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Moving forward in circles: challenges and opportunities in modeling population cycles

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Abstract

Population cycling is a widespread phenomenon, observed across a multitude of taxa in both laboratory and natural conditions. Historically, the theory associated with population cycles was tightly linked to pairwise consumer-resource interactions and studied via deterministic models, but current empirical and theoretical research reveals a much richer basis for ecological cycles. Stochasticity and seasonality can modulate or create cyclic behavior in non-intuitive ways, the high-dimensionality in ecological systems can profoundly influence cycling, and so can demographic structure and eco-evolutionary dynamics. An inclusive theory for population cycles, ranging from ecosystem-level to demographic modeling, grounded in observational or experimental data, is therefore necessary to better understand observed cyclical patterns. In turn, by gaining better insight into the drivers of population cycles, we can begin to understand the causes of cycle gain and loss, how biodiversity interacts with population cycling, and how to effectively manage wildly fluctuating populations, all of which are growing domains of ecological research.

“The affair runs always a similar course. Voles multiply. Destruction reigns. [...] The experts advise a Cure. The Cure can be almost anything: [...] a Government Commission, a culture of bacteria, poison, prayers denunciatory or tactful, a new god, a trap, a Pied Piper. The Cures have only one thing in common: with a little patience *they always work*. They have never been known entirely to fail. Likewise they have never been known to prevent the next outbreak. For the cycle of abundance and scarcity has a rhythm of its own, and the Cures are applied just when the plague of voles is going to abate through its own loss of momentum.”

– Charles Elton (1942). *Voles, Mice and Lemmings: Problems in Population Dynamics*
Clarendon Press, Oxford.

Introduction

Almost a century after the publication of Elton’s seminal paper on population cycles (Elton, 1924), we now understand and can recognize many different causes of oscillatory behavior (Kendall *et al.*, 1999; Turchin, 2003). While much of this progress has centered on well-understood consumer-resource dynamics, ongoing research continues to reveal additional areas where our knowledge is far from complete (Fig. 1). As new theoretical and empirical insights combine to reveal the diversity of drivers and modulators of cycles, we are rapidly moving beyond simple pairwise interactions toward an exciting and integrative understanding of cyclic dynamics.

Ecologists often cultivate multiple working hypotheses, and weight their relative likelihoods according to the data available (e.g., Kendall *et al.*, 2005). That hypotheses will become more or less likely over time, as a function of the data collected, is therefore well accepted. However, less attention is perhaps given to the role of mechanistic models in shaping our trains of thought. For instance, Elton believed that cycles were likely to be created by climatic oscillations (Elton, 1924), until presented with alternative models by Lotka and Volterra showing the possibility of intrinsically generated oscillations (Kingsland, 1995). Additionally, spatial gradients in cycle amplitude and periodicity were longed viewed as emerging from spatial variation in the strength of biotic interactions, due partly to convincing mechanistic models (Turchin & Hanski, 1997; Klemola *et al.*, 2002; Begon *et al.*, 2006). However, new mechanistic models (Taylor *et al.*, 2013b) now bring back the effect of abiotic factors into fashion, through seasonal forcing of vital rates (see Bjornstad *et al.*, 1995, for an early discussion of explanations of cycle gradients). Thus, broadening the set of mechanistic models that explain how cycles may arise or be modulated, either by incorporating empirical insights or using new mathematics, greatly enhances how we think about causal mechanisms. We therefore suggest that the theory on population cycles will benefit from branching out of classic consumer-resource theory, a change that is already under way (Fig. 1).

[Insert Fig 1]

In the following, we review the modeling literature on what creates population cycles, how cycles affect ecosystems, and how to manage cycles (Fig. 1). Although there are a number of models that can enrich the current theory on cycle causation, they can be broadly grouped into three sets: (1) ecosystem-level or higher-dimensional models, which include a large number of species or ecosystem compartments that can modulate ecological interactions; (2) models including demographic detail, i.e., asking whether cycles are driven by changes in survival or fecundity, age structure, or trait dynamics; (3) models including stochasticity and other forcings (e.g., seasonal) that can profoundly influence either ecosystem-level models or demographic ones. Finally, apart from uncertainties in the mechanisms causing population cycles, understanding the effects of cycles on ecosystem processes poses its own challenges for ecology, our fourth theme (Fig. 1). The ecosystem effects can be rather dramatic, as cycles within communities may play a role in biodiversity maintenance (Chesson, 2000). Understanding the ecosystem-level consequences of cycles is particularly important for populations that historically cycled but have recently become non-cyclic, and vice versa. Furthermore, many open questions remain regarding the response of cyclic populations to environmental changes (Ims *et al.*, 2008) and,

reciprocally, regarding the control of pest outbreaks (Reilly & Elder, 2014). As we show below, these questions will almost surely extend beyond the classic consumer-resource paradigm.

The snowshoe hare cycle, an enduring challenge

The snowshoe hare (*Lepus americanus*), having one of the best empirically and theoretically studied cycles (Elton & Nicholson, 1942; Royama, 1992), can be used to illustrate how recent advances and current challenges have grown out of and beyond basic predator-prey theory. Across the boreal forest of North America, hare populations exhibit 9–11 year fluctuations in abundance (Fig. 2a). The Canada lynx (*Lynx canadensis*) is the most important specialist predator of snowshoe hares and its cyclic dynamics with respect to hare fluctuations have been investigated extensively (O’Donoghue *et al.*, 1997). Phenomenological models have been fit to lynx-snowshoe hare time series, both in isolation and together, in an attempt to re-create observed patterns of numerical change (Moran, 1953; Royama, 1992; Vik *et al.*, 2008). They suggest a dynamical link between the two time series (Vik *et al.*, 2008). In order to elaborate on the classic theory, we briefly recall some basics of a consumer-resource cycle, the classic mechanism (though not the only one) to create a delayed negative feedback loop on population size (May, 1973). Much of the “new” theory we are covering in this paper (some of it, e.g., effects of stochastic forces, is in fact quite old but has been downplayed for a long time - see below) has connections to such classic consumer-resource models. In a specialist predator-prey cycle (Fig. 2 and Supplementary Appendix S1), temporary increases in the prey population support a growing number of predators until over-predation causes both populations to crash, leading to sustained oscillations of both populations. Such dynamics are commonly modeled using differential equations for the prey density, N , and the predator density, P , with the following structure:

$$\frac{dN}{dt} = \underbrace{f(N)}_{\substack{\text{prey} \\ \text{pop. growth}}} - \underbrace{g(N, P)}_{\substack{\text{functional} \\ \text{response}}} P \quad (1)$$

$$\frac{dP}{dt} = \underbrace{h(g(N, P))}_{\substack{\text{numerical} \\ \text{response}}} P - \underbrace{\mu P}_{\substack{\text{predator} \\ \text{death}}} . \quad (2)$$

The function g is known as the functional response, and describes prey consumption rates as a function of prey and predator densities, the function h is the numerical response, which describes the conversion of consumed prey into predator population growth, and μ is the predator’s per capita death rate.

[Insert Fig 2]

For certain functions h and g , sustained predator-prey oscillations are possible. For instance, an increasing and saturating functional response $g(N)$ is responsible for most limit cycles, as in the Rosenzweig-MacArthur (RM) predator-prey model (Fig. 2 and Supplementary Appendix S1, Rosenzweig & MacArthur, 1963; Turchin, 2003).

The lynx-hare cycle is, at first glance, fairly consistent with the RM model, which is a special case of the consumer-resource framework in Eqs. 1-2. However, the RM model fails to accurately reproduce some important aspects of the data, such as cycle amplitude and hare recovery after a trough (Fig. 2). Through the years, many mechanistic models have been developed in an effort to more accurately reproduce hare population cycles, for instance using a seasonal variant of the RM model, which assumes a “specialist predator pool” (without separating the various predators) that prey on hares (King & Schaffer, 2001).

The consideration of stochastic effects (e.g., environmental or demographic noise) in addition to the pairwise interaction suggested early on a role for noise in sustaining the hare-lynx cycle (Moran, 1953; Nisbet & Gurney, 1976). Using modern statistical methods, including generalized additive models and nonlinear time series analyses, Yan *et al.* (2013) found that density dependence and predation failed to generate sustained hare cycles in the absence of external forcing, but were successful when climatic effects with both stochastic and deterministic components were added, including variables

such as the North Atlantic Oscillation index (NAO) and the Southern Oscillation index (SOI). These results suggest that predation is necessary but not sufficient for the appearance of the 10-year cycles. While the specific role of noise - and environmental forcing more generally - in the snowshoe hare cycle is debated, the broader lesson is that we are still discovering new ways that stochastic effects fundamentally alter the occurrence and appearance of cycles (Fig. 1).

Increasing the dimensionality of the system by including different species and trophic levels (Fig. 1, panel 1) has also lent insight into the drivers of the snowshoe hare-lynx cycle. Earlier statistical analyses (Stenseth *et al.*, 1997) provided some support for adding dynamics of the hare's vegetation resource to the basic predator-prey model, and large-scale food supplementation experiments backed this up by showing an effect of food on hare densities (the Kluane Lake project, Krebs *et al.*, 2001). However, as Turchin (2003) highlights, removing the vegetation dynamics from models such as those proposed by King & Schaffer (2001) changes hare dynamics very little, suggesting instead no significant role of vegetation. More recent work, involving plant chemical defenses induced by hares, has considered a new aspect of this additional dimension. Models looking at the effect of hare browsing on resource quality suggest that induced defenses can suppress the recovery of hare populations from a trough (Liu *et al.*, 2013). While predation is still the key driver of cycles, this suppression creates a lag that gives cycles the correct 10-year period (Liu *et al.*, 2013). Other recent work has used higher-dimensional models to consider whether differences among predator species are significant for hare cycles. Great horned owls and coyotes have different functional responses than lynx (O'Donoghue *et al.*, 1998) and raptors, in particular, are likely able to push hare numbers lower than other predators (Hodges *et al.*, 1999). Tyson *et al.* (2010) found that the inclusion of several specialist predator populations in a model could explain the prolonged hare population troughs. In accordance, Krebs *et al.* (2014) showed, using empirical data, that variations in the cycle amplitude were related to variations in the number of predators during hare troughs. By increasing the dimensionality of the system, a more systematic understanding of this classic population cycle continues to emerge.

Even in the basic two-dimensional system, we are beginning to appreciate how cyclic dynamics may arise due to changes in the predator's or prey's physiology that affect population demography (Fig. 1, panel 2). The delayed recovery of hare reproduction during the low phase of the cycle may be attributed to maternal effects. The maternal effect hypotheses proposed that predator-induced chronic stress, which reduces hare reproduction, remains after predator densities decline (Sheriff *et al.*, 2010; Krebs, 2011; Sheriff *et al.*, 2011). Stress is propagated into the hare trough (c. 3 years) by maternal inheritance of high levels of free cortisol. This may explain why hare troughs are so low and why the cyclic period extends to 9-11 years, although quantitative models incorporating these effects are still lacking. We note that the best-fitting model of Yan *et al.* (2013), which included a 2-year delayed effect of lynx on hare growth, is in line with the maternal effect hypothesis.

The above examples illustrate that even in this well-known system, where the key role of lynx predation in driving snowshoe hare cycles was written into textbooks decades ago, ongoing, iterative theoretical development and data analysis continues to transform our understanding of the system. The mechanisms we introduced through the hare example - stochastic forces, higher dimensionality, and demographic mechanisms like those that arise due to maternal effects - are general features that can promote cycles, and each is an active area of research beyond the snowshoe hare system. In the following sections, we examine in detail these and additional areas that are at the frontier of research on population cycles.

Zooming out: considering higher-dimensional systems

Most models of cycling populations fitted to data have rather low dimensionality (typically two, sometimes three state variables). While two state variables can be enough to generate cycling, there is no guarantee that real systems obey this simplicity. In many cyclic systems, several components can interact to cause cycling. And even when all of these interactions are of the consumer-resource type, no single interaction alone may be sufficient to explain cycling. For example, natural enemies and plant defenses can act simultaneously on folivore densities, leading to oscillations that would not result from either driver alone (Elderred *et al.*, 2013). Similarly, Red Grouse population fluctuations (New *et al.*, 2009) are thought to be caused by the presence of macroparasites as well as adaptive territorial

behavior by coxks. Knowing when models with more than two state variables are warranted requires input from both the empirical perspective, to test viable hypotheses, and the theoretical perspective, to determine when new cycles have the potential to arise from the combination of multiple drivers (e.g., [Ruifrok et al., 2015](#)).

Models for food webs provide further insight into how cyclic populations affect, and are affected by, other parts of an ecosystem. The combination of several weak consumer-resource interactions can create dynamic cascades that induce oscillations in distant consumer-resource pairs ([Kadoya & McCann, 2015](#)), and the interaction of multiple oscillating consumer-resource pairs can lead to chaotic dynamics ([Benincà et al., 2009](#)). Increasing bottom-up energy fluxes or interaction strengths in food webs tends to destabilize population equilibria and induce oscillations ([May, 1973](#); [McCann et al., 1998](#); [McCann, 2000](#); [Rip & McCann, 2011](#); [Fussmann et al., 2014](#)). This so-called *principle of interaction strength* ([McCann & Gellner, 2012](#), see Glossary Box 1), sometimes also called *principle of energy flux* ([Rip & McCann, 2011](#)), turns out to be a generalization of the long known “paradox of enrichment” in consumer-resource theory that predicts decreased stability at higher nutrient supply to the prey ([Rosenzweig, 1971](#); [Fussmann et al., 2000](#)). By moving beyond pairwise interactions, generalities begin to emerge that either confirm, in this case, or refute the application of foundational theories to larger systems. Much remains to be done outside of a food web context, for instance in large competition webs or with multiple interaction types.

In the case of competitive networks, a mechanism which has long been known to induce cycling is intransitive competition, that is, competition with rock-paper-scissors (RPS) type of dynamics, inducing a succession of species in time ([May & Leonard, 1975](#); [Huisman & Weissing, 1999](#); [Laird & Schamp, 2009](#); [Allesina & Levine, 2011](#)). Although the empirical evidence for such cycles is weak (but see [Sinervo & Lively 1996](#), in a behavioral genetics context), cycles induced by succession of various types, with a mechanism very similar to the RPS cycle, have recently been evidenced by [Benincà et al. \(2015\)](#) in an rocky intertidal community.

To embrace the ecosystem-level context, time series spanning multiple species and environmental variables (e.g., [Krebs, 2011](#)) are crucial for identifying the true dimensionality of ecological fluctuations ([Abbott et al., 2009](#)). The benefits of collating multispecies time series for elucidating mechanisms can already be seen by stepping from two to three dimensions. For example, for systems with intraguild predation (IGP), cyclic dynamics may occur across multiple trophic levels ([Holt & Polis, 1997](#)). How does one decipher whether IGP promotes cycles? In classical predator-prey theory, the predator follows the prey with approximately a quarter-phase lag. IGP theory predicts that peaks of the intermediate and top predator should fall on either side of a quarter phase lag ([Hiltunen et al., 2013](#)), with the IG predator peak always preceding the top predator peak; [Hiltunen et al. \(2013\)](#) empirically validated these rich predictions about the sequence of peaks. Thus models with more dimensions introduce costs in terms of number of parameters, but also opportunities to better falsify/confirm models with data through refined predictions.

The analytical treatment and visualization of high-dimensional models, above 3 dimensions, can present significant difficulties. Special techniques may be used to reduce the dimensionality of complex models to a more tractable number (typically 2, [Indic et al. 2006](#)), by approximating some aspects of the dynamics. They usually involve projecting the high-dimensional model onto a plane or manifold so that the cycle can be represented using reconstructed coordinates in the new plane. The two-dimensional projection uses new variables ([Ives & Jansen, 1998](#)), and the overall procedure has similarities with classical approaches such as principal component analysis and eigenvalue decomposition. Though the techniques are not new, they have rarely been applied to population cycles (but see [Ives & Jansen, 1998](#); [Ripa & Ives, 2003](#)) and represent a promising avenue for future research. In molecular biology, models for oscillators can be remarkably complex (e.g., including up to 73 differential equations for the circadian clock), and efficient model reduction techniques have been developed ([Indic et al., 2006](#)); such tools could be of use to ecologists to represent large systems. A natural case occurs when the dynamics, past the transients, involve a low-dimensional attractor to which the system eventually converges. Depending on the particular model structure, other approximations may be more appropriate (e.g., if the structure is quite modular, one could study simple modules and their arrangement, [Bascompte & Melián 2005](#)).

Zooming in: the influence of demography and trait evolution

Stage structure, changes in vital rates and interactions between stages

Demography has long been known to affect population cycling, and such influences are threefold. First, the simple fact that there is some structure in the population - groups that differ in their reproduction and survival rates - can help create or amplify cycles. In a now-classic paper, [Murdoch *et al.* \(2002\)](#) contrasted short-period or cohort cycles - that are typical of intraspecific, relatively direct density dependence - with longer-period cycles that arise from the feedbacks in pairwise consumer-resource interactions (see Box 2). Cohort cycles, that emerge from age or stage structure, are believed to represent more than 50 % of all observed population cycles ([Murdoch *et al.*, 2002](#)), which motivates the development of stage- and size-structured theory ([de Roos & Persson, 2013](#)).

Second, mechanisms for cohort and consumer-resource cycles need not be fully separated, but can co-occur, or even interact and induce rich dynamical behaviors. For instance, [McCauley *et al.* \(2008\)](#) experimentally demonstrated co-existing attractors in *Daphnia*-algal systems with adult-driven cohort cycles (see Box 2 for a typology of cohort cycles and [de Roos & Persson 2013](#)). Co-existing attractors can occur when the resource has logistic growth (unlike in Box 2), and not only occur due to population structure in the consumer, as shown by [McCauley *et al.* \(2008\)](#), but also due to structure in the resource ([Wearing *et al.*, 2004](#)). The effects of age and stage structure interact most strongly with consumer-resource interactions in cannibalistic systems, where consumer and resource belong to the same species. Increasing cannibalism usually destabilizes populations and promotes oscillations ([Costantino *et al.*, 1997](#)), though in cases where populations can also be cyclic through cohort cycles ([Claessen *et al.*, 2000](#)) or multispecies trophic interactions ([Wearing *et al.*, 2004](#)), increasing cannibalism can lead to lower-amplitude cycles or no cycles for some parameter values (i.e., the responses are nonlinear). Overall, combinations of trophic mechanisms and stage structure effects can be quite unexpected.

Third, there are other, less explored ways in which demography can influence cycling. Much of cycle theory considers changes in survival as the likely proximate driver of cycles of herbivores ([Berryman, 2002](#)). However, changes in reproduction rates through direct influence of the environment ([Lomnicki, 1995](#); [Smith *et al.*, 2006](#); [de Roos *et al.*, 2009](#); [Pinot *et al.*, 2016](#)) or maternal effects ([Inchausti & Ginzburg, 2009](#)) can promote cycling. Using a combination of models and data, [Kendall *et al.* \(2005\)](#) showed that while parasitism and maternal effects (maternal body size affects the performance of offspring) can each qualitatively explain pine looper moth cycles, the latter provides parameter estimates that better match empirical measurements. Maternal effects are also implicated in annual plant population cycles ([Crone & Taylor 1996](#); [Crone 1997](#), see Box 3). How these reproduction-driven cycles could connect to the age/size-structured consumer-resource based theory ([de Roos & Persson, 2013](#)) is, to our knowledge, currently unknown and an interesting avenue for research; very likely these are akin to delayed feedback cycles, though there might be a continuum between cohort and delayed feedback cycles ([Pfaff *et al.* 2014](#), Box 2).

Hence, a better empirical characterization of demographic structure in cycling populations, changes in demographic rates (i.e., survival and reproduction), associated linkages to traits (e.g., body size), and interaction between stages, would undoubtedly improve our ability to discern the mechanisms influencing cyclic populations ([Miller & Rudolf, 2011](#); [Row *et al.*, 2014](#); Box 4). A common practice in population cycle studies is to separate “extrinsic” (predation, disease) from “intrinsic” causes (age structure, maternal effects, adaptive territoriality). However, the possibility of mixing extrinsic and intrinsic components, such as predator-driven maternal effects or cannibalistic interactions, suggests that a classification based on demographic changes (i.e., changes in survival or reproduction rates for a given age, stage or size) might be more useful in pinpointing at least the proximate causes of cycles.

Interactions between evolution and population cycles

Many features that promote population cycles are evolvable traits, which suggests that evolution can play a key role in cyclicity; for example, litter size is correlated to cyclic propensity in rodents ([Stenseth *et al.*, 1985](#)) and continuous prey adaptation has been shown to facilitate the emergence of consumer-resource cycles ([Abrams & Matsuda, 1997](#)). Evolutionary processes can occur on fast timescales: during epizootics, disease transmission rates can change rapidly due to selection for disease resistance at high pathogen abundance and selection for relaxation at low pathogen abundance, promoting oscillatory

eco-evolutionary dynamics (Elderd *et al.*, 2008). For the question of why cycles occur, a stronger understanding of both short- and long-term eco-evolutionary dynamics may be key.

In consumer-resource cycles, the cycle phase lag between the interacting species emerges as an important indicator of the underlying eco-evolutionary dynamics (Yoshida *et al.*, 2003; Becks *et al.*, 2010). In usual predator-prey cycles not involving evolution, cycles run counterclockwise on the prey-predator phase plane and prey peaks precede predator peaks by about a quarter of a cycle. The counterclockwise lag represents a fundamental result of consumer-resource models. In contrast, in a microcosm experiment algal populations were almost out of phase compared to their protist grazers, and cycles proceeded clockwise whenever algal defense mechanisms (in trade-off to their competitive ability) were allowed to evolve (Cortez & Weitz, 2014). This phenomenon, sometimes called “cryptic” or “reversed” cycling, was shown to occur in about half of the protozoan consumer-resource time series examined by Hiltunen *et al.* (2014). Although not all clockwise cycles are driven by evolution (Hiltunen *et al.*, 2014), evolution may be an important modulator of cyclic behavior in natural systems, particularly for organisms with short generation times that have a potential for rapid evolution. Without the interplay between theory and data, the potential for and the confirmation of clockwise cycling may not have emerged.

Forcing of ecological dynamics by periodic and noisy temporal variation

Forcing by environmental oscillations

Apart from endogenous ecological (e.g., consumer-resource) interactions, population cycles can also be driven by cyclic environmental variations, such as periodic changes in weather patterns (London & Yorke, 1973; Hunter & Price, 1998). Periodic or roughly periodic environmental drivers previously proposed to explain fluctuating populations include solar flare (“sunspot”) cycles (Sinclair *et al.*, 1993), the North Atlantic Oscillation (García-Comas *et al.*, 2011), the El Niño–Southern Oscillation (Stenseth *et al.*, 2002) and long-period fluctuations of ocean currents (Bernal, 1981). When the driving force induces a linear response in the system, an elegant treatment is possible using the so-called *transfer function*, which describes the system’s response to different forcing frequencies (Roberts *et al.*, 1995). For example, ecosystems with high inertia and long correlation times will exhibit a transfer function that quickly declines at higher frequencies, and will thus be most sensitive to low-frequency forcing. In contrast, the interaction of external periodic forcing with nonlinear endogenous dynamics is less well understood. Progress has been made in recent years using simulations and numerical bifurcation analyses (Dakos *et al.*, 2009; Taylor *et al.*, 2013a), and established analytical techniques from physics - such as Floquet theory (Klausmeier, 2008) - offer promising future avenues for ecology. Seasonality, in particular, is increasingly recognized as a key element in determining complex population dynamics (King & Schaffer, 2001; de Roos *et al.*, 2009; Taylor *et al.*, 2013b; Nelson *et al.*, 2013). For example, forcing can result in repeated jumps between alternative attractors in models for seasonal measles outbreaks (Aron, 1990; Keeling *et al.*, 2001), and seasonal variation of parameters has been shown to promote chaos in the classical Rosenzweig-MacArthur model (Rinaldi *et al.*, 1993). Chaos appears widespread in periodically forced non-linear systems, particularly when exogenous forcing affects multiple components or interacts with endogenous cyclicality (Dakos *et al.*, 2009; Greenman & Pasour, 2011; Benincà *et al.*, 2015). Rather strong seasonality, with a really adverse period for the organisms considered, can induce life histories where reproduction occurs only during the favorable season and survival forms (e.g., seeds, resistant eggs or larval stages) allow persistence through the adverse period, as in annual plants and insects. These dynamics can be very prone to cycling and are best modeled in discrete time (see Box 3 for models and references).

Stochasticity can also greatly enhance population cycling

Stochastic ecological modeling has revealed that random environmental perturbations and demographic stochasticity can have a vast range of effects on population cycles (Nisbet & Gurney, 1982; Black &

McKane, 2012). Perhaps the best known example is the induction of “noise-sustained oscillations” (NSO) around otherwise stable equilibria through the repeated random excitation of damped oscillators (Royama, 1992; Kendall, 2001; McKane & Newman, 2005). While NSOs exhibit a peak in their frequency spectrum, corresponding to a “characteristic frequency”, they are inherently irregular (Figs. 3c, 5) and have a decaying autocorrelation, i.e., they are *phase forgetting*. Many populations appear to have phase-forgetting cycles (Kaitala *et al.*, 1996), such as sockeye salmon (Myers *et al.*, 1998; Krkošek *et al.*, 2011), crappies (Allen & Miranda, 2001) and Dungeness crabs (Higgins *et al.*, 1997). NSOs may yield complete mathematical descriptions when noise is weak (Wiesenfeld, 1985; Aparicio & Solari, 2001; Greenman & Benton, 2005; Tomé & de Oliveira, 2009; Baxendale & Greenwood, 2011). These can show a large range of effects of noise, e.g., color in stochastic forcing - autocorrelation - can enhance resonance (Greenman & Benton, 2005). However, oscillations sustained by strong noise are usually examined numerically and effects of strong noise, which are less studied, are of great interest for ecological cycles (Box 4, see also “flickering” below).

NSOs can occur in models that exhibit damped oscillations in the absence of noise for all parameter values, or models displaying potential bifurcations towards limit cycles, such as stochastic variants of eqs. 1-2 (eqs. 3-4 and Fig. 3).

$$dN = \left(\underbrace{f(N)}_{\substack{\text{prey} \\ \text{pop. growth}}} - \underbrace{g(N, P) P}_{\substack{\text{functional} \\ \text{response}}} \right) dt + \underbrace{\sigma_1 N dW_1}_{\text{noise term}} \quad (3)$$

$$dP = \left(\underbrace{h(g(N, P)) P}_{\substack{\text{numerical} \\ \text{response}}} - \underbrace{\mu P}_{\substack{\text{predator} \\ \text{death}}} \right) dt + \underbrace{\sigma_2 P dW_2}_{\text{noise term}}. \quad (4)$$

Here, the noise terms dW_i , with variance σ_i^2 , are added as perturbations on the per capita growth rate of both species, i.e. the noise terms are proportional to population size. This corresponds to environmental stochasticity (Lande *et al.*, 2003), which amounts to introduce stochasticity in the prey intrinsic growth rate or the predator mortality rate. Eqs. (3-4) are written using differentials rather than derivatives for mathematical reasons (see e.g., Nolting & Abbott, 2016 for more details), but behave similarly to eqs. (1-2) when the noise terms tend to zero. The stochastically forced predator-prey systems can exhibit, depending on parameter values, damped oscillations towards an equilibrium point (Fig. 3a), limit cycles (Fig. 3b) or noise-sustained oscillations (Fig. 3c).

In the latter case, stochasticity can push the system towards fluctuations, before the deterministic bifurcation point is reached, on nearly the same attractor (e.g., a limit cycle) that emerges after the bifurcation (Wiesenfeld, 1985). This means that very high-amplitude fluctuations can be sustained or generated by noise, not unlike those generated by more regular, seasonal forcing (King & Schaffer, 2001; Taylor *et al.*, 2013a). However, noise can also alter the qualitative properties of limit cycles by causing irregularities in the cycle period (“jitter”) (Nisbet & Gurney, 1982; Burgers, 1999) or allowing transients far from the system’s attractor (Rohani *et al.*, 2002). The differences between noisy limit cycles and NSOs can also be visualized in the phase plane (Fig. 4; Pineda-Krch *et al.*, 2007). Noise can also induce irregular transitions between attractors, a behavior sometimes referred to as *flickering* (Fig. 5c; Box 1, Dakos *et al.*, 2013). Flickering has been reported most often for physical and chemical systems (Horsthemke & Lefever, 2006), however ecological systems with complex phase space structure are similarly sensitive to noise (Earn *et al.*, 2000; Coulson *et al.*, 2004; Ives *et al.*, 2008). Flickering can take the form of irregular population outbreaks (Dwyer *et al.*, 2004; Sharma *et al.*, 2015) or can be mistaken for predator-prey cycles (Spencer & Collie, 1996); much remains to be done to better characterize this phenomenon.

The above considerations show that stochastic effects not only have the potential to qualitatively alter cyclic population dynamics, but can even induce oscillations in systems that would otherwise be static (Fig. 5). Recognizing which particular paradigm best describes the observed fluctuations (e.g., as noisy limit cycles, NSOs or non-cyclic; Fig. 5) is non-trivial. For example, NSOs may be confused with correlated but non-cyclic fluctuations (i.e., lacking a peak in their frequency spectrum) especially when available time series are of insufficient duration. In fact, a substantial number of natural populations may have been misinterpreted as cyclic in the past (Louca & Doebeli, 2015). Because the stochastic component can itself be weakly periodic, there is clearly a continuum between purely random and

purely periodic forcing, including red (autocorrelated) and weakly periodic noise. Different scenarios may be distinguished by fitting parametric models (Kendall *et al.*, 1999; Ives *et al.*, 2008; a technique illustrated in Supplementary Appendix S2). Non-parametric methods also exist, notably based on nonlinear state space reconstruction (Sugihara *et al.*, 2012). As much-needed data are collected, these analytical tools will continue to provide additional insight into how stochasticity may drive and sustain population cycles.

[Insert Figs. 3, 4 and 5 around here]

Space and dispersal modulate observed cyclic patterns

The presence or properties of some population cycles cannot be fully explained without considering the spatial extent of populations (Ranta *et al.*, 1997), because spatially separated populations may synchronize or induce cyclicity in one another through dispersal of individuals. Empirical research shows that synchrony can extend well beyond the scales of individual dispersal (e.g., ~ 50 km vs ~ 1 km in voles, Bjørnstad *et al.*, 1999). If one assumes that the scale of synchrony should match the scale of the process that drives it, this observation would suggest that large-scale spatial synchrony might be maintained by factors other than individual dispersal (Krebs *et al.*, 2013). However, theoretical research demonstrates (Blasius *et al.*, 1999; Jansen, 1999), and empirical tests confirm (Fox *et al.*, 2011), that extended dispersal-driven synchrony can occur through phase-locking (i.e., the progressive synchronization of oscillators). Thus, the presence of intrinsic cycles has strong implications for the appearance of spatial patterns like synchrony. In addition to inducing synchrony, dispersal can damp oscillations in cyclic populations (Briggs & Hoopes, 2004). This occurs when immigration to a site is independent of (or only weakly dependent on) the local population density, because such immigration reduces local density dependence and weakens negative feedback loops. Thus, dispersal and landscape structure can interact to play a critical role in determining cycle persistence. Note, though, that the stabilizing effect of dispersal is intimately related to synchrony, because high dispersal rates are expected to reduce cycle amplitude while concurrently increasing synchrony. On the other hand, synchrony caused by factors other than dispersal (such as correlated environmental conditions, discussed below), can weaken the cycle-damping effect of dispersal (Abbott, 2011).

Apart from dispersal, synchrony can also be caused by spatially correlated environmental fluctuations that drive synchronized responses in separate populations. For example, during a particularly beneficial stochastic perturbation (e.g., very high summer growth rate due to favorable climate), most populations increase and therefore become synchronous over large spatial scales (Kerlin *et al.*, 2010). In cyclic populations, non-linear feedbacks can damp or amplify the effects of perturbations. As a result, the strength of this synchrony is predicted to be weaker than the strength of environmental correlation (Moran, 1953) and the scale and pattern of population synchrony may not generally resemble the scale or the pattern of environmental correlations (Abbott, 2007). For higher-dimensional models, phase reduction methods (Acebrón *et al.*, 2005; Goldobin *et al.*, 2010), which ignore cycle amplitudes and describe dynamics purely in terms of their phases, can help keep models tractable while retaining the key variables required to describe patterns of synchrony (Haydon *et al.*, 2001; Cazelles & Stone, 2003; Goldwyn & Hastings, 2011). Wavelet and co-spectral approaches can also help to show how spatial synchrony changes over time, particularly in relation to climatic signals (Sheppard *et al.*, 2016; Defriez *et al.*, 2016).

Spatially-lagged synchrony (or *periodic traveling waves*, see Glossary in Box 1), can theoretically arise in both homogeneous and heterogeneous environments (Sherratt & Smith, 2008), and will, according to empirical work, be shaped by landscape structure and dispersal dynamics (Bjørnstad *et al.*, 2002; Berthier *et al.*, 2014). Traveling waves can also arise during recurrent epidemic outbreaks, whereby large core cities provide the spark for the initiation of outbreaks in smaller satellite towns (Grenfell *et al.*, 2001). In the wake of a traveling wave, populations may exhibit spatiotemporal chaos (Sherratt *et al.*, 2009), though noise can prevent this transition (Petrovskii *et al.*, 2010). Landscape structure and stochasticity can thus interact to drive the appearance of local cyclic or chaotic oscillations, but more work is needed for a clearer sense of whether this occurs commonly in nature.

Large-scale studies of forest Lepidoptera represent some of the most intriguing evidence for the benefits of blending empirical data with theoretical models to understand the effects of landscape

structure on cyclic behavior. Empirical data from the larch budmoth and the forest tent caterpillar show an increase in the duration of outbreaks in fragmented habitat, prolonging the time herbivorous insects spend at cycle peaks (Roland, 1993). Because the link between forest fragmentation and insect outbreaks was disputed, Hughes *et al.* (2015) constructed a model of defoliator cycles driven by parasitoids. Their model shows that disputes in the empirical findings were a result of studies using local versus global measures of outbreaks. Moreover, it was found that forest loss can increase herbivore density and outbreak severity when parasitoids disperse further than the herbivores, because parasitoid dispersal mortality decreases the control of herbivores by parasitoids (Hughes *et al.*, 2015). Studying the effects of landscape configuration presents empirical challenges, because to study the mechanisms of cycling requires detailed local scale experiments, but habitat variation typically occurs at much larger spatial scales. Advances in computational power and the development of analytical tools that take advantage of the hierarchical nature of the data now mean models with more realistic landscape structure can be combined with data from local and large scale studies. These advances will allow researchers to bridge the gap between landscape ecology and population ecology.

How population cycling interacts with global change, biodiversity and management

Cycle gain and loss

Population cycles can disappear in response to environmental change, and this can have profound effects on an ecosystem. Cycle loss in herbivores can induce ripple effects throughout the food web in northern regions (Ims *et al.*, 2008; Millon *et al.*, 2014) and adversely affect species sharing predators with these herbivores (Kausrud *et al.*, 2008; Barraquand *et al.*, 2015). The effects are not uniformly negative, however. Since cycle loss often means a decrease in mean abundance in addition to the decrease in variability (Cornulier *et al.*, 2013), cycle loss can have positive consequences in the case of pest species. Changing environmental conditions may alter the amplitude (Nelson *et al.*, 2013) or periodicity (detected using wavelets, see Cazelles *et al.* 2008; Kausrud *et al.* 2008) in existing cycles and even cause cycle gain in previously non-cyclic populations. Overall, the emergence or disappearance of cycles under changing conditions, while often disruptive, also provides opportunities for understanding the mechanisms driving cyclic dynamics (Ims *et al.*, 2008) and may be considered a natural experiment or perturbation to the system.

Foremost, climate change has been implicated as a key driver in both cycle gain or loss. For species whose development times or foraging behavior are temperature-dependent, a changing climate can have dramatic effects on cyclic dynamics. For small mammal species, such as voles, climate change has decreased population size during the peaks of the cycle due to changes in winter growth rates (Cornulier *et al.*, 2013). Warm winters generate melt-frost events at northern latitudes, which result in less favorable conditions for herbivores accessing their food through the frozen bottom snow layers (Kausrud *et al.*, 2008; Ims *et al.*, 2008), although these results are not unequivocal (Korpela *et al.*, 2013; Gouveia *et al.*, 2015). General principles of consumer-resource theory may help predict the effects of long-term climatic changes on population cycles (O'Connor *et al.*, 2011) and, more generally, food web dynamics (Gilbert *et al.*, 2014). For example, recent bioenergetic models suggest that warming can damp oscillations in predator-prey systems (Fussmann *et al.*, 2014) and three-species food chains (Binzer *et al.*, 2012) by reducing bottom-up energy fluxes, consistent with the aforementioned principle of interaction strength in consumer-resource theory (Rip & McCann, 2011; McCann & Gellner, 2012). Cycles of populations with seasonally varying behavioral responses may be particularly affected by warming: if a predator switches its predatory behavior (functional response) between seasons, cycle gain or loss can occur as summer season length increases (Tyson & Lutscher, 2016). This points to the importance of developing models and sampling strategies that take into account both direct and indirect effects of climate change on population cycles (Post, 2013).

Changing spatial patterns can also lead to cycle gain and loss. Cycle loss in the gray-sided vole (Hörnfeldt, 2004; Ims *et al.*, 2008), originally thought to be due to climate change, was later found to be chiefly due to changes in the landscape structure (Ecke *et al.*, 2010). Theoretical studies show that habitat loss alone can cause cycle amplitude reduction and, as fragmentation occurs, cycle

loss (Strohm & Tyson, 2009; Gauduchon *et al.*, 2013). Additionally, cycle loss has been shown, in some cases, to be a precursor to extirpation as habitat loss increases (Strohm & Tyson, 2009; Maciel & Kraenkel, 2014; Vitense *et al.*, 2016), which could suggest an indicator of regional-level resilience. However, in at least one empirical, non-spatial context it is cycle gain, rather than cycle loss, that is the indicator of imminent collapse (for salmon populations, White *et al.*, 2014), which echoes theoretical work on epidemiological systems with Allee effects (Hilker *et al.*, 2009). In spatial models, an increase in amplitude may also precede population collapse for some parameter values (Maciel & Kraenkel, 2014; Vitense *et al.*, 2016). In summary, the connection between cyclic population behavior and regional persistence seems often idiosyncratic, and it is therefore very unlikely that increase or decrease in cycle amplitude could be interpreted as an early-warning signal of population collapse.

Biodiversity maintenance

Empirical studies have shown a strong effect of the periodic resource inputs provided by cyclic populations on ecosystem function and subsequent community structure. For instance, the periodic cicada provides an input of resources after the cicadas emerge, mate, and die, and these periodic nutrient pulses affect nitrogen availability and forest plant community structure (Yang, 2004). In addition, outbreaking forest insects periodically increase nitrogen availability on the forest floor, via high concentration of frass during cycle peaks. The nitrogen is readily taken up by forest floor microbes and quickly incorporated into the soil (Lovett *et al.*, 2002). Cyclic populations can also promote biodiversity through the “bird-feeder effect”, whereby insect outbreaks cause an increase in regional predators that are attracted to high local prey densities (Eveleigh *et al.*, 2007).

From the perspective of species not actively contributing to such periodic outbreaks, these outbreaks can be viewed as external resource pulses. Hence, existing resource pulse literature could help predict ecosystem-wide consequences of population cycles (Chesson *et al.*, 2004; Schmidt & Ostfeld, 2008). Models of shared predation using a representation of the focal prey as a pulse (Schmidt & Ostfeld, 2008; Barraquand *et al.*, 2015) show that cyclic species can promote alternative prey species persistence - and therefore biodiversity - whenever predator numbers are constant, yet create apparent competition whenever predators have strong numerical response to their focal prey. Hence, numerical responses of predators are key to predict the ecosystem-scale biodiversity effects of overabundant cyclic species.

Cycling has also been predicted to promote coexistence of multiple consumers competing for common resources, because on periodic orbits the average resource density can be higher than the threshold densities required for the survival of the oscillating consumers (Armstrong & McGehee, 1980). Aside from classic consumer-resource mechanisms, intransitive competition, such as rock-paper-scissors competition in which there is no overall winner, allows for competitor coexistence via cyclic dynamics (see “Zooming out” section and Huisman & Weissing, 1999; Allesina & Levine, 2011). Thus, oscillatory dynamics may result in increased biodiversity and contribute to explaining the puzzling coexistence of many similar competitors in some systems (Chesson, 2000). It remains to be tested whether these predictions would hold for realistic interaction webs (McCann & Gellner, 2012). Microcosm experiments with multiple interacting species may help resolve these uncertainties (Box 4).

Within species, cycling also interacts with genetic diversity maintenance (Norén & Angerbjörn, 2013). Following population genetics theory, population lows should be bottlenecks and reduce population diversity. But the levels of genetic diversity currently observed in cyclic species are actually higher than expected from population troughs (e.g., for lynx, mouflon, and voles, Stenseth *et al.*, 2004; Ehrlich & Jorde, 2005; Kaeuffer *et al.*, 2007; Ehrlich *et al.*, 2009). Such genetic variability is thought to be maintained notably by negatively density-dependent dispersal (more movement at low population density), which seems widespread in cyclic species (Norén & Angerbjörn, 2013). Hence, cyclic populations seem to be intrinsically robust to the erosion of their intra-specific diversity. Finally, cycling can in itself be a mechanism of genetic and phenotypic diversity maintenance, as shown by Sinervo & Lively (1996) who demonstrated the maintenance of color polymorphisms in lizards through rock-paper-scissors competition.

Management

Because of their wide variation in densities, cyclic populations present unique challenges to managers who want to keep pest densities low and game species densities high. In the introductory quote, El-

ton pessimistically concluded that most strategies to reverse outbreaks appear successful only because these strategies are applied prior to an inevitably imminent collapse of the populations. Here we describe modern strategies to control population dynamics that incorporate ecological and mathematical knowledge to suggest interventions that effectively impact population dynamics.

Management strategies can focus on population-level control (e.g., adding or removing individuals of the focal population), top-down control (e.g., augmenting predators or parasites) or bottom-up control (e.g., augmenting resources). Although these strategies have been successfully applied to control cycles (Hudson *et al.*, 1998; Korpimäki & Norrdahl, 1998; Bell *et al.*, 2012), unsuccessful attempts also occur (Hessl *et al.*, 2004) and can lead to unexpected and unwanted outcomes (Doak *et al.*, 2008). Some ways of harvesting individuals can in theory stabilize populations that would otherwise fluctuate, but care must be taken because empirical evidence shows that harvesting can also increase fluctuations, for example in plant, insect, and fish populations (Hsieh *et al.*, 2006; Shelton & Mangel, 2011).

Management strategies at the population level remove surplus individuals (Lande *et al.*, 1995; Fryxell *et al.*, 2005; Hilker & Westerhoff, 2006) or add individuals (Hilker & Westerhoff, 2005; Tung *et al.*, 2014) based on some target population threshold. This threshold can be a fixed density or be related to density changes between surveys, as is the case in Adaptive Limiter Control where populations are restocked in the event of an undesirably strong crash (Sah *et al.*, 2013; Franco & Hilker, 2013). Although these strategies are robust to the mechanisms driving fluctuations, their efficacy can depend on the census data used (Franco & Hilker, 2014) and the timing of intervention (Hilker & Liz, 2013).

To optimize the timing of intervention, mechanistic models (Desharnais *et al.*, 2001) and time series analysis (Hilker & Westerhoff, 2007) can be used to determine “hot regions” in the cycles (i.e., regions that are particularly sensitive to perturbations). Demonstrations of the “hot region” control method using laboratory experiments (Desharnais *et al.*, 2001) showed that adding a few individuals to populations of the flour beetle, *Tribolium castaneum*, in hot regions of the population cycle greatly affected population dynamics. In contrast, adding the same number of individuals in mathematically determined “cold regions” caused no change in the dynamics. A series of recent experiments with *Drosophila melanogaster* demonstrated the effectiveness of several alternative methods for stabilizing populations, including Adaptive Limiter Control (Sah *et al.*, 2013) and related strategies (Tung *et al.*, 2016a,b). Although mathematical models are not required to use these strategies (Hilker & Westerhoff, 2007), models can help determine the best timing and number of individuals that would have the most effect (Desharnais *et al.*, 2001; Franco & Hilker, 2013; Cid *et al.*, 2014; Tung *et al.*, 2014). Fitting models to data (Supplementary Appendix S2) is key to the latter analyses. This approach exemplifies how theory and empirical research can result in not only well-planned management strategies but a better understanding of cyclic dynamics.

Besides direct manipulation of population densities, populations can be managed by affecting the underlying mechanisms driving population dynamics. For instance, the parasitic nematode *Trichostrongylus tenuis* contributes to population cycles of the red grouse, *Lagopus lagopus scoticus*; treating 15%–50% of the grouse population with antiparasitics prevented crashes that were observed in the untreated populations, a pattern that could be explained by a general macroparasite model (Hudson *et al.*, 1998, though see Lambin *et al.*, 1999). Similarly, using transgenic Bt corn to decrease larval survival rates of the European corn borer, *Ostrinia nubilalis*, damped the 5–7 year population cycles of the pest in Minnesota compared to population dynamics pre-Bt corn (Bell *et al.*, 2012). Despite these successes, we should not underestimate the potential of ecological systems to surprise us and produce counter-intuitive results. For example, controlling populations could lead to stable populations with constant levels of defoliation as opposed to cyclic populations causing cycles of defoliation, but these stable populations may exhibit larger densities and thus cause increased overall defoliation (Reilly & Elderd, 2014; Stieha *et al.*, 2016). Intense monitoring is therefore needed to refine models for management based on empirical evidence.

Conclusion

We have summarized four promising research fields in contemporary research on population cycles (Fig. 1) and synthesized the current state of our knowledge, as well as important open challenges in each of them (Box 4). First, although only two species or compartments are needed to make cycles

emerge in a system of differential equations, mechanisms involving many more species are also likely to occur. Thus, a current and much-needed trend is to increase the dimensionality of systems considered, considering whole interaction webs, in both theoretical and statistical models. Multi-dimensional ecological time series are therefore required to understand cycles in their broader ecosystem context and to robustly calibrate high-dimensional models. Improved mathematical and statistical tools that link multiple sources of information will play an important role in this endeavor. Second, demographic context (stage structure, temporal patterns in vital rates and trait values, interactions between stages) can be key for understanding cyclic dynamics. Making use of the recent progress in linking data to theoretical models in demographic research (matrix models parameterized through capture-recapture, integral population models) will likely help understanding the proximate causes of cycling. Third, stochastic and seasonal forces permeate ecological systems and can induce oscillations. Although their potential role in cycling populations has been known for some time, it is currently under-appreciated. There is still much to discover about how strong and autocorrelated noise affect nonlinear systems - and how to detect such effects (Box 4). Finally, applied research aimed at understanding the consequences of changes in cyclic populations and managing cyclic species is progressing with great strides. Charles Elton saw many control actions as no better than waiting for the natural termination of outbreaks, but as cycles knocked on and off by environmental changes provide great natural experiments, and theoretical models are increasingly used to help control populations, we begin to understand how to truly manage cycles. Further progress will undoubtedly involve continual feedback between theory and empirical research, a defining feature of research on population cycles that will continue to help the field moving forward.

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Box 1 Glossary

- **flickering** repeated random transitions between alternative attractors caused by noise ([Dakos *et al.*, 2013](#))
- **noise-sustained oscillations (NSO)** oscillations caused by random perturbations of damped oscillators, sometimes known as quasi-cycles ([Nisbet & Gurney, 1982](#))
- **phase-forgetting cycles** cycles with fluctuating periods, manifested as a decaying autocorrelation ([Nisbet & Gurney, 1982](#))
- **periodic traveling wave** cyclic pattern propagating in one or more spatial directions ([Sherratt & Smith, 2008](#))
- **principle of interaction strength** increasing the energy flux through a consumer–resource interaction relative to the mortality rate of the consumer tends to destabilize the interaction ([McCann & Gellner, 2012](#))
- **stochastic resonance** the amplification of periodic forcing by random noise ([Gammaitoni *et al.*, 1998](#))

Box 2 Cohort or consumer-resource cycles?

Cohort or generation cycles have periods that are characteristically close to the development time of the focal population (Murdoch *et al.*, 2002). Using the delayed host-parasitoid model,

$$R_t = \lambda R_{t-T_R} F(R_{t-T_R}, C_{t-T_R}) + S_R R_{t-1} \quad (5)$$

$$C_t = \lambda R_{t-T_C} (1 - F(R_{t-T_C}, C_{t-T_C})) + S_C C_{t-1}, \quad (6)$$

with T_C and T_R being the consumer and resource development times, respectively, Murdoch *et al.* (2002) showed that the period of consumer-resource cycles should be approximately $4T_C + 2T_R$. Taking a consumer perspective and denoting $T_C = \tau$, they then looked at known periods of cycles of generalists versus specialist consumers. They found that cycling generalists had mostly periods $< 4\tau$ while specialists had cycles with periods $> 4\tau$, indicative of a consumer-resource cycle. Hence, cycle periodicity may provide a first hint of the qualitative causes of observed cycles. They further classified cycles into:

- “Single-generation cycles” (SGCs), for single species with direct density dependence, that tend to occur with period within $1-2\tau$ (de Roos & Persson (2013) suggest that possible generational overlap makes “cohort cycles” a clearer denomination),
- “Delayed-feedback cycles” (DFCs), for single species with a delay in their dynamics, that tend to occur with period within $2-4\tau$, and
- “Consumer-resource cycles” as typified by eqs. (1)–(2), that usually occur with period $> 4\tau$ (i.e., $4T_C + 2T_R$).

Recent research shows that SGCs and DFCs might in fact be caused by the same class of demographic processes (Pfaff *et al.*, 2014). SGCs/DFCs are widely observed in insects but also in fish, where such demographic processes interact with environmental stochasticity (White *et al.*, 2014).

Further insight into the mechanisms by which cohort cycles (SGCs) emerge can be gained using size-structured population models where the maturation processes are modelled explicitly as a function of physiological and growth processes, i.e., the redistribution of energy (de Roos & Persson, 2013). The baseline model is given by 5 key equations (de Roos & Persson, 2013) including a size variable s for consumers.

- Growth rate of resource biomass R (semi-chemostat or logistic):
 $G(R) = \rho(R_{\max} - R)$ or $G(R) = \rho R(1 - R/R_{\max})$
- Change in juvenile size distribution $c(t, s)$ with growth function $g(R, s)$ and mortality rate $d_J(R)$:
 $\frac{\partial c(t, s)}{\partial t} + \frac{\partial g(R, s)c(t, s)}{\partial s} = -d_J(R)c(t, s)$
- Increase in consumer newborns through reproduction, with reproduction function $b(R, s_m)$, s_b being the size at birth and s_m at maturity: $g(R, s_b)c(t, s_b) = b(R, s_m)C$
- Adult consumer dynamics, including transition from juveniles to adult size, as well as adult mortality with rate $d_A(R)$: $\frac{dC}{dt} = g(R, s_m)c(t, s_m) - d_A(R)C$
- Resource biomass dynamics, with consumer intake rates $w_J(R)$ and $w_A(R)$:
 $\frac{dR}{dt} = G(R) - w_J(R) \int_{s_b}^{s_m} sc(t, s)ds - w_A(R)s_m C.$

de Roos & Persson (2013) further assume that the maximum ingestion rates of juvenile is M_C and that of adults qM_C , influencing intake rates $w_J(R) = M_C \frac{R}{H_c + R}$ and $w_A(R) = qM_C \frac{R}{H_c + R}$. With semi-chemostat resource dynamics, no cycles are observed in this and other consumer-resource models *whenever adults and juveniles are trophically identical* ($q = 1$ here) (Turchin & Batzli, 2001; de Roos & Persson, 2013). Instead, cohort cycles emerge when $q \neq 1$. A major contribution of de Roos and Persson was to delineate two kinds of cohort cycles, juvenile-driven ($q < 1$, large amplitude, low juvenile/adult ratio, one dominant cohort, highly episodic reproduction) vs. adult-driven cycles ($q > 1$, lower amplitude, high juvenile/adult ratio, relatively constant size distribution, variable yet continuous reproduction). For semi-chemostat resource dynamics, cycle period/maturation delay ≈ 1 in both cases, though slightly longer for adult-driven cycles.

Box 3 Cycles in organisms with episodic life histories

The simple presence of episodic life-history events, best represented by a discrete-time model, can sometimes be enough to create population cycling, as even the simplest discrete-time models are famously prone to cycling and other complicated dynamics (May, 1974). One example of a simple model capable of complex dynamics is the Ricker Model (we follow the presentation of Gurney & Nisbet, 1998), where N_t adults produce, on average, f offspring between time t and $t+\tau$, $\tau \in [0, 1)$, and these offspring are reproductively mature by $t+1$. Offspring survival to maturity, however, decreases with adult density (such as $\text{Pr}(\text{survival}) = \exp(-\alpha N_t)$, so that the number of adults in the next generation, $N_{t+1} = fN_t \exp(-\alpha N_t)$ (or $N_{t+1} = fN_t \exp(-\alpha N_t) + s_A N_t$ if generations overlap because some fraction, s_A , of adults survive to reproduce again). As fertility f increases, populations are first stable, then exhibit 2-point cycles with overcompensation (i.e., overshooting and undershooting of a carrying capacity), then longer period cycles through period doubling and even chaos (Gurney & Nisbet, 1998). However, even in the chaotic regime, high frequencies (low periods) usually dominate the frequency spectrum of such models (Cohen, 1995). Importantly, these cycles are a low-dimensional, intraspecific phenomenon; they are not expected when interspecific density dependent feedbacks are strong, as in tightly coupled consumer-resource food webs (Murdoch *et al.*, 2002). Because annual replanting of their host plant prevents multi-year interspecific feedbacks, the cyclic outbreaks of agricultural pest insects have recently been described as such overcompensation cycles (Stieha *et al.*, 2016).

In contrast to overcompensation cycles, consumer-resource interactions and other mechanisms discussed in the main text generally lead to lower-frequency cycles that build to and descend from each peak over multiple years (Murdoch *et al.*, 2002, see main text and Box 2 for a discussion of periodicities), even with highly seasonal environments or episodic life-histories. The balance of direct, intraspecific density dependence and lagged or interspecific feedbacks will determine which type of cycle arises. For example, experimental populations of the annual plant *Cardamine pennsylvanica* exhibit multi-generational cycles due to delayed density dependence via parental effects, where high parental density reduces offspring size (Crone, 1997) and fecundity (Crone & Taylor, 1996). To model plant cycles, Crone (1997) made the following assumptions

- adult plant density N_t is proportional to seed density s_t , $N_t = a s_t$
- average plant mass w_t declines with present and parental plant density N_{t-1} so that $\ln(w_t) = a_1 - b_1 N_t - c_1 N_{t-1}$
- average plant mass and fecundity are allometrically related $f_t = a_2 w_t^{b_2}$
- seed density in the next generation is proportional to population fecundity $s_{t+1} = a_3 f_t N_t$

This then leads to the model

$$N_{t+1} = a_3 a_2 N_t e^{a_1 b_2 - b_1 b_2 N_t - c_1 b_2 N_{t-1}} \quad (7)$$

where subscripted a_i , b_i , and c_i are estimated from the data. The above model produces limit cycles of period 2 and above. Experimentally decreasing nutrient availability, however, reduces the strength of this delayed interaction (thereby increasing the relative strength of direct density dependence) and leads to a damped 2-point cycle (Molofsky *et al.*, 2014). Populations with such episodic life-histories living in strongly seasonal environments provide unique opportunities to study cycle-producing mechanisms; it is much more straightforward to test for lagged density dependent effects in discrete-time systems where the set of possible lags is both finite and naturally defined (year $t-1$, $t-2$, etc.). Annual plants are an interesting avenue for further study, because as shown above, oscillations can and do occur in plants (see also Tilman & Wedin, 1991; Gonzalez-Andujar *et al.*, 2006) and shorter time series in temporally replicated surveys - compared to animals - might hide the richness of their population dynamics.

Box 4 Future research directions in modeling population cycles

Better characterization of interactions in food webs with cyclic species

- Population densities are typically estimated from indices of high uncertainty (e.g., tracks or scat [Krebs, 2011](#), tree rings, [Cooke & Roland, 2007](#)). More **precise population estimates** (e.g., mark-recapture) and longer-term monitoring will improve statistical power, add value to proxy data, and allow testing of more complex models ([Krebs et al., 2014](#)).
- Observation-driven **high-dimensional models** are needed to understand how population cycles emerge in, and interact with, entire food webs. Multi-species microcosm experiments and some natural food webs can serve as anchors for future theories ([Benincà et al., 2008](#); [Krebs, 2011](#)).
- **Multidimensional time series** (e.g., multi-species population data, abiotic data) will be crucial for identifying the dimensionality of ecological fluctuations, using models both in the time domain ([Abbott et al., 2009](#); [Sugihara et al., 2012](#)) and in the frequency domain ([Detto et al., 2012](#)).

Better integration of individual-level processes into mechanistic population models

- The roles of **behavioral responses** (e.g., fear) and **indirect demographic effects** (e.g., maternal effects on fecundity) are increasingly recognized in the context of cyclic populations ([Sheriff et al., 2010](#); [Krebs, 2011](#); [Sheriff et al., 2011](#)), but theoretical treatments are scarce ([Kendall et al., 2005](#)). More demographic studies (e.g. [Row et al., 2014](#)) are needed.
- Understanding the **role of co-evolution in ecological cycles**, and how results from microcosm experiments apply to higher taxa and natural populations ([Yoshida et al., 2003](#); [Yoshida, 2006](#); [Becks et al., 2010](#)).
- **Trade-offs between reproduction and survival rates** in evolutionary models will need to be adjusted to measurable life history traits such as fecundity and mortality, in order to obtain testable predictions on how cyclic environments affect evolution ([Greenman et al., 2005](#); [Hoyle et al., 2011](#)).
- New tools are needed for **calibrating detailed stochastic models**, including individual-based models ([Svanbäck et al., 2009](#); [Hartig et al., 2011](#)), to data.

Understanding the effects of stochasticity on population fluctuations

- Recent work challenges the robustness of conclusions from models that assume perturbations to be weak and uncorrelated ([Reuman et al., 2008](#); [Sharma et al., 2015](#)). Future stochastic models will need to move **beyond weak white noise** by considering (1) high-amplitude perturbations and non-linear responses, as well as (2) autocorrelated (coloured) noise.
- Methods are needed for **identifying the best description of observed fluctuations**, be it as limit cycles, NSOs, non-cyclic fluctuations, or chaos ([Pineda-Krch et al., 2007](#); [Louca & Doebeli, 2015](#)), and detecting causal relationships between variables ([Sugihara et al., 2012](#)). This is essential for the construction of detailed mechanistic models ([Kendall et al., 1999](#)), and in turn, providing management strategies.
- Further exploring how **demographic** and **environmental noise** influence **traveling waves** ([Petrovskii et al., 2010](#)), in order to improve our interpretation and predictions of spatiotemporal patterns in the field.

Consequences of cycles and management

- Correctly **interpreting changes in cyclicity** as signs of population collapse or increase, or other larger ecological changes ([Ims et al., 2008](#); [White et al., 2014](#)).

- Understanding the role of cycles in **biodiversity maintenance**. For example, do cycles in key herbivores within large food webs favor top consumer coexistence?
- **Control methods** based on mathematically derived “hot regions”, so far only tested under laboratory conditions (Desharnais *et al.*, 2001), need to be evaluated **in the field**.

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Figures

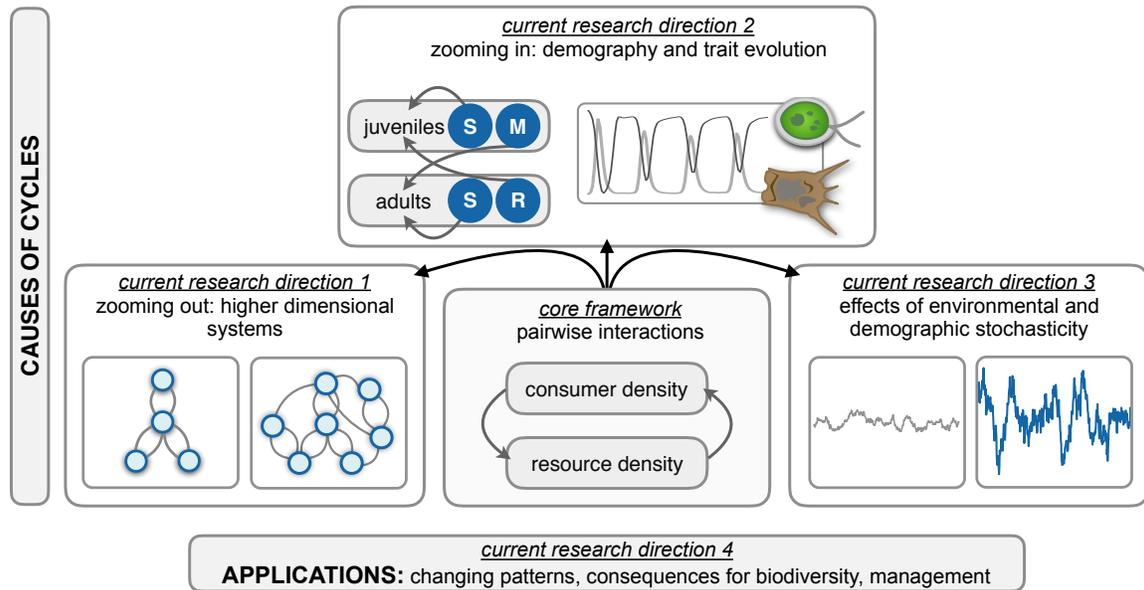


Fig. 1: Key areas in theoretical and statistical population cycle research. In panel 2, we represent flows of individuals between juvenile (top) and adult (bottom) compartments. S: survival, R: reproduction, M: maturation processes.

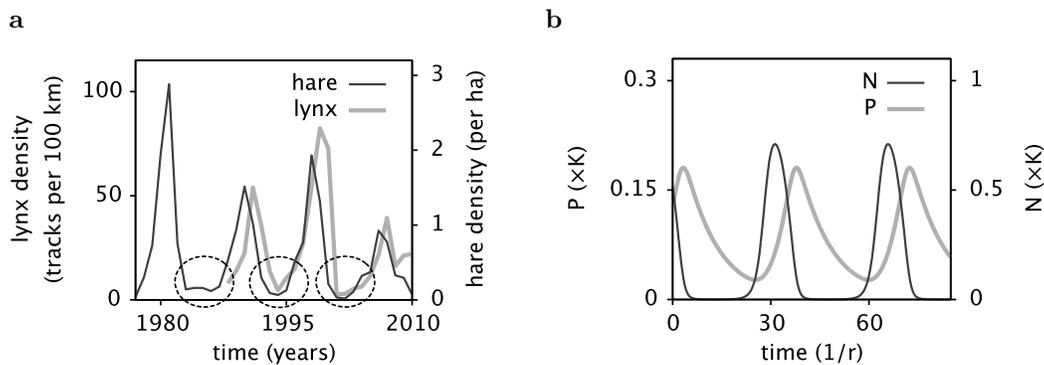


Fig. 2: (a) Snowshoe hare densities in spring (black curve) and lynx snow track densities during winter (grey curve), in Kluane Lake area, Northern Canada. Lynx winter densities are plotted over the year of the next spring. Data from Krebs (2011). Dashed circles indicate troughs of the hare cycle, which remain poorly understood. (b) Prey (N) and predator (P) population densities (relative to the prey carrying capacity K) during predator-prey cycles according to the Rosenzweig-MacArthur model (Supplementary Appendix S1). Time is relative to the inverse intrinsic prey growth rate. $K = r/\alpha$ is the prey carrying capacity. Parameters: $r = 1$, $\alpha = 1$, $c = 5$, $D = 0.4$, $e = 0.1$, $\mu = 0.1$ (equations in Supplementary Appendix S1). Unless the parameters are tweaked to unrealistic values, the predator-prey lag remains different in (a) and (b). However, lynx snow tracks imperfectly reflect lynx densities, thus the true lag is unknown.

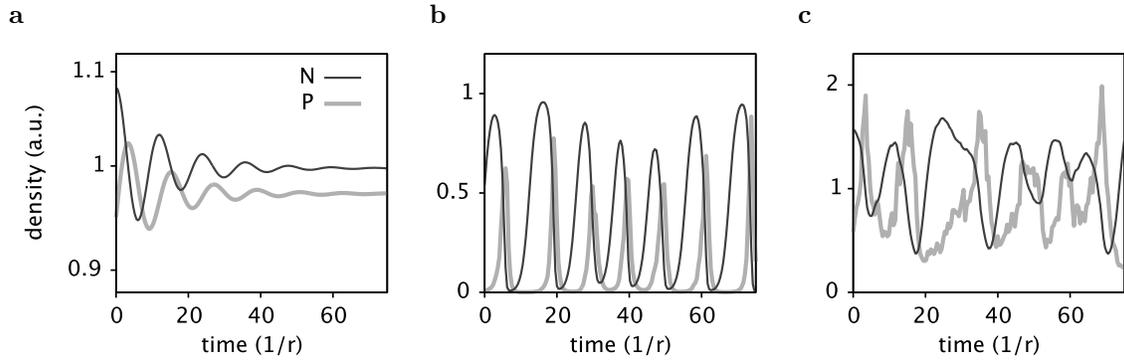


Fig. 3: Behavior of a stochastically forced predator-prey system (the Bazykin model, a variant of the RM model with a self-regulated predator; equations in Supplementary Appendix S1). The model can exhibit, depending on parameter values, (a) damped oscillations ($e = 1.4, \sigma = 0$), (b) noisy limit cycles ($e = 1.9, \sigma = 20$) or (c) phase-forgetting noise-sustained oscillations ($e = 1.4, \sigma = 20$). For all simulations $K = 1, r = 1, K_p = 100, c = 2, d = 0.2, \mu = 2$ (equations in Supplementary Appendix S1). Population sizes for prey and predators are independently rescaled to arbitrary units.

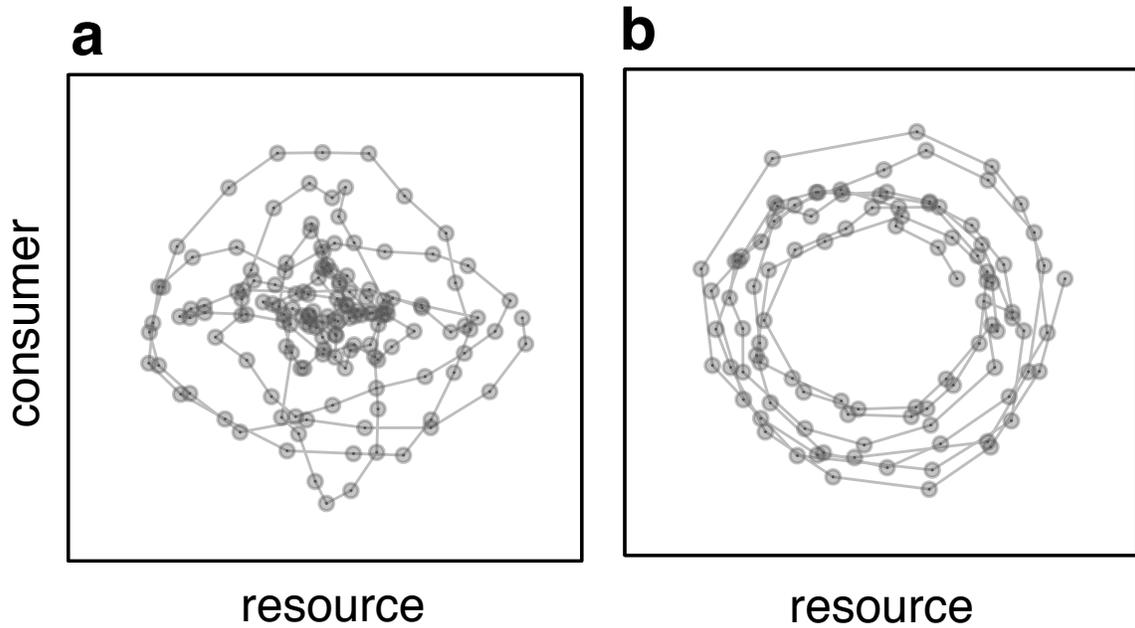


Fig. 4: Phase planes of stochastic predator-prey models: (a) Phase plane generated by noise-sustained oscillations, concentrated around the deterministic equilibrium. (b) Phase plane generated by a limit cycle perturbed by noise, concentrated around the periodic trajectory. In both figures, overlapping dots appear darker.

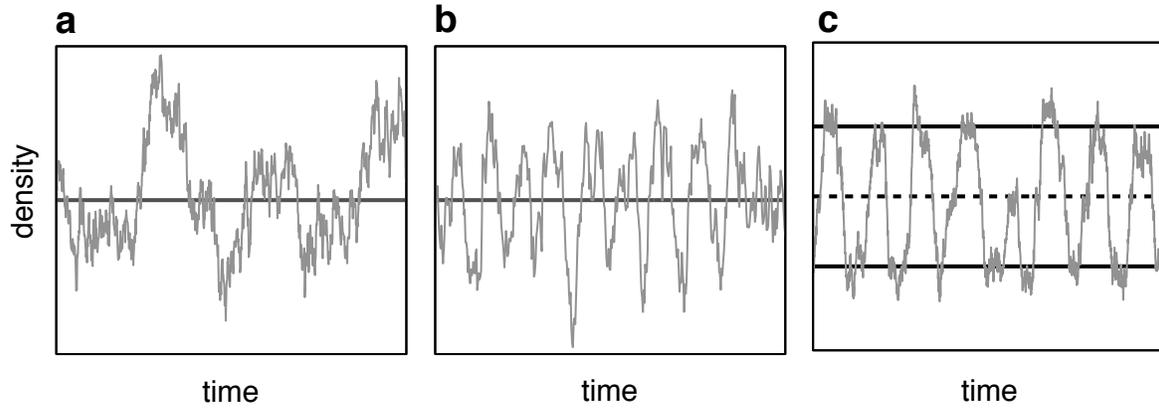


Fig. 5: (a–c): Fluctuating time series (gray curves) generated by stochastic models showing: (a) Irregular, non-periodic fluctuations around an equilibrium, (b) noise-sustained oscillations around a stable focus perturbed by white noise and (c) flickering in a bistable system subject to white noise. Solid and dashed lines represent stable and unstable equilibria, respectively. In all 3 cases, noise is essential for the emergence of the observed fluctuations.