Seasonality in Ecology: Progress and Prospects in Theory

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1 Abstract

Seasonality is an important feature of essentially all natural systems but the consequences of seasonality have been vastly underappreciated. Early work emphasized the role of seasonality in driving cyclic population dynamics, but the consequences of seasonality for ecological processes are far broader. Yet, seasonality is often not explicitly included in either empirical or theoretical studies. Many aspects of ecological dynamics can only be understood when seasonality is included, ranging from the oscillations in the incidence of childhood diseases to the coexistence of species. Through several case studies, we outline what is now known about seasonality in an ecological context and set the stage for future efforts. We discuss approaches for incorporating seasonality in mathematical models, including Floquet theory. We argue, however, that these tools are still limited in scope and more approaches need to be developed.

Keywords: annual cycle, phenology, seasonal forcing, seasonal variability, temporal variability, timescales

2 Introduction to seasonality

Seasonality is a prevalent environmental feature in diverse ecological systems driven by periodic climatic condition (Fretwell 1972, Holt 2008). Seasonality can be defined as the regular and periodic changes of a variable on an annual timescale (Williams et al. 2017). Seasonal variables relevant in ecological systems obviously include temperature and photoperiod, but also include rainfall, wind, human activity, upwelling, and resource pulses. The recognition of these varied drivers of ecological systems shows the ubiquity of seasonality.

Although ecologists clearly acknowledge the role of seasonality, in many cases seasonal factors are ignored in investigations of ecological processes and systems. There are two

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main reasons for this lack of focus on seasonality. First, from an empirical perspective, data must be collected throughout the year, and over several years, to understand the role of seasonality in ecological systems (Power et al. 2008). To examine seasonality explicitly, a control treatment with no seasonality would be needed—an often impossible manipulation in natural systems. And second, from a modeling perspective the complexity of mathematical tools needed to deal with seasonal factors presents a great challenge. Although possible numerically, periodic variability makes traditional ecological models more difficult to work with analytically. This relates to the more general problem in mathematical models of dealing with large variability (Hastings 2004). Recognizing the role of seasonality reflects a broader trend in ecology to move away from thinking of ecological systems in terms of equilibrium dynamics (Hastings 2004, Tonkin et al. 2017) and instead focus on transients and variability.

Yet, despite these difficulties in studying seasonality, a number of ecological questions can only be answered in the context of seasonality. Both persistence and coexistence of many populations depend on seasonality. For example, Power et al. (2008) examine the role seasonal flooding plays in determining food web dynamics. Only by sampling throughout the year, and across many years, were they able to show how the complex predator-prey interactions depended on the seasonal regime. A key life history aspect determining an organism's response to seasonality is whether an organism lives for a longer or shorter duration than the seasonal factor of interest. For organisms that live less than a year, a number of different strategies may be used including seasonal polyphenisms (Morehouse et al. 2013) and seed banks (Venable 2007). Conversely, long-lived organisms have to endure seasonal changes multiple times throughout their lives. From simple winter dormancy to more complex strategies, organisms have evolved a number of approaches to cope with seasonality (Forrest and Miller-Rushing 2010). Organisms may skip unfavorable seasons by shutting down their metabolisms during part of the year (e.g. hibernation) or migrating between areas that are more or less favorable (Holt and Fryxell 2011).

Because of the evolved responses of species to seasonal pressures, seasonality is directly tied to work on species phenology. Seasonal interactions and global climate change can alter the phenology of species in important ways. There can be mismatches in the timing of seasonal events, increased or decreased season lengths, and lastly, a reduction or increase in the seasonal variability (Stevenson et al. 2015). These changes can then alter the relative timescales between organism and seasonal variability. Phenological mismatches can occur between a species and its environment or between multiple species (Visser and Both 2005, Both et al. 2009). As climate change advances the timing of optimal conditions (e.g. resource availability or temperature) necessary for reproduction, or other seasonal life-history events, a particular species may become poorly suited to its environment. Climate change is also expected to change the length of seasons, which can have positive or negative consequences for individual species (Stevenson et al. 2015). Lengthened summer seasons are expected to alter ecosystem level processes that may feed back to affect individual species. For instance, permafrost in the Arctic is expected to melt more rapidly with climate change, which would release more CO_2 (Schuur et al. 2008). This will further drive long term changes in the environment that could feedback to individual organisms. Lastly, the variability (or amplitude) in environmental conditions over a course of a year may decrease. For instance, the temperature may reach lower maxes in summers and higher minimums in winter, an "eternal summer" scenario (Stevenson et al. 2015). This could be beneficial for some species

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and harmful for others.

Here, our goal is not to provide a comprehensive review of seasonality. Instead, we select specific case studies to emphasize the pervasiveness of seasonality, how ignoring seasonal dynamics prevents ecological understanding, and provide an overview of current mathematical approaches to modeling seasonality. We start by discussing the relationship between timescales and seasonality. We then discuss available mathematical tools, especially in the context of single species and infectious disease dynamics (Altizer et al. 2006). Next, we highlight these ideas for interacting species and community dynamics. Lastly, we provide some recommendations for future avenues of research. We do not discuss literature on animal migrations (Altizer et al. 2011, Dingle 2014, Teitelbaum et al. 2015) or evolution (Williams et al. 2017) as both have been extensively reviewed elsewhere.

3 Timescales and seasonality in simple models

Concepts from timescales provide the structure for organizing theoretical approaches to seasonality. As in the study by Power et al. (2008), the key concepts are embodied in simple issues of timescales related to species lifespan. Many of the basic conclusions are illustrated by a very simple model (Hastings 2012) that looked at persistence for a single species with a fixed lifespan and a temporally varying resource. Here we consider the seasonal factor as the varying resource. There are three possible relationships between the timescale of variability and the species lifespan: species lifespan longer than seasonal cycle, species lifespan on a timescale comparable to seasonal variability, or species lifespan shorter than seasonal cycle. For long-lived species, the species experiences essentially the arithmetic mean resource level, averaging across seasons and years. If the resource varies very slowly, the consumer dynamics are governed by the geometric mean resource level, which can obviously be much less than the arithmetic mean if there is large variability. No simple conclusions are possible if the timescales are comparable. As an example, small seasonal variation in certain parameters, such as transmission rates in the dynamics of childhood diseases, can lead to dynamics that have a period that is yearly or possibly more complex (Metcalf et al. 2009). This key example illustrates the idea that if underlying timescales in the process are similar to the timescales of variability complex behavior can result.

4 Single-species dynamics

The concepts illustrated by simple models point to the key issues that need to be included in more detailed approaches. Understanding the role of seasonality in ecological models requires explicit variation in parameters within the year (Table 1). One obvious approach is to start with a model in continuous time, a differential equation model, and to allow a parameter to depend explicitly on time (Rosenblat 1980). For example, a mathematical model of seasonality could simply be the continuous-time logistic population model with a temporally-varying carrying capacity. Without seasonality, the model solutions converge to a simple fixed-point attractor. However, a seasonal forcing term causes periodic solutions. These simple models show that seasonality can enrich the possible set of solutions, moving from simple equilibrium points to fluctuating populations dynamics.

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Modeling approach	**Description**	**Strength(s)**	**Weakness(es)**
Semi-discrete (hybrid) models (Mailleret and Lemesle 2009)	Combines discrete time (between years) and continuous time (within season) models	Intuitive choice for many species with seasonal reproduction. Flexible framework	Not appropriate for continuously reproducing species
Periodically-forced models solved with numerical methods	Numerical tools can be used to approximate solutions of complicated population models that include periodic forcing terms	Can be more biologically realistic.	Computationally intense. Limited solution space.
Small noise approximations	Some models allow analytical solutions if variability is small	Appropriate when seasonal forces are small in magnitude.	Limited application
Periodic matrices	Different transition matrices for each season	Includes structure or multiple species	Need to parameterize multiple matrices, one for each season
Floquet theory (Klausmeier 2010)	Allows a measurement of invasion rates in strictly periodic environments	Simple interpretation and extension of traditional eigenvalues	Often difficult to implement in practice
Successional state dynamics (Klausmeier 2010)	Approach to modeling seasonally forced food webs as series of state transitions	Analytical results are possible. Fast to simulate	Limited to species which have fast dynamics relative to seasonal forcing terms. Appropriate for species unaffected by demographic stochasticity at low population size.

Table 1: Survey of mathematical tools for modeling seasonality.

One area where seasonally-forced models have been particularly useful is in the study of infectious diseases (see review by Altizer et al. 2006). Seasonality can affect infectious disease dynamics through several mechanisms: affecting host behavior, modifying host immune responses, altering encounter rates between pathogens and hosts, and affecting the biology of disease vectors via changing season lengths and magnitude (Altizer et al. 2006, Metcalf et al. 2009, Shaman et al. 2010, Stevenson et al. 2015). One simple approach to these questions includes seasonality in the standard SEIR (susceptible, exposed, infected, recovered) epidemiological models by allowing birth and transmission to depend explicitly on time (see Box 1 in Altizer et al. (2006)). One textbook example is the outbreak of the contagious childhood disease measles in England (Bjørnstad et al. 2002, Grenfell et al. 2002). Without seasonality, models of measles would predict damped cycles, whereas measles outbreaks occur as sustained cycles. Here, the key seasonal factor was varying contact rates driven by the academic calendar. Models with the inclusion of seasonal factors accurately predict sustained, large amplitude cycles (Bjørnstad et al. 2002, Grenfell et al. 2002).

In addition to continuous-time models, the dynamics at different times of the year can be modeled separately. For species with an overwintering stage, an appropriate approach would be a hybrid model that has continuous time dynamics during part of the year (with constant parameters) and a discrete time description of survivorship during the other part of the year (Table 1). For example, White et al. (2018) modeled a collared pika (*Ochotona collaris*) population in the Yukon. The model included two parts: a continuous-time set of differential equations to represent growth and resource acquisition during the summer and a discrete-time map from the start of winter to the start of spring. The resulting dynamics were periodic cycles in population size. A related approach that would be appropriate for organisms such as corals that spawn at essentially a single time during the year would be impulsive differential equations, where there is a single reproductive pulse during the year. Simple discrete time models, including an equation for each season, can also be used to study seasonality. For example, Kot and Schaffer (1984) examined a discrete time model of a single species in a seasonal environment. They found that while mild seasonality can stabilize population dynamics, larger seasonality will destabilize the population. Recently, Betini et al. (2013) also used a two-season model and coupled it with experiments of Drosophila. They found that density-dependence and carry-over effects form one season to the next can act to stabilize population dynamics. Specifically, in the absence of seasonality there would have been decaying oscillations or chaotic dynamics as opposed to sustained oscillations when seasonality was included.

All of these mathematical models can be readily solved numerically. However, analytical approaches can be difficult to use, if not impossible. The tools typically used to analyze stability such as linearization and eigenvalues have natural analogs called Floquet multipliers (see Klausmeier (2008) for a review in an ecological context). Although Floquet multipliers can be found analytically for simple models, they are typically calculated numerically. Klausmeier (2008) showed three diverse examples where Floquet multipliers were useful: calculating fitness in structured populations, determining invasion criteria in models of competition, and in determining the stability of limit cycles. However, Floquet multipliers are limited to models of periodic systems. For stochastic or chaotic variability, more general Lyapunov exponents (Metz et al. 1992) are needed, as Lyapunov exponents are essentially analogous to Floquet multipliers.

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5 Interacting species

Much of the large body of empirical and theoretical literature on the dynamics of interacting species has ignored explicit consideration of seasonality. For example, early models of coexistence including the Lotka-Volterra competition equations as used by Gause (1934) and Tilman's R* model (Tilman 1982) did not include explicit temporal variation. More recent work has explored how these conclusions change as temporal variability is included.

Temporal variability can promote coexistence through the storage effect and relative nonlinearity (Chesson 1994, Chesson and Huntly 1997), each a form of temporal niche partitioning. The storage effect allows a particular species to experience low competition during one season, or time of year, and to store that benefit for later use (Snyder 2012). Then, two species may outperform one another, but only in different parts of the year or in different years—a partitioning of time. Species are able to store these benefits in the form of dormant seeds, long-lifespans, or in ways that directly store resources. These ideas have been empirically tested in winter annual plants in the Sonoran Desert (Angert et al. 2009). Here, a tradeoff between growth and low-resource tolerance in desert annuals allows for the coexistence of several similar species, because of interannual variability and the storage effect.

Relative nonlinearity is important in a temporally varying environment, as growth is usually a nonlinear function of competition (Ruel and Ayres 1999). If two species have different growth curves or experience different degrees of variability, each will find different periods of time to be more favorable than others. The differences present between species give the term relative nonlinearity. Because of Jensen's inequality, this allows for one species to invade the other and vice versa, thus allowing for coexistence. Although relative nonlinearity is not as important as the storage effect, it can be important in systems where oscillatory or chaotic dynamics are present (Snyder 2012).

Recent work has also highlighted how temporal heterogeneity, and in particular seasonality, can fundamentally alter results from classic predator-prey models. For example, Taylor et al. (2013a) examined a Rosenzweig-MacArthur predator-prey model (Rosenzweig and MacArthur 1963) in which prey growth rate was a sinusoidal function of time. The non-seasonal Rosenzweig-MacArthur model produces monotonic, or oscillatory, decay to equilibrium or limit cycles. With seasonal terms included in the model, multi-year cycles, quasi-periodicity, and chaos are all possible (Taylor et al. 2013a). These results are in line with past work that has shown multi-year cycles to be common in natural systems (Kendall et al. 1999). Taylor et al. (2013b) followed up this work with a more tactical model to examine the Fennoscandian vole system. This system spans a large geographical region and experiences different levels of seasonal forcing in different areas. They found that by including predation pressure from weasels and varying breeding season length, they could accurately predict the cycle lengths of the vole population sizes in different locations. This is in contrast to past work that attributed different cycles lengths only to varying predation pressures.

In order to understand how species interactions may change with global warming, an explicit consideration of seasonality is warranted. In addition to mismatches between a particular species and abiotic variables, species interactions may be altered when seasonal patterns are disrupted (Tylianakis et al. 2008). Past work has focused on pairwise interactions between species (Stevenson et al. 2015), but see Both et al. (2009) on several trophic levels. Many predators rely on timing of reproduction to be in sync with resource availability.

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This is most clearly demonstrated in the context of birds, like the great tit (*Parus major*) in the Netherlands. Reed et al. (2013) found that in response to spring warming, a mismatch occurred between the great tit's timing of reproduction and peak caterpillar abundance, the primary food for nestlings. This led to strong selection for earlier reproduction, but did not result in significant demographic consequences.

6 Community dynamics

Community ecologists have long been interested in how seasonal factors can lead to patterns in biodiversity. Janzen (1967) postulated his "seasonality hypothesis" to explain the latitudinal diversity gradient. Essentially, he proposed that organisms that lived in less seasonal environments (e.g. the tropics) would have a reduced range of physiological tolerance to temperature. This, in turn, would reduce gene flow and cause higher speciation rates in less seasonal environments. Empirical evidence for Janzen's seasonality hypothesis has been mixed, but mostly supports his core ideas (Ghalambor et al. 2006, Sheldon et al. 2015).

To better understand the role of seasonality in community dynamics, McMeans et al. (2015) called for more research on temporally forced food webs. Focusing on arctic food webs, they argue that temporally forced food webs are the norm in ecology and that including temporal variability in models has an effect on both ecosystem function and stability. Although explicit inclusion of temporal variability in food web models is a challenge both mathematically and empirically, there are some mathematical tools currently available.

A number of approaches may be applicable for modeling seasonally forced communities, including periodic matrices with interacting species, non-autonomous systems of differential equations, successional state dynamics (Klausmeier 2010), and complex simulation models (Table 1). Recently, Klausmeier (2010) developed an approach, which he termed successional state dynamics (SSD), in order to study seasonally forced food webs. The approach can be used with any ecological model (e.g. predator-prey model) that incorporates a piece-wise periodic forcing function. Essentially, SSD tracks species as common or rare, thus simplifying food web dynamics to a succession of state transitions. Klausmeier (2010) showed that SSD is only applicable in systems where the species dynamics (generation times) are fast relative to the frequency of the external timing. This may limit potential uses of SSD, but it would still be relevant in microbial, plankton, or insect food webs.

Empirical investigations of seasonality in ecological communities have demonstrated the importance of inclusion of time. Power et al. (2008) examined a seasonally pulsed river system over an 18-year period, finding that algae blooms were common in summers that proceeded strong winter flooding. They also used a series of experiments to demonstrate the of role algae consumers, and higher trophic levels, have on controlling algae biomass. They conclude by noting that after disturbances, like floods, the specific food webs that succeeded were dependent on both the flooding regime itself and members of the community present. Without an understanding of seasonal dynamics, the community differences found year-to-year would be a mystery.

Recently, Benincà et al. (2015) examined successional dynamics of a rocky intertidal system dominated either by barnacles, mussels, or algae. Using a set of periodically-forced coupled differential equations, they found that seasonal forcing in temperature could force a

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cyclic system to become chaotic. Using 20 years of abundance data, they found that their system was really on the edge of chaos, alternating between more regular, cyclic behavior and chaotic dynamics. Thus, the model dynamics would be fundamentally different in the absence of this seasonal driver. Seasonal forcing, and exogenous forces in general, can interact with intrinsic dynamics resulting in various interesting phenomena, such as chaos (Hastings et al. 1993). Thus, periodic forcing of a system that already displays periodic behavior can result in chaos (Hastings et al. 1993, Benincà et al. 2015)

With climate change, the strength of many species interactions is likely to change—largely driven by changes in phenology (Visser et al. 2004, Visser 2008). A change in the season lengths or strength of seasonal factors could lead to different population or community dynamics. For example, changing seasonal fog patterns may affect not only coastal redwoods (*Sequoia sempervirens*) but also for other members of the forest community, which may collect water caught by redwoods (Johnstone and Dawson 2010). Further, global climate change can interact with particular aspects of species biology, like their ontogeny, to further alter species interactions (Yang and Rudolf 2010). Despite the need to understand how seasonality affects community dynamics there are few available systems with enough temporal resolution to model seasonal or year-to-year changes in food web structure and composition (McMeans et al. 2015).

7 Conclusions and future directions

Recently, ecologists have begun moving away from studying equilibrium dynamics, and instead recognizing inherit temporal variability (Hastings 2004). Seasonality is a particular type of temporal variability and is ubiquitous in ecological systems. Studying seasonality explicitly leads to many important conclusions, but three stand out. First, seasonality in and of itself is an important source of variability that drives many ecological systems. As in the example of childhood diseases, seasonality played a critical role in understanding that system (Metcalf et al. 2009). It is therefore not surprising that seasonality can be a structuring force in other ecological contexts. Second, incorporating seasonality can enrich the possible dynamics possible in the system. This was particularly clear in the example of a rocky intertidal community (Benincà et al. 2015). They showed that including seasonality in temperature altered the dynamics a simple fixed point to chaotic dynamics. Lastly, seasonality is a simple form of variability, given it is periodic on a yearly timescale. Therefore, if we understand the role of seasonality in ecological systems, we could make progress towards understanding the role of environmental variability in general.

Our current dearth of knowledge on seasonal dynamics stems from both empirical and theoretical difficulties. Empirically, an understanding of seasonal forcing requires long-term observations or experiments. Therefore, data from several years, including multiple seasons, are required to characterize such a system. This should become easier and more cost-effective with increases in technology for monitoring (Pimm et al. 2015). Mathematically, we have few tools to handle large variability, like seasonality, in even simple models. Some recent applications of classical mathematical approaches (e.g. Floquet theory) are potential future avenues. However, Floquet multipliers are more of an important conceptual tool than a practical computational or analytic approach for more complicated ecological systems, like seasonal food webs where fewer approaches are available (McMeans et al. 2015).

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