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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. In ecological systems, seasonality may include variations in temperature, precipitation, or other processes. Seasonality is typically not explicitly included in either empirical or theoretical studies. However, 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. Further, studies of phenology and global climate change only make sense in the context of seasonal dynamics. Our goal is to outline what is now known about seasonality and to set the stage for future efforts. We review the effects of seasonality on ecological systems in both laboratory and field settings. We then 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. We demonstrate the range of impacts of seasonality on ecological systems and show the necessity of incorporating seasonality to understand ecological dynamics.

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

2 Introduction to seasonality

Seasonality is a nearly ubiquitous feature of ecological systems since in essentially all environments some climatic drivers are seasonal (Fretwell 1972). Seasonality can be defined as the regular and periodic changes of a variable on an annual time scale (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. One reason is simply the difficulty of doing so. 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). From a modeling perspective the complexity of mathematical tools needed to deal with seasonal factors presents a great challenge. 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.

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) demonstrated the role of seasonal flooding in determining food web dynamics of river systems. In addition, any characteristic related to phenology, or timing of life history events, is almost by definition related to seasonal dynamics. A key aspect of life history determining an organism's and population's response to seasonality is whether an organism lives for a longer or shorter duration than the seasonal factor of interest (Table 1). 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).

It is a challenge to manage and conserve species in seasonal environments without a good sense of seasonal ecology in general. A further challenge is that climate models now predict that many seasonal factors may change in timing, intensity, or duration (Stevenson et al. 2015). Consequently, to manage in a novel environment (Cuddington et al. 2013) a mechanistic understanding of the organisms of concern in relation to seasonal environmental factors is needed to make predictions of future behavior.

Our overall goals are to emphasize how ubiquitous the influence of seasonality is, how ignoring seasonal dynamics prevents ecological understanding, and provide an overall framework for understanding the impacts of seasonality. We start with general theory. We then move to disease dynamics where the inclusion of seasonal factors is clearly essential (Altizer et al. 2006) and has been relatively well understood. We move on to other, perhaps less well discussed, areas. We do not review 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. Ideas from time scales provide a key organizing principle: seasonality essentially sets a yearly or within year time scale, and the interaction with different time scales of different organisms provides a way to understand how and when seasonality matters.

	Consumer persistence depends on:	Consumer dynamics
Resource dynamics faster than population dynamics	Arithmetic mean resource level	Determined by average resource
Resources dynamics on same time scale as population dynamics	No general prediction	More complex dynamics
Resources dynamics slower than population dynamics	Geometric mean resource level	Tracks resource dynamics

Table 1: The relationship between the time scale of resource fluctuation and consumer persistence or dynamics. Modified from Hastings (2012).

3 State of the general theory

Concepts from time scales provide the structure for organizing theoretical approaches to seasonality (Table 1). For populations changing faster than yearly, explaining periodic dynamics is an important goal. For populations where longer than yearly time scales are appropriate, the role of seasonality in determining species persistence, coexistence, or population levels is the key issue. The standard simple ecological modeling approaches cannot address these questions without explicitly including seasonality.

Many of the basic conclusions and possible complications 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. There are three possible relationships between the time scale of variability of the resource and the consumer lifespan: the resource varies rapidly relative to the lifespan, the resource varies on a timescale comparable to the lifespan, or the resource varies slowly (Table 1). If the resource varies rapidly, the consumer experiences essentially the arithmetic mean resource level. 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. This essential trichotomy underlies theoretical understanding of the role of seasonality for persistence (Table 1).

For questions of dynamics key aspects of the system include the seasonal variability magnitude and the lifespan (or other relevant life history aspects) of the organisms (Table 1). A simple conclusion is that small seasonal variation in 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 time scales in the process are similar to the time scales of variability complex behavior can result.

More generally, approaching the role of seasonality in models requires explicit variation in parameters within the year (Table 2). One obvious approach is to start with a model in continuous time, a differential equation model, and have one or more of the parameters depend explicitly on time (Fig. 1 and Rosenblat 1980). A well-studied example of the

approach are the equations used in models of childhood diseases where the contact rate is assumed to be periodic in time with a period of one year, with sinusoidal variability typical (Metcalf et al. 2009). In other approaches, the dynamics at different times of the year are separated explicitly. In insects with an overwintering stage, 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 2). 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 (Kot and Schaffer 1984). 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) that unfortunately are a conceptual and potentially numerical tool rather than a truly practical analytic tool.

Adding further complications, such as spatial aspects, can lead to even more complex dynamics. What the discussion of theoretical approaches really illustrates is that one reason for the lack of appreciation of the role of seasonality has been the more limited (especially analytical) tools available for developing and analyzing models. This is particularly true, as we noted above, for the case when seasonality is likely to be most important: when the seasonal effects are large and the natural time scale of the ecological system in the absence of seasonality would not be too far from one year.

4 Infectious disease dynamics

Studies of infectious disease dynamics with mechanistic models and high quality data have emphasized how including seasonality is essential (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). Additionally, some diseases require specific seasonal conditions for outbreaks to occur. For example, influenza requires low temperature and humidity, leading to winter outbreaks in temperate climates (Shaman et al. 2010, Stevenson et al. 2015). Of course, these seasonal conditions change on a year-to-year basis, and the length and magnitude of these seasons are likely to change under climate change (Shaman et al. 2010, Stevenson et al. 2015).

Seasonality is typically included 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)). Without the explicit seasonality the models would not produce the observed cycles in the number of infected individuals.

One textbook epidemiological 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

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 using 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	Allows you to calculate growth rates in periodic environment	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 and species unaffected by demographic stochasticity at low population size

Table 2: Mathematical tools for modeling seasonality

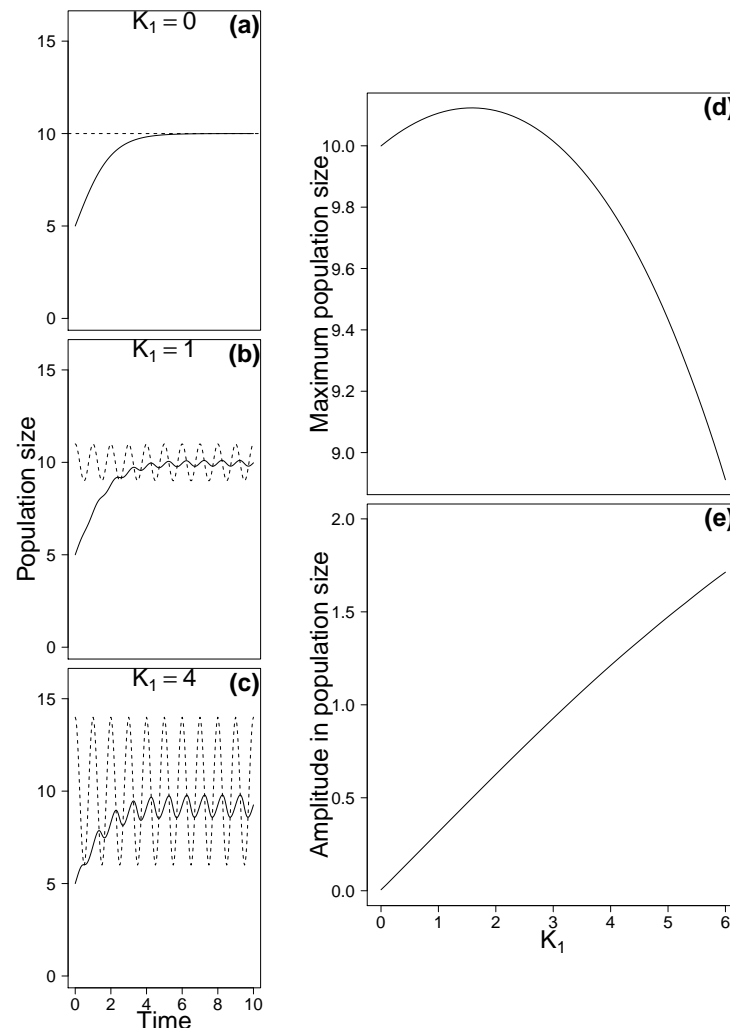


Figure 1: Seasonality can be included in simple population models by including periodic forcing terms (Rosenblat 1980). A simple example would be the logistic growth model $dN/dt = rN(1 - N/K(t))$ with $K(t) = 10 + K_1 \cos(2t)$, where there is a fluctuating carrying capacity, K . Here N is the population size, r is the intrinsic rate of growth, and t is time. Panels (a)-(c) are solutions to the forced logistic growth model with (a) $K_1 = 0$, (b) $K_1 = 1$, and (c) $K_1 = 4$. For different values of K_1 , panels (d) and (e) show the maximum population size and amplitude in population, respectively.

cycles (Bjørnstad et al. 2002, Grenfell et al. 2002). The role of spatial dynamics, primarily the heterogeneity in city size in England, interacted with seasonal dynamics and affected the spread of periodic measles outbreaks. Since this work, numerous other examples of the role of seasonality in driving disease outbreaks have been identified, including rubella incidence in Kenya (Wesolowski et al. 2015) and six childhood infections before the modern era of vaccination (Metcalf et al. 2009).

Several disease vectors are particularly sensitive to temperature, precipitation, and other seasonal factors (Altizer et al. 2013). Thus, many of these vectors outbreak during certain parts of the year and only in certain geographic locations. Because of climate change, the

timing or location of optimal conditions for these vectors has changed in many places (Altizer et al. 2013). This, in turn, has altered the spread of the diseases associated with these vectors. Perhaps of largest concern is the spread of mosquito-borne diseases like malaria and dengue (Gage et al. 2008, Thomson 2014).

Strikingly, epidemiological models without seasonal components may produce erroneous results. In addition, it is also important to study the interactions between seasonal processes and spatial heterogeneity, inherit nonlinearities, evolution, and climate change. The lessons of the importance of seasonality in epidemiology, the kinds of effects, and the ways models are developed suggest fruitful avenues for more general questions of population biology.

5 Ecological implications

In ecological systems, our understanding of seasonality has been developed mostly in terms of single species dynamics, both mathematically and empirically. A simple mathematical model of seasonality could be the logistic model with a temporally-varying carrying capacity (Fig. 1). These simple models show that seasonality can enrich the possible set of solutions, moving from simple equilibrium points to fluctuating populations dynamics (Table 3). 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 from one season to the next can act to stabilize population dynamics. Here we focus on cases where seasonality was studied in the context of multi-species communities.

5.1 Interacting species

Much of the large body of empirical and theoretical literature on the dynamics of interacting species has ignored explicit consideration of seasonality. As examples, the 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 effects. The Lotka-Volterra competition equations predict that coexistence is only possible given certain parameter values. Tilman's R^* theory explicitly models resources and predicts one species would outcompete another given a single limited resource. 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 part of the 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

System	Main finding	Seasonal factor	Modeling approach	Without (or weak) seasonality	With seasonality	Citation
Succession in intertidal area	Cyclic succession of barnacles, algae, and mussels driven by seasonal temperature fluctuations	Temperature	sinusoidal variability	Decaying oscillations	Chaotic dynamics	(Benincà et al. 2015)
Childhood measles	Sustained cycles only predicted with inclusion of seasonality in contact rates	Contact rates	sinusoidal variability	Damped cycles	Sustained cycles	(Bjørnstad et al. 2002, Grenfell et al. 2002)
Experimental <i>Drosophila</i> system	Depending on parameter values, seasonality can stabilize population dynamics	Discrete breeding season	A different population model for each season	Decaying oscillations or chaotic behavior	Sustained oscillations	(Betini et al. 2013) ∞
Rosenzweig-MacArthur model	Seasonality can move a system from simple equilibrium dynamics to more complicated dynamics	NA	seasonal forcing term	Monotonic, or oscillatory, decay to equilibrium or limit cycles	Multi-year cycles, quasi-periodicity, and chaos are all possible	(Taylor et al. 2013a)
Fennoscandian vole system	Changes in the length of the breeding season lead to changes in the period of multi-year cycles	Length of breeding season	seasonal forcing term	NA	Multi-year cycles where the period depends on the seasonal regime	(Taylor et al. 2013b)

Table 3: Examples of systems where the inclusion of seasonality was important for understanding overall ecological dynamics.

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. Similar to the one species models described earlier, seasonal forcing terms can be included in classic predator-prey models. Recently, (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 unforced 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.

One of the most important aspects of seasonality in regards to interacting species is when season lengths may change for those species in different ways. This can cause species to experience stronger or weaker interactions (Tylianakis et al. 2008). As we will see in the next section, mismatches between species are also important when examining whole ecological communities (McMeans et al. 2015).

5.2 Community dynamics

For more than two species questions about succession, coexistence, and community assemblies are important. McMeans et al. (2015) called for more research on temporally forced food webs, in particular seasonally-driven 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. Explicit inclusion of temporal variability in food web models is a challenge.

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 2). 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. 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 role of 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 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).

6 Other sources of temporal variability

Seasonality is a single example of temporal variability, one that is periodic on a yearly time scale. However, there are other sources of periodic variability on different time scales and non-periodic variability. Thus seasonality is one way to consider more general questions of temporal variability. The relationship between the time scale of variability and that of the species of interest will determine population dynamics (Table 1).

Temporal variability has long been recognized to be important in ecological systems (Gravel et al. 2011). Early work by (Lewontin and Cohen 1969) focused on a simple single-species model of population growth that introduced variability that was uncorrelated and drawn from the same random variable. They found that this variability alone could dra-

matically alter the conditions for persistence of the population—depending on the geometric growth rate instead of the arithmetic growth rate (Lewontin and Cohen 1969). Of course, temporal variability can also be correlated over time. Intuitively we know the conditions one day, or one year, can often help predict what will occur in the next time period. Not surprisingly, specific autocorrelation structure and the time scale of correlation are important in determining the effects of variability on population dynamics (Schreiber 2010). Ecological models predict much different dynamics with the inclusion of seasonality and temporal variability more generally.

In ecology, much less work has examined the role of large variability. Few mathematical tools exist for explicitly dealing with large variability (Lande et al. 2003, Hastings 2014). Either a number of simplifications are needed or more complicated simulation models can be employed. As an example, Lyles et al. (2009) examined data from a pistachio farm in tandem with a stochastic modeling framework. They found that resource switching coupled with large environmental variability might drive the masting behavior in pistachio trees. Here, large temporal variability was necessary to generate realistic model predictions.

Resource pulses are another source of large variability, often tied to abiotic and biotic factors (Yang et al. 2008, Holt 2008). One of the best-known examples of a periodic resource pulse is the emergence of cicadas (*Magicicada* spp.) on the east coast of the United States (Yang 2004). Every 17 years, these cicadas emerge and are consumed by numerous small mammals, reptiles, spiders, and other insects (Yang 2004). Outbreking insects, whether periodic or not, also provide below ground benefits as they can often increase the rate of nutrient cycling (Yang 2004). Although economic questions of resource pulses have been studied, less is known about the ecological effects of these events (Yang et al. 2008). Similar to disturbances, the specific consequences of resource pulses depend on characteristics of the pulse (magnitude, frequency and duration), the environment, and the specific players involved directly or indirectly with the pulsed resource (Yang et al. 2008). Resource pulses can allow coexistence between similar species if they are able to take advantage of the resource pulse and competition is reduced. This may also lead to species being able to define a temporal niche in relation to other species (Yang et al. 2008)

7 Seasonality and global change

Phenology is the key to many 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 time scales between organism and seasonal variability (Table 1). 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. This strong selective pressure may drive a plastic or genetic response in seasonal timing (Bradshaw and Holzapfel 2008). 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 CO₂ (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 and harmful for others. For example, warmer winters may decrease snowpack causing animals like the Collared pika to freeze during winter rain storms (COSEWIC 2011).

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. 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.

More research needs to be done on more complex systems—those with more than a single pairwise interaction (McMeans et al. 2015). In these species networks, interactions between species are expected to change seasonally and between years. Not surprisingly, including temporal forcing in food web models will alter stability and persistence of those webs. Unfortunately, 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).

8 Conclusions and implications

Recently, ecologists have begun moving away from studying equilibrium dynamics, and instead recognizing inherent temporal variability (Hastings 2004). Seasonality is a particular type of temporal variability and is ubiquitous in ecological systems and thus may be a way to study more general effects of variability. If we have a theoretical understanding of the role of seasonality in ecological systems, we could compare across systems regardless of which specific seasonal factors were at play. We also see that the time scale of seasonality interacts with the natural time scale of each species, affecting overall population dynamics (Table 1). As we have shown, an appreciation for seasonal forces is essential for understanding ecological systems, including species interactions and disease dynamics (Table 3). 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. Thus, without an understanding of seasonality we may prescribe incorrect management actions.

Global climate change is expected to alter seasonal timing, duration, and magnitude

(Stevenson et al. 2015) of seasonality. In response to climate change, there are numerous examples of changing phenologies of plant and animal species across the globe (Visser and Both 2005, Both et al. 2009). However, not all species are responding the same. Therefore, a better understanding of seasonality may help us tease apart differential responses of species to climate change.

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. Mathematically, we have few tools to handle large variability, like seasonality, in even simple models. Some recent developments (e.g. Floquet theory and non autonomous systems theory) are potential future avenues. Of course, we have even fewer tools available in more complicated ecological systems, like seasonal food webs (McMeans et al. 2015).

Studying seasonality explicitly leads to many important conclusions, but two 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 (Table 3). Second, seasonality is a simple form of variability, given it is periodic on a yearly time scale. Therefore, if we understand the role of seasonality in ecological systems, we could make progress towards understanding the role of environmental variability in general.

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