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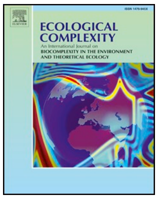

Seasonality in ecology: Progress and prospects in theory

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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 various approaches and tools for incorporating seasonality in mathematical models. We argue, however, that these tools are still limited in scope and more easily-accessible approaches need to be developed.

1. Introduction to seasonality

Seasonality can be defined as the regular and periodic changes of a condition on an annual timescale (Williams et al., 2017). Seasonality is a prevalent environmental feature in diverse ecological systems driven by periodic climatic condition (Fretwell, 1972; Holt, 2008). Seasonal variables relevant in ecological systems obviously include temperature and photoperiod, but also include rainfall, wind, human activity, upwelling, and resource pulses. From this list of examples, it is clear that seasonality can affect many ecosystem processes and therefore the dynamics of many populations and communities.

Although ecologists clearly acknowledge the role of seasonality, in many cases seasonal factors are ignored in investigations of ecological processes and systems. As one example, in identifying 100 fundamental questions in ecology, Sutherland et al. (2013) did not mention seasonality, although some questions were related to spatio-temporal dynamics. There are two 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). In situations where data can be collected at high frequency, it is then possible to use traditional time series tools (e.g. seasonal autoregressive models) to study the role of seasonality (Ghysels et al., 2001). To examine seasonality explicitly, a control treatment with no, or reduced, seasonality would be needed—an often impossible manipulation in natural systems. And second, from a modeling perspective the complexity of mathematical models needed to deal with seasonal factors presents a challenge. In particular, mathematical models with periodic variability (e.g. seasonality) are more difficult to work with analytically, although it is still possible to solve such models numerically. Thus, to incorporate temporal variability, simulation models of specific systems are often used, which can be too complicated to allow for theoretical insights. This relates to the general difficulty of analyzing mathematical models which include 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, 2001; Tonkin et al., 2017) and instead a focus on transients. Because seasonality essentially perturbs an ecological system yearly, Hastings (2014) noted “investigations of coexistence in planktonic systems have focused not only on complex dynamics, but also on the transient behavior of models [...] because, with seasonality, long-term solutions can be essentially irrelevant.” If seasonality is strictly periodic, tools to study long-term equilibrium dynamics still apply, but they still do not address questions of transients. Thus, despite difficulties in studying seasonality, a number of ecological questions can only be answered in the context of seasonality. This is particularly true for understanding transients and making short term predictions (Dietze et al., 2018).

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Both persistence and coexistence of many populations depend on seasonality (Rudolf, 2019). Many of the basic conclusions are illustrated by a simple and general theoretical consumer-resource model with a temporally varying resource (described fully in Hastings, 2012). Here we consider the seasonal factor as the varying resource. There are three possible relationships between seasonality and the species lifespan: species lifespan much longer than seasonal cycle, species lifespan on a timescale comparable to seasonal variability, or species lifespan much shorter than seasonal cycle. For long-lived species, the species experiences essentially the arithmetic mean resource level, averaging across seasons and years. Conversely, for a short-lived consumer species, the consumer dynamics are governed by the geometric mean resource level, which can be much less than the arithmetic mean. No simple conclusions are possible if the species lifespan is on a similar time scale to the seasonal cycle. For organisms that live less than a year, a number of different life-history 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. To cope with this seasonality, organisms have evolved various strategies, including shutting down metabolism during part of the year (e.g. hibernation) or migrating between areas that are more or less favorable (Forrest and Miller-Rushing, 2010; 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). Phenological mismatches can occur between a species and its environment or between multiple species (Both et al., 2009; Kharouba et al., 2018; Visser and Both, 2005). 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). Lastly, the variability (or amplitude) in environmental conditions over a course of a year may decrease. For instance, the temperature may reach lower maxima in summers and higher minima in winter, an "eternal summer" scenario (Stevenson et al., 2015). This could be beneficial for some species and harmful for others.

Here, our goal is not to provide a comprehensive review of seasonality, but instead to highlight important ecological aspects of seasonality and techniques to model them in a theoretical context. We use a series of case studies to emphasize the pervasiveness of seasonality and how ignoring seasonal dynamics prevents ecological understanding. We first discuss some available mathematical approaches and 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.

2. General models with seasonality

Understanding the role of seasonality in ecological models requires explicit variation in parameters within the year (Table 1). Following ideas that go back at least as far as (Levins, 1966), we begin with general models that incorporate the basic ideas, but not the details. Identifying, and then modeling, the specific underling biological mechanism of seasonality is key as different modeling assumptions will lead to different dynamics (Geritz and Kisdi, 2004). One obvious approach is to start with a model in continuous time, such as an ordinary differential equation, 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 in the same model causes periodic solutions. Every continuous or semi-discrete model with strict periodicity is therefore equivalent to a fully discrete model with the period as the time step. These general models show that seasonality can enrich the possible set of solutions, moving from simple equilibrium points to fluctuating population dynamics.

General discrete-time models, including an equation for each season, can also be used to study seasonality. These models include inherit time delays with the mapping from one year to the next (Geritz and Kisdi, 2004). The specific mechanisms that cause these time delays are what produce the more complex dynamics commonly observed in discrete-time systems (Geritz and Kisdi, 2004). 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.

Some situations require neither a strictly discrete- or continuous-time approach. Instead, dynamics at different times of the year can be modeled separately. For species with an overwintering stage, an appropriate approach would be a semi-discrete (or 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, Mailleret and Lemesle (2009)). For example, White et al. (2018) modeled a collared pika (*Ochotona collaris*) population in Yukon, Canada. 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 of population size on a yearly timescale. Thus, these cycles can also be viewed as a fixed-point solution if observed only once per year, i.e. a discrete-time system.

All of these mathematical models can be readily solved numerically. However, analytical tools can be difficult to use, if not impossible. For example, linear stability analysis for periodic solutions results in Floquet multipliers (Cushing, 1980; Klausmeier, 2008; Smith and Waltman, 1995; Strogatz, 2001). Although Floquet multipliers can be found analytically for simple models, they are typically calculated numerically. Klausmeier (2008) showed three different examples where Floquet multipliers can be useful: calculating fitness in structured populations, determining invasion criteria in models of competition, and in determining the stability of limit cycles. For stochastic or chaotic variability, more general tools are used (King et al., 1996; Metz et al., 1992; Rinaldi et al., 1993; Stollenwerk et al., 2017).

3. Infectious disease dynamics

Beyond single species models, 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

Table 1
Survey of modeling approaches and analysis tools for studying seasonality.

Modeling approach	Description	Strengths	Limitations
Statistical approaches	Include periodic explanatory variables (often in the form of a sine and cosine functions with periodicity on an annual time scale) in traditional time series techniques (Ghysels et al., 2001)	• Can reveal the correlative relationship between a response variable and the seasonal factor allowing for forecasting or hypothesis generation.	• Requires a lot of data to estimate effect of seasonal variable and only captures correlative patterns.
Semi-discrete models	Combines discrete-time (between years) and continuous-time (within season) models (Mailleret and Lemesle, 2009)	• Intuitive choice for many species with seasonal reproduction.	• Not appropriate for continuously reproducing species
Periodic matrix models	Different transition matrices can be built for each season (Caswell, 2001)	• Intuitive choice for many species with seasonal reproduction. • Includes within-species heterogeneity in vital rates or multiple species	• Not appropriate for continuously reproducing species • Need to parameterize multiple matrices, one for each season
Continuous-time models with periodic forcing terms	Ordinary (or partial) differential equations, stochastic differential equations, and other approaches can include periodic forcing terms and be solved numerically	• Appropriate for continuous-time systems	• Can be computationally intense to solve and cannot be solved analytically. • Not appropriate for discretely reproducing species
Analysis tool			
Small noise approximations	Some models allow analytical solutions if seasonal variability is small	• Analytical results are possible • Appropriate when seasonal forces are small in magnitude	• Limited to a narrow set of modeling situations
Floquet theory	Measures linearized stability of periodic orbits (Cushing, 1980; Klausmeier, 2008; Strogatz, 2001)	• Simple interpretation and extension of traditional eigenvalues	• Often difficult to implement in practice
Successional state dynamics	Technique to modeling seasonally forced food webs as series of state transitions (Klausmeier, 2010)	• Analytical results are possible • Fast to simulate	• Limited to species which have fast dynamics relative to seasonal forcing terms and unaffected by demographic stochasticity at low population size.

SIR (susceptible, infected, recovered) epidemiological models by allowing birth and transmission to depend explicitly on time (Altizer et al., 2006; Bauch and Earn, 2003). One textbook example is the outbreak of the contagious childhood disease measles in England (Bjørnstad et al., 2002; Grenfell et al., 2002). Without seasonality in contact rates, models of measles would predict damped cycles, whereas measles outbreaks occur as sustained cycles. In addition, seasonality can interact with other processes. For instance, Mata et al. (2019) studied a seasonally-forced stochastic differential equation. They found that, although demographic stochasticity did not alter the timing of limit cycles caused by seasonality, the amplitude of the cycles were affected. At higher levels of stochasticity, the dynamics were no longer strongly governed by the underlying deterministic skeleton, which principally contains the seasonal component (Mata et al., 2019). Focused on epidemics, Alonso et al. (2007) show that stochasticity can sustain cycles that would have otherwise dampened out, but also that this effect depends on the strength of seasonality. These more complicated infectious disease models also lead naturally to more general models of interacting species and community dynamics.

4. 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 resource-ratio hypothesis (Tilman, 1982) did not include explicit temporal variation, as that was not their focus. Tilman's approach explicitly models resources and predicts one species would out-compete another given a single limited resource. However, more recent work has built on these seminal papers to explore the consequences of adding temporal heterogeneity.

Theoretical work has shown that temporal variability can promote coexistence through several mechanisms, including the storage effect and relative nonlinearity, each a form of temporal niche partitioning (Chesson, 1994; Chesson and Huntly, 1997). Temporal niche partitioning can prevent competitive exclusion of species (Hutchinson, 1961). The storage effect allows an individual species to experience low competition during one season, or time of year, and to store that benefit (e.g. body fat) for later use (Snyder, 2012). Thus, two species may outperform one another, but only in different parts of the year or in different years. Species are able to store these benefits in the form of dormant seeds, long-lifespans, or in ways that directly store resources. Seasonality allows a particularly large degree of variation that can allow the storage effect to operate. 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 variability in seasonal rainfall and the storage effect.

Relative nonlinearity is important in a temporally varying environment, as growth is usually a nonlinear function of competition (Chesson, 1994). If two species have growth curves that respond differently to competition, each species experiences different periods of time where they are favored. The average growth rate for each species then depends on the degree of variation in competition. The variation can increase or decrease the average growth rate depending on the shape of the nonlinear functions, i.e. Jensen's effect (Ruel and Ayres, 1999). Thus, relative nonlinearity can promote coexistence when forces, like seasonality, cause fluctuations in competition (Chesson, 1994). Although relative nonlinearity is probably not as relevant in nature as the storage effect, it can be important in systems where oscillatory or chaotic dynamics are present (Snyder, 2012).

One particular area where seasonality has been considered, and can fundamentally alter results, is in predator-prey models (King and Schaffer, 2001; King et al., 1996; Rinaldi et al., 1993; Stollenwerk et al., 2017; Tyson and Lutscher, 2016). For example, the nonseasonal Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963) 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 (Gragnani and Rinaldi, 1995; Rinaldi et al., 1993; 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 the key mechanism that explained the varying cycle lengths of the vole population sizes in different locations was the length of the breeding season. 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 (Kharouba et al., 2018; Rudolf, 2019; Tylianakis et al., 2008; Tyson and Lutscher, 2016). Past work has focused on pairwise interactions between species (Stevenson et al., 2015), but see Both et al. (2009) on several trophic levels. Rudolf (2019) has recently shown how modern coexistence theory can be extended to consider species interactions in the context of seasonal regimes. More theoretical work should build on this by exploring the different ways in which seasons might change and by considering multiple trophic levels.

5. 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, like the tropics. Evidence for Janzen’s seasonality hypothesis has been mixed and depends on the specific system, but empirical work 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 described earlier are also applicable for modeling seasonally forced communities, including periodic matrices with interacting species, temporally-forced systems of differential equations, and complex simulation models (Table 1). Around a decade ago, Klausmeier (2010) borrowed ideas from physics to introduce another 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 that incorporates periodic forcing, like seasonality. Essentially, SSD reduces species abundance to a binary measure of common or rare, thus simplifying food web dynamics. 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 systems with fast generation times, e.g. 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 mechanisms for changing community structure each year would be unknown. These same ideas have investigated in other ecological systems to show how seasonality itself can maintain biodiversity (Dakos et al., 2009; Sakavara et al., 2018).

As an example, Benincà et al. (2015) examined successional dynamics of a rocky intertidal system dominated either by barnacles, mussels, or algae. Previous work had indicated that mortality rates depend on the season, as high summer temperatures cause higher mortality of both algae and mussels. 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 more broadly, can interact with intrinsic periodic dynamics resulting in chaotic dynamics (Benincà et al., 2015; Hastings et al., 1993). In general, seasonal forcing of any underlying dynamics more complex than approach to an equilibrium can lead to much more complex dynamics

With climate change, the strength of many species interactions is likely to change—largely driven by changes in phenology (Visser, 2008; Visser et al., 2004). A change in the season lengths or strength of seasonal factors could lead to different population or community dynamics. Further, global climate change can interact with particular aspects of species biology, like their ontogeny or phenology, to further alter species interactions (Rudolf, 2019; Yang and Rudolf, 2010). In these species networks, interactions between species are expected to change seasonally and between years. Not surprisingly, including temporal forcing will alter stability and persistence in models of ecological communities (McMeans et al., 2015; Rudolf, 2019). 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). For systems with available data (e.g. plant-pollinator interactions and disease dynamics), network modeling provides another framework for understanding seasonality. These dynamic, or evolutionary, network models allow for temporal fluctuations in the network topology or processes connecting the nodes (Gross and Blasius, 2008).

6. Conclusions and future directions

The study of complex dynamics in ecology goes back at least as far as the 1970’s (May, 1974; 1976), but in the last couple of decades ecologists have expanded studies of more complex dynamics and dynamics on shorter time scales, including those caused by temporal forcing (Hastings, 2004). Seasonality is a particular type of temporal forcing 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; for instance, the role seasonality plays in determining species coexistence (Rudolf, 2019). Second, incorporating seasonality can enrich the possible dynamics possible in the system (Gragnani and Rinaldi, 1995; Hastings et al., 1993; Rinaldi et al., 1993). This was particularly clear in the example of a rocky intertidal community (Benincà et al., 2015) where seasonal changes in temperature altered the dynamics a simple fixed point to chaotic dynamics. Thus, not incorporating seasonality in models can lead to an incorrect understanding of the ecological system or the application of incorrect management actions. Because seasonality can enrich system dynamics, and lead to longer transient behavior, this can also delay the time it which ecosystem managers might detect changes. Lastly, although, as we have emphasized, analytic solutions of models incorporating seasonality are difficult, these models are still easier to analyze or numerically solve than stochastic ones. Separating out the effects of amplitude and time scale of variability and keeping the external effects bounded is much easier in the context of seasonal models than stochastic ones. Thus we can make use of the idea that 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 limited understanding of seasonal dynamics stems from both empirical and theoretical difficulties. Empirically, an understanding of seasonal forcing requires long-term observations and experiments. Therefore, to ensure high statistical power, ecologists and ecosystem managers need to collect data from several years, including multiple seasons, to properly understand the role of seasonality (McMeans et al., 2015; White, 2019). Of course, data collection is often seasonal simply for logistical reasons (e.g. weather, academic calenders) (Tyson and Lutscher, 2016). This should become easier and more cost-effective with increases in technology for monitoring (Pimm et al., 2015). Although we have some mathematical tools to manage seasonal forces that are strictly periodic, much of the software typically used (e.g. AUTO, MATCONT) is not readily-accessible to ecologists. Other techniques to handle transient behavior, like that produced by seasonality, are still being developed (Vesipa and Ridolfi, 2017). Floquet multipliers are more of an important conceptual tool than a practical one, especially for more complicated ecological systems. Therefore, we need further development in accessible tools for studying temporally-forced systems in general. In addition to more development on analytical tools, other numerical approaches may hold more promise. With big data becoming the new norm in ecology, statistical approaches may enable a better understanding of the effect of seasonality across systems (Ghysels et al., 2001). Other areas of current research, including successional state dynamics and dynamic network models, point to other potential avenues that might be most relevant in more realistic, complicated ecological systems.

Ethical statement

Hereby, I, Easton White, consciously assure that for the manuscript "Seasonality in Ecology: Progress and Prospects in Theory" the following is fulfilled:

1) This material is the authors' own original work, which has not been previously published elsewhere.
2) The paper is not currently being considered for publication elsewhere.
3) The paper reflects the authors' own research and analysis in a truthful and complete manner.
4) The paper properly credits the meaningful contributions of co-authors and co-researchers.
5) The results are appropriately placed in the context of prior and existing research.
6) All sources used are properly disclosed.
7) All authors have been personally and actively involved in substantial work leading to the paper, and will take public responsibility for its content.

CRediT authorship contribution statement

Easton R. White: Conceptualization, Writing - review & editing, Writing - original draft. **Alan Hastings:** Conceptualization, Writing - review & editing, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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