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Ecological Synchrony and Metapopulation Persistence

A Dissertation submitted in partial satisfaction
of the requirements for the degree of

Doctor of Philosophy

in

Evolution, Ecology, and Organismal Biology

by

Serj Danielian

June 2022

Dissertation Committee:

Dr. Helen M. Regan, Chairperson

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ABSTRACT OF THE DISSERTATION

Ecological Synchrony and Metapopulation Persistence

by

Serj Danielian

Doctor of Philosophy, Graduate Program in Evolution, Ecology, and Organismal
Biology

University of California, Riverside, June 2022

Dr. Helen M. Regan, Chairperson

Due to habitat fragmentation, many of the populations in nature have been broken into smaller subpopulations that are connected by migration (i.e., metapopulation). Subpopulation synchrony within a metapopulation is of practical importance because it has consequences for the conservation of species. Moran effect and dispersal are the main causes of metapopulation synchrony, but the spatial distribution of subpopulations has also been shown to influence synchrony and persistence in metapopulations. In population ecology, synchrony has been shown to negatively influence persistence in metapopulations. In chapter 1 of this dissertation, I review how synchrony is studied in ecology with the aim of identifying a unifying role of synchrony across ecological processes. In this chapter, I showed a novel framework for classifying synchrony across ecological processes. I referred to synchrony that is within a single trophic level as horizontal synchrony and synchrony that takes place between species at different trophic levels as

vertical synchrony. This framework classified vertical synchrony into antagonistic synchrony (predator-prey and parasite-host) and synergetic synchrony (mutualism and commensalism). The horizontal synchrony was categorized as intraspecific synchrony (i.e., synchrony within a population), and interspecific synchrony (i.e., among species synchrony). In chapter 2, I ran theoretical simulations to investigate how the spatial distribution of subpopulations (i.e., homogeneous vs heterogeneous metapopulation networks) influences persistence in metapopulations. I showed that there appears to be an intermediate optimal amount of heterogeneity but in my study intermediate and high heterogeneity were fairly similar and both were better for persistence than homogeneous metapopulation networks. I also showed that more dispersal appears to be more beneficial than less dispersal. In chapter 3, I ran theoretical simulations to investigate the role of positive (red noise) and negative (blue noise) autocorrelations of environmental variation in large heterogeneous metapopulation networks. I showed that when the autocorrelation of environmental noise shifts from positive (red noise) to negative (blue noise), this may benefit the persistence of a species in large heterogeneous metapopulation networks. Higher dispersal between patches increased occupancy and persistence. Overall, this dissertation summarizes the role of synchrony in ecological interactions and could be a useful resource for educational purposes. It also contributes to conservation science by allowing the conservationists involved in decision-making to optimally design reserves under varying natural conditions.

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Introduction

Due to habitat fragmentation, many of the populations in nature have been broken into smaller subpopulations that are connected by migration. This concept of grouped subpopulations connected by migration (dispersal) was coined by Richard Levins (1969) as a Metapopulation. These subpopulation densities may fluctuate in a synchronous fashion within a metapopulation. Synchronized subpopulations have been observed in species of insects, human pathogens, fish, amphibians, mammals and in many other taxa (Liebhold et al. 2004). Subpopulation synchrony within a metapopulation is of practical importance because it has consequences for the conservation of species. For example, if several different populations that form a metapopulation are synchronous and achieve low densities at the same time, then the entire metapopulation or perhaps the entire species is at risk of becoming extinct (Laan and Fox 2020; Régnière and Nealis 2019; Anderson and Hayes 2018; Matter 2001; Earn et al. 2000; Heino et al. 1997). On the other hand, if the metapopulation is not synchronous and one or more populations become extinct while others survive because they had higher population densities, then the surviving populations could be the source of dispersing individuals which recolonize the locality of the extinct population. Human activity frequently results in habitat fragmentation and a barrier to dispersal, which increases the need to understand the consequences of metapopulation synchrony. Understanding synchrony at the metapopulation level could lead to better natural resource management and help in conservation decisions.

Mechanisms of metapopulation synchrony

Many of the studies have focused on the two main mechanisms of metapopulation synchrony: 1) correlation of environmental factors (Walter et al. 2021), and 2) dispersal (Abbott 2011). These mechanisms and their relative importance have been a major research question (Matter et al. 2022; Kahilainen et al. 2018; Duncan et al. 2013, Abbott and Dwyer 2008; Abbott 2007; Peltonen et al. 2002; Williams and Liebhold 2000). If dispersal is high enough, subpopulations can synchronize and increase the chances of extinction for the metapopulation (Abbot 2011; Earn et al. 2000; Hudson and Cattadori 1999). Moran (1953) was one of the first to propose environmental fluctuations as a cause of metapopulation synchrony. Moran (1953) studied the predator-prey dynamics between lynx and snowshoe hare populations throughout Canada and concluded that the synchronization of the predator-prey relationship was caused by synchronized environmental factors.

Other studies have shown that the spatial distribution of the subpopulations can have a significant influence on the synchrony and persistence of species (Gilarranz and Bascompte 2012; Holland and Hastings 2008). These studies mentioned above reported that subpopulations that have a more uniform (i.e., homogeneous) spatial distribution tend to result in more synchronous dynamics, and therefore, result in lower metapopulation persistence compared to subpopulations with less uniform distributions (i.e., heterogeneous).

Measuring metapopulation synchrony

Studies have assessed synchrony using some variant of the correlation coefficient, including Pearson and Spearman correlation coefficients, correlation in direction of changes, and correlation of high and low peaks of time series (Buonaccorsi et al. 2001). A correlation approach may mask important dynamics, which might be revealed by looking at the time scale (i.e., period) of synchrony of environmental variation (Ouyang et al. 2014). For example, one can look at just the variance of a time series, which is a single number. However, if one wanted to have a better understanding of that time series, one can break it down by frequency through the process of fast Fourier transform (Bracewell 1993; Platt and Denman 1975). The spectrum of a time series is the frequency decomposition of the variance that shows the relative contributions of variation at different time scales. If a variance is accumulated at low or high frequencies in the power spectra, this causes positive or negative autocorrelations which are named red or blue environmental noise respectively (Postuma et al. 2020; Cotto and Chevin 2020; Ruiz and Rincón 2018). For fragmented populations (i.e., metapopulation), the color of environmental noise can be reflected in the color of the population time series, and this can have a significant influence on a species' population dynamics (Desharnais et al. 2018; Massie et al. 2015). Gilljam et al. (2019) showed that the color of environmental noise such as temperature, precipitation, and frost day frequency, is associated with animal population dynamics. The strength of this association between the color of

environmental noise and population time series has been shown to be negatively influenced by the increasing inherent population growth rates (Ferguson et al. 2016). More specifically, red noise has been associated with a high extinction chance in slow-growing populations, while blue noise with fast-growing populations (García-Carreras and Reuman 2011; Schwager et al. 2006; Heino et al. 2000; Cuddington and Yodzis 1999). These associations can further be influenced by dispersal such that increasing dispersal under red noise conditions can decrease extinction chance (Mustin et al. 2013). These complex interactions are important to understand because these can have consequences for the persistence of a metapopulation.

Rationale for Chapter 1 of this dissertation

Several review papers have summarized ecological literature on the topic of synchrony in the previous decades (Duranton and Gaunet 2016; Satake et al. 2012; Abbott 2011; Liebhold et al. 2004; Spottiswoode and Møller 2004; Bjørnstad et al. 1999; Reed et al. 1997; Ims 1990). These reviews range from topics such as reproductive synchrony to synchrony of population dynamics to synchrony of animal behavior to synchrony of environmental variation. To my knowledge, there has not been a synthetic review in recent years that looks at synchrony across ecological interactions. The broad aim of the initial chapter is to fill this gap and to explore the role that synchrony, and subsequently, asynchrony, play in a lot of different processes in ecology, and not just in metapopulation persistence. The goal

of this project is to review how synchrony is studied in other ecological processes in recent years, whether there is a unifying role of synchrony across ecological process, and what its consequences for biodiversity and conservation are.

Rationale for Chapter 2 of this dissertation

A network heterogeneity is a characteristic of a metapopulation network. A heterogeneous network has high variability in the number of connections per patch, while a homogeneous network has habitat patches with a similar number of connections per patch (Zamborain-Mason et al. 2017; Gilarranz and Bascompte 2012). This heterogeneity of a metapopulation network has only been shown to have a positive influence on the metapopulation persistence (Liao et al. 2020; Lucas et al. 2019; Grilli et al. 2015; Gilarranz and Bascompte 2012; Cooper et al. 2012; Holland and Hastings 2008). A possible reason why many of these studies have not detected a negative influence of network heterogeneity on metapopulation persistence is because network structure is not emphasized on a full range of dispersal, and growth. A big point that is missing is the fact that previous work has looked at network structure and metapopulation persistence using colonization/extinction models, but not with actual population dynamic models. The broad aim of this chapter is to fill this gap.

I think that a homogeneous network should lead to high synchrony in a metapopulation and lead to high extinction. In contrast, the heterogeneous network would lead to low synchrony but a high extinction due to disconnect between

patches. Therefore, a network with intermediate heterogeneity should lead to high persistence by balancing against the negative influence of synchrony and disconnect between patches. The role of dispersal and growth rates between patches is also investigated in these interactions and how these influence persistence in metapopulation networks.

Rationale for Chapter 3 of this dissertation

Previous studies that have looked at the influence of the color of environmental noise have either used a population with a single patch (Gilljam et al. 2019; Ferguson et al. 2017; García-Carreras and Reuman 2011; Schwager et al. 2006; Cuddington and Yodzis 1999) or a metapopulation with a small number of patches (Danielian 2016; Greenman and Benton 2005; Heino 1998). We propose that the interaction of color of environmental noise with growth rate and dispersal may possibly be influenced by network heterogeneity in spatially structured large metapopulations. It remains unknown how the color of environmental noise influences survival in heterogeneous metapopulation networks. The aim of this paper is to fill this gap.

In this third chapter, I ask how does the color of noise influence persistence in large heterogeneous metapopulation networks; what role does the growth rate of subpopulations play in this interaction; and how is this interaction influenced by dispersal rate between metapopulation patches?

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Chapter 1: How Synchrony is Studied in Ecological Processes and What the Consequences of That Synchrony (or Asynchrony) is for Biodiversity.

Introduction

Synchrony is a well-known, widely studied, and fundamental phenomenon in population ecology; it is defined as coincident changes in the abundance or other time-varying demographic parameters of populations (Wang et al. 2016; Liebhold et al. 2004). Accordingly, asynchrony is defined as a lack of that synchrony. Several review papers over the past three decades have summarized the ecological literature on synchrony in individual ecological processes (Duranton and Gaunet 2016; Satake et al. 2012; Abbott 2011; Liebhold et al. 2004; Spottiswoode and Møller 2004; Bjørnstad et al. 1999; Reed et al. 1997; Ims 1990). These reviews range across topics such as synchronous reproduction, population dynamics, animal behavior, and environmental variation. The role of synchrony has been particularly well established in metapopulation dynamics and the most cited review papers on synchrony focus on the stabilizing role of dispersal in metapopulation dynamics (Abbot 2011; Liebhold et al. 2004).

Many review papers focus on a single process such as the role of synchrony in reproduction, behavior or population dynamics, but do not compare and/or contrast the role of synchrony across multiple ecological processes. To our knowledge, there has not been a synthetic review in recent years that examines synchrony across ecological interactions. A comprehensive review of the

contribution of synchrony across processes in ecology would promote a better understanding of the interactions of organisms and their environments. In this review, we aim to survey the different modes and mechanisms of synchrony in ecology to identify the circumstances under which synchrony promotes or impedes species persistence. The broad aim of this paper is to examine the roles of synchrony in a range of fundamental ecological processes and how those roles influence the biodiversity of organisms.

In this paper, we summarize the ways that synchrony occurs in population ecology and how it influences ecological outcomes. We offer a framework for differentiating the modes of synchrony in foundational ecological processes that are presented widely in ecology textbooks. We use this framework to examine synchrony across a range of ecological processes and ultimately how it affects species' survival and ultimately biodiversity.

Synchrony in Population Ecology

Intraspecific synchrony

In ecology, synchrony has been studied widely in populations, particularly in metapopulations linked by dispersal. Synchrony within a population is also known as intraspecific synchrony (Swanson and Johnson 1999; Hanski and Woiwod 1993). There are two main causes of synchrony in metapopulations: 1) correlations among environmental factors which cause subpopulations to fluctuate in the same directions (Moran Effect) and 2) dispersal (Abbott 2011) between the

subpopulations within a metapopulation in which an increase in abundance of one subpopulation compensates for a decrease in another (Laan and Fox 2020; Defriez et al. 2016; Loreau and Mazancourt, C., 2008; Liebhold et al. 2004; Kendall et al. 2000; Ranta et al. 1997). Moran (1953) was the first to propose environmental fluctuations as an underlying cause of metapopulation synchrony and identified temperature-related meteorological phenomena that contributed significantly to the synchronous oscillations of lynx and snowshoe hare population densities. Moran concluded that synchronized environmental factors in turn cause synchronization of the predator-prey relationship of lynx and snowshoe rabbits. The term "Moran effect" has ever since been used to refer to the synchronous relationship between populations that are driven by environmental variables.

On the other hand, dispersal has been described as a "double-edged sword" because while it may recolonize extirpated subpopulations at the local level, providing a stabilizing effect, it can cause synchronized fluctuations in subpopulation densities at the regional or global scale (Abbott 2011; Hudson and Cattadori 1999); ultimately leading to population collapse.

Synchrony between subpopulations can result in lower persistence of the metapopulation to which they belong. When the abundances of subpopulations within a metapopulation fluctuate synchronously, i.e., rise and fall together, subpopulations are at relatively low or high density simultaneously. If a catastrophic event, or even a "bad year", strikes a metapopulation when all subpopulations are at

low density, the chance of that metapopulation becoming extinct can be high. Alternatively, synchrony in metapopulation dynamics can play a resource limiting role by creating a strain on resources when all subpopulations within a metapopulation are at high density. When subpopulations are fluctuating asynchronously, the chances of extinction are lower because if one subpopulation is extirpated, individuals from a high-density subpopulation can recolonize this subpopulation through dispersal and lower the chance of extinction for the entire metapopulation. Under asynchronous fluctuations, resource availability is unequally distributed across subpopulations because at low density, subpopulations are likely to have sufficient or over-abundant resources to support higher densities. Conversely, at high density, subpopulations will have lower per capita resources available, possibly leading to subsequent subpopulation decline through local intra-specific competition. Therefore, asynchrony can have a resource partitioning role and thus increase the chances of metapopulation persistence (Aplet and Mckinley 2017); conversely, subpopulation synchrony can be resource limiting when all subpopulations are simultaneously at high density and thus lower the chances of metapopulation persistence. Synchrony in metapopulation dynamics lowers the chance of a metapopulation persistence (Laan and Fox 2020; Desharnais et al. 2018, Greenville et al. 2018) and thus, can have detrimental effects on biodiversity and conservation efforts. These very clear cause-effect relationships in synchronous or asynchronous population dynamics, particularly in the context of resource limitation or partitioning, raise the question of whether the synchronicity-

asynchronicity dichotomy manifests in ecological processes beyond metapopulation dynamics.

Interspecific Synchrony

Synchrony can also occur between populations of different species that are at the same or different trophic levels in a food web. The consequences of this type of synchrony are not clearly defined. For example, synchrony between two coexisting species (that are at the same trophic level) can result in resource limitation because the competing species rely on similar resources, and this synchrony can be detrimental for the survival of at least one of the species (Scranton and Vasseur 2016; Korpimäki et al. 2005). Conversely, in plant and seed-disperser interactions, synchrony of phenology between the plant and the disperser (that are at different trophic levels) can result in resource partitioning for both the seeds (because seeds avoid clustering together that would result in limited soil nutrients) and the dispersers (because dispersers often save the seed for later use) (Koenig et al. 2015; Warren and Bradford 2014). This type of synchrony that occurs between mutualistic species that are at different trophic levels can be beneficial for the survival of the species involved. Based on these examples, interspecific synchrony can be beneficial for survival in mutualistic interactions where species are at different trophic levels, and potentially be detrimental for survival for coexisting species that are at the same trophic levels. Therefore, it is useful to separate

interspecies synchronies based on the trophic levels of the interacting species. We propose a framework for synchrony to address these differences.

Framework for Classifying Synchrony

To address these differences, and to better understand the larger role of synchrony in ecological interactions, we offer a framework to classify the consequences of synchrony and asynchrony based on the trophic levels of organisms represented in the interaction. We refer to synchrony that is within a single trophic level as horizontal synchrony which is further differentiated into intraspecific (within a species) and interspecific (between species) synchrony. We refer to synchrony (or asynchrony) that takes place between species at different trophic levels as vertical synchrony (or asynchrony) which is further differentiated into antagonistic (negative interactions) and synergetic (positive interactions) following the terminology of Straub et al. (2020).

Based on these terms we divide vertical synchrony into antagonistic synchrony and synergetic synchrony. Vertical antagonistic synchrony includes predator-prey and parasite-host interactions. Vertical synergetic synchrony includes mutualism and commensalism.

The diagram below visualizes this framework.

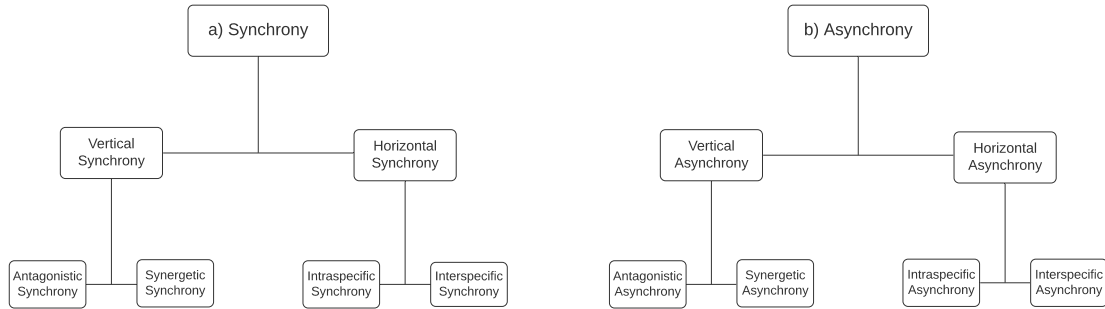


Figure 1.1. Synchrony Framework. a) Synchrony is divided into vertical and horizontal synchrony. Vertical synchrony is between species at different trophic levels and is divided into two subcategories, antagonistic (negative interactions) and synergetic (positive interactions) synchrony. Horizontal synchrony can occur within a species or between different species at the same trophic level in a food web. Horizontal synchrony is divided into two subcategories: intraspecific and interspecific synchrony (between species at the same trophic level). b) Asynchrony follows the same classification as synchrony.

Box 1. Glossary.

Synchrony	Coincident changes in the abundance or other time-varying demographic parameters (Wang et al. 2016; Liebhold et al. 2004).
Asynchrony	Asynchrony is defined as a lack of synchrony.
Vertical Synchrony	Synchrony between species of different trophic levels.
Antagonistic Synchrony	Synchrony between species of different trophic levels that has a negative effect on at least one of the species involved.

Synergetic Synchrony	Synchrony between species of different trophic levels that has a combined positive effect on the species involved.
Horizontal Synchrony	Synchrony within a species or between different species of the same trophic level.
Intraspecific Synchrony	Synchrony within a species.
Interspecific Synchrony	Synchrony between different species of the same trophic level.
Resource Limitation	Reduction in per capita growth rate of a population or of populations of all species across trophic levels due to resource availability (Osenberg and Mittelbach 1996).
Resource Partitioning	State of reduced overlap in resource use in time and space (Kumar and Mina 2018).

Methods

The list of processes in ecology reviewed in this paper is based on the typical topics that appear in popular textbooks in introductory ecology (Kumar and Mina 2018; Cain et al. 2018; Huang et al. 2018; Tyler Miller and Spoolman 2014): Allee effect, Coexistence, Competition, Disturbance, Hibernation, Extinction, Foraging, Germination, Masting, Parasitism, Resilience, Spawning, Succession, Mutualism, and

Migration (Supplemental Table 1.1). Articles were identified in the peer-reviewed literature by searching for the term "synchrony" in Web of Science along with each process listed in Supplemental Table 1.1. Search categories were limited to Ecology, Biodiversity Conservation, Environmental Sciences, Marine Freshwater biology, Limnology, Oceanography, Plant Sciences, Microbiology, and Entomology on the Web of Science website. Articles were limited to those published from 2009 to 2020 to summarize recent advances in the understanding of synchrony among ecological processes. For each paper, the relevant process was identified along with whether synchrony or asynchrony was apparent, and the kind of synchrony that had been studied (antagonistic, synergetic, intraspecific, interspecific). Synchronous (or asynchronous) processes were classified as resource partitioning or resource limiting.

Finally, the effects of (a)synchrony on biodiversity and species persistence were noted. For example, when reviewing synchrony in the context of masting, a paper by Crone (2013) found that synchronous flowering in an iteroparous perennial forb (*Astragalus scaphoides*) results in high pollen production and many seeds. This, in turn, results in the limitation of resources for these plants. However, synchronous flowering can increase the fitness of these species (Rapp et al. 2013) and positively influence the survival of these organisms. Thus, this paper identifies intraspecific synchronous flowering to be resource limiting, but it has positive consequences for species survival.

Supplemental Table 1.1 itemizes each ecological process, whether the process results in synchrony or asynchrony, the kind of (a)synchrony observed, whether the (a)synchrony results in resource partitioning or limitation and what its effects on biodiversity are. This paper focuses on peer-reviewed empirical research to provide a framework for understanding of the role of (a)synchrony in ecological processes. This review places particular focus on mutualism and masting because synchronous and asynchronous processes have been more readily observed and better established for these processes. The remaining processes are discussed in the supplemental section attached to this paper.

Mutualism

Many organisms exhibit interspecific cooperation in nature, known as mutualisms (Stone 2020). Mutualistic interactions contribute to the biodiversity, function, and stability of ecosystems (Hale et al. 2020). Such interactions have been observed in many organisms, but the most widely studied form of cooperative behavior are plant-pollinator mutualisms. It has been estimated that about 75% of crop species need insect pollination for reproduction (Daniels et al. 2020; Klein et al. 2007).

Pollinators are essential to the reproduction of most flowering plants (Kearns et al. 1998). In a mutualistic interaction of Mediterranean Palm trees (*Chamaerops humilis*) and their pollinating weevils, synchrony of flowering in the trees has been shown to attract more pollinating weevils (Jácome-Flores et al. 2018). The synchrony of flowering (intraspecific synchrony) assures abundant resources for

pollinators and this, in turn, leads to increased seed set, an increase in the plant population, and a corresponding increase in the pollinator population (Jácome-Flores et al. 2018). Likewise, to assure continuous resources are available during the pollination season, fig trees (*Ficus montana*) have been shown to have intraspecific synchrony of flowering within a tree, but intraspecific asynchrony of flowering among the trees (Chiang et al. 2018). Synchrony of flowering within a tree ensures abundant resources for their wasp pollinators (*Kradibia tentacularis*) within an individual tree (i.e., temporal synchrony within trees increasing individual tree fitness). In contrast, asynchrony of flowering among trees means that flowering occurs at different times during the pollinating season resulting in continuous resource availability for pollinators (i.e., temporal asynchrony among trees, increasing individual pollinator fitness). Here, the interplay of intraspecific synchrony and asynchrony of flowering leads to resource partitioning of nutrients for the fig tree metapopulation, and resource partitioning of seeds for the wasps. This resource partitioning for figs and wasps benefits the survival of both species. Furthermore, in certain dieocious (i.e., having male and female organs on different individuals) fig species such as *Ficus hispida* and *Ficus fistulosa*, trees exhibit asynchrony of development within sexes, but synchrony of development between sexes (Suleman et al. 2011). This means that some members within each sex develop before other members of the same sex (intrasexual asynchrony), and this provides continuous pollen for the wasp population, which in turn, benefits the fig population by providing continuous pollination services. The interplay of

asynchrony and synchrony of development of the wasp population results in resource partitioning for the wasps because there are fewer mature members of the wasp population consuming resources at one given time. This promotes the persistence of both fig and wasp populations. Here, the interplay of intraspecific synchrony and asynchrony in both examples ensures that there is continuous synergetic synchrony between plants and their pollinators. This synergetic synchrony results in resource partitioning for pollinators and seeds which benefits the survival of both the fig and wasp populations.

Changes in environmental conditions may disrupt the synchrony of plant pollinator phenology (e.g. seasonal changes such as flowering, insect development) by causing a range shift in the host organism to a more suitable environment (Maglianesi et al. 2020). The phenological synchrony of a plant pollinator interaction (synergetic synchrony) is dependent on how suitable the new environment is for the pollinator after the host experiences a range shift (Richman et al. 2020). Pollinators have been shown to shift with their host plants to assure phenological synchrony (synergetic synchrony), but this shift has its limits since extreme environmental conditions can nevertheless disrupt phenological synchrony (Harrower and Gilbert 2018). Plant species that exhibited range shifts in response to changing environmental conditions had higher synergetic synchrony with their pollinators compared to plant species that did not exhibit a similar adaptive shift (Rafferty and Ives 2011). The inability to adapt to changing environmental conditions may result in phenological asynchrony, or a mismatch in timing of emergence or activity, between

plants and their pollinators (Rafferty and Ives 2011). When a phenological mismatch (or asynchrony) increased between bumblebees and their mutualistic plants, this resulted in a decreased pollination service by bumblebees because spring flowering time shifted to an earlier date while the first bumblebee detection time did not, resulting in lower seed production (Kudo and Ida 2013). These studies indicate that climate-induced range shifts can result in asynchrony of phenology between these mutualists culminating in resource limitation for the pollinators. Subsequently, this has negative effects on the reproduction and ultimate survival of the plant species.

Asynchrony of flowering among similar species of plants (interspecific asynchrony) can result in continuous resources (i.e., spatiotemporal asynchrony of flowers) for generalist pollinators that can support pollinator survival (Bizecki Robson 2013). *Symphotrichum sericeum* is a flowering plant from the Aster family that shares generalist pollinators with other Aster species (such as *Solidago rigida*, *Rudbeckia hirta*, and *Solidago canadensis*). These species flower consecutively resulting in the continuous availability of resources for their shared pollinators (Bizecki Robson 2013). This study documented a high similarity of shared pollinator visitors and no overlap of flowering events across the different Aster species resulting in the partitioning of resources for both the plants and the pollinators: the different Aster species use nutrients at different times and the asynchrony of flowering results in a partitioning of pollen resources. Similarly, different species of insect pollinators have asynchronous seasonal abundance peaks that support continuous pollination

of shared flowering plants (Adedoja et al. 2020), thus representing resource partitioning for both the pollinators and plants.

Coinciding phenology of plants and their pollinators is what facilitates these mutualisms because the two organisms have the opportunity to interact in mutually beneficial ways. But other mutualistic interactions can occur as well in response to coinciding phenology. Spring warming temperatures often facilitate dispersal of seed-producing plants by synchronizing seed production with the emergence of foragers such as insects, birds, and small mammals (Turkia et al. 2020; Warren et al. 2011). Warren and Bradford (2014) designed an experiment in which they paired an early-blooming plant (*Anemone americana*) with a late-foraging ant species (*Aphaenogaster rudis*). They found that asynchrony in seed production and the emergence of these insects caused a failure in the dispersal mutualism leading to an accumulation of seeds around the parent plant, increased intraspecific competition and the ultimate fragmentation of populations of this plant. Here, asynchrony of phenology between *A. americana* plants and *A. rudis* ants resulted in resource limitation for the plants. When the early-blooming *A. americana* was paired with early-foraging *Aphaenogaster picea* ant species, the dispersal mutualism recovered resulting in lower intraspecific competition and partitioning of resources for the plant species. Similarly, synchrony between the density of red squirrels (*Sciurus vulgaris*) and seed production in pines (*Pinus cembra*) facilitated pine cone dispersal, resulting in resource partitioning for the pines because intraspecific competition between emergent *P. cembra* seedlings was reduced (Zong et al. 2010).

In seed dispersal mutualisms, the plant and disperser pair occur at different trophic levels, and the synchrony between the two mutualists can be thought of as vertical because the species involved are at different trophic levels. This vertical synchrony results in a partitioning of resources and is beneficial for the plants and their dispersal mutualists. In the generalist mutualists, the asynchrony of phenology among the different plants or pollinators (at the same trophic level) can be thought of as horizontal asynchrony among similar species of plants or pollinators. This horizontal asynchrony that is present in both generalist plants and pollinators results in resource partitioning for plants and pollinators and is beneficial for the survival of all the mutualist species involved. A disruption in horizontal asynchrony can result in increased competition among similar species of plants or pollinators and consequently result in a limitation of resources that is detrimental for survival. Conversely, climate-induced disruption in vertical synchrony (synchrony at different trophic levels) between mutualist species can result in resource limitation due to decreased pollination services and this can be detrimental for the survival of a plant-pollinator pair. This leads to the conclusion that vertical synchrony results in resource partitioning beneficial for survival, while vertical asynchrony results in resource limitation detrimental to survival. Conversely, horizontal synchrony results in resource limitation due to increased competition which is detrimental for survival, while horizontal asynchrony results in resource partitioning because of decreased competition and is beneficial for survival.

Masting:

Some trees may super-reproduce synchronously every few years in a process known as masting; the more synchronous the masting, the larger the number of seeds produced and the higher the chance of seeds escaping predation (Archibald et al. 2012). Synchronous mass production of seeds (horizontal-intraspecific synchrony) results in resource limitation of nutrients for the masting species, but it also allows predation escape and, therefore, is beneficial for survival. The process of masting also drives greater pollen production, greater pollination efficiency (Koenig et al. 2015), enhanced wind pollination, and increased seed dispersal (Rapp et al. 2013).

The predominant cause of masting is precipitation (Koenig et al. 2017). A masting event can be influenced by other environmental factors such as vapor pressure deficit (Wion et al. 2019; Smaill et al. 2011), aridity the year prior to the event (Ascoli et al. 2020), and temperature (Koenig et al. 2015). Masting in pistachios (*Pistacia vera*) can be influenced by local microbial communities, the underlying soil conditions or root-grafting, and these can lead to long-distance correlations of seed production (Noble et al. 2018). This intraspecific synchrony of seed production leads to resource limitation of nutrients for the masting species but is beneficial for survival through predation escape.

Even though masting may occur at population-level scales, individuals within a population can contribute differently to mass seed production (Minor and Kobe

2017; Pesendorfer et al. 2016). When measuring individual contribution to masting among the trees, individuals within a population were much less synchronized during heavy crop years compared to low fruit production years (Żywiec et al. 2012). This is because super-producers within a population have higher nutrient availability and fewer neighboring trees, higher synchrony and lower variability of masting cycles compared with other members of the population (Minor and Kobe 2017). While these super-producers may dominate seed production within a population, the entire population reaps the predator-escape benefits of masting (Minor and Kobe 2017).

Koenig et al. (2015) proposed a hypothesis known as the Phenological Synchrony Hypothesis to explain how cold and warm temperatures may impact synchronous seed production. According to this hypothesis, cold wet Spring seasons result in variable microclimatic conditions (such as daily maximum temperature for each oak tree) and this, in turn, drives phenological variability (i.e., phenological asynchrony) within a wind-pollinated oak population (*Quercus lobata*). Warm Spring temperatures result in less variability in microclimatic conditions, which leads to greater synchronous phenology across oaks within a population. Koenig et al. (2015) first found support for the Phenological Synchrony Hypothesis by confirming that warmer Spring temperatures resulted in shorter and more synchronous pollen seasons in wind-pollinated oak populations, which resulted in high acorn production. Here, the intraspecific synchrony of phenology within the trees resulted in a limitation of nutrients for the entire oak population, however,

this synchrony is beneficial for the survival of these species because of associated high fertilization rates and large acorn production. Subsequent studies confirmed that cold Spring temperatures resulted in intraspecific asynchrony of phenology that lead to low fertilization success and smaller seed crops while warmer environmental conditions result in intraspecific synchrony of phenology that lead to high fertilization success and larger seed crops (Bogdziewicz et al. 2017; Koenig et al. 2015).

The synchronous environmental variation that underpins masting events can have a corresponding synchronizing influence on organisms at higher trophic levels as well, through a consumer-resource interaction (Haynes et al. 2013, 2009).

Synchrony in consumer-resource interactions occurs through correlation of environmental variability that synchronizes abiotic basal resources which, in turn, synchronizes seed production dynamics, ultimately synchronizing the dynamics of their consumers (vertical antagonistic synchrony). An analysis of long-term data of beech (*Fagus sylvatica*) masting and two consumer rodent population densities (field vole, *Microtus agrestis*, and bank vole species, *Myodes glareolus*) showed a delayed positive correlation between the resource and the two coexisting consumers (Imholt et al. 2017). These two coexisting vole species can cause significant damage to the beech species during the synchronous outbreak of the vole species (Imholt et al. 2017). Here, synchronous masting causes a limitation of nutrients for the beech species, but it also results in predation escape for the masting species which is beneficial for their survival. The masting of beech species

causes resource partitioning for the consumers which results in synchronous outbreak in both vole species which in turn can damage the beech forest. The extent of the damage is more severe when there is a continuous snow cover in the forest that limits alternative resources for the abundant vole populations (Imholt et al. 2017). The antagonistic synchrony observed here results in resource partitioning for the consumer species, but the synchronous abundance of consumers is harmful for the masting species.

Masting events can also result in synchrony between seed producers and seed dispersers through mutualistic interactions, and this can impact predator-prey interactions between other species within a community (Zwolak et al. 2018). A study conducted in Alpine Meadows of southern Poland found that a beech (*Fagus sylvatica*) masting event increased the population density of yellow-necked mice (*Apodemus flavicollis*), releasing predation pressure on bank voles (*Microtus subterraneus*) because the two rodents share common predators (Zwolak et al. 2018). The yellow-necked mice are mutualistic dispersers for the beech species, and the resultant synergetic synchrony benefits the beech species by dispersing its seeds across space that partitions resources for the seeds. This also results in the partitioning of resources for the mice because they use the stored seeds when resources are low. This synergetic synchrony resulting in resource partitioning for the mutualistic species involved can also release predation pressure from bank voles because the yellow-necked mice are alternative prey for mice and vole common predators. There was also an increased intraspecific synchrony between

the mice and vole species, that resulted in synchronous abundance of the common predator species (Zwolak et al. 2018).

Synchronous masting events may occur among multiple species (horizontal interspecific synchrony) that benefits all species involved through increased chances of escape of seed predation. This is possible when different species use the same environmental cues for seed production (Koenig and Knops 2014). Coexisting oak species that share resources can also have synchronous masting even when the species involved have different levels of drought sensitivity and Spring temperatures (Pérez-Ramos et al. 2015). Interspecific masting can occur among different species (horizontal interspecific synchrony), and this results in resource limitation, but it also facilitates seed predation escape which benefits the survival of the species involved.

Masting can have both positive and negative effects in ecological communities. For instance, acorn masting may have caused synchronous outbreaks of gypsy moths that spread large distances in oak-pine and oak-hickory forests in North America (Haynes et al. 2013). This spread resulted in forest defoliation and billions of dollars of economic loss (Zhang et al. 2019). These studies indicate that intraspecific masting synchrony can result in vertical antagonistic synchrony between the masting species and their consumers (rodents or moths) which may cause resource limitation for other organisms.

Discussion

The biggest contribution of this work to the scientific literature on synchrony is that it classifies synchronous interactions into two directions, within a trophic level (horizontal) and between trophic levels (vertical). An organism can interact with the members of its own species (horizontal intraspecific), with the members of similar species (horizontal interspecific), and members of species at other trophic levels (vertical). The vertical interactions can be net negative (vertical antagonistic) or net positive (vertical synergetic). This framework allows us to classify different types of synchronies into subcategories that can be used to understand their role in species survival. To accomplish this, we considered whether a type of synchrony (or asynchrony) was resource partitioning or resource limiting, and whether that was beneficial for survival of species.

A few generalities arise when considering the interaction of horizontal (a)synchrony, vertical (a)synchrony, resource limitation, resource partitioning, and biodiversity conservation in all the processes considered here. Horizontal asynchrony (both intraspecific and interspecific) results in a partitioning of resources and this partitioning is beneficial for the survival of the species and biodiversity, whereas horizontal synchrony results in a limitation of resources and can potentially reduce biodiversity except when there are other factors at play such as attraction of pollinators or predator escape. Vertical synergetic synchrony results in resource partitioning for the species of higher trophic levels, and resource

limitation for the species of lower trophic levels. This is beneficial for the survival of all species involved and promotes biodiversity. Vertical synergetic asynchrony results in resource limitation for the species of higher trophic level and is detrimental for the survival all species involved. Vertical antagonistic synchrony results in resource partitioning for the consumer species but is detrimental to the survival of the resource species. Vertical antagonistic asynchrony is resource limiting for the consumer species but is beneficial for the survival of consumer species. Summarizing these generalities is one of the main contributions of this work to the scientific literature.

It was also evident from the literature survey that synchronies were associated with specific processes in the way these were studied. Horizontal intraspecific asynchrony that leads to partitioning of resources was reported in the processes of germination, hibernation, masting, mutualism, and parasitism (Supplemental Table 1.1). Horizontal interspecific synchrony was reported in the processes of mutualism and coexistence. Horizontal interspecific synchrony was reported in the processes of masting, germination, migration, and competition. Vertical antagonistic synchrony (synchrony among species of different trophic levels that has a net negative effect on one of the species) was reported in the processes of masting and succession. Vertical synergetic synchrony (synchrony among species of different trophic levels that has a net positive effect on the species) was reported in the processes of masting and mutualism.

Some of the terms, such as intraspecific or interspecific synchrony, have been used in literature before (Scranton and Vasseur 2016; Monteiro et al. 2012; Sundell and Ylönen 2008; Liebhold et al. 2004; Koenig et al. 1999; Szentkiralyi 1997; Sun et al. 1996; Toy 1991). Our synchrony framework incorporates these terms into a wider classification of synchrony and attempts to find commonalities with modern and classic literature.

Synchrony is a natural phenomenon that widely occurs among physical objects and in nature (Strogatz 2003). This work is the first of its kind that we know of to address (a)synchrony across wide topics in ecology. This is very important as it summarizes the role of this fundamental natural phenomenon in ecological interactions. This work is also useful for new ecologists interested in (a)synchrony to explore and understand its wider role in ecology. The table we present in this work (Supplemental Table 1.1) could also be a useful resource for textbooks used in undergraduate education.

Limitations of this study: Some branches of ecology use different terms to describe synchrony. For example, studies in phenological mutualism refer to the levels of synchrony as Phenological mismatch. Since this work focuses on the term “synchrony” and its role in fundamental processes in ecology, studies that refer to synchrony in different terms might be excluded from this review paper.

For future directions, a comparison of the theoretical literature with empirical literature in ecological synchrony could better bridge the observations and the

theory. A review paper that summarizes how synchrony is measured would be a useful reference tool for ecologists examining synchrony in the field across different processes and study systems.

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Supplemental Section

Supplemental Table 1.1: This table summarizes processes, the type of synchrony/asynchrony observed in that process, whether synchrony leads to limitation of resources, and its consequences for biodiversity. A more detailed description of some of the processes is found in the supplemental section.

Processes	Exhibit Synchrony and/or Asynchrony?	Kind of Synchrony/Asynchrony	Resource Partitioning or Resource Limiting?	Effects on Biodiversity	Notes	References
Allee Effect	Synchrony and Asynchrony	Intraspecific Synchrony of Reproduction in small populations; Intraspecific Asynchrony of development between the sexes	None; Resource Limiting in terms of mates	Detrimental for Biodiversity	The impact is more severe when males and females exhibit asynchronous time to maturity.	Gates and Nason 2012; Adamski et al. 2019
Coexistence	Caused by Interspecific Temporal Asynchrony	Asynchrony of Activity	Resource Partitioning	Promotes Biodiversity	Temporal asynchrony of activity is the most important driver of coexistence.	Marinho et al. 2020; de Cassia Bianchi et al. 2016; Jensen et al. 2019.
Competition	Synchrony and Asynchrony	Interspecific Synchrony of growth; Interspecific Asynchrony of Abundance	Resource Limiting when resources are available in pulses, Resource Partitioning when competition is at low levels	Promotes Biodiversity if it does not lead to extinction of organisms	Competition among species may result in a decrease in the spatiotemporal synchrony, which, in turn, can increase survival chances and promote biodiversity.	Jensen et al. 2019; Lepš <i>et al.</i> 2019
Dispersal	Synchrony	Intraspecific Synchrony of Abundance	Resource Limiting	Promotes and Demotes Biodiversity	The synchronizing effect of dispersal can be a double-edged sword in population persistence because at low levels, dispersal can cause recolonization of extinct population patches, while at high levels, it can increase the chances of extinction for a species.	Laan and Fox 2020; Abbot 2011; Régnière and Nealis 2019; Anderson et al. 2019

Processes	Exhibit Synchrony and/or Asynchrony?	Kind of Synchrony/Asynchrony	Resource Partitioning or Resource Limiting?	Effects on Biodiversity	Notes	References
Foraging	Synchrony	Intraspecific Synchrony of Foraging and Vigilance	Resource Limiting	Promotes Biodiversity	Animals foraging in synchrony is an evolutionary adaptation that increases social cohesion and results in an anti-predatory defense mechanism.	(Duranton and Gaunet 2016; van Rooij and Griffith 2013; Pays et al. 2009)
Germination	Synchrony and Asynchrony	Horizontal (i.e., Intraspecific and Interspecific) Synchrony and Asynchrony of Germination	Synchrony is Resource Limiting, while Asynchrony is Resource Partitioning	Promotes and Demotes Biodiversity	When resources are at low supply, synchronous germination leads to limitation of resources and can be detrimental to biodiversity. When resources are abundant, synchronous germination leads to limitation of resources, but it increases the chances of survival, thus promoting biodiversity.	(Rühl et al. 2016; Ranal et al. 2016; Ludewig et al. 2014; Simão et al. 2013)
Hibernation	Synchrony and Asynchrony	Intraspecific Synchrony of Torpor in social animals; Intraspecific asynchronous ending of hibernation between sexes	None; Caused by Resource Limitation; Resource Partitioning because sexes end hibernation at different times	Promotes Species Survival	Small, social hibernators synchronize their core body temperature rhythms among its individual members during the hibernation session. Males end hibernation in synchrony with other males to prepare for breeding.	(Lee et al. 2016; Nassar and Hraoui-Bloquet 2014; Olson et al. 2013)

Processes	Exhibit Synchrony and/or Asynchrony?	Kind of Synchrony/Asynchrony	Resource Partitioning or Resource Limiting?	Effects on Biodiversity	Notes	References
Masting	Synchrony and Asynchrony	Horizontal (i.e., Intraspecific and Interspecific) and Vertical (i.e., Antagonistic and Synergetic) Synchrony and Intraspecific Asynchrony of Reproduction	Horizontal synchrony results in Resource Limiting for the masting species while vertical synchrony results in Partitioning of Resources for higher trophic levels; the intraspecific asynchrony of masting is caused by Resource Partitioning	Promotes Biodiversity	The more synchronous the masting event, the higher the chances of seeds escaping predation. The process of masting drives greater pollen production, greater pollination efficiency, enhanced wind pollination due to the abundance of pollen, and enhanced dispersal of seeds. Synchronous release of seeds can also indirectly increase the density of other member species of their community (synergetic synchrony) and thus can indirectly increase the persistence of the community. The intraspecific synchrony can lead to limitation of resources, and that could be beneficial for survival if it allows species to avoid predation (foraging, germination, masting), local harsh weather (migration), colonize extinct population patches (dispersal), promote pollinator survival (mutualism) and provide ecosystem services (succession). The antagonistic synchrony between a consumer and a resource results in resource partitioning for the consumer and is beneficial for its survival, however, it is detrimental for the survival of the producer species.	(Zwolak et al. 2018; Rapp et al. 2013; Archibald et al. 2012; Haynes et al. 2009)
Migration	Synchrony and Asynchrony	Horizontal (i.e., Intraspecific and Interspecific) Synchrony of Abundance; Interspecific Asynchrony of Abundance	Resource Limiting for migrating species; Resource Partitioning due to Asynchrony with overwintering species	Promotes Biodiversity	Synchrony is known to have negative consequences for species survival, but for organisms faced with dealing with local harsh environmental conditions that may result in shortages of resources, synchronized migration might be a less costly option for survival of a species. Migrating organisms can have synchrony of abundance with overwintering species which results in partitioning of resources and is beneficial for survival.	(Tallman et al. 2019; Crewe et al. 2019; Gurarie et al. 2019; Lendrum et al. 2013)

Processes	Exhibit Synchrony and/or Asynchrony?	Kind of Synchrony/Asynchrony	Resource Partitioning or Resource Limiting?	Effects on Biodiversity	Notes	References
Mutualism	Synchrony and Asynchrony	Intraspecific Synchrony and Asynchrony of Flowering and Development, Synergetic Synchrony of Phenology	Horizontal Synchrony of flowering is Resource Limiting for plants, while horizontal Asynchrony is Resource Partitioning for plants and pollinators; Synergetic synchrony is Resource Limiting for plants, but Resource Partitioning for pollinators and seeds	Both Synchrony and Asynchrony Promote Biodiversity	The interplay of horizontal synchrony and asynchrony of flowering leads to resource partitioning of nutrients for the metapopulation of figs, and resource partitioning for seeds and the metapopulation of wasps. The synergetic synchrony assures abundant resources for pollinators, and this, in turn, leads to increased seed set and an increase in the plant population and a corresponding increase in the pollinator population. The asynchrony of flowers among different plants assures continuous resources for pollinators across time.	(Jácome-Flores et al. 2018; Chiang et al. 2018; Harrower and Gilbert 2018; Bizecki Robson 2013; Rafferty and Ives 2011; Suleman et al. 2011)
Parasitism	Synchrony and Asynchrony	Intraspecific Synchrony and Asynchrony of Abundance	Resource Partitioning at local scale, and Resource Limiting at global scale	Promotes and Demotes Biodiversity	Local or patchy parasitic outbreaks can increase the persistence of a species by decreasing its spatial synchrony. In contrast, large-scale parasitic outbreaks result in spatial synchrony of populations of species that will decrease the chances of survival, and thus, be detrimental for biodiversity.	(Hirako et al. 2018; Ramos and Drummond 2017; Wetherington et al. 2017; Roscoe et al. 2016; Duncan et al. 2015)
Resilience	Asynchrony	Caused by Horizontal Asynchrony of Abundance	Resource Partitioning	Promotes Biodiversity	Disturbance in the community can result in less synchronous dynamics that can result in a higher resilience, and this, in turn, can positively influence the survival of species and biodiversity.	(Viviani et al. 2019; Smeti et al. 2016; Sproull et al. 2016)
Spawning	Synchrony	Synchrony of Egg Release	None, since fertilization takes place inside the egg	Promotes Biodiversity	Synchronous egg release increases the chances of egg fertilization, thus promotes species survival.	(Doyle et al. 2019; Kaniewska et al. 2015)

Processes	Exhibit Synchrony and/or Asynchrony?	Kind of Synchrony/Asynchrony	Resource Partitioning or Resource Limiting?	Effects on Biodiversity	Notes	References
Succession	Synchrony	Horizontal (i.e., Intraspecific and Interspecific) Synchrony of Abundance; Vertical (i.e., Antagonistic and Synergetic) Synchrony of Abundance	Resource Limiting due to horizontal synchrony; Resource Partitioning due to Vertical Synchrony	Promotes Biodiversity	Synchronous recovery of species after a catastrophic event is beneficial because different species can provide ecosystem services for the survival of the newly established species.	(Fleeger et al. 2018; Boopathy et al. 2012.)

Allee Effect:

An Allee effect is defined as a positive correlation between density dependence and per capita growth rate; thus, declining density may result in a decline in fitness when Allee effects are present in a population (Gates and Nason 2012). Allee effects in reproduction have important implications for biodiversity and conservation because these increase the extinction risk of a population (Pavlova et al. 2016; Elliott et al. 2017). In an effort to understand the potential impacts of an Allee effect on fragmented populations of figs, Gates and Nason (2012) discovered that in smaller populations the reproduction of individuals within a population is more synchronous than in larger populations. This means that if an individual within a small population has a low reproductive output, then the rest of the population members in that population are likely to have low reproductive output as well. This has implications for the survival of these species since populations with more synchronous dynamics are known to have a higher probability of extinction. The synchronous dynamic (intraspecific synchrony) does not lead to limitation of resources here since the populations are at low density during the Allee Effect. Instead, the synchronous populations could easily go extinct in case of a catastrophic event that could wipe out populations, and possibly the species. The negative impact of the Allee effect in small populations is more severe in species where males and females reach sexual maturity at different times, exhibiting asynchronous time to maturity (Adamski et al. 2019). The asynchronous time to

maturity would increase the chances of extinction and cause further decline in the population density, leading to partitioning of resources for the remaining population. An Allee effect can increase the intraspecific synchrony of density within a population through reproductive synchrony, leading to limitation of resources. It can also cause an asynchronous time to maturity, leading to a decline in population density that would result in abundance of resources (RP), but the lack of mates within a population can be detrimental for the survival of species.

Germination

When species germinate synchronously (both intraspecific and interspecific synchrony of germination), it can put a strain on soil nutrients and leads to limiting of resources. The limitation of resources can be detrimental for survival. However, when organisms germinate asynchronously, this results in partitioning of resources, and therefore, is beneficial for survival. This concept was highlighted in a recent study which found endangered, keystone species in arable lands in Europe germinate more synchronously (results in limitation of resources), and the authors found that invasive and/or more common species usually have asynchronous germination (results in partitioning of resources) (Rühl et al. 2016). Here, the synchronous germination of local species (both intraspecific and interspecific synchrony) plays a resource limiting role, and thus, may have a detrimental impact on the survival of the local species, while the invasive species germinate asynchronously resulting in partitioning of resources. Thus, the resource

partitioning in invasive species may be one of the reasons why the invasive species may be better suited for survival compared to the local species that may utilize synchronous germination that results in limitation of resources.

The resource partitioning role of synchronous germination may not be as influential for survival in environments where the resources are in constant supply compared to environments where resources are scarce. Uniform environmental conditions, which are a characteristic of stable environmental conditions and stable resources, have a more synchronizing influence on tropical palm tree germination in Atlantic Rain Forest than less uniform environments with less stable conditions and resources (Braz et al. 2016). Although synchrony results in limitation of resources in organisms that germinate synchronously, the constant supply of resources can offset the negative influence of synchronous germination. In this case, the synchronous germination, though resource limiting, has a beneficial effect on the survival of these tropical palm trees. In contrast, in more unpredictable environments such as in Cerrado grasslands in Brazil, the germination of a widespread apomictic shrub (*Miconia albicans*) is slower and less synchronous compared to less disturbed environments (Sales et al. 2013). This indicates that in disturbed environments, organisms that partition their seed germination patterns across time and space, have a better chance of survival than those that have more synchronous germination. This does not hold true for organisms such as obligate seeders that rely on disturbance for germination (Regan et al. 2010).

Hibernation

When resources are in low supply, and environmental conditions are not very favorable, some organisms go through periods of decreased physiological activity that lasts for days or weeks. This process is known as torpor, and some mammals hibernate through multiple cycles of torpor for a prolonged time when resources are scarce, and the temperatures are the lowest in the annual cycle (Lee et al. 2016). Here, resource limitation is the cause of hibernation, and it promotes the persistence of species by limiting their use of resources that are scarce when environmental conditions are not favorable.

Social interactions can play a role in the hibernating process of social animals. Small social mammals such as arctic ground squirrels synchronize their core body temperature rhythms across individuals during the hibernation session, and this synchrony declines towards the end of the hibernation season (Olson et al. 2013). Hibernating males generally end their hibernation period in synchrony with other males to prepare for breeding while females end their hibernation one month after the males (Lee et al. 2016; Nassar and Hraoui-Bloquet 2014). This asynchronous ending of the hibernating process between different sexes may play a resource partitioning role because males are the first ones to end the hibernation period and forage for resources while the females are still hibernating. This might be another mechanism that promotes persistence in the species.

Succession

After catastrophic events that cause extinction events, organisms recolonize unoccupied habitats through the process of succession. The Deepwater Horizon oil spill in the Gulf of Mexico in 2010 was the most massive marine oil spill in the United States history and released nearly 200 million gallons of oil (Boopathy et al. 2012). As a result of this major contamination event, many marine plants were wiped out entirely along with the life they supported (Fleeger et al. 2018). Three years after the oil spill, nematodes, copepods, and annelids recovered in synchrony with the local salt-water cordgrass after the Deepwater Horizon oil spill in 2010. The synchrony of recovery was present even though the species density and diversity were much lower compared to the pre-spill era (Fleeger et al. 2018). Here, the synchronous recovery of nematodes, copepods, annelids, and local salt-water cordgrass results in limitation of resources due horizontal (intraspecific and interspecific) synchrony, and partitioning of resources due to vertical (antagonistic and synergetic) synchrony, but it is beneficial for these organisms' survival because they can provide services for each other during the process of succession.

Spawn

Some organisms release eggs synchronously to increase the chances of egg fertilization in a process known as spawning (Doyle et al. 2019). Organisms may use different environmental cues to release their eggs synchronously (Doyle et al. 2019).

Corals have been shown to synchronize their spawning using moonlight as a cue (Kaniewska et al. 2015), while other organisms such as Bluehead chub and yellowfin shiner have preferred environmental conditions such as warm and quiet waters to spawn (Kim and Kanno 2019). The warm and quiet waters provide a suitable environment for the development of the released eggs. Disturbances such as high precipitation that increase water levels and decrease water temperatures hinder spawning synchrony in these organisms (Kim and Kanno 2019). Besides environmental variables that synchronize spawning, social behaviors such as female choice may play a role in a spawning event (Brattli et al. 2018). In the sperm competition event, females of free-living arctic char species had higher synchrony of gamete release with a guarding male than with a sneaker male (Egeland et al. 2015, Brattli et al. 2018). Synchronous egg release increases the chances of fertilization for participating species and increases the persistence of these species; thus, it is beneficial to biodiversity and conservation. Spawning synchrony does not lead to partitioning or to limitation of resources since fertilization takes place inside an egg.

Foraging

Social organisms forage with the other members of their population or community to be near organisms of their kind. Animals foraging in synchrony is an evolutionary adaptation to increase social cohesion and to serve as an anti-predatory defense mechanism (Duranton and Gaunet 2016). When foraging in synchrony, organisms may synchronize other behaviors such as vigilance. During synchronous foraging,

red-necked pademelon (*Thylogale thetis*, a type of kangaroo) synchronize their vigilance to avoid predation (Pays et al. 2009). Other organisms, such as Long-tailed Finch parents forage in synchrony to reduce nest predation by limiting the amount of activity around their nest (van Rooij and Griffith 2013). The reduced activity around their nests may help these birds avoid predation, which increases the chances of survival for their offspring, and subsequently for their species. The synchrony of foraging leads to limitation of resources since the organisms consume resources at the same time, however, this leads to increased survival chances because of predation escape. Besides foraging in synchrony to avoid direct predation, some organisms synchronize their reproduction in the presence of foraging synchrony (Brandl et al. 2019). The synchronous reproduction may result in limitation of resources for the entire population, but it leads to predator satiation and allow for prey escape, thus increasing the persistence of species. The synchronous foraging can also result in increased nestling mass in wild zebra finches (Mariette and Griffith 2015). This may result in offspring that are better suited for their environment, thus increasing the chances of survival for the species. Thus, synchronous foraging may result in synchronous vigilance and synchronous reproduction, which leads to limitation of resources, but can also result in predation escape which benefits the species' survival.

Individuals within a population may synchronize their foraging behavior only with certain members of their population that have similar activity levels (Fichtel et al.

2011). Having similar activity levels means that organisms may spend a similar amount of time foraging and digesting their food. It follows that the physiology of an organism may play a role in foraging synchrony. Members of a lemur population (*Lepilemur ruficaudatus*) have been shown to synchronize their foraging with other individuals of their population of similar physiological needs according to activity-budget hypothesis (Fichtel et al. 2011). Thus, similar physiological needs of individuals within a population may result in synchronous foraging that may provide protection from predators. This, in turn, may increase the persistence of species. Even large mammals such as whales that do not have natural predators, still synchronize foraging for social cohesion (Isojunno et al. 2017). Foraging with other individuals of a population results in limitation of resources due to the simultaneous use of it but may increase population persistence by providing safety from predators and by providing social benefits such as mate availability.

Parasitism

Parasitism can be described as a type of disturbance, and it can act both as a synchronizing and as a desynchronizing force depending on the spatial scale of the parasitic infection (Hirako et al. 2018). At a local scale, parasitic infections can act like local disturbances that increase local perturbations, and thus can cause an asynchrony of the populations it is infecting (Hirako et al. 2018; Wetherington et al. 2017; Ramos and Drummond 2017; Bull and Bonsall 2010). The desynchronized population dynamics of infected species can result in resource partitioning and lead

to increased persistence of species and can promote biodiversity. Conversely, parasitic infections at a global scale can act as a synchronizing force for populations of species across vast distances, and thus be resource limiting that can decrease the chances of survival for those species (Roscoe et al. 2016; Duncan et al. 2015; Vindstad et al. 2013; Vogwill et al. 2009). Local or patchy parasitic outbreaks can increase the persistence of a species by decreasing its spatial synchrony and leading to resource partitioning, while large scale parasitic outbreaks result in spatial synchrony of populations of species and lead to limitation of resources that can decrease the chances of survival, and thus, be detrimental for biodiversity.

Resilience

When facing disturbances, organisms can often become more resilient by adapting to the disturbances. These disturbances can serve as a perturbation to a population or a community of organisms that can desynchronize their dynamics (Smeti et al. 2016). An aquatic community of fish in French Polynesia that was subjected to high disturbance resulted in a stable, less synchronous community that had high functional diversity (Viviani et al. 2019). All of these combined resulted in a more resilient community compared to a community with very little disturbance (Viviana et al. 2019). Disturbance in a community can result in less synchronous dynamics that can result in a higher resilience and this, in turn, can positively influence survival of species.

Disturbances in the form of small-scale outbreaks can decrease the spatial synchrony (Resource Partitioning) in large forests, increasing resilience and persistence in the forest community (Sproull et al. 2016). Localized outbreaks of beetles can increase the spruce forest resilience against a more severe outbreak by affecting specific patches of spruce populations, thus, desynchronizing their dynamics (Sproull et al. 2016), and leading to partitioning of resources that is beneficial for survival. Conversely, large-scale global outbreaks can spatially synchronize forest dynamics that will decrease the persistence of species (Hirako et al. 2018).

Migration

Migration is different from dispersal in that dispersal is the movement of individual organisms from their birthplace, while migration is the synchronous and directed movement of a group of organisms between distant habitats (Tallman et al. 2019). Organisms migrate in large groups seasonally to find better pastures, and this migration can be synchronized by plant phenology, winter weather (Lendrum et al. 2013), lunar cycles (Norevik et al. 2019) and immediate weather conditions (Gurarie et al. 2019). During the migration season, the departure dates for Caribou individuals from Alaska and Canada are synchronized within a population, while the arrival dates may not necessarily be synchronous (Gurarie et al. 2019). The synchronous migration (intraspecific synchrony) can be resource limiting due to groups of species moving in synchrony across space, but it can assist organisms in

better navigating towards environments with better resources and environmental conditions, thus promoting population persistence.

Population dynamics of long-distance migratory insects such as Monarch butterflies can be in temporal synchrony with other long-distance migratory insects (interspecific synchrony) but be in asynchrony (interspecific asynchrony) with other overwintering butterfly species (Crewe et al. 2019). Interspecific synchrony of density that leads to limitation of resources is known to have negative consequences for species survival, but for organisms faced with dealing with local harsh environmental conditions that may result in a shortage of resources, synchronized migration might be a less costly option for survival of a species. Thus, synchronized migration, though resource limiting, may prolong species survival and promote biodiversity.

Dispersal

Similarly to migration, dispersal of individuals can synchronize population dynamics across space (Laan and Fox 2020; Hopson and Fox 2019; Anderson et al. 2019; Régnière and Nealis 2019) which leads to limitation of resources, and this can have negative consequences for species survival. Dispersal of pests can also spatially synchronize seasonal outbreaks (Larroque et al. 2019) and have negative consequences for the survival of local species. The extent of spatial synchrony caused by dispersal can also be strongly influenced by the direction of the wind

(Vindstad et al. 2019). The synchronizing effect of dispersal can be a double-edged sword in population persistence because at low levels, dispersal can cause recolonization of locally extinct population patches, while at high levels, it can increase the chances of extinction for a species (Abbott 2011). This indicates that some dispersal is beneficial for species survival, while a high level of dispersal can be resource limiting and be detrimental for biodiversity and species survival.

Coexistence

Biodiversity conservation is promoted when spatial and temporal dynamics are asynchronous, but which of these two types of synchronies is more critical for the coexistence and persistence of species? It has been shown that temporal asynchrony of activity in mesocarnivores in the Caatinga forest of Brazil is more critical for intraspecific coexistence than spatial segregation, which can result in spatial asynchrony (Marinho et al. 2020). Both the temporal and spatial asynchronies can result in partitioning of resources, and therefore be beneficial for survival of species. Another study conducted on mid-sized carnivores in Central Pantanal, Brazil, confirms that temporal asynchrony of activity is the most important element to promote coexistence among species (Bianchi et al. 2016). Thus, the temporal asynchrony that results in partitioning of resources across time is more beneficial for survival, than spatial partitioning of resources. The temporal asynchrony of flowering has also been shown to promote coexistence among flowering species (Jensen et al. 2019). Spatial segregation has been shown to lead to temporal and

spatial asynchrony (Jensen et al. 2019). Thus, temporal asynchrony is more important than spatial segregation (that can lead to spatial asynchrony), and that spatial segregation can lead to temporal asynchrony, that promotes the coexistence of species. Temporal and spatial asynchrony (interspecific asynchrony in both case) can result in partitioning of resources that can promote species survival and biodiversity.

Competition

When biotic and abiotic resources are available in a short duration (i.e., in pulses), this can result in synchronous growth since organisms can take advantage of the temporary abundance of available resources for a short time. This clustering of abiotic resources may lead to spatiotemporal flowering synchrony (also resource limiting) that can improve pollination success, promote the coexistence of species because of the high abundance of resources during the pollination season (Jensen et al. 2019). This increased flowering synchrony that promotes mutualism (synergetic synchrony that results in resource partitioning) and coexistence (interspecific synchrony that can be resource limiting) can promote biodiversity when resources are available in a short duration.

During the synchronous flowering and pollination season, when species abundance is high, resources may become limited for the large number of organisms that depend on it, and that may create competition for soil, light, and pollination

resources (Jensen et al. 2019). Strong competition (resulted from interspecific synchrony) among bee-pollinated species may result in spatial segregation among these species and decrease the spatiotemporal synchrony of flowering resulting in partitioning of resources (Jensen et al. 2019). Thus, competition may increase the spatial distribution of organisms during the pollination season, which can decrease spatiotemporal synchrony (resource partitioning), which, in turn, can increase survival chances and promote biodiversity. The interspecific competition in a community of temperate grassland species has been shown to lead to temporal asynchrony of abundances (resource partitioning) among members of the community (Lepš et al. 2019). This asynchrony can result in increased persistence of species (Desharnais et al. 2018), and this higher persistence can have positive consequences for biodiversity conservation.

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Chapter 2: Intermediate Network Heterogeneity May Increase Persistence in Spatially Structured Metapopulations

Introduction

A metapopulation is defined as a group of spatially connected subpopulations (Levins 1969). When subpopulations within a metapopulation fluctuate synchronously, subpopulations are at low density and at high density at the same time (i.e., synchronous fluctuations). If a catastrophic event strikes a metapopulation when all subpopulation patches are at low density, the chances of that metapopulation going extinct is high.

Studies in landscape ecology view subpopulation patches as a spatially connected network of patches and have shown that the spatial distribution of these networks has consequences for the synchrony and the persistence of a metapopulation (Hanski 1998). Some of these characteristics of a spatial network include the rate of dispersal (i.e., how fast the individuals move) between patches and the level of connectivity (i.e., the number of connections that link patches) between patches (Dedrick et al. 2021). The frequency distribution of node degree across all patches or network heterogeneity is another characteristic of a network. A heterogeneous network has high variability in the number of connections per patch, while a homogeneous network has habitat patches with a similar number of connections per patch (Zamborain-Mason et al. 2017; Gilarranz and Bascompte 2012). Other characteristics of a network are the number of patches a network has, the sizes (i.e.,

carrying capacity) of patches, and how central certain patches are within a network (Zamborain-Mason et al. 2017). All these network characteristics have been shown to have consequences for synchrony and metapopulation persistence (Hakkenberg et al. 2021; López-Sánchez et al. 2021; Gilarranz 2020; Grilli et al. 2015; Gilarranz and Bascompte 2012; Grant et al. 2010; Holland and Hastings 2008; Hanski 1998), but the most attention has been focused on the dispersal rate.

At low levels, the dispersal rate may be insufficient to recolonize locally extinct population patches, while at high levels, it can cause synchronized population dynamics; both scenarios can increase the chance of extinction of the species (Hogan et al. 2012; Abbott 2011; Gouhier et al. 2010; Reed 2004; Peltonen et al. 2002; Kendall et al. 2000; Lande et al. 1999; Heino et al. 1997; Ranta et al. 1995).

Like the dispersal rate, the connectivity of patches can also exhibit similar trade-offs in that high connectivity may cause synchrony of population dynamics and increase the chances of extinction, while low connectivity may be insufficient to recolonize extirpated habitat patches (Guichard and Gouhier 2014; Salau et al. 2012; Baggio et al. 2011). Thus, an intermediate level of dispersal rate and connectivity may prolong the persistence of a metapopulation.

Contrary to the dispersal rate and the connectivity, heterogeneity of a metapopulation network has only been shown to have a positive influence on the metapopulation persistence (Liao et al. 2020; Lucas et al. 2019; Grilli et al. 2015; Gilarranz and Bascompte 2012; Cooper et al. 2012; Holland and Hastings 2008). We

suspect many studies have not detected the negative influence of network heterogeneity on metapopulation persistence because network structure is not emphasized on a full range of dispersal and growth. A big point that is missing is the fact that previous work has looked at network structure and metapopulation persistence using colonization/extinction models, but not with actual population dynamic models. We aim to fill this gap in this work.

Just like dispersal rate and connectivity, the heterogeneity of a metapopulation network will likely have positive and negative influences. Therefore, we think that a network with intermediate heterogeneity should lead to higher persistence in metapopulations than more homogeneous and heterogeneous networks. We think that a homogeneous network should lead to high synchrony in a metapopulation and lead to high extinction. In contrast, the most heterogeneous network would lead to low synchrony but a high extinction due to disconnect between patches.

Therefore, a network with intermediate heterogeneity should lead to high persistence by balancing against the negative influence of synchrony and disconnect between patches. We also investigate the role of dispersal and growth rates between patches in these interactions to influence persistence in metapopulation networks. We address these questions using a Ricker population model that incorporates a spatial parameter for connected patches with inherent growth rates that include environmental and demographic stochasticity parameters. These elements in the Ricker model allow us to generate actual population dynamics that

experience environmental and demographic stochasticity, and we estimate measures that describe the model outputs.

Methods

Overview of the model

This study was conducted using model simulations. We use the Ricker discrete-time population model (Ali et al. 2019; Travis 2003; Ranta et al. 1995; May 1976) in our simulations and include both environmental and demographic stochasticity in spatially connected metapopulation patches. We use three different spatially connected metapopulation models arranged in a ring, random, and scale-free network topologies (i.e., homogeneous, intermediately heterogeneous, and heterogeneous, respectively).

Growth Rate and Model Dynamics

The Ricker model we use has three phases: growth, emigration, and immigration. The growth phase includes both demographic and environmental stochasticity:

$$G_i(t) = \text{Binomial}(N_i(t) * e^r, e^{-r(\frac{N_i(t)}{k}) + \sigma z_i(t)}), \quad (1)$$

Where $G_i(t)$ is the population density of patch i at time t after growth has occurred, $N_i(t)$ is the density of patch i at time t , r is the per capita growth rate of a patch, k is the carrying capacity of a patch, $z_i(t)$ is the random environmental stochasticity for patch i at time t , and σ is the amplitude of environmental stochasticity at time t . The environmental stochasticity $z_i(t)$ was based on the algorithm in Chambers (1995) as

presented in Desharnais et al. (2021). We used this algorithm to draw from a Gaussian distribution with a mean of 0 and a variance of 1. The generated environmental time series were uncorrelated in time and among patches. This algorithm allowed us to generate 1024 Gaussian time series with a length of 3000-time steps per time series, and each patch in the metapopulation had a corresponding time series of 3000 environmental stochasticity values. Each metapopulation patch had a unique environmental parameter at each time step of the simulation. The demographic stochasticity is determined by the *Binomial*(n,p) equation where p successes are chosen from n trials; this accounts for stochasticity in demographic processes such as births and deaths (Ben Zion et al. 2010).

After the growth phase, the emigration phase involves calculating the number of individuals emigrating from a patch i through the binomial distribution (emigration does or does not occur):

$$E_i(t) = \text{Binomial}(G_i(t), d), \quad (2)$$

Where $E_i(t)$ is the number of individuals emigrating from patch i , and d is the dispersal rate of patch i . Each individual (after the growth phase) is chosen to emigrate with a probability d .

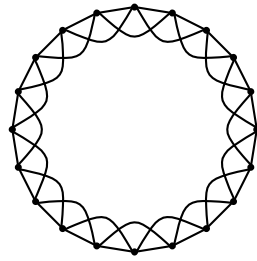
After the emigration phase, the immigration phase takes place. This is accomplished by randomly assigning each emigrant to a connected patch. This is accomplished through the following equation:

$$I_{i,j}(t) = \text{RandomSample}(E_i(t), j \text{ connected patches}), \quad (3)$$

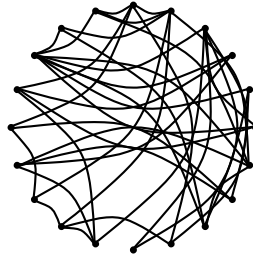
Where $I_{ij}(t)$ is the number of immigrants from patch i to patch j at time t .

Metapopulation Networks and Patch Size

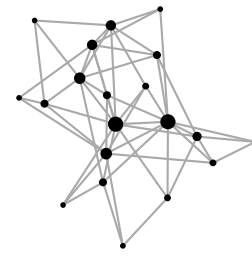
The ring network is homogeneous in its spatial distribution of metapopulation patches; here, each patch is connected to four of its closest neighbors (Holland & Hastings 2008), and dispersal can only occur between a patch and close neighbors (Figure 2.1a). This type of network topology represents patches of habitat that are evenly distributed across a landscape with uninhabitable terrain in between (Gilarranz and Bascompte 2012; Watts and Strogatz 1998). Alternatively, in random networks (we used Watts-Strogatz model to generate this type of network, MATLAB 2015), dispersing individuals can travel to near and far patches, but nearer patches have a higher probability of receiving immigrants (Figure 2.1b). This type of network has small-world properties (Holland & Hastings 2008; Watts & Strogatz 1998). This type of network is more heterogeneous than the ring network. The third type of network examined in this project is the scale-free network (we used Barabási-Albert model to generate this type of network, George 2022) (Figure 2.1c), which is very heterogeneous in its spatial distribution. This network allows long-distance dispersal and has a few well-connected metapopulation patches. Most patches have a few connections, and the degree distribution of connections follows the power law-curve with an exponent 3 (Gilarranz and Bascompte 2012; Barabasi and Albert 1999).



a) ring network



b) random network



c) scale-free network

Figure 2.1. Metapopulation network topologies. Three types of network structures were used that represent the topology of metapopulations in increasing levels of heterogeneity (Shizuka 2018). The networks displayed here have 20 patches for illustration purposes, while simulations in our study used 1024 patches. Patches in all network types have a mean of four connections to other patches: a) the ring network is the least heterogeneous and each patch is connected to its four closest neighbors; b) the random network has intermediate heterogeneity. It has randomly assigned connections among the patches, with a preference for connections to closer neighbors; c) The scale-free network is the most heterogeneous of the networks that allow random connections, and there is no preference for close neighbor connections.

This study followed Gilarranz and Bascompte (2012) by using 1024 network patches with 4096 connections, and each patch had an average of four connections with its neighbors. To link these networks with the population model, adjacency matrices were used to represent each of these undirected networks where dispersal can occur in either direction between patches. An adjacency matrix is a square matrix where the diagonal elements are the patches of a metapopulation network, and the nonzero elements across rows or columns represent directional connections to certain patches (Cahen-Fourot et al. 2020).

Simulation parameters

There were three types of nonlinear model dynamics considered in this project, undercompensating, overcompensating, and chaotic. We picked r (per capita growth rate) values in equation (1) that led to undercompensating ($r = \ln(2)$), overcompensating ($r = \ln(7)$), and chaotic ($r = \ln(17)$) dynamics in the deterministic and non-spatial version of the Ricker model. We chose these growth rate values to facilitate the numeric methods such that n_t will always be an integer (Yarri et al. 2012). Each subpopulation, or patch, was assigned an initial density that was randomly selected from the interval spanning plus or minus 10% of the carrying capacity k , which was set to be $k = 100$ for each subpopulation patch. We chose this carrying capacity value after parameterization of model to allow us to compare the across the different metapopulation dynamics. The length of each time series was 3000, and the number of iterations (i.e., simulation repetitions) was 100 for each scenario of network type, dispersal rate, and subpopulation dynamic. The simulation repetitions allowed us to calculate mean metapopulation metrics for analysis. The environmental stochasticity parameter $z_i(t)$ was based on the Gaussian distribution and was regenerated for each of the 100 simulation iterations. The amplitude of environmental stochasticity σ was set to be 2.0 for undercompensating, and 3.0 for overcompensating and chaotic dynamics. These amplitudes of noise values were chosen to highlight the influence of network structure on metapopulation persistence. Several dispersal rates were chosen to

represent the proportion of individuals emigrating from a patch. This allowed us to observe how increasing the level of movement between patches influenced metapopulation persistence. The dispersal rates used in this study were 0.00, 0.05, 0.075, 0.10, 0.15, and 0.20, indicating the probability an individual emigrates from a patch. These per patch dispersal values have been well documented in nature and are widely reported in the literature (Laan and Fox 2020; Adamski et al. 2019; Desharnais et al. 2018; Gokhale et al. 2018; Fronhofer et al. 2014; Cooper et al. 2012; Bowne and Bowers 2004). These parameter values were held constant throughout all simulations to make comparisons between simulations equitable. The programming language used was MATLAB (2021).

Model analyses

We quantified the influence of the heterogeneity of the network structure, random environmental stochasticity, and metapopulation dynamics on (quasi-)extinction risk in our simulations using several metrics. These included mean patch occupancy, mean correlation coefficient between the time series of patches within a metapopulation, mean time to extinction, and the probability of metapopulation extinction.

Mean patch occupancy was calculated by dividing the total number of occupied patches at each time step by the total number of metapopulation patches (1024) for each metapopulation iteration (Holmes et al. 2020). This was then averaged across all metapopulation iterations (i.e., simulation repetitions). If a metapopulation went

extinct before the final time step, the mean occupancy was only calculated for non-extinct time steps.

The average Pearson correlation coefficient was calculated between the pairs of subpopulations (i.e., patch) time series within a metapopulation. This correlation coefficient was then averaged among all the iterations of a metapopulation. If a metapopulation went extinct before the final time step, the correlation coefficient was only calculated for the time steps for which the metapopulation was extant.

Mean time to extinction (Roff 1974) was calculated as the average number of time steps before the metapopulation went extinct across all the iterations for each scenario. Extinction in our model occurred when all metapopulation patches simultaneously had a density of zero.

The probability of extinction was calculated by dividing the number of metapopulation iterations in which extinction occurred by the total number of metapopulation iterations (100).

Results

Figure 2.2 plots mean metapopulation occupancy (a, e, i), mean correlation (b, f, j), mean time to extinction (c, g, k), and the probability of extinction (d, h, l) for the ring, random, and scale-free networks against the dispersal rates between metapopulation patches. The columns of subplots represent undercompensating (a, b, c, d), overcompensating (e, f, g, h), and chaotic dynamics (I, j, k, l).

When looking at the results for each metapopulation metric (e.g. mean time to extinction, probability of extinction, etc.) general trends for the overcompensating and chaotic dynamics are similar. For both of the dynamics, the probability of extinction for all networks is close to 1.00 at the dispersal rate of 0.05, and less than 0.05 at the dispersal rate of 0.20 (Figure 2.2h,l). A similar pattern is also observed for the mean time to extinction where both dynamics lead to a lower mean time to extinction at the dispersal of 0.05, and a higher mean time to extinction at the dispersal rate of 2.00 (Figure 2.2g,k). The mean correlation is nearly identical for dispersal values greater than 0.10 (2.2f, j) for overcompensating and chaotic dynamics. The general trends for the undercompensating dynamic tend towards greater extinction risk, lower mean occupancy, and higher correlation. The probability of extinction is higher and the mean time to extinction is lower when dispersal rates are greater than 0.10 for the undercompensating dynamic (Figure 2.2c,d). The mean occupancy is lower for the undercompensating dynamic for all networks when dispersal values are greater than 0.10.

Across these metrics and subpopulation dynamics, random and scale-free networks have roughly similar responses. For the undercompensating dynamic, the scale-free and random networks have higher mean time to extinction (Figure 2.2c), lower probability of extinction (2.2d), and higher mean occupancy (2.2a) than the ring network for dispersal rates of >0.10 . For the overcompensating dynamic, these differences occur between dispersal values 0.075 to 0.15 (Figure 2.2e,g,h), and for the chaotic dynamic, between dispersal values 0.05 to 0.075 (2.2i,k,l). The biggest

differences in correlation coefficients among the networks occur at a dispersal rate of 0.10 for the undercompensating dynamics (2.2b), 0.75 for the overcompensating (2.2f), and 0.05 for the chaotic dynamics (2.2j). These patterns indicate that as the growth rate increases, the range of dispersal values where networks show different responses decreases.

Between the heterogeneous networks (random and scale-free), the random networks had slightly higher mean occupancy, mean time to extinction, and lower probability of extinction than random networks for higher dispersal rates. For the undercompensating dynamic, the differences in mean time to extinction and probability of extinction occurred for dispersal values >0.10 (Figure 2.2c,d), 0.075-0.10 for the overcompensating dynamic (2.2g,h), and 0.05 for the chaotic dynamic (2.2k). Despite these differences, the mean correlation coefficients were roughly similar for these networks for all dynamics (2.2b,f,j). This indicated that there was no to a very little link between correlation coefficient, mean time to extinction, and extinction probability for the random and scale-free networks. The mean occupancy was higher for the scale-free compared to the random networks for all dynamics when dispersal was greater or equal to 0.075 (2.2a,e,i).

As dispersal rate increased so did mean occupancy across all population dynamics types (2.2a,e,i); mean correlation coefficient tended to have the lowest values at intermediate dispersal rates (2.2b,f,j); and random and scale-free networks showed similar responses in extinction time and probability (2.2c,d,g,h,k,l). Ring networks

tended to have persistently higher extinction rates (and low mean time to extinction) as dispersal rate increased but eventually coincided with the other two networks for overcompensating and chaotic dynamics. This indicated that a higher level of movement among the patches could fill the empty patches faster, leading to higher persistence.

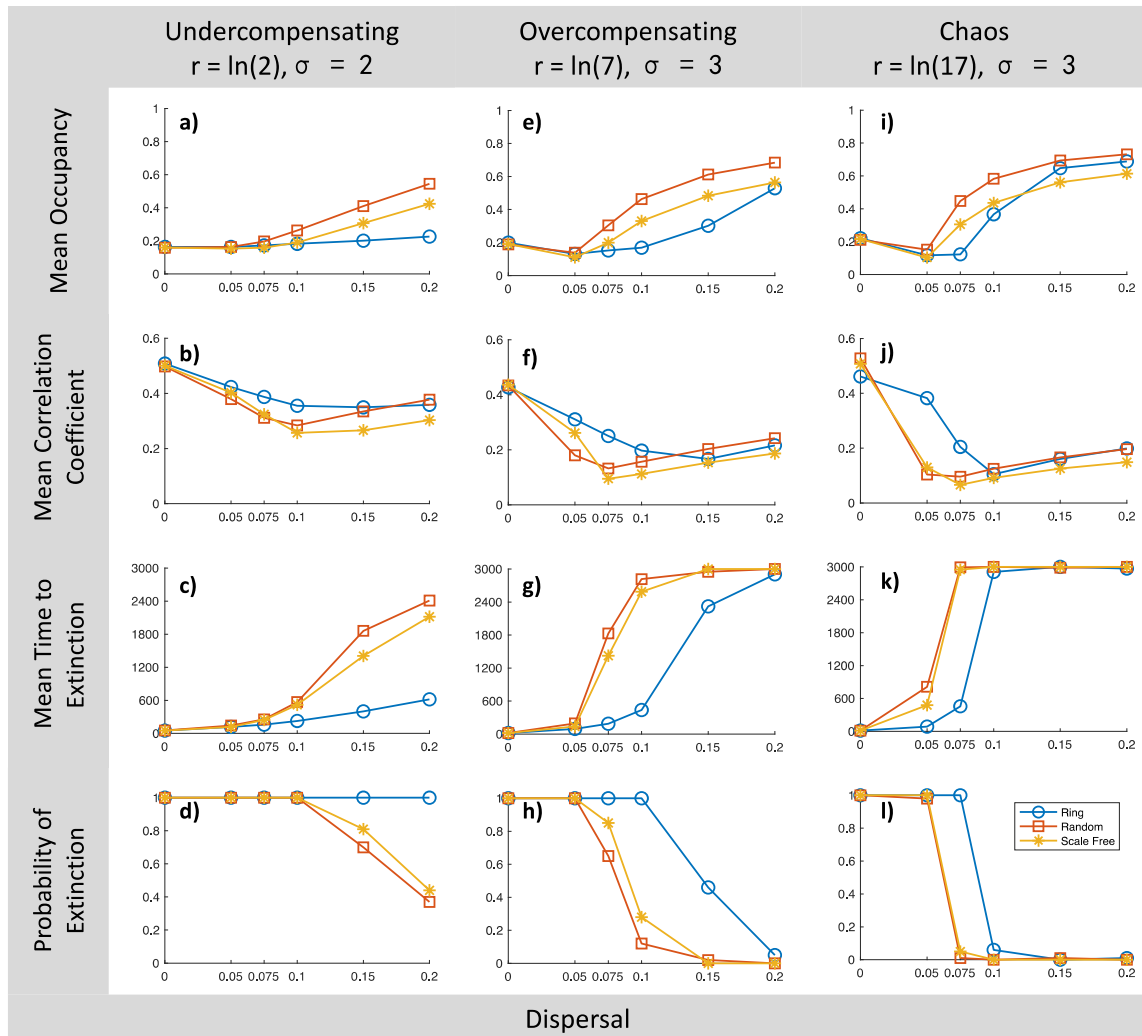


Figure 2.2. Influence of metapopulation network types (ring, random, scale-free) and metapopulation dynamics (undercompensating, $r = \ln(2)$; overcompensating, $r = \ln(7)$; chaos, $r = \ln(17)$) on the mean occupancy (a,e,i), mean correlation coefficient (b,f,j), mean time to extinction (c,g,k) and the probability of metapopulation extinction (d,h,l). The simulation parameters were: Iterations = 100 (i.e., simulation repetitions); length of time series, $t = 3000$ -time steps, amplitude of stochasticity, $\sigma = 2.0$ for undercompensating dynamics, and $\sigma = 3.0$ for overcompensating and chaotic dynamics; dispersal rates were 0.00, 0.05, 0.075, 0.10, 0.15, and 0.20; carrying capacity, $k = 7$; average number of connections = 4 per patch; total number of patches per network = 1024.

Discussion

We report four main findings in this paper: 1) heterogeneous networks increased persistence in spatially structured metapopulations; 2) networks with intermediate heterogeneity tended to lead to higher persistence for a range of dispersal rates and dynamics; 3) overcompensating and chaotic dynamics had similar patterns of metapopulation persistence; 4) increasing dispersal increased persistence in large networks.

There are clear differences between heterogeneous (random and scale-free) and homogenous (ring) networks. Both random and scale-free networks led to higher persistence and mean occupancy for higher dispersal rates for the undercompensating dynamics, and for intermediate dispersal rates for the overcompensating and chaotic dynamics. These patterns confirm what many other studies had shown in that network heterogeneity increases persistence in metapopulations (Liao et al. 2020; Lucas et al. 2019; Gilarranz and Bascompte 2012; Holland and Hastings 2008). However, our findings also indicate that there appears to be an intermediate optimal amount of heterogeneity that may benefit metapopulation persistence. This is contradictory to what many of the studies mentioned above had shown. Extreme heterogeneity in networks may negatively influence persistence by lowering occupancy. This was true for higher dispersal rates in undercompensating and intermediate for overcompensating dynamics. For all these ranges of dispersal, the most heterogeneous networks had lower

synchrony than the networks with intermediate heterogeneity. This indicates that lower synchrony is not always beneficial for persistence, contrary to what many studies believe (Laan and Fox 2020; Anderson and Hayes 2018; Abbott 2011; Liebhold et al. 2004; Ranta et al. 1995). The lower synchrony may be a result of a higher disconnect among the patches, but this does not benefit the persistence since the high disconnect also lowers patch occupancy in highly heterogeneous networks. This pattern is likely balanced by the networks with intermediate heterogeneity.

The general trends for overcompensating and chaotic dynamics are similar compared to the undercompensating dynamic. This is likely the case because higher growth rates in these dynamics hit the carrying capacity faster compared to the undercompensating dynamic. This leads to higher mean occupancy, mean time to extinction, lower correlation coefficient, and probability of extinction.

Higher dispersal rates benefited metapopulation persistence for all networks and dynamics. This is likely the case because the faster movement of individuals between patches filled up empty patches quicker. Higher dispersal rates also increased synchrony between patches (Hopson and Fox 2019; Abbott 2011; Kendall et al. 2000). We did not observe any negative influence on persistence caused by higher dispersal rates, and this is likely because the dispersal rates we used in these simulations did not fully synchronize patches. Higher dispersal rates also interacted with overcompensating and chaotic dynamics to increase metapopulation persistence. The growth rates are so high for both Overcompensating and chaos that

the patches are usually full and so don't go extinct as much – and when they do high dispersal rates fill them again.

There are a few take-away messages for conservationists or for those who are involved in a reserve design. Heterogeneity in a network is better for a metapopulation persistence than homogeneity. There appears to be an intermediate optimal amount of heterogeneity but in our study intermediate and high heterogeneity were fairly similar and both were better for persistence than homogeneous networks. In some cases, an intermediate network heterogeneity would provide the highest benefits for the metapopulation persistence. For a slow-growing subpopulation (i.e., undercompensating dynamic) the intermediate network heterogeneity would benefit the metapopulation persistence at higher dispersal rates. For a fast-growing subpopulation (i.e., overcompensating and chaotic dynamics), the network with an intermediate heterogeneity may provide the highest benefits for the metapopulation persistence at lower dispersal levels. More dispersal appears to be more beneficial than less dispersal in all cases except when homogeneous networks experience undercompensating dynamics.

The limitations of this study are that this study assumes equal dispersal rate, equal amplitude of environmental noise, and equal population growth in each patch. It also assumes that all dispersing individuals reach a destination.

Future theoretical studies should test this theory of intermediate network heterogeneity in small versus large networks to see if this theory is true for all

network sizes. Applied studies, on the other hand, can put this theory to a test by designing networks and testing the finding of this paper.

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The influence of temporal noise color on the persistence of a species in large metapopulation networks.

Introduction

A review paper by Southerland et al. (2013) identified one hundred of the most fundamental questions in the field of ecology. One of the identified questions at the population level asks how environmental noise (a.k.a. randomness) and environmental change affect population dynamics (Southerland et al. 2013). Due to habitat fragmentation, many of the populations in nature have been broken into smaller populations that are connected by migration. This concept of grouped populations connected by migration (dispersal) was coined by Richard Levins (1969) as a Metapopulation. Within a metapopulation, the group of populations are also known as subpopulations.

These subpopulation densities may fluctuate in a synchronous fashion within a metapopulation. Synchronized subpopulations have been observed in species of insects, human pathogens, fish, amphibians, mammals and in many other taxa (Liebhold et al. 2004). Subpopulation synchrony within a metapopulation is of practical importance because it has consequences for the conservation of species. For example, if several different populations that form a metapopulation are synchronous and achieve low densities at the same time, then the entire metapopulation or perhaps the entire species is at risk of becoming extinct (Laan and Fox 2020; Régnière and Nealis 2019; Anderson and Hayes 2018; Matter 2001;

Earn et al. 2000; Heino et al. 1997). On the other hand, if the metapopulation is not synchronous and one or more populations become extinct while others survive because they had higher population densities, then the surviving populations could be the source of dispersing individuals which recolonize the locality of the extinct population. Human activity frequently results in habitat fragmentation and a barrier to dispersal, which increases the need to understand the consequences of metapopulation synchrony. Understanding synchrony at the metapopulation level could lead to better natural resource management and help in conservation decisions.

Many of the studies have focused on the two main mechanisms of metapopulation synchrony: 1) correlation of environmental factors (Walter et al. 2021), 2) dispersal (Abbot 2011). These mechanisms and their relative importance have been a major research question (Matter et al. 2022; Kahilainen et al. 2018; Duncan et al. 2013, Abbott and Dwyer 2008; Abbott 2007; Peltonen et al. 2002; Williams and Liebhold 2000). If dispersal is high enough, subpopulations can synchronize and increase the chances of extinction for the metapopulation (Abbot 2011; Earn et al. 2000; Hudson and Cattadori 1999). Moran (1953) was one of the first to propose environmental fluctuations as a cause of metapopulation synchrony. Moran (1953) studied the predator-prey dynamics between lynx and snowshoe hare populations throughout Canada and concluded that synchronization of the predator-prey relationship was caused by synchronized environmental factors.

Studies have assessed synchrony using some variant of the correlation coefficient, including Pearson and Spearman correlation coefficients, correlation in direction of changes, and correlation of high and low peaks of time series (Buonaccorsi et al. 2001). A correlation approach may mask important dynamics, which might be revealed by looking at the time scale (i.e., period) of synchrony of environmental variation (Ouyang et al. 2014). For example, one can look at just the variance of a time series, which is a single number. However, if one wanted to have a better understanding of that time series, one can break it down by frequency through the process of fast Fourier transform (Bracewell 1993; Platt and Denman 1975). The spectrum of a time series is the frequency decomposition of the variance that shows the relative contributions of variation at different time scales. If a variance is accumulated at low or high frequencies in the power spectra, this causes positive or negative autocorrelations which are named red or blue noise, respectively (Postuma et al. 2020; Cotto and Chevin 2020; Ruiz and Rincón 2018).

By analogy, we can look at annual temperature data and the correlation between the weekly and monthly scales. If the correlation of this hypothetical temperature were high on the weekly scale, the color of the spectra (shown by the spectral power of environmental noise) would be blue (Figure 3.1e,f) because there is a higher frequency of weeks compared to months. Thus, if the correlation of this hypothetical temperature were high on the monthly scale, the color of the spectra would be red (Kuparinen et al. 2019; Vasseur and Yodzis 2004; Bjørnstad and Grenfell 2001) because there is a lower frequency of months compared to weeks (Figure 3.1a,b). If

the correlation were equal between weekly and monthly scales, this would be an example of white noise (Figure 3.1c,d). If the high correlation of temperature shifted from a monthly to a weekly scale, then we can say that the color of spectra for this hypothetical temperature has become bluer. Conversely, if the high correlation of temperature shifted from a weekly scale to a monthly scale, we can say that the color of spectra for this hypothetical temperature has reddened.

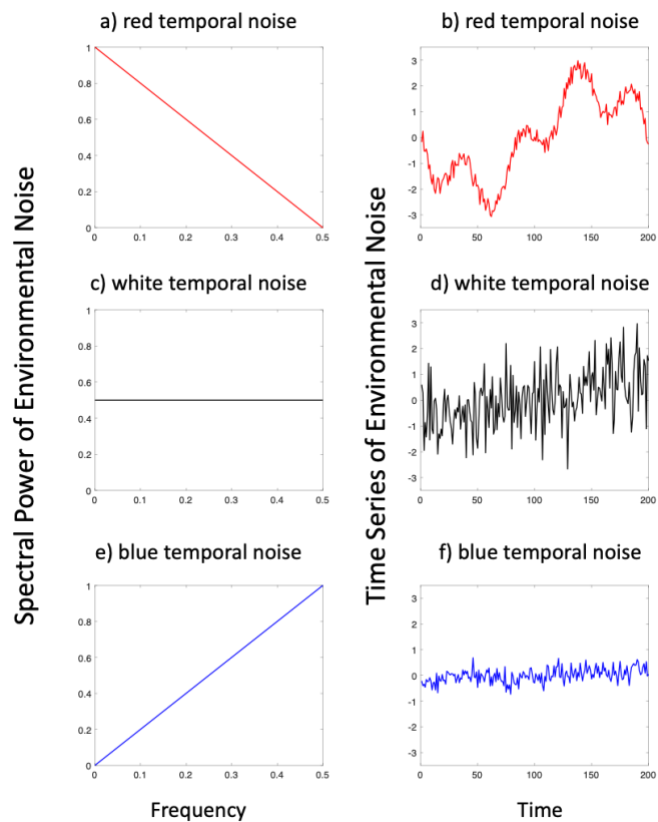


Figure 3.1. Figures a,c,e show colored environmental noise in the frequency domain where the independent variable is frequency. Figures b,d,f show the same environmental noise in the time domain where the independent variable is time. The figure is designed to highlight differences between colors of noise.

For fragmented populations (i.e., metapopulation), the color of environmental noise can be reflected in the color of the population time series, and this interaction can be complicated by the influence of local migration among fragmented habitats and local population dynamics (Desharnais et al. 2018; Massie et al. 2015). Gilljam et al. (2019) showed that the color of environmental noise such as temperature, precipitation, and frost day frequency, is associated with animal population dynamics. The strength of this association between the color of environmental noise and population time series has been shown to be negatively influenced by the increasing inherent population growth rates (Ferguson et al. 2016). More specifically, red noise has been associated with high extinction chance in slow-growing populations, while blue noise with fast-growing populations (García-Carreras and Reuman 2011; Schwager et al. 2006; Heino et al. 2000; Cuddington and Yodzis 1999). These associations can further be influenced by dispersal such that increasing dispersal under red noise conditions can decrease extinction chance (Mustin et al. 2013). These complex interactions are important to understand because these can have consequences for the persistence of metapopulations.

Other studies have also shown that metapopulation network heterogeneity (frequency distribution of patch degree across subpopulations) can also benefit metapopulation persistence (Zamborain-Mason et al. 2017; Gilarranz & Bascompte 2012). In a previous study (Danielian et al. unpublished), we suggest that a metapopulation with intermediate network heterogeneity may increase persistence compared to a metapopulation with an extreme heterogeneity. Previous studies that

have looked at the influence of the color of environmental noise have either used a population with a single patch (Gilljam et al. 2018; Ferguson et al. 2017; García-Carreras and Reuman 2011; Schwager et al. 2006; Cuddington and Yodzis 1999) or a metapopulation with a small number of patches (Danielian 2016; Greenman and Benton 2005; Heino 1998). We propose that the interaction of color of environmental noise with growth rate and dispersal may possibly be influenced by network heterogeneity in spatially structured large metapopulations. It remains unknown how the color of environmental noise influences survival in heterogeneous metapopulation networks. The aim of this paper is to fill this gap. In this present study, we ask how does the color of noise influence persistence in large heterogeneous metapopulation networks; what role does metapopulation dynamics (i.e., growth rate) play in this interaction; and how is this interaction influenced by dispersal rate between metapopulation patches? We use the Ricker discrete-time model that includes environmental noise in spatially connected metapopulation patches to answer these questions.

Methods

Overview of the model

This study was conducted using model simulations. We use the Ricker discrete-time model (Ali et al. 2019; Travis 2003; Ranta et al. 1995; May 1976) in our simulations and include both environmental and demographic noise in spatially connected metapopulation patches.

Growth Rate and Model Dynamics

The Ricker model we use has three phases: growth, emigration, and immigration.

The growth phase includes both demographic and environmental noise:

$$G_i(t) = \text{Binomial}(N_i(t) * e^r, e^{-r(\frac{N_i(t)}{k}) + \sigma z_i(t)}), \quad (1)$$

Where $G_i(t)$ is the population density of patch i at time t after growth has occurred, $N_i(t)$ is the density of patch i at time t , r is the per capita growth rate of a patch, k is the carrying capacity of a patch, $z_i(t)$ is the random environmental noise for the patch i at the time t , and σ is the amplitude of environmental noise at the time t .

Each patch in the metapopulation had a corresponding time series of 3000 environmental noise values. Each metapopulation patch had a unique environmental parameter at each simulation time step. The demographic noise is determined by the *Binomial*(n,p) equation where p successes are randomly chosen from n trials, and this randomness accounts for demographic processes such as birth, death, and competition (Ben Zion et al. 2010).

After the growth phase, the emigration phase involves calculating the number of individuals emigrating from a patch i through the binomial distribution (emigration does or does not occur):

$$E_i(t) = \text{Binomial}(G_i(t), d), \quad (2)$$

Where $E_i(t)$ is the number of individuals emigrating, and d is the dispersal rate of patch i . Each individual (after the growth phase) is chosen to emigrate with a probability d .

After the emigration phase, the immigration phase takes place. This is accomplished by randomly assigning each emigrant to a connected patch. This is accomplished through the following equation:

$$I_{i,j}(t) = \text{RandomSample}(E_i(t), j \text{ connected patches}), \quad (3)$$

Where $I_{i,j}(t)$ is the number of immigrants from patch i to patch j at time t .

Stochastic Environmental noise

The algorithm used to generate the stochastic environmental noise is based on Chambers (1995) as implemented in (Desharnais et al. 2022). This method generates a multivariate random time series based on any specified theoretical spectral matrix that is a function of frequency. Figures 3.1a,c,e help us visualize this information in a series of plots where the independent variable is the frequency, and the dependent variable is the spectral power of the time series of environmental noise. The y-axis is the spectral power that ranges from 0 to 1. For illustrative purposes, if the spectral power has a value of 1 at the frequency of 0.5, large waves of environmental variation dominate the time series of environmental noise, and the autocorrelation is positive. This is known as red noise and has a spectral power of $[0, 1]$, where 0 indicates little presence of small frequency waves, and 1 indicates large presence of large frequency waves in a time series (Figure 3.1a). On the

contrary, a blue noise has a spectral power of $[1, 0]$, where 1 indicates a high presence of small frequency waves in a time series, and a value of 0 indicates a small presence of large frequency waves in a time series (Figure 3.1e). A white noise has frequency values of $[0.5, 0.5]$. The first and the second values are the same and indicate an equal number of small and large waves of environmental variation at all frequencies (Figure 3.1c).

Metapopulation Network and Patch Size

The metapopulation network we used in this study is a random network with small-world properties (Holland & Hastings 2008; Watts & Strogatz 1998). In this type of network (used Watts-Strogatz model, MATLAB 2015), the migrating individuals can travel to near and far patches, but nearer patches have a higher probability of receiving immigrants. All metapopulation patches had an average of four connections with their neighbors, and the network had 1024 patches. An adjacency matrix was used to represent this undirected network where dispersal can occur in either direction between patches. An adjacency matrix is a square matrix where the diagonal elements are the patches of a metapopulation network, and the nonzero elements across rows or columns represent directional connections to certain patches (Cahen-Fourot et al. 2020).

Simulation parameters

There were three types of nonlinear model dynamics considered in this project, undercompensating, overcompensating, and chaotic. We picked r (per capita growth

rate) values in equation (1) that led to undercompensating ($r = \ln(2)$), overcompensating ($r = \ln(7)$), and chaotic ($r = \ln(17)$) dynamics in the deterministic non-spatial version of the model. We chose these growth rate values to facilitate the numeric methods such that n_t will always be an integer (Yarri et al. 2012). Each subpopulation, or patch, was assigned an initial density that was randomly selected from the interval spanning plus or minus 10% of the carrying capacity k which was set to be $k = 7$ for each subpopulation patch. We chose this carrying capacity value after parameterization of model to allow us to compare the results across the different metapopulation dynamics. The length of each time series was 3000, and the number of iterations (i.e., simulation repetitions) was 100 for each scenario of color of noise, dispersal rate, and subpopulation growth rate. The simulation repetitions allowed us to calculate mean metapopulation metrics for analysis. The environmental noise parameter $z_i(t)$ was regenerated for each of the 100 simulation iterations. The amplitude of environmental noise σ was set to be 2.0 for undercompensating, 4.0 for overcompensating and 6.0 for the chaotic dynamics. These amplitudes of noise values were chosen to show the influence of the color of noise on persistence. Several dispersal rates were chosen to represent the proportion of individuals emigrating from a patch. This allowed us to observe how increasing the level of movement between patches influenced metapopulation persistence. The dispersal rates used in this study were 0.00, 0.05, 0.10, and 0.20, indicating the probability an individual emigrates from a patch. These per patch dispersal values have been well documented in nature and are widely reported in

the literature (Laan & Fox 2020; Hopson & Fox 2019; Adamski et al. 2019; Gokhale et al. 2018; Fronhofer et al. 2014; Cooper et al. 2012; Bowne & Bowers 2004). These parameter values were held constant throughout all simulations to make comparisons between simulations equitable. The programming language used was MATLAB (2021).

Metapopulation metrics measured

Several metapopulation metrics were used to quantify the influence of the color of random environmental noise, dispersal rate and different metapopulation dynamics. The metrics used for all iterations were mean patch occupancy, mean correlation coefficient between the time series of patches within a metapopulation, and mean time to extinction.

Mean patch occupancy was calculated by dividing the total number of occupied patches at each time step by the total number of metapopulation patches (1024) for each metapopulation iteration (Holmes et al. 2020). This was then averaged across all metapopulation iterations (i.e., simulation repetitions). If a metapopulation went extinct before the final time step, the mean occupancy was only calculated for non-extinct time steps.

The average Pearson correlation coefficient was calculated between the pairs of subpopulations (i.e., patch) time series within a metapopulation. This correlation coefficient was then averaged among all the iterations of a metapopulation. If a

metapopulation went extinct before the final time step, the correlation coefficient was only calculated for the time steps for which the metapopulation was extant. Mean time to extinction (Roff 1974) was calculated as the average number of time steps before the metapopulation went extinct across all the iterations for each scenario. Extinction in our model occurred when all metapopulation patches simultaneously had a density of zero.

Results

Our results indicate that the blue color of environmental noise resulted in higher mean time to extinction, but white and red switched depending on dynamics (Figure 3.2c,f,i). More specifically, the blue noise had higher mean time to extinction when dispersal was greater than 0.05 for the undercompensating and chaotic dynamics, and is 0.10 for the overcompensating dynamics. Red noise resulted in higher mean time to extinction than white noise when dispersal was 0.20 for the undercompensating dynamic (3.2c), and white noise in higher mean time to extinction than red noise when dispersal was 0.20 for the chaotic dynamic (3.2i). These differences in mean time to extinction among the color of noise were likely caused by mean correlation coefficients. This is truer for blue noise as it always resulted in lower correlation coefficients except when dispersal rate was less than 0.10 for the undercompensating dynamic (3.2b). This was likely an indication that asynchrony led to higher mean time to extinction for the blue noise. However, differences in correlation coefficients did not always lead to differences in mean

time to extinction as observed in the case of chaotic dynamics when dispersal is 0.05 (3.2h,i). We did not see discernable differences in mean occupancy for the colors of noise except when dispersal was low for the undercompensating dynamic (Figure 3.2a,d,g). Mean occupancy values were similar even when mean time to extinction values were different.

Increasing dispersal increased mean occupancy (Figure 3.2a,d,g), and mean time to extinction (3.2c,f,i) for all colors of noise and dynamics, decreased correlation coefficient for the chaotic dynamic. The correlation patterns were different for the undercompensating and overcompensating dynamic. The increasing dispersal rate first decreased, then increased correlation coefficients for all colors of noise for the undercompensating dynamic, and only for the blue noise for the overcompensating dynamic.

Increasing growth rate (i.e., dynamics) led to similar outcomes in mean occupancy for the overcompensating and chaotic dynamics (3.2d,g), increased mean correlation coefficient for red and white noise for the chaotic dynamic (3.2h), switched mean time to extinction patterns between red and white noise between the undercompensating and chaotic dynamics when dispersal was 0.20 (3.2c,j).

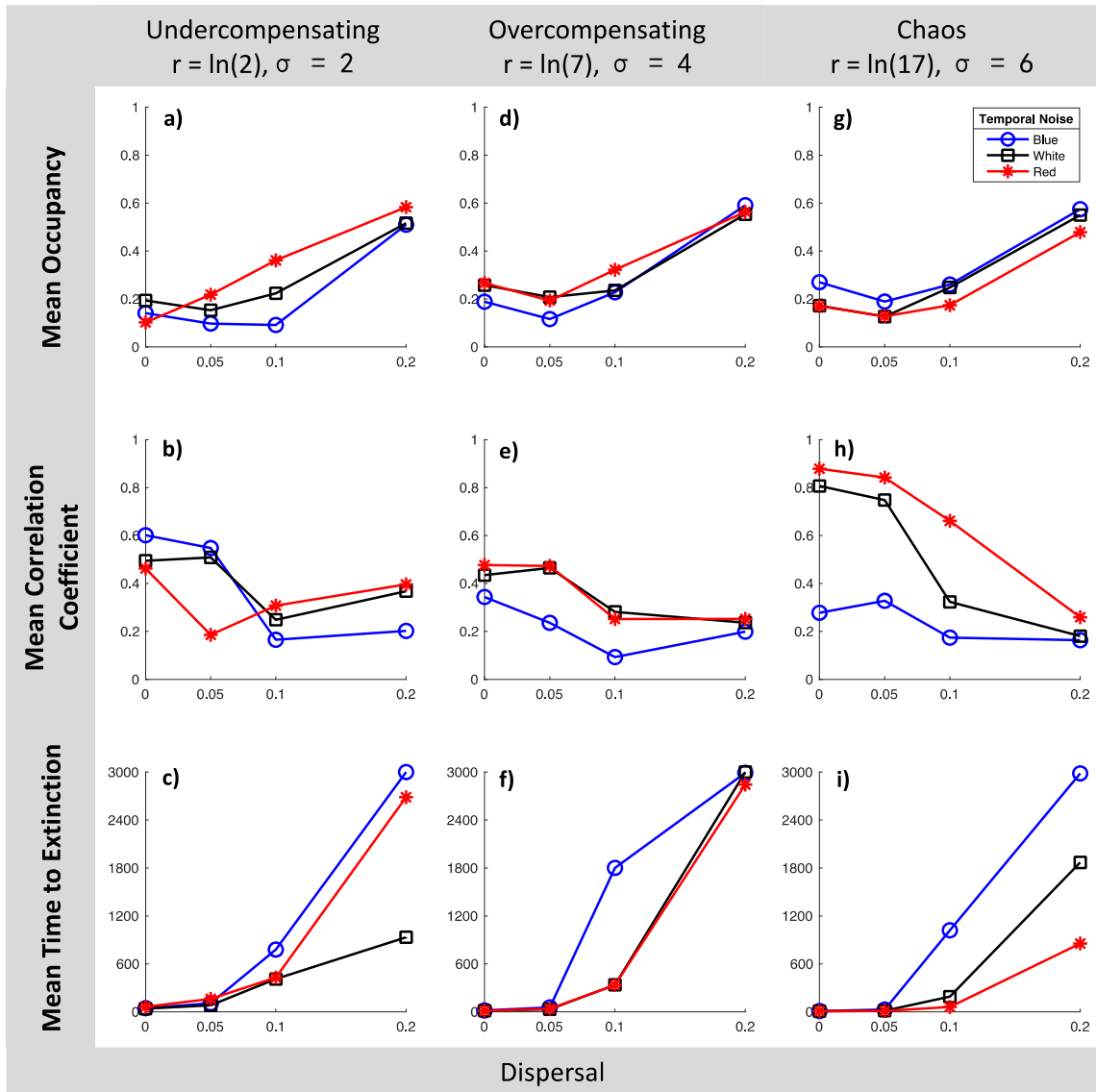


Figure 3.2. This figure shows the influence of the color of environmental noise (blue, white, red) and metapopulation dynamics (undercompensating, $r = \ln(2)$; overcompensating, $r = \ln(7)$; chaos, $r = \ln(17)$) on the mean occupancy (a,d,g), mean correlation coefficient (b,e,h), and mean time to extinction (c,f,i). The metapopulation network type used here was Random network. The simulation parameters were: Iterations = 100; length of time series, $t = 3000$ -time steps, amplitude of noise, $\sigma = 2.0$ for Undercompensating dynamics, $\sigma = 4.0$ for overcompensating, and $\sigma = 6.0$ for the chaotic dynamics; dispersal rates were 0.00, 0.05, 0.10, and 0.20; carrying capacity, $k = 7$; average number of connections = 4 per patch.

Discussion

Here are the main findings from this paper: 1) blue color of environmental noise resulted in lower synchrony and higher persistence for all dynamics; 2) mean occupancy was only meaningfully different for undercompensating dynamic and does not appear to be a predictor of persistence; 3) dispersal increased mean occupancy and persistence; 4) metapopulation dynamic reversed the pattern of persistence for the red and white colors of noise when dispersal was high.

Blue noise resulted in higher persistence for all dynamics when the dispersal rate was greater than 0.05 per patch, except for when dispersal was 0.20 for the overcompensating dynamics. It has been shown that blue environmental noise increases persistence for slow-growing populations, and red noise increases persistence in fast-growing populations (Danielian 2016; García-Carreras et al. 2011; Heino et al. 2000). Our results confirmed with the blue noise increasing persistence in slow-growing populations but contradicted the red noise increasing persistence in fast-growing populations. The major difference between our study and the studies mentioned above is that some had used a single patch model (García-Carreras et al. 2011; Heino et al. 2000) while the other had used a two-patch metapopulation model (Danielian 2016). We suspect that in a large, heterogeneous network, the rules of interaction between the color of noise and metapopulation dynamic may be different in that in a large network, blue noise increases persistence under all growth rates, while in a small network or single patch models,

blue noise only increases persistence in slow-growing populations. In all the cases where the blue noise led to high persistence in our study, the mean metapopulation correlation was the lowest among the three colors of noise results. It is also important to note that these results were true when dispersal rate was at or above a certain threshold. Then the question remains – why is it that when growth is high (overcompensating and chaos), the heterogeneous network and higher dispersal rate increases persistence when noise was blue? A possible explanation for this is that in a large heterogeneous network (had an average of four connections per patch) patches that go extinct are filled quickly by way of dispersing individuals, and high-frequency variation quickly de-synchronizes (i.e., increases asynchrony) the subpopulation dynamics between the habitat patches, and this asynchrony increases persistence when noise is blue.

We observed another unexpected result - red noise resulted in higher persistence than white noise for the undercompensating dynamics when the dispersal rate was 0.20. The red noise had similar synchrony but resulted in higher persistence than the white noise. This means that synchrony may not have been the main cause of higher persistence for the red noise. There is a possible two-step process at play here that increases persistence for red noise. First, red noise resulted in high extinction of patches when growth is undercompensating (slow), then high dispersal quickly fills the extinct patches, and therefore increase persistence when patch extinction is high (Fox et al. 2017). This may be why occupancy was high for the red noise for the undercompensating dynamics for nonzero dispersal rates.

We observed differences in mean time to extinction even when mean occupancy values were similar when growth rate was high (undercompensating and chaos). The likely reason for this is because the mean occupancy is a central tendency measure while the mean time to extinction is based on the variance of the outcome for the metapopulation.

Higher dispersal rates increased mean occupancy and mean time to extinction for all colors of noise and all dynamic. Increasing dispersal rate first decreased correlation coefficient, then increased for all colors of noise when the dynamic was undercompensating, decreased and only increased correlation coefficient for blue noise when overcompensating. This type of U-shaped pattern between dispersal and synchrony is possible when local regulatory forces such as growth and noise act on the local subpopulations, and when dispersal increases, it may overcome the influence of the noise and dynamics (Abbot 2011; Jansen 2001). Higher dispersal generally increases synchrony among metapopulation patches (Abbot 2011; Peltonen et al. 2002; Heino et al. 1997; Ranta et al. 1995). We only observed this pattern for the undercompensating dynamic for all colors of noise, and only for the blue noise for the overcompensating when dispersal was greater than 0.01. In the case of the chaotic dynamic, increasing dispersal rate decreased correlation coefficient. It is possible for increasing dispersal to lower synchrony in between patches when a species has an “extremely fast dynamic” (Koelle and Vandermeer 2004). We think the increasing dispersal between the patches may empty patches of individuals, and therefore desynchronize subpopulation dynamics.

Increasing growth is expected to lower synchrony between subpopulation patches (Ranta et al. 2000). However, this was not the case for the chaotic dynamic, as we observed synchrony to increase for red and white colors of noise, but not for blue. This might be due to how we estimate correlation coefficient in our model in that if a metapopulation goes extinct (i.e., all patch densities are zero) before the final time step of 3000, then correlation is estimated for the time steps when there is at least one surviving subpopulation. In the case of the chaotic dynamic and red noise, many of the patches go extinct and stay extinct when dispersal is low, and correlation between zero values of patch densities is high. This is likely why correlation coefficient is high in our metapopulation model when growth is very high, and as dispersal increases, dispersing individuals fill the empty patches and therefore disrupt this pattern of synchrony.

This work has implications for conservation purposes. When conservationists design habitats for preservation purposes, they should keep in mind that general rules for small network may not always apply to large spatial networks. Our findings indicate that when the autocorrelation of environmental noise shifts from positive (red color) to negative (blue color), this may benefit the persistence of a species in large heterogeneous metapopulation networks. Higher dispersal between patches increases occupancy and persistence.

The limitations of this study are that this study assumes equal dispersal rate, equal amplitude of environmental noise, and equal population growth in each patch. It also assumes that all dispersing individuals reach a destination.

For future studies, we recommend designing experiments to test these theories in laboratory or field settings.

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Conclusion

In chapter 1 of this dissertation, I proposed a novel framework for classifying synchrony across ecological processes. I referred to synchrony that is within a single trophic level as horizontal synchrony and synchrony that takes place between species at different trophic levels as vertical synchrony. I repeated the same classification categories for asynchrony. I further divided vertical synchrony into antagonistic synchrony (predator-prey and parasite-host) and synergetic synchrony (mutualism and commensalism). The horizontal synchrony was categorized as intraspecific synchrony (i.e., synchrony within a population), and interspecific synchrony (i.e., among species synchrony). This approach fills the gap between a new theory and the classic theory of intraspecific and interspecific synchrony.

In chapter 2, I showed that there appears to be an intermediate optimal amount of heterogeneity but in my study intermediate and high heterogeneity were fairly similar and both were better for persistence than homogeneous metapopulation networks. In some cases, an intermediate network heterogeneity benefited metapopulation persistence. I also showed that more dispersal appears to be more beneficial than less dispersal in all cases except when homogeneous networks had slow-growing subpopulations.

In chapter 3, I showed that when the autocorrelation of environmental noise shifts from positive (red color) to negative (blue color), this may benefit the persistence of

a species in large heterogeneous metapopulation networks. Higher dispersal between patches increased occupancy and persistence.

Chapter 1 of this dissertation is the first of its kind to address (a)synchrony across wide topics in ecology. This is important as it summarizes the role of this fundamental natural phenomenon in ecological interactions. This work is also useful for new ecologists interested in (a)synchrony to explore and understand its wider role in ecology. The table presented in chapter 1 (Supplemental Table 1.1) could also be a useful resource for textbooks used in undergraduate education. Chapter 2 and 3 contribute to the conservation science by allowing the conservationists involved in decision making to optimally design reserves under varying natural conditions.