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Arzoo Narang,<sup>1</sup> Subhendu Bhandary,<sup>1</sup> Taranjot Kaur,<sup>1</sup> Anubhav Gupta,<sup>2,3</sup> Tanmoy Banerjee,<sup>4,a)</sup> and Partha Sharathi Dutta<sup>1,b)</sup>

## AFFILIATIONS

<sup>1</sup> Department of Mathematics, Indian Institute of Technology Ropar, Rupnagar 140 001, Punjab, India

<sup>2</sup> Department of Evolutionary Biology and Environmental Studies, University of Zurich, 8057 Zurich, Switzerland

<sup>3</sup> URPP Global Change and Biodiversity, University of Zurich, 8057 Zurich, Switzerland

<sup>4</sup> Chaos and Complex Systems Research Laboratory, Department of Physics, University of Burdwan, Burdwan 713 104, West Bengal, India

<sup>a)</sup> Electronic mail: tbanerjee@phys.buruniv.ac.in

<sup>b)</sup> Author to whom correspondence should be addressed: parthasharathi@iitrpr.ac.in

## ABSTRACT

Anthropogenic global warming in this century can act as a leading factor for large scale species extinctions in the near future. Species, in order to survive, need to develop dispersal strategies depending upon their environmental niche. Based on empirical evidence only a few previous studies have addressed how dispersal can evolve with changing temperature. However, for the analytical tractability, there is a need to develop an explicit model to ask how the temperature-dependent dispersal alters ecological dynamics. We investigate the persistence of species in a spatial ecological model, where dispersal is considered as a function of temperature. Spatial persistence is of major concern and dispersal is reasonably an important factor for extinction risk in the context of promoting synchrony. Our study yields how the temperature influences species decision of dispersal, resulting in either short-range or long-range dispersal. We examine synchronous or asynchronous behavior of species under their thermal dependence of dispersal. Moreover, we also analyze the transients to study the collective behavior of species away from their final or asymptotic dynamics. One of the key findings is at the most unfavorable environmental conditions long-range dispersal works out as the driving force for the persistence of species.

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Understanding various mechanisms maintaining biodiversity is a challenging aspect of ecology. Theory and insights from the nonlinear dynamics of coupled oscillators play a significant role in this endeavor. In the metapopulation ecology, each patch (or node) is modeled as an oscillator and spatial interactions among them through dispersal often produce synchronous or asynchronous dynamics, influencing species persistence. Although various dispersal strategies have been studied in the context of species survival, climate warming is one of the major abiotic factors altering species associations and persistence. The potential for warming to alter metapopulation interactions and dynamics can be highly significant. Taking this into account, here we consider a spatial Rosenzweig-MacArthur model accounting for temperature-dependent dispersal strategy of species, characterized by their fitness under climate warming. Further,

we analyze synchronous or asynchronous, asymptotic or transient behavior of species under different thermal conditions. We emphasize that the temperature-dependent dispersal strategy can significantly contribute to maintaining species persistence at extreme temperatures. Also, transients can help us to determine the long term metapopulation dynamics under warming.

## I. INTRODUCTION

The study of spatial ecological systems has a strong significance in our understanding of the large scale population dynamics concerning the evolutionary outcomes.<sup>1,2</sup> Spatial ecologists often find metapopulation theory of utmost importance in order to understand the processes of regional extinction and recolonization of species.

The metapopulation approach adopts the view that local population interact via dispersal and gene flow.<sup>3</sup> Dispersal is expressed through the interaction of an organism with its environment; therefore, it is likely to be influenced by environmental effects.<sup>4</sup> One of the major environmental factors responsible for altering the costs and benefits of dispersal is the climate warming. Climate change has a considerable impact on species composition,<sup>5,6</sup> and current global warming is expected to cause an irreparable change to ecosystems.<sup>7</sup> Eventually, dispersal will become a central subject in order to predict species responses to environmental change.<sup>8</sup> Therefore, it is of natural interest to explore the effect of temperature on species dispersal. According to the earlier studies, dispersal, that is, considered to be an impelling cause for the persistence and stability of metapopulations could also drive the population toward extinction by increasing the degree of spatial synchrony.<sup>9–11</sup> Population stability means that the minimum density of populations in all patches is not too low, the probability of extinction is less in a given time.<sup>12</sup> Other than dispersal, environmental factors are also one of the reasons of dynamical connection,<sup>13,14</sup> which results in synchronization of spatial populations. If dispersal induces synchrony, then the synchronized populations will continue to remain in synchrony until and unless any large external perturbation drives them away.<sup>15</sup> Spatial “asynchrony” in density fluctuations is known to strengthen the metapopulation persistence. This indicates the importance to examine species dynamics due to dispersal and the extrinsic factor, which we consider to be temperature, on synchrony.

Range interaction in species dispersal is an important factor that drives interesting spatial dynamics.<sup>16</sup> Dispersal, under the influence of climate change has an impact on species range shifts,<sup>17–19</sup> either resulting in long-distance dispersal (LDD) or short-distance dispersal (SDD). We incorporate dispersal kernels that are referred to the probability to disperse to certain distances. A number of different functions are used for dispersal kernels in theoretical models of dispersal including the inverse power law,<sup>16</sup> for the present study, we consider that the network of spatially separated patches are connected by a long-range interaction that obeys a distance-dependent power law. Our choice of this particular type of dispersal kernel is also motivated by the fact that the long-range interaction plays a crucial role in many physical and biological systems. For example, in the one-dimensional Ising spin model<sup>20</sup> and spin-glass model,<sup>21</sup> interaction among the spins are governed by the long range interaction that obeys a distance-dependent power law. In neuronal systems, long-range interaction with a specific scaling has been found which controls the connectivity among the neurons.<sup>22</sup>

An appreciable amount of work has been done to study the effects of climate change and dispersal on ecosystems.<sup>8,23–31</sup> A mathematical model (predator-prey subsidy model) involving temperature to study seasonal fluctuations<sup>29</sup> and also to measure the impact of global warming and seasonality<sup>30</sup> has been investigated. Further, the influence of network structures was examined on the predator-prey subsidy system.<sup>31</sup> It was observed that in spatial structures with food scarcity, an increase in migration rates would result in the possibility of extinction of predators. Investigating delayed migration to study spatial dynamics has also been an important perspective.<sup>29,32</sup> Consequently, considerable research has been done to examine the

effect of dispersal on predator-prey dynamics.<sup>33–35</sup> However, a direct approach that incorporates temperature in spatial population models to study dispersal induced dynamics is yet to be explored. Models that investigate migratory effects are generally classified into one of the three categories: Island models, Stepping-Stone models, and Continuum models.<sup>31</sup> The key feature of “Island” model<sup>33,34</sup> is the inclusion of set of patches. It involves instantaneous migration between patches without explicitly including spatial dimensions. The “Stepping-Stone” models again consider populations being divided into patches, but the patches are now assigned fixed spatial coordinates. In such models, spatial structures significantly contribute toward determining predator-prey dynamics.<sup>31</sup> The “Continuum” models involve partial differential equations to elucidate migration of populations in continuous domain.<sup>33</sup> In this work, we link changing global mean temperature with the dispersal behavior of species by considering an ecological system, namely, a spatial Rosenzweig-MacArthur model<sup>36,37</sup> or a “Stepping-Stone” model. We demonstrate that the natal dispersal tendency depends upon the changing temperature, which further will have an impact on the species survival. We consider that at very low and high temperature ranges, species dispersal within patches is low; this arises mainly as a consequence of species “Thermal Performance Curves” (TPCs).<sup>38</sup> These curves show an exponentially inclining trend at low temperatures attain a maxima at the thermal optimum and then decline with a further increase in the temperature. Hence, as species thermal performance is low at extreme temperatures, this suppresses species ability to move and thus disperse within patches. In this paper, we try to address the following questions: How does the temperature-dependent dispersal influence the dynamics of a metapopulation? Can dispersal promote persistence of species by reducing the degree of spatial synchrony, even in the least favorable environmental conditions? Can transient state work as an indicator of species behavior in their final dynamics?

To address the above questions, we begin by analyzing the fluctuations in species density over time. We carry out different measures to learn the coherence/incoherence in species dynamics characterized by their amplitude of fluctuations, density correlations, and transient dynamics. Furthermore, we use cross-wavelet analysis to understand the long term dynamics of the system through transients. Variations in temperature that influences species dispersal leads to interesting spatiotemporal dynamics. We observe that amplitude of fluctuations in species density, averaged over large number of the system replicates, suppresses along the thermal axis up to optimum temperatures. These findings are conserved while investigating the cluster count, depicting relatively similar response of large number of species along the changing temperatures. Furthermore, the robustness of observations is rooted through the increasing synchrony measure and decreasing transients of the system. Importantly, we also find that the transient phase of the system can trace the long term synchronous or asynchronous distance-dependent dynamics. In all, our study reveals that the synchrony is minimum at the extreme conditions and comparatively more synchronized behavior is observed around the optimum temperatures, which may also be hinted by the transient state, using cross-wavelet analysis.

The paper is organized as follows: In Subsection II A, we introduce the temperature-dependent metapopulation model. The

measures used to analyze the model are defined in Subsection II B. In Sec. III, we first discuss cluster analysis and transients that are related to the collective dynamics of the model. Then, we present the cross-wavelet analysis that depicts the effects of different temperature together with the distance between patches in Subsection III E. Finally, in Sec. IV, we discuss the importance of our results and future directions.

## II. MATERIALS AND METHODS

To study the influence of temperature-dependent dispersal on spatial population dynamics, we consider prey-predator interactions within a patch and between  $n$ -spatially distributed patches. Each patch exhibits homogeneous behavior in the sense of species interactions and phenotypes. Spatial heterogeneity is introduced into the system due to temperature dependent dispersal phenomenon as well as by accounting short-range and long-range interactions of species between the patches.

### A. A metapopulation model

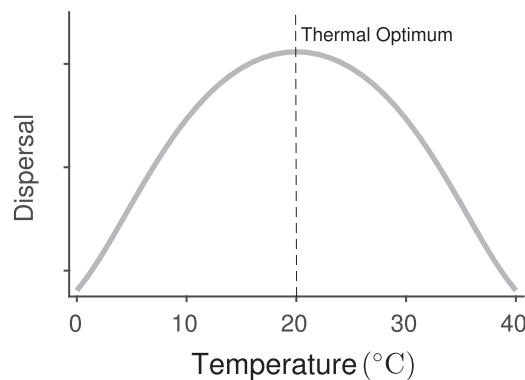
We start with the dimensionless form of a spatial Rosenzweig-MacArthur model.<sup>36,39</sup> The dynamics of a prey density ( $h_i$ ) and a predator density ( $p_i$ ) in the  $i$ th patch (node) are given as

$$\frac{dh_i}{dt} = h_i(1 - \theta h_i) - \frac{p_i h_i}{1 + h_i} + \epsilon_h \left( \frac{1}{\zeta(f(T))} \sum_{d=1}^m \frac{h_{i-d} + h_{i+d}}{d^{f(T)}} - h_i \right), \quad (1a)$$

$$\frac{dp_i}{dt} = \frac{\phi p_i h_i}{1 + h_i} - \eta p_i + \epsilon_p \left( \frac{1}{\zeta(f(T))} \sum_{d=1}^m \frac{p_{i-d} + p_{i+d}}{d^{f(T)}} - p_i \right), \quad (1b)$$

where  $i (= 1, 2, \dots, n)$  determines the index of a patch. The patch indices  $i - d$  and  $i + d$  are in correspondence with modulo the number of patches in the network (i.e.,  $n$ ).  $\theta$  is the self-regulation of prey,  $\phi$  is the conversion efficiency of the predator to convert and assimilate acquired food into energy, and  $\eta$  determines the predator's natural mortality. These factors govern the local dynamics of the interaction network. Spatiotemporal dynamics of the metapopulation are characterized by dispersal strengths of prey and predator as  $\epsilon_h$  and  $\epsilon_p$ , respectively.  $d$  is the distance between  $i$ th and  $j$ th patches, defined by the minimum number of edges required to disperse from the  $i$ th to the  $j$ th patch. We consider a regular network where all the patches are connected with other and hence accessible by the dispersing species from any patch [i.e.,  $m = (n - 1)/2$ , when the total number of patches is odd], but the dispersal density may vary depending upon the distance between the patches as well as the temperature of the habitat.

In the network, every patch is connected to all the other patches via the dispersal strength  $\epsilon_h$  or  $\epsilon_p$ , which is modulated by the distance between patches and temperature-dependent power law function



**FIG. 1.** Thermal dependence of dispersal of spatially separated species. At extreme temperatures (either very low or high), species are less likely to disperse.

$d^{-f(T)}$ , where  $T$  is the temperature.  $\zeta(f(T)) = 2 \sum_{d=1}^m d^{-f(T)}$  is the normalization constant. We consider the hypothesis that dispersal is the strongest at the optimal temperature (see Fig. 1). This is because of the fact that the intermediate temperature being a favorable temperature for the growth and survival<sup>40</sup> of species results in the active biological traits of species.<sup>38,41</sup> For example, the species attack rate follows an increasing trend, attains a maximum at the optimum temperature, and then declines, moreover, handling time also attains an optimum value at the intermediate temperature.<sup>42</sup> The temperature-dependent power law exponent  $f(T)$  governing the distance-dependent interaction strength is represented by a Gaussian function<sup>42</sup>

$$f(T) = f_{opt} \times e^{\frac{(T-T_{opt})^2}{2s^2}}, \quad (2)$$

where  $f_{opt}$  is the value of  $f$  at the optimal temperature  $T_{opt}$ . Temperature sensitivity of the function  $f(T)$  is determined by the parameter  $s$ , which also determines the performance breadth of the dispersal between the coupled patches. Throughout this work, we have considered  $f_{opt} = 0.27$ ,  $T_{opt} = 20^\circ\text{C}$ , and  $s = 11.5$ . The function  $f(T)$  holds relatively large values at extreme temperatures as compared to the intermediate temperatures. Furthermore, large values of  $f(T)$  imply less chances of species to disperse to the further habitat as compared to lower values of  $f(T)$  (except the nearest neighboring patches, i.e., for  $d = 1$ ) as prey-predator dispersal strengths are modulated via  $d^{-f(T)}$  (see Fig. 1). Therefore, species dispersal is more to further patches at intermediate temperatures in comparison with the extreme temperatures.

### B. Characteristic measures

We study spatiotemporal dynamics of the system [see Eq. (1)] for a fragmented land of 11 patches. When there is no dispersal of species from one patch to another (i.e., with  $\epsilon_h = \epsilon_p = 0$ ), species dynamics are determined by their local interaction and they exhibit oscillatory behavior. Setting it up as a benchmark for spatiotemporal interaction, first, we examine the time series of the species in the 11 patches and observe the impact of changing temperature

on the species dynamics. Our major concern is to understand what role dispersal plays in the survival of species under different thermal conditions. For this, we compute the total predator amplitude<sup>37</sup> defined as

$$\text{Total predator amplitude} = \log_{10} \left( \frac{\max \left( \sum_{i=1}^n p_i \right)}{\min \left( \sum_{i=1}^n p_i \right)} \right) \quad (3)$$

over a window of  $4\bar{M}_p$ , with  $\bar{M}_p$  as the mean period of the population cycle which is averaged over a sufficiently long time period. Synchronous system signifies more possibility of obtaining high values of predator amplitude comparative to asynchrony. In order to analyze the same, we also calculate cumulative probability of various predator amplitudes for different values of  $T$ .

Likewise to explore the outcomes of interactions between patches, we calculate correlation coefficient  $\rho_{ij}$  of a species time series at time  $t$ , between the  $i$ th and the  $j$ th patch for different values of the temperature  $T$ . Thereafter, set of patches having identical behavior are considered to form a cluster. Here, for identical behavior we refer to patches having  $\rho_{ij} > 0.999$ . Out of the  $n$  patches, we can have a  $k$ -cluster solution, where  $1(\text{global synchrony}) \leq k \leq n(\text{complete asynchrony})$ . The correlation coefficient is calculated at each time and is given by<sup>43</sup>

$$\rho_{ij} = \frac{\langle x_i x_j \rangle - \langle x_i \rangle \langle x_j \rangle}{\sqrt{\langle x_i^2 \rangle - \langle x_i \rangle^2} \sqrt{\langle x_j^2 \rangle - \langle x_j \rangle^2}}, \quad (4)$$

where  $x$  is the species density and  $\langle \dots \rangle$  is the average over the window  $[t, t + 4\bar{M}_p]$ . Using the correlation coefficient  $\rho_{ij}$ , the frequency of the occurrence of a  $k$ -cluster solution with time evolutions is calculated as

$$\text{Frequency of } k\text{-cluster} = \frac{\text{No. of } \leq k\text{-clusters}}{\text{No. of simulations}}. \quad (5)$$

Due to the possibility of the occurrence of multiple stable attractors in higher dimensional dynamical systems, here we perform large ensembles of simulations for a set of randomly chosen initial conditions.

For the permanence of our results, we carry forward our investigation by calculating the synchrony measure  $\sigma$ <sup>44</sup> with respect to the changing temperature  $T$ . The synchrony order parameter  $\sigma$  measures the amount of change in synchrony between patches along the temperature gradient and is defined as

$$\sigma = \sqrt{1 - \left\langle \frac{\sum_{i=1}^n [x_i(t) - \bar{x}(t)]^2}{\sum_{i=1}^n x_i(t)^2} \right\rangle}, \quad (6)$$

where  $\bar{x}(t) = \frac{1}{n} \sum_{i=1}^n x_i(t)$  and  $\langle \dots \rangle$  represents the average over a given time. The quantity  $\sigma$  varies at intervals 0 and 1, i.e., from no synchrony to perfect synchrony of the populations. Any intermedi-

ate value of  $\sigma$  accounts for partial synchronization of populations in the system.

The study of asymptotic or long-term dynamics is influential to understand a natural system. The asymptotic dynamics may display a constant or a periodic phase evolution or even chaos. However, while considering the large-scale dynamics, it is of great importance to realize how the population evolves with time. Another important aspect of ecological time scales is the transients, i.e., the dynamics far from the final state of a system. A lot of attention has been given to the study of transient dynamics,<sup>45,46</sup> and it is believed that the final behavior of a system may be quite different from the transient dynamics.<sup>47</sup> Therefore, it is essential to study the variations in both the transient and asymptotic dynamics.

We also split the total predator amplitude into transient and asymptotic time series, and take the median of these time series called as the “median predator amplitude” (MPA) for transient and asymptotic states. To estimate the transient time, we first used the low pass filter on the time series obtained by numerically integrating Eq. (1) following an algorithm as described in Ref. 37. MPA is taken to be an ensemble average of 100 simulations for different set of randomly chosen initial conditions in order to avoid uncertainty. We also calculate the mean fraction of time spent in the transient state along changing global mean temperature to estimate the time taken by the populations to reach a steady state under different warming conditions.

Also, there is a possibility of long transients, i.e., the system reaches asymptotic behavior after a very long time,<sup>48</sup> it is even possible that the system never attains asymptotic state within a given time frame. Therefore, in order to understand how a system evolves with time, it is important to study the behavior of system away from its final asymptotic dynamics. Here, we use wavelet analysis to study synchronization and phase relations between interacting species when the system is in transient state. Wavelet analysis is a commonly used statistical tool for investigating nonstationary time series.<sup>49</sup> Usually, periodic signals are analyzed by spectral analysis, which uses stationary time series. This sometimes works as a limitation since majority of ecological time series are nonstationary in nature, and hence, it may not be able to characterize signals whose frequency content changes with time. It is possible to overcome this hindrance by wavelet analysis, which is now regularly being used for the investigation of ecological time series.<sup>50,51</sup> In the interest of studying the relative behavior of two time series, here we use cross-wavelet analysis. It examines the fluctuations of two time series, also estimates the phase difference between these fluctuations.<sup>52</sup> Cross-wavelet analysis is a powerful tool for testing the possibility of linkages between two time series.<sup>53</sup> To study the effect of temperature and distance on species dynamics, we perform the cross-wavelet analysis by considering  $n = 33$  patches.

We use the 4th order Runge-Kutta method with  $10^{-2}$  step size to numerically integrate Eq. (1). Initial conditions of prey are independently and identically distributed, with  $\log_{10}(h_i(0))$  following a uniform distribution on the interval  $(-5, 1 + \log_{10} \hat{h})$ . Parallelly, predator initial conditions are independently and identically distributed, with  $\log_{10}(p_i(0))$  uniformly distributed on the interval  $(-5, 1 + \log_{10} \hat{p})$ .  $\hat{h} = \frac{n}{\phi - \eta}$  and  $\hat{p} = (1 + \hat{h})(1 - \theta \hat{h})$  are the respective equilibrium densities of prey and predator.

### III. RESULTS

As per the choice of  $f(T)$  and the associated thermal optimum [Eq. (2)], the system has a reflection symmetry on the either side of the thermal optimum  $T_{opt} = 20^\circ\text{C}$  (see Fig. 1). For example, the results that hold for  $T = 0^\circ\text{C}$  will also hold for  $T = 40^\circ\text{C}$ . Hence, in general, we carry out the numerical experiments for the temperature ranging from  $T = 0^\circ\text{C}$  to  $T = 20^\circ\text{C}$ .

#### A. Time series analyses and predator amplitude

We observe diverse species dynamics for different values of the temperature  $T$ . Examining the time series of predator density as well as total predator amplitude [Eq. (3)], we find that increasing temperature  $T$  up to the line of symmetry (i.e., the line at  $T = 20^\circ\text{C}$  in Fig. 1), moves the system from low to high amplitude values and, hence, less number of clusters  $k$ . Figure 2 shows the amplitude fluctuations with time for different values of temperature, and it is clearly visible by analyzing cumulative probability [see Figs. 2(k)–2(o)] that the expectation of getting high amplitude values increases with the increasing temperature.

#### B. Cluster analysis

The total predator amplitude reveals oscillatory behavior of populations indicating that the solutions of Eq. (1) can result in different synchronous states of spatially connected species depending

upon the number of clusters. Hence, we perform the cluster analysis using Eqs. (4) and (5). We observe different  $k$ -cluster solutions for different warming conditions of the habitat patch,  $k$  ranging from 1 to  $n$  cluster(s).

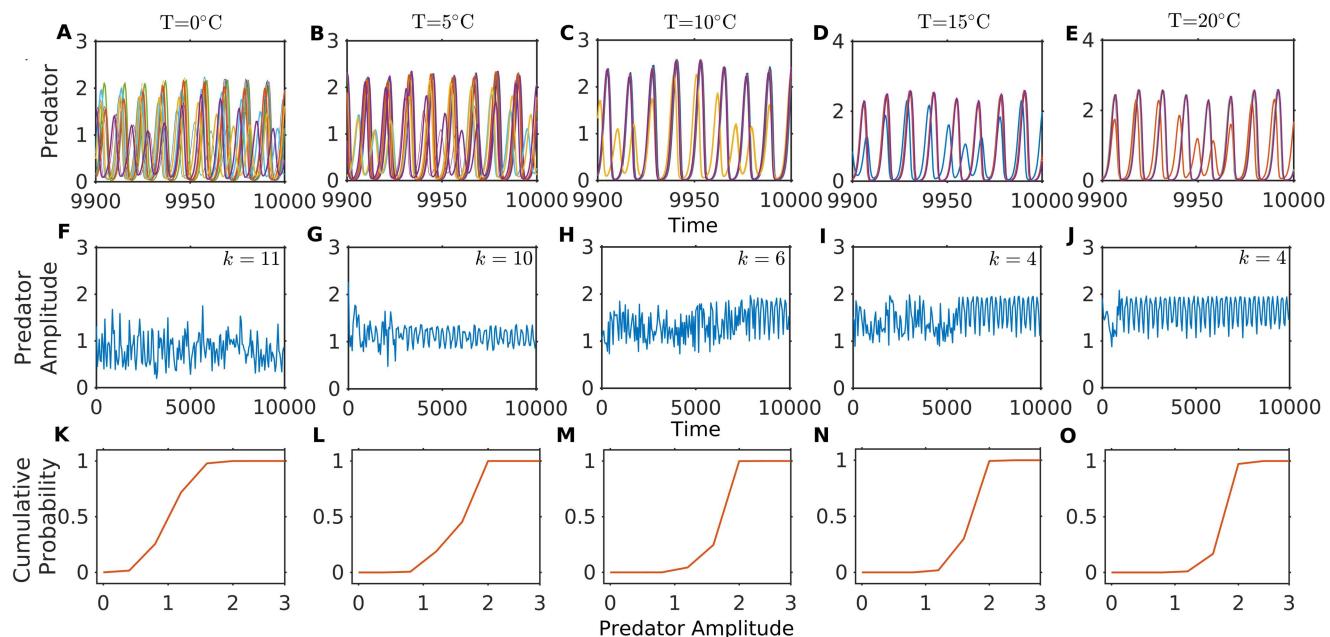
Analyzing the distribution of clusters (see Fig. 3) with changing temperature reveals an important information about the collective dynamics of the system. We observe that an increase in the temperature up to thermal optimum converges the system from high to low number of clusters.

#### C. Interpatch synchrony

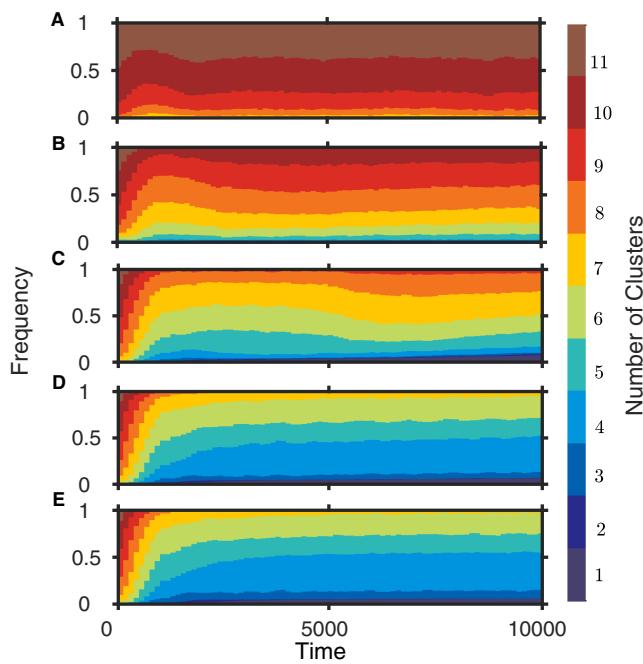
Synchrony is highly influenced by species interaction strength. High interaction strength between patches drives more synchronous behavior, when compared to low interaction strength. We calculate the synchrony order parameter  $\sigma$  [Eq. (6)] to measure the change in synchrony between patches with variations in  $T$ , it explains qualitative synchronous dynamics of the interaction network. Figure 4 depicts that the value of  $\sigma$  increases with the increasing temperature up to the thermal optimum. In fact, synchrony is the strongest at the thermal optimum and the weakest at both the temperature extremes (extreme low and extreme high temperatures).

#### D. Median predator amplitude and mean transient fraction

The MPA depicts the fluctuations in total population density, low value of MPA implies lower fluctuations and hence high chances

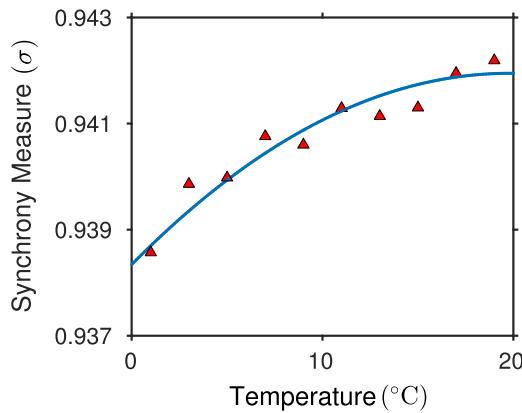


**FIG. 2.** Time series of predator species, predator amplitude, and cumulative distributions of predator amplitude along the thermal gradient  $T$ : for (a), (f), (k)  $T = 0^\circ\text{C}$ ; (b), (g), (l)  $T = 5^\circ\text{C}$ ; (c), (h), (m)  $T = 10^\circ\text{C}$ ; (d), (i), (n)  $T = 15^\circ\text{C}$ ; and (e), (j), (o)  $T = 20^\circ\text{C}$ . Local dynamics are governed by  $\theta = 0.3$ ,  $\eta = 1$ , and  $\phi = 3$ . Dispersal strengths are  $\epsilon_h = 2^{-5}$  and  $\epsilon_p = 2^{-6}$ .  $k$  denotes clusters count at different values of  $T$ .

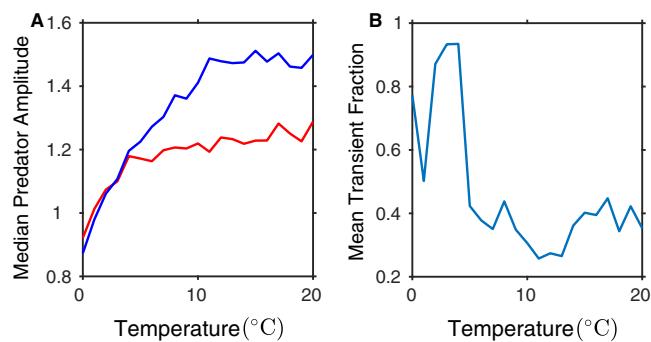


**FIG. 3.** Frequency of cluster states for different values of  $T$ : (a)  $T = 0^\circ\text{C}$ , (b)  $T = 5^\circ\text{C}$ , (c)  $T = 10^\circ\text{C}$ , (d)  $T = 15^\circ\text{C}$ , and (e)  $T = 20^\circ\text{C}$ . The system converges to high or low number of clusters depending upon the temperature. The number of clusters decrease with the increasing temperature. Local dynamics are governed by  $\theta = 0.3$ ,  $\eta = 1$ , and  $\phi = 3$ . Dispersal strengths are  $\epsilon_h = 2^{-5}$  and  $\epsilon_p = 2^{-6}$ . Each panel is the result of 100 independent simulations.

of species persistence. It is observed from Fig. 5(a) that both transient and asymptotic MPA hold lower value at low temperatures and comparatively higher value at intermediate temperature. On a related note, we also calculate mean transient fraction [see Fig. 5(b)], high



**FIG. 4.** Synchrony measure  $\sigma$  with changing  $T$ . The triangles represent the estimated value of  $\sigma$  at different values of  $T$ . The solid line is the best curve fit to the estimations. The other parameters are  $\epsilon_h = 2^{-10}$ ,  $\epsilon_p = 2^{-10}$ ,  $\phi = 2$ ,  $\eta = 1$ , and  $\theta = 0.3$ .



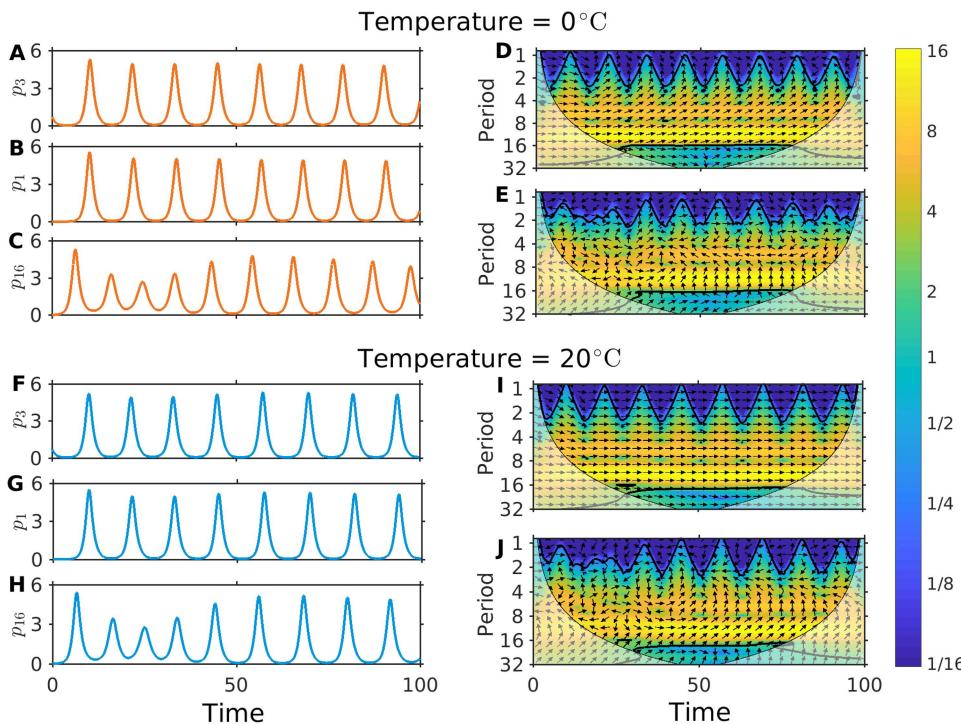
**FIG. 5.** Median predator amplitude and transient duration. (a) Median predator amplitude for the transient (red) and asymptotic (blue) solution values of  $T$ . (b) Mean fraction of the total time duration the system remains in the transient solutions with respect to temperature  $T$ . Parameter values are  $\theta = 0.3$ ,  $\eta = 1$ ,  $\phi = 3$ ,  $\epsilon_h = 2^{-5}$ , and  $\epsilon_p = 2^{-6}$ .

value of transient time corresponds to asynchronous solutions. We notice that the transient time is high around low temperatures and decreases with the increasing temperature. Hence, increasing temperature up to the thermal optimum drives the system from long transients and low amplitude solutions to lower transients and higher amplitude solutions.

### E. Cross-wavelet analysis

Wavelet analysis can be helpful to quantify and interpret powerful informations stored in the transient state.<sup>49</sup> In order to study the interactions between different time series and to understand how the behavioral state changes in a given time period, we perform cross-wavelet analysis (see Fig. 6). Black contour lines enclose a region of 95% confidence level. Wavelet transform at any point at a given time also contains information of the nearby data points and since we have considered time series of finite length, there are chances of error at the beginning and end of the time series, known as the edge effects. Cone of influence is the region of the power spectrum where edge effects might distort the signal and which is represented by the shaded region on both sides of the contour. Therefore, we confine our study to the nonshaded regions.

In accordance with the cross-wavelet analysis, the density fluctuations between predator species of two distinct patches with high common power (yellow band) is observed at a considerable periodicity of 8–16 units of time. To study the coordination between predator species of two distinct patches, we analyze the phase shift between them. At the extreme temperature  $T = 0^\circ\text{C}$ , the arrows in the eloquent common power (yellow band) reflect a phase difference of  $\approx 30^\circ$  between the fluctuations in predator density of the two nearest patches, i.e.,  $p_1$  and  $p_3$  (we consider those nearest patches where  $d$  is not equal to 1) [see Fig. 6(d)]. On the other side, a phase shift of  $\approx 90^\circ$  is observed between the fluctuations of predator species of two farthest patches, i.e.,  $p_1$  and  $p_{16}$  [see Fig. 6(e)]. When analyzed the dynamics at the thermal optimum  $T = 20^\circ\text{C}$ , the phase angle is centered around  $0^\circ$  for the predator species of nearest patches



**FIG. 6.** Time series (left panels) and cross-wavelet spectra (right panels) of the predator  $p_i$ . For two distinct temperatures: (a)–(c)  $T = 0^\circ\text{C}$  and (f)–(h)  $T = 20^\circ\text{C}$  are the time series of predator density  $p_i$ , where  $i = 1, 3, 16$  is the patch index, in three distinct patches. (d) and (i) Cross-wavelet spectra of the predator in two nearest patches  $p_1$  and  $p_3$ . (e) and (j) Cross-wavelet spectra of the predator in two farthest patches  $p_1$  and  $p_{16}$ . At  $T = 0^\circ\text{C}$ , in the case of nearest patches [(a), (b), and (d)], the predator species oscillates in phase angle of  $\approx 30^\circ$ ; for the farthest patches [(b), (c), and (e)], interactions lead to different phase angles ( $\approx 90^\circ$ ). At  $T = 20^\circ\text{C}$ , species in the nearest patches oscillate in phase, i.e.,  $0^\circ$  [(f), (g), and (i)]; in the case of farthest patches [(g), (h), and (j)], predator species show a phase drift of  $\approx 45^\circ$ . The black contour in cross-wavelet spectra encloses significant region (95% confidence level) of consideration. The color code follows a pattern from blue to yellow; blue color indicates the region with low power, whereas the yellow region is with high power. Other parameter values are  $n = 33$ ,  $\theta = 0.3$ ,  $\eta = 1$ ,  $\phi = 3$ ,  $\epsilon_h = 2^{-5}$ , and  $\epsilon_p = 2^{-6}$ .

[see Fig. 6(i)], whereas the fluctuations between two predator species of farthest patches show a phase drift of  $\approx 45^\circ$  [Fig. 6(j)].

#### IV. DISCUSSION

Understanding the effects of dispersal on population dynamics is one of the major issues in the spatial ecology. Dispersal is considered to be a “double-edged sword,”<sup>54</sup> since dispersal not only contributes toward species persistence by preventing local extinctions due to recolonization, but at some time, it can also be responsible for synchronizing the populations that can trigger the possibility of global extinction. The realization that the changing climate has a strong impact on spatial populations, communities and the whole ecosystems triggered a lot of interest on investigating the effects of temperature influenced dispersal on metapopulations.<sup>27,55</sup> Here, we have presented a mathematical-framework elucidating the effects of temperature on species dispersal. This framework illustrates how the dispersal strength that promotes synchrony at a temperature results in some form of ecological stability at a different extreme temperatures via asynchrony.

Range or habitat shifts are one of the natural ecological responses to climate change. When the temperature is not favorable,

i.e., at extreme temperatures, we have claimed interaction strength to be low which corresponds to low species dispersal, hence the intensity of LDD is low. This persuades asynchronous behavior of the population at the extreme temperatures. While at the intermediate temperatures, due to active biological traits of species, dispersal is more prompt, which makes a species efficient of going to any habitat patch. Thus, resulting in high intensity of SDD as well as moderate LDD. For instance, at the extreme temperatures, we get comparatively more number of clusters and low value of predator amplitude than that at the intermediate temperatures, which clearly depicts variations in the spatial dynamics. For different values of the temperature sensitivity  $s$ , the results are qualitatively similar. We have also observed the change in measure of synchrony with the changing temperature. Our study indicates that the synchrony order parameter holds a low value at the extreme temperatures, when compared with the value at the intermediate temperatures, including the thermal optimum.

These results hold important implications in order to understand how temperature variations affect dispersal, which further has an impact on population persistence. We find that long-range dispersal at the extreme temperatures turns out to be beneficial for the species persistence. The asynchronous behavior of populations at

extreme temperatures signifies that the minimum densities of species occur at different time instance for most of the patches, thus making the dispersing species more persistent by reducing their vulnerability toward environmental perturbation.

We also emphasize on the importance of understanding dynamics during the transient time. Corresponding to which we study the behavior of MPA differently for transient as well as asymptotic phase. The lower amplitude asymptotic solutions with higher transient duration at low temperatures [see Figs. 5(a) and 5(b)] reveal the asynchronous behavior of the system. Our study clearly demonstrates how dispersal in a regular network under the influence of increasing global temperature drives the system from asynchrony to synchrony, and to asynchrony.

Further, our study interprets the effects of climate warming on species dispersal, influencing their persistence. In view of the better understanding of evolution of such dynamics, we figure out the interactions between species of distinct patches at different temperatures through cross-wavelet analysis of few transient time series. At the extreme temperature  $T = 0^\circ\text{C}$ , the cross-wavelet analysis explores the asynchrony between the species oscillations of two nearer patches; however, the degree of asynchrony becomes stronger when we consider two further patches. This is due to the fact that the dispersal strength becomes weaker between furthest patches which results in stronger asynchrony, in comparison with the asynchrony between nearer patches. Similarly, at the optimum temperature  $T = 20^\circ\text{C}$ , we see almost synchrony in species oscillations between two nearer patches and the degree of synchrony reduces when we consider two furthest patches. In conifirmy with the phase shifts observed at  $T = 0^\circ\text{C}$  between the fluctuations of predator species of nearer and farthest patches, we state that the intensity of SDD is much more than that of LDD. On another note, based on the analysis of phase shifts at  $T = 20^\circ\text{C}$  by examining our results (Figs. 3 and 6), we claim that at intermediate temperatures, the species are resilient toward long-distance dispersal as well.

In conclusion, our study is the first step to demonstrate dispersal-temperature relationship from the perspectives of dynamical systems. We have considered a uniform model with a difference in dispersal strengths of prey and predators in each patch. Developing more mechanistic models elucidating temperature effects on dispersal by taking into account heterogeneity in the structure, and also considering intraspecific competition, which are equally substantial for the survivorship of species, is an important future direction. Further, the assumption that different species are having different temperature sensitivity may reveal interesting result. It is also important to study the dynamics of the spatial system where temperature is a function of time. This can be done by considering increase in temperature at a very slow rate (global warming<sup>56</sup>) or by assuming a periodic function (to model seasonality<sup>29</sup>). Moreover, there is a need to understand the influence of climate change on both the local and spatial ecological processes simultaneously and the long term dynamics driven by their mutual interactions.

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