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The Role of Between-Patch Dynamics in a Metapopulation: A Discrete-Time Modelling Approach

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Abstract We present a single-species metapopulation model structured by population size that is discrete in time. The novel formulation of our model allows for explicit incorporation of both the local, in space, dynamics and new details of the dispersal process. To study the impact of between-patch dynamics in the model, we construct various functions to describe density-dependent dispersal, recolonization, and between-patch stochasticity. Due to the complexity of the model, numerical simulations are used to obtain the distribution of the metapopulation. Moreover, we can use our model to predict the proportion of patches occupied, expected patch density, and variance in patch density. Our results provide insight into the influence that each of these processes play in the distribution of the metapopulation. In particular, our findings emphasize the benefit of explicitly modelling these processes. We consider two density-dependent dispersal strategies based upon individuals wanting to form average sized patches and illustrate the differences in the metapopulation distributions. For recolonization of empty suitable patches, we look at two simplistic redistribution strategies modeled as either a continuous uniform or Laplace distribution. The between-patch stochasticity is modelled using redistribution kernels where we consider both thin-tailed and fat-tailed kernels.

Keywords Metapopulation, integrodifference equations, dispersal, recolonization, stochasticity

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1 Introduction

Models for metapopulation dynamics have a rich history dating back to the original single-species model proposed by Levins (Levins, 1969b,a). Many subsequent studies on single-species metapopulation dynamics realized the limitations of the Levins model and have incorporated more biological complexity (Levin and Paine, 1974; Hastings and Wolin, 1989; Gyllenberg and Hanski, 1997; Hanski, 1998). All of these models are continuous in time and assume a large, essentially infinite, number of local populations. An alternate approach (Hastings, 1993; Gyllenberg et al., 1993; Gonzalez-Andujar and Perry, 1993) of looking at the dynamics of two local populations connected by dispersal in discrete-time leads to different analyses and results. The primary outcome of these studies found that the interaction of dispersal between patches can drive chaotic local dynamics into periodic dynamics suggesting that dispersal can have a stabilizing effect on the metapopulation dynamics. This agrees with previous work on patch modelling where the stabilizing role of dispersal arises from the inherent stochasticity in the dynamics (Hanski, 1991; Hastings, 1991). What has been missing are analyses of metapopulation models with asynchronous events with arbitrarily large numbers of local populations in discrete-time. This approach would both add biological realism and allow consideration of important biological processes.

One key issue is the effect of dispersal and colonization, encompassing both the exit from a local population and the entry into a different location. When habitat fragmentation causes local populations to become spatially isolated, a metapopulation is established and dispersal has been shown to be critical in the persistence and dynamics of the population (Dempster, 1991; Harrison et al., 1993; Ims and Yoccoz, 1997; Conradt et al., 2000). In particular, the recolonization of locally extinct patches by dispersal from other occupied patches is crucial for the persistence of the metapopulation (Hanski et al., 1996). Thus, in our considerations, we must not only have a detailed explanation for the dispersal strategy, but also for the recolonization strategy as another distinct process.

Dispersal of organisms may depend critically on the number of individuals in both the patch being left as well as the density in the patch to which the individuals disperse. This has been clearly demonstrated in careful studies (Serrano and Tella, 2003; Serrano et al., 2005) of dispersal dynamics in the Lesser Kestrel, *Falco naumanni*. Similarly, studies of the Blue-footed Booby, *Sula nebouxii*, have shown complex relationships between colony size and dispersal (Kim et al., 2009). A study of Audouin's Gull, *Larus audouinii*, (Fernández-Chacón et al., 2013) emphasized the size of the colony where migrants settle as a key factor in the choice to settle. Thus, a key feature of models for metapopulations is a detailed description of the dispersal process depending on local densities.

One key advantage of using a discrete-time model over a continuous-time model is biological realism. In particular, discrete-time models can match more closely to how observations and data collection are carried out, as well as corresponding to the discrete-time, often yearly, nature of reproduction in many organisms. The discrete-time framework is suitable for populations with different timescales between processes whereas continuous-time models are useful when the local and dispersal dynamics occur simultaneously. In addition to the avian examples of the previous paragraph, the Bay checkerspot butterfly, *Euphydryas editha bayensis*, (Harrison et al., 1988) the California spotted owl, *Strix occidentalis occidentalis*,

(LaHaye et al., 1994), and *Spartina alterniflora* (Decker and Hastings, 2020) are examples of species where the discrete-time modelling framework is better suited. The discrete-time approach will provide a link between simplifying assumptions in theoretical approaches to metapopulations and empirical data (Logue et al., 2011; Heino et al., 2015).

The discrete-time metapopulation modelling literature has been extended to include models of finite discrete-patch structure (Caswell and Cohen, 1991; Parvinen, 1999; Yakubu and Castillo-Chavez, 2002), evolution in the two-patch system (Holt and McPeek, 1996; Doebeli and Ruxton, 1997), and extensions to an infinite patch network (Parvinen, 2006, 2007). However, the discrete-time modelling framework has not received the same level of interest as its continuous-time counterpart. In this work, we aim to study a discrete-time metapopulation model with an infinite number of patches that is structured by local patch density. The model we consider has been studied previously where the focus was on the role of local, within-patch dynamics in the metapopulation distribution (Marculis et al., 2020). To emphasize the importance of the form of dispersal, we will fix the local dynamics in the model and vary the dispersal strategy, recolonization strategy, and between-patch stochasticity.

The complexity of structured populations can be incorporated into metapopulation models by considering the local populations as individuals and the local population as the metapopulation (Gyllenberg and Hanski, 1997). In these kinds of models, structure has been studied by considering the effects of local population size, patch quality, or patch age (Gyllenberg and Hanski, 1992; Levin and Paine, 1974, 1975; Hanski, 1985; Hastings and Wolin, 1989; Hastings, 1991; Hanski and Gyllenberg, 1993; Gyllenberg and Hanski, 1997). In this work, we construct a metapopulation model that structures the population according to a continuous variable describing the local population size. The goal of this endeavor is to better understand the role that between-patch dynamics play in a discrete-time metapopulation model structured by local patch density.

In this work, we develop an asynchronous discrete-time metapopulation model structured by local patch density. The upshot of our model is that the processes are explicitly defined and can be easily altered to fit data from a variety of different species. Rather than fitting our model to a specific species, we focus on the effects of changing the between-patch dynamics of density-dependent dispersal strategies, between-patch stochasticity, and recolonization of empty patches. Our model allows for explicit incorporation of these processes, and our results provide intriguing insights into how complex processes can influence metapopulation dynamics.

In the next section, we outline the mathematical model that is discrete in time but continuous in the state variable, which is a density function for the local population size. The model is broken down into two parts in order to easily comprehend how the within-patch and between-patch components interact with one another. The model is general and allows for a variety of functions describing the ecological processes; we describe a few that we will use in our numerical simulations in Section 2. The complication of the resulting integrodifference model (Lutscher, 2019) from a mathematical standpoint is that the kernel describing dispersal depends on the state variable, which is why our results are primarily numerical. Our results are presented in Section 3, where we provide figures illustrating how different types of dispersal strategies, recolonization strategies, and between-patch stochasticity

influence the metapopulation distribution. We conclude with a discussion of the results including limitations of the model and future directions.

2 Model

Integrodifference equations are discrete in time and are commonly used in theoretical ecology to model spatial spread of populations (Kot and Schaffer, 1986; Lutscher, 2019). These models were first developed with the continuous variable of interest being the population density at time t and location x. In recent years, integral projection models have been used to model demographic processes that are discrete in time and continuous in a variable other than space (e.g. size, age, or condition) (Ellner and Rees, 2006). In this study, we will use these discrete-time continuous-state models to study the metapopulation dynamics of a single species that is structured by local population density.

Our model will be split into two pieces; the within-patch dynamics and the between-patch dynamics that occur asynchronously. We assume that there are essentially an infinite number of patches equally spaced apart which allows us to treat space as an implicit feature of this model. In addition, because of the infinite patch assumption, stochasticity can be modelled as a deterministic process using redistribution kernels. There are two main processes for the within-patch dynamics: density-dependent reproduction f, and the within-patch stochasticity k_g. For the between-patch dynamics there are three main processes: density-dependent dispersal strategy d, the between-patch stochasticity k_d, and recolonization of empty patches k_r. A schematic diagram is provided in Figure 1 to illustrate the main components of our model.

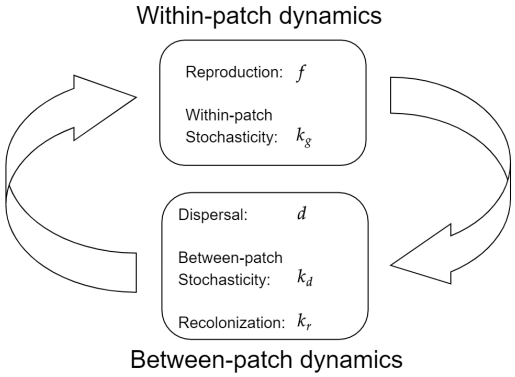

Fig. 1 A cartoon of the main dynamics in our model is illustrated here. The dynamics are broken down into two components, the within-patch dynamics and the between-patch dynamics. The within-patch dynamics are modeled by (1) and given by the top box in the figure. The between-patch dynamics are modeled by (2) and given by the bottom box in the figure.

The model that we consider has already been formulated in a previous study (Marculis et al., 2020). In our previous work, we studied the role that local dynamics play in the metapopulation distribution and persistence by fixing the between-patch dynamics. Here, we aim to address the remaining piece of understanding how

the between-patch dynamics influence the metapopulation dynamics. For completeness, we will describe the model components in full detail. Let $p_t(x)$ be the density function for the fraction of patches in the metapopulation that have x individuals at time t. Then the proportion of occupied patches is given by $\int_0^\infty p_t(x)\,dx$ and is always less than or equal to one. One can obtain the probability density function for the fraction of occupied patches by normalizing $p_t(x)$. We consider the two events of within-patch and between-patch dynamics separately. The local reproduction dynamics are density-dependent denoted by f and the within-patch stochasticity is a redistribution kernel k_g. A patch with local density z can become a patch with density y through an iteration of local reproduction and redistribution, that is $k_g(y, f(z))$. The within-patch dynamics are then given by

$$\tilde{p}_{t+1}(y) = \int_0^\infty k_g(y, f(z))p_t(z)\,dz. \tag{1}$$

We can interpret $\tilde{p}_{t+1}(y)$ as the distribution of local densities y after the within-patch dynamics but before the dispersal occurs, and $1-\int_0^\infty \tilde{p}_{t+1}(y)\,dy$ is proportion of patches that have density zero after the within-patch dynamics.

Next, we describe the second step in our model that considers the between-patch dynamics. There are three processes during this step as outlined in Figure 1: The density-dependent dispersal strategy, d, the between-patch stochasticity, k_d, and recolonization of empty patches, k_r. A patch with local density y can become a patch with density x through an iteration of dispersal and redistribution, that is $k_d(x, d(y))$. In addition, empty patches can become occupied at local density x from a patch with local density y according to the redistribution kernel, $k_r(x, y)$. The between-patch dynamics are then given by

$$\begin{aligned} p_{t+1}(x) = &\int_0^\infty k_d(x, d(y))\tilde{p}_{t+1}(y)\,dy \\ &+ \left[1 - \int_0^\infty \tilde{p}_{t+1}(y)\,dy\right] \int_0^\infty k_r(x, y)\tilde{p}_{t+1}(y)\,dy \end{aligned} \tag{2}$$

where the kernel now depends local density levels (Lutscher, 2008). The first term describes how the individuals in the metapopulation disperse, while the second term gives the dynamics for recolonization into patches that are currently unoccupied. The redistribution kernels k_g, k_d, and k_r each describe how the distribution of local patch densities change. This formulation allows for explicit modelling for the local reproduction dynamics and global dispersal dynamics. In what follows, we consider a variety of examples for the metapopulation dynamics.

2.1 Within-patch dynamics

The first step in our model is given by (1) and considers the within-patch dynamics of the local populations. In all of our simulations, to focus on the importance of the between-patch dynamics in the model, we will fix the local dynamics to have Gaussian noise and Beverton-Holt reproduction. That is,

$$k_g(y, f(z)) = \frac{1}{\sqrt{2\pi\sigma_g^2}} e^{-\frac{(y-f(z))^2}{2\sigma_g^2}} \tag{3}$$

where σ_g is the standard deviation of reproduction and

$$f(z) = \frac{Rz}{1 + \frac{(R-1)}{K} z} \tag{4}$$

where R is the growth rate, and K is the carrying capacity of the local population. Note that (3) is defined over $\mathbb{R}$ while the integration in (1) is over $\mathbb{R}^+$. This allows for some patches to be lost due to the within-patch stochasticity. In our simulations, we hold constant the parameter values to be $\sigma_g = 0.1$, $R = 5$, and $K = 1$. We choose σ_g small as to focus on the role of between-patch stochasticity, R to be large so we do not worry about metapopulation persistence, and K to be small so the recolonization step can play a role in the metapopulation distribution.

2.2 Between-patch dynamics

Recall from our model formulation that there are three main processes in (2): the density-dependent dispersal strategy, the between-patch stochasticity, and the recolonization of empty patches. For each of these three processes, we will consider two different examples of reasonable functions. In the next section, our results focus on the difference between the choice of functions used in the between-patch dynamics.

We start our description with the dispersal strategies. Let Y be a random variable that is distributed by the normalized density of $\tilde{p}_{t+1}(y)$, then the expected density of dispersers across all patches is

$$E[\alpha Y] = \alpha \int_0^\infty \frac{y\tilde{p}_{t+1}(y)}{\int_0^\infty \tilde{p}_{t+1}(y)\, dy}\, dy, \tag{5}$$

where $0 < \alpha < 1$ is the fraction of individuals expected to disperse. We consider two different dispersal strategies based around the assumption that individuals are social and prefer to be in groups (Kurvers et al., 2014). Our first strategy describes how a grouping of small patches can propagate into average sized patches. We assume that populations with above-average densities tend to remain in patches with similar density levels, thus if $y \geq E[\alpha Y]$ we would expect them to disperse according to their density y. However, when $y \leq E[\alpha Y]$, the population would disperse to patches with higher density according to the expected dispersal density. In this case, the dispersal strategy can be represented as

$$d(y) = \max\{y, E[\alpha Y]\}. \tag{6}$$

The second strategy we consider is one that also attempts to produce average size patches. Consider that populations disperse in such a way that they produce average sized patches, then we would expect $d(y) = E[\alpha Y]$ for all y. However, for small patches, there may not be enough members to disperse and produce an average sized patch, while for big patches, not enough members would be able to disperse in order to reduce the patch density to average. This behavior can be described by a shift that follows a logistic distribution with mean $E[\alpha Y]$ and scale parameter γ from the carrying capacity of the local populations. Then we get that,

$$d(y) = E[\alpha Y]\left(K + \frac{e^{-\frac{y-E[\alpha Y]}{\gamma}}}{\gamma\left(1+e^{-\frac{y-E[\alpha Y]}{\gamma}}\right)^2}\right). \tag{7}$$

A visual comparison between the two dispersal strategies is provided in Figure 2. The value $E[\alpha Y]$ alters where the sharp bend occurs in the max strategy. The quantity $KE[\alpha Y]$ determined the location for the peak of the logistic strategy. Finally, γ is the scale parameter for the logistic strategy. That is, the larger the value of γ, the more spread out the curve becomes.

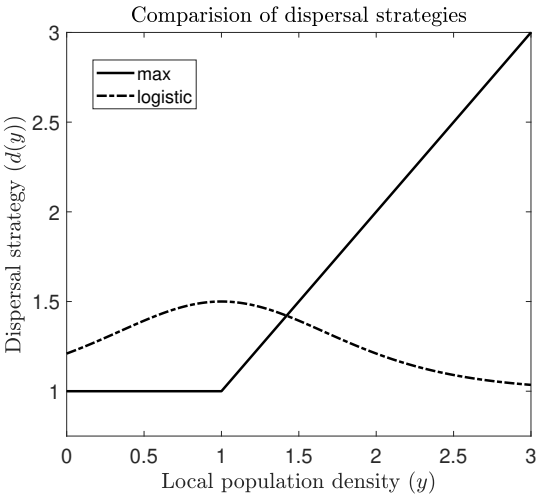

Fig. 2 Examples of the two dispersal strategies for parameter values $E[\alpha Y] = 1$, $K = 1$, and $\gamma = 0.5$. The dispersal strategy given by (6) is given by the solid line labeled max, and the dispersal strategy given by (7) is given by the dash-dot line labeled logistic.

Throughout this work we assume the redistribution kernel takes one of two forms. The first form is a thin-tailed Gaussian kernel given by

$$k_d(x, d(y)) = \frac{1}{\sqrt{2\pi\sigma_d^2}} e^{-\frac{(x-d(y))^2}{2\sigma_d^2}} \tag{8}$$

where σ_d^2 is the variance in the redistribution kernel. The second is a fat-tailed Cauchy redistribution kernel

$$k_d(x, d(y)) = \frac{1}{\pi b\left[1 + \left(\frac{x-d(y)}{b}\right)^2\right]} \tag{9}$$

where b is the scale parameter for the distribution. In (8) and (9) $d(y)$ is the density-dependent dispersal strategy for the local population with density y as described above.

The recolonization kernel k_r describes how patches with local density y colonize uninhabited patches at a local density of x. The simplest strategy is for the the individuals to be uniformly distributed from 0 to K where K is the carrying capacity of the growth function f. That is,

$$k_r(x,y) = \begin{cases} \frac{1}{K} & \text{if } 0 \le y \le K \\ 0 & \text{otherwise} \end{cases}. \tag{10}$$

Alternatively, we can let the redistribution kernel be a Laplace distribution. The form of the kernel is given by

$$k_r(x,y) = \frac{1}{2\lambda} e^{-\frac{|x-y-\mu|}{\lambda}} \tag{11}$$

where λ is the scale parameter and μ is the mean. Throughout our analyses, we assume that $\mu = 0$. This means that individuals are most likely to recolonize at the same density from which they originated.

With all the assumptions made above, the model becomes

$$\tilde{p}_{t+1}(x) = \int_0^\infty \frac{1}{\sqrt{2\pi\sigma_g^2}} e^{-\frac{\left(x - \frac{Ry}{1+\frac{R-1}{K}y}\right)^2}{2\sigma_g^2}} p_t(y)\,dy \tag{12}$$

$$\begin{aligned} p_{t+1}(x) = &\int_0^\infty k_d(x, d(y))\tilde{p}_{t+1}(y)\,dy \\ &+ \left[1 - \int_0^\infty \tilde{p}_{t+1}(y)\,dy\right] \int_0^\infty k_r(x,y)\tilde{p}_{t+1}(y)\,dy \end{aligned} \tag{13}$$

where the local within-patch dynamics are given by (12) and the between-patch dynamics are given by (13). Throughout this section, as indicated earlier, we will not alter (12) and fix the parameter values $R = 5$, $K = 1$, and $\sigma_g = 0.1$. This way we can focus on the effects of altering the dispersal strategy. In particular, we will center our attention to the three main dispersal processes; dispersal between occupied patches, recolonization of empty patches, and the between-patch stochasticity.

In the next section, we will vary the three different aspects of the between-patch dynamics to understand how each component plays a role in the metapopulation distribution. We will alter the form of the density-dependent dispersal strategy $d(y)$ in two different ways as given by (6) and (7). We will alter the functional form of k_d that will account for the between-patch stochasticity considering two different types: a thin-tailed Gaussian kernel (8), and a fat-tailed Cauchy distribution (9). Finally, we will consider two recolonization strategies. The first being that individuals recolonize uniformly in patch densities from zero to the carrying capacity K (10). The second will be a Laplace distribution with mean zero suggesting that individuals are most likely to colonize at the same density from which they originated (11).

3 Results

In this section, we will focus on how altering the between-patch dynamics in the model influence the metapopulation dynamics. In particular, we will keep the local dynamics the same across all simulations. Throughout this section, we will not alter (12) and fix the parameter values $R = 5$, $K = 1$, and $\sigma_g = 0.1$. This way we can focus on the effects of altering the dispersal strategy. In particular, we will center our attention to the two main dispersal processes; dispersal between occupied patches and recolonization of empty patches. Due to the nonlinear complexities in the redistribution kernels, our results are purely numerical. To iterate our simulations, we rely on the classical quadrature methods. All numerical simulations presented in this work were preformed in MATLAB using Simpson's rule. To deal with the semi-infinite integration, we truncated the upper bound to be twice the size of the region of interest.

The distribution of the metapopulation can be summarized by using some common statistics. First, we calculate the proportion of patches occupied at time t, $P(t)$. This is achieved by integrating the metapopulation distribution over all possible local densities,

$$P(t) = \int_0^\infty p_t(x)\,dx. \tag{14}$$

The second calculation gives the expected patch density at time t, $E(t)$. This is calculated by integrating the metapopulation distribution multiplied by the population density over all possible local densities,

$$E(t) = \int_0^\infty \frac{x p_t(x)}{\int_0^\infty p_t(x)\,dx}\,dx. \tag{15}$$

We can also compute the variance in patch density at time t, $V(t)$. This calculation is done in the following way

$$V(t) = \int_0^\infty \frac{(x - E(t))^2 p_t(x)}{\int_0^\infty p_t(x)\,dx}\,dx \tag{16}$$

where $E(t)$ is the expected patch density from (15).

We start with looking at the difference between the two density-dependent strategies for dispersal between occupied patches as outlined by (6) and (7). From Figure 3, we can begin to understand how the parameter α impacts the density-dependent dispersal strategies for the metapopulation distribution. When the expected number of dispersers is small, the dispersal strategy given by (6) shows a relatively normal distribution for the metapopulation centered about the carrying capacity. However, for the logistic dispersal strategy, the metapopulation distribution is heavily skewed toward very low local density levels suggesting that the recolonization strategy plays an important role in the metapopulation distribution. When half of the individuals are expected to disperse, as seen in the middle plot of Figure 3, the logistic dispersal strategy appears to give a lower mean value and less variation for the metapopulation distribution. For high levels of dispersers, as seen in the right plot of Figure 3, the distributions look the most similar with the logistic distribution appearing to have a slightly larger mean value and lower variance. We also observe that varying the expected fraction of individuals disperse does

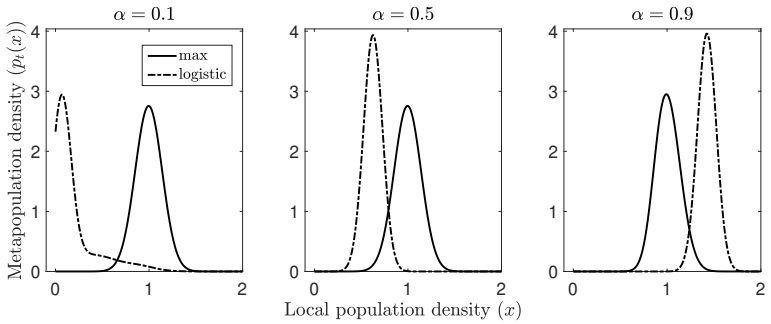

Fig. 3 In this figure we plot the metapopulation density at $t = 1000$ for three different values of the expected proportion of dispersers, $\alpha = 0.1, 0.5$, and 0.9, and for two different density-dependent dispersal strategies, max (6) (solid), and logistic (7) (dash-dot) with $\gamma = 0.5$. The between-patch stochasticity is Gaussian with $\sigma_d = 0.1$, and the recolonization strategy is given by (11) with $\lambda = 0.1$.

not appear to affect the metapopulation distribution when the dispersal strategy given by (6) is used.

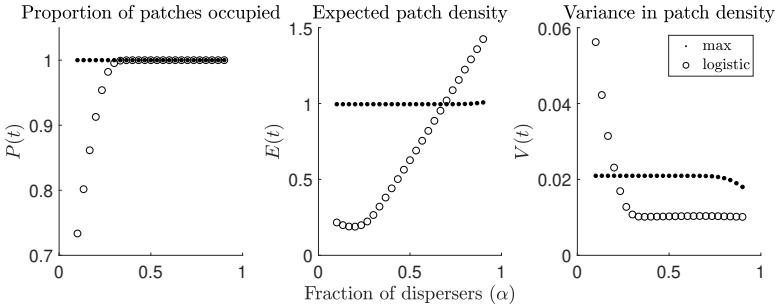

Fig. 4 In this figure we plot the proportion of patches occupied $P(t)$, the expected patch density $E(t)$, and the variance in patch density $V(t)$ at $t = 1000$. Within each plot, we calculate the three quantities for the two density-dependent dispersal strategies (6) (dots) and (7) (open circle) with $\gamma = 0.5$ for varying values of the fraction of individuals expected to disperse, α. The between-patch stochasticity is Gaussian with $\sigma_d = 0.1$ and the recolonization strategy is given by (11) with $\lambda = 0.1$.

In Figure 4 we vary the value of α, the fraction of individuals expected to disperse, and determine the proportion of patches occupied, the average patch occupancy, and the variance in patch occupancy. For the strategy given by (6) all patches are occupied when the population is persistent. For dispersal strategy (7) there is a linear increase in the proportion of patches occupied until all patches are occupied around $\alpha = 0.4$. This means that in order for all patches to be occupied, we need at least 40% of the population to disperse. The expected patch density is different for the two dispersal strategies. When the dispersal strategy is given by (6) the expected patch density is constant for $\alpha < 0.85$ and is equal to the carrying capacity $K = 1$ with a slight increase for larger α. When the dispersal strategy is given by (7) there is a linear increase in the expected patch density

once the population occupies all possible patches. Thus, for smaller values of α the expected patch density is smaller than K but then quickly exceeds K for larger α. In comparing the variance in the patch densities, we can see that both are nonincreasing with α. For values of $\alpha > 0.4$, the variance in patch density for dispersal strategy (6) is twice as large as (7). For the dispersal strategy given by (7) the variance in the patch density is equal to the variance in the dispersal strategy $\sigma_d^2 = 0.01$ for $\alpha > 0.4$ and decreases linearly up to that value.

Next, we discuss how the recolonization dynamics affect the metapopulation dynamics. We will use (6) for the dispersal strategy for $d(y)$ and let k_d be Gaussian with $\sigma_d = 0.1$. In our simulations, we vary the recolonization kernel k_r with the two kernels (10) and (11). In particular, we look at a uniform recolonization strategy and the other given by the Laplace distribution suggesting that individuals are most likely to recolonize at the same same density from which they originated.

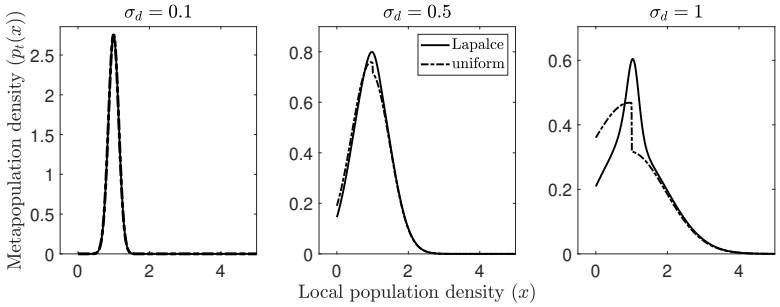

Fig. 5 In this figure we plot the metapopulation density at $t = 1000$ for three different values of the standard deviation of dispersal, $\sigma_d = 0.1, 0.5$, and 1, and for two different recolonization strategies, Laplace (11) (solid) with $\lambda = 0.1$, and uniform (10) (dash-dot). The between-patch stochasticity is Gaussian, and the density-dependent dispersal strategy is given by (6) with $\alpha = 0.5$.

In Figure 5, we plot the distribution of the metapopulations where we consider two different recolonization strategies given by a Laplace distribution and a uniform distribution. We also vary the standard deviation of dispersal σ_d to see how the metapopulation distribution is altered. In the left plot of Figure 5, the metapopulation distributions are identical because recolonization does not occur with such a small deviation in dispersal. As we increase σ_d, the variance in the metapopulation distribution increases as expected. For the Laplace recolonization kernel the metapopulation distribution remains smooth where as the uniform recolonization kernel creates a metapopulation distribution where there is a small jump in the distribution at the carrying capacity $K = 1$. As the standard deviation of dispersal becomes large as illustrated in the right plot of Figure 5, we observe that the recolonization events become more prevalent. The jump in the metapopulation distribution for the uniform recolonization strategy is accentuated. We observe in all three plots of Figure 5 that for large values of the local population density that the distributions of the metapopulation are the same because at these high density levels the recolonization does not impact the metapopulation density.

The three summary statistics for the different recolonization strategies is illustrated in Figure 6. In the left plot of Figure 6, we see that at low levels of

the standard deviation of dispersal, σ_d, that all patches are occupied for both recolonization strategies. As the standard deviation of dispersal increases, the proportion of patches occupied decreases for both recolonization strategies with the uniform recolonization yielding slightly fewer patches occupied in comparison to the Laplace recolonization strategy. The center plot of Figure 6 shows the expected patch density for the two recolonization strategies. First, it is clear that the expected patch density is larger for the Laplace recolonization strategy as compared to uniform recolonization for $\sigma_d > 0.4$ and is the same for $\sigma_d < 0.4$. For $\sigma_d < 0.4$ the expected patch density decreases and increases after the Laplace recolonization strategy. The uniform recolonization strategy shows the expected patch density to decrease for $\sigma_d < 0.5$. The variance in patch density is given in the right plot of Figure 6. Both strategies show an increasing tend in the variance as the standard deviation of dispersal increases. For larger values of σ_d, the variance in patch density is slightly larger for the uniform recolonization strategy as compared to the Laplace recolonization strategy. Overall, it appears that the recolonization strategy does not alter the three calculations in an extensive way.

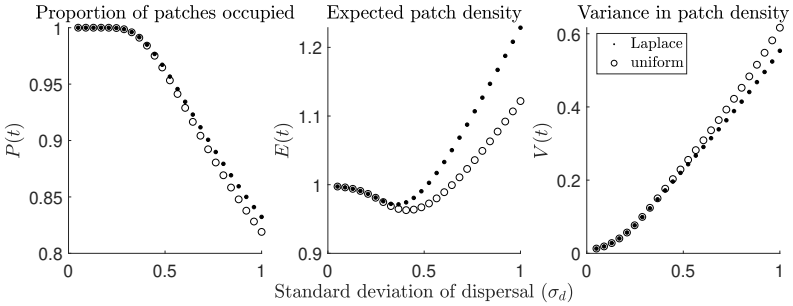

Fig. 6 In this figure we plot the proportion of patches occupied $P(t)$, the expected patch density $E(t)$, and the variance in patch density $V(t)$ at $t = 1000$. Within each plot, we calculate the three quantities for the two recolonization strategies (11) (dots) and (10) (open circle) with $\gamma = 1$ while varying the standard deviation of dispersal, σ_d. The between-patch stochasticity is Gaussian with $\sigma_d = 0.1$ and the dispersal strategy is given by (6) with $\alpha = 0.5$.

To conclude, we compare two different kinds of between-patch stochasticity with Gaussian (8) and Cauchy (9) redistribution kernels. By plotting the metapopulation distribution, we can compare the probabilities that a given patch will have a certain local population density level. Given that the Cauchy distribution has no standard deviation, setting $\sigma_d = b$ is not a good comparison between distributions. To make a sound comparison, we use the median absolute deviation. In particular, we selected a value for σ_d and found the value of b that made the two redistribution kernels have the same median absolute deviation. When the scale parameters are small, $\sigma_d = 0.1$ and $b = 0.0674$, we observe in the left plot of Figure 7 that Gaussian stochasticity predicts a higher probability for patches to have density levels about the carrying capacity; whereas, the Cauchy stochasticity has higher density levels at lower and higher densities. For intermediate scale parameters, $\sigma_d = 0.5$ and $b = 0.337$, the metapopulation distribution is altered as seen in the middle plot of Figure 7. The Cauchy stochasticity predicts more patches to have densities about the carrying capacity and for high local density levels. In the right plot of Figure

7, the metapopulation distributions for high values of the scale parameters, $\sigma_d = 1$ and $b = 0.674$, shows that the Cauchy stochasticity predicts higher probabilities when the local population density level is in a small interval about the carrying capacity and for high values of the local population density. A common theme is all three plots is that the Cauchy stochasticity predicts higher probabilities for large values of the local population density. This makes sense because of the fat-tails in the Cauchy distribution.

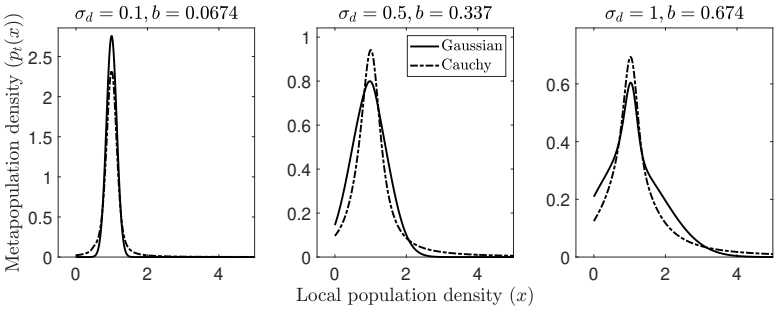

Fig. 7 In this figure we plot the metapopulation density at $t = 1000$ for three different values of the scale variables; that is, $\sigma_d = 0.1, 0.5$, and 1, and $b = 0.0674, 0.337$, and 0.674 from left to right. Within each plot, we draw the distribution for the Gaussian (solid) and Cauchy (dash-dot) redistribution kernels k_d. The density-dependent dispersal strategy is given by (6) with $\alpha = 0.5$ and the recolonization strategy is given by (11) with $\lambda = 0.1$.

To extend our understanding of the role that the between-patch stochasticity plays in the metapopulation distribution, we compute the proportion of patches occupied, the expected patch density, and the variance in patch density for varying values of the scale parameter in Figure 8. The left plot of Figure 8 shows how the proportion of patches occupied changes based on the value of the scale parameter for the between-patch stochasticity. We observe that for all values of the scale parameters the proportion of patches occupied is always larger when the between-patch stochasticity is Gaussian. For small values of σ_d all patches are occupied and decreases for $\sigma_d > 0.4$ for Gaussian stochasticity, whereas the Cauchy stochasticity has a decreasing trend for the proportion of patches occupied as the scale parameter, b, increases. In the center plot of Figure 8, we calculate the expected patch density. For small values of the scale parameter the expected patch density is approximately the carrying capacity. When the between-patch stochasticity is Cauchy, as the scale parameter increases, the expected patch density also increases. For Gaussian stochasticity, the expected patch density decreases slightly for $\sigma_d < 0.4$ and then increases past that point. The expected patch density is larger for all values of the scale parameter when the between-patch stochasticity is Cauchy. In the right plot in Figure 8, we determine the variance in patch density. It is clear that when the between-patch stochasticity is Cauchy the variance in patch density is always greater than when the between-patch stochasticity is Gaussian. We can also see that both curves are increasing as the scale parameters increase. Thus, in this example, fat-tails reduce the proportion of patches occupied, and increase the expected patch density and variance in patch density.

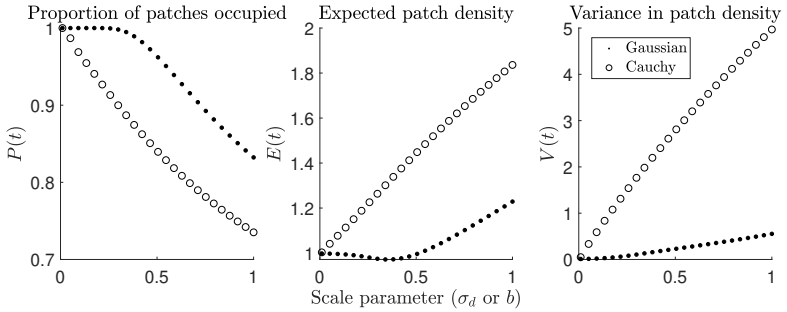

Fig. 8 In this figure we plot the proportion of patches occupied $P(t)$, the expected patch density $E(t)$, and the variance in patch density $V(t)$ at $t = 1000$. Within each plot, we calculate the three quantities for the Gaussian (dots) and Cauchy (open circle) redistribution kernels k_d for varying values of the scale parameters σ_g and b, respectively. The density-dependent dispersal strategy is given by (6) with $\alpha = 0.5$ and the recolonization strategy is given by (11) with $\lambda = 0.1$.

4 Discussion

The results presented in this work provide insight into how between-patch dynamics affect the distribution of a single-species metapopulation structured by local population size. Our results are purely numerical because of the complexity of the model. In particular, the non-linearities in the between-patch and within-patch redistribution kernels makes the model difficult to analyze. To begin making any analytical progress on the model one would need to simplify the model by removing the stochasticity. However, doing so would remove a critical component of our model. Our results focus on the roles of density-dependent dispersal, recolonization, and between-patch stochasticity by selecting different functional forms for each and varying parameters relating to these processes. The effects are summarized by plotting the stable metapopulation distribution and computing the proportion of patches occupied, expected patch density, and variance in patch density. The novelty of our model is that it is discrete in time which aligns with the processes seen in a number of real metapopulations (Harrison et al., 1988; LaHaye et al., 1994; Decker and Hastings, 2020).

The role of density-dependent dispersal is shown to have a major influence on the distribution of the metapopulation as seen in Figures 3 and 4. We constructed two different dispersal strategies centered around the concept that clustering will occur around average sized patches suggesting that individuals are social and prefer to be in groups (Kurvers et al., 2014). The proportion of individuals dispersing is observed to have a minimal effect on the density-dependent dispersal strategy given by (6) while the strategy given by (7) produces very different distributions based on the proportion of individuals dispersing. This exemplifies the previously known fact that the dispersal process of many individuals is closely tied with local density levels (Serrano and Tella, 2003; Serrano et al., 2005; Kim et al., 2009).

We find that the recolonization strategy does not influence the metapopulation distribution at large local population densities as indicated in Figure 5. However, the difference is exemplified for large values of the standard deviation in dispersal, due to a higher proportion of patches become unoccupied giving more importance to recolonization. It has been demonstrated in previous work that recolonization

is a key component for metapopulation persistence (Hanski et al., 1996) and the size of a colony is an important factor for where individuals settle (Kim et al., 2009). Thus, while this role may not have an immense effect on the distribution of the metapopulation, its importance may be observed in other aspects such as persistence and potentially in spatially explicit models.

We have shown that the thickness of the tail for the between-patch stochasticity kernel can impact the metapopulation density significantly. While the metapopulation distributions may not appear to the eye to be drastically different in Figure 7, the calculations in Figure 8 suggest differently. It is apparent that the fat-tailed kernel can decrease the proportion of patches occupied, and significantly increase the expected patch density and variance in patch density. This highlights the effect that fat-tailed kernels have on the metapopulation distribution suggesting that the tails of a probability distribution are important. This is exemplified at higher values for the scale parameter in the between-patch stochasticity. Gaussian kernels are thin-tailed are used to model random walks, but fat-tailed kernels are needed for events such as Lévy flights with a Cauchy distribution (Petrovskii et al., 2008). The intuition behind using a fat-tailed kernel for the between-patch stochasticity is that there is a small chance for individuals to deviate extremely from the norm (Clark et al., 2001). Previous studies have shown that fat-tailed long-distance dispersal in a statistically structured populations is a consequence that individuals of the same species are not identical (Petrovskii and Morozov, 2009) suggesting that fat-tailed kernels may be more prevalent in real populations than previously thought.

Although our model is quite general and can easily incorporate explicit functions for density-dependent dispersal strategies, recolonization strategies, and between-patch stochasticity, there are still a number of limitations that detract from its application to natural populations. To begin, the model only considers a single species. To include the interactions with other populations this scalar model could be extended into a system of equations for a metacommunity. The general framework of this model will follow naturally from our single-species model by using vector notation. In addition, our model makes the assumption that there are an infinite number of patches in the metapopulation. While this may be a reasonable assumption for metapopulations with a large number of local patches, and previous studies have considered a simplistic two patch system (Hastings, 1993; Gyllenberg et al., 1993; Gonzalez-Andujar and Perry, 1993), the dynamics for metapopulations with an intermediate number of patches remain uncertain. We do not consider spatially explicit populations and to increase the biological realism of our model, this would be a natural next step. This can be accomplished by including components such as habitat fragmentation (Peacock and Smith, 1997), distance between patches (Vuilleumier et al., 2007), and patch heterogeneity (Ovaskainen, 2002). As a final remark, the model does not include any explicit time-dependence. Incorporating time-dependence in the system could be a natural way of including the effects of global change (Thomas and Hanski, 2004) such as habitat degradation (Nee and May, 1992) and climate change (Anderson et al., 2009).

In the results presented in Section 3, we fix the local demographic components and vary the between-patch dispersal events. In our previous work, we did the opposite by fixing the between-patch dynamics and varying the within-patch dynamics (Marculis et al., 2020). However, variation of both components would lead to a deeper understanding of the model dynamics. Thus, there are still numerous

combinations of the functional forms in which we have still not considered. In addition, we only consider two different forms for the density-dependent dispersal strategy, recolonization strategy, and the between-patch stochasticity. While we chose these functional forms for the biological reasons indicated in the model section, there are still an endless number of other options one could choose. The upshot of this is that our model can be applied to approximate the dynamics in many natural systems by choosing an appropriate form for the within and between-patch dynamics.

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