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Original Research Article

Superdiffusivity due to resource depletion in random searches

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ABSTRACT

Animal search patterns are governed by the various movement strategies undertaken when animals encounter stimuli. The stimuli caused by resource growth and depletion can modify search patterns due to the need to finding resources. In this paper, we investigate the influence of resource depletion on the dynamics of dispersal of a population which is related to diffusion or anomalous diffusion. Our approach is to develop a population level model using partial differential equations that takes into account rules for movement based on the resource levels. Through numerical analysis, we show that the population dispersal patterns depend on the resource depletion, with superdiffusive spread in cases where the depletion rate (as given by high consumption and low replenishment) is high. This has the potential to increase searching efficiency.

1. Introduction

Consider an animal population that explores the environment by moving to nearby resource locations while avoiding places with resources depletion. The goal of each animal is to utilize the resource while minimizing energy output and maximizing search efficiency. To save energy the animal goes to nearby locations and, to increase efficiency in finding the resource, it prefers places where the resources are higher. In this way, the animal has to (i) locate nearby patches and (ii) avoid places with exhausted resources. For the first point, we consider a strategy of movement based on a localized dispersal kernel. For the second point, we consider a strategy where animals avoid places with low resource levels.

Studies of resource depletion and animal movement have questioned how the resource dynamics interact with the exploration patterns. Some studies deal with mechanistic models, often using individual based simulations (Hinsch et al., 2012; Reluga and Shaw, 2015; Avgar et al., 2016), while others include field observations (Lourenço et al., 2010; Merkle et al., 2014). Other approaches assume that individuals can use some marker other than resource levels, for instance spatial memory (Ramos-Fernandez et al., 2004; Winter, 2005; Mueller and Fagan, 2008; Van Moorter et al., 2009; Merkle et al., 2014; Berbert and Fagan, 2012; Vincenot et al., 2015; Grünbaum, 2012; Bracis et al., 2015; Potts and Lewis, 2016) or greed (Bhat et al., 2017a,b), to govern movement decisions.

In this paper, we define a mathematical model to analyze how the dynamics of resource depletion can induce an anomalous diffusion in localized random searches. The paper is organized as follows. The following subsections of this introduction present the rules and dynamics for movement and resource depletion. Section 2 shows the methods used, including the derivation of a non-dimensional model and its numerical analysis. In Section 3 we present our results. Finally, in Section 4 we discuss the results and present perspectives on future work. The Appendices contain the detailed development of our model as well as a linear stability analysis.

1.1. Movement and resource rules

Assume a disordered one-dimensional space explored by a population of many individuals who consume a resource and move randomly with a bias towards locations with high resource and away from locations with no or low resource. The resource depletion is established according to the rules of movement in the landscape. As individuals visit a location, they consume the resources in this location at a given rate.

Briefly, the individuals of a population perform a localized random walk, with a bias towards sites with higher resource levels. At each time interval Δt the individual must choose a single site. Per capita resource consumption occurs at rate α per unit of resource and the replenishment occurs exponentially in time. This

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means that the resource recovers at a rate $1/\mu$ according to a Poisson process, so the probability of recovering a resource location in time step of length Δt is approximately $\Delta t/\mu$. After the individual consumes the resource location x at time t_1, the probability of resource replenishment at location x at time $t > t_1$, is $1 - \exp[(t - t_1)/\mu]$.

1.2. Resource dynamics

Resource is consumed at rate α when an individual of a population visits a location and it recovers exponentially in time with rate $1/\mu$. We denote $u(x, t)$ to be the probability density function for the population and $r(x, t)$ to be the expected resource density distribution at location x and time t. Then the resource density at x after a time step of size Δt is given by (i) the r at x at time t, (ii) the consumption of r during time Δt, and (iii) the recovery of r during time Δt. These three elements are included in the following equation:

$$r(x, t+\Delta t) = \underbrace{r(x,t)}_{(i)} - \underbrace{r(x,t)u(x,t)\alpha\Delta t}_{(ii)} + \underbrace{(1-r)\frac{\Delta t}{\mu}}_{(iii)}. \tag{1}$$

Rearranging the terms, dividing by Δt and taking the limit of $\Delta t \to 0$, we obtain

$$\frac{\partial r}{\partial t} = -\alpha u \ r + \frac{(1-r)}{\mu}. \tag{2}$$

The first term on the right models the depletion, and the second models the replenishment to an asymptotic level of 1. We have dropped the (x, t) dependency for notational convenience, but keep in mind that resource and population densities depend on both space and time.

1.3. Movement dynamics

The probability density function for the population, $u(x, t)$, is dependent on the movement rules for individuals. To provide an expression for the dynamics of $u(x, t)$ we consider the probability of moving from a site at y to another at x, which is proportional to (i) the dispersal kernel $K(y - x;\Delta t)$ during the localized random search and to (ii) the probability that the site x has the resource r. A detailed development of this density distribution, given in Appendix A, shows that $u(x, t)$ evolves approximately according to:

$$\frac{\partial u(x,t)}{\partial t} = -\frac{\partial}{\partial x}\left[u(x,t)\left(2M_2\frac{\partial}{\partial x}\log[r(x,t)] - M_1\right)\right] + M_2\frac{\partial^2 u(x,t)}{\partial x^2}. \tag{3}$$

where M_1 is the infinitesimal first moment of the dispersal kernel describing the bias, and M_2 is the infinitesimal second moment of the dispersal kernel, in this case, the diffusion coefficient. Note that in the advective term of this equation there is a nonlinear coupling due to the resource density r. This is in terms of advection up gradients of $\log[r(x, t)]$. Observe that $\partial_x \log[r(x, t)]$ is a measure of the proportional change in resource with space, since it represents the relative variation of resource with space, $\partial_x(r)/r$.

The advection term with a log function appears from the normalization used in the transition probability for the random walk (see Appendix A). This normalization is necessary, since the transition probability varies at each step due to the resource consumption/recovery. Othmer and Stevens (1997) also have developed a similar normalization to define the dispersal of bacteria by chemotaxis. In that case, they have obtained partial differential equations for population of bacteria that move according to local environmental factors. Their work suggests that this kind of advection with a log function reveals that the bacteria possess a perception region to move (and to aggregate). In our model, it also shows that the individuals of a population can perceive the environment and use this information to decide their movement, in our case, moving towards locations with higher resources and avoiding places with resource depletion.

It is worth mentioning that, in our model, we are considering the movement but not the population growth dynamics. Thus, the total population size is constant on an infinite domain, or on a finite domain, providing there are zero-flux boundary conditions: $u(2M_2 d(\log(r))/dx - M_1) + M_2 du/dx = 0$ at $x = -L/2$ and $L/2$ where L is the length of the domain.

2. Methods

2.1. Nondimensional system

Our model depicted by Eqs. (2) and (3) specifies how the resource and the population vary with time. Before we analyze the system, it is convenient to reduce the number of parameters through adimensionalization. Therefore, we introduce the variables

$$\begin{aligned} \hat{x} &= \frac{x}{\sqrt{\mu M_2}} \\ \hat{t} &= \frac{t}{\mu} \\ \hat{u} &= u\sqrt{\mu M_2}. \end{aligned} \tag{4}$$

Thus, Eqs. (2) and (3) become

$$\frac{\partial r}{\partial t} = -\alpha\sqrt{\frac{\mu}{M_2}}ur + (1-r), \tag{5}$$

$$\frac{\partial u}{\partial t} = -\frac{\partial}{\partial x}\left[u\left(2\frac{\partial}{\partial x}\log(r) - M_1\sqrt{\frac{\mu}{M_2}}\right)\right] + \frac{\partial^2 u}{\partial x^2}, \tag{6}$$

where we have dropped the "hat" from x, t and u for convenience of notation. Observe that, now, the time scale is given by the resource depletion rate $1/\mu$ and the term related to diffusion now has unitary value. Since we focus on the effects of resource depletion on the population dispersal, we neglect the conventional advection by considering $M_1 = 0$. Note that, if M_1 is nonzero, there will be a bias to one direction, and it will hide the resource depletion effects we want to analyze. Therefore, we can consider only the effect of one parameter:

$$\beta = \alpha\sqrt{\frac{\mu}{M_2}}, \tag{7}$$

which quantifies the rate of resource depletion. Thus, our model is:

$$\frac{\partial r}{\partial t} = -\beta ur + (1-r), \tag{8}$$

$$\frac{\partial u}{\partial t} = -2\frac{\partial}{\partial x}\left[u\frac{\partial}{\partial x}\log(r)\right] + \frac{\partial^2 u}{\partial x^2}, \tag{9}$$

on a domain $x \in (-L/2, L/2)$ with boundary conditions $2udr/dx - du/dx = 0$ at $x = -L/2$ and $L/2$. We analyze these equations to understand the population dispersal dynamics dependence on resource depletion. We have also undertaken an analytical approach to evaluate the stability of spatially homogeneous solutions, which is in the Appendix B. In the next section we show our numerical analysis.

2.2. Numerical analysis

To numerically analyze the model, we used the MATLAB built-in solver “pdepe”. Because the patterns we found are unusual, we also validated the results with our own implementation using a finite difference scheme and the C++ language (not shown). We varied time t from 0 to 1 with time step $\Delta t = 0.01$, the rate of resource depletion β from 0.1 to 100. The one-dimensional space $x \in (-5, 5)$ was chosen to be large enough to avoid edge effects, with grid size of 10^{-4}. The initial condition for the population $u(x, 0)$ was given as a top hat function of height 10 and width 0.1 centered at the origin (with $\int_{-5}^{5} u(x, 0)dx = 1$), and 1 for resource ($r(x, 0) = 1$).

The quantity used to evaluate the population spread was the *reach of the population* $x_p(t)$, defined as the distance at which the population reached a lower threshold, which we choose to be $u(x_p(t), \; t) = 2 \times 10^{-5}$. Assuming symmetry of the population distribution with respect to the center, we numerically evaluate $x_p(t) > 0$. To compare with diffusive processes, we also obtained numerical solutions for the diffusion equation ($\partial_t u = \partial_{xx} u$) and its population reach $x_p(t)$.

3. Results

The pattern of spatial spread with resource depletion is significantly different than that for spread with simple diffusion. Fig. 1(a) shows the numerical solution for the population $u(x, t)$ for $t = 1$ and $\beta = \{1, 10, 100\}$, where $\beta = 0$ stands for diffusion only. Observe that both the reach and the spread pattern of the population distribution depends on β. For a small value of β, the population is concentred near the origin, but as this parameter increases, the spread also increases. We also observe the appearance of peaks in the edge of the distribution. We refer to them as *advective resource driven peaks* and they occur due to the advection induced by the resource r term from Eq. (9). The symmetric pattern, with respect to the origin, reveals that there is no other advection process inducing a bias in one direction of this spread. Comparing the population distribution for $\beta = 1$, 10 and 10^2 with the case for only diffusion ($\beta = 0$), we note that for small values of β, the population disperses in a manner similar to diffusion. As β increases, the advection due to the resource dynamics becomes an important factor. Fig. 1(b) shows how the population distribution varies with time for $\beta = 100$. We also show the resource density r with population density u in Fig. 1(c).

Observe that the population reach x_p is a concave down function of time, as shown in Fig. 2. The reach x_p shows a power-law dependence on time, as one can see in the in-set plot in Fig. 2. We fitted these curves for $t > 0.1$ to find the characteristic exponent m, so that

$$x_p \propto t^m. \tag{10}$$

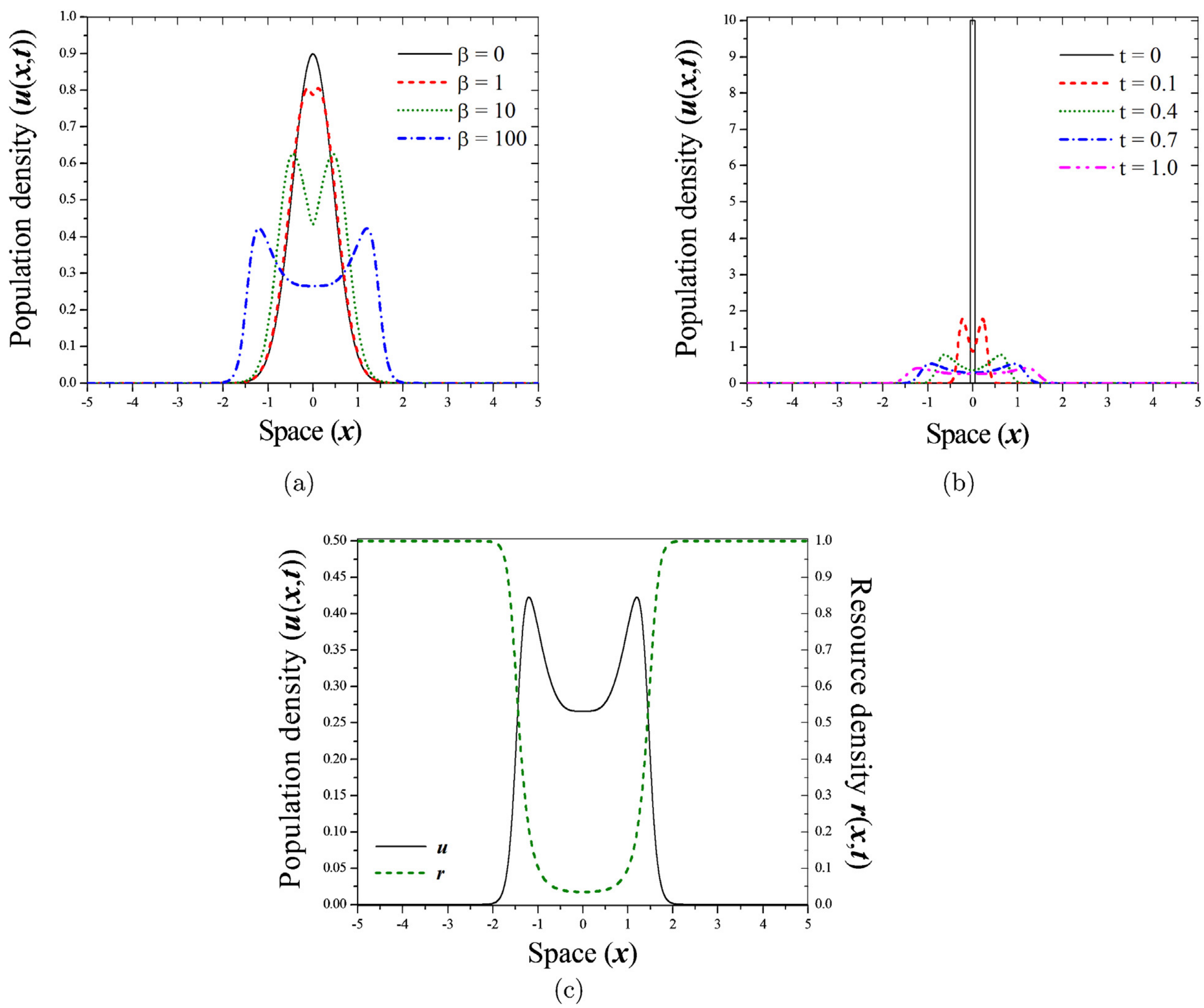

Fig. 1. Population density $u(x, t)$ for (a) $t = 1$ and $\beta = \{1, 10, 100\}$; and (b) $\beta = 100$ for a few values of time. (c) Population and resource densities for $t = 1$ and $\beta = 100$.

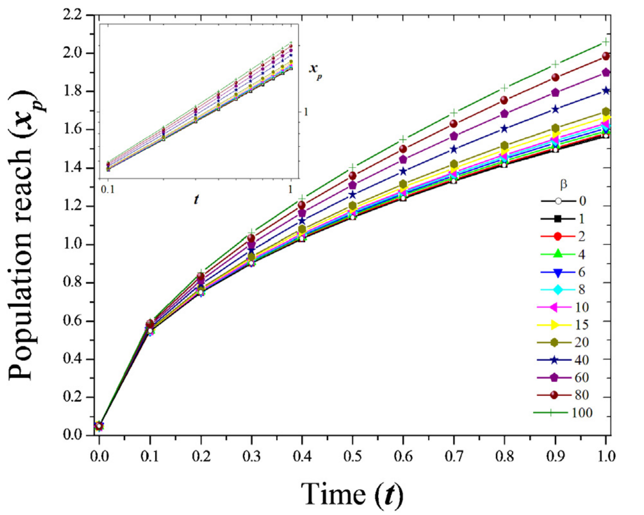

Fig. 2. Population reach x_p as function of time t for different values of β. Inset: Same data x_p as function of time t in a log-log scale, showing the power-law behavior.

Normal diffusive processes are characterized by a Gaussian distribution for the population density. The standard deviation of this distribution, which can represent the distribution reach, increases proportional to $\sqrt{t}$. Thus, for diffusion $m = 0.5$. In our model, we have $m \in (0.5, 0.6)$, which reveals the super-diffusive nature of this dynamics for large values for the strength of resource depletion β.

Fig. 3 shows the characteristic exponent m dependence on β. The model that best fits this curve is

$$m(\beta) = m_0 + a\ \log\left(\frac{\beta}{c} + 1\right), \tag{11}$$

where $m_0 = 0.5$ is the characteristic exponent for diffusion, $a = 0.135$ measures the sensitivity to resource depletion effects, and $c = 30$ is a scale factor. Using this equation in Eq.(10) yields

$$x_p \propto t^{m_0 + a\ \log(\beta/c+1)}. \tag{12}$$

To understand the effect of β on the dispersal, we considered four cases for our model dynamics:

1. $\beta = 0$: therefore $x_p \propto t^{m_0}$, and the population disperses only by Gaussian diffusion.

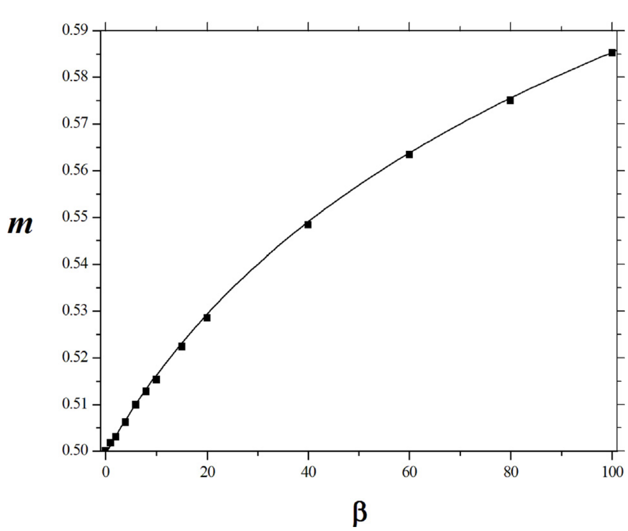

Fig. 3. Characteristic exponent m as function of β.

2. $\beta \ll c$: in this case $a\log(\beta/c+1) \approx a\beta/c \ll 1$. Therefore $x_p \propto t^{m_0}$ and the population disperses mostly by diffusion.
3. $\beta \approx c$: thus $a\log(\beta/c+1) \approx a\log 2$, and $x_p \propto t^{m_0 + a\log 2}$. Therefore, the population dispersal depends on the sensitivity a. For low values of a the dispersal is mostly diffusive, while for high levels of a the dispersal has a super-diffusive behavior.
4. $\beta \gg c$: for this case $x_p \propto t^{m_0 + a\log(\beta/c)}$, and the population has a super-diffusive behavior.

Therefore, c characterizes a crossover value for β that separates two distinct behaviors. For $\beta < 30$, the dispersal is mostly due to normal diffusion processes, and for $\beta > 30$, it has super-diffusive dispersal due to resource depletion effects.

Although we have focused on the movement of a population with individuals released near the centre of a region, we may also ask as to the behavior of a spatially solutions. Appendix B shows that the spatially solutions are stable to perturbations. In other words, the resource depletion effects will not lead to local aggregations in space.

4. Discussion

In this work we propose a model for the dispersal of populations of many individuals randomly exploring one-dimensional space and choosing their movements according to the resource levels. We established the rules for the movement and resource dynamics, and determined a system of partial differential equations for the spatial redistribution of the population. The numerical analysis of this system of equations has revealed that the dynamics is equivalent to either normal or anomalous diffusion (super-diffusion) depending on the strength resource depletion, which induces an advection in the population spread.

Explicitly, we consider a population with individuals who move via a redistribution kernel $K(y-x, \Delta t)$ restricted to the vicinity of the current location, with a preference for regions with resource density $r(x, t)$. The resource $r(x, t)$ itself is consumed in visited regions and recovers according to a Poisson process with parameter given by the replenishment rate $(1/\mu)$. Thus, if μ has a high value, then the resource density recovers slowly. This parameter μ can be interpreted as a time for a site become attractive again. Note that, with this model, individuals of this population seek to move to nearby positions, but move away from regions that have been recently exhausted.

We have translated the dynamic rules into a continuum model approach. The resource density $r(x, t)$ is described by Eq. (2), and the population density $u(x, t)$ is given by Eq. (3). Eq. (3) has a normal diffusion term and a term that contains an advective flow due to resource depletion. This term reveals that the population disperses away from regions with exhausted resources, expanding the explore new locations.

To evaluate our model, we have reduced the number of parameters by nondimensionalization and obtained the system given by Eqs. (8) and (9). This system has only one parameter, β, which characterizes the per capita rate of resource consumption per unit resource. Due to the intractability of an analytical approach, we have performed a numerical study and a stability analysis shown in Appendix B. We used the MATLAB built-in solver “pdepe” (Shampine and Reichelt, 1997) to evaluate the qualitative features of our model.

Our results show that both the reach and the spread pattern of the spatial distribution of the population depend on β (Eq. (7)). The analyzed quantity was the population reach x_p which increases with time according to a power law. The characteristic exponent m of this power law shows that for small values of β, the population disperses mainly by normal diffusion. For high values of β, the dispersal is given by an anomalous diffusion, the super-diffusion. An empirically derived connection between m and β is given in Eq. (11), and the implications for population reach are given by Eq. (12). Eq. (12) also includes two other characteristic parameters: a and c. The first represents the sensitivity of the resource effect. Biologically, it could be used to distinguish between animals species. The second, gives a crossover value for β that separates the dispersal behavior in diffusion and super-diffusion.

The classical diffusion occurs as described by the Gaussian dispersal term, whereas super-diffusion is induced by the resource depletion. Note that the resource effects occur only with respect to the movement of the population. Patterns of super-diffusion redistribution are also found through the use of other dispersal kernels, such as Levy flights (Viswanathan et al., 1999, 2011) which are distribution kernels with heavy tails. Other dynamics that show anomalous diffusion are given by models with non-Markovian random walks (Majumdar et al., 2015; Serva, 2014; Choi et al., 2012; Boyer and Romo-Cruz, 2014; Schutz and Trimper, 2004; Cressoni et al., 2007; Borges et al., 2012). However, our paper is the first that we know of to provide a plausible model for super-diffusion arising from the interplay between animal movement and resource depletion.

We show how, in the presence of resource dynamic, the individuals of a population need only search their neighborhood locally, and still can have super-diffusive movement. Further, the slower the recover of resource (larger μ), the more super-diffusive the population dispersal. By way of contrast, when there is rapid recover of the resource, the normal diffusion prevails, as discussed previously.

This behavior of avoiding sites with resource depletion as we propose here is reasonable for most foraging species, but has also been specifically reported for species such as black-tailed godwits (Lourenço et al., 2010). Some animal species can perceive variations in the site quality using prior knowledge (Dias et al., 2009). We could assume that, for species that move widely (Dias et al., 2009), some spatial memory could explain this behavior and our quantity r could possibly be understood in the context of a global spatial memory w of patch depletion, given by $w = 1 - r$. As discussed by Merkle et al. (2014) and Winter (2005), spatial memory can also relate to the temporal variability of the environment. Future work could relate spatial memory with resource depletion as a way to translate foraging decisions from individuals to a population level. At the individual level, work with bats in Winter (2005) shows how they use the memory of visited feeder sites (with resource depletion) to decide their movement and avoid depleted feeder sites. Future work could also includes incorporating different types of site quality into movement rules. One way to do, so, could be based on the dynamics presented by Bhat et al. (2017a,b), where individuals move according to a marker (greed) which can be understood as patch resource quality varying from preferable to avoidable. Lastly, an expansion to two dimensional system would make the model closer to real landscapes.

Finally, our work shows how the interplay between resource depletion and movement can induce different patterns of space use and population spread. Our model is theoretical, but only requires a single parameter, β, per individual rate of resource depletion. More complex models would have additional parameters, but would allow for a stronger connection to experimental or field studies.

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Appendix A. Development of the population dynamics

We consider a population of many individuals exploring a disordered one-dimensional space. The probability of moving from a site at y to another at x is proportional to

1. the localized dispersal kernel $K(y-x;\Delta t)$, that characterizes a localized random search and to
2. the resource density $r(x, t)$ at x. If $r(x, t)$ is high the probability of visiting this site must be high, otherwise, the probability is low.

Therefore, the probability is

$$P(y \to x) = \frac{K(y-x;\Delta t) r(x,t)}{\mathcal{N}(y,\Delta t)}, \tag{A.1}$$

where

$$\mathcal{N}(y,\Delta t) = \sum_{j\in\Omega} K(y-x_j;\Delta t) r(x_j,t) \tag{A.2}$$

is the normalization coefficient, such that $\sum_{i\in\Omega} P(y \to x_i) = 1$, with Ω a local spatial domain where the walker performs a random search for x. This coefficient is necessary, because at each step the transition probability varies according to the resource density $r(x, t)$.

Considering this situation, for one individual performance, we describe the probability of finding the individual at x after a time interval Δt by the master equation

$$\begin{aligned} u(x,t+\Delta t) &= \sum_{i\in\Omega} \frac{K(y_i-x,\Delta t) r(x,t) u(y_i,t)}{\mathcal{N}(y_i,\Delta t)} \\ &= r(x,t) \sum_{i\in\Omega} \frac{K(y_i-x,\Delta t) u(y_i,t)}{\mathcal{N}(y_i,\Delta t)}. \end{aligned} \tag{A.3}$$

For an average density, it means for several trajectories of many individuals moving independently, we can take the continuum limit on the space, and write

$$\begin{aligned} u(x,t+\Delta t) &= \int_\Omega \frac{K(y-x,\Delta t) r(x,t)}{\int_\Omega K(y-\xi;\Delta t) r(\xi,t) d\xi} u(y,t) dy \\ &= r(x,t) \int_\Omega \frac{K(y-x,\Delta t) u(y,t)}{\int_\Omega K(y-\xi;\Delta t) r(\xi,t) d\xi} dy, \end{aligned} \tag{A.4}$$

where the integration on y is also on a domain size Ω. For simplicity, let us use a truncated dispersal kernel with non-zero values only inside the domain Ω, so that

$$u(x,t+\Delta t) = r(x,t) \int_{-\infty}^{\infty} \frac{K(y-x,\Delta t) u(y,t)}{\int_{-\infty}^{\infty} K(y-\xi;\Delta t) r(\xi,t) d\xi} dy. \tag{A.5}$$

Analyzing the bottom integral using $z = y - \xi \Rightarrow \xi = y - z \Rightarrow z \in [\infty, -\infty]$, and $dz = -d\xi$

$$\begin{aligned} \int_{-\infty}^{\infty} K(y-\xi,\Delta t) r(\xi,t) d\xi &= \int_{\infty}^{-\infty} K(z,\Delta t) r(y-z,t)(-dz) \\ &= -\int_{\infty}^{-\infty} K(z,\Delta t) r(y-z,t) dz \\ &= \int_{-\infty}^{\infty} K(z,\Delta t) r(y-z,t) dz \\ &= \left[\int_{-\infty}^{\infty} K(z,\Delta t) dz\right] r(y,t) - \left[\int_{-\infty}^{\infty} z K(z,\Delta t) dz\right] \frac{\partial r(y,t)}{\partial y} \\ &\quad + \left[\int_{-\infty}^{\infty} \frac{z^2}{2} K(z,\Delta t) dz\right] \frac{\partial^2 r(y,t)}{\partial y^2} + h.o.t. \end{aligned}$$

where we have used a Taylor series expansion in the last line. Dropping the higher order terms, we obtain an approximation for the bottom integral:

$$\int_{-\infty}^{\infty} K(y-\xi,\Delta t) r(\xi,t) d\xi \approx r(y,t) + \Delta t\left[-\phi_1(\Delta t)\frac{\partial r(y,t)}{\partial y} + \phi_2(\Delta t)\frac{\partial^2 r(y,t)}{\partial y^2}\right], \quad (A.6)$$

where

$$\phi_1(\Delta t) = \frac{1}{\Delta t}\int_{-\infty}^{\infty} zK(z,\Delta t)dz \quad (A.7)$$

$$\phi_2(\Delta t) = \frac{1}{2\Delta t}\int_{-\infty}^{\infty} z^2 K(z,\Delta t)dz, \quad (A.8)$$

and

$$\lim_{\Delta t\to 0}\phi_1(\Delta t) = M_1 \equiv \text{first infinitesimal moment}. \quad (A.9)$$

$$\lim_{\Delta t\to 0}\phi_2(\Delta t) = M_2 \equiv \text{second infinitesimal moment}. \quad (A.10)$$

Substituting Eq. (A.6) in (A.5)

$$\begin{aligned} u(x,t+\Delta t) &\approx r(x,t)\int_{-\infty}^{\infty} K(y-x,\Delta t)\underbrace{\frac{u(y,t)}{r(y,t)+\Delta t\left[-\phi_1\frac{\partial r(y,t)}{\partial y}+\phi_2\frac{\partial^2 r(y,t)}{\partial y^2}\right]}}_{g(y,\Delta t)}dy \\ &\approx r(x,t)\int_{-\infty}^{\infty} K(y-x,\Delta t) g(y,\Delta t) dy\ . \end{aligned} \quad (A.11)$$

Using $\ell = y - x \Rightarrow y = \ell + x \Rightarrow \ell \in [-\infty, \infty]$ and $d\ell = dy$:

$$\begin{aligned} u(x,t+\Delta t) \approx\ & r(x,t)\textstyle\int_{-\infty}^{\infty} K(\ell,\Delta t) g(\ell+x,\Delta t) d\ell \\ =\ & r(x,t)\left\{[\textstyle\int_{-\infty}^{\infty} K(\ell,\Delta t)d\ell] g(x,t) + [\int_{-\infty}^{\infty}\ell K(\ell,\Delta t)d\ell]\dfrac{\partial g(x,t)}{\partial x}\right. \\ &\left. + \left[\int_{-\infty}^{\infty}\frac{\ell^2}{2}K(\ell,\Delta t)d\ell\right]\frac{\partial^2 g(x,t)}{\partial x^2} + h.o.t.\right\} \\ =\ & r(x,t) g(x,\Delta t) \\ &+ \Delta t\left[\phi_1\frac{\partial g(x,\Delta t)}{\partial x} + \phi_2\frac{\partial^2 g(x,\Delta t)}{\partial x^2} + \cdots\right]\Bigg\}. \end{aligned} \quad (A.12)$$

We rewrite $g(x, \Delta t)$ to leading order in Δt using $(1+\varepsilon)^{-1} \approx 1 - \varepsilon + O(\varepsilon^2)$, so that

$$\begin{aligned} g(x,\Delta t) &\approx \frac{u(x,t)}{r(x,t)} 1 + \frac{\Delta t}{r(x,t)}\left[-\phi_1\frac{\partial r(x,t)}{\partial x} + \phi_2\frac{\partial^2 r(x,t)}{\partial x^2}\right]\Bigg\}^{-1} \\ &\approx \frac{u(x,t)}{r(x,t)} + \frac{u(x,t)\Delta t}{r(x,t)^2}\left[\phi_1\frac{\partial r(x,t)}{\partial x} - \phi_2\frac{\partial^2 r(x,t)}{\partial x^2}\right]. \end{aligned} \quad (A.13)$$

Then, considering only the first order terms, we obtain

$$\begin{aligned} u(x,t+\Delta t) \approx\ & u(x,t) + \Delta t\frac{u(x,t)}{r(x,t)}\left[\phi_1\frac{\partial r(x,t)}{\partial x} - \phi_2\frac{\partial^2 r(x,t)}{\partial x^2}\right] \\ & + \Delta t\ r(x,t)\left[\phi_1\frac{\partial}{\partial x}\left(\frac{u(x,t)}{r(x,t)}\right) + \phi_2\frac{\partial^2}{\partial x^2}\left(\frac{u(x,t)}{r(x,t)}\right)\right]. \end{aligned} \quad (A.14)$$

Using

$$\frac{\partial}{\partial x}\left(\frac{u(x,t)}{r(x,t)}\right) = \frac{1}{r(x,t)}\frac{\partial u(x,t)}{\partial x} - \frac{u(x,t)}{r(x,t)^2}\frac{\partial r(x,t)}{\partial x},$$

we obtain

$$\begin{aligned} u(x,t+\Delta t) \approx\ & u(x,t) + \Delta t\phi_1\frac{\partial u(x,t)}{\partial x} - \Delta t\frac{u(x,t)}{r(x,t)}\phi_2\frac{\partial^2 r(x,t)}{\partial x^2} \\ & - 2\Delta t\frac{u(x,t)}{r(x,t)}\phi_1\frac{\partial r(x,t)}{\partial x} + \Delta t\ r(x,t)\phi_2\frac{\partial^2}{\partial x^2}\left(\frac{u(x,t)}{r(x,t)}\right). \end{aligned} \quad (A.15)$$

For the second derivative we use

$$\begin{aligned} \frac{\partial^2}{\partial x^2}\left(\frac{u(x,t)}{r(x,t)}\right) =\ & \frac{1}{r(x,t)}\frac{\partial^2 u(x,t)}{\partial x^2} - \frac{u(x,t)}{r(x,t)^2}\frac{\partial^2 r(x,t)}{\partial x^2} \\ & - \frac{2}{r(x,t)^2}\frac{\partial u(x,t)}{\partial x}\frac{\partial r(x,t)}{\partial x} + \frac{2u(x,t)}{r(x,t)^3}\left[\frac{\partial r(x,t)}{\partial x}\right]^2. \end{aligned}$$

Then

$$\begin{aligned} u(x,t+\Delta t) \approx\ & u(x,t) + \Delta t\phi_1\frac{\partial u(x,t)}{\partial x} + \Delta t\phi_2\left\{\frac{\partial^2 u(x,t)}{\partial x^2} + \frac{2u(x,t)}{r(x,t)^2}\left[\frac{\partial r(x,t)}{\partial x}\right]^2\right. \\ & \left. - \frac{2u(x,t)}{r(x,t)}\frac{\partial^2 r(x,t)}{\partial x^2} - \frac{2}{r(x,t)}\frac{\partial u(x,t)}{\partial x}\frac{\partial r(x,t)}{\partial x}\right\}. \end{aligned} \quad (A.16)$$

Dividing by Δt and taking the limit $\Delta t \to 0$, using Eqs. (A.9) and (A.10) as well, we obtain the approximation:

$$\begin{aligned} \frac{\partial u(x,t)}{\partial t} =\ & \frac{\partial u(x,t)}{\partial x}\left[M_1 - \frac{2M_2}{r(x,t)}\frac{\partial r(x,t)}{\partial x}\right] + M_2\frac{\partial^2 u(x,t)}{\partial x^2} \\ & + 2M_2\frac{u(x,t)}{r(x,t)^2}\left[\frac{\partial r(x,t)}{\partial x}\right]^2 - 2M_2\frac{u(x,t)}{r(x,t)}\frac{\partial^2 r(x,t)}{\partial x^2}. \end{aligned} \quad (A.17)$$

We rewrite the terms to get

$$\frac{\partial u(x,t)}{\partial t} = -\underbrace{\frac{\partial}{\partial x}\left[u(x,t)\left(2M_2\frac{\partial}{\partial x}\log r(x,t) - M_1\right)\right]}_{\text{Advective flux with a log function}} + \underbrace{M_2\frac{\partial^2 u(x,t)}{\partial x^2}}_{\text{Diffusive flux}}. \quad (A.18)$$

where M_1 stands for the preference for one direction, and M_2 is the diffusion coefficient. Note that in the advective term of this equation there is a nonlinear coupling due to the resource density r. Besides, this equation has an advection up gradients of $\log r(x, t)$. Observe that $\partial_x \log r(x, t)$ is some measure of locations with resource, since it represents the relative variation of space with resource, $\partial_x r/r$.

Appendix B. Linear stability analysis

To evaluate our problem, we consider zero flux boundary conditions and a given initial condition. Since we are concerned with the spatial-driven instability, we first determine the conditions for a linearly stable state in the absence of any spatial variation. Therefore, from Eq. (8) we obtain for the steady state $(u, r) = (u_0, r_0)$:

$$\frac{\partial r_0}{\partial t} = -\beta u_0 r_0 + (1 + r_0) = 0 \quad \Rightarrow r_0 = \frac{1}{1+\beta u_0}. \tag{B.1}$$

This gives us the relation between u and r at the steady state. Now, we linearize the original problem, Eqs. (8) and (9), about the steady state (u_0, r_0). Let us assume a small perturbation $|u_1|, |r_1| \ll 1$, with:

$$\binom{r_1}{u_1} = (\bar{r}\bar{u})e^{\lambda t + ikx}, \tag{B.2}$$

where λ is the eigenvalue which determines the temporal variation, and k is an eigenvalue that can be understood in the context of wavenumber. Thus, linearizing the original set of equation using with $r = r_0 + r_1$ and $u = u_0 + u_1$, we obtain:

$$\frac{\partial u_1}{\partial t} = -2\frac{\partial}{\partial x}\left[(u_0 + u_1)\frac{\partial}{\partial x}\log(r_0 + r_1)\right] + \frac{\partial^2 u_1}{\partial x^2}. \tag{B.3}$$

Evaluating the derivative of the log function, we got:

$$\frac{\partial}{\partial x}\log(r_0 + r_1) = \frac{1}{r_0 + r_1}\frac{\partial r_1}{\partial x}, \tag{B.4}$$

we can rewrite

$$\frac{1}{r_0 + r_1} = \frac{1}{r_0}\frac{1}{1 + \frac{r_1}{r_0}} = \frac{1}{r_0}\left(1 - \frac{r_1}{r_0} + \cdots\right), \tag{B.5}$$

therefore

$$\begin{aligned}\frac{\partial}{\partial x}\log(r_0 + r_1) &= \frac{1}{r_0 + r_1}\frac{\partial r_1}{\partial x}\\ &= \frac{1}{r_0}\left(1 - \frac{r_1}{r_0} + \cdots\right)\frac{\partial r_1}{\partial x}\\ &\approx \frac{1}{r_0}\frac{\partial r_1}{\partial x},\end{aligned} \tag{B.6}$$

where we keep only the first order terms. So, Eq. (B.3) becomes

$$\begin{aligned}\frac{\partial u_1}{\partial t} &\approx -2\frac{\partial}{\partial x}\left[(u_0 + u_1)\frac{1}{r_0}\frac{\partial r_1}{\partial x}\right] + \frac{\partial^2 u_1}{\partial x^2}\\ &\approx -2u_0\frac{1}{r_0}\frac{\partial^2 r_1}{\partial x^2} + \frac{\partial^2 u_1}{\partial x^2}\\ &\approx -\left(\frac{2u_0}{r_0}\right)\frac{\partial^2 r_1}{\partial x^2} + \frac{\partial^2 u_1}{\partial x^2}.\end{aligned} \tag{B.7}$$

For the r equation, we obtain

$$\begin{aligned}\frac{\partial r_1}{\partial t} &= -\beta(u_0 + u_1)(r_0 + r_1) + (1 - r_0 - r_1)\\ &= \underbrace{-\beta u_0(r_0) + (1 - r_0)}_{=0} - \beta u_1(r_0) - \beta u_0(r_1) - r_1 - \beta u_1 r_1\\ &= u_1(-\beta r_0) + r_1(-\beta u_0 - 1) + h.o.t.\\ &\approx u_1(-\beta r_0) + r_1(-\beta u_0 - 1)\ ,\end{aligned} \tag{B.8}$$

where again, we keep only the first order terms. In the matrix formalism:

$$\frac{\partial}{\partial t}\begin{bmatrix} r_1\\ u_1\end{bmatrix} = \begin{bmatrix} -(\beta u_0 + 1) & -\beta r_0\\ \left(\frac{-2u_0}{r_0}\right)\frac{\partial^2}{\partial x^2} & \frac{\partial^2}{\partial x^2}\end{bmatrix}\begin{bmatrix} r_1\\ u_1\end{bmatrix}. \tag{B.9}$$

Using Eq. (B.2) we obtain:

$$\begin{aligned}\frac{\partial}{\partial t}\begin{bmatrix} r_1\\ u_1\end{bmatrix} &= \frac{\partial}{\partial t}\begin{bmatrix} \bar{r}\\ \bar{u}\end{bmatrix}\exp(\lambda t + ikx) = \lambda\begin{bmatrix} r_1\\ u_1\end{bmatrix}\\ \frac{\partial^2}{\partial x^2}\begin{bmatrix} r_1\\ u_1\end{bmatrix} &= \frac{\partial^2}{\partial x^2}\begin{bmatrix} \bar{r}\\ \bar{u}\end{bmatrix}\exp(\lambda t + ikx) = -k^2\begin{bmatrix} r_1\\ u_1\end{bmatrix}\end{aligned} \tag{B.10}$$

Therefore,

$$\lambda\begin{bmatrix} r_1\\ u_1\end{bmatrix} = \underbrace{\begin{bmatrix} -(\beta u_0 + 1) & -\beta r_0\\ \left(\frac{2u_0}{r_0}\right)k^2 & -k^2\end{bmatrix}}_{A}\begin{bmatrix} r_1\\ u_1\end{bmatrix}\ , \tag{B.11}$$

where A is the stability matrix. We have to analyze the stability condition through the eigenvalues λ of A, namely, solving $|A - \lambda I| = 0$.

$$\begin{aligned}p(\lambda) &= \lambda^2 - \mathrm{tr}A\ \lambda + \det A = 0\\ &= \lambda^2 + \underbrace{(\beta u_0 + 1 + k^2)}_{-tr(A)}\lambda + \underbrace{(3\beta u_0 + 1)k^2}_{det(A)} = 0\ .\end{aligned} \tag{B.12}$$

Linear stability is guaranteed if Re $\lambda < 0$ (Murray, 2003). Thus, analyzing Eq. (B.12), for stability we must have $tr(A) < 0$ and $det(A) > 0$. Therefore, the stability conditions are

$$-(\beta u_0 + 1 + k^2) < 0. \tag{B.13}$$

$$(3\beta u_0 + 1)k^2 \geq 0, \tag{B.14}$$

where the equality occurs in the absence of any spatial effects, namely, if $k^2 = 0$. Note that, since $\beta > 0$ and $u_0 > 0$, these conditions are always satisfied. It means the resource consumption does not destabilize the spatially uniform stationary state.

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