On a possible origin of the fat-tailed dispersal in population dynamics

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Abstract

Populations do not remain fixed in space. Their distribution changes continuously due to the impact of environmental factors, such as wind, and/or due to self-motion of individuals. A cornerstone for understanding mechanisms of dispersal is identification of factors affecting the dispersal curve, in particular, its rate of decay at large distance. The standard random walk approach resulting in a dispersal curve with a ‘thin’ Gaussian tail was eventually opposed by the theory of Lévy flights, which predicts a more realistic ‘fat’ tail with a lower rate of decay. However, here we argue that the Gaussian large-distance asymptotics is more an artefact of an oversimplified description of the dispersing population rather than an immanent property of the random walk diffusion. Specifically, we show that, when some inherent population structure is taken into account, diffusion results in a dispersal curve with either exponential or power law rate of decay. Our theoretical results appear to be in a very good agreement with some available data.

Keywords:
Dispersal
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Diffusion
Structured population
Dispersal curve
Fat tail

1. Introduction

Understanding the mechanisms and patterns of species dispersal is a major problem in spatial ecology (Levin et al., 2003; Turchin, 1998; Clobert et al., 2001; Bullock et al., 2002; Nathan et al., 2002) and epidemiology (Pielaat et al., 2002; Brown and Bolker, 2004; Reluga et al., 2006). A standard theoretical approach to species dispersal is based on the random walk approximation (Skellam, 1951; Okubo, 1980, 1986; Okubo and Levin, 2001), i.e. Brownian motion, which results in a diffusion equation. Diffusion approximation has proved to be useful in many ecological applications (Murray, 1989; Shigesada and Kawasaki, 1997; Petrovskii and Li, 2006); however, in some cases it was found to be at variance with reality. For instance, in case of a single-point release of a given population, the random walk approach predicts the Gaussian/normal spatial distribution where the population density decreases at large distance $x$ with the asymptotical rate of decay $\exp(-x^2)$. Although it is in agreement with some data (Kareiva, 1983), there is also a growing amount of evidence, based on field studies on different species, that the rate of decay can be much slower (Taylor, 1978; Buechner, 1987; Okubo and Levin, 1989; Wilson and Thomas, 2002; Levin et al., 2003). The latter situation is often referred to as dispersal with a ‘fat tail’ (compared to the ‘thin’ Gaussian tail). Correspondingly, a dispersal function with a fat tail is usually regarded as a fingerprint of a non-Gaussian diffusion, cf. Lévy flights, when the standard random walk approximation does not apply.
In order to create a relevant theoretical framework, an alternative mathematical approach was developed based on integral-difference equations (Kot and Schaffer, 1986; Kot et al., 1996; Lewis and Pacala, 2000; Neubert and Caswell, 2000; Clark et al., 2001). It has been shown that, for an appropriately chosen dispersal kernel, their solutions may possess either exponential or a power law rate of decay.

A question which yet remains largely open is what dynamical mechanisms are behind the fat-tailed dispersal. In the case of a passive motion, e.g. seed dispersal due to the impact of wind, the fat tails can be ascribed to peculiarities of turbulent mixing (Okubo, 1980; Okubo and Levin, 1989; Nathan et al., 2002) and thus put into a more general context of ‘superdiffusion’ (Klaf ter et al., 1996). However, in case of species with an ability to self-motion, e.g. such as insects or mammals, the actual mechanism of fat tails formation remains unclear. Studies on birds (Viswanathan et al., 1996) and monkeys (Ramos-Fernandez et al., 2004) suggested that a significant deviation from the Brownian motion may take place already at the level of a single individual so that a fat-tailed dispersal curve may be a consequence of specific foraging behavior. On the other hand, there is considerable evidence that individual motion of some insects is more likely to be of Brownian type (Root and Kareiva, 1984; Okubo, 1986).

In this paper, we show that, in fact, Gaussian tail is not an inherent property of the random walk diffusion. Rather, it is a consequence of an oversimplified description of the dispersing population. On the contrary, we show that a dispersal tail with a rate of decay slower than that of the normal distribution is just an intrinsic property of diffusion motion provided that the dispersing/diffusing population is structured with respect to dispersive ability of the individuals.

2. Model and analysis

Let us consider a population described by its density \( n(x, t) \), where \( x \) is position and \( t \) is time. For the sake of simplicity, we focus on one-dimensional case. We assume that motion of the individuals can be adequately described by random walks. Evolution of the population density is then given by the diffusion equation and species diffusivity is quantified by the diffusion coefficient \( D \). It should be mentioned here that, in the case of individual diffusive motion, \( D \) gives the mean displacement per unit time, \( \langle x^2 \rangle = Dt \); therefore, \( D \) provides a certain link between the individual-level and the population-level description of dispersal.

In order to exclude the impact of specific initial conditions, we consider the case of a single-point release when \( N_0 \) individuals of the given species are set free at the moment \( t = 0 \) at the position \( x = 0 \). Random walk approximation results in the Gaussian distribution of the population density over space:

\[
     n(x, t) = \frac{N_0}{\sqrt{\pi Dt}} \exp \left( -\frac{x^2}{Dt} \right),
\]


Eq. (1) is obviously based on the assumption that all the individuals of a given population possess equal ability for self-motion so that population diffusivity can be described by a single coefficient \( D \). In reality, however, it is not so. Individuals are not identical and the parameters such as body weight, length of wings (if any), etc., can vary significantly within the same population. Moreover, most populations are structured with respect to a certain property, e.g. see Lomnicki (1988) and Cushing (1998), and that may affect dispersive ability as well. For instance, in an age-structured population very young and very old individuals are likely to possess lower ability to motion.

An immediate consequence of the above observation is that virtually any population is, actually, structured with respect to individual dispersal ability. In the simplest case, it may consist of \( K \) groups or ranks (e.g., corresponding to different life-stages), each of them being quantified by its own value of the diffusion coefficient. Correspondingly, species dispersal would be quantified by the set of parameters \( D_1, D_2, \ldots, D_K \) rather than a single value \( D \).

In a more general case, diffusivity varies continuously, which can be taken into account by introducing a diffusivity distribution function \( \phi(D) \) so that \( \phi(D) \, dD \) gives the fraction of the population which diffusivity lies between \( D \) and \( D + dD \). Let us denote the corresponding population density as \( d\rho_0(x, t) \); then, instead of Eq. (1) we now have

\[
     d\rho_0(x, t) = \frac{N_0\phi(D)}{\sqrt{\pi Dt}} \exp \left( -\frac{x^2}{Dt} \right) \, dD
\]

where \( \int_0^\infty \phi(D) \, dD = 1 \).

What is measurable in dispersive experiments is the total population density \( n(x, t) \), which arises from contributions of all possible ranks:

\[
     n(x, t) = \int d\rho_0(x, t) = \int_0^\infty \frac{N_0\phi(D)}{\sqrt{\pi Dt}} \exp \left( -\frac{x^2}{Dt} \right) \, dD
\]

 Apparently, the resultant total population distribution over space given by \( n(x, t) \) depends on \( \phi(D) \). To the best of our knowledge, there has not been any study which would give an insight as to what may be the properties of \( \phi(D) \). Thus, in order to address this issue and to check how the Gaussian spatial distribution (1) of the population density can possibly be modified by the impact of population structure, below we consider a few hypothetical cases. For all these cases we assume that \( \phi(D) \) is a unimodal distribution; what is essentially different is its asymptotical behavior for large \( D \). The larger the \( D \) larger is the typical dispersal distance of the given rank; thus, it is intuitively clear that slower rate of decay in \( \phi(D) \) may result in slower rate of decay in the population density \( n \).

Case 1. We begin with the case when \( \phi(D) \) is given by the normal distribution:

\[
     \phi(D) = \phi_1(D) = A_1 \exp \left( -\frac{(D - D_0)}{\mu}^2 \right)
\]

where \( A_1 = (\pi \mu)^{-1/2} \) is a coefficient and \( D_0 \) and \( \mu \) are the distribution center and half-width, respectively. Generally
Speaking, the normal distribution should be defined on the whole line. In the case when distribution (4) is applied to the semi-finite domain \( D > 0 \), it has to be truncated so that \( \phi(D) \equiv 0 \) for \( D < 0 \); that results in a somewhat different value of coefficient \( A_1 \). However, due to the very fast rate of decay, in case \( \mu \ll D_0 \) the normal distribution can be applied to the semi-line \( D \geq 0 \) with high precision.

For \( \phi(D) \) given by (4), an exact analytical expression for \( n(x, t) \) is not available. However, it appears possible to estimate its rate of decay at large \( x \). Omitting here the technical details for the sake of brevity, for \( \xi = x^2 / (\mu t) \gg 1 \) the integral (3–4) can be written as

\[
n(x, t) \sim x^{-1/3} \exp \left( -\kappa \xi^{2/3} [1 + \tau(\xi)] \right). \tag{5}\]

where notation \( \sim \) has the usual meaning “up to a constant coefficient,” \( \kappa \) is a numerical factor on the order of unity and \( \tau(\xi) \) is a certain function which tends to zero when \( \xi \) tends to infinity. Eq. (5) apparently means that, at any fixed moment of time, the large-distance asymptotics of the population density is given as

\[
n(x, t) \sim x^{-1/3} \exp \left( -\frac{\kappa}{(\mu t)^{2/3}} x^{2/3} \right). \tag{6}\]

Remarkably, the rate of decay appears to be slower than that of the normal distribution, although the discrepancy is not large. Curve 1 in Fig. 1 shows (in semi-logarithmic coordinates) the population density over space obtained as a result of numerical integration in (3). The population density of the corresponding unstructured population (with \( D = D_0 \)) is shown by the dotted curve which is situated very close to curve 1; in particular, their large-distance asymptotics is nearly the same.

**Case 2.** Our next example addresses the situation when the rate of decay of \( \phi(D) \) at large \( D \) is lower than Gaussian. Specifically, we are going to consider the case when \( \phi(D) \) decreases exponentially:

\[
\phi(D) = \phi_{xy}(D) = A_2 D^{-\nu} \exp \left( -\frac{D}{D_0} \right), \tag{7}\]

where \( A_2 = [\nu^{\nu-1} \Gamma(\nu + 1)]^{-1} \) is a coefficient, \( \Gamma \) is the standard Gamma-function, \( \nu \) is the characteristic diffusivity for the given species and \( \nu \) is a parameter.

With \( \phi = \phi_{xy} \), analytical integration in (3) is not possible but it is possible to estimate its asymptotical rate of decay. Omitting technical details, the population density \( n(x, t) \) given by (3) and (7) can be written as

\[
n(x, t) \sim x^{-\nu/\gamma} \exp \left( -\frac{2x}{(\nu t)^{1/\gamma}} \right). \tag{8}\]

For any fixed moment of time, Eq. (8) reduces to

\[
n(x, t) \sim x^{-\nu/\gamma} \exp \left( -\frac{2x}{(\nu t)^{1/\gamma}} \right). \tag{9}\]

Therefore, the asymptotical rate of decay in population density is now clearly different from one of the corresponding unstructured population.

Since Eq. (9) gives only an estimate and not an exact result, in order to check the prediction of lower decay rate the integral (3) with (7) was also calculated numerically. Curve 2 in Fig. 1 shows the population density over space obtained as a result of numerical integration. The rate of decay is indeed much slower now than it was in the previous case (shown by curve 1). At large distances, curve 2 comes close to a straight line, which corresponds to exponential rate of decay.

**Case 3.** Finally, we are going to consider the case when the asymptotical behavior of \( \phi(D) \) is described by a power law. For convenience of mathematical treatment, we consider the following parametrization:

\[
\phi(D) = \phi_{xy}(D) = A_3 D^{-\nu} \exp \left( -\frac{D}{D_0} \right), \quad D > 0. \tag{10}\]

Here \( \gamma > 1 \) is a parameter and \( A_3 = \nu^{\nu-1} / \Gamma(\gamma - 1) \) is a coefficient. In order to avoid the singularity at \( D = 0 \), we additionally define \( \phi_{xy}(0) = 0 \).

Now, integration in (3) can be done analytically resulting in

\[
n(x, t) = \frac{C}{\Gamma(\gamma - 1)} \left( \frac{x^2}{\nu t} \right)^{-\nu/\gamma} \exp \left( -\frac{2x}{(\nu t)^{1/\gamma}} \right). \tag{11}\]

**Fig. 1 - Population density** \( n \) **vs.** space for different choice of \( \phi(D) \). Here curve 1 is obtained for (4) with parameters \( D_0 = 3, \mu = 0.3 \) and curve 2 is obtained for (7) with \( \nu = 1 \) and \( \gamma = 2 \). Parameters are chosen in such a way that \( D_0 = |D| \), where \( D \) is the mean value of the distribution (7); thus curves 1 and 2 can be compared straightforwardly. The spatial distribution of the corresponding unstructured population (described by a single value \( D = D_0 \)) is shown by a dotted curve which practically coincides with curve 1. Curves 3 and 4 are obtained for (10) with \( \gamma = 2 \) and 3, respectively, and \( \nu = 1 \).
Obviously, at any given moment of time and for sufficiently large \( x \), from (11) we arrive at

\[ n(x, t) \sim x^{1-2\gamma}. \]  

Thus, function \( \phi(D) \) given by (10) results in a spatial distribution of the population density with the large-distance asymptotical behavior described by a power law. Curves 3 and 4 in Fig. 1 show Eq. (11) for \( \gamma = 2 \) and 3 when \( n \sim x^{-3} \) and \( x^{-5} \), respectively.

In order to check how the predictions of our model can possibly be confronted with reality, by way of example Fig. 2 shows some data on insect dispersal provided by Wilson and Thomas (2002); see their work for details of the sampling procedure. It should be mentioned that species dispersal normally takes place in two spatial dimensions and thus predictions of a 1-D model cannot be applied straightforwardly. In the case of Wilson and Thomas (2002), however, the species habitat had a clear prolate shape (with its width and length being about 400 and 3000 m, respectively) and one can hope that Eq. (3) captures essential features of the system. Indeed, there is an apparently good agreement between our theoretical results (solid curve), i.e. Eq. (3) with \( \phi(D) \) given by (10) with \( \gamma = 1.9 \), and the observed power law rate of decay in population density, cf. the dashed-and-dotted line. We want to emphasize that this agreement is obtained for biologically reasonable parameters. In particular, the value of characteristic diffusivity \( v \) that we have used (see Fig. 2 legend) is consistent with a typical diffusivity for flying insects, cf. Shigesada and Kawasaki (1997).

Interestingly, the theory appears to be in a reasonably good agreement with the data also at small and intermediate distances. The observed discrepancy can possibly be attributed to the fact that on a small spatial scale dispersal is essentially two-dimensional, and the rate of diffusive spread from a point source is higher in a 2-D system than in the corresponding 1-D system.

3. Concluding remarks

Therefore, we showed that standard random walk diffusion can result in a dispersal curve with a fat tail provided that the given population is structured according to individual motion ability. All three hypothetical types of \( \phi(D) \) considered here lead to a population density distribution with the asymptotical rate of decay lower than that of the normal distribution. In particular, Cases 2 and 3 result in exponential and power law, correspondingly. Thus, we conclude that formation of a fat-tailed dispersal curve due to the impact of the population structure is a probable mechanism in ecological populations.

We want to mention here that power laws emerging as a result of mixing of distributions with other asymptotical properties have previously been observed also in other problems of population dynamics (cf. Allen et al., 2001). That may indicate that the power laws in ecology may be more typically arising as a result of the interplay between the population or community structure and the standard distributions (such as, for instance, normal or log-normal) rather than having a fundamental meaning by themselves.

The mathematical framework that has been used increasingly often to deal with the fat-tailed population dispersal is based on integral-difference equations, see Kot and Schaffer (1986), Kot et al. (1996) and Neubert and Caswell (2000). This approach was proved to be especially useful for populations with clearly distinguished multiplication and dispersal stages. Population redistribution due to dispersal is then described as

\[ u(x, t + T) = \int_{-\infty}^{\infty} K(x - y) u(y, t) \, dy, \]  

where \( K \) is the dispersal kernel (which, by its meaning, is essentially the dispersal curve of the single-point release) and \( T \) is the duration of the dispersal stage. Provided \( K(x - y) \) has some necessary properties, i.e. being fat-tailed by itself, the population density \( u(x, t + T) \) is fat-tailed even if the original distribution \( u(x, t) \) was Gaussian or of finite support. This approach, however, tells nothing regarding how a fat-tailed dispersal curve can possibly appear; rather, the required property is postulated. In this paper, we have shown that a fat-tailed kernel may arise quite naturally as a consequence of inherent population structure with respect to individual mobility.

For the sake of mathematical clarity, here we have restricted our analysis to the case of a single point release. The corresponding initial condition is given by the \( \delta \)-function. However, we want to stress that the main result, i.e. the
fat-tailed large-distance asymptotics, remains essentially unchanged in case of any other initial condition described by a function of compact support, the total population density being described by an equation somewhat more complicated compared to (3).

In Eq. (3), integration is done over the semi-infinite domain \( D \geq 0 \). In reality, however, due to finiteness of the individual speed diffusivity should be bounded, \( 0 \leq D < D_1 \). Consequently, the spatial distribution given by (3) is only valid on a certain spatial scale. Thus, the fat-tailed dispersal curve actually provides an “intermediate asymptotics” (cf. Barenblatt, 1996) and, for sufficiently large \( x \), \( n(x, t) = 0 \) for any finite time \( t \).

Regarding further applications of our approach, an open question remains as to what biological factors may affect the shape of \( \phi(D) \) in a real population and how it can be measured and/or calculated theoretically for a given species. It seems probable that this issue also involves an evolutionary aspect. Indeed, since dispersal in general is in many ways beneficial for population functioning, cf. Clobert et al. (2001), one can expect that existence of some individuals or ranks with higher dispersive ability can make its positive impact stronger and more prominent. A population with higher proportion of such ranks, e.g. with a slower rate of decay in \( \phi(D) \), would be then less prone to extinction and thus more likely to survive in the course of evolution.

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References


