

Article

Modelling spread with context-based dispersal strategies

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Abstract

Dispersal is a context-dependent adaptive trait. Different dispersal strategies arise as species need to optimize their fitness in the ever changing quality of habitats further imposed by abiotic and biotic factors. This work reviews the spread of populations under different dispersal strategies. Namely, we address the spread of a population when dispersal is driven by habitat fragmentations, density-dependent predation and mixed propagules. The context-based dispersal can explain a variety of range dynamics. It is of common accord however that the cause and effect of dispersal could have a wider effect on population dynamics that goes beyond purely ecological nature.

Keywords dispersal strategy; density dependence; habitat fragmentation; propagule pressure; range expansion.

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1 Introduction

Dispersal plays an important role in determining population and community dynamics, from the persistence of a metapopulation (Johst et al., 2002; Levins, 1969) to the maintenance of biodiversity (Chesson, 2000; Kerr et al., 2002). It is also an important factor in predicting the potential dynamics of biological invasions as it allows individuals to change habitats and occupy the full extent of accessible niche in the environment (Roura-Pascual et al., 2009; Caplat et al., 2014; Donaldson et al., 2014). Fields and laboratory observations have shown that a multitude of processes can drive dispersal. Immediate causes include crowding and food accessibility in the local habitat. In some cases, active dispersal can be density-dependent; that is, the magnitude of dispersal depends on the local population size. For example, intense competition in a crowded area will force individuals to emigrate (positive density-dependence), while it could also impair dispersal abilities in some cases (negative density-dependence) (Ims and Andreassen, 2005; Matthysen, 2005; Nowicki and Vrabec, 2011).

Dispersal is highly affected by the individual's mobility. Indeed, mobility can reflect the physical efforts or morphological traits needed to actively disperse in nature (Berthouly-Salazar et al., 2012; Phillips et al., 2006; Simmons and Thomas, 2004), or phenotypic traits which facilitate transport by different dispersal vectors. Such is the case for example in the seed dispersal of many species, during which smaller seeds tend to be dispersed further than heavier seeds (Xiao et al., 2005). Dispersal is also particularly noticeable when juveniles leave their natal sites for new potential habitats (Gaines and Bertness, 1993; Savidge, 1987). Environmental conditions also contribute to different dispersal behaviours as individuals in quest for more favourable habitats may emigrate (Hui et al., 2012; Pärn et al., 2012). These examples are related to the dispersal strategy of individuals given its surrounding environment.

In light of biological invasions, different contexts of dispersal could result in different patterns of range expansion in nature, ranging from the extinction of the population (Thomas, 2000; Theodorou et al., 2008) to an accelerating invasion front (Cohen, 1998; Philips et al., 2014). The understanding of such patterns, especially in the early stage of the range expansion, has become an active interdisciplinary topic as efforts to control biological invasions are often expensive (Pimentel et al., 2005; Allendorf and Lundquist, 2003). The remainder of this work is devoted to the study of the population-level effects of different dispersal mechanisms using mathematical modelling.

2 Modelling Spatial Dynamics

A large body of theory has been developed over the years for modelling the spatial dynamics of populations. Mathematical and computational modelling are powerful approaches for predicting species' range dynamics. Theoretical studies of ecological spread started with the seminal work of Skellam (1951). In his studies, Skellam (1951) used the reaction-diffusion models based on partial differential equations (PDE), which had initially been developed by Fisher (1937) (see also Kolmogorov et al., 1991) for the spread of an advantageous allele in a population, in order to investigate the spread of muskrats in Europe. In this type of model, the dispersal ability and strategy are implicitly incorporated in the diffusion coefficient (Holmes et al. 1994).

Early spread models, which incorporated the movements of individuals in reaction-diffusion models using a constant diffusion term and described the growth dynamics of the population using the most simple growth function, have yielded a robust and well known prediction of a constant rate of spread in the long term. As more field data have become available, more versatile models have also been developed from the Skellam's initial case to investigate the effects of different dispersal abilities and strategies (Kinezaki et al., 2006; Sanchez-Garduno and Maini, 1994; Shigesada et al., 1986). An early review presented by Holmes et al. (1994) showed that reaction-diffusion models in the PDE framework could successfully depict numerous features of ecological phenomena and interactions. Traditional reaction-diffusion models however suffer from one major limitation, as their uses are inherently confined to populations for which demographic processes and individuals movements can continuously occur in time and space, and individuals possess normally-distributed dispersal distances over a fixed period of time (Skellam, 1951; Holmes et al., 1994).

Another line of spread models explicitly incorporates the distribution of dispersal distance to describe individuals' movement in the system. These classes of models have the advantage that the distribution of dispersal distance over a given period of time (also known as the dispersal kernel) is not necessarily a normal distribution (Kot et al., 1996). Furthermore, dispersal kernel models are available in the literature in continuous (Mollison, 1977) as well as in discrete-time (Kot et al., 1996). Like reaction-diffusion models, dispersal kernel models were used in population genetics (Weinberger, 1982) prior to their applications to population ecology. In discrete-time dispersal kernel models (known as integrodifference equations), population growth is assumed to occur during a sedentary stage whereas individual movements take place during the dispersal stage. The

models are therefore suitable for organisms with non-overlapping generations and separated growth and dispersal stages. Classic examples of such populations include annual plants and seasonal insects (Liebhold and Tobin, 2008).

In this class of model, the dispersal ability is incorporated in the dispersal kernel. Depending on the shape of the dispersal kernel, integrodifference models have yielded different range expansion patterns and have led to an attribution of the accelerating nature of range expansion to considerable long-distance dispersal (Kot et al., 1996). Like reaction-diffusion models, dispersal kernel models have been extended to incorporate different dispersal strategies (Kawasaki and Shigesada, 2007; Lutscher, 2008; Veit and Lewis, 1996; Weinberger et al., 2008).

A third line of models for spatial spread consists of stochastic and spatially explicit models (that is models that use geographical space to incorporate habitat features). Rapid advances in computer technology have allowed for extensive use of spatially explicit models for ecological spread. These are particularly powerful when incorporating demographic stochasticity as well as different landscape features such as dispersal barriers (Dunning Jr et al. 1995; Grimm and Railsback, 2005; Grimm, 1999). Although the complexity of the resulting models often does not allow mathematical investigations, computational experiments have led to momentous highlights for instance on the role of long-distance dispersal (Pearson and Dawson, 2005). Recent uses of spatially explicit models suggest the evolution of dispersal strategies can explain the accelerating nature of range expansion (Phillips et al., 2008; Travis et al., 2009) as well as different mechanisms that limit the distribution of species (Kubisch et al., 2014; Phillips, 2012).

3 Effect of Habitat Fragmentation

Environmental conditions may influence the invasion process at different stages. In particular, the rate of spread was found to be environmentally dependent for different species (Hui et al., 2011; With, 2002). A number of empirical investigations have speculated that the spatial heterogeneity of the landscape can influence the rate of spread of invasive species (Hastings et al. 2005; and references therein). Indeed, spatial heterogeneity can influence demographic as well as dispersal processes which are the keys to determining the spread of the population.

The effects of environmental heterogeneity are commonly studied using metapopulation frameworks in which subpopulations develop in response to the local habitat quality and are linked by migration behaviours. One well-established approach is based on stochastic patch occupancy model (SPOM) (Hanski and Ovaskainen, 2003; Hanski, 1998). For a landscape consisting of n habitat patches, SPOMs are formulated as Markov chains with 2^n states, where the transition probabilities for a local habitat patch from being occupied to the empty state differ among patches based on the environment heterogeneity. While the transition from occupied to empty is particularized by local extinction rates, transition from the empty state to occupied is specified by dispersal or colonisation processes.

SPOMs are usually impossible to tract mathematically as the number of habitat patches increases. It is of common practice to analyse the deterministic limit of the model (McVinish and Pollett, 2013). One of the well-known models is Levins' (1969) occupancy model, later improved by Ovaskainen and Hanski (2001) which established the invasion thresholds given the extinction and colonisation rates of the local habitat patches. Undeniably, this formulation of environmental heterogeneity has led to important breakthroughs in Ecology. The approach however is usually limited to the presence or absence of the focal species rather than its abundance in the habitat patches.

Other commonly used mathematical approaches to study the effects of environmental heterogeneity consist of reaction diffusion models. In this framework, the theory of invasion in heterogeneous environments

has a strong background especially in the continuous time (using PDEs). Namely, two implementations of spatial heterogeneity have been investigated theoretically. Shigesada et al. (1986) first proposed the spatial heterogeneity by alternating homogeneously favourable and unfavourable patches on an infinite one-dimensional environment. The growth rate and diffusion coefficient were given by periodic step functions of the locations. Another environment structure was investigated by (Kinezaki et al., 2006) by allowing the growth and dispersal parameters to vary sinusoidally in space in response to a sinusoidally distributed habitat quality. In both models, a population introduced at a local point propagated into periodic travelling waves. Estimations of the rate of spread were derived as $c = 2(\langle r \rangle_A \langle D \rangle_H)^{1/2}$ when the period of environmental change was sufficiently small, where $\langle r \rangle_A$ and $\langle D \rangle_H$ denote the spatial arithmetic mean of the growth rate and spatial harmonic mean of the diffusion coefficient respectively. This first model has an emphasis on the influence of the sizes of favourable and unfavourable patches on the rate of spread of the population. The later model on the other hand elucidated the role of the amplitude and wave length of the growth and dispersal parameters.

The spatial arrangement of habitats has also attracted interest in populations with non-overlapping generations using integrodifference equations. While some authors constructed general and robust mathematical formulae of the asymptotic rate of spread (Weinberger et al., 2008), others investigated different assumptions on the spatial heterogeneity and their influence on the population's spread (Kawasaki and Shigesada, 2007; Dewhurst and Lutscher, 2009). Kawasaki and Shigesada (2007) first proposed the patchy environment which consists of alternating favourable and unfavourable patches. The model was built with exponentially damping (Laplace) dispersal kernel. It was assumed that the spatial heterogeneity affects only the growth processes and did not influence the dispersal kernel. One important outcome of this work suggests that the presence of unfavourable patches can decrease the rate of spread dramatically. However, the population can always spread when the favourable habitats are wide enough regardless of the quality and sizes of unfavourable patches. Dewhurst and Lutscher (2009) later investigated a more general case for the same environment structure. Namely, in addition to location-dependent growth, they considered that individual dispersal behaviours are also affected by the environment for example when individuals from unfavourable locations may disperse far in an attempt to find more favourable habitats. Such dispersal behaviours were incorporated in the model by allowing the variance of the dispersal kernels to vary in space. Similar to the work of (Shigesada et al., 1986), their approach also put an emphasis on the availability of favourable habitats, that is, the proportion of favourable habitats in the environment rather than the actual sizes of the patches. A minimal proportion of favourable habitats to ensure a successful invasion as well as the asymptotic rate of spread were derived.

Recently, Ramanantoanina and Hui (2015) investigated how dispersal strategies interfere with landscape fragmentation using the same landscape structure proposed by Shigesada and Kawasaki (2007). In addition to location-dependent population growth, individual dispersal behaviours are affected by the environment in two ways. First, the dispersal distance of migrating individuals is affected by the habitat quality of their locations, for example when individuals from unfavourable locations may disperse far in an attempt to find more favourable habitats (Fahrig, 2007; Klaassen et al., 2006). Second, depending on the quality of the local habitat, only a fraction of the local population emigrates while the other individuals remain sedentary (Hui et al., 2012; Klaassen et al., 2006). Such dispersal behaviours are incorporated by using location-dependent dispersal probability. Good dispersal strategies are crucial for the survival of a population facing the ever changing environments. Limited dispersal can push populations to extinction as they cannot escape local detrimental conditions (Thomas, 2000). Emigrating from unfavourable habitats however does not help the population unless migrating individuals can find new habitats in the fragmented landscape in which they can breed (Thomas, 2000; Thomas et al., 2006).

Ramanantoanina and Hui (2015) established a formula depicting the persistence and the range expansion of a population in a periodically fragmented environment. Namely, the rate (c) at which a population expands its range satisfies

$$\bar{c} \sqrt{\frac{\ln R_{\min}}{R_{\min}}} \leq c \leq \bar{c} \sqrt{\frac{\ln R_{\max}}{R_{\max}}},$$

where $R_{\min} = \alpha + \min(\beta)$ and $R_{\max} = \alpha + \max(\beta)$, with $\alpha = p \cdot d_1 R_1 + (1-p)d_2 R_2$ and $\beta = \{(1-d_1)R_1, (1-d_2)R_2\}$; and $\bar{c} = 2pd_1R_1\sigma_1^2 + 2(1-p)d_2R_2\sigma_2^2$ whenever $R_{\max} < e$. In this inequality, the symbols R , d and σ^2 denote the growth rate, dispersal probability and a measure of the dispersal distance (namely the variance of the dispersal kernels) and the subscripts 1 and 2 refer to the vital rates in favourable and unfavourable patches respectively. The habitat quality is determined by the local growth rate, with $R_1 > 1$ in favourable patches and $R_2 \leq 1$ for unfavourable. In their analysis, p refers to the proportion of favourable patches in the available habitat.

The population will spread whenever $\alpha + \min(\beta) > 1$, which requires a balance in the survival of the migrating and sedentary populations. Even if all individuals from unfavourable patches emigrate ($d_2 = 1$) for instance, the population can spread only $pd_1R_1 + (1-p)d_2R_2 > 1$. This invasion threshold can be interpreted in different ways, namely, the invasion will be successful if (1) there are sufficient dispersers from the favourable patches: $d_1 > (1 - (1-p)R_2) / (pR_1)$ or (2) there are enough favourable patches in the environment: $p > (1 - R_2) / (d_1R_1 - R_2)$, or (3) the population can grow fast enough in the favourable patches $R_1 > (1 - (1-p)R_2) / (pd_1)$.

Habitat destruction not only can reduce the overall availability of favourable habitats, but also affect the size of the available patches (Bailey et al. 2010; Bennett and Saunders 2010). This aspect of habitat fragmentation will further reduce the chance of migrating individuals to find suitable patches (Thomas, 2000; Thomas et al., 2006). Ramanantoanina and Hui (2015) speculated that this will slow the spread of a population, which is also in accordance with field observations of insect outbreaks as natural enemies fail to control the pest due to habitat fragmentations (Ouyang et al., 2014; With, 2002).

4 Effect of Predation

Habitat suitability and the resulting dispersal behaviours are not solely determined by abiotic factors. Predation, for instance, is one of the most fundamental biotic interactions in ecology which can affect individual behaviours. Although early theories considerably advanced the understanding of predator-prey systems (Beddington et al., 1975; Berryman, 1992; Rosenzweig and MacArthur, 1963), they often implicitly assume well-mixed homogenous populations in space, namely the mean-field assumption and thus violate the reality that the spatial distribution of species is rarely homogenous but spatially autocorrelated (Fortin and Dale, 2005; Hui et al., 2010; Kokubun et al., 2008). As such, more recent models commonly use spatially explicit processes on the dynamics and viability of populations (Murray 2002; Neubert et al., 1995; Petrovskii and Li, 2005) to implement different survival strategies that can lead to the spatial heterogeneity of species distribution.

Indeed, different ways of capturing prey have been observed in predators. While some predators sit and wait for their prey at hidden places (e.g. crab spiders; Morse, 2006), others actively change their hunting ground according to prey density (e.g. pythons; Madsen and Shine, 1996). In contrast, prey can also improve its survival rate by forming swarms for anti-predation (Lindén, 2007; Siegfried and Underhill, 1975) or actively avoiding encountering potential predators (e.g. Hauzy et al., 2007; great white shark, Weng et al., 2007)). Consequently, different dispersal behaviours naturally arise from the optimization of species evolutionary fitness. Besides affecting its own survival, dispersal behaviours can also potentially affect the

invasiveness of non-invasive species as well as the spatiotemporal patterns of the invasion (Holway and Suarez, 1999; Rehage and Sih, 2004).

Various theoretical and empirical studies have highlighted different dispersal behaviours in predator-prey systems, namely the effect of prey-induced dispersal in predator's (El Abdllaoui et al., 2007; Ainseba et al., 2008; Chakraborty et al., 2007; Tao, 2010) or the effects of prey refuge and density-dependent mortality on species persistence (Forrester and Steele, 2004; Gonzalez-Olivares and Ramos-Jiliberto, 2003). Predator-prey interactions have given rise to a wide variety of spatial dynamics, ranging from spatial synchrony (i.e. the dynamics of populations at different localities coincide) to spatial chaos (Gao et al., 2007; Holyoak and Lawler, 1996; Li et al., 2005; Sherratt et al., 1997; Vasseur and Fox, 2009). While the former tend to promote the extinction of the metapopulations (Matter, 2001), the latter can boost persistence by providing refuge and promoting rescue effect (Allen, 2003).

Interspecific density-dependent dispersals do not only affect the persistence of metapopulations but also play a major role in the spread of non-native species in novel environments (Shigesada and Kawasaki, 1997; Sutherland et al., 2002). In the absence of interspecific density-dependent dispersal, Lin (2011) showed that the rate of spread as well as the density of the prey population is diminished by the presence of predators (see also Owen and Lewis, 2001; Shigesada and Kawasaki, 1997). Pan (2013) on the other hand suggested the prey population can accelerate the spread of the predator species by invading the novel environment first and thus providing resources for the predators.

A recent study (Ramanantoanina et al., 2011) suggested more complicated dynamics of the prey and predator in the presence of interspecific density-dependent dispersal behaviours, namely prey evasion (PE) and predator pursuit (PP). PE portrays the tendency of prey avoiding predators by dispersing into adjacent patches with fewer predators, while PP describes the tendency of predators to pursue the prey by moving into patches with more prey. The results suggest that rate of range expansion of the predators is closely tied with that of the prey. Indeed this is the case as the model inherently assumed that the predator feed only on one prey (specialist predator) and thus the predator's range is limited by that of the prey (Kubisch et al. 2014). The rate of spread of both species were found to be increased by weak density dependent dispersal (Tsyganov et al. 2004) but lessened as the PE and PP effects became stronger (Ramanantoanina et al., 2011).

The rates of spread resulting from the PE and PP are indeed supported by the spatial patterns of the population dynamics. When the PE effect is strong for instance, prey dispersal is solely motivated by the fear of the predators. The prey population therefore will only spread until they reach a predator-free environment at the front of the range expansion. In addition, strong PE reduces the resource available to the predators and slows down the range expansion of the species. Strong PP has similar effects on the spread of the population as it tends to suppress the prey population from range expansion by decreasing local populations.

In addition to ecological responses, recent studies speculate that PE and PP behaviours may also have resulted from evolutionary dynamics of dispersal. (Travis et al., 2013) suggested that predators are likely to evolve to higher emigration and more selective in their destination when the preys exhibit complex spatiotemporal dynamics. Selection for less prey dispersal on the other hand was predicted when predators have small home range (Barraquand and Murrell, 2012). Evenly distributed predators selects for more prey dispersal. It is of common accord that predator-prey interactions have a wide range of potential effects on either species' range which are beyond the realm of purely ecological behaviours.

5 Effect of Mixed Propagules

Clearly, dispersal is not a static characteristic even at individual level. There are growing evidences that

dispersal can vary in space and time (Berthouly-Salazar et al., 2012; Simmons and Thomas, 2004; Vander Wall, 2008). Even though some works have considered the possibility of "slow and fast" dispersers in a population (Dercote et al., 2006) and numerous simulation-based models have considered the evolution of dispersal strategies and dispersal distances in a population (Kubisch et al., 2014; Travis et al., 2009), the study of the spatiotemporal dynamics of dispersal and its impact on a species' range lags considerably behind.

Multiple dispersal strategies have also been implemented using stratified diffusion model. In this type of model, population range advances as different colonies are formed through long distance dispersal and merged into a super colony by short distance dispersal (Clark et al., 1998; Shigesada et al., 1995). Theoretical investigations suggest that Type II (biphasic range expansion in which a break of slope is observed between two linear range expansions) and Type III (a continuously accelerating range expansion, but can also be followed by a saturation when the available habitat has been fully invaded) range expansions can emerge from stratified diffusions. Such pattern of dispersal is commonly supported when propagules can be transported by multiple dispersal vectors such as wind or humans (usually leads to long-distance dispersal) or animal fur (often inducing short distance dispersal) (Aubry et al. 2006; Van Leeuwen et al., 2013; Wichmann et al., 2009).

The transport of propagules does not only depend on the dispersal vectors but also on individual traits. Non-random patterns have been observed in seed dispersal depending on the seed size (Xiao et al., 2005). Active dispersers also display variety morphological traits which yield different dispersal abilities time (Berthouly-Salazar et al., 2012; Simmons and Thomas, 2004; Vander Wall, 2008). Ramanantoanina et al. (2014) investigated the importance of such variation of dispersal abilities which are also common in the initial propagule (the introduced population) (Erfmeier et al., 2013; Merritt et al., 2010). Indeed, studies show that the initial propagule often consists of a suite of individuals with different performance ability, and assuming propagules with identical traits often leads to an underestimation of the spreading rate in animals. Furthermore, propagule size (that is, the number of individuals released into a novel area promotes the invasion success as large propagule size can efficiently counteract the positive density dependence caused by the Allee and founder effects that hamper the establishment of initial propagules in a novel ecosystem (Blackburn et al., 2013; Korsu and Huusko, 2009; Simberloff, 2009).

Ramanantoanina et al (2014) used integrodifference equations to incorporate individuals with different dispersal abilities in the initial propagule and speculated that the range advance between two generations is determined by the ability of the population at the front of the invasion. The range expansion could be accelerating due to a dynamic dispersal kernel driven by the spatial sorting for stronger dispersers at the range front. The rate of spread however eventually reaches equilibrium with median value

$$c = \sqrt{2 \ln(R)} d^2 \left(1 + \frac{\ln(R)}{12} \right) \gamma_2$$

Where $d^2 = \exp(\mu + (2\sigma^2)^{1/2} \text{erf}^{-1}(2^{1-1/n} - 1))$ when the dispersal abilities from the initial propagule follows the lognormal distribution $\ln N(\mu, \sigma^2)$ and n is the propagule size. The new formula confirms that the rate of spread increases with propagule size, more notably for more diverse initial propagule. The classic formula is shown to be a special case of the new ones, corresponding to a homogeneous initial propagule ($\sigma^2=0$).

Besides the many contexts from which dispersal strategies arise, range expansion itself imposes a selection force on dispersal during which individuals with stronger dispersal abilities are more likely to locate at the advancing range front. This phenomenon, commonly known to as spatial sorting, is supported by different evidence in nature, such as longer legs in cane toads (*Bufo marinus*) in Australia (Phillips et al., 2006), the wing shape of Indian mynas (*Acridotheres tristis*) in South Africa (Berthouly-Salazar et al., 2012), and long-winged morphs of bush crickets in UK (Simmons and Thomas, 2004). Although theoretical investigations

using diffusion of dispersal traits predict less diversity at the range front, spatial sorting has also been speculated to explain the accelerating range expansion (Bechinou et al., 2012).

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