

# Evolution of Dispersal Kernels

Andreas Gros

*Department of Animal Ecology, University of Würzburg, Germany*

## Goal

To investigate the evolution of dispersal kernels in the spatial logistic model, driven by either inter- or intraspecific competition in continuous space and time.

## Background and motivation

From an individual's perspective, dispersal may be motivated by a number of (not mutually exclusive) reasons: avoiding competition for resources (either inter- or intraspecific) (Lambin et al., 2001), minimizing kin competition (e.g. Hamilton & May, 1977; Comins, 1982; Frank, 1986; Kisdi, 2004), avoiding inbreeding (Perrin & Goudet, 2001), or coping with the temporal variability of resource availabilities (Levin et al., 1984; Travis & Dytham, 1999; Gandon & Michalakis, 2001). Generally, dispersal is favoured as long as individuals have a higher inclusive fitness when they move away from their natal habitat (Frank, 1986; Metz & Gyllenberg, 2001; Poethke & Hovestadt, 2002; Dytham, 2003). Law & Dieckmann (2000) and Law et al. (2003) showed that the "individual's-eye view" is essential in modeling and analyzing the spatial dynamics resulting from intra- and interspecific interactions. These interactions result in spatial patterns of species abundance, which develop according to the individuals' competitive abilities (Law et al., 2003). When the landscape is assumed to be homogeneous in space and time, it is only the abundance and spatial distribution of individuals that define the heterogeneous environmental conditions to which the potential for spreading adapts. This eco-evolutionary feedback results in a highly dynamic fitness landscape that exerts the selective pressures driving the evolution of dispersal traits. In the modeling approach of (Dieckmann & Law 2000), dispersal kernels are used for describing the propagation of individuals. Such kernels are defined as probability densities, with their shape determining the relative spatial distribution of an individual's offspring around its parent. Evolution in the shape of dispersal kernels in a dynamically changing environment has not been investigated to date. Any approach in this direction will have to account for the fact that, without any costs of dispersal, the evolving distances are likely to escalate evolutionarily, since this minimizes kin competition and maximizes the chance for escape from unfavorable environmental conditions -- like a highly crowded neighbourhood (Leturque & Rousset, 2002). It is therefore important to either incorporate costs of dispersal, or to reasonably limit dispersal ranges.

As we investigate the evolution of dispersal, we utilize function-valued traits, measuring the amount of dispersal over a continuum of relevant distances. Function-valued traits give a very detailed description of adaptive features in biological organisms. However, directly following the resultant stochastic dynamics of function-valued traits through individual-based simulations is a fairly complex undertaking. Therefore, the formal link between the individual-based ecology, which is fast and stochastic, and a description of the expected evolutionary process, which is slow and deterministic, has to be carefully constructed (Dieckmann et al., 2005), in order to arrive at simplified models. In this context, particular attention must be devoted to the parameterization of function-valued adaptive traits and the formulation of their

evolutionary constraints. While striving for parsimony, an exaggerated parameter-reduction can lead to spurious results because then the evolutionary dynamics can easily get trapped in local optima since low-dimensional parameterizations are prone to inhibit so-called 'extra-dimensional bypasses' (Conrad, 1990).

The modeling of small-scale interactions has already led to a better understanding of spatial population dynamics (Law et al., 2003), by enabling, e.g. species coexistence where mean-field approximations predict the extinction of less competitive species (Law & Dieckmann, 2000). Incorporation of adaptive dynamics into such models will result in an even more realistic picture of spatial population dynamics

## Research questions

I will try to find out, whether there are evolutionary attractors of dispersal kernel shape, and, given such attractors are found, how these depend on the competition regime considered in the model. For the sake of simplicity, I will concentrate on systems consisting of one and (time permitting) two species with different competitive abilities.

## Methods and work plan

The framework of adaptive dynamics of function-valued traits offers a suitable method for investigating the course and outcome of long-term evolution of dispersal kernels under the assumption of asexual inheritance (Dieckmann & Law, 1996; Dieckmann & Ferrière, 2004; Dieckmann et al., 2005). The population dynamics driving the eco-evolutionary process will incorporate resource competition owing to local intra- and interspecific competition. Such competitive interactions can be described by spatial logistic models in continuous space and time (Law et al., 2003). I will implement two individual-based models describing the polymorphic stochastic dynamics of populations with either scalar-valued or function-valued traits, which determine the shape of the corresponding dispersal kernels. To be able to identify evolutionary attractors in the shapes of dispersal kernels, it is helpful to gain a deterministic description of the same population dynamics. Therefore, it is necessary to reduce the polymorphic stochastic models (*PSM*) to corresponding monomorphic deterministic models (*MDM*). Altogether there are four models, which I describe in the following:

1. *Polymorphic stochastic model with scalar-valued adaptive traits (PSM<sup>s</sup>)*  
To derive an eco-evolutionary population dynamic with the full spectrum of stochasticity resulting from interacting and mutating individuals, I will implement an individual-based model based on spatial logistic equations for species interactions similar to the approach of Law et al. (2003). In this step, I use a bivariate Gaussian function as dispersal kernel,

$$m_i(x - x') = \frac{1}{M} \exp\left(-\frac{|x' - x|^2}{2(S_{m_i})^2}\right). \quad (1)$$

This function depends on a scalar-valued trait, as its shape is given by only one parameter: the standard deviation  $S_{m_i}$ , which denotes the trait value of the individual of species  $i$  in focus, and determines the kernel's width.

By considering natal dispersal, the dispersal kernel is directly linked to the probability for an individual of type  $i$ , located at  $x$ , to give birth to an offspring at  $x'$ :  $B_i(x, x') = b_i m_i(x - x')$ , with the intrinsic birth rate  $b_i$ .

Mutations generate variability with a probability  $\mu_i$  per birth event and mutant trait values are obtained by adding a mutation effect drawn from a Gaussian distribution with mean 0 and given (small) standard deviation.

Competition affects the probability that an individual of species  $i$  at location  $x$  dies,

$$D_i(x, p) = d_i + \sum_j d'_{ij} \int w_{ij}(x' - x) [p_j(x', t) - \delta_{ij} \delta_x(x')] dx', \quad (2)$$

with the interaction kernel

$$w_{ij}(x - x') = \frac{1}{W} \exp\left(-\frac{|x' - x|^2}{2(S_{w_{ij}})^2}\right). \quad (3)$$

The kernels are normalized so that their integrals over  $x' - x$  are equal to 1, with  $M$  and  $W$  being the normalization constants.  $d_i$  denotes a species' intrinsic death rate, whereas  $d'_{ij}$  defines the strength of influence of either intraspecific ( $i = j$ ) or interspecific ( $i \neq j$ ) competition of species  $j$  on  $i$ .  $S_{w_{ij}}$  indicates the characteristic range of competitive influence of species  $i$  on  $j$ . The local density of individuals of type  $i$  at point  $x'$  is denoted by  $p_i(x', t)$ , and the expression  $\delta_{ij} \delta_x(x')$  removes the individual of type  $i$  at  $x$ , because it does not compete with itself (Law et al., 2003).

2. *Polymorphic stochastic model with function-valued adaptive traits (PSM<sub>f</sub>)*  
The description of the birth process in this step is similar to the one above, but with the function-valued trait  $m_i(a)$ , which measures the amount of dispersal over a distance  $a \in [0, L]$ ;  $L > 0$ ,  $L$  being the upper limit for dispersal distances. To facilitate the implementation of this model, the function-valued traits will be reasonably discretized into a histogram of distance classes wherein mutations result in shifts in the dispersal amplitude of a distance class. More refined mutation models (based on explicit variance-covariance functions) may be considered later.
3. *Monomorphic deterministic model with scalar-valued adaptive traits (MDM<sub>s</sub>)*  
Assuming the ecological and the evolutionary timescale to be sufficiently separated, we regard each species within the population as monomorphic. Thus, selection has enough time to take effect before a new viable and potentially advantageous mutant replaces a resident trait:  $m_i \rightarrow m'_i$  (Dieckmann et al., 2005). To devise a spatially implicit version of our model, we use  $C(\xi)$ , the second spatial moment, which describes how pair densities vary with the distance  $\xi$  between a pair's members (Dieckmann & Law, 2000).

In the following, index 1 denotes the resident species with trait value  $S_m$  and 2 the corresponding mutant species with trait value  $S'_m$ . The differential equations describing the population dynamics of densities  $N_i$  in the resident and mutant populations are given by

$$\begin{aligned} \frac{d}{dt} N_i &= (b_i - d_i) N_i \\ -\sum_j d'_{ij} \int w_{ij}(\xi) C_{ij}(\xi) d\xi, \quad i, j \in \{1, 2\}. \end{aligned} \quad (4)$$

The dynamics of pair of densities  $C_{ij}(\xi)$  is given by

$$\frac{d}{dt} C_{ij}(\xi) = +\delta_{ij} b_i m_i(-\xi) N_i \quad (5a)$$

$$+b_i \int m_i(\xi') C_{ij}(\xi + \xi') d\xi \quad (5b)$$

$$-d_i C_{ij}(\xi) \quad (6a)$$

$$-\sum_k d'_{ik} \int w_{ik}(\xi'') T_{ijk}(\xi, \xi'') d\xi'' \quad (6b)$$

$$-d'_{ij} w_{ij}(\xi) C_{ij}(\xi) \quad (6c)$$

$$-\sum_k d'_{ik} \int w_{ik}(\xi'') T_{ijk}(\xi, \xi'') d\xi'' \quad (6d)$$

$$-d'_{ij} w_{ij}(\xi) C_{ij}(\xi) \quad (6e)$$

$$-|m_i| C_{ij}(\xi) \quad (7a)$$

$$+\int m_i(\xi') C_{ij}(\xi + \xi') d\xi' \quad (7b)$$

$$+ \langle i, j, \xi \rightarrow j, i, -\xi \rangle, \quad i, j \in \{1, 2\}, \quad (7c)$$

with the contribution of birth events (5), death events (6), and movement events (7) to changes in  $C_{ij}(\xi)$ . The term  $\langle i, j, \xi \rightarrow j, i, -\xi \rangle$  accounts for the fact that all birth and death events do not only occur to an  $i$  individual, but can also happen to the  $j$  individual of the  $ij$  pair: it is shorthand for all preceding terms after changing  $i$  to  $j$ ,  $j$  to  $i$  and  $\xi$  to  $-\xi$ . The moment closure needed for the triplet density  $T_{ijk}$  in (6b) and (6d) will be a power-2 closure (Murrell et al., 2004).

There are three time scales present in the invasion dynamics of a mutant in an established resident population: the slowest one is the development of the resident population ( $N_1, C_{11}$ ), which is considered to be at equilibrium. The intermediate timescale is the progress of the mutant population size ( $N_2$ ), and the fastest development occurs in the spatial distribution of mutants ( $C_{12}, C_{22}$ ). Thus, each iteration of the model consists of three steps: After calculating the resident dynamic, the equations for  $C_{12}, C_{22}$  can be solved, assuming them to be at a local pseudo-equilibrium, to calculate the mutant population's per capita growth rate  $\frac{1}{N_2} \frac{d}{dt} N_2$ . The latter quantity is referred to as the mutant's invasion fitness  $f(S'_m, S_m)$  in the given resident population. Its derivative,  $g(S_m) = \partial f(S'_m, S_m) / \partial S'_m|_{S'_m=S_m}$ , known as the selection gradient determines the expected rate of evolutionary change according to the canonical equation of (scalar-valued) adaptive dynamics (Dieckmann & Law, 1996),

$$\frac{d}{dt} S_m = \frac{1}{2} \mu_{S_m} \sigma_{S_m}^2 \hat{N}_m g(S_m). \quad (8)$$

Here,  $\hat{N}_m$  denotes the equilibrium population size of the resident population, and  $\mu_{S_m}$  is the fraction of mutations per birth.  $\sigma_{S_m}^2$  is the variance of the mutation distribution  $M$  (Dieckmann & Law, 1996),

$$\sigma_m^2(S_m) = \int \Delta S_m^2 M(S_m, \Delta S_m) d\Delta S_m. \quad (9)$$

#### 4. Monomorphic deterministic model with function-valued adaptive traits (MDM<sub>f</sub>)

The main difference to the step above is the switch to function-valued adaptive traits. This approach enables individuals to adapt freely their dispersal kernel in response to a ecological environment.

Based on the prerequisites provided in the step above, we solve the canonical equation, governing the expected adaptive dynamics of function-valued traits (Dieckmann et al., 2005),

$$\frac{d}{dt}m(a) = \frac{1}{2}\mu_m\hat{N}_m\int\sigma_m^2(a',a)g_m(a')da'. \quad (10)$$

Here,  $\sigma_m^2$  is the variance-covariance function of the mutation distribution  $M$  at trait value  $m$ ,

$$\sigma_m^2(a,a') = \int [m'(a') - m(a)][m'(a') - m(a)]M(m,m')dm', \quad (11)$$

where the integration extends over all feasible trait values  $m'$ . The function  $g$  is the selection gradient and is obtained as the functional derivative of the invasion fitness  $f(m',m)$ ,

$$g_m(a) = \lim_{\varepsilon \rightarrow 0} [f(m + \varepsilon\delta_a, m) - f(m, m)]/\varepsilon = \left. \frac{\partial}{\partial \varepsilon} f(m + \varepsilon\delta_a, m) \right|_{\varepsilon=0}. \quad (12)$$

The MDM models will be used to identify evolutionary attractors in the shape of dispersal kernels and the corresponding PSM models will be used for comparison. Also, by comparing the results of the scalar-valued and function-valued models, it is possible to evaluate the capacity of the simpler scalar-valued adaptive traits to approximate the kernel shapes of the more complex function-valued adaptive traits.

## Relevance and link to ADN's research plan

This project extends the work of the ADN Program on dispersal evolution, the spatial logistic equation, spatial invasion fitness, and the adaptive dynamics of function-valued traits.

## Expected output and publications

This work is intended for publication as a co-authored research article and will also be included in my PhD thesis.

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