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# Dispersal kernels: review

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## 15.1 Basic concepts and definitions

Dispersal distance, the Euclidian distance between ‘start’ and ‘end’ points of a dispersal event, is recognized as a fundamental characteristic of the dispersal process, defined here as the movement of dispersers—called diaspores, propagules, gametes, or dispersing individuals in the literature—from their natal site or their breeding home range to a new place of potential establishment. Distance constitutes the most basic spatial descriptor of dispersal. For sexually reproducing plants, pollen and seed dispersal distances outline, respectively, the net displacement of the entire lifetime track of the male gamete or the individual; for migratory animals, in contrast, the dispersal distance often constitutes a tiny proportion of the lifetime track (Nathan *et al.* 2008). Although the dispersal distance cannot capture all aspects of how dispersal shapes post-dispersal survival and subsequent population and community dynamics, it has been used extensively in this context because it represents some key features of these relationships (Janzen 1970; Connell 1971; Kot *et al.* 1996; Nathan and Muller-Landau 2000). In this chapter, we discuss the basic concepts, questions, tools, and future directions in using dispersal kernels to study the behavior and ecology of animals and plants, and refer the readers to Chapter 16 for a discussion on the evolution of dispersal and dispersal kernels (Ronce 2007).

The statistical distribution of dispersal distances in a population is termed the ‘dispersal kernel’. It is a probability density function (pdf) describing the distribution of the post-dispersal locations relative to the source point. The term ‘dispersal kernel’ is equivalent to various terms previously used in the literature such as ‘contact distribution’ (Mollison 1977) and ‘dispersal distribution’ (Tufto *et al.* 1997). These terms

encompass the probabilistic special case of the ‘dispersal curve’, a general popular term used for any graphical representation of the distribution of dispersal distances or the density of dispersing individuals at different distances from the source. The term ‘dispersal kernel’ emerged from mathematical studies of integro-differential equations for population spread (Thieme 1977; Diekmann 1978; Van den Bosch *et al.* 1990; see Box 15.1). Indeed, ‘kernel’ was used in integration theory since Hilbert (1904) and etymologically means the ‘core’, ‘nucleus’, or ‘inner part’; hence, a dispersal kernel represents the contribution of a specific core (source point) to the re-organization of certain units (e.g. individuals) in a larger entity (population). Three influential studies analysing the relationship between the shape of the dispersal kernel and population spread (Mollison 1991; Kot *et al.* 1996; Clark *et al.* 1999) popularized the term in ecology. It was then integrated successively in various fields of dispersal ecology, mostly in studies of plant seeds and pollen (e.g. Nathan and Muller-Landau 2000; Klein *et al.* 2003; Robledo-Arnuncio *et al.* 2004) and of larvae of marine organisms (e.g. Largier 2003; Siegel *et al.* 2003; Kinlan *et al.* 2005), but also in studies of various other taxa including pathogens (Skelsey *et al.* 2005), water fleas (Havel *et al.* 2002), insects (Baguette 2003), birds (van Houtan *et al.* 2007), and mammals (Revilla and Wiegand 2008). The rich ensemble of species of various taxonomic groups for which dispersal kernels were estimated is illustrated in Table 15.1.

Cousens *et al.* (2008) argued that ‘dispersal kernel’ has been used inconsistently and confusingly to denote either the distribution of the distances travelled or the distribution of the post-dispersal locations relative to the source location. Various terms were suggested to distinguish these two

**Table 15.1** Various functions used for the dispersal kernel, mostly in phenomenological approaches. Expressions for the dispersal location kernel  $k_l(r)$  have been re-parameterized to include a scale parameter ( $a$ ) homogeneous to a distance and a shape parameter ( $b$ ) determining the shape of the curve, and particularly the relative weight of long-distance events.

Kernel name	$k_l(r)$ expression*	Parameter values	Mean dispersal distance	Tail fatness	Taxonomic groups applied	Model comparison	Recommended use
Gaussian	$\frac{1}{\pi a^2} \exp\left(-\frac{r^2}{a^2}\right)$	$a > 0$	$\frac{a\sqrt{\pi}}{2}$	Thin-tailed	Pollen (Austerlitz <i>et al.</i> 2004; Goto <i>et al.</i> 2006), Seeds (Sagnard <i>et al.</i> 2007), Seedlings (Goto <i>et al.</i> 2006), Beetles (Chapman <i>et al.</i> 2007), Moths (Bianchi <i>et al.</i> 2009), Fish (Coombs and Rodriguez 2007), Birds (Van Houten <i>et al.</i> 2007—named Rayleigh therein), Mammals (Krkosek <i>et al.</i> 2007)	Poorer fits than more leptokurtic kernels in general, except occasionally for heavy seeds (Sagnard <i>et al.</i> 2007)	In general, should be used only as a reference against more leptokurtic kernels. Adequate to represent the result of dispersal through diffusion or completely random walk during a constant time.
(Negative) Exponential	$\frac{1}{2\pi a^2} \exp\left(-\frac{r}{a}\right)$	$a > 0$	$2a$	Exponential	Pollen (Austerlitz <i>et al.</i> 2004; Goto <i>et al.</i> 2006), Seeds (Willson 1993; Clark <i>et al.</i> 1999; Nathan <i>et al.</i> 2000; Sagnard <i>et al.</i> 2007; Jones and Muller-Landau 2008), Seedlings (Goto <i>et al.</i> 2006), Butterflies (Baguette 2003; Fric and Konvicka 2007), Mosquitos (Estep <i>et al.</i> 2010), Beetles (Chapman <i>et al.</i> 2007; Carrasco <i>et al.</i> 2010)	Generally outperforms the Gaussian but is outperformed by more leptokurtic kernels, except occasionally for seed dispersal and butterflies (Fric and Konvicka 2007)	In general, should be used only as a reference against more fat-tailed kernels. Represents well a travel at constant speed in a random direction with a constant stopping rate. Also obtained from a correlated random walk with settlement (Hovestadt <i>et al.</i> 2011)
Exponential Power (Gaussian for $b = 2$ ; Exponential for $b = 1$ )	$\frac{b}{2\pi a^2 \Gamma(2/b)} \exp\left(-\frac{r^b}{a^b}\right)$	$a, b > 0$	$a \frac{\Gamma(3/b)}{\Gamma(2/b)}$	$b > 1$ : thin-tailed, $b < 1$ : fat-tailed. Always thinner than power laws	Pollen (Hardy <i>et al.</i> 2004; Oddou-Muratorio <i>et al.</i> 2005, Robledo-Arnuncio and Gil 2005, Goto <i>et al.</i> 2006), Seeds (Clark <i>et al.</i> 1998, González-Martínez <i>et al.</i> 2006, Schurr <i>et al.</i> 2008), Seedlings (Ribbens <i>et al.</i> 1994 with $b=3$ , Goto <i>et al.</i> 2006), Beetles (Chapman <i>et al.</i> 2007), Moths (Bianchi <i>et al.</i> 2009), Mammals (Krkosek <i>et al.</i> 2007)	Outperforms the Gaussian, Exponential, 2Dt and Geometric functions for pollen (Austerlitz <i>et al.</i> 2004) Values for $b$ generally found from 0.3 to 0.6	Well suited for pollen dispersal. Encompasses the Gaussian and Exponential as special cases and therefore adequate for kernel's shape comparisons.

2Dt	$\frac{(b-1)}{\pi a^2} \left(1 + \frac{r^2}{a^2}\right)^{-b}$	$a > 0; b > 1$	$a \frac{\sqrt{\pi}}{2} \frac{\Gamma\left(b - \frac{3}{2}\right)}{\Gamma(b-1)}$ $\infty$ for $b < 3/2$	Fat-tailed Power-law tail	Pollen (Austerlitz <i>et al.</i> 2004; Goto <i>et al.</i> 2006), Seeds (Clark <i>et al.</i> 1999; Greene <i>et al.</i> 2004; Canham and Uriarte 2006; Schurr <i>et al.</i> 2008; Venable <i>et al.</i> 2008), Seedlings (Greene <i>et al.</i> 2004; Goto <i>et al.</i> 2006) Beetles (Carrasco <i>et al.</i> 2010, with $b = 1$ )	Outperforms many other kernels in seed dispersal studies, except occasionally the lognormal and WALD (Clark <i>et al.</i> 1999; Greene <i>et al.</i> 2004; Schurr <i>et al.</i> 2008; Jones and Muller-Landau 2008). Compares more poorly to other kernels for pollen (Austerlitz <i>et al.</i> 2004).	Well suited for seed dispersal studies. Obtained as a continuous mixture of Gaussian kernels with variance parameters distributed as the inverse of a Gamma distribution. The particular case $b = 3/2$ was obtained as the deposition location on the ground of a 3D drift Brownian motion from an elevated source when gravity is negligible (Stockmarr 2002)
(Inverse) Power-law	$\frac{(b-2)(b-1)}{2\pi a^2} \left(1 + \frac{r}{a}\right)^{-b}$	$a > 0; b > 2$	$\frac{2a}{b-3}$ $\infty$ for $b < 3$	Fat-tailed Power-law tail	Pollen (Austerlitz <i>et al.</i> 2004; Devaux <i>et al.</i> 2007)	Outperformed the exponential-power family when fitting long-distance pollen dispersal data (Devaux <i>et al.</i> 2007)	Adequate for describing very fat tails.
(Inverse) Power-law (undefined)	$\left(\frac{r}{a}\right)^{-b}$	Not a PDF (infinite integral)	Not a PDF (infinite integral)	Fat-tailed Power-law Not a PDF (infinite integral)	Seeds (Willson 1993; Nathan <i>et al.</i> 2000), Butterflies (Baguette 2003; Fric and Konvicka 2007)	Less sensitive than the negative exponential to the spatial scale of the dispersal observations (Fric and Konvicka 2007)	Have been used traditionally in numerous studies to fit dispersal curves, but does not fit the definition of a dispersal kernel since it is not a PDF. For dispersal kernel representations, should be replaced by the power-law PDF given above.
Logistic	$\frac{b}{2\pi a^2 \Gamma\left(\frac{2}{b}\right) \Gamma\left(1 - \frac{2}{b}\right)} \left(1 + \frac{r^b}{a^b}\right)^{-1}$	$a > 0; b > 2$	$a \frac{\Gamma\left(\frac{3}{b}\right) \Gamma\left(1 - \frac{3}{b}\right)}{\Gamma\left(\frac{2}{b}\right) \Gamma\left(1 - \frac{2}{b}\right)}$	Fat-tailed Power-law tail	Pollen (Klein <i>et al.</i> 2006b) Beetles (Chapman <i>et al.</i> 2007)	Like generally the power-law functions, it outperformed exponential families in Chapman <i>et al.</i> (2007)	Suitable for frequent long-distance dispersal events together with weak effect of distance close to the source

(continued)

**Table 15.1** *Continued*

Kernel name	$k_i(r)$ expression*	Parameter values	Mean dispersal distance	Tail fatness	Taxonomic groups applied	Model comparison	Recommended use
Lognormal	$\frac{1}{(2\pi)^{3/2} br^2} \exp\left(-\frac{\log(r/a)^2}{2b^2}\right)$	$a>0; b>0$	$a \exp\left(\frac{b^2}{2}\right)$	Fat-tailed	Seeds (Greene <i>et al.</i> 2004; Stoyan and Wagner 2001; Canham and Uriarte 2006; Schurr <i>et al.</i> 2008; Jones and Muller-Landau 2008), Seedlings (Greene <i>et al.</i> 2004)	Outperforms many other kernels, except occasionally the 2Dt and WALD, in seed dispersal studies (Greene <i>et al.</i> 2004; Schurr <i>et al.</i> 2008; Jones and Muller-Landau 2008).	Well suited for seed dispersal studies, especially when the peak of the distribution is presumably not at zero distance from the source (e.g. seedlings after establishment under Janzen-Connell effects)
Gaussian Mixture (particular case of the general mixture below)	$\frac{p}{\pi a_1^2} \exp\left(-\frac{r^2}{a_1^2}\right) + \frac{1-p}{\pi a_2^2} \exp\left(-\frac{r^2}{a_2^2}\right)$ $a_1, a_2 > 0$ $0 < p < 1$		$\frac{\sqrt{\pi}}{2}(pa_1 + (1-p)a_2)$	Leptokurtic Never fat-tailed	Kernel integrating several vectors	Mostly used in theoretical studies (e.g. Bialozyt <i>et al.</i> 2006; Fayard <i>et al.</i> 2009)	
General Mixture	$pK_1(r) + (1-p)K_2(r)$				Exponential + inverse power and a variety of other mixtures used for Pollen (Goto <i>et al.</i> 2006; Slavov <i>et al.</i> 2009), Seeds (Bullock and Clarke 2000), Fish (Coombs and Rodriguez 2007), Butterflies (Hovestadt <i>et al.</i> 2011)	Outperformed non-mixture kernels when tested	Very versatile, though at the cost of increased dimensionality. Well-suited if short- and long-distance dispersal are suspected to be governed by different processes or vectors.
Inverse Gaussian (Wald)	$\frac{\sqrt{b}}{\sqrt{8\pi^3} r^5} \exp\left(-\frac{b(r-a)^2}{2a^2 r}\right)$	$a > 0; b > 0$	$a$	Leptokurtic Exponential tail Mode at $r > 0$	Wind dispersed propagules (Katul <i>et al.</i> 2005; Schurr <i>et al.</i> 2008)	Outperformed exponential, lognormal and 2Dt kernels in a seed dispersal study including source effects (Schurr <i>et al.</i> 2008)	Derived from a mechanistic wind dispersal model, hence well suitable for wind dispersal studies, especially when independent information on wind dispersal parameters is available.
Weibull (Gaussian for $b = 2$ )	$\frac{b}{2\pi a^2} r^{b-2} \exp\left(-\frac{r^b}{a^b}\right)$	$a > 0; b > 0$	$a \frac{\Gamma(1/b)}{b}$	Fat-tailed for $b < 1$ Mode at $r > 0$ for $b > 2$ $k_i(0) = \infty$ for $b < 2$	Pollen (Austerlitz <i>et al.</i> 2004; Goto <i>et al.</i> 2006), Seeds (Greene <i>et al.</i> 2004; Canham and Uriarte 2006), Seedlings (Greene <i>et al.</i> 2004; Goto <i>et al.</i> 2006), Flies (Taylor <i>et al.</i> 2010, with $b = 1.5$ ), Birds (Paradis <i>et al.</i> 2002; Kesler <i>et al.</i> 2010)	Generally outperformed by other kernels, such as the 2Dt and lognormal (Greene <i>et al.</i> 2004; Jones and Muller-Landau 2008), but has sometimes provided the best fits in pollen dispersal studies (Austerlitz <i>et al.</i> 2004)	Can fit well fat tails, but should be examined against other fat-tailed kernels in general.

Gamma (Exponential for $b = 2$ )	$\frac{1}{2\pi a^2 \Gamma(b)} \left(\frac{r}{a}\right)^{b-2} \exp\left(-\frac{r}{a}\right)$	$a > 0; b > 0$	$ab$	Peaks at 0 for $b \leq 2$ $k_l(0) = \infty$ for $b < 2$ Mode at $r = 0$ for $b > 2$ Exponential tail	Birds (van Houtan <i>et al.</i> 2007)	Was outperformed by a power-law tail (log-sech) in van Houten <i>et al.</i> 2007	Can be used alternatively to the related Weibull family function
Log-sech distribution (Cauchy for $b = 1$ )	$\frac{1/(\pi^2 b r^2)}{(r/a)^{1/b} + (r/a)^{-1/b}}$	$a > 0; b > 0$	$\infty$ for $b \geq 1$	Fat-tailed Power-law tail Flat shape close to 0 for $b < 1$ Sharp decrease in 0 for $b, \geq 1$	Birds (Paradis <i>et al.</i> 2002, van Houtan <i>et al.</i> 2007), Mammals (Krkosek <i>et al.</i> 2007 used a Cauchy in a 1D space)	Outperformed the Gaussian and the gamma (van Houtan <i>et al.</i> 2007). Outperformed the non power-law tails (Weibull, Exponential) in Paradis <i>et al.</i> 2002	Suitable for frequent long-distance dispersal events together with weak effect of distance close to the source

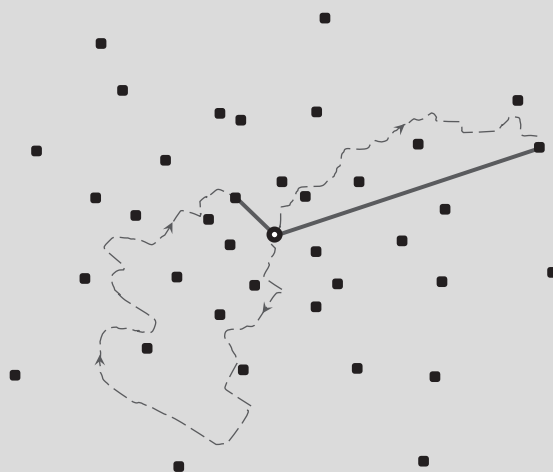
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\* For sake of consistency, for all models, we provide expressions for the dispersal location kernel  $[k_l(r)]$ . The expression can thus appear different to that originally published in the cited reference if the authors had provided the dispersal distance kernel  $[k_o(r)]$ . The relations between these two are detailed in Box 15.1.

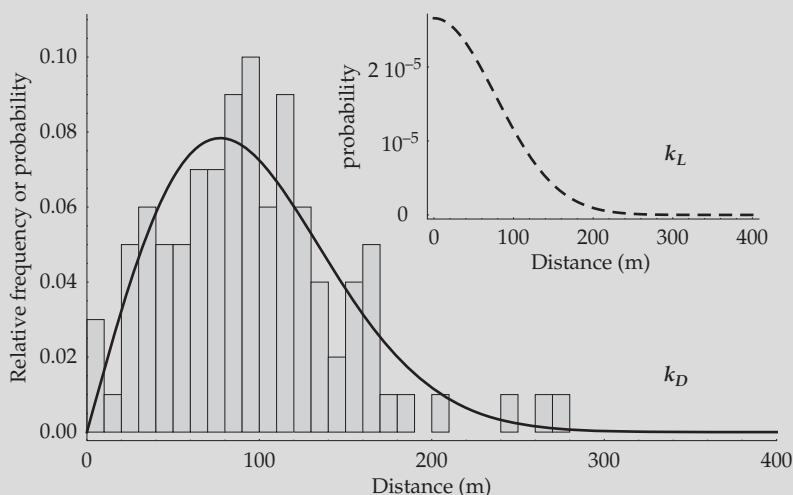
### Box 15.1 Basic formulations of dispersal kernels

Consider a single point source is the origin site of  $n$  dispersers drawn from a large population in a continuous space (Figure 15.1). The dispersal distance of each disperser is the net displacement from the source, or the Euclidian distance between the 'start' (the source) and the 'end' point of the dispersal event. The histogram (Figure 15.2) shows a hypothetical example for  $n = 100$  dispersers. Assume this histogram represents a continuous parametric distribution  $k$  characteristic of this population. Function  $k$  is a probability density function (pdf) termed the 'dispersal kernel', which can also be a discrete pdf in lattice space (Chesson and Lee 2005).

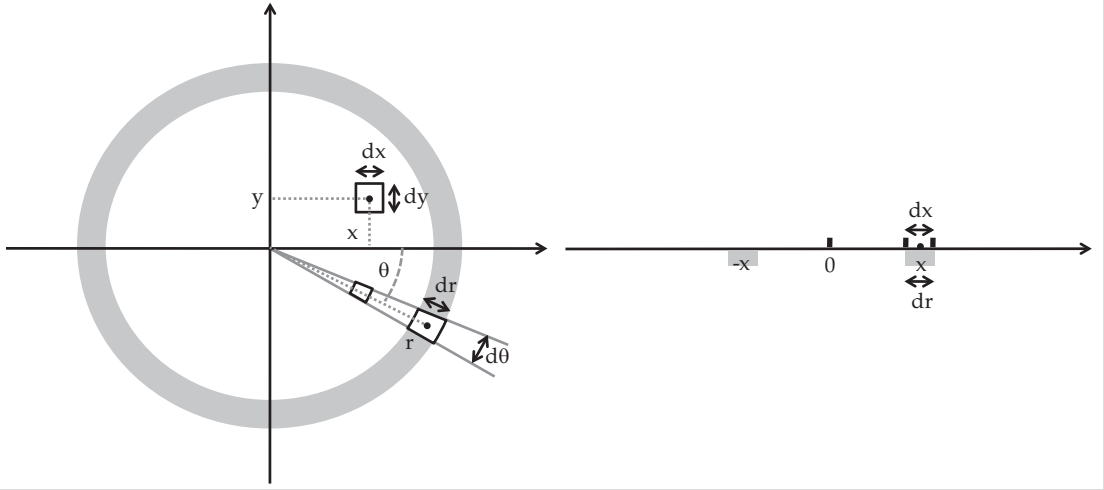
The dispersal kernel  $k$  can be defined as the pdf of the distribution of the end location of a disperser relative to the source point. It can be defined on a line or one-dimensional (1D) space, a plane or two-dimensional (2D) space, and even on a three-dimensional (3D) space for dispersal in water or canopy. This type of dispersal kernel was termed 'dispersal kernel' (Nathan and Muller-Landau 2000), 'two-dimensional (2D) dispersal kernel' (Cousens and Rawlinson 2001) or 'dispersal density kernel' (Nathan *et al.* 2008b). Here we propose the alternative term 'dispersal location kernel' to avoid confusion with 2D space and with the word 'density' of the pdf. In a 2D space, either a polar



**Figure 15.1** A schematic representation of dispersal from a single source (open circle at the center), showing the end points of dispersal events (black squares). The movement path (thin dashed line with arrows) and the dispersal distance (thick solid line) are shown for two dispersers.



**Figure 15.2** A histogram of 100 dispersal distances and the fitted dispersal distance kernel ( $k_D(r)$ , solid line); i.e. the probability density function of the distribution of the dispersal distance travelled by a disperser. We also plotted the dispersal location kernel ( $k_L(r)$ , dashed line, encapsulated figure); i.e. the probability density function of the distribution of the final location of a disperser (see Figure 5.3 in Cousens *et al.* 2008 for similar representations).



**Figure 15.3** For a source at the origin 0, the dispersal location kernel denoted as  $k_L(r)$  provides the density of the probability of the dispersal end point in the 1D, 2D, or 3D space according to the spatial dimension of the study system. For instance, in 2D space,  $k_L(r)dA$  is the probability of a dispersal end point to be within a small 2D area  $dA$  around the location  $(x,y)$  in cartesian coordinates (left picture, top half) or  $(r,\theta)$  in polar coordinates (left figure, bottom half). The surface  $dA$  depicted by the empty polygons is given by  $dx dy$  or  $r dr d\theta$ . Since a probability is unitless and  $dA$  is an area,  $k_L(r)$  is expressed in per unit area in a 2D space (see Table 15.2). The dispersal distance kernel denoted as  $k_D(r)$  is the probability density function of the dispersal distance and is 1D regardless of the space dimension (Table 15.2).  $k_D(r)dr$  equals the probability of a dispersal end point to be at a distance between  $r$  and  $r + dr$  from the origin regardless of the direction, i.e. within the grey area of the circular ring depicted in the left figure. For instance, in 1D space (right picture),  $k_L(r)dr$  is the probability to end in the white segment around  $x$  whereas  $k_D(r)dr$  is the probability to end in any of the grey segments around  $x$  and  $-x$ .

$(r, \theta)$  or a cartesian  $(x,y)$  coordinate system can be used to specify the locations of the source point  $r = 0$ , or  $(x, y) = (0,0)$  and of the final point at distance and direction  $(r, \theta)$  with coordinates  $(x, y)$ . Formally, given that  $x = r \cos(\theta)$  and  $y = r \sin(\theta)$ , the probability of having a dispersal end point in an infinitesimally small area  $dA = dx dy = r dr d\theta$  around a single point  $(x,y)$  or  $(r, \theta)$  is:

$$k_{x,y}(x,y)dA = k_{r,\theta}(r,\theta)dA, \quad (\text{Equation 15.1})$$

where  $x,y$  vary in  $(-\infty, +\infty)$ ,  $r$  in  $(0, +\infty)$  and  $\theta$  in  $(0, 2\pi)$  (Figure 15.3).

Dispersal kernels are simpler to present in polar coordinates because distance  $r$  is a meaningful variable, and because the moments of the pdf are simpler to calculate (Clark *et al.* 1999). Also, under the common assumption of radial symmetry,  $k_{r,\theta}(r, \theta)$  depends only on  $r$  and can be denoted as  $k_L(r)$ . This kernel integrates to 1 over the whole 2D space:

$$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} k_{x,y}(x,y) dx dy = \int_0^{\infty} \int_0^{2\pi} k_{r,\theta}(r,\theta) r dr d\theta = \int_0^{\infty} \int_0^{2\pi} k_L(r) r dr d\theta = 1.$$

In 1D space, the cartesian and polar systems of coordinates can also be used alternatively and provide

$$k_x(x) dx = k_{r,\theta}(r,\theta) dr, \quad (\text{Equation 15.2})$$

with  $x$  varying in  $(-\infty, +\infty)$ ,  $r$  in  $(0, +\infty)$  and  $\theta$  being either 0 or  $\pi$ . Being pdfs, these kernels integrate to unity:

$$\int_{-\infty}^{\infty} k_x(x) dx = \int_0^{\infty} k_{r,\theta}(r,0) dr + \int_0^{\infty} k_{r,\theta}(r,\pi) dr = 1.$$

An alternative formulation only provides the density of probability  $k_D(r)$  that a dispersal event ends at a distance  $r$  away from the source, regardless of the direction. The dispersal kernel  $k_D(r)$  always gives a probability per unit distance (Figure 15.3). It was termed 'distance distribution' (Nathan and Muller-Landau 2000), 'one-dimensional (1D) dispersal kernel' (Cousens and Rawlinson 2001), and 'dispersal distance kernel' (Nathan *et al.* 2008b), the latter was adopted in this review. It is defined for  $r$  in  $(0, +\infty)$  and integrates to 1 on this interval.

Location and distance kernels are related through the relations

$$k_D(r) = \int_0^{2\pi} k_{r,\theta}(r,\theta) r d\theta = 2\pi r k_L(r) \quad (\text{Equation 15.3})$$

in 2D space, and



**Box 15.1** *Continued*

$$k_D(r) = k_{R,\theta}(r, 0) + k_{R,\theta}(r, \pi) = 2k_L(r) \quad (\text{Equation 15.4})$$

in 1D space. In both (15.3) and (15.4) the last equality is restricted to the radial symmetric case.

**Table 15.2**

Space dimension	Dispersal distance kernel	Dispersal location kernel
1D	$k_D(r)$ in per unit distance	$k_L(x) = k_L(r)$ in per unit distance
2D	$k_D(r)$ in per unit distance	$k_{x,y}(x, y) = k_L(r)$ in per unit area
3D	$k_D(r)$ in per unit distance	$k_{x,y}(x, y, z) = k_L(r)$ in per unit volume

Computing the 'seed shadow' around a source, i.e. the number of dispersers at different places, requires multiplying the dispersal kernel by the total number of dispersers ( $Q$ ) originated from that source (Clark *et al.* 1999; Nathan and Muller-Landau 2000). The units are numbers per unit of distance when the  $k_D(r)$  formulation is used, and densities (individuals per unit distance, area, or volume, depending on space dimension) when the  $k_L(r)$  formulation is used. When several individual seed shadows overlap, the locations of all sources and the number of dispersers each produces interact with the dispersal kernel in a convolution product to predict the numbers or densities of dispersers. In a 2D space and assuming a single kernel for all sources, for instance, the density of dispersers arriving at location  $(x, y)$  equals

$$\int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} Q(x_i, y_i) k_{x,y}(x - x_i, y - y_i) dx_i dy_i, \quad (\text{Equation 15.5})$$

where  $(x_i, y_i)$  denotes a potential source location and  $Q(x_i, y_i)$  is the number of dispersers originated from the source per unit area. When the sources can be considered as points, these expressions of the density of dispersers arriving at location  $(x, y)$  expresses through discrete sums

$$\sum_{i: \text{all sources}} Q(x_i, y_i) k_{x,y}(x - x_i, y - y_i), \quad (\text{Equation 15.6})$$

or under isotropic dispersal

$$\sum_{i: \text{all sources}} Q(x_i, y_i) k_L(r_{xy}), \quad (\text{Equation 15.7})$$

where  $r_{i,xy}$  is the distance between  $(x_i, y_i)$  and  $(x, y)$ . Equation 15.7 is at the core of inverse modelling techniques, which employ expected disperser obtained in this way to estimate the most likely parameter values of  $k_L(r)$ , given observed densities at a set of locations (Ribbens *et al.* 1994). If the different sources are distinguishable, dispersal location kernels also allow predicting the respective proportion (rather than density) of dispersers from each individual source  $j$  arriving at a given location  $(x, y)$ :

$$\frac{Q(x_j, y_j) k_L(r_{j,xy})}{\sum_{i: \text{all sources}} Q(x_i, y_i) k_L(r_{i,xy})}, \quad (\text{Equation 15.8})$$

assuming again isotropic dispersal in 2D space and invariant kernel across sources.

alternative representations of a dispersal kernel (Nathan and Muller-Landau 2000; Cousens *et al.* 2008; Nathan *et al.* 2008b; see Box 15.1), yet none of them has been sweepingly adopted. Evaluating the shortcomings of previous suggestions, we propose the use of 'dispersal distance kernel' and 'dispersal location kernel', denoted as  $k_D$  and  $k_L$ , respectively (for details, see Box 15.1). The term dispersal kernel should not be used indiscriminately. Wrong conclusions could result from confusing  $k_D$  and  $k_L$  while comparing, for example, dispersal kernels and spread rates (Lewis *et al.* 2006). Therefore, authors should always explicitly mention what type of kernel is presented. In addition, the term 'dispersal kernel' should be reserved only for probabilistic representations of 'dispersal

curves', because it clearly disentangles fecundity and dispersal (Ribbens *et al.* 1994).

Another important confusion associated with dispersal kernels comes from ambiguous definitions of 'dispersal'. Strictly, a dispersal event ends when the movement of the disperser ends; for instance, when an animal- or wind-dispersed seed arrives to its potential establishment site, or a bird reaches a potential new breeding site. The resulting 'basic dispersal kernel' encompasses the movement and the survival of the disperser during dispersive movements. More broadly, dispersal encompasses also the 'post-arrival' survival of dispersers to include only effective dispersal events that lead to establishment and/or successful reproduction. The resulting 'effective dis-

persal kernel' can be defined using different levels of establishment and/or reproduction. In plant studies, for example, effective dispersal can refer to seedlings (e.g. González-Martínez *et al.* 2006), saplings, and even to adults of the next generation (Steinitz *et al.* 2011). Because post-arrival survival varies in time and space and with distance from the source, effective dispersal kernels can differ substantially from the basic dispersal kernels, as found when comparing kernels estimated for seeds, seedlings, and adult plants (e.g. González-Martínez *et al.* 2006; Steinitz *et al.* 2011). Effective pollen dispersal requires viable pollen transport, fertilization, and the development of a viable seed. The spatial arrangement of individual plants and the scale and shape of the pollen dispersal kernel jointly determine the structure of the mating network (Meagher and Vassiliadis 2003; Fortuna *et al.* 2008).

Similar terminological and conceptual problems also appear in dispersal studies of active movers. The dispersal concept can encompass different processes (e.g. natal dispersal and breeding dispersal) that are likely to produce different kernels. Philopatry, the settlement at the natal site, is often neglected when defining the range of dispersal events. This practice can greatly affect the estimation and usefulness of dispersal kernels and therefore the way philopatry was treated should be specified. Capture–recapture studies of active movers must cope with the challenge of identifying the starting natal site, the establishment end point or the fate of censored animals (Turchin 1998). Such difficulties can be resolved by following the complete trajectory of a dispersing animal. Nevertheless, nearly all studies based on capture–recapture or individual tracking actually estimate effective dispersal kernels, since dispersers that did not survive or establish after reaching the dispersal end point site are either unknown or deliberately excluded. In a few studies (e.g. Larsen and Boutin 1994; Anders *et al.* 1998), data on post-dispersal mortality of animals is available, and in principle, the basic and effective dispersal kernels can be compared. On the other hand, mortality during dispersal movements (before settlement) is more commonly estimated for actively dispersed animals (e.g. Larsen and Boutin 1994; Clobert *et al.* 2004; Revilla and Wiegand 2008; Johnson *et al.* 2009) than for passively dispersed animals or plants. In any case, any consideration of effective dispersal kernels necessitates clear explicit

criteria to delimit the starting and establishment sites and their temporal resolution, for both passive and active movers.

## 15.2 The questions

The dispersal kernel concept is central to fundamental research on dispersal processes and spatial patterns. Here we review several key questions covering the patterns observed in nature for dispersal kernels and their variations, the underlying mechanisms shaping them, and the large-scale consequences of dispersal kernels shapes, especially for long-distances.

### 15.2.1 What are the most common characteristics of dispersal kernels found in nature?

The history of dispersal research has experienced a drastic shift from Gaussian and Exponential dispersal kernels that dominated until the late 1990s, to various fat-tailed dispersal kernels that prevail nowadays. Early studies on actively dispersing animals, mostly insects, had already noted that dispersal location kernels are leptokurtic and thus deviate from the Gaussian case (Bateman 1950). Yet Gaussian and other exponentially-bounded kernels constitute, for example, the core mathematical feature of the classical theories of reaction-diffusion (Skellam 1951), genetic isolation by distance (Wright 1943), island biogeography (MacArthur and Wilson 1967), and spatial population ecology (Hanski 1994; Moilanen and Hanski 2001). The major drivers of the shift to fat-tailed kernels were studies demonstrating that observed population spread rates cannot be explained by simple exponentially-bounded kernels, but necessitate mixture (Lewis 1997) or fat-tailed ones (Mollison 1991; Kot *et al.* 1996; Clark 1998; Clark *et al.* 1999). In parallel, simple random walks associated to normal diffusion and Gaussian dispersal kernels have been questioned by studies showing that Lévy flights associated with anomalous diffusion and fat-tailed distributions fit animal movement data better (Viswanathan *et al.* 1996; Ramos-Fernández *et al.* 2004; Sims *et al.* 2008; but see Edwards *et al.* 2007). Nearly all studies comparing the fit of different dispersal kernels to empirical

dispersal data have concluded that fat-tailed kernels outperform thin-tailed ones. Examples span from pollen (Robledo-Arnuncio and Gil 2005; Klein *et al.* 2006b) and seeds (Bullock and Clarke 2000; Clark *et al.* 2005; González-Martínez *et al.* 2006; Robledo-Arnuncio and García 2007; Martínez and González-Taboada 2009), to fish (Fujiwara *et al.* 2006) and birds (Paradis *et al.* 2002; van Houtan *et al.* 2007). However, dispersal kernels are typically estimated from data confined to relatively small spatial scales, and the statistical properties of the far tails have rarely been tested (Niggemann *et al.* 2012).

Dispersal kernels are based on the assumption that distance is the primary factor determining the probability of connecting two sites: the farther away, the lower the probability, with the exception of the opposing trend at short distances in the case of non-zero mode. Yet dispersal data suggest that for many active movers (or passive dispersal mediated by active movers), distance-decaying kernels are insufficient. Habitat heterogeneity greatly affects the probability of arriving at any site (Thomas and Kunin 1999). Spatially structured populations comprise complex spatial distributions of breeding habitats embedded in a non-breeding habitat matrix. Here, distance-decaying kernels might suit dispersal movements within the available breeding habitat, yet dispersers moving in the matrix often follow different rules and thus, in the simplest case, require an additional kernel. The matrix itself can be highly heterogeneous, and possibly each matrix class can yield a matrix-specific kernel (Vandermeer and Carvajal 2001; Revilla *et al.* 2004). More generally, active movers make decisions affecting their trajectories as a function of their interaction with the environment and a set of trade-offs that the organisms need to take into account (Nathan *et al.* 2008a), giving rise to complex multi-peaked or spatially restricted dispersal kernels (Haas 1995; Wiens *et al.* 1997; Haddad *et al.* 2003; Fisher *et al.* 2009; Lees and Peres 2009).

### 15.2.2 Uncertainty and variability of dispersal kernels

Dispersal is a complex process affected by multiple factors, some of which are highly variable in nature,

others are difficult to estimate empirically, representing unpredictable contingencies. Three sources of uncertainties were identified in predictive studies of population rate of spread (Clark *et al.* 2003; Higgins *et al.* 2003a). The first, model uncertainty, is due to over-simplifications of the processes and sources of variability included in the model (e.g. stage structure in populations, spatial variations of the environment, variability of dispersal vectors). More detailed investigation of the movement ecology of dispersers should help to improve this aspect. The second, parameter uncertainty, is due to an imperfect knowledge/estimation of the parameters governing the processes. More powerful experimental designs and statistical analyses of large-scale datasets aim at reducing this one. Even if the dispersal kernel is known perfectly, the third source, inherent uncertainty, results from the stochastic nature of dispersal, the disproportionate effect or rare discrete events concerning dispersers or features of the landscape. Schtickzelle *et al.* (Chapter 18), for butterfly examples, found significant inter-annual variation in dispersal kernels not explained by meteorological variation. Revilla and Wiegand (2008) demonstrated that mortality patterns of resident lynx generated highly dynamic changes in the availability of settlement sites for dispersers. Consequently, the stochastic realization of the same dispersing behavior and the same survival risk deeply affected the effective dispersal kernels between years. Thus, although observed patterns might appear consistent across space, they might not be replicable along time even if all else is equal. Long-distance dispersal events typically contribute to inherent uncertainty with fatter tailed dispersal kernels and higher net reproduction rates, providing more unpredictable extreme events (Clark *et al.* 2001). Given these uncertainties, understanding to what extent dispersal kernels are repeatable and/or determined by measurable characteristics of the environment is challenging.

### 15.2.3 What determines the properties of dispersal kernels?

Dispersal, like other types of movement, depends on four different types of proximate factors: the

internal state determining the motivation to move, the motion and the navigation capacities of the individual, and external factors such as landscape properties and biotic interactions (Nathan *et al.* 2008a). Mechanistic models developed to tailor specific types of dispersal, have striven to incorporate the key processes affecting the studied dispersal system, and the system-specific parameters to investigate their role in shaping the dispersal kernels, and to enable predictions. Examples span across many taxonomic groups, growth forms, and biomes, yet perhaps the most basic distinction is between passively and actively dispersed organisms.

There are three major stages in the dispersal of organisms passively dispersed by either an abiotic or biotic vector: initiation, transport, and termination (Isard and Gage 2001). Each of these stages is associated with a key parameter: the load of the vector, its displacement velocity, and the passage time of the disperser within the vector, respectively (Nathan *et al.* 2008b). In wind-driven passive dispersal, the vector load is the number of dispersal units originated from the source, the vector displacement velocity is determined by the horizontal wind speed during transport, and the passage time is determined by attributes of the source location, the terminal velocity of the dispersal unit, and the vertical wind speed (see, for example, Thomas *et al.* 2003 for ballooning spiders, and Nathan *et al.* 2011b for wind-dispersed seeds). For animal-mediated dispersal, the vector load is the number of dispersal units taken by the animal, the vector displacement velocity is determined by the animal movement and the passage time is determined, for example, by the retention time in the gut or the fur of the animal (Tsoar *et al.* 2011). Note that the dispersal kernel itself is determined only by two basic parameters (vector displacement velocity and passage time), whereas the vector load is the multiplier, or source strength, that transforms the kernel's probabilities to numbers or densities (see Box 15.1).

Sensitivity analyses of mechanistic models have elucidated, qualitatively and quantitatively, the relative role of different biological and environmental factors in determining the properties of dispersal kernels. It has been shown, for example, that wind speed parameters have greater impact on intra-

specific variation in median dispersal distances and long-distance dispersal (LDD) compared to biological parameters (Soons *et al.* 2004; Nathan and Katul 2005). Of particular interest are atmospheric conditions favouring turbulent updrafts originating LDD (Nathan *et al.* 2002; Kuparinen *et al.* 2007a). Air movement may in turn be locally affected by physiography and canopy structure, and experimental evidence suggests that canopy opening and fragmentation tend to enhance airborne pollen dispersal distances (e.g. Bacles and Ennos 2008), a trend also noticed in insect-pollinated species (e.g. White *et al.* 2002). Effective pollen dispersal kernels are also strongly affected by pollen viability, which can drastically decrease in only a few hours (e.g. maize in hot conditions, Aylor 2004; but see Bohrerova *et al.* 2009). For animal-dispersed seeds, the movement of the animal vector, greatly affected by landscape features and complex behaviors, has the strongest effects on dispersal patterns (Russo *et al.* 2006; Spiegel and Nathan 2007; Levey *et al.* 2008). Both small- and large-scale spatial heterogeneity in the landscape can also influence the dispersal of seeds by wind (Bullock and Moy 2004; Bohrer *et al.* 2008; Pouden *et al.* 2008; Schurr *et al.* 2008).

All the discussion above assumes that there is a single major dispersal vector. Yet a problem of model uncertainty appears when important vectors are neglected or missed. In plants, for example, it has long been assumed that the 'standard' dispersal vector is the one inferred from seed morphology (van der Pijl 1982). Yet many plants, if not most, are actually dispersed by additional 'non-standard' vectors, which play a key role especially in LDD (Higgins *et al.* 2003b). The existence of multiple vectors operating at different spatial scales has been compellingly demonstrated for various plant species (Dennis and Westcott 2007; Jordano *et al.* 2007; Spiegel and Nathan 2007). A given species might be passively dispersed by many types of dispersal vectors, each potentially operating at a different scale and/or generating a different dispersal kernel. The combination of these different kernels, weighted by the relative load dispersed by each vector, constitutes the 'total dispersal kernel' (Nathan *et al.* 2008b), the complete descriptor of dispersal distances in the studied dispersal system. Overall, for

many organisms, quantifying the dispersal kernel generated by the common dispersal vector might be insufficient, because it could deviate substantially from the total dispersal kernel.

In actively dispersed organisms individuals search for a place to reproduce. However, their movement trajectory is not only affected by this aim, since they have to consider simultaneously other factors such as their perceived mortality risk and the availability of food (Nathan *et al.* 2008a), integrating the effects of several processes normally acting at different spatiotemporal scales (Fryxell *et al.* 2008; Delgado *et al.* 2010). This is presumably the most fundamental difference between passive and active dispersers. The kernels obtained for active dispersers do not purely describe the dispersal process alone, but integrate different behaviors such as food, water, or refuge search, and predator avoidance, while searching for a new place to settle. The fact that there are several simultaneous processes behind empirical movement data hinders the identification of the onset and end of dispersal *per se*. The only way to identify a dispersal event is to detect deviations from a 'normal' behaviour by defining rules based on thresholds in movement parameters estimated using moving time windows, such as changes in short-term home ranges, distance to the origin, velocities, and turning angles (e. g. Palomares *et al.* 2000; Fryxell *et al.* 2008). The existence of strong behavioural differences among individuals, in many cases due to varying personalities (e.g. McDougall *et al.* 2006; Cote and Clobert 2007), make these approaches inherently subjective, and the interpretation of who is dispersing under those rules qualitative. A typical example is the difficulty in classifying the movements of young animals moving away but eventually returning to their natal site, mimicking actual dispersal patterns (i.e. when they finally settle and reproduce). Whether those excursions are part of the normal behaviour, or an initial training of the individual for later dispersal, is very relevant because in the end dispersal is a searching process during which individuals can have lots of a priori information (e.g. dispersing badgers between adjacent groups, Macdonald *et al.* 2008), or be naïve, with a broad range of intermediate cases (McConnell *et al.* 2002; Stamps and Davis 2006; Brown *et al.* 2008).

Nevertheless, we have a strong theoretical basis to predict movement properties of searching individuals, as a function of the spatio-temporal distribution of targets and the available prior information. Trajectories can be strongly linear when the cost of moving is high and the individual has poor information on target location (Zollner and Lima 1999), leading to leptokurtic kernels. However, if the spatial autocorrelation of targets is known, the movements of dispersers should initially be restricted locally to find a nearby high quality area, given that the natal site has proved favourable. When targets are clustered, the search can be Lévy-like with long straight moves until detecting some cue on a potential target, and then performing a restricted area search (Bartumeus *et al.* 2005), leading to fat-tailed kernels. Animals can even use systematic strategies such as foray search by which individuals sample the landscape, systematically obtaining information on the absence and/or relative quality on the surrounding areas before making the dispersal decision (Conradt *et al.* 2003). Search movements are additionally modified by factors such as cueing strategies, in which individuals trade off the onset of dispersal as a function of their relative quality against conspecifics (Stevens and Bonsall 2011) or conspecific attraction (Gamble *et al.* 2007), which can overrun all the previous information available to the individual (Serrano *et al.* 2001).

Estimating multi-process kernels for active dispersers is not necessarily more complex than for passive dispersers. However, building mechanistic models remains very challenging since it requires an integrated understanding of all the processes involved, including the movements and habitat selection before dispersal. The predicted kernels depend not only on model structure, but also on the actual parameterization, the initial conditions, the temporal and spatial heterogeneity, and resolution used.

### 15.2.4 Long-distance dispersal and large-scale dynamics

Although dispersal kernels are typically fitted based on dispersal data collected at relatively short distances from the source, increasing interest in disper-

sal kernels comes largely from the recognition of LDD importance (Petit *et al.* 1997; Clark *et al.* 1999; Higgins and Richardson 1999; Cowen *et al.* 2000; Cain *et al.* 2000; Kinlan and Gaines 2003; Bowler and Benton 2005; Trakhtenbrot *et al.* 2005; Nathan 2006). The magnitude and frequency of LDD events—derived from the properties of the dispersal kernel and especially the shape parameter determining the ‘fatness’ of the distribution tail—have been found to play an important role in a variety of ecological and genetic processes: the rate of spread of an expanding population (Kot *et al.* 1996; Neubert and Caswell 2000; Clark *et al.* 2001), the response to climate changes (Nathan *et al.* 2011a), the connectivity among isolated populations (Muñoz *et al.* 2004), the survival and genetic variation in metapopulations (Sork *et al.* 1999; Bohrer *et al.* 2005), the effects of forest fragmentation (van Houtan *et al.* 2007), the spatial distribution of genetic diversity (Ibrahim *et al.* 1996; Petit 2004; Bialozyt *et al.* 2006; Wingen *et al.* 2007; Fayard *et al.* 2009), and the transfer of genes between locally adapted populations (Kuparinen *et al.* 2010). LDD can be defined in a relative way, characterizing the distance above which a given fraction of dispersal events occurs (say 1% or 1‰), or in absolute terms, characterizing the fraction of dispersal events that occurs above a given threshold distance associated with the biology of the species and the environment (Nathan *et al.* 2008b). Both definitions are intimately related to the dispersal kernel and especially to the ‘fatness’ of its tail, whose characterization remains a challenge both for mechanistic and empirical approaches.

### 15.3 The tools

Dispersal kernels can be estimated by various experimental and mechanistic modelling approaches. Section 15.2 outlines the principal components of mechanistic models of passive and active dispersal; this section focuses on experimental approaches.

Experimentally, basic dispersal kernels can be estimated from the trajectories of particular dispersers (Lagrangian approach) or from the amount and/or diversity of dispersers at particular sampling points (Eulerian approach) (Bullock *et al.* 2006). The Lagrangian approach has been applied mostly to

animals or animal-dispersed seeds or pollen, using mark/recapture (e.g., van Houtan *et al.* 2007), or tracking designs such as radio telemetry or GPS tags (e.g. Larsen and Boutin 1994; Anders *et al.* 1998; Ovaskainen *et al.* 2008; Revilla and Wiegand 2008; Johnson *et al.* 2009). It was also applied to smaller passive dispersers, through visual tracking of seeds dispersed by wind (Andersen 1991; Soons *et al.* 2004), radio tracking of tagged acorns dispersed by birds (Pons and Pausas 2007), or searching for radio-labeled gamma emitting seeds dispersed by ants (Kalisz *et al.* 1999). This approach provides a more straightforward distribution fitting compared to Eulerian methods, since dispersal end points are not confined to the sampling sites. Another advantage is the possibility of correlating disperser traits with dispersal capacities. Yet the number of dispersal units sampled is limited because tagging and tracking individual dispersers is costly. Finally, observations are concentrated on a short time period, which may be a problem if variable environmental conditions result in temporally fluctuating dispersal patterns (Skarpaas *et al.* 2011).

The Eulerian approach relies on physical or biological ‘traps’ at some particular points where dispersers are sampled. Live trapping of moving animals allows the mark and posterior recapture of individuals, including the non-invasive camera trapping (e.g. Gardner *et al.* 2010). Traps can also be containers or nets to catch seeds (e.g. Bullock and Clarke 2000 on the ground; Dauer *et al.* 2009 in the air; Middleton 1995 in water), ground plots where seeds or seedlings are collected (e.g. García *et al.* 2007), pheromone attractive systems (Qureshi *et al.* 2005), light traps or sticky traps for insects (Collier and Smith 1998), nets for catching animals (Chifflet *et al.* 2011), sticky slides or rotorods to collect pollen (e.g. Tufto *et al.* 1997), or mother-plants to sample viable pollen (e.g. Oddou-Muratorio *et al.* 2005). Some combinations of trapping systems can inform about the post-dispersal survival of dispersers (e.g. mother-plant versus sticky slides for pollen) enabling to distinguish effective dispersal from the basic dispersal kernel.

Most studies have measured the number of dispersers collected per trap. Some also measured a morphological characteristic associated to different

sources (e.g. Klein *et al.* 2003). An increasing number of studies have genotyped the dispersers at several neutral markers to assign them to their original source, more or less categorically (e.g. Jordano *et al.* 2007; Jones and Muller-Landau 2008; see following). Even when the trapping design is not explicit (e.g. 'some seedlings chosen randomly throughout a forest plot'), studies based on traps must account for the positions of the sampling sites relatively to the sources to retrieve the dispersal kernel (e.g. Figure 1 in Nathan and Muller-Landau 2000). Robledo-Arnuncio and García (2007) indeed showed that simply estimating a dispersal kernel from the effective dispersal distances without accounting for the sampling design results in biases (Jones and Muller-Landau 2008).

A first set of methods to fit the dispersal kernel relies on the information carried by the number of dispersers in the traps (Equations 15.5–15.7; Box 15.1). Observations from a single point source are the easiest to analyse (Bullock and Clarke 2000; Skarpaas *et al.* 2004). Experimental designs where several indiscernible sources are located all around the traps are analysed through inverse modelling (Ribbens *et al.* 1994; Clark *et al.* 1998; Schurr *et al.* 2008), which can be extended to consider independent seed shadows as replicates if dispersers can be assigned categorically to different sources (e.g. by means of genetic methods; Jones and Muller-Landau 2008).

Because the numbers of dispersers in the traps might be unknown (e.g. mother tree as a pollen trap) or strongly determined by external factors independent of dispersal (e.g. germination and survival rates producing seedling number variation across sampling sites), the second set of methods to estimate dispersal kernels uses the proportions from different discernible sources in the traps (Equation 15.8; Box 15.1). This solution was first used for few sources with discernible traits (e.g. different colours of kernels in corn, Klein *et al.* 2003). Next, the use of highly polymorphic neutral markers was used to conduct a categorical parentage analysis and then analyse the retrieved dispersal events (e.g. Hardy *et al.* 2004 for pollen dispersal; Robledo-Arnuncio and García 2007 for seeds). More advanced methods integrate into a single likelihood

function the Mendelian rules used in parentage analysis and the dispersal kernel and mass-action law used in spatial analysis (Adams *et al.* 1992; Burczyk *et al.* 2002; Oddou-Muratorio *et al.* 2005; Hadfield *et al.* 2006; Klein *et al.* 2008). These methods can estimate the basic dispersal kernel even if survival varies spatially, as long as the survival rate is source-independent. They rely on the probability of originating from the different sources independently of the factors affecting the probability of presence of the disperser at the sampling point. This is a clear benefit in studies sampling individuals a long time after dispersal, like settled seedlings of trees (Moran and Clark 2011).

A variety of other uses of molecular information to estimate dispersal are found in the literature and are not detailed here; these include assignments to geo-referenced populations with different allelic frequencies (e.g. Gaggiotti *et al.* 2002), patterns of isolation by distance (Hardy *et al.* 2006), and other methods from landscape genetics (Guillot *et al.* 2009), or genetic differentiation among pollen pools (TwoGener method, e.g. Austerlitz *et al.* 2004).

From historical least square estimation (e.g. Klein *et al.* 2003), the toolbox of statistical approaches has been expanded with non-parametric estimations (Chesson and Lee 2005), maximum likelihood (Tufto *et al.* 1997; Clark *et al.* 1999; Burczyk *et al.* 2002; Canham and Uriarte 2006; Schurr *et al.* 2008), and Bayesian analyses for hierarchical models (Clark *et al.* 2004; Hadfield *et al.* 2006; Snäll *et al.* 2007; Klein *et al.* 2008; Jones and Muller-Landau 2008; Moran and Clark 2011). The latter enables accounting for additional sources of variability (e.g. individual fecundity obtained as a function of basal area plus a random component in Clark *et al.* 2004; Chapter 19) and to consider jointly various types of observations (Clark and Gelfand 2006).

Optimizing the observation design can also improve the estimation of the dispersal kernel. The general objective is to cover the widest range of environments and trapping distances to sample dispersal events independently over the actual range, including rare LDD events. But the optimal sampling design is a compromise between statistical power and sampling time and costs (see Bullock *et al.* 2006 for a thorough discussion). Mathematical

and computational techniques can determine the optimal sampling distances and sampling effort at each distance (Stoyan and Wagner 2001; Skarpaas *et al.* 2005). But this requires a good *a priori* knowledge about the dispersal kernel from a pilot study or mechanistic models.

Estimating the dispersal kernel empirically requires using appropriate families of parameterized functions (e.g. Austerlitz *et al.* 2004; Greene *et al.* 2004; Klein *et al.* 2006b; Jongejans *et al.* 2008). In Table 15.1 we summarize a wide array of kernel families used in the literature, providing statistical formulations, properties, performance, and actual and recommended applications.

Dispersal kernels are first characterized by a scale parameter, providing the spatial extent of most dispersal events (e.g. mean dispersal distance). The importance of LDD is further characterized by the overall shape of the kernel indicated by the kurtosis, or alternatively by the fatness of its tail. Kurtosis is the fourth moment of the kernel and equals 0 for a Gaussian, typically mesokurtic. As noted above, the Gaussian kernel has been extensively used in dispersal research, yet this function does not model LDD realistically. The use of leptokurtic distributions to characterize dispersal is almost always necessary (Table 15.1), yet not sufficient: the exponential distribution and the mixture of two Gaussians, two leptokurtic alternatives to the Gaussian, often provide worse fits than distributions with fatter tails (Table 15.1). Thus, the shape of the tail, not only the kurtosis, should be characterized to elucidate how fast the function decreases towards zero at relatively large distances. Fat-tailed dispersal kernels decrease more slowly than any exponential (Kot *et al.* 1996), while power-law kernels (e.g. 2Dt) decrease more slowly than any exponential-power function (Klein *et al.* 2006a). Recent studies of LDD generalized the use of fat-tailed kernels, not merely leptokurtic kernels (Table 15.1). The key challenge here is to obtain data on the frequency and spatial extent of the rare LDD events (Nathan 2006).

The shape of the dispersal kernel close to the origin also varies among functions: some are strongly peaked (power-exponential with  $b < 1$ ) or even infinite at 0 (some Weibull), some show a convex shape

close to the origin (2Dt, Clark *et al.* 1999) or even increase from 0 at short distances (log-normal, Stoyan and Wagner, 2001).

When the family of functions is not adequate both near and far, the fit reaches a compromise to catch the shape of the whole function. This can result in a bad characterization of the tail. It is strongly advisable to fit a variety of dispersal families and select the best-fitting one (Bullock *et al.* 2006), when possible the more mechanistic one, yet remembering that model selection is sensitive to the study site area and that extrapolations beyond the observational scale may be problematic (Fric and Konvicka 2007; Kuparinen *et al.* 2007b). The examples given in Table 15.1 show that the Gaussian and the Exponential are (still) widely used kernels, despite their overall poor performance. The simple inverse

power-law function  $\left(\frac{r}{a}\right)^{-b}$  (Table 15.1) is a fat-tailed distribution that has long been used to fit 'dispersal curves', yet it cannot be integrated close to zero unlike other formulations of the power-law that provide true dispersal kernels (Levin *et al.* 2003; 2Dt, power-law or logistic in Table 15.1). The use of various fat-tailed distributions is steadily becoming mainstream practice, exhibiting a notable upsurge in the last decade. Different fat-tailed functions have been adopted for different taxonomic groups (Table 15.1), reflecting more field-specific research histories than biological differences among taxa. The exponential power function, for example, has been used intensively in plant dispersal research since Clark *et al.* (1998), but is rarely applied to animals.

The need for a better mechanistic interpretation of dispersal kernel parameters has led to the proposition of more sophisticated expressions, mostly for wind dispersal of seeds, in the lineage of Greene and Johnson (1989) and Okubo and Levin (1989) and recently reviewed in Nathan *et al.* (2011b). Models of animal-mediated dispersal have recently gone beyond simply multiplying animal velocity by seed passage time, to incorporate, for example, landscape heterogeneity as well (e.g. Russo *et al.* 2006; Levey *et al.* 2008). To model mechanistically how self-propelled animals move during their own dispersal, all different components of the movement ecology framework need to be incorporated



(Nathan *et al.* 2008b; Revilla and Weigand 2008; Tsoar *et al.* 2011). These components have equivalents among passively dispersing organisms (Nathan *et al.* 2008a; Wright *et al.* 2008; Bacles and Jump 2011; Tsoar *et al.* 2011), and these two basic dispersal systems, previously considered incompatible, are likely to converge.

Even when mechanistic and phenomenological models fit comparably well to a particular experimental dataset (e.g. Skarpaas *et al.* 2004), a clear benefit of mechanistic models is that they can be used both to investigate the underlying mechanisms (Section 15.2) and to provide predictions based on *a priori* knowledge of environmental conditions and biological parameters.

## 15.4 Synthesis and future directions

By providing an individual-based description of dispersal probabilities at different distances and directions, dispersal kernels are statistical tools most suited for (i) characterizing dispersal scale and direction *per se*, (ii) investigating the relation between dispersal patterns, individual traits and ecological and demographic factors, or (iii) correcting for distance effects in studies of other processes (e.g. mating systems, selection gradients, or community assemblages). Dispersal kernels are key components of biological models that need to consider individual movement in explicit space, such as reproduction, recruitment, competition, range expansion, metapopulation dynamics, population resilience to habitat disturbance, gene flow, and transgene escape.

The dispersal kernel, though, may not be ideal to address all questions. For instance, metapopulation models may not require explicit individual information and may be more efficiently parameterized using pairwise migration rates among subpopulations (e.g. Bullock *et al.* 2006). Further, commonly employed dispersal kernels (and especially phenomenological functions) provide a simple quantitative description of the average dispersal process across individuals and environments. If they are well suited for comparative and modelling purposes, they are potentially too coarse-grained for detailed descriptions of the actual dispersal pattern

when it involves complex behavioural mechanisms, intricate phenotypic correlations, and strong interactions with environmental factors, resulting in substantial inter-individual variation in dispersal ability and distance-independent fluctuations of dispersal probability across heterogeneous landscapes. In the latter case, the observed distribution of dispersal events will contain valuable information that may be lost upon oversimplified kernel fitting. The challenge will be to develop versatile enough kernels to unravel the actual variability in the dispersal process, for which mechanistic approaches are likely to excel as explicative and predictive tools. Researchers should not be discouraged by the apparent complexity of mechanistic models; we advocate efforts to acquire the helpful analytical skills and attitude required for modelling and understanding the fundamental mechanisms driving plant and animal movement.

Dispersal kernels should not be considered as goals in themselves or as fixed within species. Dispersal kernels are individually and temporally variable laws subject to many influential factors of interest. Much could be gained when modelling movement patterns using dispersal kernels by including data on morphological, physiological, behavioural, genetic, and developmental attributes of focal individuals, as well as on environmental variables, such as resource availability, landscape configuration, weather conditions, or relative abundance of intervening dispersal vectors (Nathan *et al.* 2008b). Comparative observational studies or controlled manipulation of dispersal-related traits and suspected environmental determinants are still scarce (Chapter 19), while empirical evidence is crucially needed. A careful assessment of the statistical uncertainty associated with kernel estimates, a frequently neglected issue, will be required for such kind of comparative inference. On the other hand, longitudinal studies should add the informative temporal dimension often missing in dispersal kernel evaluations. For instance, animal lifetime tracks can reveal spatio-temporal scaling properties of movement and their association with internal and external factors, to which separate dispersal kernels could be fitted in order to dissect total movement

into specific processes of interest, such as foraging, natal, or breeding dispersal.

The development of dispersal kernels reflecting LDD events accurately is a remaining issue concerning both phenomenological and mechanistic models. The limited spatial scale of observations is a key drawback of phenomenological methods, since dispersal functions with very different tails may yield similarly good fits (Kuparinen *et al.* 2007b). Mechanistic kernels are more promising since they provide a basis for generalization beyond the scale of empirical analysis, but they still confront spatial scale constraints when it comes to experimental validation of their long-distance predictions. How to progress then? For species distributed in discrete populations, among-population pairwise migration rates might prove pivotal quantities for long-distance validation of kernels. Migration rates could be independently estimated in the field, using for instance capture–recapture or individual genetic assignment procedures (Manel *et al.* 2005), and compared against the expected proportion of migrants predicted by integrating the candidate kernel across individuals in the recipient and source populations (e.g. Revilla *et al.* 2004; Klein *et al.* 2006b). Alternatively, migration rates could be combined with local dispersal data to produce better kernel fits across different spatial scales (e.g. Goto *et al.* 2006). The estimation of migration rates can however be problematic if there are many large candidate source populations or for continuously distributed species. Indeed, there might often be insurmountable difficulties in obtaining the detailed individual information required for estimating and validating dispersal kernels over both short and long distances. Whether the dispersal kernel concept remains practical and testable over very broad spatial scales is questionable. Alternative approaches not based on individual dispersers deserve further exploration, such as connectivity maps, which have proved valuable to predict long-term continental-scale movements of both passive dispersers (Muñoz *et al.* 2004) and strong flyers (Felicísimo *et al.* 2008).

Finally, dispersal kernels can be regarded as complex phenotypic traits; assessing their heritability, plasticity, and among-population genetic divergence could inform on the selection shaping them

and the ultimate evolutionary causes of dispersal (Chapter 16). For most plants and many animals, the dispersal kernel or the morphological traits affecting the dispersal kernel could be measured in provenance or progeny trials raised in common gardens, to infer genetically determined phenotypic differences among populations and their environmental and demographic correlates (Donohue *et al.* 2005; Ovaskainen *et al.* 2008). Additionally, genomic advances are providing whole genome and transcriptome sequence information (e.g. Vera *et al.* 2008), enabling functional genomic and association studies that could reveal the genetic architecture of dispersal. On this point, because short- and long-distance dispersal may rely on different mechanisms and evolve independently (Ronce 2007), dispersal kernel families used should not enforce artefactual shape constraints: the parametrization of near-the-origin and tail behaviors should be clearly separated.

Overall, the dispersal kernel concept has proven essential for dispersal research. The simplest models capture the fundamental distance-decay principle of ecology and geography (Nekola and White 1999) and were used to develop classical theories on biogeography and spatial dynamics. More complex leptokurtic and fat-tailed dispersal kernels usually better fit empirical data, at least over the necessarily limited scale of analysis, implying that the spatial extent of dispersal is much larger, possibly by several orders of magnitude (Nathan *et al.* 2011b), compared to the simple exponentially bounded functions. Recent advances in statistical analyses of the shape of dispersal kernels elucidated important phenomena such as rapid population spread. More complex formulations of mixed kernels account for higher degrees of variability in the dispersal process, yet this promising research avenue remains rather dormant thus far. Nevertheless, all these simple and advanced dispersal models are inherently limited by the basic assumption that the end point location of a disperser depends first and foremost on the distance from its source. Although partially true in all dispersal systems, distance might be only a minor determinant of the dispersal probability in many dispersal systems, particularly for actively moving organisms, and for passive movers

dispersed by active movers. For these many cases, the dispersal kernel concept should be elaborated to include additional sources of variation, accounting for landscape heterogeneity concerning the major factors determining dispersal movements. The rarely questioned assumption about independent moves of the different dispersers that jointly construct the empirical dispersal kernel should be relaxed too. Because apparently many plants and animals move, passively or actively, in a correlated manner, the scope of this phenomenon needs to be assessed, the underlying mechanisms should be unveiled, and statistical tools to cope with lack of independence should be developed. Addressing these challenges would require further refinement of methods to quantify the paths and end points of dispersers, the key features of the landscape they travel through, as well as enhancement of data analysis tools and theoretical frameworks.

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