Inferences about the capacity to disperse and migrate: from a local scale to the wider landscape

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In the present context of climate change, it is important to know as accurately as possible a species' capacity to migrate and move elsewhere. Up till now, empirical approaches have been used to evaluate such dynamics but today science has become more predictive, using approaches based on integrating models such as the one presented here — the dispersion kernel — which describes the spatial distribution of seeds dispersed from one source.

The science of ecology, as indeed biology itself, has become more predictive. The ecology of dispersion, too, has moved in this direction which involves developing models of a more quantitative nature. Thus, empirical approaches which assessed species' ability to migrate or move elsewhere on the basis of observations about the past (in particular, about episodes of recolonisation in the post-glacial era) (e.g. SKELLAM 1951; DAVIES 1981; DELCOURT & DELCOURT 1987, in MCLACHLAN et al. 2005) have gradually given way to approaches based on integrated models that incorporate the principal mechanisms involved in the movement of species, notably dispersal (e.g. HIGGINS et al. 2003, JONGEJANS et al. 2008, MACMAHON et al. 2009). Such models and the mechanisms involved are especially relevant when confronting maps that plot future climate on the basis of models of worldwide climate change with the biological processes governing the life cycles of forest species (fertility, dispersal of pollen and seeds, germination, survival, growth, recruitment) (THUILLER et al. 2008).

Dispersal kernels, a determining feature for the future of plant populations on the move
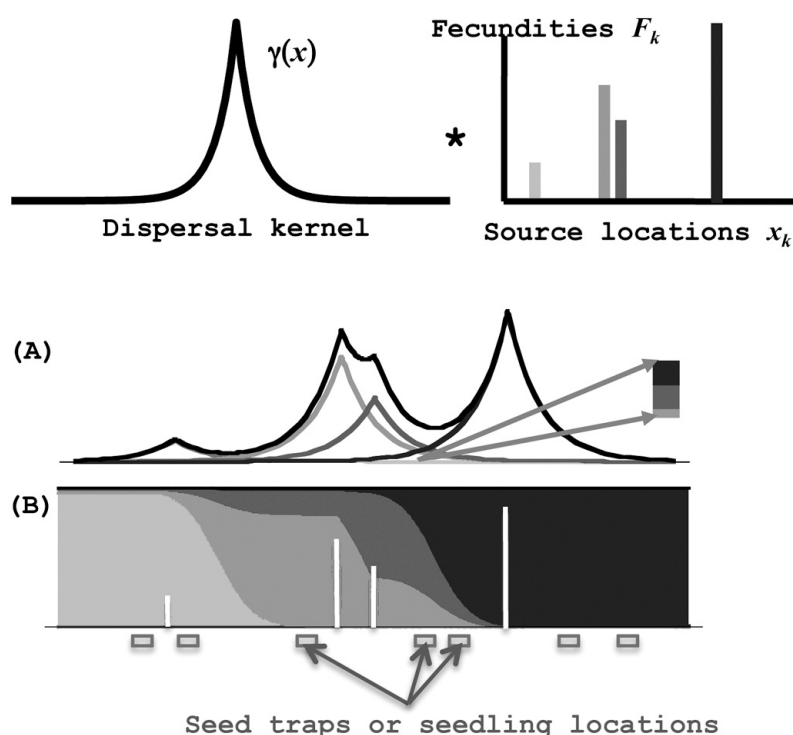
One of the main mechanisms that need to be included in predictive models is seed dispersal (which is the driving element in the movement of plants to a different area) (HIGGINS *et al.* 1999). More precisely, this means it is necessary to describe how the spatial distribution of a population of adult seed-producing trees underlies the spatial distribution of seeds after dispersal ("potential dispersal") or seedlings after germination or premature mortality ("effective dispersal") (GONZALEZ-MARTINEZ *et al.* 2006).

In recent years, the *dispersal kernel* has gradually come to the fore as a robust model for taking into account the spatial distribution of seed-producing trees ("source") and deducing the consequential "seed rain" at every point in an area (NATHAN *et al.* in press, COUSENS *et al.* 2008). This dispersal kernel is the function that describes how

each individual source distributes its seeds in its surroundings by dispersal (a probability density function, generally defined within the 2-D area in which the tree population under study is evolving). This function was first used to calculate the number of seeds expected within each plot in the given area, a number resulting from the superposition of the contribution of each individual source tree disseminating seeds (RIBBENS *et al.* 1994; CLARK *et al.* 1999). More recently, the dispersal kernel has proved to be particularly well-suited for modelling the genetic make-up of seeds arriving at a given place, a composition characterised via the contributions of the different sources relative to the total number of seeds falling (Fig. 1) (TUFTO *et al.* 1999; KLEIN *et al.* 2003).

Two characteristics of a dispersal kernel have proved to be critical for the demographics of an expanding population, especially for its rate of advance. First, a scale parameter determining the average dispersal distance; but second, and above all, the existence of dispersal over long distances signalled by the shape of the dispersal function and by its decrease for long distances (KOT *et al.* 1996; CASWELL *et al.* 2003). Even though dispersal kernels may seem similar for short distances, the significant differences in the very low rates of occurrence of rare events at long distances can alter appreciably the dynamics of colonisation (Fig. 2). There emerge quite clearly fat-tailed kernels (they decrease slower than any exponential function) which result in rapid colonisation with speed increasing over time (KOT *et al.* 1996; CLARK *et al.* 2001).

Our recent research has also shown that the shape of the dispersal kernel has an effect on the conservation and structure of genetic diversity in the course of the colonising process. FAYARD *et al.* (2009) studied this subject by simulating the destiny of an allele present at a low rate at a given time on the colonisation front. A recent study (EDMONDS *et al.*, 2004) had shown that, in the absence of long-distance dispersal, this allele was very likely to remain present at its initial location in small numbers but rare cases of "surfing" were observed during which the gene had been borne onwards by the colonisation wave, ending up at a high level in the population. This phenomenon results from the powerful impact of genetic drift that occurs on the colonisation front, reducing genetic diversity through the effect of succes-

$\gamma(x)$

Dispersal kernel

Fecundities F_k

*

Source locations x_k

(A)

(B)

Seed traps or seedling locations

sive founder effects (EXCOFFIER *et al.*, 2009). Our study has shown that fat-tailed kernels limit this phenomenon: surfing occurs less frequently, thus the genetic drift is weaker. Moreover, this property is linked particularly to the shape of the dispersal kernel and not only to the occurrence of long-distance dispersal. One possible explanation is that fat-tailed kernels lead to a greater mix of the contributions of the sources when the distance from these sources is greater, something we demonstrated in an earlier study (KLEIN *et al.*, 2006). To simplify matters, in colonisation resulting from a thin-tailed kernel, the front maintains its own drive, resulting in a gradual lessening of diversity whereas when the dispersal kernel is fat-tailed, the nucleus of the population can re-inject genetic diversity ahead of the colonisation front. A recent study centred on larch stands concluded that the hypothesis of a greater mix of contributions explained the high genetic diversity observed at the recolonisation front subsequent to the withdrawal of a glacier in a valley in Switzerland (PLUESS 2010).
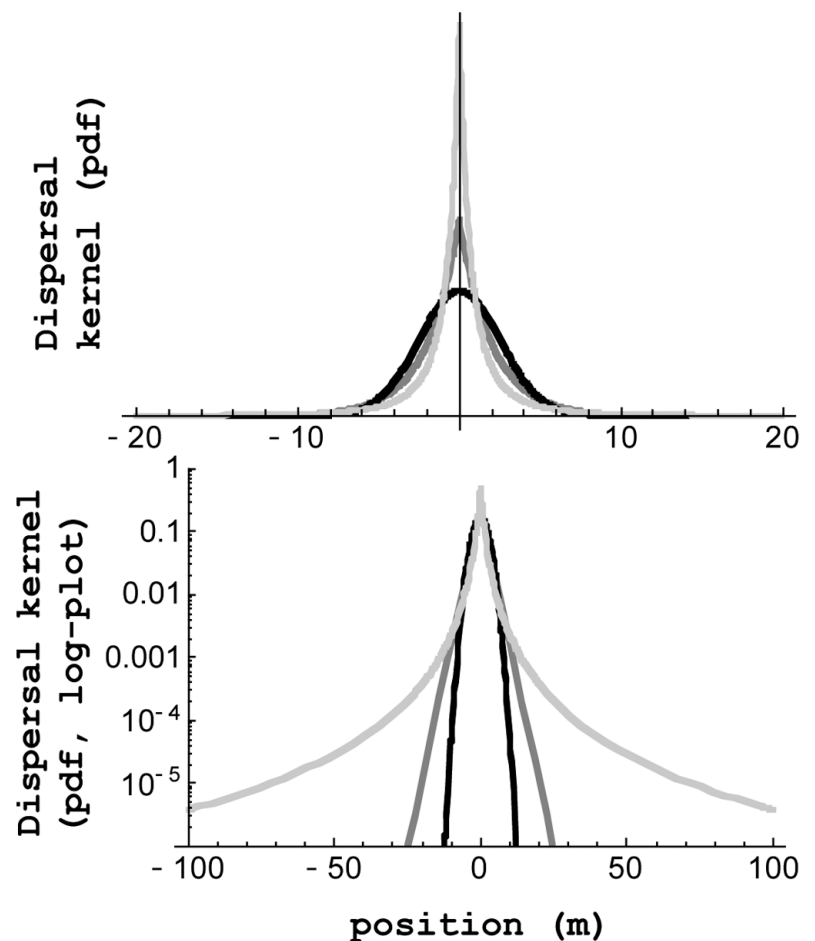
tage of being based on seed traps. Such traps are, as a rule, better adapted to dispersal by wind rather than by animals and fail to take into account other vectors of dispersal or secondary dispersal (e.g. by a second agent subsequent to previous wind dispersal). An alternative experimental approach, which is also less expensive, consists in observing the spatial distribution of successful seedlings rather than the distribution of seeds in traps (MORAN and CLARK 2011). This type of observation, while facilitating a direct appreciation of effective dispersal, is nevertheless much affected by the spatial distribution of sites favourable to the germination and flourishing of seedlings. In the first place, the favourable character of a site can be largely determined by environmental factors that are not distributed randomly over an area (competition or inter-species facilitation). And secondly, adult trees can have a negative effect on germination or survival in

Fig. 2:
Representation of dispersal kernels. Three kernels with the the same moderate dispersal distance are represented at the top on a linear scale (Gaussian kernel black; exponential kernel grey; fat-tailed kernel light grey) and below on a logarithmic scale. Although rare for all three kernels, long-distance dispersal events (> 20 m) occur at very different frequencies.

Estimating the dispersal kernel: boost from the data from genetic markers

On account of the big impact of the shape of a dispersal kernel on the capacity for movement and the conservation of genetic diversity, much experimental research has sought to make an accurate estimate of this impact over a wide range of distances (BULLOCK *et al.* 2006; JONGEJEANS *et al.* 2008).

The inverse modelling approach introduced by RIBBENS *et al.* (1994) was a landmark in the assessment of dispersal kernels. These authors were able, for the first time, to find a dispersal function at the level of an "individual" based on counting seeds in seed traps set out in tree stands: in other words, they started with observations of the accumulated contributions of a large number of sources. This statistical approach solved the problem of the superposition of individual seed shadows and provided an assessment of the kernel as well as the factors determining fecundity. This method has been widely used since its introduction but has the disadvan-

their close surroundings (a phenomenon known as the Janzen-Connell hypothesis [NATHAN & CASAGRANDI, 2006]). Two alternatives exist for adapting inverse modelling to such effects due to spatial heterogeneity in germination and survival.

The first solution, of a statistical type, consists in modelling and estimating the effects on germination and survival of some well-identified environmental variables present in the area of seedling sampling. KUNSTLER et al. (2007) used this method to take into account the favourable impact of the presence of shrub species. By developing this approach, AMM (2011) was able to study the effective dispersal of fir on the northern slope of Mont Ventoux (Provence, S.-E. France). The fir seedlings were mapped on 30 plots of 400m^2 each spread across a 400-hectare zone in which every seed source was described individually (when near to a plot) or from inventory datasheets. Variables, both biotic (surface area occupied by fir, pine and beech) and abiotic (altitude, degree of slope, soil), were recorded for each of the 30 plots and used as the explanatory basis for survival and germination in the inverse model designed to estimate the dispersal kernel. The results showed that altitude was the main variable determining the recruitment rate of the seedlings, the optimum being at a middle altitude of 1,200m. The density of the pines significantly reduced the recruitment rate. This approach also highlights the necessity to take into account the effect of environmental variables insofar as the dispersal kernel obtained when taking them into consideration (mean dispersal distance = 13.2m to 19.6m) was very different from that obtained by direct assessment based on seedlings without taking into account the impact of the environment on survival and germination (mean dispersal distance = 18m to 174m). In contrast, the dispersal kernel was much more like that for seed dispersal as estimated in a previous study on the basis of seed traps (dispersal distance = 7m). Even though the present study used a dispersal kernel allocating a large share to long-distance dispersal, it has confirmed the short average distances already reported in the literature for a number of *Abies* species.

The second solution consists in exploiting genetic data from the seedlings to trace more or less precisely the parents of the seedling (assigning parentage), in particular the mother tree dispersing the seed that resulted in the seedling (KLEIN & MURATORIO, 2011). The most effective applications of this method were those where the genotype of the mother was exactly determined by characterising maternal DNA from tissue recovered from the descendants (seed endocarps or pericarps). By way of example, JORDANO et al. (2007), with 10 micro-satellite genetic markers from *Prunus mahaleb*, were able to systematically identify the mother of an offspring when the parent was one of the 196 genotyped trees on their 26-hectare plot and in this way reconstitute the distance travelled by a seed up to 1,000m. Even in the cases where the mother tree of a descendant can be accurately pinpointed, it remains necessary in analysing the results of the parentage assignment to take into account the spatial distribution of all the sources of seeds to make a final assessment of the dispersal kernel, as was done in the inverse modelling (ROBLEDO-ARNUNCIO & GARCIA, 2007). But the analysis is no longer based on modelling the intensity of the seed rain at each trap but on the composition of the seed rain i.e. the proportion of seeds from the different sources. ROBLEDO-ARNUNCIO & GARCIA (2007) used simulations to show the improvement obtained by this method in evaluating the distances travelled. They took as an illustration the data for *Prunus mahaleb* and found a distance twice as great after factoring in the locations of the sources (278m vs. 110m).

However, there is generally no maternal tissue available for genotyping, especially when relatively old descendants are involved (up to around 40 years old). It was to deal with such cases that *seedling neighbourhood models* (SNM) and probability methods (*full probability approaches,* JONES et al., 2010) were developed, which do not seek to ascertain categorically the mothers of the sampled offspring. Instead, they assess the dispersal kernel through maximum likelihood [1], by simultaneously taking into account both genetic information (microsatellite markers of adults and seedlings governed by Mendelian laws of heredity) and spatial (localisation of seedlings governed by the dispersal kernel and the position of adult trees). These methods, introduced by BURCZYK et al. (2006), integrate the spatial aspect, as suggested by ROBLEDO-ARNUNCIO & GARCIA (2007) and discussed above, and they have been applied several times in recent years

1 - Or by a Bayesian approach, fairly comparable (e.g. Moran & Clark 2011)

(GONZALEZ-MARTINEZ *et al*, (2006); ODDOU-MURATORIO *et al.*, 2008; CHYBICKI & BURCZYK, 2010; ODDOU-MURATORIO *et al.*, 2010; MORAN & CLARK, 2011). We ourselves used them for beech stands on Mont Ventoux (BONTEMPS *et al.*, submitted) where we genotyped 257 seedlings with 10 microsatellite markers (Fig. 3). Working out the markers did not enable us to identify the parents with confidence (on average, there were 7.3 parents and 22.5 pairs of parents compatible with each seedling) but the SNM nevertheless permitted an assessment of the dispersal kernel for seeds and pollen. For the dispersal of seeds, in particular, we distinguished the young seedlings (less than 2 years old), whose rate of mortality after germination was much less than that of the older saplings and trees (3–40 years old) for which a higher level of mortality is expected due to environmental factors and density. A greater distance of dispersal was estimated for the older trees (22m) than for the young seedlings (12m), which it is tempting to explain by reference to the Janzen-Connell effects: over several years, the seedlings closer to adult trees will have suffered greater mortality, resulting in a greater distance away from the adults and, thus, from their parents. However, this bias in the method for estimating a seed dispersal kernel was not expected in theory and had never been previously studied by simulations. Therefore, we simulated 200 data profiles, including three levels of seedling mortality proportional to the density of adults in their surrounding areas, estimating the dispersal kernel for each simulation and comparing this estimate to that used for the simulations. Despite very different patterns of spatial distribution of the seedlings for the three levels of mortality, the estimated dispersal kernels displayed very similar bias. This result shows that the use of microsatellite markers and *seedling neighbourhood models* provide estimated seed dispersal kernels unaffected by effects of mortality of the Janzen-Connell type, which is the opposite of what is widely said in the literature. It also indicates that the difference in dispersal distances for young and old seedlings is engendered by another mechanism. Here, one line for further research will focus on the year-by-year variations of a dispersal kernel due to different abiotic conditions or to varying corteges of animals, depending on the year.
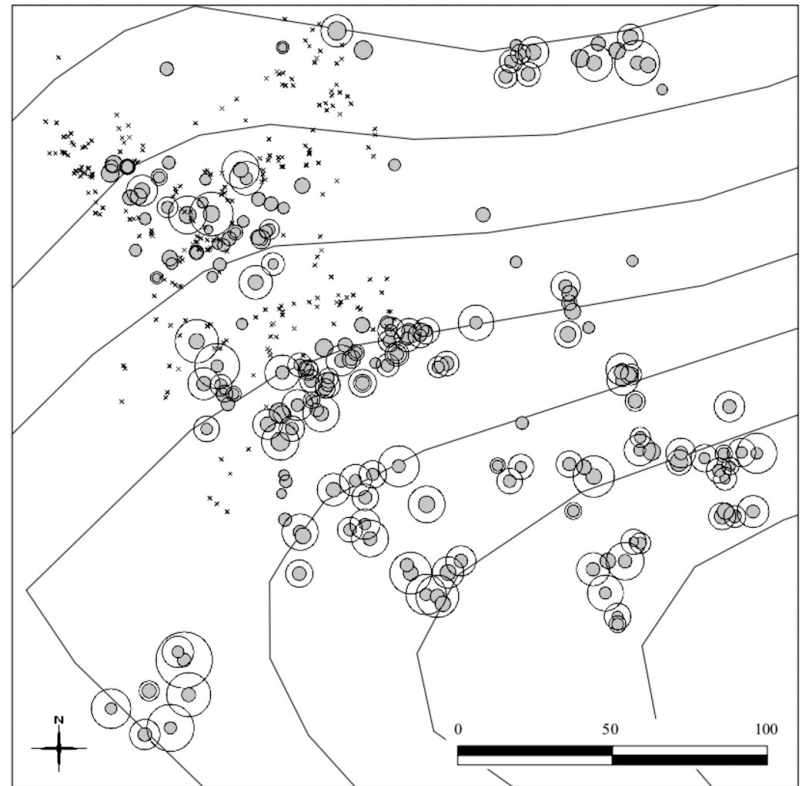
Towards analysis of large-scale dispersal

Inverse methods and derived approaches that exploit genetic data (SNM) have made it possible to characterise dispersal at the level of several hundred metres or, indeed, of several kilometres, as shown above, thanks to their statistical resolution of the problem of *seed shadow overlap* i.e. the superposition of contributions from numerous sources. Before the emergence of these methods, it was only possible to analyse dispersal patterns emanating from a single source, typically by marking seeds physically (paint, radioactivity) on a mother tree prior to their dispersal, then locating them afterwards. Such a single-source approach limited observations to a small scale and to the somewhat unreal environmental conditions that may prevail in a controlled experiment (though see BULLOCK & CLARKE (2001) for large–scale single-source experimental research).
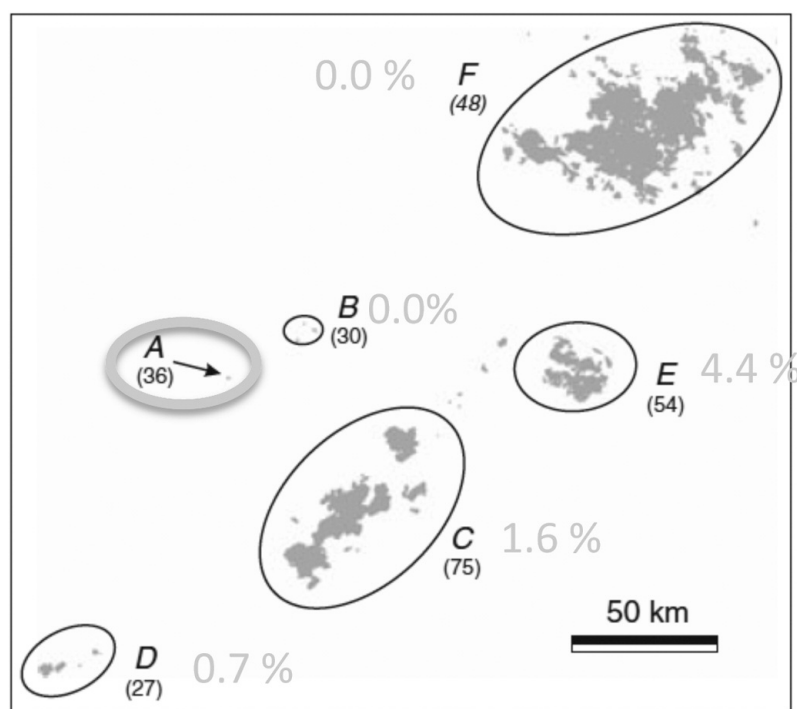
But because long distance dispersal, though rare, has important consequences, there is justification for developing the observation and modelling of dispersal processes at the much wider scales of ten or a hundred kilometres. To this end, the con-

Fig. 3:
Estimate of beech seed dispersal for a plot on Mont Ventoux. The exhaustive inventory of seed-producing adult trees (grey discs show trunk diametre, black discs stump diametre), sampling of the seedlings (crosses) and the genotyping of these individuals makes it possible to estimate the dispersal function by using a neighbourhood seedling model.

tribution of genetic markers could well prove beneficial, as shown by a recent study of pollen dispersal from *Pinus sylvestris* in scattered stands in the north of Spain (ROBLEDO-ARNUNCIO, 2011). The author used four chloroplastic microsatellite markers (paternally inherited) to identify among the five distinct populations located in a 250x250km area, the parent trees of pollen grains that had travelled a long distance (Fig.4). In finding migration levels of a few percent at distances of more than 50km, this study is the first to have shown so clearly that pollen can be blown so far by the wind and pollinate at such distances. Though their research zone provided exceptional conditions for studying gene flow at such a scale (a very small focal population, several isolated source populations and a significant genetic differentiation among the source populations), it remains important to repeat this type of study in order to characterise the dispersal functions over long distances. More generally, it is also important to investigate whether dispersal kernels constitute a good model for characterising the flow of individuals and genes at these much wider scales or whether the heterogeneous nature of plant cover as well as the structural features of landscape play a more significant role at these distances.

Over and above the statistical approaches detailed in this article, recent years have also seen the development of physical models, mechanistic to a greater or lesser degree, which have proved particularly useful (KUPARINEN, 2006). The numerous applications of the idea of using computerised simulations of physical models to predict dispersal capability (NATHAN *et al.,* 2005) and its impact on a species' ability to propagate or migrate (HIGGINS *et al.,* 1999; NATHAN *et al.,* 2011) have highlighted the features determining the occurrence of long-distance wind-borne dispersal (e.g. WRIGHT *et al.,* 2008). When allied to high-performance computers, models of air flow above a variegated canopy make it possible to simulate with precision the trajectory of seeds, pollen and spores (BOHRER *et al.,* 2008). But the features that determine the viability of seedlings and the role of animal vectors in dispersal remain difficult to model as accurately as the physics of air currents. No doubt one of the likely challenge in the years to come will be the working out of an approach combining the predictions of the mechanistic models with the empirical information obtained from the observation of long-distance dispersal in heterogeneous countryside.

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Summary

In recent years, the dispersal kernel has emerged as a modelling tool particularly well-adapted for making quantitative predictions about the capability of an individual plant to disperse its progeny and of whole populations to move further afield. This dispersal kernel function, which describes the spatial distribution of seeds disseminated from a single source, has a strong effect on the speed with which a colonisation front moves onwards by propagation, on the conservation of genetic diversity while such spreading of a plant population is under way and on the amount of gene flow over long distances. During this same period, numerous experimental and statistical methods, based on seed traps, counting established seedlings or genotyping adult trees and their offspring , have been developed to better estimate such dispersal kernels. In this article, we give a detailed account of these methods, emphasising the need to take into account the impact of environmental heterogeneity on the survival of young seedlings. And finally, we discuss lines of research for the study of dispersal kernels within a wider spatial framework (tens of kilometres).

Résumé

Pour fournir des prédictions quantitatives des capacités de dispersion des individus et de déplacement des populations, le noyau de dispersion est apparu ces dernières années comme un outil de modélisation particulièrement adapté. Cette fonction qui décrit la répartition spatiale des graines dispersées à partir d'une source, a un effet très fort sur la vitesse de propagation d'un front de colonisation, la conservation de la diversité génétique lors d'une expansion spatiale et l'intensité de flux de gènes à longue distance. De nombreuses méthodes expérimentales et statistiques, basées sur des pièges à graines, des comptages de semis installés ou le génotypage d'adultes et de leurs descendants ont été développées ces dernières années pour estimer au mieux ce noyau de dispersion. Nous détaillons ces méthodes dans cet article en insistant sur la prise en compte de l'hétérogénéité environnementale affectant la survie des semis. Finalement, nous discutons de pistes qui permettraient d'étudier les noyaux de dispersion à large échelle spatiale (dizaine de kilomètres).