

# DISPERSAL PROCESSES DRIVING PLANT MOVEMENT: RANGE SHIFTS IN A CHANGING WORLD

## Dispersal processes driving plant movement: challenges for understanding and predicting range shifts in a changing world

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### Summary

1. Dispersal ecology is a broad topical discipline that tackles important conceptual and applied issues, such as the study of the ability of plants to transmit their propagules across fragmented and managed landscapes.

2. The relevance of dispersal for plant populations is threefold because: (i) dispersal processes scale from genes and individuals that disperse (or produce propagules to be dispersed) to population dynamics and both local and regional distribution patterns; (ii) by dispersing propagules or individuals and the genes they carry, dispersal inherently links demographic and genetic dynamics across the landscape; and (iii) dispersal elicits key ecological and evolutionary processes that sustain biodiversity, such as species assembly in species-rich communities. The steady improvement of tracking devices and molecular tools that trace the movement or infer provenance of organisms and the pressing need to address conservation issues have expanded the disciplinary boundaries of dispersal ecology.

3. The discussion on the main advances on and challenges for dispersal ecology was the main motivation for the organization of a thematic topic session entitled *Dispersal processes driving plant movement: challenges for understanding and predicting range shifts in a changing world* at the Annual Meeting of the British Ecological Society (2015, Edinburgh). This session brought together researchers with different types of expertise and interests on dispersal processes and their contributions are now included in this special feature together with a few additional articles.

4. *Synthesis.* Overall, this special feature illustrates that dispersal ecology spans a broad range of research topics by integrating eight contributions that cover key aspects of this discipline: from conceptual and methodological advances to the study of the ecological and evolutionary outcomes.

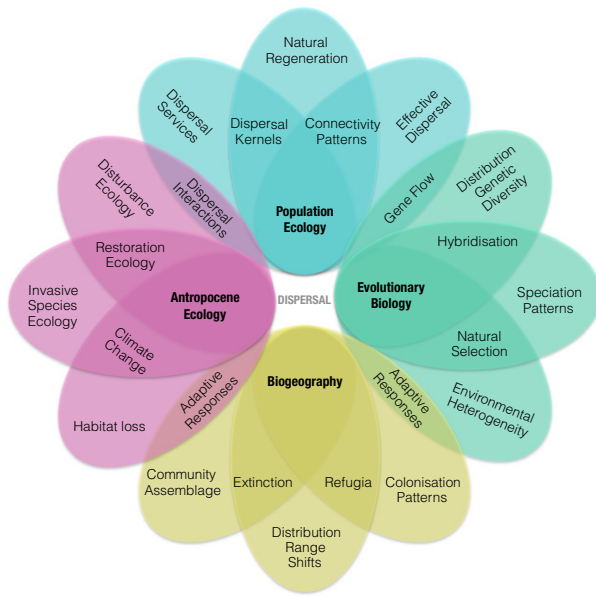
**Key-words:** anthropocene, dispersal kernels, distribution range shifts, long-distance dispersal, migration

Dispersal ecology is a broad topical discipline that assembles fundamental ecological and evolutionary processes and tackles important conceptual and applied issues (Fig. 1) (Sutherland *et al.* 2013). In an increasingly managed, fragmented and defaunated world, the ability of plants to transmit their propagules underlies colonization processes and determines range shifts (Nathan & Muller-Landau 2000; Clark, Lewis & Horvath 2001; Urban 2015). Because management must also be oriented to preserve remnant plant biodiversity, we need to

forecast the fate of plant communities inhabiting disturbed or managed landscapes by quantifying to what extent global change drivers modify the chances of plants to disperse (Tilman & Lehman 2001; Driscoll *et al.* 2014).

Understanding dispersal processes is fundamental to address a wide range of biological questions because dispersal encapsulates key biological properties. First, dispersal processes scale from genes and individuals that disperse (or produce propagules to be dispersed) to population dynamics and both local and regional distribution patterns. Local regeneration typically relies on short- to medium-distance dispersal,

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**Fig. 1.** Schematic depiction of the major ecological topics that revolve around dispersal ecology. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

whereas the geographic range that a given species or community occupies is defined by the rare arrival of long-distance dispersal (LDD) events, sometimes mediated by non-standard dispersal vectors (such as strong winds, migrating vertebrates or human transportation) (Nathan 2006). Second, by dispersing propagules or individuals and the genes they carry, dispersal inherently links demographic and genetic dynamics across the landscape (Sork *et al.* 1999). Third, dispersal underpins key ecological and evolutionary processes that sustain biodiversity, such as species assembly in species-rich communities (Hubbell 2001; Seidler & Plotkin 2006), hybridization (Petit *et al.* 2004) and speciation processes (Avice 2000).

Notably, in recent years, numerous studies have quantified how far and how often organisms move across the landscape (Cousens, Dytham & Law 2008; Clobert *et al.* 2012). The steady improvement of tracking devices and molecular tools that trace the movement or infer provenance of organisms and the pressing need to address conservation issues have expanded the disciplinary boundaries of dispersal ecology (Robledo-Arnuncio *et al.* 2014). This was the main motivation for the organization of a thematic topic session entitled *Dispersal processes driving plant movement: challenges for understanding and predicting range shifts in a changing world* at the Annual Meeting of the British Ecological Society (2015, Edinburgh). This session brought together researchers with different types of expertise and interests on dispersal processes and their contributions are now included in this special feature (SF) together with a few additional articles.

Overall, this SF illustrates that dispersal ecology spans a broad range of research topics by integrating eight contributions that cover key aspects of this discipline: from conceptual and methodological advances to the study of the ecological and evolutionary outcomes. The issue opens with

an integrative, conceptual framework to understand dispersal events as a function of the dispersal distances and the genetic neighbourhood reached by dispersed propagules (Jordano 2017). Such an integrative framework helps to explicitly link demographic and genetic effects of dispersal; its central tenet is that biologically meaningful definition of strict-sense LDD events needs consideration of geographic (distance) frames that include both population and genetic neighbourhood size references. Thus, in the case of animal-dispersed species, strict-sense LDD events are likely contributed by a minority of frugivore species within highly diversified assemblages. Farwig, Schabo & Albrecht (2017) specifically address the effects of habitat fragmentation on seed removal by frugivorous birds and mammals in relation to species-specific responses to habitat disturbance. These results indicate that seed removal may be relatively robust in spite of shifts in the frugivore community in forest fragments. The effect is likely related to functional trait complementarity and redundancy within diversified frugivore assemblages, with forest generalists and small-bodied frugivores maintaining dispersal processes in fragmented forests in temperate regions.

Yet specific dispersal functions like LDD may be negatively affected by selective losses of e.g. large-bodied frugivore species. The functional relevance of these LDD events is further explored by Horvitz *et al.* (2017) who assess the spread of 17 of China's worst invasive plant species and calculate the minimal arrival speed for the first record of each species in each county. This empirical evidence points to an unequivocal role of human-assisted dispersal, with spread patterns characterized by long jumps of tens to hundreds of kilometres and extremely fast average spread rates ( $\sim 2\text{--}4$  km per year), and highly variable scales (0.1–128.2 km per year). In general, the study of LDD still needs much more empirical data documenting the extent and frequency of these events and moving beyond exploration of species traits and habitat suitability to examine the actual patterns and the mechanisms of large-scale population spread (invasive or not). The empirical approach is particularly topical to improve our understanding and ability to model animal- and human-mediated dispersal for which mechanistic models are less advanced than those for wind-dispersed propagules.

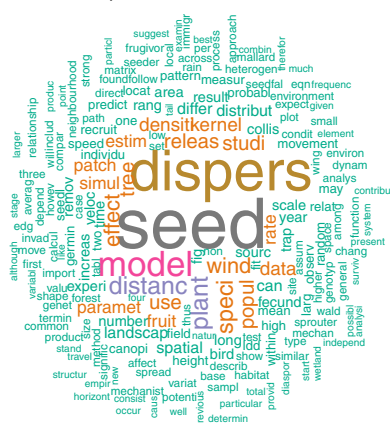
Dispersal ecologists have been gathering a wealth of empirical data on dispersal patterns obtained from direct observations, telemetry and/or the analysis of molecular markers. This offers a timely opportunity to implement two modelling exercises (Nathan 2006): (i) finding a universal best-fitting dispersal kernel that distil major features of dispersal patterns for a wide range of plant species with different dispersal mechanisms and (ii) applying novel tools that take the most of available data to delve into the tail of dispersal kernels, the most elusive part of the dispersal kernels. Both issues are covered in this SF. On the one hand, Bullock *et al.* (2017) have synthesized empirical data sets available in the literature ( $N = 168$ ) to fit and compare the performance of 11 widely used best-fitting density functions across a broad range of species and dispersal modes. No one function systematically outperformed other functions, suggesting that the best-fitted

dispersal kernel is context-dependent and researchers should fit and compare several functions, particularly if they are interested in forecasting both short- and long-distance dispersal events. Note that dispersal kernels typically integrate the action of different biotic and abiotic dispersal vectors that respond differently to the landscape (the total dispersal kernel, *sensu* Nathan 2007) and this complexity is difficult to summarize in a simple versatile function. On the other hand, empirical data sets can provide valuable insights on the extent of the tail of the dispersal kernels by applying statistics of extremes (Garcia & Borda-de-Agua 2017). Conveniently, these statistical approaches use only a subset of the observed values (particularly the large, extreme ones) to infer the probability and extent of yet unobserved, but not impossible, LDD events (Coles 2001; Katz, Brush & Parlange 2005). These very long – i.e. extreme – dispersal distance events underlie colonization patterns that eventually might result in distribution range shifts. Overall, the application of statistics of extremes opens new interesting theoretical and applied insights to move forward in understanding the consequences of rare LDD events.

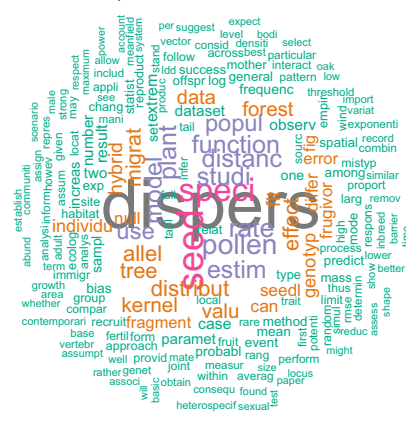
In addition to demographic consequences, dispersal is also of major importance for eco-evolutionary dynamics as local adaptation and genetic drift are determinant processes during expansions or distribution range shifts (Excoffier, Foll & Petit 2009; Kremer *et al.* 2012). In this SF, three contributions relate to this aspect by (i) considering pollen dispersal as a vector of gene flow that comes in addition to seed migration (Klein, Lagache-Navarro & Petit 2017; Robledo-Arnuncio & Gaggiotti 2017) and (ii) deciphering how the local dispersal patterns determine the variance of reproductive success and the effective population size with regard to genetic drift (Gerzabek, Oddou-Muratorio & Hampe 2017). Robledo-Arnuncio & Gaggiotti (2017) and Gerzabek, Oddou-Muratorio & Hampe (2017) both use molecular marker data to reconstruct dispersal events and raise conclusions about contemporary migration rates and/or dispersal kernels. The former is a methodological study that proposes a novel Bayesian method to estimate the effective seed and pollen migration rates among genetically differentiated populations of a landscape.

The method fully exploits population assignment likelihoods at a contemporary time-scale (i.e. jointly using parent and offspring genotypes), building upon Robledo-Arnuncio (2012), and it explicitly considers genotyping mistakes and null alleles, the two main sources of bias when estimating migration rates. It should thus emerge in the next years as a versatile method to measure pollen and seed dispersal for various plant species in human-altered landscapes or fragmented colonization fronts. This Bayesian method will also pave the way for analysing landscape genetic data with more realistic movement models at the contemporary scale. In a case study, Gerzabek, Oddou-Muratorio & Hampe (2017) apply parentage analysis within a recently established and expanding population of Pedunculate oak. More than just quantifying the highly skewed distribution of seed production and reproductive success among individuals, the study demonstrates how the long-distance seed dispersal and the disperser satiation of the scatter-hoarding jays interact with the variations of recruitment success driven by habitat and largely reshuffle the ranking of individual trees between seed production stage and seedling recruitment stage. Fully understanding the mechanisms at individual and contemporary scales is a long-lasting quest in evolutionary ecology for those aiming at predicting future eco-evolutionary dynamics, in particular under the forcing of global changes or under different management scenarios. Upscaling the consequences of dispersal mechanisms from individuals to populations is also central in Klein, Lagache-Navarro & Petit (2017), which uses simulations to investigate the determinants of realized hybridization rates. Important effects of pollen limitation, spatial clustering of a rare species and fine-scale distribution of individuals were observed in their individual-based spatially explicit simulations. The study thus underlines that it is better to *analyse, then aggregate, rather than analyse the aggregate*, following Clark *et al.* (2011). To this goal, dispersal kernels appeared once again as a powerful methodology to investigate the interaction between dispersal processes and spatial configurations, but the question of putting more reality in kernels for animal- or human-dispersed seeds and pollen still deserves important efforts in the future (Robledo-Arnuncio *et al.* 2014).

Special feature 2008



Special feature 2017



**Fig. 2.** Word clouds obtained from combining all papers contributing to the special feature issued in 2008 (left) and the current issue (right). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

The last SF about dispersal issued in the *Journal of Ecology* in 2008 examined major advances in dispersal ecology, with a strong mechanistic focus that pursued modelling complex seed dispersal processes (Bohrer *et al.* 2008; Carlo & Morales 2008; Jones & Muller-Landau 2008; Levey, Tewksbury & Bolker 2008; Schurr, Steinitz & Nathan 2008; Soons & Bullock 2008). The word cloud derived from that issue (Fig. 2a) shows that 'seed' ( $n = 1408$ ), 'dispers' ( $n = 1098$ ), 'model' ( $n = 592$ ), 'distan' ( $n = 383$ ) and 'plant' ( $n = 367$ ) were the most frequent words in that issue. The frequency of the term 'seed' was highly correlated with the frequency of 'dispers', 'releas' and 'wind', which evidences a strong trend towards mechanistic approaches to understand how propagules get dispersed, particularly in wind-dispersed plant species. The overall message of this previous SF highlighted the need of improving our predictions on how far and how often organisms move across heterogeneous landscapes by accommodating key plant features and different sources of spatial and environmental complexity to our models. Since then, much progress has been made in combining different tools and models to gain reliable dispersal estimates, including LDD events. The second word cloud (Fig. 2b), obtained from the contributions comprised in the current SF, shows a similar set of top-mentioned words: 'disperse' ( $N = 815$ ), 'specie' ( $N = 358$ ), 'seed' ( $N = 357$ ), 'plant' ( $N = 247$ ) and 'distan' ( $N = 243$ ). The most frequent word (disperse) is highly correlated with 'kernel', 'distan', 'mode' and 'vertebrate' showing an increased interest for the study of biotic dispersal vectors that mobilize propagules. The presence of 'pollen', 'genotype', 'popul' and 'allel' in the list of frequent words also depicts a trend towards demo-genetic impacts of dispersal and methodologies relying on molecular markers to trace dispersal events.

Ecological studies have demonstrated that anthropogenic activities and climate-driven changes impact the probability of organisms to persist in their current locations and, as a result, distribution ranges might shift in response to global change drivers. Yet, the consequences of climate change and anthropic actions in determining the ability of plant populations to disperse remains poorly quantified. The integration of tools providing robust measures on dispersal patterns at the local scale combined with statistical methods that allow us to scale-up local processes to global patterns is a pending task in dispersal ecology. In addition, these approaches should be extended to the study of communities and biomes where different species become connected through biotic interactions (Morales-Castilla *et al.* 2015), some of them instrumental in providing dispersal services. To forecast the fate of current biomes in a changing world, future efforts should consider the integrated effect of multiple interacting species to scale from the population- and species-levels to the community level across regional scales.

### Authors' contributions

C.G., E.K. and P.J. contributed equally to the writing of this editorial.

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### Data accessibility

This paper does not use data.

### References

- Avise, J.C. (2000) *Phylogeography: The History and Formation of Species*. Harvard University Press, Cambridge, MA, USA.
- Bohrer, G., Katul, G.G., Nathan, R., Walko, R.L. & Avissar, R. (2008) Effects of canopy heterogeneity, seed abscission and inertia on wind-driven dispersal kernels of tree seeds. *Journal of Ecology*, **96**, 569–580.
- Bullock, J.M., González, L.M., Tamme, R., Gotzenberger, L., White, S.M., Partel, M. & Hooftman, D.A.P. (2017) A synthesis of empirical plant dispersal kernels. *Journal of Ecology*, **105**, 6–19.
- Carlo, T.A. & Morales, J.M. (2008) Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. *Journal of Ecology*, **96**, 609–618.
- Clark, J.S., Bell, D.M., Hersh, M.H., Kwit, M.C., Moran, E., Salk, C., Stine, A., Valle, D. & Zhu, K. (2011) Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecology Letters*, **14**, 1273–1287.
- Clark, J.S., Lewis, M. & Horvath, L. (2001) Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist*, **157**, 537–554.
- Clobert, J., Bague, M., Benton, T. & Bullock, J. (2012) *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- Coles, S. (2001) *An Introduction to Statistical Modeling of Extreme Values*. Springer, London, UK.
- Cousens, R., Dytham, C. & Law, R. (2008) *Dispersal in Plants: A Population Perspective*. Oxford University Press, Oxford, UK.
- Driscoll, D.A., Banks, S.C., Barton, P.S. *et al.* (2014) The trajectory of dispersal research in conservation biology. Systematic review. *PLoS ONE*, **9**, e95053.
- Excoffier, L., Foll, M. & Petit, R. (2009) Genetic consequences of range expansions. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 481–501.
- Farwig, N., Schabo, D. & Albrecht, J. (2017) Trait-associated loss of frugivores in fragmented forest does not affect seed removal rates. *Journal of Ecology*, **105**, 20–28.
- García, C. & Borda-de-Agua, L. (2017) Extended dispersal kernels in a changing world: insights from statistics of extremes. *Journal of Ecology*, **105**, 63–74.
- Gerzabek, G., Oddou-Muratorio, S. & Hampe, A. (2017) Temporal change and determinants of maternal reproductive success in an expanding oak forest stand. *Journal of Ecology*, **105**, 39–48.
- Horvitz, N., Wang, R., Wan, F.H. & Nathan, R. (2017) Pervasive human-mediated large-scale invasion: analysis of spread patterns and their underlying mechanisms in 17 of China's worst invasive plants. *Journal of Ecology*, **105**, 85–94.
- Hubbell, S. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ, USA.
- Jones, F.A. & Muller-Landau, H.C. (2008) Measuring long-distance seed dispersal in complex natural environments: an evaluation and integration of classical and genetic methods. *Journal of Ecology*, **96**, 642–652.
- Jordano, P. (2017) What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of Ecology*, **105**, 75–84.
- Katz, R.W., Brush, G.S. & Parlange, M.B. (2005) Statistics of extremes: modeling ecological disturbances. *Ecology*, **86**, 1124–1134.

- Klein, E.K., Lagache-Navarro, L. & Petit, R.J. (2017) Demographic and spatial determinants of hybridization rate. *Journal of Ecology*, **105**, 29–38.
- Kremer, A., Ronce, O., Robledo-Arnuncio, J.J. *et al.* (2012) Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*, **15**, 378–392.
- Levey, D.J., Tewksbury, J.J. & Bolker, B.M. (2008) Modelling long-distance seed dispersal in heterogeneous landscapes. *Journal of Ecology*, **96**, 599–608.
- Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015) Inferring biotic interactions from proxies. *Trends in Ecology & Evolution*, **30**, 347–356.
- Nathan, R. (2006) Long-distance dispersal of plants. *Science*, **313**, 786–788.
- Nathan, R. (2007) Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. *Frugivory and Seed Dispersal: Theory and Applications in a Changing World* (eds A.J. Dennis, R. Green, E.W. Schupp & D. Westcott), pp. 252–276. Commonwealth Agricultural Bureau International, Wallingford, UK.
- Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278–285.
- Petit, R.J., Bodenes, C., Ducouso, A., Roussel, G. & Kremer, A. (2004) Hybridization as a mechanism of invasion in oaks. *New Phytologist*, **161**, 151–164.
- Robledo-Arnuncio, J.J. (2012) Joint estimation of contemporary seed and pollen dispersal rates among plant populations. *Molecular Ecology Resources*, **12**, 299–311.
- Robledo-Arnuncio, J.J. & Gaggiotti, O.E. (2017) Estimating contemporary migration rates: Effect and joint inference of inbreeding, null alleles and mistyping. *Journal of Ecology*, **105**, 49–62.
- Robledo-Arnuncio, J., Klein, E., Muller-Landau, H. & Santamaria, L. (2014) Space, time and complexity in plant dispersal ecology. *Movement Ecology*, **2**, 16.
- Schurr, F.M., Steinitz, O. & Nathan, R. (2008) Plant fecundity and seed dispersal in spatially heterogeneous environments: models, mechanisms and estimation. *Journal of Ecology*, **96**, 628–641.
- Seidler, T.G. & Plotkin, J.B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biology*, **4**, 2132–2137.
- Soons, M.B. & Bullock, J.M. (2008) Non-random seed abscission, long-distance wind dispersal and plant migration rates. *Journal of Ecology*, **96**, 581–590.
- Sork, V.L., Nason, J., Campbell, D.R. & Fernandez, J.F. (1999) Landscape approaches to historical and contemporary gene flow in plants. *Trends in Ecology & Evolution*, **14**, 219–224.
- Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J. *et al.* (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, **101**, 58–67.
- Tilman, D. & Lehman, C. (2001) Human-caused environmental change: impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences United States of America*, **98**, 5433–5440.
- Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science*, **348**, 571–573.

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