

ESSAY REVIEW

Plant functional connectivity – integrating landscape structure and effective dispersal

Alistair G. Auffret^{*,1,2}, Yessica Rico³, James M. Bullock⁴, Danny A. P. Hooftman^{4,5}, Robin J. Pakeman⁶, Merel B. Soons⁷, Alberto Suárez-Esteban^{8,9}, Anna Traveset¹⁰, Helene H. Wagner¹¹ and Sara A. O. Cousins¹

¹Biogeography and Geomatics, Department of Physical Geography, Stockholm University, 10691 Stockholm, Sweden;

²Department of Biology, University of York, York YO10 5DD, UK; ³CONACYT, Instituto de Ecología, A.C., Centro Regional del Bajío, Av. Lázaro Cardenas 253, Pátzcuaro, Michoacán 61600, México; ⁴NERC Centre for Ecology & Hydrology, Benson Lane, Wallingford, Oxfordshire OX10 8BB, UK; ⁵Lactuca: Environmental Data Analyses and Modelling, 1112 NC Diemen, The Netherlands; ⁶The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH, UK; ⁷Ecology & Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands; ⁸Department of Renewable Resources, University of Alberta, 116 St. and 85 Ave., Edmonton, AB T6G 2R3, Canada; ⁹Yukon Research Centre, Yukon College, 500 College Drive, Whitehorse, YT Y1A 5K4, Canada;

¹⁰Mediterranean Institute of Advanced Studies (UIB-CSIC), C/Miquel Marqués 21, 07190-Esporles, Mallorca, Balearic Islands, Spain; and ¹¹Department of Ecology and Evolutionary Biology, University of Toronto, 3359 Mississauga Road, Mississauga, ON L5L 1C6, Canada

Summary

1. Dispersal is essential for species to survive the threats of habitat destruction and climate change. Combining descriptions of dispersal ability with those of landscape structure, the concept of functional connectivity has been popular for understanding and predicting species' spatial responses to environmental change.

2. Following recent advances, the functional connectivity concept is now able to move beyond landscape structure to consider more explicitly how other external factors such as climate and resources affect species movement. We argue that these factors, in addition to a consideration of the complete dispersal process, are critical for an accurate understanding of functional connectivity for plant species in response to environmental change.

3. We use recent advances in dispersal, landscape and molecular ecology to describe how a range of external factors can influence effective dispersal in plant species, and how the resulting functional connectivity can be assessed.

4. Synthesis. We define plant functional connectivity as *the effective dispersal of propagules or pollen among habitat patches in a landscape*. Plant functional connectivity is determined by a combination of landscape structure, interactions between plant, environment and dispersal vectors, and the successful establishment of individuals. We hope that this consolidation of recent research will help focus future connectivity research and conservation.

Key-words: biodiversity conservation, climate change, gene flow, habitat fragmentation, landscape ecology, landscape genetics, pollen dispersal, pollination, seed dispersal

The importance of dispersal and connectivity

Dispersal is a key life-history process, with the movement of individuals or propagules impacting populations, species and communities from short-term ecological to long-term evolutionary time-scales (Nathan *et al.* 2008; Bonte *et al.* 2012).

Of current interest is the role of dispersal during periods of environmental change, particularly anthropogenic habitat destruction and climate change (Hampe 2011; McConkey *et al.* 2012; Baguette *et al.* 2013). Habitat loss results in smaller, fewer and more isolated populations at local, landscape and regional scales. A reduction in dispersal between populations can cause them to become increasingly affected by the cumulative effects of genetic drift and reduced gene

*Correspondence author. E-mail: alistair.auffret@natgeo.su.se

flow, resulting in fitness loss and an erosion of genetic diversity. This can leave them less resilient to environmental and demographic stochasticity and more likely to go extinct (Leimu *et al.* 2006; Vranckx *et al.* 2012). A lack of dispersal among isolated populations also leads to population decline, with a lower chance of populations being rescued or suitable patches being (re-)colonized resulting in biodiversity losses (Ibáñez *et al.* 2014). Dispersal is also required for organisms to migrate successfully to more suitable climates in response to climate change (Hampe 2011).

By linking dispersal with the physical environment, the concept of *connectivity* has been useful for understanding how, and predicting where, organisms disperse, often in relation to environmental change. The connectivity concept was introduced by Taylor *et al.* (1993) as *the degree to which the landscape facilitates or impedes movement among resource patches*. Since then, its most enduring development has been the identification of the structural and functional components of landscape connectivity. *Structural connectivity* describes the physical aspects of the landscape and the configuration of habitat patches, while *functional connectivity* is defined as *the behavioural responses of an organism to the various landscape elements*, referring to the actual flow of individuals and their genes among habitat patches (Tischendorf & Fahrig 2000). This became the prevailing definition which is still cited today (Baguette *et al.* 2013; Aavik, Holderegger & Bolliger 2014). As different species can respond differently to a particular landscape structure, functional connectivity is necessarily species-specific, and is commonly measured using estimated dispersal distances, rates of movement through different categories of land-cover and other active interactions with different types of habitat and with the matrix (Calabrese & Fagan 2004; Vogt *et al.* 2009; Watts & Handley 2010).

Integrating landscape structure and effective dispersal

Understanding how dispersal and landscape interact to determine species occurrences and responses to environmental change is extremely valuable. However, researchers are increasingly appreciating that there are other factors and processes beyond landscape structure that can influence dispersal among habitat patches. For example, the movement ecology paradigm, which aims to unify research relating to different types of movement across species and scales, considers that a range of external factors can affect how and where organisms move (Nathan *et al.* 2008). Along with the spatial structure of the landscape, paths of movement are determined by factors such as climate and the presence of resources, mutualistic species or predators, and their interactions with landscape structure and the characteristics of the organism in question (Nathan *et al.* 2008; Vasudev *et al.* 2015). At the landscape scale, many of the external factors affecting movement have been studied in the context of the matrix, the variations of which can affect species movement *per se*, as well as influencing immigration into habitat patches through interactions

with the biotic and abiotic environment (Driscoll *et al.* 2013). Although it is clear that movement is affected by more than landscape structure, external factors such as behaviour of individuals and species interactions have only rarely been considered as components of functional connectivity (Bélisle 2005; Betts *et al.* 2015a), and these factors are largely specific to animals. Suggestions for the assessment of functional connectivity are still generally based on coupling movement and landscape structure only (Vogt *et al.* 2009; Watts & Handley 2010; Luque, Saura & Fortin 2012).

In addition to the movement of an individual, there are other stages of dispersal that can be affected by landscape structure and external factors, with consequences for functional connectivity. Dispersal can be split into three distinct phases comprising (i) departure, (ii) transfer (or movement) and (iii) arrival (Bonte *et al.* 2012). Therefore, processes occurring pre- and post-transfer in the habitat patches connected by species movement are also important in determining functional connectivity. As advances in molecular ecological methods and a reduction in costs mean that we can increasingly measure exactly how populations are connected in space (Luque, Saura & Fortin 2012; Baguette *et al.* 2013), it is important that we understand mechanistically the full range of factors and processes that lead to successful dispersal across landscapes. Therefore, it is vital that the functional connectivity concept considers how dispersal is affected by both landscape and other external factors, and that all stages of the dispersal process are included explicitly. With a focus on plant species, we draw upon recent work in the dispersal and connectivity literature to show how interactions between organism, landscape and dispersal affect functional connectivity in space and time, and how methodological advances can be used for its assessment.

Plant functional connectivity

We define plant functional connectivity as *the effective dispersal of propagules or pollen among habitat patches in a landscape*. Functional connectivity has generally been considered in terms of individuals of species actively responding to landscape structure, which is generally only applicable to mobile animals. For most plant species, dispersal involves the transfer of propagules (such as seeds, spores, bulbs and other plant fragments) and/or pollen via biotic and abiotic vectors. Therefore, plant functional connectivity can change not only as a result of a modification of landscape structure but also with changes in the type, behaviour or abundance of dispersal vectors, or the plants' ability to use these vectors. Furthermore, for functional connectivity to be realized, the dispersal of propagules and pollen must be *effective* (Schupp, Jordano & Gómez 2010). This means seeds must not only arrive (following seed dispersal) or be produced (following pollen dispersal) but must also result in the establishment of a new adult plant. From a genetic perspective, resulting individuals must also reproduce for their genes to be integrated into the population. As a consequence, plant functional connectivity depends on

processes at both source and recipient habitat patches and in the matrix, as well as on the characteristics and behaviour of relevant dispersal vectors of propagules and pollen (Fig. 1). In their application of the movement ecology paradigm to plants, Damschen *et al.* (2008) added seed dispersal vector identity to landscape structure as an additional factor influencing plant movement. In the following sections, we describe explicitly how dispersal by different vectors of seeds and pollen are affected by and interact with factors both dependent on, and independent of, landscape structure, and how this dispersal then leads to functional connectivity.

CONNECTIVITY THROUGH SEED DISPERSAL

Studies of functional connectivity in plants very often focus on the dispersal of seeds between isolated habitat patches (e.g. Rico, Boehmer & Wagner 2012; Mueller *et al.* 2014). At the source population, seed production is an important determinant of the amount of dispersal, and is governed by pollination, resource availability and a range of environmental conditions, which can vary with or independently of landscape change (Soons & Heil 2002). The abscission of seeds from parent plants, as well as their transfer across the landscape and arrival in recipient habitats can occur biotically and abiotically. We describe these separately below, although the majority of plant species can be dispersed by multiple vectors (Ozinga *et al.* 2004).

Biotic seed dispersal

Biotic dispersal over the distances required to transport seeds between habitat patches generally involves the attachment to (epizoochory), ingestion by (endozoochory) or caching by (synzoochory) animals. As such, functional connectivity for plants is affected by how *other organisms* respond to (changes in) landscape structure, or by changes in the interaction between plant and vector (McConkey *et al.* 2012). Following seed production, functional connectivity through biotic dispersal first depends on the presence of dispersers that ingest or deliberately move the seeds, or to which seeds become attached. Animal dispersers then determine the potential for functional connectivity through their movement and behaviour (Jansen *et al.* 2012; González-Varo, López-Bao & Guitián 2013). This movement and the subsequent detachment or deposition of seeds (behaviourally determined or otherwise) can in turn be influenced by landscape structure. For example, linear landscape elements and variation in matrix quality can affect movement in seed-dispersing animals (Magrath, Larrinaga & Santamaría 2012; Suárez-Esteban, Delibes & Fedriani 2013), and habitat selection can cause non-random seed deposition in particular landscape elements (directed dispersal; Carlo *et al.* 2013). In these cases, changes in landscape structure would be expected eventually to affect functional connectivity. However, biotic seed dispersal can also be affected by other factors. For example, changes in climate (Mokany, Prasad & Westcott 2014),

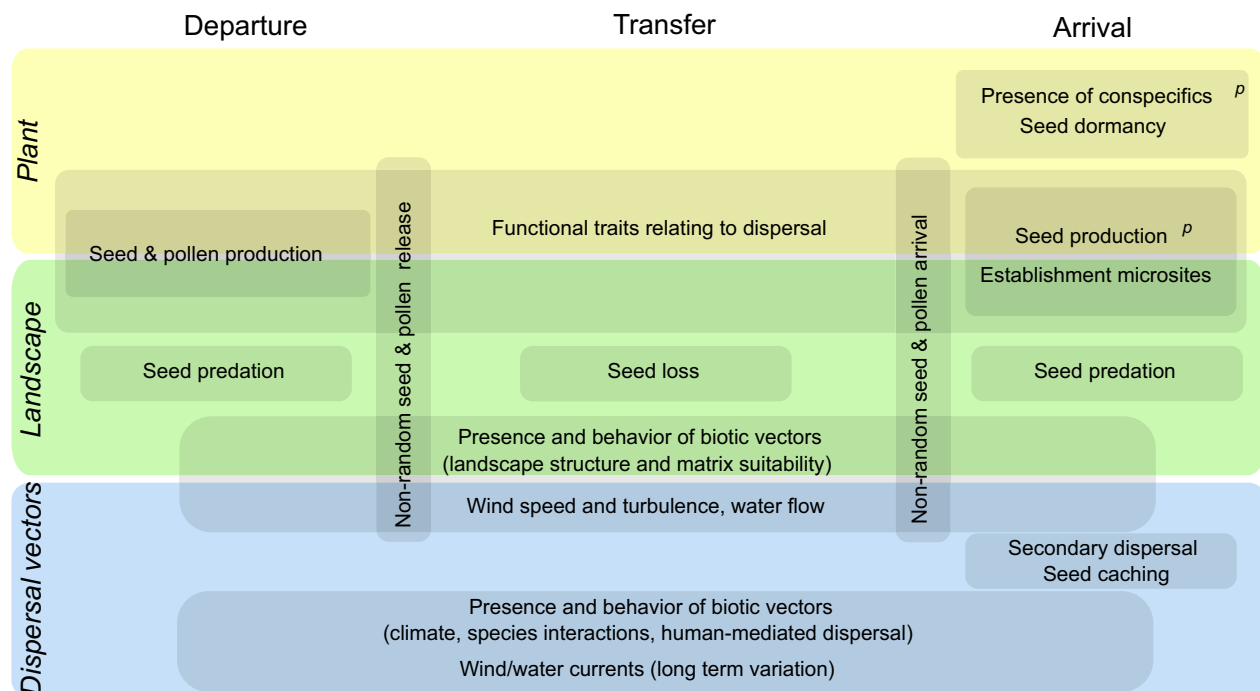


Fig. 1. Landscape factors can be important determinants of plant functional connectivity, but their influence extends well beyond connecting structures in the landscape. The landscape's influence is always mediated by the plant species or dispersal vector, while fluctuations or changes in the transfer of seed and pollen dispersers as well as long-term climate change can alter functional connectivity without an associated change in landscape structure. The functional traits of the plant species of interest determine the likelihood of dispersal by different vectors, as well as establishment or eventual seed dormancy. Most factors are common between functional connectivity by seed dispersal and pollination, although effective pollination also depends on the presence of conspecifics and the production of seeds following pollination (denoted by p). [Colour figure can be viewed at wileyonlinelibrary.com]

hunting practices (Markl *et al.* 2012) and the introduction of non-native dispersal vectors (Traveset & Richardson 2014) can all influence seed dispersal indirectly via effects on – and interactions between – the populations of animal dispersers. These factors can not only interact with landscape structure but can also occur independently, affecting the *quality* of seed dispersal (Schupp, Jordano & Gómez 2010), and as a consequence the potential for functional connectivity.

Humans act as another biotic dispersal vector, being able to disperse seeds over long distances. Seeds can become attached to clothing, vehicles or goods, and subsequent dispersal at different scales is determined by landscape and patterns of movement (Niggemann *et al.* 2009). In addition, humans can manipulate patterns of functional connectivity through the transportation of other biotic dispersers such as grazing livestock between isolated habitat patches, without associated changes in structural connectivity (Rico, Boehmer & Wagner 2012).

Abiotic seed dispersal

Beyond gravity, abiotic dispersal vector occurs mainly via wind and water. For species transported by wind, abscission is partially controlled by wind speed and turbulence, as well as temperature (Maurer *et al.* 2013). Unlike biotic dispersal, whereby seeds of very different morphologies are able to disperse long distances (Bullock *et al.* 2017), long-distance seed dispersal by wind is associated with seeds that are released relatively high in the vegetation and those which fall slowly (Tackenberg, Poschlod & Bonn 2003). Once airborne, vegetation structure, landscape configuration and topography can all affect the distance and direction seeds disperse across the matrix (Damschen *et al.* 2014; Trakhtenbrot, Katul & Nathan 2014). Projected changes in temperature and wind speeds associated with future climate change, along with interactions with habitat fragmentation are also expected to affect seed dispersal patterns and consequently the functional connectivity of populations at landscape and larger spatial and temporal scales (Soons, Nathan & Katul 2004; Kuparinen *et al.* 2009; Bullock *et al.* 2012). As with biotic dispersal, directed dispersal to suitable sites can also occur via abiotic vectors, particularly water (Soons *et al.* 2017). Exactly where these seeds arrive is generally determined by longer term flow patterns in channels, tides and oceanic currents (Vargas *et al.* 2014; Favre-Bac *et al.* 2016), which could vary in response to future changes in landscape and climate.

Arrival and establishment

For functional connectivity to be realized, seeds do not only have to arrive at the recipient habitat, they must also establish and grow into adult plants, which is an important bottleneck (Uriarte *et al.* 2010; Hampe 2011). The presence of microsites such as rock debris, anthills or animal burrows has been found to promote such establishment and complete the process of functional connectivity (Rico, Boehmer & Wagner 2012). For biotically dispersed species, suitable establishment

microsites can be created through disturbance by the seed-dispersing animal (Faust *et al.* 2011). Secondary dispersal by ants (myrmecochory) and seed caching animals of seeds that have already been dispersed across a landscape by other biotic and abiotic vectors can also improve the potential for establishment in a new patch (Vander Wall 2003; Gallegos, Hensen & Schleuning 2014). On the other hand, seed predation occurring either pre- or post-dispersal can negatively affect functional connectivity, and is related to conditions in the site and surrounding landscape (Orrock & Damschen 2005).

CONNECTIVITY THROUGH POLLEN FLOW

The exchange of pollen offers another way by which genes can be moved between distinct plant populations. Because conspecifics need to be present and flowering at the recipient patch to ensure functional connectivity, dispersal of pollen contributes solely to the persistence of plant species where they already occur, potentially preventing inbreeding depression and harbouring among-population adaptive genetic diversity (Keller & Waller 2002; González-Varo *et al.* 2010). Like seeds, pollen can be dispersed abiotically by wind and water, or biotically via animals (mainly insects, but also a range of vertebrate species; Ollerton, Winfree & Tarrant 2011).

For plant species dependent on biotic pollination to produce seeds, functional connectivity depends to a large extent on pollinator identity, density and behaviour. Pollinator movement and successful pollination are influenced by habitat composition and landscape configuration, including the presence of habitat corridors (Townsend & Levey 2005; Hadley & Betts 2012). Some plant species are even able to control pollination through recognition of avian pollinator species (Betts, Hadley & Kress 2015b). Pollinator movement can be influenced not only directly by landscape factors, for example, insect pollinators also interact with other factors such as wind speed and direction (Ahmed *et al.* 2009). The presence of pollinators in a landscape can also be affected by climate-driven phenological changes (Kudo & Ida 2013) or shifts in the pollinator community through extinction, immigration or invasion. The loss of a single pollinator species can reduce seed production through modifying the foraging behaviour of other pollinators (Brosi & Briggs 2013), while the competitive displacement of different types of native by non-native pollinators can reduce plant fitness by increasing self-pollination and by creating hybrids between related non-native and native plants (Morales & Traveset 2008; Morales *et al.* 2013).

The dispersal of pollen by wind is thought to have evolved such that pollen flow is facilitated where pollen or pollinator limitation is a potential issue, such as in areas with sparse plant occurrences (Culley, Weller & Sakai 2002). Like seed dispersal, the transfer of pollen among plant populations by wind is affected by landscape structure (Shohami & Nathan 2014). It might also be expected that like wind-dispersed seeds, longer term and larger scale patterns of pollen flow might be affected by climate change influencing wind speed and turbulence, and their resulting interactions with landscape

structure. For abiotic pollen dispersal by water, the distance and direction of pollen transfer depends mainly on water flow and currents. Following successful pollen transfer by either biotic or abiotic means, plant functional connectivity depends on appropriate conditions for pollination and seed production in the recipient patch, and later establishment following local or among-patch seed transfer.

SEED BANKS AND FUNCTIONAL CONNECTIVITY

The potential for some plant species to persist in seed banks means that the realization of functional connectivity can be delayed for long periods of time following seed production after among-patch pollen flow (Fig. 2a), or following seed arrival to a new patch (Fig. 2b). For these species, persistent seed banks can be important for allowing populations to survive periods of unsuitable environmental conditions (Snyder 2006), and provide a useful strategy to retain the potential for connectivity when establishment is not immediately possible. Some seed-banking plant species require a specific environmental cue (such as fire) to break dormancy for the eventual realization of functional connectivity. The potential to persist in a seed bank is not only a useful strategy but it also provides a challenge for understanding patterns of functional connectivity based solely on the observation and analysis of established plant populations (Rico, Boehmer & Wagner 2012; Aavik *et al.* 2013). Seed bank persistence through periods of environmental unsuitability might also be regarded as functional connectivity, where the transfer stage of dispersal

corresponds to transfer through time rather than space (Fig. 2c). Like functional connectivity in space, such dispersal in time can promote genetic diversity (Honnay *et al.* 2008; Falahati-Anbaran, Lundemo & Stenøien 2014). However, just as anthropogenic environmental change can affect functional connectivity through its effects on abiotic and biotic dispersal vectors, climate change and nitrogen deposition can also have negative effects on seed bank survival, reducing the potential for delayed colonization independent of landscape processes (Ooi 2012; Basto *et al.* 2015).

Assessing plant functional connectivity

The multitude of different factors affecting the functional connectivity of plant species means that its assessment is challenging. The expanding field of landscape genetics is extremely valuable for understanding how populations are functionally connected in space and time (Luque, Saura & Fortin 2012; Baguette *et al.* 2013). However, recent advances in a range of other methods such as dispersal modelling and pollination network analysis could also be very useful in shedding light on specific interactions between dispersal, landscape and other relevant factors, and for gaining a broad understanding of functional connectivity for groups of species or communities. Below, we discuss some recent methodological advances, which we expect will facilitate future research in the field.

LANDSCAPE GENETICS

As functional connectivity is ultimately concerned with gene flow in time and space, landscape genetics provide a useful methodological toolbox to measure realized connectivity by explicitly incorporating spatial information to investigate gene flow in a landscape (Holderegger *et al.* 2010; Dyer 2015a; Fig. 3). Empirical genetic studies have shown that extant plant populations are functionally connected at the landscape and regional scales largely as a result of pollen flow (Dick *et al.* 2008), while seed dispersal has a larger impact at the local scale by creating fine-scale genetic structure (Epperson 2007; Rico & Wagner 2016). Understanding the role of landscape features in determining genetic structure is essential for understanding plant functional connectivity. Comparing landscape metrics with the F_{ST} estimate of genetic differentiation (Slatkin 1987) as a proxy for gene flow is one method of doing so. For instance, landscape-scale gene flow in the grassland plant *Lychis flos-cuculi* is restricted by forest cover, while measures of grassland structural connectivity have no effect (Aavik, Holderegger & Bolliger 2014). Using a molecular approach in this way shows that structural connectivity should not be automatically equated with functional connectivity. However, a concern regarding indirect measures of gene flow such as F_{ST} is that they are integrated measures of historical functional connectivity over several generations and thus are not likely to capture contemporary landscape changes (Holderegger *et al.* 2010; Aavik, Holderegger & Bolliger 2014; Epps & Keyghobadi 2015).

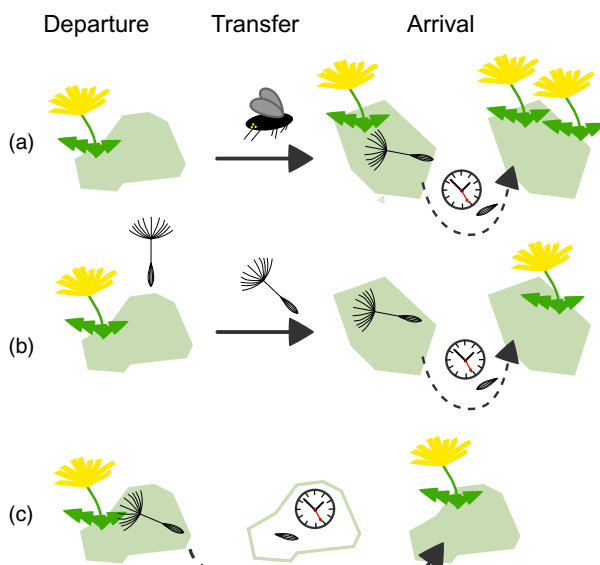
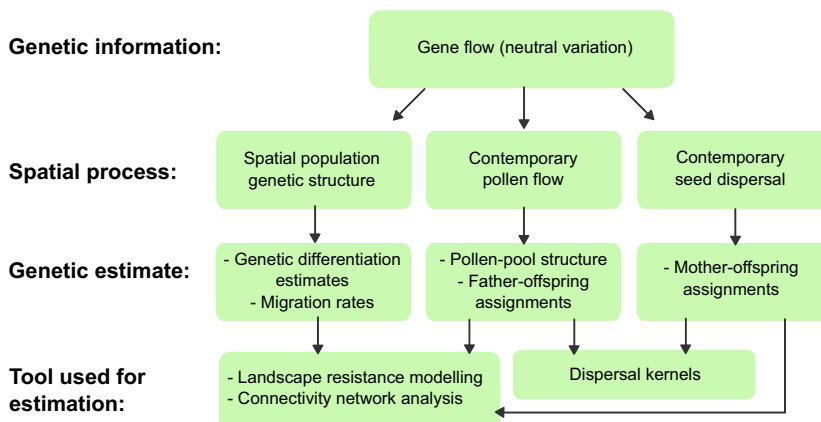


Fig. 2. The potential role of seed banks in plant functional connectivity. Seed dormancy (clock indicates time passing) in the recipient habitat following the dispersal of pollen (a) or seeds (b) in the recipient habitat patch can delay the realization of functional connectivity in space. The dormancy of seeds produced within the source population can be considered to 'connect' populations in time, buffering temporal environmental heterogeneity (c). [Colour figure can be viewed at wileyonlinelibrary.com]

Fig. 3. Conceptual model relating different spatial landscape processes to genetic estimates and the appropriate molecular ecological methods for quantifying plant functional connectivity. [Colour figure can be viewed at wileyonlinelibrary.com]



In contrast, direct approaches such as parentage analyses that estimate gene flow over one or few mating events offer great potential since they reveal how gene flow is related to the current landscape (Jones *et al.* 2010; Moran & Clark 2012). Specifically, paternity analyses evaluate effective pollen dispersal by comparing the genotype of the mother plant and the offspring to a pool of potential fathers to assign the most likely father. This can in turn be linked to landscape features, as done by Kamm *et al.* (2010), who found that open areas enhanced pollen-mediated gene flow for two isolated populations of the insect-pollinated forest tree *Sorbus domestica*. A useful approach that does not require sampling the potential fathers is the analysis of pollen pool structure. This method compares the genotypes of mothers scattered across the landscape along with their offspring to estimate the effective number of pollen donors, effective mating neighbourhood size and effective pollen dispersal kernels (Smouse *et al.* 2001; Sork *et al.* 2002). Creating a pollination network from this information can then be used to link paternal genetic connectivity to landscape features such as matrix quality (Dyer *et al.* 2012), and to quantify how between-site and at-site habitat characteristics differentially influence vector movements (DiLeo *et al.* 2014; Dyer 2015b).

Seed dispersal, on the other hand, is evaluated genetically through maternity analysis. This allows the quantification of seed dispersal distances and direction, as well as the dispersal effectiveness of available vectors (Jones & Muller-Landau 2008; Robledo-Arnuncio *et al.* 2012). By genotyping the maternally inherited endocarp (which in some species is transported with the seed) of dispersed seeds and relating it to the source 'mother' tree, Jordano *et al.* (2007) were able to identify how animal seed dispersers differentially deposited seeds of the same species over different distances and into different habitat types. Using these methods to measure contemporary gene flow, it is possible to assess the effects of landscape structure and dispersal vectors on relative contributions of pollen and seed dispersal to functional connectivity. While such analyses require large genetic resources due to the large numbers of offspring and potential parents required to be sampled at the landscape, the ongoing developments and reduction in costs of molecular techniques will facilitate the transition of studying a single species and a single landscape to multiple

co-occurring species in a landscape or one species in replicate landscapes. This will aid the understanding of how different stages and processes involved in functional connectivity relate to genetic structure across landscapes and will be important to generate more accurate predictive models for conservation and management in the light of rapid environmental change.

SEED DISPERSAL

The transfer stage of dispersal has typically been most studied, and several recent advances have the potential to improve the understanding of this critical phase. For biotic dispersal, the identification of vectors following dispersal by ingestion is now possible thanks to DNA barcoding (González-Varo, Arroyo & Jordano 2014), and the prediction of seed detachment from animal fur has been generalized by Bullock *et al.* (2011). When the vector is known, the distance and direction of biotic dispersal from a known source can be measured using stable isotopes following the isotope marking of parent plants (Carlo *et al.* 2013). These advances in the measurement of dispersal can be used to improve the modelling of dispersal kernels, which can be represented by statistical fitting of functions to detailed dispersal data (Bullock *et al.* 2017), and the dispersal process can be modelled mechanistically (Nathan *et al.* 2011). As connectivity represents the combination of landscape and dispersal ability, understanding how landscape structure affects dispersal kernels is important. Indeed, Côrtes & Uriarte (2013) suggested that the behavioural responses of animals to habitat and landscape structure is a key element for determining the distance and direction of biotic dispersal. For abiotic dispersal, recent developments have opened the possibility of modelling wind dispersal in relation to landscape structure (Trakhtenbrot, Katul & Nathan 2014). While these issues are important in understanding and predicting how dispersal kernels are influenced by a changing environment, such models are generally only concerned with the transfer stage of seed dispersal. Seed production, seed predation, seed banking, the presence of germination microsites and germination ability are also important determinants for functional connectivity (Soons & Heil 2002; Orrock & Damschen 2005; Rico, Boehmer & Wagner 2012), and should be incorporated into future mechanistic models.

An exciting implication of recent developments in both dispersal modelling and landscape genetics is the potential for molecular data regarding functional connectivity to be used to validate and improve mechanistic dispersal (including pollen) models, facilitating a more accurate understanding of current functional connectivity following recent environmental change, as well as its prediction under different future scenarios. This is of great relevance, as assessing to what extent the interplay between gene flow and selection might enable plant species to adapt effectively to rapid environmental changes remains a major challenge (Holderegger *et al.* 2010).

POLLEN FLOW

Spatial patterns of biotic pollen flow have often been investigated by mapping pollination networks. However, it is only recently that researchers have looked beyond the direct transfer of pollen between flowering conspecifics, even though most biotically pollinated plants are visited by many pollinators, which in turn visit a wide array of plant species. By identifying the diversity of pollen grains on stigmas in plant communities (Fang & Huang 2013), or by building theoretical networks between plant species sharing known pollinators (Padrón, Nogales & Traveset 2011), the transfer of pollen between individuals of different species (interspecific pollen transfer) can be assessed. Interspecific pollen transfer can lead not only to positive interactions due to increased pollinator attraction but also to negative interactions by potentially reducing the effectiveness of pollen transfer between conspecifics (Morales & Traveset 2008). Understanding these interactions between plant species and their mutual pollinators can be valuable for assessing how changes in pollinator abundances due to changes in landscape structure or the introduction of non-native plants or pollinators can affect plant functional connectivity for individual species or at the community level.

PLANT FUNCTIONAL TRAITS

While other recent advances can be useful for an improved understanding of a certain stage of plant functional connectivity, the use of functional traits provides the potential for some generalization of plant functional connectivity across plant communities within a landscape. For some dispersal mechanisms it is by now well-established which functional traits determine seed dispersal potential. Dispersal across landscapes by wind is dependent on relative plant height and appropriate seed traits (Tackenberg, Poschlod & Bonn 2003; Nathan *et al.* 2011). Similarly, seed buoyancy is important for predicting dispersal in water (Carthey *et al.* 2016; Soons *et al.* 2017), and different traits are associated with dispersal by animals via attachment and ingestion (Albert *et al.* 2015). Yet, some functional traits (such as buoyancy or capacity to survive gut passage) are notoriously difficult to quantify consistently for large numbers of species. Currently, coarse distinctions between species' dispersal capacities can be estimated from plant functional traits (Thomson *et al.* 2010; Tamme *et al.* 2014), although future work on standardized measurements of

important traits such as buoyancy and seed gut passage survival will be critical for generalizations regarding the effects of environmental changes on dispersal and connectivity. Furthermore, the importance of establishment and variation in site conditions means that traits related to both competition and dispersal are found to interact with landscape structure to determine species turnover following environmental change (Hemrová & Münzbergová 2015; Auffret *et al.* 2017). Understanding which traits relate to specific environmental changes and to the whole dispersal process offers a potential way forward to predicting how the functional connectivity of whole plant communities will respond to future changes or management interventions.

Concluding remarks

Plant functional connectivity, here defined as the effective dispersal of organisms across a landscape, has a huge impact on ecological responses to environmental change. For plants, the realization of functional connectivity involves the dispersal of both propagules and pollen by biotic or abiotic vectors, and includes the production of seeds and pollen at the source patch as well as the successful establishment of new individuals at the recipient patch. The different stages of effective dispersal are all affected by landscape, as well as a range of external factors and their interactions. Despite this complexity, recent methodological advances in landscape genetics, mechanistic dispersal modelling and ecological network analysis can help us understand how environmental change affects how and where plants move across landscapes. We hope researchers and managers working with functional connectivity will continue to consider landscape-dependent and landscape-independent factors affecting dispersal, as well as all stages of the dispersal process (Fig. 1), for the benefit of future research and conservation.

Authors' contributions

A.G.A. conceived the project and built the consortium with assistance from S.A.O.C., with all authors contributing to the development of the ideas presented. A.G.A. led the writing, with input from all authors regarding paper structure and content. All authors approved the publication of the paper.

Acknowledgements

A.G.A. and S.A.O.C. are supported by the strategic research program EkoKlim at Stockholm University and the Swedish Research Council Formas (2015-1065). J.M.B. and D.A.P.H. were supported by NERC-UK projects NEC05264 and NEC05593. R.J.P. was supported by funding from the Scottish Government's Rural and Environment Science and Analytical Services Division. Y.R. was supported by the National Council of Science of Mexico. M.B.S. was supported by the Netherlands Organization for Scientific Research (NWO-ALW). A.T. was supported by funding from the Spanish Government (CGL2013-44386-P). H.H.W. was supported by a Discovery grant from the National Sciences and Engineering Research Council of Canada. We are very grateful for the comments of two anonymous reviewers, which were extremely helpful in improving upon previous drafts of the manuscript.

Data accessibility

This paper does not use data.

References

- Aavik, T., Holderegger, R. & Bolliger, J. (2014) The structural and functional connectivity of the grassland plant *Lychnis flos-cuculi*. *Heredity*, **112**, 471–478.
- Aavik, T., Holderegger, R., Edwards, P.J. & Billeter, R. (2013) Patterns of contemporary gene flow suggest low functional connectivity of grasslands in a fragmented agricultural landscape. *Journal of Applied Ecology*, **50**, 395–403.
- Ahmed, S., Compton, S.G., Butlin, R.K. & Gilmartin, P.M. (2009) Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences United States of America*, **106**, 20342–20347.
- Albert, A., Auffret, A.G., Cosyns, E. *et al.* (2015) Seed dispersal by ungulates as an ecological filter: a trait-based meta-analysis. *Oikos*, **124**, 1109–1120.
- Auffret, A.G., Aggemyr, E., Plue, J. & Cousins, S.A.O. (2017) Spatial scale and specialization affect how biogeography and functional traits predict long-term patterns of community turnover. *Functional Ecology*, **31**, 436–443.
- Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013) Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, **88**, 310–326.
- Basto, S., Thompson, K., Phoenix, G., Sloan, V., Leake, J. & Rees, M. (2015) Long-term nitrogen deposition depletes grassland seed banks. *Nature Communications*, **6**, 7185.
- Bélisle, M. (2005) Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology*, **86**, 1988–1995.
- Betts, M.G., Hadley, A.S. & Kress, W.J. (2015b) Pollinator recognition by a keystone tropical plant. *Proceedings of the National Academy of Sciences United States of America*, **112**, 3433–3438.
- Betts, M.G., Gutzwiller, K.J., Smith, M.J., Robinson, W.D. & Hadley, A.S. (2015a) Improving inferences about functional connectivity from animal translocation experiments. *Landscape Ecology*, **30**, 585–593.
- Bonte, D., Van Dyck, H., Bullock, J.M. *et al.* (2012) Costs of dispersal. *Biological Reviews*, **87**, 290–312.
- Brosi, B.J. & Briggs, H.M. (2013) Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proceedings of the National Academy of Sciences United States of America*, **110**, 13044–13048.
- Bullock, J.M., Galsworthy, S.J., Manzano, P., Poschlod, P., Eichberg, C., Walker, K. & Wichmann, M.C. (2011) Process-based functions for seed retention on animals: a test of improved descriptions of dispersal using multiple data sets. *Oikos*, **120**, 1201–1208.
- Bullock, J.M., White, S.M., Prudhomme, C., Tansey, C., Perea, R. & Hooftman, D.A.P. (2012) Modelling spread of British wind-dispersed plants under future wind speeds in a changing climate. *Journal of Ecology*, **100**, 104–115.
- Bullock, J.M., González, L.M., Tamme, R., Götzenberger, L., White, S.M., Pärtel, M. & Hooftman, D.A.P. (2017) A synthesis of empirical plant dispersal kernels. *Journal of Ecology*, **105**, 6–19.
- Calabrese, J.M. & Fagan, W.F. (2004) A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment*, **2**, 529–536.
- Carlo, T.A., García, D., Martínez, D., Gleditsch, J.M. & Morales, J.M. (2013) Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. *Ecology*, **94**, 301–307.
- Carthey, A.J.R., Fryirs, K.A., Ralph, T.J., Bu, H. & Leishman, M.R. (2016) How seed traits predict floating times: a biophysical process model for hydrochorous seed transport behaviour in fluvial systems. *Freshwater Biology*, **61**, 19–31.
- Córtés, M.C. & Uriarte, M. (2013) Integrating frugivory and animal movement: a review of the evidence and implications for scaling seed dispersal. *Biological Reviews of the Cambridge Philosophical Society*, **88**, 255–272.
- Culley, T.M., Weller, S.G. & Sakai, A.K. (2002) The evolution of wind pollination in angiosperms. *Trends in Ecology & Evolution*, **17**, 361–369.
- Damschen, E.I., Brudvig, L.A., Haddad, N.M., Levey, D.J., Orrock, J.L. & Tewksbury, J.J. (2008) The movement ecology and dynamics of plant communities in fragmented landscapes. *Proceedings of the National Academy of Sciences United States of America*, **105**, 19078–19083.
- Damschen, E.I., Baker, D.V., Bohrer, G. *et al.* (2014) How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proceedings of the National Academy of Sciences United States of America*, **111**, 3484–3489.
- Dick, C.W., Hardy, O.J., Jones, F.A. & Petit, R.J. (2008) Spatial scales of pollen and seed-mediated gene flow in tropical rain forest trees. *Tropical Plant Biology*, **1**, 20–33.
- DiLeo, M.F., Siu, J.C., Rhodes, M.K., López-Villalobos, A., Redwine, A., Ksiazek, K. & Dyer, R.J. (2014) The gravity of pollination: integrating at-site features into spatial analysis of contemporary pollen movement. *Molecular Ecology*, **23**, 3973–3982.
- Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B. & Smith, A.L. (2013) Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution*, **28**, 605–613.
- Dyer, R.J. (2015a) Landscapes and plant population genetics. *Landscape Genetics* (eds N. Balkenhol, S.A. Cushman, A.T. Storfer & L.P. Waits), pp. 181–198. John Wiley & Sons, Chichester, UK.
- Dyer, R.J. (2015b) Population graphs and landscape genetics. *Annual Review of Ecology, Evolution, and Systematics*, **46**, 327–342.
- Dyer, R.J., Chan, D.M., Gardiakos, V.A. & Meadows, C.A. (2012) Pollination graphs: quantifying pollen pool covariance networks and the influence of intervening landscape on genetic connectivity in the North American understory tree, *Cornus florida* L. *Landscape Ecology*, **27**, 239–251.
- Epperson, B.K. (2007) Plant dispersal, neighbourhood size and isolation by distance. *Molecular Ecology*, **16**, 3854–3865.
- Epps, C.W. & Keyghobadi, N. (2015) Landscape genetics in a changing world: disentangling historical and contemporary influences and inferring change. *Molecular Ecology*, **24**, 6021–6040.
- Falahati-Anbaran, M., Lundemo, S. & Stenoien, H.K. (2014) Seed dispersal in time can counteract the effect of gene flow between natural populations of *Arabidopsis thaliana*. *New Phytologist*, **202**, 1043–1054.
- Fang, Q. & Huang, S.-Q. (2013) A directed network analysis of heterospecific pollen transfer in a biodiverse community. *Ecology*, **94**, 1176–1185.
- Faust, C., Eichberg, C., Storm, C. & Schwabe, A. (2011) Post-dispersal impact on seed fate by livestock trampling – A gap of knowledge. *Basic and Applied Ecology*, **12**, 215–226.
- Favre-Bac, L., Mony, C., Ernoul, A., Burel, F. & Arnaud, J.-F. (2016) Ditch network sustains functional connectivity and influences patterns of gene flow in an intensive agricultural landscape. *Heredity*, **116**, 200–212.
- Gallegos, S.C., Hensen, I. & Schleuning, M. (2014) Secondary dispersal by ants promotes forest regeneration after deforestation. *Journal of Ecology*, **102**, 659–666.
- González-Varo, J.P., Arroyo, J.M. & Jordano, P. (2014) Who dispersed the seeds? The use of DNA barcoding in frugivory and seed dispersal studies. *Methods in Ecology and Evolution*, **5**, 806–814.
- González-Varo, J.P., López-Bao, J.V. & Guitián, J. (2013) Functional diversity among seed dispersal kernels generated by carnivorous mammals. *Journal of Animal Ecology*, **82**, 562–571.
- González-Varo, J.P., Albaladejo, R.G., Aparicio, A. & Arroyo, J. (2010) Linking genetic diversity, mating patterns and progeny performance in fragmented populations of a Mediterranean shrub. *Journal of Applied Ecology*, **47**, 1242–1252.
- Hadley, A.S. & Betts, M.G. (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. *Biological Reviews*, **87**, 526–544.
- Hampe, A. (2011) Plants on the move: the role of seed dispersal and initial population establishment for climate-driven range expansions. *Acta Oecologica*, **37**, 666–673.
- Hemrová, L. & Münzbergová, Z. (2015) The effects of plant traits on species' responses to present and historical patch configurations and patch age. *Oikos*, **124**, 437–445.
- Holderegger, R., Buehler, D., Gugerli, F. & Manel, S. (2010) Landscape genetics of plants. *Trends in Plant Science*, **15**, 675–683.
- Honnay, O., Bossuyt, B., Jacquemyn, H., Shimono, A. & Uchiyama, K. (2008) Can a seed bank maintain the genetic variation in the above ground plant population? *Oikos*, **117**, 1–5.
- Ibáñez, I., Katz, D.S.W., Peltier, D., Wolf, S.M. & Connor Barrie, B.T. (2014) Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. *Journal of Ecology*, **102**, 882–895.
- Jansen, P.A., Hirsch, B.T., Emsens, W.-J., Zamora-Gutierrez, V., Wikelski, M. & Kays, R. (2012) Thieving rodents as substitute dispersers of megafaunal seeds. *Proceedings of the National Academy of Sciences United States of America*, **109**, 12610–12615.
- 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.
- Jones, A.G., Small, C.M., Paczolt, K.A. & Ratterman, N.L. (2010) A practical guide to methods of parentage analysis. *Molecular Ecology Resources*, **10**, 6–30.
- Jordano, P., García, C., Godoy, J.A. & García-Castaño, J.L. (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences United States of America*, **104**, 3278–3282.

- Kamm, U., Gugerli, F., Rotach, P., Edwards, P. & Holderegger, R. (2010) Open areas in a landscape enhance pollen-mediated gene flow of a tree species: evidence from northern Switzerland. *Landscape Ecology*, **25**, 903–911.
- Keller, L.F. & Waller, D.M. (2002) Inbreeding effects in wild populations. *Trends in Ecology & Evolution*, **17**, 230–241.
- Kudo, G. & Ida, T.Y. (2013) Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology*, **94**, 2311–2320.
- Kuparinen, A., Katul, G., Nathan, R. & Schurr, F.M. (2009) Increases in air temperature can promote wind-driven dispersal and spread of plants. *Proceedings of the Royal Society of London B: Biological Sciences*, **276**, 3081–3087.
- Leimu, R., Mutikainen, P., Koricheva, J. & Fischer, M. (2006) How general are positive relationships between plant population size, fitness and genetic variation? *Journal of Ecology*, **94**, 942–952.
- Luque, S., Saura, S. & Fortin, M.-J. (2012) Landscape connectivity analysis for conservation: insights from combining new methods with ecological and genetic data. *Landscape Ecology*, **27**, 153–157.
- Magrath, A., Larrinaga, A.R. & Santamaría, L. (2012) Effects of matrix characteristics and interpatch distance on functional connectivity in fragmented temperate rainforests. *Conservation Biology*, **26**, 238–247.
- Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J. & Böhning-Gaese, K. (2012) Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology*, **26**, 1072–1081.
- Maurer, K.D., Bohrer, G., Medvigy, D. & Wright, S.J. (2013) The timing of abscission affects dispersal distance in a wind-dispersed tropical tree. *Functional Ecology*, **27**, 208–218.
- McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H. & Santamaría, L. (2012) Seed dispersal in changing landscapes. *Biological Conservation*, **146**, 1–13.
- Mokany, K., Prasad, S. & Westcott, D.A. (2014) Loss of frugivore seed dispersal services under climate change. *Nature Communications*, **5**, 3971.
- Morales, C.L. & Traveset, A. (2008) Interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. *Critical Reviews in Plant Sciences*, **27**, 221–238.
- Morales, C.L., Arbetman, M.P., Cameron, S.A. & Aizen, M.A. (2013) Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment*, **11**, 529–534.
- Moran, E.V. & Clark, J.S. (2012) Between-site differences in the scale of dispersal and gene flow in red oak. *PLoS ONE*, **7**, e36492.
- Mueller, T., Lenz, J., Caprano, T., Fiedler, W. & Böhning-Gaese, K. (2014) Large frugivorous birds facilitate functional connectivity of fragmented landscapes. *Journal of Applied Ecology*, **51**, 684–692.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. (2008) A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences United States of America*, **105**, 19052–19059.
- Nathan, R., Katul, G.G., Bohrer, G., Kuparinen, A., Soons, M.B., Thompson, S.E., Trakhtenbrot, A. & Horn, H.S. (2011) Mechanistic models of seed dispersal by wind. *Theoretical Ecology*, **4**, 113–132.
- Niggemann, M., Jetzkowitz, J., Brunzel, S., Wichmann, M.C. & Bialozyt, R. (2009) Distribution patterns of plants explained by human movement behaviour. *Ecological Modelling*, **220**, 1339–1346.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.
- Ooi, M.K.J. (2012) Seed bank persistence and climate change. *Seed Science Research*, **22**, S53–S60.
- Orrock, J.L. & Damschen, E.I. (2005) Corridors cause differential seed predation. *Ecological Applications*, **15**, 793–798.
- Ozinga, W.A., Bekker, R.M., Schaminée, J.H.J. & Van Groenendaal, J.M. (2004) Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology*, **92**, 767–777.
- Padrón, B., Nogales, M. & Traveset, A. (2011) Alternative approaches of transforming bimodal into unimodal mutualistic networks. The usefulness of preserving weighted information. *Basic and Applied Ecology*, **12**, 713–721.
- Rico, Y., Boehmer, H.J. & Wagner, H.H. (2012) Determinants of actual functional connectivity for calcareous grassland communities linked by rotational sheep grazing. *Landscape Ecology*, **27**, 199–209.
- Rico, Y. & Wagner, H.H. (2016) Reduced fine-scale spatial genetic structure in grazed populations of *Dianthus carthusianorum*. *Heredity*, **117**, 367–374.
- Robledo-Arnuncio, J.J., Grivet, D., Smouse, P.E. & Sork, V.L. (2012) PSA: software for parental structure analysis of seed or seedling patches. *Molecular Ecology Resources*, **12**, 1180–1189.
- Schupp, E.W., Jordano, P. & Gómez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, **188**, 333–353.
- Shohami, D. & Nathan, R. (2014) Fire-induced population reduction and landscape opening increases gene flow via pollen dispersal in *Pinus halepensis*. *Molecular Ecology*, **23**, 70–81.
- Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science*, **236**, 787–792.
- Smouse, P.E., Dyer, R.J., Westfall, R.D. & Sork, V.L. (2001) Two-generation analysis of pollen flow across a landscape. I. male gamete heterogeneity among females. *Evolution*, **55**, 260–271.
- Snyder, R.E. (2006) Multiple risk reduction mechanisms: can dormancy substitute for dispersal? *Ecology Letters*, **9**, 1106–1114.
- Soons, M.B. & Heil, G.W. (2002) Reduced colonization capacity in fragmented populations of wind-dispersed grassland forbs. *Journal of Ecology*, **90**, 1033–1043.
- Soons, M.B., Nathan, R. & Katul, G.G. (2004) Human effects on long-distance wind dispersal and colonization by grassland plants. *Ecology*, **85**, 3069–3079.
- Soons, M.B., de Groot, G.A., Cuesta Ramirez, M.T., Fraaije, R.G.A., Verhoeven, J.T.A. & de Jager, M. (2017) Directed dispersal by an abiotic vector: wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water. *Functional Ecology*, **31**, 499–508.
- Sork, V.L., Davis, F.W., Smouse, P.E., Apsit, V.J., Dyer, R.J., Fernandez-M, J.F. & Kuhn, B. (2002) Pollen movement in declining populations of California Valley oak, *Quercus lobata*: where have all the fathers gone? *Molecular Ecology*, **11**, 1657–1668.
- Suárez-Esteban, A., Delibes, M. & Fedriani, J.M. (2013) Barriers or corridors? The overlooked role of unpaved roads in endozoochorous seed dispersal. *Journal of Applied Ecology*, **50**, 767–774.
- Tackenberg, O., Poschlod, P. & Bonn, S. (2003) Assessment of wind dispersal potential in plant species. *Ecological Monographs*, **73**, 191–205.
- Tamme, R., Götzenberger, L., Zobel, M., Bullock, J.M., Hooftman, D.A.P., Kaasik, A. & Pärtel, M. (2014) Predicting species' maximum dispersal distances from simple plant traits. *Ecology*, **95**, 505–513.
- Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos*, **68**, 571.
- Thomson, F.J., Moles, A.T., Auld, T.D., Ramp, D., Ren, S. & Kingsford, R.T. (2010) Chasing the unknown: predicting seed dispersal mechanisms from plant traits. *Journal of Ecology*, **98**, 1310–1318.
- Tischendorf, L. & Fahrig, L. (2000) On the usage and measurement of landscape connectivity. *Oikos*, **90**, 7–19.
- Townsend, P.A. & Levey, D.J. (2005) An experimental test of whether habitat corridors affect pollen transfer. *Ecology*, **86**, 466–475.
- Trakhtenbrot, A., Katul, G.G. & Nathan, R. (2014) Mechanistic modeling of seed dispersal by wind over hilly terrain. *Ecological Modelling*, **274**, 29–40.
- Traveset, A. & Richardson, D.M. (2014) Mutualistic interactions and biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 89–113.
- Uriarte, M., Bruna, E.M., Rubim, P., Anciães, M. & Jonckheere, I. (2010) Effects of forest fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site limitation. *Ecology*, **91**, 1317–1328.
- Vander Wall, S.B. (2003) Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos*, **100**, 25–34.
- Vargas, P., Nogales, M., Jaramillo, P., Olesen, J.M., Traveset, A. & Heleno, R. (2014) Plant colonization across the Galápagos Islands: success of the sea dispersal syndrome. *Botanical Journal of the Linnean Society*, **174**, 349–358.
- Vasudev, D., Fletcher, R.J., Goswami, V.R. & Krishnadas, M. (2015) From dispersal constraints to landscape connectivity: lessons from species distribution modeling. *Ecography*, **38**, 967–978.
- Vogt, P., Ferrari, J.R., Lookingbill, T.R., Gardner, R.H., Riitters, K.H. & Ostapowicz, K. (2009) Mapping functional connectivity. *Ecological Indicators*, **9**, 64–71.
- Vranckx, G., Jacquemyn, H., Muys, B. & Honnay, O. (2012) Meta-analysis of susceptibility of woody plants to loss of genetic diversity through habitat fragmentation. *Conservation Biology*, **26**, 228–237.
- Watts, K. & Handley, P. (2010) Developing a functional connectivity indicator to detect change in fragmented landscapes. *Ecological Indicators*, **10**, 552–557.

Received 21 September 2016; accepted 13 January 2017

Handling Editor: Yvonne Buckley