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Integrating microorganism and macroorganism dispersal: modes, techniques and challenges with particular focus on co-dispersal

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ABSTRACT

Whatever their size and the ecosystem they live in, all organisms may disperse at some stage of their life cycle. Dispersal dynamics are to a varying extent dependent on organismal size, life history, ecological niche, survival capacities and phylogeny. Moves towards a synthesis in dispersal ecology have focused primarily on vertebrates and higher plants, yet recent studies suggest that the dispersal of microorganisms and macroorganisms has much more in common than previously assumed. The dispersal of one organism enables co-dispersal for many others, smaller in size. There is an increasing need for a more integrated approach to study dispersal within the context of organismal interactions and their environments. Such an approach is facilitated by recent developments of powerful indirect techniques that enable tracking of microorganisms and macroorganisms over multiple spatial and temporal scales. Likewise, dispersal modelling and theoretical models of the consequences of dispersal can inspire empirical studies across the entire size spectrum. Simultaneously studying the relationships between dispersal of microorganisms and macroorganisms, and accounting for dispersal through time and space, will allow us to better understand the functioning and dynamics of communities and ecosystems, and to make better predictions of future dispersal patterns, changes in biodiversity and connectivity.

RÉSUMÉ

Tous les organismes, quels soient leur taille ou l'écosystème dans lequel ils vivent, peuvent se disperser et être dispersés à un moment donné de leur cycle de vie. Les dynamiques de dispersion de ces organismes dépendent, en partie, de leur taille, de leur mode de vie, de leur niches écologiques, de leur capacités de survie et de leur phylogénie. Des synthèses visant l'écologie de la dispersion des organismes ont principalement été élaborées sur le thème des vertébrés et des plantes, cependant de nouvelles études suggèrent que la dispersion des microorganismes et des macroorganismes sont plus similaires que prévu. C'est le cas notamment de la dispersion d'un organisme capable de transporter avec lui d'autres organismes plus petits en taille. Il devient alors nécessaire d'aborder le sujet de la dispersion des organismes en appliquant une approche intégrée, considérant l'interaction entre différentes tailles d'organismes et entre eux et leurs environnements. Cette approche est facilitée par le développement récent de puissantes techniques de détections permettant le suivi des microorganismes et des macroorganismes à différentes échelles spatiales et temporelles. De même, l'utilisation de la modélisation de la dispersion et des modèles théoriques basés sur les conséquences de la dispersion des organismes peuvent inspirer des études empiriques sur l'ensemble du spectre de taille des organismes. Par conséquent, l'étude de la dispersion des organismes considérant les relations entre microorganismes et macroorganismes à différentes échelles de temps et d'espace fournira une meilleure compréhension du fonctionnement et de la dynamique des communautés et des écosystèmes, et améliorera les modèles de dispersion, de changements de biodiversité et de connectivité.

Introduction

Dispersal can be defined as the voluntary or involuntary movement of an organism from its natal/reproductive site to a new one where sexual or asexual reproduction occurs. Dispersal can have major effects at the population and ecosystem levels, and may influence evolutionary dynamics via subsequent adaptation to novel

environments. Therefore, understanding the factors that influence dispersal is a central question in ecology and evolution.

Body size is one key determinant of dispersal potential as size determines the physical forces acting on organisms, which in turn influence their form and hence the mechanics and energetics of different dispersal modes (e.g., Finlay 2002; De Bie et al. 2012). Size influences the velocity and distance that an organism can actively or passively move and, in turn, the costs and benefits of its dispersal.

Dispersal is a universal phenomenon that occurs both in microorganisms (i.e. those below 500 μm in length) and in macroorganisms at different stages of their life cycles (e.g. as spores/cysts, gametes/eggs, pollen, ramets, juveniles or adults). Traditionally, organisms have been classified into microorganisms (microbes) and macroorganisms on the basis of whether they are visible to the naked human eye, a size threshold which is rather arbitrary in terms of its consequences for dispersal. In recent years there have been important efforts to develop a unified framework and synthesis for dispersal ecology (see, e.g., Clobert et al. 2012), but the overwhelming emphasis has been on macroorganisms, especially vertebrates. Yet the time is ripe to develop a more holistic understanding of both microorganism and macroorganism dispersal, and move towards a common framework for both. This requires paying particular attention to co-dispersal (see Appendix 1 for full definition) in which many microorganisms disperse through associations with animal vectors (e.g., Garmyn et al. 2012). To date, studies have focused largely on dispersal of individual macroorganisms ignoring the concomitant dispersal of, for example, parasites and associated microorganisms. Indeed, co-dispersal is a little used term (only 27 papers figuring "codispersal" or "co-dispersal" as a topic were found in a "Web of Knowledge" search on 22 July 2015, compared with 167,680 for "dispersal"). A particularly well-known example of co-dispersal is provided by Dutch elm disease (Webber 2000), in which bark beetles carry the spores of saprotrophic fungal pathogens that increase food supply to the beetles but have a drastic effect on the tree hosts. However, co-dispersed organisms do not necessarily provide a benefit to their vectors.

Microbial ecology has developed quickly as a field in recent decades with molecular techniques facilitating the study of microbes that cannot be cultured. Thanks to their small size, it is now arguably faster to characterize microbial communities in a given habitat through genetic approaches (metagenomic analyses) than to characterize many macroorganism communities. Distributions are partly a function of dispersal capacity, and studying the distributions of microorganisms across a range of locations

is now regularly undertaken by microbial ecologists, in a manner comparable with the pioneering studies of the distribution of macroorganisms from the eighteenth century onwards (e.g. by Linnaeus, Darwin, Wallace, etc.).

Microbial taxa have the potential to be distributed ubiquitously because of their very short generation time, small size and capacity for rapid local adaptation and ease of transport (e.g., Beijerinck 1913; Finlay 2002). However, the ubiquity rule has not been universally supported and is hotly debated. Indeed, just as for macroorganisms, a dispersal limitation has been identified for many microbes, including diatoms (e.g., Vanormelingen et al. 2007), cyanobacteria (e.g., Papke et al. 2003) and bacteria (e.g., Woodcock et al. 2007). Furthermore, the life histories of many organisms incorporate stages that span micro-scales and macro-scales (e.g. macroalgae–gametes, trees–pollen, animals–sperm/eggs; Figure 1). Although dispersal often primarily occurs at one stage (e.g. larvae of marine benthic invertebrates, adult insects), it may be achieved across the life cycle in other organisms (e.g. free spawning fish, copepods). These considerations suggest that the dispersal of microorganisms and macroorganisms share many common themes and constraints.

In this review article we compare the dispersal of microorganisms and macroorganisms, and highlight the need to expand studies of the causes and consequences of co-dispersal (including vectors, their microbiomes and other co-dispersed organisms). Additionally, we review techniques that are valuable to study dispersal across the spectrum of organism size, and suggest avenues for future investigations based on integrated studies.

Dispersal means for microorganisms and macroorganisms

Microorganisms and macroorganisms share means of dispersal (Figure 1) among which we distinguished those that actively disperse and those that are dispersed by biotic vectors (co-dispersal) or by abiotic factors (passive dispersal). The energetic costs of active dispersal increase disproportionately with body size (Bonte et al. 2012) and thus represent a potential constraint across scales. Large organisms can actively disperse over large scales (metres to kilometres) by expending energy to propel themselves through the environment using appendages (e.g. legs, tails, wings, fins) or by muscular contractions of the body (e.g. worms, jellyfish). Microorganisms similarly expend energy for movement over smaller spatial scales (centimetres to metres, e.g. diurnal migration) via cilia and flagellae (e.g. bacteria, protists, invertebrate larvae) or pseudopodia (e.g. amoebae; see examples in Jahn & Bovee 1965). Microalgae actively move in aquatic systems with or against the main flow, sometimes drifting faster and
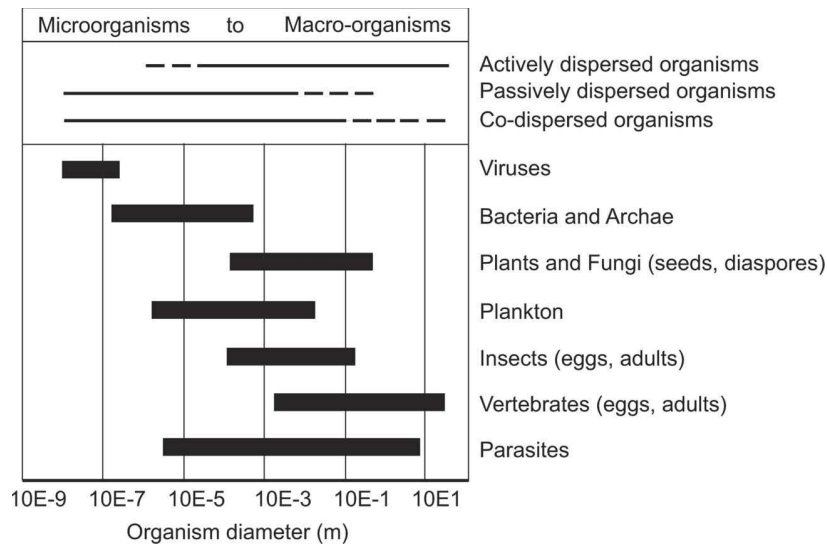
Figure 1. Schematic diagram illustrating how microorganisms and macroorganisms share basic dispersal modes.

Note: Organism size is represented as diameter (m), calculated as minimum – maximum length. The general relative importance of active dispersal (top line), passive dispersal (second line, e.g. via abiotic factors such wind, waterflow or thermal fluxes) and co-dispersal (third line, including parasitism) is shown. The dashed line indicates how a particular dispersal mode may apply to an organism group, but with a low probability. Parasites can include microorganisms and macroorganisms.

Source: The values of shortest/longest organism per category were taken from the literature (Mettenleiter & Sobrino 2008; Ghedin & Claverie 2005); bacteria and archaea, Schulz and Jørgensen (2001); plants as spores, Erdtman (1986); plants as seeds, Swamy et al. (2004) and Blackmore et al. (2012); plankton, Finlay (2002); insects, Mockford (1997) and Parker & Johnston (2006); vertebrates, Rittmeyer et al. (2012) and Calambokidis & Steiger (1997); and parasites, Fishman (1998) and Gubanov (1951).

diffusing less than passive tracers or nutrients (Croze et al. 2013). However, such movements in microorganisms are unlikely to contribute in any meaningful way to dispersal when external abiotic forces overwhelm their directed movements or when co-dispersal dominates.

Active dispersers can be excellent co-dispersal vectors for a range of smaller organisms over large distances (see Table 1 for examples). Propagules of plants and invertebrates retained in the intestines of waterfowl can travel for up to several days (Proctor 1968; García-Álvarez et al. 2015), long enough to be dispersed for hundreds or thousands of kilometres (Viana et al. 2013). Co-dispersal has also been demonstrated for many microorganisms (Table 1) including bacteria hitchhiking on zooplankton (Grossart et al. 2010) or zooplankton eggs carried by insects (van de Meutter et al. 2008).

In many cases, organisms assumed to disperse by abiotic means are co-dispersed. For instance, seeds assigned to a "wind dispersal syndrome" based on their morphology can be dispersed by waterbirds (Brochet et al. 2009). Many internal/external parasites and pathogens achieve dispersal with their hosts (Table 2). Co-dispersal is an understudied process that involves complex networks of association between organisms (Figure 2) that may be dispersed over different geographic scales. Furthermore, co-dispersed microorganisms sometimes promote or impede host

dispersal (Table 2) and are often dispersed to new suitable environments with consequences for community composition, ecosystem dynamics and biogeographical patterns (e.g., Vagvolgyi 1975; Muñoz et al. 2013). Therefore, identifying these networks is a key step towards tracing the movement patterns of both vector and co-dispersed organisms. For example, an analysis of avian haemosporidian parasites in breeding grounds recently revealed the migration route and location of the wintering grounds of the avian hosts (Synek et al. 2013).

External forces (e.g. wind, water or thermal fluxes) can carry organisms passively to new environments. Thus, organisms can unwillingly or willingly disperse without expending energy to achieve dispersal. Some macroorganisms take advantage of abiotic factors to passively disperse. They have evolved traits that enable them to become airborne despite their large size. These include seeds with plumes (Howe & Smallwood 1982), light snail shells (Vagvolgyi 1975) and silk threads for ballooning arachnids (Szymkowiak et al. 2007). Aquatic and atmospheric currents are also an efficient way to transport microorganisms (Lacey and West 2006; Sharma et al. 2007; Smith et al. 2011; Croze et al. 2013). Many microbes have evolved ways to become airborne and to maintain viability in the inhospitable atmospheric environment (Schlichting 1974; Broady 1996; Womack et al. 2010). Owing to their

Table 1. Examples of biotic vectors used for dispersal.

Vector type	Mechanism	References
Anthropogenic	Boats	Gollasch (2007), Griffiths et al. (1991)
	Clothes and boots	Perrigo et al. (2012), Waterkeyn et al. (2010), Perotti & Braig (2009)
	Food transportation	Broady & Smith (1994)
	Landscape modification	Suarez-Esteban et al. (2013)
Animal	Zooplankton transporting microorganisms	Grossart et al. (2010)
	Fish transporting copepod eggs and seeds	Bartholmé et al. (2005), Pollux (2011)
	Insects transporting zooplankton eggs, fungal spores and mites	van de Meutter et al. (2008), Andersen et al. (2012), Perotti & Braig (2009)
	Waterbirds transporting seeds, bryozoans, ostracods and chironomids	Green & Sánchez (2006), Green et al. (2013), García-Álvarez et al. (2015)
	Birds transporting microorganisms in their feathers, nasal cavity, nostrils, or toes	Bisson et al. (2009), Brito-Echeverria et al. (2009), Lewis et al. (2014), Mascarenhas et al. (2010), Garmyn et al. (2012)
	Bird selecting ferns and mosses for nest construction	Osorio-Zuñiga et al. (2014)
	Terrestrial animals transporting seeds	Römermann et al. (2005)
Multi-level transportations	Waterbirds transporting zooplankton transporting bacteria	Andras & Ebert (2013)
	Seed-infesting insects transported in bird guts	Hernandez (2011)
	Ciliates transported by ostracods transported by tree frogs dispersing between bromeliads	Sabagh et al. (2011)
	Birds transporting ticks and tick-pathogens that cause mammalian diseases	Cohen et al. (2015)
	Humans transporting birds that are parasitized by mites	Mascarenhas et al. (2010)

Table 2. Parasitism and consequences for host–parasite dispersal.

Impact	Example
Impede host dispersal by reducing host motility	Ectoparasites limit dispersal distances of infected Great tits (Heeb et al. 1999)
	Bacteria reduce dispersal of ciliates towards congeners (Fellous et al. 2010)
	Protozoans limit the flight speed of parasitized Monarch butterflies (Bradley & Altizer 2005)
	Protists slow the swimming speed of parasitized chain-forming phytoplankton (Park et al. 2004)
Facilitate host dispersal by fleeing source of infection	Parasites induce an increase in the number of winged offspring in female aphids (Sloggett & Weisser 2002)
	Ectoparasite abundance influences natal dispersal between colonies of nesting cliff swallows (Brown & Brown 1992)
	Protozoans influence the migration of butterflies (Bartel et al. 2011)
Facilitate infection of hosts at different locations (Thomas et al. 2005; Lion et al. 2006)	Dispersal of parasites between breeding areas: scaly-leg mites (Latta 2003)
	Dispersal of parasites between the hosts' wintering and breeding grounds (Palinauskas et al. 2011)
Facilitate infection of multiple ecologically distinct hosts (to complete their life cycle)	Trematode facilitates ingestion of Killifish by birds, which are the final hosts (Lafferty & Morris 1996)
	Trematode facilitates the ingestion of snails by rats (Prugnolle et al. 2005)
	Cestodes facilitate the ingestion of *Artemia* by birds (Sánchez et al. 2013)
Parasite facilitates its dispersal by allowing multiple host transmission	Parasites transmitted to avian hosts via mosquitoes (Palinauskas et al. 2011)
	Trematodes transmitted to avian hosts via marine snails (Keeney et al. 2009)
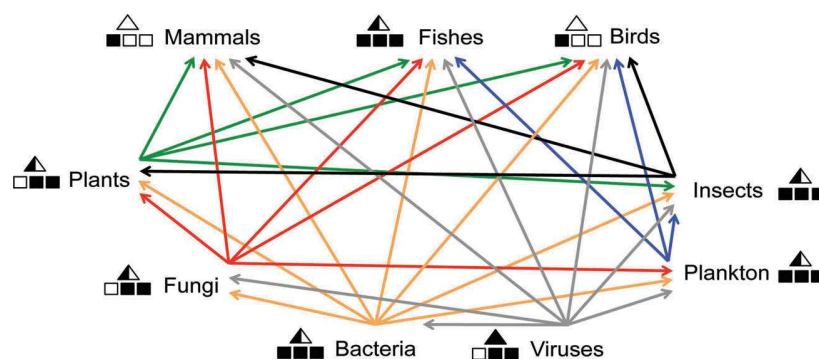
Figure 2. Schematic example of biotic networks resulting from co-dispersal.

Note: Triangles indicate the capacity of the taxa to carry parasites (white) or be parasitic (black), or both (in a qualitative, not quantitative manner). Rectangles are made up of three equal squares and indicate whether the taxa are dispersing actively (white = no, black = yes) (first square), dispersing passively (second square) or co-dispersed by a biotic vector (third square). Arrows connect the dispersed taxon to its vector. Many organisms can disperse alone (actively or passively) or together (via a biotic vector). See examples in Tables 1 and 2.

relatively large surface to volume ratios, small microbes (<20 μm) tend to have a lower deposition rate and a higher dispersal capacity than larger microbes (Hinds 1999). Small microbes can be carried by the wind for hours to weeks, a sufficient time for transport between continents (Wilkinson et al. 2012) or possibly between hemispheres (Lacey & West 2006; Després et al. 2012), and then settle in a new habitat (Genitsaris et al. 2011).

Co-dispersal distances and survival of small organisms

Many studies suggest that dispersal distances for passive dispersers can be negatively correlated with body mass (Jenkins et al. 2007; Yang et al. 2010). Thus, large-bodied groups of passive dispersers often exhibit stronger spatial clustering (de Bie et al. 2012), while microorganisms are associated with a greater range of dispersal distances (Finlay 2002; Jenkins et al. 2007). In contrast, dispersal distance correlates positively with body mass for active dispersers (Jenkins et al. 2007) and also with habitat connectivity (de Bie et al. 2012), especially for freshwater taxa (e.g. fish, amphibians). These results suggest that passive-dispersing and co-dispersing organisms may have longer tails to their dispersal kernels than many active dispersers. Wind, migratory birds and human activities in particular (see Table 1) can disperse these organisms over large distances.

Patterns of distribution and gene flow in organisms co-dispersed by migratory vectors are related to the migration routes of these vectors. This has been clearly demonstrated for pathogens such as avian influenza and macroorganisms such as freshwater bryozoans and branchiopods (Freeland et al. 2000; Figuerola et al. 2005; Muñoz et al. 2013), but has also been suggested for various other microorganisms such as microalgae, archaea (Cellamare et al. 2010; Dyall-Smith et al. 2011) and parasites (e.g. myxozoans; Koel et al. 2010). Co-dispersers with long retention times in the gut are transported great distances by migratory birds (Viana et al. 2013; García-Álvarez et al. 2015). Moreover, many microorganisms and macroorganisms disperse using multiple vectors (Appendix 1; e.g. Table 1, Figure 2) and this may increase both the frequency and spread of dispersal. Indeed, multiple vectors are likely to be the norm for co-dispersed species, with low specificity of interactions, as is well documented for plant-frugivore mutualisms (Bascompte & Jordano 2014).

Upon arrival in a new environment, effective dispersal may be promoted by rapid reproduction but impeded in an otherwise suitable habitat by priority effects that occur when the order of colonization in a developing community influences community composition and population

structure. Asexual reproduction has been widely recognized since Elton (1927) as an advantage for establishment following dispersal, because a single colonist may found a population in the absence of Allee effects. This is more frequent in microorganisms but can also allow rapid expansion of parthenogenic macroorganisms (e.g., Muñoz et al. 2010). Similarly, monoecious (i.e. unisexual) Characeae (stoneworts) are far more likely to have colonized oceanic islands than dioecious ones (Proctor 1980). Many organisms have a surprisingly high dispersal capacity with a reasonably high chance of establishing populations in a new habitat, escaping competition and other selection pressures – for example, asexual rotifers (Wilson & Sherman 2010) and obligately sexual amphipods (Wellborn & Capps 2013).

Another key determinant of dispersal in both microorganisms and macroorganisms is the ability to form resting stages, which themselves facilitate transportation. These resting stages are resistant to adverse conditions during co-dispersal and can also become buried in sediment (forming a seed bank), enabling temporal dispersal (e.g. rescue effect; Lennon & Jones 2011). Recolonization of an African lake by cladoceran ephippia retained in sediments following a prolonged period of extinction illustrates the effectiveness of such temporal dispersal (Mergeay et al. 2007). Demonstration of viability over decadal to centennial scales – for example, copepod eggs and cladoceran ephippia (Hairston et al. 1995; Frisch et al. 2014) or diatoms (McQuoid et al. 2002) – suggests strong selection for temporal dispersal via extended dormancy in some plankton groups.

Paradoxically, in both microorganisms and macroorganisms with high dispersal ability, pronounced genetic differentiation can be observed amongst local populations. These patterns can be produced by founder effects combined with rapid local adaptation that enables monopolization of resources (the Monopolization Hypothesis, see Appendix 1; De Meester et al. 2002), precluding successful colonization by incoming propagules of the same species (i.e. preventing effective dispersal). Dispersal appears to be less impeded by monopolization effects in aquatic taxa with life histories that are likely to be associated with slower local adaptation, such as infrequent sexual reproduction or slow population growth (e.g. bryozoans, obligately parthenogenetic zooplankton, macrophytes; De Meester et al. 2002; Okamura & Freeland 2002; Muñoz et al. 2010). Monopolization effects have been repeatedly observed in microalgae, cladocerans and rotifers (e.g., Louette et al. 2008; van Gremberghe et al. 2009; Michaloudi et al. 2012; Alcantara-Rodriguez et al. 2012) and are likely to be widespread in bacteria. However, they have also been reported in much larger organisms such as fish

(Bradbury et al. 2008) and terrestrial higher plants (van der Merwe et al. 2010).

Dutch elm disease illustrates how genetic differentiation in co-dispersed organisms can also be generated by hybridization, particularly when the intervention of a new vector making intercontinental movements (i.e. humans) moves fungal plant pathogens into new areas, where they can then co-disperse with the same kinds of vectors used in their native range (i.e. bark beetles; Brasier 2001).

Techniques to measure dispersal of microorganisms and macroorganisms

Multiple techniques allow detection and tracking of dispersing organisms. In the following we consider several techniques that are increasingly used for the study of dispersal for both macroorganisms and microorganisms (further examples in Table 3).

Direct tracking methods have been used for decades, including "mark-recapture" of vertebrates and the measurement of plant dispersal using seed traps (e.g., Bullock et al. 2002). Technical progress has permitted the development of efficient tracking devices that can be attached to organisms to follow their movements in increasing detail. These devices are improving over time, enabling high specificity, longer recording times and enhanced time-resolution (e.g., Wikelski et al. 2007; Guilford et al. 2011; Vandenabeele et al. 2013; Table 3). While most of the electronic and tagging devices are developed for large organisms, they are gradually getting smaller and are being applied to a wider range of organisms – for example, radio-tracking of bees (Hagen et al. 2011) and quantum nanoparticle tagging in zooplankton (Ekvall et al. 2013; Table 3).

However, indirect tracking is the most common means of assessing organism dispersal. It is much easier to sample organisms (or descendants) after they have dispersed than to monitor them during dispersal. We review some of the techniques that enable indirect tracking of microorganism and macroorganism dispersal (see also Table 3). To date, most approaches involve indirectly monitoring the dispersal of macroorganisms.

For some species, stable isotope ratios can provide a spatially unbiased marker for detecting long-distance dispersal events (Hobson 2005) and for identifying the origin of organisms that move across isotopic boundaries. Although the spatial resolution is low, the ability to collect and analyse large amounts of data and to detect long-distance dispersal movements provides important advantages compared with conventional "mark-recapture" techniques. Stable isotopes have successfully been used to infer dispersal of macroorganisms such as birds (Hobson et al. 2004; Studds et al. 2012; van Wilgenburg et al. 2012), mammals (Pauli et al. 2012) and insects (Caudill 2003; Macneale et al. 2005). The development of models that utilize multiple isotopes (Hobson et al. 2012) or combine isotopes with other sources of data – for example, genetic data (Chabot et al. 2012), morphological traits (Rushing et al. 2014) or abundance (Royle & Rubenstein 2004) – will greatly expand our ability to study long-distance dispersal in many organisms. To our knowledge, these techniques have not yet been applied to studying patterns of dispersal in microbes, but combining isotopic studies of vector dispersal with studies of the diversity of microbes that are co-dispersing should enable further insights into the dispersal routes of microorganisms.

Table 3. Organism dispersal: detection and tracking techniques and their applications.

Techniques available	Example of use of tracking techniques
Electronic devices	Track macroorganism and microorganism dispersal using remote sensor, satellite tracking, video records, geolocators, laser radar or unmanned planes: macroorganisms, Witt et al. (2010), Klaassen et al. (2011), Bouten et al. (2013), Anderson and Gaston (2013), Lundin et al. (2011) and Brydegaard et al. (2009); microorganisms, Ekvall et al. (2013), Menden-Deuer (2010) and Fellous et al. (2010)
Molecular markers	
Ancient DNA	Assess temporal dispersal (Cermeño et al. 2013) and causes of dispersal (Coolen et al. 2004; Rull 2012; Jørgensen et al. 2012)
Environmental DNA and metabarcoding	Investigate the origin and direction of dispersal (Valentini et al. 2009, 2010; Jerde et al. 2011; Boyer et al. 2012; Dejean et al. 2012; Takahara et al. 2013) and investigate community interactions with regard to dispersal (Thomsen et al. 2012a, 2012b; Foote et al. 2012; Bienert et al. 2012; Yoccoz et al. 2012; Schnell et al. 2012; Calvignac-Spencer et al. 2013)
Population genetic markers	Link gene flow to dispersal (Bradbury et al. 2008; Casteleyn et al. 2010; McCusker & Bentzen 2010)
Real-time polymerase chain reaction and mass spectrometry	Quantify biodiversity and functional genes associated with dispersal (Hill et al. 1999; Christensen et al. 2011)
Stable isotopes	Assess the origin of dispersal in relation to habitat quality and trophic interactions (Rubenstein & Hobson 2004; Macneale et al. 2005)
Real-time fluorescence detectors	Determine organism size and concentration of airborne organisms (Hairston et al. 1997)
Landscape genetics	Quantify the effects of landscape features or climate on dispersal (McRae & Beier 2007; Storfer et al. 2010; Dudaniec et al. 2012, 2013) and co-dispersal (James et al. 2011; Côté et al. 2012)
Air samplers	Sample airborne dispersing microorganisms according to size on medium, agar or filters (Lacey & West 2006; Després et al. 2012)

Numerous methods using genetic markers have been applied to study organism dispersal (see for review Green & Bohannan 2006; Clobert et al. 2012; Hanson et al. 2012). Two techniques are particularly notable for enabling new insights into dispersal of taxa that are endangered, rare, cryptic, inaccessible or effectively invisible. The two techniques, environmental DNA (eDNA) and ancient DNA (aDNA), are based on detecting DNA that is present in environmental samples and are applicable to both microorganisms and macroorganisms (Appendix 1).

The examination of eDNA barcoding and metabarcoding (reviewed in Taberlet et al. 2012) is a powerful approach to identify the presence of microorganisms and macroorganisms, even at low density (Thomsen et al. 2012a), at any stage of their life cycle using traces of intracellular/extracellular DNA and the DNA of intact organisms (Bass et al. 2015) present in terrestrial or aquatic ecosystems. The technique has been used to track dispersal of invasive species, and to estimate the origin and direction of microorganism and macroorganism dispersal (Table 3). Samples aged from less than a month (Dejean et al. 2011; Thomsen et al. 2012a) to 450,000 years (Willerslev et al. 2007) have been processed successfully, allowing the description of past community composition, community interactions (Schnell et al. 2012) and insights into dispersal.

For older samples, the analysis of aDNA (see Table 3) can provide new insights into spatial and temporal scales of dispersal. The approach is best suited for studying organisms in well-preserved and dateable (marine and lake) sediments and in certain soil types (e.g. permafrost). The analysis of aDNA has been used to identify community assembly through time and to determine the presence and the nature of dispersal barriers (Gregory-Eaves & Beisner 2011; Rull 2012) – for example, in microorganisms (Cermeño & Falkowski 2009; Cermeño et al. 2010, 2013) and in macroorganisms (Willersley & Cooper 2005). The technique offers exciting opportunities to investigate historical dispersal patterns and the role of temporal dispersal that may be achieved via long-term dormancy of highly resistant propagules (Mergeay et al. 2007; Lundholm et al. 2011).

Combining morphological features and genetic markers (e.g. mitochondrial and ribosomal genes) in biogeographic and phylogeographic studies allows us to understand the relationship between the distribution of a species and its dispersal, revealing recent and historical dispersal events both for microorganisms and macroorganisms. Broad distributions are themselves suggestive of high dispersal ability, as recognized by Darwin (1859). While many microorganisms demonstrate widespread distributions, true ubiquity is debated. Apparent broad ranges may sometimes be explained by poor taxonomic resolution, when for instance the method of identification used or the threshold employed to define taxonomic levels may be inappropriate (Green & Bohannan 2006). Biogeographical patterns of occurrence in both microorganisms and macroorganisms have been revised after the identification of cryptic species (e.g., Amato et al. 2007; Bickford et al. 2007; see Appendix 1). The rapid extension of molecular studies from single markers to whole genome sequencing greatly enhances progress in this field.

New challenges and directions

Most dispersal studies have focused on active dispersal of small to large macroorganisms and passive dispersal of microorganisms. To more fully understand dispersal it is particularly important to further investigate: dispersal across life cycles; the impact of the three dispersal means (active, passive and co-dispersal) on microorganism distribution; and the ecological and evolutionary consequences of the networks of links between microorganisms and macroorganisms arising from co-dispersal. In the following we consider new directions and challenges for future dispersal research.

The effects of landscape (or seascape) heterogeneity on genetic dispersal and structure have been investigated for both microorganisms and macroorganisms (e.g., Storfer et al. 2010; Scheckenbach et al. 2010) via landscape genetic approaches (Appendix 1; see Tables 1 and 3). Landscape effects on microorganism dispersal have mainly been inferred *post hoc* (e.g., Whitaker et al. 2003; Heinzelman et al. 2012) rather than quantitatively, or are addressed within the context of host–pathogen interactions (reviewed in Biek & Real 2010). A key challenge is how to link spatial genetic processes occurring from small (Nunan et al. 2002) to large (Anderson et al. 2010) scales with those occurring in microorganisms to macroorganisms. This might be achieved by developing multi-level models within a landscape genetics approach that simultaneously considers spatial and temporal scales as predictors of genetic patterns characterized by isolation-by-resistance (Dudaniec et al. 2013). This will help to avoid spatial and temporal mismatches because of ecological differences between organisms (i.e. due to generation time, dispersal behaviour) or similar responses of these organisms to their environment, such as the type of land use (microorganisms: Ranjard et al. 2013; macroorganisms: Goldberg & Waits 2010), vegetation (microorganisms: Kuske et al. 2002; macroorganisms: Dudaniec et al. 2013), temperature (microorganisms: Ward et al. 1998, macroorganisms: Manel et al. 2012) and nutrients (microorganisms: Nunan et al. 2002; macroorganisms: Andrew et al. 2012). Simulation modelling of genetic data in combination with landscape or climate change data projections can also be used to predict future dispersal patterns (e.g. for invasive or reintroduced species;

Balkenhol & Landguth 2011). In many cases these are predictions made for macroorganisms that are vectors for many co-dispersed organisms.

Mechanistic modelling of migration and other dispersive movements enable routes, timing and individual differences in movements to be explored and understood (Bauer & Klaassen 2013). Although most modelling approaches are focused on active dispersers, passively dispersing organisms may be examined using biophysical transport models (e.g. in seascape genetics; Riginos & Liggins 2013). Extensive transport models for pollen may be used with minor modifications to model microorganism dispersal. There is great scope for incorporating co-dispersal into movement models of actively dispersing vectors, as recommended by Bauer and Klaassen (2013), who incorporated epidemiological details into migration models to generate insights into the spread of diseases. Furthermore, the costs of dispersal vary at each dispersal step (pre-emigration, initiation, transfer and settlement) and these should be considered independently (Bonte et al. 2012). Dispersal costs at the transfer stage are considered important in microorganisms (Bonte et al. 2012), but other steps have received little, if any, attention. For macroorganisms with multiple dispersal stages, explicit modelling of each step has rarely been done. This could provide crucial insights into spatial and temporal dynamics and improve our ability to predict how species respond to global change (Travis et al. 2012). Moreover, information gained in landscape genetic studies may be used to simulate dispersal across resistance-defined landscapes while incorporating species' life history traits as additional predictors (e.g. software CDPOP; Landguth & Cushman 2010). This resistance-based approach may be viewed as an extension to the least-cost path approach to modelling dispersal pathways, the latter referring to the "single path of least cost between points" and the former "the cumulative average cost of multiple paths between points", and are usually calculated from raster-based landscape data (McRae & Beier 2007). Although most commonly used in landscape genetic studies, these approaches have also been used in ecological studies (reviewed in Zeller et al. 2012) and show promise for use within future complex dispersal models.

A third challenge is to improve quantification of passive dispersal. The passive dispersal of microorganisms that utilize air and water as dispersal vectors remains underestimated, mainly because of technical limitations (Lacey & West 2006; Després et al. 2012). We see an increased need to perform experiments to test how microorganisms can further use, and maybe alter, their environment to influence their dispersal (e.g. through a role as ice nuclei and cloud condensation nuclei for bacteria and protists; Després et al. 2012; D'Souza et al. 2013). Combined studies of environmental samples and sequencing approaches (e.g. high throughput) can be employed to characterize the diversity of airborne microbial taxa and reflect their dispersal capacity. There is also a need to clarify the role of wind dispersal for macroorganisms – for example, how far can zooplankton eggs of different sizes be dispersed by this means? What is the role of storms in moving macroorganisms such as fish (Bajkov 1949)? In many cases it also remains unclear the extent to which some macroorganisms disperse actively by swimming or passively by currents, and both can be important in the same population (e.g. fish larvae; Swearer & Shima 2010; Williams et al. 2012).

Many species interact to jointly influence joint dispersal dynamics in complex ways (Figure 2), and such co-dispersal of organisms from one environment to another has important ramifications for understanding biogeographical patterns, community dynamics and adaptive traits, as well as for conservation and management strategies. The following key questions remain unanswered: how extensive is co-dispersal? What are the implications of such co-dispersal for the establishment of communities in novel habitats? What are the dispersal dynamics of taxa co-dispersing with macroorganisms? How does co-dispersal contribute to metacommunity dynamics and ecosystem function?

The broad distributions of many microorganisms and the significant contributions of parasites to community biomass (e.g. exceeding that of top predators in an estuarine system; Kuris et al. 2008) provide evidence for the importance and extent of co-dispersal in the natural world. Landscape genetic approaches can be used to distinguish current from historical dispersal processes by quantifying the effect of landscape features according to the "resistance" they impose on gene flow (Storfer et al. 2010; Dudaniec et al. 2012). Such approaches could enhance our understanding of how co-dispersal contributes to mutual landscape genetic patterns, accounting for the temporal variation in genetic versus landscape changes (Anderson et al. 2010; Dudaniec et al. 2012, 2013; Hand et al. 2015).

Last but not least, we emphasize the need for further investigation into use of multiple vectors for dispersal. So far, multiple vectors have been investigated mainly in pathogens of economic importance (e.g. Dutch Elm disease) or organisms that rely on different vectors to complete their life cycle (e.g. parasites with complex life cycles), but many other organisms are co-dispersed in a facultative way (Table 1, Figure 2). Even rare long-distance co-dispersal events by unusual vectors over large scales can generate a more cosmopolitan distribution than expected in these taxa. Screening the biodiversity dispersed within different vectors will identify

co-dispersal networks and give us a better understanding of the distribution of organisms and the means and consequences of their dispersal. Examining the dispersal of species within networks that quantify species interactions is a powerful way to investigate the importance of multiple dispersal vectors within communities – for example, plant-frugivore (Carlo & Yang 2011; Mello et al. 2011) and bird/mammal-mite (Latta 2003; Perotti & Braig 2009; Mascarenhas et al. 2010). The networks of interactions between dispersed taxa and their vectors can be considered "the architecture of biodiversity" (Bascompte & Jordano 2014).

Conclusions

It is sobering to reflect on just how little we know about how far, and by what means, most taxa on this planet disperse. However, we anticipate that in the near future many currently unknown dispersal relationships will be identified and quantified. We may even obtain insights into ancient co-dispersal, as recently exemplified by evidence for the passive dispersal of collembolans by mayflies noted by chance in fossilized amber (Penney et al. 2012). Combinations of well-established and next-generation techniques will help unveil distribution patterns and community interactions and so better define dispersal routes and co-dispersal interactions. New modelling approaches will bring insight into how communities interact during dispersal, how to predict dispersal in a changing world and how to design effective protected areas or corridors for dispersal. It is particularly clear that future research should invest more focus on co-dispersal in microorganisms and macroorganisms and that empirical studies of dispersal need to be broadened in scale, sample size and taxonomic scope, combining both field and laboratory studies, without adhering to old assumptions that dispersal traits are predictable *per se* based on organism size and morphology. We are looking forward to seeing increased collaborations between population biologists, ocean and atmospheric physicists, landscape ecologists and modellers to create a more holistic view of how organism movements result in functional communities that may be better conserved by more informed stewardship.

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Disclosure statement

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Appendix 1. Key definitions

Ancient DNA (aDNA) corresponds to DNA extracted from fossil remains, ancient specimens or traces from biological sources (Pääbo et al. 1989).

Environmental DNA (eDNA) metabarcoding is a bio-molecular multi-specific approach used to track and detect specific groups of organisms using universal primers to characterize DNA (both extracellular and in intact tiny organisms) present in environmental samples (e.g. air, water or soil) (Taberlet et al. 2012; Bass et al. 2015).

Co-dispersal is passive transport of an organism by biotic vectors. This includes phoresy, hitch-hiking, endozoochory (transportation of seeds, spores or other propagules inside the animal body after ingestion) and epizoochory (transportation outside the animal after attachment). It also includes the transport of parasites, symbionts and commensalists inside and outside the body.

Landscape genetics links the fields of landscape ecology, population genetics and spatial statistics to reveal quantitative relationships between landscape features and gene flow (Manel et al. 2003).

Monopolization hypothesis (De Meester et al. 2002) was proposed to explain restricted gene flow in organisms that have high capacity for dispersal. Strong natural selection combined with founder effects leads to distinct locally-adapted genotypes that monopolize the available habitat, preventing establishment of new immigrants.

Cryptic species are two or more species that are not distinguishable based on their morphology but which are sexually isolated and genetically differentiated.

Multiple vectors correspond to several taxa that act as vectors for a single dispersed species.