Integrating micro and macro-organism 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 focussed primarily on vertebrates and higher plants, yet recent studies suggest that the dispersal of micro- and macro-organisms have 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 micro- and macro-organisms 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 micro- and macro-organisms, 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.

Keywords

co-dispersal, detection and tracking techniques, dispersal ecology, integrated approach, organism size

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 level, 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 macro-organisms 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 macro-organisms 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 (e.g. see Clobert et al. 2012), but the overwhelming emphasis has been on macro-organisms, especially vertebrates. Yet the time is ripe to develop a more holistic understanding of both micro- and macro-organism dispersal, and move towards a common framework for both. This requires paying particular attention to co-dispersal (see Box 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 macro-organisms ignoring the concomitant dispersal of e.g.

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 22/07/2015, 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 as molecular techniques have facilitated 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 macro-organism 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 to the pioneering studies of the distribution of macro-organisms from the 18th 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 macro-organisms, 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 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 micro- and macro-organisms share many common themes and constraints.

In this review paper we compare the dispersal of micro- and macro-organisms, 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.

1. Dispersal means for micro- and macro-organisms

Micro- and macro-organisms 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 meters, e.g. diurnal migration) via cilia and flagellae (e.g. bacteria, protists, invertebrate larvae) or pseudopodia (e.g. amoebae; see examples in Jahn and Bovee 1965). Microalgae actively move in aquatic systems with or against the main flow, sometimes drifting faster and 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 kilometers (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 macro-organisms 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 and 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 (Croze et al. 2013; Lacey and West 2006; Sharma et al. 2007; Smith et al. 2011). 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). Due to their relatively large surface to volume ratios, small microbes ($< 20 \mu\text{m}$) 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 and West 2006; Després et al. 2012), and then settle in a new habitat (Genitsaris et al. 2011).

2. 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- 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 macro-organisms 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; Dyll-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 micro- and macro-organisms disperse using multiple vectors (Box 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 and Jordano 2014).

Upon arrival to a new environment, effective dispersal may be promoted by rapid reproduction but impeded in otherwise suitable habitat by priority effects that occur when the order of colonisation 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 macro-organisms (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 (e.g. asexual rotifers:

Wilson and Sherman 2010; obligately sexual amphipods: Wellborn and Capps 2013).

Another key determinant of dispersal in both micro- and macro-organisms 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 and Jones 2011). Recolonisation 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 (e.g. copepod eggs and cladoceran ephippia: Hairston et al. 1995, Frisch et al. 2014; diatoms: McQuoid et al. 2002) suggests strong selection for temporal dispersal via extended dormancy in some plankton groups.

Paradoxically, in both micro- and macro-organisms 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, De Meester et al. 2002, see Box 1), 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 and Freeland 2002; Muñoz et al. 2010). Monopolization effects have been repeatedly observed in microalgae, cladocerans and rotifers (e.g. van Gremberghe et al. 2009; Michaloudi et al. 2012; Louette et al. 2008; 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).

3. Techniques to measure dispersal of micro- and macro-organisms

Multiple techniques allow detecting and tracking dispersing organisms. Below we consider several techniques that are increasingly used for the study of dispersal for both macro- and micro- organisms (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 (e.g. radio-tracking of bees: Hagen et al. 2011; 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. Below we review some of the techniques that enable

indirect tracking of micro- and macro-organism dispersal (see also Table 3). To date, most approaches involve indirectly monitoring the dispersal of macro-organisms.

For some species, stable isotope ratios can provide a spatially unbiased marker for detecting long-distance dispersal events (Hobson et al. 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 to conventional ‘mark-recapture’ techniques. Stable isotopes have successfully been used to infer dispersal of macro-organisms 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 (e.g. genetic data: Chabot et al. 2012; morphological traits: Rushing et al. 2013, or abundance: Royle and 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.

Numerous methods using genetic markers have been applied to study organism dispersal (see Green and Bohannan 2006; Clobert et al. 2012; Hanson et al. 2012 for review). Two techniques are particularly notable for enabling new insights on dispersal of taxa that are endangered, rare, cryptic, inaccessible or effectively invisible. The two techniques, Environmental DNA (eDNA) and Ancient DNA (aDNA), use traces of DNA that organisms have left behind, recently or in the past, and are applicable to both micro- and macro-organisms (Box 1).

The examination of eDNA barcoding and metabarcoding (reviewed in Taberlet et al. 2012) is a powerful approach to identify the presence of micro- and macro-organisms, even at low density (Thomsen et al. 2012a), at any stage of their life-cycle using traces of intra/extracellular DNA 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 micro- and macro-organism 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 ancient DNA (see aDNA, Table 2) 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 and Beisner 2011; Rull 2012; e.g. in microorganisms: Cermeno and Falkowski 2009, Cermeno et al. 2010, 2013, and in macro-organisms: Willersley and 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 micro- and macro-organisms. 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 and Bohannan 2006). Biogeographical patterns of occurrence in both micro- and macro-organisms have been revised after the identification of cryptic species (e.g. Amato et al. 2007; Bickford et al. 2007; see Box 1). The rapid extension of molecular studies from single markers to whole genome sequencing enable greatly enhances progress in this field.

4. New challenges and directions

Most dispersal studies have focused on active dispersal of small to large macro-organisms and passive dispersal of microorganisms. To more fully understand dispersal it is particularly important to further investigate: 1) dispersal across life cycles, 2) the impact of the three dispersal means (active, passive, and co-dispersal) on microorganism distribution, and 3) the ecological and evolutionary consequences of the networks of links between micro- and macro-organisms arising from co-dispersal. Below 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 micro- and macro-organisms (e.g. Storfer et al. 2010; Scheckenbach et al. 2010) via landscape genetic approaches (Box 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 and 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 micro- to macro-organisms. 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 characterised by isolation-by-resistance (Dudaniec et al. 2013). This will help to avoid spatial and temporal mismatches due to ecological differences between organisms (i.e. due to generation time, dispersal behavior) or to similar responses of these organisms to their environment such as the type of land use (micro: Ranjard et al. 2013; macro: Goldberg and Waits 2010), vegetation (micro: Kuske et al. 2002; macro: Dudaniec et al. 2013), temperature (micro: Ward et al. 1998, macro: Manel et al. 2012) and nutrients (micro: Nunan et al. 2002; macro: 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 and Landguth 2011). In many cases these are predictions made for macro-organisms 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 and Klaassen 2013). Although most modelling approaches are focussed on active dispersers, passively dispersing organisms may be examined using biophysical transport models (e.g. in seascape genetics: Riginos and Liggins 2013). In plant ecology, 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 macro-organisms 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 and 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 and 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 due to technical limitations (Lacey and 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 characterise the diversity of airborne microbial taxa and reflect their dispersal capacity. There is also a need to clarify the role of wind dispersal

for macro-organisms, e.g. how far can zooplankton eggs of different sizes be dispersed by this means? What is the role of storms in moving macro-organisms such as fish (Bajkov 1949)? In many cases it also remains unclear the extent to which some macro-organisms disperse actively by swimming or passively by currents, and both can be important in the same population (e.g. fish larvae: Swearer and 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 macro-organisms? 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 of 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 e.g. multiple dispersal vectors within communities (e.g. plant-frugivore (Carlo et al. 2011; Mello et al. 2011) and bird/human-mite (Latta 2003; Perotti and Braig 2009; Mascarenhas et al. 2010)). The networks of interactions between dispersed taxa and their vectors can be considered as "the architecture of biodiversity" (Bascompte and 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 micro- and macro-organisms and that empirical studies of dispersal need to be broadened in scale, sample size and taxonomic scope, combining both field and lab 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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Box 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 from traces of DNA present in environment samples (e.g. air, water, or soil) (Taberlet et al. 2012).

Co-dispersal: 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: The 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: 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.

Figure and legends

Figure 1 – Schematic diagram illustrating how micro- and macro- organisms share basic dispersal modes. 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) are shown. The dashed line indicates how a particular dispersal mode may apply to an organism group, but with a low probability. Parasites can include micro- and macro-organisms. The values of shortest/longest organism per category were taken from the following literature: Mettenleiter and Sobrino 2008, Ghedin and Claverie 2005; bacteria and archaea: Schulz and Jørgensen 2001; plants as spores: Erdtman 1986; plants as seeds: Krishna Swamy et al. 2004, Blackmore et al. 2012; plankton: Finlay 2002; insects: Mockford 1997, Parker and Johnston 2006; vertebrates: Rittmeyer et al. 2012, Calambokidis and Steiger 1997; and parasites: Fishman 1998, Gubanov 1951.

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1083 Figure 2 – Schematic example of biotic networks resulting from co-dispersal. Triangles
 1084 indicate the capacity of the taxa to carry parasites (white) or be parasitic (black), or both (in a
 1085 qualitative, not quantitative manner). Rectangles are made up of three equal squares and
 1086 indicate if the taxa are dispersing actively (white = no, black = yes) (first square), passively
 1087 (second square) or are co-dispersed by a biotic vector (third square). Arrows connect the
 1088 dispersed taxon to its vector. Many organisms can disperse alone (actively or passively) or
 1089 together (via a biotic vector). See examples in Tables 1 and 2.

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1091 **Table 1- Examples of biotic vectors used for dispersal.**

Vector type	Mechanism	References
Anthropogenic	<ul style="list-style-type: none"> - boats - clothes and boots - food transportation - landscape modification 	<p>Gollash et al. 2007, Griffiths et al. 1991</p> <p>Perrigo et al. 2012, Waterkeyn et al. 2010, Perotti and Braig 2009</p> <p>Broadly and Smith 1994</p> <p>Suarez-Esteban et al. 2013</p>
Animal	<ul style="list-style-type: none"> - Zooplankton transporting microorganisms - Fish transporting copepod eggs and seeds - Insects transporting zooplankton eggs, fungal spores and mites - Waterbirds transporting seeds, bryozoans, ostracods and chironomids - Birds transporting microorganisms in their feathers, nasal cavity, nostrils, or toes - Bird selecting ferns and mosses for nest construction - Terrestrial animals transporting seeds 	<p>Grossart et al. 2010</p> <p>Bartholme et al. 2005, Pollux 2011</p> <p>van de Meutter et al. 2008, Andersen et al. 2012, Perotti and Braig 2009</p> <p>Green and Sánchez 2006, Green et al. 2013, García-Álvarez et al. 2015</p> <p>Bisson et al. 2009, Brito-Echeverria et al. 2009, Lewis et al. 2014, Mascarenhas et al. 2010, Garmyn et al. 2012</p> <p>Osorio-Zuñiga et al. 2014</p> <p>Romermann et al. 2005</p>
Multi-level transportations	<ul style="list-style-type: none"> - Waterbirds transporting zooplankton transporting bacteria - Seed-infesting insects transported in bird guts - Ciliates transported by ostracods transported by treefrogs dispersing between bromeliads - Bird transporting ticks and tick-pathogens associated to mammalian diseases - Humans transporting birds parasitized by mites 	<p>Andras and Ebert 2013</p> <p>Hernandez 2011</p> <p>Sabagh et al. 2011</p> <p>Cohen et al. 2015</p> <p>Mascarenhas et al. 2010</p>

1093 **Table 2- Parasitism and consequences for host-parasite dispersal.**

Impact	Example
Impede host dispersal by reducing host motility	<ul style="list-style-type: none"> - 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 and Altizer 2005) - Protists slow the swimming speed of parasitized chain-forming phytoplankton (Park et al. 2004)
Facilitate host dispersal by fleeing source of infection	<ul style="list-style-type: none"> - Parasites induce an increase in the number of winged offspring in female aphids (Sloggett and Weisser 2002) - Ectoparasite abundance influences natal dispersal between colonies of nesting cliff swallows (Brown and 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)	<ul style="list-style-type: none"> - 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)	<ul style="list-style-type: none"> - Trematode facilitates ingestion of Killifish by birds, which are the final hosts (Lafferty and Morris 1996) - Trematode facilitate the ingestion of snails by rats (Prugnolle et al. 2005) - Cestodes facilitate the ingestion of <i>Artemia</i> by birds (Sánchez et al. 2013)
Parasite facilitates its dispersal by allowing multiple host transmission	<ul style="list-style-type: none"> - Parasites transmitted to avian hosts via mosquitoes (Palinauskas et al. 2011) - Trematodes transmitted to avian hosts via marine snails (Keeney et al. 2009)

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1096 **Table 3- Organism dispersal: detection and tracking techniques and their applications**

Techniques available	Example of use of tracking techniques
Electronic device	Track macro and microorganism dispersal using remote sensor, satellite tracking, video records, geolocators, Laser radar, or unmanned planes (macro: Witt et al. 2010, Klaassen et al. 2011, Bouten et al. 2013, Anderson and Gaston 2013, Lundin et al. 2011, Brydegaard et al. 2009, micro: Ekvall et al. 2013, Menden-Deuer 2010, Fellous et al. 2010)
Molecular markers	<ul style="list-style-type: none"> - <i>Ancient DNA</i>: Assess temporal dispersal (Cermenio et al. 2013) and causes of dispersal (Coolen et al. 2004, Rull 2012, Jørgensen et al. 2012) - <i>Environmental DNA and metabarcoding</i>: Investigate the origin and direction of dispersal (Dejean et al. 2012, Jerde et al. 2011, Takahara et al. 2013, Valentini et al. 2009, 2010; Boyer et al. 2012) and to 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) - <i>Population genetic markers</i>: Link gene flow to dispersal (McCusker and Bentzen 2010, Bradbury et al. 2008, Casteleyn et al. 2010) - <i>Real-time PCR and mass spectrometry</i>: Quantify biodiversity and functional genes associated with dispersal (Christensen et al. 2011, Hill et al. 1999) - <i>Stable isotopes</i>: Assess the origin of dispersal in relation to habitat quality and trophic interactions (Rubenstein and Hobson 2004, Macneale et al. 2005) - <i>Real-time fluorescence detectors</i>: 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 and Beier 2007, Storfer et al. 2010, Dudaniec et al. 2012, 2013) and co-dispersal (Côté et al. 2012, James et al. 2011)
Air samplers	Sample airborne dispersing microorganisms according to size on medium, agar or filters (Lacey and West 2006, Després et al. 2012)

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