Editorial: Animal-Mediated Dispersal in Understudied Systems

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Animals disperse many smaller organisms by ingesting, transporting and egesting propagules (endozoochory) or by carrying propagules attached to their exterior (epizoochory). Both forms of animal-mediated dispersal are generally well studied, but most previous work focused only on a few kinds of species interactions. For example, seed dispersal by frugivorous birds and mammals, scatter-hoarding by small mammals, seed dispersal by ants, and dispersal of grasses and herbs by large herbivores have been investigated in detail. In contrast, other kinds of zoochory remain relatively unexplored, such as dispersal of propagules of aquatic invertebrates, or dispersal by vectors such as granivorous birds, fish, and reptiles. Our current knowledge on zoochory may be biased, overlooking important yet unidentified species interactions.

This Research Topic provides 14 new studies on zoochory in understudied dispersal systems to fill this gap. This collection includes reviews, statistical modelling, network analyses, field observations and analyses of historical data. This identifies new interactions, and presents new methods and ideas for future work. The publications in this Research Topic highlight seven key points or lessons.

First, much of the plant dispersal literature is dominated by dispersal syndromes assigned based on the morphology of seeds and fruits. However, many of the studies collected here show that syndromes are not reliable and should not be assumed to reflect actual dispersal mechanisms in the absence of field studies. The "endozoochory syndrome" is generally applied exclusively to plants with a fleshy fruit and equated with "frugivory", thereby ignoring that many non-fleshy fruits may also be dispersed by endozoochory. This collection demonstrates how a wide variety of plant species generally assumed to rely on abiotic dispersal can be dispersed by endozoochory: Corvids (Green et al., 2019), Cyprinidae fish (Boedeltje et al., 2019) and ungulates (Baltzinger et al., 2019) all disperse seeds without fleshy fruits. Additionally, the epizoochory syndrome often fails to predict what plants are actually dispersed via epizoochory by mammals (Baltzinger et al., 2019).

Second, our dispersal topic shows that zoochory is not exclusive to plants, but also applies to an understudied range of other organisms – including animal propagules. Hessen et al. (2019) remind us how important zoochory of invertebrates such as cladocerans and copepods by migratory birds is, especially in areas such as the Arctic where species need to shift their distributions quickly due to climate change. Okamura et al. (2019) show us in their review that bryozoans have proved to be an excellent model of invertebrate zoochory by waterbirds, since these organisms are detected with remarkable regularity in field studies on many continents. Ironically, this taxonomic group (moss animals) – so poorly known by the general public and even by most biologists – has proved to be perhaps the best example of animal-mediated dispersal of other animals.

Third, a wide range of often-overlooked animal dispersers is identified. Parrots – often deemed only seed predators – are identified as key vectors of palm seeds and large nut-like seeds (Blanco et al., 2019; Tella et al., 2019), European Corvidae are rediscovered as endozoochorous vectors of over 150 plant species of which the majority lacks fleshy fruits (Green et al., 2019), three temperate fish species disperse vegetative fragments of many vascular plants, mosses and charophytes (Boedeltje et al., 2019), and fleshy fruits are consumed by 470 different lizard species (Valido and Olesen, 2019). Several studies highlight that zoochory can occur by introduced animals, including ungulates (Baltzinger et al., 2019), goats (*Capra hircus*) and pine martens (*Martes martes*) (Muñoz-Gallego et al., 2019). This collection of studies therefore emphasizes the wide taxonomic range of vectors involved in zoochory.

A fourth key lesson is that current species interactions should be viewed in an evolutionary context (Blanco et al., 2019; González-Castro et al., 2019; Muñoz-Gallego et al., 2019; Tella et al., 2019). Plant-animal mutualisms may have evolved and then later have been disrupted by extinctions of the disperser animals. Historical dispersal interactions can be rescued by new interactions with new disperser species. Muñoz-Gallego et al. (2019) describe how two invasive mammals currently disperse a dwarf palm species, after its original dispersal vector went extinct. Blanco et al. (2019) investigate the potential of livestock to replace extinct megafauna, and González-Castro et al. (2019) identify two present-day vectors for the almost extinct plant Canary Islands dragon tree *Dracaena*.

A fifth lesson we can learn is that zoochory seems omnipresent across biomes and continents. While zoochory is most extensively studied in tropical forests and Mediterranean ecosystems, it also seems frequent for example in aquatic ecosystems, at high latitudes and in urbanized areas (Boedeltje et al., 2019; Gelmi-Candusso and Hämäläinen, 2019; Hessen et al., 2019; Okamura et al., 2019). Studying species dispersal in freshwater ecosystems and at higher latitudes such as the Arctic and Antarctic is increasingly important due to the relatively strong impacts of global change there. Zoochory may be a key mechanism for species to cope with habitat reduction and fragmentation, but still more research is needed.

A sixth lesson is that zoochory can take many forms. Baltzinger et al. (2019) review the importance of seed dispersal by ungulates via endozoochory compared to epizoochory, and secondary dispersal compared to primary dispersal. They distinguish primary epizoochory (direct adhesion to fur) from secondary epizoochory (seed-containing mud adhering to animals, or transfer through contact with conspecifics), and show both overlap and complementarity of the different mechanisms. Thinking of endozoochory we usually assume seed passage through the entire alimentary canal and egestion in faeces. However, also regurgitation is an important and understudied endozoochory process, both in mammals (Baltzinger et al., 2019; Delibes et al., 2019) and in birds whether as loose seeds or in pellets (González-Castro et al., 2019; Green et al., 2019). Delibes et al. (2019) focus on the spitting of seeds from the cud that occurs in mammalian ruminants, identifying at least 48 plant species belonging to 21 families that are dispersed this way. Spitting and regurgitation of seeds before digestion seems an especially important mechanism for larger-sized seeds, and it is here reported for ruminants (Blanco et al., 2019; Delibes et al., 2019) and birds (González-Castro et al., 2019). For parrots and Eurasian blackcaps (*Sylvia atricapilla*), another dispersal mechanism (estomatochory) is also reported: these birds handle the fruits for consumption and disperse the seeds without having ingested them (Blanco et al., 2019; González-Castro et al., 2019; Tella et al., 2019). Such synzoochory is also particularly relevant for large-seeded plants.

A final lesson we can learn from this collection of studies is that there are many new directions and technical advances that can benefit future studies. Hessen et al. (2019) highlights the importance of taking into account local species sorting and spatial scales. Even though zoochory may be frequent, community structures are importantly determined by many confounding parameters and even extensive zoochory does not have to affect communities e.g. owing to priority effects (Hessen et al., 2019). Kleyheeg et al. (2019) estimated seed rain based on tracking data of migratory mallards (*Anas platyrhynchos*) and their experimental seed retention times. A comprehensive modelling exercise estimates how many seeds are deposited in aquatic habitats along their migratory flyways. Coughlan et al. (2019) provide a model that can be used to quantify the role of different dispersers, or intraspecific differences among animals in dispersal importance, and rank species along an axis of importance. New approaches advocated include genetic tools for assessing waterbird-mediated transport of bryozoans (Okamura et al., 2019), and the use of dynamic seed dispersal networks to assess seed dispersal in fragmented and rapidly changing urban landscapes (Gelmi-Candusso and Hämäläinen, 2019). These new approaches will further expand the studied taxonomic range, for instance by facilitating the detection and tracking of microbial propagules such as moss spores or pathogens. All publications include many suggestions for future research directions.

In conclusion, these 14 publications jointly illustrate the extensive taxonomic range of zoochory, its omnipresence across biomes and the many ways by which animals can disperse a variety of animal and plant propagules. We hope that this Research Topic will function as a useful reference for future work on the importance of zoochory in its broadest sense, helping to emphasize its importance as a cosmopolitan source of connectivity. With global change and human pressure on ecosystems increasing, it is important to understand the contribution of natural and anthropogenic connectivity to the survival of native species and the spread of alien species worldwide. We hope this Research Topic provides an improved understanding of the contribution of zoochory to this connectivity – and hope it stimulates further investigation of zoochory in understudied systems.

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