Migratory birds as global dispersal vectors

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Abstract

Propagule dispersal beyond local scales has been considered rare and unpredictable. However, for many plants, invertebrates and microbes dispersed by birds, long distance dispersal (LDD) might be regularly achieved when mediated by migratory movements. Because LDD operates over spatial extents spanning hundreds to thousands of kilometers, it can promote rapid range shifts and determine species distributions. We review evidence supporting this widespread LDD service and propose a conceptual framework for estimating LDD by migratory birds. Although further research and validation efforts are still needed, we show that current knowledge can be used to make more realistic estimations of LDD mediated by regular bird migrations, thus refining current predictions of its ecological and evolutionary consequences.

The need to quantify long distance dispersal

Long distance dispersal (LDD) allows organisms to cross population boundaries, move among habitat patches and colonize remote areas, thus having important ecological, biogeographical and evolutionary consequences [1-3]. Its study and quantification has been, however, hindered by the low frequency of LDD events, the difficulty of tracking propagules (see Glossary) over large geographic scales, and the unpredictable nature of LDD vectors operating at such scales (such as ocean currents, extreme meteorological events and animals moving over long distances) [4].

Animal vectors are diverse and provide LDD services in a wide range of ecosystems and biogeographic regions. Examples of animal vectors able to disperse seeds over distances of hundreds to thousands of meters include Amazonian fish (<5 km) [5], Asian elephants (3 up to 5.8 km) [6], North American deer (<3 km) [7] and African hornbills (<6.9 km) [8]. Fruit bats and pigeons are also known to disperse seeds of many plant species over tens of kilometers throughout the tropics and in some subtropical regions [9, 10]. But among animal vectors, birds have the highest potential to mediate propagule LDD, especially during migration (>1,000 km) [11].

However, dispersal is hard to measure and quantify, especially LDD events. Therefore, the study of biodiversity distribution has been hindered by a deficient understanding and incorporation of dispersal, namely through the use of theoretical and arbitrary dispersal kernels. The most popular example is species distributions models (SDMs), which either disregard dispersal or incorporate very crude formulations of dispersal kernels (e.g. [12, 13]). Moreover, many studies on phylo- and bio-geographic patterns (reviewed in [2, 14]) argue that LDD promoted by birds is the only parsimonious explanation for such patterns in many taxa, including angiosperms [15, 16], bryophytes [17, 18], freshwater zooplankton [19, 20], marine snails [21] and ticks [22].

The potential of birds to mediate LDD of a vast number and diversity of organisms (see Box 1) provides a solid conceptual and methodological background to study vectored LDD and progress towards its quantification. Albeit still limited by technological and methodological constraints, progress so far allows for much better LDD estimations than before. We review the vectoring role of birds, especially of migratory birds, and propose an improved conceptual framework for understanding and estimating bird-mediated LDD beyond the scale of local populations.

Overlooked vectoring potential of migratory birds

Birds are probably the most abundant and competent vertebrate vectors [23]. They can disperse propagules both internally, following voluntary or involuntary ingestion of propagules (endozoochory), and externally, following attachment of propagules to feathers or legs. Birds also transport entire organisms, including pathogens and parasites, in both ways [24, 25] (Box 1).

Among birds, migratory species can be key LDD vectors because: (i) they move seasonally over broad spatial scales and can overcome major geographical barriers; (ii) they stop at sites with similar habitat characteristics along their migration routes, increasing the probability of successful establishment of dispersed propagules (i.e. they provide directed dispersal); and (iii) they are diverse, abundant and ubiquitous. Nearly one fifth (19%) of the 10,064 extant bird species on Earth (BirdLife International) are fully migratory [26] and many other species make long-distance movements (such as altitudinal or irruptive movements) as well as dispersal movements. Although migratory birds occur all over the world, the vast majority occurs in higher latitudes, especially in the northern hemisphere [26]. This means that LDD by migratory birds can be expected to be more frequent and relevant in the temperate region of the northern hemisphere, although the role of altitudinal, intra-tropical, temperate-tropical (e.g. by frugivorous songbirds [27]) and trans-hemispheric (e.g. by waders [28]) migrations should not be neglected.

Quantifying LDD by birds engaged in long-distance movements is a daunting task, as propagules must be sampled while the bird is in flight or immediately after stopping, but increasing evidence provides convincing support for this phenomenon. For example, 1.2% of passerine and gallinaceous birds intercepted by falcons while migrating over the ocean from Europe to Africa were found to transport ingested seeds (endozoochory) of at least five plant species [29]; and eight species of trans-equatorial migrant waders, captured in their arctic breeding grounds shortly before migration, were found to have bryophyte diaspores attached to their plumage, suggesting that these birds transport plant propagules towards their wintering grounds [30]. Numerous studies of seed dispersal to and between oceanic islands also suggest that marine and migratory birds are important LDD vectors (see review in [31]). The most striking example comes from Surtsey Island, a volcanic island nearby Iceland whose flora is dominated by bird-dispersed angiosperms (64% of species [31]), and where a single passerine species arriving from migration was found to carry seeds of 30 different plant species [32]. Dispersal of parasites and pathogens during bird migration also provides illustrative examples. Molecular analysis showed that 0.2% of the migrating birds sampled in an offshore island of New England were infested with ticks originating from coastal Maine (9.7 km away), 20% of which were infected with Lyme disease, a pathogen that was absent from the island [22]. Similarly, the spread of West Nile Virus across North America and the transcontinental spread of avian Influenza were mediated by migratory songbirds and migratory waterfowl, respectively [24].

As expected, LDD by migratory birds seems to be more frequent in the temperate region of the northern hemisphere. However, this bias might also reflect the larger number of studies undertaken in this region. In the tropical, subtropical and southern-temperate regions, many bird species fly long distances within short time periods, during both migration and other long-distance displacements. Examples of suitable long-distance dispersal vectors from these regions include hornbills in tropical Africa (<290 km) [8], oilbirds and pigeons in South America (>100 km) [33, 34], with-eyes, bulbuls and mousebirds in South Africa (<400 km) [35], waterfowl in Australia (hundreds of kilometers) [36] and gulls all over the world (hundreds of kilometers to and between oceanic islands) [31].

Although all the aforementioned studies are of key importance to establish the likelihood and scale of LDD by birds, they are not suited for estimating realistic dispersal patterns (e.g. dispersal kernels), due to their opportunistic nature (only a handful of species and localities available), low sample sizes and limited spatial accuracy in the determination of source populations. Moreover, propagules from each different vectored species may be dispersed by a diverse guild of vectors, each of them with different vectoring capacities, adding a level of complexity to the use of observational studies to understand vectored LDD. To overcome these limitations, mechanistic (process-based) models can be used to estimate potential LDD [4]. Despite recent methodological progress in estimating dispersal of organisms transported by migratory birds (e.g. [11, 37]), the lack of a unified conceptual framework has hindered the achievement of more realistic estimations and predictions to date.

A framework for the study of LDD by migratory birds

Propagule dispersal comprises three consecutive phases: initiation (propagule uptake by the vector), transport (propagule movement along with the vector) and deposition (propagule retrieval following transport) [4]. To understand the various determinants of each of these three phases, it is particularly useful to consider the Movement Ecology Framework proposed by Nathan *et al*. (2008) [38], which comprises four basic components: internal state, motion capacity, navigation capacity and external factors. Below we build on this conceptual framework to provide a mechanistic model of propagule movement mediated by migratory birds (see the conceptual model in Figure 1). Because propagule movement is mediated by the vector, the movement ecology of the vectored organism should be regarded as nested within the movement ecology of the bird vector [10]. This general framework can be applied to all kinds of propagules, though there are obvious differences among them (e.g. diaspores vs. parasites) that are not extensively reviewed here. For example, most parasites and pathogens, but not other propagules, can (i) influence the vector's behavior, movement and dispersal capacity, especially if disease is involved, and (ii) propagate while retained in the vector, thus increasing their dispersal effectiveness.

Propagule uptake

The dispersal process initiates when the vector acquires the propagule. Hence, it is contingent upon the biotic interaction between the vector (in this case the migratory bird) and the vectored organism (through its propagules) – thus, on their spatial, temporal and ecological overlap. Phenological synchrony between propagule production and vector visitation has been observed in several regions and biomes. For example, many terrestrial and aquatic plants produce their fruits during the autumn migration of frugivores and waterbirds, respectively [39, 40]. Further, the odds of acquiring parasites and pathogens are expected to be high during migration, because migratory birds are known to congregate in great numbers in key stopover areas along flyways. The probability of encounter between vectors and propagules represents the "navigational" capacity of the vectored organisms and is determined, for instance, by propagule traits that attract the dispersal vector and/or allow propagule uptake (e.g. production of fleshy fruits promoting ingestion, adhesive structures promoting attachment, and air- or vector-borne disease propagules promoting transmission) [10, 41].

Overall, the initiation phase is driven by (i) the internal state of the vector, namely its necessity to replenish energy for migratory flights [42], which determines the identity and quantity of acquired propagules; and (ii) the internal state and navigation capacity of the vectored organisms, which determine the characteristics, phenology (time of production) and abundance of their propagules. External factors can also affect the initiation phase: for example, climatic conditions can influence propagule production, attractiveness and availability, while meteorological conditions can influence migration time and stopover use by birds.

Transport: bird movement

Following the initiation phase, migratory birds start or resume migration (see Box 2) and transport internal and/or attached propagules. The duration and distance of the migratory flight depend on the birds' navigational and motion capacities, particularly on the trade-off between energy consumption and total migration time. This trade-off forms the basis of the "optimal migration" theory [42, 43] and defines the different (optimal) migratory strategies observed amongst different bird species, which in turn determine propagule LDD patterns [44].

From the vectored organism's perspective, its "motion" capacity depends on: (i) the retention time of propagules, which is determined by a number of propagule traits (notably size; e.g. [45], but also presence of specialized structures [46]); (ii) their resistance to the aggression encountered in the bird’s body (gut environment and immune responses, for internal dispersal), or to the environmental conditions at the vector’s exterior while in movement. External factors, such as landscape configuration and weather conditions, affect vector (and thus propagule) movement by shaping its movement decisions and route [47, 48].

Propagule deposition

Finally, propagules are released and deposited, either during flight, probably resulting in establishment failure, or after the bird stops, often in a habitat type comparable to that of departure, thus increasing the chances of propagule successful establishment. Stopping over during migration depends on the navigational capacity of the bird, i.e. on its ability to find shelter and food *en route*, and its internal state (willingness to stop). The deposition of viable propagules depends on their resistance to the internal or external conditions experienced during transport and their retention time (see Box 3). Germination, hatching and/or transmission of transported propagules depend on the effects of the conditions endured during transport and the propagule's internal state, as determined by the life-history of the species and modulated by propagule traits (e.g. coat permeability and presence of dormancies) and environmental cues (e.g. photoperiod and temperature). External factors such as habitat characteristics will also determine the fate of retrieved propagules.

Effectiveness of LDD

The realization of dispersal depends on its effectiveness, i.e. on the combination of successful transportation and deposition of viable propagules, plus their successful establishment and reproduction. Such effectiveness is critically related to the gains and costs involved in reaching distant habitat patches through LDD (e.g. [49]), and ultimately depends on the constraints posed by a combination of abiotic and biotic filtering of arriving propagules. The expected establishment challenges further increase uncertainty to the whole LDD process.

Dispersal effectiveness can be measured by the product of the number of propagules dispersed by a vector and the probability that they produce a new adult (i.e., by the quantity and quality components of dispersal) [50]. Field studies in aquatic ecosystems report high prevalence of propagules in waterbird droppings (45% for aquatic plants and 32% for invertebrates, on average), with high germination or hatching potential (36% and 30%, respectively) [51]. Terrestrial birds also ingest and disperse large amounts of propagules, especially seeds, during their migration [27, 52, 53]. Many of the seeds defecated by frugivorous birds remain viable after transportation, and most show enhanced (36-41%) or unaffected (45-48%) germination frequency and rate (N=153 and 103 plant species for germination frequency and rate, respectively) [54]. These numbers are all the more important if one considers the large population numbers of bird vectors: e.g. two migratory bird species, one waterfowl (mallard) and one passerine (European pied-flycatcher) known to ingest large quantities of propagules during migration [51, 52], have a worldwide population which surpasses 19 and 40 million birds, respectively (according to BirdLife International). Therefore, these birds alone likely disperse hundreds of thousands to millions of viable propagules each year. Passerines are generally more abundant than waterbirds, but the latter can acquire larger propagule loads, make longer migratory flights (Box 2) and retain propagules over longer periods (Box 3); thus the amount of propagules that reach a given distance is expected to depend on a tradeoff between the number of vectors (which generally decreases with body size; [55]) and their motion and propagule retention capacities (which generally increases with body size; see Box 2 and 3). Successful colonization and establishment in the destiny will ultimately depend on niche processes. As such, LDD might be more effective in aquatic ecosystems because waterbirds are more likely to fly from and to waterbodies – which are relatively homogeneous habitats. Indeed, the broad distribution of many aquatic organisms has been often attributed to the relative homogeneity of the aquatic environment (see [56] for a discussion). Nevertheless, recruitment probabilities in general may increase through phenotypic plasticity [56], rapid adaptation to local conditions [57], and directed local-scale dispersal to suitable microhabitats [58].

Ecological consequences of LDD

Migratory birds can promote the movement and connectivity of many taxa over extremely large spatial scales, with important ecological consequences. They can promote large-scale connectivity in anthropogenic (e.g. forest-pasture mosaics) and naturally isolated (e.g. lakes and wetlands, mountain tops) landscapes [59, 60]; as well as the colonization of distant habitat patches, including those in different continents [24, 61] or hemispheres [16, 17], and on oceanic islands [29, 62], hence contributing to the formation of phylo- and biogeographic patterns. LDD can also accelerate the spread of biological invasions [63, 64], parasites and pathogens [22, 24], and is likely to mediate the responses of species and populations to global change [64-66].

Estimation of ecological consequences: rapid range shifts

LDD is predicted to accelerate greatly the rate of dispersal across large spatial extents. However, and despite the wide acknowledgement of its importance in modern modeling platforms (e.g. [12, 13, 67]), the dispersal component of current species distribution models (SDMs) remains poorly defined. In most cases, it assumes either unlimited dispersal or an arbitrary dispersal kernel applied across all species. In the few studies that include dispersal kernels estimated for specific species, such estimates do not contemplate the role of LDD by non-standard vectors such as migratory birds (e.g. [68]). We argue that the conceptual framework presented here, together with the increasing amount of published evidence, may allow for the incorporation of more realistic predictions of the frequency and scale of LDD provided by migratory birds to a considerable number of species – albeit accurate predictions of the distance and direction of LDD events will only be attainable if both bird movement and propagule retention time are accurately parameterized (see Box 2 and 3).

In Figure 2, we illustrate how to estimate and predict rapid range shifts for species dispersed by migratory birds, based on the conceptual framework presented above. This example can constitute a methodological basis to foster the incorporation of LDD potential in species distribution modeling. For a given species and/or population distributed over a given area and dispersed by a given set of migratory bird species, we estimate its possible range shift within one year (one spring and one autumn migration). The core model component is the dispersal kernel, which was estimated according to a mechanistic model [11]. Bird migratory-flight distances (see Box 2) are combined with propagule retention times (see Box 3) to produce the dispersal kernel. Note that, if the model is to be parameterized for pathogen dispersal, the effect of the infection (i.e., propagule retention) on the migration capacity of vector birds should be adequately incorporated (see Box 3 and references therein).

Once the dispersal kernel is estimated, habitat suitability along the migration flyway must be determined to estimate the combined probability of propagule arrival and establishment in a given locality. Habitat suitability might be estimated through niche modeling, incorporating whenever possible the interaction between abiotic, biotic and stochastic population and community factors. The example in Figure 2 provides the possible range shifts of a vectored population across a full migratory cycle (one spring and autumn migration), which may be easily run over multiple years. If the goal is to predict future range shifts (e.g. following climate change), stepping-stone LDD events should be included by complementing these models with demographic models predicting propagule production at each new site of establishment (e.g. [67]).

Hypothesis testing and model validation

LDD predictions might be tested using a combination of direct observations and analysis of their ecological consequences. Direct observations of LDD (e.g. [29]) might be achieved by examining birds arriving from long-distance flights, such as those killed while in active migration by predators, human hunters or collision with man-made structures (e.g. lighthouses or wind turbines). The origin of collected propagules might then be traced using stable isotopes or genetic markers (see [69] for a review). For example, LDD frequencies observed empirically in one study (1.2 % of the sampled migrating birds were transporting at least one propagule [29]) is comparable with mechanistic-model estimates (yielding LDD frequencies of ≤3.5% of the migrating birds [11]).

Ecological consequences, namely distributional patterns, can be investigated using taxonomic assessments, phylogenetic analyses, genomic analyses, niche modeling, and computational techniques for modeling evolutionary data (see [2] for an overview). Inference made from distributional patterns might be used to validate LDD predictions. For example, it has been shown that the distribution of aquatic and land angiosperms [70, 71], zooplankton [19, 20], and pathogens [24] can be explained by regular dispersal along the migratory routes of their potential bird vectors. While regular LDD might take place at ecological time scales, providing a feasible response mechanism to rapid environmental changes such as climate change, rare events that promote the colonization of remote areas and generate disjunct distributions, such as bipolar distributions (e.g. [16]), might take place at evolutionary time scales [2], posing insurmountable challenges to the possibility of predicting their occurrence.

Concluding remarks and future directions

A wide range of organisms uses the LDD services provided by birds; hence more accurate LDD estimations might be achieved by incorporating the birds' vectoring potential and thus the full dispersal potential of vectored organisms. The study of diaspore (e.g. seed) dispersal and pathogen dispersal have traditionally been studied in parallel research lines, but studying the common and distinct processes underlying their dispersal might contribute to and cross-fertilize both research lines. The proposed framework constitutes a first step towards a general mechanistic understanding of bird-mediated LDD.

Although data is still limited for many vector and vectored species, LDD estimations based on mechanistic models and allometric relationships (see Box 4) provide more reliable estimates than the most commonly assumed dispersal scenarios (of unlimited or arbitrary dispersal capacity). Our ability to quantify and predict LDD by migratory birds will critically depend on the effectiveness of dispersal: (i) LDD might be more predictable if propagules are frequently acquired along migratory routes (e.g. [24, 29, 41, 52, 72]), and (ii) LDD might be largely unpredictable whenever propagule transportation occurs at very low frequency, especially in the case of extreme events spanning very large distances (hundreds to thousands of kilometers; e.g. [15, 16]). Movement tracking technology is expected to boost research on species range dynamics that will contribute to understand global patterns of biodiversity [72].

The conceptual framework proposed here can be used to derive and test specific hypotheses about the effects of LDD on (i) colonization patterns and connectivity, and consequent biogeographic patterns, and (ii) the spread of parasites, pathogens and invasive species. Reliable estimations of LDD will aid in (1) improving species distribution models (SDMs), by indicating where and when species, including invaders and disease, can reach suitable habitat patches, (2) choosing adequate scales to survey the distribution of biodiversity (e.g. spatial and temporal turnover in local communities), and (3) predicting species responses to global change. Therefore, it will have clear implications for the conservation of biological diversity and the sustainable use of ecosystem services.

Box 1. Diversity and LDD potential of organisms dispersed by birds

A wide array of different taxa use the LDD services provided by birds. Microorganisms, including viruses, bacteria and protozoans, live in or on birds and can travel along with them. The most known examples are emergent infectious diseases such as avian Influenza and West Nile Virus [24], but other microorganisms can be dispersed in association with other propagules dispersed by birds, including diaspore parasites [74] and viruses and bacteria associated to ectoparasites (e.g. Lyme disease in ticks [22]). The spores of fungi [75], as well as the diaspores of many plant taxa, including bryophytes [30], ferns [2], conifers (e.g. [76]) and both aquatic and land angiosperms (e.g. [23, 51]) are also frequently dispersed by birds. Among invertebrates, we highlight ectoparasites (e.g. fleas and ticks; e.g. [22]), land [77] and aquatic [78] snails, and aquatic microinvertebrates such as rotifers and crustaceans, but other invertebrates such as flies, hemipterans and other arthropods, as well as nematodes and other worms, can also be dispersed occasionally by birds (e.g. [79]). Birds disperse all these organisms as dormant propagules (e.g. plant seeds, invertebrate cysts and resting eggs), fragments (typically for plants) and/or whole individuals (e.g. snails attached to feet and/or plumage, pathogens and parasites travelling with or within the vector). Vectored dispersal can be triggered by (1) the intentional lure provided by an associated reward, such as the pulp consumed by frugivores, (2) a predation event, in which a fraction of the propagules survives gut passage (e.g. granivory), (3) involuntary ingestion, such as the consumption of seeds and cysts by filter-feeding birds, (4) attachment of propagules to the vector's body (e.g. to the bird's feet or feathers), or (5) the transmission of pathogens or parasites. Some of the mentioned organisms are known to use bird-mediated LDD services, including plants, invertebrates (mainly zooplankton) and parasites (see main text), but empirical evidence is scarce for the vast majority.

Vectored dispersal generally occurs over small spatial scales. Plants, for example, are rarely dispersed over more than 1,500 m [65]. However, LDD operates beyond the scale of a local population, ranging from the landscape scale (at which LDD links metapopulations and metacommunities) to the regional and biogeographical scales (at which LDD leads to the colonization of distant and remote areas). In Figure I we provide some examples of vectored LDD operating at different spatial scales.

Box 2. Bird migration patterns

Migration is a directional movement between separate breeding and wintering areas. Birds undertake extraordinary migratory journeys, crossing hundreds or thousands of kilometers, often over entire continents or between them. Migration consists, in most cases, of a series of consecutive long-distance flights interspersed with stopover periods for resting and feeding (but see [80] for extreme, non-stop flights of waders across the entire Pacific ocean). The distance and frequency of non-stop migratory flights (Figure I), which set the potential for propagule LDD, are the result of species-specific migration strategies, defined according to a trade-off between time, energy and safety [42, 43]. During migration, birds spend most of their time feeding and resting at stopover sites, thus generating local-scale dispersal. In contrast, migratory flights can be expected to promote less frequent, long distance dispersal events. If propagules are retained long enough, birds can transport them over hundreds of kilometers – and occasionally over more than one thousand kilometers (Figure I).

Migratory distances can be either measured with ringing or satellite-tracking data, or estimated using theoretical calculations based on aerodynamic theory (Box 4). Maximum migratory distances calculated from empirical data are shorter than those derived from theoretical calculations, which probably reflects the influence of individual strategies and external factors such as landscape configuration (e.g. movement barriers). Despite the rapid increase in the use of satellite-based tracking technologies, detailed movement data are still lacking for a large proportion of bird species, in particular smaller species such as passerines. This means that detailed knowledge of migratory routes and connectivity is still lacking for most bird species, especially high-frequency data obtained at large spatio-temporal scales. We expect technological advances in animal tracking (already under development and test) to improve our knowledge in a near future, namely through the production of smaller and lighter satellite tags [81]. It will allow a deeper mechanistic understanding of the processes determining flight performance in migrating birds, which in turn will promote the refinement of mechanistic models (e.g. Box 4).

Box 3. Propagule retention time

Propagule retention time is often considered to be the most important determinant of dispersal kernels [11, 82], yet the morphological traits, physiological processes and environmental factors behind its intra- and inter-specific variation are still poorly understood. For ingested propagules, the range of gut retention times (GRT) varies greatly among taxa: in passerines GRT peaks at 20 to 60 minutes [54] and show distribution tails that do not extend beyond a few hours, whereas in waterbirds GRT peaks at 1 to 11 hours and show long tails reaching 72 hours (e.g. [83, 84]; Figure I). GRT scales positively with body mass in passerines [85] but negatively in waterbirds [11]. These contrasting relationships might be related to a trade-off between GRT (larger birds have longer guts through which propagules take longer to pass) and propagule survival (larger birds have stronger gizzards that destroy a higher proportion of propagules that spend longer periods within them), though further research is still needed. For externally-attached propagules, the only study that measured attachment time to bird feathers showed an exponential decrease of retention time up to a maximum of nine hours, strongly associated with preening and ruffling rates [86]; and for pathogens, the duration of infection (i.e., retention time) is variable. For example, the duration of infection by West Nile virus in various bird orders and by Influenza A in mallards peaks at approx. 3 days, extending up to 7 and 34 days, respectively [87, 88]. Other endoparasites (e.g. *Plasmodium*) and ectoparasites (e.g. ticks) cause life-lasting infections in birds.

It is also worth noting that propagule retention and flying activity might influence each other, but we still lack a methodology to measure retention time while birds are flying. A study on the effect of physical activity (swimming) on seed retention time using mallards showed enhanced propagule survival but slightly shorter retention times at higher physical activity [89]. On the other hand, travelling with the extra weight of a large (ingested) propagule load might affect flying performance [90]. Parasites and pathogens might also affect the birds' physical condition and migratory performance, such as in swans infected by Influenza, which delayed the start of their migratory flights for more than a month, until the end of the infectious period [91] – but not in two passerine vectors (Swainson's thrush and gray catbird) experimentally infected with West-Nile Virus, whose migratory activity was unaffected [92].

Box 4. Allometric scaling

The size of organisms is an important determinant of many vital physiological and behavioral processes [93]. Hence, body mass (M) is often related to many morphological and functional traits (Y) by this general expression, where b is the scaling exponent [93]:

$$Y = Y_0 M^b$$

Let U be the flight speed and R the propagule retention time. Dispersal distance (D) can be estimated as:

$$D = c\, U\, R$$

where c is a correction factor for departures from the assumption of linear movement at constant speed from propagule uptake to release (adapted from [94]). U scales to the body mass of animal vectors [94]:

$$U = 15.9\, M^{0.13}$$

For internal dispersal, R scales also to the body mass of the animal ingesting the propagule, so that:

$$R = R_0 M^b$$

where R_0 and b take different values for different functional groups (e.g. passerines vs. waterfowl [11, 85]).

These formulae provide a rough estimate of the maximal (or potential) dispersal distance, assuming that the vectoring animal keeps on moving until the propagule is released. But for dispersal to be effective in most cases, the vector must land before the propagule is released, i.e. the flight time (T) must be equal or shorter than the retention time ($T \leq R$). We can estimate flight time according to the equation:

$$T = k^{-1} \ln(1+f)$$

where K is the rate of mass loss and f is the relative fuel load. The flight distance (Y) is the multiplication of the flight time by the flight speed [43]:

$$Y = U\ k^{-1}\ \ln(1+f)$$

Flight time and distance can be expected to scale with body mass, as k is inversely related to metabolic power consumption during flight (P). P shows the following empirical relationship with body mass [95]:

$$P = 53.65\ M^{0.74}$$

whose exponent is higher for calculations based on the aerodynamic theory [96], where:

$$P = 44.05\ M^{0.975}$$

These calculations have a number of limitations. Firstly, they are based on the conservative assumption that only fat, rather than fat and protein, is burned during the migratory flight. Second, they focus on estimating maximum (i.e. potential) flight time and distance, which might not be good indicators of the overall migration strategy. Instead, mode migratory distances might be obtained by using usual, rather than maximum, fat loads. In this sense, it is important to note that maximum dispersal distances set the potential limit for one-step LDD (Figure I), even though mode distances (which are far more frequent) are often large enough to result in LDD.

Outstanding Questions

Dispersal ecology

- What characteristics (besides body mass) determine the vectoring capacity of birds during migration?
- Can allometric scaling be used to estimate multi-vector dispersal kernels?

- How flying activity, particularly during migration, modifies propagule retention time? Experiments measuring propagule retention time of birds flying on wind tunnels can provide a solution to this question.

- How many propagules are dispersed by migratory birds each year and at which scale? I.e., how strong is the propagule pressure generated by migratory birds at different spatial scales? Can major stopover areas where migrating birds congregate function as hotspots for propagule deposition?

Ecological consequences

- What is the colonization success of species and individuals dispersed by migratory birds? Can deposition hotspots (such as major stopover areas) promote colonization and maintain or boost regional diversity?

- Does LDD mediated by migratory birds influence metapopulation and metacommunity dynamics, particularly in fragmented habitats? Will the observed declines in migratory bird populations reduce the connectivity between populations?

- Can the dispersal services provided by migratory birds determine phylo- and bio-geographic patterns?

- To what extent can the vectoring role of migratory birds accelerate the rate of range expansion and shifts? Will it suffice to compensate for the impact of climate change?

- What is the role of migrating birds as mobile linkers among ecosystems, particularly as providers of ecosystem services?

Conservation biology

- Which types of invasive species can be (regularly) dispersed by migratory birds?

- Can migratory birds accelerate the spread of pathogens? What characteristics of pathogens favour their dispersal?
- Can species distribution models, particularly those used to predict range adjustments and design conservation strategies, incorporate predictable LDD estimates?

Glossary

Endozoochory: dispersal of propagules inside an animal vector

Epizoochory: dispersal of propagules attached to an animal vector

Disjunct distribution: species showing large discontinuities in their distribution (e.g. transoceanic and bipolar distributions).

Dispersal kernel: a probability distribution of dispersal distances and the associated spatial distribution of dispersal units.

Dispersal vector: any agent transporting propagules (e.g. birds or wind).

Long distance dispersal (LDD): dispersal acting beyond local scales, typically across population boundaries.

Propagule: a vectored dispersal unit.

Range shift: shift in the geographic distribution of species, often in response to environmental change (e.g. climate change).

Tail of probability distribution: the range of a given variable (e.g. dispersal distance) that has a disproportionate low occurrence probability, whose length and thickness depend on the distribution kurtosis and skewness. LDD is characterized by right-skewed, leptokurtic distributions (i.e. large distance values occur at low probability).

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Figure legends

Figure 1. Movement ecology framework for propagules dispersed by migratory birds. Note that, independently of propagule adaptations to its vectors and thus to movement, propagule movement relies on the vector movement as its key external factor, and thus the vectored organisms' movement is nested within the vectors' movement (see [10]).

Figure 2. Estimation of rapid range shifts mediated by migratory birds: example of a population present in Doñana National Park, Spain, dispersed by a waterfowl species weighing 300g (orange line in the dispersal kernel) and migrating along a route (orange polygon) within the Palaearctic-African flyway. The grey line corresponds to a waterfowl species weighing 1 kg (for comparison purposes). Dispersal kernels were parameterized according to empirical data and estimated according to a mechanistic model [11], where LDD was considered as dispersal mediated by bird migratory flights, i.e. flights >100 km. Habitat suitability was assumed to be within the range 10-25 ºC of maximum March temperature (note that this is only an example; temperature information was obtained from [97]). The probability of arrival and establishment in a suitable location corresponds to (1 - cumulative distance frequency) (grey scale corresponding to the dispersal kernel above).

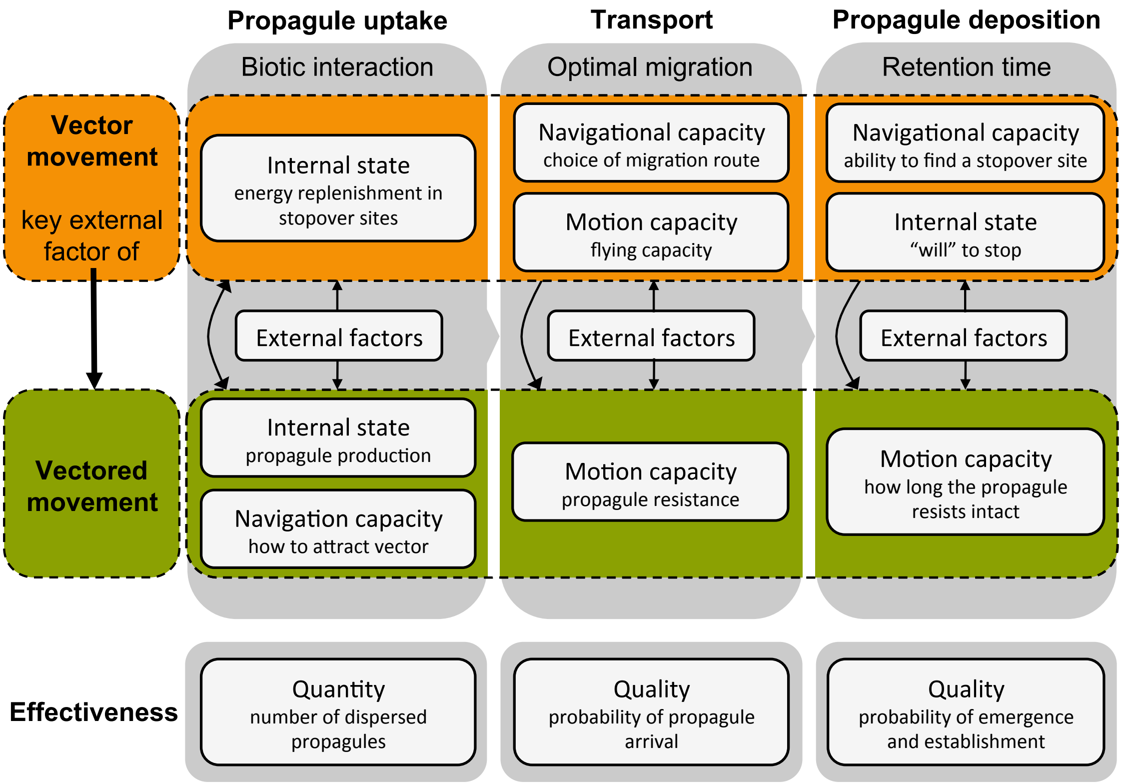
Figure I (Box 1). Examples of vectored LDD operating at different spatial scales: (A) ticks and Lyme disease dispersed by migratory landbirds over 37 km [22], (B) macrophyte seeds and zooplankton eggs dispersed by migratory waterfowl over distances ranging from tens to hundreds of kilometers [11], (C) terrestrial plant seeds dispersed by migratory passerines over ~1,000 km [29, 32], and (D) bryophyte diaspores dispersed by transequatorial migrant shorebirds over distances up to 15,000 km [30]. Solid and dashed arrows correspond to examples of dispersal events either directly observed or supported by compelling evidence, respectively.

Figure I (Box 2). Frequency distribution of migratory distances for waterfowl (Anatidae; A; data from [11]) and passerines (mostly frugivores; B; data read from [98]). Distances were obtained from ringing data by measuring the distance between two consecutive sightings within a period of six (A) or seven (B) days. Within these time periods, most waterfowl make only a single migratory movement (see [44] for details); passerines, nevertheless, can make more than one migratory flight. Distances <50 km were excluded.

Figure I (Box 3). Probability distribution of gut retention times. (A) Waterfowl: lognormal distribution fitted to aggregated experimental raw-data (individual gut retention times of plant seeds fed to seven duck species [11]). (B) Passerines: lognormal distribution fitted to summarized experimental data (mean and standard deviation of the gut retention time of inert tracers fed to 13 passerine species [82]). The dashed line represents retention times beyond the standard deviation.

Figure I (Box 4). Maximum range distances of bird migratory flights as a function of body mass, calculated according to empirical (A) and allometric (B) relationships. Allometric relationships were based on the bird's maximum fuel-loading capacity (hmax = 1.42 mass - 0.0554; [99]). Maximum fuel loads (fmax) were estimated as hmax-1, and power consumption was transformed into mass loss by converting 37.6 kJ into one gram of fat (assuming that only fat is burned; [100]).

Figure 1



Propagule uptake
Transport
Propagule deposition
Biotic interaction
Optimal migration
Retention time
Vector movement
key external factor of
Internal state
energy replenishment in stopover sites
Navigational capacity
choice of migration route
Motion capacity
flying capacity
Navigational capacity
ability to find a stopover site
Internal state
"will" to stop
External factors
External factors
External factors
Vectored movement
Internal state
propagule production
Navigation capacity
how to attract vector
Motion capacity
propagule resistance
Motion capacity
how long the propagule resists intact
Effectiveness
Quantity
number of dispersed propagules
Quality
probability of propagule arrival
Quality
probability of emergence and establishment

Figure 2

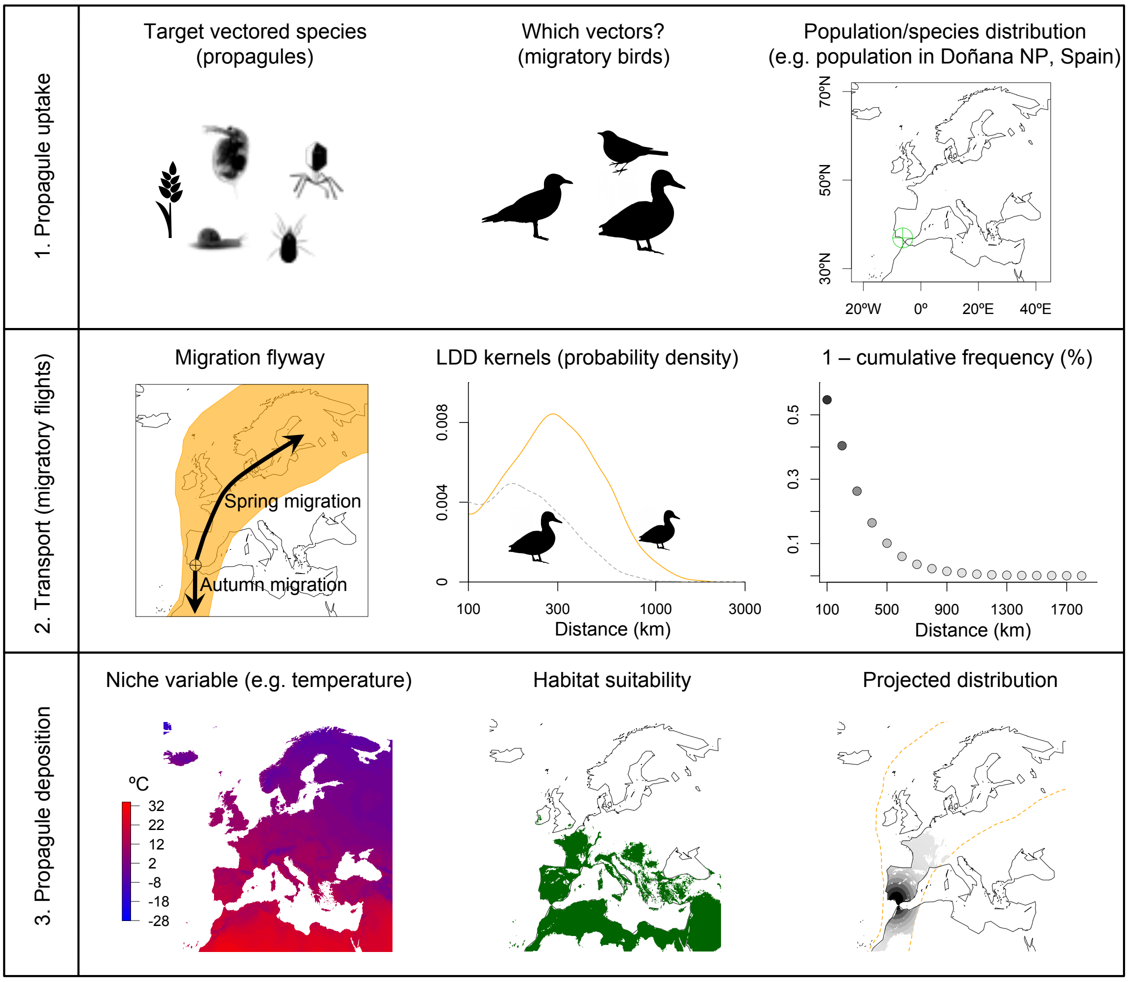
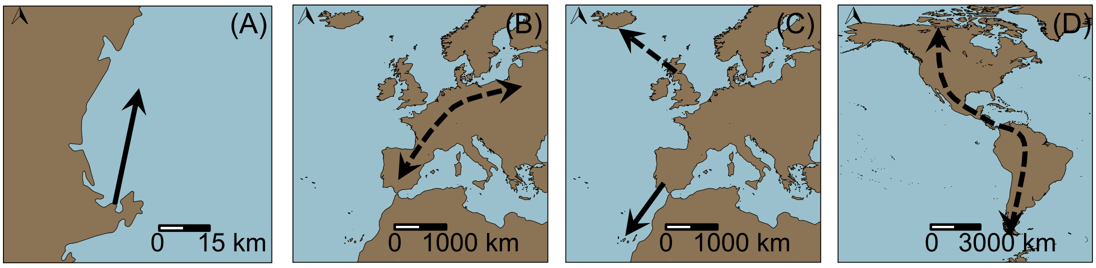

1. Propagule uptake
Target vectored species
(propagules)
Which vectors?
(migratory birds)
Population/species distribution
(e.g. population in Doñana NP, Spain)
70ºN
50ºN
30ºN
20ºW
0º
20ºE
40ºE
2. Transport (migratory flights)
Migration flyway
Spring migration
Autumn migration
LDD kernels (probability density)
0.008
0.004
0
100
300
1000
3000
Distance (km)
1 – cumulative frequency (%)
0.5
0.3
0.1
100
500
900
1300
1700
Distance (km)
3. Propagule deposition
Niche variable (e.g. temperature)
ºC
32
22
12
2
-8
-18
-28
Habitat suitability
Projected distribution

Figure I - Box 1



824 Figure I - Box 2

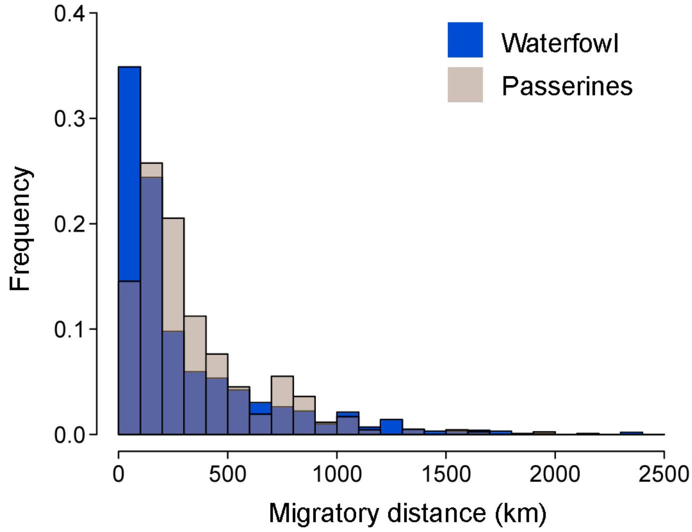


Figure I - Box 3

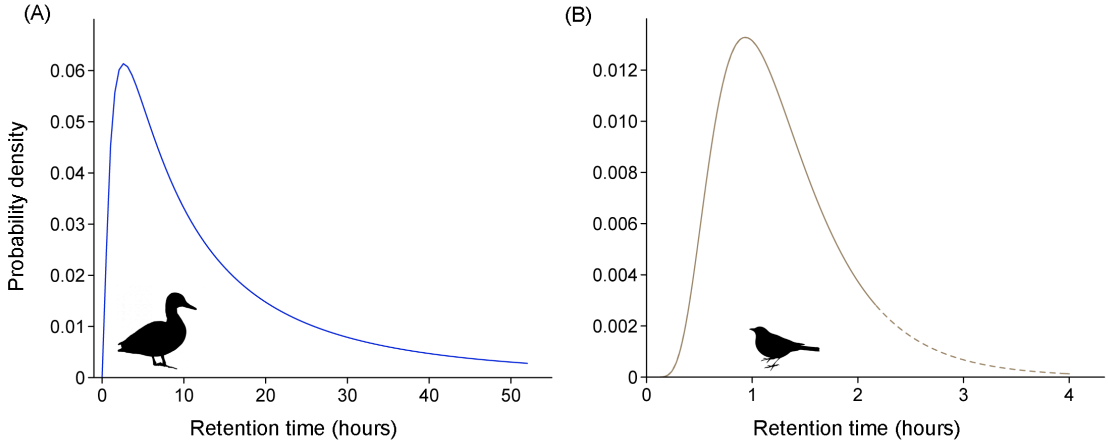


Figure I - Box 4