

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 $\leq 3.5\%$ 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].

436

437 **Box 4. Allometric scaling**

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

442
$$Y = Y_0 M^b$$

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

445
$$D = c U R$$

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

449
$$U = 15.9 M^{0.13}$$

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

452
$$R = R_0 M^b$$

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

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

460
$$T = k^{-1} \ln(1+f)$$

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?

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

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

492

493 *Ecological consequences*

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

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

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

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

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

506

507 *Conservation biology*

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

509 - Can migratory birds accelerate the spread of pathogens? What characteristics of
510 pathogens favour their dispersal?
511 - Can species distribution models, particularly those used to predict range adjustments
512 and design conservation strategies, incorporate predictable LDD estimates?
513

514 **Glossary**

515 **Endozoochory**: dispersal of propagules inside an animal vector

516 **Epizoochory**: dispersal of propagules attached to an animal vector

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

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

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

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

524 **Propagule**: a vectored dispersal unit.

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

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

531

532 **Acknowledgements**

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References

1. De Queiroz, A. (2014) *The monkey's voyage: how improbable journeys shaped the history of life*. Basic Books.
2. Gillespie, R.G., *et al.* (2012) Long-distance dispersal: a framework for hypothesis testing. *Trends Ecol. Evol.* 27, 47-56.
3. Nathan, R. and Nathan, O. (2014) Unlikely yet pivotal long dispersals. *Science* 344, 153-154.
4. Nathan, R., *et al.* (2008) Mechanisms of long-distance seed dispersal. *Trends Ecol. Evol.* 23, 638-647.
5. Anderson, J.T., *et al.* (2011) Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proc. R. Soc. B*, rspb20110155.
6. Campos-Arceiz, A., *et al.* (2008) Behaviour rather than diet mediates seasonal differences in seed dispersal by Asian elephants. *Ecology* 89, 2684-2691.
7. Vellend, M., *et al.* (2003) Dispersal of *Trillium* seeds by deer: implications for long-distance migration of forest herbs. *Ecology* 84, 1067-1072.
8. Holbrook, K.M., *et al.* (2002) Implications of long-distance movements of frugivorous rain forest hornbills. *Ecography* 25, 745-749.
9. Corlett, R.T. (2009) Seed dispersal distances and plant migration potential in tropical East Asia. *Biotropica* 41, 592-598.

- 557 10. Tsoar, A., *et al.* (2011) A movement ecology approach to study seed dispersal
558 and plant invasion: an overview and application of seed dispersal by fruit bats.
559 In *Fifty years of invasion ecology: the legacy of Charles Elton* (Richardson,
560 D.M., ed), pp. 103-119, Wiley-Blackwell.
- 561 11. Viana, D.S., *et al.* (2013) Allometric scaling of long-distance seed dispersal by
562 migratory birds. *Am. Nat.* 181, 649-662.
- 563 12. Elith*, J., *et al.* (2006) Novel methods improve prediction of species'
564 distributions from occurrence data. *Ecography* 29, 129-151.
- 565 13. Phillips, S.J., *et al.* (2006) Maximum entropy modeling of species geographic
566 distributions. *Ecol. Model.* 190, 231-259.
- 567 14. Mummenhoff, K. and Franzke, A. (2007) Gone with the bird: Late tertiary and
568 quaternary intercontinental long-distance dispersal and allopolyploidization in
569 plants. *Syst. Biodivers.* 5, 255-260.
- 570 15. Le Roux, J.J., *et al.* (2014) Relatedness defies biogeography: the tale of two
571 island endemics (*Acacia heterophylla* and *A. koa*). *New Phytol.* 204, 230-242.
- 572 16. Popp, M., *et al.* (2011) A single Mid-Pleistocene long-distance dispersal by a
573 bird can explain the extreme bipolar disjunction in crowberries (*Empetrum*).
574 *Proc. Natl. Acad. Sci. USA* 108, 6520-6525.
- 575 17. Lewis, L.R., *et al.* (2014) Direct long-distance dispersal shapes a New World
576 amphitropical disjunction in the dispersal-limited dung moss *Tetraplodon*
577 (Bryopsida: Splachnaceae). *J. Biogeogr.* 41, 2385-2395.
- 578 18. Piñeiro, R., *et al.* (2012) Circumarctic dispersal and long-distance colonization
579 of South America: the moss genus *Cinclidium*. *J. Biogeogr.* 39, 2041-2051.
- 580 19. Figuerola, J., *et al.* (2005) Invertebrate eggs can fly: evidence of waterfowl-
581 mediated gene flow in aquatic invertebrates. *Am. Nat.* 165, 274-280.

- 582 20. Muñoz, J., *et al.* (2013) Bird migratory flyways influence the phylogeography of
583 the invasive brine shrimp *Artemia franciscana* in its native American range.
584 *PeerJ* 1, e200.
- 585 21. Miura, O., *et al.* (2011) Flying shells: historical dispersal of marine snails across
586 Central America. *Proc. R. Soc. B* 282.
- 587 22. Smith, R.P., *et al.* (1996) Role of bird migration in the long-distance dispersal of
588 *Ixodes dammini*, the vector of Lyme disease. *J. Infect. Dis.* 174, 221-224.
- 589 23. Stiles, F.G. (2000) Animals as seed dispersers. In *Seeds: the ecology of*
590 *regeneration in plant communities* (Fenner, M., ed), pp. 111-124, CABI
591 Publishing.
- 592 24. Altizer, S., *et al.* (2011) Animal migration and infectious disease risk. *Science*
593 331, 296-302.
- 594 25. Fenton, A., *et al.* (2002) Parasite transmission: reconciling theory and reality. *J.*
595 *Anim. Ecol.* 71, 893-905.
- 596 26. Somveille, M., *et al.* (2013) Mapping global diversity patterns for migratory
597 birds. *PLoS ONE* 8, e70907.
- 598 27. Chesser, R.T. and Levey, D.J. (1998) Austral migrants and the evolution of
599 migration in New World birds: diet, habitat, and migration revisited. *Am. Nat.*
600 152, 311-319.
- 601 28. Conklin, J.R., *et al.* (2010) Breeding latitude drives individual schedules in a
602 trans-hemispheric migrant bird. *Nat. Commun.* 1, 67.
- 603 29. Viana, D.S., *et al.* (2016) Overseas seed dispersal by migratory birds. *Proc. R.*
604 *Soc. B* 283.
- 605 30. Lewis, L.R., *et al.* (2014) First evidence of bryophyte diaspores in the plumage
606 of transequatorial migrant birds. *PeerJ* 2, e424.

- 607 31. Nogales, M., *et al.* (2012) Evidence for overlooked mechanisms of long-distance
608 seed dispersal to and between oceanic islands. *New Phytol.* 194, 313-317.
- 609 32. Fridriksson, S. (1975) *Surtsey: evolution of life on a volcanic island*.
610 Butterworths.
- 611 33. Bucher, E.H. and Bocco, P.J. (2009) Reassessing the importance of granivorous
612 pigeons as massive, long-distance seed dispersers. *Ecology* 90, 2321-2327.
- 613 34. Holland, R.A., *et al.* (2009) The secret life of oilbirds: new insights into the
614 movement ecology of a unique avian frugivore. *PLoS ONE* 4, e8264.
- 615 35. Mokotjomela, T.M., *et al.* (2013) Potential seed dispersal distances of native and
616 non-native fleshy fruiting shrubs in the South African Mediterranean climate
617 region. *Plant Ecol.* 214, 1127-1137.
- 618 36. Raulings, E., *et al.* (2011) Do birds of a feather disperse plants together?
619 *Freshwat. Biol.* 56, 1390-1402.
- 620 37. Lebarbenchon, C., *et al.* (2009) Spread of avian Influenza viruses by common
621 teal (*Anas crecca*) in Europe. *PLoS ONE* 4, e7289.
- 622 38. Nathan, R., *et al.* (2008) A movement ecology paradigm for unifying organismal
623 movement research. *Proc. Natl. Acad. Sci. USA* 105, 19052-19059.
- 624 39. Burns, K.C. (2002) Seed dispersal facilitation and geographic consistency in
625 bird–fruit abundance patterns. *Global Ecol. Biogeogr.* 11, 253-259.
- 626 40. Figuerola, J., *et al.* (2003) Passive internal transport of aquatic organisms by
627 waterfowl in Doñana, south-west Spain. *Global Ecol. Biogeogr.* 12, 427-436.
- 628 41. Wright, S.J., *et al.* (2008) Understanding strategies for seed dispersal by wind
629 under contrasting atmospheric conditions. *Proc. Natl. Acad. Sci. USA* 105,
630 19084-19089.

- 631 42. Alerstam, T. (2011) Optimal bird migration revisited. *Journal of Ornithology*
632 152, 5-23.
- 633 43. Hedenström, A. (2008) Adaptations to migration in birds: behavioural strategies,
634 morphology and scaling effects. *Phil. Trans. R. Soc. B* 363, 287-299.
- 635 44. Viana, D.S., *et al.* (2013) Migratory strategies of waterbirds shape the
636 continental-scale dispersal of aquatic organisms. *Ecography* 36, 430-438.
- 637 45. Soons, M.B., *et al.* (2008) Small seed size increases the potential for dispersal of
638 wetland plants by ducks. *J. Ecol.* 96, 619-627.
- 639 46. Sorensen, A.E. (1986) Seed dispersal by adhesion. *Annu. Rev. Ecol. Syst.* 17,
640 443-463.
- 641 47. McCabe, J.D. and Olsen, B.J. (2015) Landscape-scale habitat availability, and
642 not local geography, predicts migratory landbird stopover across the Gulf of
643 Maine. *J. Avian Biol.* 46, 395-405.
- 644 48. Shamoun-Baranes, J., *et al.* (2010) Stochastic atmospheric assistance and the use
645 of emergency staging sites by migrants. *Proc. R. Soc. B* 277, 1505-1511.
- 646 49. Caughlin, T.T., *et al.* (2014) The importance of long-distance seed dispersal for
647 the demography and distribution of a canopy tree species. *Ecology* 95, 952-962.
- 648 50. Schupp, E.W., *et al.* (2010) Seed dispersal effectiveness revisited: a conceptual
649 review. *New Phytol.* 188, 333-353.
- 650 51. Van Leeuwen, C.H.A., *et al.* (2012) Gut travellers: internal dispersal of aquatic
651 organisms by waterfowl. *J. Biogeogr.* 39, 2031-2040.
- 652 52. Costa, J.M., *et al.* (2014) Endozoochory largely outweighs epizoochory in
653 migrating passerines. *J. Avian Biol.* 45, 59-64.
- 654 53. Herrera, C.M. (1984) A study of avian frugivores, bird-dispersed plants, and
655 their interaction in Mediterranean scrublands. *Ecol. Monogr.* 54, 1-23.

- 656 54. Traveset, A. (1998) Effect of seed passage through vertebrate frugivores' guts on
657 germination: a review. *Perspect. Plant Ecol. Evol. Syst.* 1, 151-190.
- 658 55. Nee, S., *et al.* (1991) The relationship between abundance and body size in
659 British birds. *Nature* 351, 312-313.
- 660 56. Santamaría, L. (2002) Why are most aquatic plants widely distributed?
661 Dispersal, clonal growth and small-scale heterogeneity in a stressful
662 environment. *Acta Oecol.* 23, 137-154.
- 663 57. De Meester, L., *et al.* (2002) The Monopolization Hypothesis and the dispersal-
664 gene flow paradox in aquatic organisms. *Acta Oecol.* 23, 121-135.
- 665 58. Carlo, T.A. and Tewksbury, J.J. (2014) Directness and tempo of avian seed
666 dispersal increases emergence of wild chiltepins in desert grasslands. *J. Ecol.*
667 102, 248-255.
- 668 59. Amezcaga, J.M., *et al.* (2002) Biotic wetland connectivity—supporting a new
669 approach for wetland policy. *Acta Oecol.* 23, 213-222.
- 670 60. Levey, D.J., *et al.* (2008) Modelling long-distance seed dispersal in
671 heterogeneous landscapes. *J. Ecol.* 96, 599-608.
- 672 61. Yu, S., *et al.* (2014) Species diversity and distribution of *Ruppia* in China:
673 Potential roles of long-distance dispersal and environmental factors. *J. Syst.*
674 *Evol.* 52, 231-239.
- 675 62. Heleno, R. and Vargas, P. (2015) How do islands become green? *Global Ecol.*
676 *Biogeogr.* 24, 518-526.
- 677 63. Green, A.J. (2015) The importance of waterbirds as an overlooked pathway of
678 invasion for alien species. *Divers. Distrib.* 22, 239–247.
- 679 64. Trakhtenbrot, A., *et al.* (2005) The importance of long-distance dispersal in
680 biodiversity conservation. *Divers. Distrib.* 11, 173-181.

- 681 65. Corlett, R.T. and Westcott, D.A. (2013) Will plant movements keep up with
682 climate change? *Trends Ecol. Evol.* 28, 482-488.
- 683 66. Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science*
684 348, 571-573.
- 685 67. Bocedi, G., *et al.* (2014) RangeShifter: a platform for modelling spatial eco-
686 evolutionary dynamics and species' responses to environmental changes.
687 *Methods Ecol. Evol.* 5, 388-396.
- 688 68. Cunze, S., *et al.* (2013) Are plant species able to keep pace with the rapidly
689 changing climate? *PLoS ONE* 8, e67909.
- 690 69. Wang, B.C. and Smith, T.B. (2002) Closing the seed dispersal loop. *Trends*
691 *Ecol. Evol.* 17, 379-386.
- 692 70. Hampe, A., *et al.* (2003) Rangewide phylogeography of a bird-dispersed
693 Eurasian shrub: contrasting Mediterranean and temperate glacial refugia. *Mol.*
694 *Ecol.* 12, 3415-3426.
- 695 71. King, R.A., *et al.* (2002) Population differentiation of *Potamogeton pectinatus*
696 in the Baltic Sea with reference to waterfowl dispersal. *Mol. Ecol.* 11, 1947-
697 1956.
- 698 72. Brochet, A.-L., *et al.* (2009) The role of migratory ducks in the long-distance
699 dispersal of native plants and the spread of exotic plants in Europe. *Ecography*
700 32, 919-928.
- 701 73. Jönsson, K.A., *et al.* (2016) Tracking animal dispersal: from individual
702 movement to community assembly and global range dynamics. *Trends Ecol.*
703 *Evol.* 31, 204-214.
- 704 74. Del Rio, C.M., *et al.* (1996) Seed dispersers as disease vectors: bird transmission
705 of mistletoe seeds to plant hosts. *Ecology*, 912-921.

- 706 75. Malloch, D. and Blackwell, M. (1992) Dispersal of fungal diaspores. In *The*
707 *fungal community: its organization and role in the ecosystem* (Dighton, J., *et al.*,
708 eds), pp. 147-171, Marcel Dekker Inc.
- 709 76. Tomback, D.F. and Linhart, Y.B. (1990) The evolution of bird-dispersed pines.
710 *Evol. Ecol.* 4, 185-219.
- 711 77. Wada, S., *et al.* (2012) Snails can survive passage through a bird's digestive
712 system. *J. Biogeogr.* 39, 69-73.
- 713 78. van Leeuwen, C.H.A., *et al.* (2012) Experimental quantification of long distance
714 dispersal potential of aquatic snails in the gut of migratory birds. *PLoS ONE* 7,
715 e32292.
- 716 79. Frisch, D., *et al.* (2007) High dispersal capacity of a broad spectrum of aquatic
717 invertebrates via waterbirds. *Aquat. Sci.* 69, 568-574.
- 718 80. Gill, R.E., *et al.* (2009) Extreme endurance flights by landbirds crossing the
719 Pacific Ocean: ecological corridor rather than barrier? *Proc. R. Soc. B* 276, 447-
720 457.
- 721 81. Kays, R., *et al.* (2015) Terrestrial animal tracking as an eye on life and planet.
722 *Science* 348, aaa2478.
- 723 82. Guttal, V., *et al.* (2011) Retention time variability as a mechanism for animal
724 mediated long-distance dispersal. *PLoS ONE* 6, e28447.
- 725 83. Charalambidou, I., *et al.* (2005) Digestive plasticity in mallard ducks modulates
726 dispersal probabilities of aquatic plants and crustaceans. *Funct. Ecol.* 19, 513-
727 519.
- 728 84. Charalambidou, I., *et al.* (2003) Effect of ingestion by five avian dispersers on
729 the retention time, retrieval and germination of *Ruppia maritima* seeds. *Funct.*
730 *Ecol.* 17, 747-753.

- 731 85. Karasov, W.H. (1990) Digestion in birds: chemical and physiological
732 determinants and ecological implications. *Stud. Avian Biol.* 13, 391-415.
- 733 86. Yumoto, T. (1999) Seed dispersal by Salvin's curassow, *Mitu salvini* (Cracidae),
734 in a tropical forest of Colombia: direct measurements of dispersal distance.
735 *Biotropica* 31, 654-660.
- 736 87. Komar, N., *et al.* (2003) Experimental infection of North American birds with
737 the New York 1999 strain of West Nile virus. *Emerging Infect. Dis.* 9, 311-322.
- 738 88. Latorre-Margalef, N., *et al.* (2009) Effects of Influenza A virus infection on
739 migrating mallard ducks. *Proc. R. Soc. B* 276, 1029-1036.
- 740 89. Kleyheeg, E., *et al.* (2015) Bird-mediated seed dispersal: reduced digestive
741 efficiency in active birds modulates the dispersal capacity of plant seeds. *Oikos*
742 124, 899-907.
- 743 90. Piersma, T. and Gill, R.E., Jr. (1998) Guts don't fly: small digestive organs in
744 obese bar-tailed godwits. *Auk* 115, 196-203.
- 745 91. Van Gils, J.A., *et al.* (2007) Hampered foraging and migratory performance in
746 swans infected with low-pathogenic avian Influenza A virus. *PLoS ONE* 2,
747 e184.
- 748 92. Owen, J., *et al.* (2006) Migrating birds as dispersal vehicles for West Nile virus.
749 *EcoHealth* 3, 79-85.
- 750 93. West, G.B., *et al.* (1997) A general model for the origin of allometric scaling
751 laws in biology. *Science* 276, 122-126.
- 752 94. Schurr, F.M., *et al.* (2009) Long-Distance Seed Dispersal. In *Annual plant*
753 *reviews: fruit development and seed dispersal*, pp. 204-237, Wiley-Blackwell.
- 754 95. Hedenström, A. (2010) Extreme endurance migration: what is the limit to non-
755 stop flight? *PLoS Biol.* 8, e1000362.

- 756 96. McWilliams, S.R., *et al.* (2004) Flying, fasting, and feeding in birds during
757 migration: a nutritional and physiological ecology perspective. *J. Avian Biol.* 35,
758 377-393.
- 759 97. Hijmans, R.J., *et al.* (2005) Very high resolution interpolated climate surfaces
760 for global land areas. *Int. J. Climatol.* 25, 1965-1978.
- 761 98. Hall-Karlsson, K.S.S. and Fransson, T. (2008) How far do birds fly during one
762 migratory flight stage? *Ringing Migr.* 24, 95-100.
- 763 99. Hedenström, A. and Ålerstam, T. (1992) Climbing performance of migrating
764 birds as a basis for estimating limits for fuel-carrying capacity and muscle work.
765 *J. Exp. Biol.* 164, 19-38.
- 766 100. Jenni, L. and Jenni-Eiermann, S. (1998) Fuel supply and metabolic constraints
767 in migrating birds. *J. Avian Biol.* 29, 521-528.
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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 °C 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

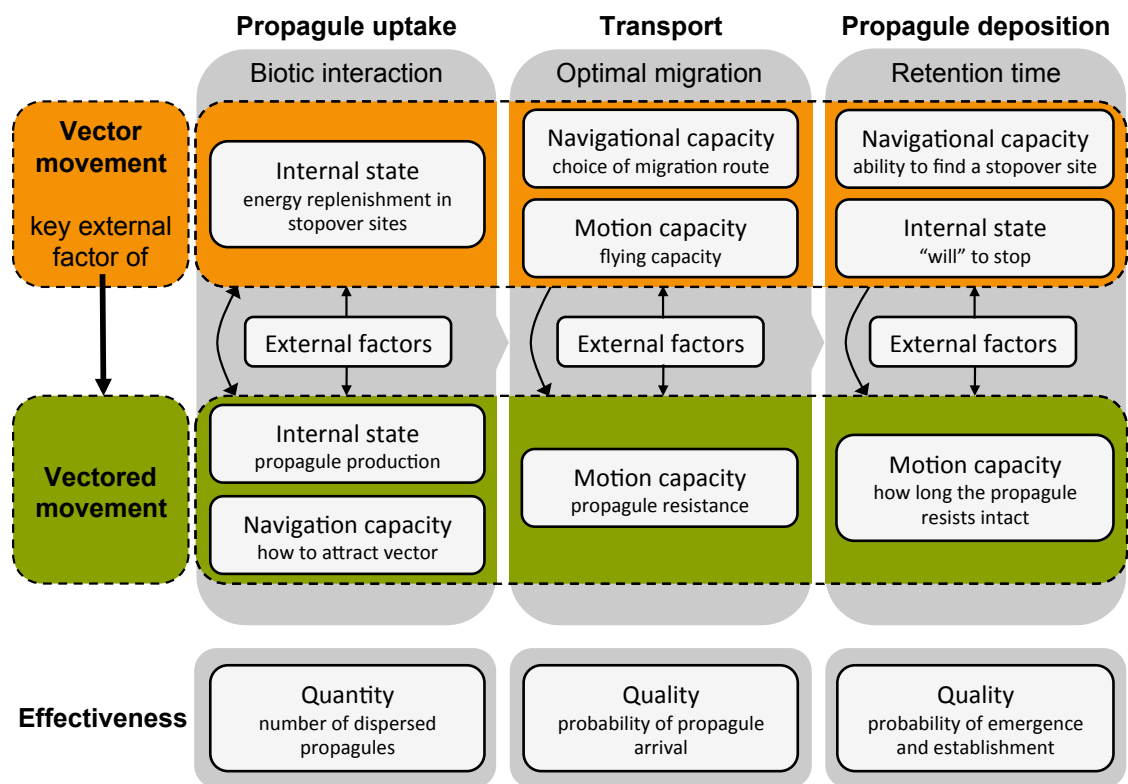
diaspores dispersed by transequatorial migrant shorebirds over distances up to 15,000 km [30]. Solid and dashed arrows correspond to examples of dispersal events either directly observed or supported by compelling evidence, respectively.

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 ($h_{\max} = 1.42 \text{ mass}^{-0.0554}$; [99]). Maximum fuel loads (f_{\max}) were estimated as $h_{\max}-1$, 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]).

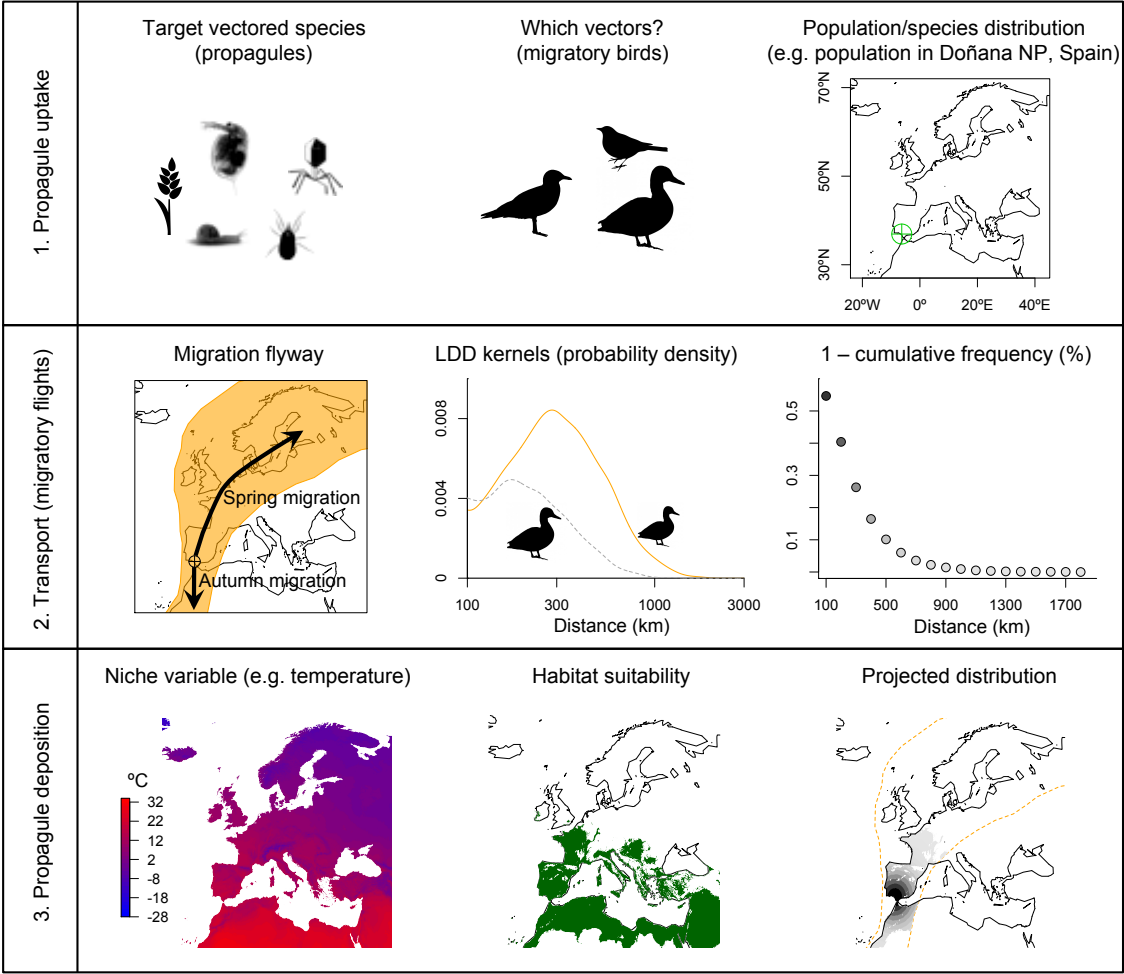
818 Figure 1



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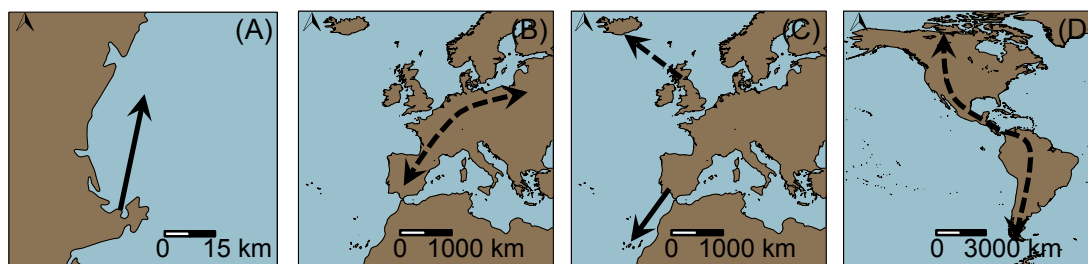
820 Figure 2



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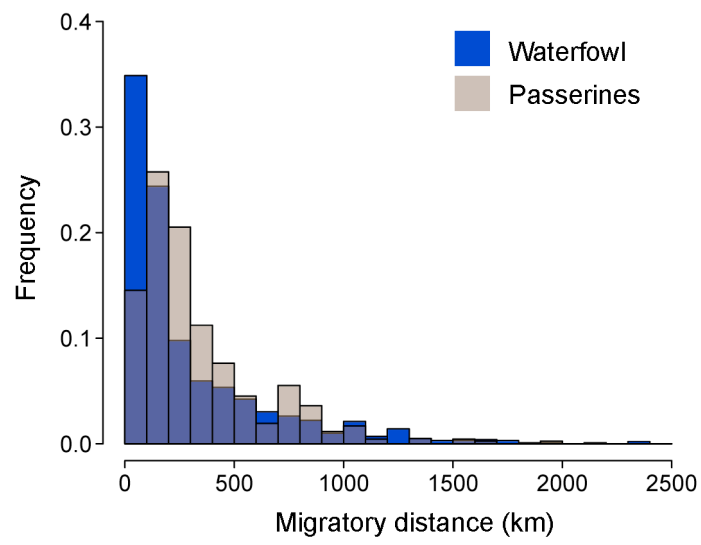
822 Figure I - Box 1



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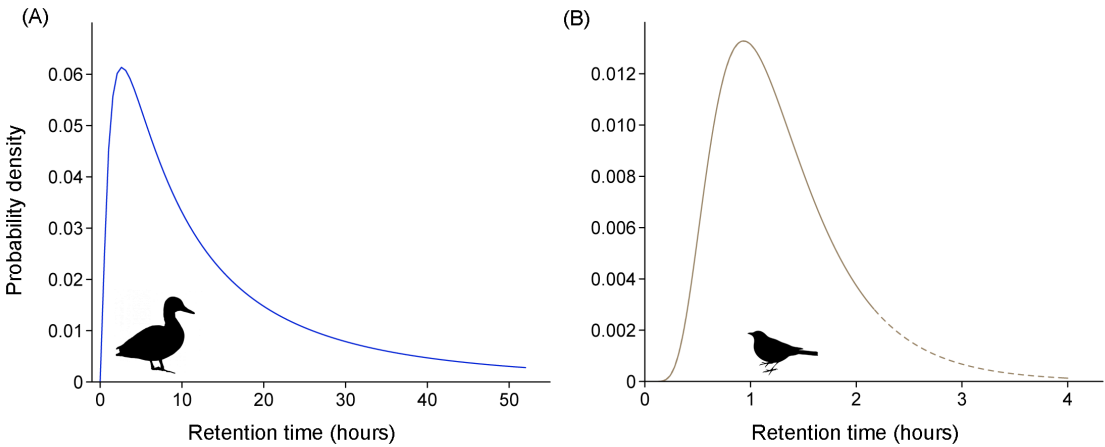
824 Figure I - Box 2



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826 Figure I - Box 3



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