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EDITORIAL

Long-distance dispersal research: building a network of yellow brick roads

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ABSTRACT

This special issue of *Diversity and Distributions* presents six papers that contribute to the assembly of a general research agenda for studying long-distance dispersal (LDD) across a variety of taxonomic groups (e.g. birds, fish, aquatic invertebrates and plants), ecosystems (e.g. terrestrial and marine ecosystems, wetlands and grasslands) and thematic fields (e.g. biological transport, marine biology, biogeochemistry and biodiversity conservation). This editorial emphasizes the need to develop a network integrating different research approaches ('yellow brick roads') to address the great challenge ('finding the end of the rainbow') of quantifying, understanding and predicting LDD and its implications. I review the key avenues for future research suggested in the special issue contributions, and stress the critical importance of properly considering the spatial and temporal scales relevant to the process and system of interests. I propose combining absolute and proportional definitions of LDD as a default practice in any investigation of LDD processes. When LDD is defined primarily by an absolute critical distance that characterizes key feature(s) of the system of interest, a quantitative assessment of the proportion of dispersal events expected to move beyond this critical threshold distance should also be provided. When LDD is defined primarily by a certain small fraction of dispersal events that travel longer than all others, an estimate of the absolute distance associated with this high percentile at the tail of the dispersal curve should also be added.

Keywords

Biodiversity conservation, biological invasions, biological transport, complexity, interdisciplinary research, large-scale movements, long-distance dispersal, scale effects, spatial ecology, spatial spread.

FINDING YOUR WAY(S) IN THE (RE-DISCOVERED) LAND OF OZ

Interest in dispersal has risen rapidly over the last 15 years (Nathan, 2003) with a recent disproportionate increase in interest particularly in long-distance dispersal (LDD) (Fig. 1). In fact, the existence of these typically rare events of long movements, and their disproportionate importance to populations, species and communities, has long been recognized by the likes of Darwin (1859) and Wallace (1876). Nevertheless, interest in LDD lay dormant over most of the previous century, especially between the 1960s and 1980s, when LDD was considered unquantifiable, unpredictable and unimportant (see Nathan, 2001 for review). An important positive outcome of this period for dispersal research was a clear recognition of the evolutionary and ecological significance of the vast majority of dispersal events of individuals travelling fairly short distances (e.g. Janzen, 1970; Hamilton & May, 1977; Lidicker & Caldwell, 1982).

Early in this recent LDD renaissance, British plant ecologist Jonathan Silvertown published a short discussion-type article with the captivating title: 'Dorothy's dilemma and the unification of plant population biology' (Silvertown, 1991). Dorothy's dilemma, '*to find a way to the end of the rainbow*', was solved by travelling along the yellow brick road. Silvertown used this metaphor to encourage plant ecologists to look beyond their '*limited vision, bounded by the population edge*', to '*find the all-important tails of the seed dispersal curve*'. He emphasized one such yellow brick road for studying LDD: ecologists should look at larger scales than they normally do, and should employ genetic tools to quantify LDD through estimates of gene flow rates and genetic structure differentiation. The potential of this specific methodological approach for studying LDD has been emphasized recently (Ouborg *et al.*, 1999; Cain *et al.*, 2000; Godoy & Jordano, 2001; Spong & Creel, 2001; Nathan *et al.*, 2003; Telfer *et al.*, 2003; He *et al.*, 2004). While acknowledging the great potential of genetic tools for studying LDD, the goal of this special issue is to explore

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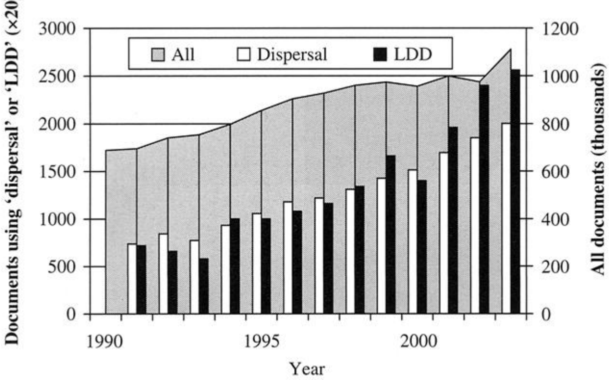

Figure 1 A rapid recent increase in the relative frequency of publications using the word 'dispersal' (open columns) and especially the phrase 'long-distance dispersal' (LDD, filled columns) in their title, keywords or abstract, compared to the smaller increase in the total number of publications (grey columns) included in the Science Citation Index (ISI Web of knowledge), over the years 1991–2003. Search for LDD was ('long-distance' or 'long-range') and 'dispersal'. The number of publications using LDD is multiplied by a factor of 20 to match the number of publications using dispersal. Most publications use dispersal in the ecological sense (see Nathan, 2003).

new avenues for studying LDD and to advance integration among alternative methods, chiefly by means of interdisciplinary research. LDD processes are typical examples of complex biological systems, for which single approach solutions are probably not appropriate or realistic. Therefore, using Silvertown's metaphor, this special issue advocates the establishment of a network of yellow brick roads for addressing the high complexity and uncertainty associated with LDD.

In this editorial, I attempt to synthesize some of the major topics highlighted in the six contributions from this special issue. First, I summarize the major avenues for future research and emphasize possible links among the different approaches. Then, I discuss two fundamental problems, the sensitivity of LDD to scale and the definition of LDD, in relation to the diverse opinions presented in this special issue.

A NETWORK OF YELLOW BRICK ROADS

The six contributions from this special issue cover a broad spectrum of organisms, ecosystems and thematic fields, embracing a variety of spatial scales and methodological approaches (Table 1). All contributions strongly recommend a shift from the rather narrative and qualitative analyses, which are being employed by most researchers today, to more concrete and quantitative examinations of LDD; as well as acknowledging the overwhelming challenge involved with such a demanding shift. To facilitate the journey to 'the end of the rainbow', this special issue highlights some yellow brick roads that provide new insights and better understanding of LDD patterns, processes and implications.

Nathan *et al.* (2005) advocate the development of a new methodological approach for studying multi-scale effects of atmosphere dynamics on aerial transport processes. This mechanistic approach combines detailed atmospheric models with high-resolution data on the relatively long movements of airborne organisms. Soons & Ozinga (2005) used a mechanistic wind dispersal model to evaluate LDD ability of wind-dispersed grassland plants. This model incorporates the effects of small-scale turbulent eddy motion, which can drastically affect LDD of small airborne organisms (Nathan *et al.*, 2002; Soons *et al.*, 2004), but does not deal with the effects of large-scale atmospheric processes, nor does incorporate effects of structural heterogeneity in the landscape. The atmospheric models recommended by Nathan *et al.* (2005) can incorporate atmospheric processes operating on a broad range of scales as well as virtually any type of landscape heterogeneity. While admitting the immense challenge

Table 1 Summary of the key features of the contributions in this special issue

Contribution	Organisms	LDD definition*	Spatial scale of LDD $\log_{10}$(meters)	Suggested yellow brick road
Nathan *et al.*	Airborne biota	Both	2–6	Developing mechanistic models of biological transport based on multiscale atmospheric models
Kinlan *et al.*	Marine biota	Both	2–6	Distinguishing between dispersal beyond the local population and extreme LDD and their relative importance for different ecological processes
Green and Figuerola	Bird-dispersed aquatic invertebrates	Absolute distance	4–6	Recognizing the importance of a specific LDD mechanism, and how it could be quantified
Hobson	Mostly birds	Absolute distance	5–6	Using stable isotopes to quantify LDD over large scales
Soons and Ozinga	Wind-dispersed plants	Proportional distance	−2–3	Integrating mechanistic models and regional monitoring data to evaluate the role of LDD in species regional survival
Trakhtenbrot *et al.*	All	Both	2–5 (6–7 human-mediated LDD)	Identifying tools for incorporating LDD in biodiversity conservation

*Two general types of LDD definitions: absolute distance and proportional distance (see text).

involved with developing such an interdisciplinary modelling framework, Nathan *et al.* (2005) illustrate why this approach could be highly rewarding for quantifying, predicting and understanding aerial LDD processes.

Kinlan *et al.* (2005) laid out an innovative framework for examining the role of LDD in marine systems. They call for reconsidering the LDD definition and placing it in the context of some old chestnuts of marine ecology, including the relative openness of marine demography. They outlined an ambitious agenda that should provoke new ideas among scholars of LDD in the terrestrial ecosystem as well. Because data and tools for implementing the framework suggested by Kinlan *et al.* (2005) are still lacking, they illustrate the potential of their approach with some preliminary analysis of data and theory that give insight into marine LDD. They also emphasize the need to refine marine transport models by incorporating realistic modelling of turbulent mixing processes, which may be as influential in the hydrosphere (Cowen, 2002) as they are in the atmosphere (Nathan *et al.*, 2005). A major challenge will be to integrate realistic hydrodynamic models with the complex behaviours (swimming, vertical shifts) exhibited by many marine species during the dispersal phase (Cowen *et al.*, 2003).

Darwin (1859) devoted two chapters (XII and XIII) of his *The Origin of Species* to discuss a variety of LDD mechanisms and their implications for species geographical distribution. One of the LDD mechanisms he discussed, the passive transport of aquatic plants and invertebrates by migrating waterbirds, has been virtually neglected ever since. Green & Figuerola (2005) argue that waterbirds transport, either internally or externally, enormous numbers of invertebrate propagules over distances of up to thousands of kilometres. They suggest specific hypotheses about the relationship between the main migratory flyways and abundance, distribution, and genetic and species diversity of aquatic invertebrates. They also outlined some directions for investigating these hypotheses, including large-scale comparisons of species composition, small-scale field studies on bird feeding strategies, gut retention times, propagule survival and movements, and tests of genetic differentiation between wetlands on and off migratory flyways. Genetic tools hold great promise for LDD research and their integration with other methods has also been suggested by Hobson (2005) and Kinlan *et al.* (2005).

Motivated by recent advances in applying stable isotope techniques to study migratory connectivity (mostly of birds), Hobson (2005) proposed possible ways this technique may be applied to the study of LDD. He particularly emphasized the promise of this technique in identifying new immigrants, presumably arriving through LDD, by detecting isotopic outliers within an isotopically known population. Hobson suggested that the combination of this technique with other methods is the key to improve the rather coarse resolution currently available by stable isotopes (as mentioned below). Artificial isotopic enrichment, one of the techniques highlighted by Hobson (2005), could be particularly useful for marking aquatic invertebrates studied by Green & Figuerola (2005). Natural and artificial chemical tags are also an emerging tool in marine LDD research (Kinlan *et al.*, 2005), which opens another possibility for cross-system synergy in approaches.

Soons & Ozinga (2005) presented a broad comparative study combining three independent data sets, two using long-term and large-scale surveys to estimate regional survival of a large number of wind-dispersed grassland plant species, and the third, using a mechanistic model to estimate their LDD ability. They found that LDD explains a greater proportion of the variance in regional plant survival than short-distance dispersal, and has a roughly equivalent effect to that of seed longevity. However, they also found that in time periods of increasing nutrient availabilities, such as the second half of the 20th century in the Netherlands, LDD was much less important for regional plant survival than plant nutrient requirement. While this special issue generally emphasizes the importance of LDD, an important take-home message from this study is the need to put LDD in the right perspective, and recognize circumstances where postdispersal processes are of overriding importance.

LDD plays a key role in determining a variety of ecological processes and therefore, should often be considered in a conservation context. In reality, this is very rarely done, mainly because of the great difficulty and high uncertainty inherent in estimating LDD rates. The importance of considering LDD in conservation plans for the design of marine reserves and sustainable harvest of exploited fish species (Kinlan *et al.*, 2005), and the control of invasive exotic species (Green & Figuerola, 2005) and regional survival of plants (Soons & Ozinga, 2005) are emphasized in this special issue. Trakhtenbrot *et al.* (2005) reviewed the topic and clarified the relative importance of LDD for major conservation issues. They discussed the pros and cons of qualitative and quantitative tools and explore how information on LDD can help guide management decisions. They distinguished among cases of *excessive LDD*, in which high LDD levels of alien invasive species and genetically modified organisms threaten the survival of native species, and cases of *insufficient LDD*, where low LDD levels threaten the survival of indigenous species inhabiting fragmented landscapes or undergoing range shifts in response to changing environmental conditions. An important challenge in the establishment of a network of yellow brick roads for studying LDD is implementing tools to assess LDD, including human-mediated events, as standard practice in conservation practices.

THE CRITICAL IMPORTANCE OF SCALE

One of the main insights gained from ecological research over the last two decades has been broad recognition of the importance of considering the spatial and temporal scales of ecological and evolutionary processes (Levin, 1992; Tilman & Kareiva, 1997; Silvertown & Antonovics, 2001; Chave & Levin, 2003). Dispersal in general and LDD in particular are among the most fundamental processes responsible for sensitivity to scale; hence, LDD constitutes a major impetus for growing recognition of the importance of scale-dependent processes. It is therefore not surprising that all the contributions from this issue — working on different processes operating over a variety of spatial scales (Table 1) — strongly emphasize the need to properly consider scale effects. All together, they highlight different 'scale problems' associated with LDD.

Nathan *et al.* (2005) emphasized the importance of short-term and small-scale events for long-term large-scale aerial biological transport processes. A diverse set of organisms, ranging from tiny spores, seeds and insects to the much larger birds, utilize the atmosphere for passive or active journeys of various lengths and durations. While it is commonly recognized that such aerial transport processes are strongly affected by long-term (> days) and large-scale (> tens of kilometres) variation in atmospheric conditions, the role of atmospheric processes operating at much shorter (< minutes) and smaller (< hundreds of meters) scales has traditionally been neglected. Yet, some small-scale airflow characteristics such as turbulent gusts and coherent eddy motion can largely determine the onset and fate of aerial journeys.

Kinlan *et al.* (2005) demonstrated the substantial variation in the typical scale of marine species dispersal, ranging over five orders of magnitude even when the comparison is restricted to organisms with sedentary adults. They show a considerable discrepancy between estimates of average dispersal distance and estimates of rate of spread across several taxonomic groups. This suggests that information on the mean properties of the dispersal process may not be very informative about extreme events that are important for large-scale colonization. Higgins *et al.* (2003) reached a similar conclusion for terrestrial plants, demonstrating substantial disparity between the mechanisms inferred from seed morphology, which mediate the short-distance dispersal of most seeds, and the 'nonstandard' mechanisms that actually drive LDD. Kinlan *et al.* (2005) further analysed the general positive relationship between the scale of the 'local' population of sedentary adults and the level of propagule retention. In conclusion, they argue that any evaluation of the role of LDD in marine systems, as well as any examination of common concepts such as 'self-recruitment' and 'openness', must be explicitly linked to the scale of the process and the organization unit (population/species/community) of interest.

Green & Figuerola (2005) emphasized the role of spatial scale in LDD of aquatic invertebrates in relation to the major flyways of migratory waterbirds. They argue that invertebrate community structure should vary among wetlands not only because of local interactions such as competition and predation (Shurin, 2000), but also as a result of waterbird migratory movements. The spatial scales of LDD as defined by Green & Figuerola (2005) are relatively large (Table 1), because waterbirds can transport invertebrate propagules over very long distances during their migratory flights. Hobson (2005) defines equal or even larger scales (Table 1). Detection of LDD events by stable isotope markers depends first and foremost on the scale of the isotopic landscape, which is currently rather coarse (Hobson, 2005). Studies using deuterium isotope markers in feathers can distinguish the source location at a resolution of approximately 300 m in altitude and 1.5 degrees (~170 km) in latitude (estimated for North America). This coarse resolution renders the stable isotope technique inefficient for most LDD events in most species; yet it offers a unique opportunity to detect extreme LDD events. This opportunity is particularly attractive because organisms are 'self-marked' as they feed and therefore, the highly demanding mass marking of capture-recapture applications is not necessary.

Finally, scale effects are tremendously important for considering LDD in management decisions (Trakhtenbrot *et al.*, 2005). Assessment of conservation practices must consider the huge interspecific variation in LDD; the five orders of magnitude difference reported by Kinlan *et al.* (2005) is not unique to marine systems, wherein the difference of six orders of magnitude in LDD ability was estimated by Soons & Ozinga (2005) for 190 wind-dispersed plant species of north-west European grasslands (Table 1). In fact, the concepts of excessive and insufficient LDD of Trakhtenbrot *et al.* (2005) are inherently scale-dependent, and therefore any implementation of LDD in conservation efforts should entail sensitivity analysis of the scales over which LDD is estimated. Overall, the need to explicitly incorporate LDD in conservation decisions further emphasizes the need to develop a multiscale view in evaluating conservation strategies (Doak *et al.*, 1992; Schwartz, 1999; Levin, 2000; Hartley & Kunin, 2003).

LDD DEFINITION

Among the multiple methodological challenges involved in studying LDD (Nathan *et al.*, 2003), the question of definition is of primary importance. Although each of the six contributions from this special issue addressed this challenging question in a different (case- and context-specific) way (Table 1), two general types of definitions can be distinguished. First, the *absolute distance* definition, assigns LDD events as dispersal beyond a certain threshold distance, whereas the second, the *proportional distance* definition, assigns LDD events as those reaching distances that are longer than those reached by most other dispersing individuals.

The exact threshold values selected for the absolute distance LDD definition are typically arbitrary, but their order of magnitude should reasonably reflect the scale of the process in question. In some cases, the LDD scales (or the screening capacity of the applied technique) are only partially known, imposing a rather coarse definition; for example, Hobson (2005) defines LDD at regional (hundreds of kilometres) to continental (thousands of kilometres) scales, over which long-distance movements of highly mobile organisms such as birds might be detected by stable isotopes. A more specific definition is given by Green & Figuerola (2005), who define bird-mediated LDD of aquatic invertebrates using a threshold distance of 10 km between wetlands that are not connected hydrologically. One of the two definitions proposed by Kinlan *et al.* (2005) (their case-I LDD) refers to the boundary of the area over which adults of the local population interact and reproduce. This type of LDD definition is more commonly applied in the literature; nevertheless, Kinlan *et al.* (2005) warn that identification of the distance that best characterizes the 'local' scale is not necessarily as trivial as it is often considered. Other natural sources of an absolute distance scale may include the average size of discrete habitat patches, or the length scale of variation in local demographic processes (growth, mortality, and/or fecundity).

Studies using the proportional distance LDD definition select an arbitrary high percentile of the dispersal distances distribution to distinguish LDD. Soons & Ozinga (2005), for example, designated the 99th percentile of the simulated dispersal kernels of wind-dispersed seeds as a measure of LDD ability, whereas Kinlan *et al.* (2005) (their case-II LDD) use extreme-value distributions to estimate the farthest distance travelled by an individual in a discrete period of time. In practice, this type of LDD definition is not broadly applicable, mostly because it requires the distribution of dispersal distances to be known or to be amenable to reliable estimation. For instance, Green & Figuerola (2005) noted that the paucity of data on bird-mediated dispersal distance distributions of aquatic invertebrates precludes a proportional definition of LDD in this system. However, the combination of process-based models that motivate the form of a dispersal kernel (e.g. Kinlan *et al.*, 2005; Nathan *et al.*, 2005) with improved LDD data may lead to increasing applicability of this measure.

These two types of LDD definitions can be interpreted as mutually exclusive if taken to their extremes. On one hand, the absolute distance can be defined independently of the dispersal characteristics of the species or population in question. Kinlan *et al.* (2005), for example, offer as one definition of a threshold for their case-I LDD the boundaries of the area where (non-dispersing) adults interact and breed, irrespective of the area where (dispersing) larvae may occur. On the other hand, the proportional distance can be defined while completely ignoring any characteristic of the system that is not related to dispersal. For example, the 99th percentile threshold used by Soons & Ozinga (2005) to assess LDD ability depends exclusively on dispersal-related characteristics, regardless of the patchiness of the landscape. Trakhtenbrot *et al.* (2005) argued that the proportional distance definition should be preferred in conservation contexts in problems of excessive LDD (e.g. if the main concern is the estimate of LDD ability in nonindigenous elements). If the main concern is to alert for cases in which LDD might be insufficient to place individuals beyond a certain distance, such as the typical interpatch distance in fragmented landscape, the absolute distance definition should be the primary first choice.

Determining two mutually exclusive definitions of LDD can therefore be valuable for some theoretical and practical purposes. Nevertheless, the use of one type of LDD definition while completely ignoring the other might be confusing and even misleading. Nathan *et al.* (2003; p. 263) gave an example of a proportional LDD definition (99th percentile) estimated from simulations of wind-dispersed seeds in a dense forest vs. open landscape, resulting in an LDD threshold of three vs. 200 meters, respectively. While the latter value may correspond to interpatch distance in moderately fragmented forested landscapes, the former is evidently an inappropriate measure, as LDD events would fall within the crown projection of the source tree. Kinlan *et al.* (2005) raised similar concerns, emphasizing that the distinction they made between their case-I and case-II LDD in marine systems is based on the substantial difference between the typical scale of movements of sedentary adults (used to define case-I LDD) and larvae (case-II). If the difference between the movement scales of dispersing vs. reproductive (nondispersing) individuals is much less pronounced, as is the case for certain marine species either lacking larvae or with highly mobile adults, and perhaps for many terrestrial species, these two definitions are expected to collapse into a one operative criterion.

The overall conclusion emerging from this discussion is that the two types of LDD definitions should be considered as complementary rather than competing alternatives. I propose combining absolute and proportional definitions as a default practice in any investigation of LDD processes. This will provide adequate information for any specific case under study and would help avoid inappropriate or ambiguous definitions. If the absolute distance definition is the logical first choice, (e.g. when one wishes to assess interpatch connectivity in a fragmented landscape), information on the proportion of individuals that travel equal or longer distances than the specified threshold should be added. For instance, LDD could be defined as '1000 m (0.1%)', where 0.1% indicates the 99.9th percentile at the tail of the dispersal curve. If the proportional distance definition is the first logical choice, (e.g. when we wish to compare LDD ability of invasive species), information on the absolute distance associated with this high percentile should be added. For instance, LDD could be defined as '0.1% (1000 m)'. Determining an absolute distance LDD definition is considered less difficult than determining a proportional distance definition. Nevertheless, any attempt to resolve these specific problems of definition, and to address other challenges involved with collecting, analysing and interpreting LDD data, is best undertaken by more than one approach. Assembling an interdisciplinary network of yellow brick roads is probably the only way to address the difficulties associated with LDD research.

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