

The importance of long-distance dispersal in biodiversity conservation

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ABSTRACT

Dispersal is universally considered important for biodiversity conservation. However, the significance of long- as opposed to short-distance dispersal is insufficiently recognized in the conservation context. Long-distance dispersal (LDD) events, although typically rare, are crucial to population spread and to maintenance of genetic connectivity. The main threats to global biodiversity involve excessive LDD of elements alien to ecosystems and insufficient dispersal of native species, for example, because of habitat fragmentation. In this paper, we attempt to bridge the gap in the treatment of LDD by reviewing the conservation issues for which LDD is most important. We then demonstrate how taking LDD into consideration can improve conservation management decisions.

Keywords

Biodiversity conservation, biological invasions, climate change, connectivity, invasive species, long-distance dispersal, management, mechanistic models, reintroduction.

INTRODUCTION

Global biodiversity is threatened by several human-induced processes. The most severe current threats are land use change and invasive species. Climate change is already affecting species distributions and its future impacts are predicted to be extensive (Sala et al., 2000). An additional threat that has emerged recently is the escape of genetically modified organisms (GMOs) or parts of their genotypes (Dale et al., 2002). Dispersal, defined as the movement of organisms, their propagules, or their genes (e.g. pollen in plants) away from the source (Stenseth et al., 1992; Turchin, 1998; Clobert et al., 2001; Nathan, 2001; Bullock et al., 2002; Petit, 2004), plays a central role in all four threats. Land use changes lead to a reduction in habitat area and to fragmentation, which as a rule reduces connectivity between patches. Climate change alters the geographical location of suitable climatic niches, resulting in shifts in species distributions. In extreme cases, the entire future climatically suitable niche lies outside the present species range, necessitating migration for the species to survive. For invasive species and GMOs, the threat to biodiversity conversely results from excessive movement of elements not native to the ecosystem.

In both terrestrial and marine ecosystems, most dispersing units move relatively short distances away from the source; long-distance dispersal (LDD) events are typically rare in both plants (Harper, 1977; Willson, 1993) and animals (Paradis *et al.*, 1998;

Paradis et al., 2002), although they are probably more prevalent in marine systems (Kinlan & Gaines, 2003; Kinlan et al., 2005). An extensive literature addresses the importance of dispersal in biodiversity conservation (e.g. Ellstrand, 1992; Strykstra et al., 1998; Sweanor et al., 2000; Cooper & Walters, 2002; Honnay et al., 2002; Haddad et al., 2003). However, these studies rarely take into consideration the differences between short- and long-distance dispersal (although see Sutherland et al., 2000; Amezaga et al., 2002; Higgins et al., 2003b; Yamamura, 2004).

What constitutes LDD can be highly case-specific. The mechanisms behind LDD often include both those that operate in the short-distance dispersal of the species and those unique to LDD (e.g. Higgins et al., 2003c) (see Tools for quantifying LDD: Defining LDD for discussion of LDD definition). Because of the conceptual complexity in defining LDD and the frequently severe difficulty in documenting it (Nathan et al., 2003), the scope and importance of LDD is often greatly underestimated. LDD events can be much more important for population dynamics and genetic composition than their low frequency might suggest. Ecologically, LDD is central to several population processes (Nathan, 2001; Levin et al., 2003), especially in heterogeneous environments (Bolker & Pacala, 1999). Most importantly, it determines to a large extent the rate of population spread (Kot et al., 1996; Clark, 1998; Turchin, 1998; Shigesada & Kawasaki, 2002; Levin et al., 2003; Green & Figuerola, 2005). In the context of the threats identified above, the relevant issues are

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DOI: 10.1111/j.1366-9516.2005.00156.x

expansion of invasive species, range shift as a result of climate change and reintroduction programs. LDD also allows recolonization in naturally patchy or fragmented environments that harbour metapopulations. Last, but not least, LDD is important for exchanging genetic information, facilitating genetic connectivity between fragmented patches, thus promoting longterm species survival. But LDD also allows the spread of genes from GMOs to their native relatives. To sum up, the main conservation issues where LDD is important fall into two categories: (1) cases where insufficient dispersal of the native species threatens their own survival (i.e. habitat fragmentation and range shifts as a result of climatic change), and (2) cases where excessive dispersal of elements alien to the ecosystem threatens the survival of other (native) species (i.e. invasive species and GMOs). Accordingly, conservation management practices are needed to enhance LDD in the former case and suppress it in the latter. Reintroduction programs are unusual in incorporating both these categories: LDD is required for the species to recolonize its historic range, but excessive LDD could bring the population into conflict with humans.

This article reviews the role of LDD in biodiversity conservation. We first address in detail the relative importance of LDD for leading conservation issues. Second, we examine the qualitative and quantitative tools for assessment of LDD ability, their merits and drawbacks, and recommend the tools adequate for different conservation needs. Finally, we briefly explore how information on LDD can help in guiding conservation management decisions.

ASSESSMENT OF LDD IMPORTANCE

Excessive LDD

For invasive species, LDD ability is only one of several factors that indicate high invasiveness. Other species traits, such as lack of habitat specificity, and case-specific factors, such as introduction effort, may be no less important. Therefore, we assigned very high importance of LDD for the generalist species, and moderate for the other invasives (Table 1). For GMOs, the ability to impact native species is a function of two types of LDD. First, there is a potential for 'traditional' LDD via seed-set or other whole-organism spread. Second, and even more alarming, is the

potential for spread of genome fragments through hybridization with wild relatives (Table 1).

Insufficient LDD

Threatened species often occur in small and geographically restricted populations. These small populations are most threatened by extinction resulting from demographic, genetic and environmental stochasticity. Often, multiple small populations exist at a considerable distance from one another. Dispersal is then crucial for metapopulation dynamics to emerge: subpopulation genetic diversification, re-colonization of sites where a subpopulation has become extinct, and establishment of new subpopulations. Although some subpopulations may be relatively near to one another, others will be distant. Where LDD ability is naturally insufficient, or where fragmentation has rendered subpopulation distances greater than the LDD ability of the species, long-term species survival will be threatened unless LDD can be re-established (Table 1). For such species, the whole dispersal kernel (Nathan et al., 2003) should be studied, as LDD alone might not be sufficient for their survival. All other species affected by fragmentation are also expected to benefit from LDD, but to a lesser extent (Table 1).

In the case of climate change, those species with a narrow climatic niche (i.e. the subset of habitat specialists that are 'climate specialists'), are likely to be most affected. These species have the greatest chance of most of their present geographical range to become climatically inappropriate. For such species, survival depends on rapid migration. Given the rapid rate of anthropogenic climate change, short-distance dispersal of the kind already documented (e.g. Parmesan, 1996) may not be sufficient. In those cases, high LDD ability will be crucial for the survival of the species (Table 1). Similarly, because the number of dispersers in threatened species is usually low, LDD would be highly important for the realization of rapid migration in these species (Table 1).

Reintroduction programs

Reintroduction programs for threatened species often serve to establish core populations which are then expected to spread and

Table 1 Importance of long-distance dispersal by problem type, conservation issue and species characteristics; + stands for important; ++ for very important; blank: not relevant

Problem type	Торіс	Nonthreatened species		
		Habitat generalists	Habitat specialists	Threatened species
Excessive dispersal	Invasion	++	+	
	GMOs	++	++	
		(Having wild relatives)		
Insufficient dispersal	Climate change	+	++	++
	_		(Narrow climatic range)	
	Fragmentation	+	+	++
Either insufficient or excessive dispersal	Reintroduction			++

recolonize further parts of the species' historic range. Because LDD ability is a key factor shaping the rate of spread, understanding LDD parameters is important in designing the number and spatial configuration of release points. It also determines whether the reintroduced individuals and their progeny will stay within the boundaries of the protected area where they were released, or will come into contact with humans, as has been the case with wolf reintroductions in the United States (Mech, 1995). In the presence of remaining native populations, LDD is also important to allow contact with them and sustain high genetic diversity of the reintroduced population (Forbes & Boyd, 1997). We therefore regard LDD as highly important for the success of these programs (Table 1).

Interaction with environment characteristics

The landscape structure is a key factor in evaluating LDD in the conservation context. The permeability of landscapes to dispersal affects the rate of both population spread and exchange of genetic information, hence its relevance to all the conservation topics we address. In a fragmented or naturally patchy landscape, the distances between patches should be compared to the scale of short- and long-distance dispersal, when assessing the level of connectivity among patches (Lavorel et al., 1995). Assuming that there is no establishment in the matrix, LDD will be most important at intermediate distances. When the distances are too large, extreme LDD events, which are normally exceedingly rare, would be the only mechanism to allow connectivity. When distances are too short, connectivity can be achieved also without LDD. In the context of range shifts, where in most cases LDD determines the rate of population spread, in fragmented landscapes this may be the only way for spread. On larger spatial scales, the proportion of fragmented landscape from the whole species range is of importance. The higher the degree of fragmentation, the more important is LDD for inter-population connectivity.

TOOLS FOR QUANTIFYING LDD

The scarcity of LDD and its inherent uncertainty render it difficult to define, observe and quantify (Koenig *et al.*, 1996; Nathan *et al.*, 2003). This makes the inclusion of LDD in conservation planning a challenge, and may be responsible for the relative paucity of references to it in this context.

In this section, we first discuss how LDD may be operationally defined in a way that can be useful in a conservation context. Following the formulation of a suitable working definition for LDD, the species LDD ability should be evaluated. At present, few tools for measuring LDD directly are available to help conservation efforts, although considerable efforts are currently devoted to this challenge (Nathan, 2003). Therefore, indirect assessments of LDD ability are needed. We then review existing tools for both qualitative and quantitative assessment of LDD ability. The former can at best inform us about the likelihood of dispersing long distances relative to other species in the same taxon, whereas the latter quantifies the probability of dispersal to a given distance in particular landscapes. The final part of

this section offers advice on how to select the most appropriate assessment tool for a given need from among those listed.

Defining LDD

Mechanisms responsible for LDD events can either be the same 'standard' mechanisms responsible for the short-distance dispersal of most propagules (or individuals) or 'nonstandard' mechanisms that are uniquely associated with LDD (Higgins *et al.*, 2003c). As a result of this duality, the morphological characteristics that typically signify the key mechanism of short-distance dispersal might be uninformative about LDD, as was shown for plant seeds (Higgins *et al.*, 2003c).

When detailed information is lacking experts familiar with the species in question often qualitatively determine the definition of LDD. In the less common cases where sufficient biological information is available, the frequency distribution of dispersal distances (Nathan & Muller-Landau, 2000) may be obtainable from either direct measurements or indirect estimates. In both cases, LDD can be operationally defined as a certain (high) percentile of the cumulative distribution that includes all known dispersal mechanisms (Nathan *et al.*, 2003); it may also be defined on the base of a certain threshold of absolute dispersal distance that is much longer than the median dispersal distance, or both. Such numerical estimates are preferable to generalized approximations.

For threats of excessive dispersal, maximal dispersal distances are of most interest for interspecific comparison of threat potential. This is equivalent to looking at a high percentile of the cumulative distribution. For threats involving insufficient dispersal, the main interest is in the probability of dispersal to a specified absolute distance (e.g. the typical interpatch distances or the distances between the present range and the projected future climatically suitable range). Therefore, for these cases, a combined definition should be used.

Conservation actions often must take place on restricted time scales, and the LDD probability is usually low. Therefore, the number of realized LDD events depends crucially on the source strength (i.e. on the total number of dispersing units). Invoking the precautionary principle, the threshold for defining LDD in cases of insufficient dispersal should be set most conservatively (i.e. relatively low percentile of the cumulative distribution) for threatened species with low fecundity.

We emphasize that in any consideration of the consequences of LDD for conservation, the potential for LDD and the source strength are necessary but not sufficient information. The other basic property that should be evaluated is the probability of establishment once a propagule arrives, which determines if an LDD event will actually lead to successful recruitment (Nathan *et al.*, 2003). Yet, evaluating establishment probabilities of propagules that underwent LDD is still a most challenging unresolved task.

Oualitative assessment

Qualitative assessment of LDD ability is based on proxies. For passive dispersal, in which the organism relies on a particular

transport mode or species for dispersal, LDD ability can be inferred from information on the effectiveness of the LDD vector. In the absence of direct observations on the effectiveness of the identified LDD vector, or if the identity of the key LDD vectors is unknown, LDD ability is usually inferred according to certain propagule characteristics that are associated with plausible LDD vector(s). For plant seeds, these characteristics, called 'morphological dispersal syndrome' (sensu Higgins et al., 2003c), include for example lightweight pappi or wings as indicators of dispersal by wind, barbs and hooks indicating attachment to animals, and fleshy pulp pointing to endozoochory. For other passively dispersed organisms, such characteristics may include size (Figuerola & Green, 2002), mass, and floating devices (for water-mediated dispersal).

Actively dispersing organisms can be grossly classified by their movement mode. More precise estimations of LDD ability are based on morphological characteristics, such as body size or wing length (Paradis *et al.*, 1998), or on life-history traits, such as diet type and migratory status (Paradis *et al.*, 1998; Sutherland *et al.*, 2000). The finding of a positive correlation, after controlling body size, between home range size and maximal dispersal distance in mammals (Bowman *et al.*, 2002), facilitates qualitative assessment of LDD ability, because quantification of home range size is considerably less demanding than measuring LDD. Behavioural traits may also be important predictors of LDD ability. For example, Rehage & Sih (2004) showed that species of *Gambusia* fish characterized by greater boldness (demonstrated by enhanced exploratory behaviour) dispersed farther in experimental streams than did less bold taxa.

The main advantage of a qualitative assessment of LDD over a quantitative one lies in the relative accessibility of the required information. Yet, it should be kept in mind that such qualitative proxies for dispersal ability do not always prove informative about LDD, because of the uncertainty involved with the identity of LDD mechanism. This uncertainty can lead to underestimation of LDD ability — a desired outcome for insufficient LDD cases, but far from helpful in situations of excessive LDD.

Quantitative assessment

Unlike qualitative tools, quantitative assessment provides precise predictions regarding levels of LDD. Two types of quantitative models are typically used, ones that are mechanistic in nature and ones that are phenomenological. Both demand more data than are required for qualitative assessments, and have additional advantages and disadvantages that are discussed below.

Mechanistic models

These models use data on factors affecting dispersal to predict the magnitude and frequency of LDD. The explicit treatment of processes enables simulating different scenarios, including the changes in parameter values that are caused by the human impacts that threaten biodiversity. For example, wind characteristics are different in open and closed vegetation, and such differences are especially important in fragmented landscapes. Mechanistic models of seed dispersal by wind can incorporate these differences (e.g. Nathan *et al.*, 2002a, 2005). They provide the means for evaluating the consequences of alternative conservation practices, and can predict LDD independently of observation data. Unfortunately, mechanistic models of LDD currently exist for only some of the known dispersal processes. Models for passive LDD by wind and by water currents are now available (Cowen *et al.*, 2000; Nathan *et al.*, 2002b, 2005). Soons & Ozinga (2005), for example, applied a mechanistic wind dispersal model to help assess plant response to environmental changes. Active movement of organisms is much more complicated to model, because of the high variability in behavioural and environmental factors (Higgins *et al.*, 2003a), and mechanistic models of active dispersal tend to be case-specific (e.g. South & Kenward, 2001; Macdonald & Rushton, 2003).

High complexity, compared to phenomenological models, is characteristic of all mechanistic models, because they usually include more parameters (Higgins & Richardson, 1996). This can be a disadvantage, as estimating parameter values may be challenging. The complexity also renders mechanistic models computationally expensive, as they often require a large number of simulations (Nathan *et al.*, 2003, 2005).

Phenomenological models

An alternative to mechanistic modelling is using phenomenological models such as fitting a curve for the observed dispersal distances (e.g. Clark, 1998), without explicitly considering the dispersal process. Such models have been used for passively dispersed taxa (Wolfenbarger, 1946; Wolfenbarger, 1959), especially plant seeds (e.g. Willson, 1993; Cain *et al.*, 1998; Clark, 1998; Nathan *et al.*, 2000), pollen (Austerlitz *et al.*, 2004) and spores (Gregory, 1945), and for actively dispersing animals, including birds (e.g. Paradis *et al.*, 2002) and insects (Taylor, 1978; Kuras *et al.*, 2003). One or more functional forms are often fitted to the data, and the criterion for selecting among them is usually the best statistical fit. To emphasize the fit in the 'tail' representing LDD and to account for both short- and long-distance dispersal data, a mixture of functions is sometimes fitted (e.g. Higgins & Richardson, 1999; Higgins *et al.*, 2003c).

The main advantage of phenomenological models is their simplicity compared to mechanistic ones. When no mechanistic model is available, as is often the case, they are, in fact, the only tool available for quantitative assessment. The main disadvantage is that phenomenological models provide no insight into the dispersal mechanism(s). The 'correct' model is chosen mostly based on best statistical fit, not on theoretical insights. Moreover, these models only enable prediction for the range of distances and the habitat for which they were calibrated. Given that data are nearly always limited to short-distance dispersal (see previous discussion on Tools for quantifying LDD), this general constraint of phenomenological models entails a particular disadvantage for applying this approach to model LDD for conservation purposes. Extrapolation from short-distance dispersal to LDD is problematic, and one cannot decide a priori whether extrapolation will lead to conservative or inflated estimates of LDD ability.

Despite the abovementioned shortcomings, we anticipate continued widespread use of these models. To test their predictive abilities more rigorously, we propose excluding the longest observed distances during the curve fitting stage, then extrapolating the fitted function to the full observed distances' range, and finally testing the accuracy of the prediction against this independent data subset. High accuracy may indicate that it is possible to further extrapolate the results to greater distances, for which data collection is impractical.

Additional factors to consider when quantifying LDD

Evaluation of LDD for conservation purposes must consider the possible interactions between the processes that threaten biodiversity and dispersability. Fecundity, dispersal and establishment might all be affected. We shall now discuss the interactions relevant to some major conservation issues.

Excessive LDD

At a global scale, the introduction of invasive species to new locations is achieved through human-aided transport across major geographical barriers (Richardson et al., 2000b). In evaluating the LDD ability of potentially invasive species, one must consider that subsequent population spread within invaded regions is often also facilitated by human-mediated LDD. An example for this process was provided by Suarez et al. (2001) for the spread of Argentine ants in the USA. They found that estimated annual spread distances showed a bimodal distribution, with short distances corresponding to local dispersal by colony budding and long distances resulting from human-aided LDD. Similarly, Arnaud et al. (2003) found that in the sugar beet (Beta vulgaris ssp. vulgaris), there was no extensive transfer of pollen to wild sugar beets (B. vulgaris ssp. maritima), but there was an escape of weedy cultivated lineages attributed to human-mediated LDD of seeds. Thus, while most studies on dispersal in GMOs have addressed pollen dispersal, human-induced seed dispersal should also be considered.

We recommend that assessment of LDD for invading species and GMOs be extended to include investigation of the human-mediated dispersal vectors for each species. When the human-mediated vector is known, it is possible to use the assessment tools discussed previously to evaluate its contribution to LDD. One example of such study is Buchan & Padilla's (1999) work on dispersal of zebra mussels by recreational boaters. They showed that qualitative assessment of LDD based on the boater movement patterns was better at predicting spread than diffusion models based on the biology of the species and its inherent dispersal ability. This is probably also the case for many other invasive species. Therefore, attempts to build detailed spread models based primarily on species traits are probably not very useful.

Additionally, invasion may increase the species fecundity, hence realized LDD, relative to its natural populations, either because of lack of natural enemies, or the result of altered genetic composition (e.g. Hönig *et al.*, 1992; Wolfe, 2002; Leger & Rice,

2003). Furthermore, the conditions favouring, or deterring, the establishment of alien propagules dispersed over long distances need to be evaluated when assessing their invasive potential.

Insufficient LDD

Habitat fragmentation can break down movement processes, one of the reasons being that the matrix between patches often impedes movement (e.g. Richardson et al., 2000a; Ricketts, 2001; Higgins et al., 2003b); and negatively affect source strength, influencing both short and long-distance dispersal. Therefore, both for active and passive dispersal, the most likely effect of increased fragmentation on LDD is to reduce dispersal distances. However, effects at edges can be extremely complex (Cadenasso & Pickett, 2001). For example, certain types of fragmentation might actually increase LDD distances of wind-dispersed organisms, because of high turbulence on the edge of forested and open vegetation (Nathan et al., 2002a). The negative effects of fragmentation on source strength can result from a decline in population size and from reduced fecundity. Negative effects on fecundity were demonstrated for lizards (Boudjemadi et al., 1999) and for wind-dispersed plants (Soons & Heil, 2002). Soons & Heil (2002) have also shown that the range of dispersal distances was altered in fragmented landscapes, probably resulting from inbreeding depression that affected seed morphology. It is important to emphasize that LDD might actually increase in importance in fragmented vs. intact habitats, despite a decrease in absolute dispersal distances, because LDD might become the major way to biologically connect patches that are no longer physically linked.

For climate change, there is some evidence that range extension may be coupled with selection for increased dispersability. Thomas *et al.* (2001) provide an example of higher proportions of long-winged morphs in newly established populations of bush crickets. Another concern is that while propagules might disperse sufficiently long distances to reach suitable habitats, other environmental features of these remote sites may not be favourable for their establishment. Such effects are hard to predict, but they should be considered in assessing LDD when appropriate data on the subject are available.

Recommendations for selecting assessment tool

The information presented underscores the importance of considering LDD when conducting conservation research and management projects. Although it is enough, in some cases, to do so in a qualitative way, it is often desirable to quantitatively evaluate levels of LDD. Quantitative assessment of LDD ability is highly informative but is also very costly in terms of data collection, time, and computational demands. Because resources for conservation and management are always limited, we recommend restricting the use of quantitative assessments for two main situations. As a rule, it should be undertaken for addressing the most crucial threats, and especially for preventing excessive LDD. It should also be applied for addressing less severe cases when an inappropriate management decision (presumably resulting from

misleading qualitative assessment) has the potential to be particularly costly. For example, in cases of insufficient dispersal, qualitative assessment resulting in conservative estimates of LDD is not problematic unless resulting in costly management actions, such as human assisted translocation of individuals (Peters, 1992; Honnay *et al.*, 2002; Watkinson & Gill, 2002).

When threats of excessive LDD are identified, an immediate action is often required. Therefore, as a first step, qualitative assessment should be conducted to rapidly screen all potentially threatening species. The resulting conservative estimates of LDD ability will define the highest priorities for action. Then, attempts should be made to identify nonstandard dispersal vectors, and especially human-mediated dispersal, for all species (e.g. Ruiz & Carlton, 2003). A reassessment of LDD potential may be needed once such vectors are discovered. The last step would be different for invasive species and GMOs. The large number of invasive species precludes quantitative assessment of LDD for all of them. Such evaluation should only be undertaken for species possessing characteristics that increase their potential to be invasive. In the case of GMOs, which can be kept under strict control until approval is granted, quantitative assessment of LDD should be employed for each GM species. When there is a need for quantitative evaluation, we strongly recommend the use of mechanistic models if applicable. Furthermore, if direct empirical quantification is feasible, it should be used to test the power of mechanistic models as general predictive tools, rather than merely to estimate LDD ability.

MANAGEMENT FOR/AGAINST LDD

Developing conservation management plans that take LDD into account is as challenging as the task of assessing the level of LDD. We are aware of few management actions unique to LDD as opposed to short-distance dispersal. Nevertheless, the inclusion of data on LDD can guide the choice between the management options available for controlling dispersal. Furthermore, when unique LDD mechanisms are known, they should be specifically addressed in the management plans. For example, because waterfowl serve as an LDD vector for many aquatic invertebrates, it was suggested to take into consideration their migration routes when constructing wetland reserve networks, so as to increase interwetland connectivity (Amezaga *et al.*, 2002).

As a first step, knowledge of LDD potential can be used in constructing biologically meaningful population models for directing management decisions. One type of such models is aimed at estimating population spread, for forecasting the rate of spread of invasive species, reintroduced populations, or species tracing climatic range shift. Other models might incorporate data on LDD to assess whether the existing interfragment connectivity is sufficient for metapopulation survival and for maintaining adequate genetic diversity. These estimations can be used in further management decisions, and assist in deciding whether direct intervention is desired. For instance, the primary tool to prevent spread of invasive species at its initial steps is biosafety protocols for species import (e.g. Pheloung *et al.*, 1999; Williams & West, 2000). Quantitative assessment of LDD ability

could improve the screening process employed by these protocols.

CONCLUSIONS

Long-distance dispersal is highly relevant to the most pressing biodiversity conservation problems facing us today, and is likely to become even more important as the impacts of global climate change intensify, and human-mediated dispersal of species proliferates. Nevertheless, the issue remains under-appreciated by the conservation community, which has traditionally focused on the importance of short-distance dispersal. To adequately incorporate LDD in conservation plans, it is essential to distinguish between two fundamental contexts: excessive LDD of nonindigenous elements, and insufficient LDD of native species. Despite the difficulties in definition and quantification, various tools are currently available for evaluating the potential for LDD. Implementing assessment of LDD as a standard routine in conservation practice would give rise to better management decisions.

ACKNOWLEDGEMENTS

RN acknowledges support from the National Science Foundation (IBN-9981620), the German-Israeli Foundation (GIF 2006–1032.12/2000), the Israeli Science Foundation (ISF-474/02), the US-Israel Binational Science Foundation (BSF 229/2002), and the International Arid Land Consortium (IALC-03R/25). DMR acknowledges support from the DST Centre of Excellence for Invasion Biology.

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