Migration potential as a new predictor of long-distance dispersal rate for plants

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Abstract

How biotic and abiotic factors interact to shape the overall pattern of dispersal of propagules is critical in understanding the evolution of dispersal mechanisms as well as predicting dispersal rates between patchily-distributed habitats. But which plant traits, demographic and/or habitat factors best predict the capacity for dispersal? We introduce the concept of migration potential ($v$), a readily interpretable parameter that combines recruitment efficiency (recruits per adult / seeds per adult per dispersal cycle) with level of habitat occupancy for predicting effective long-distance dispersal (LDD) of seeds. Using our empirical (genotype assignment) estimates of LDD and statistics on life-history traits and demographic features for contrasting co-occurring shrub species as a test case, and comparing with alternative plant traits, we demonstrate that rate of LDD is best described as a simple function of $v$. As the direct consequence of life-history and demographic traits in a specific environmental context, $v$ has the potential to predict LDD rates in both stable and changing ecosystems.
Dispersal is a fundamental life-history trait that has evolved in almost every taxon, and affects almost all ecological and evolutionary processes (Levin et al. 2003; Ronce 2007). For plants, long-distance dispersal (LDD) refers to the movement of propagules away from their source beyond an extended threshold distance, determined by key biological or physical features, at the tail end of the dispersal kernel (Nathan 2006; Levey et al. 2008). Despite its rarity compared with primary dispersal, LDD is disproportionately important for species persistence in fragmented landscapes (Tittler et al. 2006), colonization including non-native invasions (Caswell et al. 2003), metapopulation dynamics (Husband and Barrett 1996) and range shifts in response to climate change (Alsos et al. 2007, Fitzpatrick et al. 2008). An ability to predict the capacity for LDD is required to better manage species’ responses to environmental changes such as global warming, habitat loss, and presence of invasive species (Kokk and López-Sepulcre 2006). But which plant traits, demographic and/or habitat factors best predict the capacity for LDD?

Theoretical models regularly assume that LDD rates are related to life-history traits (Eriksson and Jokobsson 1999) and habitat availability (Travis and Dytham 1999; Barton et al. 2009). However, until now these models have not been tested using empirical evidence involving species (ideally co-occurring) with contrasting life-history traits, demographic rates and dispersal patterns. In addition to overcoming the technological and methodological challenges in measuring LDD rates (Nathan 2006), an efficient framework for combining information about life-history traits, population dynamics and habitat specificity is needed in order to relate such estimates to a parameter describing LDD rates across diverse ecological settings (Ronce 2007; Holyoak et al. 2008). Here, we use theory to develop a suitable parameter, migration potential, as a product of recruitment efficiency
and habitat occupancy. A comprehensive data set we collected over eight (genetically based estimates of LDD rate) and 25 (life-history and demographic attributes) years provided a unique opportunity to test the model. We show that migration potential can accurately predict LDD rate for multiple co-occurring species, and is superior to other possible predictors for this data set.

**Study system**

The study area is located in fire-prone Mediterranean-type shrublands on the Eneabba Plain, southwestern Australia, with an estimated mean fire return interval of ~13 years (Miller *et al.* 2007). The sandplain is characterized by a gentle dune–swale topography, with plant communities differing between dunes and swales, creating a spatially explicit metapopulation system for dune-dwelling species. In an area of 15 km², sand dunes were identified and mapped. Four shrub species, *Banksia attenuata*, *B. candolleana*, *B. hookeriana* (Proteaceae), and *Daviesia triflora* (Papilionaceae) were investigated. These species are common members of the dune crest community but are absent from the intervening swales (typically 0.1–1 km wide), i.e. they exist in a naturally fragmented system with discrete populations on each dune. The four species differ markedly in life-history traits and demographic rates, including population density, plant height, fire response, seed set (fecundity), seedbank type, seed mass, recruitment rate and lifespan (Table 1). Consequently, these four species are representative of the spectrum of major life history traits and demographic characters present in the region. Dispersal events measured for this synthesis occurred simultaneously after the last fire (1998), and demographic data were collected for plants of similar age. Thus, our data are representative of normal patterns
in this community. The juvenile recruits identified were six to eight years old at the time of sampling and had high probability of survival to maturity (Enright and Lamont 1989, 1992).

**LDD rates**

In our system, LDD refers to inter-patch (between dune populations) seed movement resulting in recruitment of a new individual, i.e. effective dispersal. Inter-patch movement is a discrete event that occurs beyond the boundary of the source population (Levey et al. 2008). LDD rate refers to the fraction of sampled individuals per population that were assigned, based on comparative genotype using population likelihood assignment tests, to a population other than that from which they were collected (Rannala and Mountain 1997). In a set of interconnected populations, assignment of individuals to source populations on the basis of genotypic variation has been demonstrated as a powerful, and indeed sometimes the only, tool available to precisely measure effective LDD rate (Nathan et al. 2003; Paekau et al. 2004; Sork and Smouse 2006). To determine inter-population LDD, the log-likelihood of each individual originating from each source population was calculated following Bayesian-based methods (Rannala and Mountain 1997; Piry et al. 2004). An unambiguous assignment was accepted when the difference between the largest and the second largest log-likelihood was above a threshold stringency level, which provides a conservative test for the identification of seed immigrants that excludes inter-population hybrids and early backcrosses as belonging to the resident population (He et al. 2009a). An inter-population dispersal event was accepted if an individual was unambiguously assigned to a population other than that from which it was collected.
We previously determined the inter-population LDD rate and its spatial scale for *B. attenuata* (microsatellites; He et al. 2009), *B. hookeriana* (AFLP, microsatellites; He et al. 2004, 2010), and *D. triflora* (microsatellites, He et al. 2009b) in the study area. The LDD rate of *B. hookeriana* was estimated using AFLP (He et al. 2004) and microsatellite (He et al. 2010) markers for independent sets of samples collected in the same region and averaged. Both tests resulted in similar rates and spatial scale of dispersal, suggesting the measured LDD rates are likely to be accurate for these species. The LDD rate of *B. candolleana* was determined using microsatellite DNA markers for 529 individuals collected from 15 populations and the same statistical population allocation procedures used as for the other banksias (Merwin L, He T, Krauss SL, Lamont BB, Enright NJ unpublished).

**Life-history traits and demographic features**

Data on life-history traits and demographic attributes were collected for the four study species (Table 1). The traits/attributes examined were those considered most likely to influence LDD: lifespan, fire response, seed production (per hectare), recruits per parent (since the last fire) and seed mass. Available information on traits and demographic attributes were collated from > 25 years of demographic/life-history studies on the banksias (Enright and Lamont 1989, 1992; Enright et al. 1998; Lamont et al. 2007). Lifespan was estimated as maximum possible age of an individual plant. Seed production (per ha) was calculated as fecundity per plant × population density (ha⁻¹).

**Habitat occupancy**
The 3 × 5 km study area was surveyed for occurrence of the three banksias and *Daviesia triflora*. We recorded the number of dunes (populations) where each species occurred in our survey area of 36 dunes. For each species, habitat occupancy was calculated as the fraction of dunes with the species present.

**Predictive model**

*Recruitment efficiency.* Evolutionary theory predicts that the cost of dispersal will be a strong selective force in the evolution of dispersal mechanisms, so that a lower dispersal cost results in greater dispersal rate (Ronce 2007; Cheptou et al. 2008; Dytham 2009; Riba et al. 2009). We focus here on effective LDD, i.e. long-distance dispersal plus successful post-dispersal recruitment. The ratio of number of recruits per adult to number of seeds dispersed per adult is an estimate of the efficiency with which seeds produce recruits, incorporating mortality filters during dispersal, germination and establishment, i.e. seed-to-adult survival probability (Nathan 2006). We refer to this measure as recruitment efficiency ($r$), an inverse estimate of dispersal cost. At least in our study system, it is not evident that immigrants have superior fitness over locally dispersed seeds (He et al. 2009a), so we assume that locally and inter-population dispersed seeds do not differ in their establishment success. However, a high $r$ in some species could result from wide microsite tolerances that would favour higher effective dispersal rates. Assuming a negative correlation between LDD rate (the fraction of immigrants per unit population at a given point in time, $v$) and dispersal cost (inverse of recruitment efficiency, $r$) (Cheptou et al. 2008; Dytham 2009), it is expected that: $v = a_1 \times r + a_2$ where $a_1$ and $a_2$ are constants (see (1) below).

*Habitat occupancy.* Theory predicts that inter-population dispersal rate is generally
correlated with habitat availability in a stable system (Travis and Dytham 1999). However, seeds may fail to reach all available sites favorable for their establishment and survival (dispersal limitation, Hubbell et al. 1999), or competitive exclusion may prevent the successful establishment of species competing for the same resources (Hardin 1960). Therefore, we define habitat occupancy ($h_o$), as the fraction of suitable habitat patches within the reference area that is occupied by that species. This measure incorporates habitat availability as affected by possible dispersal limitations and the biotic interactions encountered after germination within each patch that ultimately determine if a population will establish there. The following is then expected: $v = a_1 \times h_o + a_2$.

Migration potential. Given recruitment efficiency ($r$) and habitat occupancy ($h_o$), as defined above, LDD rate, $v$, for any species can be expressed as:

$$v = a_1 \times r \times h_o + a_2$$  \hspace{1cm} (1)

where $a_1$ is an ecosystem-specific coefficient (slope of the relationship) and $a_2$ is the minimum LDD rate for any species to survive in that system (LDD intercept when $r$ or $h_o = 0$). We define a single variable, migration potential ($m$), as $m = r \times h_o$. Therefore, formula 1 can be rewritten as:

$$v = a_1 \times m + a_2$$  \hspace{1cm} (2)

Correlations

We calculated recruitment efficiency ($r$), habitat occupancy ($h_o$) and migration potential ($m$) as outlined above for our four study species. Simple linear correlations with their known LDD rate ($v$) were applied to reveal any trends. Relationships between LDD rate and other life history traits/demographic attributes (Table 1) were also explored as
alternative explanations. Theoretical lines were added, passing through the origin (zero trait value, zero dispersal) and the means of the LDD rate and trait values for the four species as defining coordinates. Significance was taken at $P = 0.05$.

**Results and Discussion**

We determined LDD rates ($v$) and spatial scale (distance between source and sink populations for LDD events) for four co-occurring shrub species in a highly speciose, fire-prone Mediterranean-type shrubland using molecular microsatellite markers and statistical population-assignment tests. All four species demonstrated dispersal to distant habitat patches within the study area of 15 km$^2$, with the percentage of individuals assigned to a population other than that from which they were sampled (LDD rate) of 0.017–0.062 (Table 2)—that is, between 1.7% and 6.2% of sampled individuals were inferred to be immigrants. For these four species, LDD rate ($v$) increased monotonically with recruitment efficiency ($r$), but displayed only a weak relationship with habitat occupancy ($h_o$) (Fig. 1a,b). However, migration potential ($m$), a product of habitat occupancy and recruitment efficiency, displayed a highly significant association with LDD rate (Fig. 1c). A linear fit of dispersal rate ($v$) to migration potential ($m$) for our data gives: $v = 34m + 0.017$ ($P = 0.0008$), with an estimated minimum LDD rate for species to survive in this shrubland system ($a_2$) of 1.7% (Fig. 1c). Thus, we demonstrate that migration potential, a consequence of habitat occupancy interacting with recruitment efficiency, successfully predicts LDD rates in this ecosystem.

These four species display contrasting life-history and demographic properties, including marked differences in primary dispersal mechanism/vector, seed mass, fecundity
and seed production, recruitment rate and lifespan (Table 1). However, none of these
variables predicted dispersal rate as effectively as migration potential (Fig. 2). Although the
nonsprouter–resprouter dichotomy is often viewed as a key determinant of population
dynamics in fire-prone Mediterranean-type ecosystems (Bond and Midgley 2001; Lamont
and Wiens 2003), it did not appear to control LDD rates in the three banksias (Fig. 2). LDD
rate is expected to increase with increasing seed production (more propagules to disperse),
as well as the inverse of lifespan (because greater generation turnover rate has the potential
to produce more propagules per unit time, Willson 1993). In our system, such correlations
were not statistically significant ($P > 0.05$), indicating weak power for these parameters in
predicting LDD rate (Fig. 2 a,b).

Although seed size has been suggested as one of the key attributes affecting dispersal
rates (Eriksson and Jokobsson 1999), we did not see this relationship with LDD rate (Fig.
2c), perhaps a consequence of conflicting effects on fitness (Gomez 2004). LDD rate did
increase monotonically with recruitment rate but only marginally significantly so on a
logarithmic scale (Fig. 2d, $P = 0.06$), suggesting that effective dispersal is related to
recruitment success. Although we found no relationship between seed dispersal vectors and
dispersal rates, our results do lend support to previous suggestions that LDD is usually
achieved by non-standard agents (Higgins et al. 2003; Nathan 2006;): wind vortices (dust-
devils) rather than surface winds in the case of the banksias (He et al. 2004, 2009a, 2010),
and large birds (emu, *Dromaius novaehollandiae*) rather than ants in the case of *Daviesia
triflora* (He et al. 2009b).

Our study of multiple co-occurring species in spatially explicit habitats demonstrated
that LDD capability of a species is influenced by the species attributes interacting in a
specific environmental setting. Although our analysis was restricted to a single ecosystem, and the species in the analysis only cover a fraction of the spectrum of variation in life history/demographic traits among plants, the current formulation provides a framework for further analyses in which empirical evidence for effective dispersal can be tested against hypothesized relationships between dispersal and life history, demographic and habitat attributes. For example, increased mobility has been proposed to involve trade-offs with other life-history traits (Ronce 2007). To establish such a relationship, comparing species with similar dispersal mechanisms may be necessary. In this study, LDD of the wind-dispersed banksias supported the expectation of a trade-off for increased dispersibility, but adding the animal-dispersed species annulled the relationship.

LDD rate is the consequence of many interacting life-history traits, each of which may have a different and potentially contrasting influence on dispersal and/or post-dispersal establishment. Recruitment efficiency ($r$) represents the outcomes of interacting life-history/demographic traits (germinability, competitiveness, microhabitat tolerances), and is a measure of the success with which seeds produce successful recruits, i.e. seed-to-adult survival probability (Nathan 2006). Effective dispersal is not only influenced by the availability of suitable habitats, but by how many sites are already occupied as a consequence of ecological processes such as dispersal limitation and/or competitive exclusion at the population scale. Habitat occupancy captures this, and serves well as a parameter for use in ecological and evolutionary models of dispersal. Migration potential $(m)$, as a consequence of interacting life-history traits, demographic attributes and habitat specificity, is a unifying predictor of effective LDD rate that provides a simple yet effective solution in dealing with the many factors controlling LDD success. While it appears to be
the only suitable data currently available, our test of the model was limited to just four
species. We encourage researchers with suitable data to test this model in their own system,
or to use the critical variables we have identified as a guide to what additional data should
be collected to help interpret their own LDD data.

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Table 1 Life-history traits (mean ± standard deviation) and demographic rates typical for the four study species in a mature stand 12–15 years after the last fire*

<table>
<thead>
<tr>
<th>Species</th>
<th>B. hookeriana</th>
<th>B. attenuata</th>
<th>B. candolleana</th>
<th>D. triflora</th>
</tr>
</thead>
<tbody>
<tr>
<td>Life history</td>
<td>Fire-killed</td>
<td>Resprouter</td>
<td>Resprouter (clonal)</td>
<td>Resprouter</td>
</tr>
<tr>
<td>Population density (ha⁻¹)</td>
<td>828±92</td>
<td>305±32</td>
<td>149±16</td>
<td>177±21</td>
</tr>
<tr>
<td>Recruitment rate (recruits adult⁻¹ per dispersal cycle)</td>
<td>1</td>
<td>0.06</td>
<td>0.007</td>
<td>0.004</td>
</tr>
<tr>
<td>Fecundity (seeds adult⁻¹)</td>
<td>370±34</td>
<td>55±4</td>
<td>32±3</td>
<td>225±22</td>
</tr>
<tr>
<td>Seed mass (mg)</td>
<td>45±6</td>
<td>101±12</td>
<td>210±50</td>
<td>13±1.5</td>
</tr>
<tr>
<td>Lifespan (year)</td>
<td>40</td>
<td>300</td>
<td>1200</td>
<td>500</td>
</tr>
</tbody>
</table>

* Data were obtained or re-calculated from Enright and Lamont (1989, 1992); Enright et al. (1998) and Lamont et al. (2007), or authors’ unpublished data.
Table 2. LDD rates, spatial extent and seed dispersal mechanisms for the four study species. Maximum distances may have been constrained by the size of the study area (3 km × 5 km), so longer distances are possible. N: number of individuals genotyped; P: number of populations sampled; R: resprouter after fire; N: nonsprouter, killed by fire.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size</th>
<th>LDD rate ( v )</th>
<th>Average distance of LDD ± sd and (range (km))</th>
<th>Primary/LDD mechanism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Banksia attenuata R</td>
<td>788 (27)</td>
<td>0.055</td>
<td>1.4±0.7 (0.2–2.6)</td>
<td>Wind/Wind vortex</td>
</tr>
<tr>
<td>Banksia hookeriana N</td>
<td>582 (18)(^b)</td>
<td>0.062</td>
<td>1.1±0.7 (0.3–3.3)</td>
<td>Wind/Wind vortex</td>
</tr>
<tr>
<td></td>
<td>221 (20)(^c)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Banksia candolleana R</td>
<td>529 (15)</td>
<td>0.021</td>
<td>1.1±0.9 (0.3–2.3)</td>
<td>Wind/Wind vortex</td>
</tr>
<tr>
<td>Daviesia triflora R</td>
<td>764 (23)</td>
<td>0.017(^d)</td>
<td>1.3±0.6 (0.4–2.4)</td>
<td>Ant/Emu</td>
</tr>
</tbody>
</table>

\(^a\), He et al. 2009a; \(^b\), He et al. 2010; \(^c\), He et al. 2004; \(^d\), He et al. 2009b
Figure legends

Figure 1. Migration potential \( m = r \times h_o \), defined as the product of recruitment efficiency and habitat occupancy, displays a highly significant association with empirically determined LDD rates \( v \) among our four study species. Broken lines represent theoretical predictions constrained to pass through the origin (i.e. zero trait value, zero LDD rate) and the coordinate defined by mean x and mean y of the LDD rates and trait values for the four study species.

Figure 2. Association of demographic/life history traits to empirically determined rates of long-distance dispersal of seeds \( v \) for the four study species. Broken lines represent theoretical predictions constrained to pass through the origin (i.e. zero trait value, zero LDD rate) and means of the LDD rate and trait values for the four species. Lifespan is estimated as maximum possible age of an individual plant. Recruitment rate is the net number of recruits present over a time interval sufficient for recruitment to have occurred, compared with the number of adults present just prior to the start of the period.
Figure 1.
Figure 2.