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

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27 **Abstract**

28 How biotic and abiotic factors interact to shape the overall pattern of dispersal of
29 propagules is critical in understanding the evolution of dispersal mechanisms as well as
30 predicting dispersal rates between patchily-distributed habitats. But which plant traits,
31 demographic and/or habitat factors best predict the capacity for dispersal? We introduce the
32 concept of migration potential (ν), a readily interpretable parameter that combines
33 recruitment efficiency (recruits per adult / seeds per adult per dispersal cycle) with level of
34 habitat occupancy for predicting effective long-distance dispersal (LDD) of seeds. Using
35 our empirical (genotype assignment) estimates of LDD and statistics on life-history traits
36 and demographic features for contrasting co-occurring shrub species as a test case, and
37 comparing with alternative plant traits, we demonstrate that rate of LDD is best described
38 as a simple function of ν . As the direct consequence of life-history and demographic traits
39 in a specific environmental context, ν has the potential to predict LDD rates in both stable
40 and changing ecosystems.

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50 Dispersal is a fundamental life-history trait that has evolved in almost every taxon, and
51 affects almost all ecological and evolutionary processes (Levin et al. 2003; Ronce 2007).
52 For plants, long-distance dispersal (LDD) refers to the movement of propagules away from
53 their source beyond an extended threshold distance, determined by key biological or
54 physical features, at the tail end of the dispersal kernel (Nathan 2006; Levey et al. 2008).
55 Despite its rarity compared with primary dispersal, LDD is disproportionately important for
56 species persistence in fragmented landscapes (Tittler et al. 2006), colonization including
57 non-native invasions (Caswell et al. 2003), metapopulation dynamics (Husband and Barrett
58 1996) and range shifts in response to climate change (Alsos et al. 2007, Fitzpatrick et al.
59 2008). An ability to predict the capacity for LDD is required to better manage species'
60 responses to environmental changes such as global warming, habitat loss, and presence of
61 invasive species (Kokk and López-Sepulcre 2006). But which plant traits, demographic
62 and/or habitat factors best predict the capacity for LDD?

63 Theoretical models regularly assume that LDD rates are related to life-history traits
64 (Eriksson and Jokobsson 1999) and habitat availability (Travis and Dytham 1999; Barton et
65 al. 2009). However, until now these models have not been tested using empirical evidence
66 involving species (ideally co-occurring) with contrasting life-history traits, demographic
67 rates and dispersal patterns. In addition to overcoming the technological and
68 methodological challenges in measuring LDD rates (Nathan 2006), an efficient framework
69 for combining information about life-history traits, population dynamics and habitat
70 specificity is needed in order to relate such estimates to a parameter describing LDD rates
71 across diverse ecological settings (Ronce 2007; Holyoak et al. 2008). Here, we use theory
72 to develop a suitable parameter, migration potential, as a product of recruitment efficiency

73 and habitat occupancy. A comprehensive data set we collected over eight (genetically based
74 estimates of LDD rate) and 25 (life-history and demographic attributes) years provided a
75 unique opportunity to test the model. We show that migration potential can accurately
76 predict LDD rate for multiple co-occurring species, and is superior to other possible
77 predictors for this data set.

78

79 **Study system**

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

96 in this community. The juvenile recruits identified were six to eight years old at the time of
97 sampling and had high probability of survival to maturity (Enright and Lamont 1989,
98 1992).

99

100 **LDD rates**

101 In our system, LDD refers to inter-patch (between dune populations) seed movement
102 resulting in recruitment of a new individual, i.e. effective dispersal. Inter-patch movement
103 is a discrete event that occurs beyond the boundary of the source population (Levey et al.
104 2008). LDD rate refers to the fraction of sampled individuals per population that were
105 assigned, based on comparative genotype using population likelihood assignment tests, to a
106 population other than that from which they were collected (Rannala and Mountain 1997).
107 In a set of interconnected populations, assignment of individuals to source populations on
108 the basis of genotypic variation has been demonstrated as a powerful, and indeed
109 sometimes the only, tool available to precisely measure effective LDD rate (Nathan et al.
110 2003; Paekau et al. 2004; Sork and Smouse 2006). To determine inter-population LDD, the
111 log-likelihood of each individual originating from each source population was calculated
112 following Bayesian-based methods (Rannala and Mountain 1997; Piry et al. 2004). An
113 unambiguous assignment was accepted when the difference between the largest and the
114 second largest log-likelihood was above a threshold stringency level, which provides a
115 conservative test for the identification of seed immigrants that excludes interpopulation
116 hybrids and early backcrosses as belonging to the resident population (He et al. 2009a). An
117 inter-population dispersal event was accepted if an individual was unambiguously assigned
118 to a population other than that from which it was collected.

119 We previously determined the inter-population LDD rate and its spatial scale for *B.*
120 *attenuata* (microsatellites; He et al. 2009), *B. hookeriana* (AFLP, microsatellites; He et al.
121 2004, 2010), and *D. triflora* (microsatellites, He et al. 2009b) in the study area. The LDD
122 rate of *B. hookeriana* was estimated using AFLP (He et al. 2004) and microsatellite (He et
123 al. 2010) markers for independent sets of samples collected in the same region and
124 averaged. Both tests resulted in similar rates and spatial scale of dispersal, suggesting the
125 measured LDD rates are likely to be accurate for these species. The LDD rate of *B.*
126 *candolleana* was determined using microsatellite DNA markers for 529 individuals
127 collected from 15 populations and the same statistical population allocation procedures
128 used as for the other banksias (Merwin L, He T, Krauss SL, Lamont BB, Enright NJ
129 unpublished).

130

131 **Life-history traits and demographic features**

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

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141 **Habitat occupancy**

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

146

147 **Predictive model**

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

164 *Habitat occupancy*. Theory predicts that inter-population dispersal rate is generally

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

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

$$176 \quad v = a_1 \times r \times h_o + a_2 \quad (1)$$

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

$$181 \quad v = a_1 \times m + a_2 \quad (2)$$

182

183 **Correlations**

184 We calculated recruitment efficiency (r), habitat occupancy (h_o) and migration potential
185 (m) as outlined above for our four study species. Simple linear correlations with their
186 known LDD rate (v) were applied to reveal any trends. Relationships between LDD rate
187 and other life history traits/demographic attributes (Table 1) were also explored as

188 alternative explanations. Theoretical lines were added, passing through the origin (zero trait
189 value, zero dispersal) and the means of the LDD rate and trait values for the four species as
190 defining coordinates. Significance was taken at $P = 0.05$.

191

192 **Results and Discussion**

193 We determined LDD rates (v) and spatial scale (distance between source and sink
194 populations for LDD events) for four co-occurring shrub species in a highly speciose, fire-
195 prone Mediterranean-type shrubland using molecular microsatellite markers and statistical
196 population-assignment tests. All four species demonstrated dispersal to distant habitat
197 patches within the study area of 15 km^2 , with the percentage of individuals assigned to a
198 population other than that from which they were sampled (LDD rate) of 0.017–0.062
199 (Table 2) — that is, between 1.7% and 6.2% of sampled individuals were inferred to be
200 immigrants. For these four species, LDD rate (v) increased monotonically with recruitment
201 efficiency (r), but displayed only a weak relationship with habitat occupancy (h_o) (Fig.
202 1a,b). However, migration potential (m), a product of habitat occupancy and recruitment
203 efficiency, displayed a highly significant association with LDD rate (Fig. 1c). A linear fit of
204 dispersal rate (v) to migration potential (m) for our data gives: $v = 34m + 0.017$ ($P =$
205 0.0008), with an estimated minimum LDD rate for species to survive in this shrubland
206 system (a_2) of 1.7% (Fig. 1c). Thus, we demonstrate that migration potential, a
207 consequence of habitat occupancy interacting with recruitment efficiency, successfully
208 predicts LDD rates in this ecosystem.

209 These four species display contrasting life-history and demographic properties,
210 including marked differences in primary dispersal mechanism/vector, seed mass, fecundity

211 and seed production, recruitment rate and lifespan (Table 1). However, none of these
212 variables predicted dispersal rate as effectively as migration potential (Fig. 2). Although the
213 nonsprouter–resprouter dichotomy is often viewed as a key determinant of population
214 dynamics in fire-prone Mediterranean-type ecosystems (Bond and Midgley 2001; Lamont
215 and Wiens 2003), it did not appear to control LDD rates in the three banksias (Fig. 2). LDD
216 rate is expected to increase with increasing seed production (more propagules to disperse),
217 as well as the inverse of lifespan (because greater generation turnover rate has the potential
218 to produce more propagules per unit time, Willson 1993). In our system, such correlations
219 were not statistically significant ($P > 0.05$), indicating weak power for these parameters in
220 predicting LDD rate (Fig. 2 a,b).

221 Although seed size has been suggested as one of the key attributes affecting dispersal
222 rates (Eriksson and Jokobsson 1999), we did not see this relationship with LDD rate (Fig.
223 2c), perhaps a consequence of conflicting effects on fitness (Gomez 2004). LDD rate did
224 increase monotonically with recruitment rate but only marginally significantly so on a
225 logarithmic scale (Fig. 2d, $P = 0.06$), suggesting that effective dispersal is related to
226 recruitment success. Although we found no relationship between seed dispersal vectors and
227 dispersal rates, our results do lend support to previous suggestions that LDD is usually
228 achieved by non-standard agents (Higgins et al. 2003; Nathan 2006;): wind vortices (dust-
229 devils) rather than surface winds in the case of the banksias (He et al. 2004, 2009a, 2010),
230 and large birds (emu, *Dromaius novaehollandiae*) rather than ants in the case of *Daviesia*
231 *triflora* (He et al. 2009b).

232 Our study of multiple co-occurring species in spatially explicit habitats demonstrated
233 that LDD capability of a species is influenced by the species attributes interacting in a

234 specific environmental setting. Although our analysis was restricted to a single ecosystem,
235 and the species in the analysis only cover a fraction of the spectrum of variation in life
236 history/demographic traits among plants, the current formulation provides a framework for
237 further analyses in which empirical evidence for effective dispersal can be tested against
238 hypothesized relationships between dispersal and life history, demographic and habitat
239 attributes. For example, increased mobility has been proposed to involve trade-offs with
240 other life-history traits (Ronce 2007). To establish such a relationship, comparing species
241 with similar dispersal mechanisms may be necessary. In this study, LDD of the wind-
242 dispersed banksias supported the expectation of a trade-off for increased dispersibility, but
243 adding the animal-dispersed species annulled the relationship.

244 LDD rate is the consequence of many interacting life-history traits, each of which
245 may have a different and potentially contrasting influence on dispersal and/or post-dispersal
246 establishment. Recruitment efficiency (r) represents the outcomes of interacting life-
247 history/demographic traits (germinability, competitiveness, microhabitat tolerances), and is
248 a measure of the success with which seeds produce successful recruits, i.e. seed-to-adult
249 survival probability (Nathan 2006). Effective dispersal is not only influenced by the
250 availability of suitable habitats, but by how many sites are already occupied as a
251 consequence of ecological processes such as dispersal limitation and/or competitive
252 exclusion at the population scale. Habitat occupancy captures this, and serves well as a
253 parameter for use in ecological and evolutionary models of dispersal. Migration potential
254 (m), as a consequence of interacting life-history traits, demographic attributes and habitat
255 specificity, is a unifying predictor of effective LDD rate that provides a simple yet effective
256 solution in dealing with the many factors controlling LDD success. While it appears to be

257 the only suitable data currently available, our test of the model was limited to just four
258 species. We encourage researchers with suitable data to test this model in their own system,
259 or to use the critical variables we have identified as a guide to what additional data should
260 be collected to help interpret their own LDD data.

261

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

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

* 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.

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374 Table 2. LDD rates, spatial extent and seed dispersal mechanisms for the four study
375 species. Maximum distances may have been constrained by the size of the study area (3 km
376 × 5 km), so longer distances are possible. N: number of individuals genotyped; P: number
377 of populations sampled; R: resprouter after fire; N: nonsprouter, killed by fire.

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

378 a, He et al. 2009a; b, He et al. 2010; c, He et al. 2004; d, He et al. 2009b

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388 Figure legends

389

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

396

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

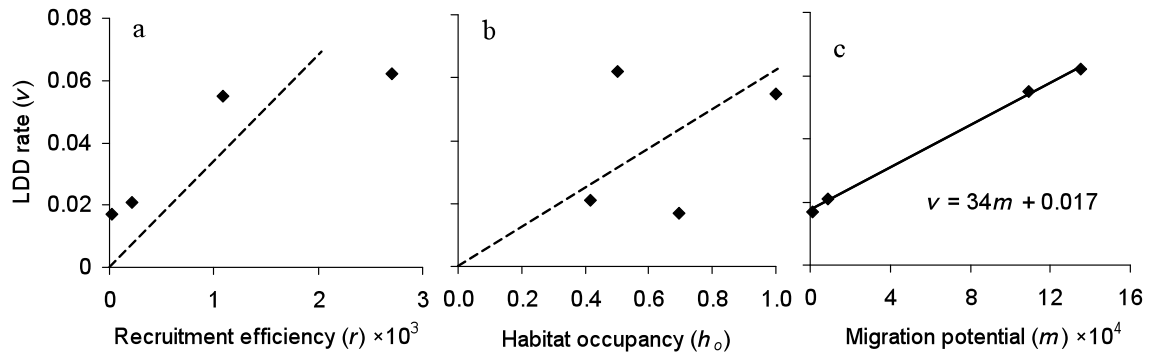
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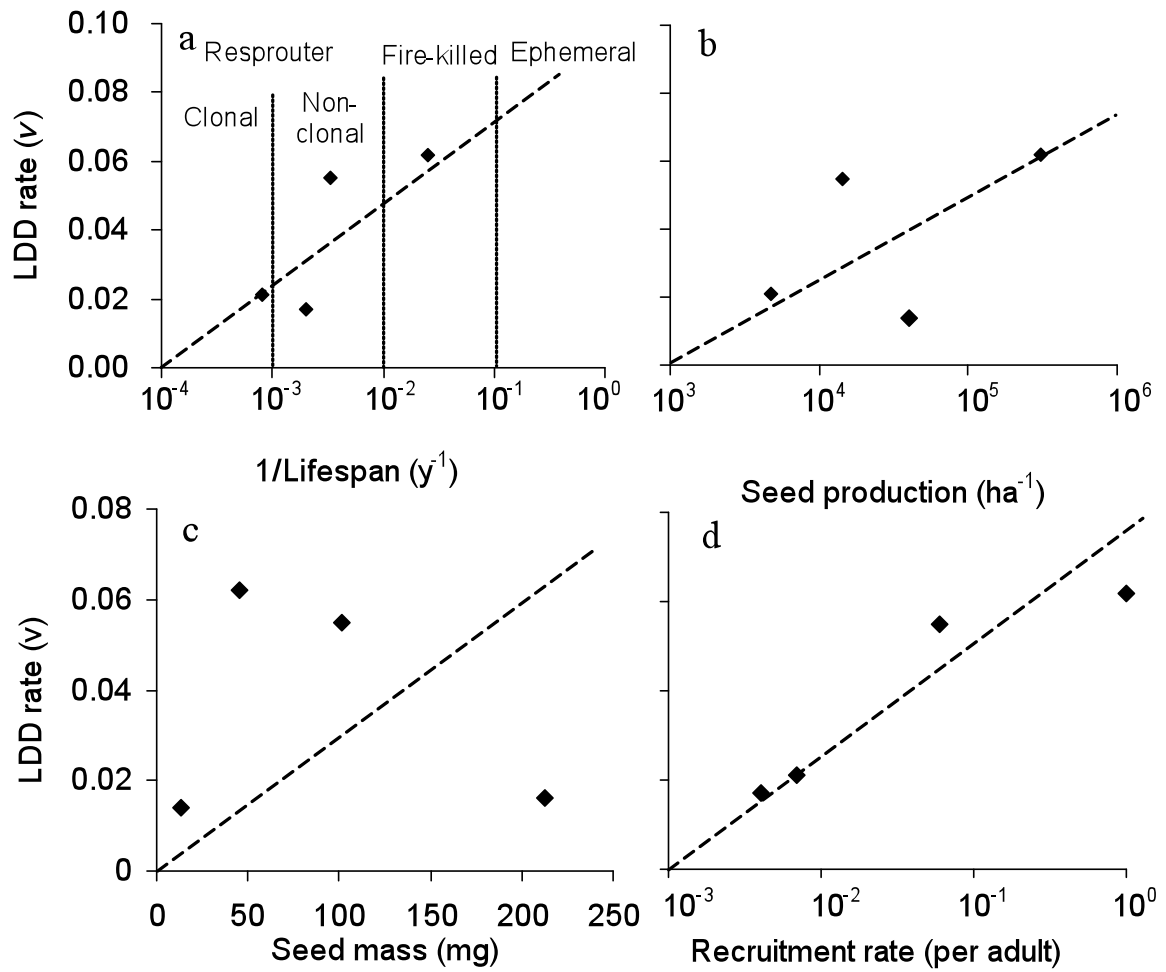
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410 Figure 1.

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413 Figure 2.

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