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Demographic consequences for a threatened plant after the loss of its only disperser. Habitat suitability buffers limited seed dispersal

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21 Running title: Demographic consequences in *Daphne rodriguezii*

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22   ***Abstract***

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24   Seed dispersal links the end of a plant's reproductive cycle with the establishment of new

25   recruits. Dispersal over short distances may lead to the local aggregation of individuals,

26   slower population growth and, ultimately, to lower population densities. In this study, we

27   analyse the demographic consequences for the shrub *Daphne rodriguezii* after the loss of its

28   only seed disperser in an island ecosystem (Menorca Island, W Mediterranean). During a

29   period of 8-10 years, we collected demographic data from five populations, four where the

30   disperser is extinct (disrupted) and the only one in which it still persists (undisrupted). We

31   calculated basic deterministic variables, analysed life table response experiments (LTRE)

32   and their covariation among demographic traits, and simulated future population

33   vulnerability. Population growth rate (λ) was either stable or negative and independent of

34   whether the population was disrupted or not. Current and past population dynamics were

35   similar in the two largest populations (one being the undisrupted), which suggests that the

36   environmental conditions allow them to be stable regardless of seed disperser presence.

37   Variation in λ was dependent on rainfall variability and was highly influenced by stasis and

38   growth. There also existed trade-offs between the former life traits and fecundity, which

39   indicate strong competition when resources are limiting (e.g. high plant aggregation due to

40   limited seed dispersal or low rainfall), and that could ultimately affect high-elasticity

41   demographic traits. Our study suggests that the population dynamic of *D. rodriguezii* is

42   stable under the current conditions, and that where dispersal is limiting, important

43   environmental changes (e.g. in habitat suitability and/or rainfall regime) might lead to local

44   extinctions.

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46   KEYWORDS: Covariation between vital rates, plant-disperser interactions, LTREs,

47   Matrix population models, Mutualism disruption

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Introduction

The phase of seed dispersal links the end of the reproductive cycle of adult plants with the establishment of recruits, and can thus significantly influence the population dynamics of plant species (Wang and Smith 2002; Levin et al., 2003; Howe and Miriti 2004; Cousens et al., 2008). All other factors being equal, seed dispersal over short distances may lead to local aggregation of plants, slower population growth and, ultimately, to lower population densities (Levin et al., 2003; Cousens et al., 2008). This pattern may emerge in environments which vary greatly in space since seedlings have very different chances of survival depending on the site they arrive at (e.g. in ecological succession or habitat degradation). Under such circumstances, the biased survival of seedlings in sites to which seeds have been dispersed results in pervasive and positive demographic impacts (Miriti et al., 2001; Godínez-Álvarez et al., 2002; Brodie et al., 2009a; Brodie et al., 2009b). Alternatively, mother plants might be concentrated in patches highly favourable for plant survival, suggesting that the disadvantage of local dispersal (i.e. seedlings emerging below adults may have high density-dependent competition) must be weighed against the disadvantage of wider dispersal into less suitable habitats (Cousens et al., 2008).

Vital rates (e.g. survival, fecundity, growth) determine the demographic parameters that describe the development of individuals throughout life-cycle transitions (de Kroon et al., 2000). In addition to disentangling which of these demographic transitions influence plant population dynamics, it is crucial to estimate those environmental variables linked to any of them (Boyce et al., 2006; Buckley et al., 2010) and if they buffer or delay the effects of environmental disturbances (Honnay et al., 2005). In long-lived species, the greater the variation in transitions (e.g. seed-to-

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73   seedling transitions), the lower is the elasticity value (defined as the relative change in

74   population growth rate resulting from small relative changes in the matrix elements; de

75   Kroon et al., 2000; Zuidema and Franco 2001) and the less likely that such transitions

76   will influence the population growth rate (Pfister 1998; Doak et al., 2005). Despite

77   stasis (i.e. the probability of surviving and remaining in a given stage from one

78   recording date to the next; Zuidema and Franco 2001) having the highest elasticity of

79   the life-cycle transitions (Silvertown et al., 1996), it is important to estimate the

80   correlation between stasis and the rest of transitions in determining elasticity values

81   (Lambers et al., 1989; Roff 2002). Plant-animal interactions (pollination, seed dispersal,

82   seed predation, etc) influence low-elasticity transitions (fecundity in long-lived species),

83   but it is also possible that their demographic effect on plant population dynamics is

84   stronger than previously thought (Ehrlén 2002; Godínez-Álvarez and Jordano 2007), as

85   fecundity can covariate with high-elasticity transitions (Boyce et al., 2006).

86   Our study is focused on *Daphne rodriguezii*, an endemic and endangered shrub

87   of Menorca Island (Balearic Islands, W Mediterranean). In this species, seedling

88   survival depends highly on other nurse-plant species (Traveset and Riera 2005;

89   Rodríguez-Pérez and Traveset 2010), and seedlings and adults are highly associated

90   with the abundance of shrub cover (Rodríguez-Pérez et al., in press). This suggests that

91   the suitability of appropriate sites for plant recruitment is key for the stability of

92   population dynamics. Compared to all other Menorcan populations, there is a greater

93   abundance and regeneration in plants inhabiting Colom Islet, a small islet near Menorca

94   (Traveset and Riera 2005). There is no evidence of historical disturbance in these

95   populations (P. Fraga pers. com.) and, thus, Traveset and Riera (2005) suggest that the

96   main cause of population decline in Menorca is the loss of its only seed disperser, the

97   frugivorous lizard *Podarcis lilfordi*. Most fruits remain undispersed below mother

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98   plants in Menorcan populations (disrupted populations, hereafter), whereas in Colom

99   Islet (undisrupted population, hereafter) *P. lilfordi* defecates seeds in habitats

100   appropriate for seedling establishment (Traveset and Riera 2005; Rodríguez-Pérez and

101   Traveset 2010; Rodríguez-Pérez et al., in press). In the disrupted populations, seedlings

102   recruit under mother plants creating high density clumps which ultimately have a low

103   survival probability (Rodríguez-Pérez et al., submitted). In the close vicinity of adult

104   plants, plant aggregation is much higher in disrupted than in undisrupted populations

105   (Rodríguez-Pérez et al., submitted). We can thus hypothesize that if co-specific

106   competition is strong, the lack of seed dispersers could have a greater negative effect for

107   the population dynamics of the disrupted populations. Much empirical evidence exists

108   in relation to the influence of the failure of mutualists on the early regeneration stages of

109   their plant partners, but there is still little evidence on whether these disruptions cascade

110   into the plant population dynamics (but see , for instance, Christian 2001; Sharam et al.,

111   2009; Anderson et al., 2011). Here, we studied the demography of D. rodriguezii over a

112   period of eight to ten years in a total of five populations. The data obtained were used to

113   construct matrix population models in order to answer two questions: a) Do undisrupted

114   and disrupted populations differ in their past, present and future population dynamics?

115   and b) How do life-cycle transitions (stasis, growth, retrogression, fecundity) vary,

116   interact and influence population growth rate?

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118   ***Material and methods***

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120   **Study species**

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122   *Daphne rodriguezii* Teixidor (Thymelaeaceae) is an evergreen shrub that reaches

123   up to 1.5 m in height and lives no longer than 50 years (Rodríguez-Pérez et al. unpubl.

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124   data). It inhabits coastal shrublands and grows mostly under shrubs of *Phillyrea latifolia*

125   subsp. *media*, *Pistacia lentiscus* and *Erica multiflora* (Appendix 1). The distribution of

126   *D. rodriguezii* is highly fragmented and mainly scattered throughout the north-western

127   part of Menorca Island. It is also present in Colom Islet, a small islet (c. 60 ha) very

128   close to Menorca (c. 250 m offshore) and with similar climatic conditions (temperature

129   and precipitation) than Menorca (see Appendix 1). From January to March, new shoots

130   develop, just before flowering. Fruit set is consistently low (<10% of flowers turn into

131   fruits) and selfing is infrequent (Traveset and Riera 2005; Rodríguez-Pérez and Traveset

132   2011). *D. rodriguezii* reproduces only through seeds. Orange-red drupes develop from

133   May through June and, at Colom Islet, are consumed by the endemic lizard *Podarcis*

134   *lilfordi*. This frugivore is its only seed disperser and it only coexists with *D. rodriguezii*

135   there (Traveset and Riera 2005; Rodríguez-Pérez and Traveset 2010). The passage of

136   seeds through the digestive tract of lizards does not affect their germination capacity

137   (Santamaría et al. 2007; Rodríguez-Pérez and Traveset 2010). The proportion of post-

138   dispersal seed predation varies between populations (Traveset and Riera 2005), but it is

139   consistently very high (i.e. it is independent of the presence of the seed disperser) and

140   mostly caused by rodents (Traveset and Riera 2005; Appendix 1). All of the unpredated

141   seeds from Menorcan populations are de-pulped by ants and beetles (pers. obs.).

142   However, seeds are left intact, have high chances of germination (pulp removal de-

143   inhibits seed germination capacity; Santamaría et al 2007), and are usually left in the

144   close vicinity of mother plants, where survival probabilities are proportionally lower

145   (Rodríguez-Pérez et al., submitted).

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147   **Field data collection**

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149   We considered five plots within each population which are representative of a)

150   the whole range of the species distribution (Appendix 2), b) the range of population

151   sizes and c) the disperser presence (disrupted *vs*. undisrupted): four disrupted in

152   Menorca (Porter, Mesquida, Pudent and Favàritx ranging from 50 and 300 individuals)

153   and the only undisrupted population in Colom Islet (with up to 18,000 individuals). For

154   more biological information, see Appendix 1. In 1999, we initially monitored three

155   populations (Porter, Mesquida and Colom Islet). In the first two, we marked (with

156   permanent metallic tags) all the plants that were detected during intensive surveys

157   throughout each plot. Subsequent surveys confirmed we had marked all plants in the

158   population. Due to the high plant density in Colom Islet (about ten-times higher than in

159   disrupted plots, see Appendix 1), we selected a smaller plot of c. 80 m^2 and we tagged

160   and monitored all individuals in it. This plot appeared representative of a large (and

161   comparable) area in the undisrupted population (see Appendix 1). In subsequent years,

162   we included plots from two other disrupted populations (Pudent in 2000 and Favàritx in

163   2001) where the proportion of monitored plants ranged from 60-75% of the entire

164   population (pers. obs.).

165   For each plant, we measured height, maximum crown diameter, and fruit crop.

166   Plant measures were recorded in yearly field surveys before the summer (in early May).

167   At this time, most fruits begin to ripen (and are quickly removed by lizards in Colom

168   Islet) whereas new seedlings emerge early in the year (between November and March).

169   We tagged and measured new recruits in each field survey. A total of 1,073 plants were

170   marked and monitored during the entire study period. The study concluded with the

171   2008 survey.

172   **Plant size categorization**
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174   Before building projection matrices, plants were grouped into size-classes. The

175   volume of the cylinder enclosing each plant was used as a biological criterion to

176   categorize plants. This volume was log transformed and grouped into five size-classes,

177   using the *k*-means clustering method in STATISTICA 6.0 (Statsoft Inc. 2005). We also

178   checked if the classes to which each plant had been assigned were heterogeneous

179   enough by using independent criteria (such as plant survival and mean flower

180   production), and found that they were indeed different [Generalized Linear Models:

181     $\chi^2 > 186.5$, d.f = 4, $p < 0.0001$, for both analyses; GENMOD procedure, SAS statistical

182   software]. In the entire study, we used the following size-class boundaries: (1) seedlings

183   (Sdl, no reproduction, smaller than 30 cm^3), (2) juveniles (Juv, <10% reproducing

184   yearly, smaller than $2*10^3$ cm^3) (3) small reproductives (S Rep, <25% reproducing

185   yearly, smaller than $1*10^4$ cm^3), (4) medium reproductives (M Rep, c. 75% reproducing

186   yearly, smaller than $6*10^4$ cm^3) and (5) large reproductives (L Rep, c. 90% reproducing

187   yearly, larger than $6*10^4$ cm^3). *D. rodriguezii* does not have a seed bank (Traveset and

188   Riera 2005), and this stage was thus not considered as a new size-class.

189   **Deterministic demographic analysis – current and past demographic**
190   **trends and influence on vital rates**
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192   For each pair of consecutive years, we constructed a total of 42 projection

193   matrices (seven to nine for each plot). The annual fecundity of each size-class was

194   calculated as the fruit number multiplied by the probability of surviving post-dispersal

195   seed predation and seedling emergence (see Appendix 3). The deterministic population

196   growth rate (λ), or dominant eigenvalues, and their confidence intervals (95%) were

197   obtained following Alvarez-Buylla and Slatkin (1993). For each plot, the stable-class

198   distribution (or dominant right eigenvector) was compared with the observed

199   distribution using a G-test. These estimates were averaged by years. To combine life-

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200   cycle and size-class transition, we added matrix elements following the methodology

201   described in Caswell (2001, p. 206-256). The deterministic λ, sensitivity (i.e. dominant

202   eigenvalue to small changes in each of the elements of the projection matrix), elasticity

203   (i.e. sensitivity of the dominant eigenvalue to proportional changes), reproductive value

204   (i.e. left eigenvector of the dominant eigenvalue) and stable-class distribution were

205   calculated with the software PopTools 3.0.3 (Hood 2008). For more information about

206   general methodology applied to matrix population models, see Caswell (2001).

207   **Spatial and temporal variability on plant fate: log-linear models**
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209   We performed log-linear models to identify the effect of size-class, plot and year

210   on the current plant fate (transition from t to $t+1$). We built a four-way contingency

211   table of counts of observed transitions, including the following variables: size-class in t

212   (C), plot (P), year (Y) and fate (i.e., size-class in $t+1$; F). In addition to the five size-

213   classes described above, death was included as another class in the fate effect. We

214   considered only hierarchical models, in which the presence of a given interaction

215   implies the presence of all lower-order interactions; for instance, a CYP interaction

216   includes the effects of CY, CP, YP, besides the separate effects of C, Y and P. The

217   model goodness-of-fit (G^2) was calculated by comparing each model with the saturated

218   one (CYP, which includes all the effects). In order to test the within-class variability, we

219   also analysed the effects of plot and year on the fate of each size-class.

220   Contrasts between specific factors were calculated as the difference between G^2

221   for the two models (ΔG^2). ΔG^2 values closer to zero mean that a given reduced model

222   fits as well as the saturated model (i.e. reduced models with smaller ΔG^2 values

223   explained proportionally better the observed plant fate). Because we dealt with a two-

224   way factor design (year and plot), each effect was tested in two different ways,

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225   depending on whether models included only the tested effect (mutual independence,

226   suggesting that *P* was independent of *Y* and *Y* was independent of *P*) or whether this

227   was subsequently added to a model that previously did not include it (conditional

228   independence, which denotes the partial association between *PY* and *YP*). For more

229   information about this methodology applied to demographic data, see Caswell (2001, p.

230   326-335).

231   **Stochastic simulations: future trends**
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233   To estimate the future viability of *D. rodriguezii*, simulations were performed

234   multiplying the distribution of size-classes using a matrix drawn at random each time.

235   We chose this methodology as it preserves the correlation structure among vital rates

236   (Menges 2000). This is a fair assumption, considering that we detected demographic

237   trade-offs between vital rates in our study species (see *Results*). In order to check the

238   independence of the environmental conditions in the different years measured, we

239   analysed the correlation in rainfall among years. For instance, high-rainfall years could

240   be followed by low-rainfall years (negative autocorrelation), whereas high-rainfall years

241   might occur in strings (positive autocorrelation). In our case, we detected a positive

242   autocorrelation in rainfall but this trend was weak (i.e. Spearman $R^2 = 0.11$, value

243   averaged by plots); hence, we consider that environmental conditions of a given year are

244   independent from those of the previous one.

245   Furthermore, we wanted to separate the effect of population size and its past

246   population dynamics and thus we simulated each plot (500 replicates) under the same

247   initial size (*n*=100) and the size-class distributions (averaged across plots and years).

248   The stochastic λ was then calculated as $\log \lambda s = (\log N_t - \log N_0)/t$ (Caswell 2001, p. 387-

249   401), N_0 and N_t being the initial (observed) and the after-simulation plot sizes,

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250   respectively. The proportion of iterations that led to population extinction (i.e. all plants

251   of a given plot died) was used as a *proxy* to calculate its vulnerability to future

252   extinctions. Simulations were performed using a specified 'visual program'

253   implemented in Microsoft Excel (K. Lehtilä, X. Picó). Since this procedure does not

254   include demographic stochasticity and density-dependent survival (see Brook 2000 for

255   discrepancies and concordances between observed and estimated projections) we

256   projected plots up to a short-time scale (up to the maximum age of older individuals, see

257   *Study species*). Unless otherwise indicated, average values are reported as mean ±

258   standard error (± 1 SE).

259   Life table response experiments (LTREs): decomposing spatial and
260   temporal variability of population dynamics
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262   Life table response experiments (LTREs) allow the decomposition of the

263   observed variance of λ into life-history transitions (Caswell 2001, p. 258-

264   278). This μετηοδ αδδρεσσεσ τηε εξτεντ το ωηιχη εαχη ματριξ εντρψ ισ ρεσπον

265   σιβλε φορ χηανγεσ ιν τηε λ value of a given matrix, as compared to the λ value of the

266   average matrix. In the present study, 'plot' and 'year' were considered and analysed as

267   fixed effects due to the different intrinsic traits of each plot (presence of seed disperser,

268   population size) and year (specific abiotic conditions, see Appendix 1). Effects of main

269   factors and their interactions were decomposed into 'contributions' (i.e. deviance of the

270   corresponding matrix element to the mean matrix; Caswell 2001, p. 261). For each life-

271   history trait, we first assessed whether the overall contribution forof each matrix (42)

272   was correlated with its □. In our case, we also calculated the relative λ of each matrix

273   ($\Delta\lambda$) based on: a) differences among plots within the same year (i.e. the λ value and the

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274   yearly averaged λ), and b) differences among years within the same plot (i.e., between

275   each □ value and the □ averaged □by plots).

276   Given that rainfall is one of the most variable environmental factors in arid and

277   semiarid environments and may influence the population dynamics of long-lived

278   species (Marrero-Gómez et al., 2007), we further explored if the temporal variability in

279   'contributions' was associated to annual rainfall. Hence, we correlated the yearly-

280   decomposed contributions with the averaged annual rainfall of the five studied plots;

281   rainfall data came from the closest meteorological station of each plot (i.e. not farther

282   than 5 km away; data from the Balearic Meteorological Institute).

283   In addition to computing the overall effect, 'contributions' were summed across

284   positive and negative values (net effects) separately for life-history transitions and plot.

285   This dissecting procedure provides a clearer biological picture of vital rates, since it

286   explores how positive and negative contributions compensate each other, and highlights

287   hidden trade-offs between life-history elements (Jongejans and de Kroon 2005).

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289   *Results*

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291   **Population dynamics: past, present and future trends**
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293   In all plots, the most abundant individuals were those in the reproductive size-classes

294   (>50%; Fig. 1). The plots with the highest proportions of reproductives (63%, on

295   average) were all disrupted, whereas the undisrupted and one of the disrupted plots

296   (Porter) had a high proportion of seedlings and juveniles (37%; Fig. 1). Plots from the

297   two largest populations (Pudent and Colom Islet) had similar observed and stable-class

298   distributions (Fig. 1). In the other plots, there was discordance between observed and

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299   stable-class distributions, suggesting that these plots were currently in transient

300   dynamics.

301   Pooling all size-classes, plant fate was found to be rather variable and such

302   variation was better explained by the plot effect (i.e. ΔG^2 values were smaller; Table 1).

303   A plot effect was found to be more important in seedlings' and small reproductives' fate,

304   whereas the year effect was the most important for juveniles. For small reproductives

305   and juveniles, there was no year effect (Table 1). In the case of medium and large

306   reproductives, conditional dependence explained plant fate better (i.e. conditional ΔG^2

307   values were smaller than marginal values; Table 1).

308   During the study period, deterministic λ either decreased or was stable in each

309   plot, regardless of the absence of the disperser (Fig. 2). Mesquida and Pudent had, on

310   average, relatively high values of λ due to their high stasis of reproductive adults

311   (Appendix 3). By contrast, the other plots had low values of λ, due to the low survival

312   and high retrogression of large reproductives (Porter and Colom Islet), low survival of

313   small reproductives and juveniles (Porter) and low fecundity (Favàritx; Appendix 3).

314   The lowest λ in Colom Islet was found in 2004 (see Fig. 2), due to an unusual low stasis

315   (and survival) of medium reproductives (c. 38% lower than average); the λ for this year

316   was likely extreme for the population dynamics of this population due to non-different

317   observed and stable-class distributions (Fig. 1).

318   Stochastic simulations showed that the vulnerability for the next 50 years was

319   moderate on Colom Islet (21%). When we excluded the projection matrix of 2004 in the

320   simulations, the vulnerability decreased up to 5.8% in the latter plot. Vulnerability was

321   also moderate in two out of four disrupted plots (Porter: 38.0% and Favàritx 18.6%)

322   whereas it was almost null (<0.1%) in the others (Pudent and Mesquida).

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Spatial-temporal variability, interaction among vital rates and their influence on λ

As in many long-lived species, stasis accounted for most of the elasticity (90.9%±3.0; Appendix 3) and the lowest variability of life-cycle transitions (Appendix 4). By contrast, fecundity had high variability but low elasticity. Reproductive plants were the size-classes with the highest elasticity (88.6%±2.23), specifically, medium (37.4%±5.7) and large reproductives (29.5%±6.2). Both size-classes accounted for the lowest variability in stasis (1.31 and 1.36, respectively; Appendix 4).

Overall, LTREs showed that the observed variability in deterministic λ mostly depended on the 'plot x year' interaction (44.8%), followed by year (33.2%) and plot (21.9%). The difference between observed and modelled λ (i.e. calculated from the decomposed contributions of each life-history transition) was rather low (1.54%±0.16), indicating that the two-way decomposition of the variance fitted well with the observed λ. When we decomposed the relative contribution of each year and correlated it to annual rainfall, we did not observe any trend (Spearman R= 0.233, *p*= 0.552). However, when we removed the year 1999 (there was an inverse trend between contribution for that year and rainfall; see Fig. 4a) and we repeated the analysis, we detected a significant association between both variables (Spearman R= 0.762, *p*= 0.0368) suggesting that an important fraction of the contribution variability depended on annual rainfall. According to the variability in life-cycle transitions, only the $\Delta\lambda$ regarding the differences among plots was significantly associated with the relative contribution of each transition (Table 2). Specifically, the $\Delta\lambda$ was positively correlated to the contributions of stasis and growth (Fig. 3). Such variation did not depend on rainfall variability since it was not correlated to contributions for either life-cycle transition (see

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349   Table 2). We also detected trade-offs between contributions: fecundity was correlated

350   negatively and positively, respectively, to stasis and retrogression (Appendix 4).

351   Within plots, the magnitude of contributions by life-cycle transitions was highly

352   variable. Stasis was the most important element in two disrupted plots (Mesquida and

353   Favàritx); in the former, this life-cycle transition was responsible for its relatively high

354   value in λ (Fig. 4c) whereas in the latter, its positive contribution was unbalanced by the

355   negative effect of the rest of life-cycle transitions (Fig. 4e). In Colom Islet, by contrast,

356   contributions were negative in most life-cycle transitions (especially stasis and growth),

357   which finally resulted in an overall relatively low contribution (Fig. 4f). The positive

358   contributions of stasis and growth on Pudent were responsible for its overall positive

359   effect (Fig. 4d). Despite the fact that fecundity contribution was strongly positive on

360   Porter, the relatively low plot effect was due to its low stasis and growth (Fig. 4b).

361

362   ***Discussion***

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364   **How did the variability and interaction among vital rates affect the population**
365   **dynamics of *D. rodriguezii*?**

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367   Persistence of plant populations greatly depends on the fluctuations of environmental

368   conditions (Menges 2000; Doak et al., 2005; Boyce et al., 2006; Salguero-Gómez and

369   de Kroon 2010; Buckley et al., 2010). In the case of *D. rodriguezii*, plant fate varied

370   much among plots for seedlings and medium reproductives (both pooled), but showed

371   to be independent of environmental variability (year or plot) for juveniles and small and

372   large reproductives. Despite most of the observed variability in deterministic population

373   growth rate (λ) was intrinsically "random" (i.e. 45%), an also important fraction (33%)

374   was explained by temporal variability. After decomposing the λ variability among

375   years, we detected that the relative contributions depended on rainfall; in other words,

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376   lower and higher rainfall than average (c. 550 mm) cascaded into a negative and

377   positive λ, respectively, in *D. rodriguezii*. Our results agree with those of Marrero-

378   Gómez et al. (2007) who found that the population dynamics of the narrow endemic

379   shrub *Helianthemum juliae* in the Canary Islands is also affected by rainfall. These

380   authors argue that rainfall (highly variable in arid and semiarid environments) could be

381   an environmental factor influencing the population dynamics of long-lived species. The

382   greater temporal variation in plant populations is partly scale-dependent due to similar

383   environmental factors in spatially close populations (Buckley et al., 2010). In our case,

384   study plots were located less than 40 km apart from each other, suggesting that

385   environmental conditions (in this case, rainfall) are equivalent and potentially

386   meaningful for the population dynamics of the five studied populations of *D.*

387   *rodriguezii*. Our findings further suggest that λ was also explained by an important

388   fraction of its variability decomposed by life-cycle transitions, specifically, its

389   dependence on stasis and growth. Our data did not allow us to detect correlations

390   between rainfall and λ variability decomposed by life-cycle transitions, suggesting that

391   the contribution of vital rates to λ is compensated within plots (Jongejans and de Kroon

392   2005).

393   Even though the rest of low-elasticity life-cycle transitions (growth,

394   retrogression and fecundity) contribute relatively little to λ, we detected demographic

395   trade-offs among them at the plot level. In Mesquida and Pudent, for instance, positive

396   contributions in stasis and/or growth compensate the negative contributions for the rest

397   of life-cycle transitions, and λ was thus higher than average in both plots. By contrast,

398   the relatively low λ for the rest of the plots resulted from a negative contribution in most

399   life-cycle transitions. Due to resource limitation, physiological allocation in one vital

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400   rate may also be detrimental to the other vital rates (Lambers et al., 1989; Roff 2002). In

401   *D. rodriguezii*, positive contributions to fertility were weakly associated with negative

402   and positive contributions to stasis and retrogression, respectively. Fertility is the most

403   variable life-cycle transition in *D. rodriguezii* (as it occurs in the rest of long-lived

404   species; Silvertown et al., 1996) which suggests that high investment of resources in

405   fruit production during the reproductive season could strongly influence the rest of the

406   life-cycle transitions. Our hypothesis could thus be supported at the plot level. For

407   instance, Porter showed the highest contribution to fertility but the lowest λ of the five

408   studied plots, probably due to its high fruit production per plant (Appendix 1) and low

409   stasis of reproductives (Appendix 2). By contrast, Pudent and Mesquida have

410   comparatively low fruit production (Appendix 1), which probably translates into high

411   stasis and the most stable λ of the studied populations.

412   When individuals share the same environment, vital rates could be directly

413   correlated to the close environmental conditions (Doak et al., 2005). Lack of seed

414   dispersal leads to local aggregation of recruits and adults, which in turn leads to higher

415   competition for space and resources (Harper 1977). Here we detected negative

416   correlations in the variance of life-cycle transitions, interactions which could be

417   magnified when recruits compete for resources with adults in "good" years (when

418   rainfall is higher than average; Rodríguez-Pérez and Traveset 2010). This is what

419   probably occurs in our disrupted populations, since recruits achieve high local densities

420   and have proportionally lower probabilities of survival in the close proximity of

421   reproductives (Rodriguez-Perez et al. submitted). Thus, our findings point out to the

422   necessity of studying also the variability of ecological determinants that affect vital rates

423   when predicting its demographic consequences into plant species (Salguero-Gómez and

424   de Kroon 2010).

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Is the loss of its disperser important for the population dynamics of *D. rodriguezzi*?

Despite the broad evidence that seed dispersal is important for plant population dynamics (Wang and Smith 2002; Levin et al., 2003; Howe and Miriti 2004), there are few examples examining its effect within the entire plant's life cycle. In those cases, seed dispersal 'matters' for population dynamics because the frugivores dispersing more seeds increase their germination capacity and/or move them also to high quality sites for seedling establishment (Godínez-Álvarez et al., 2002; Brodie et al., 2009a; Brodie et al., 2009b). In the present study, however, we found that λ of the undisrupted population is similar to that in half of the disrupted ones. This is probably because short-term regeneration processes such as emergence (i.e. ingestion does not affect seed germination) and seedling survival (i.e. survival is consistently high under nurse plants) do not depend on the presence or absence of the seed disperser (Traveset and Riera 2005; Rodríguez-Pérez and Traveset 2010).

In spatially heterogeneous environments, adult plants are likely to be located in patches which are highly favourable for survival and, thus, local dispersal may be more advantageous than longer dispersal (as habitats might be less suitable) for the population dynamics (Cousens et al., 2008). Regardless of the presence of the disperser, reproductives of *D. rodriguezii* are mostly concentrated under nurse shrubs (Rodríguez-Pérez et al., in press), which happen to be the best places for seedling survival (Traveset and Riera 2005; Rodríguez-Pérez and Traveset 2010). We also observed that λ remains approximately stable in two disrupted plots (Mesquida and Pudent) and that it is independent of population size (Appendix 1). Since environmental variability is a measure to predict species population dynamics in heterogeneous landscapes (Wiegand et al., 1999; Chisholm and Wintle 2007), it is likely that the two latter disrupted

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451 populations remain demographically stable because habitat features in them are

452 appropriate for the species persistence. Long-living forest plants can have remnant

453 populations not in equilibrium with the current degree of habitat fragmentation (Honnay

454 *et al.,* 2005), which is attributed to the still optimal conditions in habitat fragments. In

455 our case, however, three of the four disrupted populations are in transient dynamics (see

456 Fig. 1), which suggests that their current population instability might be due to changes

457 in habitat quality.

458   Where lizards still persist, *D. rodriguezii* maintains high levels of plant

459 regeneration (i.e. seedlings and juveniles are proportionally more abundant than

460 reproductives) and a stable λ (if we exclude the unusual year, 2004). In Colom islet,

461 most plants are located in high-quality sites (Rodríguez-Pérez et al., in press) and they

462 are less aggregated at small distances than in the populations without lizards

463 (Rodríguez-Pérez et al., in prep). This allows the islet population to respond to any

464 environmental disturbance, because dispersers can move seeds into high-quality habitat

465 patches. A revealing study by Miriti et al. (2001) detected that changes in survival of

466 isolated adults of a perennial desert shrub (despite lower success during early stages of

467 recruitment) have greater influence on λ than changes in survival of adults close to

468 neighbours. Consequently, the importance of seed dispersal for the population dynamics

469 of long-lived plants may emerge in the long-term, and this is independent of whether its

470 effects on the population dynamics are positive (Godínez-Álvarez et al., 2002; Brodie et

471 al., 2009a; Brodie et al., 2009b), neutral (present work) or negative (Miriti *et al.,* 2001).

472   The few studies examining whether the failure of mutualisms has implications

473 for plant population dynamics, point to strong cascading effects (Christian 2001;

474 Sharam et al., 2009; Anderson et al., 2011). In our case, such an effect does not appear

475 to be so strong, at least from a demographic viewpoint. *D. rodriguezii* is highly

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476   associated with nurse plants (Traveset and Riera 2005; Rodríguez-Pérez et al., in press),

477   and positive plant-plant interactions seem thus one of the main forces governing its

478   population dynamics. This leads to assume that its populations could remain stable

479   within the current environmental conditions, independently of the seed-disperser

480   presence. Yearly rainfall (as a *proxy* of resource availability) includes demographic

481   "noise" in the population dynamics of *D. rodriguezii*: when rainfall is below the

482   average, λ declined (present work) but there is no competition of recruits beneath adults

483   (Rodríguez-Pérez & Traveset 2010). This suggests that plant-plant interactions buffer

484   population dynamics when resources are limiting, allowing a proportionally higher

485   survival of recruits when seed disperser is absent.

486   Since environmental factors strongly influence the population dynamics of

487   perennial plants (Buckley et al., 2010), it is thus likely that such demographic effects

488   influence *D. rodriguezii* by changes in the abundance of high-quality habitats. If this is

489   the case, seed dispersal would matter (Howe and Miriti 2004) because it would be a

490   demographic process helping to stabilize population dynamics in case of environmental

491   variability (Levin et al., 2003; Cousens et al., 2008). In disrupted populations, plants

492   currently live in high-quality 'islands' of habitat (i.e. habitat features fulfil the

493   ecological conditions to maintain stabilized populations) and, having lost the seed

494   dispersal capacity, they are not able to move between habitat patches (Rodríguez-Pérez

495   et al., in press). Consequently, plant species may face local extinctions under moderate-

496   to-strong changes in habitat quality (Cousens et al., 2008).

497   In short, the demographic consequences on *D. rodriguezii* may not be so

498   dramatic after the loss of its seed disperser, provided that habitat quality remains stable.

499   This may create time-lags to population extinctions that can take up to thousands of

500   years to come into completion (Sax and Gaines 2008).

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612   Table 1 - Log-linear analyses for the effect of plot (P) and year (Y) on the plant fate,

613   including the matrices decomposed by plant size-classes. Each effect over plant fate was

614   explored as the difference between the dependent-effect model and the saturated model

615   (see material & methods). The effects of including another factor under parenthesis test

616   for conditional independencey (see Caswell 2001, p. 326-335); i.e., P (Y) means that the

617   effect of plot (P) when added to a model already contained years (Y). In all analyses, the

618   P x Y interaction effect was never significant ($\Delta G2 > 58.0$, $p = 1.000$, for all analyses).

619   *** p <0.001 ** p <0.01 *p <0.05 † p <0.1

620

	All Stages		Seedling		Juvenile		S Rep		M Rep		L Rep	
Effect	**Δdf**	**ΔG²**	**Δdf**	**ΔG²**	**Δdf**	**ΔG²**	**Δdf**	**ΔG²**	**Δdf**	**ΔG²**	**Δdf**	**ΔG²**
Y	200	226.7†	40	70.0**	40	34.4 n.s.	40	38.0 n.s.	40	61.0*	40	23.7 n.s.
P	100	196.3***	20	34.7*	20	47.2**	20	27.9 n.s.	20	34.4*	20	52.1***
P (Y)	100	204.9***	20	43.5**	20	52.7***	20	28.8†	20	31.6*	20	48.3***
Y (P)	200	235.4*	40	78.8***	40	39.5 n.s.	40	38.9 n.s.	40	58.2*	40	19.9 n.s.

621

622 Table 2 – Spearman-rank correlations between the contributions of each matrix ($n =$

623 42), in respect to (a) λ, (b,c) the relative λ and (d) annual rainfall. The relative λ of each

624 matrix (Δλ) was calculated following two criteria: b) in respect to differences between

625 each λ value and the averaged λ by plots within the same year, and c) to differences

626 between each λ value and the yearly-averaged λ within the same plot. Additionally, we

627 correlated the contributions for each matrix with the annual rainfall. For more

628 information, see *Material and Methods.*

	Life-cycle transition	R	t (n-2)	*p*
a) λ	Stasis	0.210	1.36	0.181
	Fecundity	-0.108	-0.688	0.495
	Growth	0.259	1.70	0.098
	Retrogression	0.198	1.28	0.209
b) Δλ by plots	Stasis	0.647	5.37	<0.0001
	Fecundity	-0.015	-0.094	0.926
	Growth	0.420	2.92	0.006
	Retrogression	0.065	0.411	0.683
c) Δλ by years	Stasis	0.244	1.59	0.119
	Fecundity	0.038	0.242	0.810
	Growth	0.092	0.586	0.561
	Retrogression	0.246	1.61	0.116
d) Rainfall	Stasis	0.036	0.229	0.820
	Fecundity	0.046	0.290	0.773
	Growth	-0.034	-0.217	0.829
	Retrogression	0.160	1.028	0.310

629

630

631   Figure captions

632   Figure 1 - Average distribution of individuals belonging to the observed (black bars)

633   and the stable-stage (white bars) size-classes. For each plot, we calculated the

634   significance between observed and stable-stage proportions. Year variability is

635   denoted in error bars (± 1 SE). Abbreviations: Sdl: seedlings, Juv: juveniles, S, M,

636   L Rep: small, medium and large reproductives.

637

638   Figure 2 - Deterministic population growth rate (λ; ± 95% CI) across plots and years.

639   Confidence intervals were calculated following Alvarez-Buylla and Slatkin

640   (1993). Dashed line represents the λ at stability (i.e. λ=1). For each plot, we also

641   showed the average λ across years.

642

643   Figure 3 - Contribution of each vital rate to the variance of the population growth rate

644   (X axes), in respect to the relative population growth rate ($\Delta\lambda$, Y axes). For each λ

645   value, we calculated its $\Delta\lambda$ in respect to the averaged λ by plots, since it explained

646   the contributions of two out of four vital rates (Table 2). Note that the values of

647   each plot are denoted with different symbols.

648

649   Figure 4 - Contributions to the average matrix in λ (a) across years and (b-h) vital-rate

650   transitions. For years, we plotted contributions yearly-decomposed (bars and left

651   Y-axes); in other words, positive contributions (white bars) meant a proportionally

652   higher value for a given year than the average contribution. We also showed the

653   mean annual rainfall averaged by plots (grey line and right Y-axes); the average

654   value for the whole studied period was c. 550 mm. For vital-rates [i.e., fecundity

655   (F), stasis (S), growth (G) and retrogression (R)], the total contribution for each

656   plot (γ) was decomposed and grouped into positive and negative contributions

657   (white and black bars, respectively).

658   Appendix 1 – Differences between plots in some abiotic and biotic traits. Disrupted

659   plots (i.e. without the presence of the seed disperser: Porter, Mesquida, Pudent and

660   Favàritx) are located in Menorca Island whereas the undisrupted plot (i.e. the disperser

661   is present there; Colom Islet) was in an Islet nearby Menorca (c. 250 m offshore).

662   Climatic information (rainfall and temperature) came from the closest meteorological

663   station of each plot (no longer than 5 km; data from the Balearic Meteorological

664   Institute) and soil variables (conductivity, organic matter and total nitrogen [N:

665   Kjeldahl's method]) from 5 soils samples collected up to 5cm in depth; samples were

666   sampled and analysed in 2002 by the Agriculture Department of the Balearic Islands.

667   We also estimated plant plot size, plant density (in each study site plot), percentage of

668   plant occurrence under shrubs and fruit crop and fruit set (averaged for each year); these

669   estimates were based on the number of reproductive plants. Shrub abundance was

670   calculated from a habitat map (1:1000 cartography) included in a GIS platform; this

671   map have the following categories: open habitat (i.e. bare soil and rocks) and shrubs

672   (i.e., *Phillyrea latifolia*, *Pistacia lentiscus*, *Erica multifolia*, *Rosmarinus officinalis* and

673   *Santolina chamaecyparisus*). In previous studies, we estimated post-dispersal seed

674   predation and seedling emergence by field experiments (Traveset & Riera 2005;

675   Rodríguez-Pérez & Traveset 2010); the average values of these experiments are shown

676   here.

677

Abiotic and biotic traits	Porter	Mesquida	Pudent	Favàritx	Colom Islet
Abiotic					
Plot sampling area (m^2)	7480.2	5741.0	4142.2	2959.3	80.0
Rainfall per year (mm)	541.8	548.4	579.4	440.8	589.5
Average temperature (Celsius)	16.5	16.9	16.8	16.9	16.8
Facing slope	S	W	W	W	W
Average distance to sea (m)	50	110	90	80	50
Soil conductivity (dS/m)	2.28	1.63	3.30	1.09	5.08
Organic matter (%)	8.66	8.06	2.70	2.44	3.50
Total Nitrogen in soil (mg N/L)	0.67	0.61	0.16	0.14	0.22
Biotic					
Plant plot size	48	47	298	168	c.18,000
Plant density (Plant/m^2)	0.033	0.041	0.045	0.051	0.447
Shrub abundance (%)	63.7	68.5	86.4	86.9	74.4
Plant occurrence under shrubs (%)	57.2	80.5	81.8	73.5	81.2
Fruit crop	9.4±7.4	4.3±4.8	4.9±4.9	6.0±7.3	6.0±4.8
Post-dispersal seed predation (%)	78.4	60.7	91.5	99.5	97.3
Seedling emergence (%)	26.9	43.9	23.0	15.7	42.1
Presence of seed disperser	No	No	No	No	Yes

678

679   In a larger area (i.e. 3619.2 m^2) and a few meters apart from the monitoring plot

680   in Colom Islet, we also measured the abundance of plants by size-classes (see

681   Rodríguez-Pérez et al., in press). There, we found an also high plant density (this time,

682   six-times higher than disrupted plots) and that the size-class plant abundance (see Fig.

683   1) did not differ between those two plots ($\chi^2_{10} = 10.0$, p = 0.265). This indicates that our

684   monitored (but small) undisrupted plot is representative of the population dynamics of a

685   large area in our undisrupted population (Colom Islet).

686

687   References

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698   a spatially-explicit analysis of a plant-disperser interaction. – Ecography

699 Appendix 2 - Location of study sites of *D. rodriguezii*. Black dots show names and

700 locations of study populations in the Menorca Island.
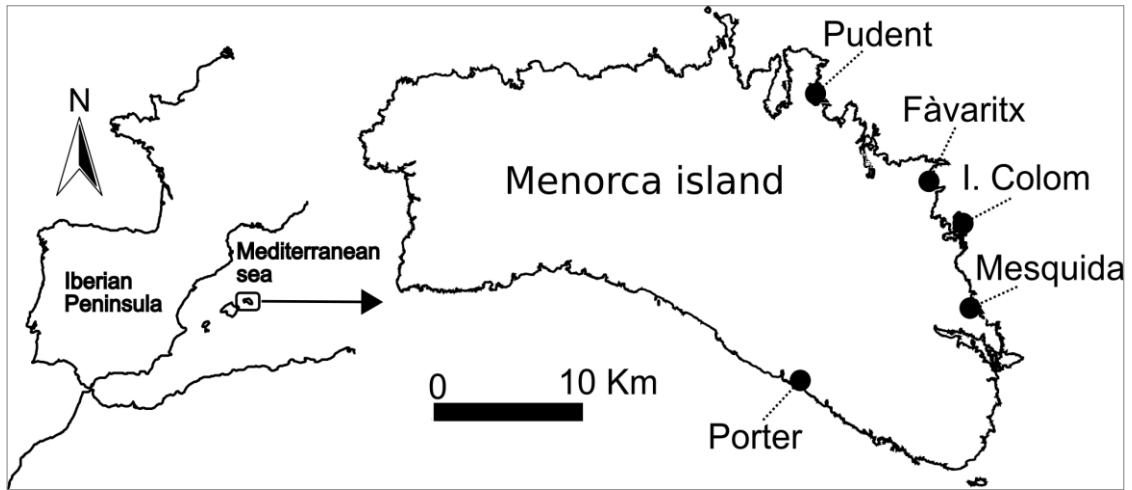
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702

703   Appendix 3 - Average transition and elasticity elements per each year, plot, life-cycle

704   and size-class of *D. rodriguezii*. For each matrix, each column (j) represents the

705   transition p_{ij} of a given size-class at time t and the rows (i) at time t+1. p_{ii} is the

706   transition of remaining in the same size-class (stasis), $p_{i>j}$ to regressing to a smaller size-

707   class (retrogression) and $p_{i<j}$ of promoting to a higher size-class (growth).

708   Fecundity, or the averaged number of seedlings that each size-class contributed

709   to each matrix, was calculated after accounting for the fruit crop per each size-class, the

710   probability of post-dispersal seed predation and the seedling emergence (see Appendix

711   1). When this information was not available from a particular year, we used the average

712   of other years in that plot. In all plots, seed germination experiments were run from

713   2000 and 2005 (Traveset & Riera 2005; Rodriguez-Perez & Traveset 2011) whereas

714   post-dispersal seed predation experiments from 2002 to 2005 (Traveset & Riera 2005;

715   unpubl. data).

716   In some years, some transitions were not observed in a given plot. For instance,

717   reproductive individuals frequently did not grow and/or retrogress in a particular year;

718   in other words, all individuals remain alive or (if any) become dead. In consequence, we

719   modify matrices in order to include those unobserved events according to a conservative

720   approach. These transitions were estimated following $p_{ij}*=1/n$, in which *n* represents the

721   sample size of a given size-class in each matrix. The maximum transition value to be

722   modified was 0.1. In case that both growth and retrogression were not observed for a

723   given size-class, $p_{ij}*$ was evenly distributed across life-cycle transitions. We only

724   modified those transitions that grew and retrogressed only one stage (i.e. j+1, j-1,

725   respectively). Finally, $p_{ij}*$ was removed from stasis since each column have to sum 1.0.

	Stage at time t+1	Transition probabilities					Elasticity				
		Sdl	Juv	S Rep	M Rep	L Rep	Sdl	Juv	S Rep	M Rep	L Rep
Porter	Sdl	0.3270	0.0165	0.1039	0.2690	1.3916	0.0284	0.0006	0.0011	0.0022	0.0066
	Juv	0.1315	0.7132	0.0513	0.0069	0.0000	0.0105	0.1139	0.0033	0.0003	0.0000
	S Rep	0.0000	0.0569	0.7279	0.0450	0.0000	0.0000	0.0135	0.0869	0.0069	0.0000
	M Rep	0.0000	0.0000	0.0602	0.8317	0.1057	0.0000	0.0000	0.0160	0.4540	0.0151
	L Rep	0.0000	0.0000	0.0000	0.0533	0.7900	0.0000	0.0000	0.0000	0.0217	0.2190
Mesquida	Sdl	0.5427	0.0000	0.0456	0.0562	0.1610	0.0054	0.0000	0.0015	0.0012	0.0025
	Juv	0.1647	0.7963	0.0594	0.0222	0.0175	0.0052	0.1491	0.0106	0.0022	0.0013
	S Rep	0.0000	0.1167	0.8653	0.0556	0.0000	0.0000	0.0193	0.2828	0.0125	0.0000
	M Rep	0.0000	0.0000	0.0568	0.8248	0.0880	0.0000	0.0000	0.0197	0.2473	0.0151
	L Rep	0.0000	0.0000	0.0000	0.0638	0.8556	0.0000	0.0000	0.0000	0.0189	0.2053
Pudent	Sdl	0.3958	0.0022	0.0270	0.0631	0.1647	0.0063	0.0000	0.0011	0.0028	0.0064
	Juv	0.1637	0.7489	0.0346	0.0042	0.0000	0.0102	0.0493	0.0017	0.0009	0.0000
	S Rep	0.0000	0.1384	0.7658	0.0519	0.0000	0.0000	0.0127	0.1303	0.0127	0.0000
	M Rep	0.0000	0.0000	0.1342	0.8262	0.0736	0.0000	0.0000	0.0227	0.3616	0.0206
	L Rep	0.0000	0.0000	0.0000	0.0790	0.8820	0.0000	0.0000	0.0000	0.0270	0.3339
Fàvaritx	Sdl	0.5671	0.0002	0.0019	0.0100	0.0157	0.0020	0.0000	0.0000	0.0004	0.0007
	Juv	0.1075	0.7435	0.0487	0.0000	0.0000	0.0011	0.0352	0.0072	0.0000	0.0000
	S Rep	0.0000	0.1210	0.7579	0.0517	0.0000	0.0000	0.0082	0.2413	0.0129	0.0000
	M Rep	0.0000	0.0000	0.0925	0.8347	0.0428	0.0000	0.0000	0.0140	0.2575	0.0115
	L Rep	0.0000	0.0000	0.0000	0.0440	0.9037	0.0000	0.0000	0.0000	0.0121	0.3959
Colom	Sdl	0.4272	0.0018	0.0165	0.0554	0.2804	0.0093	0.0001	0.0007	0.0049	0.0032
	Juv	0.1595	0.8029	0.0336	0.0103	0.0058	0.0090	0.1768	0.0050	0.0013	0.0000
	S Rep	0.0000	0.0738	0.7264	0.0411	0.0184	0.0000	0.0150	0.1505	0.0150	0.0009
	M Rep	0.0000	0.0030	0.1464	0.8443	0.1400	0.0000	0.0002	0.0245	0.4250	0.0150
	L Rep	0.0000	0.0000	0.0048	0.0377	0.7491	0.0000	0.0000	0.0006	0.0185	0.1246
		Stage at time t					Stage at time t				

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References

Traveset, A. and Riera, N. 2005. Disruption of a plant-lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. – Conservation Biology 19: 421-431.

Rodríguez-Pérez, J. and Traveset, A. 2010. Seed dispersal effectiveness in a plant–lizard interaction and its consequences for plant regeneration after disperser loss. – Plant Ecology 207: 269-280.
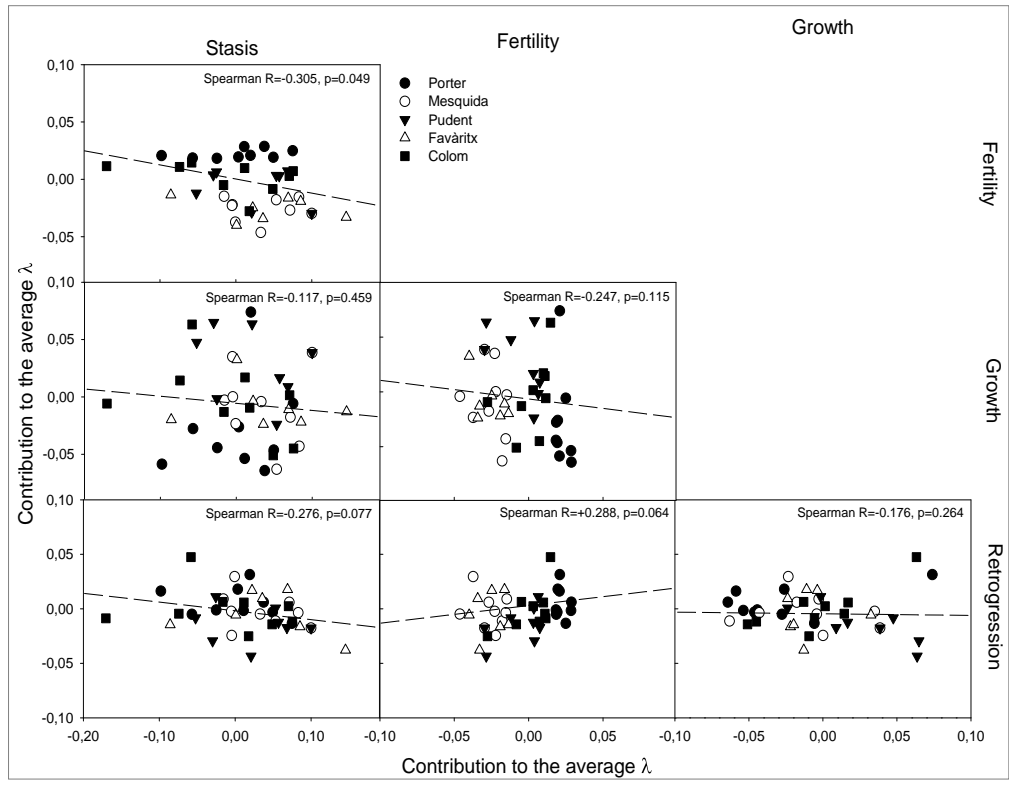
737 Appendix 4 – Coefficient of variation (CV) of life-cycle transitions for each plant size-

738 class. CV was calculated by plots (black symbols) and by years (white symbols). Stasis,

739 growth and retrogression values came from transitions of matrix elements; fertility

740 values from the number of seedlings (i.e. the fruit crop after including the probability of

741 post-dispersal seed predation and seedling emergence).
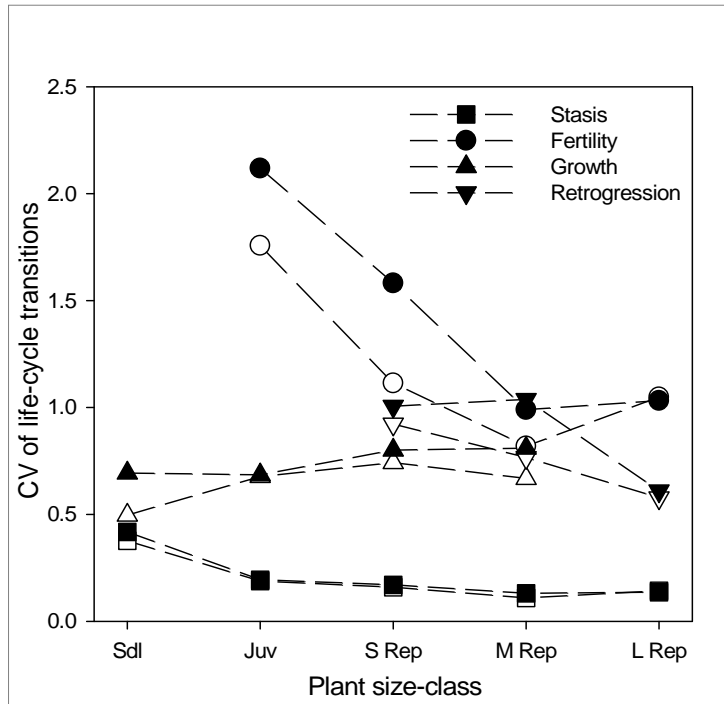
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743   Appendix 5 – Correlations of contributions between life-cycle transitions. Each point

744   represents the contribution of each plot and year for a given matrix element. Note that

745   the value for each plot was depicted in different symbols.

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