Coexistence and the niche in a nurse-cactus interaction: is cyclic dynamics justified?

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5   dynamics justified?

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Abstract

1. The interaction between the nurse plant *Larrea tridentata* and the cacti *Cylindropuntia leptocaulis* is thought to follow cyclical-replacement dynamics. However, the required changing nature of their interaction, from facilitation to competition, has not been investigated through their full life cycle.

2. In order to test the hypothesised cyclical dynamics, we compared the demography of four sub-populations (LA = *Larrea* associated to *Cylindropuntia*; CA = *Cylindropuntia* associated to *Larrea*, LS = solitary *Larrea*; CS = solitary *Cylindropuntia*) in the Mapimí Biosphere Reserve, Mexico, over the period 2008-2015. This allowed us to compare their demography at varying levels of the generally low and unpredictable limiting resource, water. Given the protection afforded to *C. leptocaulis* seedlings by *L. tridentata* and their presumed increasingly competitive effect on *L. tridentata*, which would justify the expectation of cyclic replacement dynamics, we expected to find a zero or positive *per capita* rate of population growth ($r \geq 0$) in CA and LS, and a negative one in CS and LA.

3. The overall r over the study period was close to equilibrium ($r=0$) for both LA and LS, with no significant difference between them. In contrast, and as expected, r of CA was consistently and significantly larger than that for CS. In both species, λ ($=e^r$) was positively correlated with annual rainfall with no significant difference between LA and LS and a significant difference between CA and CS in this relationship. *L. tridentata* can exist alone and coexist with *C. leptocaulis* across the levels of precipitation experienced at the study site, while *C. leptocaulis* cannot persist in the absence of *L. tridentata*. The cyclical dynamics of replacement does not occur in this system and, given the static nature of the evidence on which the original conclusion was based, it is unlikely to exist as a general rule across the species' geographic range.

49   **4.** *Synthesis*: Our findings stress the importance of elucidating the demographic

50   mechanisms that allow species competing for a common limiting resource to coexist

51   when the resource varies temporally, and expose the difficulty of identifying a species'

52   ecological niche in the absence of detailed, long-term demographic information.

53

54   **Keywords:** coexistence, competition, facilitation, matrix models, niche, resource

55   fluctuations, plant population and community dynamics.

56

57   Introduction

58   Plant-plant interactions are a determining factor in the structuring of plant

59   communities (e.g., Grace & Tilman 1990; Pugnaire 2011) and the nature of these

60   interactions in arid environments has received considerable attention in the literature.

61   After the first observations that the recruitment of many species in arid environments

62   was favoured by a shaded microenvironment located under the canopy of shrubs

63   (Shreve 1931; Niering, Whittaker & Lowe 1963), many studies have confirmed the

64   relevance of facilitation (Flores & Jurado 2003), and its prevalence has been confirmed

65   at different ecological scales (see reviews by Brooker *et al*. 2007 and Callaway 2007).

66   On the other hand, the importance of competition in structuring vegetation in arid

67   environments has generated a substantial amount of work showing that in these

68   unproductive environments plants compete intensely for the most limiting resource,

69   water (see reviews by Fowler 1986 and Goldberg & Barton 1992), yet have evolved

70   morphological, physiological and demographic mechanisms that allow them to coexist

71   (Goldberg & Novoplansky 1997; Nobel 1997; Schwinning & Ehleringer 2001;

72   Silvertown 2004; Verhulst *et al.* 2008; Cazares-Martinez, Montaña & Franco. 2010;

73   Ferrer, Montaña & Franco 2015).

74   The final outcome of the combination of these positive and negative effects

75   depends on their integration throughout the species' life cycle in a constantly changing

76   environment (Bertness & Callaway 1994; Holzapfel & Mahall 1999; Brooker &

77   Callaghan 1998). These effects also change with the ontogeny of the interacting species

78   (Miriti 2006; Armas & Pugnaire 2009; Flores-Torres & Montaña 2015), with positive

79   effects dominating the initial life cycle stages of the favoured species and negative

80   effects dominating when it becomes an adult, which could presumably result in

81   competitive exclusion of the facilitator or nurse plant. This has led authors to

82   hypothesise that small-scale plant to plant interactions, such as those occurring under

83   the canopy of individual plants, determine the composition and structure of desert

84   communities (Vasek & Lund 1980; McAuliffe 1988; Yeaton & Romero-Manzanares

85   1986; Soriano *et al*. 1994; Cody 1996).

86   Based on observational data, Yeaton (1978) proposed a cyclical-dynamics model

87   between two species in the Northern Chihuahuan Desert. According to Yeaton's model,

88   the sequence begins with the establishment of *Larrea tridentata* (creosote bush) in an

89   open space and the subsequent establishment of *Cylindropuntia leptocaulis* (desert

90   Christmas cactus or desert Christmas cholla) under its canopy, a consequence of seeds

91   being transported and deposited under *Larrea* plants by birds and rodents. Eventually, *L.*

92   *tridentata* dies due to water limitation as water availability at the deeper soil levels that

93   its roots occupy decreases due to the development of the shallow root system of *C.*

94   *leptocaulis*. The cactus, in turn, dies as it ages and its shallow root system is exposed

95   due to the activity of burrowing rodents and wind/water erosion. The cycle may restart

96   with the establishment of a new creosote bush in the now open space. In contrast to this

97   hypothesis, Flores-Torres and Montaña (2012) found that recruitment of *C. leptocaulis*

98   under *L. tridentata* shrubs in the Southern Chihuahuan Desert was mostly via vegetative

99   propagation of stem segments rather than from seed. They also found that, although

100   *Larrea* facilitates the clonal establishment of the cactus, it is rarely replaced by it

101   (Flores-Torres & Montaña 2015). Long-term coexistence of the individual plants would

102   suggests that the hypothesised cyclical dynamics of replacement might not occur.

103   The facilitation-competition effect in the interaction between pairs of species in

104   arid environments has been studied with a variety of approaches including physiological

105   and morphological responses, quantification of growth and reproduction, and variation

106   in spatial distribution (McAuliffe 1984, 1988; Flores-Martínez, Ezcurra, & Sánchez-

107   Colón 1994, 1998; Flores-Torres & Montaña 2015). Demographic studies, however,

108   have tended to concentrate on the positive demographic effect on the nursed plant,

109   whether native (Godínez-Alvarez, Valiente-Banuet & Valiente-Banuet 1999; Esparza-

110   Olguín, Valverde & Vilchis-Anaya 2002, Esparza-Olguín, Valverde & Mandujano 2005)

111   or introduced (Griffith *et al.* 2010). No study, however, has considered the population

112   dynamics of the two interacting species over their whole life cycle to try and determine

113   whether the outcome is one of competitive exclusion or coexistence. This issue is of

114   relevance to what is perhaps the most important question in ecology: how do species

115   limited by the same resource(s) coexist? This question is at the root of the concept of a

116   species' unique niche (Hutchinson 1957; Case & Gilpin 1974; Tilman 1982).

117   In order to investigate the overall long-term effect of both positive and negative

118   interactions on the population dynamics of a shrub-cactus interaction, we monitored the

119   population dynamics of *Larrea tridentata* and *Cylindropuntia leptocaulis* in an area of

120   the Southern Chihuahuan Desert over seven annual periods (2008-2015) that covered a

121   wide range of the interannual variation in rainfall. The individuals of each species were

122   categorised into two sub-populations defined by the presence or absence of an

123   interacting individual of the other species. This allowed us to test the hypothesis of

124 replacement and possible cyclical dynamics between the two species, which our recent

125 study suggested is artefactual (Flores-Torres & Montaña 2015). More broadly, it

126 allowed us to identify the components of their population dynamics that allow them to

127 coexist, that is to say, the features of their dynamics that furnish them with a specific

128 niche.

129

Materials and methods

131 *Study area*

132 The study took place in the area around the Desert Laboratory in the Mapimí

133 Biosphere Reserve (MBR) (Southern Chihuahuan Desert 26º 41' N and 103º 45' W,

134 1100 m above sea level, and 28.8 ºC mean annual temperature). The records at the

135 Desert Laboratory meteorological station over a 30 year period (1978-2007) revealed a

136 mean annual precipitation of 279.3 ± 16.6 mm (mean ± standard error), while the

137 figures for the study period (June 2008-May 2015) were 260.6 ± 37 mm ($n = 7$). The

138 annual precipitation data collected over the study period were added up for each year of

139 study (June to May) to investigate its influence on fecundity and predicted asymptotic

140 population growth. The shrubland vegetation of the area is dominated by *Larrea*

141 *tridentata*, *Jatropha dioica*, *Prosopis glandulosa* var *torreyana*, *Opuntia rastrera*,

142 *Castela texana*, *Partenium incanum*, *Opuntia microdasys*, and *Fouqueria splendens*.

143 The terrain has a gentle slope (2-5%) and the soils are gravelly sandy loam to clay loam

144 (Montaña 1990).

145 *Study species*

146 .*Cylindropuntia leptocaulis* DC. (Cactaceae) is a profusely branched shrub 0.5-

147 1.8 m tall (Anderson 2001) with a well-defined woody trunk and a multitude of short,

148   terminal, cylindrical, photosynthetic stem segments (Bobich & Nobel 2001; Evans *et al.*

149   2004). These segments detach easily from the plant allowing recruitment near the

150   mother plant, and presumably also zoochorous dispersal when segments become

151   attached by their spines to animals' skin, feathers or fur. To our knowledge, however,

152   zoochorous dispersal has never been studied/quantified. *Cylindropuntia leptocaulis*

153   produces hermaphrodite flowers, and globous red fruits. It produces abundant seed in

154   wet years (e.g., ~64 000 seeds ha^{-1} in 2010) and fails to produce fruit in dry years

155   (Flores-Torres 2013). However, its main form of recruitment in the study zone during

156   the study period was by clonal propagation by means of the rooting of broken stem

157   segments (Flores-Torres & Montaña 2012). Its distribution comprises most North

158   American deserts (Bravo-Hollis 1978).

159   On the other hand, *Larrea tridentata* (Sesse and Moç. ex DC.) Coville

160   (Zygophyllaceae) is an evergreen microphilic shrub, densely branched from its base,

161   0.6-3 m tall. It is the dominant shrub in all North American warm deserts (MacMahon

162   1979). In the study area, it produces abundant seed in good years (e.g., ~450,000 seeds

163   ha^{-1} in 2010) and this production is unaffected by the amount of precipitation (this

164   study). Seedling establishment in the study area, however, only occurred during wet

165   years, and we only observed recruitment of new seedlings in 2014 and 2015 (51 and 83

166   individuals respectively), when precipitation was above average.

167   *Data collection*

168   In June 2008 we labelled 618 individuals of *L. tridentata*, 314 of them growing

169   in association with *C. leptocaulis* (henceforth subpopulation LA, or just LA) and 304

170   growing alone (henceforth LS). A similar procedure was followed with 628 *C.*

171   *leptocaulis* cacti, with 314 growing associated to *L. tridentata*, usually under its canopy

172   (subpopulation CA), and 314 growing alone (henceforth CS). A similar approach to

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classification of plants with and without neighbours of other species (with potential positive or negative reciprocal population-level effects) was adopted by Miriti, Wright & Howe (2001) and Griffith (2010). The rationale for the grouping of individuals into those with and without neighbours is that, in addition to the ability to evaluate the consequences of the interaction (relative to the subpopulation without it) on specific vital rates (survival, growth and fecundity), it is possible to evaluate their joint effect on overall population growth as a measure of fitness. This type of population subdivision is standard practice in human demography when investigating the population dynamics of subgroups, such as races or geographic origins (e.g., Hamilton 2004).

All plants were inside four plots of different sizes located in the vicinity of the Desert Laboratory and covering a total area of 2.6 ha. Marked plants of both species were measured for height and two diameters (major and minor axes), and re-measured in June of every year from 2008 to 2015. In each annual census new individuals, the product of either sexual reproduction (in *L. tridentata*) or vegetative propagation (in *C. leptocaulis*) were incorporated to the census, measured, and subsequently monitored as all previously established plants. For each new recruit of *C. leptocaulis*, the nearest adult plant of the same species was considered its mother plant. This is justified because shed terminal shoots fall directly below the mother plant and our observations suggest zoochorous dispersal is rare. Our observations also indicated that all established plants, (≥ one year-old) were able to shed terminal shoots that clone the genet. This assumption was not necessary for *L. tridentata* because fecundity (as seedling recruitment) was allocated in proportion to seed production as a function of size (see explanation of seed set and fecundity estimation in the next two sections).

Based on Yeaton (1978) and our own observations (Flores-Torres & Montaña 2012, 2015), we expected the change of status from associated to solitary to be a

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198   relatively rare event. Indeed, over the seven year period only 17 out of the initial 314

199   LA died resulting in 17 CA becoming CS (5.4% or <0.8% per year). On the other hand,

200   the death of 103 out of 314 CA (which went against expectation) released this number

201   of LAs from the interaction. Nonetheless, because of possible time lags in the negative

202   effects of the interaction, we decided to keep these recently released LA under this

203   category for the demographic analyses described below covering the seven-year period.

204   In the case of LS being colonised by *C. leptocaulis*, thus becoming LA, the cactus was

205   too small to produce any observable effects on the demography of *L. tridentata* even

206   after seven years. Moreover, colonisation occurred 27 times over the seven year period,

207   and only six of these survived to 2015 (a recruitment rate of <2% over the seven year

208   period or <0.3% per year). As for CS becoming CA, this transition did not take place

209   because, as expected, recruitment only occurred under *L. tridentata*. If anything, the

210   decision of keeping individuals in their initially observed condition would reduce the

211   observed differences between associated and solitary ones, making the testing of these

212   differences more stringent.

213   *Population structure and seed set/clonal set*

214   Individual plant volume was estimated as the volume of an (inverted) elliptic

215   cone ($V = \pi h r_1 r_2 / 3$, where h is height, and r_1 and r_2 are the semimajor and semiminor

216   axes, respectively). Based on their estimated volume, individual plants were classified

217   into one of five stages. For *L. tridentata*, these stages were: J1 ≤ 0.03 m^3 < A1 ≤ 0.20 m^3

218   < A2 ≤ 0.50 m^3 < A3 ≤ 1.00 m^3 < A4 > 1.00 m^3; for *C. leptocaulis*: J1 ≤ 0.008 m^3 < J2 ≤

219   0.033 m^3 < A1 ≤ 0.09 m^3 < A2 ≤ 0.20 m^3 < A3 > 0.20 m^3.

220   Flores-Torres and Montaña (2015) showed that association did not affect fruit

221   production in *L. tridentata*, i.e., it produces the same average number of fruits whether

222   they were solitary or associated with an individual of *C. leptocaulis*. Therefore, in

9

223   October each year the fruits of ten solitary individuals were counted in each size class of

224   *L. tridentata*. With these data the average number of fruits per individual was regressed

225   against canopy volume, and individual seed production estimated from this regression

226   given each individual's volume and the fact that each fruit bears four seeds. Total annual

227   seed production was then calculated by adding the predicted seed production from these

228   regressions for all reproductive individuals within the study areas, and standardised to

229   seed set per hectare.

230   *C. leptocaulis* at Mapimí establishes primarily by vegetative propagation

231   (Flores-Torres & Montaña 2012), and we found only two recruits of sexual origin in the

232   seven years of study. Consequently, we assumed that fecundity for this species

233   corresponded to clonal propagation for both CS and CA. The total annual production of

234   rooted stems was calculated by adding up their number over the whole study area and

235   standardising it per hectare. By analogy to seed set, we call this variable clonal set.

236   *Population dynamics*

237   Asymptotic matrix population models were employed to determine essential

238   demographic properties of the populations in each study year, as well as over the whole

239   study period. The standard matrix population model has the form $N_{t+1} = AN_t$, where N

240   represents, in this case, a five-row column vector of abundances in each of the five

241   stages defined above for each species at two successive times, t and $t+1$, and A is a 5 x 5

242   matrix whose coefficients, a_{ij}, represent the demographic contributions that an

243   individual in size class j makes to size class i over the time interval t to $t+1$ (Caswell

244   2001). The a_{ij} coefficients were of four types: probability of permanence in the same

245   stage, probability of transition to further stages of the life cycle, probability of transition

246   to previous stages of the life cycle, and individual fecundity, all measured over an

247   annual interval. These coefficients were calculated for each stage, subpopulation and

species for each year of study. Except for fecundity, these coefficients were simply the

proportion of surviving individuals staying or moving to any other stage in the course of

a year (Caswell 2001).

Fecundity, on the other hand, was estimated employing the anonymous

reproduction method (Caswell 2001, p. 173). For *L. tridentata*, the fecundity of each

individual was calculated by multiplying the total number of new recruits (seedlings) at

time $t+1$ by the proportion of seeds produced by it at time t (the ratio of their estimated

number of seeds produced and the total number of seeds produced by their respective

subpopulation in a particular year). From these individual fecundities, the estimation of

the average individual fecundity in each stage is straightforward. Similarly, for *C.*

leptocaulis, individual clonal fecundity was calculated by multiplying the number of

surviving rooted stem fragments at time $t+1$ by the ratio of the number of clones

estimated to have been produced by each individual and the number of clones produced

by the entire subpopulation. The per capita clonal fecundity was obtained from the

average individual fecundity of individuals in each stage.

In total, seven annual transition matrices (2008-2009 to 2014-2015) and a

pooled matrix (from data from all seven periods pooled together) were constructed for

each subpopulation. In order to prevent non-convergence of matrix models in years

without recruitment, which does not permit estimation of some parameter values, the

establishment of a single recruit was assumed. Similarly, to avoid the absence of

mortality (i.e., survival=1) in the last stage, which inflates longevity, an additional dead

individual was assumed. With fecundity and mortality having opposite effects on

population growth their minimal increase resulted in differences in the estimated rate of

population growth between observed and altered matrices in the thousandths (e.g., from

$\lambda=0.99417$ without alteration to $\lambda=0.99371$ when modified for the CA population in

279   Projections for annual and pooled matrices were carried out employing the

280   program STAGECOACH (Cochran & Ellner 1992). In addition to the finite rate of

281   population increase ($\lambda = e^r$, r is the intrinsic rate of population increase) and its

282   corresponding right and left eigenvectors (equivalent to the stable stage distribution and

283   the reproductive value distribution, respectively), the program calculates sensitivity and

284   elasticity matrices, plus the expected age-specific survival and fecundity schedules, life

285   expectancy at birth (L, the expected lifespan), and average age of the parents of a cohort

286   ($\bar{A}$), among other age-related parameters. The STAGECOACH output was then

287   employed to determine the elasticity of λ to changes in each of the basic vital rates

288   embedded in the matrix coefficients (survival σ, growth γ, retrogression ρ and fecundity

289   or recruitment φ) following the method outlined by Franco and Silvertown (2004).

290   *Statistical analyses*

291   Comparison of individual parameters, such as seed set/clonal set and population

292   growth rate (λ) as functions of precipitation and factor subpopulation (associated or

293   solitary) were subject to regression and ANCOVA in SPSS 23 (IBM 2016).

294

Results

296   *L. tridentata*'s seed-set did not correlate with rainfall and did not differ between

297   the two subpopulations (precipitation effect $F_{1,11} = 0.2$, $P = 0.67$; subpopulation effect

298    $F_{1,11} = 0.003$, $P = 0.96$; Fig. 1A). On the other hand, clonal production (clonal set) in *C.*

299   *leptocaulis* correlated with precipitation and the slope did not differ between

300   subpopulations at $P=0.05$ (precipitation effect $F_{1,12} = 17.5$, $P = 0.001$; interaction

301   subpopulation x precipitation $F_{1,12} = 2.9$, $P = 0.12$; Fig. 1B).

302   In *L. tridentata*, the relationship between annual λ and total annual precipitation

303   was positive (Fig. 2A; $R^2 = 0.34$, $F_{1,12} = 7.55$, $P = 0.018$) and there was no difference in

304   either intercept or slope between LA and LS (ANCOVA rainfall effect: $F_{1,10} = 6.307$, P

305    $= 0.031$; sub-population effect: $F_{1,10} = 0.016$, $P = 0.902$; interaction rainfall $\times$

306   subpopulation: $F_{1,10} = 0.025$, $P = 0.878$). The pooled matrices' λs (2008-2015) indicated

307   that both subpopulations were near but above equilibrium ($\lambda_{LS} = 1.036$ and $\lambda_{LA} =$

308   1.022). On the other hand, the average λs from the seven annual matrices gave slightly

309   lower values that included the pooled matrix's λs within their standard error ($\lambda_{LS} =$

310   1.014 ± 0.022 and $\lambda_{LA} = 1.012 \pm 0.019$).

311   The positive relationship between annual λ and total annual precipitation for *C.*

312   *leptocaulis* better fitted a power model than a linear one (Fig. 2B), with a significance

313   difference in the power coefficient ("slope") between λ_{CA} and λ_{CS} (ANCOVA of log(λ)

314   *vs.* log(rainfall) including intercept, rainfall effect: $F_{1,11} = 14.28$, $P = 0.003$;

315   subpopulation effect: $F_{1,11} = 3.86$, $P = 0.075$; ANCOVA excluding intercept which did

316   not show difference in the first model, rainfall effect: $F_{1,11} = 6.01$, $P = 0.032$; sub-

317   population effect: $F_{2,11} = 18.92$, $P < 0.001$). The λ of the pooled matrices indicated that

318   subpopulation CS would tend to decrease while CA would tend to grow ($\lambda_{CS} = 0.939$

319   and $\lambda_{CA} = 1.032$), and the average of the predicted individual year's λs gave lower

320   estimates that slightly accentuated their difference ($\lambda_{CS} = 0.868 \pm 0.054$, $\lambda_{CA} = 1.007 \pm$

321   0.071). When looking at the changing value of the projected rate of population increase

322   for each year of study, in years when $\lambda \leq 1$, $\lambda_{LS} \leq \lambda_{LA}$ (Fig. 2C), but when $\lambda > 1$, either

323   subpopulation could have larger λ. On the other hand, $\lambda_{CA} > \lambda_{CS} < 1$ in all years (Fig.

324   2D). We did not attempt to evaluate the statistical differences between the long-term λ

325   values between each species subpopulations for either species because their correlation

326   with rainfall means a significant proportion of the year to year variance was due to this

327   correlation, not to stochastic variation. That is, variation was not random noise or error

328   in the determination of λ, but deterministic variation driven mostly by differences in the

329   abundance of the limiting resource. Thus, the significance (or lack of) of their

330   differences, assuming that their variation represents random noise, is irrelevant to the

331   question of how resource abundance affects their population dynamics: it does.

332   The elasticity analyses of the pooled matrices showed a consistent pattern of

333   vital rate contribution for both species with survival contributing between one and two

334   orders of magnitude more than growth, retrogression and fecundity to changes in

335   population growth rate (Fig. 3 A & B). The most striking differences were those

336   between the two subpopulations of *C. leptocualis* in the elasticities of retrogression and

337   fecundity, which were lower and higher, respectively, when associated to *L. tridentata*.

338   Of note also was the lower elasticity of growth, retrogression and fecundity in LA

339   compared to LS. Finally, compared to their corresponding solitary conspecifics, there is

340   a contrasting pattern of change in elasticity throughout the life cycle, continuously

341   increasing in LA and decreasing in the adult stages of CA (Fig. 3 C & D). The stable

342   stage distributions for the two associated subpopulations of *L. tridentata* and *C.*

343   *leptocualis* followed a similar pattern to that of their elasticities (Fig. 4 A & B).

344   The projection of life table schedules from the pooled matrices revealed that life

345   expectancy at birth, which we took as the maximum expected lifespan (*L*), was almost

346   an order of magnitude larger for *L. tridentata* (L_{LA}, = 406 years, L_{LS} = 177 years) than it

347   was for *C. leptocaulis* (L_{CA}, = 46 years, L_{CS} = 33 years; Fig 5). Association with the

348 other species produced lower early survival and larger late survival in *L. tridentata* (Fig.

349 5A), but a consistently higher survival throughout the whole life cycle for *C. leptocaulis*

350 (Fig. 5B). Fecundity was higher for isolated than for associated *L. tridentata* (Fig. 4C),

351 with the opposite pattern and wider differences between associated and solitary

352 individuals for *C. leptocaulis* (Fig. 5D). Finally, the standardised distribution of

353 reproductive value revealed that the maximum reproductive value of the four

354 subpopulations (LA = 98 yr, LS = 65 yr, CA = 15 yr and CS = 10 yr) corresponded to

355 24%, 37%, 33% and 30% of their respective lifespan.

356

357 **Discussion**

358 *Population growth*

359 Our seven years of detailed demographic information allowed us to conclude

360 that *Cylindropuntia* was dependent on *Larrea* to remain viable ($r = \ln(\lambda) \geq 0$). Without

361 the protection afforded by *Larrea* in the early stages of *Cylindropuntia*'s life cycle, the

362 latter would tend towards extinction (Fig. 2). In contrast to Yeaton's (1978) assertion,

363 there was no evidence that *Cylindropuntia* would drive the population of *Larrea*

364 towards extinction, as it was capable of maintaining long-term positive population

365 growth with or without the presumed competition exerted by *Cylindropuntia* (Fig. 2). In

366 particular, clonal recruitment played a significant role in the maintenance of viable

367 population growth in CA whose total number of clonal recruits over the seven years of

368 study were 403, while those in CS were 84. Most of the CA clones were recruited under

369 their mother plant, thus not influencing the status of LA. These and those under or near

370 CS had a large mortality which resulted in the low successful recruitment under LS

371 mentioned in the methods section. Nonetheless, CA maintained higher fertility

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372 (expressed as clonal recruitment) than CS (Fig. 5D). Sexual (seedling) recruitment of

373 *Cylindropuntia* was infrequent and depended on sufficient water for fruit production and

374 germination (Flores-Torres & Montaña 2012, 2015). We only observed two seedlings of

375 this species over the seven year period, and the species failed to produce fruits in the

376 two driest years. As in species of *Opuntia* (under which it was previously classified), the

377 recruitment maintaining the population of *Cylindropuntia* occurs via vegetative

378 propagation (Mandujano *et al*. 2001; Mandujano, Golubov & Huenneke 2007; Keeler &

379 Tenhumberg 2011).

380   For *Larrea*, the opposite was true, with fertility being higher in LS than in LA

381 (Fig. 5C). *Larrea*, which did not show a seed set response to resource abundance (Fig.

382 1), achieved positive rates of population growth through seedling recruitment in wet

383 years and generally lower mortality. Thus, the number of dead plants over the whole

384 study period was: LA = 18, LS = 30, CA = 105, CS = 202, with the majority of deaths in

385 *Larrea* occurring in the juvenile stage (LA=13 and LS=21). Furthermore, as stated in

386 the methods section, no individuals of *L. tridentata* belonging to the largest stage died

387 during the study period. Cyclical dynamics demands that *Cylindropuntia* kills its host in

388 a large proportion of cases (Table 2 in Yeaton 1978), but this was not the case in our

389 seven-year study. In fact, *Larrea* survived better when in association with

390 *Cylindropuntia*. These differences in mortality were reflected in their projected

391 longevities, which followed the order: LA > LS > CA > CS, with the first being over an

392 order of magnitude longer than the last (Fig. 5A & B). Clearly, *Larrea* outlives

393 *Cylindropuntia* by an order of magnitude, especially when in association.

394   *Elasticity*

395   As in other shrubs of arid zones (Silvertown *et al.* 1996; Golubov *et al*. 1999;

396 Miriti, Wright & Howe 2001; Jiménez-Lobato & Valverde 2005; Verhulst *et al*. 2008;

397   Ferrer, Montaña & Franco 2015), the elasticity of survival (σ) dominated in all four

398   subpopulations. *Larrea* was able to compensate for the decrease in the contribution of

399   growth (γ) and fecundity (φ) to population growth rate, when in association with

400   *Cylindropuntia*, by increasing the contribution of survival (σ). This change confirms the

401   slight but consistent negative effect of *Cylindropuntia* on *Larrea* (Flores-Torres &

402   Montaña 2015) (Fig. 3A). For *Cylindropuntia*, the main benefit of the association was

403   the increase in the relative contribution of recruitment (φ). This confirms and further

404   emphasises the importance of the interaction for recruitment, as it does in other cacti

405   species (Godínez-Álvarez, Valiente-Banuet & Valiente-Banuet 1999; Esparza-Olguín,

406   Valverde & Vilchis-Anaya 2002, Esparza-Olguín, Valverde & Mandujano 2005).

407   Elasticity also emphasised the increasing contribution of adults in LA, compared

408   to the relatively constant contribution of all adult stages in LS, and the importance of

409   early life cycle stages in CA and late stages in CS. These patterns are to a certain extent

410   mirrored in the projected stable stage distributions (Fig. 4), which show the relative

411   abundances expected at demographic equilibrium when employing all seven years' data

412   (pooled matrix). The positive effects of the interaction on the cactus are not limited to

413   the establishment phase, and its demographic consequences are carried over into further

414   stages of the life cycle (Pugnaire, Haase & Puigdefábregas 1996; Tirado & Pugnaire

415   2003).

416   Overall, the elasticity results highlight the importance of quantifying the

417   changing value of positive and negative effects on each species throughout their life

418   cycle, and the contribution made by individual demographic parameters.

419   *Life history*

420   The higher survival and longer lifespan of *Larrea*, particularly when in

421   interaction with *Cylindropuntia*, rules out the idea that it can be competitively excluded

422 by *Cylindropuntia*. In fact, it seems that by growing more slowly in the presence of

423 *Cylindropuntia*, *Larrea* senesces at a slower pace. This is evocative of the dietary

424 restriction hypothesis in animals (Piper *et al.* 2011, but see critique by Sohal & Forster

425 2014) and coincides with known physiological responses to resource limitation in plants

426 (e.g., Tardieu & Davies 1993, Passioura 2002). We hypothesise that the slower growth

427 of LA delays it from reaching a height at which vessel embolism during a dry year

428 would be likely to kill it (Jarbeau, Ewers & Davis 1995; Ryan & Yoder 1997; Koch *et*

429 *al.* 2004). This would also be aided by the development of a deeper root system. It is

430 known that although fine roots of *Larrea* are distributed within the first 30 cm below the

431 surface, individual roots may reach down to 5 m (Gibbens & Lenz 2001), while cacti

432 roots tend to remain near the soil surface (Cannon 1913). Our own studies have revealed

433 that, in the study area, the horizontal spread (linear dimension) of the superficial roots of

434 *Cylindropuntia*, which are mostly concentrated in the first 32 cm below the soil surface,

435 is over twice that of canopy spread (Flores Torres & Montaña 2015). On the other hand,

436 Briones *et al.* (1996) found that, in this same area, the roots of adult *Larrea* plants are

437 distributed to depths >75 cm, with a peak in root density at 22.5 cm. The presence of

438 hydraulic lift in *Larrea* and "rain roots" in *Cylindropuntia* also result in differences in

439 the time that it takes them to absorb readily available water and, thus, on photosynthetic

440 efficiency (Flores Torres & Montaña 2015). Taken together, those results indicate that,

441 although both species are limited by the abundance of water, *Larrea* can withstand

442 drought better than *Cylindropuntia*.

443   At stable stage distribution, LS would be dominated by younger individuals

444 while LA would be dominated by individuals in the largest stage (Fig 4), which is

445 reflected in their corresponding expected lifespan – shorter in LS and longer in LA (Fig.

446 5). Young *Larrea* do not provide sufficient protection from the sun and are therefore not

447 colonised by *Cylindropuntia*. Because of their larger size, old *Larrea* shrubs would have

448 coexisted with several generations of *Cylindropuntia*, offering them better conditions

449 than smaller, younger shrubs (Tewksbury & Lloyd 2001; Navarro-Cano *et al.* 2015;

450 Amghar *et al.* 2016). Finally, individuals of *Cylindropuntia* can only survive on their

451 own once the plant has grown to a sufficiently large size.

452   *Population-level consequences of the interaction in this and in previous work*

453   While the interaction clearly involves facilitation in favour of the cactus, the fact

454 that water is the most important limiting resource would suggest fierce competition

455 leading to competitive exclusion of one species. Yet, this does not happen and the two

456 species coexist indefinitely. The dynamics of the interaction results in apparently

457 stochastic, yet deterministic population fluctuations driven by the abundance of the

458 limiting resource. While the process of capturing rain fast, which allows *Cylindropuntia*

459 to reach optimal water levels for photosynthesis earlier, may suggest a kind of benign

460 parasitism on *Larrea*, the higher tolerance for water loss of *Larrea* allows it to sit and

461 wait until conditions improve. This slower pace of life when in interaction with

462 *Cylindropuntia* allows *Larrea* to live longer, confirming previous suggestions of a few

463 hundred years' lifespan (Goldberg & Turner 1986; Bowers 2005). As a consequence, its

464 elasticity increases with stage. In contrast, in *Cylindropuntia* elasticity increased in the

465 first three stages, but decreased in the last two – it had a shorter lifespan, confirming a

466 previously estimated maximum lifespan of 50 years (Goldberg & Turner 1986). In the

467 war of attrition for the limiting resource, it is *Cylindropuntia*, not *Larrea*, that is

468 eventually eliminated.

469   Flores-Torres and Montaña (2015) found that although *Cylindropuntia* had

470 negative effects on growth and vigour of *Larrea* (in an irrigation experiment), the

471 frequency of naturally occurring dead adult shrubs associated to live cacti was lower

19

472 than expected by chance. This indicates that the exclusion of *Larrea* is an infrequent

473 event which promotes the aggregated spatial distribution of both species. This has also

474 been reported for other coexisting species competing for water in arid environments

475 (Fonteyn & Mahall 1981; Nobel 1997; Silvertown 2004).

476 As we observed in two coexisting salt bushes with contrasting maximum sizes

477 and lifespan in the same study zone, the two species coexist because, in terms of

478 population growth, each one does better at opposite extremes of abundance of the

479 limiting resource (Verhulst *et al*. 2008; Cázares-Martínez, Montaña & Franco. 2010). If

480 we adopt the r-K continuum of life histories to compare the two interacting species,

481 *Cylindropuntia* (and *Atriplex acanthocarpa* in Verhulst *et al.* 2008 and Cázares-

482 Martínez, Montaña & Franco. 2010) behaves more as an *r*-selected species, being

483 shorter living and benefiting more when the resource is abundant. On the other hand,

484 *Larrea* (like *A. canescens* in the two previous references) behaves as a *K*-selected

485 species, which is longer living and can withstand resource scarcity better. The two

486 interacting species coexists despite competing (i.e., being limited by the same limiting

487 resource) all the time. We documented a similar effect in a study of one species,

488 *Flourensia cernua*, in two contiguous and contrasting habitats in the same study zone

489 that represented, respectively, a source and a sink population (Ferrer, Montaña & Franco

490 2015). In each habitat, *F. cernua* was limited by the same resource, water, but the

491 respective populations had contrasting demographics. In the less productive, source

492 habitat it had a slower demography with a longer lifespan, thus behaving as a *K*-selected

493 species. In the more productive, sink habitat its demography was faster and its lifespan

494 shorter, and constantly tended towards extinction due to competition with the grass

495 *Pleuraphis mutica*. It behaved as an *r*-selected species.

496   All these studies demonstrate that, in order to understand the conditions that

497   allow coexistence, and thus characterise each species unique niche, it is necessary to

498   elucidate the changing nature of the interaction with ontogeny, the plasticity of the

499   relative contribution of demographic parameters to fitness (as measured by λ), and,

500   crucially, the influence of variation in the abundance of the limiting resource.

501

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510

Authors' contributions

512   The study was conceived by CM and MF. Field data were collected by AFT and CM.

513   AFT conducted the analyses with guidance from CM and MF. AFT and MF wrote the

514   final paper.

515

Data accessibility

517   This data from the study will be archived in the form of matrix models in the

518   COMPADRE database (http://www.compadre-db.org/).

519

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FIGURE LEGENDS

708 Figure 1. The variation in seed set and clonal recruitment per unit area with the amount

709 of annual rainfall experienced at the Mapimi Biosphere Reserve, Mexico, for (A) two

710 subpopulations of *L. tridentata* (squares) and (B) two subpopulations of *C. leptocaulis*

711 (circles). For each species, the subpopulations were defined by whether individuals

712 were found in intimate proximity with a member of the other species (filled symbols

713 and continuous line) or on their own (empty symbols and dashed line).

714

715 Figure 2. The relationship between the finite rate of population increase (λ) and total

716 annual rainfall (from June one year to May the following year) for (A) two

717 subpopulations of *L. tridentata* (squares) and (B) two subpopulations of *C. leptocaulis*

718 (circles). In order to witness the temporal changes, the information is also presented as a

719 time sequence over the study period (C & D). Filled symbols represent plants in a

720 nurse-cactus association and empty symbols represent solitary plants.

721

722 Figure 3. The elasticity of individual vital rates (survival, growth, retrogression and

723 fecundity) summed across all life cycle stages (A & B), and for each life cycle stage

724 summed across vital rates (C & D), for *L. tridentata* (A and C) and *C. leptocaulis* (B &

725 D). Filled bars represent plants in a nurse-cactus association and empty bars represent

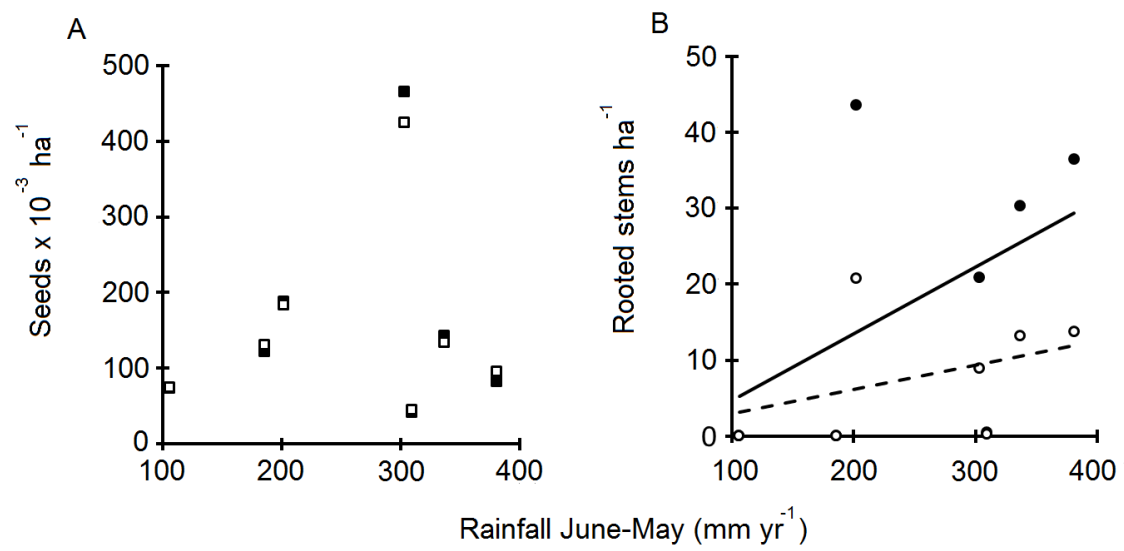726 solitary plants. Note logarithmic axis in A & B.

727

728 Figure 4. Stable stage distribution (**w**, dominant right eigenvector) from pooled matrices

729 for the period 2008-2015 in *L. tridentata* (A) and *C. leptocaulis* (B). Empty bars

730 represent solitary plants (LS & CS) and filled bars plants associated with individuals of

731 the other species (LA & CA). J = juvenile categories, A = adult categories.

732

733   Figure 5. Projected survival (l_x), fecundity (f_x) and reproductive value (v_x) as functions

734   of age (x) from the projection of pooled matrices (2008-2015) of *L. tridentata* (A, C &

735   E) and *C. leptocaulis* (B, D & F). Continuous lines represent associated plants and

736   dotted lines represent solitary plants. Note the one-order magnitude difference in the x-

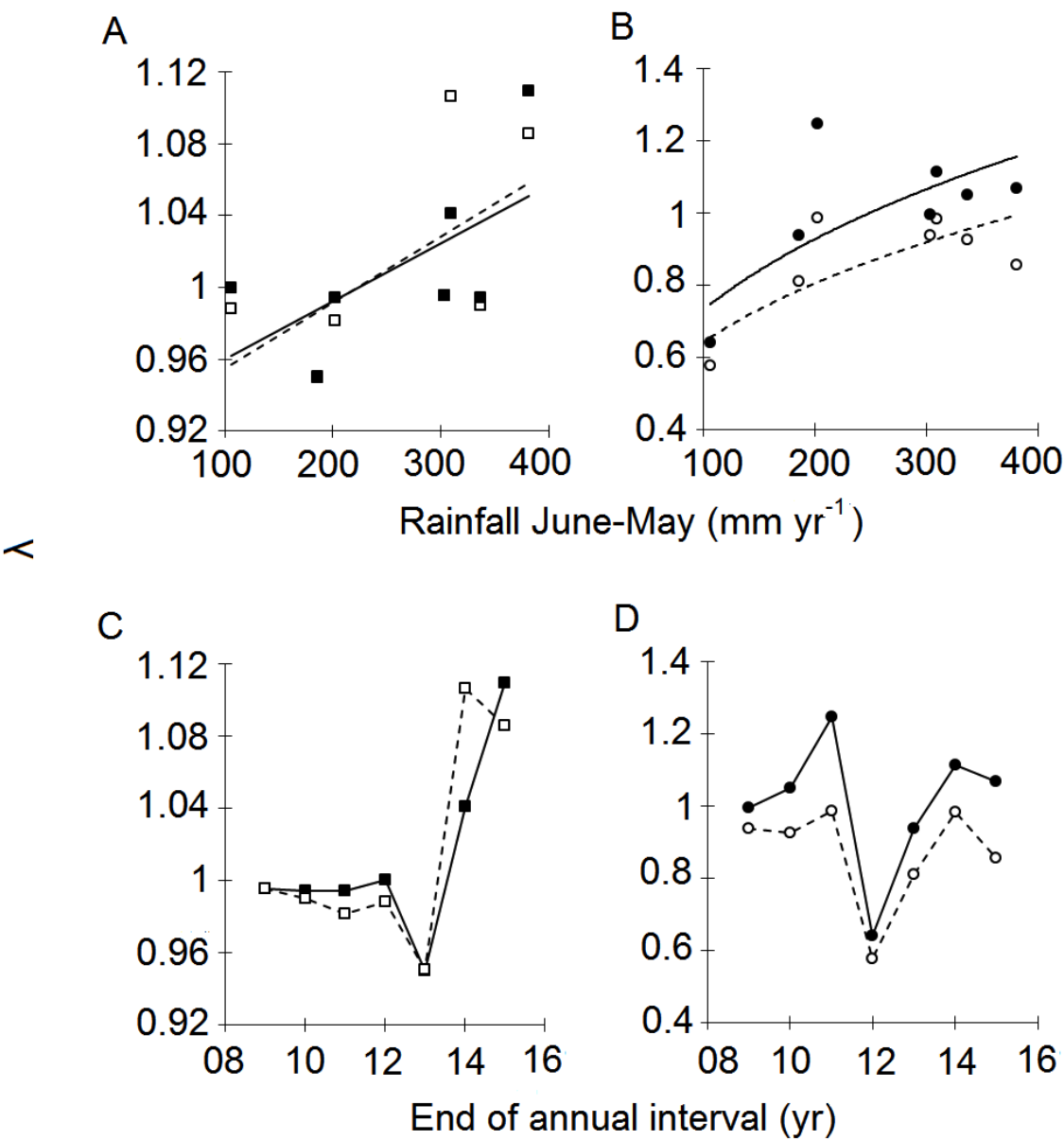737   axis scale for the two species.
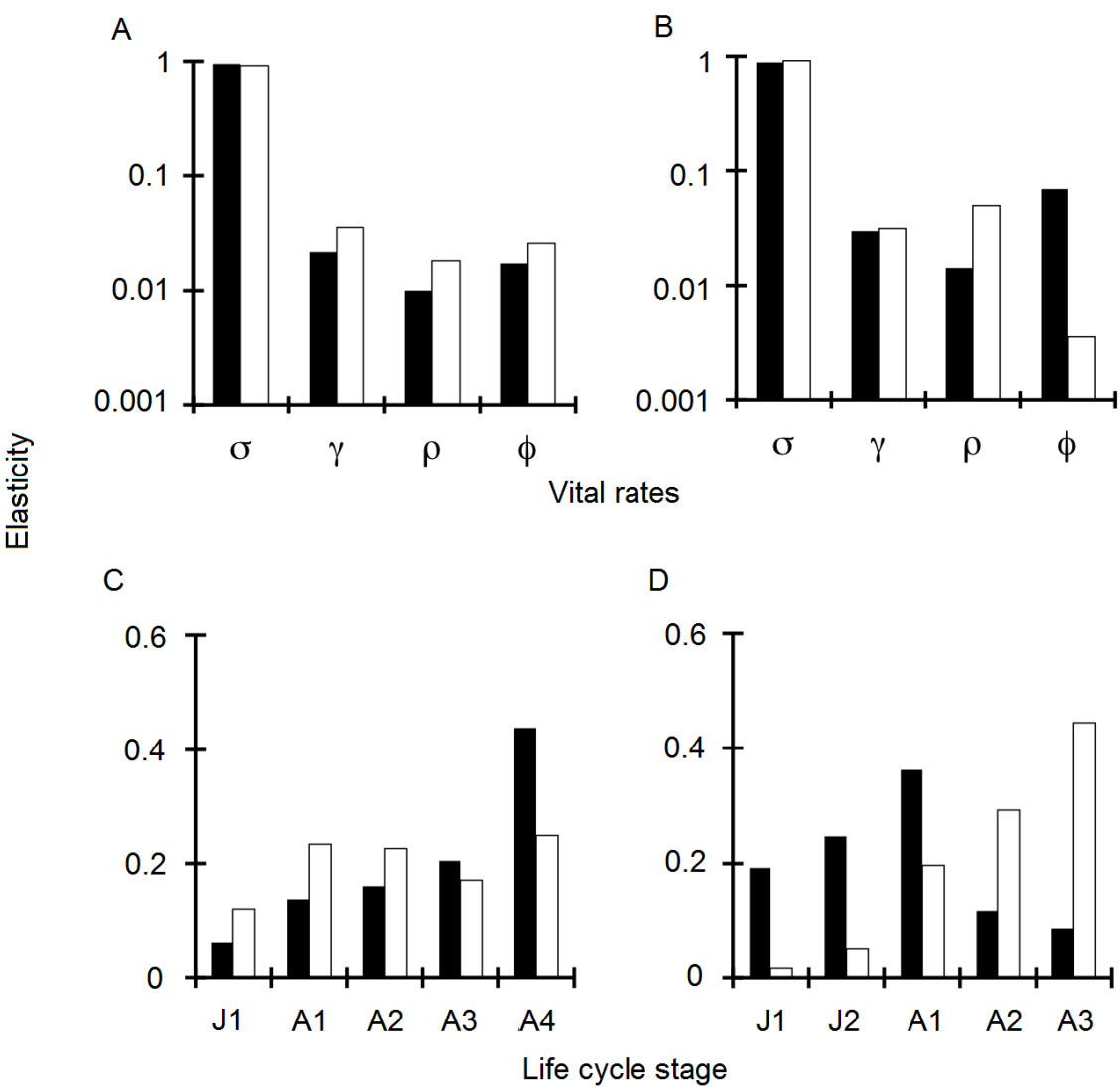
738   Figure 1

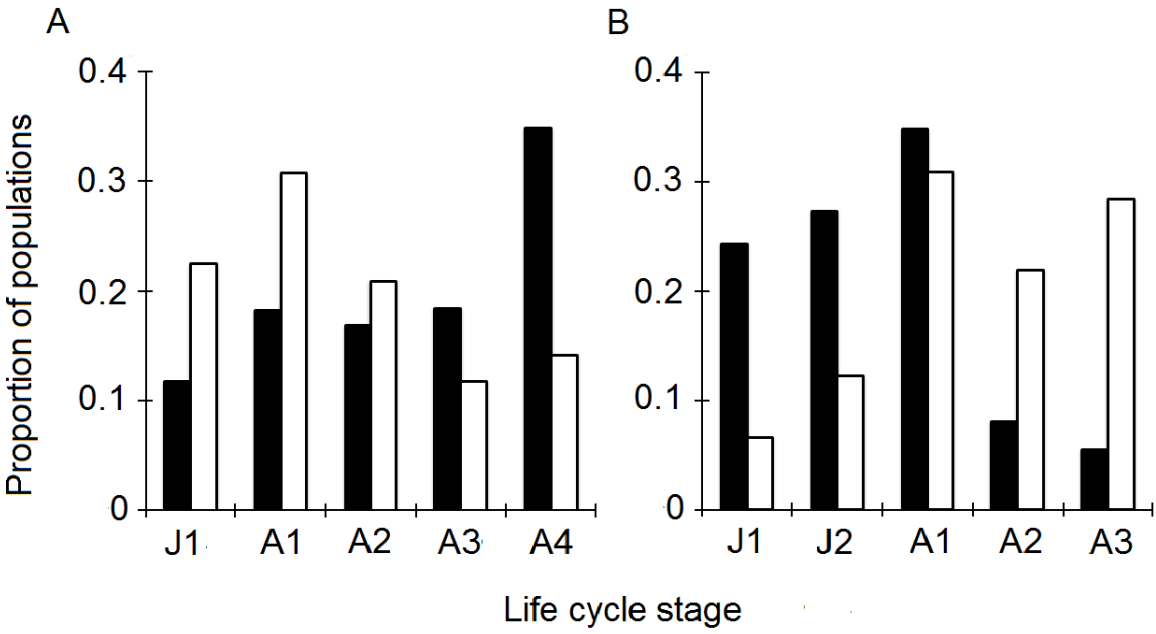739

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742 Figure 2

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Figure 3

751

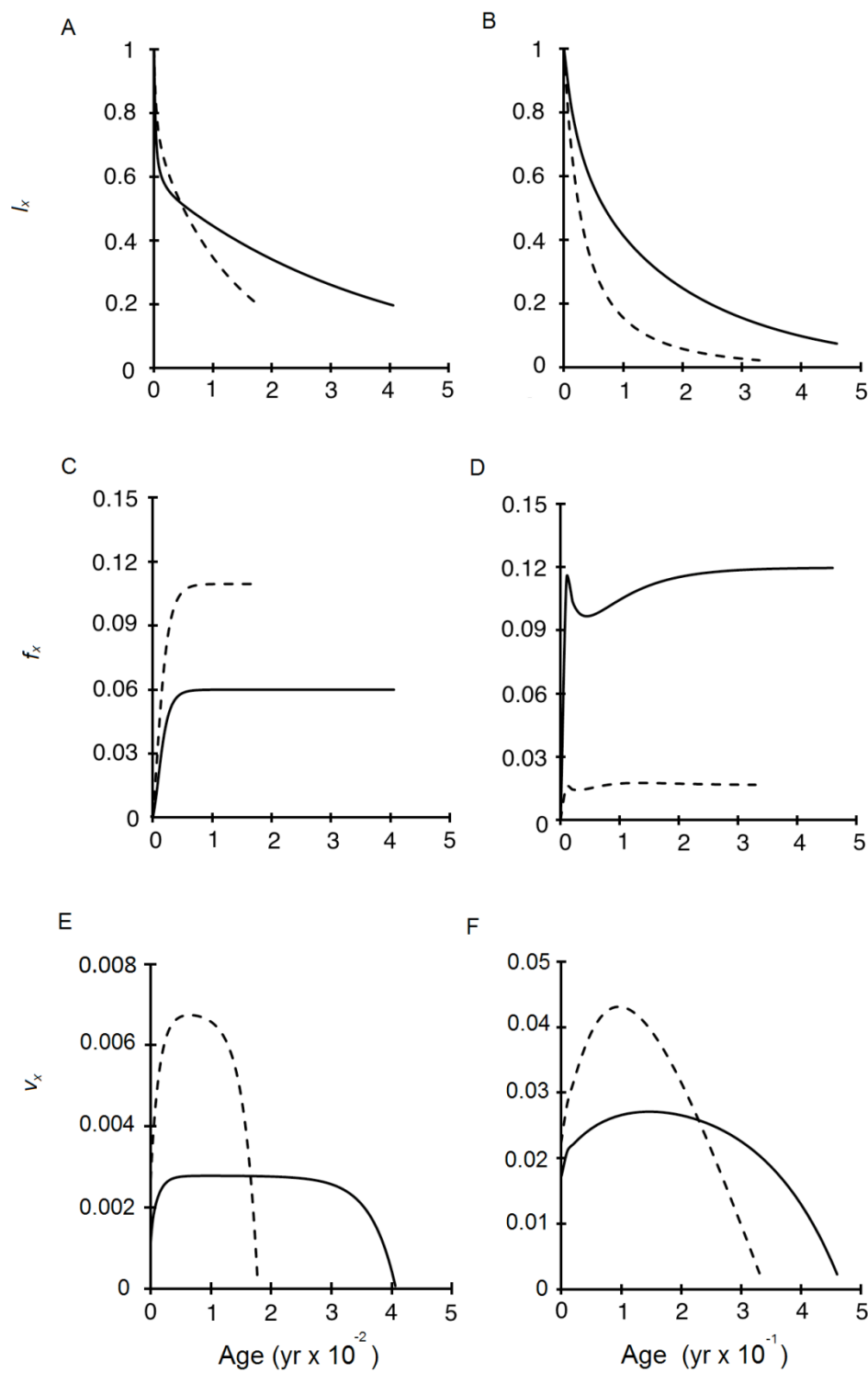754   Figure 5

A

B

C

D

E

F

Age (yr x 10^{-2})

Age (yr x 10^{-1})

755

756