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Coexistence and the niche in a nurse-cactus interaction: is cyclic
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.

4. *Synthesis*: Our findings stress the importance of elucidating the demographic mechanisms that allow species competing for a common limiting resource to coexist when the resource varies temporally, and expose the difficulty of identifying a species' ecological niche in the absence of detailed, long-term demographic information.

Keywords: coexistence, competition, facilitation, matrix models, niche, resource fluctuations, plant population and community dynamics.

Introduction

Plant-plant interactions are a determining factor in the structuring of plant communities (e.g., Grace & Tilman 1990; Pugnaire 2011) and the nature of these interactions in arid environments has received considerable attention in the literature. After the first observations that the recruitment of many species in arid environments was favoured by a shaded microenvironment located under the canopy of shrubs (Shreve 1931; Niering, Whittaker & Lowe 1963), many studies have confirmed the relevance of facilitation (Flores & Jurado 2003), and its prevalence has been confirmed at different ecological scales (see reviews by Brooker *et al.* 2007 and Callaway 2007). On the other hand, the importance of competition in structuring vegetation in arid environments has generated a substantial amount of work showing that in these unproductive environments plants compete intensely for the most limiting resource, water (see reviews by Fowler 1986 and Goldberg & Barton 1992), yet have evolved morphological, physiological and demographic mechanisms that allow them to coexist (Goldberg & Novoplansky 1997; Nobel 1997; Schwinning & Ehleringer 2001; Silvertown 2004; Verhulst *et al.* 2008; Cazares-Martinez, Montaña & Franco. 2010; Ferrer, Montaña & Franco 2015).

The final outcome of the combination of these positive and negative effects depends on their integration throughout the species' life cycle in a constantly changing environment (Bertness & Callaway 1994; Holzapfel & Mahall 1999; Brooker & Callaghan 1998). These effects also change with the ontogeny of the interacting species (Miriti 2006; Armas & Pugnaire 2009; Flores-Torres & Montaña 2015), with positive effects dominating the initial life cycle stages of the favoured species and negative effects dominating when it becomes an adult, which could presumably result in competitive exclusion of the facilitator or nurse plant. This has led authors to hypothesise that small-scale plant to plant interactions, such as those occurring under the canopy of individual plants, determine the composition and structure of desert communities (Vasek & Lund 1980; McAuliffe 1988; Yeaton & Romero-Manzanares 1986; Soriano *et al.* 1994; Cody 1996).

Based on observational data, Yeaton (1978) proposed a cyclical-dynamics model between two species in the Northern Chihuahuan Desert. According to Yeaton's model, the sequence begins with the establishment of *Larrea tridentata* (creosote bush) in an open space and the subsequent establishment of *Cylindropuntia leptocaulis* (desert Christmas cactus or desert Christmas cholla) under its canopy, a consequence of seeds being transported and deposited under *Larrea* plants by birds and rodents. Eventually, *L. tridentata* dies due to water limitation as water availability at the deeper soil levels that its roots occupy decreases due to the development of the shallow root system of *C. leptocaulis*. The cactus, in turn, dies as it ages and its shallow root system is exposed due to the activity of burrowing rodents and wind/water erosion. The cycle may restart with the establishment of a new creosote bush in the now open space. In contrast to this hypothesis, Flores-Torres and Montaña (2012) found that recruitment of *C. leptocaulis* under *L. tridentata* shrubs in the Southern Chihuahuan Desert was mostly via vegetative

propagation of stem segments rather than from seed. They also found that, although *Larrea* facilitates the clonal establishment of the cactus, it is rarely replaced by it (Flores-Torres & Montaña 2015). Long-term coexistence of the individual plants would suggest that the hypothesised cyclical dynamics of replacement might not occur.

The facilitation-competition effect in the interaction between pairs of species in arid environments has been studied with a variety of approaches including physiological and morphological responses, quantification of growth and reproduction, and variation in spatial distribution (McAuliffe 1984, 1988; Flores-Martínez, Ezcurra, & Sánchez-Colón 1994, 1998; Flores-Torres & Montaña 2015). Demographic studies, however, have tended to concentrate on the positive demographic effect on the nursed plant, whether native (Godínez-Alvarez, Valiente-Banuet & Valiente-Banuet 1999; Esparza-Olguín, Valverde & Vilchis-Anaya 2002, Esparza-Olguín, Valverde & Mandujano 2005) or introduced (Griffith *et al.* 2010). No study, however, has considered the population dynamics of the two interacting species over their whole life cycle to try and determine whether the outcome is one of competitive exclusion or coexistence. This issue is of relevance to what is perhaps the most important question in ecology: how do species limited by the same resource(s) coexist? This question is at the root of the concept of a species' unique niche (Hutchinson 1957; Case & Gilpin 1974; Tilman 1982).

In order to investigate the overall long-term effect of both positive and negative interactions on the population dynamics of a shrub-cactus interaction, we monitored the population dynamics of *Larrea tridentata* and *Cylindropuntia leptocaulis* in an area of the Southern Chihuahuan Desert over seven annual periods (2008-2015) that covered a wide range of the interannual variation in rainfall. The individuals of each species were categorised into two sub-populations defined by the presence or absence of an interacting individual of the other species. This allowed us to test the hypothesis of

replacement and possible cyclical dynamics between the two species, which our recent study suggested is artefactual (Flores-Torres & Montaña 2015). More broadly, it allowed us to identify the components of their population dynamics that allow them to coexist, that is to say, the features of their dynamics that furnish them with a specific niche.

Materials and methods

Study area

The study took place in the area around the Desert Laboratory in the Mapimí Biosphere Reserve (MBR) (Southern Chihuahuan Desert 26° 41' N and 103° 45' W, 1100 m above sea level, and 28.8 °C mean annual temperature). The records at the Desert Laboratory meteorological station over a 30 year period (1978-2007) revealed a mean annual precipitation of 279.3 ± 16.6 mm (mean \pm standard error), while the figures for the study period (June 2008-May 2015) were 260.6 ± 37 mm ($n = 7$). The annual precipitation data collected over the study period were added up for each year of study (June to May) to investigate its influence on fecundity and predicted asymptotic population growth. The shrubland vegetation of the area is dominated by *Larrea tridentata*, *Jatropha dioica*, *Prosopis glandulosa* var *torreyana*, *Opuntia rastrera*, *Castela texana*, *Partenium incanum*, *Opuntia microdasys*, and *Fouqueria splendens*. The terrain has a gentle slope (2-5%) and the soils are gravelly sandy loam to clay loam (Montaña 1990).

Study species

Cylindropuntia leptocaulis DC. (Cactaceae) is a profusely branched shrub 0.5-1.8 m tall (Anderson 2001) with a well-defined woody trunk and a multitude of short,

terminal, cylindrical, photosynthetic stem segments (Bobich & Nobel 2001; Evans *et al.* 2004). These segments detach easily from the plant allowing recruitment near the mother plant, and presumably also zoochorous dispersal when segments become attached by their spines to animals' skin, feathers or fur. To our knowledge, however, zoochorous dispersal has never been studied/quantified. *Cylindropuntia leptocaulis* produces hermaphrodite flowers, and globous red fruits. It produces abundant seed in wet years (e.g., ~64 000 seeds ha⁻¹ in 2010) and fails to produce fruit in dry years (Flores-Torres 2013). However, its main form of recruitment in the study zone during the study period was by clonal propagation by means of the rooting of broken stem segments (Flores-Torres & Montaña 2012). Its distribution comprises most North American deserts (Bravo-Hollis 1978).

On the other hand, *Larrea tridentata* (Sesse and Moç. ex DC.) Coville (Zygophyllaceae) is an evergreen microphilic shrub, densely branched from its base, 0.6-3 m tall. It is the dominant shrub in all North American warm deserts (MacMahon 1979). In the study area, it produces abundant seed in good years (e.g., ~450,000 seeds ha⁻¹ in 2010) and this production is unaffected by the amount of precipitation (this study). Seedling establishment in the study area, however, only occurred during wet years, and we only observed recruitment of new seedlings in 2014 and 2015 (51 and 83 individuals respectively), when precipitation was above average.

Data collection

In June 2008 we labelled 618 individuals of *L. tridentata*, 314 of them growing in association with *C. leptocaulis* (henceforth subpopulation LA, or just LA) and 304 growing alone (henceforth LS). A similar procedure was followed with 628 *C. leptocaulis* cacti, with 314 growing associated to *L. tridentata*, usually under its canopy (subpopulation CA), and 314 growing alone (henceforth CS). A similar approach to

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, (\geq 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

relatively rare event. Indeed, over the seven year period only 17 out of the initial 314 LA died resulting in 17 CA becoming CS (5.4% or <0.8% per year). On the other hand, the death of 103 out of 314 CA (which went against expectation) released this number of LAs from the interaction. Nonetheless, because of possible time lags in the negative effects of the interaction, we decided to keep these recently released LA under this category for the demographic analyses described below covering the seven-year period. In the case of LS being colonised by *C. leptocaulis*, thus becoming LA, the cactus was too small to produce any observable effects on the demography of *L. tridentata* even after seven years. Moreover, colonisation occurred 27 times over the seven year period, and only six of these survived to 2015 (a recruitment rate of <2% over the seven year period or <0.3% per year). As for CS becoming CA, this transition did not take place because, as expected, recruitment only occurred under *L. tridentata*. If anything, the decision of keeping individuals in their initially observed condition would reduce the observed differences between associated and solitary ones, making the testing of these differences more stringent.

Population structure and seed set/clonal set

Individual plant volume was estimated as the volume of an (inverted) elliptic cone ($V = \pi h r_1 r_2 / 3$, where h is height, and r_1 and r_2 are the semimajor and semiminor axes, respectively). Based on their estimated volume, individual plants were classified into one of five stages. For *L. tridentata*, these stages were: $J1 \leq 0.03 \text{ m}^3 < A1 \leq 0.20 \text{ m}^3 < A2 \leq 0.50 \text{ m}^3 < A3 \leq 1.00 \text{ m}^3 < A4 > 1.00 \text{ m}^3$; for *C. leptocaulis*: $J1 \leq 0.008 \text{ m}^3 < J2 \leq 0.033 \text{ m}^3 < A1 \leq 0.09 \text{ m}^3 < A2 \leq 0.20 \text{ m}^3 < A3 > 0.20 \text{ m}^3$.

Flores-Torres and Montaña (2015) showed that association did not affect fruit production in *L. tridentata*, i.e., it produces the same average number of fruits whether they were solitary or associated with an individual of *C. leptocaulis*. Therefore, in

October each year the fruits of ten solitary individuals were counted in each size class of *L. tridentata*. With these data the average number of fruits per individual was regressed against canopy volume, and individual seed production estimated from this regression given each individual's volume and the fact that each fruit bears four seeds. Total annual seed production was then calculated by adding the predicted seed production from these regressions for all reproductive individuals within the study areas, and standardised to seed set per hectare.

C. leptocaulis at Mapimí establishes primarily by vegetative propagation (Flores-Torres & Montaña 2012), and we found only two recruits of sexual origin in the seven years of study. Consequently, we assumed that fecundity for this species corresponded to clonal propagation for both CS and CA. The total annual production of rooted stems was calculated by adding up their number over the whole study area and standardising it per hectare. By analogy to seed set, we call this variable clonal set.

Population dynamics

Asymptotic matrix population models were employed to determine essential demographic properties of the populations in each study year, as well as over the whole study period. The standard matrix population model has the form $N_{t+1} = AN_t$, where N represents, in this case, a five-row column vector of abundances in each of the five stages defined above for each species at two successive times, t and $t+1$, and A is a 5 x 5 matrix whose coefficients, a_{ij} , represent the demographic contributions that an individual in size class j makes to size class i over the time interval t to $t+1$ (Caswell 2001). The a_{ij} coefficients were of four types: probability of permanence in the same stage, probability of transition to further stages of the life cycle, probability of transition to previous stages of the life cycle, and individual fecundity, all measured over an 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

2008-2009). This is congruent with the level of precision obtained from a total sample size per population of ~300 individuals. The assumption of one recruit was not necessary for the pooled matrices because recruitment occurred in one or more years. However, one dead adult in the last age category was assumed to have occurred in one year for *L. tridentata* because no deaths occurred in the last stage of this species in either condition throughout the seven year study period.

Projections for annual and pooled matrices were carried out employing the program STAGECOACH (Cochran & Ellner 1992). In addition to the finite rate of population increase ($\lambda = e^r$, r is the intrinsic rate of population increase) and its corresponding right and left eigenvectors (equivalent to the stable stage distribution and the reproductive value distribution, respectively), the program calculates sensitivity and elasticity matrices, plus the expected age-specific survival and fecundity schedules, life expectancy at birth (L , the expected lifespan), and average age of the parents of a cohort (\bar{A}), among other age-related parameters. The STAGECOACH output was then employed to determine the elasticity of λ to changes in each of the basic vital rates embedded in the matrix coefficients (survival σ , growth γ , retrogression ρ and fecundity or recruitment ϕ) following the method outlined by Franco and Silvertown (2004).

Statistical analyses

Comparison of individual parameters, such as seed set/clonal set and population growth rate (λ) as functions of precipitation and factor subpopulation (associated or solitary) were subject to regression and ANCOVA in SPSS 23 (IBM 2016).

Results

L. tridentata's seed-set did not correlate with rainfall and did not differ between 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' λ s (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 λ s from the seven annual matrices gave slightly
309 lower values that included the pooled matrix's λ s 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 $\log(\lambda)$
314 vs. $\log(\text{rainfall})$ 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 λ s 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

subpopulation could have larger λ . On the other hand, $\lambda_{CA} > \lambda_{CS} < 1$ in all years (Fig. 2D). We did not attempt to evaluate the statistical differences between the long-term λ values between each species subpopulations for either species because their correlation with rainfall means a significant proportion of the year to year variance was due to this correlation, not to stochastic variation. **That is, variation was not random noise or error in the determination of λ , but deterministic variation driven mostly by differences in the abundance of the limiting resource.** Thus, the significance (or lack of) of their differences, assuming that their variation represents random noise, is irrelevant to the question of how resource abundance affects their population dynamics: **it does.**

The elasticity analyses of the pooled matrices showed a consistent pattern of vital rate contribution for both species with survival contributing between one and two orders of magnitude more than growth, retrogression and fecundity to changes in population growth rate (Fig. 3 A & B). The most striking differences were those between the two subpopulations of *C. leptocaulis* in the elasticities of retrogression and fecundity, which were lower and higher, respectively, when associated to *L. tridentata*. Of note also was the lower elasticity of growth, retrogression and fecundity in LA compared to LS. Finally, compared to their corresponding solitary conspecifics, there is a contrasting pattern of change in elasticity throughout the life cycle, continuously increasing in LA and decreasing in the adult stages of CA (Fig. 3 C & D). The stable stage distributions for the two associated subpopulations of *L. tridentata* and *C. leptocaulis* followed a similar pattern to that of their elasticities (Fig. 4 A & B).

The projection of life table schedules from the pooled matrices revealed that life expectancy at birth, which we took as the maximum expected lifespan (L), was almost an order of magnitude larger for *L. tridentata* ($L_{LA} = 406$ years, $L_{LS} = 177$ years) than it was for *C. leptocaulis* ($L_{CA} = 46$ years, $L_{CS} = 33$ years; Fig 5). Association with the

other species produced lower early survival and larger late survival in *L. tridentata* (Fig. 5A), but a consistently higher survival throughout the whole life cycle for *C. leptocaulis* (Fig. 5B). Fecundity was higher for isolated than for associated *L. tridentata* (Fig. 4C), with the opposite pattern and wider differences between associated and solitary individuals for *C. leptocaulis* (Fig. 5D). Finally, the standardised distribution of reproductive value revealed that the maximum reproductive value of the four subpopulations (LA = 98 yr, LS = 65 yr, CA = 15 yr and CS = 10 yr) corresponded to 24%, 37%, 33% and 30% of their respective lifespan.

Discussion

Population growth

Our seven years of detailed demographic information allowed us to conclude that *Cylindropuntia* was dependent on *Larrea* to remain viable ($r = \ln(\lambda) \geq 0$). Without the protection afforded by *Larrea* in the early stages of *Cylindropuntia*'s life cycle, the latter would tend towards extinction (Fig. 2). In contrast to Yeaton's (1978) assertion, there was no evidence that *Cylindropuntia* would drive the population of *Larrea* towards extinction, as it was capable of maintaining long-term positive population growth with or without the presumed competition exerted by *Cylindropuntia* (Fig. 2). In particular, clonal recruitment played a significant role in the maintenance of viable population growth in CA whose total number of clonal recruits over the seven years of study were 403, while those in CS were 84. Most of the CA clones were recruited under their mother plant, thus not influencing the status of LA. These and those under or near CS had a large mortality which resulted in the low successful recruitment under LS mentioned in the methods section. Nonetheless, CA maintained higher fertility

(expressed as clonal recruitment) than CS (Fig. 5D). Sexual (seedling) recruitment of *Cylindropuntia* was infrequent and depended on sufficient water for fruit production and germination (Flores-Torres & Montaña 2012, 2015). We only observed two seedlings of this species over the seven year period, and the species failed to produce fruits in the two driest years. As in species of *Opuntia* (under which it was previously classified), the recruitment maintaining the population of *Cylindropuntia* occurs via vegetative propagation (Mandujano *et al.* 2001; Mandujano, Golubov & Huenneke 2007; Keeler & Tenhumberg 2011).

For *Larrea*, the opposite was true, with fertility being higher in LS than in LA (Fig. 5C). *Larrea*, which did not show a seed set response to resource abundance (Fig. 1), achieved positive rates of population growth through seedling recruitment in wet years and generally lower mortality. Thus, the number of dead plants over the whole study period was: LA = 18, LS = 30, CA = 105, CS = 202, with the majority of deaths in *Larrea* occurring in the juvenile stage (LA=13 and LS=21). Furthermore, as stated in the methods section, no individuals of *L. tridentata* belonging to the largest stage died during the study period. Cyclical dynamics demands that *Cylindropuntia* kills its host in a large proportion of cases (Table 2 in Yeaton 1978), but this was not the case in our seven-year study. In fact, *Larrea* survived better when in association with *Cylindropuntia*. These differences in mortality were reflected in their projected longevity, which followed the order: LA > LS > CA > CS, with the first being over an order of magnitude longer than the last (Fig. 5A & B). Clearly, *Larrea* outlives *Cylindropuntia* by an order of magnitude, especially when in association.

Elasticity

As in other shrubs of arid zones (Silvertown *et al.* 1996; Golubov *et al.* 1999; Miriti, Wright & Howe 2001; Jiménez-Lobato & Valverde 2005; Verhulst *et al.* 2008;

Ferrer, Montaña & Franco 2015), the elasticity of survival (σ) dominated in all four subpopulations. *Larrea* was able to compensate for the decrease in the contribution of growth (γ) and fecundity (ϕ) to population growth rate, when in association with *Cylindropuntia*, by increasing the contribution of survival (σ). This change confirms the slight but consistent negative effect of *Cylindropuntia* on *Larrea* (Flores-Torres & Montaña 2015) (Fig. 3A). For *Cylindropuntia*, the main benefit of the association was the increase in the relative contribution of recruitment (ϕ). This confirms and further emphasises the importance of the interaction for recruitment, as it does in other cacti species (Godínez-Álvarez, Valiente-Banuet & Valiente-Banuet 1999; Esparza-Olgún, Valverde & Vilchis-Anaya 2002, Esparza-Olgún, Valverde & Mandujano 2005).

Elasticity also emphasised the increasing contribution of adults in LA, compared to the relatively constant contribution of all adult stages in LS, and the importance of early life cycle stages in CA and late stages in CS. These patterns are to a certain extent mirrored in the projected stable stage distributions (Fig. 4), which show the relative abundances expected at demographic equilibrium when employing all seven years' data (pooled matrix). The positive effects of the interaction on the cactus are not limited to the establishment phase, and its demographic consequences are carried over into further stages of the life cycle (Pugnaire, Haase & Puigdefábregas 1996; Tirado & Pugnaire 2003).

Overall, the elasticity results highlight the importance of quantifying the changing value of positive and negative effects on each species throughout their life cycle, and the contribution made by individual demographic parameters.

Life history

The higher survival and longer lifespan of *Larrea*, particularly when in interaction with *Cylindropuntia*, rules out the idea that it can be competitively excluded

by *Cylindropuntia*. In fact, it seems that by growing more slowly in the presence of *Cylindropuntia*, *Larrea* senesces at a slower pace. This is evocative of the dietary restriction hypothesis in animals (Piper *et al.* 2011, but see critique by Sohal & Forster 2014) and coincides with known physiological responses to resource limitation in plants (e.g., Tardieu & Davies 1993, Passioura 2002). We hypothesise that the slower growth of LA delays it from reaching a height at which vessel embolism during a dry year would be likely to kill it (Jarbeau, Ewers & Davis 1995; Ryan & Yoder 1997; Koch *et al.* 2004). This would also be aided by the development of a deeper root system. It is known that although fine roots of *Larrea* are distributed within the first 30 cm below the surface, individual roots may reach down to 5 m (Gibbens & Lenz 2001), while cacti roots tend to remain near the soil surface (Cannon 1913). Our own studies have revealed that, in the study area, the horizontal spread (linear dimension) of the superficial roots of *Cylindropuntia*, which are mostly concentrated in the first 32 cm below the soil surface, is over twice that of canopy spread (Flores Torres & Montaña 2015). On the other hand, Briones *et al.* (1996) found that, in this same area, the roots of adult *Larrea* plants are distributed to depths >75 cm, with a peak in root density at 22.5 cm. The presence of hydraulic lift in *Larrea* and “rain roots” in *Cylindropuntia* also result in differences in the time that it takes them to absorb readily available water and, thus, on photosynthetic efficiency (Flores Torres & Montaña 2015). Taken together, those results indicate that, although both species are limited by the abundance of water, *Larrea* can withstand drought better than *Cylindropuntia*.

At stable stage distribution, LS would be dominated by younger individuals while LA would be dominated by individuals in the largest stage (Fig 4), which is reflected in their corresponding expected lifespan – shorter in LS and longer in LA (Fig. 5). Young *Larrea* do not provide sufficient protection from the sun and are therefore not

colonised by *Cylindropuntia*. Because of their larger size, old *Larrea* shrubs would have coexisted with several generations of *Cylindropuntia*, offering them better conditions than smaller, younger shrubs (Tewksbury & Lloyd 2001; Navarro-Cano *et al.* 2015; Amghar *et al.* 2016). Finally, individuals of *Cylindropuntia* can only survive on their own once the plant has grown to a sufficiently large size.

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

While the interaction clearly involves facilitation in favour of the cactus, the fact that water is the most important limiting resource would suggest fierce competition leading to competitive exclusion of one species. Yet, this does not happen and the two species coexist indefinitely. The dynamics of the interaction results in apparently stochastic, yet deterministic population fluctuations driven by the abundance of the limiting resource. While the process of capturing rain fast, which allows *Cylindropuntia* to reach optimal water levels for photosynthesis earlier, may suggest a kind of benign parasitism on *Larrea*, the higher tolerance for water loss of *Larrea* allows it to sit and wait until conditions improve. This slower pace of life when in interaction with *Cylindropuntia* allows *Larrea* to live longer, confirming previous suggestions of a few hundred years' lifespan (Goldberg & Turner 1986; Bowers 2005). As a consequence, its elasticity increases with stage. In contrast, in *Cylindropuntia* elasticity increased in the first three stages, but decreased in the last two – it had a shorter lifespan, confirming a previously estimated maximum lifespan of 50 years (Goldberg & Turner 1986). In the war of attrition for the limiting resource, it is *Cylindropuntia*, not *Larrea*, that is eventually eliminated.

Flores-Torres and Montaña (2015) found that although *Cylindropuntia* had negative effects on growth and vigour of *Larrea* (in an irrigation experiment), the frequency of naturally occurring dead adult shrubs associated to live cacti was lower

than expected by chance. This indicates that the exclusion of *Larrea* is an infrequent event which promotes the aggregated spatial distribution of both species. This has also been reported for other coexisting species competing for water in arid environments (Fonteyn & Mahall 1981; Nobel 1997; Silvertown 2004).

As we observed in two coexisting salt bushes with contrasting maximum sizes and lifespan in the same study zone, the two species coexist because, in terms of population growth, each one does better at opposite extremes of abundance of the limiting resource (Verhulst *et al.* 2008; Cázares-Martínez, Montaña & Franco. 2010). If we adopt the r-K continuum of life histories to compare the two interacting species, *Cylindropuntia* (and *Atriplex acanthocarpa* in Verhulst *et al.* 2008 and Cázares-Martínez, Montaña & Franco. 2010) behaves more as an *r*-selected species, being shorter living and benefiting more when the resource is abundant. On the other hand, *Larrea* (like *A. canescens* in the two previous references) behaves as a *K*-selected species, which is longer living and can withstand resource scarcity better. The two interacting species coexists despite competing (i.e., being limited by the same limiting resource) all the time. We documented a similar effect in a study of one species, *Flourensia cernua*, in two contiguous and contrasting habitats in the same study zone that represented, respectively, a source and a sink population (Ferrer, Montaña & Franco 2015). In each habitat, *F. cernua* was limited by the same resource, water, but the respective populations had contrasting demographics. In the less productive, source habitat it had a slower demography with a longer lifespan, thus behaving as a *K*-selected species. In the more productive, sink habitat its demography was faster and its lifespan shorter, and constantly tended towards extinction due to competition with the grass *Pleuraphis mutica*. It behaved as an *r*-selected species.

All these studies demonstrate that, in order to understand the conditions that allow coexistence, and thus characterise each species unique niche, it is necessary to elucidate the changing nature of the interaction with ontogeny, the plasticity of the relative contribution of demographic parameters to fitness (as measured by λ), and, crucially, the influence of variation in the abundance of the limiting resource.

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Authors' contributions

The study was conceived by CM and MF. Field data were collected by AFT and CM. AFT conducted the analyses with guidance from CM and MF. AFT and MF wrote the final paper.

Data accessibility

This data from the study will be archived in the form of matrix models in the COMPADRE database (<http://www.compadre-db.org/>).

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FIGURE LEGENDS

Figure 1. The variation in seed set and clonal recruitment per unit area with the amount of annual rainfall experienced at the Mapimi Biosphere Reserve, Mexico, for (A) two subpopulations of *L. tridentata* (squares) and (B) two subpopulations of *C. leptocaulis* (circles). For each species, the subpopulations were defined by whether individuals were found in intimate proximity with a member of the other species (filled symbols and continuous line) or on their own (empty symbols and dashed line).

Figure 2. The relationship between the finite rate of population increase (λ) and total annual rainfall (from June one year to May the following year) for (A) two subpopulations of *L. tridentata* (squares) and (B) two subpopulations of *C. leptocaulis* (circles). In order to witness the temporal changes, the information is also presented as a time sequence over the study period (C & D). Filled symbols represent plants in a nurse-cactus association and empty symbols represent solitary plants.

Figure 3. The elasticity of individual vital rates (survival, growth, retrogression and fecundity) summed across all life cycle stages (A & B), and for each life cycle stage summed across vital rates (C & D), for *L. tridentata* (A and C) and *C. leptocaulis* (B & D). Filled bars represent plants in a nurse-cactus association and empty bars represent solitary plants. Note logarithmic axis in A & B.

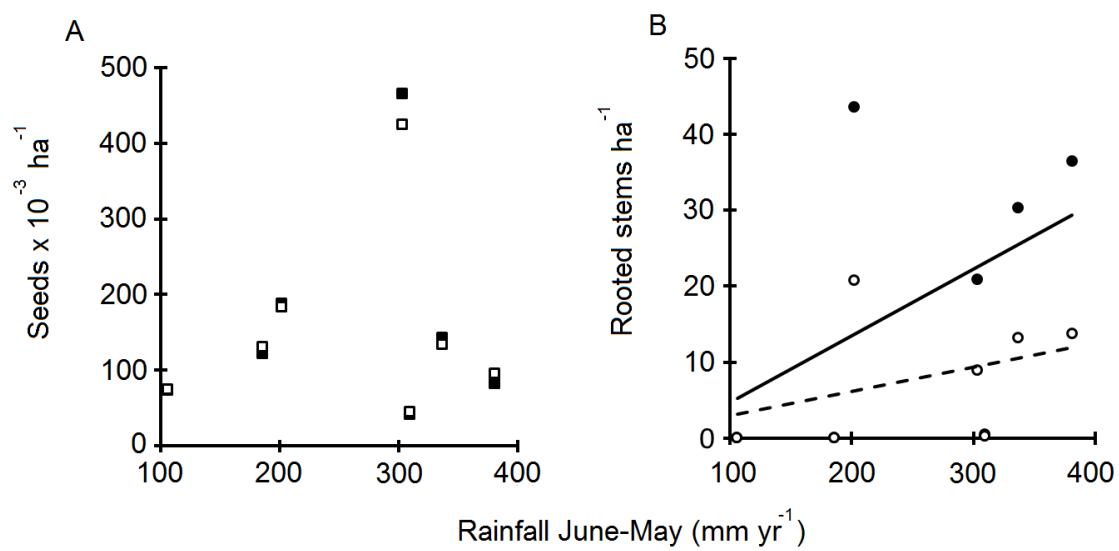
Figure 4. Stable stage distribution (\mathbf{w} , dominant right eigenvector) from pooled matrices for the period 2008-2015 in *L. tridentata* (A) and *C. leptocaulis* (B). Empty bars represent solitary plants (LS & CS) and filled bars plants associated with individuals of the other species (LA & CA). 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

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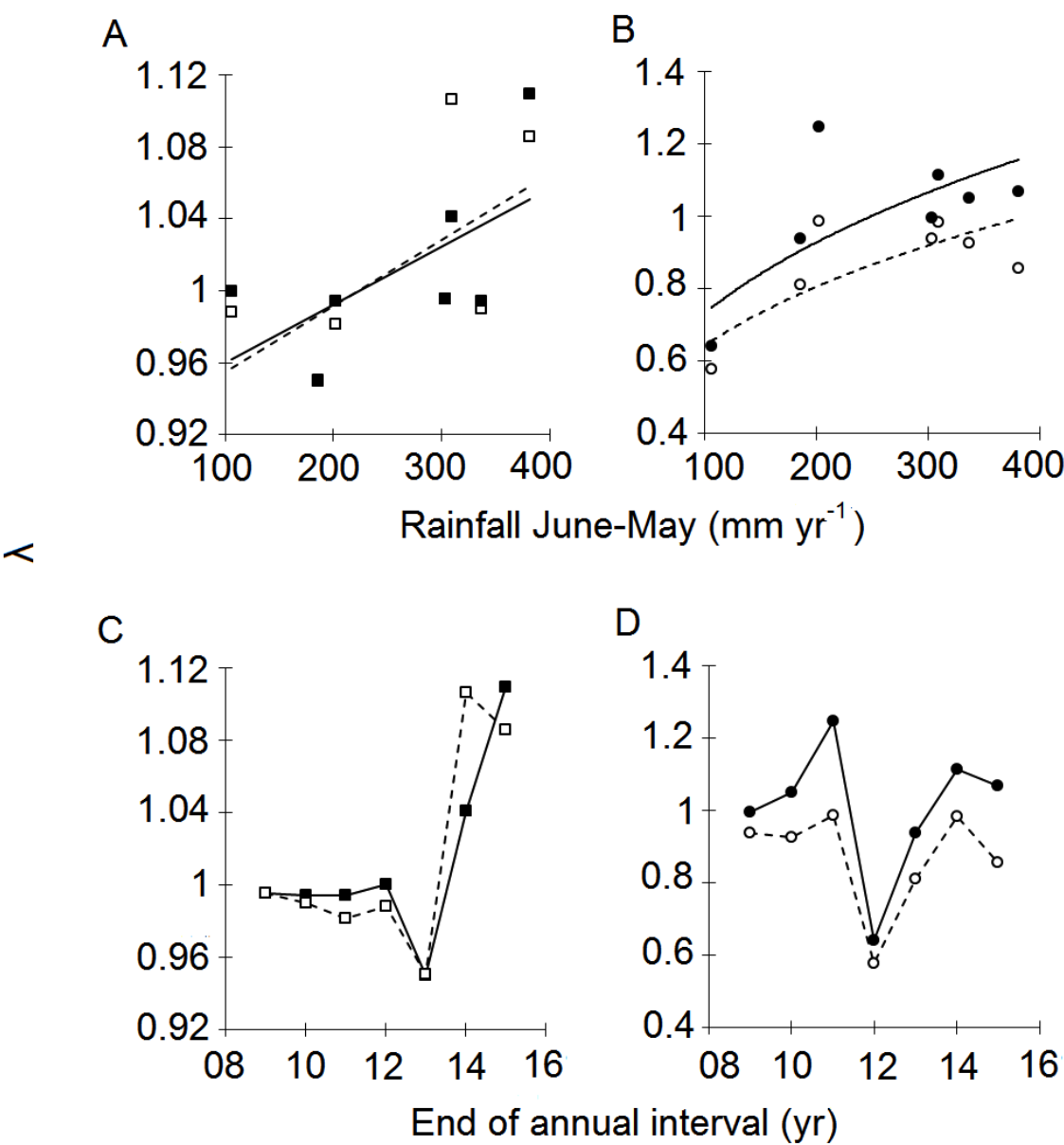


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742 Figure 2

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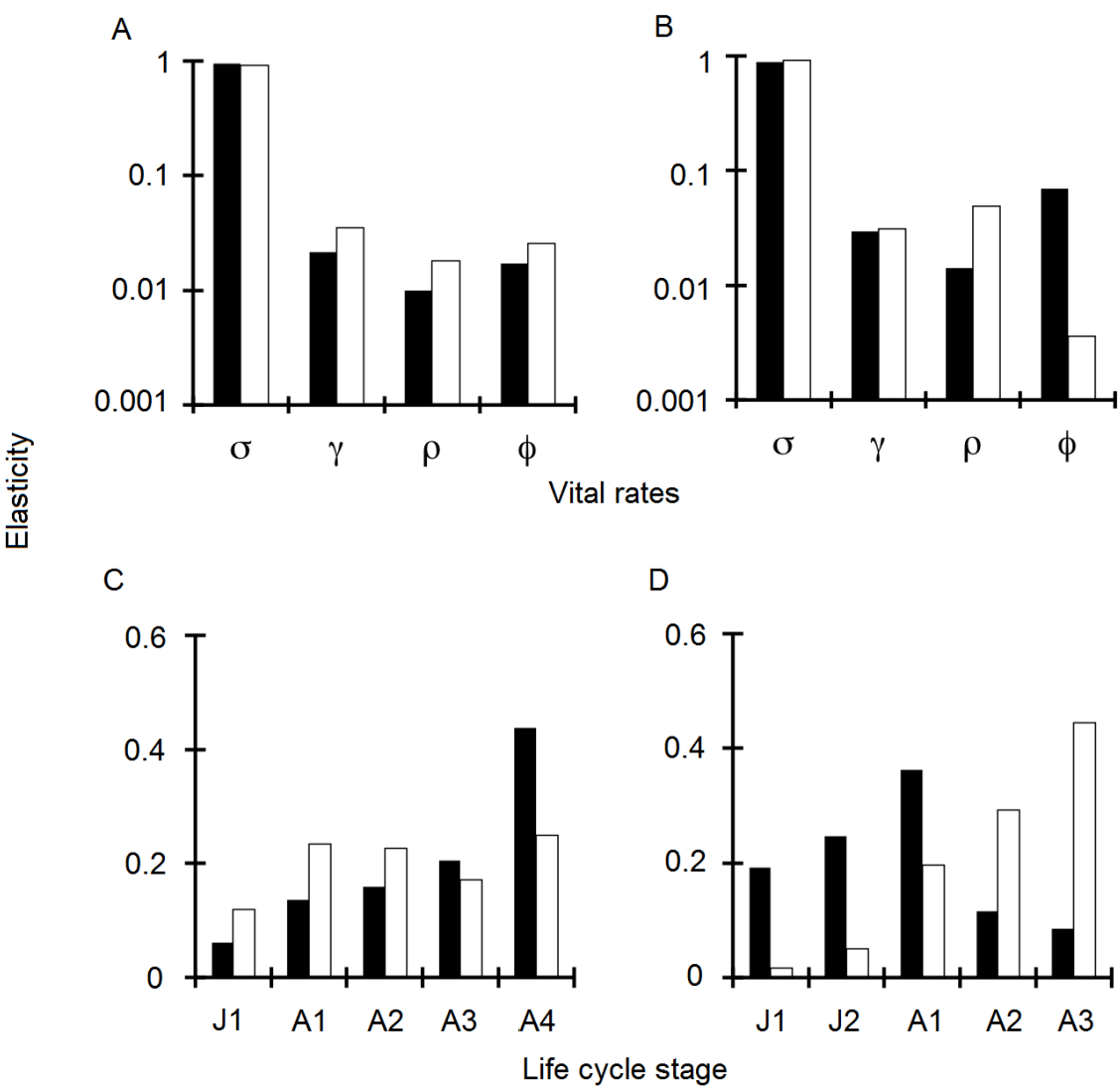


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746 Figure 3

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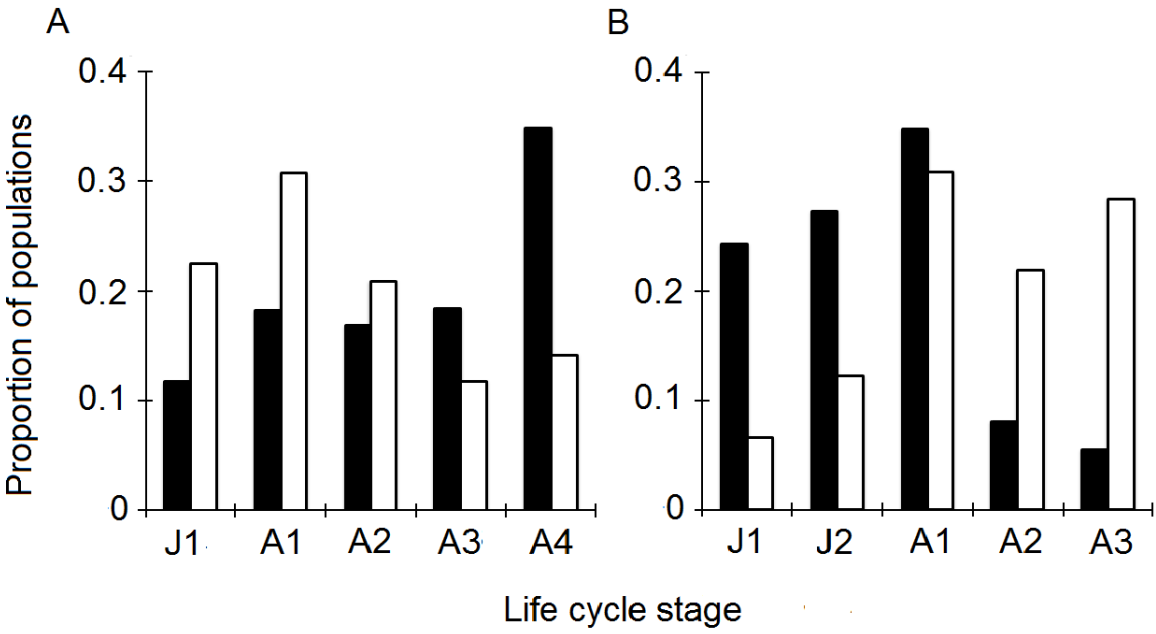


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750 Figure 4

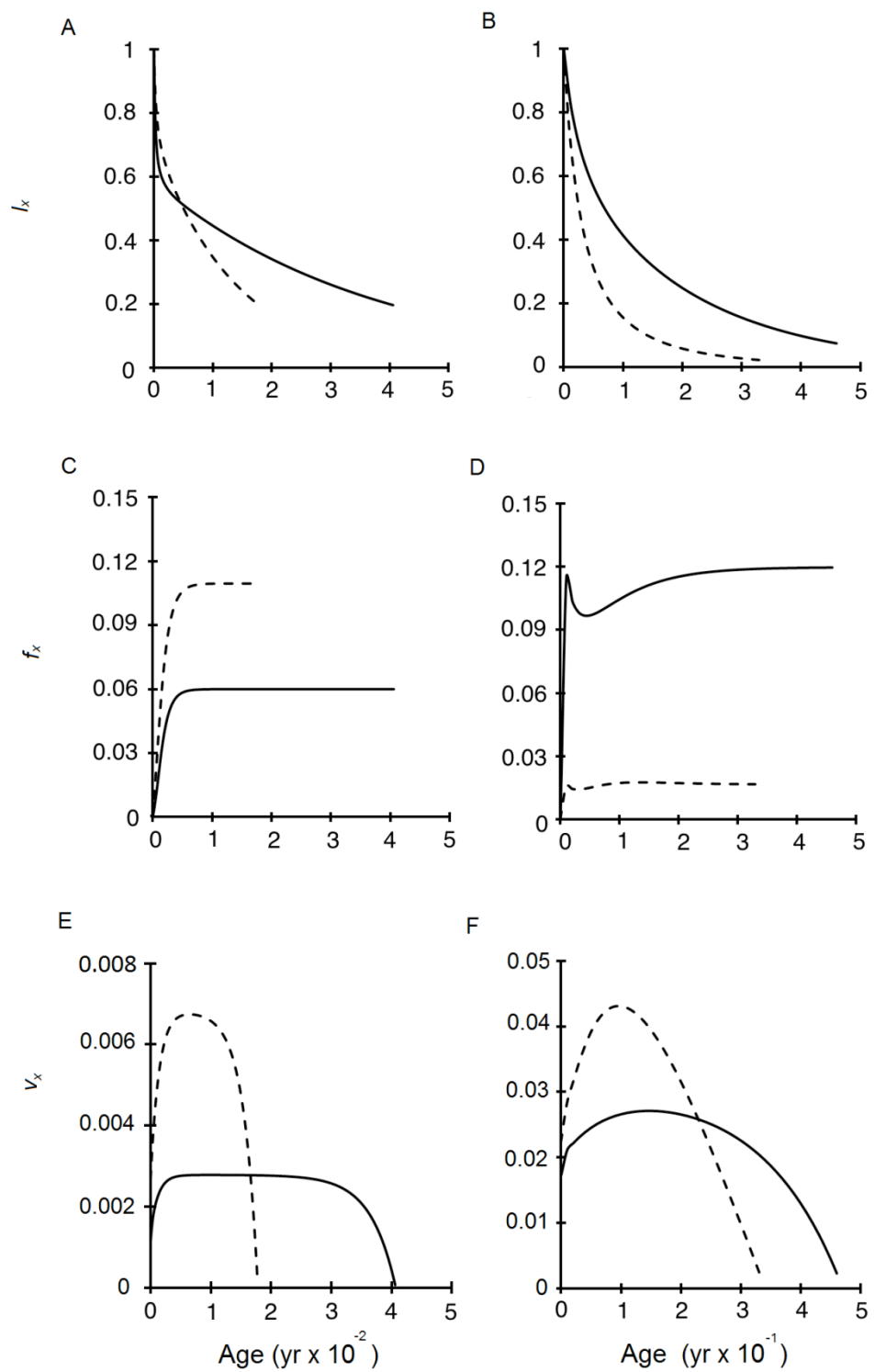
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754 Figure 5



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