Ontogenetic shift from facilitation to competition in a desert shrub

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Summary

1 Spatiotemporal responses to habitat conditions are important components of plant population and community dynamics. Plant stage or size is a common predictor of plant performance for a range of ecological conditions, including responses to neighbours. Plant response to local conditions varies from seedling establishment through to senescence, with strong implications for population regulation.

2 I investigated size-dependent responses to near adult neighbours among a uniquely quantitative sample of mapped juvenile and adult bur-sage (*Ambrosia dumosa*), a common shrub in the Colorado Desert of California.

3 Analyses of juvenile establishment and survival for two 5-year census periods from 1984 to 1989 and 1989 to 1994 determined that germination and survival was greater for juveniles located under adults compared with away from adults. However, analyses of neighbour effects on growth of plants from the 1984 cohort showed that near adult neighbours improved juvenile growth over the 10-year interval from 1984 to 1994, but reduced adult growth.

4 A size-dependent, ontogenetic shift occurs because neighbouring adult plants significantly improve the demographic performance of juveniles, but diminish that of larger established plants.

5 The ontogenetic niche shift may be a useful framework to describe such differential responses of juvenile and adult plants. The utility of this framework is that responses to spatial and temporal variability in the environment are clearly demonstrated through ontogenetic constraints on plant performance, which provide an alternative mechanism of coexistence within and between species.

Key-words: *Ambrosia dumosa*, demography, desert plants, ontogenetic shifts, population ecology, spatial ecology

Introduction

The size of an organism is an indicator of a wide range of ecological and evolutionary processes. The variation that an organism experiences throughout ontogeny is often orders of magnitude greater than the variation that exists among individuals of similar age or stage, across multiple species in a given habitat. Ontogenetic variation in habitat use has been studied in plant populations either by explicit manipulation of abiotic variables to determine limitations attributable to ontogenetic stage (Parrish & Bazzaz 1985) or by consideration of limiting conditions attributable to a single stage (Hunter 2003; persistence niche: Bond & Midgley 2001; regeneration niche: Grubb 1977; safe site: Harper 1977). Plants do not actively seek ideal habitats, but they experience distinct differences in tolerances to extrinsic factors at different developmental stages (Turner *et al*. 1969; Parrish & Bazzaz 1985; Franco & Nobel 1989; Lyons & Barnes 1998). A consequence is that distinct differences exist in the success of coexisting cohorts that may share a given habitat but that belong to different life-history stages (Alliende & Harper 1989). It is unclear if responses to extrinsic factors experienced at one developmental stage are consistent with responses at all ontogenetic stages or if ontogenetic stage causes shifts in plant responses to specific resources or levels of resources.

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Ontogenetic shifts can be assessed directly or indirectly. As an alternative to the direct manipulation of limiting resources to assess changes in niche requirements (e.g. Parrish & Bazzaz 1985), I propose to follow the responses of different stages or size classes of a plant population that occur under contrasting regimes of specific habitat conditions. Stage-specific demographic responses to contrasting environmental regimes or along an ecological gradient document shifts in habitat suitability and define the presence of ontogenetic shifts. On first principles, the probability of survival increases as plants grow (see Pfister 1998), and therefore the demographic responses of small juvenile plants will be expressed as differences in growth and mortality rates, but that of larger plants will be in the main limited to differences in performance such as growth or reproductive allocation. The underlying assumption is that performance will be enhanced where local conditions are most favourable.

I address ontogenetic shifts using demographic data from a population of the long-lived desert shrub *Ambrosia dumosa* (Gray) Payne (Asteraceae). *A. dumosa* is a good candidate to evaluate niche shifts between facilitated establishment and competitive suppression. It exists in clumped distributions that suggest facilitative interactions (Wright & Howe 1987; Miriti *et al.* 1998), but adult plants that are isolated by at least one canopy diameter from conspecifics make the most significant contribution to population growth (Miriti *et al.* 2001). Most juveniles occur within the canopy space of a conspecific adult, but isolated juveniles are conspicuous. These observations suggest two probable mechanisms for population regulation of *A. dumosa*: (i) plants that are isolated from neighbours from seedling establishment through to adult senescence show greater performance at all demographic stages and drive population dynamics, or (ii) demographic performance in response to neighbours is stage-dependent, with young plants benefiting from close adult proximity and large plants benefiting from isolation. The second mechanism suggests an ontogenetic shift (Fig. 1) within *A. dumosa* defined by the distinct demographic performances of plants with and without close adult neighbours and characterized by the contrasting spatial distributions of juveniles and adults.

My evaluation of ontogenetic shifts in response to adult near neighbours involves two steps: (i) determination of the response of new seedlings to adult neighbours and (ii) determination of the response of established juveniles and adults to adult neighbours.

Considering the first step, location under an adult canopy may enhance germination and seedling growth; however, competitive interactions owing to crowding from other juveniles (peers) that also occupy these favourable sites may eventually reduce seedling survival and growth, effectively overriding the benefits of facilitation. Establishment site therefore generates contrasting effects on the survival of newly established plants. I use these contrasting effects of establishment site to generate four partially exclusive hypotheses to
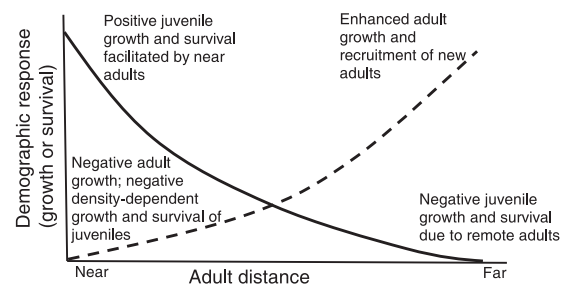

Fig. 1 Conceptual diagram of a general ontogenetic shift in response to adult near neighbours. Juveniles (indicated by the bold curve) are expected to respond positively at one end of the gradient, but adults (indicated by the dashed curve) are expected to respond positively at the opposite end of this gradient. An ontogenetic shift occurs not only due to the distinct responses of juveniles and adults at opposite ends of the gradient, but also due to the poor performance of adults under the conditions that favour juveniles. The trajectory of juvenile or adult responses may not be even along the gradient, as indicated by the nonlinear curve. Plant responses conform to an ontogenetic shift, with juvenile growth and survival favoured with near adult neighbours and adult growth favoured with remote adult neighbours.

test the persistence of juveniles in response to adult canopies: (i) juveniles under an adult canopy have higher survival than those that are not (nurse effect); (ii) clumped juveniles under adult canopies have lower survival than isolated juveniles under adults (peer competition diminishes the nurse effect); (iii) juveniles in clumps away from adult canopies have higher survival than clumped juveniles under adults (adult competition overrides peer competition); and (iv) juveniles isolated from both adults and peers show higher survival (negative density dependence overrides nurse effects). The null hypothesis (v) predicts that juvenile survival is independent of proximity to peers or adults.

The second step is to determine if seedling responses to adult proximity are consistent for the range of plant sizes present in the population. Once seeds germinate, I assume that differences in plant performance that can be attributed to near adult neighbours are likely to be expressed as differences in growth. An ontogenetic shift occurs if neighbouring adult plants significantly improve the demographic performance of juveniles, but diminish that of larger established plants.

Methods

STUDY SITE AND SPECIES

Demographic data for > 6000 *Ambrosia dumosa* are from ongoing censuses of plants within a permanent study hectare that was established in 1984 in Joshua Tree National Park (Wright & Howe 1987; Miriti *et al.* 1998). The study site is on a bajada that slopes gently (≤ 4%) to the north-west of the Eagle Mountains, 10 km south of the transition from the Colorado Desert to the Mojave Desert (115°47′ W, 33°46′ N; elevation 1006 m). Rainfall typically occurs during the winter months

(see Went 1949), and averaged 18.5 cm yr^{-1} at the Cottonwood Spring ranger station (2 km away) from 1970 to 1984 (National Park Service records). Drought conditions occurred during the 1989–94 interval but not the 1984–89 interval as measured by the Palmer drought severity index (PDSI), a measure of drought severity that is calculated considering both precipitation levels and temperature (PDSI obtained from the National Climatic Data Center at the National Oceanic and Atmospheric Association). Mean PDSI for winter 1989 was –3.76, indicating 'severe' drought, and mean PDSI for winter 1990 was –4.49, indicating 'extreme' drought.

Woody perennial shrubs and cacti were tagged, measured and mapped on a fixed grid in 1984. Censuses occurred at 5-year intervals, in 1989 and 1994, and captured significant growth, recruitment and mortality (Wright & Howe 1987; Miriti *et al*. 2001, 1998). Plant height, canopy major and minor axes, and mortality were censused for all tagged plants, and new recruits were tagged and measured. Plant volume was calculated by treating shrubs as oblate spheroids (see Miriti *et al*. 2001). Plant volumes were log$_2$-transformed. The presence or absence of flower buds, inflorescences or infructescences indicated reproductive status. The volume at which the steepest increase in the proportion of plants presenting reproductive structures occurred was used as the size cut-off between juveniles and adults (see Wright & Howe 1987).

JUVENILE SURVIVAL IN RESPONSE TO GERMINATION SITE

Hypotheses of juvenile survival as a function of proximity to adult conspecifics were tested using 'new juveniles' for each of the two census intervals. New juveniles were defined as plants that were not present during the preceding census and therefore germinated within the 5-year interval between censuses. Plants from the initial 1984 census were considered as new juveniles if they fell within the size interval determined by calculating the mean and one standard deviation of new juveniles identified in 1989.

Juveniles were divided into four categories based on two factors, location relative to an adult canopy and presence of at least one juvenile neighbour, each with two levels (presence or absence). The four categories were: (i) underneath an adult canopy and clumped, (ii) underneath an adult canopy and isolated, (iii) away from an adult and clumped, and (iv) away from an adult canopy and isolated. A juvenile was considered underneath an adult canopy if its x,y coordinates fell within the circle defined by the x,y coordinates (focus) and the major axis (diameter) of an adult. Mean nearest-neighbour distance for juveniles was 0.44 m; to determine juvenile isolation, 0.44 was rounded to 0.50. Isolated juveniles had no juvenile neighbour within 0.50 m of its x,y coordinates; clumped juveniles had at least one juvenile neighbour within 0.50 m.

Juvenile survival as a function of proximity to an adult and presence of neighbours was determined from the census data and organized in a three-way contingency table. The effects of canopy (C) and neighbours (I) on survivorship (S) were evaluated using log-linear analyses (TABLES subprogram of SYSTAT 5.03), which tests for independence among the effects of categorical variables (Agresti 1990). I constructed hierarchical models with the goodness of fit of a given model assessed using the log-likelihood ratio (G^2). The significance of an interaction was evaluated by testing the change in G^2 following the addition or deletion of a term from the model being constructed.

JUVENILE AND ADULT GROWTH IN RESPONSE TO ADULT PROXIMITY

Because plant survival increases as individuals grow, I used growth of established plants to evaluate demographic consequences of proximity to adult neighbours. For this analysis, I confined the data set to the 1984 cohort and used plant x,y locations to determine distance to the nearest adult neighbour. This restriction permitted a 10-year window of observation in which juvenile growth was not skewed by the more precarious demography of newly established juveniles (see Pfister 1998). Furthermore, 10 years provided sufficient time for small juveniles present in 1984 to reach reproductive size and therefore the opportunity to observe responses to adult neighbours.

Juveniles and adults were analysed separately. Growth was calculated as the difference between plant volumes for consecutive censuses. The dependence of growth on adult neighbour distance is confounded by plant size because small plants can grow much more than larger plants; therefore, plant size was also included as an independent variable. I used quantile regressions (Cade & Guo 2000; Cade & Noon 2003) to evaluate the following model:

$$y = \beta_0 + x_1\beta_1 + x_2\beta_2 + \varepsilon$$

where y refers to growth during a census interval, x_1 refers to adult neighbour distance at the start of the census interval and x_2 refers to plant volume at the start of the census interval; ε is a random error term (Cade & Guo 2000). Sample estimates of β at quantile τ, $\beta(\tau)$, τ ($\tau \in [0,1]$), reflect parameter estimates at that quantile.

Quantile regression is an effective tool for determining the relationship between predictor and response variables when unmeasured variation causes heterogeneous responses to a signal or signals. Whereas conventional regression methods evaluate the mean response to predictor variables ($\tau = 0.50$), quantile regression can evaluate the relationship between predictor and response variables for all parts of a distribution. The ability to detect significant relationships between variables throughout the distribution is especially useful for detecting ontogenetic shifts. If growth is
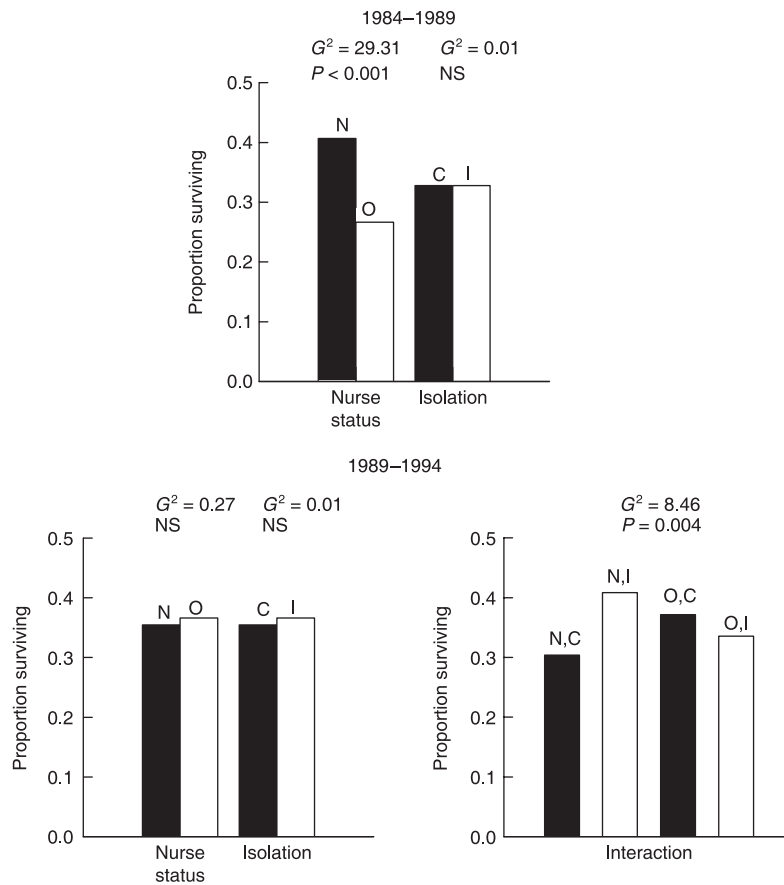
1984–1989

$G^2 = 29.31$ $G^2 = 0.01$
$P < 0.001$ NS

1989–1994

$G^2 = 0.27$ $G^2 = 0.01$
NS   NS

$G^2 = 8.46$
$P = 0.004$

Fig. 2 Observed proportional survival of new juveniles established at the start of the 1984–89 and 1989–94 census intervals plotted in response to location under an adult nurse, and juvenile clumping. Letters above the bars indicate juvenile condition: N, under a nurse; O, away from a nurse; I, isolated from juvenile neighbours; C, clumped with at least one juvenile neighbour. Log-linear analyses were used to test the significance of juvenile survival in response to these variables. *G*-statistics, which compare observed and expected survival, and significance of nurse status and isolation from juveniles are included above each graph (NS, not significant). Survival during the 1984–89 interval was enhanced by adult nurses (*P* < 0.001) independent of juvenile clumping. For the 1989–94 interval, neither nurse status nor juvenile clumping alone explained survival. A significant interaction (*P* = 0.004) occurred in which nurse plants enhanced survival of isolated juveniles, but juveniles away from a nurse benefited from occurring in a clump of juveniles.

enhanced for some surviving plants near adults while simultaneously negative density-dependent growth stunts growth for other survivors, the mean response to near adults would be insignificant. I used least absolute deviation to quantify growth responses for all quantiles using the Blossom software package (Blossom ver. W2003.02). *P*-values were determined using 10 000 iterations of the rank-score test.

Results

JUVENILE SURVIVAL IN RESPONSE TO GERMINATION SITE

Log-linear analyses used comparisons of observed and expected values of juvenile survival for the two census intervals in response to proximity to an adult canopy and isolation (Fig. 2). For the 1984–89 cohort, there were no significant interactions among the effects of canopy and clumping, but proximity to an adult canopy significantly enhanced juvenile survivorship. More juveniles survived and fewer died under an adult can-

opy than expected by chance (*P* < 0.001). The presence of juvenile neighbours had no effect on peer survivorship. For the 1989–94 cohort, there was an interaction between the effects of canopy and isolation on juvenile survivorship (*P* = 0.004): survival was high for clumped juveniles under adults and for isolated juveniles away from adults. Neither juvenile neighbours nor adult canopies alone yielded significant effects.

JUVENILE AND ADULT GROWTH AS A FUNCTION OF ADULT PROXIMITY

Juvenile and adult growth were analysed from 1984 to 1994 for the cohort of plants present in the initial 1984 census and did not include juveniles first recorded in 1989. Juvenile growth was more variable than adult growth for both census intervals, and growth was greatest during the 1989–94 census interval (1984–89 mean juvenile growth = −1.880, σ = 2.694; 1989–94 mean juvenile growth = 3.141, σ = 2.567; 1984–89 mean adult growth = −0.247, σ = 0.984; 1989–94 mean adult growth = −0.119, σ = 0.840).
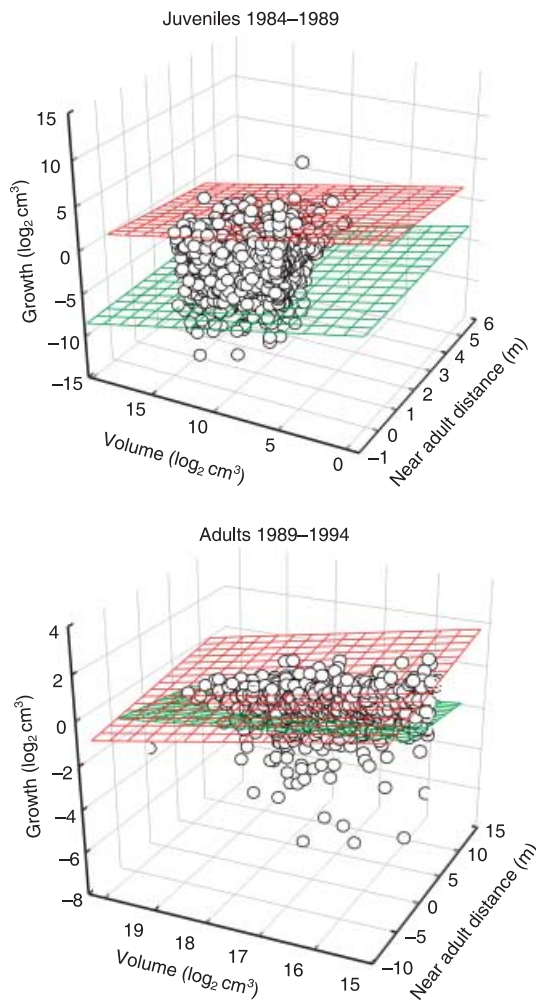
Juveniles 1984–1989

Adults 1989–1994

Fig. 3 Scatter diagrams of plant growth of the 1984 cohort in response to plant volume ($\log_2$ volume, cm^3) and adult neighbour distance during the 10-year period from 1984 to 1994. Each point represents growth of an individual *Ambrosia dumosa*. Significant quantile regression surfaces are inserted as red or green planes. The position of regression surfaces is determined by the quantile (τ) that yields a significant response. Red planes indicate growth along the upper edge of the response surface ($\tau > 0.50$) and green planes indicate growth along the lower edge of the response surface ($\tau < 0.50$). For the 1984–89 interval, both positive and negative growth of juveniles was significantly influenced by near adult neighbours, suggesting that near adults facilitate growth, but density-dependent interactions among juveniles also reduce growth. For the 1989–94 interval, adult growth increased as distance to adult neighbours increased.

Quantile regression showed that the effects of adult neighbours on focal plant growth depend on plant size (Fig. 3); the smallest juveniles displayed the greatest positive growth. For the 1984–89 census interval, growth responded at both the upper and the lower edge of the distribution, with the greatest magnitude of both positive and negative growth displayed for plants with near adult neighbours (1984–89 $\tau \mid 0.96$, $y = 5.17 - 0.27x_1 - 0.26x_2$, $P = 0.003$; $\tau \mid 0.27$, $y = -2.01 + 0.21x_1 - 0.16x_2$,

$P = 0.06$). Because growth analyses are confined to the 1984 cohort, the analysis of juvenile growth for the 1989–94 interval is not presented.

As with juveniles, adult growth was not independent of adult neighbour distance and plant size; smaller adults showed the greatest amount of positive growth. Positive growth of adults was negligible during the 1984–89 interval; for the 1989–94 census interval, adults showed significant responses along the upper edge of the distribution, showing that positive growth improved when adult neighbours were remote ($\tau \mid 0.92$ $y = 7.90 + 0.05x_1 - 0.43x_2$, $P = 0.0016$). Along the lower edge of the distribution, near adult neighbours reduced the intensity of negative growth during both census intervals (1984–89: $\tau \mid 0.07$, $y = -4.50 - 0.12x_1 + 0.21x_2$, $P = 0.04$; 1989–94: $\tau \mid 0.20$, $y = 3.88 - 0.06x_1 - 0.25x_2$, $P = 0.07$).

Differences in the response to adult neighbours as plants grew were dramatic. Within the *A. dumosa* population, 54% (1984–89) and 59% (1989–94) of surviving new juveniles were under an adult canopy, whereas more than 70% of older reproductives occurred in isolation. Further examination of the 1984 cohort revealed that after 10 years, there was no difference in the percentage of juveniles that recruited into adult size classes as a function of proximity to an adult canopy (7.6% canopy juveniles vs. 7.3% isolated juveniles), despite the clear earlier advantage to seedlings under adults. For this population, in which mean age of first reproduction was estimated to be > 80 years (Miriti 1999), juveniles outgrew the advantage of protection of an adult canopy within the first 10 years of life.

In summary, the 1984 cohort was analysed to determine growth responses of adults and juveniles to near adult neighbours. This longitudinal observation of growth was such that juvenile responses were stronger during the 1984–89 interval but adult responses were more apparent during the 1989–94 interval. The best explanation is that sufficient time had elapsed to permit 1984 juveniles to reach reproductive size. Juveniles grew most with adult near neighbours while adults grew most when they were isolated.

Discussion

The perennial shrub bur-sage (*Ambrosia dumosa*) shows an ontogenetic shift in response to adult neighbours: seedlings and juveniles are facilitated by adult neighbours, but larger plants compete with adult neighbours. Interspecific examples of change in interaction sign are sometimes termed parasitic (Wilson & Nisbet 1997), but ontogenetic shifts may provide a general framework for such changes.

The responses of juveniles and adults of *A. dumosa* provide an example of the significance of ontogenetic variation when the habitat requirements of early stages conflict with and are not just different from those of mature stages (Wayne & Bazzaz 1991; Schupp 1995). Juveniles of long-lived species often occur in habitats

distinct from those of adults (Alliende & Harper 1989), which suggests that individuals that successfully reach maturity either possessed the ability to tolerate conditions that eliminate most immatures or benefited from a mechanism that changed local conditions. At the individual level, the change in interaction sign is associated with changing requirements and tolerances of seedlings as compared with adults. Among new recruits, close proximity to an adult canopy enhances growth and survival, although later loss of these young plants may be attributed to peer competition, competition with adults or both when resources become limiting as seedlings grow. At the population level, the shift in interaction sign attributable to adult proximity is probably a mechanism that determines the projection that isolated plants drive population dynamics of *A. dumosa* at this study site (Miriti *et al*. 2001).

Ontogenetic stage limits tolerances to abiotic conditions (Parrish & Bazzaz 1985), and ontogenetic constraints are sometimes considered a critical component of population dynamics (Grubb 1977; Harper 1977; Bond & Midgley 2001; Hunter 2003). Such ontogenetic constraints are often critical in understanding and managing plant populations in which particular life stages require specific conditions not shared by other life stages. For instance, Valverde & Silvertown (1997) used simulations to explore extinction scenarios based upon frequency of gap openings for *Primula vulgaris*, an understory herb which recruits in light gaps. Similarly, Menges (1990) demonstrated the requirement of ephemeral riverbanks for the successful establishment of *Pedicularis furbishiae*, which must avoid shading from other species in order to establish. In these species all stages of the population may reside in a given area and still risk local extinction if conditions required for a single ontogenetic transition are absent. Population fate rests on requirements that are unique to one ontogenetic stage and to which the other stages are indifferent. Shifts in the ideal conditions for life-history stages document ontogenetic changes in the way that individuals interact with their environment with clear consequences for overall population dynamics.

An alternative paradigm to the significance of ontogenetic stage determining interaction sign is that shifting conditions alternately favour positive facilitative or negative competitive interactions among plants (Callaway 1995; Bertness & Leonard 1997; Callaway & Walker 1997; Goldberg & Novoplansky 1997; Hacker & Gaines 1997; Holmgren *et al*. 1997; Bertness 1998; Goldberg *et al*. 1999; Holzapfel & Mahall 1999). Tension between facilitation and competition certainly exists in desert plants. Within a size class, changes in resource abundance attributable to drought or other factors might easily tip the balance between facilitation and competition, as suggested by seedling survival in my study during the 1989–94 interval, which included drought conditions (but see Tielbörger & Kadmon 2000; Maestre *et al*. 2005). Dormann & Brooker (2002) suggest a model relating the importance of competition, rather than its occurrence, to a gradient of environmental harshness. If ontogeny influences the importance of competition, resulting in greater differences in resource use and competitive effect within a species than between similar size classes of different species (Werner & Gilliam 1984), the demographic consequences of an ontogenetic shift are important. Experimental manipulations will help to resolve the prevalence of these strategies.

Spatiotemporal dynamics are an important component of the ontogenetic shift here documented. The spatiotemporal dynamics of this shift agree with a recent summary of spatial coexistence in plant communities, which presents three axes of ecological differences that promote coexistence: resource partitioning, temporal niche partitioning and spatial niche partitioning (Amarasekare 2003). Ontogenetic shifts in this study represent temporal shifts in resource use that lack spatial partitioning but determine the sign and intensity of interactions among neighbours, which in turn influences the spatial distribution of the population.

In summary, the present study describes an ontogenetic shift from facilitation to competition among small and large plants attributable to adult neighbour proximity. The generality of ontogenetic shifts in plant populations remains to be determined, but the recognition that juvenile and adult plants express distinct responses to habitat conditions suggests broad significance of these dynamics.

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