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Facilitation drives 65 years of vegetation change in the Sonoran Desert

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Abstract. Ecological processes of low-productivity ecosystems have long been considered to be driven by abiotic controls with biotic interactions playing an insignificant role. However, existing studies present conflicting evidence concerning the roles of these factors, in part due to the short temporal extent of most data sets and inability to test indirect effects of environmental variables modulated by biotic interactions. Using structural equation modeling to analyze 65 years of perennial vegetation change in the Sonoran Desert, we found that precipitation had a stronger positive effect on recruitment beneath existing canopies than in open microsites due to reduced evaporation rates. Variation in perennial canopy cover had additional facilitative effects on juvenile recruitment, which was indirectly driven by effects of density and precipitation on cover. Mortality was strongly influenced by competition as indicated by negative density-dependence, whereas precipitation had no effect. The combined direct, indirect, and interactive facilitative effects of precipitation and cover on recruitment were substantial, as was the effect of competition on mortality, providing strong evidence for dual control of community dynamics by climate and biotic interactions. Through an empirically derived simulation model, we also found that the positive feedback of density on cover produces unique temporal abundance patterns, buffering changes in abundance from high frequency variation in precipitation, amplifying effects of low frequency variation, and decoupling community abundance from precipitation patterns at high abundance. Such dynamics should be generally applicable to low-productivity systems in which facilitation is important and can only be understood within the context of long-term variation in climatic patterns. This predictive model can be applied to better manage low-productivity ecosystems, in which variation in biogeochemical processes and trophic dynamics may be driven by positive density-dependent feedbacks that influence temporal abundance and productivity patterns.

Key words: arid; density dependence; productivity; SEM; stability; stress gradient; structural equation modeling; Tumamoc Hill.

Introduction

The relative importance and manner in which biotic and abiotic factors drive ecological processes is a long-standing issue in ecology, and has been studied extensively in moderate to high-productivity environments (Connell and Slatyer 1977, May 1984, Sousa 1984, Houlahan et al. 2007). Resource supply rates, disturbances and biotic interactions vary substantially in their effects on autotroph demographic rates along environmental gradients (Grime 1977, Bertness and Callaway 1994, Goldberg and Novoplansky 1997), resulting in different relative effects of these drivers on vegetation dynamics that are not sufficiently understood in low-productivity biomes, particularly deserts (Shreve 1929, Bowers and Turner 2002, Bowers et al. 2004). Desert perennial vegetation dynamics are both slow (Goldberg and Turner 1986, McAuliffe 1988, Cody 2000) and understudied, with few data sets available for analysis (but see Miriti 2007). In addition, both climatic and biotic regulation of under- and over-dispersed spatial patterns, suggesting facilitation and competition, respectively, have been observed (Yeaton et al. 1977, Larrea-Alcazar and Soriano 2006, Miriti et al. 2007), but their relative importance for recruitment and mortality rates has not been thoroughly assessed. Finally, there is no clear model for how abiotic factors modulate the outcome of biotic interactions to generate temporal abundance patterns in low-productivity biomes. While focusing on organismal responses to water limitation has provided important insights into the ecology of desert plants (Noy-Meir 1973), a broader perspective that incorporates the simultaneous direct

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and indirect effects of climatic variation and biotic interactions on community dynamics is necessary for scaling up to population and community-level patterns.

Indeed, several lines of evidence suggest that facilitation and competition should both have important impacts (though on different aspects) of desert perennial plant community dynamics. Seedling growth and survival of many species is substantially greater beneath the canopy of a mature plant than in the open (McAuliffe 1988, Callaway 1995), due variously to protection from stresses such as extreme temperatures and predation as well as enhancement of soil moisture and fertility (Flores and Jurado 2003). This facilitative effect is ubiquitous in arid systems and can influence recruitment independently or by modulating climatic effects (Greenlee and Callaway 1996, Tielbörger and Kadmon 2000). Similarly, competition can negatively affect the size (Yeaton et al. 1977), physiological status (Fonteyn and Mahall 1981), and survival of neighboring plants (Miriti et al. 1998), thereby potentially impacting mortality rates. Both competition and facilitation occur simultaneously in plant communities (Callaway and Walker 1997), and need to be considered in concert to gain a good understanding of their roles in demographic processes.

The importance of precipitation in determining the establishment and survival of desert perennials is certain, but the demographic patterns generated by precipitation over long time periods are less predictable. Extreme events certainly impact desert plant communities (Brown et al. 1997, Miriti et al. 2007), however less extreme variation in precipitation may have little or no immediate effect on recruitment or mortality (Bowers and Turner 2002, Bowers 2005). This may in part be a matter of scale: resource limitation and climatic extremes are visually apparent in arid systems, with precipitation rapidly triggering biotic processes such as germination and metabolic regulation on very short time scales (Noy-Meir 1973, Reynolds et al. 2004) and driving ecosystem state changes on centennial or broader time scales (Schlesinger et al. 1990). However, these processes may be transient or occurring in the background, respectively, relative to the temporal scales at which recruitment and mortality occur (Shreve 1917, Bowers and Turner 2001, Bowers et al. 2004). Recruitment and mortality are processes that often require several years to be fully realized, and due to the sessile nature and longevity of perennial plants both positive and negative effects of neighbors are likely to be persistent. Facilitation occurs over multiple years before a seedling becomes established, and likewise competitive interactions can occur for many years before leading to mortality of one or the other competitor (Miriti et al. 1998). Thus, recruitment and mortality must be assessed at an appropriate timescale in order to determine their likely effects on community dynamics.

Precipitation patterns may also primarily influence recruitment and mortality by altering the outcomes of biotic interactions or by indirect effects via some intermediary factor. For example, biotic interactions can shift from facilitation to competition across years due to variation in water availability (Greenlee and Callaway 1996, Tielbörger and Kadmon 2000). Precipitation may also influence recruitment and mortality indirectly by determining the amount of standing biomass and therefore the amount of canopy cover to protect young seedlings from high irradiance or herbivory. In order to account for all of these potential drivers, both positive and negative interactions should be considered in a manner that accounts for their unique effects on recruitment and mortality, as should the potential for abiotic variables to influence dynamics indirectly and by modulating biotic interactions (Fig. 1). These processes are often considered independently, but such an approach does not provide a comprehensive picture of ecological patterns or processes.

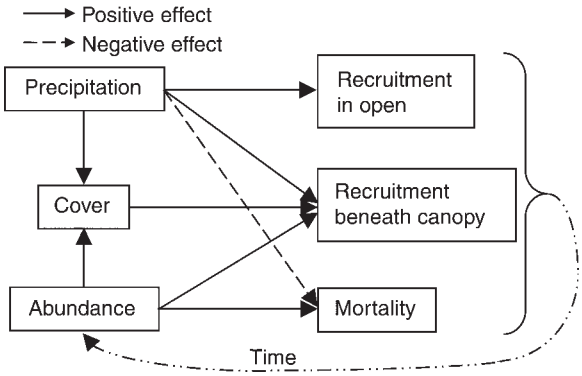

FIG. 1. Hypothetical structural equation model with possible temporal feedback. Straight arrows indicate positive (solid) and negative (dashed) causal effects. Effects of abundance or cover on mortality represent competition, while effects on recruitment represent facilitation.

To quantify the direct and indirect roles of abiotic and biotic factors in driving long-term dynamics in a low-productivity ecosystem, we used structural equation modeling (SEM) to analyze 65 years of permanent plot data from a site in the Sonoran Desert in which all perennial plants were mapped at approximately decadal intervals. This temporal scale is appropriate for assessing dynamics of slow-changing desert vegetation in which recruitment and mortality are a function of climatic variation and biotic interactions over many years (Cody 2000). To assess whether facilitation was occurring in our study plots, we also determined whether plants tended to recruit preferentially beneath existing canopies and if the degree of this preference increased with precipitation, the latter suggesting a modulation of climatic variation by plant canopies (e.g., Greenlee and Callaway 1996). We then used a simulation model derived from our SEM results to assess the temporal patterns generated by facilitation and competition, with random variation in precipitation. Quantifying the effects of climate and biotic interactions on recruitment

and mortality is clearly important, but it does not immediately predict the temporal patterns generated by these drivers. An empirical data set represents one of any number of general patterns that can be generated by the same set of processes, particularly if there is a random component to any of the driving variables, as is the case for precipitation in deserts. Thus, we used a simulation model to visualize and predict the consequences of independent and interactive effects of biotic interactions and climate on temporal abundance patterns to gain insight into the general effects of these different factors on dynamics.

Methods

Site description

This study was conducted using long-term data collected at Tumamoc Hill (32°13′ N, 111°00′ W), an isolated outcrop of the Tucson Mountains, Pima County, Arizona, USA. The study site, established as the Desert Laboratory of the Carnegie Institution of Washington in 1903, encompasses about 352 ha and includes Tumamoc Hill proper, a rocky, basaltic-andesitic knoll (760–948 m above sea level), and the level or gently rolling plain to the west (725–760 m above sea level). We used data from a set of eight contiguous 100-m^2 plots established in 1928 located on the flat alluvial fan (Area B in Shreve 1917, 1929, Shreve and Hinckley 1937, Goldberg and Turner 1986). Each plot was censused seven times at approximately decadal intervals from 1936–2001, with the locations of all perennial canopies and stem bases mapped during each census. Decadal monitoring is consistent with the characteristic cycling of wet and dry periods in the region (Goldberg and Turner 1986) and is appropriate for assessing recruitment and survival of woody and succulent desert plants (Goldberg and Turner 1986, Cody 2000).

Study-site vegetation is typical of the Arizona Upland subdivision of the Sonoran Desert. The most abundant species are *Ambrosia deltoidea*, *Krameria grayi*, *Opuntia engelmannii*, and several *Cylindropuntia* species, while less abundant but larger species such as *Larrea tridentata*, *Parkinsonia microphylla*, and *Fouquieria splendens* contribute substantially to cover. Domestic livestock have been excluded from the study site since 1907. Annual precipitation (300 mm) is seasonally distributed as a highly variable winter–early spring (November–March, 110 mm), an arid late spring (April–June, 20 mm), a predictable summer monsoon (July–August, 120 mm), and a highly variable autumn (September–October, 50 mm). Average maximum and minimum daily temperatures are 18.6° and 2.4°C during January, the coldest month, and 37.9° and 22.8°C in June, the hottest month (Sellers et al. 1985).

Data extraction

To estimate recruitment and mortality we constructed digital coverages of each of the eight plots for each of the six time intervals (census t and $t + 1$) using GIS software (ESRI 2003). Perennial abundance (hereafter "density") and cover were determined at each census, as was the cover of each plant that recruited or died in order to account for changes in cover due to these processes. The microenvironment of each new plant was recorded to estimate the regeneration niche within each plot and interval. Microenvironment was defined as either "open" (bare ground not beneath a perennial canopy) or "vegetated" (beneath a perennial canopy), based on the position of the trunk of a new recruit. As canopy size and configuration could vary substantially between censuses, new recruits in an open microsite during one census and vegetated in another were counted as 0.5 covered and 0.5 vegetated. For each plot at each time interval, a χ^2 statistic was calculated as an estimate of recruitment niche. The number of new recruits in open microsites was compared to the expected value based on proportion of bare ground within a plot, then assigned a positive sign if the number of recruits expected to occur in the open was greater than the number observed, and a negative sign if expected is less than observed. This variable, which we term recruitment niche score (RNS), is an indicator of the relative trend toward establishment beneath perennial canopies (positive) or in bare microsites (negative). We use this metric rather than simply conducting a chi-square test for two reasons. First, the number of new recruits during any time interval was insufficient to attain any statistical power for a chi-square test. Comparing RNS across plots and over time still allows us to statistically test if the preponderance of RNSs is positive or negative. Second, this is a useful index of the degree of facilitation that can be related to predictor variables (in this case, precipitation) to determine the context-dependence of facilitation.

Daily rainfall and temperature data from the University of Arizona weather station (32°13′ N, 110°57′ W; <5 km from study site) were used to calculate mean annual precipitation as during each census interval. Total precipitation for summer (May–August), fall (September–October), and winter/spring (November–April) were calculated for each year, and their average calculated for each time interval. Extreme events have been shown to play an important role in driving community dynamics in arid regions (Brown et al. 1997, Miriti et al. 2007), so we also determined the maximum seasonal totals for each time interval. Mean annual precipitation (MAP) and average annual number of precipitation events (one or more consecutive days of rain) were also calculated. Multicollinearity among precipitation variables was substantial, so we conducted a principal components analysis (PCA) to create orthogonal predictor variables for regression analysis. All but two precipitation variables (summer maximum and winter maximum) had large positive eigenvectors for the first principal component. Summer maximum and winter maximum were the only variables with large

eigenvectors for the second and third components, respectively, and based on a scree test only these first three principal components explained sufficient variation in the data set to be retained. Therefore, the orthogonal variables MAP, summer maximum and winter maximum were the only precipitation variables used in analyses of RNS. Only MAP was used for the SEM analysis, since it was least likely to be influenced by measurement error due to the substantial local-scale variation in precipitation observed at the field site (Humphrey 1933).

Statistical analysis

We conducted two analyses to determine if facilitation was occurring in our study plots and if the intensity of facilitation varied in time with precipitation. First, we used a two-tailed t test to determine if, and in which direction, RNS differed from zero. Second, to determine if facilitation enhanced recruitment in response to increased precipitation, we conducted multiple regressions with the three precipitation variables as predictors and the average RNS across all eight plots during each time interval. For each regression analysis, Akaike's information criterion with a small sample-size correction (AIC_c; McQuarrie and Tsai 1998) was used to select the best regression model within SAS (SAS Institute 2003). All variables were normally distributed and error variances were consistent, conforming to the assumptions of the general linear model.

We used SEM to determine the direct and indirect effects of abiotic and biotic factors in regulating recruitment and mortality (Grace 2006). The biotic variables used for SEM analysis were the density at the beginning of each interval and the average cover over each time interval. Since we did not know when plants recruited during an interval, using initial density was considered the best approach in that small, new plants were unlikely to function as benefactors and seedlings that germinate beneath a soon dead canopy are unlikely to survive on average. Average cover was used because individual plant canopies could grow or contract. The number of new recruits in the open, number establishing beneath canopies and number of dead plants were all divided by the interval length in years, and along with MAP were all $\log_{10}$+1 transformed in order to achieve normality and remove heteroscedasticity. The SEM analyses were conducted in Mplus v. 5.2 (Muthén and Muthén 2007) with a multilevel, or hierarchical, analysis where plots were treated as clusters to account for temporal dependence between census intervals from the same plot. The analysis was based on unstandardized coefficients (correlations), with standardized coefficients reported in order to account for different units of measure across variables.

Simulation model

We performed simulations that included all significant bivariate relationships from the structural equation model (see Results; Fig. 3). We used the discrete time function,

$$\frac{N_{t+1}}{N_t} = (\alpha + \beta)P + \gamma C - \delta N + \varepsilon$$

where cover $C = \zeta N + \eta P$, N is abundance, and P is a normally distributed random driving variable (in this case precipitation). The parameters α and β are the recruitment rates driven by P in the open and beneath canopies, respectively, γ is the recruitment rate driven by cover, δ is the mortality rate due to abundance, ε is a constant change in abundance due to unexplained recruitment and mortality, and ζ and η are the rates of change in cover due to variation in abundance and P, respectively. The null expectations for abundance and cover dynamics were modeled solely as a function of P (γ, δ, and $\zeta = 0$), then effects of cover and abundance were included to determine if they generated unique dynamics. All simulations were performed with MATLAB (MathWorks 2008).

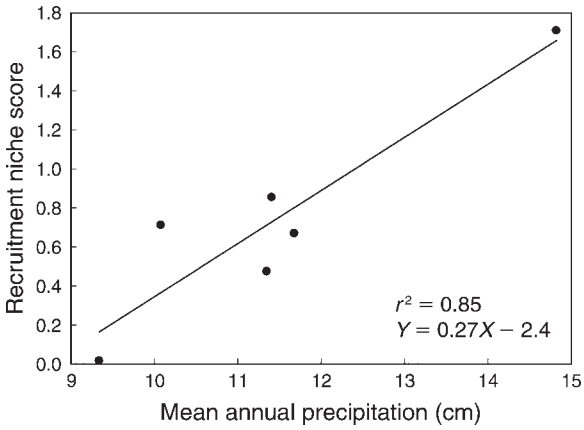

FIG. 2. Community-level recruitment niche score (RNS) as a function of variation in precipitation over time. RNS values are averaged across plots for each time interval, with larger positive values indicating greater facilitative effect.

RESULTS

Controls on recruitment and mortality

The average community RNS was significantly greater than zero ($RNS_{mean} = 0.74$, $t_{(36,2)} = 3.37$; $P = 0.002$), indicating that the preponderance of species experienced facilitative benefits during recruitment. Over time, RNS was also strongly positively correlated with MAP ($r^2 = 0.85$, df = 5; $P = 0.009$; Fig. 2), but neither of the other precipitation variables. Thus, in wetter intervals recruitment increased substantially more beneath canopies than in the open, indicating that the direct effect of precipitation on recruitment beneath canopies was different and greater than its effect in the open, thereby justifying its inclusion in the structural equation model.

Overall, the observed data did not differ significantly from the hypothesized structural equation model ($\chi^2_{(3)} =$

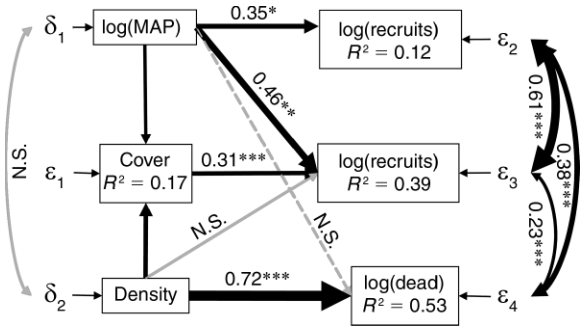

FIG. 3. Results of structural equation modeling (SEM) analysis. Gray arrows indicate nonsignificant (N.S., $P > 0.05$) bivariate relationships. The breadth of an arrow indicates the magnitude of the standardized path coefficient, which is presented numerically above each path. Curved, double-headed arrows indicate correlations between error variables for exogenous (δ) and endogenous (ε) variables.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

3.39; $P = 0.34$). However, the predicted effects of MAP on mortality and of density on recruitment beneath canopies were not significant (Fig. 3). MAP did directly influence recruitment, with a substantially stronger effect on recruitment beneath canopies than in the open. MAP and density also significantly affected cover, although the effect of density was somewhat stronger. In turn, cover directly influenced the number of recruits beneath existing canopies, but was not correlated with recruitment in the open or total recruitment (see Appendix A), indicating that the effect of cover on recruitment was due to enhanced recruitment beneath canopies. Finally, density had a strong positive effect on mortality.

Simulation model

Facilitation substantially affected abundance dynamics in several ways, depending on the frequency and direction of variation in precipitation. The impact of high frequency variation in precipitation was stabilized by facilitation (Fig. 4a), due to continued recruitment in periods with low precipitation coupled with a slow response to increased precipitation due to the positive density dependence of cover. In contrast, the effect of low frequency variation in precipitation was amplified by facilitation due to increasingly strong positive feedbacks as abundance, and therefore cover, increases, although precipitous declines in abundance can follow if precipitation declines persistently, due to declines in cover driven directly by long-term drought (Fig. 4b). Perhaps most striking are the lag effects of facilitation on responsiveness to precipitation at peak community abundance (Fig. 4c), which can result in relative stasis for multiple decades following persistent declines in precipitation before declines in abundance occur. At high abundance, community dynamics become desynchronized from precipitation due to strong positive feedbacks. Thus, the community response to variation in precipitation can be highly variable, but is predictable when considered relative to long term average abundance and precipitation patterns.

DISCUSSION

Over the course of 65 years in the Sonoran Desert, direct, indirect, and interactive effects of precipitation, cover, and density influenced patterns of recruitment and mortality in the perennial plant community in complex ways. Our statistical model accurately predicted these demographic rates (but with two important nonsignificant effects), and through simulations we show that facilitation can buffer the effects of high frequency variation in precipitation while amplifying the effects of low frequency climatic variation, potentially leading to slow responses to drought and decoupling of climate and community dynamics. Only through several lines of evidence—spatially explicit data that permit assessment of the microsite regeneration niche, the temporal context-dependence of facilitation, and indirect effects—were we able to differentiate the causes of variation in recruitment and mortality.

The effects of existing plant canopies on microenvironmental conditions varied substantially in time, producing interesting facilitative effects on recruitment. Since facilitation is by definition a positive plant–plant interaction, the simplest prediction would be that positive density-dependence of recruitment should be

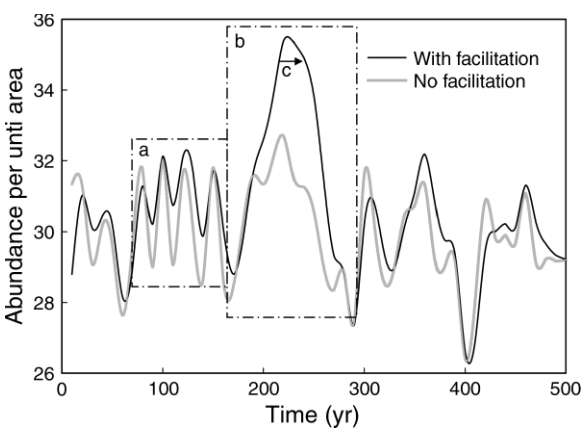

FIG. 4. Simulations of temporal abundance patterns with and without facilitation. Highlighted areas are: (a) buffering of dynamics by facilitation with high-frequency background recruitment, (b) amplification of dynamics by facilitation with low-frequency background recruitment, and (c) four-decade lag effect of facilitation at high abundance. The control (no facilitation) parameters were $\alpha + \beta = 0.75$, $\gamma = 0.002$, $\delta = 0.005$, $\varepsilon = 0.85$, $\zeta = 0$, $\eta = 20$; with facilitation, $\alpha + \beta = 0.5$, $\gamma = 0.002$, $\delta = 0.005$, $\varepsilon = 1$, $\zeta = 10$, $\eta = 10$. The parameters α and β are the recruitment rates driven by P (a normally distributed random driving variable, in this case, precipitation) in the open and beneath canopies, respectively, γ is the recruitment rate driven by cover, δ is the mortality rate due to abundance, ε is a constant change in abundance due to unexplained recruitment and mortality, and ζ and η are the rates of change in cover due to variation in abundance and P, respectively.

observed through time. However, the SEM results showed no direct effect of density on recruitment. The direct effect of cover instead suggests that the "core" area of a benefactor rather than simply its presence determines facilitative influence (McAuliffe 1986). While cover and recruitment beneath canopies could be trivially correlated, it would then be expected that cover would be negatively correlated with recruitment in the open, which it was not. The less stressful or resource rich microsite beneath perennial canopies improves recruitment, as evidenced by the positive average RNS, such that an increase in cover improves conditions for recruitment at the plot scale. The interaction between cover and precipitation exhibited by the strong positive relationship between precipitation and RNS demonstrates that plant canopies at least in part facilitate recruitment via reduced evaporation rates. Combined with the fact that the direct effect of precipitation on recruitment was greater beneath canopies than in the open suggests that, while this effect is independent of the amount of cover, existing canopies amplify the effect of precipitation on recruitment by retaining soil moisture longer than in the open. The positive relationship between facilitation and precipitation observed here supports the findings of Maestre et al. (2005) and Tielbörger and Kadmon (2000) in other arid systems, although the plateau effect observed by the latter for reproductive output did not occur for recruitment in our study.

While the direct and indirect causes of recruitment were rather complex, mortality was largely determined by variation in density, presumably due to competition. It is somewhat surprising that precipitation had no effect on mortality, but this finding corroborates the absence of a climatic signature with respect to mortality patterns found in other studies (Pierson and Turner 1998, Bowers and Turner 2001), as well as the effect of competition on nearest-neighbor size–distance relationships (Yeaton et al. 1977). However, extreme drought has been shown to impact mortality in the Mojave Desert (Miriti 2007, Miriti et al. 2007) and elsewhere in the southwest United States, but these broad-scale patterns may not be revealed in the present data set due to the relatively small size of the study plots.

While our structural equation model successfully predicted the variation observed in our data set, substantial variation was left unexplained. Species-specific responses to climatic variation (Goldberg and Turner 1986) and unique competitive and facilitative effects and responses (Yeaton et al. 1977, Larrea-Alcazar and Soriano 2006) would probably explain additional variation in the endogenous variables we measured. However, we believe our approach is preferable to a more complex analysis for several reasons. First, the extensive temporal reach of this historically important data set comes at a cost to the size and replication of plots so that the abundance of any single species is not sufficient to carry out species-level SEM analyses with sufficient statistical power. In addition, while many facilitative and competitive interactions in arid environments have been shown to be very species-specific through static spatial studies (McAuliffe 1986, 1988, Miriti et al. 2001), such relationships are highly variable in both space and time (Greenlee and Callaway 1996, Nobel and Bobich 2002, Riginos et al. 2005). In fact, we found that the RNS of *Ambrosia deltoidea*, the most abundant species in our plot and one that has been shown to be highly spatially negatively correlated with existing canopies elsewhere (McAuliffe 1988) did in fact have a positive RNS that increased dramatically with precipitation over time in our plots (Appendix B). Therefore even species that may a priori be considered unaffected by facilitation may in fact exhibit positive responses to neighbors, the magnitude of which can vary substantially in time. Likewise, the strength of the correlation between density and mortality suggests that most plants compete with multiple neighbors due to substantial overlap of wide spreading root systems, likely making assessment of intraspecific or pair-wise interspecific interactions irrelevant, if not impossible. Incorporating species-specific data would also greatly reduce the generality of our conclusions, which support the conceptualization of ecological communities as complex networks of interacting entities that may be best described in terms of composite variables (McGill et al. 2006).

The consequences of facilitation for community dynamics in arid environments have been explored within the context of circular succession (Yeaton 1978), directional succession (Shreve 1917, McAuliffe 1988, Wiegand et al. 2004) and host–parasite dynamics (Vandermeer 1980), but this is the first study to demonstrate the unique dynamics generated by community-level facilitation within the context of temporal variation in resource availability. Arid climates are not characterized simply by limitation of water for biological processes but also by the inherent variability in its supply (Noy-Meir 1973). If this is expressed as frequent variation in precipitation at a decadal scale the effects of precipitation are likely to be buffered by facilitative interactions, thereby enhancing community stability. In contrast, a persistent increase in precipitation leads to a strong positive feedback loop via facilitation that, over longer periods of time, leads to a more rapid increase in abundance than expected based solely on precipitation. Responses to declines in precipitation are buffered due to this same positive feedback, which in the short term creates resistance to declines in abundance but that in the long term is not sufficient to maintain high densities, eventually resulting in a rapid decline in abundance due to very low recruitment. This is true at the plot scale, but across a landscape plots may not be entirely in synch due to the scales at which density vs. precipitation vary. Underlying stochastic processes influence demographic rates at small scales (McAuliffe 1988) such that, even with a strong, consistent effect of precipitation across a

landscape stochastic variation in recruitment and mortality at the plot scale may result in little or no climatic signature across plots, even though at the landscape scale there is an effect of precipitation. In contrast to most metapopulation models (DeAngelis and Waterhouse 1987), positive density dependence via facilitation and not propagule limitation means that synchronicity is unlikely to be attained even with high connectedness among plots. Thus, arid systems must be considered at multiple scales in order to best predict variation in ecological patterns and processes. Lamentably, there are not enough long-term demography plots scattered across the same hydroclimatic area to evaluate either the degree or spatiotemporal scales of ecological synchrony for perennial plants in the Sonoran or any other desert.

Interestingly, the interactions between abundance, cover, and precipitation may also explain some of the observed interannual variation in net primary productivity (NPP) that is not explained by variation in precipitation found in other studies (e.g., Yahdjian and Sala 2006). Recruitment can have a large effect on variation in cover, such that wet antecedent conditions may produce a greater than expected increase in cover (and therefore NPP) due to the positive feedback of facilitation. Cover could also increase more than expected following a dry period if abundance is relatively high, or increase less than expected following a period of high or average precipitation if abundance is low. The rates of demographic responsiveness relative to the frequency of fluctuations in resource availability therefore determine not only whether facilitation stabilizes or destabilizes changes in plant community abundance, but possibly the dynamics of biogeochemical processes via controls on productivity, and of higher trophic levels through bottom up control. The relevant demographic rates must be considered relative to long-term variation in climatic drivers, emphasizing the importance of long-term research for effectively predicting and managing the stability of low-productivity ecosystems, especially considering their relative fragility with respect to anthropogenic disturbances. Given the predicted changes in total precipitation, frequency, and magnitude of precipitation events in the coming decades, particularly in the hot deserts of North America (Institute for the Study of Planet Earth 2000), understanding the role of facilitation in driving ecosystem dynamics will be essential for conserving biodiversity and the ecosystem services provided by arid and semi-arid ecosystems.

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APPENDIX A

Correlation matrix and standard deviations (*Ecological Archives* E091-080-A1).

APPENDIX B

Regeneration niche of *Ambrosia deltoidea* (*Ecological Archives* E091-080-A2).