

LETTER

Rainfall variability and fine-scale life history tradeoffs help drive niche partitioning in a desert annual plant community

Robert K. Shriver

University Program in Ecology,
Duke University, Durham, NC
27708, USA

*Correspondence: E-mail:
robert.shriver@duke.edu

Abstract

Tradeoffs have long been an essential part of the canon explaining the maintenance of species diversity. Despite the intuitive appeal of the idea that no species can be a master of all trades, there has been a scarcity of linked demographic and physiological evidence to support the role of resource use tradeoffs in natural systems. Using five species of Chihuahuan desert summer annual plants, I show that demographic tradeoffs driven by short-term soil moisture variation act as a mechanism to allow multiple species to partition a limiting resource. Specifically, by achieving highest fitness in either rainfall pulse or interpulse periods, variability reduces fitness differences through time that could promote coexistence on a limiting resource. Differences in fitness are explained in part by the response of photosynthesis to changing soil moisture. My results suggest that increasing weather variability, as predicted under climate change, could increase the opportunity for coexistence in this community.

Keywords

Comparative demography, comparative ecophysiology, intraannual variability, niche partitioning, resource pulses, resource variability, species coexistence, tradeoffs.

Ecology Letters (2017) 20: 1231–1241

INTRODUCTION

How diverse communities of species are maintained on a small set of shared limiting resources is an enduring paradox in ecology (Hutchinson 1961). Tradeoffs have played a fundamental role in the development of theory to explain observations of high species diversity (Tilman 1982; Kneitel & Chase 2004). Because resources are limited and environments often variable, maximum fitness in one set of conditions is assumed to come at the cost of lower fitness in another. Tradeoffs can help to promote species coexistence if, for example, rapid colonisation comes at a cost of lower competitive ability (Levins & Culver 1971), or if plant species can specialise on the uptake of one resource (e.g. sunlight) at the cost of another (e.g. nitrogen) (Tilman 1982, 1985). Alternatively, two or more species can capitalise on the same resource through performance tradeoffs as a function of resource availability (Fig. 1, Chesson 2000; Chesson *et al.* 2004). If species differ in their fitness and resource use in response to resource availability, fluctuations in resource availability can reduce fitness differences over time, and concentrate competition within, rather than among species. Despite the intuitive simplicity of resource fluctuations and tradeoffs as a mechanism for creating niche differences, empirical evidence supporting the role of tradeoffs in resource partitioning in natural communities is conspicuously lacking (Clark *et al.* 2003; Silvertown 2004; Adler *et al.* 2013). With widespread predictions of increases in intra- and inter-annual climate variability, the role of climate variability in creating niche differences and promoting coexistence has received increasing attention (Adler *et al.* 2006, 2009; Angert *et al.* 2009). However, little attention has been paid to how dynamic physiological responses of organisms to variable environments dictate changing demographic performance and niche partitioning.

Because competition for resources occurs through shared resource pools, understanding how changes in resource variability will alter community structure would be greatly benefited by explicitly linking ecophysiological processes that control resource use to demographic performance (metrics that underlie much of coexistence theory). However, one significant roadblock is the difficulty in quantifying demographic performance at the timescale over which a resource is varying. For example, if physiological responses to resource fluctuations are happening on daily or weekly timescales but fitness is only quantified annually, then the salient variation in fitness that helps create niche differences will be missed. Stable coexistence over years or decades requires that the long-term fitness of competing species is equivalent (through a combination of mechanisms that equalise fitness differences and promote intraspecific density dependence; Chesson 2000; Hillerislambers *et al.* 2012) but mechanisms that create niche differences can occur at much finer timescales. This mismatch in scales could lead to the impression that species do not differ in their performance or are seemingly functionally 'neutral', when in reality we are aggregating over important short-term fitness differences (Clark *et al.* 2011). Thus, in order to understand how fluctuations in resources may promote coexistence, demographic performance must be measured over appropriate timescales.

Water limited ecosystems are an appealing place to study the link between fluctuating resource availability and tradeoffs because, unlike many resources, the use of water by plants is relatively easy to measure. Plants in arid environments face an inherent physiological tradeoff between carbon uptake through photosynthesis and water use through transpiration. Closing stomata limits water loss and reduces the risk of embolism, but these benefits come at the risk of carbon starvation and ultimately mortality (McDowell *et al.* 2008; McDowell 2011).

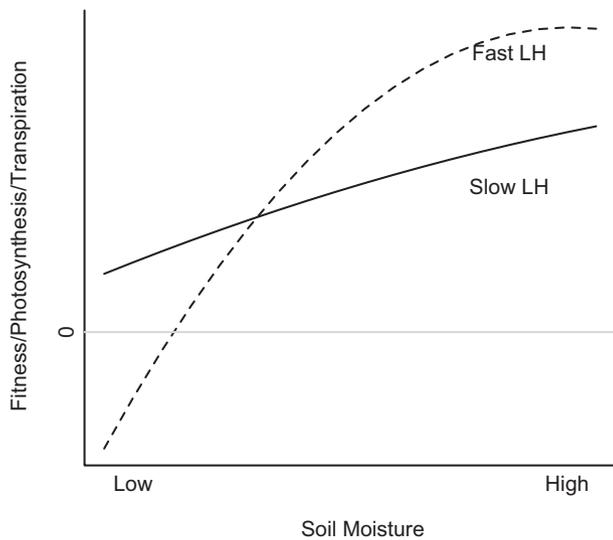


Figure 1 Hypothesised responses of daily fitness, photosynthesis, and transpiration to soil moisture for fast life history (fast growth-low survival) and slow life history species (slow growth-high survival) (Chesson 2000; Chesson *et al.* 2004). Tradeoffs allow each species to have the highest fitness in one set of conditions, slow LH when resources are low and fast LH when resources are high, thus reducing fitness differences through time. (Chesson 2000; Chesson *et al.* 2004). Fast LH species show greater rates of photosynthesis and higher fitness at high soil moisture than slow LH species. At low soil moisture, photosynthesis of Fast LH species declines rapidly leading to negative carbon balance, low survival, and low fitness compared to slow LH species. Stabilisation of coexistence requires species alter resource abundance in way that favours competitors (See Discussion). Patterns of transpiration could help to stabilise coexistence if relatively higher transpiration (lower water use efficiency) by fast LH species shortens rainfall pulse durations when fast LH species are abundant, more rapidly creating conditions that favour slow LH species. In contrast, lower transpiration (higher water use efficiency) by slow LH species could lengthen rainfall pulse durations when slow LH species are abundant, favouring fast LH species.

Conversely, leaving stomata open reduces the risk of mortality from carbon starvation, but this strategy can lead to greater risk to embolism and has been empirically associated with lower responsiveness to environmental conditions (McDowell *et al.* 2008), limiting photosynthesis and growth in wetter conditions. Differences in water use strategies have been shown to have important consequences for population growth and community structure (Angert *et al.* 2009). And, a rich theoretical literature has hypothesised that variability created by rainfall pulses can help create niche differences if some species specialise on water use in pulse periods while others do best during interpulse periods (Goldberg & Novoplansky 1997; Schwinning & Ehleringer 2001; Chesson *et al.* 2004; Huxman *et al.* 2008). Climate change is expected to increase the size of rainfall events (pulses), but also the length of dry periods in between (interpulse) periods in many ecosystems worldwide (Christensen *et al.* 2007). Therefore, understanding the role of rainfall variability in creating niche difference will be critical for forecasting how biodiversity will respond to climate change.

Here, I investigate whether variable rainfall patterns during the Chihuahuan desert summer monsoon drive fitness trade-offs, and in turn help to create niche differences, in five species of annual plants. These common species represent the

ecological diversity of annual plant species found in Chihuahuan desert including: two C4 grasses, two C4 forbs and one C3 forb. Species grow concurrently during a 2–3 month rainy season, when available soil moisture fluctuates between intense drought (interpulses) and near total saturation (pulses) (e.g. Fig. 3c). In previous work in this system, I quantified the demographic responses of these plants to soil moisture, demonstrating differences in how species' demographic rates respond to short-term variability. Specifically, fast growth at high soil moisture comes at the cost of lower survival in dry conditions, and vice versa (Shriver 2016). Here, I first examine whether these demographic rates lead to differently shaped fitness responses such that the species with highest fitness changes as a function of soil moisture. This resource-driven variation in rank fitness is the hallmark of resource use trade-offs (Chesson *et al.* 2004; Adler *et al.* 2013). Second, I examine whether physiological differences in carbon uptake and water use can elucidate the mechanism that drives fitness differences and create niche differences among species. Specifically, I hypothesise that species with a fast life history (fast growth-low survival; one grass and one forb) have lower fitness and rates of carbon uptake in dry conditions than slow life history species (slow growth-high survival) but that this cost is countered by the benefit of higher fitness and carbon uptake in wet conditions. This leads to faster maximum growth rates, greater sensitivity to environmental conditions and greater variability in growth rates for low survival species, as has been observed in many systems (Jenkins & Pallardy 1995; Suarez *et al.* 2004; McDowell *et al.* 2008). This tradeoff between fitness in wet and dry conditions, controlled by photosynthesis, along with variation in soil moisture could act to reduce fitness differences among species and promote resource partitioning through time. By connecting physiological processes to demographic patterns, I explicitly link resource uptake and use to observed life history tradeoffs and niche differentiation.

METHODS AND MATERIALS

Field data were collected at the Jornada Basin LTER in the Chihuahuan Desert of southern New Mexico USA. The field site, on the north end of the Doña Ana Mountains, is dominated by patchy, perennial bunch grasses and ephemeral annual plants. I concentrate on five of the most common annual plant species that compose ~ 40% of the annual plant cover in an average year: *Bouteloua barbata* (BOBA), *Boerhavia intermedia* (BOIN), *Eriogonum abertianum* (ERAB), *Panicum hirticaule* (PAHI) and *Tidestromia lanuginosa* (TILA). These species include two C4 grasses (BOBA, PAHI), two C4 forbs (BOIN, TILA) and one C3 forb (ERAB). Unlike their winter annual counterparts, most Chihuahuan desert summer annuals have been shown to have low levels of innate seed dormancy and wide germination conditions, and seeds of most species germinate during the first few large rain events of each season (Freas & Kemp 1983; Kemp 1983; Bachelet *et al.* 1988). The C3 species, ERAB, is an exception; it germinates during winter rains and survives a dry period before reinitiating growth and reproduction in the monsoon (Fox 1989). This life history meant that ERAB was not present in two study years 2013 and 2014, when winter rains were minimal.

Experimental design and environmental covariates

I measured how growth, reproduction and survival of all five species responded to soil moisture. To increase the range of observed soil moisture, I established 15 rainout shelters and adjacent control plots during 2012 and 2013. Rainout shelters were designed to reduce rainfall by ~20%, while still allowing light to pass through open areas and the clear plastic roofing (Yahdjian & Sala 2002; Levine, McEachern & Cowan 2010). Palruf roofing allows ~90% light transmittance leading to only ~2% total reduction in light levels under shelters. Similar shelters have been shown to have limited effect on temperatures within the plot, and effectively reduce rainfall with insignificant treatment artefacts on plant growth (Vogel *et al.* 2013). I measured soil moisture in plots using both stationary soil moisture probes (Decagon 10HS, Pullman, WA, USA) and a portable soil moisture probe (Campbell Scientific Hydrosense, Logan, UT, USA). To account for differences in probe calibration, probe measurements were rescaled to one another using concurrent measurements, when available (See Appendix S1 for further details).

Demographic and fitness data

In Shriver (2016), I quantified the demographic response of these five species to daily environmental conditions. Briefly, individuals of the five focal species in the plots were measured for size, number of flowers and fruits, and survival at ~2-week intervals during the monsoon season of 2012 and 2013. For the C4 grasses (BOBA and PAHI), the C3 forb (ERAB) and one of the C4 forbs (BOIN), size was measured as the length from the ground to the tip of the terminal stem or leaf. The other C4 forb (TILA), which grows radially near the ground, was measured by its two-dimensional area, determined by the length of the major and minor axis across the plant and the percent area missing from an idealised ellipse defined by those axes. To deal with nonlinearity in the increase of TILA size, area^{1/2} was used for modelling growth. I measured vital rates on 203 BOBA, 316 BOIN, 317 ERAB, 664 TILA and 229 PAHI individuals, for a total of 7818 individual 2-week measurements or 87 121 plant-days across all species.

I fit demographic models using a Bayesian state-space modelling approach that downscales bi-weekly plant censuses to understand how plant demographic rates respond to day-to-day environmental variation (Shriver 2016). By sharing information across census intervals these models infer the daily response of each species to environmental conditions, reconstructing how daily conditions led to observed vital rate changes over 2-week intervals. Models included linear effects of daily soil moisture, temperature, distance-weighted neighbour biomass, and plant size, all two-way interactions of soil moisture, temperature and neighbour biomass, and random individual effects. It was observed that plants rarely die in response to one stressful day, so in the survival model a moving average of environmental conditions in the five preceding days was used as a compromise to capture short- and longer-term conditions that lead to mortality.

Using demographic parameter estimates derived from the analyses in Shriver (2016), in this paper I explore whether the

fast-slow life history tradeoff helps reduce fitness differences by allowing each life history to be most fit in wet or dry conditions, and how physiological responses to soil moisture drive resource partitioning. I am interested in the response of the five annual plant species to soil moisture, so I condition responses on a fixed value for other covariates to allow a straightforward comparison. Temperature was fixed at 35.17 °C, the average for July (often the month of greatest growth). The demographic and fitness responses of species to the average temperature over the monsoon season (32.2 °C), which do not differ qualitatively, are presented in the Appendix S1 (Figs S1, S2 and S3). Neighbour biomass was fixed at the average from 2012 to 2013, although the overall response to neighbour biomass for all species, except ERAB, are generally weak (Fig. S4).

Fitness for a plant on any given day, t , can be thought of as the cumulative probability that it survives until that day multiplied by the cumulative number of flowers produced; this can be written as:

$$\log \left((f_{i,t-1} * r_{i,t})(s_{i,t-1} * p_{i,t}) \right)$$

where $f_{i,t-1}$ is the number of flowers of individual, i , on day $t-1$, $r_{i,t}$ is the daily relative reproductive rate ($f_{i,t}/f_{i,t-1}$), $s_{i,t-1}$ is the cumulative survival probability, and $p_{i,t}$ is the daily survival probability. This relationship can be rearranged as:

$$\log \left((f_{i,t-1} * s_{i,t-1})(r_{i,t} * p_{i,t}) \right)$$

where the first term summarises cumulative effects of the past, and the second is the contribution of each individual day, the daily fitness increment. For $r_{i,t}$ and $p_{i,t}$, I used the posterior probability of an average individual's response to soil moisture (i.e. parameter uncertainty). I then used daily fitness increment in two analyses. In one analysis, I quantified daily fitness increment as a function of soil moisture, conditional on plant size of 15 cm, the approximate minimum size at which physiological measurements could be taken. In the second analysis, I simulated the response of each species' fitness to three soil moisture scenarios: one in which rainfall is pulsed with 25 mm rainfall events on days 1 and 24 (similar to soil moisture dynamics seen in the monsoon season, e.g. Fig. 3c and d), and two other scenarios in which soil moisture is held constant at the low (0.037 VWC) and the high values (0.165 VWC). Soil moisture dynamics were simulated using a soil moisture model fit to field collected data that includes three processes: soil moisture inputs through rainfall and reductions in soil moisture through evapotranspiration and drainage (Shriver 2016). In each simulation, plants were allowed to grow, and then changes in size then impacted reproduction and survival. Starting plant size was 15 cm for all species, $f_{i,t}$ of 1.

Physiological data collection and modelling

Physiological data were collected throughout the mid to late monsoon season (August and September) of 2014 and 2015 at ~4–7 day intervals. Physiological measurements required that plants typically reach about 15 cm in size; because of this, and the later than average start of the monsoon in 2014 and 2015, July measurements were not possible. Focal individuals

of the five species large enough for physiological measurement were randomly selected from plants within plots.

I measured photosynthetic and transpiration rates in the field using a LICOR-6400 (LICOR Biosciences, Lincoln, Nebraska) with a standard leaf chamber and a red-blue LED light source. I conducted measurements between late-morning and mid-day at a constant chamber temperature (32 °C), constant light intensity (1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$), constant airflow rate (500 $\mu\text{mol s}^{-1}$), and ambient CO_2 concentration (~360–380 ppm). For each individual, three measurements were taken within 1–2 min. I standardised the measurements to leaf area by taking a photograph of each leaf with a scale bar and digitising the area using ImageJ software (National Institutes of Health, Bethesda, Maryland). Measurements were taken in both rainout shelter and control plots. Although rainout shelters intercept a small amount of available light (~2%), this is likely to have had little to no effect on the interpretation of how soil moisture affected physiological processes because light levels within the LICOR-6400 chamber were held constant during measurement. In total the number of plant-day measurements for each species was 47 BOBA, 52 BOIN, 22 ERAB, 46 PAHI, 50 TILA.

I modelled photosynthetic rate (a) and transpiration rate (w) as functions of soil moisture in a Bayesian framework. For each species, these physiological parameters were modelled as latent multivariate normal response variables constrained by the data taken at each sampling time (observation model), and environmental conditions (process model). The process model is,

$$[a, w]_{i,t} \sim \boldsymbol{\mu}_{i,t} + \boldsymbol{\alpha}_i + \boldsymbol{\varepsilon}_{i,t}$$

$$\boldsymbol{\mu}_{i,t} \sim \mathbf{b}_0 + \mathbf{b}_1 \left(\frac{m_{i,t}}{\theta + m_{i,t}} \right)$$

$$\boldsymbol{\alpha}_i \sim N_2(0, \Lambda)$$

$$\boldsymbol{\varepsilon}_{i,t} \sim N_2(0, \Sigma)$$

The functional form of $\boldsymbol{\mu}_{i,t}$ is a version of the common Monod saturating resource use function (Clark *et al.* 2003), where \mathbf{b}_0 and \mathbf{b}_1 describe the intercept and rate of the response of photosynthesis and transpiration to soil moisture ($m_{i,t}$), and θ is the half saturation parameter for the response of photosynthesis and transpiration. The model included individual random effects ($\boldsymbol{\alpha}_i$) and process error ($\boldsymbol{\varepsilon}_{i,t}$) which are both two-dimensional multivariate normal distributions (N_2) with mean 0 and covariance Λ and Σ respectively.

The observation model took into account that measurement precision can vary for each individual each sampling day by allowing normally distributed observation error for photosynthesis and transpiration ($\sigma_{i,t}^2$ and $\tau_{i,t}^2$ respectively) to vary by individual and day based on the three measured values (j) for photosynthesis ($A_{i,t,j}$) and transpiration ($W_{i,t,j}$).

$$\prod_3^{j=1} N(A_{i,t,j} | a_{i,t}, \sigma_{i,t}^2)$$

$$\prod_3^{j=1} N(W_{i,t,j} | w_{i,t}, \tau_{i,t}^2)$$

Physiological models were fit using JAGS (Just Another Gibbs Sampler) in R run for 20 000 iterations with a burn-in

period of 2000 iterations. All species were assigned the same informative, but weak, priors to limit posteriors to physiologically realistic parameter space (See Supporting Information 1 for full model details, prior assignments, and parameter estimates).

Species differ in their allocation of carbon to leaf area vs. leaf structural tissues. Even with the same area-specific photosynthetic and transpiration rates, species with higher specific leaf area (SLA), i.e. more leaf area per unit biomass, invest comparatively less biomass in achieving similar amounts of carbon uptake and water loss (Huxman *et al.* 2008). Scaling physiological rates by biomass allowed a comparison of each species payoff in photosynthesis, or cost in transpiration, that was based on biomass investment in leaf tissue, rather than leaf area. I rescaled leaf-area standardised models of photosynthesis and transpiration described above by each species mean SLA (see Table S4). Unfortunately, ERAB was not present when SLA measurement were taken, so only area standardised measurements are presented (See Fig. S5).

To quantify tradeoffs and the relationship between fitness and physiology, I examined correlations between daily fitness increments and photosynthetic rates at minimum and maximum soil moisture. To do this I used Pearson correlations coefficients between mean daily fitness increments and photosynthetic rates at 0 VWC and 0.2 VWC of C4 species, species for which full photosynthetic data was available.

RESULTS

Demography and fitness

Demographic analysis based on the models from Shriver (2016) showed that species generally fell along a tradeoff of growth in wet conditions and survival in dry conditions. The fast life history species (C4 forb BOIN and grass PAHI) maintain growth rates nearly double that of the slow life history species (C4 forb TILA and grass BOBA) in wet conditions, but survival rates for BOIN and PAHI were ~1% lower each day in dry conditions than TILA and BOBA (Fig. 2). Similarly, reproductive rates for BOIN and PAHI were much more responsive to environmental variation than TILA and BOBA. ERAB (C3 forb) had the lowest growth rates and survival rates of all species across soil moisture availability.

Both slow life history species (TILA and BOBA) had highest daily fitness increment increase at low soil moisture (~0.06 volumetric water content (VWC) or lower) but very little change in performance as soil moisture increased (Fig. 3). In the case of BOBA, performance on average declined slightly as soil moisture increased. In contrast, fast life history species (BOBA and PAHI) had lower demographic performance at low soil moisture, but had the highest performance under wet conditions (nearly doubling from low to high soil moisture). Finally, C3 species (ERAB) did not have the highest demographic performance relative to other species at any soil moisture level, but its own performance was highest at high soil moisture. Figures 3c and d show that soil moisture dynamics span the range of this fitness tradeoff.

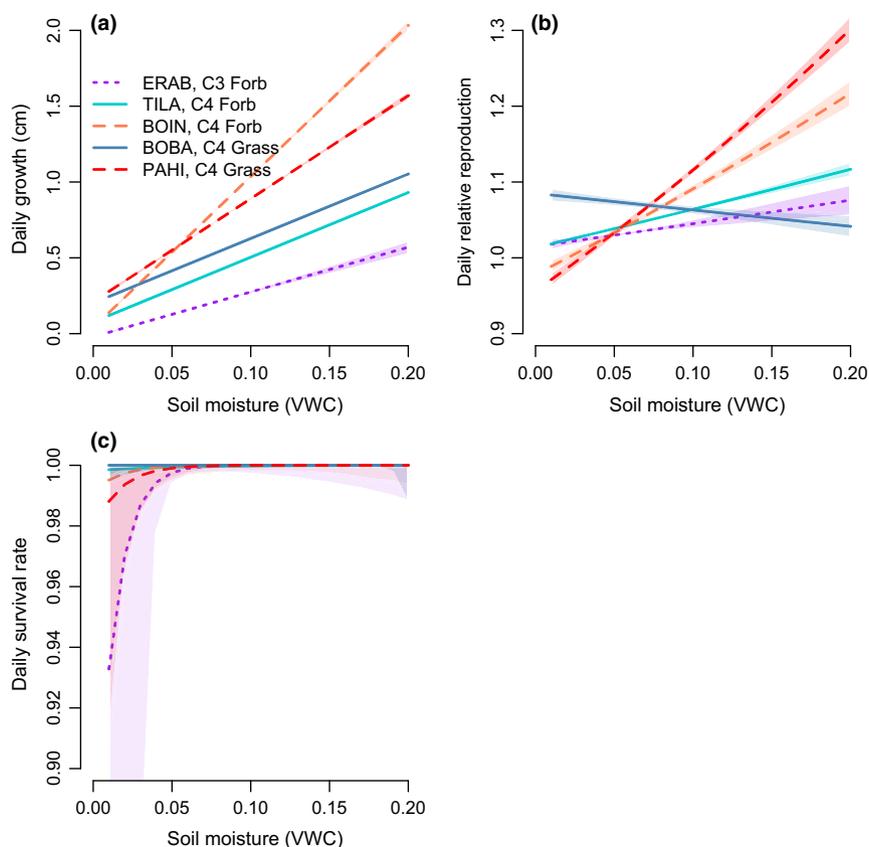


Figure 2 Demographic responses of five annual plant species to changes in soil moisture. (a) Daily growth (cm/day), (b) Daily relative reproduction ($\text{flowers}_{t+1}/\text{flowers}_t$), (c) Daily survival rate. For the purposes of comparison, all other predictor variables in the demographic models were held constant: temperature 35.17 °C, neighbour biomass at the average observed for years 2012 and 2013, and plant size of 15 cm. Shaded region covers the 95% CI of the mean response to soil moisture (i.e. parameter uncertainty).

Resource uptake and use

All species increased photosynthesis and transpiration with increasing moisture (Fig. 4). Consistent with my hypothesis, slow life history species (TILA and BOBA) maintained photosynthetic rates above zero in the driest conditions. (Fig. 4a). The fast LH species (BOIN and PAHI) both showed zero or negative carbon balance (net respiration) in the driest conditions (Fig. 4a and b, Table S2). Similarly, fast life history species showed greater rates of transpiration in most conditions (Fig. 4c and d). However, contrary to my hypotheses fast life history species only surpass slow life history species' photosynthetic rate at high soil moisture in the grasses, while there is little difference in the forbs. ERAB, not adjusted for SLA, photosynthesis remained relatively low and invariant in response to soil moisture (Fig. S5).

Fitness and physiological tradeoffs

Minimum and maximum daily fitness increment were highly negatively correlated, $\rho = -0.98$ (Fig. 5a), indicating that higher maximum daily fitness increment comes at the cost of lower minimum daily fitness increment. Counter to expectations higher maximum photosynthetic rates were not uniformly associated with lower minimum rates, $\rho = 0.28$

(Fig. 5c). However, this result was primarily driven by differences in the magnitude of maximum photosynthetic rates between grasses and forbs. As expected, minimum and maximum daily fitness increment and photosynthetic rate were positively related, but the relationship was much stronger for minimum rates ($\rho = 0.91$, Fig. 5c), than maximum ($\rho = 0.29$, Fig. 5d). In addition, increasing photosynthetic rates were associated with increasing daily fitness across all species, $\rho = 0.79$ (Fig. 5e).

Pulse-interpulse tradeoffs

To show differences in fitness longitudinally in response to changing soil moisture I also simulated the response of all five species to low soil moisture conditions, high soil moisture conditions, and a rainfall pulse-interpulse cycle. As hypothesised, the slow life history species (TILA and BOBA) had consistently higher daily fitness increment in dry conditions (Fig. 6b), leading to cumulative fitness $\sim 9\text{--}11\times$ higher than fast life history species (Fig. 6c). In contrast, the pattern is reversed at consistently high soil moisture, where the fast life history species (BOIN and PAHI) have higher daily fitness increment and cumulative fitness $\sim 0.25\text{--}1\times$ higher (Fig. 6e and f). With fluctuating moisture from rainfall pulses the forb and grass species with the highest fitness increment differed

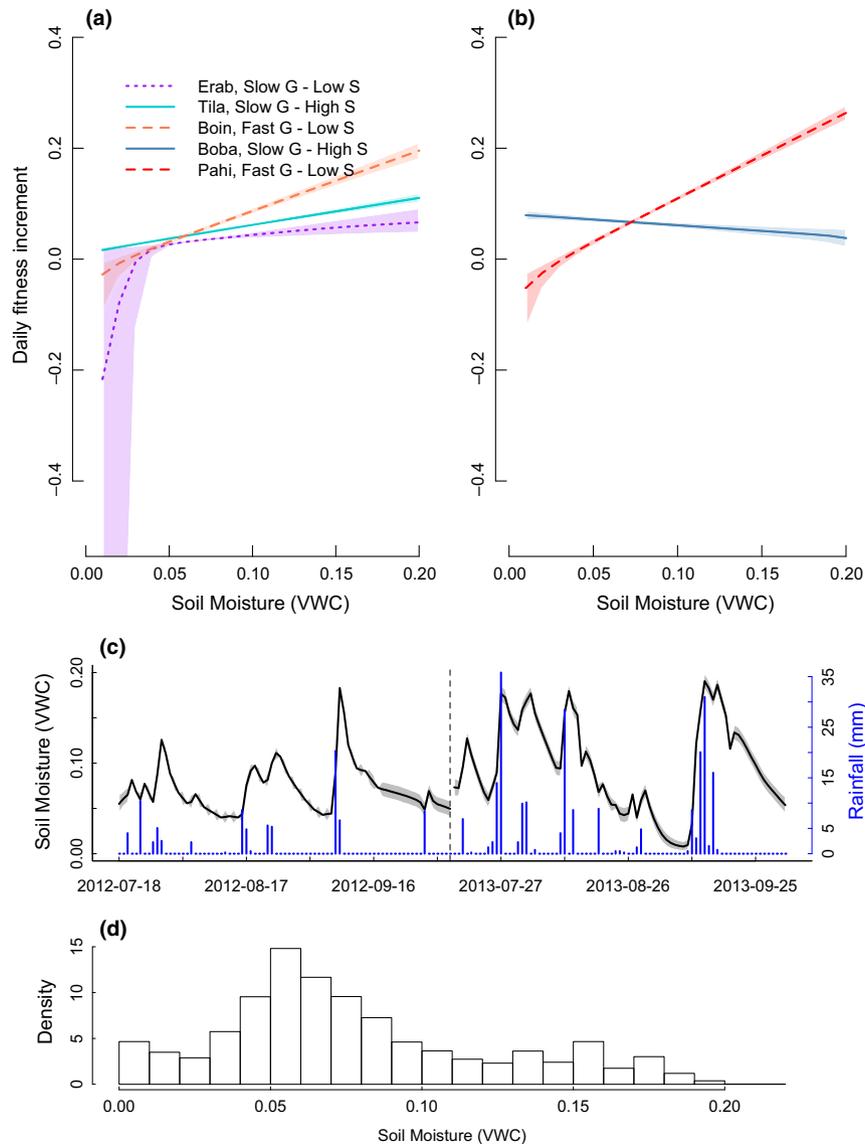


Figure 3 Daily fitness increment in response to soil moisture for (a) forbs and (b) grasses. In addition, (c) Soil moisture (black) and rainfall (blue) time series for one randomly selected plot over the 2012 and 2013 monsoon season. Daily fitness increment is quantified as the product of daily relative reproduction (fruit and flowers produced) and the daily probability of survival, $\log(r_{i,t} p_{i,t})$. Solid lines are slow life history species, long-dashed lines are fast life history species, and the short-dashed line is the slow-growth, low-survival C3 species. Shaded interval covers the 95% CI for the mean response of each species to soil moisture (i.e. parameter uncertainty). For the purposes of comparison, all other variables in the demographic models were held constant: temperature is 35.17 °C, neighbour biomass is the average observed for years 2012 and 2013, plant size is 15 cm.

between rainfall pulses and interpulse periods (Fig. 6h). Fast life history species show greater responsiveness to soil moisture variation and had the greatest daily fitness increase following rainfall. Once soil moisture had declined to ~0.07–0.05 VWC, several days after rainfall, slow life history species were favoured with greater daily increases in fitness. Slow life history species continued to be favoured until another rainfall pulse occurs. These fluctuating fitness advantages led to the total differences in cumulative fitness to be greatly reduced compared to the low and high rainfall scenarios, differences of only 0.15–0.19x (Fig. 6i). Finally, the slow growing, low survival C3 (ERAB) species was unable to have the highest daily fitness increases in any of the simulated conditions.

DISCUSSION

Rainfall variability, resource pulses and desert plants

My results indicate that rainfall pulses and life history trade-offs in growth, survival and reproduction can act to reduce fitness differences through time and promote niche partitioning, and that physiological differences among life histories help drive patterns of resource partitioning. Each grass and forb species, except ERAB, was able to have the highest fitness in either rainfall pulse or interpulse periods (Figs 3 and 6e). Rainfall events and rapid evapotranspiration could create variation in soil moisture in the shallow soil layers used by these annual plants allowing partitioning in time. But

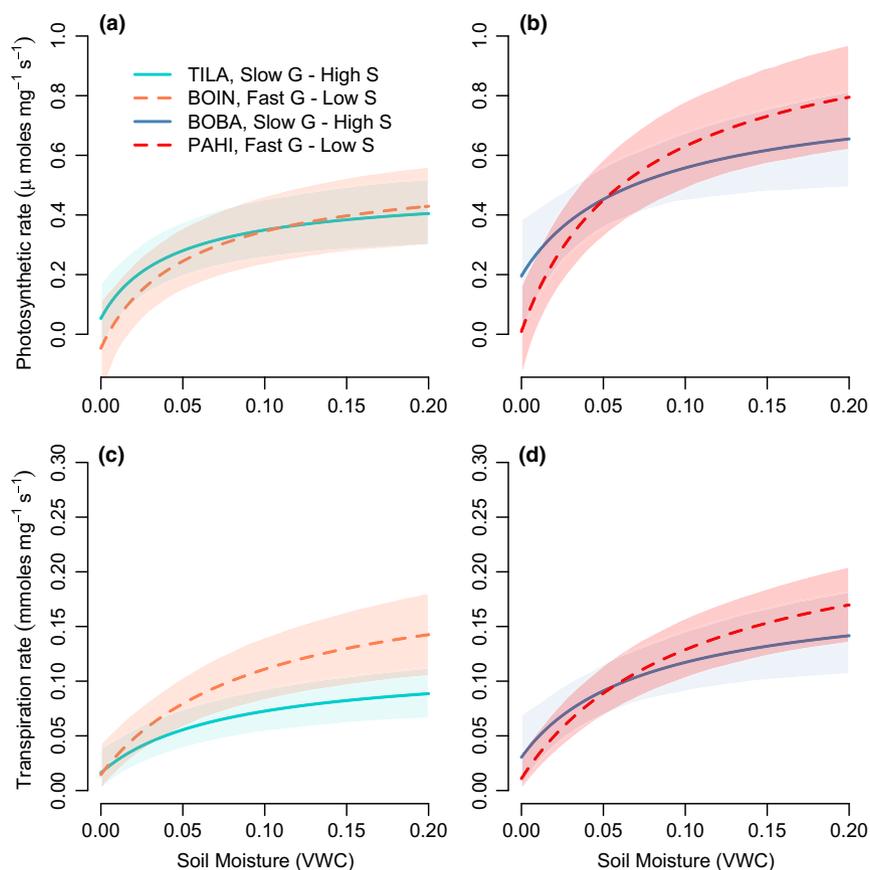


Figure 4 The response of (a and b) photosynthesis and (c and d) transpiration to changing soil moisture adjusted for species specific leaf area for (a and c) C4 forbs, and (b and d) C4 grasses. Shaded intervals are 95% CI for the average species response to soil moisture (i.e. parameter uncertainty). Units are per mg of dry leaf biomass.

importantly, changes in performance that drive this tradeoff track changes in soil moisture that happen daily. Although over longer time scales, rainfall variability could lead to near equivalent cumulative fitness across species, important differences that allow species to partition resources in time occur at much shorter time scales (Fig. 6). While annual variability may be key in understanding some drivers of coexistence (e.g. Chesson 2000; Adler *et al.* 2006; Angert *et al.* 2009), my results suggest that one major shortcoming of focusing on fitness at only one scale is that it integrates over variability that may be key to understanding other ways species partition resources. However, the relevant scale of variation likely differs from species to species depending on their biology, for example while daily variation in soil moisture is relevant for annual plants, it is likely that deeper rooted organism such as trees experience moisture variation on much longer timescales. Indeed, investigating how demographic rates and fitness changes at multiple temporal scales will likely be key to understanding how many populations and communities will respond to changes in both average conditions and in short-term variability due to climate change (Scranton *et al.* 2016; Shriver 2016).

A growing literature on winter annual plants in the Sonoran desert has greatly expanded our understanding of how annual plants cope with variable environments. Yet key differences in

winter and summer desert annuals provide an interesting, and mostly unexplored, contrast for how plants cope with variable environments. First, summer monsoon rains, although temporally variable, are quite reliable in the Chihuahuan and Sonoran deserts compared to winter rains. July and August are the only months to have always recorded rainfall at the Jornada Basin in 80+ years (Wainwright *et al.* 2006). While the role of winter annual seed dormancy and seed banks in buffering populations and species coexistence is well established (Venable 2007; Kimball *et al.* 2010), less is known about summer annuals. The reliability of rainfall, and lack of innate seed dormancy have led some to hypothesise that buffering through seed banks may be less important for structuring the summer annual plant communities (Freas & Kemp 1983; Kemp 1983), and species typically germinate following initial summer rains (Bachelet *et al.* 1988). Thus, mechanisms that allow partitioning of resources through time among continuously co-occurring species are likely to be key in maintaining diversity in this community (Chesson *et al.* 2004).

Demography and ecophysiology

Plants in arid environments must balance carbon uptake and water loss. I found that high rates of mortality and low fitness increments at low soil moisture were associated with less

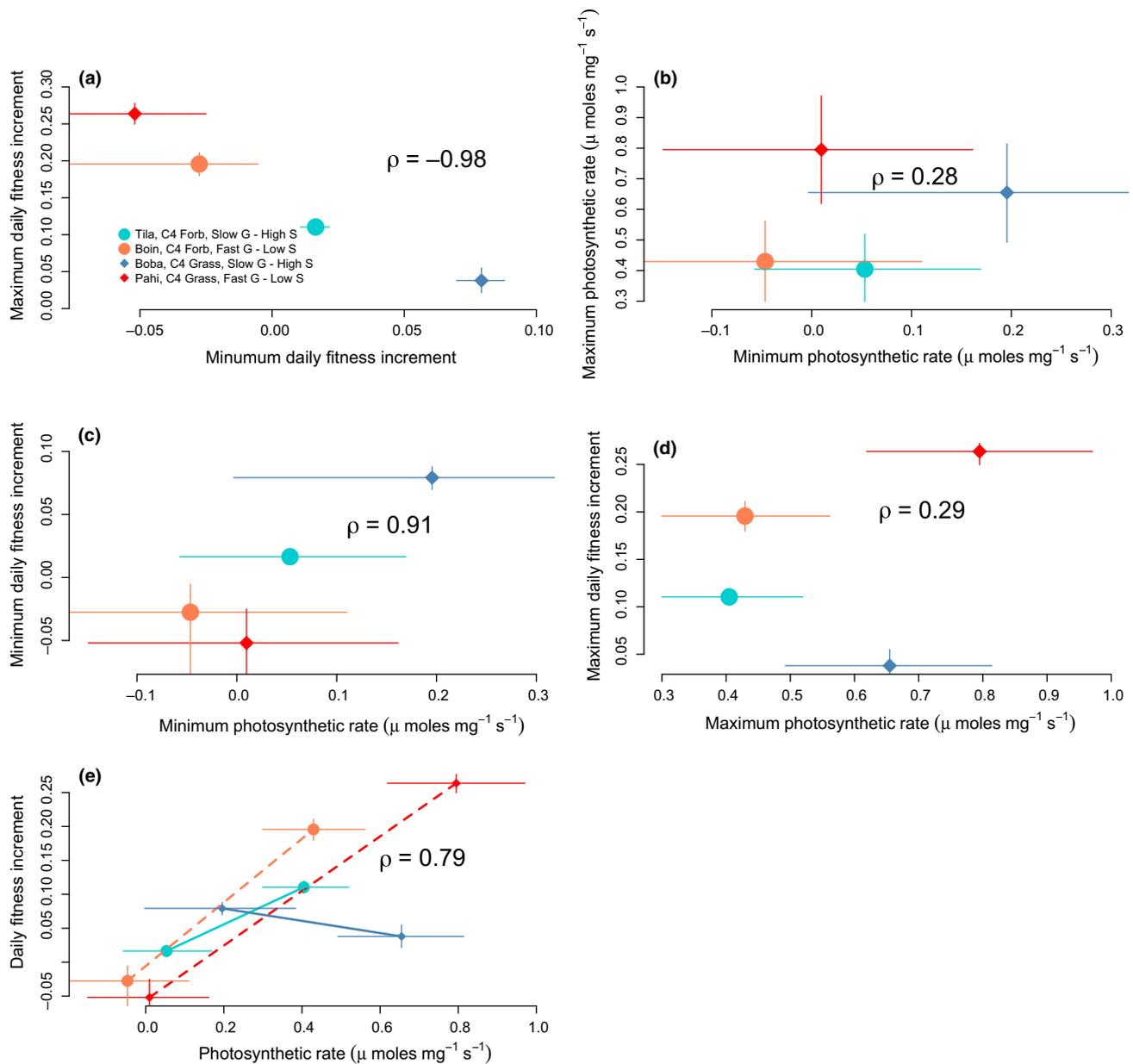


Figure 5 Tradeoffs in performance between (a) daily fitness increment at minimum (0 VWC) and maximum soil moisture (0.20 VWC), and (b) photosynthetic rate at minimum and maximum soil moisture. And, relationships between (c) daily fitness increment and photosynthetic rate at minimum soil moisture, (d) daily fitness increment and photosynthetic rate at maximum soil moisture, and (e) daily fitness increment and photosynthesis at minimum and maximum soil moisture for all species. Error bars cover 95% CI around estimates.

carbon uptake (Fig. 5c), near net zero or negative carbon balance (although with a 95% CI overlap of positive values), perhaps leading to carbon starvation as previous work has suggested (McDowell *et al.* 2008). However, the exact mechanism controlling plant mortality are often still unresolved (Sala *et al.* 2010). This finding also indicates that TILA and BOBA's ability to generally maintain positive carbon balance at low soil moisture may come at the cost of lower fitness at high soil moisture (Fig. 5). Patterns of leaf photosynthesis, however, show conflicting evidence of tradeoffs in photosynthetic rates at high soil moisture. While the fast life history grass (PAHI) had a higher photosynthetic rate than its slower

counterpart (BOBA), there was little difference in forbs (Figs 4 and 5). Fast-slow tradeoffs in reproduction and survival are common in plants (Salguero-Gómez *et al.* 2016), these findings suggest that work based on linking demography to common physiological limitations may be able to help in elucidating the functional basis of widespread tradeoffs.

Fitness, resource use and coexistence theory

A wealth of research on the role of variability in coexistence theory (*sensu* Chesson 2000) has greatly advanced our understanding of how many species can coexist in diverse

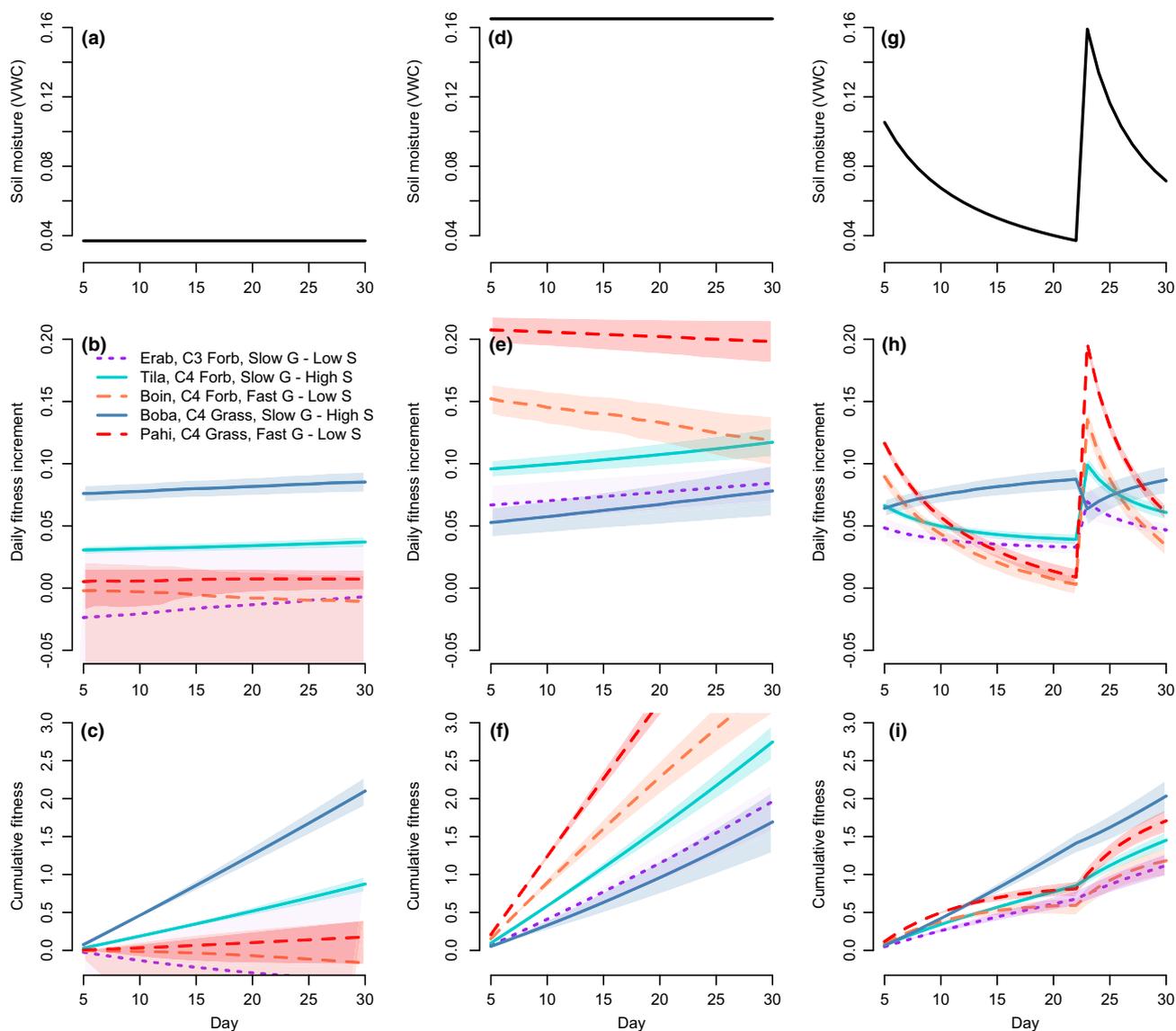


Figure 6 Simulated daily changes in fitness in three scenarios: Constant low soil moisture (a, b and c), constant high soil moisture (d and e and f), and soil moisture fluctuations from rainfall pulses (g, h and i). Simulations include effect of soil moisture on plant growth, survival and reproduction. For the purposes of comparison, all other variables in the demographic models were held constant: temperature 35.17 °C, neighbour biomass at the average observed for years 2012 and 2013. Starting plant size and $f_{i,t}$ was 15 cm and 1 respectively. Shaded intervals cover the 95% CI.

communities. This work has created a set of demographic mechanisms that allow for coexistence of multiple species in variable environments. A better understanding of how physiological processes control demographic patterns and how these same processes change resource availability could further expand our understanding of the demographic and physiological constraints that allow many species to coexist, and provide a clear link between resource mechanistic approaches to coexistence and those based on demographic and population models.

In addition to tradeoffs that reduce fitness differences, to stabilise coexistence species themselves should modify resource abundance in a way that favours competitors, allowing competitors to invade from low density in order to safeguard coexistence (Chesson 2000; Chesson *et al.* 2004; Adler *et al.* 2013). Large events favour fast life history species (BOIN and

PAHI), but higher rates of transpiration by fast life history species (Fig. 4c and d) could more quickly reduce soil moisture when these species are abundant, leading to low soil moisture conditions that favour slow life history species (TILA and BOBA). Conversely, slower rates of transpiration by slow life history species (Fig. 4c and d) could extend the length of high soil moisture conditions when slow life history species are abundant allowing a greater advantage for fast life history species. While patterns of faster transpiration by fast life history species is consistent with predictions of what would be required for stable coexistence, quantifying whether soil moisture fluctuations alone are strong enough to stabilise coexistence requires quantifying both the density of each species through time and the impact that individuals of each species have on soil moisture. This work provides a first step in

beginning to link physiological patterns of resource use and uptake, to demographic tradeoffs and niche partitioning.

But the questions remain, how do grasses and forbs of the same life history partition resources and how does ERAB remain in a community where it is never the most fit forb? First, grasses and forbs have different rooting structures, extensive fibrous roots vs. a central tap root that may allow belowground resource partitioning (Fargione & Tilman 2005). Differences in predawn leaf water potential provide some evidence that these differences in rooting structure may lead to below ground partitioning (See Appendix S2 and Fig. S9). Second, ERAB has a unique life history in this community that lends itself to seasonal competition avoidance. ERAB germinates much earlier than other summer annuals (Fox 1989). Given that ERAB is most susceptible to negative effects from high neighbour biomass (Fig. S4) this may give ERAB a period in which it is able to use water and grow in relative isolation, which could allow it to avoid competition.

Climate change implications

While the impact of increasing weather variability may be in many cases negative when considering single species alone, these results and others suggest that variability plays an essential role in maintaining biodiversity in some ecosystems (Adler *et al.* 2006; Angert *et al.* 2009). Climate change predictions for the Chihuahuan desert, and many ecosystems, (Christensen *et al.* 2007), indicate that rain events in the future are likely to be larger with longer dry periods in between. This amplification of the rainfall pulse-interpulse cycle could further insure that conditions will at times be optimal for each of these species, and allow for continued diversity in this desert ecosystem. Although, this requires that dry interpulse periods are short enough to allow all species to persist. Regardless, taking into account intra-annual weather variability will likely be key to understanding how changes in limiting resources will affect population dynamics and community composition and structure in the future.

AUTHORSHIP

RKS designed and performed this research and is the sole author.

ACKNOWLEDGEMENTS

I thank WF Morris, L Leverett, R Dalton, L Carley, B Bachelot, A Louthan, and two anonymous reviewers for their valuable feedback on this manuscript. I thank P Corcoran, C Maxwell, J Anderson, D Thatcher and the Jornada staff for their field support. This research was supported by grants from the Native Plant Society of New Mexico and Duke Biology. Additionally, this material is based upon work supported by the National Science Foundation Graduate Research Fellowship (DGF 1106401). Weather data sets were provided by the Jornada Basin Long-Term Ecological Research (LTER) project. Funding for these weather data was provided by the US National Science Foundation (Grant DEB-1235828).

REFERENCES

- Adler, P.B., HilleRisLambers, J., Kyriakidis, P.C., Guan, Q. & Levine, J.M. (2006). Climate variability has a stabilizing effect on the coexistence of prairie grasses. *Proc. Natl Acad. Sci. USA*, 103, 12793–12798.
- Adler, P.B., HilleRisLambers, J. & Levine, J.M. (2009). Weak effect of climate variability on coexistence in a sagebrush steppe community. Weak on coexistence effect of climate variability in a sagebrush steppe community. *Ecology*, 90, 3303–3312.
- Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. (2013). Trait-based tests of coexistence mechanisms. *Ecol. Lett.*, 16, 1294–1306.
- Angert, A.L., Huxman, T.E., Chesson, P. & Venable, D.L. (2009). Functional tradeoffs determine species coexistence via the storage effect. *Proc. Natl Acad. Sci. USA*, 106, 11641–11645.
- Bachelet, D., Wondzell, S.M. & Reynolds, J.F. (1988). A Simulation Model Using Environmental Cues to Predict Phenologies of Winter and Summer Annuals in the Northern Chihuahuan Desert. In: *Advances in Environmental Modelling*. Elsevier, Amsterdam, pp. 235–260.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.
- Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K. *et al.* (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia*, 141, 236–253.
- Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I. *et al.* (2007). Regional climate projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M. & Averyt, K.B., *et al.*). Cambridge University Press, Cambridge, pp. 849–940.
- Clark, J.S., Mohan, J., Dietze, M. & Ibanez, I. (2003). Coexistence: how to identify trophic trade-offs. *Ecology*, 84, 17–31.
- Clark, J.S., Bell, D.M., Hersh, M.H., Kwit, M.C., Moran, E., Salk, C. *et al.* (2011). Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecol. Lett.*, 14, 1273–1287.
- Fargione, J. & Tilman, D. (2005). Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. *Oecologia*, 143, 598–606.
- Fox, G. (1989). Consequences of flowering-time variation in a desert annual: adaptation and history. *Ecology*, 70, 1294–1306.
- Freas, K. & Kemp, P. (1983). Some relationships between environmental reliability and seed dormancy in desert annual plants. *J. Ecol.*, 71, 211–217.
- Goldberg, D. & Novoplansky, A. (1997). On the relative importance of competition in unproductive environments. *J. Ecol.*, 85, 409–418.
- HillerisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. & Mayfield, M.M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annu. Rev. Ecol. Evol. Syst.*, 43, 227–248.
- Hutchinson, G.E. (1961). The paradox of the plankton. *Am. Nat.*, 95, 137–145.
- Huxman, T., Barron-Gafford, G. & Gerst, K. (2008). Photosynthetic resource-use efficiency and demographic variability in desert winter annual plants. *Ecology*, 89, 1554–1563.
- Jenkins, M.A. & Pallardy, S. (1995). The influence of drought on red oak group growth and mortality in the Missouri Ozarks. *Can. J. For. Res.*, 25, 1119–1127.
- Kemp, P.R. (1983). Phenological patterns of chihuahuan desert plants in relation to the timing of water availability. *J. Ecol.*, 71, 427–436.
- Kimball, S., Angert, A.L., Huxman, T.E. & Venable, D.L. (2010). Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Glob. Chang. Biol.*, 16, 1555–1565.
- Kneitel, J.M. & Chase, J.M. (2004). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.*, 7, 69–80.
- Levins, R. & Culver, D. (1971). Regional coexistence of species and competition between rare species. *Proc. Natl Acad. Sci.*, 68, 1246–1248.

- Levine, J.M., McEachern, A.K. & Cowan, C. (2010). Do competitors modulate rare plant response to precipitation change? *Ecology*, 91(1), 130–140.
- McDowell, N.G. (2011). Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol.*, 155, 1051–1059.
- McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T. *et al.* (2008). Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.*, 178, 719–739.
- Sala, A., Piper, F. & Hoch, G. (2010). Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytol.*, 186, 274–281.
- Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C. *et al.* (2016). Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proc. Natl Acad. Sci.*, 113, 230–235.
- Schwinning, S. & Ehleringer, J.R. (2001). Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *J. Ecol.*, 89, 464–480.
- Scranton, K., Lummaa, V. & Stearns, S. (2016). The importance of timescale of fitness metric for estimates of selection on human life-history traits during a demographic transition. *Ecol. Lett.*, 19, 854–61.
- Shriver, R.K. (2016). Quantifying how short-term environmental variation leads to long-term demographic responses to climate change. *J. Ecol.*, 104, 65–78.
- Silvertown, J. (2004). Plant coexistence and the niche. *Trends Ecol. Evol.*, 19, 605–611.
- Suarez, M.L., Ghermandi, L. & Kitzberger, T. (2004). Factors predisposing episodic drought induced tree mortality in Nothofagus–site, climatic sensitivity and growth trends. *J. Ecol.*, 92, 954–966.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1985). The Resource-Ratio hypothesis of plant succession. *Am. Nat.* 125, 827–852
- Venable, D.L. (2007). Bet hedging in a guild of desert annuals. *Ecology*, 88, 1086–1090.
- Vogel, A., Fester, T., Eisenhauer, N., Scherer-Lorenzen, M., Schmid, B., Weisser, W.W. & Weigelt, A. (2013). Separating drought effects from roof artifacts on ecosystem processes in a grassland drought experiment. *PLoS one*, 8(8), 1–10.
- Wainwright, J. (2006). Climate and climatological variations in the Jornada basin. In: *Structure and Function of a Chihuahuan Desert Ecosystem* (eds Havstad, K.M., Huenneke, L.F. & Schlesinger, W.H.). Oxford, New York, pp. 44–80
- Yahdjian, L. & Sala, O.E. (2002). A rainout shelter design for intercepting different amounts of rainfall. *Oecologia*, 133(2), 95–101.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Editor, Elsa Cleland

Manuscript received 1 March 2017

First decision made 14 April 2017

Second decision made 26 June 2017

Manuscript accepted 3 July 2017