

LETTER

Functional trait trade-off and species abundance: insights from a multi-decadal study

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Abstract

Phylogenetically informed trait comparisons across entire communities show promise in advancing community ecology. We use this approach to better understand the composition of a community of winter annual plants with multiple decades of monitoring and detailed morphological, phenological and physiological measurements. Previous research on this system revealed a physiological trade-off among dominant species that accurately predicts population and community dynamics. Here we expanded our investigation to 51 species, representing 96% of individual plants recorded over 30 years, and analysed trait relationships in the context of species abundance and phylogenetic relationships. We found that the functional-trait trade-off scales to the entire community, albeit with diminished strength. It is strongest for dominant species and weakens as progressively rarer species are included. The trade-off has been consistently expressed over three decades of environmental change despite some turnover in the identity of dominant species.

Keywords

Abundance, annual plants, coexistence, community phylogenetics, functional traits, macroecology, physiological trade-offs.

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INTRODUCTION

Ecophysiological trait trade-offs are commonly used as organising principles for understanding population and community processes. Organisms must balance allocation to growth, survival and reproduction to maximise fitness within the constraints of finite resources. For example, at the population level, the trade-offs between defence versus growth and reproduction is crucial in predicting predator-prey cycles (Strauss *et al.* 2002; Yoshida *et al.* 2004; Lind *et al.* 2013). At the community level, trade-offs between traits such as growth and mortality among tropical tree species (Wright *et al.* 2003, 2010; Poorter & Markesteijn 2008), competitive ability and herbivore resistance in plants (Kempel *et al.* 2011), or seedling development and new habitat occupation in a hyperdiverse temperate region (Chen *et al.* 2018) help us understand the evolution of diverse life history strategies. Such trade-offs among species within a community result in varied physiological responses to the environment that lead to different patterns of demography, adaptation and distribution. Thus, trade-offs form the basis of niche partitioning among species and have been shown to underpin species coexistence mechanisms (Tilman 2004; Angert *et al.* 2009).

The trait-based approach requires knowledge of which trait trade-offs are important for defining species niches and niche definition is best accomplished with detailed population dynamic information linking traits to fitness (McGill *et al.* 2006; Litchman *et al.* 2007; Kimball *et al.* 2012, 2013). Relatively simple systems such as desert annual plant communities are exceptionally well-suited for such an approach since dynamics are fast and patterns of variation in populations and environment can be documented in a relatively short time (Angert *et al.* 2009; Huxman *et al.* 2013). We have previously shown that a trade-off between growth rate and water-use

efficiency is important in defining species niches of dominant species in a desert annual plant community (Angert *et al.* 2007, 2009, 2010; Huxman *et al.* 2008, 2013).

Such trade-offs between water-use efficiency and growth potential are well known in plants (Bai *et al.* 2008; Gebrekirstos *et al.* 2011). CO₂ uptake and water vapour loss through stomata are tightly linked, such that in general high photosynthetic rates cannot be achieved without subsequent high water losses. Likewise, adaptations to increase water-use efficiency usually come at a cost that reduces rates of carbon gain or alters allocation to growth (Smith *et al.* 1997). Many adaptations to increase water-use efficiency are known, including small cell size and thick cell walls which help protect against plasmolysis, greater allocation to roots at the expense of above-ground photosynthetic tissues, small, dissected leaves, thick cuticles, sunken stomata, succulence/CAM, phenological strategies such as leaf abscission strategies and the annual growth habit (Orians & Solbrig 1977; Solbrig & Orians 1977). All these adaptations constrain carbon accumulation and allocation to growth, thus contributing to the water-use efficiency/growth rate trade-off.

The trade-off between carbon gain and water transpiration is related to the trade-off between water-use efficiency and nitrogen-use efficiency (Field *et al.* 1983; Patterson *et al.* 1997; Hooper & Johnson 1999; Gong *et al.* 2011), to the 'leaf economic spectrum' (Wright *et al.* 2004) and to the C-S axis of Grime's C-S-R triangle (Grime 1977). Many adaptations that operate to adjust one of these trade-offs incidentally influence the other ones resulting in the correlations that underlie the 'fast-slow' trait spectrum which has been described at organ, individual and ecosystem scales (Reich 2014).

The trade-off between water-use efficiency and growth rate is expressed as plastic responses to the environment (Gong *et al.* 2011; da Silva Lobato *et al.* 2016), genetic variation

within populations (Saldana *et al.* 2007; Nemeskéri *et al.* 2012), population or cultivar differences along environmental gradients (Lizana *et al.* 2006; Munoz-Perea *et al.* 2007; Rizza *et al.* 2012), and species differences (Tsialtas *et al.* 2001; Nemeskéri *et al.* 2012). Population and species differences along environmental gradients reflect the filtering aspect of community construction (Saldana *et al.* 2007; Kimball *et al.* 2010). While few studies have focused on divergent positions along the trade-off within communities as an example of limiting similarity promoting species coexistence (but see Angert *et al.* 2009), this idea has long been explicit in the literature (Orians & Solbrig 1977; Solbrig & Orians 1977; Fowler 1986). Nonetheless, no studies to our knowledge have discussed the existence of the trade-off within communities in terms of species abundance. Some have related position along the trade-off to abundance from the standpoint of environmental filtering, e.g., water-use efficiency has been related to abundance in arid environments (Tsialtas *et al.* 2001), or have used abundance to calculate community mean trait values (reviewed in Funk *et al.* 2017).

A strong trade-off between relative growth rate (RGR) and water-use efficiency (WUE) has been identified for nine focal species in a winter annual plant community (described extensively in Angert *et al.* 2007 and Huxman *et al.* 2008). These nine species represent 60% of individual plants occurring in long-term plots in a desert winter annual study system. The inverse relationship between RGR and WUE has been shown to allow these dominant species in the community to uniquely respond to temporal abiotic variation, with each species taking advantage of different environmental conditions (Kimball *et al.* 2010, 2011, 2012). These functional differences have been shown to underlie species coexistence via the temporal storage effect (Angert *et al.* 2009) and show predictive relationships with phenological, morphological and seed-stage characteristics important for fitness in these species (Angert *et al.* 2010; Kimball *et al.* 2011; Huang *et al.* 2016). Moreover, our study site has become hotter and drier over three decades and winter rains have arrived increasingly later in the season, shifting germination to colder periods and favouring cold-adapted species with high WUE (Kimball *et al.* 2010 and Huxman *et al.* 2013). Despite multi-decadal changes in species relative abundance, species diversity has not declined (Venable & Kimball 2013).

Most studies of functional-trait trade-offs that organise communities focus on a few to a dozen or so dominant species or functional groups (Litchman *et al.* 2007; Angert *et al.* 2009). However, complete enumeration of species richness in plant communities often reveals many more species, including many rare species and it is unclear whether niche differentiation alone is adequate to explain such high numbers of species (Tilman & Pacala 1993; Silvertown 2004). Such concerns have lead ecologists to consider that species diversity may be explained by a multitude of processes acting at different scales (Bengtsson *et al.* 1994; Loreau & Mouquet 1999; Kneitel & Chase 2004) and that some species in a community may even be maladapted to local conditions (Mouquet & Loreau 2003; Esther *et al.* 2008).

Here we extend the analysis of this WUE-RGR functional-trait trade-off to 51 winter annual species constituting 96% of

the individual plants seen in our permanent plots over 30 years. We evaluate the trade-off for this expanded species list in a phylogenetic context and explore its relationship to species abundances. Specifically, we ask: (1) How does the WUE-RGR trade-off for the entire community compare to that of the dominant species? (2) How does species abundance relate to whether a species follows a community-organising trade-off? (3) As community composition changes over time in response to multidecadal environmental change, what happens to the trade-off and to species positions along the trade-off?

MATERIALS AND METHODS

Field site

Field work was conducted at the 115-year-old Desert Laboratory now owned by the University of Arizona and Pima County, AZ, USA (32.2129° N, 111.0062° W, 723 m a.s.l.). The central feature of the Desert Laboratory is Tumamoc Hill, a volcanic hill and alluvial, gently sloping flat (Phillips 1976). Our research is conducted on the creosote flats northwest of Tumamoc Hill and on the lower northern and western slopes of the hill itself. The soil in this area is variable and is predominantly sandy, clay and rocky (see Pantastico-Caldas & Venable 1993 for a thorough description). The site receives about 300 mm of rain annually, with roughly half falling during summer monsoons, and most of the remainder falling between October and April, the growing season for winter annual plants.

Functional trait measurements

In the 2007–2008 winter growing season, multiple physiological traits were measured for the 51 winter annual plant species considered here (Table 1). One to three randomly selected individuals of each species were harvested at roughly weekly intervals (~eight plants total from four dates for each species) during the main growing season (February and March). All annual plant species present in our study area that occurred in sufficient numbers for our protocol were used. Harvested plants were separated into root, leaf, stem and reproductive organs to estimate biomass allocation and leaf area. Leaf area was measured with a Licor 3100 Leaf Area Scanner (Licor, Nebraska, USA).

From these measurements we calculated specific leaf area (SLA; leaf: leaf dry mass), leaf area ratio (LAR; leaf area: total dry mass) and leaf mass ratio (LMR; leaf mass: total dry mass). Our sequential harvest data could not be used to directly calculate RGR since we attempted to harvest only pre-reproductive plants for stable isotope analysis. These annual plants develop rapidly and we were not able to collect enough sequential samples before the onset of reproduction to get a reliable direct measurement of RGR. Instead we constructed a surrogate for RGR from its constitutive components based on our previous understanding of RGR construction in our system (Angert *et al.* 2007, 2009, 2010; Huxman *et al.* 2008, 2013). RGR (rate of dry mass production per unit dry mass) is, by definition, the product of NAR (rate of dry mass production per unit leaf area) and LAR

Table 1 Species used in this study. Nomenclature is consistent with previous work in the system; when different, current synonymy is indicated in parentheses

Species code	Family	Species name in paper
AMIN	Boraginaceae	<i>Amsinckia intermedia</i> Fisch. & C.A. Mey.
ASNU	Fabaceae	<i>Astragalus nuttallianus</i> Dc.
BOIN	Apiaceae	<i>Bowlesia incana</i> Ruiz & Pav.
CACH	Onagraceae	<i>Camissonia chamaenerioides</i> (<i>Eremothera chamaenerioides</i> (A. Gray) W.L. Wagner & Hoch)
CAEX	Orobanchaceae	<i>Castilleja exserta</i> (A. Heller) T. I. Chuang & Heckard
CHST	Asteraceae	<i>Chaenactis stevioides</i> Hook. & Arn.
CHBR	Polygonaceae	<i>Chorizanthe brevicornu</i> Torr.
CRAN	Boraginaceae	<i>Cryptantha angustifolia</i> (Torr.) Greene
CRBA	Boraginaceae	<i>Cryptantha barbigera</i> (A. Gray) Greene
CRPT	Boraginaceae	<i>Cryptantha pterocarya</i> (Torr.) Greene
DAPU	Apiaceae	<i>Daucus pusillis</i> Michx.
DEPI	Brassicaceae	<i>Descurainia pinnata</i> (Walter) Britton
DRCU	Brassicaceae	<i>Draba cuneifolia</i> Torr. & A. Gray
ERDI	Polemoniaceae	<i>Eriastrum diffusum</i> (A. Gray) H. Mason
ERDE	Polygonaceae	<i>Eriogonum deflexum</i> Torr.
ERTR	Polygonaceae	<i>Eriogonum trichopes</i> Torr.
ERLA	Asteraceae	<i>Eriophyllum lanosum</i> (A. Gray) A. Gray
ERCI	Geraniaceae	<i>Erodium cicutarium</i> (L.) L'Hér. ex Aiton
ERTE	Geraniaceae	<i>Erodium texanum</i> A. Gray
ESCA	Papaveraceae	<i>Eschscholzia californica</i> Cham.
EUCH	Boraginaceae	<i>Eucrypta chrysanthemifolia</i> (Benth.) Greene
EUMI	Boraginaceae	<i>Eucrypta micrantha</i> (Torr.) A. Heller
EVMU	Asteraceae	<i>Evax multicaulis</i> (<i>Evax verna</i> Raf.)
GULA	Brassicaceae	<i>Caulanthus lasiophyllus</i> (Hook. & Arn.) Payson
HAPA	Boraginaceae	<i>Harpagonella palmeri</i> A. Gray
HEHI	Caryophyllaceae	<i>Herniaria hirsuta</i> L.
LARE	Boraginaceae	<i>Lappula redowskii</i> (<i>Lappula</i> <i>occidentalis</i> (S. Wats.) Greene)
LELA	Brassicaceae	<i>Lepidium lasiocarpum</i> Nutt.
LEGO	Brassicaceae	<i>Lesquerella gordonii</i> (A. Gray) S. Watson
LIBI	Polemoniaceae	<i>Linanthus bigelovii</i> (A. Gray) Greene
LOHU	Fabaceae	<i>Lotus humistratus</i> (<i>Acmispon</i> <i>brachycarpus</i> (Benth.) D.D. Sokoloff)
LOTO	Fabaceae	<i>Lotus tomentellus</i> (<i>Acmispon</i> <i>strigosus</i> (Nutt.) Brouillet)
LUCO	Fabaceae	<i>Lupinus concinnus</i> J. Agardh
LUSP	Fabaceae	<i>Lupinus sparsiflorus</i> Benth.
MAPA	Brassicaceae	<i>Matthiola parviflora</i> Kuntze
MEAL	Loasaceae	<i>Mentzelia albicaulis</i> (Douglas) Douglas ex Torr. & A. Gray
MOBE	Asteraceae	<i>Monoptilon bellioides</i> (A. Gray) H.M. Hall
OEPR	Onagraceae	<i>Oenothera primiveris</i> A. Gray
PEHE	Boraginaceae	<i>Pectocarya heterocarpa</i> (I.M. Johnst.) I.M. Johnst.
PERE	Boraginaceae	<i>Pectocarya recurvata</i> I.M. Johnst.
PHCR	Boraginaceae	<i>Phacelia crenulata</i> Torr. ex S. Watson
PHDI	Boraginaceae	<i>Phacelia distans</i> Benth.
PLAR	Boraginaceae	<i>Plagiobothrys arizonicus</i> (A. Gray) A. Gray

(continued)

Table 1. (continued)

Species code	Family	Species name in paper
PLIN	Plantaginaceae	<i>Plantago insularis</i> (<i>Plantago ovata</i> Forssk.)
PLPA	Plantaginaceae	<i>Plantago patagonica</i> Jacq.
SCBA	Poaceae	<i>Schismus barbatus</i> (L.) Thell.
SIAN	Caryophyllaceae	<i>Silene antirrhina</i> L.
SIIR	Brassicaceae	<i>Sisymbrium irio</i> L.
SPEC	Apiaceae	<i>Spermolepis echinata</i> (Nutt. ex DC.) Heller
STCA	Brassicaceae	<i>Strepantanthus carinatus</i> C. Wright ex A. Gray
STMI	Asteraceae	<i>Stylocline micropoides</i> A. Gray

(total plant leaf area/total plant dry mass). In turn, LAR is the product of SLA (leaf area per unit dry mass) and LMR (total plant leaf dry mass/total plant dry mass). Previous growth analysis using 2005-season harvests of individuals over time showed that among species differences in whole plant RGR are determined more by LAR than by NAR (Angert *et al.* 2007) and that interspecific NAR variation appears to be associated with differences in nitrogen allocation and differential within-season activity affecting WUE rather than driving big differences in RGR (Huxman *et al.* 2008). So, we constructed an RGR surrogate from a principal components analysis (PCA) of its primary constitutive components, LAR, SLA and LMR (prcomp procedure, R Core Team 2018). SLA and LAR data were natural log transformed to improve normality and reduce the importance of outliers. The first PC explained 60.53% of the variation in the original three variables and correlated positively with SLA (loading = 0.67), LAR (loading = 0.72) and LMR (loading = 0.19). To confirm that our PC1 score measures a similar signal of growth capacity to harvest-based RGR, we analysed the correspondence of PC1 with the sequential-harvested-calculated RGR measurements in Angert *et al.* (2007) using the species common to both studies. We also confirmed that PC1 showed the same strong trade-off with WUE as harvest-calculated RGR.

The leaves collected prior to reproduction were oven-dried for carbon isotope analysis to calculate Δ , a time-integrated measure of water-use efficiency calculated as $\Delta = (\delta a - \delta p) / (1 + \delta p / 1000)$, where δa is the $\delta^{13}\text{C}$ ratio of CO_2 in the atmosphere (assumed to be -8‰) and δp is the measured carbon isotope ratio of the dry leaf tissue (Farquhar *et al.* 1989). Leaf samples from three individuals of each species were analysed separately for carbon isotopes, then averaged.

Functional trade-off analysis

To examine the strength of the trade-off between intrinsic WUE (Δ) and our RGR surrogate (PC1; hereafter, 'RGR') while accounting for shared evolutionary history, we conducted phylogenetic generalised least squares analyses (PGLS; Symonds & Blomberg 2014, see Appendix 1A for a brief description of PGLS). To avoid overcorrection of the data we calculated Pagel's λ separately for each regression model and used it to adjust the error covariance matrix (Pagel 1997;

Freckleton *et al.* 2002; Revell 2010). Pagel's λ in this context is a measure of the strength of phylogenetic signal (inertia) in regression residuals. This was implemented with the `ppls` function in the R package `caper` v. 0.5.2. (Orme 2013). The phylogenetic tree of our 51 annual plant species employed in our analyses was constructed using the most recent and comprehensive molecular phylogeny of land plants (see Appendix 1B for details of assembly; Zanne *et al.* 2014).

The role of species abundance

Demographic measurements on 72 permanent plots at the Desert Laboratory provide yearly estimates of the number of germinating and surviving plants per m^2 (see Gremer *et al.* 2016 for methodological details and plot history). We estimated the average germination density of each species from 2005 to 2015 to get a time-averaged density for an interval that brackets the 2007–08 season in which our data were collected. This specific range was somewhat arbitrarily chosen but a decadal average overlapping the study season was used to capture general trends in species abundance. Similar trends are found using only 2007–2008 abundances and below we assess the role of shifting windows of abundance on the robustness of our results.

We assessed the strength of the trade-off with respect to 2005–2015 average species abundances by running a PGLS for the six most abundant species and then repeating this analysis, adding one additional species in each iteration, in the order of decreasing average abundance (Table S1). We also repeated this procedure with random selections of six initial species and randomly pulled subsequent species additions without replacement. The random selections were repeated 100 times for each number of species. We then compared the dynamics of the coefficient of determination (R^2) and associated P -values between the density-ordered species addition and the randomly-ordered additions. Finally, we conducted a weighted regression analysis using species abundances as weights.

The trade-off across time

To explore the possibility that the WUE-RGR trade-off changes as species composition shifts across decades, we calculated average abundances of species for consecutive non-overlapping 5-year periods across the 32 years between 1983 and 2014 (the first period used for averaging was 7 years: 1983–1989). We averaged 5-year periods to increase our chances of uncovering multidecadal trends and to simplify data presentation (there were no significant differences using yearly abundances). Using these average abundances, a weighted regression was conducted on RGR vs. WUE with time interval and interval \times WUE interaction as covariates. If interval is significant the trade-off shifts in intercept across time intervals. If interval \times WUE interaction is significant, the slope of the trade-off varies across intervals. Because we used the same values of WUE and RGR for each species for all intervals, only the weights (abundances) differed across intervals. Thus we used a randomisation procedure to create null distributions to test the significance of slope and intercept

differences across time intervals. The six average abundances of each species were randomly reassigned to the six five- or seven-year intervals for that same species. Then the F -statistics for interval and interval by WUE were calculated from the regression described above. This was repeated 2000 times to create null distributions of F for intercept and slope differences. Slope or intercept was deemed to vary significantly across time intervals if the F -statistics using the true abundances was greater than 95% of the F 's generated using randomised abundances.

RESULTS

We found a significant positive correlation between our RGR surrogate (PC1) based on LAR, SLA and LMA measured in 2008 and RGR calculated from sequential harvests from the field site in 2005 (Fig. S1, $R^2 = 0.46$, $P = 0.04$). Also, our RGR surrogate has a similar-strength trade-off with WUE as the sequential-harvest RGR used by Angert *et al.* (2009) for the same nine dominant species and species also had similar positions along the trade-off axis (Fig. 1a, $R^2 = 0.55$, $P = 0.02$, $\lambda = 0.43$). These consistencies make us confident that our RGR surrogate is capturing the same signal of 'growth potential under favourable conditions' that trades off with WUE for dominant species.

When we analysed all 51 species using phylogenetic generalised least squares, we found that the trade-off was also present ($R^2 = 0.07$, $P = 0.03$, $\lambda = 0.54$; Fig. 1b). When we weighted the regression by 2005–2015 species abundance, the trade-off using 51 species became highly significant with a much higher coefficient of determination ($R^2 = 0.53$, $P < 0.00001$, Fig. 1c). Since species contribute to this regression in proportion to their abundance, the many minor community members do not dominate the weighted analysis.

When species were added in order of decreasing abundance to the PGLS (starting with the five most abundant species), the coefficient of determination started at $R^2 > 0.80$ and steadily decreased eventually being < 0.1 (Fig. 2a). All analyses up to and including the addition of the 35th species had $P < 0.05$. Beyond that $P > 0.05$ until it dropped back under 0.05 with the addition of the rarest two species at which point the analysis converged to the result presented above for the PGLS of the full 51 species ($R^2 = 0.07$, $P = 0.03$).

When we repeated this analysis using a random set of five starting species and randomly choosing species to be added sequentially (i.e. disregarding species abundance), the five-species regressions were seldom significant and median R^2 was around 0.3, dropping quickly to around 0.1 with the progressive random inclusion of additional species (Fig. 2b). Median P values were > 0.05 for all regressions with < 39 species, dropping below 0.05, thereafter, again converging to the same result from above when all 51 species were finally included (Fig. S2).

Neither the slope nor intercept differed significantly across the 5-to-7-year intervals spanning 1983 to 2014 using regression weighted by abundance (Fig. 3a; randomization test, intercept differences, $P = 0.42$; slope differences, $P = 0.43$). There were no significant differences when individual year densities were used for this analysis either. Thus, the nature of

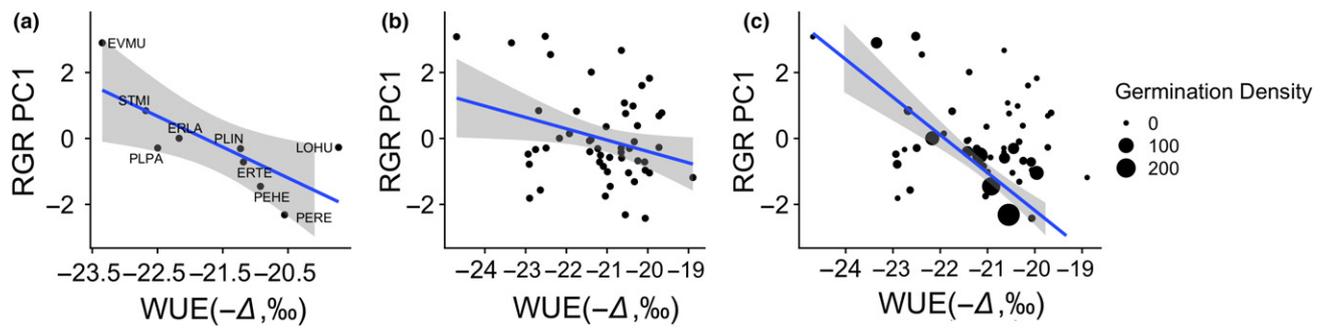


Figure 1 (a) Functional-trait trade-off between WUE and an RGR surrogate for nine dominant species used in previous research. Blue line represents PGLS regression line ($R^2 = 0.44$, $P = 0.03$, $\lambda = 0.43$). (b) Functional-trait trade-off between WUE and the RGR surrogate for all 51 species present in the community. Each dot represents one species on functional-trait trade-off axes. The PGLS regression line ($R^2 = 0.071$, $P = 0.033$, $\lambda = 0.54$) is similar to the ordinary least squares regression line (not shown). (c) Abundance-weighted regression of WUE vs. RGR surrogate trait values for 51 species ($P < 0.00001$). Dot sizes indicate relative species abundance.

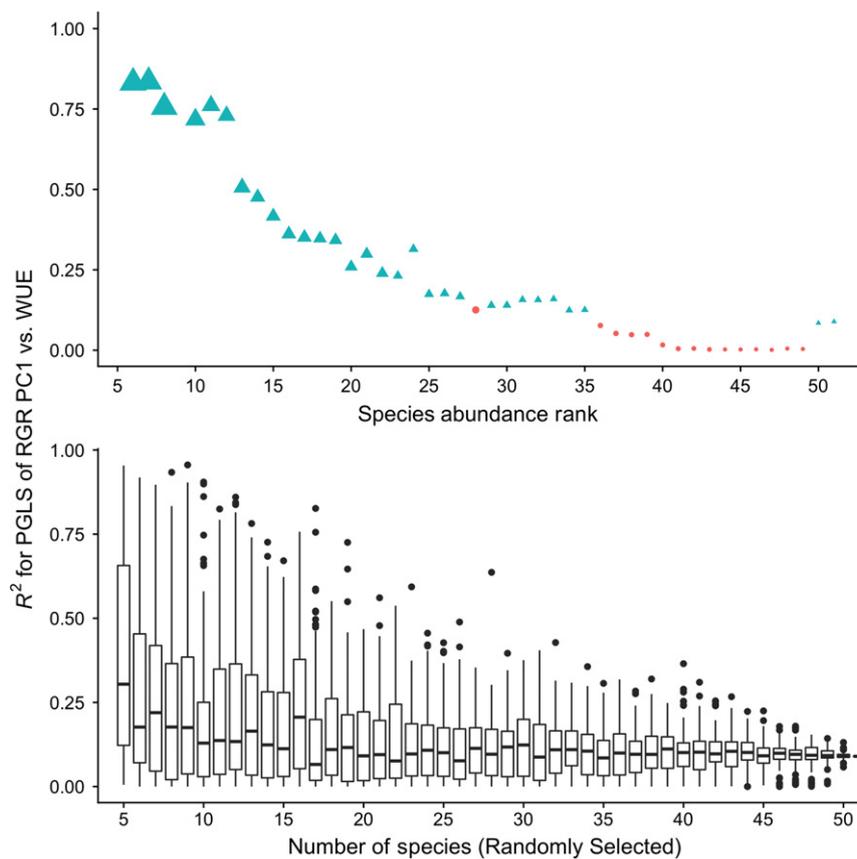


Figure 2 (a) PGLS R^2 's start high and progressively decline as more species are added sequentially by declining abundance rank. R^2 's with $P < 0.05$ are represented by triangles; dots indicate $P > 0.05$. The size of the markers represents the relative abundance of the last species added. (b) Whisker plots for R^2 's for 100 replicates of random selection of X species where X goes from 5 to 51. The open bar represents the 25–75% quartiles and the thick horizontal line represents the median. In contrast to (a) median R^2 's are uniformly low when species are selected at random with regard to abundance.

the community trade-off line did not change across three decades in response to changing species relative abundances. However, the community shifted position along the trade-off line over time, with species with higher WUE and lower RGR increasing in abundance relative to species with lower WUE and higher RGR (community abundance-weighted average RGR progressively declined while weighted average WUE progressively increased, Fig. 3b).

DISCUSSION

Comprehensive community research programs are crucial for advances in community ecology, and are needed to make better predictions of responses to environmental change (McGill *et al.* 2006; Huxman *et al.* 2013). To achieve this, we must move beyond focal-species interactions and consider entire communities and the mechanistic underpinnings of population

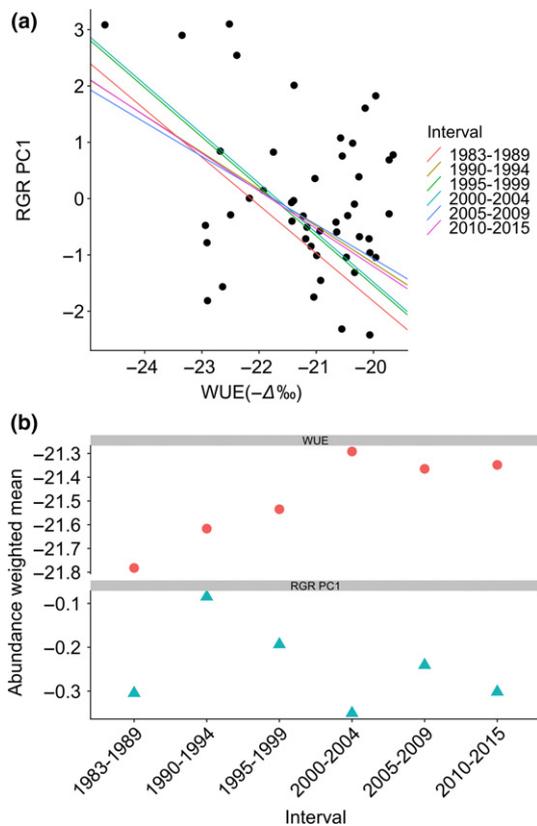


Figure 3 (a) Functional-trait trade-off between WUE and RGR for all species present in the community over 30 years. Regressions weighted by species abundances averaged across consecutive 5-to-7-year intervals are similar across the three decades. Each dot represents one species on functional-trait trade-off axes. (b) Change across 5-to-7-year intervals in community-abundance-weighted average WUE (Δ) and abundance-weighted average RGR surrogate.

dynamics within them. Here we focused on a system in which the physiological mechanisms of population dynamic responses to abiotic and biotic environmental factors have been studied extensively for nine abundant annual plant species (Angert *et al.* 2007, 2009; Barron-Gafford *et al.* 2013; Gremer *et al.* 2013; Huxman *et al.* 2013). When we extended the analysis of an interspecific trade-off between WUE and RGR to over 50 species constituting the 96% of individuals in the community we found that it scaled to the entire winter annual plant community, albeit with weaker explanatory power. The trade-off was strongest for dominant species and diminished as progressively rarer species were added, raising interesting questions regarding community organization and the role of rare species. Finally, we showed that, even as the weather from September to May became hotter by 0.05 °C and precipitation decreased by 6.6 mm (Kimball *et al.* 2010) and species relative abundances shifted, the slope and intercept of the trade-off line did not change over three decades.

The trade-off and species abundance

In a water-limited, high-light study area, a functional trade-off between WUE and RGR is expected due to physiological

limitations on photosynthetic gas exchange from plant canopies (Huxman *et al.* 2008; Gong *et al.* 2011). So why, when we consider the larger annual plant community, do we see such high residual variance compared to that for just the dominant species? The 10 most abundant species had residuals less than 1 SD from the trade-off line whereas half of the remaining species had residuals greater than 1 SD from the line (Fig. 1c). Also, why do we see so many rare apparent 'Darwinian demons' with both high WUE and RGR?

One reason may be that this environment requires a specific balance between functional traits. Huxman *et al.* (2013) showed that photosynthetic light capturing capacity of these winter annuals is high relative to carboxylation capacity, with ratios exceeding those typically found in other angiosperms (Wullschlegel 1993). Because light-capturing enzymes are highly temperature sensitive, this has been interpreted in terms of adaptation to low temperature growing conditions of winter annuals (Harley *et al.* 1992; Gremer *et al.* 2012; Huxman *et al.* 2013). Furthermore, among our dominant focal species, those with high WUE had the highest ratios of photosynthetic light-capturing capacity to carboxylation capacity suggesting an association of WUE species with low temperature photosynthesis, later confirmed by phenological and laboratory studies (Kimball *et al.* 2010, 2011; Gremer *et al.* 2012). Such specialisation to environmental conditions is likely driving the apparent trade-off we see in the community. Desert ecosystems are known for being nutrient limited. Low precipitation limits nutrient availability to plants and result in soil carbonate accumulation. The resulting alkalinity leads to low availability of P and other nutrients (Lajtha & Schlesinger 1988; Misra & Tyler 2000). Likewise, low precipitation limits biological N cycling thereby limiting N availability (Noy-Meir 1973; Schimel & Parton 1986; Fisher *et al.* 1987). In a nutrient-limited environment species that fall above the trade-off line may be investing too much nitrogen to both RGR and WUE, requiring more resources than are typically available and paying high respiratory costs (Barron-Gafford *et al.* 2013). Contrastingly, species that fall below the trade-off line may be investing too little nitrogen in RGR and WUE which would make them inferior competitors (Gremer *et al.* 2013). In this case, the trade-off line would represent the 'on-average' ideal investment range of nitrogen between WUE and RGR required to occupy primary niche space in this community given the expected rainfall-temperature covariation seen in the contemporary history.

One possible explanation of these non-optimal trait combinations is that some of these rare species may be recent introductions that have not had time to evolve to the trade-off constraint. None of the nine dominant species on which the trade-off was described in previous research is introduced. Only four of the 51 species in this study are introduced and two of these (*Erodium cicutarium* and *Schismus barbatus*) are abundant, lie close to the trade-off line, and are considered naturalised. The other two introduced species (*Matthiola parviflora* and *Sisymbrium irio*) are less abundant, high WUE and high RGR species with the second and fourth highest residuals. Thus while recent introduction may explain the deviation of these two species, it cannot provide a general explanation for why the majority of the rare species stray from the trade-off line.

An additional possibility is that the rare species that don't follow the trade-off are common under different environmental conditions that predominate elsewhere within our broader geographic region. This is true regionally for some plants like *Oenothera primiveris* which are more common in hotter drier parts of the Sonoran Desert and, on a more local scale, for many of the other rare plants in our study like *Eschscholzia mexicana* which are often common in southeastern Arizona, but not at the Desert Laboratory. In this case rare species not on the local trade-off line are likely members of a larger geographic species pool that survive locally as sink populations maintained by dispersal or perhaps in rare microhabitat conditions that are more common elsewhere (Shmida & Ellner 1984; Loreau & Mouquet 1999; Chesson 2000a; Zelený *et al.* 2010). In this scenario, gene flow from their core habitats may impede local adaptation to conditions at Tumamoc.

In addition, rare microhabitat conditions can also occur in time (Shmida & Ellner 1984; Chesson 2000b). In the Sonoran Desert, reliably wet periods that immediately follow winter rainfall are significantly cooler than dry pre-storm periods by 1.5–4.5°C for several days, regardless of event size (Huxman *et al.* 2008). Species on the WUE end of the trade-off line may be optimised for photosynthetic performance during these short low-temperature periods immediately following rain. In years when precipitation events are small and soil moisture evaporates quickly, species at this end of the trade-off are more successful than higher RGR species that have better performance when rainfall events are large and soil moisture persists after temperatures have returned to pre-storm levels (Kimball *et al.* 2012). The species on the WUE end of the trade-off also do well in years when rainfall occurs early in the growing season when temperatures are cooler, while species at the RGR end of the trade-off do well when rainfall occurs under warmer conditions later in the season (Kimball *et al.* 2011). These are general patterns of environmental variation that permit species at different positions along the trade-off line to maintain high average abundance. But there may be rare years that break the association of small rainfall events with cooler temperatures and large rainfall events with higher temperatures. Also, the normal pattern of early growing seasonal precipitation occurring at lower temperatures than late seasonal precipitation may occasionally be broken. Such unusual environmental patterns may contribute to the persistence at low density of species that are off the trade-off line. Theoretical investigations suggest that adaptation to limited, unique temporal or spatial environments, may result in especially strong negative frequency dependence which strongly buffers species from extinction, though at low population sizes (Yenni *et al.* 2012). Yenni *et al.* (2017) analysed data from 90 communities including our Sonoran Desert winter annual community and found an intriguing pattern of stronger negative frequency dependence with rarity. This suggests that limited, unique environments may indeed be responsible for rare species being farther from the trade-off line obeyed by the dominant species in our system. Common to all these explanations is the idea that rarer species farther from the trade-off line are less adapted to the commonly occurring conditions at the Desert Laboratory than are the common species.

Trade-off invariance through time

Understanding how community wide trade-offs change with shifting climate trends will provide key insights to predict changes in community composition and diversity (Kimball *et al.* 2016; Dwyer & Laughlin 2017). In our system the position of the trade-off line associated with community dominance has not shifted, despite warming and drying of the climate. While the climate has shifted over three decades, we can hypothesise that the size-frequency distribution of rainfall has not changed dramatically, leaving the optimal trade-off unchanged. Under such circumstances we expect species with lower growth rates and greater WUE to increase or replace others resulting in shifts in position along an invariant community trade-off, and this is what we found. Thus, an emergent property, the community functional trade-off, is less variable in response to environmental change than species composition. This is reminiscent of Ernest and Brown's concept of ecosystem homeostasis whereby ecosystem level properties are predicted to vary less than species composition (Ernest & Brown 2001). In contrast, if the size-frequency distribution of rainfall and its association with temperature were to undergo more radical changes, we would expect the position (slope or intercept) of the trade-off line associated with high species abundances to change as well.

We used fixed trait values for each species in this analysis. Although we recognise that trait values may change with environmental change through space or time, variation is typically less within than between species (reviewed in Siefert *et al.* 2015). Indeed, for all the traits used in this paper, intraspecific variation due to microhabitat variation in 2008 was insignificant relative to interspecific variation.

Further research into the reasons for this trade-off invariance and to determine its limits and generality for other systems will greatly enhance our ability to predict community responses to ongoing climate change.

What is the role of rare species?

While apparently maladapted to the local environment at present, rare species may provide a reservoir of potential pre-adapted replacement species when new climatic conditions disfavour the currently abundant species. Indeed, some species that were rare in the cooler and wetter 1980s have become abundant in the warmer, drier conditions today and some species that were abundant in the 1980s are rare now [see individual species abundance graphs in Venable & Kimball (2013)]. Despite such shifts in species composition, the species diversity has neither declined nor increased (Venable & Kimball 2013) and the dominant species still follow the trade-off, year-to-year. Given the relatively rapid dynamics of annual plants, these dozens of low-density species that are presumably better adapted to historically infrequent conditions may guarantee substantial resilience of species diversity when environments change. It will be informative to monitor the dynamics of the trade-off and species abundances going forward to evaluate the continued invariance of the trade-off and the resilience of species diversity. This will be especially

insightful if hydroclimatic conditions change significantly, resulting in different size-frequency distributions of rainfall events and their covariation with temperature both during and following rainfall events.

We found a significant phylogenetically corrected trade-off between relative growth rate and water-use efficiency that was strong for dominant species and weaker community wide. Proximity to the trade-off line may confer fitness and permit large population sizes, yet many species farther from the trade-off line persist at lower numbers. While some species went from rare to abundant and vice versa over the three decades studied, the position of the trade-off was unaltered. Thus, species turnover is not neutral but involves species that follow a specific set of rules in terms of trait optimization. This study demonstrates the value of investigating functional-trait trade-offs relevant to major selective pressures and applying them to an entire community of organisms to understand the mechanistic underpinnings of past and contemporary population dynamics amidst global change. Rare and apparently maladapted species may provide an important source of diversity resilience in the face of global change.

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AUTHORSHIP

XYG, TEH and DLV designed the experiment, DLV and TEH collected data. XYG analysed trait data and JPS performed phylogenetic analyses. XYG, JPS and UB wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

DATA ACCESSIBILITY STATEMENT

The data supporting the results are archived at <https://doi.org/10.6084/m9.figshare.6438686.v1>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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