Terrestrial carbon balance in a drier world: the effects of water availability in southwestern North America

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Abstract

Global modeling efforts indicate semiarid regions dominate the increasing trend and interannual variation of net CO_2 exchange with the atmosphere, mainly driven by water availability. Many semiarid regions are expected to undergo climatic drying, but the impacts on net CO_2 exchange are poorly understood due to limited semiarid flux observations. Here we evaluated 121 site-years of annual eddy covariance measurements of net and gross CO_2 exchange (photosynthesis and respiration), precipitation, and evapotranspiration (ET) in 21 semiarid North American ecosystems with an observed range of 100 – 1000 mm in annual precipitation and records of 4–9 years each. In addition to evaluating spatial relationships among CO_2 and water fluxes across sites, we separately quantified site-level temporal relationships, representing sensitivity to interannual variation. Across the climatic and ecological gradient, photosynthesis showed a saturating spatial relationship to precipitation, whereas the photosynthesis–ET relationship was linear, suggesting ET was a better proxy for water available to drive CO_2 exchanges after hydrologic losses. Both photosynthesis and respiration showed similar site-level sensitivity to interannual changes in ET among the 21 ecosystems. Furthermore, these temporal relationships were not different from the spatial relationships of long-term mean CO_2 exchanges with climatic ET. Consequently, a hypothetical 100-mm change in ET, whether short term or long term, was predicted to alter net ecosystem production (NEP) by 64 $gCm^{-2} yr^{-1}$. Most of the unexplained NEP variability was related to persistent, site-specific function, suggesting prioritization of research on slow-changing controls. Common temporal and spatial sensitivity to water availability increases our confidence that site-level responses to interannual weather can be extrapolated for prediction of CO_2 exchanges over decadal and longer timescales relevant to societal response to climate change.

Keywords: carbon dioxide, climate, ecosystem, evapotranspiration, net ecosystem exchange, net ecosystem production, photosynthesis, productivity, respiration, semiarid, water

Introduction

Semiarid ecosystems dominate the global trend of increasing net CO_2 uptake from the atmosphere and contribute the greatest fraction to atmospheric CO_2 interannual variation (Poulter *et al.*, 2014; Ahlström *et al.*, 2015). In many semiarid regions, interannual variability of precipitation far exceeds current precipitation

trends, creating natural experiments for predicting ecosystem response to future climate. Because water is a primary control of CO_2 exchange in semiarid ecosystems (Huxman *et al.*, 2004; Bai *et al.*, 2008), there is growing concern that future changes in water availability may alter their important capacity to mitigate anthropogenic emissions (Sala *et al.*, 2012; Carvalhais *et al.*, 2014). In this paper, we use observations from an ecological and climatic gradient in semiarid southwestern North America, where precipitation is expected to

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decline on average but become more variable by the mid-21st century (Seager *et al.*, 2007; Cayan *et al.*, 2010; Wuebbles *et al.*, 2013; Cook *et al.*, 2015). Other regions may become wetter, and the approach employed here is equally applicable to positive or negative changes in climatic moisture.

Net exchange of CO_2 between ecosystems and the atmosphere may be quantified as net ecosystem production (NEP), the small difference between opposing fluxes of assimilation via gross ecosystem photosynthesis (GEP), and release by ecosystem respiration (R_{eco}) (Eqn 1).

$$NEP = GEP - R_{eco} \qquad (1)$$

In this paper, we use the term 'CO$_2$ exchanges' to refer collectively to NEP and its component fluxes GEP and R_{eco}. CO_2 exchanges are controlled both by fast-changing factors, primarily ecophysiological sensitivity to weather, and by slow-changing ecosystem demographic factors including plant community (species, age, structure) and biogeochemical pools, which reflect climate and legacies of disturbance (Barford *et al.*, 2001; Schwalm *et al.*, 2012; Vicente-Serrano *et al.*, 2013; Friend *et al.*, 2014; Reichstein *et al.*, 2014). These slow-changing factors constrain ecophysiological response to weather (Knapp & Smith, 2001; Huxman *et al.*, 2004; Sala *et al.*, 2012), meaning CO_2 exchanges depend on interactions between slow and fast factors. Slow factors are less well studied than fast ones, and ecosystem process models often emphasize fast ecophysiology, such as meteorological controls on photosynthesis. Observations are lacking to assess the accuracy of extrapolating well-studied fast ecophysiology to predict NEP over decadal and longer timescales, resulting in highly uncertain projections of future climate over the timescales important for societal decision-making (Sitch *et al.*, 2008; Friedlingstein *et al.*, 2013).

The well-studied relationship between precipitation and vegetation productivity supports inferences about GEP under altered water availability. First, the productivity response is expected to follow an initially modest trajectory but increase in magnitude after slow plant community adaptation; this has been inferred, using a space-for-time substitution, from steeper spatial relationships between productivity and precipitation across sites with different climates than temporally among years at a site (Hsu *et al.*, 2012; Sala *et al.*, 2012; Jin & Goulden, 2014). Moreover, ecosystem adaptation to altered climatic water availability may change the sensitivity of production to temporal variation in water availability (i.e., altered slow factors regulate fast response). Because temporal slopes tend to be steeper at drier sites (Huxman *et al.*, 2004; Hsu *et al.*, 2012; Sala *et al.*, 2012; Jin & Goulden, 2014), we can expect that cli-

matic drying in southwestern North America would increase ecosystem sensitivity to interannual weather variation. Increased sensitivity would then multiply the impact of expected increases in precipitation variability. While spatial and temporal precipitation–productivity relationships are among the most extensive datasets of climate–ecosystem interactions, it remains unclear whether the above expectations can be extrapolated to NEP, because the impacts of water availability on respiration are less well understood.

Observed relationships between water availability and respiration are relatively scarce in comparison with those of productivity. Temperature has received much emphasis as a kinetic driver of R_{eco} over short time-scales (i.e., hours to days), but recent studies indicate that water availability, mediated by vegetation activity, is an important control of annual-scale R_{eco} (Mahecha *et al.*, 2010; Wang *et al.*, 2010). Diverse measurements indicate that GEP is a strong driver of R_{eco}, probably because it provides photosynthates for both autotrophic and heterotrophic respiration (Ayres & Lombardero, 2000; Högberg *et al.*, 2001; Janssens *et al.*, 2001; Ryan & Law, 2005; Baldocchi, 2008; Wang *et al.*, 2010). The typical approach in prior syntheses of annual eddy covariance datasets has been to combine site-years, often resulting in linear spatial relationships between R_{eco} and GEP with slopes of ~0.7–0.9, sometimes with separate relationships for site classes (i.e., vegetation, disturbance) (Baldocchi, 2008; Lasslop *et al.*, 2010; Yu *et al.*, 2013; Chen *et al.*, 2015). However, site-specific differences in R_{eco} may dominate variability in annual NEP across sites (Valentini *et al.*, 2000), possibly because legacies of disturbance alter the relationship between long-term mean respiration and productivity (Baldocchi, 2008; Chen *et al.*, 2015). Therefore, in the present analysis, we maintained the distinct identity of each site and quantified an offset between the mean annual CO_2 flux at each site and the spatial relationship.

An additional challenge is quantifying water available to drive ecosystem CO_2 exchanges. Soil moisture is commonly recognized as a primary control on both photosynthesis and respiration in semiarid systems. However, soil moisture measurements can be difficult to compare across sites, and asynchrony of soil moisture with other ecological constraints (e.g., phenology, energy) may confound annual-scale analysis. As the input to soil moisture, precipitation (P) is the most common proxy for water availability, although the annual local water balance reflects hydrologic partitioning of P to runoff and drainage losses (Q), storage changes (S), and ET (Eqn 2).

$$P = ET + Q - S \qquad (2)$$

In semiarid regions, annual S is small (Scott, 2010). Meanwhile, intense precipitation may exceed infiltration capacity, especially during the southwest monsoon, causing significant runoff which does not contribute to local CO_2 exchanges. Runoff tends to be larger in wetter years and at wetter sites, increasing the amount by which precipitation overestimates available water (Ponce-Campos *et al.*, 2013). Therefore, in addition to precipitation, we used ET as a proxy of water availability. In semiarid ecosystems, ET represents primarily the efflux of soil moisture, and it has long been recognized as a more accurate metric of the water available to drive plant and soil CO_2 cycling (Rosenzweig, 1968; Schwalm *et al.*, 2010; Ponce-Campos *et al.*, 2013). However, a lack of measurements has limited understanding of the relationship between ET and CO_2 exchanges, especially for semiarid sites, where ecosystem function is particularly sensitive to water. Maturing eddy covariance datasets help answer this challenge by simultaneously quantifying ecosystem-scale ET with NEP and its components GEP and R_{eco} (Goulden *et al.*, 1996). Use of ET would also capture any influence from ecosystem access to groundwater (Thompson *et al.*, 2011), although the available data suggest that groundwater does not play a significant role in the network of semiarid, upland sites studied here.

Here we quantified the effects of water availability (P, ET) on NEP and its components GEP and R_{eco} across 21 eddy covariance sites representing the climatic and ecological demography of semiarid southwestern North America. We used the interannual variation of ecosystem CO_2 exchanges to quantify site-level temporal relationships (Lauenroth & Sala, 1992; Knapp & Smith, 2001; Huxman *et al.*, 2004). Cross-site spatial relationships were fit to site mean values across the climatic and ecological gradients, and we employed a space-for-time substitution to draw inferences about ecosystem CO_2 exchange under future climatic water availability (Hsu *et al.*, 2012; Sala *et al.*, 2012; Jin & Goulden, 2014). To improve understanding of semiarid ecosystem–atmosphere CO_2 exchanges, we addressed three questions: (i) How does the temporal sensitivity of semiarid ecosystem CO_2 fluxes to interannual water availability vary among sites with different climatic water availability? (ii) How do the temporal sensitivities of ecosystem CO_2 fluxes to interannual water availability compare to cross-site spatial relationships with climatic water availability? (iii) What is the relative importance of spatial and temporal water availability variations in regulating semiarid NEP? In contrast to models, atmospheric inversions, or remote-sensing estimates, the unique dataset of semiarid ecosystem measurements assembled here allows in-depth analysis of how NEP and its component fluxes respond to spatial and temporal variations in water availability.

Methods and materials

Study sites

We identified 21 eddy covariance flux sites with 4–9 years of measurements (mean of 6 years, total $n = 121$) representing the climate and ecosystems of the southwestern US and northern Mexico (Fig. 1, Table 1, Fig. S1), a region that is water-limited at the annual scale (i.e., potential evapotranspiration > precipitation). Observations were made between 1999 and 2013, with most occurring after 2004 (Table 1). The major regional ecosystem types represented are desert, arid tropical scrub, chaparral, grassland, savanna, pinyon, and juniper woodlands, and forests including ponderosa, mixed conifer, oak/pine, and tropical deciduous forest. Site descriptions are available for the US sites at www.ameriflux.lbl.gov and for the Mexico sites at www.flux-data.org. Climate for the study sites and region was characterized with mean annual precipitation and temperature (Fig. S1) for the period 1950–2000 using the 30 arc-second WorldClim dataset (www.worldclim.org). Based on the ANUSPLIN algorithm, WorldClim is comparable to PRISM (www.prism.oregonstate.edu) but offers worldwide coverage (Parra & Monahan, 2008). Mean annual precipitation ranged from 150 to 750 mm, while mean annual temperature ranged from 1 to 24 °C. Most sites had some history of management or disturbance, although the availability and precision of such data varied (Table S1). One chaparral site (so2) had a stand-replacing fire. The postfire observations were treated separately and appear as a 21st site in the analysis (so2B).

Flux data collection and processing

We used annually integrated sums of precipitation and high-frequency (30 min) measurements of net CO_2 exchange and water vapor flux and estimates of GEP and R_{eco} derived from the net CO_2 exchange measurements. Measurements of terrestrial-atmosphere gas flux were made at the ecosystem level using the eddy covariance technique (Goulden *et al.*, 1996). Data collection and regular calibrations of eddy covariance flux measurement systems followed accepted guidelines (Lee *et al.*, 2006). Observations of net CO_2 exchange with insufficient turbulent mixing were screened using a friction velocity filter (Reichstein *et al.*, 2005). Gross fluxes were initially partitioned from the net CO_2 exchange measurements based on the observed relationship between nighttime respiration and temperature, which was then used to separately derive daytime GEP and R_{eco} (Reichstein *et al.*, 2005). At several sites with recurring periods of insufficient nighttime turbulent mixing to determine a robust respiration–temperature relationship, gross fluxes were instead partitioned using a light response curve fit to daytime net CO_2 flux (Lasslop *et al.*, 2010). Previous comparisons have shown good agreement among approaches at the annual scale (differences <10%) (Desai *et al.*,
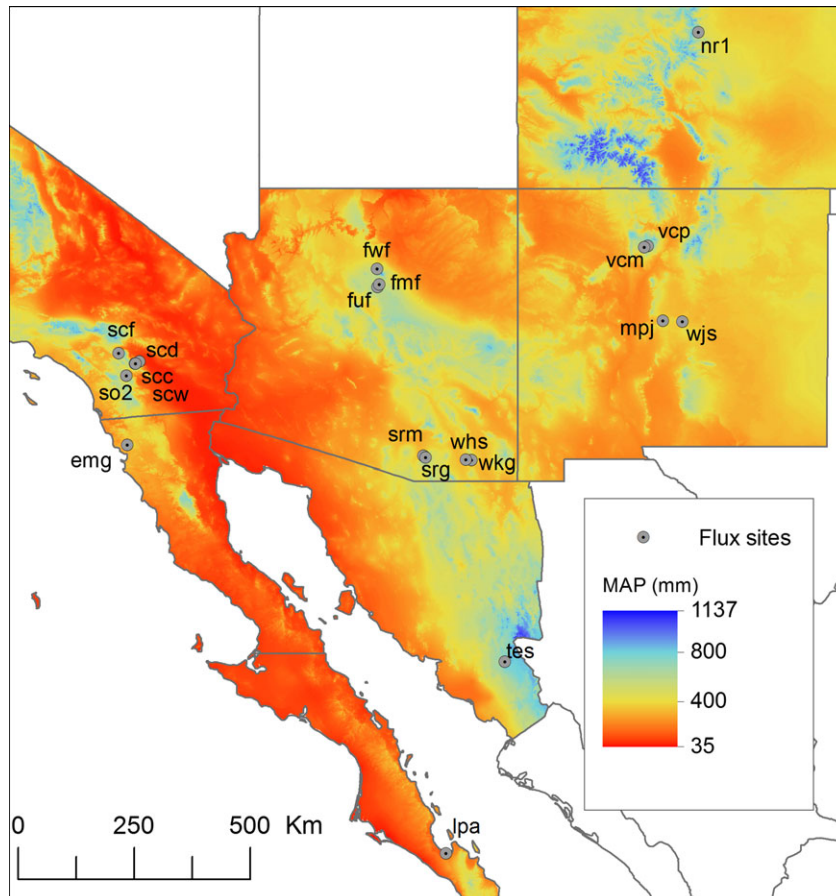
Fig. 1 Map of eddy covariance flux observation sites in southwestern North America. The shaded area shows mean annual precipitation (MAP, 1950-2000) for the region including the states of Colorado, New Mexico, Arizona, Southern California, Sonora, Baja Norte, and Baja Sur. For sites codes and descriptions, see Table 1.

2008; Lasslop *et al.*, 2010). Here, we found that the choice of partitioning method did not alter any of our conclusions.

Annual CO_2 and water vapor flux sums were calculated using a hydrologic year running November 1 to October 31. At two sites, fluxes for the months of November and December were estimated in one hydrologic year (emg-2007, so2-1999) using the mean weekly observed fluxes of the remaining years. November and December are relatively dormant months at these Mediterranean chaparral sites, together comprising only 9–12% of mean annual fluxes.

Separation of fast and slow factors controlling ecosystem CO_2 exchanges

We interpreted our results using an ecological approach developed to separate temporal and spatial variability in plot-scale precipitation–productivity relationships and associate them with fast and slow controls, respectively (Fig. 2a) (Lauenroth & Sala, 1992; Huxman *et al.*, 2004; Sala *et al.*, 2012). Site-level temporal relationships represent ecophysiological responses to fast-changing factors such as weather (i.e., annual water availability), while spatial relationships determined from mean annual values at each site reflect slow-changing

controls such as plant community adaptation to climate (Lauenroth & Sala, 1992; Chen *et al.*, 2015) (Fig. 2b). Employing a space-for-time substitution allows inferences to be drawn about ecosystem response to future conditions (Hsu *et al.*, 2012; Sala *et al.*, 2012; Jin & Goulden, 2014). We modified the existing approach by quantifying site offsets (Fig. 2a), which are attributed to slow controls not captured by the spatial relationship, such as confounding environmental factors or legacies of disturbance (Baldocchi, 2008; Chen *et al.*, 2015). This spatial–temporal approach differs from the more common practice in synthesis studies of eddy covariance data in which a single relationship between two variables is determined across the pooled site-years or classes thereof (e.g., vegetation class, disturbance). The single response determined in this manner is usually similar to the spatial relationship but is weighted by unequal years of observation among sites.

Results

GEP ranged from 67 to 1140 gC m^{-2} yr^{-1} (Fig. 3). The spatial relationship of GEP to precipitation was positive and gradually saturating (Fig. 3a), consistent with prior observations of ANPP or remotely sensed greenness

Table 1 Site descriptions, mean climate*, and observation years

Site ID	Description	MAP (mm)	MAT (°C)	Obs. Years	PI	Site references
US-scd	Southern California desert	132	21.4	2007–2012	Goulden	Goulden et al. (2012)
MX-lpa	La Paz arid tropical scrub	167	23.6	2003–2008	Oechel	Hastings et al. (2005), Bell et al. (2012)
MX-emg	El Mogor chaparral	327	16.1	2008–2013	Vargas	Leon et al. (2014)
US-wjs	Tablelands juniper savanna	349	10.9	2009–2013	Litvak	Anderson-Teixeira et al. (2011)
US-whs	Walnut Gulch Lucky Hills shrubland	352	16.8	2008–2013	Scott	Scott (2010)
US-wkg	Walnut Gulch Kendall grassland	386	15.8	2005–2013	Scott	Scott et al. (2010)
US-scw	Southern California pinyon-juniper	403	14.1	2007–2013	Goulden	Goulden et al. (2012)
US-scc	Southern California chaparral	409	13.9	2007–2013	Goulden	Goulden et al. (2012)
US-srm	Santa Rita mesquite savanna	421	17.7	2005–2013	Scott	Scott et al. (2009)
US-mpj	Heritage Land Conservancy pinyon-juniper	423	9.6	2009–2013	Litvak	Anderson-Teixeira et al. (2011)
US-srg	Santa Rita grassland	494	16.7	2009–2013	Scott	Scott et al. (2015)
US-fwf	Flagstaff ponderosa postwildfire	535	6.5	2007–2010	Kolb	Dore et al. (2010, 2012)
US-vcp	Valles Caldera ponderosa forest	547	5.7	2008–2012	Litvak	Dore et al. (2010, 2012)
US-so2/so2B†	Sky Oaks Old Stand chaparral	558	13	1999–02, 2005–08	Oechel	Luo et al. (2007)
US-fmf	Flagstaff managed ponderosa pine	580	7.4	2007–2010	Kolb	Dore et al. (2010, 2012)
US-fuf	Flagstaff unmanaged ponderosa pine	607	7.1	2006–2010	Kolb	Dore et al. (2010, 2012)
US-nr1	Niwot Ridge subalpine mixed conifer	654	0.7	2001–2002, 2007–2012	Blanken	Monson et al. (2002)
US-scf	Southern California oak pine forest	692	10.9	2007–2012	Goulden	Goulden et al. (2012)
MX-tes	Tesopaco semiarid tropical savanna	721	23	2005–2008	Yepez, Garatuza	Verduzco et al. (2015)
US-vcm	Valles Caldera mixed conifer forest	724	2.9	2008–2012	Litvak	Anderson-Teixeira et al. (2011)

*Mean annual temperature (MAT) and mean annual precipitation (MAP) 1950–2000 from the WorldClim 1-km dataset [www.worldclim.org].

†Observations collected at so2 after a 2003 wildfire are denoted 'so2B' and analyzed as a unique site.

(Huxman et al., 2004; Hsu et al., 2012; Jin & Goulden, 2014). In contrast, use of ET as the water availability metric revealed a linear relationship, as predicted by a hydrologic model (Zhang et al., 2001; Ponce-Campos et al., 2013), with an intercept of ~80 mm on the ET axis (horizontal) and a slope of 1.79 gC mm^{-1} H$_2$O. Temporal slopes between GEP and ET (i.e., production sensitivity to interannual variations in available water) showed no trend across the climatic gradient, in contrast to the declining sensitivity of productivity to *precipitation* shown here (Fig. 3a) and reported previously (Huxman et al., 2004; Hsu et al., 2012; Sala et al., 2012). Therefore, we combined GEP and ET observations from all sites (n = 121 site-years), expressed as deviations from site means, to determine a common temporal slope of 1.46 gC mm^{-1} H$_2$O, which explained 71% of GEP temporal variation and was not significantly different from the spatial slope (Fig. 3b inset). Hence, both temporal variation in available water at a site and differences in climatic water availability across sites had the same effect on annual productivity.

Ecosystem respiration (R_{eco}) ranged from 139 to 981 gC m^{-2} yr^{-1}. There was a linear spatial relationship between R_{eco} and ET (Fig. S3) with a slope of 0.78 gC mm^{-1} H$_2$O, but the relationship was relatively weak (R^2 = 0.27, P < 0.01). Instead, there was a stronger spatial relationship between R_{eco} and GEP (Fig. 4, R^2 = 0.65, P < 0.001). This CO$_2$ balance between GEP and R_{eco} defines NEP (Eqn 1), and the spatial slope indicated an average increase of 64 gC m^{-2} annually respired for each 100 gC m^{-2} of increased annual photosynthesis. Temporal slopes between R_{eco} and GEP showed no trend across the productivity gradient. The temporal slope fit to interannual deviations from the means of all sites was 0.56 (R^2 = 0.52, P < 0.001), meaning that on average across the 21 semiarid ecosystems, 56% of GEP interannual variation was counteracted by R_{eco} interannual variation within the same year (Fig. 4 inset). Three sites with known disturbance (Table S1, lpa, fmf, fwf) had the lowest temporal slopes (Fig. S4). The temporal and spatial slopes between R_{eco} and GEP were not different. Therefore, respiration showed the same average relationship to interannual productivity variation, which depends upon interannual water availability, as to long-term site productivity, which depends upon climatic water availability.
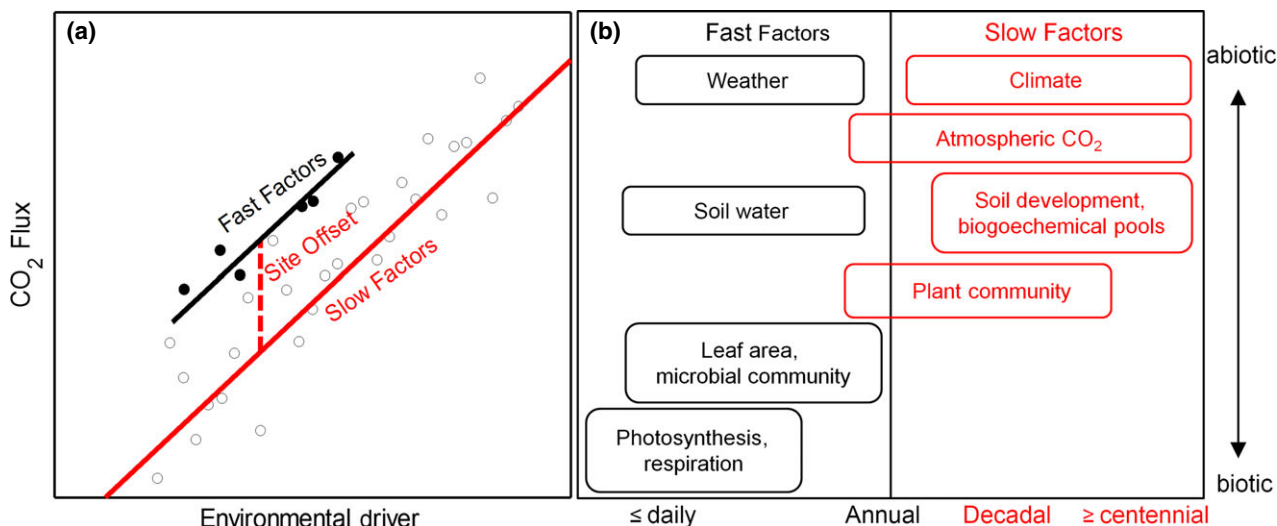
Fig. 2 Interpretation of spatial (red) and temporal (black) relationships in multi-site ecosystem synthesis studies including illustration with hypothetical observations (a) and a conceptual diagram showing timescales of several factors regulating ecosystem function (b). Slow factors regulate the cross-site spatial relationship between average values of an environmental driver (e.g. water availability) and the CO_2 flux, while fast factors control the CO_2 flux response to temporal variability of the driver. In (a), the site offset represents slow factors not scaling with the driver, such as disturbance effects on soil carbon or plant stem density. In (b), the vertical axis represents a gradient from abiotic to biotic factors. Please see the online version of the article for references to color.
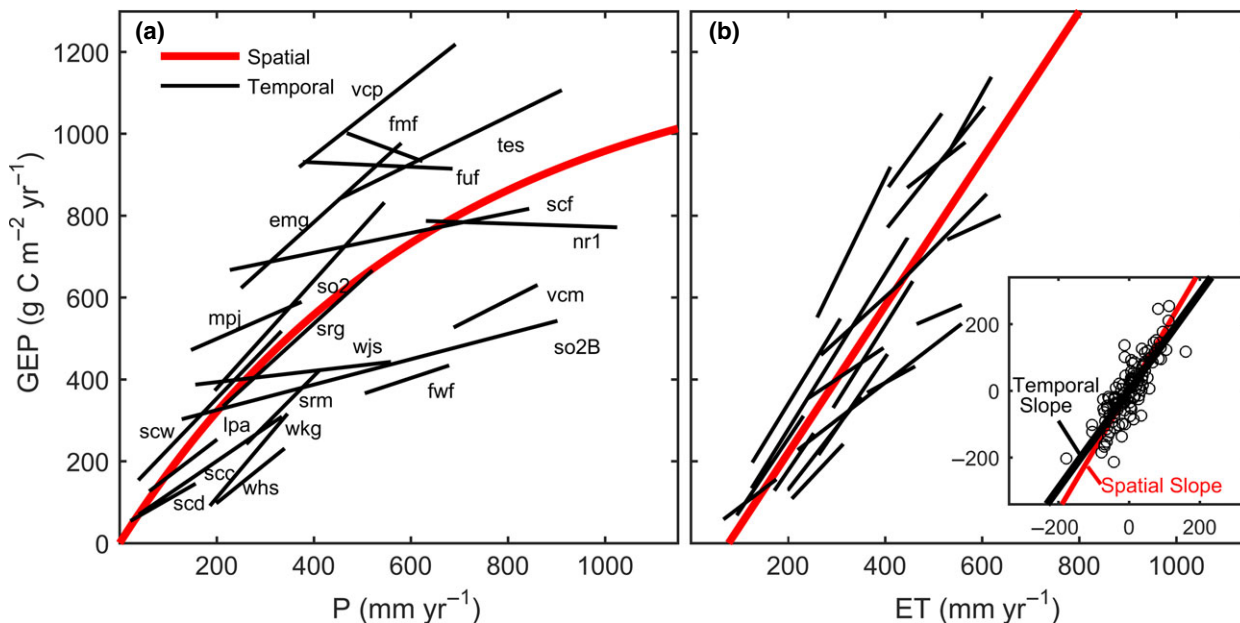

Fig. 3 Relationships of annual gross photosynthesis (GEP) with precipitation (P) (a) and with evapotranspiration (ET), a metric of water available to drive ecosystem CO_2 cycling after subtracting hydrologic losses from precipitation (b). Linear fits estimate the temporal (that is, interannual) relationships at each site (small black lines). In (a) the spatial relationship of $\overline{GEP}$ to mean precipitation $\overline{P}$ (red curve) is described by a negative exponential (Huxman *et al.*, 2004) $\overline{GEP} = 1218(1 - \exp(-0.001532\overline{P}))$, $n = 21$ sites, $R^2 = 0.52$, $P < 0.001$), while in (b) the spatial relationship to mean ET is linear: $\overline{GEP} = 1.79\overline{ET} - 139$, $n = 21$, $R^2 = 0.73$, $P < 0.001$. In (b) the inset shows the annual GEP and ET expressed as deviations from each site's mean using the same units as the main figure. The temporal slope fit to this combination of all sites (1.46 gCmm^{-1} H$_2$O, $n = 121$ site-years, $R^2 = 0.71$, $P < 0.001$) was not different from the spatial slope ($P > 0.05$). To identify individual sites, see Fig. S2.

Semiarid ecosystems showed a positive linear spatial relationship between climatic water availability (mean ET) and NEP with a slope of 0.95 gC mm^{-1} H$_2$O (Fig. 5a). The spatial relationship intercepted the ET axis (horizontal) at 286 mm, suggesting a water availability threshold for net CO$_2$ source/sink function in southwestern North America during the early 21st century. Temporal slopes between ET and NEP were positive and showed no trends in sensitivity of NEP to ET across the site gradient in climatic water availability. The temporal slope fit to interannual deviations at all sites was 0.62 gC mm^{-1} H$_2$O, $R^2 = 0.26$, $P < 0.001$, not shown).

We used partial variance decomposition (Bevington & Robinson, 2002) to quantify the percentage of NEP variance explained by the relationships of GEP with ET and of R_{eco} with GEP including spatial relationships, site offsets, and temporal relationships, as well as unexplained variability around the temporal models (Fig. 2a). We found 63% of NEP variance could be explained by just the spatial relationships of GEP with ET (42%) and of R_{eco} with GEP (21%) (Fig. 5b). Most of the remaining NEP variability (26%) was related to site offsets. Meanwhile, only an additional 8% of NEP variance was explained by the addition of temporal relationships for each site, while 4% remained unexplained.
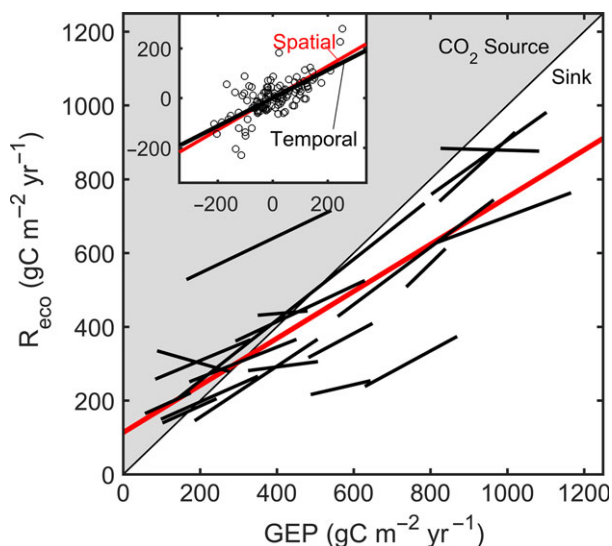

Fig. 4 The relationship of annual ecosystem respiration (R$_{eco}$) to gross photosynthesis (GEP). The spatial relationship of mean $\overline{R_{eco}}$ to $\overline{GEP}$ across sites was described by a linear fit (thick red line): $\overline{R_{eco}} = 0.64\overline{GEP} + 113$, $n = 21$ sites, $R^2 = 0.65$, $P < 0.001$. The inset shows the annual GEP and R$_{eco}$ expressed as deviations from each site's mean using the same units as the main figure. The temporal slope fit to this combination of all sites (0.56, $n = 121$, $R^2 = 0.52$, $P < 0.001$) was not different from the spatial slope. To identify individual sites, see Fig. S4.

Discussion

We found a tendency toward similar spatial and temporal responses of annual CO$_2$ exchanges to water availability variations across a climatic and ecological gradient of semiarid ecosystems (Figs 3b and 4). Therefore, we did not find evidence supporting the expectation that ecosystem response to altered water availability would initially follow a shallow temporal slope, then a steeper spatial slope representing slow climate adaptation. Instead, similar spatial and temporal slopes increase our confidence that fast ecophysiological responses are useful for predicting NEP under future climatic water availability. A central tendency in temporal sensitivities of CO$_2$ exchanges to water among sites suggested that climatic drying (or wetting) should not be expected to change CO$_2$ exchange sensitivity to moisture. Most of the unexplained NEP variance across this regional dataset was related to site offsets in mean CO$_2$ fluxes, suggesting a need for future research to prioritize site-specific controls.

Productivity relationships with available water

A linear spatial relationship between GEP and ET suggests that semiarid ecosystems use marginal differences in climatic water availability with common efficiency (Fig. 3b) and that saturating relationships between productivity and precipitation (Fig. 3a), (Huxman *et al.*, 2004; Hsu *et al.*, 2012; Jin & Goulden, 2014) reflect, at least in part, increasing hydrologic losses at wetter sites (Eqn 2) (Ponce-Campos *et al.*, 2013). Here, a horizontal intercept of ~80 mm ET in the spatial relationship (Fig. 3b) implies a minimum threshold of climatic water availability below which vegetation productivity is negligible, and all water remaining after runoff losses is evaporated. While this represents an extrapolation, the inclusion of dry sites makes the extrapolation small relative to the range of observations.

A common temporal relationship between GEP and ET across the climatic and ecological gradient (Fig. 3b inset) implies that if expected regional drying drives ecosystem shifts (e.g., forest to savanna and grassland to shrubland), this will not necessarily constrain a site's capacity for response to water availability. Vegetation change can alter the amount of precipitation which becomes ecosystem-available (i.e., the hydrologic partitioning of P between ET and Q, Eqn 2), but this would be captured by our use of ET as the water availability metric (Scott *et al.*, 2014). Our finding that temporal and spatial slopes did not differ from one another contrasts with results suggesting that reduced climatic water availability would drive down productivity initially along a shallower interannual slope, then subsequently
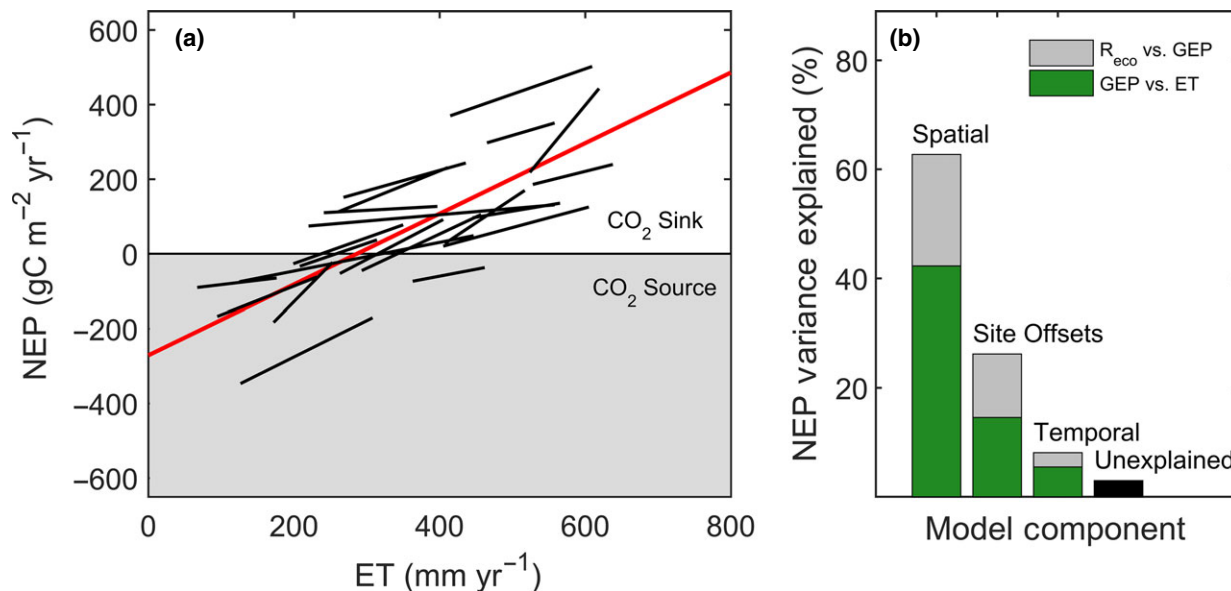
Fig. 5 The relationship between annual net ecosystem production and evapotranspiration (a) and the percentages of NEP variance explained by the spatial and temporal relationships among productivity, respiration, and evapotranspiration (b). In (a), the linear spatial relationship was $\overline{NEP} = 0.95\overline{ET} - 271$; $n = 121$; $P < 0.001$; $R^2 = 0.60$. At the horizontal intercept of the spatial model (NEP = 0) ET is 286 mm y^{-1}. In (b), GEP was predicted from spatial and temporal relationships with ET (Fig. 3b), and R_{eco} was predicted from relationships with GEP (Fig. 4). The four model components (bars) shown are described in Fig. 2a.

along a steeper spatial slope reflecting vegetation community adaptation (Sala *et al.*, 2012; Jin & Goulden, 2014). Our sites were similar to these studies in both climatic precipitation and ecosystem functional types, and our finding of similar spatial and temporal slopes likely results from use of ET, which removes from consideration the portion of precipitation not available to drive local CO_2 cycling (Eqn 2). It is likely that at a site, more (less) precipitation results in more (less) hydrologic loss (Zhang *et al.*, 2001; Ponce-Campos *et al.*, 2013), flattening the apparent temporal slopes of productivity to precipitation. Meanwhile, the underlying efficiency with which ecosystems utilize an increment of available water for productivity ($\Delta GEP/\Delta ET$) appears to remain relatively constant both temporally and spatially (Fig. 3b). Unexplained variability in the temporal relationship of ET with GEP could reflect interannual differences in hydrologic partitioning of ET between evaporation and transpiration, ecosystem constraints resulting from water availability in earlier years, or the timing and size of precipitation events throughout the year. However, unexplained temporal variation contributed <5% to NEP variance (Fig. 5b).

Respiration relationships with available water and productivity

Our finding that R_{eco} was related weakly to ET (Fig. S3) and more strongly to GEP (Fig. 4) is consistent with

direct and indirect control of R_{eco} by water. ET represents primarily the efflux of soil moisture remaining after hydrologic losses from precipitation (Eqn 2), which can limit heterotrophic respiration of accumulated labile carbon until a precipitation pulse wets the soil (Sponseller, 2007; Jenerette *et al.*, 2008). However, this direct control of heterotrophic respiration by water is more likely to regulate the timing of respiration within a season than alter annual sums of R_{eco}. Annual respiration is more likely controlled by water availability indirectly through plant production of photosynthates (Mahecha *et al.*, 2010; Wang *et al.*, 2010), which are respired by plant tissue and root-associated mycorrhizae and stimulate heterotrophic respiration (Högberg *et al.*, 2001; Janssens *et al.*, 2001; Ryan & Law, 2005; Sampson *et al.*, 2007; Baldocchi, 2008; Vargas *et al.*, 2011).

A common temporal slope of R_{eco} to GEP (0.56) found by combining all sites (Fig. 4 inset) builds upon the finding that respiration was half as sensitive as productivity to drought (Schwalm *et al.*, 2010) by showing that this relationship holds more generally for wetting or drying within the entire range of observed variation. The temporal slope also falls within reported ratios of *autotrophic* respiration to productivity in forests ($R_a/GEP \sim 0.53–0.57$) (Waring *et al.*, 1998; Litton *et al.*, 2007). This may mean that in these semiarid ecosystems, interannual variation of R_{eco} reflects mainly the response of plants to changes in water availability and resulting

photosynthate production. In such a scenario, multi-year mean R_{eco} at a site may be viewed as a baseline regulated by slow-changing factors including plant biomass and soil carbon pools. Although we lack the measurements to separately quantify the components of R_{eco} here, this scenario illustrates how separation of temporal and spatial relationships across multitemporal, multisite studies (Fig. 2) can suggest new hypotheses for ecosystem function.

The spatial slope of R_{eco} to GEP (0.64) for southwest North American semiarid ecosystems (Fig. 4) was smaller than that reported in several prior studies (~0.7–0.9) (Law *et al.*, 2002; Baldocchi, 2008; Lasslop *et al.*, 2010; Chen *et al.*, 2015). It was more similar to that found in a recent synthesis across eddy covariance sites in China (0.68) with greater representation of semiarid ecosystems (Yu *et al.*, 2013). One possible explanation for the lower spatial slope found here is that this study represents a period of drought in southwestern North America (Seager & Vecchi, 2010; Scott *et al.*, 2015) during which ecosystem respiration is elevated relative to productivity (Van der Molen *et al.*, 2011; Scott *et al.*, 2015). Therefore, the drier sites often functioned as carbon sources to the atmosphere (Fig. 4), increasing the vertical intercept and reducing the slope of the spatial relationship. Although there has been discussion in the literature about spurious correlation between R_{eco} and GEP, a recent analysis of FLUXNET sites found a similar relationship between these two fluxes ($R_{eco} = 0.71$GEP + 153, $R^2 = 0.76$) and showed that most of their correlation was not spurious, especially for annual sums (Baldocchi *et al.*, 2015).

Relationships of NEP with interannual and climatic differences in available water

Our results show that semiarid NEP depends on how water availability drives counteracting responses in productivity and respiration, both spatially and temporally. The spatial relationship of R_{eco} with GEP (Fig. 4) intersects the 1 : 1 line at ~315 gCm^{-2} yr^{-1}, suggesting that sites with average productivity above 315 gCm^{-2} yr^{-1} tended to function as net CO_2 sinks ($R_{eco} <$ GEP), while those sites below this productivity threshold tended to be sources ($R_{eco} >$ GEP). We calculate a similar source/sink threshold at a productivity of ~ 250 gCm^{-2} yr^{-1} in the ChinaFlux dataset of Yu *et al.* (2013). Our productivity threshold of 315 gCm^{-2} yr^{-1} corresponds to a climatic water availability of ~255 mm (Fig. 3b), illustrating why NEP tended to switch from negative to positive near this value of ET (Fig. 5a). Mass conservation precludes the driest sites from functioning indefinitely as carbon sources, and caution should be applied in extrapolating these results, which

represent a period of drought in southwestern North America (Seager & Vecchi, 2010; Scott *et al.*, 2015). Drought may shift a number of long-lasting constraints such as plant community and soil carbon pools, possibly reducing GEP and increasing R_{eco} (Van der Molen *et al.*, 2011), similar to the 'disturbance offset' suggested in other multisite flux data syntheses (Baldocchi, 2008; Chen *et al.*, 2015).

Using the empirical approach shown in Fig. 2 and the combined observations from the 21 sites, we find that NEP was equally sensitive to interannual variations in water availability and differences in average climatic water availability (Fig. 6). First we posit a change, which could be positive or negative, of 100 mm in available water, estimated from ET. For the case where the change represents interannual weather variation (Fast pathway), we use the temporal slopes of GEP to ET and R_{eco} to GEP. Temporal variation of 100 mm in available water is predicted to change GEP by 146 gCm^{-2} yr^{-1}, of which 56% is counteracted by Δ R_{eco} within the same year, resulting in predicted ΔNEP magnitude of 64 gCm^{-2} yr^{-1}. For a difference in climatic water availability (slow pathway), we use the spatial slopes, which predict ΔGEP of 179 gCm^{-2} yr^{-1}, 64% of which is counteracted by long-term mean respiration, resulting in the same predicted ΔNEP magnitude of 64 gCm^{-2} yr^{-1}. This result (Fig. 6) contrasts with our initial expectation that NEP would be more sensitive to climatic shifts than to interannual variation, inferred from steeper spatial than temporal slopes in precipitation–productivity relationships (Hsu *et al.*, 2012; Sala *et al.*, 2012; Jin & Goulden, 2014). Our predicted NEP sensitivity to water falls within the range estimated from models and atmospheric inversions over Australia, 25–100 gCm^{-2} yr^{-1} per mm (deviation from mean growing season P) (Poulter *et al.*, 2014), providing terrestrial observation-based support for the idea that semiarid region NEP dominates the interannual variability of global atmospheric CO_2 (Ahlström *et al.*, 2015).

We are cautious about extrapolating the NEP responses predicted in Fig. 6. The results represent a specific region and time period, as mentioned above. Furthermore, we employ a space-for-time substitution assuming that water availability is the main driver of differences in ecosystem CO_2 cycling in space and time, and we cannot account for future climatic changes not represented by our climatic and ecological gradient. Notably, changes in atmospheric temperature, vapor pressure deficit (VPD), and CO_2 concentration could influence plant community structure or alter GEP by changing leaf-level water-use efficiency (Morgan *et al.*, 2007; Donohue *et al.*, 2013; Keenan *et al.*, 2013; Friend *et al.*, 2014). Here, we found no relationship between
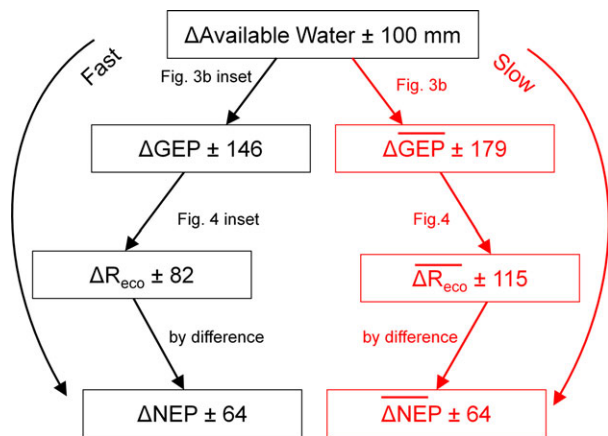
Fig. 6 The effects of water availability on semiarid ecosystem CO_2 exchange with the atmosphere for a hypothetical change of 100 mm in water availability (positive or negative). The left side illustrates the average fast response of NEP to temporal variation in water availability at a site, while the right side predicts a similar impact from a shift in climatic water availability, inferred from cross-site spatial relationships. CO_2 exchange terms have units of $gCm^{-2}y^{-1}$. Overbars along slow pathway denote long-term mean values.

annual temperature or VPD and water-use efficiency (not shown). Meanwhile, data suggest that in hot and dry regions such as southwestern North America, productivity depends mainly upon water availability, not atmospheric CO_2 (Newingham *et al.*, 2014; Reeves *et al.*, 2014). It is not our intention that Fig. 6 should be interpreted as a prediction for future NEP in southwestern North America. Accordingly, we do not attempt to quantify or propagate uncertainty in measurements, data processing, linear models, or the pathway linking ET, GEP, R_{eco}, and NEP. Instead, we view Fig. 6 as illustrating comparison of fast and slow factors regulating CO_2 exchanges across multitemporal, multisite ecological datasets (Fig. 2).

Because CO_2 exchanges showed common spatial and temporal relationships to water availability, most of the unexplained NEP variation was related to slow (i.e., persisting throughout the observation years) site-specific offsets from the spatial relationships (Fig. 5b, offsets for each site shown in Table S1). We detected no associations between offsets and mean annual temperature, vapor pressure deficit, seasonality of precipitation, or plant functional type. Although complex terrain can pose challenges for eddy covariance measurement and data processing (Baldocchi, 2008), we detected no association of site offsets with elevation or with sites described in the literature as having somewhat complex terrain (see Table 1 for literature references). Errors in partitioning of NEP into its component fluxes could contribute to offsets, but offset

magnitude at many sites (up to 50–70%) exceeded expected systematic partitioning errors (~10%) (Desai *et al.*, 2008; Lasslop *et al.*, 2010). Many of the largest offsets suggested associations with site demography and history, supporting the 'disturbance offset' concept (Baldocchi, 2008; Chen *et al.*, 2015). For example, the most positive GEP offsets were associated with disturbances that killed some plants without changing the biome type (Fig. S2, Table S1, sites fmf, emg), consistent with demographic shifts toward younger plants during recovery from moderate disturbance (Baldocchi, 2008; Amiro *et al.*, 2010). A stand-replacing chaparral fire was associated with a change in GEP offset from positive to negative (so2, so2B), consistent with reductions in stem density, leaf area, and root development. At the high-elevation sites vcm and nr1, negative GEP offsets could be due to snow sublimation, which reduces the fraction of water available to support photosynthesis. In the carbon balance regulating NEP, the most positive R_{eco} offset relative to GEP (Figs 4 and S4, Table S1) was associated with drought at scw, where plant mortality likely reduced photosynthesis while increasing substrate for heterotrophic respiration (Harmon *et al.*, 2011). The chaparral site (so2) R_{eco} offset switched from positive to negative following wildfire (so2B), possibly because combustion reduced the carbon pools available to support long-term average respiration. At vcm, a negative R_{eco} offset could indicate asynchrony of temperature and water limitations on respiration at this high-elevation, seasonally dry site, or respiration inhibition related to elevated nitrogen deposition (Janssens *et al.*, 2010).

Directions for future work to improve understanding of terrestrial CO_2 exchanges

While offsets at some sites were consistent with plausible causes (Table S1), a rigorous analysis was precluded because these sites, like many others, lack consistent observations of slow factors likely to regulate offsets (Fig. 2) (Litton *et al.*, 2007; Baldocchi, 2008; Tang *et al.*, 2014). Studies based on coordinated flux meso-networks deployed across forest age gradients offer a valuable counterexample (Amiro *et al.*, 2010), but a greater number and diversity of sites reporting nonflux observations are needed to support inferences about slow-changing controls from synthesis studies. Alternatively, very long term records at a site may reveal shifts in mean flux relationships, such as water-use efficiency (Keenan *et al.*, 2013). We expect maturing datasets in semiarid ecosystems may be promising for such site-based study, because the slow factors likely driving site offsets (Fig. 2) tend to change more frequently and

rapidly in semiarid ecosystems than in forests (e.g., drought alters grassland species assemblage (Moran *et al.*, 2014), recurrent fire alters chaparral biomass pools (Keeley, 1986)).

Our results support the use of ecosystem-scale ET to represent water availability, although it remains an imperfect proxy. As compared with precipitation, ET showed a stronger relationship with GEP (Fig. 3). In eddy covariance studies, ET is measured using the same instruments and methodology as the CO_2 exchanges, and represents the same spatial footprint, whereas precipitation measurements involve different instrumental challenges and assumptions (Rasmussen *et al.*, 2012; Shuttleworth, 2012). Use of ET instead of P removed hydrologic losses from the estimated water availability (Eqn 2). Although Q likely varies with terrain, soils, and the within-year distribution of precipitation events, our results confirm that losses increase in wetter years and at wetter sites, impacting both spatial and temporal models of productivity (Fig. 3). Further advances in understanding of hydrologic controls on ecosystem CO_2 exchanges depend on quantifying how precipitation is partitioned among hydrologic losses, transpiration, and abiotic evaporative losses (Newman *et al.*, 2006).

The spatial–temporal empirical framework used here (Fig. 2) integrates several decades of ecological thought on fast and slow factors controlling productivity with the promising field of whole-ecosystem carbon and water flux observations. We suggest this approach of maintaining site identity could be employed in cross-site synthesis studies whenever sufficient data exist to quantify site mean fluxes and site-level temporal relationships. Although robust statistical treatment of individual sites is challenging when site records are relatively short (<10 years), inferences about ecosystem function may be drawn from the collective patterns of site-level temporal relationships across gradients of important drivers (Huxman *et al.*, 2004). There is a need to compare the results of the present study across global networks of long-term eddy covariance sites, including for controls other than water and/or nonlinear relationships. Separation of fast and slow controls across broad networks of ecosystem measurements should enable learning about timescales of important factors regulating ecosystem function, informing priorities for observation and improving predictive ecosystem models.

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Author contributions

J.A.B., R.L.S., and M.L.G. conceived the study. J.A.B. assembled the data, produced preliminary results, and wrote the manuscript. All authors analyzed data, contributed to the interpretation of results, and helped revise the manuscript. The authors declare no conflict of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Climate for the region and the 21 sites.
Figure S2. Relationships of GEP with ET, as in Main Text Fig. 3b, with site codes added.
Figure S3. Relationships of R_{eco} with ET.
Figure S4. Relationships of Reco with GEP, as in Main Text Fig. 4, with site codes added.
Table S1. Site disturbance histories and site offsets from spatial relationships.