Reply to Referee # 1

Comment #1: This is an interesting modelling study examining how dryland ecosystem carbon fluxes respond to precipitation anomalies arriving at interannual and interdecadal time scales. Results are unsurprising but make a few valuable points about the nonlinearities (thresholds and filters) in carbon flux responses to wet and dry events. Findings are heavily dependent on the model's approach. Interpretations need to be revisited in a few places. The writing needs to be improved. Insights regarding mechanisms get disappointingly little attention in terms of quantitative analysis. But overall this paper makes a useful contribution.

Re: Thanks to the reviewer for considering our modelling study interesting and for providing several constructive comments. We reply to each of your comments/suggestions in the following.

Comment #2: Line 121: If the third question is to identify the mechanisms that are responsible for legacy effects, why then do you make an assumption that allows only a single answer? The methods chosen do not seem to allow for you to identify the mechanisms responsible. Instead, the mechanisms are hard-wired into the PALS, pulse-reserve modeling framework that has been adopted, so there is no real discovery to be had.

Re: We agree with the reviewer that the mechanisms that are responsible for the modeled legacy dynamics are already built in the model. We deleted the third question.

Comment #3: Section 2.3: Calibration / Validation makes incomplete and weak use of the data: The approach for model cal/val should be improved with cross-validation and bootstrapping. Fit the model (calibrate it) many times with different subsamples of the observations and then select model parameters based on the best-fit results from validation with the remaining observations.

Re: The reviewer suggests a more rigorous way of model calibration and validation. However, the PALS model we used is written in the STELLA platform, which hinders us from making the automated model runs necessary to complete this type of model calibration. We therefore calibrated the model within the platform by adjusting some of the key parameters such as photosynthate allocation ratios, death rates of plant organs, and decomposition coefficients of litter and soil organic matter to reach the best fit between the simulated and observed fluxes.

Comment #4: Mechanisms are not deeply explored and evidenced, which is especially disappointing given that this is a modeling study in which case you know everything and how everything works. A revision should seek to give more attention to exposing the specific mechanisms that give rise to the reported dynamics.

Re: We have revised the explanations for the modeled legacy dynamics in the discussion section 4.2 (lines 476-555). We hope these revisions would be helpful in understanding our work.

Comment #5: Line 59: "the savanna ecosystem", clarify which or where... certainly not all globally?

Re: The mesquite savanna ecosystem is located on the Santa Rita Experimental Range (SRER), 45 km south of Tucson, AZ, UAS. The grassland ecosystem is located on the Walnut Gulch Experimental Watershed (WGEW), 11 km east of Tombstone, Arizona, USA. We have clarified that there is one ecosystem (a savanna and a grassland) in each of the two study (Scott et al. 2009 and Hamerlynck et al. 2013), and both of them are located in southeastern Arizona, USA.

Comment # 6: Line 64: consider examining Williams et al. 2006, which does explore legacies on interannual and interdecadal time scales to some degree, and citing as appropriate.

Re: We revised the sentence to appreciate the modeling study by Williams et al. 2006 on how increased rainfall variability may influence dryland vegetation production at interannual and interdecadal scales (line 63-66).

Comment #7: Line 70-71: consider reviewing and citing contributions by Huxman et al. 2004 in Nature and Huxman et al. 2004 in Oecologia.

Re: These studies showed the importance of precipitation pulse size and frequency in controlling the activity of plants and microbes in aridland ecosystems. Hysteresis effects between rainfall pulses (i.e., precipitation legacy effects at rainfall event scale) were also analyzed in these studies. We have cited Huxman et al., 2004a, b (the two Oecologia papers) in line 55 and Huxman et al., 2004c (the Nature paper) in line 74.

Comment #8: Line 76 - 77: consider renaming "structural attributes" to replace "attributes".

Re: The word "attributes" has been replaced with "carryovers" (line 79).

Comment #9: Line 91: consider including citation of Williams et al. 2009 in Oecologia which also shows lagged effects for respiration.

Re: The work has been cited in Line 92. Thanks for the recommendation.

Comment #10: Section 2.1: Some key details of the model need to be presented a little more fully. -What phenomenological model has been adopted for representing canopy stomatal resistance, and plant photosynthesis (e.g. Jarvis-type, or Farqhar and Ball-Berry)? - What are the details of how soil moisture influences plant productivity, plant respiration, and heterotrophic respiration? -Is the model's allocation strategy trained to respond to seasonal, interannual and interdecadal variations in water availability? This is a key for the present study but the data rarely exist to parameterize such dynamic behaviors in models.

Re: Since these key model details have been presented in our previous publications, we did not describe them in detail in this manuscript. Specifically, the algorithms for calculating plant production, photosynthesis, stomatal conductance, and their relations

with water and nitrogen conditions are presented in equations (10) through (14) in Shen et al. (2005, Ecological Modelling, 189, 1-24); the algorithms for calculating autotrophic respiration, heterotrophic respiration, and their relations with temperature, moisture, and nitrogen conditions are presented in equations (A4) through (A11) in Shen et al. (2009, Global Change Biology, 15, 2274-2294).

To present all these detail model descriptions, it would take about 5-6 more manuscript pages. We therefore only added some brief descriptions as suggested by the reviewer in lines 165-181 to help potential readers to examine these key mechanisms built into the model.

Comment #11: Line 219 +: Explain what is "annual" for this paper. This may seem like a detail but it can be really important for assessing "legacies" or carry-over effects. Is it water year (October to September) or calendar (January to December) or some other time period? How does it encompass the two growing seasons and dry seasons? It would be most logical to start your "annual" period at the end of the longer of the two dry seasons, meaning the end of your warm dry season, or end of June.

Re: In line 219 (line 230 in the revised manuscript), "annual" refers to the calendar year (January-December). For calculating seasonal fluxes, "annual" refers to December (of a previous year) to November (of a current year), which has been defined in lines 231-232. For calculating yearly "or annual" fluxes, we used the calendar year (January-December) for the reason that annual ecosystem carbon fluxes are usually reported in the literature on the basis of a calendar year. We added one sentence to clarify this (Line 235-236).

Comment #12: Line 240: Why do you use SPI to assess legacies? Using a standard-normal, statistical translation of absolute values can significantly distort the physiological / ecological meaning or implication of a precipitation anomaly. I recommend you consider sticking with the absolute precipitation anomalies to avoid creating artificial, spurious lags or legacies.

Re: The main purpose of using SPI is to indicate whether a particular year is a wet, a normal or a dry year (see Fig. 1). SPI is also used in the Spearman correlation analysis (see Table 1). We actually tried both SPI and absolute PPT amount in this analysis; both indices received exactly the same correlation coefficients and the significance levels. In Fig. 6, SPI is also used to indicate year type (wet, normal or dry) and to show whether the direction of legacy effects differ among year types. The quantification of legacy effects is solely based on the carbon fluxes simulated (see the equation on page 16), not on the PPT amount or its anomalies.

Comment #13: Figure 2: It seems odd that the model fit for NEP is so poor for the calibration period while so strong for the validation period. Note that the calibration period always has NEP > 0 while the validation period has a year of NEP < 0. **Re:** Intuitively, the model fit should be better for the calibration than the validation period. But that is not the case in our study, mainly because the three validation years

have much larger precipitation variation (229-404 mm) than that in the four calibration years (285-329 mm). The larger precipitation variation in the validation years results in larger GEP, Re and NEP variations (see the new Fig. 2) that are better captured by the model simulations. In the original Fig. 2, NEP actually is always less than 0 (i.e. C source; see the open dots in Fig. 2d) in the calibration period, while there are two years with NEP>0 (i.e., C sink; see the open dots in Fig. 2h) in the validation period. We don't know what confused the reviewer, but this now can be seen more clearly in the new Fig. 2d.

Comment #14: Figure 2: is the R2 shown here for all seasons pooled together? That seems odd. They should each be regressed independently or else only show one of them. The R2 for each season (CS, WS, Annual) pooled is ill-advised.

Re: We agree with the reviewer that pooling all seasonal and annual data together to conduct a regression analysis is logically wrong. Thanks to the reviewer for the constructive comment. We re-conducted such analysis separately for each of the two growing seasons and the calibration and validation years. A new Fig. 2 has been created to present these new results. However, we only showed the comparisons between the observed and simulated fluxes at the annual scale in the new Fig. 2 (left panels), with seasonal comparisons being presented in the supplementary Figure S3, since this modeling analysis is mainly focused on the interannual and interdecadal scales.

Comment #15: Your analysis should show early on (e.g. before Fig 3) observed carbon fluxes versus precipitation for annual, CS, and WS periods to describe a baseline portion of variation explained without considering legacy effects.

Re: Following the reviewer's suggestion, we conducted a new analysis on the relations of the observed (and simulated) fluxes versus precipitation under the baseline PPT conditions (i.e. without changing the previous- or current- year precipitation). The results are shown in the new Fig. 2 (right panels). It is noted here that although the portion of the annual carbon flux variations can be explained largely (R^2 mostly > 0.70) by current-year precipitation, that inseparably contains the legacy impacts from previous-years. This is also the main logical basis of our simulation design, i.e. by changing the previous- and current-year precipitation separately to discriminate the previous- and current-year precipitation effects on current-year carbon fluxes.

Comment #16: Section 2.3: the writing in this section is poor and needs to be improved. Line 252: "faster" is odd diction Line 253: ".. of the variations in observed ones" has awkward diction and syntax. Line 257: "explanative" is incorrect (explanatory)

Re: Based on the new Fig. 2, we revised the section to report the new results (Line 262-299). "faster" has been replaced with "larger" (line 263). "explanative" has been corrected to "explanatory" (line 292).

Comment #17: Year 2006: The model performed poorly for this year, and it was suspected that this is because of an extreme drought impact. Taking this to be the case, doesn't this imply that the model is not capable of capturing drought responses, and if so, doesn't this call into question the use of the model for the intended application... to study lag or legacy drought impacts which are likely to be strongest and most important in the extreme cases?! Even if you intend to study "non-extreme influences of legacies (Line 265)", the fact that the model performance bounces back to being just fine following the 2006 drought seems to argue that there are only negligible legacy effects from extreme precipitation anomalies. This point should be brought out and discussed more critically.

Re: The model is calibrated by pursuing a best fit between the simulated and observed gross primary production (GEP) and ecosystem respiration (Re) in four calibration years (2004-2007). It is therefore not surprising that the model performed well in terms of GEP and Re with the R² being larger than 0.6 (see new Fig. 2b, c), but performed poorly in terms of NEP in these four years with the R² of 0.0001 at the annual scale (Fig. 2d), because NEP is actually calculated from GEP and Rec. We identified that this was mainly due to the poor performance in 2006, a year with an extremely dry cool growing season. If the data of this year were excluded, the R² for NEP could reach above 0.70. The model performed very well in the three validation years (2008-2010), with R² values for different fluxes being all larger than 0.9 (see Fig. 2, left panels). These model calibration and validation results indicate that the model is capable of capturing the annual variations of ecosystem-level fluxes including NEP in 6 out of the 7 years (2004-2010), with 2006 being an exception. We think that the poor performance in 2006 is mainly because the built-in empirical relations between the rate of tissue death (or plant mortality) and the influential factors (e.g., air temperature, soil moisture, and plant phenology) account for more "normal" climate conditions rather than extreme conditions. Although there are many studies that have documented that extreme drought can cause more severe plant mortality, the quantitative or empirical relation between drought severity and plant mortality rate for the studied mesquite savanna ecosystem is still lacking, which hinders us to incorporate more robust relations into the model. Considering such extreme cool-season drought as in 2006 only occurred once in the 30-year simulation period, we therefore think the overall model performance is acceptable. We briefly explained such possible reasons in the discussion section (see lines 550-556).

Comment #18: Line 271: there is no single threshold or cutoff for what is acceptable model performance. a cut-off of 50% would seem absurd for some contexts. **Re:** R²>0.5 was suggested as a rough criteria to assess hydrological models (Moriasi et al. 2007, Transactions of the ASABE, 50, 885-900). For the three calibration years, the R²s for the observed *versus* simulated fluxes were all >0.9 (see new Fig. 2, left panels). We therefore deleted the sentence and the citation.

Comment #19: Model experiment designs for both interannual and interdecadal

variations look good.

Re: Thanks.

Comment #20: Why are legacy effects calculated as a cumulative anomaly over the simulation period? Certainly the effect size would then depend on the year in which an interannual perturbation was imposed, for example, having a large opportunity for legacy effects if a perturbation occurred in 1995 than if a perturbation occurred in 2010.

Re: At the inter-decadal scale, we divided the 30-year period into two sub-periods based on the baseline PPT conditions showing in Fig. 1. While calculating the subperiod-scale fluxes, we used the cumulative fluxes throughout the subperiod and the legacy effects were further calculated based on the cumulative flux anomalies. This is analogous to what we would get annual fluxes by summing up all daily fluxes in a year.

Comment #21: Fig 3: typo in (a) for "Cuurent"

Re: Fixed.

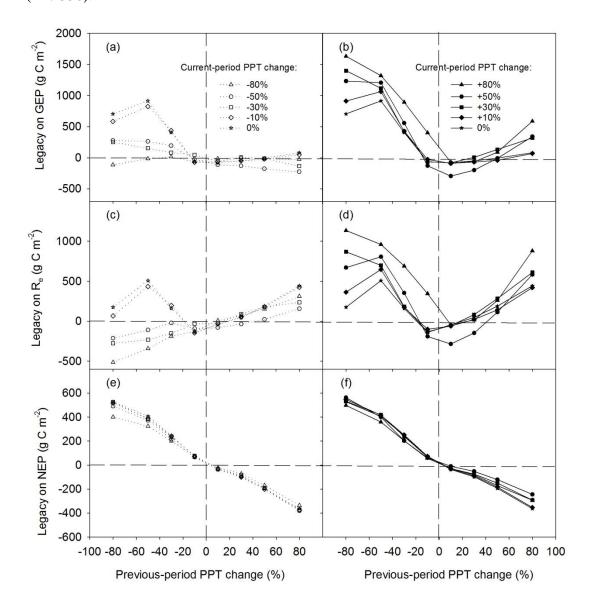
Comment #22: The model's results of the interdecadal legacy seem rather obvious... not that this is all bad but it does limit the paper's contributions of discovery and insight to some degree, especially because results are model-based. A dry prior period knocks vegetation back such that the current period has more growth and less respiration. A wet prior period allows more vegetation growth which elevates respiration in the current period but has little effect on GEP. However, it is puzzling that a prior dry period elevates GEP. What model dynamic explains this? [later it comes out that this is purportedly related to an accumulation of soil nitrogen that becomes available – which is possible but raises some other questions as raised below.]

Re: It was puzzling to us too that a prior dry period/year elevates current-period/year GEP, since aboveground net primary production (ANPP) has been found to have a negative response to a prior dry year. By the notion, GEP and ANPP should all reflect "production". But ANPP of dryland ecosystems is often estimated by harvesting biomass, so we argue that field observed ANPP is actually "biomass". Our simulation results showed that biomass had a negative response to a prior dry year (see Fig. 5a,b and Fig. 8a, b), which is consistent with what has been found in field studies for ANPP. In the PALS model, GEP is calculated based on the photosynthesis rate that is linearly related to nitrogen availability, indicating that accumulated N in a prior dry year can stimulate GEP in a current year especially when water is not limiting. That explains why a prior dry year imposes mostly positive legacy impacts on current-year GEP when the current-year PPT was increased (see Fig. 3b) but impose no impacts or even negative impacts on GEP when the current-year PPT was reduced (see Fig. 3a).

Comment #23: Line 326: "wet legacies imposed mostly negative impacts on

current-period GEP". This is not consistent with what I see in Figure 3a, where it looks like a wet legacy has little to no effect on GEP.

Re: The statement was made in terms of the sign (positive or negative) of the numbers plotted in Fig. 3a, which can be better seen (in the figure below) with the zero lines being added. But in terms of the magnitude of the numbers, the effects are indeed very small. We therefore replaced "mostly negative" will "little" in the text (line 350).



Comment #24: Fig 5. This must be showing anomalies in states not absolutes, right? This should be clarified in the y-axis labels with a delta in front of each label.

Re: No, those are not absolute flux values. They are the legacy effects calculated as the difference between the current-period flux with previous-period PPT change and that without previous-period PPT change (see the equation in page 17 for how we define legacy effects). To avoid ambiguity, we added a delta in front of each label as the reviewer suggested and explained what that means in the figure caption (lines 864-866).

Comment #25: Explain how the legacy duration is quantified. Is it somehow weighted by the magnitude of response so that subtle differences many years later are ignored? Also, explain why, mechanistically, it is so variable.

Re: The legacy duration means how long the legacy lasts after a PPT perturbation in one particular year. It is quantified as the number of years until the impacts on NEP vanish (i.e. the carbon fluxes equal to those under baseline PPT conditions). For example, a decrease in PPT by 30% in year 1982 caused carbon flux changes in the following 4 years (i.e. 1983-1986) compared with the fluxes without changing 1982 PPT, then the legacy duration is 4 years (see Fig. 6a). We added one sentence in the caption of Fig. 6 to clarify this. Similar to the direction and magnitude of the legacies, the lasting duration of the legacies were very variable as well, mainly because yearly PPT (see Fig. 1) and the corresponding PPT alterations were very variable.

Comment #26: Explain the odd results of a -30% prior year interannual precipitation perturbation for year 2000, which really stands out. Also, where is this year's data point in Figure 7? It seems to have been selectively removed, no? There is no reason to treat it as an outlier, this being a set of model results with no room for sampling error as you would otherwise have with observationally based study.

Re: The odd result (or exceptionally high value) is actually for year 1999 (see Fig. 6, left column), which is a result of a -30% PPT change in 1998. We double checked our dataThe odd numbers in 1999 and 1984 were resulted from a mistake during legacy calculation and they have been corrected in this revision (see Fig. 6).

Comment #27: Line 452: the second mechanism is poorly explained. please clarify, particularly regarding what is meant by "if the resources produced ... were not completely lost...".

Comment #28: Line 459: The third mechanism is not a mechanism at all. What is being stated here?

Re: The first mechanism explains why a biogeochemical carryover (e.g. SOM) can cause changes in flux rates. The second mechanism explains why biogeochemical materials (e.g., biomass or SOM) can be carried over. The third mechanism explains why different types of biogeochemical carryovers (e.g. nitrogen) can form legacy impacts on carbon fluxes. We have revised the descriptions of these mechanisms (see line 476-492).

Comment #29: Lines 460 to 476: The argumentation is unclear here. You point out that your simulation results do not show a soil water carryover effect, but then you go on to state that it should be considered to be a potential mechanism. Do you mean that you think your model is wrong in that it lacks this mechanism? Why? What justifies this speculation, which is inconsistent with your findings? What would be done to include this?

Re: We wanted to emphasize that water carryover was not a major contributor at interdecadal and interannual scales, but it could potentially be important at seasonal or

event scales. Since we did not analyze the legacy effects at seasonal or event scales, we deleted the unrelated descriptions from lines 503-508.

Comment #30: Line 482: If Nsoil is high in a dry legacy because plant uptake has been squashed, why is GEP elevated post-dry period when the plants have to invest in acquiring N that they would have otherwise had? THis mechanism in the model seems odd to me. Is a sudden pulse of N better at supporting GEP than a plant canopy that already possessed that N? Perhaps some of that N would have otherwise been tied up in nonphotosynthesizing plant parts (stems, roots), but is that what really happens? **Re:** The model assumes that plant growth or photosynthesis is directly modified by N availability as in the following equation:

$$G_j = X_{Ivs} \bullet SLA_j \bullet A_{\max,j} \bullet (12 / 0.46) \bullet F_c \bullet F_t \bullet S_j^N$$

where G_j is the amount of daily plant growth (g dry mass m⁻²) for functional type j, X_{lvs} is the leaf dry mass (g), SLA is the specific leaf area (m² g⁻¹), $A_{max,j}$ is the maximum potential net photosynthetic rate (mol CO_2 m⁻² s⁻¹), 12 (g) is the mass of C per mol CO_2 , 0.46 is the average C content (46%) in plant tissues, R_{loss} is the respiratory loss of photosynthetic production per day, F_t is the temperature influence factor (for forbs and grasses, not for shrubs and annuals), F_c (2/ π × photoperiod × 3600) is a conversion factor (changing time unit from second to day), and S_i^N is a

linear scalar accounting for the effect of leaf N on $A_{max,j}$ (see Eqn. (13) in Shen et al. 2005, Ecological Modelling, 189, 1-24). Based on this model assumption, high soil N availability would result in larger plant growth or GEP when water is also available. The PALS model also assumes plants take nitrogen directly from soils and allocated to different organs (leaves, stems, and roots). It is biochemically possible the some stored N in stems and roots may be used for photosynthesis in leaves. But this has not been incorporated into PALS.

Comment #31: Diction and syntax are troubled throughout this section. example: 488: "The N enhancement as dry legacies also explains..."

Re: "The N enhancement as" is replaced with "The carryover of N from" (line 521).

Comment #32: Overall, it seems appropriate to put the magnitude of these legacy effects into the context of the magnitude of effects from current-year or current-season precipitation anomalies.

Re: We don't truly understand the comment. Is that what we have done in Table 1, Fig. 4 and Fig. 7?

Comment #33: Line 523: poor wording here.

Re: The description has been reworded (lines 571-576).

Comment #34: Line 523: This paragraph, including speculation and needed new directions, seems out of place in the conclusions section and would be more

appropriate at the end of the discussion section.

Re: We moved the paragraph to the end of the discussion section and revised it accordingly (Lines 544-550).

Comment #35: Citations:

Re: The five references have been cited in the revised version.

Abstract

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The precipitation legacy effect, defined as the impact of historical precipitation (PPT) on extant ecosystem dynamics, has been recognized as an important driver in shaping the temporal variability of dryland aboveground primary production (ANPP) and soil respiration. How the PPT legacy influences whole ecosystem-level carbon (C) fluxes has rarely been quantitatively assessed, particularly at longer temporal scales. We parameterized a process-based ecosystem model to a semiarid savanna ecosystem in southwestern US, calibrated and evaluated the model performance based on 7 years of eddy covariance measurements, and conducted two sets of simulation experiments to assess interdecadal and interannual scale PPT legacy effects over a 30-yr simulation period. The results showed that decreasing the previous period/year PPT (dry legacy) always imposed positive impacts on net ecosystem production (NEP) whereas increasing the previous period/year PPT (wet legacy) had negative impacts on NEP. The simulated dry legacy impacts were mostly positive on gross ecosystem production (GEP) and negative on ecosystem respiration (R_e) but the wet legacy impacts were mostly negative on GEP and positive on R_e. Although the direction and magnitude of GEP and R_e responses to the simulated dry and wet legacies were influenced by both the previous and current PPT conditions, the NEP responses were predominantly determined by the previous PPT characteristics including rainfall amount, seasonality and event size distribution. Larger PPT difference between periods/years resulted in larger legacy impacts, with dry legacies fostering more C sequestration and wet legacies more C release. By analyzing the resource pool (C, N, and H₂O) responses to the simulated dry and wet legacies, we found that the carryover of soil N between periods/years was

- 22 mainly responsible for the GEP responses while the carryovers of plant biomass, litter and soil
- organic matter were mainly responsible for the R_{e} responses. These simulation results suggest
- that previous PPT conditions can exert substantial legacy impacts on current ecosystem C
- balance, which should be taken into account while assessing the response of dryland ecosystem
- 26 C dynamics to future PPT regime changes.
- 27 **Keywords:** AmeriFlux, carbon flux, lagged effect, biogeochemical carryover, ecosystem
- 28 modeling, semiarid-, legacy

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1 Introduction

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Drylands play an important role in global carbon (C) cycle and future C sequestration 32 (Houghton et al., 1999; Asner et al., 2003), as they cover 30-45% of the earth's land surface 33 (Asner et al., 2003; Reynolds et al., 2007), store about 15% of the global soil organic carbon 34 (Schlesinger, 1991), and represent 30-35% of the terrestrial net primary production (Field et al., 35 1998). Driven by sporadic precipitation (PPT) and nonlinear biological responses, dryland C 36 37 fluxes are especially variable across time and space (Maestre et al., 2012; Collins et al., 2014), making the prediction of dryland C budgets a challenging task (Jenerette et al., 2012). 38 Moreover, climate models predict that the intra- and inter-annual PPT variability may be further 39 40 intensified in dryland regions with longer drought durations and more large-sized events (Solomon et al., 2007; Diffenbaugh et al., 2008; Cook and Seager, 2013). Further, sequences of 41 wet years followed by sequences of dry years and vice versa are also increasingly likely (Peters 42 43 et al., 2012; Sala et al., 2012). Understanding the response of dryland ecosystem C fluxes to PPT variation is, therefore, important to characterizing the global C cycle and predicting how 44 future PPT regime changes will affect dryland C balance. 45 46 As a measure of ecosystem C balance, net ecosystem production (NEP) has a value that is positive when an ecosystem accumulates C and negative when an ecosystem loses C. Dryland 47 NEP has been thought to be closely tied to current-year PPT amount, with wetter than average 48 49 years being a C sink, drier than average years being a C source, and years with average rainfall being C neutral (Flanagan et al., 2002; Hastings et al., 2005). In addition, the precipitation 50 legacy effect, defined as the impact of past PPT conditions on the current structure and 51

functioning of ecosystems (Lauenroth and Sala, 1992; Sala et al., 2012; Monger et al., 2015), has 52 been found to play an important role in shaping the temporal variability of dryland ecosystem C 53 fluxes (Knapp et al., 2002; Heisler and Weltzin, 2006; Sala et al., 2012; Ogle et al., 2014; 54 <u>Huxman et al., 2004a, b</u>). For example, Hasting et al. (2005) attributed the C sink status of a 55 desert shrub ecosystem in the early spring of 2002 to the above-average rainfall in the late fall of 56 Scott et al. (2009) and Hamerlynck et al. (2013) found that the cool season (Dec - Apr) 57 58 drought was followed by an unusually large net C loss during the following warm monsoon season (Jul - Sep) in a semiarid savanna and a semidesert grassland ecosystems in southweastern 59 Arizona, USA. Moreover, the savanna ecosystem has recently been a net C source and one 60 61 hypothesized explanation is current respiration of organic C that accumulated in the preceding wetter decade (Scott et al., 2009), but has yet been tested. While these studies reveal the 62 existence of PPT legacy effects on NEP at the seasonal scale, only a few studies have 63 64 quantitatively assessed the contribution of PPT legacy to the temporal variability of dryland NEP at interannual and interdecadal time scales has not been quantitatively assessed (Williams and 65 Albertson, 2006), mainly because it is methodologically difficult to separate the past and current 66 67 PPT impacts on C fluxes with observational data (Sala et al., 2012), and there is a general lack of field manipulative experiments to address the PPT legacies at these scales (Reichmann et al., 68 2013a). 69 70 Much of our current understanding of the PPT legacy effects on dryland C fluxes is based on the aboveground net primary production (ANPP). A number of studies have documented that 71 dryland ANPP is not only linearly related to current-year PPT, but also closely related to the PPT 72

amount and seasonality several months to years before (Lauenroth and Sala, 1992; Oesterheld et 73 al., 2001; Huxman et al., 2004c). For example, field studies have found a positive wet legacy 74 effect where ANPP is higher than expected if preceded by a wetter year, or a negative dry legacy 75 76 effect where ANPP is lower than expected if preceded by a drier year (Jobbagy and Sala, 2000; Oesterheld et al., 2001; Wiegand et al., 2004; Sherry et al., 2008; Sala et al., 2012). Proposed 77 mechanisms explaining such observed PPT legacy effects on ANPP mainly involve the structural 78 79 carryovers of structural attributes between years. The structural attributes, which can include be leaf and root biomass (Oesterheld et al., 2001), the composition of species differing in rooting 80 depth and phenology (Paruelo et al., 1999; Jobbagy and Sala, 2000; Jenerette et al., 2010), or the 81 82 density of seeds, tillers and plant individuals (Oesterheld et al., 2001; Yahdjian and Sala, 2006; Reichmann et al., 2013a). Alternatively, production may be lower than expected if proceeded 83 by a wet period (a negative wet legacy effect) or higher than expected if preceded by a dry period 84 85 (a positive dry legacy effect) (Jenerette et al., 2010). Such PPT legacy effects may be influenced more by biogeochemical effects carryovers that influence the resource availability to 86 respond to current PPT (Evans and Burke, 2013; Reichmann et al., 2013b), whereby increased 87 88 growth in response to a higher PPT can reduce the available nutrients (e.g. nitrogen (N)) for the following period and *vice versa*. Although various mechanisms have been proposed for the 89 PPT legacy impacts on ANPP, few of them have been rigorously tested, and the key underlying 90 91 mechanisms still remain poorly understood (Sherry et al., 2008; Sala et al., 2012; Monger et al., 2015; Williams et al., 2009). 92

Soil respiration (R_s) , as a major component of ecosystem C efflux, has also been found to have

lagged responses to PPT variations (Sponseller, 2007; Ma et al., 2012; Cable et al., 2013; Huxman et al., 2004b). This is particularly true at the event scale; after a period of drought, a rainfall event can result in a pulse of CO₂ efflux that may be orders of magnitude larger than that before the event and then decline exponentially for a few days to weeks (Xu et al., 2004; Jenerette et al., 2008; Borken and Matzner, 2009; Cable et al., 2013). At a seasonal scale, Vargas et al. (2010) found no lags between R_s and soil moisture across 13 vegetation types including four grasslands; but Hamerlynck et al. (2013) presented longer-term ecosystem flux data that suggest seasonal drought legacy affects ecosystem respiration (R_e) in a semi-desert grassland in southeastern AZ, US. They posited that the increased C substrate availability resulting from the previous cool-season drought induced plant mortality was responsible for the higher R_e in the following monsoon season. However, very few studies have been devoted to understanding the PPT legacy impacts on dryland respiration at greater than seasonal timescales. In this study, we conducted simulation experiments with a widely-used dryland ecosystem model, Patch Arid Land Simulator (PALS; Kemp et al. 1997, 2003; Reynolds et al. 2004; Shen et al. 2009), to analyze the PPT legacy effects on ecosystem-level C fluxes including NEP, gross ecosystem production (GEP), and R_e. The PALS model was built on the pulse-reserve concept (Noy-Meir, 1973) and had been used to analyze the impacts of antecedent moisture conditions and the lagged responses of different plant functional types in three North American deserts at the rainfall event scale (Reynolds et al., 2004). We parameterized, calibrated, and evaluated the model based on the long-term eddy covariance measured fluxes at a semidesert savanna ecosystem in southwestern US (Scott et al., 2009) to analyze the PPT legacy effects at

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three two questions. First, what are the direction and magnitude of ecosystem C flux responses to dry and wet legacies? We expected that the PPT legacy impacts would occur over annual and decadal scales in correspondence to PPT fluctuations at these scales and the dry and wet legacy impacts would differ in direction and magnitude. Second, how are the direction and magnitude of PPT legacy effects related to the PPT characteristics of both the previous and the current year / period? For PPT characteristics, we were not only interested in the annual and seasonal PPT amount but also between-event interval and event size distribution since all these variables are widely-recognized key PPT features to dryland ecosystems. Third, what are the mechanisms responsible for the PPT legacy effects? We assumed that changes in the structural and biogeochemical pools/reserves (C, N, and H₂O) resulting from changes in previous year / period PPT would influence current ecosystem C fluxes as conceptualized in the pulse reserve framework and implemented in the PALS model.

2 Methods

2.1 Model description

PALS is a process-based ecosystem model that consists of four modules: atmospheric forcing, a water cycling and energy budget, plant production and respiration, and soil organic matter (SOM) decomposition and heterotrophic respiration (R_h). The four modules are interactively linked by the cycling of C, N, and H_2O through the atmosphere-plant-soil continuum. The PALS model explicitly considers seven plant functional types (FTs) commonly found in the

North American warm deserts: evergreen shrub, deciduous shrub, perennial forb, perennial C₃ 136 and C₄ grasses, and native and exotic C₃ annual grasses (Reynolds et al., 1997; Shen et al., 2009). 137 Since the detailed model structure and mechanistic relationships have been presented in several 138 publications (Kemp et al., 1997, 2003; Reynolds et al., 1997, 2000, 2004; Gao & Reynolds, 2003; 139 Shen et al., 2005, 2008a, 2008b, 2009), here we briefly describe the four modules and refer 140 interested audience to the specific literature. 141 The atmospheric driving force module reads in data for atmospheric driving variables (e.g. 142 atmospheric [CO₂], N deposition rate, daily maximum and minimum air temperatures, 143 precipitation, relative humidity, and solar radiation), and based on these driving variables, 144 145 calculates other important variables such as vapor pressure deficit (VPD) that determines stomatal conductance and soil temperature that influences SOM decomposition and soil 146 respiration. Calculations of VPD and soil temperature can be found in Equations (2) - (7) in 147 148 Shen et al. (2005). The water cycling and energy budget module mainly calculates soil water contents at six 149 layers, the rates of water infiltration into and percolation out of a layer, and water losses via 150 151 evaporation and transpiration from different layers. Water infiltration and percolation rates of a layer are determined by the effective PPT reaching the soil surface, previous water content, and 152 the water holding capacity as a function of soil texture (Shen et al., 2005). Soil evaporation is 153

determined by soil water availability and energy available in the two top soil layers (10 cm in

of roots in each layer for all plant FTs (Kemp et al., 1997; Shen et al., 2008b). Canopy

depth). Water uptake by plants is partitioned among the soil layers according to the proportion

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transpiration is calculated by using the energy budget and the canopy stomatal resistance (Reynolds et al., 2000; Gao and Reynolds, 2003).

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The plant production and respiration module mainly simulates phenology, primary production, growth and maintenance respiration, photosynthate allocation, and litterfall of each plant FT. Three major phenophases (i.e. dates of germination, leafing, and dormancy) are determined in PALS based on the observed dates, air temperature, and precipitation (Shen et al., 2009). Primary production for each FT is calculated based on the leaf area, potential net photosynthetic rate, stomatal conductance, leaf N content modifier, and the difference between intercellular and atmospheric [CO₂]. The plant photosynthesis rate is estimated as a product of stomatal conductance and the partial pressure gradient between atmospheric and intercellular [CO₂]. The stomatal conductance is calculated as an exponential function of leaf water potential and a linear relationship to decreasing atmospheric vapor deficit (see Equations (10) - (14) in Shen et al., 2005). Photosynthate is allocated to different plant organs (leaf, stem, and root) using fixed allocation ratios after subtracting the maintenance respiration, which is estimated as a function of live biomass, basal respiration rate, and modifiers of temperature and plant water potential (Shen et al., 2008a). Growth respiration is calculated based on the growth yield coefficient and the net photosynthate used for growth (Shen et al., 2008a). Litterfall amount is mainly determined as a function of observed dormancy dates, maximum air temperature and drought conditions (Shen et al., 2008a; Shen et al., 2009).

The SOM decomposition and heterotrophic respiration module simulates the decomposition of metabolic and structural litter material, SOM in active, slow and passive pools, and CO₂

emissions associated with these decomposition processes (Kemp et al., 2003 and Shen et al., 2009). The SOM decomposition rate or heterotrophic rate is calculated as thea first-order kinetics rate with a of decomposition coefficient and multiplied by the pool size, which are further modified by the temperature and moisture scalars (see Equations (A4)-(A11) in Shen et al., 2009). In addition, this module also simulates the dynamics of soil mineral N pool by using N mineralization and atmospheric deposition as the major inputs, and plant N uptake and leaching loss as the major outputs. Among these the N mineralization and plant uptake processes are modeled in more detail while the rates of the other processes are basically assigned with empirical constant values. The N mineralization processes are directly coupled to litter and SOM decomposition processes and are calculated as a product of the C flow rates and the C/N ratio of the corresponding litter or SOM pools (Parton et al., 1993; Kemp et al., 2003). The plant N uptake is a product of water transpiration and N concentration in soil solution (see Equation (8) in Shen et al., 2008b).

2.2 Model parameterization

For this study, we modified and parameterized PALS to represent an upland mesquite savanna ecosystem in the Santa Rita Experimental Range (SRER; 31.8214° N, 110.8661° W, elevation 1116 m), about 45 km south of Tucson, AZ, USA. Soils at this site are a deep sandy loam (Scott et al., 2009), and the mean groundwater depth likely exceeds 100 m (Barron-Gafford et al., 2013). Precipitation was therefore considered as the only source of water input into the system. Based on the vegetation composition (Scott et al., 2009), there were five major plant FTs

included in PALS: shrub (e.g. Prosopis velutina), subshrub (e.g. Isocoma tenuisecta), C₄ perennial grass (e.g. Digitaria californica), perennial forb (e.g. Ambrosia psilostachya), and C₃ annual grass, among which the velvet mesquite shrub with average height of ca. 2.5 m accounted for ~35% of the total canopy cover and other FTs (mainly perennial grasses) accounted for ~22% (Scott et al., 2009). Therefore, we derived the site-characteristic parameters for the two major FTs (shrub and perennial grass) from previous studies carried out in SRER, with those for the other FTs being adopted from a generic parameter dataset for the PALS model to be used in the North American warm deserts (Reynolds et al., 2004; Shen et al., 2005). These site-specific parameters mainly included plant-related parameters (e.g. canopy cover, C allocation ratio, rooting distribution ratio, and the initial values of living and dead plant biomass pools) and soil-related parameters (e.g. soil chemical and physical properties, C/N ratios, decomposition rates, and initial values of the litter and SOM pools). The values of these parameters are provided in Supplementary Table S1, with cited literature also being listed below the table. For the climatic variables used to drive the PALS model, we compiled a 30-year meteorological dataset that included daily precipitation (PPT), maximum and minimum air temperatures (T_{max} and T_{min}), relative humidity (RH), and total solar radiation (S_{rad}) from 1981 to 2010. The T_{max}, T_{min}, RH, and S_{rad} data from 1981-1990 were observations from the Tucson Weather Station (about 50 km north of the mesquite savanna site and lower elevation) and obtained through the Arizona Meteorological Network online data access (AZMET: http://ag.arizona.edu/azmet). The remaining 20 years (1991-2010) of T_{max}, T_{min}, RH and S_{rad} data were observations from the Kendall Weather Station (about 85 km east of the mesquite

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savanna site and slightly higher elevation) and obtained through the Southwest Watershed Research Center (SWRC) online data access (http://www.tucson.ars.ag.gov/dap/). PPT data were observations from the Santa Rita Watershed rain gage #5 (1.5 km from the site) and obtained also from the SWRC online data access. These different sources of meteorological data were adjusted based on the 7 years (2004-2010) of the meteorological data obtained from the AmeriFlux eddy-covariance flux tower at the mesquite savanna site (US-SRM, see Supplementary Figure S1). At last, we used the AZMET and SWRC data from 1981 to 2003 plus the flux tower data from 2004 to 2010 to drive the model. Since our simulation experiment was based on the manipulations of the 30-year (1981-2010) PPT data, we report the PPT characteristics here in more detail. In the past 30 years, the mean annual PPT amount was 401 mm at the site, slightly greater than the long-term (1937-2007) mean of 377 mm (Scott et al., 2009). Based on the seasonal PPT amountFor the analysis at the seasonal scale, we distinguished four seasons with their mean PPT being listed in parenthesis: the cool growing season from Dec to Mar (cool-GS, 104 mm), the warm dry season from Apr to Jun (warm-DS, 27 mm), the warm growing season from Jul to Sep (warm-GS, 223 mm), and the cool dry season from Oct to Nov (cool-DS, 47 mm). For the analysis at the annual or decadal scales, we used calendar year (Jan-Dec) as the time unit to compute and present the annual PPT and C fluxes. At the site, as in many other dryland regions (Sala et al., 1992; Heisler-White et al., 2008), most rainy days have only light amounts. About 80 % of daily rainfall was < 10 mm, with medium- to large-sized events (10 - 50 mm) accounting for about 20% and only 10 events larger than 50 mm in the 30 years. The no-rain-day duration between events (hereafter

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between-event interval or BEI) was ~5 days on average in the warm-GS and ~10 days in the cool-GS.

To further assess the degree of dryness/wetness of a particular year or growing season relative to the normal annual or seasonal rainfall, we computed the Standard Precipitation Index (SPI) for the 30 years and the 2 growing seasons of each year using the software SPI_SL-6 (available at http://drought.unl.edu/MonitoringTools), with SPI ≈ 0 indicating a normal year/season, SPI < 0 a dry year/season, and SPI > 0 a wet year/season. Based on the computed SPI, the 30 years were divided into two periods: a wet period from 1981-1994 with mean annual rainfall of 465 mm and a dry period from 1995 to 2010 with mean annual rainfall of 345 mm (Fig. 1a). The 1995-2010 dry period was dominated by cool-GS drought (Fig. 1b), whereas the warm-GS seemed to be wetter in the 1981-1994 wet period (Fig. 1c). These SPI values were used to analyze the relationships between PPT legacy effect and PPT amount.

2.3 Model calibration and evaluation

After model parameterization, we calibrated the model based on four years (2004-2007) of CO₂ and H₂O flux data monitored using the eddy covariance technique at the savanna site. Detailed descriptions of instrumentation, sensor heights and orientations, and data processing procedures for the eddy covariance data can be found in Scott et al. (2009). During model calibration, we mainly adjusted the parameter values of photosynthate allocation ratios, live biomass death rates, and SOM decomposition rates to achieve a best fit between modeled and observed GEP and R_e. The model performed well in capturing the seasonal variation patterns

of actual evapotranspiration (AET), GEP, R_e, and NEP in the four <u>calibration</u> years (Supplementary Figure Fig. S2), with faster larger C exchanges fluxes during the warm-GS. At seasonal and the annual scales, simulated AET, GEP, and R_e could explain explained over 690% of the variations in the observed onesobservations (Fig. 2, left panels). Compared to AET, GEP, and R_e,B), but the correlation between the simulated and observed NEP was very weakerweak This was mainly due to the poor match in 2006: because the model substantially (Fig. 2d). overestimated GEP (120 g C m⁻² simulated versus 52 g C m⁻² observed) during in the warmcool-GS of 2006 but underestimated R_e during the cool-GS (Supplementary Figure Fig. S32). If the data of this year were excluded, the explanatory power for annual and seasonal NEP was could reachreached 5274%. Possible causes for the poor model performance in 2006 shall be discussed later in the discussion section. Since our goal was to use an empirically plausible model to understand the long-term temporal variations in ecosystem fluxes, we consider the calibration results acceptable. Year 2006 had extreme cool-GS drought with the SPI = -2.09 (Fig. 1b) and rainfall of 35 mm less than half of those in the other three years. This cool-GS drought may have caused increased plant mortality similar to that reported for a semi-desert grassland nearby our study site (Scott et al., 2010; Hamerlynck et al., 2013). Wesuspect that the model failed to capture such extreme drought impacts and resulted in the poorperformance in 2006, since the empirical relations describing plant mortality and climateconditions in PALS account for more normal, rather than extreme, conditions. This is appropriate for our study as we are examining non-extreme influences of legacies.

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The model performance was further evaluated by assessing the degree of correlation between

the PALS-simulated and flux-tower-measured C and H₂O fluxes from 2008 through 2010, which were not used for model calibration. The coefficients of determination (R²), which describe the proportion of the variance in measured data explained by the model, were all larger than 0.98 at the seasonal and annual scales in the three validation years (2008-2010; Fig. 2, right left panels). Model performance is typically considered to be acceptable with R² value > 0.5 (Moriasi et al., 2007). These evaluation results indicate that the model was capable of capturing the temporal variability of observed fluxes at seasonal and the annual scales. Furthermore, we also analyzed the relationships between the observed and simulated fluxes and the corresponding current-year PPT to see how the flux variations explained by current-year PPT under baseline conditions (i.e. the PPT variations showing in Fig. 1). The explanatory power (R²) for both the observed and simulated fluxes were mostly over 70% (Fig. 2, right panels), which further indicates that the model is capable of capturing the impacts of PPT variability on ecosystem fluxes. However, such explanatory power of current-year PPT inseparably contains the contribution from previous-year PPT under the baseline PPT conditions. The following simulation experiments were therefore designed to discriminate the contributions by previous- and current-year PPT impacts. Since our goal was to use an empirically plausible model to understand long-term temporal variations of ecosystem fluxes, we therefore consider the overall model performance acceptable.

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2.4 Simulation experiments

We designed two sets of simulation experiments to examine the interdecadal and interannual PPT legacy effects. To analyze the interdecadal legacy effects, we first changed the PPT of the

14-year previous period (1981-1994) by 0%, \pm 10%, \pm 30%, \pm 50% and \pm 80% (multipliers of existing daily PPT amounts in the record) while keeping the 16-year current-period (1995-2010) PPT unchanged. After these manipulations, the average PPT of the previous period ranged from 93 mm corresponding to the 80% of decrease to 837 mm corresponding to the 80% of increase. This design detects how changes in previous-period PPT influence the current-period C fluxes and the associated C pool dynamics. On top of each previous period PPT manipulation level, we further changed the current-period PPT by 0%, $\pm 10\%$, $\pm 30\%$, \pm 50%, and \pm 80%, which resulted in the average current-period PPT varying from 69 mm to 621 This design detects how changes in the current-period PPT influence the legacies resulting from changes in the previous-period PPT. As a result, we made 73 simulation runs corresponding to the 73 combinations of the above previous- and current-period PPT manipulations (9 previous PPT levels times 8 current PPT levels plus 1 baseline run). To analyze the interannual legacy, we changed the PPT of each individual year by $\pm 30\%$ while keeping the PPT of the subsequent years unchanged. This design resulted in 54 simulation runs (27 years from 1981-2007 times 2 PPT manipulation levels) and illustrates the effects of changes in the PPT of the previous one year on the C fluxes and resource pools of the current year(s). After a 30% of PPT change, annual PPT ranged from 162 mm to 925 mm in the 27 years, which was large enough to cover the PPT interannual variation at the study site. Another consideration of using 30% as the PPT manipulation level was that future projected annual PPT variation in dryland regions will be -30% to +25% (Bates et al., 2008; Maestre et al., 2012).

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2.5 Data analysis

Legacy effect was quantified as the C flux (or resource pool size) of the current-period/year after PPT changes in the previous-period/year minus that without PPT changes in the previous-period/year. As an example, the following equation calculates the legacy effect of increasing the previous-period PPT by 30% on the current-period NEP:

$$Legacy_{NEP} = \Delta NEP = NEP_{PPT+30\%}^{CP} - NEP_{PPT+0\%}^{CP}$$

where $NEP_{PPT+30\%}^{CP}$ is the cumulative NEP throughout the current period (1995-2010) under a 30% of previous-period (1981-1994) PPT increase; $NEP_{PPT+0\%}^{CP}$ is the cumulative NEP throughout the current period with no previous-period PPT change (or baseline PPT conditions showing n in Fig. 1). This method directly quantifies whether changes in PPT of the previous period will impose a positive, negative, or no legacy effect on the C fluxes (or resource pools) of the current period. For simplicity, hereafter we refer to the legacy effect resulting from the decreased previous-period/year PPT as the dry legacy and that resulting from the increased previous-period/year PPT as the wet legacy. Spearman correlation analysis was used to detect the relationships between legacy effects and PPT characteristics, including SPI, BEI, and the number of large (≥ 10 mm) versus small (< 10 mm) events at yearly and seasonal scales. The correlation analysis was performed in SPSS 16.0 (Chicago, IL, USA).

3 Results

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3.1 Interdecadal legacy

Changes in the PPT of the previous period (1981-1994) imposed obvious legacy impacts on the C fluxes of the current period (1995-2010). The direction of the simulated interdecadal dry and wet legacies on GEP and Re was dependent upon the direction of both the previous- and current-period PPT changes. When the current-period PPT was reduced (Fig. 3, left panels), the simulated dry legacies imposed mostly positive impacts on the current-period GEP (Fig. 3a) but negative impacts on R_e (Fig. 3c); whereas wet legacies imposed mostly negative impacts on the current-period GEP (Fig. 3a) but mostly positive impacts on R_e (Fig. 3c). When the current-period PPT was enhanced (Fig. 3, right panel), both the dry and wet legacies imposed mostly positive impacts on GEP and R_e (Fig. 3b, d). Regardless of current-period PPT changes, NEP always responded positively to the dry legacies but negatively to the wet legacies (Fig. 3e, f), indicating that the direction of NEP responses to the PPT legacies was predominantly determined by the direction of the previous-period PPT changes. The simulated absolute magnitude of the PPT legacies on ecosystem C fluxes (i.e. GEP, R_e, and NEP) generally increased with the absolute magnitude of changes in the previous-period PPT (Fig. 3, Fig. 4). Increasing the current-period PPT generally amplified the legacy effects compared to decreasing the current-period PPT (comparing the left to the right panels of Fig. 3). The magnitude of the PPT legacies was also significantly correlated with the PPT difference between the previous and current period ($\triangle PPT$, equals to the current-period PPT minus the

previous-period PPT; Fig. 4). If the previous period was wetter than the current period (i.e. Δ PPT < 0 or a wet-to-dry period transition), the legacy effect on R_e was negatively related with Δ PPT (Fig. 4c) but that on NEP was positively related with Δ PPT (Fig. 4e), indicating more current-period C release after a wetter previous period. In contrast, if the previous period was drier than the current period (i.e. Δ PPT > 0 or a dry-to-wet period transition), the correlations were all positive for GEP, R_e and NEP (Fig. 4, right panels), indicating more current period C sequestration after a drier previous period.

The resource pool dynamics were also shaped by the alterations in the previous- and current-period PPTs. We only showed the 30% decrease and increase in the previous- and current-period PPT (i.e. 4 out of 72 pairs of PPT change combinations) as representative examples in Fig. 5, because the major response patterns for the other paired combinations were similar. The duration of the PPT legacy impacts generally lasted for about 6-8 years for plant biomass, litter mass and soil water content (SWC), but much longer for soil organic matter (SOM) and soil mineral N (N_{soil}) (Fig. 5). Based on the resource pool responses in the early 1-2 years (i.e. 1995 and 1996) of the current period, the dry legacies imposed negative impacts on biomass, litter and SOM (Fig. 5a-f), but positive impacts on N_{soil} (Fig. 5g-h). Contrastingly, the wet legacies imposed positive impacts on biomass, litter and SOM (Fig. 5a-f), but negative impacts on N_{soil} (Fig. 5g-h). Similar to the influences on C fluxes, increasing the current-period PPT (Fig. 5, right panels) amplified the legacy impacts on biomass and litter (Fig. 5a-d), and hastened the recovery rates of SOM and N_{soil} to their baseline levels (Fig. 5e-h).

3.2 Interannual legacy

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At the interannual scale, a 30% decrease or increase in the PPT of one previous year could cause have the legacy impacts lasting for 2-12 following years (Fig. 6a-b). The simulated dry legacies had mostly positive impacts on GEP (Fig. 6c) and NEP (Fig. 6g) but negative impacts on R_e (Fig. 6e). Conversely, the simulated wet legacies imposed mostly negative impacts on GEP (Fig. 6d) and NEP (Fig. 6h) but positive impacts on R_e (Fig. 6f). However, both the direction and magnitude of the simulated dry and wet legacies were very variable and idiosyncratic at this timescale, depending on the C fluxes of interest and the PPT conditions of specific years. The correlation analysis showed that the simulated dry and wet legacies on NEP were only significantly related with the previous-year PPT conditions including annual and warm-GS SPI, BEI, and number of large events (NE>10 mm; P<0.05; Table 1), but not the current-year PPT conditions (Table 1). With respect to GEP and R_e responses, only the wet legacies were found to be significantly correlated with some of these PPT variables (P<0.05; Table 1). Further examining the correlation between the PPT legacy effects and the PPT difference between two consecutive years (i.e. $\Delta PPT = current$ -year PPT minus previous-year PPT), we found that only R_e and NEP responses were significantly correlated with Δ PPT if Δ PPT <0 (i.e. under a wet-to-dry year transition; Fig. 7c, e). To analyze the interannual PPT legacy impacts on the dynamics of resource pools (i.e. biomass, litter, SOM, N_{soil}, and SWC), two wet years (1983 and 1994) with positive SPI and two dry years (1986 and 1995) with negative SPI (see Fig. 1a) were chosen as examples. The simulated dry legacies had negative impacts on biomass, litter and SOM, but positive impacts on N_{soil} and SWC in the first current year (Fig. 8). In contrast, wet legacies imposed just the opposite direction of impacts on the five resource pools. The simulated PPT legacy impacts on the resource pools could also last for several years, and the direction and magnitude of the legacy impacts in the following years could differ from those in the first year as described above. For example, increasing the PPT of 1995 by 30% caused a positive legacy impact on the biomass of the first following year (i.e. 1996) but it became negative in the latter following years (e.g. in 1998; Fig. 8b), further indicating that current-year PPT conditions could influence the direction and magnitude of the previous-year PPT legacies.

4 Discussion

4.1 Direction and magnitude of the simulated PPT legacies

Through this simulation analysis, we demonstrated that previous PPT could impose substantial legacy impacts on current ecosystem C fluxes at interannual and interdecadal timescales. A major finding was that the direction and magnitude of the simulated PPT legacies on NEP were predominantly determined by the previous PPT changes. However, the legacy impacts on the two processes (GEP and R_e) determining NEP (NEP = GEP - R_e) were largely influenced by both the previous and current PPT changes (Fig. 3a-d, Fig. 6c-f). The main reason was that alterations in current PPT influenced GEP and R_e in the same direction (e.g. increasing current PPT stimulated both GEP and R_e) while alterations in previous PPT influenced GEP and R_e in the opposite direction (Fig. 3a-d, Fig.6c-f). These simulation results imply that the direction of the PPT legacy impacts on NEP can be inferred from previous PPT conditions: a previous drier

condition may foster more C sequestration in a current wet period/year and a previous wetter condition may cause more C release in a current dry period/year.

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Based on the eddy covariance measured NEP, Scott et al. (2009) found that the mesquite savanna ecosystem was a net CO₂ source during the four below-average-rainfall years from 2004 through 2007. They ascribed the net release of C by the system to the cool-GS drought, but also suspected that the system was likely "burning off" much of the C sequestered during the previous wet period (~1975-1995) (Scott et al., 2009). Our simulation results of the positive wet legacy effects on SOM and negative effects on NEP (Fig. 4c, e) support this hypothesis that the accumulated SOM during the previous-wet period (Fig. 5e, f) contributed to the C released during the current dry period. We also found that larger between-period/year PPT difference could result in larger legacy effects (Fig. 4 and Fig. 7), which is in agreement with what have been found in some field studies. For example, the magnitude of drought legacy on ANPP is proportional to the severity of the drought (Yahdjian and Sala, 2006; Swemmer et al., 2007), and dry- or wet-year legacies on ANPP are linearly related to the PPT difference between years (Sala et al., 2012; Reichmann et al., 2013a). Our simulation analysis detected that not only annual PPT amount but also finer scale PPT characteristics such as GS-rainfall, BEI, and event size could be important in determining the interannual-scale PPT legacy effects (Table 1). These simulation results suggest that PPT legacies may play an more important role in shaping the temporal variability of dryland ecosystem C fluxes under the projected increase in future PPT variability (Solomon et al., 2007; Cook and Seager, 2013).

Evidence suggests that dDryland ecosystems are commonly thought to be a C sink in wet

years, a C source in dry years, and C neutral in normal years (Flanagan et al., 2002; Hastings et al., 2005). While recent studies have shown the importance of other factors including growing season length (Xu and Baldocchi, 2004; Ma et al., 2007), seasonal drought (Scott et al., 2009; Scott et al., 2010; Hamerlynck et al., 2013), and other factors such as temperature and vegetation composition (Hui et al., 2003; Hamerlynck et al., 2010; Barron-Gafford et al., 2012; Scott et al., 2014). Our simulation results indicate PPT legacies may also have important consequences to ecosystem C dynamics. For example, PPT was wetter than normal in 1987 with the SPI of 1.21, but with the NEP was of -85 g C m⁻² yr⁻¹ (a C source), due to the negative wet legacy impacts on NEP several previous wet years before (see Fig. 6h). PPT was nearly normal in 2008 with the SPI of 0.09, but with the simulated NEP was of 79.6 g C m⁻² yr⁻¹ and the observed NEP of 69.2 g C m⁻²-yr⁻¹-(a C sink), again due to the positive dry legacy impacts on NEP from several previous dry years (see Fig. 6g). In a recent analysis on 14 years (1997-2011) of eddy covariance measurements, Zielis et al. (2014) reported that inclusion of previous year's weather (PPT and temperature) into the linear predicting models for NEP increased the explained variance to 53% compared to 20% without accounting for previous year's weather, indicating that previous year's weather also played an important role in the Switzerland subalpine spruce forest. Although we compared some response patterns generated from this simulation study with those derived from field observations, there exists no field study that, to our knowledge, is comparable to our simulation experiment to allow us conducting a direct comparison between the simulated and observed responses. The simulation experimental design of this study may provide helpful insights into designing field manipulative experiments to further test the modeled patterns.

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4.2 Potential mechanisms of the modeled PPT legacies

There are three basic mechanisms explaining why PPT legacy impacts can occur in the model system like PALS. First, the rate of C fluxes is a function of not only various influential factors (e.g. PPT and temperature) but also the pool size itself. For example, soil heterotrophic CO₂ efflux (R_b) rate is a product of the decomposition coefficient, the size of the SOM pool, and two scalar functions accounting for temperature and moisture influences (Kemp et al., 2003; Shen et al., 2009). Therefore, the altered SOM pool size from previous PPT changes can affect current R_h. Second, different C pools have different turnover rates that determines whether biogeochemical materials (e.g. biomass or SOM) can be carried over. If the resources-material (e.g. water, biomass and SOM) produced in a previous legacy year has a turnover rate less than one year, then it would not be carried over to the next year to form a legacy impact were not completely lost from the pool/reserve due to slower turnover rate, the resources may be carried over to the current year and influence the C fluxes as explained in the first mechanism. In addition, the turnover rates of different C pools also determines how long the legacy lasts. For example, SOM pools in the model have relatively slower turnover rates than biomass pools (Shen et al., 2005; Shen et al., 2008b), thus resulting in the longer-lasting legacy impacts on SOM than on biomass or litter pools (Fig. 5 and Fig. 8). Third, the interactions between carbon fluxes and resource (e.g. N and water) availability also determine the direction and magnitude of legacy effects. For example, N carryover as a legacy of a prior dry period (Fig. 5g, h) can impose impacts on the current-period GEP only when the current-period PPT is not so limiting

(Fig. 3b). It would impose little or no legacy impacts on GEP when the current-period PPT is very limiting (Fig. 3a). C, N and H₂O cycling processes are closely coupled in the PALS model. Carried over resources (e.g. C and N) can therefore interact with current PPT conditions to influence the responses of current fluxes. Based on these general model mechanisms, below we discuss more specifically on the major responsive patterns of response and the responsible biogeochemical carryovers found in this study.

An intuitive first explanation for the simulated wet legacies would be the carryover of water.

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However, in most cases soil water carryover did not occur because the wet and dry legacies on SWC were mostly negative or close to zero at the beginning of the current period/year (Fig. 5i-j; Soil water carryover was therefore not the major contributor to the modeled PPT legacy effects at interdecadal and interannual scales. This simulation result corroborates with those of field studies that have shown that carryover of water across long temporal scales is rare in dryland ecosystems, because the rainy growing seasons or wet years are often separated by dry dormant seasons or dry years resulting in short residence times of water in the system-(Oesterheld et al., 2001; Reichmann et al., 2013a; Scott et al., 2014). However, it is noted herethat the carryover of soil water might be possible at finer temporal scales. For example, Raz Yaseef et al. (2012) reported that water from large storms could infiltrate into deep soillayers, be stored there for longer periods of time and carried over across seasons/months (alsosee Wiegand et al., 2004). Thus, carryover of stored soil water should be considered as one of the potential mechanisms while addressing the PPT legacy effects at seasonal or event scales.

The carryover of soil N (N_{soil}) is mainly responsible for the modeled GEP responses. In the

PALS model, the photosynthetic rate is linearly related to N availability if plant N demand is not fulfilled (Reynolds et al., 2004; Shen et al., 2005). Therefore, The enhanced N_{soil} as from dry legacies (Fig. 5g, h and Fig. 8g, h) therefore resulted in the mostly positive responses of GEP (Fig. 3a, b and Fig. 6c). Conversely, the reduced N_{soil} by from wet legacies (Fig. 5g, h and Fig. 8g, h) resulted in the mostly negative responses of GEP (Fig. 3a, b and Fig. 6d). The simulated dry legacies increased N_{soil} mainly by decreasing PPT suppressed plant growth that limited and therefore N uptake. This, which is consistent with many field measurements that N_{soil} accumulates under drought conditions (Reynolds et al., 1999; Yahdjian et al., 2006; de Vries et al., 2012; Evans and Burke, 2013; Reichmann et al., 2013b). Also similar to our simulation results, field studies found that N uptake increases and N_{soil} decreases under wet conditions in dryland ecosystems (McCulley et al., 2009; Reichmann et al., 2013b). The carryover of N enhancement as from dry legacies also explains why the simulated dry legacy impacts on NEP were positive (Fig. 3e, f and Fig. 6g), particularly under the circumstance of the dry-to-wet period/year transition (Fig. 4e, Fig. 7e). The N_{soil} carried over from the previous dry period/year and the current wetter conditions ameliorated both the N and H₂O limitations on GEP, therefore resulted resulting in more C sequestration in the current period/year. The carryover of organic matter (biomass, litter and SOM) is mainly responsible for the modeled R_e responses. In the PALS model, the autotrophic (R_a) and heterotrophic (R_h) respiration rates are linearly related to the size of biomass, litter and SOM pools (Kemp et al., 2003; Shen et al., 2008a; Shen et al., 2009). The previous wet condition stimulated biomass, litter and SOM accumulation (Fig. 5 and Fig. 8) which therefore resulted in the mostly positive

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wet legacy impacts on R_e (Fig. 3c, d and Fig. 6f). Conversely, the dry legacy decreased these pools (Fig. 5 and Fig. 8) and therefore resulted in the mostly negative dry legacy impacts on R_e (Fig. 3c, d and Fig. 6e). Contrary to our simulation results that dry legacies are mostly negative on SOM and R_h, S_Some field studies suggest that the labile C resulting from litter decomposition in a dry season may stimulate R_h in the following wet season (Jenerette et al., 2008; Scott et al., 2009; Ma et al., 2012), i.e. the dry season had a positive legacy impact on the labile C pool and R_h, which is contrary to our simulation result that dry legacies are mostly negative on SOM and R_h.—This is mainly likely because the labile soil C pool in the PALS model only accounts for ~3% of the total SOM and has a very short residence time (1.7 year; see Supplementary Table S1); small amount of seasonal labile C carryover therefore may not exert obvious legacy impacts on SOM and R_h across interannual and interdecadal scales. These results imply that the PPT legacy effects differs in direction and magnitude, depending on the type of C fluxes underconsideration, the type of legacies (i.e. dry vs wet), and the temporal scale of analysis. While this simulation analysis mainly addressed the PPT legacy impacts on dryland ecosystem C fluxes from a biogeochemical perspective, structural shifts in vegetation composition such as woody plant encroachment (Potts et al., 2008; Scott et al., 2014) exotic species invasion (Hamerlynck et al., 2010; Scott et al., 2010), and changes in microbial communities (de Vries et al., 2012; Evans and Wallenstein, 2012; Collins et al., 2014), may also interact with the biogeochemical processes to shape the PPT legacy effects on the temporal variability of dryland <u>C fluxes.</u> Furthermore, we need to better understand the legacy effects of extreme events such as the cool-GS drought in 2006 (see Fig. 1b) need better understanding in order to so that these

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important events can be adequately simulated incorporate the adequate mechanisms into the model. This cool-GS drought may have caused increased plant mortality as reported for a semi-desert grassland nearby our study site (Scott et al., 2010; Hamerlynck et al., 2013), but that has been poorly represented in the model and may have caused the overestimation of the modeled NEP in comparison with the observed one (see Fig. 2c). Future studies incorporating both the structural and biogeochemical aspects and involving multiple temporal scales are needed in order to achieve a more comprehensive understanding of the PPT legacy effects on dryland ecosystem C dynamics.

5 Conclusions

In summary, Through this simulation analysis, we learned through this simulation analysis that:

i) previous PPT conditions can impose substantial legacy impacts on the C balance of dryland ecosystems, with dry legacies fostering more current C sequestration and wet legacies causing more current C release; ii) the responses of ecosystem C fluxes to the simulated dry and wet legacies are mostly opposite in direction and asymmetrical in magnitude, with dry legacies being greater for GEP than for Re and wet legacies being greater for Re than for GEP; iii) the carryover of Nsoil is mainly responsible for the GEP responses, and the carryovers of biomass, litter and SOM are mainly responsible for the Re responses; and iv) the simulated PPT legacy effects can last for several years even with a one-year PPT change and therefore the direction and magnitude of interannual PPT legacy effects are less predictable at interannual than at interdecadal sealeones. TheseOur-simulation results imply-suggest that dryland ecosystems in southwestern US may emit more C that was sequestered in the past into the atmosphere with the predicted

decreasing drying trends in future PPT amount the region (Seager et al., 2007; Solomon et al., 2007), dryland ecosystems in southwestern US may emit more C that was sequestered in the past into the atmosphere. With the projected more extreme and variable PPT regime (Seager et al., 2007; Solomon et al., 2007; Diffenbaugh et al., 2008), t; the temporal variability of ecosystem C fluxes may be further intensified in the region due to the increasing PPT variability and the associated legacy impacts. While this simulation analysis mainly addressed the PPT legacy impacts on dryland ecosystem C fluxes from a biogeochemical perspective, structural shifts in vegetation composition such as woody plant encroachment (Potts et al., 2008; Scott et al., 2014) exotic species invasion (Hamerlynck et al., 2010; Scott et al., 2010), and changes in microbial communities (de Vries et al., 2012; Evans and Wallenstein, 2012; Collins et al., 2014), may also interact with the biogeochemical processes to shape the PPT legacy effects on the temporal variability of dryland C fluxes. Future studies incorporating both the structural and biogeochemical aspects and involving multiple temporal scales are needed in order to achieve a more comprehensive understanding of the PPT legacy effects on dryland ecosystem C dynamics.

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References

- Asner, G. P., Archer, S., Hughes, R. F., Ansley, R. J., and Wessman, C. A.: Net changes in
- regional woody vegetation cover and carbon storage in Texas Drylands, 1937-1999, Global
- 601 Change Biol., 9, 316-335, 2003.
- Barron-Gafford, G. A., Scott, R. L., Jenerette, G. D., Hamerlynck, E. P., and Huxman, T. E.:
- Landscape and environmental controls over leaf and ecosystem carbon dioxide fluxes under
- woody plant expansion, J. Ecol., 101, 1471-1483, 2013.
- Barron-Gafford, G. A., Scott, R. L., Jenerette, G. D., Hamerlynck, E. P., and Huxman, T. E.:
- Temperature and precipitation controls over leaf- and ecosystem-level CO₂ flux along a
- woody plant encroachment gradient, Global Change Biol., 18, 1389-1400, 2012.
- Bates, B. C., Kundzewicz, Z. W., Wu, S., and Palutikof, J. P. (Eds.): Climate Change and Water.
- Technical Paper of the Intergovernmental Panel on Climate Change, IPCC Secretariat,
- 610 Genenva, 2008.
- Borken, W. and Matzner, E.: Reappraisal of drying and wetting effects on C and N
- mineralization and fluxes in soils, Global Change Biol., 15, 808-824, 2009.
- 613 Cable, J. M., Ogle, K., Barron-Gafford, G. A., Bentley, L. P., Cable, W. L., Scott, R. L., Williams,
- D. G., and Huxman, T. E.: Antecedent conditions influence soil respiration differences in
- shrub and grass patches, Ecosystems, 16, 1230-1247, 2013.
- 616 Collins, S. L., Belnap, J., Grimm, N. B., Rudgers, J. A., Dahm, C. N., D'Odorico, P., Litvak, M.,
- Natvig, D. O., Peters, D. C., Pockman, W. T., Sinsabaugh, R. L., and Wolf, B. O.: A
- multiscale, hierarchical model of pulse dynamics in arid-land ecosystems, Annu. Rev. Ecol.

- 619 Evol. S., 45, 397-419, 2014.
- 620 Cook, B. I. and Seager, R.: The response of the North American Monsoon to increased
- greenhouse gas forcing, J. Geophys. Res. Atmos., 118, 1690-1699, 2013.
- de Vries, F. T., Liiri, M. E., Bjornlund, L., Setala, H. M., Christensen, S., and Bardgett, R. D.:
- Legacy effects of drought on plant growth and the soil food web, Oecologia, 170, 821-833,
- 624 2012.
- Diffenbaugh, N. S., Giorgi, F., and Pal, J. S.: Climate change hotspots in the United States,
- Geophys. Res. Lett., 35, 116709, doi: 16710.11029/12008GL035075, 2008.
- 627 Evans, S. E. and Burke, I. C.: Carbon and nitrogen decoupling under an 11-year drought in the
- shortgrass steppe, Ecosystems, 16, 20-33, 2013.
- 629 Evans, S. E. and Wallenstein, M. D.: Soil microbial community response to drying and rewetting
- stress: does historical precipitation regime matter?, Biogeochemistry, 109, 101-116, 2012.
- Field, C. B., Behrenfeld, M. J., Randerson, J. T., and Falkowski, P.: Primary production of the
- biosphere: Integrating terrestrial and oceanic components, Science, 281, 237-240, 1998.
- Flanagan, L. B., Wever, L. A., and Carlson, P. J.: Seasonal and interannual variation in carbon
- dioxide exchange and carbon balance in a northern temperate grassland, Global Change
- Biol., 8, 599-615, 2002.
- 636 Gao, Q. and Reynolds, J. F.: Historical shrub-grass transitions in the northern Chihuahuan Desert:
- modeling the effects of shifting rainfall seasonality and event size over a landscape gradient,
- Global Change Biol., 9, 1475-1493, 2003.
- Hamerlynck, E. P., Scott, R. L., and Barron-Gafford, G. A.: Consequences of cool-season

drought-induced plant mortality to Chihuahuan Desert grassland ecosystem and soil respiration dynamics, Ecosystems, 16, 1178-1191, 2013.

141: 295-305, 2004a.

Hamerlynck, E. P., Scott, R. L., Moran, M. S., Keefer, T. O., and Huxman, T. E.: Growing season ecosystem and leaf-level gas exchange of an exotic and native semiarid bunchgrass,

Oecologia, 163, 561-570, 2010.

Hastings, S. J., Oechel, W. C., and Muhlia-Melo, A.: Diurnal, seasonal and annual variation in the net ecosystem CO₂ exchange of a desert shrub community (Sarcocaulescent) in Baja California, Mexico, Global Change Biol., 11, 927-939, 2005.

Heisler-White, J. L., Knapp, A. K., and Kelly, E. F.: Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland, Oecologia, 158, 129-140, 2008.

Heisler, J. L. and Weltzin, J. F.: Variability matters: towards a perspective on the influence of precipitation on terrestrial ecosystems, New Phytol., 172, 189-192, 2006.

Houghton, R. A., Hackler, J. L., and Lawrence, K. T.: The US carbon budget: Contributions from land-use change, Science, 285, 574-578, 1999.

Hui, D. F., Luo, Y. Q., and Katul, G.: Partitioning interannual variability in net ecosystem exchange into climatic variability and functional change, Tree Physiol., 23, 433-442, 2003.

Huxman, T. E., Cable, J. M., Ignace, D. D., Eilts, J. A., English, N. B., Weltzin, J., and Willimas,

D. G.: Response of net ecosystem gas exchange to a simulated precipitation pulse in a

semi-arid grassland: the role of native versus non-native grasses and soil texture, Oecologia,

- Huxman, T. E., Snyder, K. A., Tissue, D., Leffler, A. J., Ogle, K., Pockman, W. T., Sandquist, D.
- R., Potts, D. L., and Schwinning, S.: Precipitation pulses and carbon fluxes in semiarid and
- arid ecosystems, Oecologia, 141: 254-268, 2004b.
- 664 Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D.,
- Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte,
- J., Kock, G. W., Schwinning, S., Small, E. E., and Willimas, D. G.: Convergence across
- biomes to a common rain-use efficiency, Nature, 429, 651-654, 2004c.
- Jenerette, G. D., Barron-Gafford, G. A., Guswa, A. J., McDonnell, J. J., and Villegas, J. C.:
- Organization of complexity in water limited ecohydrology, Ecohydrology, 5, 184-199, 2012.
- Jenerette, G. D., Scott, R. L., and Huete, A. R.: Functional differences between summer and
- winter season rain assessed with MODIS-derived phenology in a semi-arid region, J. Veg.
- 672 Sci., 21, 16-30, 2010.
- Jenerette, G. D., Scott, R. L., and Huxman, T. E.: Whole ecosystem metabolic pulses following
- 674 precipitation events, Funct. Ecol., 22, 924-930, 2008.
- Jobbagy, E. G. and Sala, O. E.: Controls of grass and shrub aboveground production in the
- Patagonian steppe, Ecol. Appl., 10, 541-549, 2000.
- Kemp, P. R., Reynolds, J. F., Pachepsky, Y., and Chen, J. L.: A comparative modeling study of
- soil water dynamics in a desert ecosystem, Water Resour. Res., 33, 73-90, 1997.
- Kemp, P. R., Reynolds, J. F., Virginia, R. A., and Whitford, W. G.: Decomposition of leaf and
- root litter of Chihuahuan desert shrubs: effects of three years of summer drought, J. Arid
- Environ., 53, 21-39, 2003.

- Knapp, A. K., Fay, P. A., Blair, J. M., Collins, S. L., Smith, M. D., Carlisle, J. D., Harper, C. W.,
- Danner, B. T., Lett, M. S., and McCarron, J. K.: Rainfall variability, carbon cycling, and
- plant species diversity in a mesic grassland, Science, 298, 2202-2205, 2002.
- Lauenroth, W. K. and Sala, O. E.: Long-term forage production of North-American shortgrass
- steppe, Ecol. Appl., 2, 397-403, 1992.
- Ma, S. Y., Baldocchi, D. D., Hatala, J. A., Detto, M., and Yuste, J. C.: Are rain-induced
- ecosystem respiration pulses enhanced by legacies of antecedent photodegradation in
- semi-arid environments?, Agr. Forest Meteorol., 154, 203-213, 2012.
- 690 Ma, S. Y., Baldocchi, D. D., Xu, L. K., and Hehn, T.: Inter-annual variability in carbon dioxide
- exchange of an oak/grass savanna and open grassland in California, Agr. Forest Meteorol.,
- 692 147, 157-171, 2007.
- Maestre, F. T., Salguero-Gomez, R., and Quero, J. L.: It is getting hotter in here: determining and
- projecting the impacts of global environmental change on drylands Introduction, Philos. T.
- 695 R. Soc. B., 367, 3062-3075, 2012.
- McCulley, R. L., Burke, I. C., and Lauenroth, W. K.: Conservation of nitrogen increases with
- 697 precipitation across a major grassland gradient in the Central Great Plains of North America,
- 698 Oecologia, 159, 571-581, 2009.
- Monger, C., Sala, O. E., Duniway, M. C., Goldfus, H., Meir, I. A., Poch, R. M., Throop, H. L.,
- and Vivoni, E. R.: Legacy effects in linked ecological-soil-geomorphic systems of drylands,
- 701 Front. Ecol. Environ., 13, 13-19, 2015.
- 702 Moriasi, D. N., Arnold, J. G., Van Liew, M. W., Bingner, R. L., Harmel, R. D., and Veith, T. L.:

- 703 Model evaluation guidelines for systematic quantification of accuracy in watershed
- rough simulations, Transactions of the Asabe, 50, 885-900, 2007.
- Noy-Meir, I.: Desert ecosystems: environment and producers, Annu. Rev. Ecol. Evol. S., 4,
- 706 25-51, 1973.
- Oesterheld, M., Loreti, J., Semmartin, M., and Sala, O. E.: Inter-annual variation in primary
- production of a semi-arid grassland related to previous-year production, J. Veg. Sci., 12,
- 709 137-142, 2001.
- Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., Loik,
- M. E., and Tissue, D. T.: Quantifying ecological memory in plant and ecosystem processes,
- 712 Ecol. Lett., 2014.
- Parton, W. J., Scurlock, J. M. O., Ojima, D. S., Gilmanov, T. G., Scholes, R. J., Schimel, D. S.,
- Kirchner, T., Menaut, J. C., Seastedt, T., Moya, E. G., Kamnalrut, A., and Kinyamario, J. I.:
- Observations and modeling of biomass and soil organic-matter dynamics for the grassland
- biome worldwide, Global Biogeochem. Cy., 7, 785-809, 1993.
- Paruelo, J. M., Lauenroth, W. K., Burke, I. C., and Sala, O. E.: Grassland precipitation-use
- efficiency varies across a resource gradient, Ecosystems, 2, 64-68, 1999.
- Peters, D. P. C., Yao, J., Sala, O. E., and Anderson, J. P.: Directional climate change and potential
- reversal of desertification in arid and semiarid ecosystems, Global Change Biol., 18,
- 721 151-163, 2012.
- Potts, D. L., Scott, R. L., Cable, J. M., Huxman, T. E., and Williams, D. G.: Sensitivity of
- mesquite shrubland CO₂ exchange to precipitation in contrasting landscape settings,

- 724 Ecology, 89, 2900-2910, 2008.
- 725 Raz-Yaseef, N., Yakir, D., Schiller, G., and Cohen, S.: Dynamics of evapotranspiration
- 726 partitioning in a semi-arid forest as affected by temporal rainfall patterns, Agr. Forest
- 727 Meteorol., 157, 77-85, 2012.
- Reichmann, L. G., Sala, O. E., and Peters, D. P. C.: Precipitation legacies in desert grassland
- primary production occur through previous-year tiller density, Ecology, 94, 435-443, 2013a.
- Reichmann, L. G., Sala, O. E., and Peters, D. P. C.: Water controls on nitrogen transformations
- and stocks in an arid ecosystem, Ecosphere, 4, 1-17, 2013b.
- Reynolds, J. F., Kemp, P. R., Ogle, K., and Fernandez, R. J.: Modifying the 'pulse-reserve'
- paradigm for deserts of North America: precipitation pulses, soil water, and plant responses,
- 734 Oecologia, 141, 194-210, 2004.
- Reynolds, J. F., Kemp, P. R., and Tenhunen, J. D.: Effects of long-term rainfall variability on
- evapotranspiration and soil water distribution in the Chihuahuan Desert: A modeling
- 737 analysis, Plant Ecol., 150, 145-159, 2000.
- Reynolds, J. F., Stafford Smith, D. M., Lambin, E. F., Turner, B. L., Mortimore, M., Batterbury, S.
- P. J., Downing, T. E., Dowlatabadi, H., Fernandez, R. J., Herrick, J. E., Huber-Sannwald, E.,
- Jiang, H., Leemans, R., Lynam, T., Maestre, F. T., Ayarza, M., and Walker, B.: Global
- desertification: Building a science for dryland development, Science, 316, 847-851, 2007.
- Reynolds, J. F., Virginia, R. A., Kemp, P. R., de Soyza, A. G., and Tremmel, D. C.: Impact of
- drought on desert shrubs: Effects of seasonality and degree of resource island development,
- 744 Ecol. Monogr., 69, 69-106, 1999.

- Reynolds, J. F., Virginia, R. A., and Schlesinger, W. H.: Defining functional types for models of
- desertification. In: Plant Functional Types: Their Relevance to Ecosystem Properties and
- Global Change, Shugart, T. M. and Woodward, F. I. (Eds.), Cambridge University Press,
- 748 Cambridge, 1997.
- Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbagy, E., and Peters, D.: Legacies of
- precipitation fluctuations on primary production: theory and data synthesis, Philos. T. R.
- 751 Soc. B., 367, 3135-3144, 2012.
- Sala, O. E., Lauenroth, W. K., and Parton, W. J.: Long-term soil-water dynamics in the shortgrass
- 753 steppe, Ecology, 73, 1175-1181, 1992.
- Schlesinger, W. H.: Biogeochemistry: An Analysis of Global Change, Academic Press Inc, San
- 755 Diego, CA., 1991.
- Scott, R. L., Hamerlynck, E. P., Jenerette, G. D., Moran, M. S., and Barron-Gafford, G. A.:
- Carbon dioxide exchange in a semidesert grassland through drought-induced vegetation
- change, J. Geophys. Res. Biogeosci., 115, G03026, doi: 03010.01029/02010JG001348,
- 759 2010.
- Scott, R. L., Huxman, T. E., Barron-Gafford, G. A., Jenerette, G. D., Young, J. M., and
- Hamerlynck, E. P.: When vegetation change alters ecosystem water availability, Global
- 762 Change Biol., 20, 2198-2210, 2014.
- Scott, R. L., Jenerette, G. D., Potts, D. L., and Huxman, T. E.: Effects of seasonal drought on net
- carbon dioxide exchange from a woody-plant-encroached semiarid grassland, J. Geophys.
- Res. Biogeosci., 114, G04004, doi: 04010.01029/02008JG000900, 2009.

- Seager, R., Ting, M. F., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H. P., Harnik, N.,
- Leetmaa, A., Lau, N. C., Li, C. H., Velez, J., and Naik, N.: Model projections of an
- imminent transition to a more arid climate in southwestern North America, Science, 316,
- 769 1181-1184, 2007.
- Shen, W. J., Jenerette, G. D., Hui, D. F., Phillips, R. P., and Ren, H.: Effects of changing
- precipitation regimes on dryland soil respiration and C pool dynamics at rainfall event,
- seasonal and interannual scales, J. Geophys. Res. Biogeosci., 113, G03024, doi:
- 773 03010.01029/02008JG000685, 2008a.
- Shen, W. J., Reynolds, J. F., and Hui, D. F.: Responses of dryland soil respiration and soil carbon
- pool size to abrupt vs. gradual and individual vs. combined changes in soil temperature,
- precipitation, and atmospheric [CO₂]: a simulation analysis, Global Change Biol., 15,
- 777 2274-2294, 2009.
- Shen, W. J., Wu, J. G., Grimm, N. B., and Hope, D.: Effects of urbanization-induced
- environmental changes on ecosystem functioning in the Phoenix metropolitan region, USA,
- 780 Ecosystems, 11, 138-155, 2008b.
- Shen, W. J., Wu, J. G., Kemp, P. R., Reynolds, J. F., and Grimm, N. B.: Simulating the dynamics
- of primary productivity of a Sonoran ecosystem: Model parameterization and validation,
- 783 Ecol. Model., 189, 1-24, 2005.
- Sherry, R. A., Weng, E. S., Arnone, J. A., Johnson, D. W., Schimel, D. S., Verburg, P. S., Wallace,
- L. L., and Luo, Y. Q.: Lagged effects of experimental warming and doubled precipitation on
- annual and seasonal aboveground biomass production in a tallgrass prairie, Global Change

- 787 Biol., 14, 2923-2936, 2008.
- Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., and Miller,
- H. L. (Eds.): Climate Change 2007: The Physical Science Basis, Cambridge University
- 790 Press, Cambridge, 2007.
- 791 Sponseller, R. A.: Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem, Global
- 792 Change Biol., 13, 426-436, 2007.
- Swemmer, A. M., Knapp, A. K., and Snyman, H. A.: Intra-seasonal precipitation patterns and
- above-ground productivity in three perennial grasslands, J. Ecol., 95, 780-788, 2007.
- Vargas, R., Baldocchi, D. D., Allen, M. F., Bahn, M., Black, T. A., Collins, S. L., Yuste, J. C.,
- Hirano, T., Jassal, R. S., Pumpanen, J., and Tang, J. W.: Looking deeper into the soil:
- biophysical controls and seasonal lags of soil CO₂ production and efflux, Ecol. Appl., 20,
- 798 1569-1582, 2010.
- Wiegand, T., Snyman, H. A., Kellner, K., and Paruelo, J. M.: Do grasslands have a memory:
- Modeling phytomass production of a semiarid South African grassland, Ecosystems, 7,
- 801 243-258, 2004.
- Willimas, C. A. and Albertson, J. D.: Dynamical effects of the statistical structure of annual
- rainfall on dryland vegetation, Global Change Biol., 12, 777-792, 2006.
- Williams, C. A., Hanan, N., Scholes, R. J., and Kutsch, W.: Complexity in water and carbon
- dioxide fluxes following rain pulses in an african savanna, Oecologia, 161, 469-480, 2009.
- 806 Xu, L. K. and Baldocchi, D. D.: Seasonal variation in carbon dioxide exchange over a
- Mediterranean annual grassland in California, Agr. Forest Meteorol., 123, 79-96, 2004.

808	Xu, L. K., Baldocchi, D. D., and Tang, J. W.: How soil moisture, rain pulses, and growth alter the
809	response of ecosystem respiration to temperature, Global Biogeochem. Cy., 18, GB4002,
810	doi: 4010.1029/2004GB002281, 2004.
811	Yahdjian, L. and Sala, O. E.: Vegetation structure constrains primary production response to
812	water availability in the Patagonian steppe, Ecology, 87, 952-962, 2006.
813	Yahdjian, L., Sala, O. E., and Austin, A. T.: Differential controls of water input on litter
814	decomposition and nitrogen dynamics in the Patagonian Steppe, Ecosystems, 9, 128-141,
815	2006.
816	Zielis, S., Etzold, S., Zweifel, R., Eugster, W., Haeni, M., and Buchmann, N.: NEP of a Swiss
817	subalpine forest is significantly driven not only by current but also by previous year's
818	weather, Biogeosciences, 11, 1627-1635, 2014.
819	
820	

Table 1. Spearman correlation coefficients between legacy effects and precipitation characteristics at an interannual scale.

Precipitation	Dry legacy (previous-year PPT -30%)			Wet legacy (previous-year PPT +30%)			
characteristics	∆GEP	$\underline{\underline{\Lambda}}R_{e}$	<u>∆</u> NEP	∆GEP	$\underline{\underline{\Delta}}R_{e}$	∆NEP	
Previous-year PPT characteristics							
Yearly SPI	ns	ns	0.560**	-0.545**	ns	-0.757**	
Warm-GS SPI	ns	ns	0.579**	ns	ns	-0.626***	
Yearly NE>10 mm	ns	ns	0.442*	-0.446*	ns	-0.636**	
Warm-GS NE>10 mm	ns	ns	0.445*	ns	ns	-0.575***	
Current-year PPT characteristics							
Yearly SPI	ns	ns	ns	-0.482*	-0.467*	ns	
Warm-GS SPI	ns	ns	ns	ns	-0.399*	ns	
Yearly BEI	ns	ns	ns	0.409*	ns	ns	
Yearly NE>10 mm	ns	ns	ns	-0.394*	ns	ns	

Abbreviations: PPT: precipitation; SPI: standard precipitation index; GEP: gross primary production; R_e : ecosystem respiration; NEP: net ecosystem production; GS: growing season; BEI: between-event interval; NE: number of events. * and ** - Correlations are significant at the 0.05 and 0.01 levels (2-tailed), respectively; ns – not significant.

Figure captions

Figure 1. Annual and growing-season rainfall and the corresponding standard precipitation index (SPI) in the 30 years (1981-2010) at the Santa Rita Experimental Range (SRER) mesquite savanna site. The cool growing season (cool-GS) is from Dec through Mar and warm-GS from Jul through Sep. Dots represent annual or seasonal rainfall and bars the corresponding standard precipitation index.

Figure 2. Comparison of the model-simulated water and carbon fluxes with the eddy covariance observed onesobservations at the mesquite savanna site. Left panels show the seasonal and annual fluxes (2004-2007) used for model calibration. Right panels show the seasonal and annual fluxes (2008-2010) used for model validation. R² is the coefficient of determination describing the proportion of the variance in measured fluxes explained by the model. CS represents the cool season from Oct to Mar and WS the warm season from Apr to Sep. AET represents actual evapotranspiration; GEP gross ecosystem production, Re total ecosystem respiration, and NEP net ecosystem production.

Figure 3. Interdecadal legacy effects of changing the previous-period (1981-1994)

precipitation on the cumulative carbon fluxes of the current period (1995-2010). Interdecadal legacy effects on carbon fluxes (e.g. ΔΝΕΡ) are calculated as the difference between the current-period flux with previous-period PPT changes and that without previous-period PPT changes. Dashed lines with open symbols represent different levels of decreasing (left panels) the

current-period precipitation (PPT). Solid lines with filled symbols represent increasing (right panels) the current-period precipitation.

Figure 4. Spearman correlations of interdecadal precipitation legacy effects with the precipitation difference between periods (ΔPPT). Interdecadal ΔPPT is calculated as the mean PPT of the current period (1995-2010) minus that of the previous period (1981-1994). Interdecadal legacy effects on carbon fluxes (e.g. ΔNEP) are calculated as the difference between the current-period flux with previous-period PPT changes and that without previous-period PPT changes. Sample size is 41 for the wet-to-dry period transition (left panels) and 23 for the dry-to-wet period transition (right panels). GEP represents gross ecosystem production, R_e ecosystem respiration, and NEP net ecosystem production. R_e is the coefficient of determination and P is probability.

Figure 5. Interdecadal precipitation legacy effects on the resource pool dynamics. Left panels show the resource pool responses under a 30% of decrease while right panels show those under a 30% of increase in the precipitation (PPT) of the current period from 1995-2010.

Legacy effects on pool size (e.g. ΔBiomass) are quantified as the difference between the current-period pool size with previous-period PPT change and that without previous-period PPT change. Dashed lines represent a 30% of decrease while solid lines represent a 30% of increase in the precipitation of the previous period from 1981-1994. SOM represents soil organic matter, N_{soil} soil mineral nitrogen, and SWC soil water content.

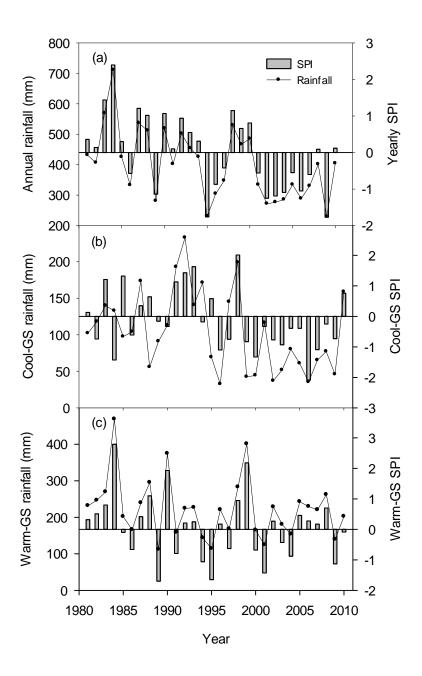
Figure 6. Interannual precipitation legacy effects on the ecosystem carbon fluxes. (a) and (b) show the lasting duration of dry (left panels) and wet (right panels) legacies, respectively. The legacy lasting duration is quantified as the number of years during which the legacy impacts on NEP resulting from a previous-year PPT change exists. (c) through (h) show gross ecosystem production (GEP), ecosystem respiration (R_e) and net ecosystem production (NEP) responses.

Bars in the background represent yearly standard precipitation index (SPI).

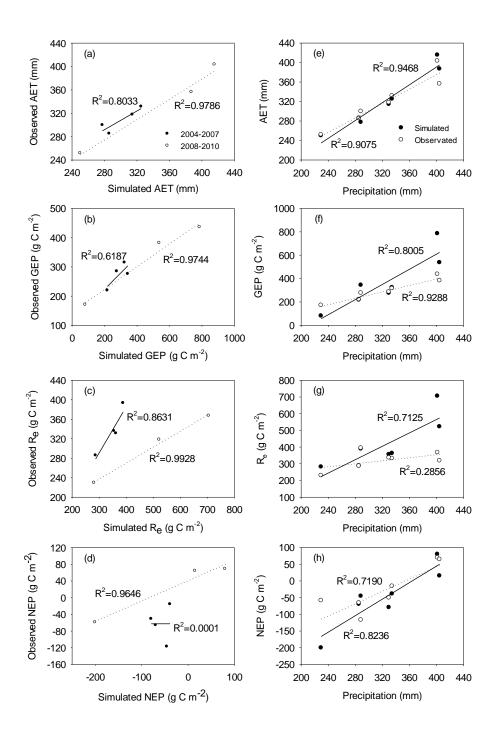
Figure 7. Spearman correlations of interannual precipitation legacy effects with the precipitation difference between years (ΔPPT). Interannual ΔPPT is calculated as current-year PPT minus previous-year PPT. Sample size is 26 for the wet-to-dry year transition (left panels) and 27 for the dry-to-wet year transition (right panels). GEP represents gross ecosystem production, R_e ecosystem respiration, and NEP net ecosystem production. R^2 is the coefficient of determination and P is probability.

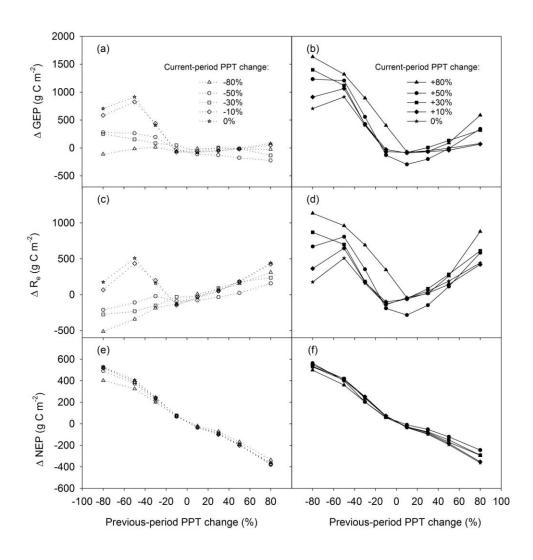
Figure 8. Interannual precipitation legacy effects on resource pool dynamics. Left panels show the legacy effects on pool dynamics in two representative wet years while right panels for two representative dry years. Legacy effects on pool size (e.g. ΔBiomass) are quantified as the difference between the current-year pool size with previous-year PPT change and that without previous-year PPT change. Solid lines represent a 30% decrease while dashed lines represent a 30% increase in the previous-year precipitation (PPT). SOM represents soil organic matter,

 N_{soil} soil mineral nitrogen, and SWC soil water content.

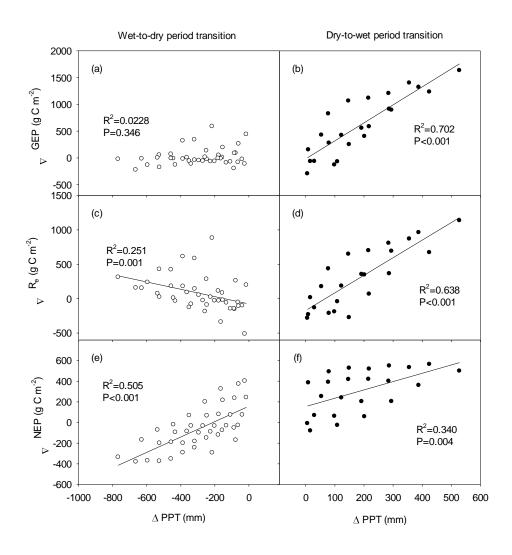


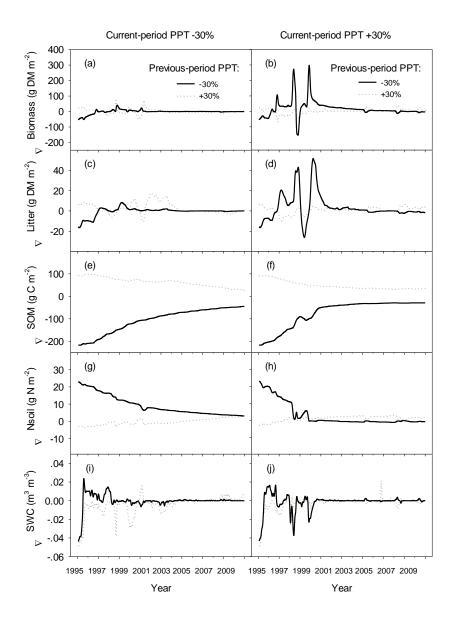
897 FIG. 2





906907 FIG. 4908





916917 FIG. 6918

