Hydrological and ecological responses of ecosystems to extreme precipitation regimes: A test of empirical-based hypotheses with an ecosystem model

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ABSTRACT

Many uncertainties exist in our quest to understand and predict how terrestrial ecosystems will respond to climate change. A particularly challenging issue is how increases in extreme precipitation regimes, which are characterized by larger but fewer individual precipitation events, will impact ecosystems. Based on a wide-ranging review of empirical studies of both hydrological and ecological processes, Knapp et al. (2008) generated a suite of hypotheses positing how these processes would respond to an increase in extreme precipitation regimes and, from this, concluded that mesic ecosystems would be more detrimentally impacted than xeric ones. In this study we present the first thorough test of these hypotheses by examining how forest, shrubland, grassland and desert ecosystems of the Tibetan Plateau, having very different vegetation and climate characteristics, respond to more extreme rainfall regimes. We accomplished this by using a simulation model (Biome-BGC) to examine the integrated behavior of these ecosystems based on the simultaneous responses and interactions of 10 hydrological and ecological processes: runoff, canopy evaporation, soil evaporation, soil water storage, transpiration, net primary productivity, soil respiration, net ecosystem exchange, nitrogen [N] mineralization, and N leaching. We ran forty-year simulations (1986–2008) where we manipulated mean growing season precipitation to create more extreme intra-annual precipitation regimes characterized by lower precipitation frequencies, longer dry periods, and larger individual (daily) precipitation events. When compared to ambient conditions, our simulations showed that increases in extreme rainfall regimes (1) impacted all hydrological processes in mesic ecosystems, resulting in a reduction of soil mineral N due to increased leaching; and (2) enhanced plant growth in xeric ecosystems, leading to larger and denser canopies and higher light interception. The responses of hydrological processes tended to follow Knapp et al.’s hypotheses more so than ecological responses. Overall, responses of mesic ecosystems closely followed the hypotheses but xeric ecosystems were highly variable and only weakly consistent with them. Our findings provide new insights as to how more extreme rainfall regimes may potentially affect the functioning of terrestrial ecosystems.

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1. Introduction

Anticipating how terrestrial ecosystems will respond to climate change is one of the greatest challenges in ecology (Fay et al., 2011; Heisler-White et al., 2008; Knapp et al., 2015; Smith, 2011; Zhang et al., 2013). Of special interest are changing precipitation regimes because the variability of rainfall and the frequency of extreme events are increasing worldwide (Easterling et al., 2000; Groisman et al., 2005; Min et al., 2011). Observations reveal an increased intensity of extreme precipitation events at mid and high latitudes (Liu and Zipser, 2015) and climatic models predict that intra-annual rainfall variability will intensify, which will shift current rainfall regimes towards more extreme ones with lower precipitation frequency, longer dry periods, and larger individual precipitation...
events worldwide (IPCC, 2013). This is significant because alterations in the frequency and size of rainfall events – alone or in combination with changes in the total amount of rainfall received – have the potential to affect ecological processes such as the establishment, survival, phenology and growth of plants (Reynolds et al., 1999; Sher et al., 2004), the composition and diversity of ecological communities (Ilg et al., 2008; Knapp et al., 2002), above- and below-ground productivity (Heisler-White et al., 2008; Maestre and Reynolds, 2007), nitrogen cycling (Bloor and Bardgett, 2012; Kong et al., 2013) and soil respiration (Fay et al., 2011; Parton et al., 2012).

Based on a review of the literature, Knapp et al. (2008) generated a suite of hypotheses (presented in Fig. 1a) positing how various hydrological (e.g., runoff, soil water storage) and ecological (e.g., net primary productivity [NPP], nitrogen [N] mineralization) processes in mesic versus xeric ecosystems – would potentially respond to more extreme precipitation regimes. Knapp et al. (2008) concluded that more extreme precipitation regimes will be more detrimental in mesic as compared to xeric ecosystems. They conjecture that larger, but less frequent, precipitation events will increase the duration and severity of soil water stress in mesic ecosystems when intervals between rainfall events increase; in addition, increased water stress will result in decreased NPP and N mineralization. In contrast, in xeric systems more extreme precipitation regimes will potentially decrease overall evaporative losses, which will lead to greater soil water storage and increased NPP.

While the empirical studies synthesized by Knapp et al. (2008) provide key insights on how plants and ecosystems may respond to extreme precipitation regimes, they have limitations. Field and greenhouse/common garden typically focus on a particular species or ecosystem, last for only a few years, are usually limited to a single precipitation extreme regime, and represent only a small fraction of the experiments needed to tease apart the myriad of interactions and feedbacks likely to occur in the future. Furthermore, due to differences in methodologies, sampling designs and measurement variables, experiments usually cannot be easily compared (Vicca et al., 2012) and do not adequately represent the types of precipitation scenarios expected in the future (Beier et al., 2012). Although some of the limitations of empirical studies can be addressed by the establishment of long-term field studies that are event-oriented and/or deal with multiple biophysical and ecosystem response processes (e.g., Fay et al., 2011; Fraser et al., 2012; Jentsch et al., 2007),
it is clear that a wholly-empirical approach is not sufficient to understand and predict how terrestrial ecosystems will respond to extreme precipitation regimes.

Process-based simulation modeling thus has a vital role to play in predicting the future state of ecosystems (Clark et al., 2001) and as a diagnostic tool for extrapolating existing, but limited, empirical knowledge of individual processes into a more comprehensive understanding of potential long-term changes in ecosystems (Reynolds et al., 2001). While numerous models have been used to explore how changes in rainfall variability, amount, timing and event size may potentially affect the specific ecological and hydrological processes examined by Knapp et al. (2008, Fig. 1a), e.g., plant growth, phenology, transpiration, infiltration (e.g., Gerten et al., 2008; Notaro, 2008; Peng et al., 2013; Reynolds et al., 2004; Xu et al., 2015; Zhou et al., 2008), how they will impact whole ecosystems is less clear (Reyer et al., 2013; Weltzin et al., 2003; Wu et al., 2011).

In this study we test Knapp et al.’s (2008) hypotheses by using an ecosystem model to examine the integrated behavior of ecosystems of the Tibetan Plateau. The Tibetan Plateau is an excellent region for testing these hypotheses because it is home to diverse ecosystems (from mesic forests to xeric deserts), is characterized by a large precipitation gradient (Aldenderfer and Yinong, 2004; Ni, 2000), and is one of the most sensitive regions in the world to climate change (Diffenbaugh and Giorgi, 2012; Spicer et al., 2003). To our knowledge, this study represents the first thorough test of Knapp et al.’s (2008) hypotheses because we simultaneously examine the responses of 10 hydrological (runoff, canopy evaporation, soil evaporation, soil water storage, transpiration) and ecological (NPP, soil respiration, net ecosystem exchange, N mineralization, N leaching) processes to more extreme rainfall regimes across ecosystems with differing vegetation and climatic characteristics. Following Knapp et al. (2008) we restrict our definition of an extreme precipitation regime to an increase in intra-annual variability, which leads to a shift from current patterns to a precipitation regime where the frequency of precipitation is lower, there are longer dry periods, and individual (daily) precipitation events are larger.

2. Materials and methods

2.1. Study area

We selected four sites in the Tibetan Plateau (TP): a forest (Gongga), shrubland (Zhuwagen), grassland (Haibei) and desert (Delingha). As shown in Fig. 1b, these sites span a wide range of mean annual precipitation (MAP) and aridity (based on the aridity index [AI], the ratio of annual precipitation to potential evapotranspiration; UNESCO, 1979). Based on AI, the forest is classified as mesic, the shrubland as dry sub-humid, the grassland as semi-arid, and the desert as arid (Fig. 1b). The growing season extends from May to September and the mean growing season precipitation (MGSP), as a percent of MAP over the 1969–2008 period, is 75% for Gongga (forest), 55% for Zhuwagen (shrubland), 84% for Haibei (grassland) and 83% for Delingha (desert).

2.2. Ecosystem model

2.2.1. Overview

We used Biome-BGC, a biogeochemical-ecosystem model that focuses on coupled water, carbon (C) and N fluxes and stocks scaled to a per square meter basis. Over the time course of a simulation Biome-BGC estimates fluxes and stocks of water, C, and N and estimates of net ecosystem exchange (NEE) and net primary production (NPP) at daily, monthly, or annual time scales (in the present study we used the daily version). Complete technical descriptions of Biome-BGC are available elsewhere (e.g., Numerical Terradynamic Simulation Group, 2015; Running and Hunt, 1993; White et al., 2000), including a lengthy bibliography of applications of the model in hundreds of studies across different biome types of the world (see Numerical Terradynamic Simulation Group, 2015).

2.2.2. Model parameterization

To parameterize Biome-BGC, three types of data are required: (i) site characteristics (e.g., soil texture and depth, elevation); (ii) meteorological data (precipitation, temperature, etc.); and (iii) eco-physiological parameters (e.g. canopy light extinction, maximum photosynthetic rates, leaf carbon to nitrogen ratios, dead wood lignin proportion). Complete details of how we parameterized Biome-BGC for the Tibetan Plateau, including specific numerical values and soil properties for the four sites in the present study, are given in Ye et al. (2013). An overview is provided below.

First, for site characteristics and meteorological data of our four sites on the Tibetan Plateau we obtained baseline values on soil types, elevation, species composition, stand density and so forth from various sources, including published literature, online databases, the Soil Database of China, and the China Meteorological Administration Data Sharing Service System. For each site, daily meteorological observations were available from 1969 to 2008 including temperature (daily maximum and minimum) and precipitation (hereafter we refer to this as “ambient” precipitation). In addition, we used the mountain climate simulator, MT-CLIM, to estimate daily near-surface meteorological parameters (day length, solar radiation, etc.).

Second, we used generic values for many of the ecosystem parameters following protocols in White et al. (2000) and the Numerical Terradynamic Simulation Group (2015) although site-specific values were used when available. For example, in the forest site (dominated by Abies and Picea) we used the average values of these two species for ecophysiological processes; for the shrub biome (where there is a paucity of data for the Tibetan Plateau) we relied solely on default generic values; for the grassland site we averaged the generic ecophysiological parameter values for C3-dominated high-elevation herb-meadow, dry-meadow, and steppe-meadow biome types; and lastly, for the desert site we used the average of generic values for grassland biomes since the dominant plant functional types were the same as C3 grasslands.

2.2.3. Model validation

A brief description of key points related to model validation of Biome-BGC for the Tibetan Plateau are given in Ye et al. (2014). Model validation was based solely on NPP and gross primary production (GPP) estimates obtained from published field studies. This was because NPP and GPP data were readily available for our study sites while other key indicators of ecosystem function (e.g., energy flux, nutrient cycling, soil water content) were not (at least for different biome types and in comparable formats).

We compiled a range of independent NPP and GPP observations from 11 different sites (three in forest, shrubland and grassland; two in deserts) on the Tibetan Plateau (site descriptions in Appendix B, Ye et al., 2014). We ran simulations of Biome-BGC using 40-yr meteorological data from each site, noting that it was not possible to reproduce the exact conditions under which the observations were obtained. The linear regression for model predictions against observations yielded an $R^2 = 0.83$ ($p < 0.01$) (Fig. 2 in Ye et al., 2013), which confirmed that Biome-BGC was operating well within the range of known values of productivity for the four biomes on the Tibetan Plateau. In this paper, we only show results for a single site in each climatic zone (i.e., mesic, dry sub-humid, semi-arid, and arid) since trends for the other sites in the same climatic zone were similar.
To further examine the validity of Biome-BGC, we compared it to the empirical model QZ-NPP (Luo et al., 2002). QZ-NPP is a nonlinear equation fitted by Luo et al. (2002) using mean annual temperature (MAT), mean annual precipitation (MAP) and NPP data from 160 forest and 35 alpine meadow sites across the Tibetan Plateau (no desert biomes were included; \( r = 0.8369, P < 0.0001 \)). We applied QZ-NPP using the annual values for the 40-yr record of MAT and MAP data from the forest, shrubland and grassland sites included in the present study and compared its predictions of NPP to the annual values gleaned from daily estimates of NPP estimated by Biome-BGC. The linear regression comparing the predictions of QZ-NPP against Biome-BGC predictions yielded an \( R^2 = 0.91 \) (\( p < 0.0001 \)) (see Fig. 2E, Appendix E in Ye et al., 2014; other details omitted here).

We have no direct validation of Biome-BGC on the Tibetan Plateau for the hydrological processes considered in the present paper. However, we are confident in the efficacy of the model since (i) it was originally developed to simulate ecosystem hydrological processes (Running, 1994; Running and Hunt, 1993) and has been extensively applied and validated for all of the hydrological processes considered in the present paper (see Numerical Terradynamic Simulation Group, 2015); and (ii) NPP and GPP are two processes that are considered fundamental, synthetic proxies of overall ecosystem function (Chapin et al., 2009; Knapp and Smith, 2001; Pan et al., 2014; White et al., 2000; Zhang et al., 2013).

2.2.4. Key processes examined

To test Knapp et al.’s (2008) hypotheses, we selected the following hydrological (H) and ecological processes to examine in detail: runoff \( (H_{\text{runoff}}) \), soil evaporation \( (H_{\text{EvapSoil}}) \), interception \( (H_{\text{EvapCanopy}}) \), soil storage \( (H_{\text{storage}}) \), NPP, soil respiration \( (R_s) \), NEE, and N mineralization \( (N_{\text{min}}) \). Although not included in Knapp et al.’s (2008) review, we also evaluated plant transpiration \( (H_{\text{trans}}) \) and nitrogen loss \( (N_{\text{loss}}) \), defined here as the ratio of leached N to \( N_{\text{min}} \).

Precipitation in Biome-BGC is partitioned into canopy interception (based on leaf area index and a user-defined interception rate), which is subject to evaporation \( (H_{\text{EvapCanopy}}) \) and infiltration (all non-intercepted precipitation, which is added to \( H_{\text{storage}} \)). Runoff is a function of \( H_{\text{storage}} \), the saturation and field capacity of the soil, and occurs only when \( H_{\text{storage}} \) exceeds field capacity. All \( H_{\text{storage}} \) above saturation runs-off immediately, whereas half above field capacity is lost (an exponential delay) to drainage. Note that Knapp et al. (2008) treat runoff and deep drainage as distinct processes, whereas in Biome-BGC they are combined into a single variable. The Penman-Monteith equation (Monteith and Unsworth, 2008) is used to calculate \( H_{\text{EvapSoil}}, H_{\text{EvapCanopy}}, \) and \( H_{\text{trans}} \). Mineralization adds N to the system whereas losses due to leaching are a function of \( H_{\text{runoff}} \). Maintenance respiration is a function of temperature and plant N content, and growth respiration is a constant proportion (30%) of all new tissue growth. Maximum rates of decomposition and C loss (via \( R_s \)) are modified by soil temperature and \( H_{\text{storage}} \). Modeled NEE is calculated as the difference between NPP and \( R_s \), which is equivalent to net ecosystem production (NEP) (Randerson et al., 2002).

2.2.5. Growing season simulations

As noted above, Biome-BGC uses a daily time step and requires daily meteorological data. Hence, we ran the model using the 40-yr daily meteorological observations from 1969 to 2008 but restrict our analysis to output during the growing season (May–September). This is done because Knapp et al.’s (2008) hypotheses apply only to growing season precipitation. Hence, precipitation that occurs outside the growing season is not part of the present study other than via its impact on initial conditions of the hydrological and ecological processes (see Section 2.2.4) at the start of the growing season.

2.3. Growing season precipitation scenarios

Using the 40-yr daily precipitation record for each site, a frequency analysis of growing season precipitation event size (the total amount of rainfall in a day) was constructed (Fig. 2a). Using this as a guide we created three scenarios (S1–S3), which differ in MGSP and intra-annual variability (extreme precipitation regimes characterized by lower precipitation frequency, longer dry periods, and larger individual precipitation events; see Figs. 3 and 4). To examine projected change in precipitation, it is important to analyze the impacts of changes in both intra-annual variability and total amounts. For example, heavy precipitation will increases despite projected decreases in total amount in some regions and total rainfall from heavy rainfalls will increase in the 21st century over many areas of the globe (Seneviratne et al., 2012).

To accomplish this we ranked all daily growing season precipitation events at each site over the 1969–2008 period according to their size, and used the k-th percentile as the cumulative relative frequency, such that \( k \% \) of the total events lie below and (100–k)% of the them lie above (Fig. 2b). At the same precipitation size, cumulative frequency were highest for desert, followed by grassland, shrubland and forest, respectively (Fig. 2b). Next, we defined precipitation extremes as event sizes higher than a spe-
cific $k$-th percentile (as done in AR5 of the IPCC, 2013) and to increase intra-annual variability, we progressively excluded growing season daily precipitation events lower than the $k$-th percentile.

We considered percentiles from the 60-th to the 96-th to increase periods between rainfall events because (i) events lower than 60-th were negligible (compare Fig. 2a and b), and (ii) the maximum events recorded for some years were ≤ 96-th percentile. Although numerous researchers have characterized differences in precipitation regimes in terms of precipitation events >$x$-th percentile of all events (e.g., Knapp et al., 2015; Reichstein et al., 2013; Seneviratne...
et al., 2012), our approach is novel since it enables us to explore a continuum of increasingly intensified rainfall regimes rather than only two or three fixed regimes (such as shown in Fig. 4).

In S1, total growing season precipitation (P_gs) was unchanged, that is, equal to ambient. To increase intra-annual variability in S1, total excluded precipitation (P_excluded) for each percentile (i.e., k = 60, 62, ..., 94, 96) was proportionally added back to the remaining precipitation events (P_remaining = P_gs - P_excluded) by multiplying each by the ratio P_excluded/P_gs. This conserves the total growing season precipitation (P_gs) since P_remaining × P_gs/P_remaining = P_remaining/P gs. By excluding events lower than the k-th percentile and by adding these back to the remaining events, we increased intra-annual variability during the growing season by (1) increasing the size of daily events, (2) decreasing the total number of daily events, and (3) augmenting the length of dry intervals (for S1, see the first column of Fig. 3). By adding the excluded rainfall back to the remaining events, we did not change the order of rain events in the daily time series. The same scheme was used for S2 and S3, except that MGSP was increased in S2 by adding back 2P_excluded whereas in S3 MGSP was decreased by eliminating all P_excluded. This scheme led to a 60% increase in MGSP in S2 and a 60% decrease in MGSP in S3, both of which were relatively close to the wettest and driest growing season precipitation observed over the 40-yr record of the sites. A summary of the resulting MGSP (for each k-th percentile) for each ecosystem is shown in Fig. 4a-d.

To quantify the intra-annual variability of precipitation, the coefficient of variability (CV) of the 40-yr growing season daily precipitation at each k-th percentile was computed (CV). The CV is scaled by a mean and is thus a very common, robust way to summarize intra-annual variability of precipitation (e.g., Anyah and Qiu, 2012; Fatichi et al., 2012; Kripalani et al., 2007). The amount of rainfall in a single day is a single rainfall event; since the goal is to quantify the dispersion or variation of daily precipitation, days with no precipitation are of course included in the calculation of CV.

At each k percentile, 40-yr daily simulations of Biome-BGC were conducted to generate the figures presented here. In each scenario, we calculated the relative change of each hydrological (H_unoif, HEvapCanopy, H_storage, H_trans) and ecological (NPP, R_g, NEE, N_min, Nloss) process, X, as follows:

\[
X_{rel} = \frac{\bar{X}_k - \bar{X}_{amb}}{\bar{X}_{amb}}
\]

where \(\bar{X}_k\) and \(\bar{X}_{amb}\) are the 40-yr means of process X at the k-th percentile and at ambient conditions, respectively. In total, over 3.5 million daily simulations were required to conduct the analyses presented here (240 40-yr simulations of 3 scenarios × 4 sites × 20 k-th percentiles progressively removed).

3. Results

3.1. Precipitation variability and length of dry days

The effect of excluding all individual rainfall events lower than the k-th percentile on CV for each ecosystem type is presented in Fig. 4e. The pattern of generated CVs varied significantly by ecosystem due to the predominance of small events, total precipitation (Fig. 2), and ambient CVs. For example, CV in precipitation in the desert and grassland sites did not reach a 10% increase over their ambient values until k = 90 and k = 80, respectively; in contrast, this occurred at k = 62 and k = 66 in the forest and shrubland, respectively. Although the largest CVs generated (at k = 96) were similar for all sites (ranging from 518% in forest to 548% in desert), there was a stark contrast in the actual increase in over CV_{amb} (at ambient) for each site: for example, 243% over CV_{amb} in forest but only 71% in desert (Fig. 4e).

At ambient precipitation, the mean length of dry days is 0.47 days in forests, 0.5 days in shrubland, 1.83 days in grassland and 2.87 days in deserts. Excluding rainfall events lower than the k-th percentile led to an increase in the mean length of dry days at all sites (Fig. 4f). The length of dry days at all sites converged at k ≥ 74 despite their differences in total precipitation and CVs. The
longest period of dry days was about 23 days for all sites at $k = 96$ (Fig. 4f).

3.2. Hydrological processes

3.2.1. Runoff
Under ambient MGSP (S1), the response of $H_{\text{runoff}}$ to increasing precipitation extremes was most sensitive in the forest and least sensitive in the desert (Fig. 5). In both forest and shrubland ecosystems, $H_{\text{runoff}}$ increased linearly with increasing CV, whereas the grassland and desert sites did not respond to extreme events until maximum precipitation variability (Fig. 5).

With increasing MGSP (S2, Fig. 4a), total $H_{\text{runoff}}$ from all ecosystems increased as compared to ambient conditions (S1) but was greatest in the forest and grassland. Maximum $H_{\text{runoff}}$ in the desert reached 78% of total precipitation (an increase of 17% over S1). $H_{\text{runoff}}$ in the shrubland was again linearly-related to increased variability but the magnitude of the response relative to S1 was small. While $H_{\text{runoff}}$ from grassland was evident only at the highest extremes, the increase in $H_{\text{runoff}}$ (as compared to ambient MGSP) was much larger relative to the shrubland or desert sites. $H_{\text{runoff}}$ in the desert site was evident only under most extreme conditions ($k = 96$).

For runoff, when comparing $H_{\text{runoff}}$ under ambient to the most extreme variation in S3, we found a 17% to 2% decline in the forest. Unexpectedly, there was a slight increase in $H_{\text{runoff}}$ in the shrubland whereas the grassland and desert sites did not exhibit any response (Fig. 5).

3.2.2. Canopy evaporation
In S1 the impact of increasing variability on $H_{\text{EvapCanopy}}$ was greatest (but opposite) in the forest and desert sites. At maximum variability, $H_{\text{EvapCanopy}}$ declined and increased by 72% and 53% in the in forest and desert sites, respectively (Fig. 5). In both ecosystems, $H_{\text{EvapCanopy}}$ was relatively insensitive to increasing CV until $k = 86$, corresponding to a 64% increase in CV in forest and 9% in the desert. In contrast, the shrubland and grassland did not exhibit any response until precipitation variability was at CV96 (Fig. 5).

Under S2, $H_{\text{EvapCanopy}}$ in forest, shrubland and grassland ecosystems exhibited a nonlinear, unimodal response to increasing extremes; of the three, the forest was least responsive. In shrubland $H_{\text{EvapCanopy}}$ increased 5–77% with increases in CV between 9 and 187%, while $H_{\text{EvapCanopy}}$ in the grassland increased 3–77%, with an increase in CV between 1 and 151%. In the desert, $H_{\text{EvapCanopy}}$ increased linearly with increasing CV, with the highest increase (216%) occurring at $k = 96$. In S3, $H_{\text{EvapCanopy}}$ in all ecosystems displayed a similar exponential decay-type response, with low rates of change and with the largest declines occurring at the highest extremes (i.e., $k \geq 90$).

3.2.3. Soil evaporation
Soil evaporation decreased exponentially with increasing CV in the forest, shrubland and grassland (Fig. 5). The forest site was highly sensitive to even small changes in precipitation variability regardless of MGSP and scenario. For example, at $k = 60$ $H_{\text{EvapSoil}}$ decreased by about 26% in each scenario with only a 9% increase in CV; at maximum CV, $H_{\text{EvapSoil}}$ was 90% less than ambient. The pattern of $H_{\text{EvapSoil}}$ with increasing CV found in the shrubland and grassland was nearly identical to that observed in the forest under S1 and S2. However, $H_{\text{EvapSoil}}$ was about 77% less than ambient at maximum CV in S3 (Fig. 5).

Regardless of scenario, the desert site was unresponsive until precipitation variability increased to about 5% above ambient values where, at this point, $H_{\text{EvapSoil}}$ dropped to ca. 11% less than ambient and above this declined to 66–71% of ambient at CV96 (Fig. 5).

3.2.4. Soil water storage
Forest $H_{\text{storage}}$ steadily decreased with increased CV in both S1 and S3 (Fig. 5). However, the largest decrease in S1 did not occur until $k = 92$, whereas in S3 the decline was immediate (although initially not large). In stark contrast to the other sites, $H_{\text{storage}}$ in the forest had a unimodal response to increased extreme events in S2: storage steadily increased up to 9%, which corresponded to increased CV of 17%, but declined thereafter, falling to 2% less than ambient at maximum CV. The behavior of $H_{\text{storage}}$ for the other three ecosystems was similar (Fig. 5): $H_{\text{storage}}$ increased about 11–17% in S1; 23–26% in S2; and declined 2–5% in the shrubland and grassland (no response in the desert site) in S3.

3.2.5. Plant transpiration
In all scenarios, forest $H_{\text{trans}}$ increased 3–4% above its ambient value with a 9% increase in CV (Fig. 5) and remained unchanged up to a 35% increase at CV76. Thereafter, $H_{\text{trans}}$ declined 12–14% in S1–S2 and 36% in S3.

Transpiration in both shrubland and grassland ecosystems increased nonlinearly under S1 and S2 but decreased linearly in S3. In the shrubland, at CV$_{94}$, $H_{\text{trans}}$ rose to a maximum of 22% in S1 and 54% in S2. In the grassland, $H_{\text{trans}}$ increased to a maximum of 22% in S1 at CV$_{94}$ and reached a 54% increase in S2 at CV$_{96}$ (Fig. 5). In S3, $H_{\text{trans}}$ in the shrubland and grassland rapidly declined, eventually to 36% less than ambient at the maximum CV.

The effect of increasing CV in S1and S2 on transpiration was greatest in the desert. For example, in both S1and S2, desert $H_{\text{trans}}$ rapidly increased with increasing precipitation extremes, up to a 88% increase in S1 and a 167% increase in S2 (corresponding to a 71% rise in CV). The desert had a similar response with other sites under S3 (a negative, linear decline; Fig. 5).

3.3. Ecological processes

3.3.1. Net primary production
Increasing precipitation extremes and decreasing MGSP led to a reduction of NPP in all ecosystems (S3; Fig. 6). At the maximum extreme, the relative decline in NPP for the shrubland (58%) and grassland (55%) was larger than for the forest (27%) and desert (22%). The forest differed from the other ecosystems in that NPP also declined in scenarios S1 and S2.

In S1, NPP in the shrubland and grassland increased in a unimodal manner to a maximum of about 8% above NPP under ambient conditions. This nonlinearity was evident for these two ecosystems in S2 as well: NPP increased 36% above ambient when CV increased 150% in the shrubland and 148% in the grassland. Similar to plant transpiration (Fig. 5), NPP in the desert was the most sensitive to increasing CV (and more so in S2 than S1). When CV reached a maximum of 350%, NPP increased 148% in S2 and 70% in S1, respectively.

3.3.2. Soil respiration and N mineralization
Responses in soil respiration ($R_{\text{f}}$) and nitrogen mineralization ($N_{\text{min}}$) resembled those of NPP (Fig. 6). Changes in $N_{\text{min}}$ and NPP were nearly identical, whereas the decline of $R_{\text{f}}$ was larger than NPP under S3 in the forest, with ~32% in respiration versus ~27% in NPP at the highest CV (Fig. 6). In S2, increase in $R_{\text{f}}$ was higher than NPP in the shrubland, grassland and desert. At maximum precipitation extremes (CV96), increases in $R_{\text{f}}$ and NPP were 54% versus 34% in the shrubland, 34% versus 22% in the grassland and 175% versus 148% in the desert. In other cases, patterns of $R_{\text{f}}$ and NPP were nearly indistinguishable.
3.3. Net ecosystem exchange

In S1, NEE exhibited a unimodal pattern for all sites (Fig. 6), slightly increasing with increasing CV, peaking at 2% (at CV90) in the forest, 5% (at CV94) in the shrubland, 3% (at CV78) in the forest and 15% (at CV92) in the desert. When CV reached maximum, NEE declined in each system. This nonlinear behavior was most evident in S3 in the forest and in S2 in the shrubland, grassland and desert (Fig. 6).

The forest differed from the other sites in that NEE decreased in S2 (Fig. 6); however, it was unresponsive until CV70 and dropped 19% below ambient at the highest level of variability. NEE was most sensitive to increasing intra-annual precipitation variability under S3 in the shrubland and grassland sites. With an increase in CV of about 10–300% (k = 60 through k = 96), NEE declined 3–58% and 1–61% below ambient in the shrubland and grassland sites, respectively. Although less sensitive as compared to the shrubland and grassland, in the desert ecosystem NEE decreased linearly with increasing CV (from 5–223%) to 1–22% below ambient (Fig. 6).

3.3.4. Nitrogen leaching

Nitrogen loss (the ratio of N leached and N\text{min}) was most sensitive to increased extreme rainfall regimes in the forest ecosystem (Fig. 6). Under ambient MGSP (S1), N losses via leaching accounted for 1% of N\text{min} at k = ambient and 4% at k = 96 in forest. With increasing MGSP (S2), N leached from the forest increased as compared to ambient (S1); maximum N losses through leaching reached 9% (an increase of 8% over ambient). As expected, decreasing the amount of MGSP (S3) decreased N leaching in forest as compared to S1 and S2. Under the most extreme variability (k = 96), N losses through leaching in forest decreased to 0% of N\text{min}. Compared to ambient conditions, this represents a drop of 1% of N loss. The shrubland and grassland sites did not respond until intra-annual precipitation variability was maximum, and their response was slight (Fig. 6). N loss was highest under S2 and lowest under S3 in both ecosystems. The desert site did not respond to any of the three scenarios (Fig. 6).

4. Discussion

4.1. Correspondence of hydrological and ecological processes to hypotheses

Based on our study of ecosystems of the Tibetan Plateau, we ranked the individual hydrological and ecological processes according to their overall correspondence with Knapp et al.’s (2008) hypotheses. As shown in Fig. 1e, soil evaporation was the most consistent hydrological process (100% agreement) whereas canopy interception had the lowest correspondence at 56%. With regard to the ecological processes, net primary production had the highest correspondence with 78% agreement and net ecosystem exchange the lowest correspondence (22% agreement) to Knapp et al.’s (2008) hypotheses. While interesting, this ranking represents only a coarse generalization: what is most important are the key interactions and feedbacks between these hydrological and ecological processes, which ultimately contribute to the underlying dynamics of ecosystems.

4.2. Ecosystem-level interactions between hydrological and ecological processes

Knapp et al. (2008) hypothesized that extreme rainfall regimes would impact mesic ecosystems by increasing the duration and severity of soil water stress. Our simulations were consistent with hypothesis as we found that intensified intra-annual rainfall variability had a detrimental impact on hydrological processes in the forest ecosystem (Fig. 1c): runoff increased, canopy interception decreased, and soil water storage decreased (soil water evaporation decreased due to less water being retained in the system). Greater vertical soil water movement also resulted in increased leaching of dissolved nutrients (as found by Gerten et al., 2008; Kong et al., 2013). More extreme precipitation regimes also resulted in more than half of the annual precipitation being lost from the forest ecosystem via outflow (S1 and S2). Not only did this reduce soil
water storage but also decreased soil mineral N due to substantial leaching (e.g., Elrashidi et al., 2005; Kong et al., 2013; Zhou et al., 2008).

With regard to another hydrological process, Knapp et al. (2008) hypothesized that larger precipitation events will result in water infiltration to deeper soil layers where it will be less prone to evaporative losses. Since Biome-BGC contains only a single soil layer, it is suitable to test this hypothesis? We concluded that it is since soil evaporation is calculated by scaling potential evaporation by days since the last rain (DSR), i.e., actual evaporation = constant × potential evaporation/DSR2 (details in Numerical Terradynamic Simulation Group, 2015; Taiz and Zeiger, 2006). Hence, larger, less frequent, rain events will increase DSR and thus decrease soil evaporation, which is consistent with Knapp et al.’s (2008) hypothesis.

In addition, Knapp et al. (2008) predicted that proportional losses of precipitation to canopy interception and evaporation should be reduced with increased precipitation event size. Our results do not support this prediction: we found increased canopy interception and evaporation in xeric ecosystems with intensification of extreme precipitation. Our simulations suggest that extreme events in xeric ecosystems will enhance plant growth, resulting in larger and denser canopies and higher interception. Denser canopies also led to greater intercepted radiation (Jones, 1992) and thus higher canopy evaporation.

Although Knapp et al. (2008) did not explicitly address plant transpiration, they posited that greater precipitation extremes should result in less soil water available for primary production in mesic systems, and more water available for biotic activity in xeric systems. We found that the amount of soil water accessed by plants decreased in mesic and increased in xeric ecosystems. However, the positive effects of increased precipitation extremes on biotic activity (plant transpiration) in xeric ecosystems was reduced by decreased MGSP, which is consistent with the findings of Smith (2011).

Xeric ecosystems on the Tibetan Plateau are likely to benefit from intensified rainfall extremes regime, but only as long as MGSP remains the same or increases. This is consistent with other studies reporting that inter-annual climate variation in drylands is a larger source of variation in NPP than intra-annual rainfall variability (D’Odorico and Bhattachan, 2012; Gerten et al., 2008; Knapp et al., 2015). NPP decreased in all three scenarios in the mesic forest site, a response driven by the direct impacts of decreasing soil water availability (as discussed above). In a modeling study of seven distinct ecosystems with a MAP gradient of 642–1554 mm, Gerten et al. (2008) reported that NPP only responded slightly to increased precipitation extremes. Our simulations show that the mesic forest and xeric desert sites are most responsive to increased intra-annual precipitation variability. Furthermore, the response of NPP to precipitation extremes also depends on the magnitude of precipitation events imposed. For example, Heisler-White et al. (2008) experimentally manipulated plots in a semi-arid grassland and found that plots receiving the largest rain events had higher aboveground NPP than those receiving intermediate but more frequent events (although both cases had larger aboveground NPP than under ambient conditions).

We found that the soil water content increased yet NPP decreased in the mesic forest site under S2, which can be explained by increased N losses via leaching. These findings support studies that suggest a negative effect of extreme rainfall events on soil N result in a decrease in NPP (e.g., Kong et al., 2013; Zhou et al., 2008). Therefore, an important consequence of extreme rainfall events in the mesic forest site was N losses through leaching, which could reduce rainfall use efficiency because water inputs from extreme rainfall events may be lost from the system. In contrast, we found that soil water was the key factor controlling the xeric desert ecosystem because N losses through leaching did not respond to increased precipitation extremes.

Decreasing soil respiration (RN) in the forest matched the hypotheses of Knapp et al. (2008) under all three scenarios (Fig. 1c). This was probably due to decreases in both soil moisture and substrate supply (such as litter) caused by decreased NPP (Thomey et al., 2011). In Biome-BGC, RN is a function of soil water, temperature, and decomposition of both soil organic matter and litter. The latter is directly determined by biomass and NPP; thus in S3, with decreased MGSP and intensified precipitation extremes, RN and NPP responses in both the mesic and xeric ecosystems were similar (Fig. 1c). While field results from drylands indicate that both RN and NPP increase with a more extreme rainfall regime (Parton et al., 2012; Thomey et al., 2011; Vargas et al., 2012), this applies to conditions represented by S1 and S2, but not by S3, as our model results clearly show (Fig. 1c).

Our simulations predict decreased Nmin in mesic ecosystem under all three scenarios, which is consistent with Knapp et al. (2008)’s hypotheses. However, and counter to Knapp et al. (2008), we found increased Nmin with a more extreme precipitation regime in xeric ecosystems (Fig. 1c). Based on the rationale that C and Nmin can be enhanced as a result of repeated drying and rewetting cycles (Fierer and Schimel, 2002; Miller et al., 2005), Knapp et al. (2008) hypothesized that reductions in the frequency of rainfall events could decrease microbial activity and biogeochemical cycling in the upper soil profile. However, Borken and Matzner (2009) found that, despite the generally observed pulse in net C and Nmin following the rewetting of dry soils, cumulative C and Nmin rates were mostly smaller than those observed in soils with continuous optimum moisture levels. These results indicate that, in the long term, transient increases in soil moisture after wetting cannot compensate for small Nmin rates caused by low soil moisture. Therefore, the increased Nmin found in xeric ecosystems was likely due to the increased soil moisture with the intensification of precipitation extremes. Under S3, Nmin decreased at all sites with a simultaneous increasing precipitation intra-annual variability and decreasing MGSP, which was likely due to the decreased soil moisture (e.g., Borken and Matzner, 2009). Knapp et al. (2008) suggested that the impact of precipitation extremes on NEE will depend on the relative change in the magnitude of the opposing C fluxes of NPP and soil respiration, and would most likely vary in direction and magnitude among mesic and xeric ecosystems, making it difficult to predict. We found this to be the case, as our simulations revealed several nonlinear responses of NEE with increasing intra-annual precipitation variability, and both increases and decreases can occur in both mesic and xeric ecosystems.

4.3. Ecosystem response to extreme precipitation regimes

The use of an ecosystem model, in concert with three precipitation scenarios, enabled us to explore the simultaneous responses, interactions and feedbacks of multiple hydrological and ecological processes, and the mechanisms underlying them, to increasingly intensified rainfall regimes in different ecosystems of the Tibetan Plateau. In spite of much uncertainty, it is unequivocal that extreme precipitation regimes will result in changes in water, N and C cycles (Heisler-White et al., 2008; Knapp et al., 2015; Kong et al., 2013).

In general, we conclude that mesic ecosystems closely follow Knapp et al.’s (2008) hypotheses and will most likely be more detrimentally impacted by extreme precipitation regimes than other ecosystem types. At the other end of the moisture spectrum, we find that xeric sites are highly variable and only weakly follow the hypotheses for hydrological processes (67% in both the xeric grassland and desert ecosystems, Fig. 1e) and poorly for the ecological processes (33%–42% agreement; Fig. 1e). The shrubland, which is intermediate between mesic and xeric, tend to follow Knapp et al.’s
hypotheses for hydrological processes (75%–83% agreement, keeping in mind that mesic versus xeric only differ for soil water storage; Fig. 1e); in contrast, the ecological processes in the shrubland are highly inconsistent regardless if compared to mesic or xeric ecosystems. The study of, and interest in, the ecological consequences of climatic extremes have greatly expanded in the past decade (Fay et al., 2011; Heisler-White et al., 2008; Knapp et al., 2015; Zhang et al., 2013). Despite a growing body of literature, there is a paucity of detailed knowledge on the magnitude, type and various combinations of climate extremes that may occur in the future (Smith, 2011). While it is uncertain if ecosystems in other parts of the world will respond as these in the Tibetan Plateau, our study represents an important test of Knapp et al.’s (2008) hypotheses because in a previous study in the Tibetan Plateau we found that both temperature and precipitation alone – and in concert – had significant, nonlinear, interacting effects on ecosystem dynamics (Ye et al., 2014). In addition to the hydrological and ecological processes considered in this study, other processes will also simultaneously change, including pollination, seed dispersal, granivory, and herbivory (Wu et al., 2011). Nevertheless, our findings provide novel insights as to how more extreme rainfall regimes may potentially affect the functioning of terrestrial ecosystems, and contribute to our understanding of the role of biotic and abiotic attributes as modulators of ecosystem responses to climate change.

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