When savannas recover from overgrazing, ecohydrological connectivity collapses

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Abstract

Grasslands and savannas across the globe have undergone a dramatic transition over the past century. Historical overgrazing has set in motion a cascade of events ranging from desertification in arid climates to woody plant encroachment (WPE) in semiarid and subhumid climates. In recent decades, grazing pressure on many of these landscapes has declined significantly, and where rainfall is sufficient (as in most semiarid and subhumid settings), herbaceous vegetation in intercanopy areas will recover. An important question is, how has this transition altered ecohydrological connectivity (overland flow and runoff–runon dynamics)? A woody-plant-encroached, subhumid savanna site in South Texas with a history of heavy grazing (but ungrazed since 1981) was used as a model landscape to address this question. Overland flow, soil moisture, and field saturated hydraulic conductivity ($K_{fs}$) were measured along a catena extending from the upland savanna-parkland areas to the downslope, more densely wooded areas. For comparison, $K_{fs}$ and infiltrability were also measured at a moderately grazed upland site 14 km east of our study site, selected as a surrogate for past conditions at our site. In contrast to the prevailing hypothesis that the downslope areas ('drainage-woodlands') at our study site have continued to be supported by runoff generated from the upland areas, our measurements yielded no evidence for the redistribution of water from the uplands to the drainage areas under the current ungrazed conditions. Further, $K_{fs}$ at the ungrazed study site was two orders of magnitude higher than that at the grazed site and infiltrability was twice as high at the ungrazed site than the grazed site. These findings, coupled with historical information from the site, strongly suggest that historical overgrazing amplified the runoff–runon process, resulting in significant subsidies of water from the uplands to the drainage areas. Then, with the relaxation of grazing pressure and subsequent landscape recovery, redistribution of water via surface runoff was relatively rare. We believe that our results are generalizable for savannas that have recovered from overgrazing. When these savannas are heavily grazed, ecohydrological connectivity is greatly increased; but if grazing pressure relaxes, ecohydrological connectivity will collapse. These changes in ecohydrological connectivity have important, but not always well understood, ecological consequences.

Introduction

Woody plant encroachment (WPE) has significantly altered grasslands and savannas across the globe (Van Auken 2009, Pyne 2016, Stevens et al 2016). In the Southern Great Plains and southwestern regions of the United States, the transition of grasslands and open savannas to woodlands or shrublands is linked to the extremely heavy grazing by domestic livestock during the late 19th and early 20th century, which led to a cascade of consequences, ultimately disrupting the stabilizing fire-feedback cycles (Walker et al 1981, Wilcox et al 2018b). In addition, the severe overgrazing significantly amplified surface runoff generation and
erosion processes (Trimble and Mendel 1995, Wilcox et al 2003), which fundamentally altered how water is redistributed across the landscape (Ludwig et al 2005, Turnbull et al 2012). This altered redistribution of water, sediment, and nutrient resources via increased overland flow can be conceptualized as an increase in ecohydrological connectivity (Ludwig et al 2005, D’Odorico et al 2010). In recent decades, grazing by domestic livestock in US savanna systems has declined precipitously, and stocking densities are at a fraction of their historical peaks (Wilcox et al 2012). At present there is much more vegetation on the landscape than under the overgrazed conditions, and the coverage of woody plants remains high (Wilcox et al 2018a, 2018b). Such large-scale increases in vegetation cover have the potential to significantly alter streamflow and groundwater recharge (Wilcox et al 2008, Wilcox and Huang 2010, Zou et al 2014), primarily by increasing both soil infiltrability and evapotranspiration (Qiao et al 2017).

The runoff–runon process has been identified as a key ecohydrological function in many drylands. Non-degraded landscapes are considered to be ‘resource conserving’ because the transfer of water occurs at relatively small scales, with areas of lesser vegetation providing water to nearby vegetation patches. A degraded landscape, on the other hand, can be described as ‘leaky’ because water, sediment, and nutrients are effectively transported elsewhere and lost from the system (Wilcox et al 2003, Ludwig et al 2005). Thus, while ecohydrological connectivity may have played a strong role in degradation of some landscapes (Okin et al 2009a, 2009b), Turnbull et al 2012), it is also a key trait of functional or ‘resource-conserving’ landscapes (Ludwig and Tongway 1995, Wilcox et al 2017). With overgrazing and subsequent recovery, the same landscape may undergo both these changes—i.e., a phase of amplified connectivity that destabilizes the system followed by a phase of decreased connectivity that improves system stability. These two processes have rarely been explicitly examined on the same landscape over time, to determine the extent and magnitude of changes in ecohydrological connectivity (as expressed by runoff–runon dynamics) as a landscape recovers from intensive grazing.

The results of such an examination are likely to differ depending on moisture regimes. For most arid landscapes, prolonged overgrazing leads to more or less permanent desertification (Schlesinger et al 1990). However, for most savanna systems—which are characterized by semi-arid and subhumid climates—the vegetation in the intercanopy areas recovers with the cessation of overgrazing (Wilcox et al 2008, Archer et al 2017). It is these latter systems that are the subject of our investigations. To date, relatively little work has been done in such ecosystems to quantify the extent to which grazing and subsequent recovery alter runoff–runon dynamics or ecohydrological connectivity.

To examine these issues, we used a subtropical savanna within the La Copita Research Area (LCRA) in South Texas as a model landscape. This region offers an excellent setting for these investigations, because of (1) its pattern of two distinct landform types: upland savannas surrounded by low-lying woodlands (hereafter referred to as ‘drainage-woodlands’) that have been heavily encroached by woody plants and exhibit a banded vegetation pattern (see figure 1); (2) its history of grazing and of extensive WPE (Archer 1989, Hibbard et al 2009); and (3) the abundance of information already available about woody plant development and carbon accumulation in these two landforms (Boutton et al 1999, 2009).

Aerial photographs and travel accounts (Humphrey 1958) from the early 20th century (figure 1) indicate that the two landforms were even more distinct in the past, with the early WPE occurring mostly in the drainage-woodlands. Additional evidence confirming this early pattern of WPE was provided by Boutton et al (1998), who found that a greater amount of soil organic carbon (SOC) accumulated in the drainage-woodlands than in the uplands, and that the mean age of woody plants in the drainage-woodlands was greater than in the uplands. Additionally, based on the mean residence time of 14C and δ13C values of SOC in the two landforms, Boutton et al (1999) have suggested that the process of WPE started around 150 years ago—roughly the time of the introduction of heavy grazing.

While the differences in progression of WPE and the associated differences in SOC accumulation across the
uplands/drainage-woodlands transition are well established, no clear mechanism for these differences has been identified or proved empirically. Boutton et al (1999) mention that these differences are associated with higher soil moisture in the drainage-woodlands, but this prevailing notion is an assumption; in reality, differences in soil moisture between the drainage-woodlands and the uplands have never been assessed properly. Previous measurements made by Bai et al (2012) were limited to a depth of 15 cm.

In a number of dryland regions, banded vegetation networks and clusters have been shown to capture runoff and exhibit higher productivity owing to excess soil moisture—including Australia (Dunkerley and Brown 1995, Dunkerley 2002), Niger (Hiernaux and Gérard 1999, Valentin and d’Herbès 1999), and North America (Cornet et al 1988, Reid et al 1999, Bhark and Small 2003). It is reasonable to expect that like the Tiger bush landscapes in Niger, the drainage-woodlands in LCRA act as ‘water harvesters’.

The main goal of our research, then, was to test the prevailing hypothesis that the drainage-woodlands are still subsidized by runoff generated from upslope areas following large rain events. Consistent with the observations made by Wilcox and Huang (2010) and Zou et al (2014) regarding the impact of WPE on streamflow and runoff generation, we hypothesized that while runoff–run off may still be subsidizing the drainage-woodlands with excess moisture, the strength of the runoff–runoff process itself must have declined with the relaxation of grazing pressure and the increased woody plant cover in the uplands as well as in the woodlands.

Site description

We carried out this study at the Texas Agricultural Experiment Station’s La Copita Research Area (LCRA) (27° 40’N, 98° 12’W), situated 15 km southwest of the city of Alice in Jim Wells County, Texas, USA. The region is part of the Tamaulipan Biotic province, which extends from northeastern Mexico to southern Texas, and consisted largely of grasslands at least until the 1850s (Bartlett 1854). The process of WPE has been noted since the late 1800s (Humphrey 1958, Johnston 1963), and the region has now largely converted into a thorn woodland (Archer et al 1988). Prior to around 1830, the primary grazers were relatively small numbers of domestic animals (cattle and horses) and native species, including deer and antelope. Beginning around 1830 and lasting until the turn of the century, the area endured a period of extremely heavy grazing by sheep and cattle (Lehmann 1969). Although grazing pressure in the region remained high into the 1960s, it was still much lower than previous levels. Before becoming a research site, the LCRA property was a cattle ranch, owned and operated by the same family since around 1850, and has a history of moderate to heavy continuous grazing (Archer 1995). It has not been grazed by domestic livestock since 1981.

The climate of LCRA is subtropical, with a mean annual temperature of 22°C and mean annual rainfall of 660 mm with high inter-annual variability (CV = 34%) (NOAA climate data, Alice weather station). The precipitation pattern is usually bimodal, with most of the rainfall occurring over the months of March to May and August to September, and is characterized by a predominance of small rain events (<20 mm) and a few larger events (50–100 mm). The high inter-annual variability is primarily driven by rare extreme events brought by hurricanes or tropical storms.

Elevations at LCRA range between 75 and 90 m. The landscape exhibits a subtle topographic undulation with slopes of 1%–3%, and is characterized largely by two distinct landforms: uplands and drainage-woodlands. Aerial photographs of the landscape reveal that the latter, which is covered with dense, woody vegetation, surrounds the savanna-like uplands in a regular pattern (figure 1). The formation underlying these woodlands typically includes deep-seated faults, contributing to the dissolution of the caliche bedrock. Soils on the uplands largely correspond to the Runge series (Typic Argiustolls), whereas the drainage-woodland soils correspond to Clayevre or Racombes series (Pachic Argiustolls). Surface soil textures in the uplands are fine sandy loams, whereas those of the drainage-woodlands are fine loams (Loomis 1989, Boutton et al 1998). Almost all soils have a thick argillic horizon (sandy clay loams to sandy clays in both the uplands and the drainage-woodland areas), but the uplands also exhibit scattered non-argillic inclusions.

These landforms also differ with respect to vegetation. The drainage-woodlands are known to have been densely wooded since at least the early 20th century (Johnston 1963, Barton 1974). The vegetation of the uplands has always been marked by a savanna-parkland physiognomy. It has been suggested that development of woody vegetation on the uplands started within the non-argillic inclusions of the landscape, then expanded to the soils with the argillic horizon (Archer et al 1988). The current woody plant composition includes a diverse number of species, the major ones being Diospyros texana, Xanthoxylum fagara, Condalia hookeri, Ziziphus obtusfolia, and Prosopis glandulosa (Basant, unpublished surveys). The dominant grass genera include Aristida, Chloris, Bouteloua, Eragrostis, Paspalum, and Tridens (Coffey 1986). Some commonly found species in the herbaceous patches on uplands are Aristida purpurea, Bouteloua rigidiseta, and Eragrostis intermedia.

Because we obviously have no data from the LCRA site representing the intensively grazed conditions of the past century, we selected a second upland site 14 km east of LCRA to serve as a surrogate. Although much less heavily grazed than was typical of the region...
in the past, this second site has remained moderately grazed (at a rate of 10 ac/AU) over the last decade and represents a reasonable surrogate for past conditions at our site. Soil pedon and slope attributes here are similar to those of the LCRA study site. The vegetation is dominated by *Prosopis glandulosa*, *Vachelia farnesiana*, and *Celtis pallida*, with large portions of bare intercanopy. Forbs and grasses present in some portions of this surrogate site are dominated by *Buchloe dactyloides*, *Chloris ciliata*, *Panicum virgatum*, *Heteropogon contortus*, and *Cenchrus ciliaris*.

**Methods**

We made three sets of measurements: (1) overland flow measured from large runoff plots, for 20 months (October 2016–June 2018); (2) soil moisture, for 12 months (September 2016–September 2017); and (3) soil infiltration capacity (measured at the surrogate site as well as in the canopy and intercanopy zones of the uplands area at LCRA, to enable comparison with the prior heavily grazed conditions).

**Overland flow measurements**

In the uplands adjacent to the drainage-woodlands, three large runoff plots were set up on sloping terrain—each measuring 4 m × 11 m. These plots were monitored for overland flow from October 2016 to June 2018. Each plot was enclosed on all four sides with metal sheeting, inserted into the soil to a depth of 10 cm. Plots R1 and R2 represented an intercanopy area, with a mix of bare ground and herbaceous cover;
Plot R3 was delineated around a central shrub surrounded by herbaceous vegetation and bare ground (figure 2). Plots R1, R2, and R3 had slopes of 0.4%, 2%, and 3%, respectively. Runoff from the plots was recorded by means of a tipping-bucket apparatus that was connected to a Hobo Onset event logger. Every tip was equivalent to 0.025 mm. Rainfall in an area close to the plots was also measured by means of a tipping-bucket apparatus (least count = 0.2 mm) coupled with a Hobo Onset event logger.

Soil moisture measurements

From September 2016 to September 2017, soil moisture was measured with a neutron moisture meter CPN 503 DR Hydroprobe (Instrotek Inc). Access tubes were installed at 32 locations along a catena of the LCRA study site: six in the drainage-woodlands and 26 in the uplands (figure 3). Upland locations were distributed between woody plant groves with non-argillic soils (N = 7) and areas with soils having an argillic horizon—including both shrub clusters and intercanopy zones (N = 19). In each access tube, soil moisture was measured at intervals of 20 cm, to a depth of 140 cm. Readings were taken about every two weeks (table A1 is available online at stacks.iop.org/ERL/15/054001/mmedia), and we ensured that soil moisture was recorded soon after all the larger rainfall events. Following completion of measurements for the study period, we also included an additional measurement made after another large rain event in June 2018, because it was the largest rain event in the last three years.

We converted neutron count ratios for all depths and dates to volumetric moisture content, using site-specific calibrations. We then converted volumetric moisture content data to total profile water in mm. For each access tube, soil water to a depth of 140 cm was estimated by adding up the water content of all the depth intervals. For each date on which soil moisture was measured, cumulative water was summarized;
and mean and standard deviation values were calculated separately for upland groves, upland intercanopy zones, upland shrub clusters, and drainage-woodlands. Standard error values for all these measurements were also reported.

**Field saturated hydraulic conductivity and infiltrability measurements**

Field saturated hydraulic conductivity ($K_s$) was determined by means of BEST (Beekman Estimator of Soil Transfer) infiltration tests, wherein the BEST parameters (Lassabatère et al 2006) are based on the method developed by Bagarello et al (2014). The BEST infiltration tests were carried out using a ring (diameter = 110 mm) inserted to a shallow depth without disturbing the soil. At every point, a fixed small volume of water was poured recurrently, and the infiltration time for each fixed volume was measured until steady-state infiltration was reached (figure A4).

Two different upland locations at LCRA were selected for these measurements, as well as a location at the surrogate upland site. At LCRA, $K_s$ was measured at a total of 89 points—45 in intercanopy areas, 31 in canopy areas, and 13 in zones on the edges of canopy areas. At the surrogate upland site, measurements were made at 30 points—20 in intercanopy and 10 in canopy areas. The BEST simulation model (Bagarello et al 2014) was used to calculate the $K_s$ values from the raw infiltration data obtained in the field. The $K_s$ values for canopy, intercanopy, and edge zones were log-converted, followed by one-way analysis of variance (ANOVA) and Tukey’s Honest Significant Difference test.

$K_s$ measurements were complemented with five sets of infiltration measurements using drip-type infiltrometers (0.65 m x 0.65 m) similar to that described in Blackburn et al (1974) and Wilcox et al (2007) (figure A5). Rainfall simulation was applied at a rate of 154.5 mm hr$^{-1}$, and runoff was collected and measured every 2 min. Two runs were carried out for each location: first a ‘dry-run,’ after which the wetted surfaces were covered with tarpaulin sheets, and then a ‘wet run’ the next day. The mean infiltration curves for the two sites were compared and the results interpreted on the basis of terminal infiltration rate.

**Results**

**Overland flow**

During the 20 months of observation, overland flow was negligible. Even for the largest rain events of this period (96 and 130 mm d$^{-1}$), overland flow amounted to 0.5% and 0.3% of rainfall, respectively (tables 1, A4). Historical precipitation records are not available for LCRA. However, precipitation records from the nearby Alice weather station suggest that a 100 mm d$^{-1}$ event may be occurring every year, whereas events greater than 150 mm d$^{-1}$ are rarer (once every decade). At the same time, precipitation data from the three nearby weather stations (table A2) suggest considerable spatial variability. In general, larger storms in the LCRA region appear to be fewer and less intense than in the Alice region. The largest rainfall event measured during the study period (130 mm d$^{-1}$) has a return interval of about five years (NOAA Atlas-14).

**Soil moisture**

Consistent with our overland flow results, measurements of soil moisture from the different locations within the landscape showed no evidence of transfer of water from the uplands to the drainage-woodland areas. Instead, during the wettest periods the intercanopy and shrub-cluster areas of the uplands were slightly wetter than the drainage-woodlands (figure 6, table A3). These upland zones also exhibited the highest soil moisture throughout the year—in contrast to the upland grove locations, which were the driest of all the locations at LCRA (figure A1). The drainage-woodlands maintained soil moisture levels often comparable to those of the upland intercanopy areas (figure A1). Even though the surface soil moisture (20 to 40 cm) in the drainage-woodlands was often higher than that of the intermediate and deeper soils (figure A2), this occurred independent of the larger rainfall events. We believe that this difference could be attributed to suppressed evaporation rates due to greater canopy and litter cover in the drainage-woodlands.

**Field saturated hydraulic conductivity and infiltrability**

Field saturated hydraulic conductivity was about eight times greater under the canopy areas than in the

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**Table 1.** Details of runoff events with total precipitation and the corresponding surface runoff generated from the three plots.

| Date          | Event size (mm) | Vol (L) | Depth (mm) | Vol (L) | Depth (mm) | Vol (L) | Depth (mm) |
|---------------|-----------------|---------|------------|---------|------------|---------|------------|
| December 2016 | 130.8           | 0       | NA         | 168     | 0.4        | 190.4   | 0.5        |
| May 2017      | 95.4            | 0       | NA         | 0       | NA         | 89.6    | 0.2        |
| June 2017     | 30.6            | 0       | NA         | 0       | NA         | 22.4    | 0.1        |
| December 2017 | 63.2            | 0       | NA         | 0       | NA         | 0       | NA         |
| June 2018     | 166.6           | 0       | NA         | 0       | NA         | 110     | 0.3        |
intercanopy areas of the uplands (figure 7). At the same time, intercanopy \( K_s \) values were also quite high (table 2). From these results we can conclude that under ungrazed conditions, these soils have high infiltrability, which is especially enhanced by the presence of shrubs. Comparison of the \( K_s \) and infiltrability results from the ungrazed LCRA uplands with those from the

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**Table 2.** Summary of field saturated hydraulic conductivity values measured for different covers at the two sites.

| Cover          | Units (mm hr\(^{-1}\)) | \( K_s \) (mean) | \( K_s \) (median) | \( K_s \) (max) | \( K_s \) (min) | Q1   | Q3   |
|----------------|------------------------|------------------|-------------------|----------------|----------------|------|------|
| Intercanopy (Ungrazed) |                       | 161.5            | 126.5             | 485.3          | 42.2           | 74.9 | 220.8|
| Canopy (Ungrazed)      |                       | 852.7            | 845.3             | 2238.7         | 421.7          | 672.9| 1096.5|
| Edges (Ungrazed)       |                       | 609.9            | 279.9             | 1936.4         | 1.5            | 151.7| 1025.7|
| Intercanopy (Grazed)   |                       | 4.3              | 4.3               | 7.2            | 1.6            | 2.4  | 6.1  |
| Canopy (Grazed)        |                       | 4.7              | 4.7               | 6.7            | 3.1            | 4.1  | 5.3  |
grazed surrogate site showed that both parameters were much greater for the ungrazed site. Infiltrability at the ungrazed LCRA site was approximately double that at the grazed surrogate site (figure 8), and \( K_{fs} \) for intercanopy areas at the ungrazed LCRA site was almost two orders of magnitude greater than that for intercanopy areas at the grazed surrogate site (figure 7). Interestingly, at the grazed site there was no difference in \( K_{fs} \) between canopy and intercanopy zones.

**Discussion**

The combination of rangeland recovery and WPE alters ecohydrological connectivity

Almost 40 years after the suspension of grazing, we find no evidence that water from the uplands is being routed to drainage areas at LCRA. These findings are contrary to the prevailing hypothesis that drainage areas continue to receive water subsidies and are more mesic than the uplands (Archer 1995, Wu and Archer 2005, Parker et al 2010). During the 20 months of our study, overland flow was nonexistent despite some relatively large rainfall events. Our soil moisture measurements also provide strong evidence that there is little if any redistribution of water from the uplands to the lower-lying drainage-woodlands. If such redistribution were occurring, there would be dramatic differences in soil moisture between the two landforms. For example, in banded vegetation drylands of Australia, soil moisture levels were 5 times higher in downslope tree groves than in adjacent upland intercanopy areas (Ludwig et al 2005). In contrast, our measurements showed insignificant differences in soil moisture. Further, our comparison of soil infiltrability and field saturated hydraulic conductivity between our ungrazed study site and the nearby grazed site demonstrates that even moderate grazing pressure dramatically diminished soil infiltrability and likely led to much higher surface runoff. Weltz and Blackburn (1995) monitored runoff from large (5 m × 7 m) plots over a 20-month period at our study site and found that runoff was still being generated from the upland areas 40 years ago (soon after the removal of livestock). They found that for rainfall events larger than 100 mm, runoff could be as high as 8% of rainfall. It is quite likely that 150 years ago, when the site was subjected to severe overgrazing, runoff from the uplands into the drainage areas was much higher.

The prevailing evidence suggests that relaxation of grazing along with an increase in woody plants has greatly reduced hydrologic connectivity between the uplands and the drainage areas—which could explain the complete cessation of subsidy inputs to the drainage-woodlands. We postulate that at our site, the drainage areas were more mesic under the overgrazed conditions of the past, owing to a more ecohydrologically connected state. While fire suppression and grazing may have been the primary triggers for recruitment and expansion of woody plants, it is likely that the greater water availability in the drainage-woodlands made this location more favorable for WPE. This proposition is supported by the higher SOC accumulation and the greater mean age of stands in the drainage-woodlands, noted by Boutton et al (1998). In other words, the hydrological state of the landscape must have been a crucial factor in determining the patterns of recruitment in the earlier stages of WPE.
Increased ecohdrological connectivity plays a crucial role in landscape evolution

WPE and grazing together have altered the hydrology in grasslands to a significant degree, as reflected by changes in hydrological processes at both the patch scale and the watershed scale (Huxman et al 2005, Wilcox et al 2017). But how these changes influence the process of landscape evolution and state-transition has remained little explored. On the basis of our current knowledge about the mechanisms at work in such environments, we propose a ‘pathway’ that illustrates how this landscape may have evolved since the end of the 19th century (figure 9).

Phase 1 (pre 1800–1830): before the introduction of cattle grazing by the Europeans in the 1700s, the South Texas plains were largely grasslands with few trees (‘wild horse deserts’) (Bartlett 1854, Johnston 1963). Most likely these grasslands were maintained by recurring fires, facilitated by Native Americans (Pyne 2001) leading to a stabilizing fire feedback (Bond and Parr 2010, Staver et al 2011). Primary grazers were deer, antelope, and small numbers of domestic horses and cattle (Lehmann 1969). Rooting depth in these grasslands was generally shallow, confined to the upper soil layers (<50 cm) (Boutton et al 1999, Zhou et al 2017), which allowed for...
more deep drainage than in woodlands (Weltz and Blackburn 1995).

**Phase 2 (1830s to early 1900s):** Following the increasing European settlement in South Texas, which led to a dramatic increase in sheep and cattle grazing (Lehmann 1969), two significant ecological changes took place: (1) a reduction in herbaceous vegetation and creating of bare patches, which disrupted the stabilizing fire feedbacks (Wilcox et al 2018a) and (2) compaction of soil due to cattle movement, which caused a rapid decline in infiltration (Wood and Blackburn 1981, Blackburn 1983, Trimble and Mendel 1995). In the wake of these changes, the region’s hydrology shifted from high infiltration to poor infiltration and frequent overland flows. As a result, overland flow from the uplands increased soil moisture in the drainage-woodlands at the expense of soil moisture recharge in the uplands. While the absence of fire spurred the rate of tree recruitment overall, the greater wetness in the drainage-woodlands allowed for higher recruitment rates than in the uplands (Boutton et al 1998).

**Phase 3 (early 1900s to mid 1900s):** By the early 20th century grazing pressure remained heavy but was probably reduced from the extremely heavy grazing in the 1800s (Wilcox et al 2012). The distinct pattern of denser drainage-woodlands surrounding open upland areas was strongly developed (aerial images; Barton 1974). With continued grazing, runoff regimes may have declined some but not significantly. However, more woody plants continued to sprout in the upland areas, helped by widespread seed dispersal and edaphic factors (Archer et al 1988, Loomis 1989, Zhou et al 2017).

**Phase 4 (mid 1900s–1980):** This phase saw the reversal of the early ecohydrological shifts. It is marked by a continuous decline in grazing pressure along with the introduction of better range management practices (Wilcox et al 2012), both of which have helped infiltration recovery. WPE on the uplands following the decline in grazing benefited from runoff-runon while at the same time reducing the strength and scale of runoff processes (Ludwig et al 1999). Stroh (2004) and Wu and Archer (2005) have noted that the boundaries of the drainage-woodlands remained dynamic until recent decades, suggesting that this area may have benefited from lateral subsidies until recently.

**Phase 5 (present day):** From our observations, it is evident that lateral subsidies have declined because of the substantial rise in infiltration rates in the uplands. We did not find evidence of a higher soil moisture regime in the drainage-woodlands. In other words, it is likely that in its current ecohydrological state, the elevation itself does not confer any advantage to the vegetation networks.

**Implications**

In this study we have provided strong evidence that in subhumid savannas, overgrazing leads to increased ecohydrological connectivity through amplification of the runoff-runon process (at our site, this greater connectivity historically enabled supplementary water from the uplands to be carried to the downslope drainage areas). With the relaxation of grazing, ecohydrological connectivity effectively collapses. The long-term ecological response of a particular system to this change is not well understood. An important question is—how generalizable are our findings? Do they apply to all landscapes that have gone through a cycle of intensive grazing followed by relatively light or no grazing? The patterns observed at LCRA (figure 9), we believe, are applicable not only to South Texas shrublands but also other low-relief savannas in subhumid climates. Quite simply, when these savanna systems are overgrazed, water will be distributed differently, with more water being supplied to low-lying areas. If the savannas are allowed to recover from overgrazing, ecohydrological connectivity will revert to pre-grazing patterns. Questions remain. For example, how will the current landscape and vegetation—which has been converted to a very different state from the pre-grazing one—respond to this ecohydrological shift? There most likely will be a significant time-lag before ecological responses to such a shift are manifested (Wilcox et al 2018a). In the case of our study site, the vegetation patterns in the drainage-woodlands are not representative of present hydrological conditions. Consideration of the legacy of disturbances such as overgrazing can help us better understand the mechanisms underlying landscape evolution.

While we believe that as a general rule the influence of grazing pressure on ecohydrological connectivity must be explicitly taken into account, it must also be recognized that the ecological and hydrological responses, as well as the scale of response, will differ depending on a number of factors—including climate, soils, and topography. In the savannas of the Rolling Plains of Texas, for example, when rangeland conditions improved following a decline in grazing pressure, river flows decreased by as much as 70% (Wilcox et al 2008). These changes, while ecologically positive, have meant that water-supply reservoirs are no longer filling up. In contrast, in the karst Edwards Plateau region of Texas, improved rangeland reservoirs from the wake of dramatic declines in stocking density have resulted in higher groundwater recharge and increased spring flow (Wilcox and Huang 2010). Both types of changes have regional-scale consequences. Studies in other grasslands and savanna systems are needed, to elucidate the ecological consequences of changes in ecohydrological connectivity—in particular, the influence of grazing on ecohydrology.
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Data statement

The data that support the findings of this study are openly available at [https://doi.org/10.25412/1.iop.11608233.v1](https://doi.org/10.25412/1.iop.11608233.v1)

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