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Nonlinear groundwater influence on biophysical indicators of ecosystem services

Jiangxiao Qiu[1,7]*, Samuel C. Zipper[2,3,7], Melissa Motew[4], Eric G. Booth[5,6], Christopher J. Kucharik[4,6] and Steven P. Loheide[5]

Groundwater is a fundamental control on biophysical processes underpinning essential ecosystem services (ES). However, interactions and feedbacks among groundwater, climate and multiple ES remain less well understood. We investigated groundwater effects on a portfolio of food, water and biogeochemical ES indicators in an urbanizing agricultural watershed. Our results show that food production, water quality and quantity, and flood control are most sensitive to groundwater, with the strongest responses under wet and dry climate extremes. Climate mediates groundwater effects, such that several ES have synergies during dry climate, but trade-offs (groundwater increased some ES but declined others) under wet climate. There is substantial spatial heterogeneity in groundwater effects on ES, which is driven primarily by water table depth (WTD) and is also sensitive to soil texture and land cover. Most ES indicators respond nonlinearly to WTD when groundwater is within a critical depth (approximately 2.5 m) of land surface, indicating that small WTD changes can have disproportionately large effects on ES in shallow groundwater areas. Within this critical WTD, increasingly shallow groundwater leads to nonlinear increases in surface flood risk, sediment erosion and phosphorus yield; nonlinear decreases in drainage to the deep vadose zone and thus groundwater recharge; and bidirectional responses of crop and grass production, carbon storage and nitrate leaching. Our study illustrates the complex role of groundwater in affecting multiple ES and highlights that strategically managing groundwater may enhance ES resilience to climate extremes in shallow groundwater settings.

Depletion of groundwater, the world's largest non-frozen freshwater resource, is widespread and accelerating at local and global scales[1–3], posing substantial sustainability challenges[4,5]. Besides serving domestic, industrial and agricultural needs, groundwater is a fundamental yet often underappreciated belowground control on biological, chemical and physical processes from bedrock to the plant canopy[6]. Previous research has demonstrated that shallow groundwater exerts a strong influence on water and energy budgets[7–9], which could have cascading effects on ecosystem services (ES)[6,10], such as food production, water quality and quantity, and carbon storage. However, previous work has primarily focused on groundwater effects on an individual ES under present climatic conditions, and therefore the dependence of multiple ES and their interactions on groundwater and climate remains unclear.

Groundwater primarily influences ES by altering ecological, hydrological and biogeochemical processes occurring at or near the land surface. These biophysical processes underlie the production of a wide range of ES, especially in agricultural landscapes that are managed primarily for food production but also sustain other human benefits[11–14]. For example, crop yield represents an ecosystem's capacity to produce food either for direct human consumption or livestock fodder[15]; drainage replenishes aquifers that sustain human freshwater needs[16]; nitrate leaching increases groundwater nitrate levels with detrimental impacts on human health; excess phosphorus yield degrades surface-water quality and interferes with safe human water uses[17,18]; carbon sequestration and storage play a vital role in regulating regional and global climate[19]; and extreme runoff is related to the capacity of landscapes to regulate stormwater and reduce flood damages[20]. By altering these key biophysical processes, groundwater ultimately affects ES essential for human livelihoods.

Groundwater can affect processes underpinning ES in a complex, service-dependent and potentially nonlinear manner[21], and thus ignoring groundwater in models used to assess ES may result in systematic biases[22,23]. For example, shallow groundwater can enhance crop yield by increasing root zone water availability (a concept known as 'groundwater yield subsidy')[24], particularly during dry years, but reduce yield during wet years when shallow groundwater leads to plant oxygen stress[25]. Shallow groundwater can also decrease a landscape's capacity to regulate flooding by reducing subsurface storage capacity, thereby increasing runoff generation during precipitation events[26,27]. These effects may further cascade to ES related to soil retention and water quality, because overland flow is a major hydrologic pathway through which sediment and phosphorus are transported[28]. Moreover, groundwater has complex effects on nutrient cycling. On the one hand, shallow groundwater can retain nutrients in or near the root zone, potentially increasing ecosystem productivity, crop yield and nutrient uptake[29,30]. On the other hand, shallow groundwater may facilitate nutrient movement through the subsurface (for example, via drainage), thus contaminating water resources[29].

While the ecohydrological effects of groundwater are recognized and understood conceptually, comprehensive research on the interactions, nonlinearities and feedbacks between groundwater, climate and multiple ES remains rare. In fact, most research for quantifying and forecasting ES is focused on aboveground drivers (for example,

[1]School of Forest Resources and Conservation, Fort Lauderdale Research and Education Center, University of Florida, Davie, FL, USA. [2]Department of Civil Engineering, University of Victoria, Victoria, British Columbia, Canada. [3]Department of Earth and Planetary Sciences, McGill University, Montreal, Quebec, Canada. [4]Nelson Institute Center for Sustainability and the Global Environment, University of Wisconsin–Madison, Madison, WI, USA. [5]Department of Civil and Environmental Engineering, University of Wisconsin–Madison, Madison, WI, USA. [6]Department of Agronomy, University of Wisconsin–Madison, Madison, WI, USA. [7]These authors contributed equally: Jiangxiao Qiu, Samuel C. Zipper *e-mail: qiuj@ufl.edu

Table 1 | List of ecosystem services in the Yahara Watershed (Wisconsin, USA), quantified at 220 m × 220 m spatial resolution, with corresponding biophysical indicators and units

Ecosystem service	Biophysical indicator	Unit
Provisioning		
Crop production[a]	Annual total crop (corn, soybean and small grains) yield	$t\ ha^{-1}$
Grass production	Annual total forage crops and grass (alfalfa, hay and pasture) yield	$kg\ ha^{-1}$
Freshwater supply	Annual total drainage from bottom of soil column to groundwater or deep vadose zone	mm
Regulating		
Groundwater quality	Annual total nitrate leached at the bottom of soil profile	$kg\ ha^{-1}$
Surface-water quality	Annual total phosphorus yield in runoff	$kg\ ha^{-1}$
Flood regulation	Annual total number of days with daily runoff >10 mm	d
Climate regulation	Annual total ecosystem carbon storage (including soil, aboveground and belowground biomass and deadwood/litter carbon pools)	$MgC\ ha^{-1}$
Soil retention	Annual total sediment yield in runoff	$t\ ha^{-1}$

[a]Original model outputs are in $bu\ ac^{-1}$ (unit), which we converted as $1\ bu\ ac^{-1} = 0.0626\ t\ ha^{-1}$, based on corn as the dominant crop (https://www.extension.iastate.edu/agdm/wholefarm/html/c6-80.html).

climate and land-use effects on ES[10,15]), and few explicitly consider groundwater processes and feedbacks. Although previous research has addressed interactions between shallow groundwater, soil texture and land cover, much of this work is constrained to field scales and/or under contemporary and static environmental conditions (as opposed to shifting drivers of change)[21,31,32]. Thus, it remains unclear how groundwater alters the magnitude and spatial patterning of a range of ES indicators at landscape scales, and whether groundwater effects are mediated by factors such as climate, soil and/or land cover. Such a holistic, landscape-scale and dynamic perspective is crucial for understanding ES trade-offs and synergies influenced by groundwater, and informing landscape management and environmental policy that aims to balance multiple targets simultaneously[33]. Knowledge of groundwater effects on ES is also needed for large-scale initiatives, such as the United Nations Sustainable Development Goals[34], to achieve global food and water security.

Here we used a process-based terrestrial ecosystem model, Agroecosystem Integrated BIosphere Simulator (Agro-IBIS)[25,35,36], to investigate groundwater effects on indicators of eight ES (Table 1) under contrasting climate extremes. We focused on an exemplar urbanizing agricultural watershed (Yahara Watershed, Wisconsin, USA) (Fig. 1) because: (1) biophysical conditions and stressors on ES in this watershed typify many agricultural landscapes in the midwestern United States (a crucial food production region) and similar production regions around the world[11]; (2) this region has substantial spatial variation in groundwater levels and minimal tile drainage, presenting a wide variety of possible groundwater–ES interactions[37]; and (3) extensive model input data (for example, meteorological, land use/cover, farming and other management practices) and field observations are available for modelling at fine spatial-temporal scales (that is, 220 m resolution and an hourly time step). Details on study region, model setup, calibration and validation can be found in the Methods and Supplementary Information. We performed a 2 × 3 factorial design for model simulations, systematically simulating groundwater presence ('with') or absence ('without') (Supplementary Fig. 2) and varying climate conditions (dry, average and wet meteorological inputs). By comparing results between presence and absence of groundwater in our simulations, we were able to isolate and capture the full range of potential groundwater effects on ES. Such an approach can also estimate the bias of land surface and ES models that do not include a representation of groundwater, which essentially equals the difference between simulations 'with groundwater' and 'without groundwater'. All six scenarios were simulated for a focal period of 12 yr that comprises three commonly adopted crop rotations in our study region, following spin-ups of the water, energy and nutrient cycles from 1786 to 2013. Model outputs of key ecological processes underlying ES production were selected as the biophysical indicators of ES (Table 1) for subsequent analyses, following refs. [11,12]. Detailed descriptions on the rationale and human relevance of ES indicators are provided in the Supplementary Information.

Nonlinear and spatially variable ES responses to groundwater

Substantial spatial heterogeneity in the magnitude and direction of groundwater effects on ES indicators (that is, exceeding one order of magnitude) occurred throughout the landscape (Fig. 1 and Supplementary Fig. 3). As one example, phosphorus yield more than doubled in 5.9%, 6.8% and 8.5% of agricultural lands under dry, average and wet climates, respectively, due to groundwater (Supplementary Fig. 4). Similarly, under average climate, the 5% of the landscape where groundwater had the largest impact on extreme runoff was approximately 2.3 times more sensitive than the watershed mean (that is, 0.93 d with runoff > 10 mm; Fig. 2).

Across all ES indicators and climate conditions, locations most susceptible to groundwater effects corresponded to areas with the shallowest groundwater (Fig. 1 and Supplementary Fig. 3). This suggests that water table depth (WTD) is a critical underlying factor driving the spatial variability in groundwater effects. To quantify this relationship, we examined the response of each ES indicator to WTD at the pixel level. Our analysis showed that groundwater effects were strong and nonlinear when the water table was within approximately 2.5 m of the land surface for most ES, with almost negligible impacts at deeper WTD (Fig. 2 and Supplementary Figs. 5 and 6).

Relationships between groundwater effects and WTD were also strongly influenced by climate. Specifically, groundwater increased crop yield when the WTD was <2.5 m in the dry climate, whereas crop yield decreased when the WTD was <1 m in average and wet climate conditions (Fig. 2a). Groundwater effects on grass production were smaller in magnitude than crops, with relatively few grid cells affected by shallow groundwater, but groundwater had a primarily positive effect in dry and average climates and a negative effect in the wet climate (Fig. 2b). Groundwater presence decreased drainage (a proxy for potential freshwater supply) across all WTDs, with nonlinear declines at WTD < 2.5 m and the sharpest declines in the dry climate and the smallest response in the average climate (Fig. 2c). Similarly, nitrate leaching (a major contributor to degraded groundwater quality) increased at WTD < 2.5 m in the dry climate, with a shallower WTD threshold (~1 m) in average and wet climates (Fig. 2d). Extreme runoff days, phosphorus and sediment yield (inverse indicators for flood regulation, surface-water quality and soil retention) all increased in similar nonlinear manners to groundwater (Fig. 2e,f,h) with sharp increases when WTD < 1.5 m. Such patterns were most evident in the wet climate, indicating that groundwater-driven increases in overland flow generation has cascading effects on other related ES. Groundwater effects on

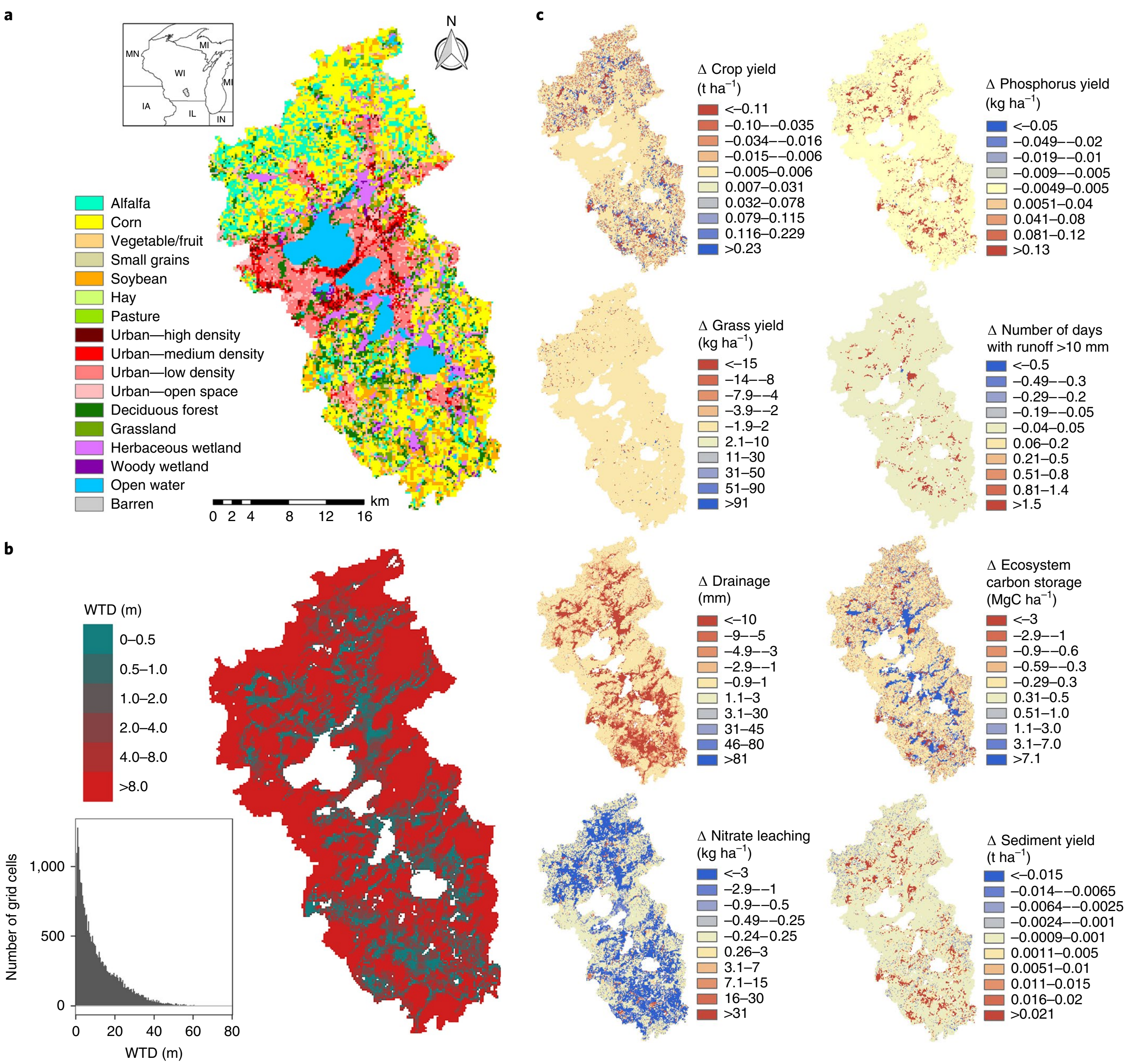

Fig. 1 | Land use/cover, WTD and groundwater effects on ES indicators in the Yahara Watershed. a, Land use/cover of the Yahara Watershed for 2014 at the modelling grid scale (that is, 220 m × 220 m resolution). Inset map shows the geographic location of the watershed in the Wisconsin and the upper Midwest, USA. **b**, Spatial distribution of WTD within the model domain, with inset figure showing the histogram of WTD. **c**, Spatial variability of groundwater effects on ES indicators modelled under average climate conditions. Results for wet and dry climates are shown in Supplementary Fig. 3. Calculations were based on differences in the means of 12 yr simulations at 220 m × 220 m grid cell between model runs with and without groundwater. Red colours indicate declines in ES provision and blue colours indicate increases in service supply due to groundwater. White colour indicates surface water (that is, lakes and ponds) in the watershed.

ecosystem carbon storage (a proxy for climate regulation) were more variable than other ES indicators, with both positive and negative effects at WTD < 2.5 m across all climates (Fig. 2g).

Sensitivity of groundwater effects to land cover and soil

Land cover and soil type also contributed to variability in ES responses to WTD (Fig. 3 and Supplementary Figs. 7 and 8). Certain ES indicators were more sensitive to soil texture than land cover; for example, changes in extreme runoff days, drainage and sediment yield were more pronounced in fine-grained soils. In contrast, other ES indicators were more sensitive to land cover than soil texture; for example, ecosystem carbon storage primarily increased in grasslands and wetlands with the presence of shallow groundwater but decreased in forests with groundwater present. In agricultural and urban land covers, ecosystem carbon storage increased at intermediate WTD but decreased at very small WTD. These results further previous work[7] showing how soil and land cover control groundwater effects on surface energy and water balances, and our findings demonstrate that these changes can extend to affect multiple societally relevant ES indicators.

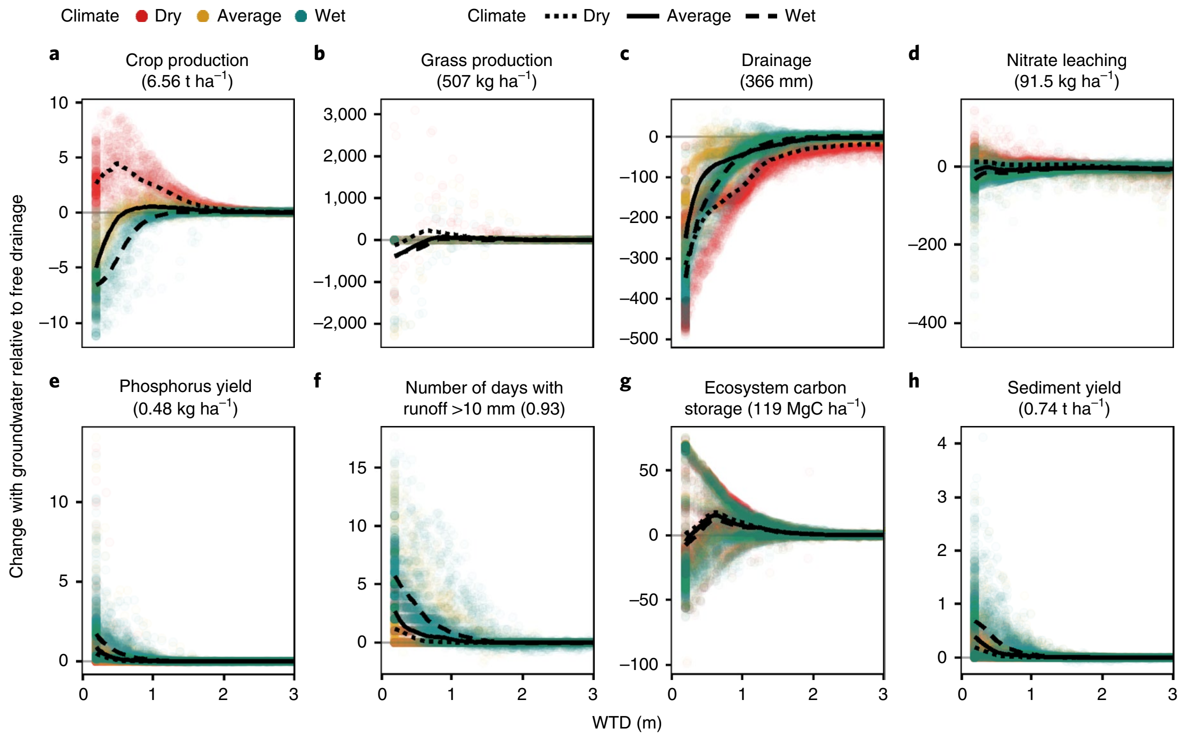

Fig. 2 | Groundwater effects on ES indicators at the grid-cell level, as a function of WTD. Lines represent smoothed loess function fitted separately for all grid cells across the watershed, with dotted, solid and dashed lines representing best fits under dry, average and wet climate conditions, respectively. The coloured points (red, brown and blue) show the modelling results under dry, average and wet climates, respectively. Numerical values in plot header are the reference for comparison, calculated as the watershed means for each ES indicator under average climate with no groundwater. Supplementary Fig. 5 shows the same data with a limited *y*-axis range to illustrate smaller responses to WTD.

Groundwater effects on ES mediated by climate

Since ES provision is strongly influenced by the scale of analysis[38], we further scaled up to examine ES responses to groundwater and climate at the watershed level, using general linear mixed-effects models with repeated measures, based on differences in watershed means between with and without groundwater simulations. Our results showed that groundwater significantly affected all ES indicators evaluated in this study, with direction and magnitude of effects varying among ES (Fig. 4 and Supplementary Figs. 9 and 10). Comparing across all ES indicators, crop production, drainage, phosphorus yield and number of days with runoff >10 mm had the largest responses to groundwater at the watershed scale, with effects up to 10–20% for certain climates (Supplementary Fig. 9), which are substantial as an aggregated watershed average and represent a potential bias for regional ES assessments without explicit consideration of groundwater.

Climate also mediated groundwater effects on ES indicators at the watershed scale (all $P < 0.001$, analysis of variance), with strongest effects under wet and dry climate extremes. For example, groundwater increased watershed-mean crop yield by 0.18 t^{-1} ha^{-1} (9%) in the dry climate, but reduced crop yield in average and wet climates (Fig. 4a). A similar pattern was observed for grass yield (Fig. 4b). Other ES responded to groundwater presence in the same direction under different climate conditions, but with varying magnitude. For example, groundwater presence reduced drainage, with the greatest declines (−33 mm yr^{-1} or −21%) when the climate was dry (Fig. 4c). Groundwater reduced watershed-mean nitrate leaching by −1.2 to −3.2 kg ha^{-1}, with moderate differences across climates (Fig. 4d). Such effects are non-trivial given the health implications of nitrate in drinking water, and effects at local scales (for example, grid cells) can be much larger (Fig. 1 and Supplementary Fig. 3). Moreover, groundwater uniformly increased phosphorus and sediment yield, and number of days with runoff >10 mm, with the smallest increase in the dry climate and largest increase in wet climate (Fig. 4e,f,h). Groundwater also increased ecosystem carbon storage with the largest increase in the dry climate (Fig. 4g).

Mechanisms underpinning groundwater effects

Our results highlight the dependence of ES indicators on the complex interplay among factors operating at different timescales: soil formation (centuries to millennia), land cover (years to decades), WTD (weeks to years) and weather conditions (days to weeks). A diverse set of mechanisms contributes to groundwater effects on ES indicators studied here. For productivity-based ES (crop/grass production), groundwater effects are beneficial in dry years but detrimental in wet years (Figs. 2 and 4). This is consistent with previous work showing groundwater yield subsidies from increased plant water availability under dry conditions but penalties due to anoxic conditions during wet conditions[24,25,39]. In contrast, for ES dependent on surface runoff (that is, extreme runoff days, phosphorus and sediment yield), responses are highly nonlinear to WTD and sensitive to soil texture, which governs infiltration capacity (Figs. 2 and 3). For these ES, infiltration is lower with shallower groundwater (due to reduced available subsurface storage) and finer soil texture (due to decreased hydraulic conductivity), leading to more runoff generation and associated phosphorus and sediment yields[26,40,41].

Responses of ES dependent on groundwater flux (that is, drainage and nitrate leaching) have complex relationships with WTD, because drainage can be either positive or negative (equating to groundwater recharge or discharge, respectively). We observed a sharp decrease in simulated drainage in all three climate conditions when WTD < 2.5 m, with the smallest response in the average climate condition (Fig. 2). The decrease in drainage occurs because groundwater weakens the hydraulic gradient at the bottom of the

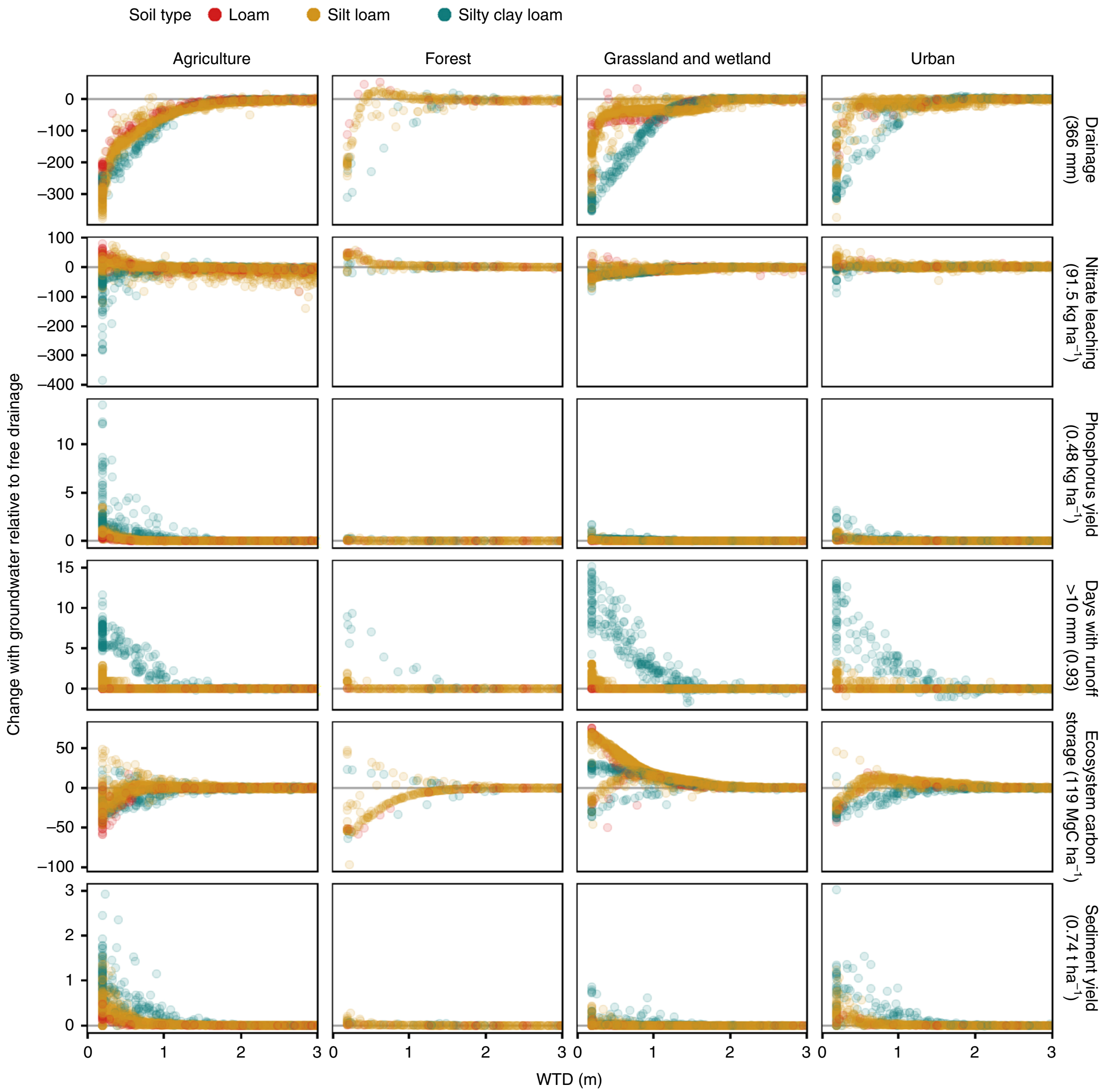

Fig. 3 | Influence of land use/cover and soil texture on groundwater effects on ES indicators at the grid-cell level. Models were run under the average climate condition, separated by five major types of land use/cover (column) and three dominant soil types in the watershed (colour coded). Numerical values in the side labels are the reference for comparison, calculated as watershed means for each ES under average climate with no groundwater. Results for crop and grass production can be found in Supplementary Fig. 7.

soil column (leading to decreased positive drainage) and creates groundwater discharge via capillary rise (leading to increased negative drainage), both of which strongly depend on soil hydraulic properties. Thus, ignoring shallow groundwater can overestimate net drainage in areas where groundwater contributes to evapotranspiration of vegetation, particularly during wet and dry conditions when the water table may be out of equilibrium[42–44].

Nitrate leaching, a function of drainage and soil nitrate concentrations, shows a more variable response to WTD than drainage with substantial variability at WTD < 1 m (Fig. 2). In the presence of groundwater, nitrate leaching increased in some pixels (especially those with shallow groundwater) despite decreased drainage (Fig. 1 and Supplementary Fig. 3), indicating that shallow groundwater increased soil nitrate concentrations. While previous work has shown that greater denitrification can occur with elevated soil moisture (thus decreasing nitrate leaching)[45], we attribute this result to enhanced nitrate availability in the soil column due to higher soil moisture, which increases N mineralization from carbon decomposition and makes additional nitrate available in soil solution to leach[35,46]. Further research such as controlled field experiments is needed to tease apart the relative importance of different N processes in governing groundwater effects on soil nitrate leaching.

Implications of groundwater effects on ES provision

Nonlinear and heterogeneous groundwater effects on ES indicators highlight the need for researchers and resource managers to consider groundwater as an explicit driver of ES dynamics, especially when the WTD is within the identified critical depth of approximately 2.5 m, as in 22% of our study domain (Fig. 1) and >25% of global terrestrial land[47]. Responses of ES indicators to WTD vary with both soil texture and land cover (Fig. 3), suggesting that soil hydraulic properties (a function of soil type) and rooting depth (a function of land cover) are mechanisms that determine groundwater regulation of ES. Thus, our results are likely generalizable to many agricultural landscapes with shallow groundwater and similar land covers (for example, corn and soybean) and soil textures

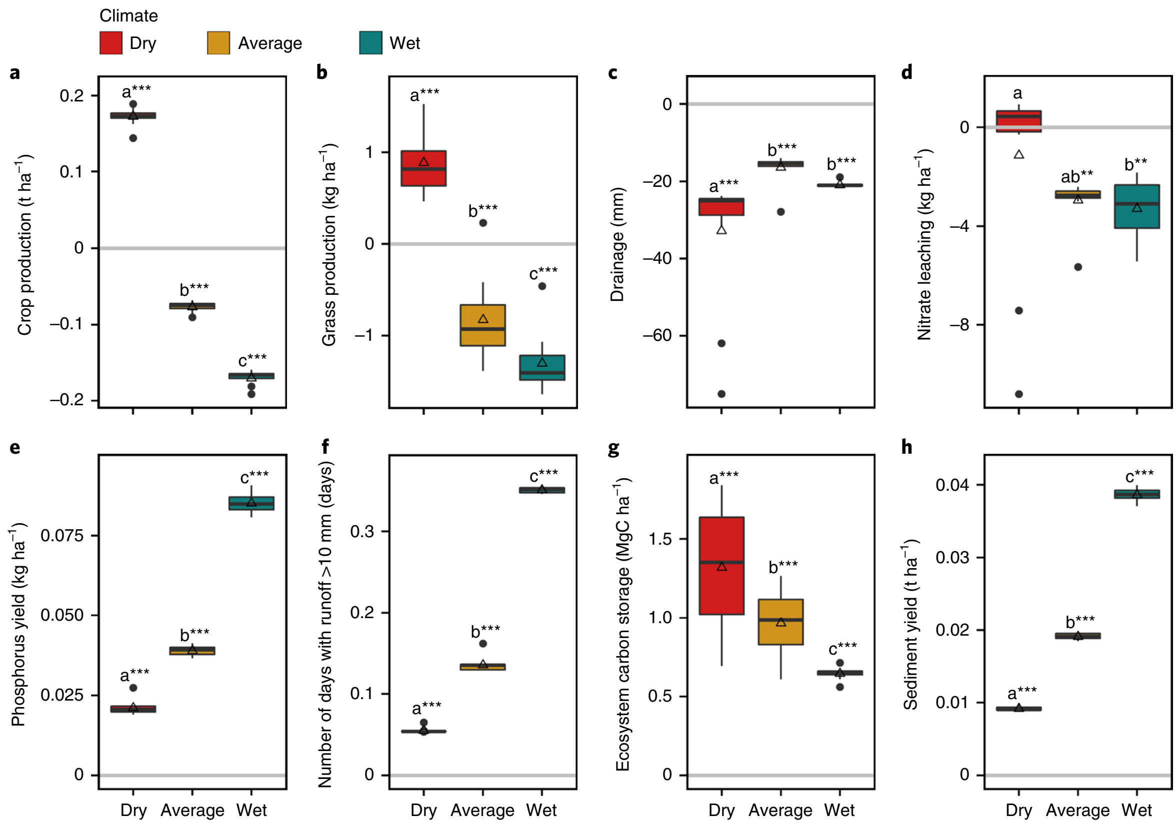

Fig. 4 | Differences in modelled ES indicators with and without groundwater. Calculations were based on 12 yr simulations summarized at the watershed scale and across three climate conditions. For a given ES indicator (each panel), boxplots with different letters are significantly different based on Tukey multiple comparison ($\alpha = 0.05$). Asterisks denote level of significance testing against zero (***$P < 0.001$, **$P < 0.01$, *$P < 0.05$) and triangles show the mean values of changes in ES indicators.

(for example, silt loam) to the Yahara Watershed. These include critical global agricultural regions such as the US Midwest, Northeast China and regions of Argentina[48].

Our research underscores the importance of integrating groundwater effects on water, energy and biogeochemical cycling in contemporary ES models in shallow groundwater settings. Although the magnitude of groundwater effects on many ES indicators is modest at the watershed scale, neglecting groundwater may cause systematic bias and overlook hotspots in the landscape where groundwater has a disproportionately large effect. However, including groundwater effects can be challenging due to limited groundwater and aquifer data as well as increased uncertainty and computational cost associated with greater model complexity[49]. While researchers are starting to address effects of land-surface anthropogenic changes, such as human-modification of landscapes, on ES provision, their indirect effects through altering groundwater levels (for example, pumping) are even less well known[39], but can be nontrivial and extend to ES beyond freshwater supply. Although integrated surface–subsurface ecohydrological models are becoming increasingly advanced and capable of simulating ecosystem processes[50,51], their use remains primarily confined to the ecohydrology community due to high complexity and computational requirements of these models. Interdisciplinary, ES-focused modelling linking aboveground and belowground drivers, processes and interactions across scales as well as connecting ES production to demand will be fruitful avenues of future ES research and critical for improving long-term ES resilience[38,52–55]. Furthermore, our research enriches an emerging literature on effects of multiple drivers and their interactions on ES, and provides evidence that ES responses can be nonlinear and have threshold effects under certain biophysical conditions (for example, WTD < ~2.5 m)[16,56,57].

From a management standpoint, our results suggest that land managers must be aware of how WTD varies across landscapes to select and implement practices that take advantage of potential groundwater-related benefits while avoiding negative impacts. A spatial perspective is critical given that watershed-level changes can mask substantial geographic variations, which may be much greater in magnitude or differ in direction from watershed-average changes (Figs. 1 and 4 and Supplementary Fig. 3). For instance, targeting practices such as manure spreading to areas with deeper groundwater may be more effective in reducing phosphorus yield to avoid water-quality impairment, due to the strong response of sediment and phosphorus yield to shallow groundwater. In addition, nonlinear ES responses to groundwater indicate leverage points where small changes in groundwater levels can have substantial effects on ES[16]. This highlights that local actions and fine-scale management to manipulate WTD (for example, managed tile drainage systems) may be an effective tool for maximizing beneficial ES, though tile drainage is currently rare in our study watershed (<7% of cropland)[58].

Effective groundwater-informed ES management requires a holistic and dynamic perspective, particularly given that ES interactions driven by groundwater can shift between synergies and trade-offs depending on climate conditions. For example, in shallow groundwater settings, some ES indicators that have synergistic relationships under dry climates due to the buffering effects of shallow groundwater (for example, food supply and other regulating ES such as water quality and flood control) instead have lose–lose outcomes during wet climates. Also, for a given location, groundwater effects can be positive for certain ES but negative for others (for example, nitrate leaching versus phosphorus yield)

(Fig. 1 and Supplementary Fig. 3), suggesting the persistence of spatial trade-offs due to groundwater effects and the need to account for these interactions in ES management[11,59]. Furthermore, improved understanding of the potential for groundwater to laterally transmit impacts of land use/cover and management decisions through the subsurface (for example, refs. [9,39]) is necessary to effectively manage groundwater–ES interactions at the landscape scale, although such dynamics were not captured in our static representation of groundwater and the one-dimensional Agro-IBIS model. Finally, climate also mediates ES response to WTD at local (grid cell) scales, indicating that managing groundwater levels will require dynamic adjustments (for example, controlled tile drainage systems) in response to growing-season weather conditions to maximize multiple ES and avoid undesirable trade-offs.

It is important to acknowledge that our study focuses on biophysical indicators representing the production of ES. Future research is needed to integrate biophysical assessments with social data (for example, population, human demands) to determine the extent to which groundwater influences ES valued by beneficiaries. This is challenging due to a number of factors not considered in our biophysical analysis, including but not limited to (1) scale mismatch in ES production, demand, consumption and management[38,60], (2) potential threshold effects (ecological, social and heath)[18,61] and (3) intricacy in linking ES production to demand and use[52]. One example of scale mismatch is that groundwater affects carbon storage at local scales; nevertheless, carbon storage is beneficial for regulating climate at regional to global scales. Another example is that groundwater effects on nitrate leaching can be significant at the local scale, but such effects are only relevant for ES delivery if drinking water directly comes from private wells at the same scale. One example of threshold effect is that changes in drainage (a proxy for groundwater recharge and potential drinking water supply) can be highly valued in water-scarce environments, but inconsequential or even harmful in water-surplus settings[21]. Similarly, groundwater effects on nitrate leaching would have substantially different value if such effects increase nitrate levels above $10\,\mathrm{mg\,l^{-1}}$ (that is, maximum contaminant levels per Environmental Protection Agency regulations). One example of intricacy in connecting ES production to demand and use is that reduced drainage due to shallow groundwater could potentially decrease water supply; however, when the water table is high, it also means that water supply may not be in shortage and thus reduced drainage is of marginally less value to demand and use of ES.

Conclusion

Our study demonstrates that groundwater has spatially variable, nonlinear and climate-dependent effects on a portfolio of ES. Shallow groundwater significantly affects all ES indicators studied and effects are especially pronounced for food production, water quality and quantity, and flood regulation. Climate mediates groundwater effects, such that several ES indicators have synergies during dry climate, but trade-offs (that is, groundwater increased some ES but decreased others) under wet climate conditions. Groundwater effects on ES are also spatially heterogeneous, with substantial effects in locations with shallow groundwater, but negligible effects where groundwater is deep. Most ES respond nonlinearly to groundwater with the largest changes when the water table is within a critical depth of approximately 2.5 m. Such nonlinear responses are likely determined by rooting depth and soil hydraulic properties, and thus may be generalizable to similar agricultural landscapes around the world.

Our study provides compelling evidence that groundwater is a key mechanism affecting multiple ES responses to climate, and underscores the importance of accounting for groundwater and climate variability simultaneously when assessing and managing ES in environments with shallow groundwater. We highlight the need for scientists to address interactions between groundwater, land-surface processes and climate in ES research, and for managers to consider groundwater as a potential driver of ES in settings with near-surface groundwater. Our results suggest that current human alterations of the WTD (for example, groundwater pumping, tile drainage) may significantly affect key ecosystem processes and ES provision at different scales, and strategically managing groundwater resources may enhance ES resilience to future climate extremes and increased climate variability.

Methods

Biophysical modelling. We used Agro-IBIS, a grid-based terrestrial ecosystem model, to quantify groundwater effects on ES indicators. Agro-IBIS is a version of the IBIS global dynamic vegetation model[35,62,63] that simulates carbon, nutrients, water and energy cycles for a suite of plant functional types at hourly resolution. Agro-IBIS has been modified to simulate agricultural plant functional types, including corn, soybean, wheat, pasture and alfalfa, with different land use and management practices. Recently, the soil water and heat transport algorithms of Agro-IBIS were replaced with those from the HYDRUS-1D variably saturated flow model[64]. This new version described in ref. [25] allows for physically based simulation of groundwater in the soil column using one-dimensional pressure head-based form of the Richards' equation (Supplementary equation (1))[65]. The version of Agro-IBIS used for the present study has been thoroughly calibrated and validated for the Yahara Watershed[24,25,36], including under both excessively dry (water stress) and wet (oxygen stress) conditions in a shallow groundwater environment[24].

To simulate conditions with and without groundwater, we used two different hydraulic boundary conditions at the bottom of each 10 m soil column model domain (representing each grid cell in the watershed), following refs. [24,25,42]. For simulations without groundwater, the bottom boundary condition allowed for free drainage (vertical hydraulic gradient = 1). For simulations with groundwater, we represented the water table as a temporally constant specified pressure head boundary condition at the bottom of domain (Supplementary Fig. 2). Input bottom boundary conditions for the Yahara Watershed were calculated from a steady-state solution of a three-dimensional regional groundwater flow model (MODFLOW-NWT) calibrated to the 2006–2012 period[37], which was adjusted to avoid locations with water table rising above the land surface (see Supplementary Information for further details). Representing the water table as a static pressure head boundary condition is an approximation, as in reality the water table fluctuates through time due to inputs and outputs to the groundwater flow system. Our factorial simulation design simplifies groundwater as absent or as a static trait, allowing us to rigorously isolate and examine groundwater effects on land-surface processes by quantifying the full range of groundwater effects on ES indicators. This also provides an indication of bias introduced by the 'no groundwater' status quo of many land-surface models. Ongoing efforts that fully couple Agro-IBIS with the MODFLOW groundwater model will be well positioned to advance this research[39]. Other model inputs, including meteorological drivers, land use/cover, nutrient application and soil texture, are based on historical and publicly available data for the watershed and have been described in details in refs. [36,66].

Factorial model simulation design. To address our research questions, we designed a full factorial set of model simulations that systematically varied climate and presence/absence of groundwater. Agro-IBIS requires precipitation, air temperature, wind speed, incoming shortwave radiation and relative humidity as meteorological inputs. To generate realistic climate scenarios, we selected years from the historical record that captured drier-than-normal (2012), average (2011) and wetter-than-normal (2013) conditions in southern Wisconsin (Supplementary Fig. 11). Annual precipitation was 541, 829 and 1,080 mm for these years, with reference evapotranspiration of 900, 754 and 722 mm, respectively. For a given climate, simulations were performed with and without groundwater (that is, free drainage) and all other variables remained the same among the paired simulations. Given these three climate scenarios (that is, dry, average and wet conditions) and two groundwater conditions (that is, presence and absence), a total of six scenarios were simulated and analysed.

All simulations were preceded by a 175 yr spin-up (1786–1960) in which carbon and nitrogen pools were allowed to reach equilibrium, followed by a 25 yr spin-up (1961–1985) in which phosphorus pools were allowed to reach equilibrium in response to historical application rates of manure and fertilizer (see ref. [36] for more details). Meteorological input data for 1986–2013 were obtained from weather stations in Arlington (Wisconsin), Dane County Regional Airport (Madison, Wisconsin) and the National Centers for Environmental Prediction. For all spin-up years before 1986, random meteorological years from the 1986–2013 period were used. Following the spin-ups of carbon, nitrogen and phosphorus pools, each of the six simulations was performed for 12 yr (that is, three crop rotations) using repeated meteorological data from the three selected climate conditions of interest (that is, 2012 for dry, 2011 for average and 2013 for wet). We chose a window of 12 yr as a focal period of analysis to reduce effects of antecedent conditions and averaged across 12 yr to avoid the arbitrariness of selecting a single year. Our results showed that 12 yr is sufficient for our analysis since most ES indicators tended to reach a dynamic equilibrium within a few years (Supplementary Fig. 10). Model outputs were selected that capture key ecological processes that underlie the production or condition of ES for subsequent analyses[11,16]. Since we intended to test effects of climate extremes on groundwater–ES relationships, we used the same meteorological data in our simulations—a common approach in modelling groundwater dynamics and feedbacks[7,8,39]. Nonetheless, we did also compare our results with simulations of actual weather and found overall consistent patterns (Supplementary Figs. 10 and 12).

Statistical analyses. For each simulation, we summarized indicators of all ES annually at two spatial scales—220 m × 220 m grid cells and watershed. At the grid-cell scale, we performed overlay analysis to identify locales where groundwater effects were most pronounced. We also generated cumulative frequency distribution plots for the changes in each ES indicator at the grid-cell level. At the watershed level, we calculated watershed differences in ES indicators between model runs with and without groundwater for each climate condition to identify which ES were most affected by groundwater. Analysis was performed separately for simulations from different climate conditions. Absolute changes (for both grid-cell and watershed scales) are presented in the main text, which allow for comparison of actual groundwater effects across different climate for a given ES, but we also present percent changes (for both grid-cell and watershed scales) as Supplementary Figs. 6, 8, 9 as percent differences allow for comparison of groundwater effects across multiple ES. Percent changes for a given ES *j* were calculated separately for each climate scenarios using the equation: $(ES_{groundwater,i,j} - ES_{no\text{-}groundwater,i,j}) / ES_{no\text{-}groundwater,i,j}$, where *i* represents values for *i*th climate conditions). Since Agro-IBIS is a one-dimensional model, transport processes between grid cells were not considered.

To examine the relationship between groundwater effects and WTD and to detect potential nonlinear responses, we plotted differences in ES indicators between model runs with and without groundwater (that is, groundwater effects) against WTD for each ES and climate at the grid-cell level. To assess the robustness of ES responses to WTD across different land covers and soils, we generated additional plots with land cover and soil as additional mediating factors under average climate. To test groundwater effects at the watershed scale and whether effects were mediated by climate, we performed general linear mixed-effects models to handle repeated measures and to avoid pseudo-replication. All statistical analyses were performed in R 3.3[67]. In the linear mixed-effects models, the response variable was the difference between watershed means of ES indicators modelled with and without groundwater. Main effects included climate (as a categorical variable with three levels) and random effects included year nested within climate. Models were fitted using restricted maximum likelihood, and significance of differences was tested using Tukey's multiple comparison with the 'glht' function in the 'multcomp' package in R[68]. Residual plots were assessed for assumptions of normality and homogeneity of variance; no violations were detected. General linear mixed-effect models were analysed using the 'lme4' R package[69], and significance of fixed effects was evaluated using the Satterthwaite's approximation for degrees of freedom in the 'lmerTest' R package[70].

Data availability

The datasets generated and analysed in this study are available from the authors upon request.

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Author contributions

J.Q. and S.C.Z. designed the research and analysed data. J.Q., S.C.Z., M.M. and E.G.B. performed the research. J.Q., S.C.Z., M.M., E.G.B., C.J.K. and S.P.L. interpreted the results. J.Q. and S.C.Z. led the writing process and all authors contributed substantially with commentary, edits and revisions.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to J.Q.

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