PNAS
www.pnas.org

Main Manuscript for

Groundwater dependence of riparian woodlands and the disrupting effect of anthropogenically altered streamflow

Melissa M. Rohde*[1,2], John C. Stella[3], Dar Roberts[4], Michael Bliss Singer[5,6,7]

[1]Graduate Program in Environmental Science, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY, 13210, USA
[2]The Nature Conservancy, 201 Mission Street, 4th Floor, San Francisco, CA, 94105, USA
[3]Department of Sustainable Resources Management, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY, 13210, USA
[4]Department of Geography, University of California, Santa Barbara, 1832 Ellison Hall, Santa Barbara, CA 93106, USA
[5]School of Earth and Environmental Sciences, Cardiff University, Main Building, Park Place, Cardiff, CF10 3AT, UK
[6]Water Research Institute, Cardiff University, The Sir Martin Francis Building, Museum Avenue Cardiff, CF10 3AX, UK
[7]Earth Research Institute, University of California, Santa Barbara, 6832 Ellison Hall, Santa Barbara, CA 93106, USA

*Corresponding Author: Melissa M. Rohde
Email: mmrohde@esf.edu

Author Contributions: MMR, JS, DR, MBS designed research and wrote the paper. MMR and JS performed research and analyzed data.
Competing Interest Statement: The authors declare no conflicts of interest.
Classification: Physical and Biological Sciences (Major Classification) and Sustainability Science (Minor Classification).
Keywords: Riparian vegetation, Groundwater, Streamflow, NDVI, California

This PDF file includes:

Main Text
Figures 1 to 4

Abstract

Riparian ecosystems fundamentally depend on groundwater, especially in dryland regions, yet their water requirements and sources are rarely considered in water resource management decisions. Until recently, technological limitations and data gaps have hindered assessment of groundwater influences on riparian ecosystem health at the spatial and temporal scales relevant to policy and management. Here we analyze Sentinel-2 derived Normalized Difference Vegetation Index (NDVI; n=5,335,472 observations), field-based groundwater elevation (n=32,051 observations), and streamflow alteration data for riparian woodland communities (n=22,153 polygons) over a five-year period (2015-2020) across California. We find that riparian woodlands exhibit a stress response with deeper groundwater, as evidenced by concurrent declines in greenness represented by NDVI. Furthermore, we find greater seasonal coupling of canopy greenness to groundwater for vegetation along streams with natural flow regimes in comparison to anthropogenically altered streams, particularly in the most water-limited regions. These patterns suggest that many riparian woodlands in California are subsidized by water management practices. Riparian woodland communities rely on naturally variable groundwater and streamflow components to sustain key ecological processes, such as recruitment and succession. Altered flow regimes that stabilize streamflow throughout the year and artificially enhance water supplies to riparian vegetation in the dry season disrupt the seasonal cycles of abiotic drivers to which these Mediterranean forests are adapted. Consequently, our analysis suggests that many riparian ecosystems have become reliant on anthropogenically altered flow regimes, making them more vulnerable and less resilient to rapid hydrologic change, and potentially leading to future riparian forest loss across increasingly stressed dryland regions.

Significance Statement

Riparian ecosystems are biodiversity hotspots under intense pressure from multiple stressors. In most water-limited regions, high human water use from agricultural and urban development eclipses environmental water needs and intensifies ecosystem water stress. In particular, adequate consideration of riparian water needs in water resource management is lacking. Here we show that in California, riparian vegetation exhibit: A) seasonal canopy stress responses to deeper groundwater, and B) greater groundwater coupling along streams with natural flow regimes compared to anthropogenically altered streams. We conclude that water subsidies in altered stream systems reduce groundwater dependence of riparian woodlands, undermine their adaptations and resilience to natural hydrologic variation, and ultimately threaten their sustainability under dual threats of increased water demand and a changing climate.

Main Text

Introduction

Riparian ecosystems are hotspots for biodiversity, hosting a wide range of aquatic and terrestrial species. Yet, they are some of the most endangered ecosystems globally (1, 2) since they often exist at the epicenter of urbanization and intensive agriculture. Biodiversity and ecosystem functioning in fluvial environments is largely regulated by shallow alluvial groundwater and its interconnection with surface flow regimes. For many river systems, shallow groundwater is a critical ecological resource – sustaining baseflow throughout the year in perennial streams and supporting intermittent discharge in drylands when the groundwater table intersects the land surface. In addition to regulating flow, groundwater sustains aquatic ecosystems by providing thermoregulation and contributing minerals and oxygen. In terrestrial environments, groundwater provides a subsurface water source to deeply rooted plant species, enabling them to buffer the effects of dry periods (3). Since shallow groundwater along rivers interact with surface water, anthropogenic alteration of streamflow and pumping of local aquifers to meet high societal demand are often at odds with the flow needs for various species and can induce water stress to both aquatic and terrestrial species at critical life stages. These trends are exacerbated in dryland regions, where small but persistent changes in the water balance may have large ecological impacts, further threatening the long-term sustainability of native riparian ecosystems (4, 5).

Phreatophyte trees are foundation species in riparian ecosystems that rely on groundwater and are effective indicators of ecosystem health, especially since they can be monitored using a variety of approaches at different scales (6). Although documented instances of extensive tree mortality, crown die-back, growth decline and poor recruitment exist within groundwater-dependent riparian ecosystems (7–9), there remain critical uncertainties in how strongly riparian woodlands respond to seasonal and interannual fluctuations in water table depth, and how groundwater dependence varies across regions and between natural and altered surface water regimes. Riparian vegetation communities occurring within dryland regions are heavily reliant on low-flow and high-flow components of surface water and groundwater regimes (10, 11). This is because key life-history processes such as propagule dispersal, germination, and establishment are regulated by various characteristics of the flow regime and their interactions with geomorphic and biotic processes (12–14). For example, riparian tree recruitment typically occurs after large floods when propagules are transported onto point bars and the floodplains of naturally flowing rivers. As the river stage declines, the root networks of new germinants grow vigorously to maintain contact with the water table as it declines throughout the growing season. If spring flows are truncated or otherwise anthropogenically modified, or the water table recedes too quickly, new cohorts fail to recruit. Native riparian species that are adapted to these seasonal interconnections between surface water and groundwater are often outcompeted by non-native or upland species where groundwater and surface flow regimes are strongly altered, thus contributing to habitat and biodiversity loss (15–17). In this context, we set out to: A) characterize when and where riparian ecosystems exhibit stress responses to seasonal groundwater table declines; and B) evaluate influences of natural versus anthropogenically altered surface flow regimes on riparian ecosystem groundwater reliance.

Until recently, riparian woodlands have been difficult to study at the landscape scale because they are typically excluded from systematic ground-level forest and agriculture monitoring programs (18). However, remotely-sensed indicators such as the Normalized Difference Vegetation Index (NDVI), a measure of canopy greenness linked to water stress responses such as leaf functioning, growth, and mortality (19), show promise for detecting phreatophyte responses to groundwater. Studies linking NDVI to groundwater levels in Northern China (20), East Coast U.S. (21), Nevada (22), and California (23) have all observed NDVI declines with increasing depth to groundwater (DTG), but they are limited in regional scope and spatial resolution. This is because sensor resolution on Earth observation satellites such as MODIS (250-m) and Landsat (30-m), are too coarse to effectively monitor riparian woodlands, which are typically distributed along river networks in narrow and discontinuous patches (24). When pixels

are large relative to vegetation patches and comprise a functionally diverse set of species, only some of which rely on groundwater, this “mixed-pixel” problem can obscure the detection of phreatophyte responses to groundwater availability (6, 20). In this study, we exploit the finer resolution (10-m) of the European Space Agency’s Sentinel-2 satellite, launched in 2015, to link riparian ecosystem responses (NDVI) to groundwater levels and surface water flow regimes across a broad range of riparian systems in California (USA), and to estimate where and when riparian vegetation is most reliant on groundwater.

California is of global ecological interest since it is one of the world’s top biodiversity hotspots (25), containing more species than the rest of the US and Canada (26). Riparian ecosystems in California coexist with a multi-billion dollar agricultural industry and 40 million people, epitomizing the ongoing global challenge of balancing social, economic, and environmental water needs. The state of California is a recent leader in sustainable groundwater management, since it is one out of only four jurisdictions globally that legally require managers to consider ecosystem impacts when designing sustainability metrics and monitoring programs (27). California’s water systems are highly altered and engineered to redistribute water across the state’s hydrologic regions, from the water-rich Sacramento River region to the semi-arid south where precipitation is low and evaporative losses are high (SI Appendix; Fig. S1). Due to intensive agriculture and urbanization, the riparian ecosystems that exist today within California’s Central Valley represent only ~5% of the floodplain habitat that was present nearly a century ago (28, 29). These remaining riparian habitats continue to be stressed by groundwater overdraft (30), climate change (31, 32), and a surface water system that is highly altered (33, 34) and over-allocated (35). With more than 90% of all freshwater species endemic to California already vulnerable to extinction within the next 100 years (36, 37), it is imperative that groundwater and surface water are managed to protect the broad ecohydrologic niches within natural riparian environments that support biodiversity and ecosystem function.

We coupled Sentinel-2 derived NDVI measurements (n=5,335,472 observations) with field-based groundwater data (n=32,051 groundwater depth measurements), and streamflow alteration indices for three major phreatophytic riparian woodland communities (n=22,153 mapped vegetation polygons) over a five-year period (2015-2020) across California. We focused on mapped vegetation types dominated by phreatophyte species that are ubiquitous throughout the state: *Salix gooddingii* (Goodding’s willow; “willow”), *Populus fremontii* (Fremont cottonwood; “cottonwood”), and *Quercus lobata* (valley oak; “oak”). By combining these large spatiotemporal datasets, we linked NDVI to groundwater and streamflow data to test whether canopy greenness varied with groundwater depth across different woodland communities, hydrologic regions, seasons, and surface flow regimes. We show that: (A) willow, cottonwood, and oak woodlands all exhibit stress responses to groundwater availability as evidenced by declines in NDVI with deeper groundwater; and (B) for vegetation along altered streams, NDVI was elevated and the coupling of greenness with groundwater was weak, compared to natural flow regimes. We conclude that current water management and infrastructure have profoundly altered natural hydrology in a manner that has impacted riparian woodlands. This has manifested in subsidies to groundwater-dependent riparian ecosystems, which in turn, promote high aseasonal growth and function, but with little opportunity for regeneration or natural succession trajectories. These alterations have the potential to lessen the adaptive capacity of riparian vegetation communities in drylands, making them vulnerable and less resilient to climatic changes or water management decisions that affect subsurface water availability.

Results

NDVI and Groundwater Depth

The magnitude and variability of NDVI differ over time between the three riparian phreatophytic woodland communities and show strong spatial variations between hydrologic regions (Figure 1, SI Appendix and Tables S1-S3). Depth to groundwater (DTG) is a significant predictor of NDVI for all vegetation types, and in all cases greenness declines with deeper groundwater (Fig. 2; SI

Appendix, Table S4). The strongest effect (i.e., steepest negative slope) occurs in oak woodlands, in which the response is significantly different from willow, which has the most modest response to DTG (shallowest slope) across the three vegetation types (SI Appendix, Table S5). Cottonwoods exhibit an intermediate response, which does not differ significantly from either willow or oak. These rankings of groundwater dependence follow relative differences in maximum rooting depth among the three communities and their positions within the riparian landscape. As pioneer riparian species, cottonwood and willow colonize channel boundaries, young point bars and low floodplains, with typical rooting depths of ≤2.5 m (38, 39) under natural conditions. The weaker NDVI response to DTG for willow woodlands compared to cottonwood and oak woodlands may reflect differences in fluvial niches. Riparian willows occur in locations with stable and shallow groundwater that support a narrower range of seasonal drought stress conditions than oak, and thus they lack the latter's deep root systems. Valley oak is a later successional species and more drought tolerant in the riparian biome, occupying older and higher fluvial surfaces, with rooting depths of up to 7.5 m in alluvial systems (40) and up to 15 m in fractured rock systems (41). The NDVI-DTG trends across vegetation types vary across hydrologic regions, with the most significant groundwater-dependent relationships occurring in the Central Coast, North Lahontan, Sacramento River, and South Coast (willow only) regions (SI Appendix, Fig. S2 and Table S6).

Surface water influences on NDVI and groundwater depth

Of the total statewide extent of riparian woodlands considered in the study (57,900 ha across all vegetation polygons), 30% of the woodland area occurs along natural stream reaches and 70% occurs along stream reaches with an altered regime (Fig. 3a). We compared the NDVI-DTG trends for each vegetation polygon that had locally available well data by its respective flow modification regime (Natural or Altered; n=582 polygons). DTG was a significant linear predictor of riparian woodland NDVI in both natural and altered systems (Fig. 3b), but the effect is significantly stronger (steeper slope) for vegetation along natural streams (SI Appendix, Table S7). The more robust NDVI-DTG trend for natural streams, observed primarily in the Sacramento River, San Francisco Bay, and Central Coast regions, suggest a greater groundwater reliance with canopy water stress levels that are directly linked to water supply via DTG, relative to altered streams where the relationship is weaker (SI Appendix, Fig. S3 and Table S8).

Distinct seasonal trends are evident in the NDVI-DTG relationships between the wetter northern regions compared to the drier regions in the south. In the Sacramento River region (SI Appendix, Fig. S4a and Table S9), for example, NDVI declines significantly with deeper DTG during spring and summer, and the negative NDVI-DTG slope is steeper in the summer. This suggests a stronger groundwater reliance later in the growing season when vapor pressure deficits (VPD) are highest and soil moisture is low. The weaker influence of DTG on canopy greenness earlier in the spring may reflect both the lower VPD, as well as greater water availability from prior precipitation and elevated snowmelt-driven streamflow along the Sacramento River and its tributaries. In contrast, the South Lahontan region in southeastern California has no significant NDVI trend with DTG in either season (SI Appendix, Fig. S4b and Table S10). In this region, riparian phreatophytes occur only as disparate patches of cottonwood woodlands along a portion of the Mojave River adjacent to a wastewater treatment facility, which provides a substantial perennial water source to the local river channel and its linked shallow groundwater aquifer (SI Appendix, Fig. S5 and S6). The lack of a relationship between groundwater depth and canopy greenness in this arid climate exemplifies the strong anthropogenic control over hydrology for the riparian woodlands.

Flow alteration can be quantified by examining whether seasonal flows are inflated (subsidized) or depleted (abstracted) for riparian vegetation patches adjacent to streams with long-term gauge records. We investigated the effect of seasonal flow alteration by comparing the NDVI response of riparian vegetation patches along streams with inflated and depleted flows (n=1891 vegetation polygons; Fig. 3c). NDVI was lower in summer compared to spring for vegetation under both inflated and depleted flow alteration classes, which is consistent with the expected higher water stress in plants in summer due to reduced water availability (^{2} =744.21, df=3, p<0.001; SI Appendix, Table S11). However, in both seasons, riparian NDVI values along stream reaches with inflated flow were elevated relative to depleted stream reaches. Seasonal differences in NDVI

under both flow alteration classes suggest a tightly coupled vegetation response to the strong seasonal shifts in water availability from precipitation-derived soil moisture in spring towards perennial groundwater in this Mediterranean climate region. However, elevated NDVI along inflated streams (Fig. 3c) suggests more uniform water availability throughout the growing season, as a result of water subsidies associated with conveyance infrastructure and regulated streamflow regimes.

Discussion

Vegetation greenness decreases with groundwater depth

Across California, we found riparian woodlands to be very sensitive to groundwater depth both seasonally and across a wide range of regional hydrologic regimes. Riparian canopy greenness (NDVI), a measure of vegetation health, varied systematically with DTG during the growing season for willow, cottonwood, and oak woodlands (Fig. 2). In locations where deeper groundwater depths coincide with lower NDVI, decreased greenness can be attributed to a wide range of physiological responses such as reduced transpiration and photosynthesis, increased intrinsic water use efficiency, drought-induced leaf abscission, branch and canopy dieback, and cavitation-induced mortality (6, 8, 9, 14). We observe a strong coupling of NDVI with DTG, particularly along natural streams, which is consistent with other studies that found positive correlations between NDVI and precipitation (22) and negative correlations between NDVI and groundwater depth (20–23). However, this is the first study to also observe the influence of surface water flow regimes on mediating the NDVI and DTG relationship, which can be explained by the same processes of focused recharge through riverbeds that are common in drylands (42).

Riparian vegetation relies on groundwater, but some are being subsidized by managed water sources

Under natural conditions, groundwater reliance within California's Mediterranean climate biomes is expected to be highest in the late summer when precipitation is absent, soil moisture is low, evaporative demand is high, and surface water flow in rivers and streams is diminished (43). However, natural groundwater reliance may be disrupted by hydrologic subsidies due to anthropogenic alteration of streamflow. As human water demand and concerns about water security intensify, natural hydrology is increasingly altered through surface water diversions into canals and regulated rivers, extensive groundwater pumping, and significant discharges of recycled wastewater downstream of treatment facilities (33, 34). The consequences of groundwater pumping on deepening water tables and loss of water access by riparian plants are well documented (8, 44). What is less well understood is to what degree altered flow regimes that redistribute water in the dry season augment local shallow alluvial aquifers and provide a supplemental water supply for riparian vegetation (42).

Here, we show that along altered streams, NDVI is higher during the growing season with all other factors equal, and the adverse effect of groundwater depth on NDVI is diminished compared to natural stream systems (Fig. 3b). This strongly suggests that stream alteration, particularly inflated flows, subsidizes riparian phreatophytes, enabling them to maintain high photosynthetic function and water status even during periods of high VPD (Fig. 3c). This is especially the case in drier regions of California (e.g., San Joaquin River, Tulare Lake, South Lahontan), where there is a long history of groundwater depletion due to pumping and most extant stands of phreatophytes occur along streams with inflated or perennial flow conditions due to human activities (e.g., wastewater treatment discharge or summer water deliveries). These results further suggest that a large proportion of California's native riparian woodlands are at least partially maintained by altered surface water regimes and built water infrastructure rather than by the historical and natural seasonal groundwater cycles to which they are adapted.

We provide a graphical conceptual model (Fig. 4) illustrating how NDVI varies seasonally across natural versus altered hydrologic regimes as a function of available subsurface water. Along natural streams, NDVI shows strong seasonal changes associated with greater net water deficit

in summer (Fig. 4b) versus spring (Fig. 4a). Along altered streams, where baseflow discharge is often augmented by agricultural and municipal water conveyance schedules or perennial inputs of treated wastewater from urban areas, NDVI remains high despite deeper regional groundwater levels in the summer (Fig. 4c and 4d). These managed water regimes alter interactions between surface and groundwater, artificially subsidizing deeply rooted plants with consequently greater canopy function and productivity than would otherwise be possible during the annual dry season.

Despite the hydrologic stability that these subsidies provide to extant riparian woodlands, they disrupt natural ecological processes and life history stages of species that are adapted to the fluvial disturbance regime and seasonally variable hydrology of this Mediterranean climate region (14, 24). For example, seed release and dispersal success of native pioneer trees depend on spring flood timing (13), and low summer base flows allow for them to establish and outcompete non-native species with less-adaptive life histories (15, 16). Flood-driven channel migration and cutoff events, which are greatly reduced in altered systems, are critical processes for maintaining native riparian forests over time (45, 46). Although modified surface flow regimes that recharge aquifers can promote short-term growth and function of existing woodland trees. In the absence of recruitment and succession processes, these flow subsidies promote the homogenization of forest age and size structure, greater invasion by non-native species, divergent forest succession and ultimately the transition to novel ecosystems (47, 48). In addition, faster growth induced by water subsidies may promote earlier mortality, a phenomena that is observed globally across many biomes (49). Fast growth is associated with low wood density and high hydraulic conductivity, among other traits that make trees vulnerable at an early age to drought cavitation, attack by pathogens and insect pests, and mechanical damage. Together, with other human stressors including climate change, widespread hydrologic alteration in California and other dryland regions, the long-term fate of native riparian woodlands is threatened; especially where there are ongoing tradeoffs between water diversions, water recycling and instream ecosystem flow needs (4, 5). In light of the combined legacy of large-scale riparian woodland conversion to agriculture, groundwater overdraft, and weakened abiotic/biotic ecosystem linkages through flow alteration and water subsidies, the preservation of these crucial habitats for rare and endemic species now relies on the deliberate, coordinated management of resource and government agencies.

Remote sensing is a promising tool for ecosystem and resource management

Prompted by the recent historic drought, California passed the Sustainable Groundwater Management Act (SGMA) in 2014 to minimize groundwater depletion and regulate its use (50). Under SGMA, local groundwater sustainability agencies are required to achieve sustainability by 2040 by bringing basins into balance and preventing adverse impacts to groundwater-dependent ecosystems (GDEs). There are significant theoretical and data gaps on the ecohydrology of GDEs across broad regions, including California, where the management challenges mirror those of many water-limited regions globally (27).

Achieving sustainable water management in California requires a science-based approach that is feasible and efficient to inform water allocation decisions and support multiple objectives. The coupling of high spatial and temporal resolution of Sentinel-2 satellite imagery with the powerful computing capacity of the Google Earth Engine platform (51) offers a new opportunity for practitioners to monitor regional changes in riparian vegetation in response to water availability, which can integrate ecological considerations into water resource planning and management decisions. By pairing Sentinel-2 derived NDVI data with concurrent field-based DTG measurements, water agencies can infer how groundwater conditions are affecting riparian vegetation communities in their basins so that appropriate thresholds and objectives are established in groundwater sustainability plans.

Conclusion

In this study, we found that vegetation greenness (NDVI) was decoupled from groundwater dynamics for riparian woodlands occurring along hydrologically altered streams compared to those along natural streams. This suggests that native riparian woodlands are opportunistic in

their water use, but vulnerable to changes in water management that may subsequently threaten their long-term sustainability. Though altered flow regimes can offer supplemental water sources that alleviate seasonal drought stress, they also undermine the ecological processes and life history stages that are adapted to the hydrologic variability inherent of Mediterranean climates. Thus, the elevated canopy greenness and aseasonality evident in hydrologically altered riparian woodlands may be masking their extreme vulnerability to rapid hydrologic shifts. In the absence of restoration of natural hydrologic processes, the long-term sustainability of remnant native riparian woodlands in California may require extensive floodplain reforestation and similarly intensive water management approaches. The compound legacy of extensive conversion of riparian woodlands to agriculture and urban land uses and the wholesale disruption of natural surface and groundwater flow regimes, create major challenges for preserving and restoring remnant riparian habitats and their ecohydrologic functioning.

Materials and Methods

Vegetation data acquisition and processing

Vegetation data

The study scope comprised riparian vegetation throughout California that was dominated by phreatophytic woody species as delineated in the California Department of Water Resources' Natural Communities Commonly Associated with Groundwater (NC) dataset (52). The NC dataset contains 98,275 delineated polygons that correspond to vegetation types commonly associated with groundwater (phreatophytes), and we identified three deciduous vegetation alliances (n= 22,153 polygons) representative of riparian environments along large-order streams throughout the state: (1) *Populus fremontii* (cottonwood), (2) *Salix goodingii* (willow), and (3) *Quercus lobata* (valley oak). Details of the dataset is provided in the SI Appendix.

Satellite imagery processing

We compiled, processed and analyzed Sentinel-2, Level-1C satellite imagery acquired between June 23, 2015 and September 30, 2020 for the riparian woodland polygons using Google Earth Engine (51). A supervised classification was performed to include only vegetation canopy pixels by masking out those dominated by bare ground. NDVI, which is a common index used in remote sensing to quantify vegetation 'greenness', was calculated for crown-classified pixels within the vegetation polygons; data processing and analysis details are presented in the SI. NDVI is a dimensionless index that ranges from -1 to 1, where values closer to 1 indicate vegetation with a higher density of green leaves and values close to zero (<0.20) indicate no vegetation. Values <0 denote the presence of surface water.

Hydrology data acquisition and processing

Groundwater

Groundwater level data from observation wells (n=3,951) were downloaded from the California Department of Water Resources' SGMA Data Viewer (53). Wells that monitor groundwater within shallow unconfined aquifers were selected because roots of riparian phreatophyte species typically do not penetrate confining layers or extend >30 m below the ground surface (38, 54). Depth to groundwater (DTG) was calculated for riparian vegetation by subtracting the groundwater elevation at the closest shallow monitoring well from the averaged land surface elevation of each vegetation polygon; data processing details are presented in the SI. After selecting vegetation polygons that met our selection criteria of being <1 km from a shallow groundwater monitoring well with measurements within the study period (June 23, 2015 and September 30, 2020), 747 polygons from the NC dataset were selected for evaluating recent trends between groundwater and vegetation.

Because the groundwater level and NDVI data were collected at different dates and frequencies (e.g., biannual groundwater levels versus NDVI ~10 days), NDVI data were linearly interpolated to derive a daily NDVI measurement for each vegetation polygon, which could then be matched with observed groundwater level data. To avoid temporal autocorrelation due to polygons sampled repeatedly within a season, median values of NDVI and DTG values were calculated for

each polygon according to season for all years in the study (2016-2020) for spring (Apr-Jun) and summer (July-Sept). Because all three vegetation types in this study are winter deciduous, only NDVI and groundwater data with paired dates within the growing season (spring and summer) were included for this study. These comprised 3,560 paired observations from 591 vegetation polygons.

Streamflow Data
We designated all stream reaches adjacent to riparian woodland polygons into two groups — natural or altered flow regimes — based on The National Hydrography Dataset (NHD) drainage features (e.g., rivers, streams, canals/ditches, pipelines; (55)) and the U.S. Geological Survey national flow modification dataset (e.g., high and low flow magnitude, variability, and duration; (34)); data processing and analysis details are presented in the SI.

Statewide streamflow data were accessed from The Nature Conservancy's Natural Flows Database (56), which contains observed streamflow data from stream gauges (n=1241 stream segments) and estimates of natural flows (expected streamflow in the absence of human modification) for all streams and rivers in California (n=171,167 stream segments) from 1950-2015 (33). We identified 1891 vegetation polygons included in this study that were within 1 km of a river reach and had at least five full years of monthly observed and estimated flows between 1996-2015 (n=89 stream segments). To quantify the degree of flow alteration by stream reach, we calculated a monthly ratio of observed/estimated streamflow. Data processing and analysis details are presented in the SI. We then classified the streamflow within each stream reach as "depleted" if the median observed/estimated ratio was <1, indicating that more than half of the recorded observed flows within a season were less than the expected value for that location. Streamflow was classified as "inflated" if the median observed/estimated ratio was >1. This conservative approach tests whether differences in NDVI can be explained by the degree of flow alteration and whether these differences are distinct for inflated (subsidized) versus depleted flows. If flow alteration is not an important explanatory variable of NDVI, all these distributions should be equivalent (statistically similar).

Statistical Analyses
All data analysis and statistical tests were performed using the programming language R (R Core Team, version 3.6.1) (57). Comparisons of NDVI and DTG relationships among vegetation types, hydrologic regions and seasons were made using linear mixed models (*'lme4'* and *'lmerTest'* packages) with random effects for polygon (to account for repeat measurements in multiple years) and for hydrologic region (to account for similar climate and environmental conditions). Post-hoc pairwise comparisons were made using Tukey estimated marginal means (*'emmeans'* package). NDVI and DTG relationships were determined using a linear mixed model (*'lmer'* function) by designating season as a fixed effect and polygon ID as a random effect. For a pairwise comparison of median NDVI across seasons and flow alteration classes (inflated, depleted), Wilcox and Kruskal tests were used. Goodness of fit for linear mixed models (58) were determined using the ('MuMIn' package); see SI Appendix for details. Our analyses utilize a statistical significance threshold of $p<0.05$.

Acknowledgments
Support for this work came from the U.S. National Science Foundation (BCS-1660490, EAR-1700517 and EAR-1700517) and the U.S. Department of Defense's Strategic Environmental Research and Development Program (RC18-1006). The authors thank Jeanette Howard, Kirk Klausmeyer, Julie Zimmerman, and Tanushree Biswas for their feedback on this research and manuscript. The code developed for this study can be found at https://github.com/melrohde/CA_RiparianGDE. The post-processed datasets are also available from the Environmental Data Initiative archive (https://environmentaldatainitiative.org/).

References

1. J. S. Albert, *et al.*, Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio*, 1–10 (2020).
2. D. Dudgeon, *et al.*, Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol Rev* **81**, 163–182 (2006).
3. M. Mayes, *et al.*, Climate sensitivity of water use by riparian woodlands at landscape scales. *Hydrol Process* **34**, 4884–4903 (2020).
4. L. G. Perry, D. C. Andersen, L. V. Reynolds, S. M. Nelson, P. B. Shafroth, Vulnerability of riparian ecosystems to elevated CO2 and climate change in arid and semiarid western North America. *Global Change Biol* **18**, 821–842 (2012).
5. K. R. Hultine, *et al.*, Climate change perils for dioecious plant species. *Nat Plants* **2**, 16109 (2016).
6. D. Eamus, S. Zolfaghar, R. Villalobos-Vega, J. Cleverly, A. Huete, Groundwater-dependent ecosystems: recent insights from satellite and field-based studies. *Hydrol. Earth Syst. Sci.* **19**, 4229–4256 (2015).
7. E. Naumburg, R. Mata-gonzalez, R. G. Hunter, T. Mclendon, D. W. Martin, Phreatophytic Vegetation and Groundwater Fluctuations: A Review of Current Research and Application of Ecosystem Response Modeling with an Emphasis on Great Basin Vegetation. *Environmental Management* **35**, 726–740 (2005).
8. M. L. Scott, P. B. Shafroth, G. T. Auble, Responses of Riparian Cottonwoods to Alluvial Water Table Declines. *Environmental Management* **23**, 347–358 (1999).
9. J. C. Stella, J. Riddle, H. Piégay, M. Gagnage, M.-L. Trémélo, Climate and local geomorphic interactions drive patterns of riparian forest decline along a Mediterranean Basin river. *Geomorphology* **202**, 101–114 (2013).
10. J. C. Stromberg, V. B. Beauchamp, M. D. Dixon, S. J. Lite, C. Paradzick, Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. *Freshwater Biol* **52**, 651–679 (2007).
11. R. M. Diehl, A. C. Wilcox, J. C. Stella, Evaluation of the integrated riparian ecosystem response to future flow regimes on semiarid rivers in Colorado, USA. *J Environ Manage* **271**, 111037 (2020).
12. D. M. Merritt, E. E. Wohl, Processes governing hydrochory along rivers: Hydraulics, hydrology, and dispersal phenology. *Ecol Appl* **12**, 1071–1087 (2002).
13. J. C. Stella, J. J. Battles, B. K. Orr, J. R. McBride, Synchrony of Seed Dispersal, Hydrology and Local Climate in a Semi-arid River Reach in California. *Ecosystems* **9**, 1200–1214 (2006).
14. S. B. Rood, J. H. Braatne, F. M. R. Hughes, Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiol* **23**, 1113–1124 (2003).
15. J. C. Stromberg, *et al.*, Altered stream-flow regimes and invasive plant species: the Tamarix case. *Global Ecol Biogeogr* **16**, 381–393 (2007).
16. D. M. Merritt, N. L. R. Poff, Shifting dominance of riparian Populus and Tamarix along gradients of flow alteration in western North American rivers. *Ecol Appl* **20**, 135–152 (2010).
17. R. Froend, B. Sommer, Phreatophytic vegetation response to climatic and abstraction-induced groundwater drawdown: Examples of long-term spatial and temporal variability in community response. *Ecol Eng* **36**, 1191–1200 (2010).
18. S. Dufour, P. M. Rodríguez-González, M. Laslier, Tracing the scientific trajectory of riparian vegetation studies: Main topics, approaches and needs in a globally changing world. *Sci Total Environ* **653**, 1168–1185 (2018).
19. M. M. Gómez-Sapiens, *et al.*, Effect of an environmental flow on vegetation growth and health using ground and remote sensing metrics. *Hydrol Process* **34**, 1682–1696 (2020).
20. J. Lv, *et al.*, Groundwater-dependent distribution of vegetation in Hailiutu River catchment, a semi-arid region in China. *Ecohydrology* **6**, 142–149 (2012).
21. C. Aguilar, J. C. Zinnert, M. J. Polo, D. R. Young, NDVI as an indicator for changes in water availability to woody vegetation. *Ecological Indicators* **23**, 290–300 (2012).
22. J. Huntington, *et al.*, Assessing the role of climate and resource management on groundwater dependent ecosystem changes in arid environments with the Landsat archive. *Remote Sensing of Environment* **185**, 186–197 (2016).
23. P. Gong, X. Miao, K. Tate, C. Battaglia, G. S. Biging, Water table level in relation to EO-1 ALI and ETM+ data over a mountainous meadow in California. *Can J Remote Sens* **30**, 691–696 (2004).

24. J. C. Stella, P. M. Rodríguez-González, S. Dufour, J. Bendix, Riparian vegetation research in Mediterranean-climate regions: common patterns, ecological processes, and considerations for management. *Hydrobiologia* **719**, 291–315 (2013).
25. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
26. R. Calsbeek, J. N. Thompson, J. E. Richardson, Patterns of molecular evolution and diversification in a biodiversity hotspot: the California Floristic Province. *Mol Ecol* **12**, 1021–1029 (2003).
27. M. M. Rohde, R. Froend, J. Howard, A Global Synthesis of Managing Groundwater Dependent Ecosystems Under Sustainable Groundwater Policy. *Groundw* **55**, 293–301 (2017).
28. P. B. Moyle, J. E. Williams, Biodiversity Loss in the Temperate Zone: Decline of the Native Fish Fauna of California. *Conserv Biol* **4**, 275–284 (1990).
29. N. E. Seavy, *et al.*, Why Climate Change Makes Riparian Restoration More Important than Ever: Recommendations for Practice and Research. *Ecol Restor* **27**, 330–338 (2009).
30. B. R. Scanlon, L. Longuevergne, D. Long, Ground referencing GRACE satellite estimates of groundwater storage changes in the California Central Valley, USA. *Water Resources Research* **48**, 587 (2012).
31. T. E. W. Grantham, D. M. Carlisle, G. J. McCabe, J. K. Howard, Sensitivity of streamflow to climate change in California. *Climatic Change* **118**, 10676 (2018).
32. D. L. Swain, B. Langenbrunner, J. D. Neelin, A. Hall, Increasing precipitation volatility in twenty-first-century California. *Nature Climate Change* **8**, 1–10 (2018).
33. J. K. H. Zimmerman, *et al.*, Patterns and magnitude of flow alteration in California, USA. *Freshwater Biol* **63**, 859–873 (2018).
34. D. M. Carlisle, *et al.*, "Flow Modification in the Nation's Streams and Rivers" (U.S. Geological Survey, 2019).
35. T. E. Grantham, J. H. Viers, 100 years of California's water rights system: patterns, trends and uncertainty. *Environ Res Lett* **9**, 084012 (2014).
36. P. B. Moyle, J. V. E. Katz, R. M. Quiñones, Rapid decline of California's native inland fishes: A status assessment. *Biol Conserv* **144**, 2414–2423 (2011).
37. J. K. Howard, *et al.*, Patterns of Freshwater Species Richness, Endemism, and Vulnerability in California. *PLoS ONE* **10**, e0130710 (2015).
38. J. C. Stromberg, Root patterns and hydrogeomorphic niches of riparian plants in the American Southwest. *J Arid Environ* **94**, 1–9 (2013).
39. P. B. Shafroth, J. C. Stromberg, D. T. Patten, Woody riparian vegetation response to different alluvial water table regimes. *Western North American Naturalist* (2000).
40. H. J. Schenk, R. B. Jackson, Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**, 480–494 (2002).
41. D. C. Lewis, R. H. Burgy, The Relationship between oak tree roots and groundwater in fractured rock as determined by tritium tracing. *J Geophys Res* **69**, 2579–2588 (1964).
42. E. A. Quichimbo, M. B. Singer, M. O. Cuthbert, Characterising groundwater–surface water interactions in idealised ephemeral stream systems. *Hydrol Process* **34**, 3792–3806 (2020).
43. K. R. Hultine, S. E. Bush, J. R. Ehleringer, Ecophysiology of riparian cottonwood and willow before, during, and after two years of soil water removal. *Ecol Appl* **20**, 347–361 (2010).
44. D. J. Cooper, D. R. D'Amico, M. L. Scott, Physiological and Morphological Response Patterns of Populus deltoides to Alluvial Groundwater Pumping. *Environmental Management* **31**, 215–226 (2003).
45. D. J. Cooper, D. C. Andersen, R. A. Chimner, Multiple pathways for woody plant establishment on floodplains at local to regional scales. *J Ecol* **91**, 182–196 (2003).
46. J. C. Stella, *et al.*, The Role of Abandoned Channels as Refugia for Sustaining Pioneer Riparian Forest Ecosystems. *Ecosystems* **14**, 776–790 (2011).
47. W. C. Johnson, *et al.*, Forty Years of Vegetation Change on the Missouri River Floodplain. *Bioscience* **62**, 123–135 (2012).
48. P. Janssen, *et al.*, Divergence of riparian forest composition and functional traits from natural succession along a degraded river with multiple stressor legacies. *Sci Total Environ* **721**, 137730 (2020).
49. R. J. W. Brienen, *et al.*, Forest carbon sink neutralized by pervasive growth-lifespan trade-offs. *Nat Commun* **11**, 4241 (2020).
50. S. of California, Sustainable Groundwater Management Act (2014).

51. N. Gorelick, *et al.*, Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sens Environ* **202**, 18–27 (2017).
52. C. D. of W. Resources, Natural Communities Commonly Associated with Groundwater (NCCAG) Dataset (2018) (May 15, 2020).
53. C. D. of W. Resources, SGMA Data Viewer (n.d.) (December 19, 2020).
54. Y. Fan, G. Miguez-Macho, E. G. Jobbágy, R. B. Jackson, C. Otero-Casal, Hydrologic regulation of plant rooting depth. *Proc National Acad Sci* **114**, 10572–10577 (2017).
55. H. S. Corporation, NHD Plus - NHDPlus Version 2 (n.d.) (December 19, 2020).
56. J. K. H. Zimmerman, *et al.*, "California Unimpaired Flows Database v2.0.1" (The Nature Conservancy, 2020).
57. R. D. C. Team, R: A Language and Environment for Statistical Computing (2008).
58. S. Nakagawa, H. Schielzeth, A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol Evol* **4**, 133–142 (2013).

Figures and Tables

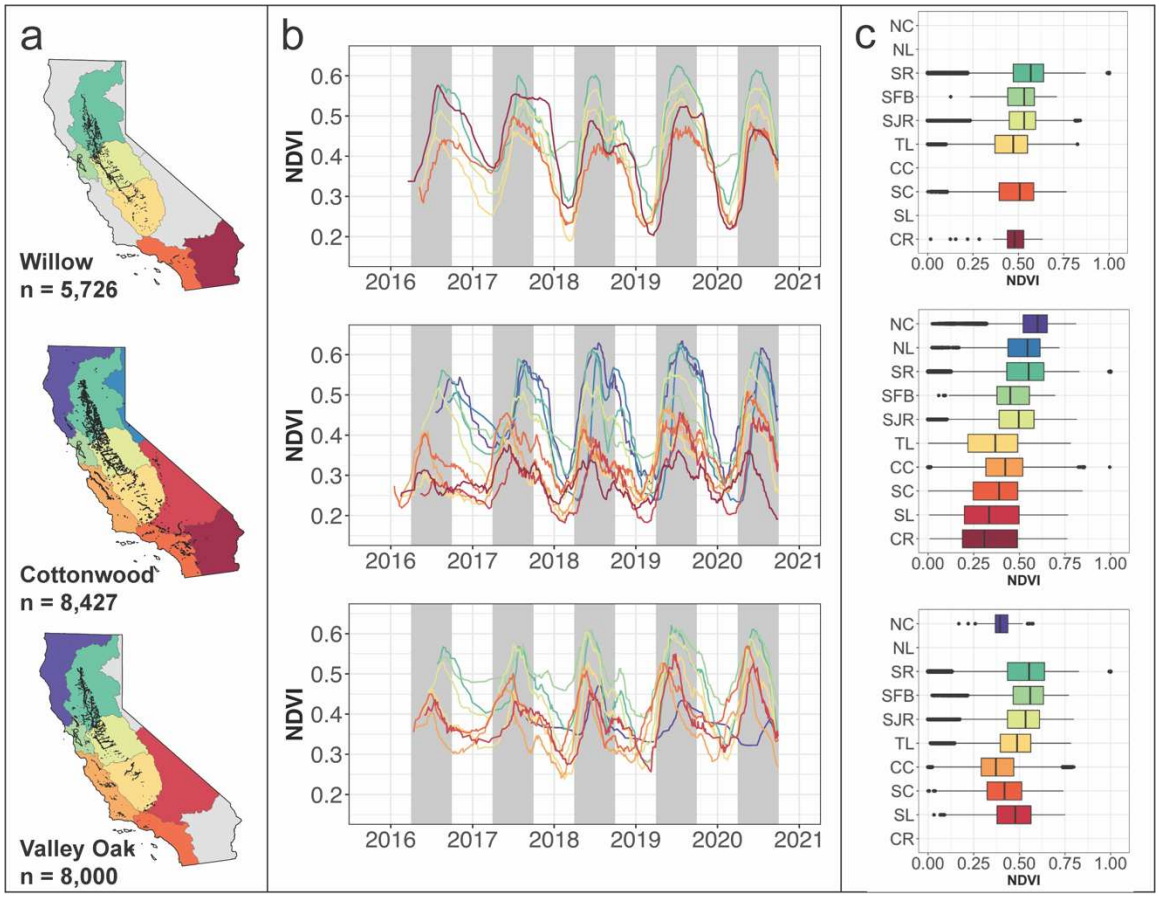

Figure 1. NDVI trends by hydrologic region. (a) Spatial distribution of riparian vegetation types (black polygons) within each hydrologic region (colors). (b) NDVI time series of 2016-2020 with annual growing seasons (Apr-Sept; highlighted in grey) for willow, cottonwood, and oak woodland vegetation types. Each line represents the median value for all mapped vegetation polygons within each hydrologic region. (c) Interquartile ranges (IQR; 25th to 75th quantiles) and median polygon values within the growing season. Outlying points beyond the minimum (Q1-1.5*IQR) and maximum (Q3+1.5*IQR) are plotted individually. Hydrologic regions include the North Coast (NC), North Lahontan (NL), Sacramento River (SR), SF Bay (SFB), San Joaquin River (SJR), Tulare Lake (TL), Central Coast (CC), South Coast (SC), South Lahontan (SL), and Colorado River (CR). Hydrologic regions shaded in gray indicate those with no mapped polygons for that vegetation type.

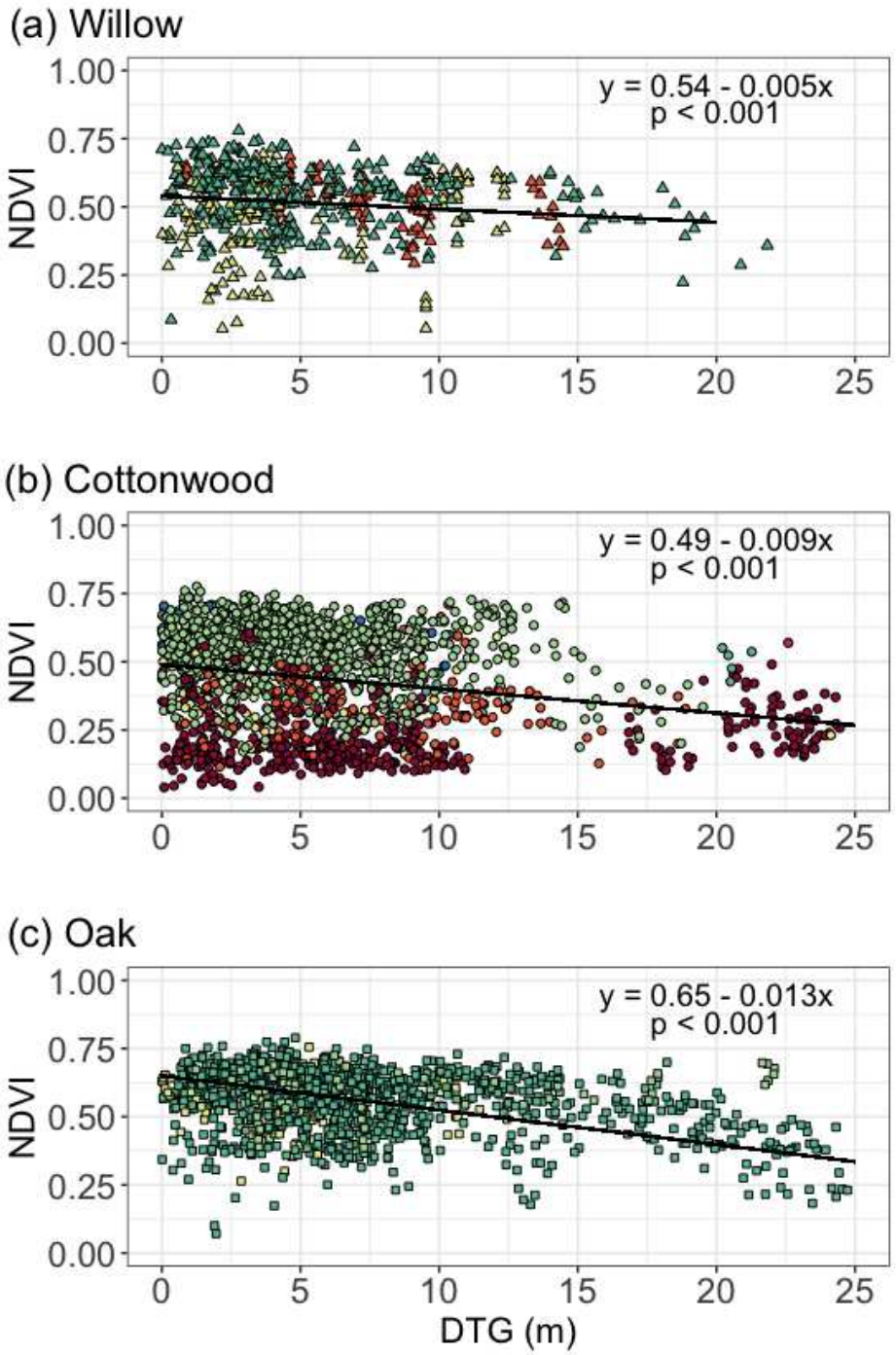

Figure 2. Linear mixed-effects regression models of NDVI and depth to groundwater (DTG) for (a) willow, (b) cottonwood, and (c) oak vegetation types. Each data point represents a vegetation polygon's spring or summer median NDVI value and the corresponding DTG data for a given year. The colors correspond to hydrologic regions (see Fig. 1).

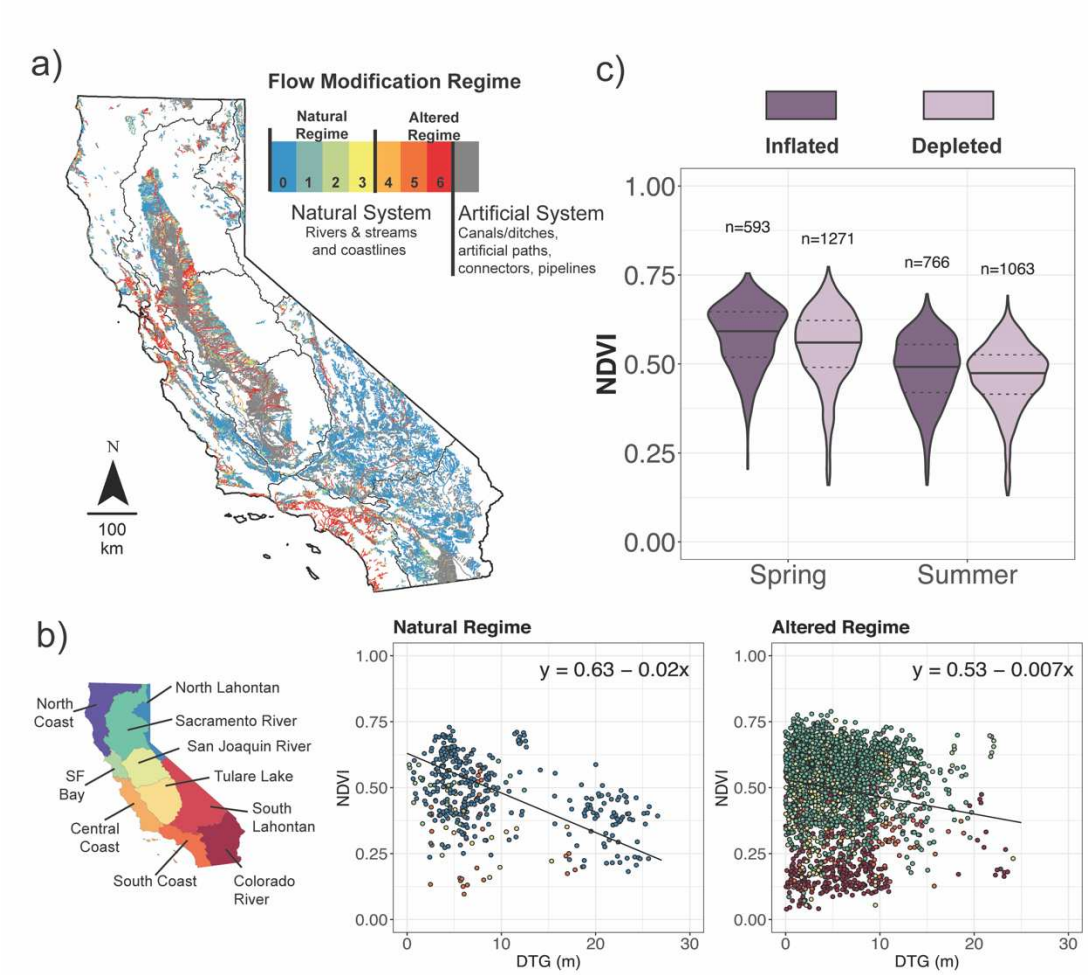

Figure 3. Riparian vegetation responses (NDVI) to groundwater and flow regimes. (a) Flow modification regime (34, 55) for all waterways within California's groundwater basins (n=82,504 waterway segments) (34, 56) (b) NDVI and DTG trendlines by flow modification regime (panel a) for vegetation (n=582 polygons) within 1 km of a well included in this study. The NDVI-DTG trends are significantly different between flow regimes, with steeper slopes in natural versus altered regimes ($p<0.001$). The color points correspond to hydrologic regions indicated on the inset map. (c) Median seasonal NDVI violin plots classified by flow alteration (inflated and depleted) for vegetation (n=1891 polygons) within 1 km of a stream gauge with observed and estimated flow data (56). The dashed lines denote the 25th and 75th percentiles and the solid line denote the 50th percentile. All groups were significantly different from each other ($p<0.001$).

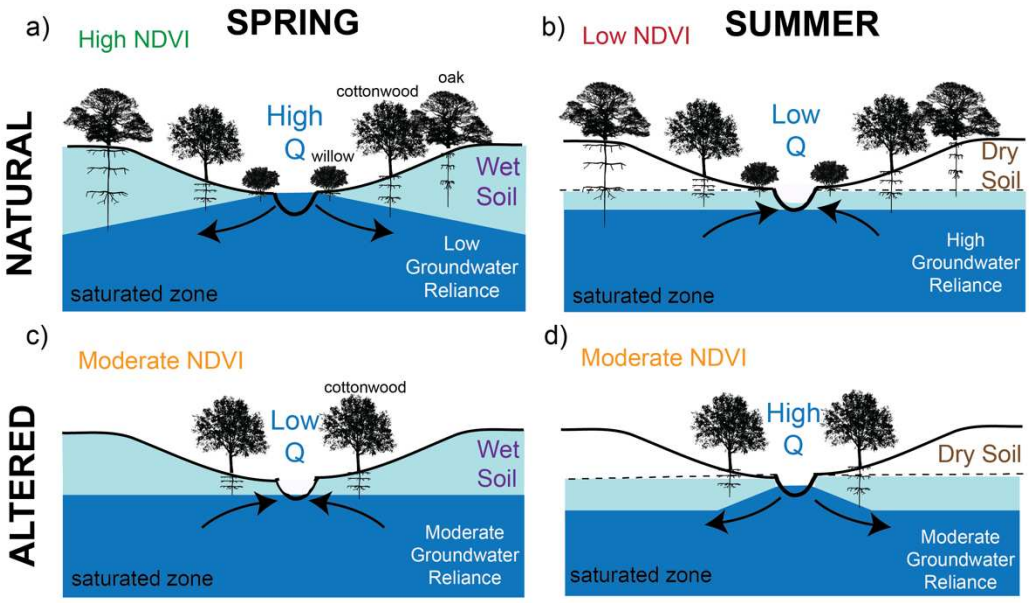

Figure 4. Conceptual model of riparian vegetation reliance on groundwater under different seasonal and surface water influences: (a) natural streams - spring, (b) natural streams - summer, (c) altered streams - spring, (d) altered streams - summer. Seasonal hydrologic variability of natural streams results in greater NDVI differences between spring and summer, compared to altered streams in which water subsidies minimize seasonal NDVI changes. Surface flow (Q) and groundwater are depicted in dark blue, soil moisture in light blue, and the capillary fringe is represented by the dashed line.