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MONITORING THE WETLAND LANDSCAPE: WHITE-FACED IBIS (PLEGADIS CHIHI)
BREEDING HABITAT AS A MODEL ASSEMBLAGE

By

SHEA PALMER COONS

B.S., Colorado State University, Fort Collins, CO, 2015

Thesis

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Approved by:

Scott Whittenburg, Associate Dean of the Graduate School
Graduate School

Dr. Victoria J. Dreitz, Chair
Wildlife Biology Program, Department of Ecosystem and Conservation Sciences

Patrick Donnelly
U.S. Fish and Wildlife Service

Dr. Winsor Lowe
Wildlife Biology Program, Department of Biological Sciences

Dr. John Kimball
Systems Ecology Program, Department of Ecosystem and Conservation Sciences

Monitoring the wetland landscape: white-faced ibis (*Plegadis chihi*) breeding habitat as a model system

Chairperson: Dr. Victoria Dreitz

ABSTRACT

Wetlands structure landscape biodiversity by providing critical habitat to numerous fish and wildlife species. However, climate change, growing human populations, and shifting land use practices strain limited water supplies that sustain wetlands in the semi-arid western US. Conserving a wetland network with prominent value to wildlife is paramount to ensure future security of habitat and ecosystem processes. Here, I use white-faced ibis (*Plegadis chihi*; hereafter ‘ibis’) breeding colonies as a model system to identify and monitor a landscape-scale wetland network across the semi-arid western US. Ibis serve an important role in marking ecologically important wetland networks because they require a wide range of wetland habitats near colony locations for nesting and foraging. My analysis encompasses 153 breeding colonies in eight regions, derived from ecoregions, located on private and public lands. I evaluate long-term (1988-2020) patterns of wetland availability at ibis breeding colonies using surface water as a proxy for wetland flooding. Surface water trends are examined based on individual colony, region, ownership, hydrology (i.e. annual duration of wetland flooding), and wetland types (e.g. flood-irrigated agriculture, managed wetlands). To identify landscape drivers influencing flooding patterns, I link long-term trends to regional climate and anthropogenic factors. Analysis shows that approximately 60% of individual colony locations experienced wetland drying, and 5 of the 8 regions showed significant declines in wetland availability. Snow-water equivalent, daily minimum temperature, and irrigation were prevalent drivers of wetland trends. Publicly managed wildlife refuges, a central component to the colony network, were specifically impacted by patterns of wetland drying. These areas provide important over-water nesting locations in semi-permanent wetlands. Additionally, declines in flood-irrigated agriculture impacted adjacent ibis colonies through reduced foraging habitat. While underlying mechanisms influencing individual wetland sites are complex, pervasive drying of nesting and foraging habitat imperils the wetland network resiliency. Regional coordination and private-public partnerships are key to the long-term viability of a wetland network that benefits ibis and numerous other wetland-dependent species.

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INTRODUCTION

Occupying less than four percent of the land area in the western US (hereafter, ‘the West’; Tiner 2003), wetlands have a disproportionately high value compared to their footprint on the landscape (Costanza et al. 1997). They provide critical ecosystem services via flood and drought mitigation, water purification, erosion prevention, carbon sequestration, and groundwater recharge (Mitsch and Gosselink 2000; Mitsch et al. 2013). Additionally, highly biodiverse environments are found within wetlands, providing habitat for numerous fish and wildlife species (Ward et al. 1999; Mitsch and Gosselink 2000; Kingsford et al. 2016). However, wetlands have suffered considerable loss and degradation (Dahl and Johnson 1991; Mitsch and Gosselink 2000). Climate change, increased water use, land use change, pollution, invasive species, and stream flow alterations drive the continued loss of wetlands worldwide and decrease their ability to provide ecosystem services.

Wetland systems in the western US reflect the combined effects of an arid climate regime and human demands for water. Annual precipitation largely falls as snow in winter, and the bulk of the available water is spring snowmelt and subsequent runoff (Stewart et al. 2004; Hamlet et al. 2007). With limited precipitation during the growing season, many producers rely on irrigation to fulfill crop water requirements. As a result, irrigation accounts for over 80% of consumptive water use in the West (Dieter et al. 2018), with the associated infrastructure and runoff shaping wetland hydrology (Downard and Endter-Wada 2013). Additionally, human population growth in the West outpaces other regions in the US and drives cropland expansion and urbanization (Czech et al. 2000; Hansen et al. 2002; Lark et al. 2015). Current rates of use,

coupled with increasing demands, put considerable stress on already strained water supplies and may have lasting ramifications for wetlands and wildlife.

Water balance alterations due to climate change further reshape hydrological processes and systems across the West, particularly wetlands. While wetland temporal and spatial dynamics reflect natural variations in hydrology and climate, uninterrupted climate trends are expected to cause broad wetland loss or reductions (Johnson et al. 2005; Records et al. 2014). Climate models predict higher temperatures that will impact wetland systems via decreased soil moisture (Schlaepfer et al. 2017), reduced snowpacks (Smith and Wagner 2006), and lowered streamflows (Perry et al. 2012). Additionally, precipitation and evapotranspiration, two factors that govern the extent of surface water, may shift in timing and magnitude (Trenberth et al. 2003; Hamlet et al. 2007). Consequently, climate change will magnify current pressures on wetland systems and establish a new normal for wetland processes.

Inundation and drought regimes are fundamental to wetland processes, yet, increased hydrologic variability predicted by climate models can critically impair wetland processes (Burkett and Kusler 2000; Salimi et al. 2021). Applying metapopulation theory to wetlands provides insights into mitigating climate change effects on these dynamic ecosystems. Metapopulation theory is often applied to wildlife and plant populations but is also a relevant approach for examining abiotic resources. Bennetts and Kitchens (1997) use the metapopulation concept to develop conservation strategies for a wetland-dependent species, the endangered snail kite (*Rostrhamus sociabilis*). The US snail kite population is regulated by periodic drought of the Florida peninsula wetland network (Takekawa and Beissinger 1989). Consequently, viewing individual wetlands as part of a “meta-habitat” encourages the conservation of this species (Bennetts and Kitchens 1997; Mooij et al. 2002). This strategy extends metapopulation concepts

to landscape features, where small networks of wetlands face greater extinction risk than large wetland networks (Hanski 1998). Similarly, conserving wetlands across a broad spatial extent increases the probability that some wetlands will remain inundated during detrimental local drying or flooding events, as it is unlikely that a single drought or flood event will impact the entire region (Bennetts and Kitchens 1997).

Changing climate regimes and increasing human demands will determine water allocation in the West, leaving limited water resources for wildlife needs. Conserving a wetland network with prominent wildlife value will ensure the future security of essential habitat and ecosystem processes that sustain waterbirds and other wetland-dependent species. White-faced ibis (*Plegadis chihi*; hereafter 'ibis'), a wading bird reliant on wetlands throughout its annual cycle, can serve an important role in marking ecologically diverse landscapes. Because their reliance on spatially broad and diverse wetlands aligns with the needs of other wetland-dependent wildlife, ibis are a useful umbrella species for a functional wetland network. Ibis breed and forage exclusively in wetlands across the western US, including California, Colorado, Oregon, Idaho, Wyoming, Nevada, Utah, and Montana (Smiley and Keinath 2003). Successful breeding depends on high wetland diversity that supports the energetic demands of raising offspring and daily migrations between nesting and foraging locations. For example, ibis often use semi-permanently flooded wetlands (29-184 cm deep) with tall emergent vegetation for nesting habitat (Ryder and Manry 1994; Herzog et al. 2020), while surrounding temporary and seasonal wetlands (5-25 cm deep) provide foraging opportunities (Smiley and Keinath 2003; Safran 1997; Safran et al. 2000). Additionally, ibis are highly mobile and respond to unpredictable wetland conditions by relocating to other regions when habitat deteriorates (Ryder 1967). Changes in ibis presence and abundance are conspicuous because of their unique

appearance and high observability, making them a useful indicator for shifting wetland states. Therefore, identifying wetland systems important to ibis dictates the wetlands of highest conservation priority at a spatial scale relevant to migratory birds.

Climate change, growing human populations, and shifting land use practices mean an uncertain future for many wetlands across the West. Physical loss of wetlands (e.g. drainage, conversion to agriculture, etc.) in the US has slowed (Davidson et al. 2014). However, functional atrophy continues to impact wetlands through prolonged drying, altered inundation timing, and unsuitable salinity or water depths. While many migratory waterbird species, including ibis, are at risk of significant range losses (Langham et al. 2015), few studies have examined the status of the wetland network supporting continental movements of migratory waterbirds. My research objectives address the following: 1) How is ibis breeding habitat changing across the western US?, 2) How are these changes reflected across individual colony locations, ecologically distinct regions, land tenure, hydrology, and land-use type?, 3) What are the relative importance of climate and anthropogenic influences in driving inundation within ibis habitat?. I use ibis breeding colonies to identify and monitor a wetland network that supports other wetland-dependent fish and wildlife species. Surface water hydrology served as a proxy for wetland function and facilitated the evaluation of shifting habitat conditions in and around colony locations. I also measured factors influencing wetland trends, including ownership, hydrology (i.e. annual duration of wetland flooding), and land-use practices (e.g. flood-irrigated agriculture, managed wetlands). To identify landscape drivers influencing hydrology patterns, I linked long-term trends to regional climate and anthropogenic factors. My results measure wetland resilience across the western US and inform conservation actions targeting a wetland network that sustains migratory waterbird viability.

METHODS

STUDY AREA

This study encompassed a network of ibis breeding habitats associated with 153 known colonies located in the Intermountain West and western Great Plains including the states of California, Colorado, Idaho, Nevada, Montana, Oregon, Utah, and Wyoming (Figure 1). The ecological setting is characterized by aridity, the prevalence of public lands, agriculture, rapid human population growth, and diverse habitats and topography. Because agriculture accounts for over 80% of surface water use in the western US (Dieter et al. 2018), irrigation infrastructure has heavily shaped wetland hydrology and distribution (Downard and Endter-Wada 2013).

Though widely distributed and essential for ibis, wetlands cover a relatively small footprint; approximately one to three percent of the western US land surface is classified as wetlands (Tiner 2003). The aridity and precipitation cycles of the study area produce wetlands that alternate between periods of drought and flooding. I identified wetland study sites using state and federal ibis colony survey records from 1984 to 2019, which produced a comprehensive collection of 153 documented ibis breeding colonies. These locations included inactive sites that previously hosted colonies in addition to currently active colony locations. Colony sites located in California's Central Valley were excluded because highly managed water systems, particularly irrigation water conveyance, govern nearly all wetland hydrology in this region (Hanak and Lund 2012). Consequently, hydrology patterns in the Central Valley reflect active manipulation that may be decoupled from climate factors, unlike other regions found in the Intermountain West and Great Plains. Breeding colony establishment depends upon the suitability of nesting habitat at the colony location as well as the availability of foraging in

surrounding wetlands (Bray and Klebenow 1988, Smiley and Keinath 2003). I buffered breeding colony locations by 18 km because ibis forage predominantly within this distance (Bray and Klebenow 1988). References to colony locations hereafter are inclusive of wetlands at the colony site and surrounding 18 km radius.

Precipitation seasonality defines vegetative patterns and water availability within the Great Plains and Intermountain West. Summer rainfall is the primary form of precipitation in the Great Plains and some areas in the Intermountain West (Lauenroth and Bradford 2009; Lauenroth et al. 2014). Other areas in the Intermountain West receive most of their precipitation as snow in the winter with a summer minimum (Cayan 1996). Both regions are characterized by a semi-arid climate with relatively high evapotranspiration and low precipitation (Williams 1999; Mckinstry et al. 2004). Within the Intermountain West, the bulk of the available water is spring snowmelt and the subsequent runoff (Stewart et al. 2004; Hamlet et al. 2007), which supplies the majority of the annual stream discharge supporting freshwater lakes and seasonally and semi-permanently flooded wetlands (Cayan 1996).

Breeding colony locations span a spectrum of land uses and ecosystems. Subsequently, I grouped ibis colony sites by ecoregions to normalize unique climate and anthropogenic drivers influencing wetland processes. Ecoregion is a geographical framework denoting areas with similar ecosystem components and processes (Omernik and Griffith 2014). This framework facilitates ecosystem management by incorporating biotic and abiotic components, including humans, defining each ecoregion. Level III ecoregions (Omerinik and Griffith 2014) aggregated by peak precipitation timing and water storage dynamics (hereafter ‘regions’) provided a hydrologically relevant framework to group ibis breeding colonies. Ibis breeding colony locations are within eight ecoregions: Great Basin-Colorado Plateau, Mojave-Sonoran Deserts,

Northern Rockies, Middle Rockies, Southern Rockies and Basins, Northern Plains, Southern Plains, and Pacific Northwest (Figure 1). The Great Basin-Colorado Plateau is an arid to semiarid region characterized by cold deserts with a dry continental climate (Wilken et al. 2011). The Northern Rockies, Middle Rockies, and Southern Rockies and Basins regions experience peak precipitation in the winter; however, each region exhibits differences in climate patterns. Pacific maritime influences in the Northern Rockies foster a wetter climate than the other Rockies regions (Wilken et al. 2011). In contrast, the Southern Rockies and Basins region have earlier snowmelt than the Northern and Middle Rockies regions (Mckinstry et al. 2004; Wilken et al. 2011). Southern Plains and Northern Plains are semi-arid prairies that receive the majority of precipitation during the summer months; however, the Northern Plains region has a slightly cooler climate than the Southern Plains (Mckinstry et al. 2004; Lauenroth and Bradford 2009). The Pacific Northwest region has the wettest climate of the regions, while the Mojave-Sonoran Deserts region is the driest (Wilken et al. 2011).

WETLAND SURFACE WATER MODELLING

Surface water area, or wetland flooding, was quantified at 153 ibis breeding colony sites and periphery wetlands across 37 years, 1984 to 2020. Monthly monitoring (Apr-Aug) was concurrent with annual ibis nesting, chick rearing, and pre-migration events. Additional monitoring of March, September, and October was used for determining wetland inundation regimes. I analyzed wetland flooding within individual sites (site-level) and across each region (region-level) using satellite imagery, which is an effective method for capturing large-scale wetland information (Jin et al. 2017; Huang et al. 2014). Landsat 5 Thematic Mapper (1984-2011) and Landsat 8 Operational Land Imager (2013-2020) satellite imagery were used to capture hydrologic patterns within individual wetlands. The year 2012 was excluded due to a gap

in satellite coverage. Landsat revisit time was 16 d and spatial resolution was 30 m. Satellite imagery binned by calendar month (Mar-Oct) was averaged into a single multispectral image using a 5-year rolling median. Landsat pixel quality attributes generated by the CFMASK algorithm (Foga et al. 2017) allowed me to mask imagery pixels containing clouds, cloud shadows, snow, and ice in all images. This approach captured the variability of wetland habitat while reducing the interference of clouds, cloud shadows, snow, and ice in monitoring the wetland landscape. I applied an extended rolling median to individual months when persistent cloud cover obscured wetland observations. To prevent artificial trends due to suboptimal imagery quality, early spring imagery (i.e. March and April) was excluded from locations where persistent cloud cover could not be corrected with an extended rolling median.

Following the methods that Donnelly et al. (2019; 2020) outlined, I used a constrained spectral mixture analysis (SMA; Adams and Gillespie 2006) to classify imagery and produce monthly estimates of wetland extent. An SMA estimates the proportion of water within each 30x30 m pixel that forms a Landsat satellite image (Jin et al. 2017). This method accounts for flooding in areas with shallow, turbid water and interspersed emergent vegetation that reduce detectability (DeVries et al., 2017). I assumed full inundation of a pixel when water was present, and I omitted pixels with less than 25% water from summaries to reduce the overestimation of surface water extent (Donnelly et al. 2020). The SMA included all unmasked pixels in the visible, near-infrared, and short-wave infrared bands. Identical methods used by Donnelly et al. (2019) estimated the accuracy of surface water determinations to be 93%-98%. Similar time-series wetland inundation studies have produced comparable accuracy (Jin et al. 2017).

Training data for SMA is minimal and requires spectral endmember classification. Spectral endmembers serve as reference points for “pure” spectra corresponding to land cover

classes and enable the SMA to identify the spectral composites of mixed pixels in a satellite image. Spectral endmember training site locations represented water, wetland vegetation, upland, shrub, and soil land cover types. I generated water and wetland vegetation endmembers using the normalized difference water and normalized difference vegetation indices, respectively (Box et al. 1989; McFeeters 1996). The endmembers for upland, shrub, and soil were generated from static plots identified through 30 m multispectral satellite imagery. Shrub plots were characterized by dense, dark-leaved shrubs or conifers. Upland plots included shrublands with high amounts of exposed soil and low vegetative productivity. Soil plots included areas with surface mineral deposits.

Results from SMA analyses were spatially clipped and summarized using polygons delineating wetland areas (Table 1). This process removed anthropogenic features (e.g. houses, cities) and other potential sources of false water positives (topographic shadow, asphalt, and conifers) from the SMA (DeVries et al. 2017). Polygon attributes described land ownership (public, private; Figure 2a) and wetland type (managed wetlands, natural wetlands, riverine wetlands, flood-irrigated agriculture; Figure 2b), which I classified using satellite imagery. Pixel attributes described the flooding duration (i.e. hydroperiod; temporary, seasonal, semi-permanent; Figure 3) of inundated pixels. Table 2 provides attribute definitions, Figure 4 illustrates the distribution of wetland attributes within each region, and Tables S1-S8 provide the amount of each wetland attribute within each region.

WETLAND HYDROPERIOD MODELLING

Wetland hydroperiod, timing and duration of wetland flooding, is a key delimiter of water depth, vegetative structure, and foraging associated with waterbird wetland use (Bancroft et al. 2002; Foti et al. 2012). For example, ibis often use semi-permanently flooded wetlands (29-

184 cm deep) with tall emergent vegetation for nesting habitat (Ryder and Manry 1994; Herzog et al. 2020) while surrounding temporary and seasonal wetlands (5-25 cm deep) provide foraging opportunities (Smiley and Keinath 2003; Safran 1997; Safran et al. 2000). Wetland hydroperiods were defined by totaling the number of months an individual pixel was inundated from March to October using the monthly surface water models described previously (see example in Figure 3). I classified hydroperiods as the following: 1) temporary wetlands contain surface water for brief periods, flooded for three months or less during the growing season (Cowardin et al. 1979), 2) seasonal wetlands were flooded for extended periods, four to six months, but often dry out by the end of the growing season (Cowardin et al. 1979) and 3), semi-permanent wetlands contain surface water for the extent of the growing season, at least seven months.

WETLAND DRIVERS

I examined cropland irrigation and climate variables (Table 3) as predictors of wetland flooding trends. Because agriculture accounts for >89% of surface water use in the western US (Maupin et al. 2014), I used annual estimates of irrigated crop area derived from irrMapper (Ketchum et al. 2020) to assess potential impacts on wetland change. This dataset uses remote sensing to provide an annual, 30 m resolution, binary classification of land as irrigated or non-irrigated (Ketchum et al. 2020). Imagery was available from 1986 to 2019 with a classification accuracy of 97.8% (Ketchum et al. 2020). National Wildlife Refuges (NWR), Wildlife Management Areas (WMA), State Wildlife Areas (SWA), Waterfowl Production Areas (WPA), and Migratory Bird Refuges (MBR) were omitted to reduce false positives resulting in overestimation of irrigation.

Annual climate variables were extracted by water year, October 1 to September 30, from TerraClimate, a global 4 km gridded monthly climate dataset for terrestrial surfaces (Abatzoglou

et al. 2018). The North American water year, beginning October 1, corresponds to when water storage (e.g. snowmelt and runoff) from the previous water year is exhausted due to high evaporative demand and summer drying (Dingman 2002). TerraClimate data was available for 1984-2019. The relatively high spatial resolution and broad temporal record of IrrMapper and TerraClimate aligned with the resolution of SMA results, making them ideal datasets for obtaining continuous irrigation and climate record spanning the study region.

Extracted climate and agriculture layers were clipped and summarized by watershed using USGS 4-digit hydrologic units (Tables S9-S14; Seaber et al. 1987) and intersected with ibis colony locations to spatially join results with wetland trends. The 4-digit hydrologic units encompass river system drainages, a reach of a river and its accompanying tributaries, a closed basin(s), or a coastal drainage area formed from a group of streams (Seaber et al. 1987). Twenty-eight subregions encompassed all colony sites in the study area (Figure 5). Using this approach made it possible to measure interactions between colony wetlands and hydrologically connected processes occurring across a watershed.

STATISTICAL ANALYSIS

Site-level and region-level comparisons of surface water, irrigation area, and climate variables occurred across two equal periods: 1988-2003 (T1) and 2004-2020 (T2). Partitioning the data into these two equal length time periods reduced subjectivity in the division of the data. Additionally, both time periods included >15 years, which captured multiple cycles of major climate phenomena: El Niño - Southern Oscillation and the Pacific Decadal Oscillation (Ropeleski and Halpert 1986; Mantua et al. 1997; Trenberth 1997). These climate controls alter hydrology over relatively short periods but have little influence on long-term trends (Kurtzman

and Scanlon 2007). Consequently, the >15 year time periods account for inter-annual climate variability and prevent artifact trends due to these climate phenonema.

I used the nonparametric Wilcoxon test as an exploratory mechanism to understand broad ecological change in western wetlands. The Wilcoxon test has commonly been used to evaluate shifts in the central tendency of hydrological time series that demonstrate non-normal distributions and censored data (Lazaro 1976; Yue and Wang 2002; Donnelly et al. 2020). Additionally, the Wilcoxon test simplifies trends and is robust against outliers and nonlinear patterns. These attributes make the Wilcoxon test appropriate for comparing differences between T1 and T2 means. First, I aggregated colony sites into regional subsets and used the Wilcoxon test to determine regional changes in total surface water. I also tested regional surface water differences based on land ownership, wetland type, and hydroperiod. To explore geographic patterns within regions, Wilcoxon tests were used on the total surface water within individual colony sites. I also examined changes based on land ownership, wetland type, and hydroperiod at the site level. While monthly surface water data included measurements from March-October, region and site-level comparisons used the mean surface water measurement from April-August to better measure annual habitat availability during ibis nesting, chick rearing, and pre-migration events. Additional data from March, September, and October were used for classifying hydroperiods and comparing monthly surface water changes.

I used p value to measure the significance strength where a p value ≤ 0.05 represented significant change. All p values are uncorrected, which limits Type II error and prevents exclusion of potentially important differences in surface water. However, inflated Type I error increases occurrences of insignificant results falsely marked as significant, particularly in site-level comparisons. Consequently, percent change, variability, and on-the-ground hydrological

contexts should also be considered when interpreting significance of surface water change. Surface water variability and change were visualized using boxplots (Figure 6).

I used random forest regression tree analysis (RF; Breiman 2001) to attribute the importance of climate and agricultural variables to long-term wetland change. RF provides a non-parametric measure of variable importance (VIMP). The VIMP score facilitates identification of key predictor variables, where a higher VIMP score indicates a stronger relationship between the predictor variable and response variable. While RF does not reveal directional relationships, identifying predictors aids in understanding ecosystem processes and interpretation of climate and land use change forecasts impacting local wetland systems. Ecological data with non-normal distributions, such as the data used in this study, are an appropriate application for RF. The two-step randomization process of RF decorrelates trees, lowers variance, and reduces bias (Ishwaran and Lu 2019). Five thousand trees were used for all model runs, and confidence interval calculations used double bootstrap subsampling ($n = 500$, $\alpha = 0.5$; Ishwaran and Lu 2019). For analysis, I grouped colonies by region and hydroperiod class (i.e. temporary, seasonal, and semi-permanent) to isolate unique climate and anthropogenic drivers. While RF analyses revealed the most important predictors of wetland change, it did not reveal the direction of influence. Predictors aid in the interpretation of climate and land use change forecasts and their potential impacts to local wetland conditions.

DATA PROCESSING

Google Earth Engine was used to process all images and perform raster-based analyses (Gorelick et al. 2017). QGIS was used for all GIS analyses (QGIS Development Team 2021). The R environment was used to conduct statistical analyses (RStudio Team, 2020; R Core Team 2020).

RESULTS

Analyses revealed that all regions exhibited differences in long-term trends and experienced substantial interannual variability. For instance, wetland conditions at Malheur Lake, OR exhibited a downward trajectory characterized by considerable fluctuations (Figure 7). Approximately 60% (n=92) of sites in the ibis network (n=153) showed statistically significant ($p < 0.05$) wetland loss due to surface water drying from 1988 to 2020 (Figure 8). Declines were pervasive in 5 of 8 regions with annual trends varying in severity and demonstrating strong linear declines (Figure 9; Table 4). Over half (56%) of colony network locations were located in the Great Basin-Colorado Plateau (87), with the Northern Plains (15) and Southern Rockies and Basins (23) containing approximately a quarter of sites. The remaining 18% of colony locations occurred in the Middle Rockies (11), Pacific Northwest (7), Southern Plains (6), Northern Rockies (3), and Mojave-Sonoran Deserts (1).

Regions experienced significant declines in some or all associated colony sites, except for the Mojave-Sonoran Deserts, where no change was detected (Table 4). Over half of sites (55) in the Great Basin-Colorado Plateau demonstrated significant declines. The Northern Rockies, Middle Rockies, Southern Rockies and Basins, Northern Plains, Southern Plains, and Pacific Northwest each exhibited decreased flooding at some or all colony locations (Table 4). The only region containing sites with significantly increased flooding was the Northern Plains.

Public wetlands accounted for over half of flooded hectares in 7 of 8 regions and were highly concentrated on managed wetland complexes, including 57 federal and state managed wildlife refuges (e.g. NWRs, MBRs, WPAs, WMAs, SWAs; Table S15). Semi-permanent wetlands supporting ibis nesting habitat via tall emergent vegetation characterized these managed wetlands (Tables S1-S8). In contrast, privately managed wetlands were rare (<10% of

managed wetlands). At least one third of foraging habitat (i.e. temporary and seasonal wetlands) was found on private lands in 6 of 8 regions, thereby complementing public wetland resources through substantial provision of foraging habitats. Additionally, flood-irrigated agriculture, an important foraging resource for ibis (Moulton et al. 2013), was associated with approximately 88% of sites.

Analysis within individual sites revealed that surface water decreases were not exclusive to any single land ownership, wetland type, or hydroperiod class. Over half of all sites experienced significant drying of either private (52% of sites) or public (63% of sites) wetlands. Declines in both nesting (semi-permanent wetlands) and foraging habitats (seasonal and temporary wetlands) were evident across sites; semi-permanent wetland flooding decreased at 97 sites (63%), seasonal wetlands at 70 sites (46%), and temporary wetlands at 31 sites (20%). Results based on wetland type predominantly exhibited significant decreases where managed wetlands and natural wetlands decreased at over 40% of sites. Flood-irrigated agriculture, an important foraging resource for ibis, also declined at over 40% of sites. Riverine wetlands decreased at approximately a quarter of sites.

REGIONAL TRENDS

Great Basin-Colorado Plateau:

Fifty-five ibis colonies in the Great Basin-Colorado Plateau experienced significant wetland loss. Overall surface water decreased by 28% (-73,637 ha; Table 4; Figure 6). Declines were significant in all months (Mar-Oct), but were most pronounced in late summer (Jul-Sept) when monthly losses exceeded 30% (Figure 10). Public wetland availability was nearly three times more than private. However, because proportional losses were similar for wetlands found

on public (-29%) and private (-28%) land, more hectares of public wetlands were lost to drying: public wetland flooding decreased by 54,519 ha while private wetland flooding decreased by 19,119 ha (Figure 11; Table 5). Semi-permanent wetlands were the only hydroperiod class exhibiting declines (-45%, -72,839 ha). Results based on wetland type showed significant shifts in surface water for all types, except for riverine features. The greatest losses occurred in natural and managed wetlands where declines were 37% (-26,887 ha) and 27% (-39,569 ha), respectively.

Middle Rockies:

Overall surface water availability remained stable from T1 to T2 (Figure 6) in the Middle Rockies, even though 6 of 11 colonies experienced significant changes in surface water (Table 4). Monthly results (Figure 10) showed significant declines for March (-23%), August (-19%), and June (-8%). Public wetland resources did not show any significant change in surface water extent (Figure 11; Table 6). In contrast, private wetland resources demonstrated significant declines (-16%, -924 ha). Changes across hydroperiods were insignificant. Results based on wetland type showed significant shifts for riverine (-7%, -230 ha) and flood-irrigated agriculture (-35%, -599 ha).

Mojave-Sonoran Deserts:

Mojave-Sonoran Deserts did not have significant change in overall surface water from T1 to T2 (Figure 6). Monthly surface water (Figure 10) demonstrated significant shifts for June (25%) and September (20%). Temporary wetlands were the only hydroperiod class exhibiting significant change (+32%, +14 ha). The Mojave-Sonoran Deserts was one of two regions that experienced significant increases in temporary wetlands. Results based on land ownership and

wetland type did not reveal any significant results (Figure 11; Table 7). The single site in this region is spring fed and associated with a managed wetland complex (Ash Meadows NWR).

Northern Plains:

Similar to the Middle Rockies and Mojave-Sonoran Desert, the Northern Plains did not demonstrate significant change in overall surface water from T1 to T2 (Figure 6). However, 6 individual colony locations showed significant decreases and 4 showed significant increases. Monthly surface water showed significant results for primarily late season months (Jul-Oct) when monthly losses exceeded 8% (Figure 10). March also showed significant decreases (-16%). Private wetland resources did not show any significant change in surface water (Figure 11; Table 8). In contrast, public wetland resources demonstrated significant decreases (-7%, -732 ha). Significant change occurred for seasonal (-7%, -213 ha) and semi-permanent (-9%, -721 ha) hydroperiod classes. Temporary wetlands did not show any significant changes between time periods. Results based on wetland type revealed significant results for riverine (-11%, -200 ha), flood-irrigated agriculture (-15%, -79 ha), and managed (-13%, -918 ha) wetland types.

Northern Rockies:

All sites (n=3) in the Northern Rockies experienced significant wetland loss. Overall surface water sustained a decrease of 12% (-434 ha; Table 4; Figure 6). Declines were significant in all months (Mar-Oct), but were most pronounced in September and October when losses exceeded 20% (Figure 10). Significant decreases occurred in both public (-11%, -355 ha) and private (-20%, -79 ha) surface water (Figure 11; Table 9). Semi-permanent wetlands were the only hydroperiod class exhibiting significant change (-15%, -412 ha; Table 8). Results based on wetland type did not reveal any significant results.

Pacific Northwest:

Three of the seven ibis colonies in the Pacific Northwest experienced significant decreases. Overall surface water decreased by -15% (-4,460 ha; Figure 6). Monthly results showed significant declines for all months except April and June. Losses were most pronounced in October (-35.7%; Figure 10). Private wetland resources did not show any significant change in surface water while public wetland resources demonstrated significant decreases (-20%, -3,926 ha; Figure 11; Table 10). Significant change occurred for temporary (+19%, +1,025 ha) and semi-permanent wetlands (-34%, -4,997 ha). The Mojave-Sonoran Deserts and Pacific Northwest were the only regions where temporary wetlands increased from T1 to T2. Results based on wetland type demonstrated significant results for natural wetlands (-15%, -2,785 ha) and flood-irrigated agriculture (-15%, -605 ha).

Southern Plains:

All sites (n=6) in the Southern Plains experienced significant wetland loss. Overall surface water decreased by 43% (-3,043 ha), the most extensive decline of all regions (Table 4; Figure 6). Declines were significant in all months (Mar-Oct) but were most pronounced late in the season (Aug-Oct) when monthly losses exceeded 45% (Figure 10). Significant decreases occurred in both public (-49%) and private (-32%) surface water (Figure 11; Table 11). Changes across hydroperiods were significant for seasonal (-24%, -283 ha) and semi-permanent (-51%, -2,696 ha) wetlands. All wetland types had significant results for decreased surface water from T1 to T2.

Southern Rockies and Basins:

Within the Southern Rockies and Basins, 57% of the ibis colonies (13/23 ibis colonies) experienced significant changes. Overall surface water declined by -20% (-6,594 ha; Figure 6; Table 4). Monthly results showed significant decreases for all months except for April (Figure 10). The greatest declines occurred in March (-27%), August (-26%), and September (-27%). This region differed from other regions in that private wetlands accounted for over half of the surface water. Additionally, 46% of the total wet hectares were associated with flood-irrigated agriculture, highlighting the extensive presence of this foraging resource. All ownership, wetland type, and hydroperiod classifications had significant results for decreased surface water (Table 12). The strongest declines occurred in public (-25%, -3,064 ha; Figure 11), managed (-26%, -2,550 ha), and semi-permanent (-24%, -2,379 ha) wetland classifications.

VARIABLE IMPORTANCE AND TRENDS

No variable presented as the single most important predictor of wetland flooding across all regions, however, snow water equivalent, minimum daily temperature, and irrigation extent were the most common drivers of wetland flooding (Figure 12). Snowmelt timing and volume governs streamflow volume, groundwater recharge, and soil moisture, in turn influencing wetland inundation (Stewart et al. 2004; Lauenroth et al. 2014; Coles et al. 2017). Snow water equivalent was an important predictor of wetland flooding in the Northern Plains, Pacific Northwest, Southern Plains, and Southern Rockies and Basins. Each of these regions is characterized by snow-dominated basins where snowpack influences water availability (Mote 2003; Stewart 2009; Snyder et al. 2019). Analysis examining watershed-level changes to snow water equivalent were statistically insignificant in all watersheds. However, previous studies

examining snowpack changes over longer temporal periods have reported declining snowpack throughout the western US (Mote et al. 2005; Stewart et al. 2009).

Temperature is a key driver of evapotranspiration and precipitation patterns (Dingman 2002; Hamlet et al. 2005). Daily minimum temperature, in particular, can have strong effects on plant water-requirements (Hatfield et al. 2011) where increased temperatures heighten crop water needs, thereby driving increased water withdrawals that impact wetland availability. The RF analysis resulted in high VIMP values for minimum daily temperature across several hydroperiods and regions, including those found in the Great Basin-Colorado Plateau, Middle Rockies, Mojave-Sonoran Deserts, Northern Rockies, Pacific Northwest, and the Southern Rockies and Basins. Trend analysis results indicate increases in minimum daily temperature over time, primarily within the Great Basin-Colorado Plateau.

Irrigation has shaped wetland inundation in agriculture-dominated basins via water withdrawals, groundwater recharge, stream return flow (Downard and Endter-Wada 2013). All watersheds in this study contained irrigated agriculture, ranging from 12,500 to > 1 million hectares, but irrigation was the primary predictor in only five regions. Irrigation had high VIMP scores in the Great Basin-Colorado Plateau, Middle Rockies, Northern Plains, Pacific Northwest, and Southern Plains. Furthermore, results indicate expansion of irrigated agriculture that will further impact water supplies in some regions. Statistically significant increases occurred across eight watersheds and two regions, including the Great Basin-Colorado Plateau (+12,710 ha) and the Pacific Northwest (+20,902 ha).

Precipitation, evapotranspiration, and runoff were less common predictors of wetland flooding, but did present as primary drivers in the Great Basin-Colorado Plateau, Mojave-Sonoran Deserts, Northern Plains, and Northern Rockies (Figure 12). Linear regression analyses

showed significant results for decreases in evapotranspiration and precipitation within two watersheds in the Southern Rockies and Basins and the Southern Plains. Changes to precipitation, runoff, and snow water equivalent were statistically insignificant in all watersheds.

DISCUSSION

This study is the first long-term monitoring of the wetland network that supports breeding ibis in the western US. Ibis breeding habitat has reached a tipping point where pervasive drying, particularly in the Great Basin-Colorado Plateau, signals a partial network collapse. Growing human water demands compromise wetland resiliency further. While widespread drying of closed basin lakes (i.e. Great Salt Lake; Donnelly et al. 2020) partly explains decreased wetland availability, concurrent desiccation of semi-permanent wetlands outside basin lake systems confirms broader ecosystem impacts. A broad-scale wetland network enables ibis to exploit wetland availability in response to dynamic conditions. However, with fewer available wetland sites, ibis populations may experience reduced plasticity in their response to drought. Consequently, targeted conservation of a landscape-scale wetland network will facilitate the long-term viability of ibis. My study evaluated the ecological effects of wetland loss across the US ibis breeding distribution while providing a framework for conserving a wetland network that mutually benefits ibis and other wildlife.

THE WETLAND NETWORK: DEFINITION AND STATUS

The nomadic nature of ibis, their diverse wetland needs, and broad spatial requirements make them a umbrella species for defining an ecologically meaningful wetland network. Wetlands are an important regulatory feature for ibis populations in the West, and as a result, ibis populations are intrinsically tied to hydrological patterns in the region. As documented in this

study (Table 4; Figure 7), high interannual variability of wetland flooding results in annual intermittency of breeding areas. This habitat variability supports nomadic behavioral traits that allow ibis to compensate for changing conditions with movements commensurate to wetland temporal and spatial dynamics (Ryder 1967; Earnst et al. 1998). As a result, ibis selection of breeding habitat mirrors wetland availability on the landscape. For example, during the early 1980s, increases in population numbers in Oregon were not reflective of recruitment from local populations (Ivey et al. 1988). Rather, increases were partially due to birds relocating from other regions that experienced reduced nest habitat (Ivey et al. 1988; Earnst et al. 1998).

Wetland diversity, not just availability, plays a key role in determining colony distributions. Proximity to a diversity of wetlands influences the utility of an individual wetland to waterbirds (Naugle et al. 1999). Wide-ranging species, such as ibis, are particularly dependent on the presence of periphery wetlands because they must travel between wetlands to find ephemeral prey resources (Bray and Klebenow 1988; Craig and Beal 1992; Niemuth et al. 2006; Kelly et al. 2008). For example, Moulton et al. (2013) speculated that decreased ibis breeding at Market Lake WMA, Idaho was partly due to the reduced availability of foraging wetlands in the surrounding landscape. Since wetland diversity and availability are inherent to an ibis-dictated wetland network, ibis breeding colonies signify the status of wetlands in the West. However, my results reiterate a pattern supported by other studies. Namely, that widespread drying of basin lakes and their associated wetlands fractures the connectivity of the wetland mosaic sustaining numerous migratory waterbirds.

The inequity of drying amongst regions reduces wetland redundancy that otherwise buffers against localized disruptions to habitat availability. The Great Basin-Colorado Plateau region exemplifies the loss of wetland redundancy. Of the individual colony sites with decreased

wetland flooding, over half of the colonies were located in the Great Basin-Colorado Plateau. This drying pattern is consistent with recent studies documenting climate-induced shifts in water availability across the Great Basin and similar arid or semi-arid regions (Wurtsbaugh et al. 2017; Wang et al. 2018; Haig et al. 2019). However, continued drying raises concerns over the future viability of stopover sites that sustain millions of migratory waterbirds. Over two million birds migrate through Southern Oregon and Northeastern California (Fleskes and Yee 2007; Warnock et al. 1998), and over one million birds migrate through the Great Salt Lake area (Paul and Manning 2002). Numerous birds migrate through other key wetland sites throughout the region (Oring and Reed 1997; Warnock et al. 1998; IWJV 2013). Similar results from other studies suggest these critical wetland sites face additional deterioration, which will limit waterbird populations through restricted migration connectivity and degraded stopover locations (Lee et al. 2015; Haig et al. 2019; Donnelly et al. 2020).

With a diminished presence of water on the landscape, ibis will likely make maladaptive selections of wetland habitat with suboptimal water quality. Elevated salinity from reduced inflows adversely impacts chick survival, as young waterbirds are not adapted to heavy salt loads (Rubega and Robinson 1989; Gutiérrez 2014). Additionally, excessive salinity levels inhibit invertebrate production, leading to trophic collapse of food resources essential to ibis and other waterbirds (Herbst 2006; Herbst et al. 2014). The ties between salinity and waterbird abundance were illustrated at Lake Abert, Oregon, US where depressed invertebrate and waterbird numbers occurred in response to extremely high or low salinity levels (Senner et al. 2018). Furthermore, without sufficient inflows from other sources, contaminants from irrigation inputs become concentrated within wetlands and act as point-source pollution. The interrelated effects of water

shortages and increasing salinity create an ecological trap where ibis will have to select between desiccated wetlands and sparse high quality habitat.

Reduced wetland flooding at the margins of the breeding season indicates potential for phenological mismatch between ibis migration and available wetland habitat. This study found pronounced decreases in wetland flooding during March and July-October, effectively reducing the extent of spring and fall wetland habitat. These time periods align with energetically demanding migration and breeding events for ibis (Ryder 1967). Additionally, waterbird breeding success is linked to the extent and quality of spring habitat (Gunnarsson et al. 2006; Morrison et al. 2007; Zarzycki 2017). Shifts in water quantity and quality can limit food resources via asynchrony between ibis movement and invertebrate productivity. Consequently, misalignment of migration and wetland flooding could result in unmet energetic demands, thereby limiting ibis populations.

THE WETLAND NETWORK: CHANGES AND THREATS

The wetland network transcends land ownership boundaries, encompassing a patchwork of private working lands, public multi-use areas, and protected complexes. Yet, the interrelationships between these different land tenures are complex and often tied to water availability. Wetlands are not isolated from the surrounding land use practices (Tsai et al. 2007; Bodhinayake and Cheng Si 2004; van der Kamp et al. 1999). As a result, the efficacy of protected wetlands can be limited or enhanced by the surrounding landscape (Beatty et al. 2014). Inundation patterns within managed wetland complexes often hinge on water-use decisions of upstream landowners (Downard and Endter-Wada 2013). Additionally, private working lands complement managed wetlands by providing foraging habitat and augmenting landscape

connectivity and migratory pathways. Consequently, a holistic perspective inclusive of public and private land relationships provides the greatest capacity for a functional wetland network.

Public lands underpinned observed patterns of colony distributions, forming a west-wide network of state and federally managed wetland areas. Privately managed wetlands were rare and associated with waterfowl hunting clubs. While most wetlands lie on private land in the West (Heimlich et al. 1998), over half of the colony wetlands were publicly owned, except within the Southern Rockies and Basins. State and federally managed wetland complexes support some of the largest ibis breeding colonies: breeding ibis numbering over 10,000 individuals have been documented at each Klamath and Bear Lake NWRs, Bear River MBR, and Market Lake WMA (Cavitt et al. 2014). However, the results of this study revealed widespread drying across public wetlands. Many managed wetland complexes originated from initiatives to conserve and manage migratory waterbirds using a system of land protections (Scott et al. 2004). As a result, these managed wetlands frequently serve migratory waterbirds as islands of refugia in a matrix of anthropogenic development (Scott et al. 2004; Beatty et al. 2014). The loss of these sites would substantially alter the current wetland mosaic. Therefore managed wetlands are a key vulnerability in sustaining a viable breeding habitat network for ibis.

The importance of managed wetlands to ibis breeding was evident in this study. However, limited protections afforded to the water resources supplying these wetlands make them sensitive to changes in neighboring water uses. For instance, subsurface irrigation drainage from agriculture is a significant source of toxic contaminants within adjacent wetlands (Lemly et al. 1993). Reduced freshwater inflows to these impacted wetlands further exacerbate the potential for decreased water quality. For example, at Stillwater NWR, toxicity studies following massive die-offs of fish and wildlife in the mid-1980s identified high levels of contaminants

from subsurface irrigation (Lemly et al. 1993). Managers responded by closing the implicated agricultural drainage sites entering the refuge. Acquisition of additional water rights provided further security for Stillwater's wetlands.

Klamath and Tule Lake NWRs illustrate another example. Competition for water resources between federal wildlife refuges, Native American tribes, threatened and endangered species, and irrigators in the Upper Klamath Basin resulted in the dewatering of substantial portions of the Lower Klamath and Tule Lake NWRs in 2001 (Burke et al. 2004). These two refuges rely on agricultural drain water and return flows to maintain refuge wetlands. Consequently, the magnitude of water delivery to farmers determines the water quantity available to the NWRs. The listing of several fish species under the Endangered Species Act further amplified the stress on an already strained water supply. The synergistic effects of drought, water level requirements in Upper Klamath Lake, and streamflow needs for endangered species in the Klamath River curtailed water available for irrigation. As a result, refuges were impacted with substantially reduced water levels and severe deterioration of wetland habitat for waterbirds. While periodic drought is inherent to wetland hydrology, extended water shortages negatively affect ibis nesting habitat. For instance, tall emergent vegetation used for nesting requires relatively stable water conditions through the warm season (i.e. hardstem bulrush, alkali bulrush, etc; Rohal et al. 2017). These examples demonstrate that geographically distant yet hydrologically connected activities can considerably impact water availability within publicly protected refuges.

The water management challenges Stillwater, Klamath, and Tule Lake NWRs face are not unique. Water quantity and quality issues pose the greatest threats to refuges nationwide (Bauch et al. 2021). Consequently, refuges often lie at the nexus of competing uses for

agriculture, human demands, and wildlife needs. Changes in wetland flooding may reflect surrounding land use alterations, changing water needs, or climatic shifts. However, as the previous examples illustrate, underlying mechanisms influencing wetland flooding on managed refuges are complex. To maintain future resilience, refuge managers must account for public values and the neighboring water users (Downard and Endter-Wada 2013).

Ibis and agriculture are inexorably linked through shared water resources, and understanding this relationship provides a key clue to maintaining network functionality. Agricultural development historically contributed substantially to wetland loss (Davidson 2014) and continues to introduce pollutants and contaminants to wetland systems (Lemly 1993). Paradoxically, certain agricultural practices afford benefits to the ibis network that are twofold: 1) flood-irrigated fields provide important food resources; 2) excess irrigation water is a significant input sustaining some wetland systems. Flood-irrigated agriculture, specifically, acts as a surrogate for natural wetlands in providing important foraging resources for many waterbird species (Hartman and Keiller 2010; King et al. 2010). Ibis are particularly dependent on these ephemeral wetlands for foraging, using flood-irrigated fields at a higher frequency than their availability on the landscape (Moulton et al. 2013). In addition to providing foraging opportunities, flood irrigation practices create and sustain wetlands that would otherwise not exist (Peck et al. 2004). Seepage from canals and flood irrigation outflow recharges groundwater, which in turn discharges to wetlands (Kendy 2006; Fernald et al. 2007; Sueltenfuss et al. 2013). However, an expanding agricultural footprint and current irrigation rates further deplete groundwater and other inputs to wetland systems (Jolly et al. 2008; Scanlon et al. 2012). Successful outcomes will depend on establishing a balance between meeting crop production requirements while supporting wetland habitat resilience.

This study revealed distinct declines in flood-irrigated agriculture, impacting ibis breeding sites through reduced foraging resources and water inputs to wetlands. Shifts in flood-irrigated agriculture extent were unequivocal and aligned with trends observed by other studies (Schaible et al. 2010). However, I acknowledge using Landsat data with a 16-day revisit cycle limited detection of some short-duration flooding events. These trends may be partly explained by evolving land-use patterns that reshape irrigation practices throughout the West. For one, urbanization and industry propel land conversion and development that, in turn, reduces irrigation opportunities (Baker et al. 2014). Water conservation efforts place social, economic, and political pressure on irrigators to improve irrigation efficiency in drought-impacted communities, which can have unintended consequences for nearby wetlands (Huntsinger et al. 2017). Increasing irrigation efficiency (via lining ditches, installing sprinkler irrigation, etc.) can simultaneously lead to expanded irrigated acreage and decreased groundwater recharge; thus consuming more water and reducing hydrological inputs to wetlands (Peck and Lovvorn 2001; Kendy and Bredehoeft 2006; Ward and Pulido-Velazquez 2008; Pfeiffer and Lin 2014; Huntsinger et al. 2017). For instance, concurrent changes in irrigation practices and groundwater development contributed to disrupted hydrology at Camas NWR, Idaho. Earlier runoff increased groundwater withdrawals, and more water-efficient irrigation practices (achieved by converting flood-irrigation to sprinkler irrigation) collectively altered natural groundwater and surface water inflows to the refuge. The subsequently lowered water table (~ 5 m decline) reduced wetland area by 25% and necessitated groundwater pumping to maintain the remaining refuge wetlands (Rattray 2017; USFWS 2014). Similar impacts occurred at another refuge in the basin, Market Lake WMA, where spring outputs have declined by 75% (Hendricks 2014; Rydalch 2014). Shrinking refuge wetlands and disappearing foraging resources beyond refuge boundaries likely

account for long term ibis nesting declines at these Idaho wildlife refuges. (USFWS 2014; Moulton et al. 2013). Once regular and numerous visitors, ibis are now sporadic users, suggesting that ibis relocated to take advantage of favorable habitat conditions elsewhere (USFWS 2014).

Irrigation practices are one constituent of an ensemble of interconnected factors redefining the ‘new normal’ for west-wide wetland availability. My analysis demonstrates average minimum daily temperature and snow water equivalent are predominant drivers of wetland flooding. However, shifting climate regimes are altering the role these climate variables play in wetland processes. Climate models predict more frequent and severe drought and deluge conditions (Cook et al. 2004; Diffenbaugh et al. 2017). Consequently, anomalies in climate may mirror future conditions that will ultimately alter or impair wetland processes. Additionally, temperatures are projected to continue rising, especially in the winter and during night (Snyder et al. 2019). Warmer temperatures at night reduce crop yields, increase the potential for water stress, and elevate evaporative demand (Hatfield et al. 2011), causing increased agricultural water needs (Mix et al. 2010; Elliott et al. 2014). Furthermore, increasing temperatures alter precipitation patterns, diminish snowpacks, and advance snowmelt timing (Stewart et al. 2004; Stewart et al. 2005), which directly impact soil moisture, groundwater recharge, and wetland inundation timing and volume (Stewart et al. 2004; Stewart et al. 2005; Smith and Wagner 2006; Perry et al. 2012; Records et al. 2014). These climate variables amplify anthropogenic stressors on wetland systems, leaving ibis and other migratory species with fewer options for refugia when extreme conditions occur.

Human populations are rapidly growing throughout the western US, and the ensuing increases in water demands exacerbate water deficits. Competition among agricultural,

municipal, and industrial uses for over-allocated water supplies is often the impetus for water conservation and transfer schemes that inadvertently harm wetlands. New water demands pressure urban centers to implement infrastructure that ensures future water security. For example, Utah has initiated plans to supply forecasted urban water needs by diverting 220,000 acre-feet of water annually from the Bear River (Fornataro 2008). This water diversion jeopardizes wetland habitat at the downstream Bear River MBR, designated as a hemispherically and globally important shorebird area. Similarly, rapid human population growth in Las Vegas, Nevada, has compelled the state to pursue extraction of over 200,00 acre-feet annually from a regional groundwater aquifer (Deacon et al. 2007). With the approval of the water right applications, this large-scale groundwater withdrawal would reduce spring discharge that sustains regional waterbird habitats, including several ibis breeding sites.

When untapped water resources are unobtainable, municipal and industrial water users have resigned to purchasing agricultural water rights. The resulting competition makes selling a water right more lucrative than decades of farm production (Dozier et al. 2017). Producers can also profit from temporarily fallowing a field and transferring the unused water to urban and industrial users without relinquishing their water rights (McMahon and Smith 2013; Dilling et al. 2019). Not only do these ‘buy-and-dry’ scenarios eliminate valuable foraging resources for birds, but they frequently involve transferring water out of the basin, which reduces local wetland availability (Dozier et al. 2017; Dilling et al. 2019). Water policies meant to reduce water consumption can also unintentionally suppress wetland conservation efforts. For example, the community in the San Luis Valley (SLV), Colorado, implemented a groundwater withdrawal tax to curb excessive groundwater pumping (Cody et al. 2015). As shown in this study, private lands play a prominent role in supplementing wetland resources within the SLV. Local wetlands

provide critical stopover sites for a multitude of migratory waterbirds, including mallards (Jeske et al. 1994), sandhill cranes (Laubhan and Gammonley 2001), and the largest ibis breeding colonies in Colorado (Earnst et al. 1998). The groundwater tax may be lauded as progress towards wetland conservation. However, it indirectly hindered private wetland protections by reducing incentives for landowners to place land into conservation easements (Kelley 2017).

FINDING SOLUTIONS

Ibis are emblematic of the relationship between agriculture and wetlands. Yet, ibis are often an unintended casualty of water conservation initiatives that seek to increase irrigation efficiencies and redirect water from agriculture to municipal use. My results demonstrate a clear need for conservation strategies that prioritize the protection of the ibis breeding network. Climate projections indicate continued deterioration of wetland conditions, and these uninterrupted trends in drying will lead to the inevitable collapse of the western wetland network. Wetland conservation will undoubtedly benefit ibis and numerous other species. I suggest the following steps to assure the long-term viability of the wetland network:

(1) *Coordinate conservation efforts at regional and flyway levels.* A successful wetland network spans multiple watersheds and regions, includes diverse wetlands, and preserves natural wetland processes. Like many waterbirds inhabiting arid regions, ibis interact with the landscape at spatial scales larger than a single wetland or watershed (Roshier et al. 2001). Nomadism and high mobility enable ibis to leverage broad scale wetland availability in response to changing geographic distributions of suitable wetlands. Consequently, system-wide droughts have more adverse impacts on ibis than local events (Mooij et al. 2002). A large-scale wetland mosaic

ensures the availability of favorable habitats during localized water scarcity. Coordination at regional or continental scales will be paramount to executing water management strategies that prevent system collapse and preserve connectivity between regions. Continental conservation planning can capitalize on the analytical framework provided herein to target water-related bottlenecks that limit ibis populations.

(2) *Value wildlife benefits of flood irrigation practices.* A wetland network that integrates both nesting and periphery wetlands preserves the wetland diversity necessary for ibis life history requirements. Moreover, effective management plans need to consider adjacent agricultural practices. Assuming all irrigation practices adversely affect wetlands neglects the complex and critical relationships between wetlands, ibis, and farming practices. Crop-level and local irrigation data lack the appropriate spatial and temporal coverage needed to examine the effects of different irrigation schemes on hydrology. However, previous research demonstrates that irrigation's timing, method, and location greatly influence wetland availability (Bishop et al. 2010; Hassanli et al. 2009; Pfeiffer and Lin 2014). To preserve valuable foraging resources that flood-irrigated fields produce, managers can employ volunteer incentive-based programs, such as the NRCS Farm Bill and FWS Partners for Fish and Wildlife Program. These programs offer technical and financial assistance for practices, activities, and enhancements that improve wildlife habitat on private land, thus providing a pathway for private landowners to advance wetland network protections.

(3) *Provide support to publicly managed wetland systems.* Publicly protected wildlife refuges form the backbone of the ibis breeding network. Many refuges must balance the cumulative

effects of pollutants and hydrologic alterations (i.e. dams, impoundments, flow regulation, groundwater extraction) beyond their boundaries. Given these stressors and projected climate change effects, refuge operations will need to prioritize wetland adaptability. In some instances, manipulating water levels may decouple these sites from climate effects, but ties to upstream water users and diminishing water resources can undermine these management actions. Securing additional water supplies through water rights, negotiations with other water users or conservation easements will be critical for mitigating impacts of water scarcity (Downard and Endter-Wada 2013; Beatty et al. 2014). However, adequate inflows should not be equated with stable water levels as preserving dynamic wetland processes via periodic drying is an important component in invertebrate prey availability and nesting vegetation (van der Valk 2005; McInerney et al. 2017). Management approaches need to consider the hydrological and socio-political context of a wetland complex to better develop relationships between hydrologically connected water-users. Thus, partnerships between refuge managers and adjacent landowners will be necessary to collectively develop strategies that shape wetland inundation and maintain the conservation capacity of refuges within the ibis breeding network.

(4) *Implement fine-scale habitat quality assessments.* For this study, I assumed that selected wetland sites represent wetlands across the West and that wetland distribution determines habitat availability at broad scales. However, by only assessing broad scale wetland availability, I did not address the wetland processes and habitat characteristics at finer scales that also structure waterbird populations. As a result, wetland area estimates may overestimate habitat availability. Previous work has established that ibis habitat quality is contingent on various characteristics such as nesting vegetation, water depth, and water salinity (Burger and Miller 1977; Safran et al.

2000; Taft et al. 2000; Senner et al. 2018; Herzog et al. 2020). Therefore, assessing fine-scale habitat quality in parallel with large-scale wetland management will further inform accurate habitat availability for ibis.

(5) *Account for the full lifecycle, especially migratory pathways.* Winter habitat quality is linked with the timing of spring migration and physical condition upon arrival to breeding grounds, two determinants of fitness for migratory birds (Sherry and Holmes 1996; McNamara et al. 1998; Marra et al. 1998; Kokko 1999). Yet, as with many migratory bird species, the lack of long-term monitoring leaves us with a poor understanding of ibis migration and wintering networks (Webster et al. 2002; Ryder 1967). There is an inextricable link between winter and breeding periods for migratory birds, whereby events occurring at any point during the annual cycle can impact success in the next phase (Webster et al. 2002). Because ibis use habitats throughout North America, wetland management strategies must encompass water needs throughout the entire annual cycle to better account for the factors driving the ibis population. Using consistent and synchronized surveys, future monitoring of ibis movement patterns will reveal a complete wetland network, including intra-seasonal and migratory pathway movements.

(6) *Support water policies that maintain wetland resiliency.* This study did not account for groundwater hydrology and anthropogenic diversions and inputs to wetlands. However, this study's landscape changes in wetland extent are consistent with recent studies documenting changes in landscape water quality and quantity (Wurtsbaugh et al. 2017; Wang et al. 2018; Haig et al. 2019). Few undeveloped water resources accommodate increasing populations or replenish diminishing rivers and aquifers (Anderson and Woosley 2005). Declining water resources indicate a need for policies that simultaneously lower urban and agricultural water consumption

and preserve ecologically valuable irrigation practices that sustain wetlands and a suite of wetland-dependent species.

Limited research and surveys leave many questions about ibis unanswered. However, my in-depth analysis of western wetlands reiterates the value of the ibis breeding network to other wetland species and serves as the foyer to future research related to ibis. Furthermore, linking research to on-the-ground applications will be fundamental to accelerating ibis and wetland conservation. To bridge the gap commonly found between research accomplishments and management implementation (Sands et al. 2012), I developed an interactive web application that makes my data directly available to natural resource managers:

<https://sheacoons.users.earthengine.app/view/wet-wfib-beta-11>. This web application and accompanying user guide integrate the science found herein to reduce uncertainties in management decisions and advance wildlife management goals. Effective conservation strategies will also integrate local ecological, social, political, and economic contexts, as each acts synergistically to produce unique hydrologic challenges. Additionally, this study has established the interdependence of public wildlife refuges and private agriculture. Thus, refuge managers and producers will need to work in tandem to maintain wetland diversity. I encourage the use of my results to generate local and regional partnerships and develop ibis breeding network protections.

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FIGURES

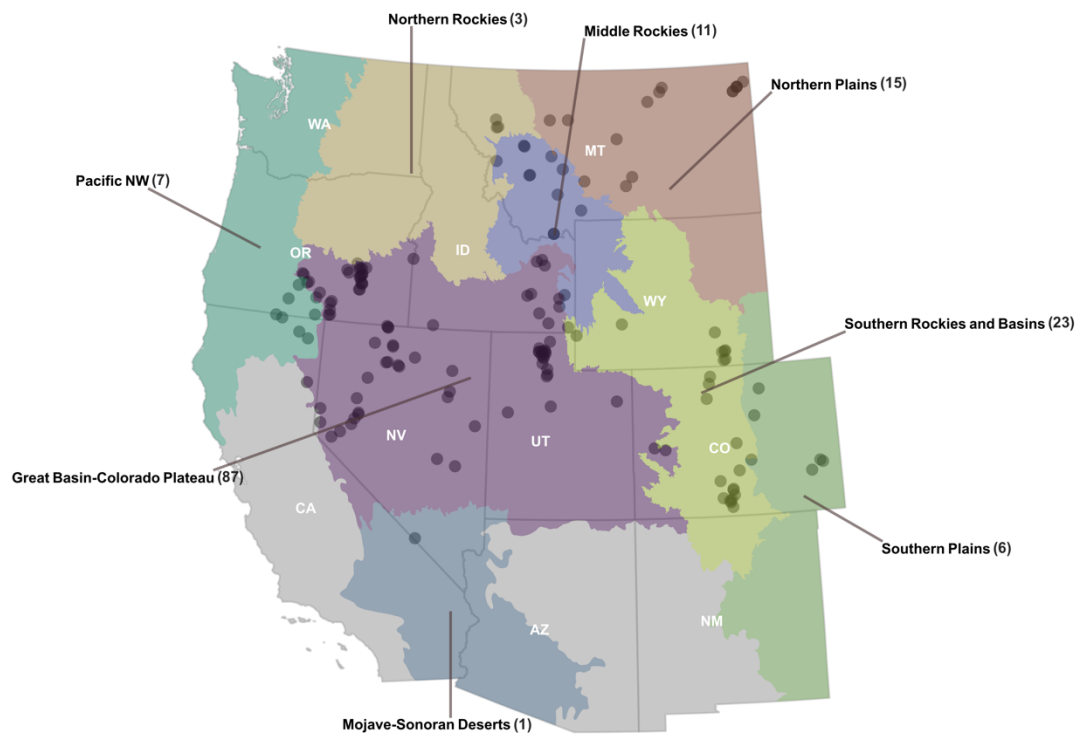


Figure 1: Ibis colony locations (black points, $n = 153$) identifying extent of wetland network evaluation overlaying western US state boundaries. The differed colored areas represent ecoregions used to summarize climate and agricultural drivers influencing wetland change. The number of individual colonies found within a given ecoregion is noted in parenthesis.

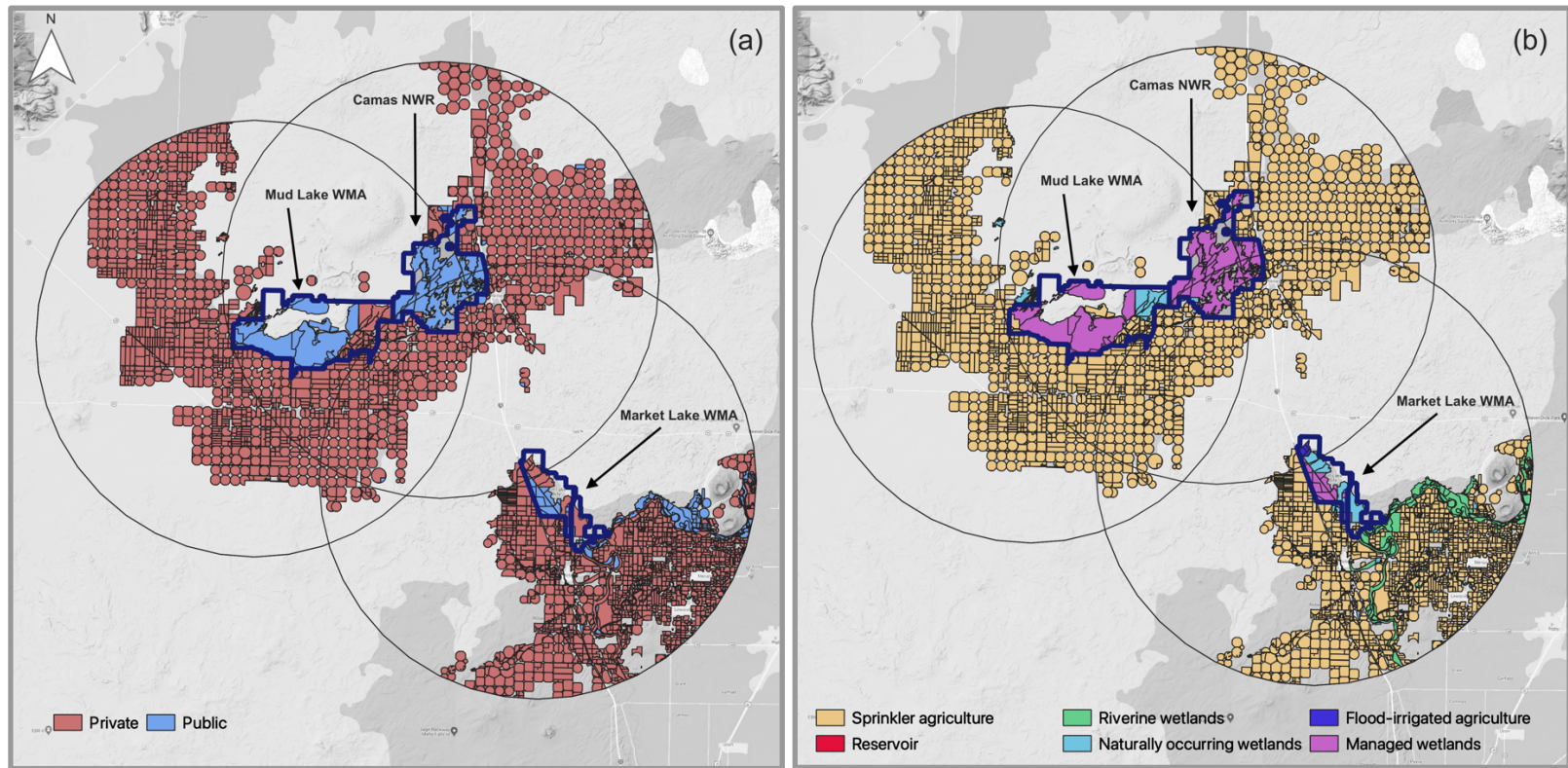


Figure 2: Illustration of the polygon attributes delineating land tenure (a) and wetland type (b) across 18 km of ibis breeding locations at Mud Lake WMA, Market Lake WMA, and Camas NWR, Idaho USA. Three foraging radii (18 km) are noted by black borders. Bold blue borders define refuge boundaries.

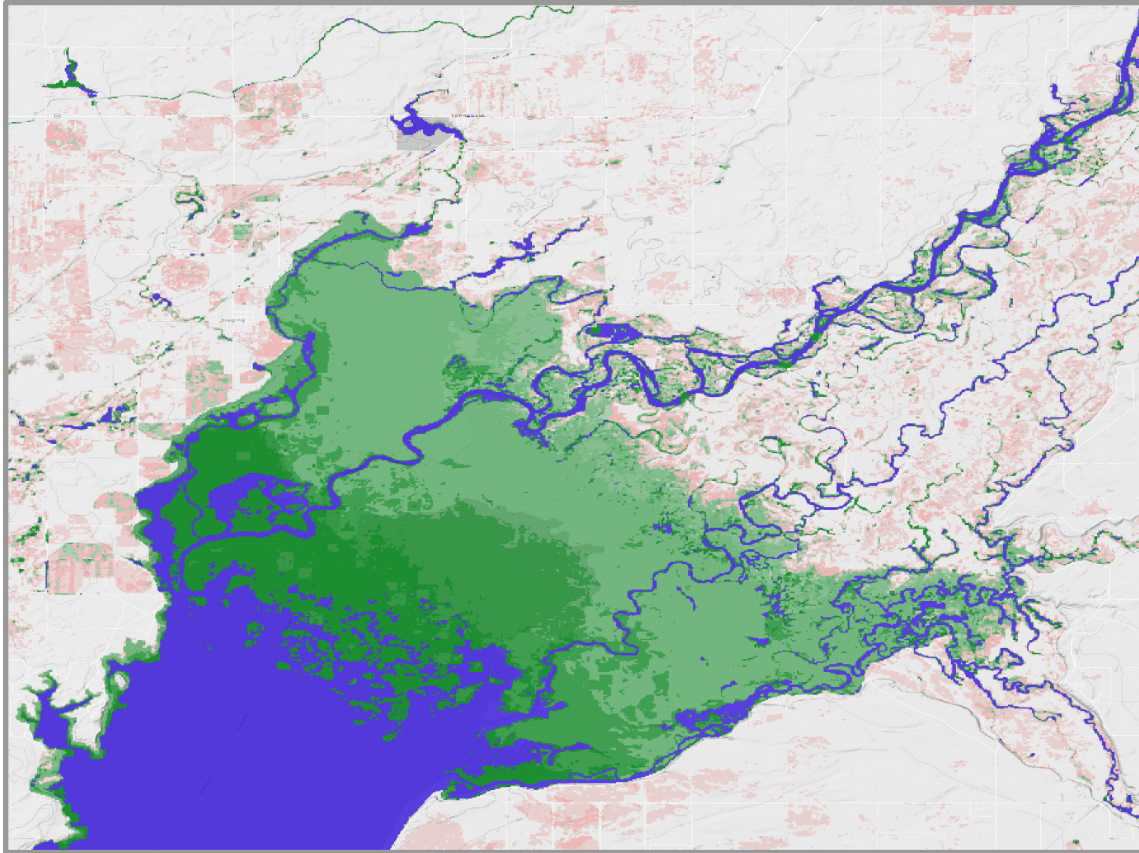


Figure 3: Illustration of wetland hydroperiod in American Falls Reservoir, Idaho. Hydroperiod data for this image were derived from median surface water extent occurring during 2016-2020. Wetlands are displayed by hydroperiod class: pink - temporary (flooded ≤ 3 months), green - seasonal (flooded > 3 and ≤ 6 months), and blue - semi-permanent (flooded ≥ 7 months). Wetlands are absent in white areas in the illustration.

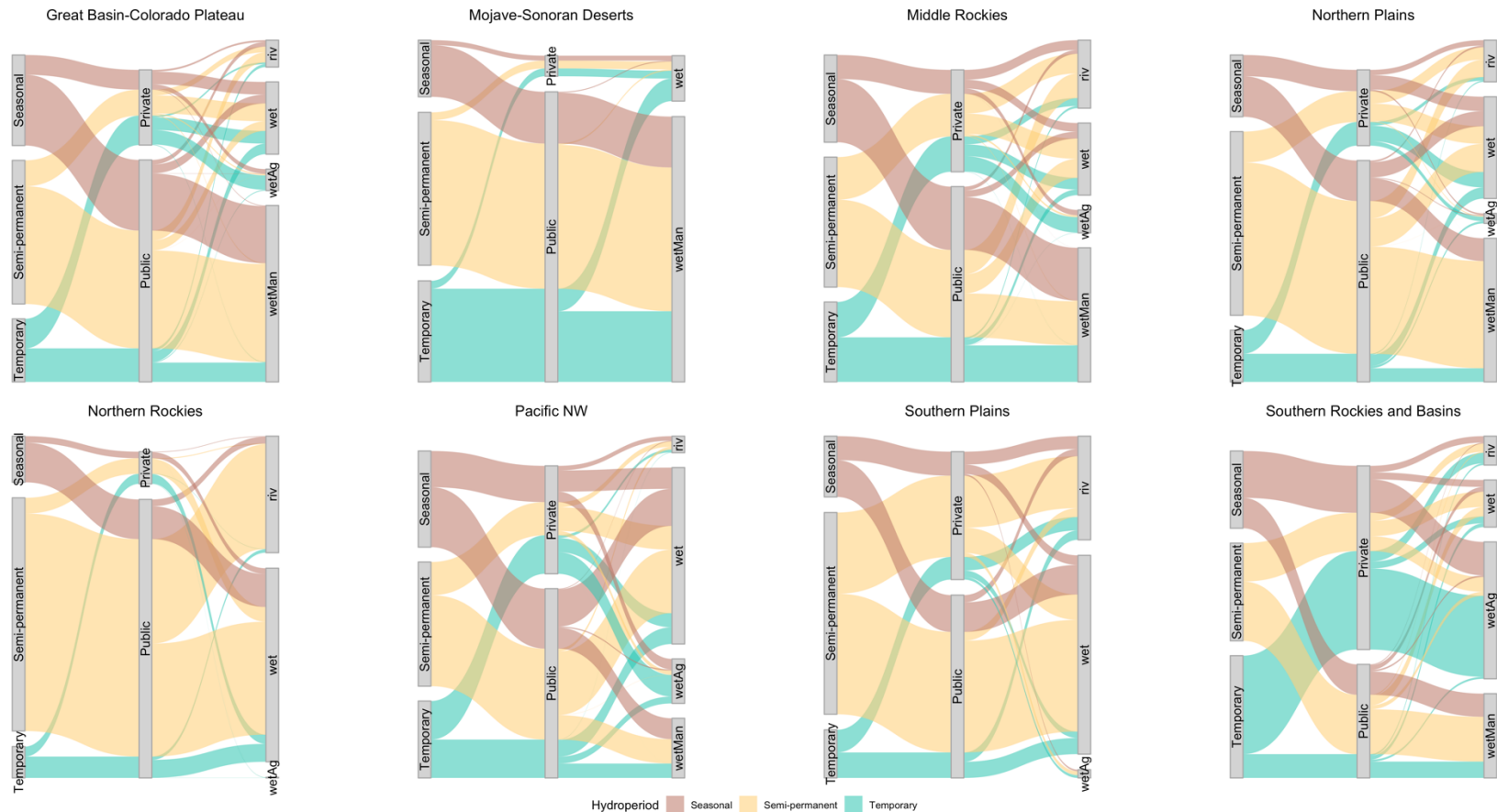


Figure 4: Parallel set diagram showing how surface water is classified within each region. The thickness of each curved line represents the amount of surface water associated with temporary (light blue), semi-permanent (yellow), and seasonal (red) wetlands. These curved lines are further subdivided by land ownership (private, public) and wetland type (managed, “wetMan”; natural; “wet”, flood-irrigated agriculture; “wetAg”, and riverine; “riv”) as read left to right. These subdivisions indicate the amount of surface water in each hydroperiod that is associated with each land ownership and wetland type category.

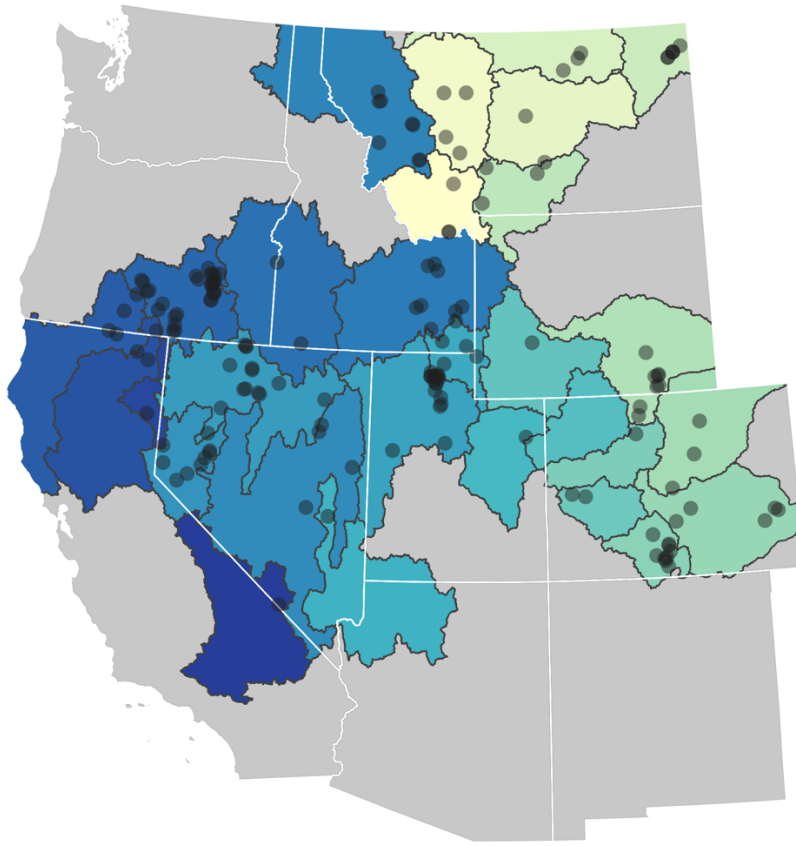


Figure 5: Map of USGS 4-digit Hydrologic Units (Seaber et al. 1987) used to summarize climate and irrigation data. Gray circles denote ibis breeding colony sites.

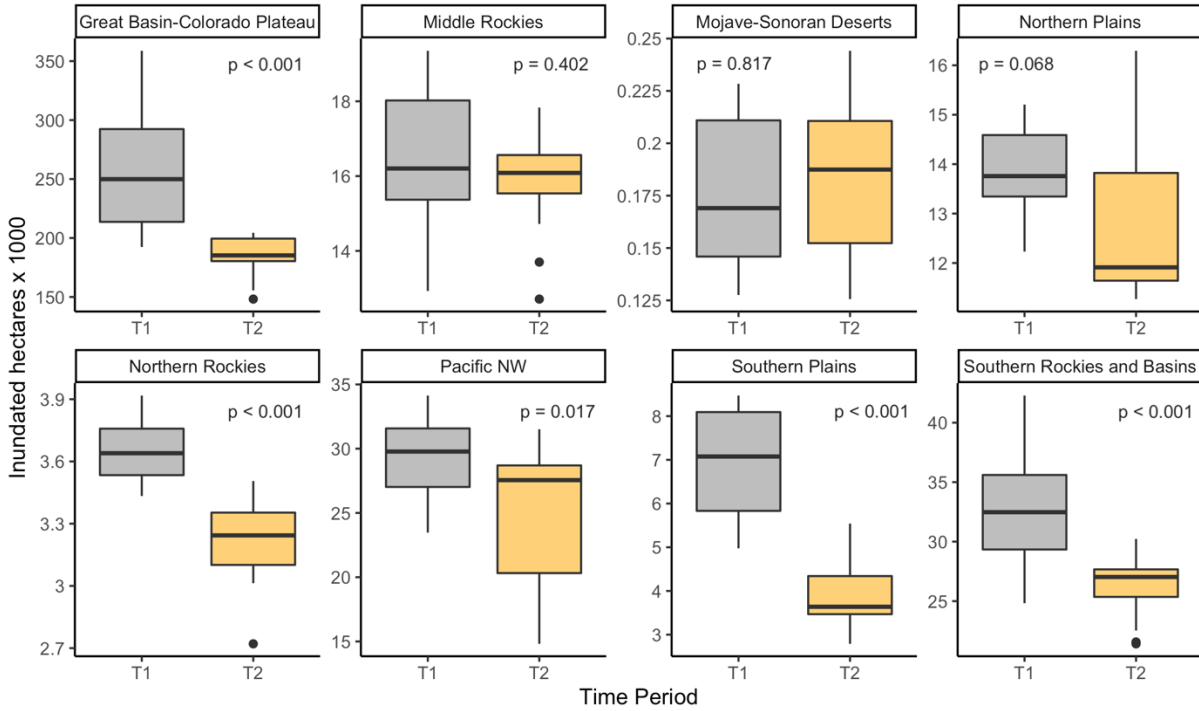


Figure 6: Boxplots of total surface water area for each region between monitoring periods (T1: 1988-2003; T2: 2004-2020).

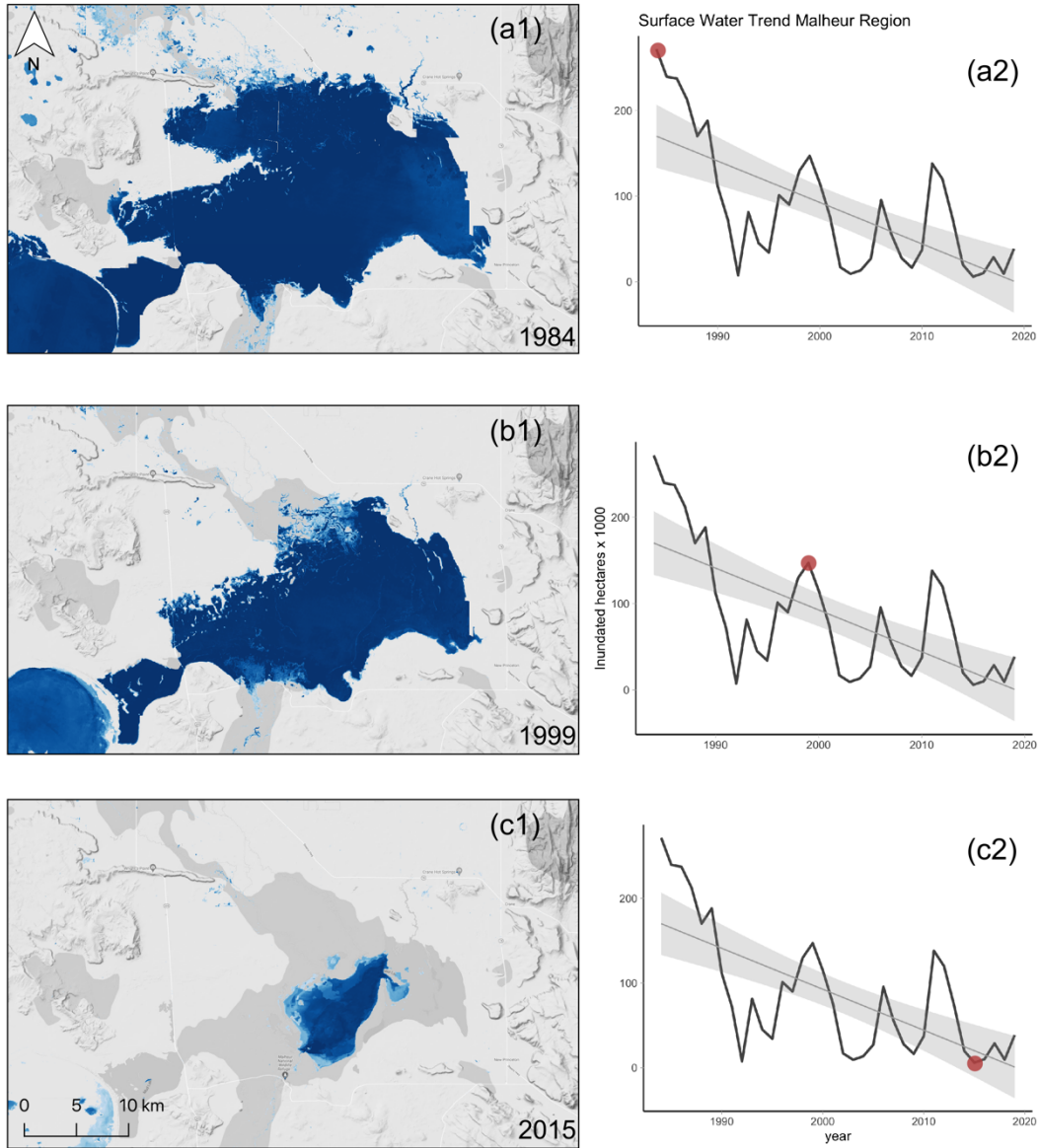


Figure 7: Annual time series of surface water for Malheur Lake, OR, USA for the years 1984 (a1), 1999 (b1), and 2015 (c1). Graphs (a2, b2, c3) depict wetland flooding trends from 1984 to 2020. The thin straight lines are the least-squares best fit with 95% CI for the slope in gray. Red points indicate the year of water surface area depicted.

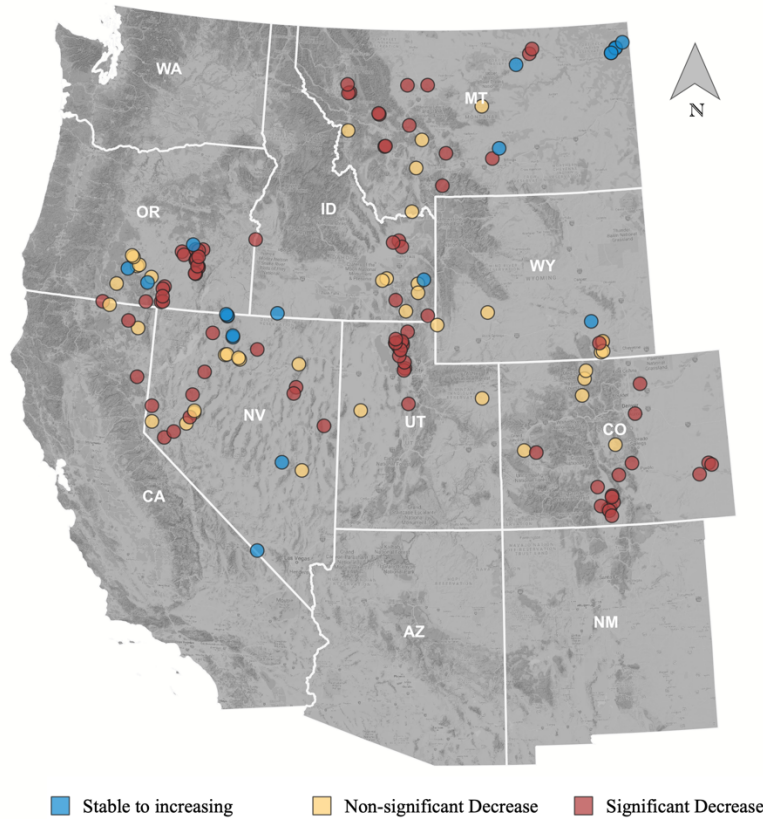


Figure 8: Map of wetland trends at individual ibis colony sites. Colors indicate the significance of change in wetland flooding: light blue is non-significant and significant increases, yellow is non-significant decreases, and red is significant decreases in flooding from T1 (1988-2003) to T2 (2004-2020).

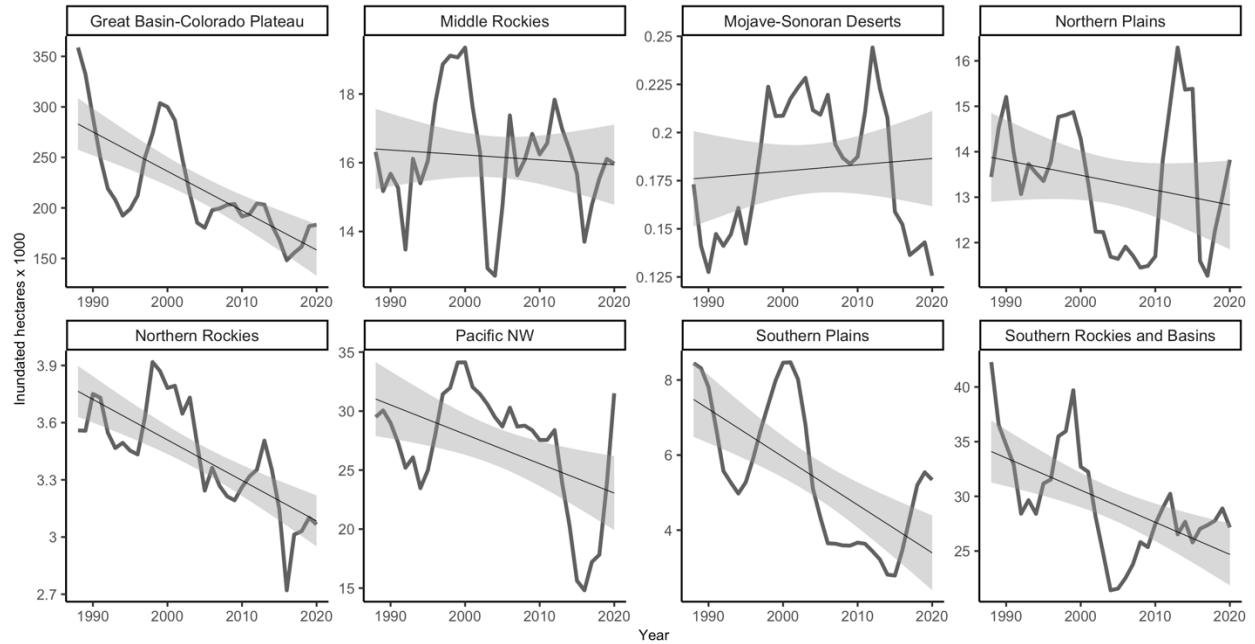


Figure 9: Annual (1988-2020) water surface area trends for wetlands within each region. The straight line is the least-squares best fit with 95% CI for the slope in gray.

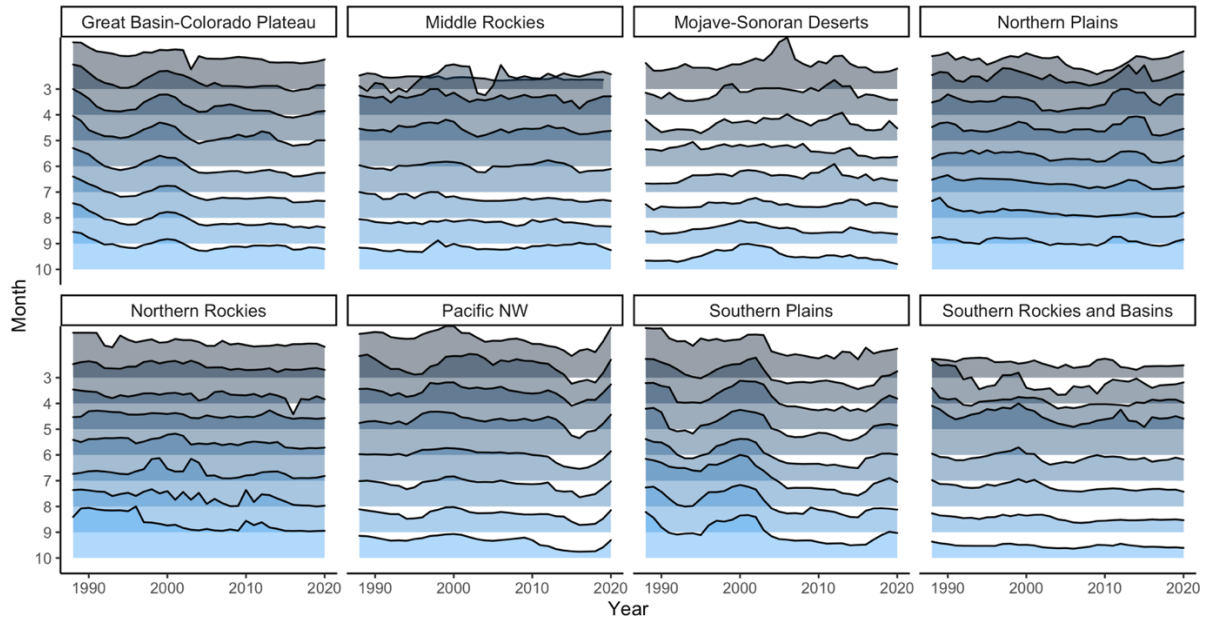


Figure 10: Monthly (March-October) surface water area trends from 1988-2020 for each region.

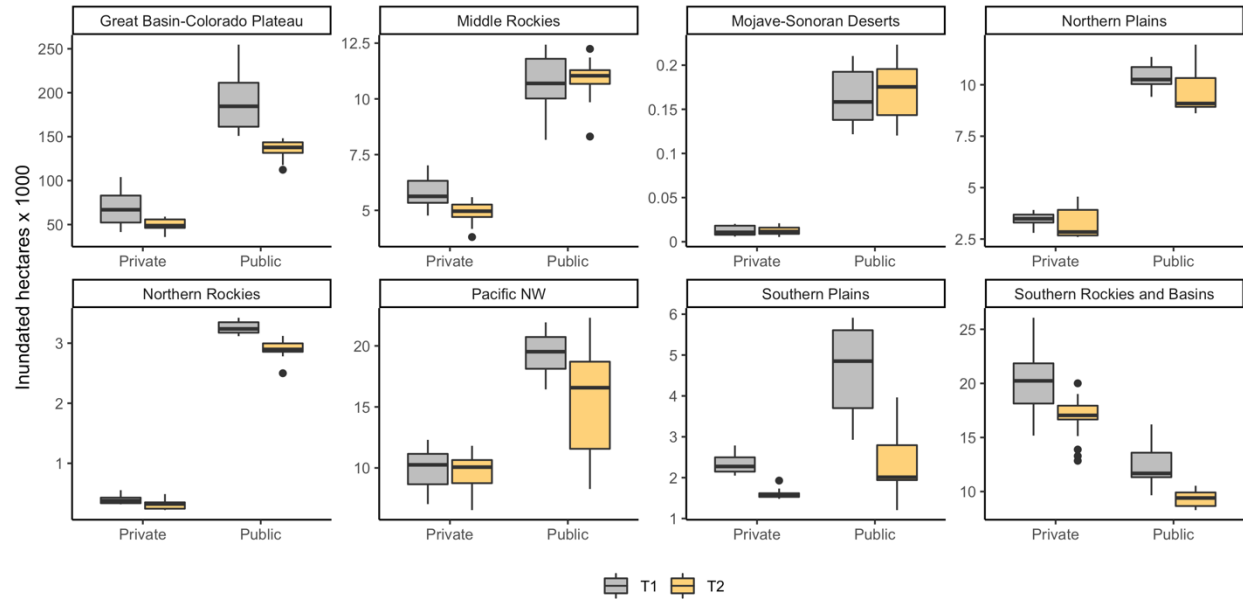


Figure 11: Boxplots of private and public water surface area for each region between monitoring periods (T1: 1988-2003; T2: 2004-2020).

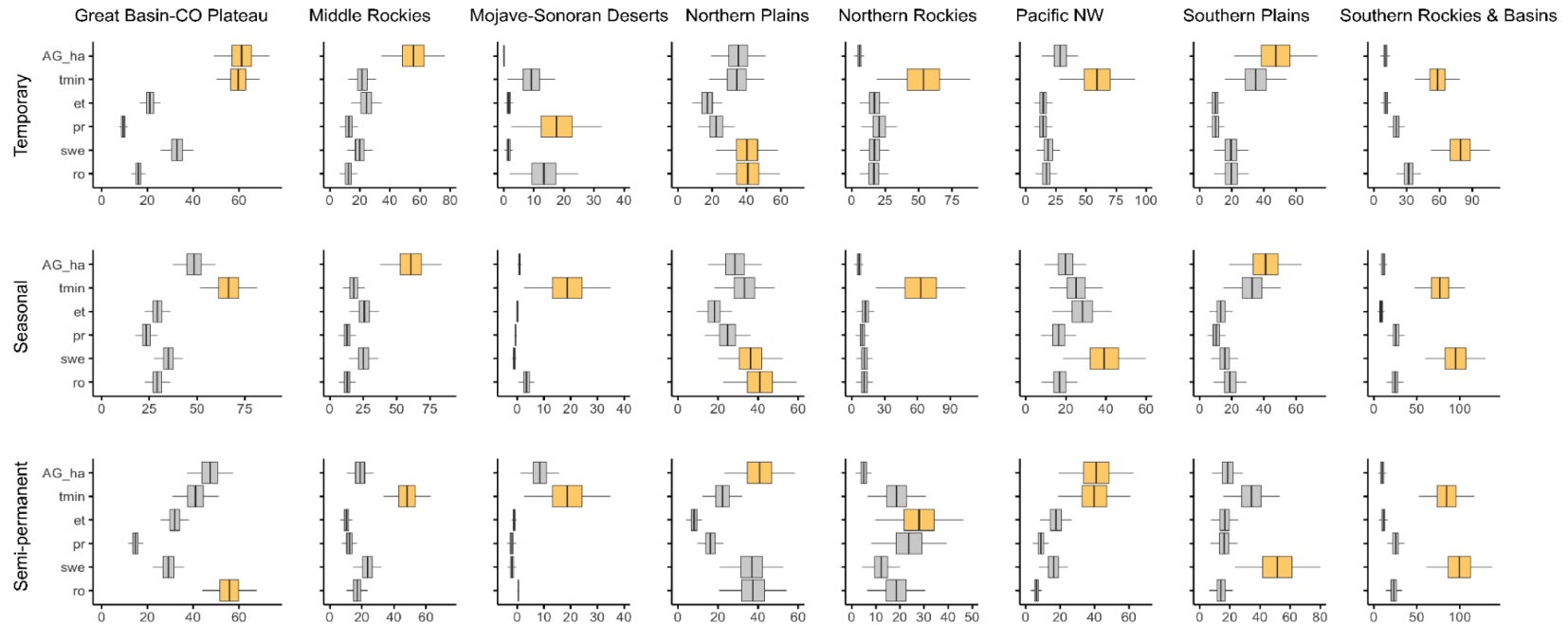


Figure 12: Predictive variable importance (VIMP) results from the random forest regression tree analysis of annual surface water area (1988-2020) in temporary, seasonal and semi-permanent wetlands. The left and right sides of the box are the 25th and 75th percentiles, respectively. The vertical line splitting the box is the median. The left and right whiskers are 5th and 95th percentiles, respectively. Predictor variables include: irrigated agricultural area (AG_ha); average daily minimum temperature (tmin); evapotranspiration (et); precipitation (pr); snow-water equivalent (swe); runoff (ro).

TABLES

Table 1: Example data of the surface water data derived from spectral mixture analysis. Surface water area (measured in hectares) is the sum of inundated pixels in a given polygon.

Polygon ID	Site Name	Region	Ownership	Wetland Type	Hydroperiod	Month	Year	Surface Water Area (ha)
267712	Cokeville Meadows NWR	Southern Rockies and Basins	Public	Managed	Semi-permanent	May	2020	0.0000
106042	Humboldt WMA	Great Basin-Colorado Plateau	Public	Managed	Seasonal	Sept	2001	0.0000
259310	Utah Lake	Great Basin-Colorado Plateau	Private	Natural	Temporary	Oct	1990	0.1376
88489	Pablo NWR	Northern Rockies	Private	Natural	Semi-permanent	Jul	2004	0.0000
63593	Grass Lake NWR	Northern Plains	Public	Managed	Seasonal	Jul	1991	0.0123
271376	Medicine Lake NWR	Northern Plains	Public	Natural	Temporary	Jul	2001	0.0000
238748	Layton Wetlands	Great Basin-Colorado Plateau	Private	Natural	Temporary	June	2001	0.0000
154167	Island Ranch	Great Basin-Colorado Plateau	Private	Flood-irrigated	Seasonal	Mar	1996	0.4885
116420	Secret Soldier	Great Basin-Colorado Plateau	Private	Riverine	Temporary	Jul	1989	0.0000
130248	Sycan Marsh	Pacific NW	Public	Natural	Semi-permanent	May	1992	0.0000

Table 2: Wetland functional type resolutions and descriptions. Surface water area values were summed across all regions and calculated as the T2 (2004-2020) average to represent current landscape conditions.

Attribute Class	Resolution	Attribute	Definition	Surface Water Area (ha)
Wetland Type	Polygon	Riverine	Riparian and riverine systems.	27875
		Natural	Natural wetland systems.	76659
		Flood-Irrigated	Wetlands associated with flood-irrigated agriculture, including those found in riparian floodplains and hay meadows.	34071
		Managed	Wetlands managed specifically for wildlife, including public refuges.	133563
Hydroperiod	Pixel	Seasonal	Flooded >3 and <6 months	82079
		Semi-permanent	Flooded > 6 months	123362
		Temporary	Flooded < 3 months	66727
Land Tenure	Polygon	Private	Privately owned land	85366
		Public	Publicly owned land: NWR, MBR, WMA, SWA, WPA	186802

Table 3: Predictor variables used in the random forest regression tree analysis. Variables were either related to agriculture or climate. Sources used to extract variable data are listed next to the associated variable.

Wetland Flooding Predictor Variables		Source
Agriculture	Annual area of irrigated agriculture	IrrMapper (Ketchum et al. 2020)
	Evapotranspiration	TerraClimate (Abatzoglou et al. 2018)
	Precipitation	TerraClimate
Climate	Runoff	TerraClimate
	Snow water equivalent	TerraClimate
	Minimum daily temperature	TerraClimate

Table 4: Summary of the area of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020). Summaries are partitioned by region. The column labeled “Significant Sites” indicates the number of ibis colony sites with significant change ($p \leq 0.05$) derived from a Wilcoxon test.

Region	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Dif	Significant Sites
Great Basin-Colorado Plateau	258634	50101	184997	17621	-73637	-28	55/87
Middle Rockies	16529	1956	15832	1292	-697	-4	6/11
Mojave-Sonoran Deserts	178	36	184	35	6	4	0/1
Northern Plains	13823	892	12909	1693	-914	-7	10/15*
Northern Rockies	3648	153	3214	193	-434	-12	3/3
Pacific Northwest	29334	3245	24874	5566	-4460	-15	3/7
Southern Plains	7006	1275	3963	865	-3043	-43	6/6
Southern Rockies and Basins	32789	4552	26196	2562	-6594	-20	13/23

* The Northern Plains had 4 sites with significant increases in surface water and 6 sites with significant decreases in surface water. This region was the only region with colony sites demonstrating significant increases.

Table 5: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Great Basin-Colorado Plateau. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Great Basin-Colorado Plateau								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	68098	19007	48979	7350	-19119	-28	0.002
	Public	190536	31195	136017	10675	-54519	-29	< 0.001
Wetland Type	Riverine	19316	3943	16943	2287	-2373	-12	0.094
	Natural	71941	24062	45054	4452	-26887	-37	< 0.001
	Flood-irrigated	20468	7180	15660	3415	-4808	-23	0.045
	Managed	146910	16766	107340	9094	-39569	-27	< 0.001
Hydroperiod	Temporary	39474	8318	40344	7034	870	2	0.929
	Seasonal	58547	11548	56878	6514	-1669	-3	0.817
	Semi-permanent	160614	41406	87775	7826	-72839	-45	< 0.001

Table 6: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Middle Rockies. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Middle Rockies								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	5848	747	4925	505	-924	-16	< 0.001
	Public	10681	1267	10907	905	227	2	0.606
Wetland Type	Riverine	3397	246	3167	146	-230	-7	0.017
	Natural	3898	428	3628	342	-270	-7	0.146
	Flood-irrigated	1723	392	1123	269	-599	-35	< 0.001
	Managed	7511	1026	7913	764	402	5	0.260
Hydroperiod	Temporary	5619	663	4805	1373	-815	-14	0.217
	Seasonal	5270	1260	4911	850	-359	-7	0.382
	Semi-permanent	5640	414	6116	858	476	8	0.110

Table 7: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Mojave-Sonoran Deserts. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Mojave-Sonoran Deserts								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	13	5	12	5	0	-2	1.000
	Public	165	31	172	31	7	4	0.736
Wetland Type	Riverine	20	7	23	7	3	16	0.127
	Managed	158	30	161	33	3	2	0.901
Hydroperiod	Temporary	43	11	57	13	14	32	0.004
	Seasonal	42	16	37	12	-5	-12	0.260
	Semi-permanent	93	23	91	18	-2	-3	0.510

Table 8: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Northern Plains. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Northern Plains								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	3466	341	3284	724	-182	-5	0.231
	Public	10357	572	9625	1015	-732	-7	0.012
Wetland Type	Riverine	1899	106	1699	110	-200	-11	< 0.001
	Natural	4346	488	4628	1075	282	7	0.901
	Flood-irrigated	525	87	447	199	-79	-15	0.049
	Managed	7053	349	6135	524	-918	-13	< 0.001
Hydroperiod	Temporary	2448	266	2469	669	21	1	0.444
	Seasonal	3198	314	2984	740	-213	-7	0.045
	Semi-permanent	8177	763	7456	496	-721	-9	0.005

Table 9: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Northern Rockies. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Northern Rockies								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	391	70	312	70	-79	-20	0.007
	Public	3257	102	2902	136	-355	-11	< 0.001
Wetland Type	Riverine	1249	21	1179	41	-70	-6	< 0.001
	Natural	2389	138	2030	157	-359	-15	< 0.001
	Flood-irrigated	10	5	5	5	-5	-46	0.009
Hydroperiod	Temporary	310	121	325	109	15	5	0.657
	Seasonal	592	147	555	224	-37	-6	0.118
	Semi-permanent	2746	185	2334	268	-412	-15	< 0.001

Table 10: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Pacific NW. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Pacific Northwest								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	9966	1597	9431	1645	-535	-5	0.309
	Public	19369	1676	15443	4232	-3926	-20	0.003
Wetland Type	Riverine	1414	212	1345	128	-69	-5	0.276
	Natural	18019	2213	15234	2878	-2785	-15	0.008
	Flood-irrigated	4125	533	3520	859	-605	-15	0.019
	Managed	5776	494	4775	2049	-1001	-17	0.127
Hydroperiod	Temporary	5536	742	6561	785	1025	19	0.001
	Seasonal	9253	1887	8764	1421	-488	-5	0.958
	Semi-permanent	14545	1737	9548	4373	-4997	-34	< 0.001

Table 11: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Southern Plains. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Southern Plains								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	2344	228	1594	108	-750	-32	< 0.001
	Public	4662	1078	2369	840	-2293	-49	< 0.001
Wetland Type	Riverine	1984	247	1281	73	-703	-35	< 0.001
	Natural	4887	1090	2579	868	-2307	-47	< 0.001
	Flood-irrigated	135	10	102	12	-33	-24	< 0.001
Hydroperiod	Temporary	625	161	562	109	-63	-10	0.423
	Seasonal	1113	294	830	204	-283	-25	0.001
	Semi-permanent	5267	1484	2571	790	-2696	-51	< 0.001

Table 12: Summary of wetland flooding change measured as the difference of means between monitoring periods (T1:1988-2003, T2: 2004-2020) in the Southern Rockies and Basins. Summaries are partitioned by land ownership, wetland type, and hydroperiod. The column labelled “*p* value” indicates significance of change ($p \leq 0.05$) derived from a Wilcoxon test.

Southern Rockies and Basins								
Attribute Class	Attribute	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	<i>p</i> value
Ownership	Private	20359	2961	16830	1983	-3530	-17	< 0.001
	Public	12430	1809	9366	704	-3064	-25	< 0.001
Wetland Type	Riverine	2585	439	2262	294	-323	-13	0.031
	Natural	4156	441	3483	550	-673	-16	0.001
	Flood-irrigated	16260	2435	13213	1677	-3047	-19	< 0.001
	Managed	9787	1664	7238	520	-2550	-26	< 0.001
Hydroperiod	Temporary	13801	1839	11604	1521	-2196	-16	0.002
	Seasonal	9139	1279	7120	908	-2018	-22	< 0.001
	Semi-permanent	9850	2201	7471	899	-2379	-24	< 0.001

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Table S1: Great Basin-Colorado Plateau - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Semi-permanent	Public	Managed	59592
Seasonal	Public	Managed	34689
Temporary	Public	Managed	11755
Semi-permanent	Private	Natural	10859
Temporary	Private	Flood-irrigated	8730
Temporary	Private	Natural	7720
Seasonal	Private	Natural	7687
Temporary	Public	Natural	6449
Semi-permanent	Public	Riverine	6064
Semi-permanent	Public	Natural	5904
Seasonal	Public	Natural	5366
Semi-permanent	Private	Riverine	3552
Seasonal	Private	Flood-irrigated	2847
Seasonal	Public	Riverine	2827
Temporary	Public	Riverine	1745
Temporary	Private	Riverine	1104
Seasonal	Private	Riverine	1099
Semi-permanent	Private	Flood-irrigated	804
Semi-permanent	Private	Managed	560
Temporary	Public	Flood-irrigated	494
Seasonal	Private	Managed	418
Temporary	Private	Managed	392
Seasonal	Public	Flood-irrigated	158
Semi-permanent	Public	Flood-irrigated	82

Table S2: Middle Rockies - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Seasonal	Public	Managed	2336
Semi-permanent	Public	Managed	1945
Temporary	Public	Managed	1619
Semi-permanent	Public	Riverine	1088
Semi-permanent	Private	Natural	901
Semi-permanent	Private	Riverine	873
Semi-permanent	Public	Natural	842
Temporary	Private	Flood-irrigated	686
Temporary	Private	Natural	517
Seasonal	Private	Riverine	436
Seasonal	Private	Natural	387
Temporary	Private	Riverine	352
Seasonal	Public	Natural	299
Temporary	Public	Natural	250
Seasonal	Private	Flood-irrigated	237
Seasonal	Public	Riverine	169
Temporary	Public	Riverine	96
Semi-permanent	Private	Flood-irrigated	81
Semi-permanent	Private	Managed	32
Temporary	Public	Flood-irrigated	12
Temporary	Private	Managed	12
Seasonal	Private	Managed	3
Seasonal	Public	Flood-irrigated	0.5

Table S3: Mojave-Sonoran Deserts - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Semi-permanent	Public	Managed	85
Temporary	Public	Managed	42
Seasonal	Public	Managed	30
Temporary	Public	Natural	13
Temporary	Private	Natural	5
Semi-permanent	Private	Natural	5
Seasonal	Private	Natural	3
Semi-permanent	Public	Natural	1
Seasonal	Public	Natural	1

Table S4: Northern Plains - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Semi-permanent	Public	Managed	4211
Semi-permanent	Public	Natural	1104
Seasonal	Public	Managed	896
Semi-permanent	Private	Natural	690
Semi-permanent	Public	Riverine	685
Temporary	Private	Natural	608
Seasonal	Public	Natural	597
Seasonal	Private	Natural	562
Temporary	Public	Managed	537
Semi-permanent	Private	Riverine	487
Temporary	Public	Natural	437
Seasonal	Private	Riverine	210
Temporary	Private	Flood-irrigated	175
Temporary	Private	Riverine	145
Temporary	Public	Flood-irrigated	85
Seasonal	Public	Riverine	67
Seasonal	Private	Flood-irrigated	62
Temporary	Public	Riverine	45
Semi-permanent	Private	Flood-irrigated	35
Seasonal	Public	Flood-irrigated	30
Semi-permanent	Public	Flood-irrigated	4
Seasonal	Private	Managed	1
Semi-permanent	Private	Managed	0.4
Temporary	Private	Managed	0.3

Table S5: Northern Rockies - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Semi-permanent	Public	Natural	1126
Semi-permanent	Public	Riverine	1042
Seasonal	Public	Natural	327
Temporary	Public	Natural	178
Semi-permanent	Private	Natural	148
Temporary	Private	Natural	92
Seasonal	Public	Riverine	68
Seasonal	Private	Natural	59
Temporary	Public	Riverine	33
Semi-permanent	Private	Riverine	9
Seasonal	Private	Riverine	6
Temporary	Private	Riverine	4
Temporary	Private	Flood-irrigated	4
Temporary	Public	Flood-irrigated	2
Semi-permanent	Private	Flood-irrigated	0.4
Seasonal	Private	Flood-irrigated	0.2

Table S6: Pacific Northwest - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Semi-permanent	Public	Natural	4759
Seasonal	Public	Natural	2776
Semi-permanent	Public	Managed	1825
Semi-permanent	Private	Natural	1779
Temporary	Private	Flood-irrigated	1621
Seasonal	Private	Natural	1594
Seasonal	Public	Managed	1567
Temporary	Public	Natural	1257
Temporary	Public	Managed	1077
Temporary	Private	Natural	1059
Seasonal	Private	Flood-irrigated	781
Temporary	Public	Flood-irrigated	512
Semi-permanent	Private	Riverine	394
Seasonal	Private	Riverine	339
Semi-permanent	Private	Flood-irrigated	316
Semi-permanent	Public	Riverine	217
Temporary	Private	Riverine	206
Seasonal	Public	Flood-irrigated	92
Seasonal	Public	Riverine	57
Temporary	Public	Riverine	29
Semi-permanent	Public	Flood-irrigated	15
Temporary	Private	Managed	1
Seasonal	Private	Managed	0.4
Semi-permanent	Private	Managed	0.1

Table S7: Southern Plains - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Semi-permanent	Public	Natural	1414
Semi-permanent	Private	Riverine	657
Seasonal	Public	Natural	374
Semi-permanent	Private	Natural	321
Temporary	Public	Natural	204
Temporary	Private	Riverine	171
Seasonal	Private	Riverine	162
Seasonal	Private	Natural	121
Temporary	Public	Riverine	118
Semi-permanent	Public	Riverine	112
Seasonal	Public	Riverine	92
Temporary	Private	Natural	81
Semi-permanent	Private	Flood-irrigated	50
Temporary	Private	Flood-irrigated	34
Seasonal	Private	Flood-irrigated	20

Table S8: Southern Rockies and Basins - Wetland surface area measured for each variation of overlapping wetland attributes: hydroperiod, land ownership, and wetland type. Wetland area is measured in hectares.

Hydroperiod	Ownership	Wetland Type	Wetland Area (ha)
Temporary	Private	Flood-irrigated	5824
Semi-permanent	Public	Managed	3221
Seasonal	Private	Flood-irrigated	2401
Seasonal	Public	Managed	1665
Temporary	Public	Managed	1172
Semi-permanent	Private	Natural	1099
Semi-permanent	Private	Flood-irrigated	1067
Temporary	Private	Riverine	759
Semi-permanent	Public	Natural	682
Semi-permanent	Private	Riverine	591
Seasonal	Private	Natural	501
Temporary	Private	Natural	493
Seasonal	Private	Riverine	465
Seasonal	Public	Natural	340
Semi-permanent	Public	Flood-irrigated	287
Temporary	Public	Natural	272
Temporary	Public	Flood-irrigated	141
Temporary	Public	Riverine	125
Seasonal	Public	Flood-irrigated	116
Semi-permanent	Public	Riverine	78
Seasonal	Public	Riverine	64

Table S9: Evapotranspiration - Changes between periods T1 (1988-2003) and T2 (2003-2020) and the Wilcoxon test and linear regression statistical test results of significance on the annual time series.

Region	T1 (mm)	SD1	T2 (mm)	SD2	Change (mm)	% Difference	Num. Wilcox-<i>p</i> Significant	Num. LM-<i>p</i> Significant
Great Basin-Colorado Plateau	2571	476	2635	469	64	2	0/12	0/12
Middle Rockies	3505	532	3519	310	15	1	0/5	0/5
Mojave-Sonoran Deserts	1358	434	1385	525	27	2	0/1	0/1
Northern Plains	3357	549	3492	466	134	4	0/5	0/5
Northern Rockies	4290	453	4101	298	-189	-4	0/1	0/1
Pacific NW	5129	442	5109	486	-20	0	0/2	0/2
Southern Plains	3580	566	3359	564	-221	-6	0/2	1/2
Southern Rockies and Basins	3261	528	3216	459	-45	-1	0/7	1/7

Table S10: Precipitation - Changes between periods T1 (1988-2003) and T2 (2003-2020) and the Wilcoxon test and linear regression statistical test results of significance on the annual time series.

Region	T1 (mm)	SD1	T2 (mm)	SD2	Change (mm)	% Difference	Num. Wilcox-<i>p</i> Significant	Num. LM-<i>p</i> Significant
Great Basin-Colorado Plateau	312	77	320	76	9	3	0/12	0/12
Middle Rockies	458	89	460	49	2	1	0/5	0/5
Mojave-Sonoran Deserts	165	64	167	75	2	1	0/1	0/1
Northern Plains	372	66	389	58	17	5	0/5	0/5
Northern Rockies	694	122	665	48	-28	-4	0/1	0/1
Pacific NW	937	254	920	274	-17	-2	0/2	0/2
Southern Plains	388	64	366	64	-22	-6	0/2	1/2
Southern Rockies and Basins	377	73	377	63	-1	0	0/7	1/7

Table S11: Snow-water equivalent - Changes between periods T1 (1988-2003) and T2 (2003-2020) and the Wilcoxon test and linear regression statistical test results of significance on the annual time series.

Region	T1 (mm)	SD1	T2 (mm)	SD2	Change (mm)	% Difference	Num. Wilcox-<i>p</i> Significant	Num. LM-<i>p</i> Significant
Great Basin-Colorado Plateau	249	101	265	97	15	5	0/12	0/12
Middle Rockies	509	178	521	146	12	6	0/5	0/5
Mojave-Sonoran Deserts	80	37	78	42	-2	-3	0/1	0/1
Northern Plains	213	79	229	94	16	10	0/5	0/5
Northern Rockies	955	338	925	237	-30	-3	0/1	0/1
Pacific NW	175	91	175	92	0	0	0/2	0/2
Southern Plains	127	37	135	39	8	6	0/2	0/2
Southern Rockies and Basins	317	89	349	93	32	9	0/7	0/7

Table S12: Runoff - Changes between periods T1 (1988-2003) and T2 (2003-2020) and the Wilcoxon test and linear regression statistical test results of significance on the annual time series.

Region	T1 (mm)	SD1	T2 (mm)	SD2	Change (mm)	% Difference	Num. Wilcox-<i>p</i> Significant	Num. LM-<i>p</i> Significant
Great Basin-Colorado Plateau	54	33	57	37	2	6	0/12	0/12
Middle Rockies	107	46	109	38	2	5	0/5	0/5
Mojave-Sonoran Deserts	28	23	28	24	-1	-2	0/1	0/1
Northern Plains	36	12	40	16	4	13	0/5	0/5
Northern Rockies	264	102	257	63	-7	-3	0/1	0/1
Pacific NW	424	224	407	244	-17	-4	0/2	0/2
Southern Plains	30	8	30	9	0	-1	0/2	0/2
Southern Rockies and Basins	51	21	55	23	4	5	0/7	0/7

Table S13: Average minimum daily temperature - Changes between periods T1 (1988-2003) and T2 (2003-2020) and the Wilcoxon test and linear regression statistical test results of significance on the annual time series.

Region	T1 (C°)	SD1	T2 (C°)	SD2	Change (C°)	% Difference	Num. Wilcox-<i>p</i> Significant	Num. LM-<i>p</i> Significant
Great Basin-Colorado Plateau	1	7	7	6	5	125	7/12	9/12
Middle Rockies	-24	6	-21	7	3	15	1/5	1/5
Mojave-Sonoran Deserts	81	6	89	6	9	11	1/1	1/1
Northern Plains	-15	7	-13	9	2	16	0/5	0/5
Northern Rockies	-21	6	-18	6	3	13	0/1	0/1
Pacific NW	35	6	39	5	4	12	0/2	2/2
Southern Plains	4	4	7	6	3	297	0/2	2/2
Southern Rockies and Basins	-22	5	-19	7	2	90	0/7	3/7

Table S14: Agricultural irrigation area - Changes between periods T1 (1988-2003) and T2 (2003-2020) and the Wilcoxon test and linear regression statistical test results of significance on the annual time series.

Region	T1 (ha)	SD1	T2 (ha)	SD2	Change (ha)	% Difference	Num. Wilcox-<i>p</i> Significant	Num. LM-<i>p</i> Significant
Great Basin-Colorado Plateau	177327	21045	190037	15391	12710	12	6/12	8/12
Middle Rockies	318728	41399	331898	30029	13171	3	0/5	1/5
Mojave-Sonoran Deserts	17502	1564	17819	929	317	2	0/1	1/1
Northern Plains	60406	16044	69228	21119	8822	19	0/5	2/5
Northern Rockies	177733	30458	165649	22808	-12085	-7	0/1	0/1
Pacific NW	422625	24410	443526	19320	20902	4	1/2	1/2
Southern Plains	297596	43387	274870	39564	-22726	-8	0/2	0/2
Southern Rockies and Basins	158699	27078	160305	27941	1605	7	2/7	3/7

Table S15: State and Federally managed wildlife refuge sites included in analysis.

State Managed	State	Federally Managed	State
Honey Lake SWA	CA	Modoc NWR	CA
San Luis Lake SWA	CO	Lower Klamath NWR	CA/OR
Russell Lakes SWA	CO	Tule Lake NWR	CA/OR
Queens SWA	CO	Alamosa NWR	CO
Fort Boise WMA	ID	Monte Vista NWR	CO
Sterling WMA	ID	Blanca Wetlands	CO
Scripps WMA	NV	Bear Lake NWR	ID
Alkali Lake WMA	NV	Oxford Slough WPA	ID
Mason Valley WMA	NV	Grays Lake NWR	ID
Carson Lake Pasture	NV	Camas NWR	ID
Humboldt WMA	NV	Market Lake WMA	ID
Franklin Lake WMA	NV	Mud Lake WMA	ID
Railroad Valley WMA	NV	Ruby Lake NWR	NV
W.E. Kirch WMA	NV	Stillwater NWR	NV
Warm Springs WMA	MT	Ash Meadows NWR	NV
Canyon Ferry WMA	MT	Medicine Lake NWR	MT
Lake Helena WMA	MT	Red Rock Lakes NWR	MT
Freezeout Lake WMA	MT	Lee Metcalf NWR	MT
Summer Lake Wildlife Area	OR	Pablo NWR	MT
Farmington Bay WMA	UT	Ninepipe NWR	MT
Ogden Bay WMA	UT	Benton Lake NWR	MT
Harold Crane WMA	UT	Spidel WPA	MT
Willard Spur	UT	Grass Lake NWR	MT
Public Shooting Grounds WMA	UT	Bowdoin NWR	MT
		Medicine Lake NWR	MT
		Warner Wetlands	OR
		Malheur NWR	OR
		Fish Springs NWR	UT
		Ouray NWR	UT
		Bear River MBR	UT
		Cokeville Meadows NWR	WY
		Bamforth Lake NWR	WY
		Hutton Lake NWR	WY