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Great Sand Dunes National Park and Preserve

Ungulate Use and Wetland Condition in the Ungulate Management Plan Baseline Period (2016–2019)



Elk (*Cervus canadensis*) graze an herbaceous wetland in the escape dunes to the west of the main dune field in the Little Spring Creek headwaters, Great Sand Dunes National Park and Preserve, 2016.

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Great Sand Dunes National Park and Preserve: Ungulate use and wetland condition in the ungulate management plan baseline period (2016–2019)

Science Report NPS/SR—2025/258

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Abstract

This report presents baseline (2016–2019) results from Ungulate Management Plan (UMP) monitoring of sensitive and important wetlands at Great Sand Dunes National Park and Preserve (GRSA) by the Rocky Mountain Network. At GRSA's request we also include several management recommendations in the Discussion.

Wetlands harbor disproportionately high levels of biodiversity and support iconic species like elk (*Cervus canadensis*) and bison (*Bison bison*). We develop Ungulate Use Indices (UUIs) from dung, collar, and camera trap data to quantify elk and bison use of wetlands. We estimate Wetland Condition Indices (WCIs) using bioassessment methods that model a synthetic response in wetland vegetation to ungulate use. WCIs provide a single number that encapsulates the condition or ecological integrity of wetlands used by elk and bison. WCIs stand alone, but we enhance their application via interpretation of their component metrics. We augment WCIs with four hand-picked (HP) metrics. Finally, we develop novel assessment points (APs) in consultation with park resource management staff that place results into classes of the best, intermediate, and worst conditions in the baseline data.

WCI models successfully capture a large portion of the variation in wetland condition response to ungulate use—much more than single metrics alone. Baseline condition of many sand sheet wetlands was poor, with almost 40% and 66% of herbaceous and woody sites degraded by elk and bison use, respectively. Two HP metrics, iris (*Iris missouriensis*) and silverweed (*Potentilla anserina*) cover in herbaceous sites, and the density of browsed willow and cottonwood (Salicaceae) in woody sites, are emblematic of these poor conditions. Over 50% of sites were in the worst condition classes for these two metrics. However, should the park effectively manage elk and bison into the future and pursue other important restoration goals, our models suggest these and other indicators of wetland condition could improve.

Baseline ungulate use and wetland condition will be compared to future UMP wetland monitoring results as GRSA resource management seeks to reduce elk and bison use of wetlands by lowering density and hazing animals. GRSA expects to approach this process in an adaptive way and may add other active and passive ungulate management strategies as warranted. The ability of a WCI to consolidate variation in wetland condition response supports a high statistical power to detect future changes. Its direct connection to park management actions is an important application of ecological monitoring that will assist GRSA resource management into the future.

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Introduction

Great Sand Dunes National Park and Preserve (GRSA), located in the high San Luis Valley of south-central Colorado (Figure 1), has globally significant biodiversity (NPS 2007), largely from its wide range of habitats and microclimates. Although the park was established to protect the tallest sand dunes in North America, wetlands are the most ecologically important of the park's habitats (Schweiger et al. 2017). Wetlands have a highly disproportionate, relative to their area, share of the park's plants and provide critical ecological support of iconic species such as elk (*Cervus canadensis*) and bison (*Bison bison*). They are also the most productive areas in the park's sand sheet zone—true ribbons of green nestled within the park's high desert ecosystems (Figure 2). Finally, wetlands are intimately connected to the hydrologic support systems that maintain the dunes and are a useful indicator of this core process at GRSA. Yet wetlands are also at risk in GRSA (Figure 3). They have been subjected to decades of human disturbance (Schweiger et al. 2017), with elk, bison, and historical cattle (*Bos taurus*) use likely far exceeding the carrying capacity of these areas (Schoenecker 2012; Wockner et al. 2015; Zeigenfuss and Schoenecker 2021). All these stressors have degraded wetland condition (NPS 2018).

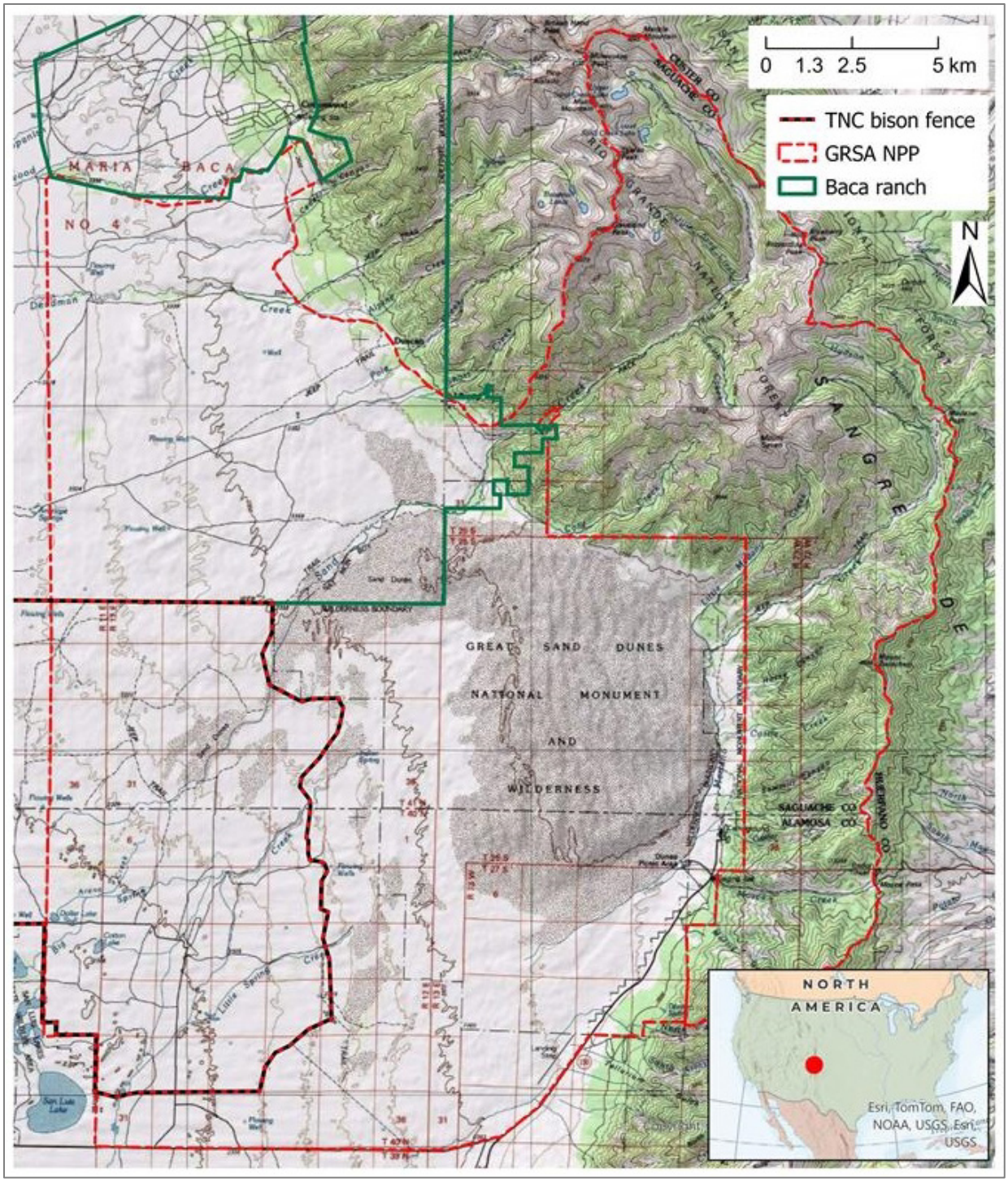


Figure 1. Great Sand Dunes National Park and Preserve (GRSA) land ownership. Inset shows location of GRSA in the U.S. The Nature Conservancy maintains a fence (TNC bison fence) that bounds a 16,100 ha bison pasture. This pasture defines two ungulate use zones: bison and elk habitat inside the fence and elk only outside the fence. A small buffer of “elk and some bison” (not shown) occurs along the boundary of the fence as it is episodically broken and bison trespass into this zone. Note that “Great Sand Dunes National Monument and Wilderness” is a former name for the park. NPS



Figure 2. Productive herbaceous wetland (site 407) in an exclosure along Little Spring Creek, Great Sand Dunes National Park and Preserve. Field crews experience joy in these places. NPS / B. SCHWEIGER



Figure 3. A rare combination of elk and bison simultaneously graze an herbaceous wetland (site 204) just outside the bison fence at Great Sand Dunes National Park and Preserve, 2018. NPS

Because wetland habitats are among the resources at risk from high levels of ungulate use, the GRSA General Management Plan (NPS 2007) required NPS to develop an Ungulate Management Plan and Environmental Impact Statement (UMP/EIS or hereafter, UMP; NPS 2018). The UMP outlines potential future management of elk and bison in GRSA to support long-term protection of resources and coordinates NPS management activities with partners across the broader eastern San Luis Valley landscape. Wetlands are identified in the UMP as the primary ecosystem type to which ungulate management should be linked via a desired wetland condition (NPS 2018). It also requires wetlands monitoring to "1) inform the development of quantitative ecological and vegetation thresholds; 2) inform whether ungulate management activities are helping to move wetlands towards desired conditions; and 3) better understand how other drivers, such as hydrology and climate, influence wetland health" (NPS 2018).

GRSA and the National Park Service (NPS) Inventory and Monitoring Program's Rocky Mountain Network (the network) began long term ecological monitoring of wetlands in 2010 (Schweiger et al. 2017). In 2016, this work was modified to better fit the needs of the UMP with more intensive sampling over a baseline period (2016–2019, also referred to as Phase 1). This baseline period was

prior to the park managing elk or bison. Data collected during the baseline period and described in this report are used to determine gradients in ungulate use that contribute to degradation of wetland habitat. Ungulate Use Indices (UUIs) are developed and incorporated into models that relate ungulate use to Wetland Condition Indices (WCIs) and hand-picked (HP) individual indicators developed by GRSA and the network. The data within the UUIs, WCIs and HP indicators (plus all supporting environmental data) are planned to be collected into the future of the UMP when GRSA begins managing elk (Phase 2) and bison (Phase 3). Monitoring results and their assessment will be integrated into the park's adaptive management of elk and bison and their habitat.

Bison, elk, mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*) were native to the area until about 1900 when bison were extirpated, and numbers of the other species were much reduced (Meany and Van Vuren 1993). Elk and pronghorn survived in small numbers (Warren 1910; Cary 1911; Swift 1945), and some animals likely moved back into the area from surrounding populations to the north and south, as well as from nearby animal releases by the Colorado Division of Wildlife (now known as Colorado Parks and Wildlife [CPW]) from the 1910s through the 1960s (Swift 1945; Colorado Division of Wildlife 2010). Elk were rarely noted in the study area prior to the late 1990s (Colorado Division Wildlife 2010). Elk roam freely throughout the study area, including the Medano Ranch bison pasture. In the late 1980s a commercial bison herd was established on private lands of the Medano Ranch. Bison are restricted to a fenced 16,100 ha area on the Medano Ranch that lies about half within the boundary of GRSA and half within the boundary of the Baca National Wildlife Refuge to the park's west and north (see Figure 1). Ungulate populations in the valley are regulated by hunting, except for bison, which are gathered and culled annually to maintain population levels. Finally, moose (*Alces alces*) have recently begun to expand their range into the study area but are present at low numbers.

Bison population data are collected by Zapata Partners and the United States Geological Service (USGS) during annual roundup and culling of the bison herd each November. Schoenecker (2012) and Schoenecker et al. (2015) developed a bison demographic model through 2012 based on data collected from 1993 to 2011 (this was later extended to 2018; K. Schoenecker, Ecologist, USGS, personal communication, 2020). Estimated bison population size varied from 1993 to 2018, ranging from a low of roughly 1,000 animals in 2004 to a high of about 2,500 animals in 2014 (note that this is about the same high count value as in the much larger Yellowstone National Park). During the first three years of the baseline period, bison population size averaged around 2,150 animals (numbers are not available for 2019 but they are likely similar to the previous three years).

Post-hunt elk population estimates from Colorado Parks and Wildlife (CPW 2005–2020) from 2005 to 2020 are only available for a larger spatial extent (General Management Unit [GMU] 82), which includes Great Sand Dunes National Park and Preserve. These suggest a general downward trend in elk population size from 2005 to roughly 2015, but from 2016 to 2020, the elk population appeared to be increasing (CPW 2005–2020). These estimates are modeled based on biannual aerial game surveys and annual hunter harvest data. However, available data on elk population applies to the entirety of GMU 82 and cannot reliably be downscaled to a smaller reporting area, such as the park.

Phase 2 of the UMP includes management of the elk population beginning in 2020. Phase 3 occurs when the park gains control of the bison herd and can initiate a preferred option for bison management as specified in the UMP EIS (date to be determined). Importantly, ungulate use of wetland habitat has a complex relationship with population size—it may or may not track with how many elk and/or bison are on the landscape. The UUIs we develop in this report and in Zeigenfuss et al. (2024) are intended to correct for this and provide a more direct estimate of potential degradation to wetland condition from ungulate use.

Monitoring objectives

UMP baseline monitoring objectives are as follows. All objectives are designed to be flexible ("adaptive management") as we learn or respond to changes in funding:

1. Develop and estimate the baseline status of Ungulate Use Indices (UUIs) in woody and herbaceous wetlands.
2. Develop and estimate the baseline status of Wetland Condition Indices (WCIs) relative to ungulate use in woody and herbaceous wetlands. By design, WCIs control for environmental gradients that may also influence wetland condition.
3. Develop and estimate the baseline status of select hand-picked (HP) indicators of wetland condition relative to ungulate use in woody and herbaceous wetlands. HP metrics are adjusted for environmental gradients that influence wetland condition. Select raw or unadjusted results are included to help in metric interpretation.
4. For UUIs, WCIs and HP indicators, document and assess patterns across wetland condition classes derived from park-supported assessment points (APs) and management-relevant drivers of condition, including exclosure, year, ungulate use type, and wetland subtype.

Purpose of this report

This report summarizes and interprets 2016–2019 baseline (Phase 1) results from Rocky Mountain Network and collaborator monitoring. Its primary purpose is to summarize baseline ungulate use and wetland condition that will be compared to future monitoring data as the park manages elk (in Phase 2, 2020–2025) and elk and bison (in Phase 3, dates to be determined). At the park's request, we also include content on possible future scenarios of ungulate management and the implications of these choices on ungulate use and wetland condition.

Importantly, a fundamental connection between ungulate use and wetland response structures our choices of which metrics to include in this report and how they are addressed. For example, we focus on WCIs because we assume they link changes in wetland condition caused by changes in ungulate use (Grace 2024). We also choose HP metrics based on a demonstrable response to ungulate use—if an HP metric, adjusted for other factors that influence it, is not affected by ungulate use, it is likely less useful for the goals of the UMP. Numerically connecting a monitoring response to an important park management action is a desired, but often elusive, objective in NPS long term monitoring. The UMP provides an explicit context to meet this goal.

We do not include final results on the effect of park management of elk numbers and distribution on wetland condition. Rather these results will be presented in UMP reports to be developed in the future. We recognize that providing information about the effects of ungulate management on wetland condition is very important and that timely information is needed for park management decisions. However, many wetland responses take “ecological time” to develop, and we should not expect these results to materialize over a time frame shorter than 5 to 10 years. We will produce interim products (visualizers, brief summaries, etc.) that address management needs with the best available information. Careful estimation of a management relevant ecological baseline is also critical for UMP, and this report presents that effort.

Methods

The following sections present brief summaries of how and why sites were selected, how data were collected in the field and/or harvested from ancillary sources, and how data were analyzed and interpreted. For additional content on our methods, see Schweiger, Gage, Driver et al. (2015), Schweiger, Gage, Haynes et al. (2015), Schweiger et al. (2017), Zeigenfuss et al. (2024), and various appendices to this report.

Sample design and statistical inference

We selected 74 sample sites across the sand sheet using a targeted design approach. Sites were located in wetland complexes using a sample frame developed for the 2010 Rocky Mountain Network wetland survey (Schweiger, Gage, Driver et al. 2015; Schweiger et al. 2017; Figure 4) in a Geographic Information System (GIS). Wetland complex polygons were originally delineated as a sample frame based on NPS vegetation mapping (Salas et al. 2011), National Wetland Inventory data (USFWS 1991), and select field reconnaissance. Sites were allocated across wetland type based roughly on the extent of wetland in each as nested within ungulate usage zones (see Figure 1). We utilized a subset of existing USGS exclosures, paired unenclosed sites, and existing network long term sample locations within these wetland types and ungulate use categories, as possible. Sites were designated for sampling in panels from 2016 to 2020; however, sampling in 2020 was canceled due to the Covid-19 pandemic and these events reallocated as possible. Approximately 10% of sample events were designated as revisits within and across years. We sampled these 74 sites a total of 103 times in the baseline period.

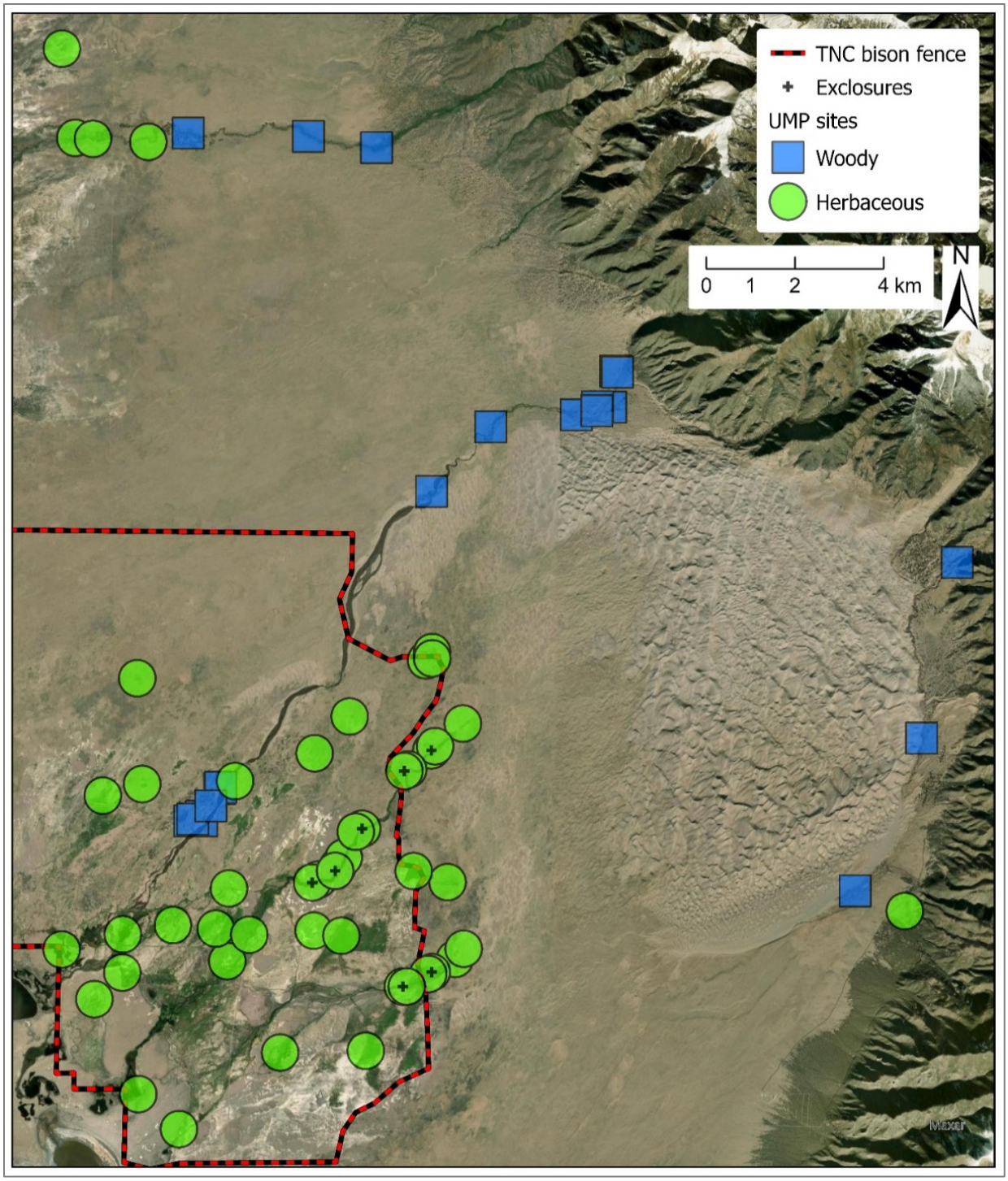


Figure 4. Great Sand Dunes National Park and Preserve Ungulate Management Plan (UMP) sample sites, 2016–2019. Map includes a Nature Conservancy (TNC) fence that bounds the bison pasture. NPS

We carefully considered a randomized or targeted sample design approach and determined that a targeted (not randomized) sampling design was the best approach to meet the needs of the UMP. We lacked sufficient detail on small scale variability and especially ungulate use to support an efficient

randomized design. A randomized design would have also complicated the incorporation of existing sites into the design. The choice of a targeted sample design means, strictly speaking, that our results apply only to sampled UMP sites. However, we expect many results are generalizable to some broader resource like "the cottonwood and willow woody wetlands of the sand sheet," but this inference is done with unknown bias and should be approached cautiously.

Field methods

Sample sites

Sample sites were confirmed in the field on their first visit. Confirmation included evaluating a site's accessibility and its wetland status. Adjustments in the GIS-defined wetland complex were made for access (i.e., safety) and wetland boundary. Sites adopted from previous monitoring by the network, GRSA or USGS were also evaluated and adjusted in case wetland type and boundaries had changed. Sample sites include up to three variants of sample plots or specific sampling locations (Figure 5). All sites have "core plots" located at or near the location defined in the sample design process. Sites also included zero to five additional sample plots of two types. First, Poo-Releve-Wood plots (PRW; note we retain the informal term "poo" for consistency with field protocol documents—in the literature this is "dung" or "pellet"; but see Poggenburg et al. 2018 for a humorous comment on his terminology) were used to sample dung, herbaceous vegetation (with a simpler releve method) and woody vegetation. They were located based on differences in vegetation type not sampled by the core plot, with crews placing PRW plots in each unique vegetation type in a complex. Variation in vegetation type generally matches smaller scale topographic variation likely to drive ground water elevation, allowing PRW plots to be located prior to actual vegetation sampling. Second, Poo (P) plots were added to a site if the core and PRW plots did not sample extant dung density in the site. Some sites could be sufficiently sampled with a single core plot. The number of PRW and P plots was set to a maximum of five given logistical constraints, and we have no sites in the design where more than five PRW or P plots were needed.



Figure 5. Detail of an example sample site ("GRSA_210") along Big Spring Creek showing a wetland complex (red polygon) and three sample plots (a core, a Poo-Releve-Wood [PRW], and a Poo [P]; green stars) for Great Sand Dunes National Park and Preserve Ungulate Management Plan monitoring, 2016–2019. NPS

For all plots not already established as part of previous monitoring, a sample plot center was located by blindly throwing a marker over a crew member's shoulder. Following Schweiger et al. (2016), core plots consisted of a 10 × 10 m square plot (100 m^2) with four nested 1 × 1 m (1 m^2) subplots for detailed understory vegetation sampling. PRW and P plots used a circular 5.6 m radius plot (100 m^2) with four 4-m diameter nested subplots for woody seedling counts in core and PRW plots. Most core sites included a shallow (usually less than 2 m deep) groundwater monitoring well. Finally, 10 core plots in unique wetland complexes were selected as camera trap locations. Sites selected for camera deployment covered most wetland habitat and ungulate use types, but coverage was limited by the small number of cameras that we could deploy and from which we could reasonably analyze data.

Primary field data: vegetation, hydrology, soil, disturbance, and dung counts

Sampling and field methods are detailed in Schweiger, Gage, Haynes, et al. (2015) and Zeigenfuss et al. (2024). They are based on standardized protocols developed by NPS, USGS, US Environmental Protection Agency (EPA), and our academic collaborators. In summary, plots are sampled for species level vegetation (Figure 6), woody plant density, woody plant percent dead and ungulate browse, soil chemistry, ground water depth, categorical human and ungulate disturbance, and elk and bison dung counts.



Figure 6. Sampling an herbaceous wetland site at Great Sand Dunes National Park and Preserve, 2016. NPS / B. SCHWEIGER

Elk and bison collars

Zeigenfuss et al. (2024) present details on elk and bison collar methods. In summary, very high frequency (VHF) or global positioning system (GPS) collars were deployed by USGS in 2005 through 2007 on 65 elk and 18 bison (Schoenecker 2012; Schoenecker et al. 2015, 2022). In 2019, NPS researchers fitted 35 elk with GPS collars. In this report we use elk collar data from 2019 through April 2020 and the 2005–2007 bison data (with several assumptions and harmonization for the old bison data as described in Zeigenfuss et al. (2024)). A total of 3,746 bison and 28,414 elk locations were used for our analysis. The fix rate for elk was two per day and for bison one to two times per week.

Wildlife camera traps

Automated trail camera data from 10 wetland sites were used to characterize baseline ungulate use. Cameras used motion activated triggering and data used in baseline analyses included late June 2016 through June 2020. Cameras pointed towards the core plot in each site but were assumed to record ungulate activity associated with a site as a whole. Cameras were mounted on exclosures or other pre-existing structures where available, or on posts driven into the ground. The detection range of the cameras was 60 ft (18.3 m). Zeigenfuss et al. (2024) presents additional wildlife camera trap method details.

Analytical methods

UMP analytical methods are focused on developing estimates of baseline ungulate use and wetland condition from 2016 to 2019. These estimates are done via indices, metrics or indicators (these terms are used interchangeably), and the development of metrics is thus one of our central analytical processes. Some metrics were derived and involved multiple analytical steps, while others were relatively simple. To interpret these metrics, we summarize each visually and/or via tables using standard statistical methods to estimate status (i.e., means, medians) and variance across various spatial or temporal subdivisions in our baseline sample. Where relevant we also test for differences across space or time with a variety of models as data form dictates (although formal trend models will be presented in future reports). We do not emphasize hypotheses testing in this report but do report p-values. We treat statistical significance as a somewhat fluid concept (*sensu* Wellek 2017) and consider a p-value of around < 0.10 as likely meaningful (or "statistically significant"). However, we also interpret patterns at higher p-value levels if there are ecological reasons to do so. Note that for simplicity in tests across multiple categories (i.e., year), we report an overall p-value and for any individual or paired test only p-values that are around or below 0.10 (i.e., for a test of 2016 vs. 2017 in a model of all years). All analyses were conducted in R (R Core Team 2024).

Sample units

UMP data are collected across all plots in a site and summarized to the sample event site scale. We control for varying sampled area across sites in metrics as needed. We build metrics and summarize data for herbaceous variables using a single sample event at each site (the first sample at a site). Revisit herbaceous sample events are used in various ways, such as estimating within year temporal variance and in validation of WCI model structure. For woody sites we had to use all events in our analyses given sample size constraints (note that woody spatial or map-based visuals only show a

single event at each site). We use several methods for randomly sampling woody events to create calibration datasets. This may introduce some autocorrelation effects into woody results, but we feel this is likely minor (and unavoidable).

Wetland vegetation ordination

Patterns in wetland vegetation community structure are important as they help determine what variables might best inform the WCI, for example by revealing how key environmental variables like ground water depth might relate to vegetation structure and indicators of ecological integrity. We apply ordination to classify sites into wetland types. We used Sorenson (Bray-Curtis) distance matrices calculated from relative abundances. Species occurring in less than three plots were first removed. Based on an examination of the distance matrices, a parametric ordination method of principal coordinates analyses was used with the "extended distance" method to deal with samples with low similarity (De'ath 1999).

Ordination models, coupled with our ecological experience, were also used to identify environmental variables (see the "Environmental adjustments" section below) for use in subsequent WCI models and to adjust HP metrics. We estimated significance of environmental variables in ordinations with permutation-based goodness of fit statistics. Final environmental variables were selected based on this significance and their ecological interpretation.

Vegetation metrics

Vegetation metrics are direct and purposefully one-dimensional assays of vegetation composition and structure. We generated over 600 vegetation metrics within multiple groups: floristic quality (conservatism), life span (i.e., perennial vs. annual), life form (i.e., forb or woody cover), nativity or degree of invasion, noxiousness, taxonomic diversity, taxonomic composition, wetland status, salt tolerance, height, woody plant condition (browse, dieback, and dead stem percentages), and woody plant density (by taxa, height, and browsed percentage). This is a large number of metrics, but given complex patterns in vegetation, potentially not enough to fully describe vegetation condition. A central point of our core analytical methodology is to select from a large number of metrics those that are most informative. Summaries of our approach to metric definition and estimation are in Schweiger et al. (2016, 2017). We present the methods, units, and range for metrics that appear in this report in more detail in Appendix A.

Ungulate Use Indices

Ungulate use data from dung counts, telemetry collars, and camera traps were developed into site scale UUIs that estimate the intensity of use by elk and/or bison of wetland habitat. UUIs serve as critical baseline indicators that will be compared to UUI results from Phase 2 and 3. All UUI indices are constructed and scaled such that smaller numbers indicate lower ungulate use.

Each method for measuring ungulate use has advantages and disadvantages as source data for a UUI. Dung counts, while simple and cost effective, may underestimate use if animals do not defecate in the habitat of interest and this likely varies by ungulate species and habitat. Dung counts are also unable to resolve seasonal or finer temporal patterns and must be treated as annual estimates. Telemetry provides temporally and spatially extensive data. However, collars are expensive and

often only a limited number of animals will be fitted with collars. Collar data cannot provide information on size of animal groups using a particular area and may result in a UUI that underestimates actual use at a site. Camera-based UUIs are ideal for resolving many of the potential problems with dung count and collar-based UUIs. The method works especially well in most GRSA wetlands where there is not heavy undergrowth or complex topography. Cameras not only detect animal presence, but also type of activity, group size, and duration of visit to a site. Like collars, partitioning of animal use by season or finer temporal scales can be determined and cameras are better than collars for tying use to a particular location on a landscape. Camera-based UUIs capture use at a site whether the animal defecates or not during their visit and are thus likely to better estimate use than dung counts. However, cameras are subject to malfunction, limited battery life, and data collection is limited by size of the data card. Gathering data without large gaps requires regular maintenance visits. Malfunction is highly likely because curious animals are often drawn to camera noise and like to rub on posts holding cameras in place. Most importantly, cameras generate an enormous amount of data that have real data management and interpretation implications.

We initially generated over 300 unique UUI variants from our three ungulate use methods. Including the effect of dung disappearance (Figure 7) and patterns with select vegetation and environmental variables, we simplified this to 59 candidate UUIs (6 dung, 29 collar, 24 camera). Camera based UUIs tended to have the best relationships and often revealed interesting patterns across space and time (Zeigenfuss et al. (2024). However, with only 10 camera sites, camera-based UUIs could not provide the spatial coverage required to model wetland response across all our sample sites. We therefore created models that combined the best UUIs from each data source into “camera-like” UUIs that captured many of the advantages of the camera based versions without the need to have a camera at all sample sites. Further testing of these camera-like UUIs, including estimating trial WCIs, resulted in the final two (camera-like) UUIs used in this report—one each for woody and herbaceous wetland types. Appendix A provides additional summary of UUI methods and the camera-like estimation. For full documentation of our UUI methodology, see Zeigenfuss et al. (2024).



Figure 7. Marking dung piles to track detectability and decay rates in an herbaceous wetland (site 302) at Great Sand Dunes National Park and Preserve, 2020. NPS / B. SCHWEIGER

Wetland Condition Indices

Wetland Condition Indices (WCIs) are model-based estimates of wetland condition that synthesize, evaluate, and combine a large number of individual vegetation metrics to assess ecological integrity. The UMP EIS and several network reports use the term "ecological integrity" as a more nuanced term for condition (we use the terms interchangeably in this report). Integrity is a complex concept that has been used in ecological monitoring of wetlands and other systems worldwide for decades (i.e., Cairns 1977; Noss 1990). Ecological integrity is the capacity to support and maintain a balanced, integrated, and adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitats of the region (Karr 1991). It conceptually aligns (Rodhouse et al. 2016) with the NPS mandate to manage parks " … unimpaired for the enjoyment of future generations" as laid out in the 1916 NPS Organic Act. It is a

multidimensional concept and single indicators are insufficient to characterize it. WCIs synthesize, evaluate and combine a large number of individual vegetation metrics to better estimate integrity. Similar approaches using names like “Indices of Biotic Integrity” or “Multimetric Indices” have been developed over the years for wetlands (Lemly and Rocchio 2009; Faber-Langendoen et al. 2019; Magee et al. 2019; Keddy et al. 2020) including in GRSA (Schweiger et al. 2017).

We build WCIs by selecting a subset of vegetation metrics that in combination have the highest level of unique ecological response to a disturbance gradient (Schoolmaster et al. 2012; Schoolmaster, Grace, Schweiger, Mitchell et al. 2013; Schoolmaster Grace, Schweiger, Guntenspergen et al. 2013). A WCI summarizes this information into a single numeric index value for each vegetation sample event. We use information theoretic and model selection statistical tools to include the smallest subset of vegetation metrics that, for a given dataset, respond with a guaranteed statistically best multivariate response to a given disturbance gradient. A WCI controls for confounding effects of important environmental gradients (see the “Environmental adjustment” section below) that can also drive patterns in vegetation metrics. Appendix A further summarizes our methods and presents additional detail on WCI model derivation—see also Schoolmaster et al. (2012) and Schoolmaster, Grace, Schweiger, Mitchell et al. (2013) and Schoolmaster Grace, Schweiger, Guntenspergen et al. (2013).

WCI models developed for UMP are unique in two important ways. First, they are based on ungulate use as the disturbance gradient against which wetland condition is scaled. Schweiger et al. (2017) also developed WCI models but used a simpler qualitative UUI. We know of no other WCI that uses a gradient other than human disturbance to build estimates of condition. Second, we focus WCI models on metrics of declining wetland condition with increasing ungulate use. This is necessary because of the complex response of vegetation to ungulate use. Many natural systems have coevolved (Leibold 1996; Terborgh 2015) herbivore–vegetation relationships where ungulate use can lead to improved habitat conditions (i.e., Ratajczak et al. 2022). Following guidance from the UMP EIS, we separated all candidate vegetation metrics into two sets: “decreaser” metrics and “increaser” metrics. Decreaser metrics are indicators of a reduced ecological condition (which can be either a positive or negative change in the metric numerically) in response to ungulate use. We construct WCIs presented here from decreaser metrics only. An increasing condition in response to ungulate use is likely important but will need to be developed in the future. Our focus on the decreasing wetland condition response to ungulate use is a central assumption behind the work presented in this report. We use the term “decreaser” to describe both metrics that are indicators of a declining condition with increased ungulate use and the WCI models created from decreaser metrics exclusively.

Hand-picked metrics

WCI-based estimates of condition are ideally suited to the goals of the UMP EIS. They present a simple, single indicator number to resource managers that quantify the response of wetland condition to ungulate use across space and time. However, deriving a WCI is analytically complex and they are not necessarily the only way park resource management might seek to understand or estimate baseline wetland conditions on the GRSA sand sheet. Single, well-constructed and easily-interpreted

metrics can have clearer management application and causal relationships (Grace et al. 2012; Schweiger et al. 2016) with disturbances such as ungulate use. We therefore developed hand-picked (HP) metrics in consultation with GRSA resource management as additional indicators of wetland condition impacted by ungulate use.

Choosing HP metrics is guided by several criteria. First, we prioritized park-selected metrics. Second, a HP metric needs to have meaningful and interpretable correlation with a UUI, as this suggests the metric will respond to ungulate management. As with the vegetation metrics analyzed in a WCI, any HP response to a UUI must also account for confounded correlation with key environmental gradients (see below). HP metrics adjusted for environmental gradients almost always have a better correlation with a UUI across space and time. Third, an HP metric should have at least some interpretable spatial pattern across UMP sites. Fourth, an HP metric should have relatively low variation across years in the baseline sample (this was not a hard and fast rule, as the impact of temporal patterns can be modeled). Fifth, we examined the presence and interpretation of an exclosure effect (attempts to remove ungulate use via fences) and a useful HP metric can be interpreted at least in part based on how it responds to exclosures. Sixth, we used the authors' best professional experience. Finally, we reviewed relevant literature for guidance on the best indicators relative to UMP objectives. We will carefully evaluate the capacity of each of the HP metrics used in this report to support useful management, and in the future, remove those that don't perform well or add additional metrics if needed. This process resulted in four high priority HP metrics.

Density of browsed willow and cottonwood

First, we develop a metric that combines browse estimates with the density of Salicaceae (willow and cottonwood) plants in woody sites and is expressed in raw format as browsed plants per meter squared. It is calculated as the product of mean percent browse (as a proportion, 0 to 1) and the density of all cottonwood and willow plants in a site (as plants per m^2). This metric can be interpreted in a general way as the density of willow and cottonwood with ungulate browse. It ranges from 0 to an unbounded maxima for high density and high browse (in our baseline data this maxima is 0.9 browsed plants / m^2). Given multistemmed morphology, especially in willows but occasionally also cottonwood when buried by sand, what exactly an individual "plant" is and what can be efficiently counted by field crews is complex. Our methods approximate this as best possible by defining consistent sampling units that we assume are individual plants (Schweiger et al. 2016). Browse on preferred species like willow is a classic indicator of degraded condition from ungulate use (Johnston et al. 2007; Rhodes et al. 2018; Kauffman et al. 2023; Miller et al. 2023). We assume that higher browse is directly related to higher ungulate use and that this is a driver of lower condition (Skovlin 2021). Importantly, we use this metric as an indicator of wetland condition, not of ungulate browse itself.

Cover of iris and silverweed

Second, we estimate the absolute cover of *Iris missouriensis* (iris) and *Potentilla anserina* (silverweed) at herbaceous sites (Figure 8). These two taxa have a similar response to ungulate use. They are both decreaser metrics (but that increase numerically with an increasing UUI). They are highly resistant to or even take advantage of the type of disturbance created by large ungulates and

are often associated with degraded habitat conditions because of their near monocultures in heavily used sites. Using both species captures this response more fully. This metric conceptually ranges from 0 to an unbounded maxima (for a very high cover). We assume it increases with ungulate use.



Figure 8. Grazing tolerant species in herbaceous wetlands at Great Sand Dunes National Park and Preserve. (Left) iris, (right) silverweed and iris (silverweed is the silver gray foliage under the taller iris). Inset image (top) shows detail of silverweed. (LEFT) NPS / K. ZYBKO, (TOP) M.M. R (CC BY-NC 2.0) in iNaturalist (from http://www.flickr.com/photos/46774986@N02/4717663334), (RIGHT). NPS / B. SCHWEIGER

Conservatism of graminoids

Third, we develop an index of conservatism of graminoids weighted by their cover in herbaceous wetlands. Conservatism describes a species' fidelity to a specific habitat or range of environmental conditions absent "non-natural" disturbance (Wilhelm and Ladd 1988; Herman et al. 1997; Matthews et al. 2015). Stressors like ungulate use outside a natural, sustainable level may fall into this category of "non-natural" disturbance. Thus, it may cause shifts in ecological processes and habitat conditions and push disturbance regimes outside a natural range of intensity, frequency, and duration. Highly conservative species are not able to quickly respond to such rapid alterations compared to broad-niche generalists (low conservatism) and are often the first to disappear from habitats heavily impacted by disturbance. The composition of conservative species at a particular site integrates spatial and temporal impacts and is often used as an indicator of ecological integrity. Conservatism is an expert opinion species level index based on "C-scores" that range from 0 for invasive nonnatives to 10 for highly conservative species. Colorado's C-scores were originally assigned in 2007 (Rocchio 2007a, b) and updated in 2020 (Smith et al. 2020). They have been empirically tested and shown to be a useful way to assess condition in Colorado (Rocchio 2007a, b) and in other systems (Matthews

et al. 2015; Kutcher and Forester 2018). We selected this as one of our HP metrics given the support in the literature for the use of conservatism in applied resource management (i.e., Mabry et al. 2018; Miller et al. 2016; Smith et al. 2020). Cover weighting of this metric scales the index by the relative cover of low to high C-scored taxa, improving its representation of site characteristics.

Wetland affinity

Fourth, we estimate an index of wetland affinity weighted by cover in woody sites (Loheide and Gorelick 2007). Wetland affinity measures the prevalence of species that have a demonstrated ability to achieve maturity and reproduce in wetlands (Tiner 2012). Affinity is quantified via categorical scores developed by experts that are often empirically verified (Gage et al. 2016; Magee et al. 2019). Wetland affinity is a common indicator in wetland condition assessments (i.e., Ervin et al. 2006; Mack 2007) and Rocky Mountain Network wetland analyses (see Schweiger et al. 2017 for a detailed treatment of this in ROMO). Sites with higher wetland affinity include more wetland obligates, reflecting a higher (wetter) and/or more importantly a stable water table, which reflects a better condition. Because the mix of species at a site responds over time and space to variation in hydrologic regime, wetland affinity integrates seasonal and annual fluctuations in groundwater levels (Grace et al. 2012). It is a useful proxy (Loheide and Gorelick 2007) for more complex and expensive measures of groundwater hydrologic regime, which is appropriate for long-term UMP monitoring. We calculate this metric as the cover weighted mean of wetland affinity scores in a sample.

Environmental adjustment

We developed several ancillary datasets (interchangeably referred to as "environmental data") to control for important drivers of wetland condition that can be confounded with the influence of ungulates use on condition. Environmental data were generated by the network as part of UMP sampling, other network protocols, or gathered from state or other federal agencies and academic collaborators. Major categories included climate and water balance, landscape composition, disturbance, spatial context (i.e., distance to the nearest sand dune), and vegetation production. Several variables were modeled, for example, to downscale remotely sensed data to a site scale or to derive moving averages or lags across years. Appendix B summarizes key environmental data used in UMP baseline analyses.

Adjusting indicators for any confounded effects of environmental gradients is a central part of UMP analysis. Adjustment is embedded in the WCI algorithms as it is the only way to ensure that the component metrics in a WCI are included because of their response to ungulate use rather than some extraneous driver of less interest to park management. Likewise, HP metrics must be adjusted to understand their relationship to ungulate use. HP metrics were selected in part because of an expectation that they respond to UUIs and thus will inform choices by GRSA in the management of ungulates. If a response pattern we see in an HP metric across space and or time is because of an important environmental gradient like ground water depth, an unknown amount of information in a data summary of the raw metric is confounded with the gradient (i.e., water table depth) and we won't know if an HP metric's change is because of ungulate use or because of covariance with the gradient (or more likely, both). Appendix B presents a summary of our linear model-based

adjustment methodology (and an example). Adjusted data are still in the same units as raw data and can be interpreted in the same way as raw data. However, occasionally adjustment can be strong enough that the scale of the response is flipped (i.e., positive correlations with the UUI become negative). Adjusted variables are also scaled to range from 0 to 10 following Blocksom (2003). This allows metrics with very different ranges to be treated in a consistent way in WCIs and other models, which enhances stability and reduces multicollinearity (but removes the "natural" scale of a variable).

Raw versions of WCI component or HP metrics should be interpreted with caution as they do not provide insight on the role of environmental gradients on status or trend estimates. Metric data in a raw unadjusted form remains, nevertheless, important as they have more familiar ranges of values, reflect what a park resource manager sees on the ground, and connect directly to the complete ecological context driving vegetation response and not just ungulate use. We therefore include select summaries of unadjusted data in our results.

Power

To help evaluate the quality of our core indicators we developed a simulation-based approach to estimate the minimum detectable difference between baseline and future results given sampling constraints, indicator statistical attributes, a target power level at 0.80, and an alpha of 0.10. A power of 0.80 defines the probability that a statistical test will correctly reject a null hypothesis of no difference (for example between baseline and Phase 2 means) when the alternative hypothesis is true (i.e., detect a true effect if it exists). An alpha of 0.10 sets the probability of observing a result given that the null hypothesis is true (i.e., the chance of incorrectly rejecting the null hypothesis of no difference between baseline and Phase 2, assuming it is true). Our alpha is slightly higher than the classic default of 0.05, but we feel it is appropriate for highly variable ecological data. Our simulations used a sample size, mean, and standard deviation for each indicator from baseline data and assumed a similar sample size, standard deviation, and mean as in the baseline for Phase 2 results. We iterated across small increments in a difference from an indicator's baseline mean to its possible Phase 2 mean and compared these using a two-sample t-test until our power and alpha values were exceeded. The expected mean in the Phase 2 sample at this point, differenced from its baseline counterpart, was output as the minimum detectable percent difference for each indicator. We consider a 10% or less detectable change useful.

Assessment

Assessment is the process by which the condition of an ecological resource, such as a single wetland or a population of wetlands in a park, is placed into classes or along a gradient that describe or interpret this condition (Stoddard et al. 2006). In broad stroke, the Rocky Mountain Network assessment process is based on developing and then comparing monitoring results to numeric assessment points (APs; Bennetts et al. 2007). APs are values of an indicator where scientists and managers have together agreed that they want to assess the status or trend of a resource relative to program goals, potential concerns, or natural variation. APs establish boundaries in a gradient between alternate states or classes in measures of disturbance or ecological response. In the most colloquial sense, condition classes defined by APs can be labeled as "good" or "bad." Data used to

set these APs can come from a variety of sources and there are many considerations in selecting source datasets. The network has developed assessment methodology in several protocols and previous reports, including wetlands in Rocky Mountain National Park (ROMO), GRSA, and Florissant Fossil Beds National Monument (FLFO; Schweiger et al. 2016, 2017, 2022) and streams in Glacier National Park (GLAC; Schweiger et al. 2018, 2024). These reports include additional details on our assessment process.

Wetlands on the GRSA sand sheet are unique (NPS 2007) and their assessment presents at least three challenges. First, there are few if any comparable wetland condition data in the literature on which valid APs might be based. Second, the disturbance gradient of interest in UMP, ungulate use, is novel and can be complex with both negative and positive impacts of ungulate use on wetland condition. Third, given the level of native ungulate and historical bison and cattle disturbance to sand sheet wetlands over the years, coupled with extensive historical and ongoing human use, we do not expect UMP baseline conditions to include a pristine reference state. Rather we interpret baseline condition classes as the "*best/intermediate/worst available,*" and over time and across space we assess changes in wetland condition and ungulate condition relative to these benchmarks.

Park-supported a priori baseline condition classes

We implemented a baseline assessment strategy using the expert opinion of park natural resource staff to classify wetland condition on the sand sheet. We tasked park staff with decades of experience working on park wetlands to independently rank UMP herbaceous and woody sites into ecological condition classes. We directed that condition should be conceptualized as in response to or relative to ungulate use. We did not provide any UMP data to park staff other than site locations and photos to reduce circularity (although the process was conducted after park staff saw a draft summary of UMP baseline results).

Park staff ranked UMP sites into three baseline condition classes and provided this to the network. We made minor revisions for consistency in terminology and for consistent application across woody and herbaceous wetland types. The final result from park evaluation was sites in three classes: "best available baseline condition" (11 sites, or 15% of all sites), "intermediate baseline condition" (10, 13%), and "worst baseline condition" (53, 72%). The park-based condition class for all sites is mapped in Figure 9. Select examples of best and worst condition classes are in Figure 10 for woody sites and Figure 11 for herbaceous sites—although we stress caution using single point in time photos for assessing a site's wetland condition.

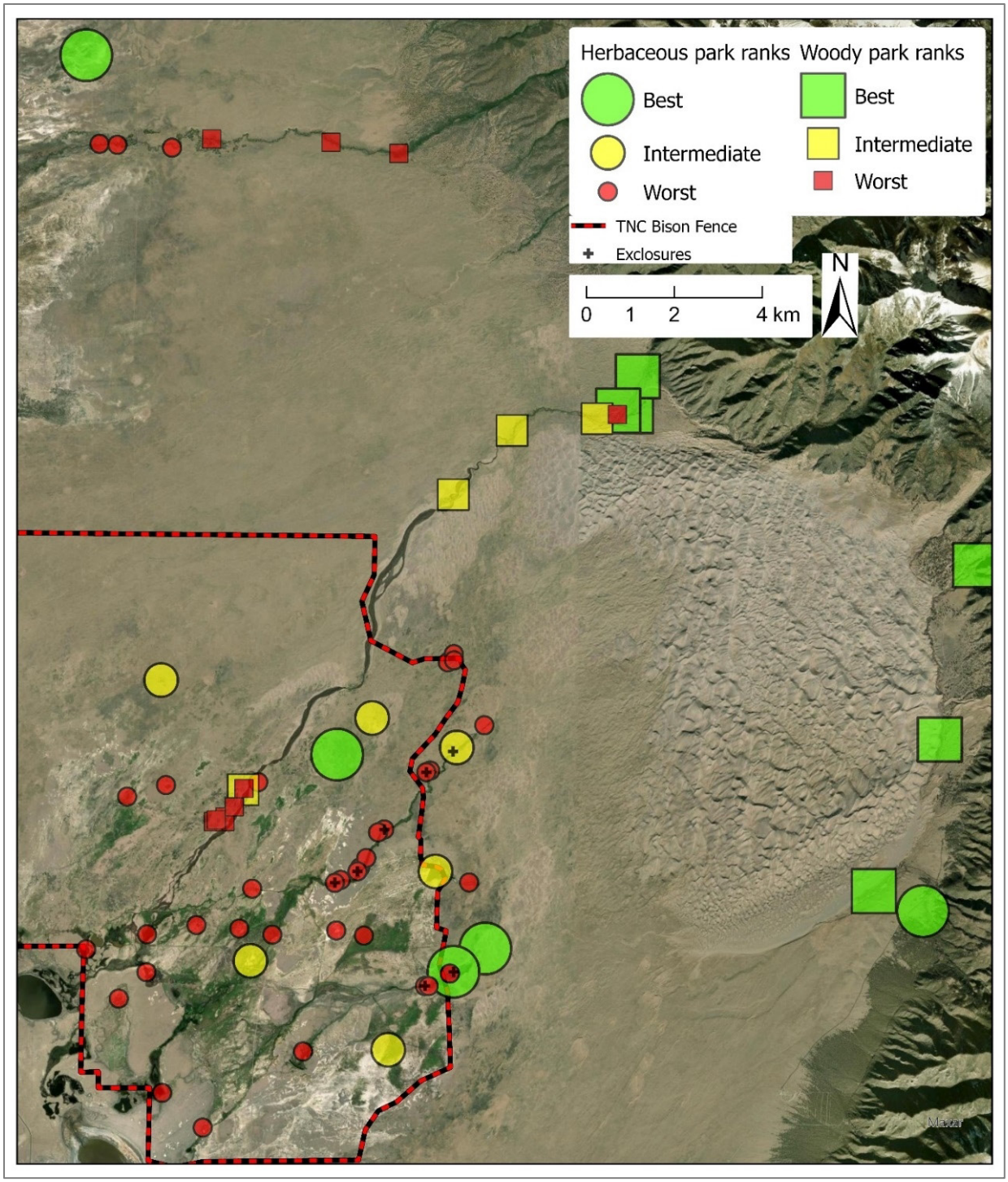


Figure 9. Park baseline classifications of woody (squares) and herbaceous (circles) Ungulate Management Plan wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Not all sites are visible given overlapping points. NPS



Figure 10. Example best and worst available condition woody wetlands at Great Sand Dunes National Park and Preserve. Top image is a best available condition willow dominated site (site 252) adjacent to Medano Creek. Bottom image is a worst available condition willow dominated site (site 212) near Sand Creek. As noted in the text, condition assessment using single photos should be done with caution. NPS / B. SCHWEIGER



Figure 11. Example best and worst available condition herbaceous wetlands at Great Sand Dunes National Park and Preserve. Top image is a best available condition sedge dominated site (site 201) to the east of the main dune field. Bottom image is a worst available condition iris and silverweed dominated site (site 136) in the north central portion of the sand sheet. Both sites have a ground water dominated hydrology. NPS / B. SCHWEIGER

To broaden and generalize these *a priori* classifications, we followed well-established methods used by the US EPA (Stoddard et al. 2008; US EPA 2016), several state (CDPHE 2012; Suplee et al. 2005) and other monitoring programs (Marshall and Lemly 2020), and by the network. We have also implemented this reference condition development approach broadly in Rocky Mountain Network monitoring, including in GLAC for streams, ROMO for streams and wetlands, FLFO for wetlands, and previously in GRSA wetlands. The basics of this method are to use an independent sample of reference or other condition class sites (the parks provided this for UMP as above), derive statistics from this sample of sites, and then apply these to a larger population to classify all sites. Following this approach, we calculated a median or mean (depending on the impact of outliers and other distributional constraints) in UUI and WCI indices across sites ranked in best and intermediate condition classes by the park and used these means or medians as thresholds for all remaining sites, placing all UUI and WCI values into best, intermediate and worst categories based on these breaks. In some cases, this rescoring did shift a park ranked site into new classes; we allowed this, assuming that the park's ranking sought to define a typical condition and that this was better estimated from the distributions created across park staff rankings. To score HP metrics, we used WCI condition classes developed as above to set thresholds in an HP metric (best, intermediate, and worst). We use WCI-based classes to score HP metrics instead of the HP metric values at park ranked sites as we expect park staff evaluated site condition as a generalized wetland condition versus by each individual HP metric. WCIs, by definition, estimate this general ecological condition.

Data availability

Data presented in this report are available in quality-checked data packages on DataStore within the NPS Integrated Resource Management Applications (IRMA) portal.

A complete list of Rocky Mountain Network data packages is available at: Data Packages (U.S. National Park Service) (nps.gov). Individual data package components are listed below:

- Site Event Metadata: DataStore - Wetlands Ecological Integrity Sample Site and Sample Event metadata data package at Florissant Fossil Beds National Monument, Great Sand Dunes National Park, and Rocky Mountain National Park 2007-2022 (nps.gov)
- Herbaceous Vegetation: DataStore - Wetlands Ecological Integrity Vegetation data package 2007-2022 at Florissant Fossil Beds National Monument, Great Sand Dunes National Park, and Rocky Mountain National Park. (nps.gov)
- Woody Vegetation: DataStore - Wetlands Ecological Integrity Woody Vegetation at Florissant Fossil Beds National Monument, Great Sand Dunes National Park, and Rocky Mountain National Park 2007-2021 (nps.gov)
- Depth to Water Hand: DataStore - Wetlands Ecological Integrity (WEI) Depth to Water Hand Measurements datasets metadata template files for use with the EMLAssemblyLine R package (nps.gov)
- Dung counts: DataStore - Ungulate Use Pellet Count Analysis data package - Great Sand Dunes National Park 2016-2022 (nps.gov)

- Soil Chemistry: DataStore - Wetlands Ecological Integrity (WEI) Soil Chemistry dataset metadata template files for use with the EMLAssemblyLine R package (nps.gov)
- Discrete Water Quality Logger: DataStore - Wetlands Ecological Integrity (WEI) Discrete Water Quality Logger Data Package, 2007-2022, for Florissant Fossil Beds National Monument, Glacier National Park, Great Sand Dunes National Park, and Rocky Mountain National Park. (nps.gov)

Results

The following sections present summaries of our core results organized by indicator category. Interpretation of key results that are most relevant to the park's management of ungulate use to improve wetland condition follows in the Discussion.

Wetland vegetation overview

Baseline Ungulate Management Plan (UMP) results fundamentally depend on the taxonomic accuracy of UMP vegetation data. The central results presented in this report are based on our vegetation data, as will future Phase 2 and 3 analyses. We therefore include a high-level summary of UMP vegetation below and a full taxa list with associated metrics in Appendix C.

We recorded a total of 266 species within 53 families across all 2016 to 2019 sample events. Species richness varied across wetland type, with 146 and 196 species in woody and herbaceous sites (several species occur in both types). The most speciose families were *Poaceae* (grasses) and *Asteraceae* (composites) in herbaceous and woody sites. The most abundant families in terms of total absolute cover across all records were *Cyperaceae* (sedges) in herbaceous sites and *Salicaceae* (willows) in woody sites. The most abundant species in both herbaceous and woody sites was *Juncus arcticus* (Baltic rush). In herbaceous sites the next two most abundant taxa were *Carex nebrascensis* (Nebraska sedge) and *C. simulata* (short beaked sedge). In woody sites, *Populus angustifolia* (narrowleaf cottonwood) and *Salix exigua* (narrowleaf willow) were the second and third most abundant species.

Over 604 vascular plant species have been identified in the park and preserve as a whole (Spackman-Panjabi et al. 2004). With wetlands comprising only approximately 4.7% of the area of the park, the 266 species in UMP samples account for a disproportionate level (44%) of the vascular plant diversity in the park. We see this "biodiversity hotspot" result in all our wetland monitoring in Rocky Mountain Network (the network) parks—it is a significant reason why wetlands are so important.

Wetland vegetation ordination

Ordinations revealed a high-level break between sites with and without a woody overstory. Within the herbaceous type, salt flats, wet meadows, and marshes were distinguishable but sample size constraints limited this. In the woody type, cottonwood- and willow-dominated sites were distinguishable. This classification largely matches previous work at Great Sand Dunes National Park and Preserve (GRSA) (Salas et al. 2010; Schweiger et al. 2016). Given real sample size constraints, we choose to structure all UMP results by herbaceous or woody types. We assume that the relevant ecological response unique to any nested wetland type is sufficiently captured at this level, but we recognize there will be important variation omitted by using these general types. We summarize these constraints in the Discussion.

Final environmental gradients

Using ordination results and ecological expertise, we selected 10 environmental variables to model in our Wetland Condition Indices (WCIs) and hand-picked (HP) metrics to help isolate changes in

response to ungulate use (i.e., Figure 12). Key summaries of these variables are given in Table 1 and Appendix B. Nearly all these variables were markedly different in nonparametric comparisons between herbaceous and woody wetland types (only bare ground was similar), suggesting our two selected wetland types have real ecological differences. Univariate correlations with the Ungulate Use Index (UUI) were also often strong, supporting the need to remove confounded signal (approximated by these correlations) in the WCI and HP metrics. Note that our methods do this adjustment with a more robust multivariate approach than reflected in the simple correlations in Table 1.



Figure 12. Salt flat herbaceous wetland (site 427) with high salinity (as reflected in the salt deposits visible in the image) at Great Sand Dunes National Park and Preserve, 2018. The models presented in this report adjust for important environmental drivers like soil salinity. NPS / B. SCHWEIGER

Table 1. Summary statistics for environmental variables used in Ungulate Management Plan analyses by wetland type, Great Sand Dunes National Park and Preserve, 2016–2019. All variables were markedly different in nonparametric comparisons across herbaceous and woody wetland types except for bare ground. SD: standard deviation. CV: coefficient of variation. Corr: Pearson correlation values.

Environmental variable, unit of measure	Herbaceous mean	Herbaceous median	Herbaceous SD	Herbaceous CV	Woody mean	Woody median	Woody SD	Woody CV	Corr. with woody UUI	Corr. with herbaceous UUI
Depth to ground water (DTW), cm	−61.09	−64.55	43.03	70.43	−118.82	−124.55	38.75	32.61	−0.05	0.14
Landscape disturbance (LDI), index	126.96	86.20	119.35	94.01	74.04	74.07	46.91	63.36	0.06	**0.57** [A]
Soil salinity from sodium absorption (SAR), ratio	7.01	3.32	11.43	163.06	0.41	0.29	0.36	87.48	0.09	0.04
Bare ground (BRE), %	22.74	11.75	25.68	112.91	23.91	15.29	24.15	101.01	**0.23** [A]	0.07
Litter cover (LIT), %	41.88	44.74	29.74	71.00	56.33	54.14	30.20	53.61	**−0.28** [A]	0.07
Elevation (ELEV), m	2323.03	2321.95	25.81	1.11	2364.93	2315.06	71.69	3.03	**−0.77** [A]	**−0.42** [A]
Production, 5-year mean (PROD), index	509.57	501.80	56.17	11.02	135.80	139.36	69.03	50.83	**−0.28** [A]	−0.09
Temperature as growing degree days, 5-year mean (GDD), index	2756.95	2761.30	33.38	1.21	2697.72	2725.05	82.93	3.07	**0.71** [A]	**0.41** [A]
Climatic deficit, lagged 3 years (D), mm	61.81	72.24	41.21	66.67	91.36	105.84	39.14	42.84	**0.14** [A]	0.11
Soil moisture, 5-year mean (SOIL), mm	66.99	63.96	27.36	40.85	38.08	34.25	11.72	30.79	**0.11** [A]	0.09

[A] Correlation values in **bold** have p-values ≤ 0.10.

Ungulate Use Indices

The focus of this report is on camera-like UUIs (for additional details see Appendix A). We also present UUIs developed from dung data alone in Appendix D, in case a UUI based on a more cost-effective sampling method is desired in the future. Additional UUI results are presented in Zeigenfuss et al. (2024).

The UUI used in woody sites is based only on elk while the UUI for herbaceous sites is derived from both bison and elk with bison data weighted by the approximate ratio of bison to elk body size. Elk are the primary users of woody wetland while both species use herbaceous sites (Schoenecker et al. 2022). UUI values for herbaceous sites well outside of the bison fence are also based on elk and bison but the bison contribution to these scores is zero. This body size-based coefficient is applied to dung data so it appears in both the camera-like UUI presented below and the dung-only UUI in Appendix D. All UUIs are scaled such that smaller numbers (less use) are "better" under the important assumption that a decrease in condition from increased ungulate use is what matters to UMP management goals. We do not normalize UUIs across woody and herbaceous variants (see the different Y-axes on figures in this section), so UUIs should not be interpreted across woody and herbaceous sites.

Summary statistics for herbaceous and woody UUIs, including park-supported baseline APs, are in Table 2. We estimate that the UUIs will have acceptable power to detect a change of 4 to 8% in a mean UUI when compared with Phase 2 and 3 results for herbaceous and woody wetlands. The herbaceous camera-like UUI has almost twice the power of the dung-only variant (see Appendix D). The woody camera-like UUI also has more power than the dung-only version, but the difference is less perhaps because there is less variation across woody than herbaceous sites (but also because of a smaller sample size in woody sites).

Table 2. Summary of Ungulate Use Indices (UUI) in woody (W) and herbaceous (H) wetland sites at Great Sand Dunes National Park and Preserve, 2016 to 2019. AP: park-based assessment points; SD: standard deviation; CV: coefficient of variation. Minimum (Min.) detectable difference (statistical power) is the smallest percent change resolvable when comparisons are made between baseline and Phase 2 or 3 means.

UUI metric, raw/adjusted, (wetland type)	Best baseline condition AP	Worst baseline condition AP	Mean	Median	SD	CV (%)	Min. detectable difference (%)
UUI camera-like (H)	≤ 4.18 [A]	≥ 22.31 [A]	21.26	22.13	11.79	55.48	3.99
UUI camera-like (W)	≤ 0.59 [B]	≥ 1.30 [B]	1.92	2.01	1.21	63.12	8.27

[A] AP estimated using median.

[B] AP estimated using mean.

Patterns across baseline condition classes

Figure 13 and Figure 14 show patterns in a baseline herbaceous wetland UUI across park management-defined condition classes by group and spatially. Figure 15 and Figure 16 show these same patterns for the woody wetland UUI.

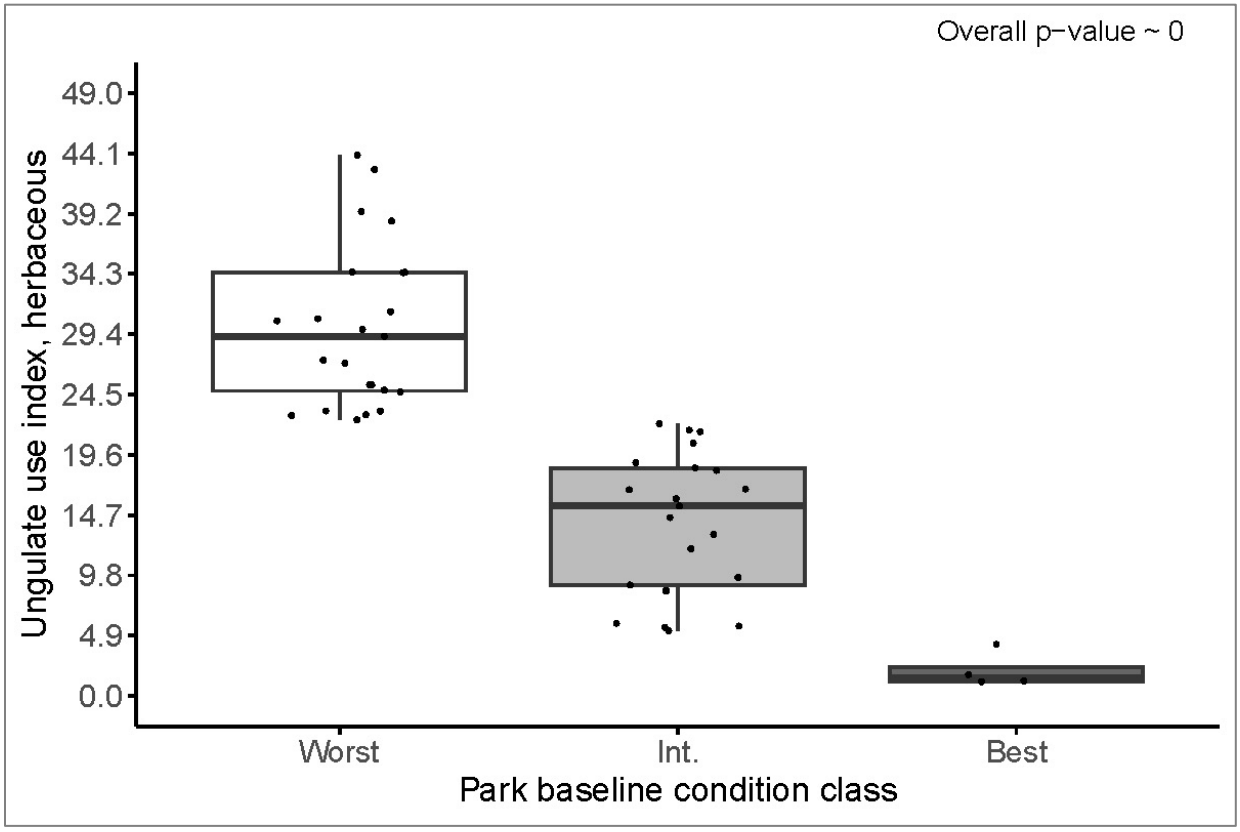


Figure 13. Ungulate Use Index (UUI) for herbaceous wetland sites across park-supported condition classes at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test, with "p-value ~ 0" indicating a vanishingly small probability. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

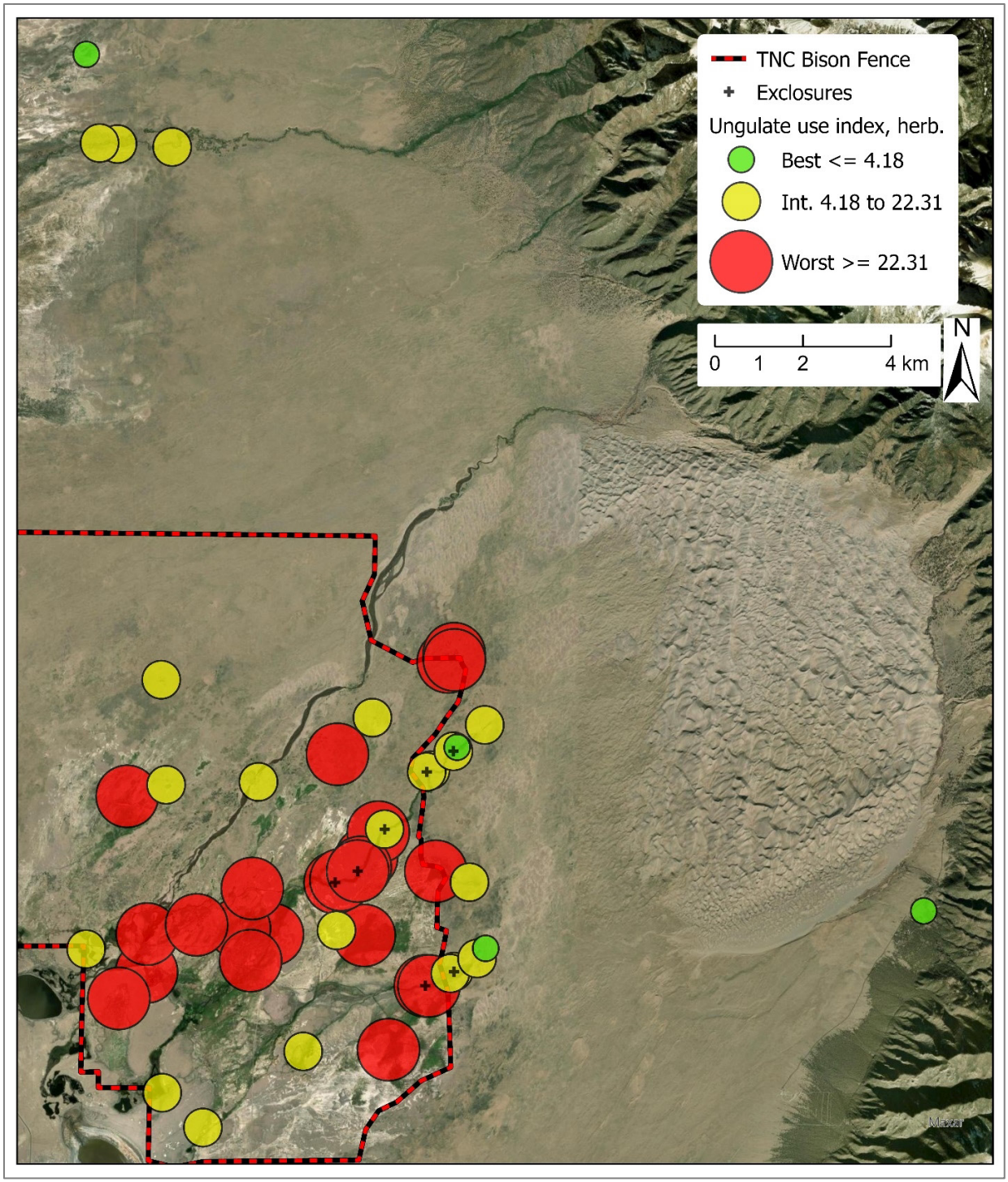


Figure 14. Ungulate Use Index in herbaceous wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Only the first visit is shown at sites with more than one sample. Point colors and size are based on condition classes as defined by park staff, with smaller green points for a best available, yellow medium size for an intermediate ("Int."), and red larger sized for worst condition. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible, given overlapping points. NPS

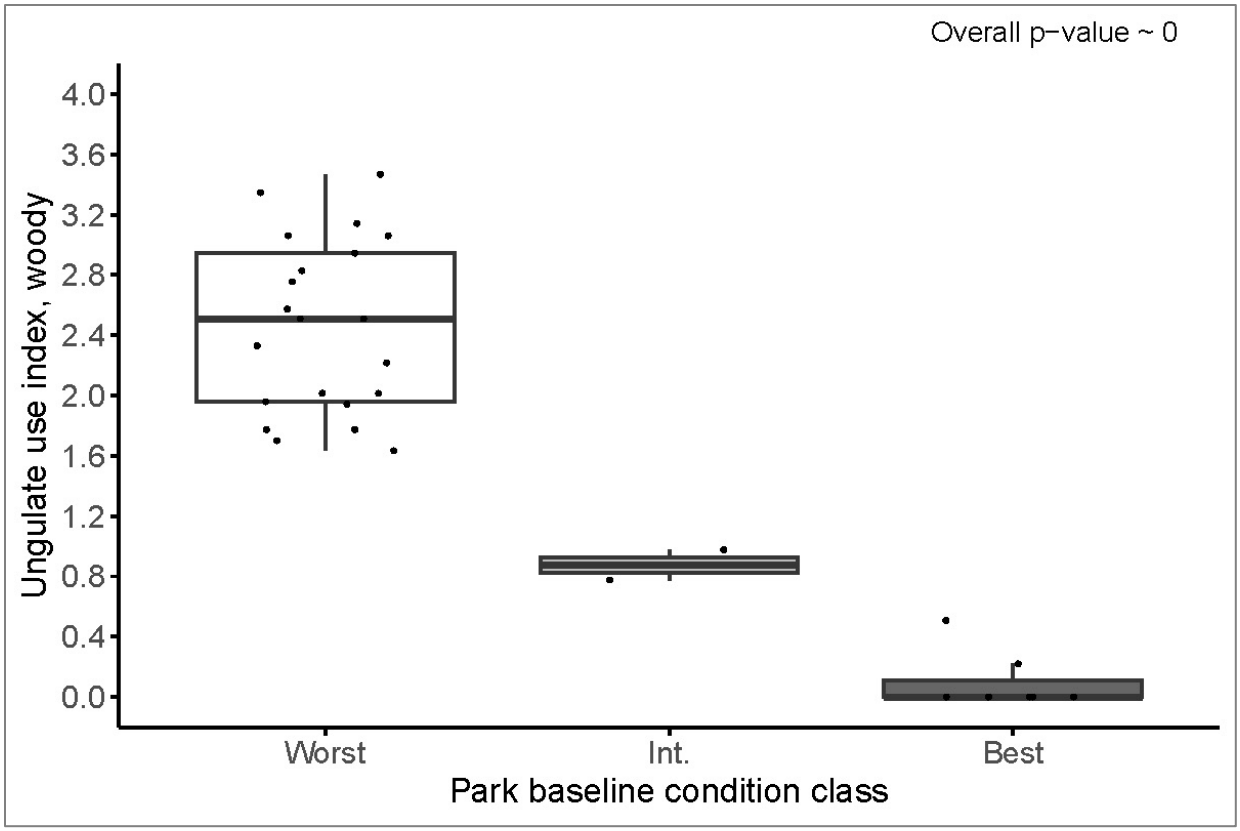


Figure 15. Ungulate Use Index (UUI) for woody wetland sites across park-supported condition classes at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test, with “p-value ~ 0” indicating a vanishingly small probability. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

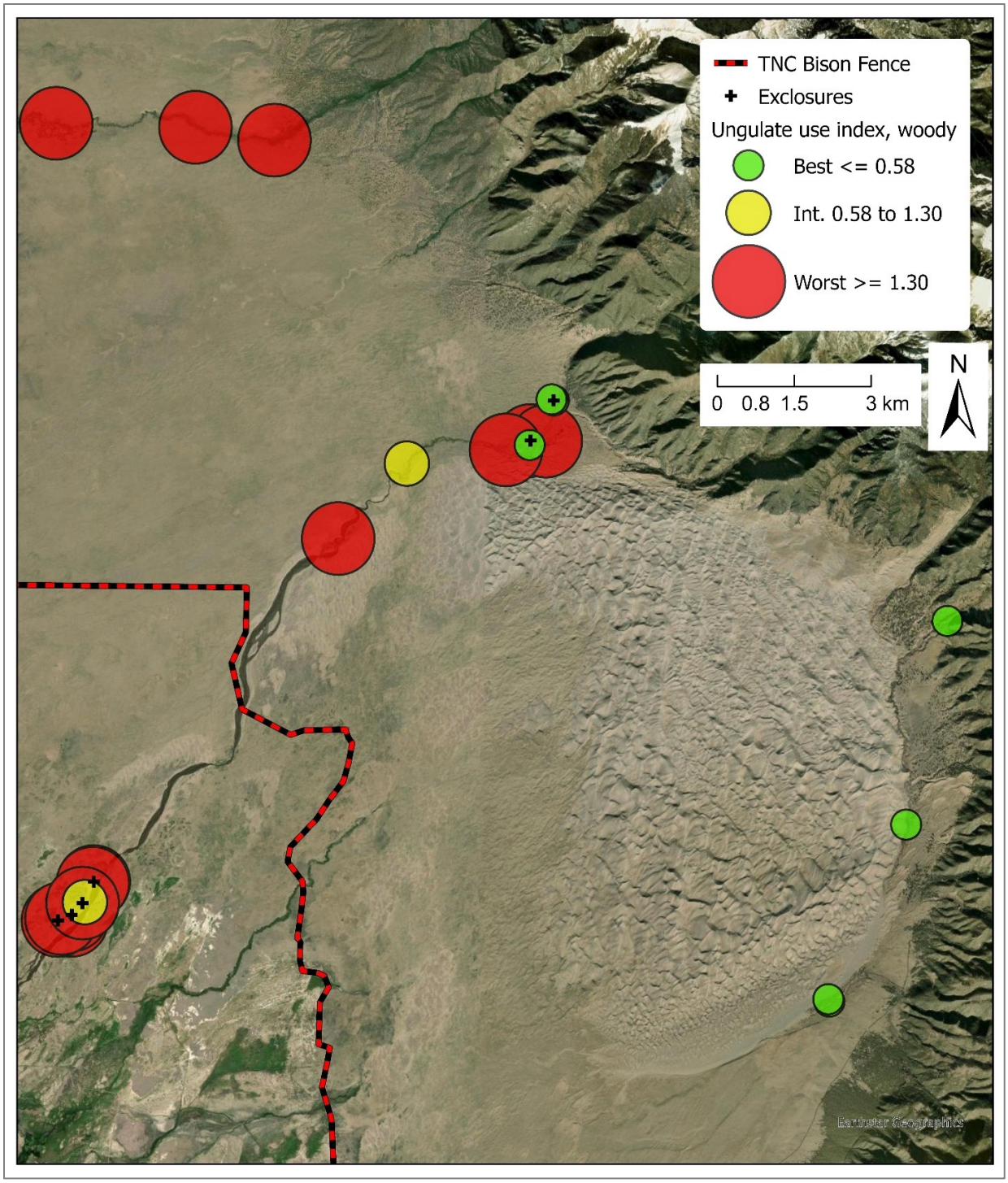


Figure 16. Ungulate Use Index (UUI) in woody wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Only the first visit is shown at sites with more than one sample. Point colors and size are based on condition classes as defined by park staff with smaller green points for a best available, yellow medium size for an intermediate ("Int."), and red larger sized for worst condition state. Points with black crosses are sites inside an ungulate exclosure. NPS

Across all herbaceous sites, 8% were in a park-supported baseline best condition class (less ungulate use) and 49% were above (more use) a baseline worst condition class, with overall and pair-wise p-values both well below 0.001. While the majority of herbaceous sites are inside the bison fence (elk and bison use zone), and we have a smaller and thus less reliable sample of herbaceous wetland outside the bison pasture, there is a clear pattern for higher use where both species impact herbaceous sites (inside the bison fence), with a general reduction in UUIs as sites are further from the bison pasture.

Baseline woody UUIs had similar general patterns as in herbaceous sites, with 22% in a baseline best available class and 70% in a worst available baseline class (overall and pair-wise p-values well below 0.001). Use was higher inside the bison fence where both elk and bison occur. However, several sites, far removed from the bison fence along Deadman Creek and unexclosed sites along Sand Creek near the mountain front, were also heavily impacted by (only elk) use.

Patterns across important management variables

Ungulate use (as estimated by UUI) in both herbaceous and woody wetlands had complex patterns across variables important to park management, such as exclosures, years, use by elk only or elk and bison, and wetland type. See the figures in Appendix E for more information on patterns in UUIs across park management relevant variables.

Surprisingly, there was no exclosure effect in herbaceous sites, with median UUI levels nearly the same across exclosed, unexclosed sites adjacent to exclosures, and sites removed from any exclosure. There was a marginal exclosure effect in woody sites ($p = 0.06$), but this is due to significantly lower ($p = 0.01$) use in unexclosed sites spatially removed from exclosures. While use was higher in paired unexclosed woody sites adjacent to exclosures, this was not significant. Note that our sample size is low and this might change with more data. However, in the UMP baseline, an overall woody exclosure effect appears to be driven by sites along the mountain front having no ungulate use at all. As discussed further below, these results indicate that the UMP exclosures have generally failed or, at least during our baseline, they did not effectively remove use from inside their boundaries relative to outside them.

Ungulate use varied across years (overall $p = 0.04$), with 2017 lower than 2018 ($p = 0.03$) and 2019 ($p = 0.04$) and marginally lower than 2016 ($p = 0.12$). Woody UUIs did not vary across years. There was a marked and significant pattern across ungulate use types, with herbaceous and woody UUIs roughly twice as high in elk and bison use areas versus elk only ($p < 0.001$ for both). This mirrors the finer-grained pattern we see in map-based comparisons across individual sites, with more high use sites in areas where both elk and bison can use wetlands (Figures 14 and 15). Finally, while we do not include secondary wetland types in much of our UMP interpretation, there was no difference across herbaceous types (salt flats, wet meadows, or marshes), but the UUI was higher in willow sites relative to cottonwood-dominated wetland sites ($p = 0.025$).

Wetland Condition Indices

Wetland Condition Indices (WCIs) are the primary focus of UMP monitoring and the core baseline results in this report. We report WCIs developed from camera-like UUIs adjusted for our environmental covariates (see Table 1). Appendix D includes alternate WCIs based on dung-only UUIs. These UUIs and WCIs are similar to the camera-like versions, with good explanation of variance and largely interpretable component metrics. We include them in this report in case WCIs based on a more cost-effective ungulate use sampling method are desired in the future. However, they do not validate as well as the camera-like WCIs, generally have lower power, and, while this is qualitative, they omit details of elk and bison use captured by cameras.

Summary statistics for each WCI, including park-supported baseline APs are presented in Table 3. WCIs range from 0 to 10 and are scaled such that larger numbers are "better" under the important assumption that a decrease in condition from increased ungulate use is what matters to UMP management goals. WCI methods apply a consistent scaling across woody and herbaceous models so it is appropriate to interpret WCI results across wetland type. WCI in both wetland types will likely have a useful minimally detectable difference (statistical power) when the models are applied to future comparisons. We estimate that WCI will have power to detect a change of 1.6% to 3.5% in mean WCI when compared with Phase 2 or 3 results in herbaceous and woody wetlands—these are both small enough changes that they are likely to be ecologically meaningful. Both camera-like WCIs have more power than the dung-only versions presented in Appendix D. In particular the herbaceous camera-like model will likely detect a mean minimum change around half as small as the dung-only based WCI.

Table 3. Summary of Wetland Condition Indices (WCI) in woody (W) and herbaceous (H) wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. The r^2 is from a linear model of the adjusted WCI and UUI; AP: park-based assessment points; Med.: median; SD: standard deviation; CV: coefficient of variation. Minimum (Min.) detectable difference (statistical power) is the smallest percent change resolvable when comparisons are made between baseline and Phase 2 or 3 means.

WCI (wetland type)	Best baseline condition AP	Worst baseline condition AP	r^2	Mean	Median	SD	CV (%)	Min. detectable difference (%)
WCI (H)	≥ 6.19 [A]	≤ 5.05 [A]	0.64	5.24	5.35	1.20	22.90	1.65
WCI (W)	≥ 7.07 [B]	≤ 5.87 [B]	0.89	5.39	5.16	1.43	26.55	3.48

[A] AP estimated using mean.

[B] AP estimated using median.

Relationships between wetland condition and ungulate use

Final herbaceous and woody WCIs are presented relative to the UUI gradient on which they are based in Figure 17 and Figure 18. Both relationships are strong, with adjusted r^2 of 0.64 and 0.89 for herbaceous and woody models. This suggests that from two thirds to nearly 90% of the variability in each WCI response was explained by UUI. This is a good sign for the model's predictive powers.

Each had a strong negative linear correlation with UUI (herbaceous: −0.80; woody: −0.94), reflecting our focus on the negative consequences of ungulate use.

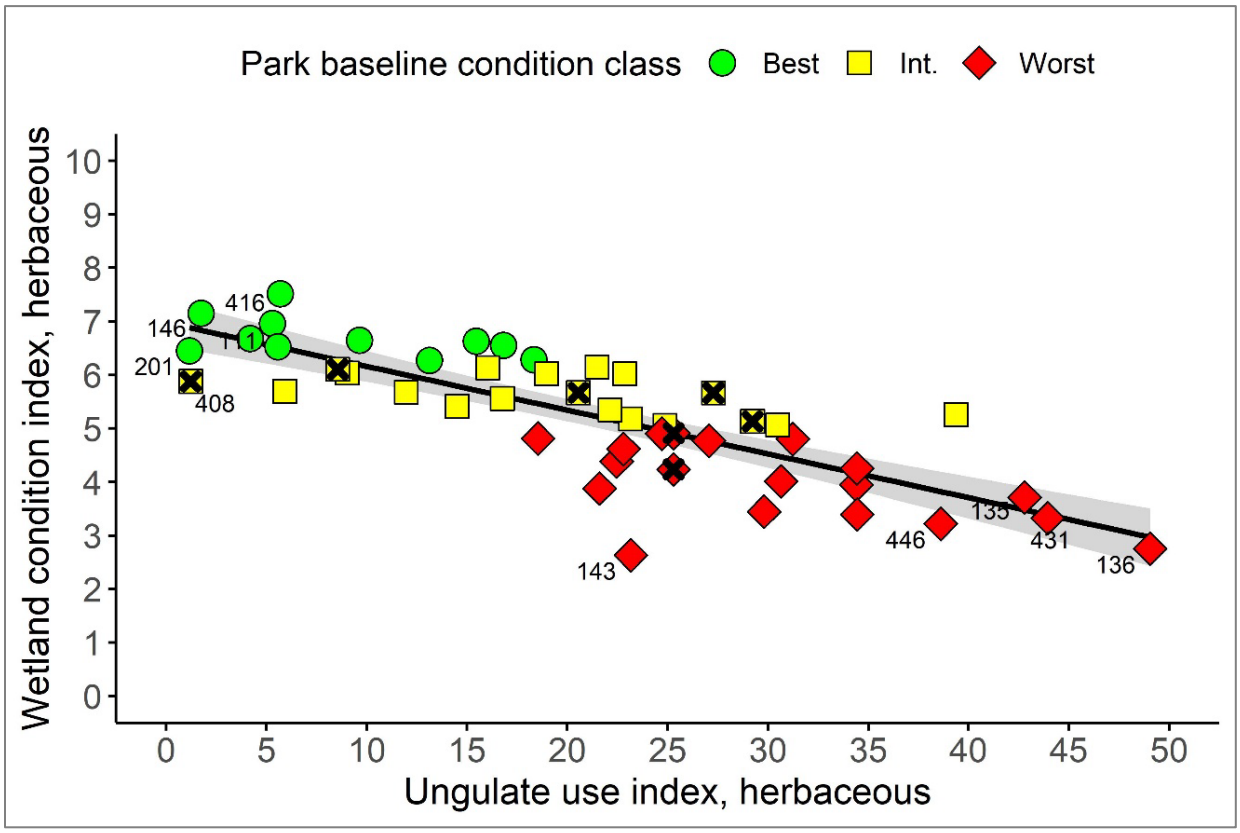


Figure 17. Relationship of Wetland Condition Index and Ungulate Use Index for herbaceous wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Linear fit (correlation = −0.80, $p \leq 0.001$, adjusted $r^2 = 0.64$) and its 95% confidence interval are shown with the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition, with green circles for "best available," yellow squares for "intermediate," (Int.), and red diamonds for "worst" classes. Points with black crosses are sites inside an ungulate exclosure. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst WCI and/or UUI ranges are labeled with their site number. Not all sites are visible given overlapping points. NPS

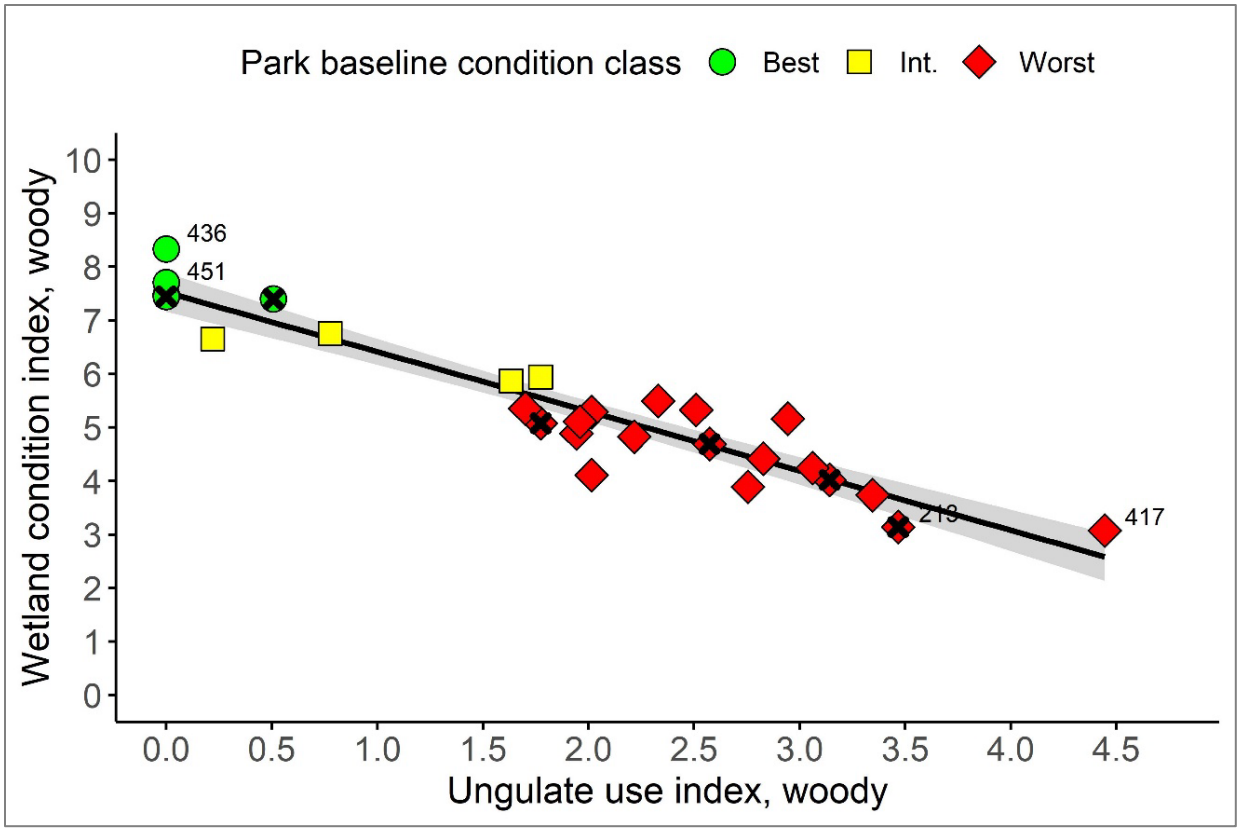


Figure 18. Relationship of Wetland Condition Index and Ungulate Use Index for woody wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Linear fit (correlation = −0.94, $p \leq 0.001$, adjusted $r^2 = 0.89$) and its 95% confidence interval are shown by the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition with green circles for "best," yellow squares for "intermediate" (Int.), and red diamonds for "worst" classes. Points with black crosses are sites inside an ungulate exclosure. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst WCI and/or UUI ranges are labeled with their site number. Not all sites are visible given overlapping points (three of the five best sites have WCI values very close to 7.4, two of which have UUI = 0 and thus overlap). NPS

Component metrics

A WCI consists of component metrics that, as a group and when controlled for confounding environmental gradients, best respond statistically to the ungulate use disturbance gradient (Schoolmaster et al. 2012; Schoolmaster, Grace, Schweiger, Mitchell et al. 2013; Schoolmaster Grace, Schweiger, Guntenspergen et al. 2013; see also Appendix A). Interpreting individual component metrics is useful and we do this in the Discussion. However, WCIs are standalone—they are the most important result for the UMP to help the park meet the wetland ecological integrity goals set forth in the EIS.

Table 4 and Table 5 present the component metrics in the herbaceous and woody WCIs. The overall correlations between the WCI and UUI for both models are markedly stronger than any of individual component metric correlations with UUI, confirming the statistical and ecological advantage and parsimony of a WCI. We often refer to this as the "ghost in the machinery" of WCI modeling. These

tables also include coefficients for how each component metric is adjusted by the environmental variables applied in the models. These may be interpreted as the influence of a given environmental variable on a UUI with all other variables held constant. This must be done with caution given different units of measure or scale for most environmental predictors. Note we retain environmental variables that have zero values within and across all component metrics (i.e., production in the herbaceous model) because these variables still influence (statistically) other variables in the model. There may also be interpretative value in variables with zero valued coefficients or influence within and across models (e.g., it is interesting that sodium absorption ratio (SAR) had non-zero values in the woody WCI across all component metrics but not in the herbaceous model).

Table 4. Final component metrics of Wetland Condition Index (WCI) for herbaceous wetland sites, Great Sand Dunes National Park and Preserve, 2016–2019. Correlation (corr.) with ungulate use (UUI) is given before (raw) and after (adjusted, Adj.) adjustment and scaling by 10 environmental covariates listed in the table. Each component variable's model intercept (int.) and coefficients for the environmental covariates are shown. Human disturbance (LDI); Depth to ground water (DTW); Sodium absorption ratio (SAR); Bare ground (BRE); Litter cover (LIT); Elevation (ELEV); Production, 5-year mean (PROD); Temperature as growing degree days, 5-year mean (GDD); Climatic deficit, lagged 3 years (D); Soil moisture, 5-year mean (SOIL). See Table 1 for units of measure and other details of the environmental variables.

Metric name, (units)	Adj. corr. with UUI	Raw corr. with UUI	Adj. model int.	UUI	LDI	DTW	SAR	BRE	LIT	ELEV	PROD	GDD	D	SOIL
Woody species richness, (count)	−0.469	−0.468	2.168	−0.052	0	0	0	0	0	0	0	0	0	0
Relative cover of salt intolerant species, (%)	0.450	0.280	17.507	0.004	0	0	0	0	0	−0.004	0	−0.003	0	0.001
Iris & silverweed absolute cover, %	0.412	0.316	8.783	0.342	0	0	0	−0.136	−0.147	0	0	0	0	0
Total height of sedges, (cm)	−0.349	−0.212	185.408	−1.688	0	0.782	0	0	0	0	0	0	−0.825	0
Wetland affinity, cover weighted, (index)	−0.264	−0.061	19.266	−0.010	0	0.008	0	−0.013	−0.006	−0.006	0	0	0	−0.009
Nonnative species richness, (count)	0.179	0.136	1.499	0.020	0	0	0	0	0	0	0	0	0	0
Dominance of graminoids, (index) [A]	0.090	−0.186	57.600	0.149	−0.074	0	0	−0.448	−0.452	0	0	0	0	0

[A] Metrics in italics are considered minor, with little direct influence on the WCI and are not interpreted.

Table 5. Final component metrics of Wetland Condition Index (WCI) for woody wetland sites, Great Sand Dunes National Park and Preserve, 2016–2019. Correlation (corr.) with ungulate use (UUI) is given before (raw) and after (adjusted, Adj.) adjustment and scaling by 10 environmental covariates listed in the table. Each component variable's model intercept and coefficients for the environmental covariates are shown. Human disturbance (LDI); Depth to ground water (DTW); Sodium absorption ratio (SAR); Bare ground (BRE); Litter cover (LIT); Elevation (ELEV); Production, 5-year mean (PROD); Temperature as growing degree days, 5-year mean (GDD); Climatic deficit, lagged 3 years (D); Soil moisture, 5-year mean (SOIL). See Table 1 for units of measure and other details of the environmental variables.

Metric name (units)	Adj. corr. with UUI	Raw corr. with UUI	Adj. model intercept	UUI	LDI	DTW	SAR	BRE	LIT	ELEV	PROD	GDD	D	SOIL
Density of browsed willows & cottonwood, (browsed plants/m^2)	0.80	0.34	−25.166	0.129	0	−0.003	0	0	0	0.006	0	0.004	0	0.011
Percentage of rabbit brush 0.5 to 1.0 m tall, (%)	0.64	0.54	−25.298	16.774	0	0	0	0	0.380	0	0	0	0	0
Total cover of salt intolerant species, (%)	0.57	−0.01	112.942	1.844	0	0	7.312	0	0	0	0	−0.046	0	0.167
Ratio of willow and cottonwood cover to all woody cover, (index)	−0.48	−0.26	0.645	−0.039	0	0	−0.160	0	−0.003	0	0	0	0	0
Density of sandbar willow, 0.5 to 1.0 m tall, (plants/m^2)	0.18	0.33	0.024	0.003	0	0	0.024	0	0	0	−0.0002	0	0	0
Dominance all species, (index) [A]	0.005	0.12	104.383	0.086	0	0	0	0	−0.470	0	0	0	0	−0.970

[A] Metrics in italics are considered minor, with little direct influence on the WCI and are not interpreted.

Patterns across baseline condition classes

Figure 19 and Figure 20 show patterns in the herbaceous WCI across park management-defined condition classes by group and spatially. Across all herbaceous sites, 22% were in a baseline best condition and 39% were in a baseline worst condition (with overall and pair-wise p-values both well below 0.001). While the majority of herbaceous sites are inside the bison fence (elk and bison use zone), and we have a less reliable sample of herbaceous wetland outside the bison pasture, there is a clear pattern for lower WCI where both species impact herbaceous sites (inside the bison fence), with an increase in WCI as sites are further from the bison pasture. The shift to higher condition outside the fence is dramatic, with a clear increase in WCI even in sites near the fence. The categorical test had overall and pair-wise p-values well below 0.001 and are thus meaningful and significant.

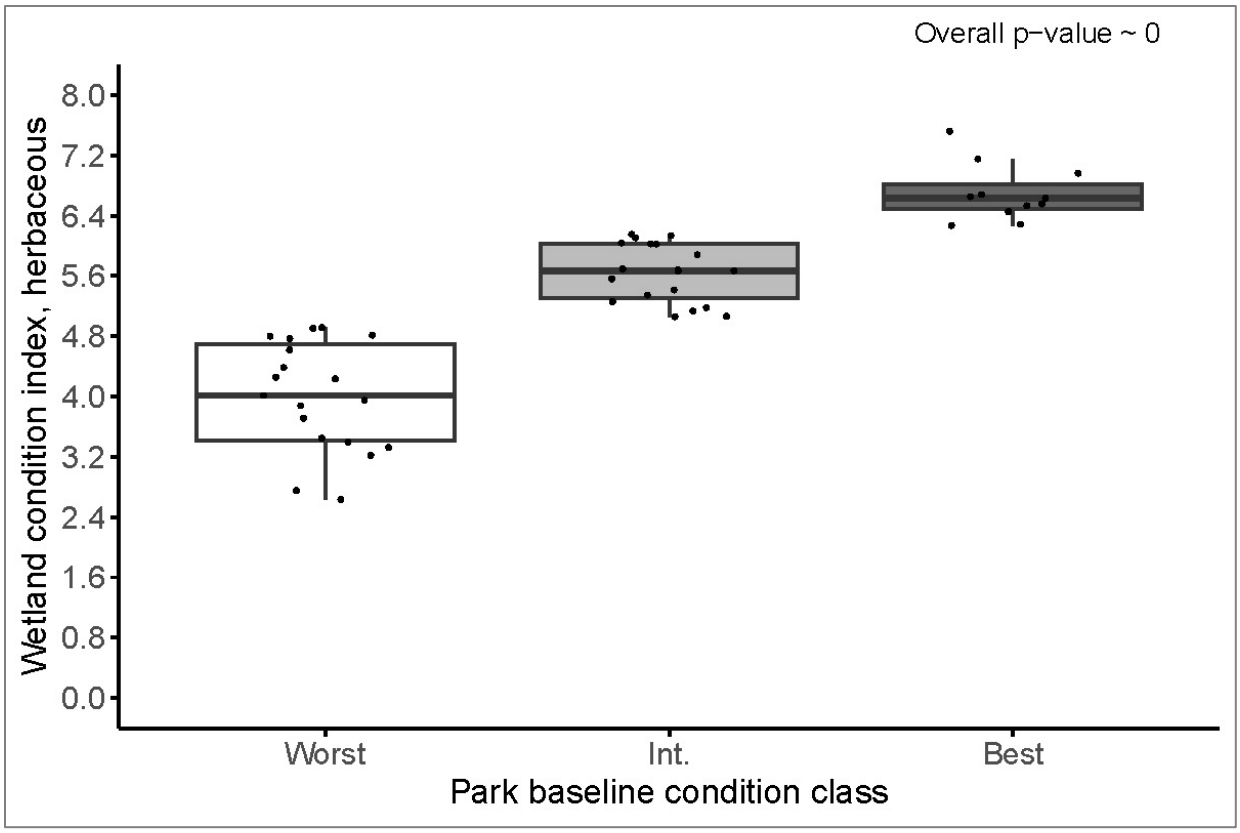


Figure 19. Wetland Condition Index for herbaceous wetland sites across park-supported condition classes at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test, with "p-value ~ 0" indicating a vanishingly small probability. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

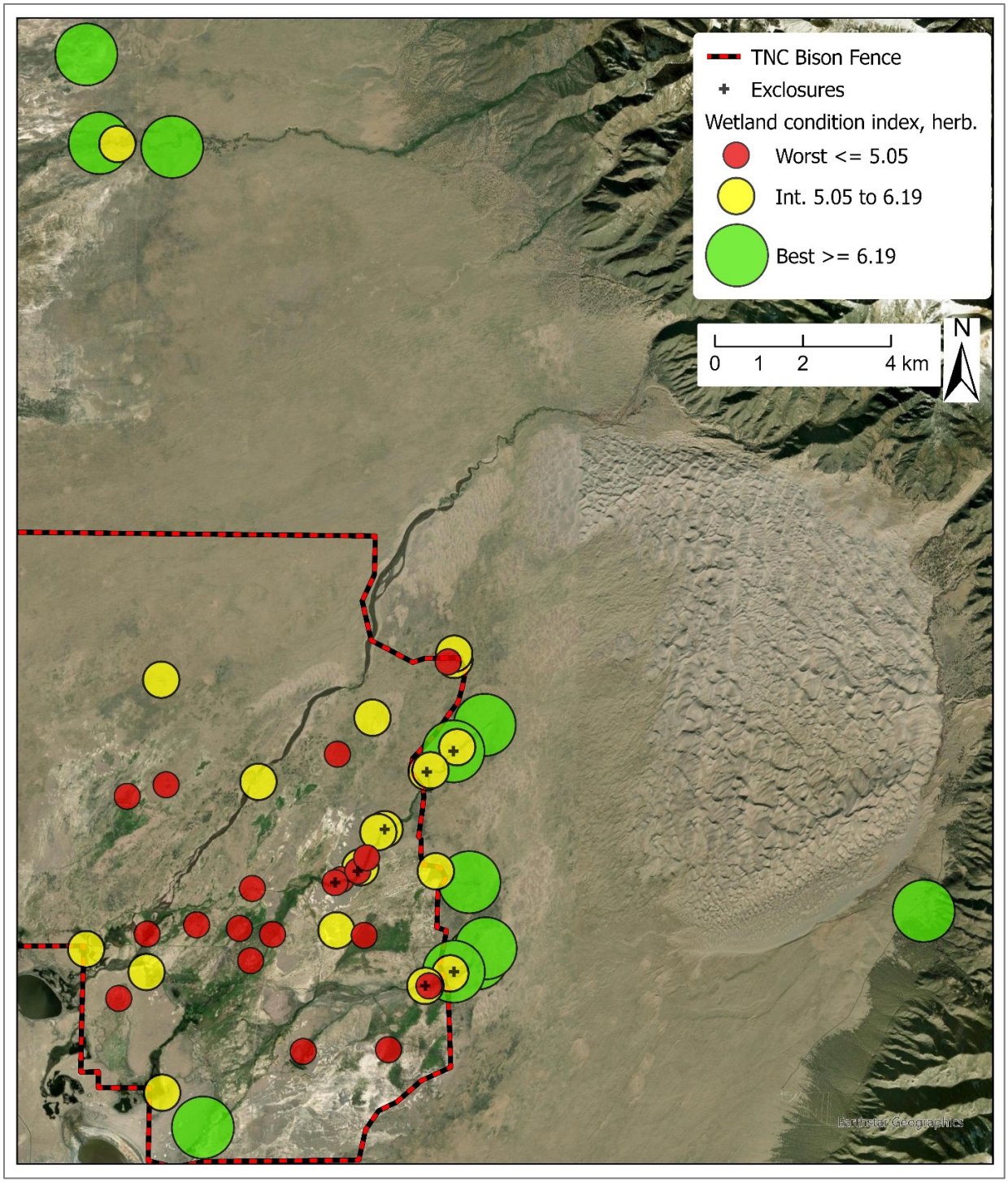


Figure 20. Wetland Condition Index in herbaceous wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Only first visit shown at sites with more than one sample. Point colors and size are based on condition classes as defined by park staff, with larger green points for a best available, yellow medium size for an intermediate ("Int."), and smaller red a worst condition state. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. NPS

Figure 21 and Figure 22 show patterns in the woody WCI across park management defined condition classes by group and spatially. Baseline woody WCI had similar general patterns as in the herbaceous model, with fewer sites (18%) in a baseline best condition and more (66%) in the baseline worst class ($p < 0.001$). Most woody sites inside the bison fence (elk and bison use zone) were in a worst condition class, with WCI increasing in sites further from the bison pasture. However, several sites, well removed from the bison fence along Deadman Creek and unexclosed sites along Sand Creek near the mountain front, were still heavily impacted by (only elk) use and had lower WCI.

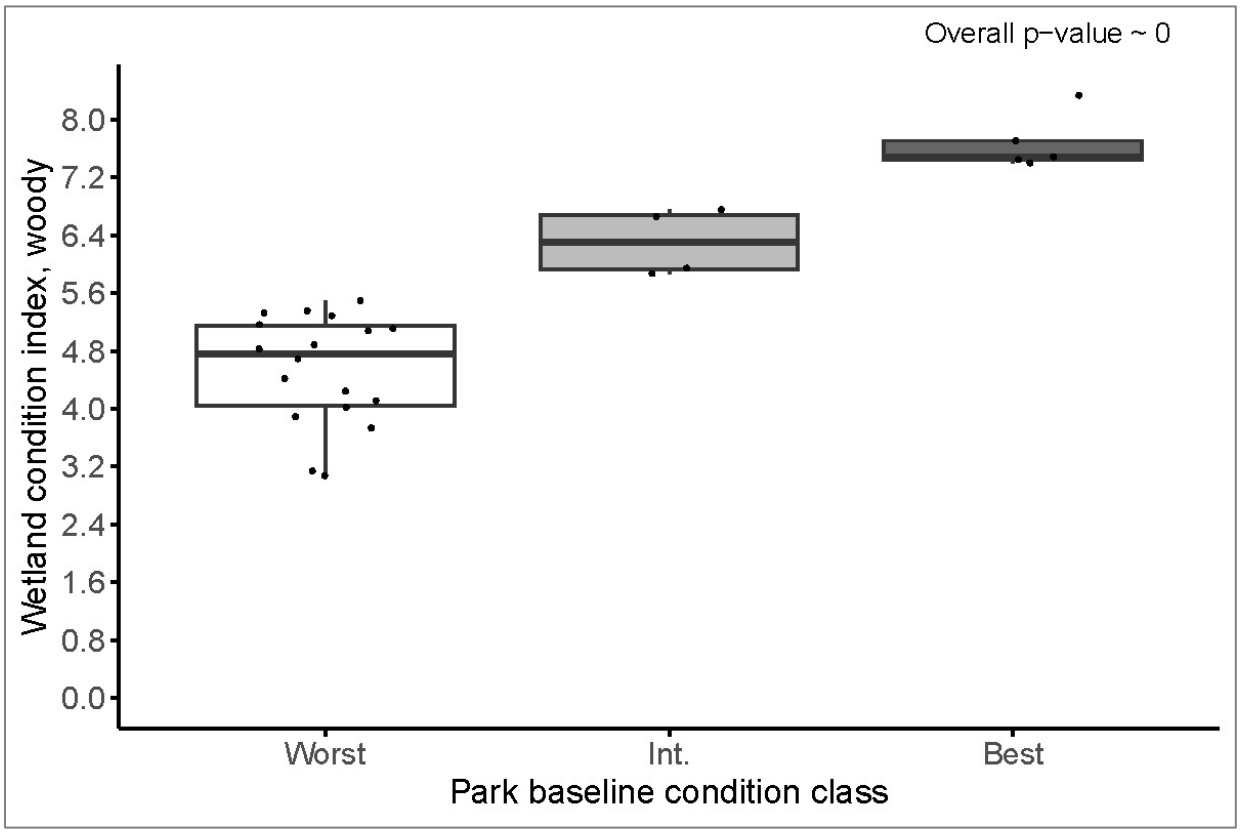


Figure 21. Wetland Condition Index for woody wetland sites across park-supported condition classes at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test, with "p-value ~ 0" indicating a vanishingly small probability. Select individual paired comparison p-values are reported in text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

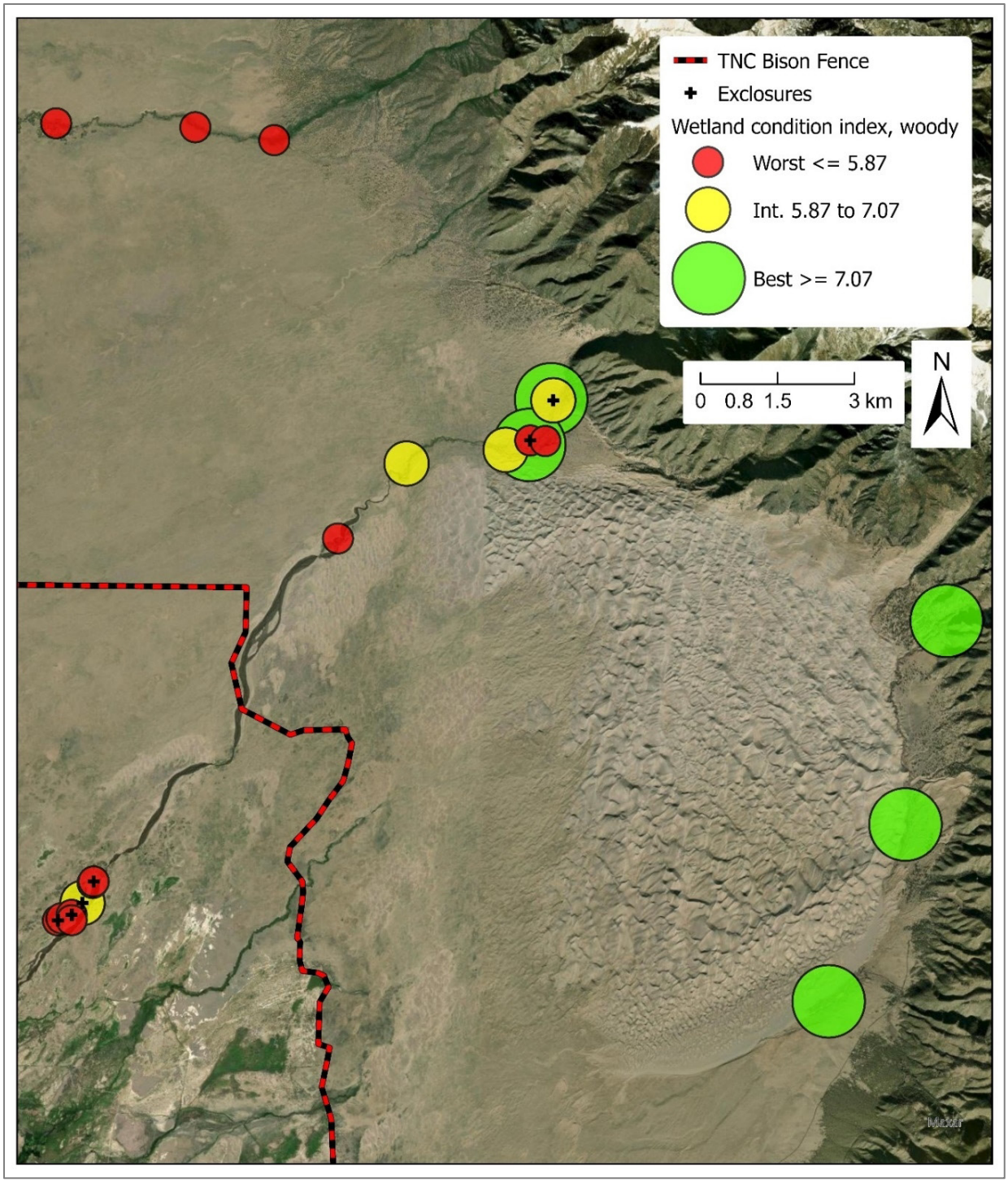


Figure 22. Wetland Condition Index at woody wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Only first visit shown at sites with more than one sample. Point colors and size are based on condition classes as defined by park staff, with larger green points for a best available, yellow medium size for an intermediate (“Int.”), and smaller red a worst condition state. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. NPS

Patterns across important management variables

Given the strong relationships between the UUIs and WCIs in woody and herbaceous sites, many of the patterns summarized here for WCI are similar to those presented above for UUIs. See the figures in Appendix E for more information on patterns in WCI across park management relevant variables.

WCIs in herbaceous and woody wetlands were remarkably similar across exclosures, sites adjacent to exclosures, and in sites well removed from exclosures. Woody WCI was marginally higher in sites spatially removed from exclosures when compared to sites adjacent to exclosures ($p = 0.07$). However, as with UUI, this pattern is not an exclosure effect per se; rather, it likely reflects the impacts of higher use from both elk and bison inside the bison fence where the majority of exclosures are located. These results suggest that exclosures had little impact on wetland condition in our baseline data. As discussed further below, this is likely due to exclosure failures in 2016–2019, as well as wetland recovery from any initially reduced ungulate use when the exclosures were constructed some 10 years prior to the UMP baseline period.

The herbaceous WCI varied across years (overall $p = 0.04$), peaking in 2017, with 2018 and 2019 lower than 2017 ($p = 0.09$ and $p = 0.03$). The WCI was also lower in 2019 than 2018 ($p = 0.05$). Annual patterns in the woody WCI were more stable, with no detectable difference between years. There was a strong pattern across ungulate use in both wetland types, with the herbaceous WCI higher with only elk use ($p < 0.0001$)—this mirrors the finer-grained pattern we see in map-based comparisons across individual sites (Figures 20 and 22). The woody WCI also varied strongly across ungulate zones (overall $p < 0.001$), with condition in the elk only and elk with some bison zones much higher than in the elk and bison zone ($p < 0.001$ for each). Finally, there was no difference across herbaceous types (salt flats, wet meadows, or marshes), yet in woody sites, WCI was notably higher in cottonwood sites versus willow ($p < 0.001$).

Hand-picked metrics

Summary statistics for the four HP metrics, in both raw and adjusted form, are presented in Table 6. We include the numeric threshold values for each metric's park-supported baseline AP—these are critical results central to the interpretation of UMP data. All adjusted HP metrics range from 0 to 10. They have units that are the same as their raw version; however, adjusted HP metrics include sufficient "statistical content" that we treat them as indices. Raw HP metrics are real-valued and have specific ranges (but conservatism and wetland affinity are still indices in their raw form). Results for HP metrics are specific to woody or herbaceous sites as indicated in the tables and associated text.

Table 6. Summary statistics for hand-picked (HP) metrics in woody (W) and herbaceous (H) wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. The r^2 is from a linear model of an adjusted HP metric and Ungulate Use Index. Assessment points (AP) are the threshold values for each metric's park-based assessment point; Med.: median; SD: standard deviation; CV: coefficient of variation. Minimum (Min.) detectable difference (statistical power) is the smallest percent change resolvable when comparisons are made between baseline and Phase 2 or 3 means (see the "Power" section). Metrics shaded gray are also component metrics in a Wetland Condition Index.

Metric name, units, (wetland type)	Best baseline condition AP	Worst baseline condition AP	r^2	Mean	Med.	SD	CV (%)	Min. detectable difference (%)
Adjusted: density of browsed willows and cottonwood, index, (W) [A]	≤ 2.16 [B]	≥ 3.81 [B]	0.64	4.94	4.09	2.97	60.0	6.85
Raw: density of browsed willows and cottonwood, browsed plants/m^2, (W)	≤ 0.034 [C]	≥ 0.053 [C]	0.08	0.14	0.059	0.23	160.0	18.27
Adjusted: iris and silverweed absolute cover, index, (H) [A]	≤ 1.54 [C]	≥ 2.83 [C]	0.16	3.52	2.88	2.67	75.83	5.46
Raw: iris and silverweed absolute cover, raw, % (H)	≤ 2.30 [C]	≥ 3.85 [C]	0.08	7.63	2.81	10.85	142.09	10.24
Adjusted: conservatism graminoids cover, weighted, index, (H) [A]	≥ 6.98 [C]	≤ 4.20 [C]	0.07	4.44	4.13	3.01	67.76	4.88
Raw: conservatism graminoids cover, weighted, raw, index, (H)	≥ 4.93 [B]	≤ 4.44 [B]	0.00	4.54	4.62	8.85	78.78	11.35
Adjusted: wetland affinity, index, (W)	≥ 6.35 [C]	≤ 3.00 [C]	0.01	5.60	5.90	3.04	54.22	3.90
Raw: wetland affinity, raw, index, (W)	≥ 3.62 [B]	≤ 2.74 [B]	0.00	3.45	3.49	0.42	72.14	7.38

[A] Metrics are components in a Wetland Condition Index, also shown shaded in gray.

[B] AP estimated using median.

[C] AP estimated using mean.

Table 7 gives correlations with UUI and the adjustment details for each HP metric. Note that the direction of the correlation with UUI indicates if smaller numbers are "better" (positive correlation) or "worse" (negative correlation) under the important assumption that a decrease in condition from increased ungulate use is what matters to UMP management goals. As noted for the WCI, we retain environmental variables that have zero values within and across HP metrics because these variables influence the coefficients of variables that have non-zero values and there may still be interpretative value in a variable with a zero valued influence. See Appendix B for additional detail on the adjustment process. We interpret raw results for all HP metrics (as well as raw WCI component metrics) in the Discussion as this may help or support an intuitive understanding of our results. However, all assessment of changes from the baseline should be done using adjusted HP metrics.

Adjustment for environmental gradients increased (relative to the raw data) the correlation with UUI for all HP metrics and the amount of variation explained by linear models (the adjusted r^2) of an HP and its UUI (Table 6, linear model figures in Appendix E). In some cases, these higher r^2 values suggest adjustment might almost triple the likelihood that future monitoring will show a change (i.e., predict a decrease in browse with a decrease in UUI resulting from park management actions). Adjustment also reduces the level of variation across sites (best seen in smaller coefficients of variation). This supports better power models, often with two to three times smaller minimum detectable differences likely when comparisons are made with adjusted data to Phase 2 and 3 results. Network monitoring at our current sample effort will not likely detect changes in HP metrics due to changes in ungulate management without adjustment for confounded environmental variables.

Table 7. Adjustment model specifications for hand-picked (HP) metrics in woody (W) and herbaceous (H) wetland sites, Great Sand Dunes National Park and Preserve, 2016–2019. Correlation (corr.) with ungulate use (UUI) is given before (raw) and after (adjusted, Adj.) adjustment and scaling by 10 environmental covariates listed in the table. Each component variable's model intercept (int.) and coefficients for the environmental covariates are shown. Human disturbance (LDI); Depth to ground water (DTW); Sodium absorption ratio (SAR); Bare ground (BRE); Litter cover (LIT); Elevation (ELEV); Production, 5-year mean (PROD); Temperature as growing degree days, 5-year mean (GDD); Climatic deficit, lagged 3 years (D); Soil moisture, 5-year mean (SOIL). For units of measure and other details of the environmental variables, see Table 1.

Metric name, units, (wetland type)	Adj. corr. With UUI	Raw corr. With UUI	Adj. model int.	UUI	LDI	DTW	SAR	BRE	LIT	ELEV	PROD	GDD	D	SOIL
Density of browsed willows and cottonwood, browsed plants/m^2, (W)	0.80	0.34	−25.166	0.129	0	−0.003	0	0	0	0.006	0	0.004	0	0.011
Iris and silverweed absolute cover, %, (H)	0.412	0.316	8.783	0.342	0	0	0	−0.136	−0.147	0	0	0	0	0
Conservatism graminoids cover weighted, index, (H)	−0.29	−0.12	5.53	−0.017	0	0.01	0	0	0	0	0	0	0	0
Wetland affinity, index, (W)	−0.29	−0.08	4.070	−0.085	0	0	0	0	−0.008	0	0	0	0	0

Patterns across baseline condition classes

Figure 23 shows all four adjusted HP metrics across park-supported condition classes. Importantly, these results are not raw values (i.e., neither absolute or relative cover)—they are adjusted for correlations with environmental gradients and scaled to a common range. With the exception of wetland affinity in woody sites, over 50% of each HP metric was in the worst condition class, suggesting that the majority of sites had higher density of browsed willow and cottonwood, less conservative graminoids, and more iris and silverweed cover than the park-supported baseline worst AP. Only wetland affinity in woody sites was below this majority threshold, with 26% of sites in a baseline worst class. All these patterns had overall and pairwise p-values well below 0.001 and are thus meaningful and significant. Note that the "overall p-value" gives the probability across all comparisons (i.e., are there any differences) in each panel while pair-wise p-values presented in text are specific to a comparison between two groups.

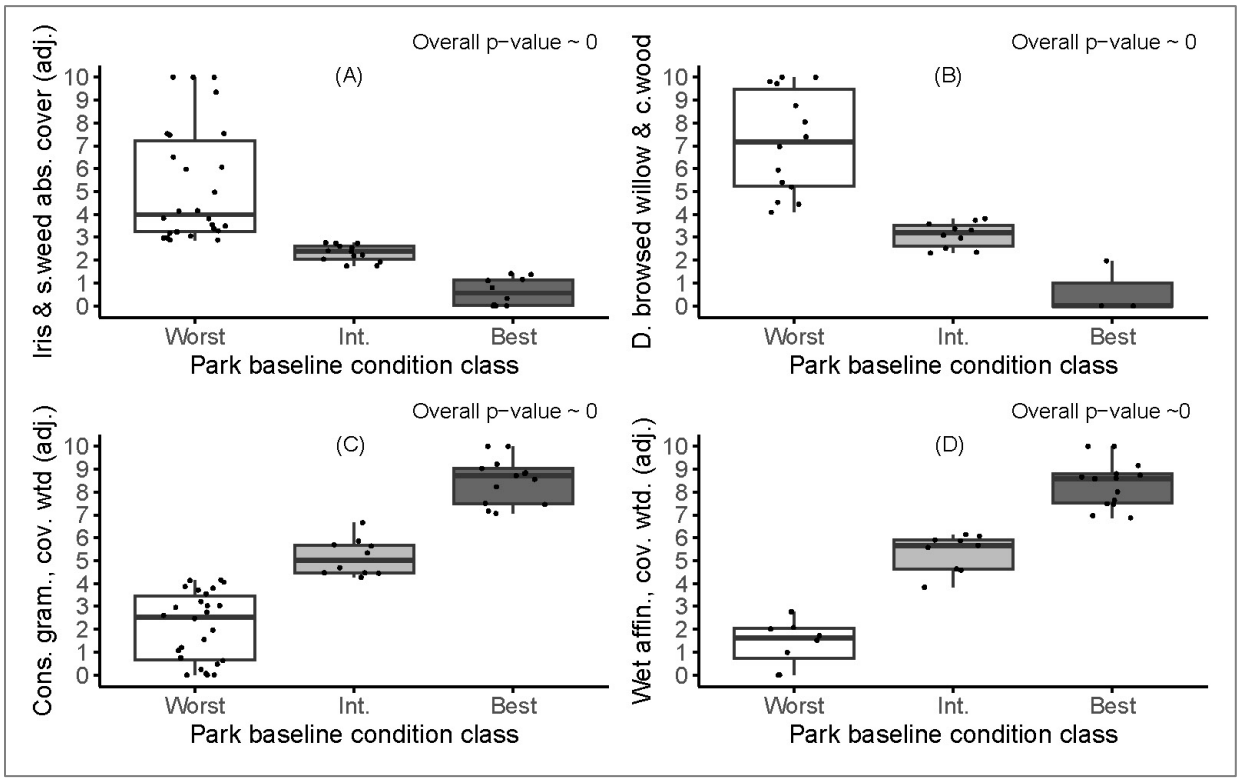


Figure 23. Patterns in hand-picked (HP) metrics across park-supported condition classes at Great Sand Dunes National Park and Preserve, 2016–2019. (A) iris and silverweed cover at herbaceous sites, (B) browsed willow and cottonwood density at woody sites, (C) conservatism of graminoids at herbaceous sites, and (D) wetland affinity at woody sites. All HP metrics are adjusted. An overall p-value is shown from a Wilcox nonparametric test with "p-value ~ 0" indicating a vanishingly small probability. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

Figure 24 and Figure 25 show spatial patterns for all four adjusted HP metrics by park-supported condition classes. All four HP metrics had complex patterns across space. The bison pasture, where

both elk and bison use wetlands, tended to have more worst condition sites, but this is confounded with uneven samples of unequally distributed wetland across the bison fence. Wetland affinity in woody sites and conservatism of graminoids in herbaceous sites were often in a best available condition at sites well-removed from the bison pasture, but the density of browsed willow and cottonwood could be in worst condition (higher browse) in these remote sites. As expected, using single univariate indicators, it is difficult to synthesize patterns into a single theme (that is what the WCI models are for).

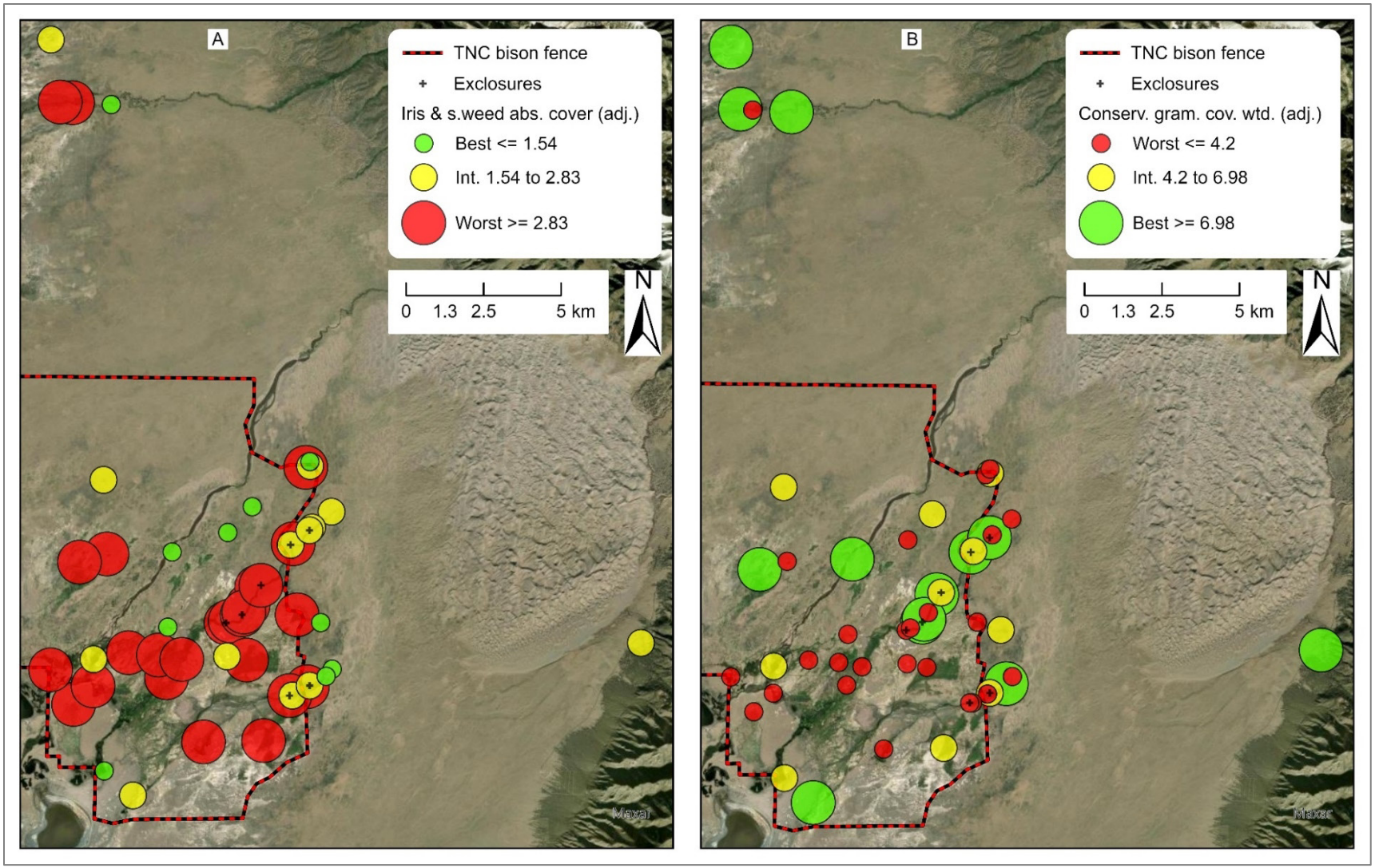


Figure 24. Adjusted results for hand-picked metrics at herbaceous sites at Great Sand Dunes National Park and Preserve, 2016–2019. (A) iris and silverweed absolute cover, and (B) conservatism of graminoids. Point colors follow condition classes as defined by park staff with larger green points for a best available, yellow medium sized points for an intermediate ("Int."), and smaller red points for a worst condition state. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible, given overlapping points. NPS

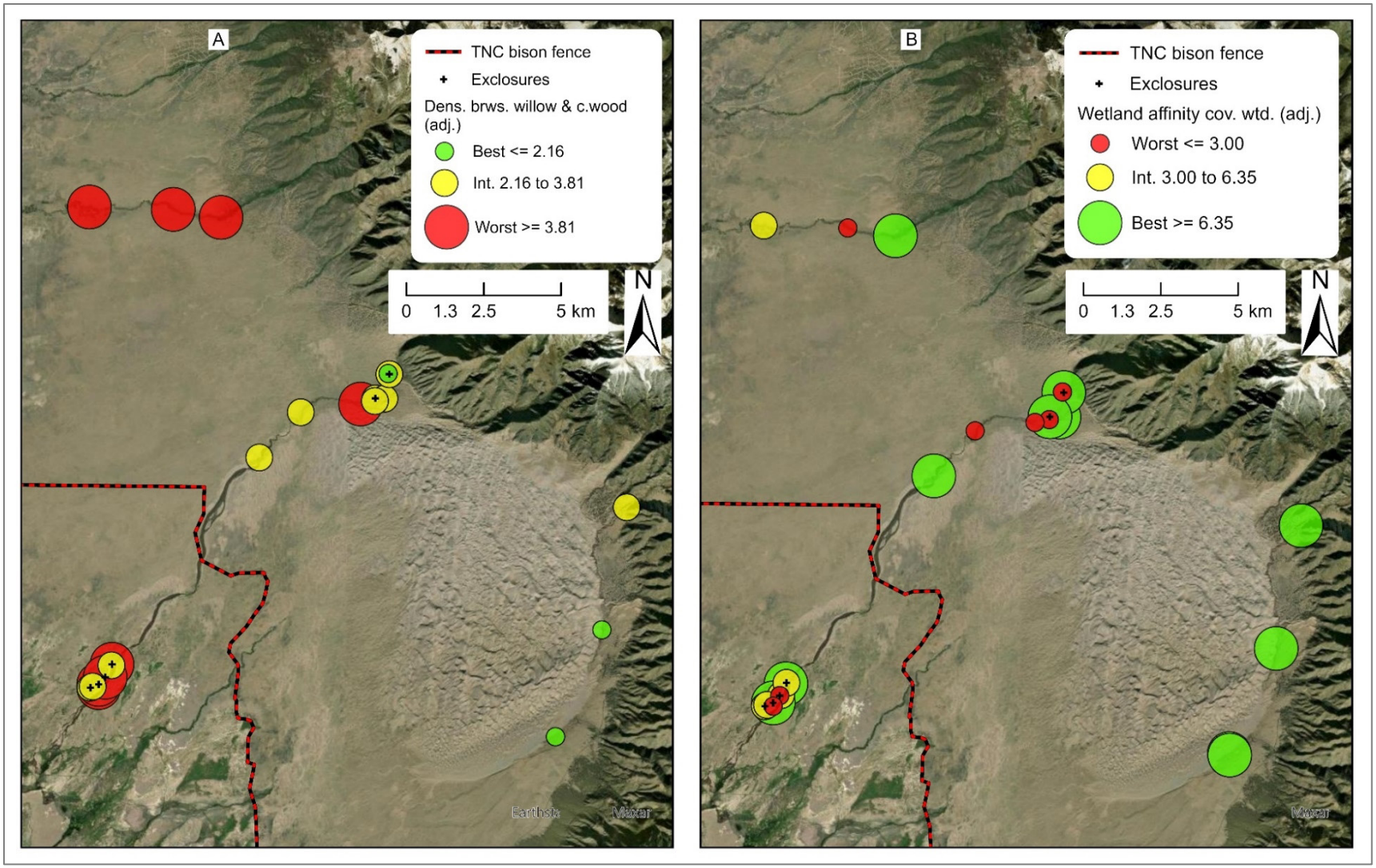


Figure 25. Adjusted results for hand-picked metrics at woody sites at Great Sand Dunes National Park and Preserve, 2016–2019. (A) density of browsed willow and cottonwood, and (B) wetland affinity. Point colors follow condition classes as defined by park staff, with larger green points for a best available, yellow medium sized points for an intermediate (“Int.”), and smaller red points a worst condition state. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. NPS

Patterns across important management variables

The four HP metrics had complex patterns across variables important to park management, such as exclosures, years, use by elk only or elk and bison, and wetland type. See the figures in Appendix E for more information on patterns in HP metrics across park management relevant variables.

Similar to UUI and WCI, there was a lack of a clear exclosure effect. There were nonsignificant increases in the density of browsed willow and cottonwood and wetland affinity in paired unexclosed sites as we might expect, but also there was higher cover of conservative graminoids in paired sites, and iris and silverweed cover was essentially identical across paired sites. As discussed further below, these results indicate that the UMP exclosures have generally failed, or, at least during our baseline period, they did not perform as expected.

Unlike with UUI and WCI, there was also no clear effect of years on any HP metric. All overall tests were strongly nonsignificant and there was no clear pattern across years in any paired comparison. This is perhaps surprising but welcome as it suggests these metrics are less influenced by annual variation. There were some likely meaningful differences across ungulate use zones. For the two woody HP metrics (with only two classes, elk and bison or elk only use), there was notably higher browse where sites were used by both species ($p = 0.006$). There was also a higher density of browsed willow and cottonwood in willow relative to cottonwood woody subtypes ($p = 0.02$). Conservative graminoids as a woody wetland HP metric were more common in elk only when compared to elk and bison use areas ($p = 0.04$). For the two herbaceous HP metrics (with a third use class of elk and some bison), there was a difference in iris and silverweed cover (overall $p = 0.006$), with notably higher cover in both elk and elk and bison use relative to elk and some bison ($p = 0.005$) and elk only ($p = 0.06$).

Discussion

In this section we interpret 2016–2019 baseline Ungulate Management Plan (UMP) results. Zeigenfuss et al. (2024) present a similar treatment of Ungulate Use Indices (UUI) and should be reviewed by park managers along with this report. As requested by Great Sand Dunes National Park and Preserve (GRSA) management, we emphasize how our results might apply to the park's ongoing and future management of ungulates as described in the UMP EIS.

Many of our interpretations are based on park-supported UMP assessment points (APs) presented throughout this report. These APs are the first time since the Rocky Mountain Network (the network) began its monitoring work in 2004 that meaningful numeric condition thresholds have been sourced from a park partner. They provide a way to place UMP results that fall along a Wetland Condition Index (WCI), UUI, or hand-picked (HP) metric gradient into best/intermediate/worst available condition classes. We expect these baseline APs to be foundational moving forward and allow a meaningful tracking of change relative to baseline conditions. To be clear, they are specific to the UMP project and they are not applicable as a viable broad-scale set of thresholds for wetland monitoring and assessment writ large.

Assumptions

Our work is based on a conceptual model of the causal relationships (Grace 2024; Grace et al. 2024) within ungulate and wetland ecology and how these are relevant to the connections that link management actions to wetland condition. We make two key assumptions to support this as a causal process. First, we assume a negative response in wetland condition to increased ungulate use (i.e., Figure 26). Much of this report focuses on developing WCI models and HP metrics that estimate this relationship. Second, we assume a negative response in ungulate use to management actions (in contrast to a positive relationship such as from supplemental feeding). We recognize that these are complex assumptions. There is supporting evidence in the literature that hazing, culling, active hunting, and exclosures can decrease ungulate habitat use (Jones et al. 2021; Kloppers et al. 2005). Likewise, there are many examples from multiple systems showing how ungulate use can negatively impact habitat condition (i.e., Johnston et al. 2007; Frank et al. 2016; Rhodes et al. 2018; Kauffman et al. 2023; Miller et al. 2023). Note that we discuss how we deal with positive effects of ungulate use on condition in a separate section below.



Figure 26. Heavy ungulate disturbance (mostly bison) in a likely degraded herbaceous wetland near sites 447 and 429, Great Sand Dunes National Park and Preserve, 2020. NPS / B. SCHWEIGER

Our two core assumptions are a large simplification of all the covariates, latent variables, and various other complicating factors in play. Yet they allow us to conceptually connect management action on ungulates to wetland condition response. We do not have a perfect statistical treatment of all the details relevant in this causal chain (*sensu* Dee et al. 2023) but this is acceptable (Grace 2024). A lack of complete information is actually another reason to develop WCI models that can help focus park management of elk, and eventually bison, to improve wetland condition. In summary, we have enough mechanistic knowledge to treat the relationship between ungulate use and wetland condition as a likely causal process.

Nevertheless, there are complex relationships among ecosystem drivers and species level (if not individual plant) responses that are beyond WCI applications. WCIs show the direction of change in complex systems—much like the familiar Dow Jones Index can mirror important macroeconomic patterns—but may not provide the details needed to fully understand mechanisms. We have developed detailed causal models based on WCIs in other network parks. For example, Schweiger et al. (2016) develop a detailed treatment of wetland response in Rocky Mountain National Park

(ROMO) to human disturbance that uses as its basis or starting point a WCI. Future work might do the same for the GRSA UMP.

Within both of our core assumptions, we recognize that there are other drivers that can enhance wetland condition or impact ungulate use. For example, condition can be improved through changes in structures that influence ground water (i.e., ditches) and disease, or change in seasonal migration patterns can impact ungulate use (as seen in ROMO; Zeigenfuss and Johnson 2015). GRSA resource management of ungulates is adaptive; park staff will evaluate the success of hazing and culling efforts and could consider other management actions, such as additional exclosures or reproductive control. As of 2024, GRSA resource staff were not directly restoring wetlands through actions such as watering wetlands, pulling weeds, or planting conservative species. If the park performs vegetation management or hydrologic restoration (e.g., via removal of ditches and/or wells), we may be able to adjust our WCI models (much like we currently do for environmental gradients) or add tools to assess the response of wetland condition to these actions.

Increasing wetland condition with increasing ungulate use

As we developed our WCIs we saw several complex vegetation metric responses to UUI. There was a clear majority that responded in a way that indicated increasing ungulate use was degrading wetland condition. There were several that had no detectable response. There were also a sizeable set that responded in a way that suggested increasing ungulate use was improving wetland condition. We introduce these concepts in the Methods section of this report where we label these types of indicators as "increasers." We call metrics that suggest a degrading condition with more ungulate use "decreasers." Schweiger et al. (2017) also identified several increaser metrics in a large dataset developed from the 2010 survey of GRSA sand sheet wetlands. Our WCI methods evaluate all candidate metrics fed into the algorithm, carefully accounting for multivariate correlation and outputting the statistically best and smallest set based on the correlation with UUI. Our methods drop candidate metrics without a meaningful response. However, including both decreaser and increasers metrics in the same WCI model estimation process proved to be problematic, with metrics essentially "canceling each other out." Therefore, in consultation with the park, we elected to focus our WCI only on a decreaser effect. We identified all metrics that were indicators of an increasing wetland condition and removed them from the modelling process.

This does not mean we think an increaser response is unimportant for UMP. Beneficial effects of sustainable ungulate use, for example elevated vegetation productivity, are well documented in the literature (Leibold 1996; Milchunas and Lauenroth 1993; Chesson 2000: Koerner et al. 2018; Ratajczak et al. 2022) Perhaps more importantly, ranchers and native peoples, including in the San Luis Valley, have known for centuries that herbivores can increase biodiversity by preferentially grazing or browsing on plant species that are otherwise competitively dominant. Large ungulates like elk and bison at GRSA evolved digestive systems and selective foraging that can reduce the abundance of palatable species (usually grasses) that dominate in the absence of grazers, resulting in increased species richness in many grasslands globally (and we see this in UMP data). Large ungulates also create small-scale heterogeneity in nutrient availability and grazing frequency, which should theoretically increase plant diversity.

The Rocky Mountain Network and GRSA made the choice to focus the WCI models presented in this report on the decreaser effect for two reasons. First, we believe that the decreaser response is the dominant process occurring on the sand sheet under current conditions (see Figure 26) and the one the park most needs to address. In general, herbaceous and woody wetlands on the sand sheet are degraded; many having been heavily grazed for decades. They often have lower (drier) water tables than wetlands in other landscapes given their high desert context. Many have also been heavily used by humans for ranching, other agricultural land uses, and, more recently, for recreation (Schweiger et al. 2017). By focusing on the decreaser response we believe we are helping the park understand and address the most critical response. Second, we only had the capacity to address the higher priority decreaser effect internally. We believe that research on the increaser phenomenon is a good candidate for external collaboration.

The bison factor

Bison account for an overwhelming proportion, relative to elk, of the ungulate use in herbaceous sites inside and near the bison fence (where both elk and bison utilize wetland). Detailed, site-specific time budgets and habitat use studies are needed to fully understand the complex resource partitioning by these two species (i.e., Schoenecker et al. 2022). We can approximate the relative role or impact of elk vs. bison in our data using ratios of dung-only elk to elk and bison UUIs. These estimates suggest that bison are likely responsible for 85 to 90% of the UUI effect on herbaceous sites where these two species overlap in the bison pasture (and just outside the fence line during periods when the fence is damaged in the "elk and some bison zone"). It is likely that heavy bison use strongly influences the herbaceous WCI, and bison are the dominant cause of degraded herbaceous wetland. We expect that even our best condition baseline herbaceous sites are, in a relative sense, degraded and heavily disturbed with reduced WCI and HP metric scores.

Phase 2 ungulate management does not include changes to the way bison are currently managed, and it is currently unclear when the park will gain control over the bison herd. The park's inability to change management of bison during Phase 2 presents a real challenge to improving the condition of herbaceous wetlands inside the bison fence because this is where most of the herbaceous wetlands on the sand sheet are located. Thus, the condition of the herbaceous wetland type, as a whole, is not likely to improve when the network analyzes Phase 2 data from 2020 to 2025. This is important for all stakeholders in UMP to understand. Reducing bison numbers on the sand sheet could create a large-scale shift in the food web and should assist with the overall goal of improved wetland conditions.

Interpretation of wetland condition indices, hand-picked and component metrics

In the following discussion we interpret Wetland Condition Indices in some detail via summaries of the relevant ecology behind patterns in their component and hand-picked metrics. While there is a lot of variation at the scale of individual species, there are some plant species that are likely useful indicators of condition within select component and HP metrics, and we include species level patterns in our interpretation as warranted. We hope that this level of detail increases the parks faculty with these tools and enhances their application in Phase 2 and 3 of the UMP.

We stress, however, that the use of component and HP metrics in isolation should be done with caution. Component metrics are in a WCI because of a multivariate response to ungulate use, which can be different than a simple bivariate pattern. Likewise, HP metrics may not capture the many multifaceted and nuanced responses of a wetland to ungulate use as their univariate nature cannot account for covariance or interactions with other metrics. A good example of this would be one HP metric placing a site in a best condition category while another places it in a worst condition class. Nevertheless, we think the following discussion will help the park understand and use baseline results.

Hand-picked metrics for herbaceous wetlands

Analysis of our baseline data indicates that the cover of iris and silverweed decreases and the conservatism of graminoid taxa increases with lower ungulate use. These changes should also reflect movement of sites into higher wetland condition. These expectations are based on environmentally adjusted versions of these metrics. Environmental adjustment is a statistical process that accounts for variation in a metric that is due to drivers other than UUI. It allows interpretation to focus on how ungulate use might drive a response. We use the vernacular phrase "all else being equal" several times in the discussion below as shorthand for the adjustment process. To be clear, many of the species within these two HP metrics are long lived perennials and are well established in sites with high ungulate use (i.e., iris absolute cover often approaches 50%). Our models suggest this is linked to ungulate use and thus might change with a change in use, but it is likely that additional management actions beyond reducing use are needed to break any stasis in the cover of species like iris or silverweed.

Iris and silverweed cover (also a WCI component metric)

Iris and silverweed cover is one of the most diagnostic and simplest responses we include in this report. It has a strong relationship with UUI and is included as a component metric in the herbaceous WCI. Iris and silverweed have a similar response to ungulate use—both are resistant to the type of disturbance created by large ungulates and readily expand in overgrazed systems (Figure 27, see also Figure 8; Eckert et al. 1973; Cuassolo et al. 2020; Otfinowski et al. 2022). Silverweed is also fairly palatable (Li et al. 2013), suggesting an additional incentive for ungulates to utilize wetlands where it is common. Using both species in a single metric captures this response more fully and likely better accommodates site level variation. It also generalizes the response better to the herbaceous wetland type we use. These two species are often labeled as increasers in overgrazed systems. We mention this to clarify how this relates to our removal of an "increaser response" described above. Iris and silverweed increase in cover with grazing but this almost always is related to a decrease in wetland condition (i.e., Jones 2005). This metric is therefore appropriately included as a decreaser HP metric and within our WCI decreaser model.



Figure 27. Near monoculture of *Iris missouriensis* (iris) in an herbaceous wetland (site 136), Great Sand Dunes National Park and Preserve, 2017. This site is the lowest condition herbaceous site based on our Wetland Condition Index in our baseline dataset. Note that condition assessment using single photos should be done with caution (see Figure 11 for a different view of this site in a drier year).
NPS / B. SCHWEIGER

To facilitate interpretation of possible change in iris and silverweed cover given management by the park of elk, and eventually bison, we also use a more familiar unadjusted or "raw" data form of the metric. An improved wetland condition from lower ungulate use, all else being equal, should decrease the absolute cover of these two species. Sites transitioning into a best category might have iris and silverweed maximum absolute cover reduced to around 10% (the baseline maximum was 67%). If sites instead remain or move into a worst condition class, absolute cover might be higher than the baseline maxima and potentially exceed 70% at the most heavily used herbaceous sites. As noted, these possible futures are extrapolated from baseline relationships with UUI and it is likely that additional management actions might be needed, including to break the long-term persistence of iris and silverweed at many of our sites.

Adjustment for iris and silverweed cover includes two environmental gradients, both with negative correlations: bare ground and litter cover. In many systems, more bare ground leads to more opportunistic taxa, like these two species, and more litter leads to less of such species (i.e., in

ROMO, Pritekel et al. 2006). We see this effect for litter on iris and silverweed cover in the herbaceous WCI but not for the bare ground variable. The pattern with bare ground may be buried in statistical minutiae and/or be unique to GRSA or other sandy substrate dominated landscapes. Bare ground on the sand sheet is dynamic, shifting rapidly as sand is blown about (Figure 28). The highly variable nature of bare ground cover at GRSA might also change the classic relationship between increased bare ground facilitating taxa like iris and silverweed or make it difficult for single point in time estimates to capture the dynamic. More work is likely needed on this issue.



Figure 28. Changes in bare ground cover across a single year at site 302 in the Little Spring Creek headwaters, Great Sand Dunes National Park and Preserve, (top) 2021 and 2022 (bottom). Given slightly different orientation of the images, the blue and red arrows point to common shrubs across the two years. NPS / K. DRIVER

Conservatism of graminoids (also a WCI component metric)

Conservatism is based on the expert opinion of the fidelity of species to specific habitats or environmental conditions that lack severe disturbance (Wilhelm and Ladd 1988; Herman et al. 1997; Matthews et al. 2015). Scores (known as "C-scores") range from 0 for invasive nonnatives to 10 for conservative species. Cover weighting scales the index by the relative cover of low to high C-scored taxa. We assume that conservative graminoids decrease with increased ungulate use. High C-score graminoids in sand sheet wetlands include *Spartina gracilis* (alkali cordgrass), *Amphiscirpus nevadensis* (Nevada bulrush), *Calamagrostis stricta* (slimstem reedgrass; Figure 29), *Catabrosa aquatica* (water whorlgrass), and *Triglochin palustris* (marsh arrowgrass).



Figure 29. High C-score graminoid *Calamagrostis stricta* (slimstem reedgrass) as part of the vegetation community in a Wetland Condition Index best condition herbaceous wetland along Deadman Creek, Great Sand Dunes National Park and Preserve, 2022. Most of the graminoid cover at this site (424) was slimstem reedgrass. NPS / B. SCHWEIGER

An improved wetland condition from lower ungulate use should, all else being equal, increase the conservatism of graminoids in UMP sites. In raw form, best sites will have more conservative species and/or more cover of these species. Scores in a typical best site might exceed 6.0 (the baseline range

is about 2 to 6), indicating a higher level of conservative graminoids in the sample. In worst sites this might fall below a score of 2.0 (suggesting fewer conservative graminoids).

The adjustment process for conservatism of graminoids includes one environmental gradient, depth to ground water, with a positive relationship or an increase in conservatism of graminoids with wetter conditions. Many conservative graminoids are also wetland obligates that respond positively to wetter conditions. Improving ground water is an active restoration consideration for the park, and controlling for this in future applications of the WCI will be important to understand the effects of ungulate management.

WCI component metrics for herbaceous wetlands

Our analysis suggests that improved condition of herbaceous wetlands will be characterized by the following changes in WCI component metrics (see Table 4). With lower ungulate use, all else being equal, we expect increased woody richness, increased total height of *Carex*, and increased wetland affinity. We also expect reduced cover of salt intolerants, reduced iris and silverweed cover (also an HP metric, see above for its interpretation) and reduced invasive species richness. We omit interpretation of the dominant graminoid component metric given its very small correlation with UUI (see Table 4). It is relevant in the WCI but primarily in the statistical support of the other component metrics in the model.

Woody species richness

Woody species are a less obvious component of herbaceous wetland sites (in contrast with woody wetland sites where they are the dominant vegetation form). Often there are only a few woody species in UMP herbaceous sites. They may exist on the margins or as small inclusions in the herbaceous vegetation. However, woody plants can still create important structure that provides shade and temperature regulation, stabilizes soils, and supports niche expansion that enhances biodiversity in woody wetlands (Keddy 1989; Anderson and Leopold 2002; Battaglia and Sharitz 2006; DeWine and Cooper 2008).

An improved wetland condition from lower ungulate use should, all else being equal, increase woody species richness. Improved woody species richness may simply mean maintaining the count of woody species in place. Or condition may respond in a complex way to the addition of only one or two woody taxa. Alternatively, condition may be sensitive to decreasing woody species richness, with accelerated loss of condition if only a few woody taxa are lost. It is more difficult to numerically define expected changes driven by the park's management of UUI with this metric as there are not a lot of woody species to theoretically add to the species pool. Only *Sarcobatus vermiculatus* (greasewood)*, Salix exigua, S. eriocephala* (Missouri River willow)*, S. bebbiana* (Bebb willow), *Populus tremuloides* (quaking aspen), *Populus angustifolia*, *Juniperus scopulorum* (Rocky Mountain juniper), *Chrysothamnus linifolius* (spearleaf rabbitbrush), and *Ericameria nauseosa* (rubber rabbitbrush) were found in herbaceous UMP sites. A more practical interpretation of this metric may be to maintain the current woody species at sites to help support good wetland condition.

Woody species richness is one of the few metrics where adjustment by environmental gradients is inconsequential (i.e., there are no non-zero values for any coefficient in Table 4). Woody species in herbaceous wetlands may be too infrequent for variation in their occurrence to be picked up by the adjustment process. Additional work may be needed to better understand this.

Cover of salt intolerant species (herbaceous)

Salt tolerant, or halophytic species, are an important component of UMP wetland vegetation. Halophytes are plants that thrive in environments with high salinity, such as sabkha saline semi-deserts (much of GRSA's sand sheet). They have physiological and morphological adaptations to survive and reproduce in conditions that would be hostile to most other plant species. Salinity levels in GRSA wetlands may be high. For example, comparisons of GRSA and ROMO wetlands of the same type (i.e., woody riparian to woody riparian) show that, on average, GRSA sites have from two to three times sodium absorption ratio (SAR) values (unpublished Rocky Mountain Network data). Salt flats, which are one wetland type included in our herbaceous wetlands, have SAR values almost 30x typical values in other UMP wetland types. Given the high salinity in these soils, we assume that higher salt tolerance (i.e., higher halophytic species cover) is a desirable aspect of wetland vegetation on the GRSA sand sheet and characterizes higher condition sites. There is some evidence for halophytes being more common in higher quality systems similar to GRSA (i.e., Yilmaz et al. 2020), but this likely needs more research for application to monitoring and assessment. There is good support in other systems (but not GRSA as far as we could resolve) for using halophytes in remediation to actively improve condition (i.e., De Lange et al. 2013; Farzi et al. 2017), which indirectly suggests an association with higher quality herbaceous wetlands.

Salt tolerance scores were derived from USDA (2024) and Smith et al. (2020), with select adjustment for GRSA specific application (David Cooper, Senior Research Scientist, Colorado State University, pers. comm. with B. Schweiger, 10/2016). Note that the computational form of this metric (sum of relative cover of salt intolerant taxa) that was included in the herbaceous WCI was salt *intolerance,* or the inverse of the salt tolerance of halophytes as described above. Essentially, the WCI model found meaningful statistical differences from the more intuitive salt tolerance metric form and included the role of salt tolerance via an intolerant metric version. This makes the interpretation of this response a bit tricky, but it still aligns with our description of the relevant ecology above. Moreover, we include a broad range of wetland types in herbaceous wetland class—not all are salt flats, and we would expect variability in this metric by these finer scale wetland types. That is, we would expect that some wetlands in best condition will have low to no halophytes just because of their underlying wetland type.

An improved herbaceous wetland condition from lower ungulate use should, all else being equal, lower the cover of salt intolerants (this is a double negative, but that is the relationship and why we interpret this metric more from a halophyte cover perspective). In raw data form, salt intolerant total relative cover may drop to a maximum of around 25% (the baseline range was 0 to 52%). If sites instead remain, or move into a worst condition class, intolerant cover might max out above 50%. We might see typical important halophytes at UMP herbaceous sites including *Muhlenbergia asperifolia* (scratch grass) and *Triglochin maritima* (seaside arrowgrass) increasing as UUI decreases and WCI

increases. Arrowgrass is also a fairly conservative species and its presence in a site would further support higher condition status.

Adjustment for salt intolerant species cover includes three environmental gradients: a positive effect of soil moisture, a negative effect of elevation, and a negative effect of growing degree days (as a proxy for air temperature). All three of these likely are related to the location of sites, with salt intolerant species cover increasing at sites with more soil moisture and sites that are cooler at higher elevations. Many plant species respond to these three factors in an intuitive way and this adjustment will be important in future applications of the WCI.

Height of sedges

Sedges (*Carex* spp.) are a typical herbaceous wetland plant with 15 species across all UMP sites. We estimate sedge height by summing the maximum height across each *Carex* sp. recorded in a site. An improved wetland condition from lower ungulate use, all else being equal, should increase the total height of sedges (Figure 30). In raw form, best sites could have total sedge height around 1.5 m (out of a range of ~ 0.10 to 1.5 m). In poorer condition sites this might fall to around 0.5 m.



Figure 30. Tall sedge stand in an herbaceous wetland near site 211, Great Sand Dunes National Park and Preserve, 2016. NPS / B. SCHWEIGER

While “more is not always more” in the natural world, increased sedge height with better condition is an intuitive response and is often used in this way in monitoring and assessment (i.e., Mollard et al. 2013; Sabo et al. 2023). In particular, Lou et al. (2016) found that sedge height was responsive to disturbance gradients in floodplain wetlands, although there was important species-level variation. Height (often described as “stubble height”) has a direct negative response to grazing (i.e., Bryant et al. 2006), and increasingly tall *Carex* likely enhances or reflects good condition, perhaps as a structural component of a site’s flora (much like woody plants can). The most common sedges in UMP data include *Carex nebrascensis, C. utriculata* (Northwest Territory sedge)*, C. simulata, C. praegracilis* (clustered field sedge)*, C. pellita* (woolly sedge) and *C. aquatilis* (water sedge). Of these, *C. simulata* and *C. pellita* are conservative taxa and thus also likely useful indicators of higher quality habitat in terms of conservatism. Most common sedges (i.e., *C. aquatilis, C. nebrascensis, C. pellita, C. praegracilis,* and *C. utriculata*) in UMP sites have a similar typical height at maturity of around 0.40 to 0.50 meters (D. Cooper, Senior Research Scientist, Colorado State University, pers. comm. with B. Schweiger, 11/2016). *Carex simulata* can be shorter (around 0.30 m), and this may introduce an unknown source of error in this metric as we do not adjust height values for their expected natural maxima. There is no clear pattern for *C. simulata* occurring in best or worst sites so we assume that this is largely not a factor in driving this metric.

Our adjustment model shows that the effect of sedge height in the WCI is influenced by elevated (i.e., wetter) ground water and decreased drought (as climatic deficit, see Appendix B). The park is actively seeking to improve hydrologic processes on the sand sheet, but there is not much that can be done about climate-driven increasing drought and related effects on water availability. Should the park be successful in raising water tables, we will need to control for changes in ground water depths in our modeling so we can be sure that any change in WCI is due to UUI and not wetter conditions.

Wetland affinity (herbaceous)

Wetland affinity measures the ability of a species because of morphological or physiological adaptations and/or reproductive strategies to achieve maturity and reproduce in wetlands. Wetland affinity is an expert opinion species level score (Tiner 2012). Note that we inverse the usual scale such that obligate taxa have a score of 5 and upland species a 0 score (as we feel this is more intuitive). Cover weighting scales the index by the relative cover of taxa with a wetland affinity score. Several of the more common sedges, including *Carex nebrascensis* and *C. utriculata,* are obligate wetland species in UMP sites. Other less common obligate wetland species include *Amphiscirpus nevadensis*, *Catabrosa aquatica*, and *Spartina gracilis*. These last three taxa are also conservative, and an increase in these might suggest an increased overall condition in terms of conservative graminoid cover (see above).

An improved wetland condition from lower ungulate use, all else being equal, should lead to increased wetland affinity in herbaceous sites. In raw form, best sites could have wetland affinity scores up to around 5, indicating a high level of obligate wetland taxa at sites (range is 0 to 5, with higher scores for “wetter” communities of species). In worst sites this might fall to a score under 4.0, with more facultative wetland or even upland taxa. The abbreviated range in metric values covering best to worst sites is likely because wetland affinity, both in herbaceous and woody sites (see

Figure 25b), varies across a relatively small numeric range across the UUI gradient, and because UMP sites are wetlands, so even degraded site scores are still on the higher side.

Adjustment for wetland affinity includes a complex set of five environmental gradients: a positive effect of ground water depth and negative effects of bare ground, litter, elevation (from the lowest site to the highest on the sand sheet) and soil moisture. Of these, three have a relatively intuitive interpretation. Wetter conditions (higher ground water) likely increases wetland obligate cover. Lower bare ground and litter cover also likely increase wetland obligate cover as wetter sites will likely have less of these "non wet" ground cover types. The elevation and soil moisture effects are a bit counterintuitive as higher elevation sites are usually wetter and higher soil moisture sites usually have higher ground water. With five non-zero coefficients in this adjustment model, the role of any single variable will depend on the others. These two variables may thus interact with the others in complex ways that will require more work to sort out.

Nonnative species richness

Nonnative, invasive species have well-established undesirable effects on ecosystem function (Byers et al. 2002; Levine et al. 2003; Fridley et al. 2007). They have been linked to reduced overall species diversity (Meiners et al. 2001), altered resource dynamics (Ehrenfeld 2003), and shifted interactions between species (Christian and Wilson 1999). They are often introduced through intentional or unintentional human action (Pysek et al. 2004; Fertig 2011), and they tend to be a focus of park management, including at GRSA. We recorded a total of 36 nonnative species across all UMP samples (see Appendix C). Using nativity designations from the Colorado Natural Heritage Program (Smith et al. 2020), the most common nonnatives were *Lepidium latifolium* (broadleaved pepperweed), *Polygonum aviculare* (prostrate knotweed), and *Cirsium arvense* (Canada thistle). These species are somewhat ubiquitous and may not be all that relevant to changes in richness (unless their broad distribution is more substantially reduced). Ten nonnatives were also more typical of upland habitat and likely occurred on the margins of our sites—these may only impact changes in nonnative richness should a site completely convert to an upland (and these species are then more able to invade a site's drier soils). Levels of ungulate use at some sites inside the bison fence may be near a level that might, if coupled with hydrologic changes, transition a site from a wetland to an upland via removal of preferred or more palatable wetland vegetation (see Figure 26). Seven nonnative species were wetland obligates or facultative wetland taxa typical of worst condition sites, including *Phragmites australis* (common reed), *Persicaria maculosa* (spotted lady's thumb), *Puccinellia distans* (weeping alkaligrass), *Polypogon monspeliensis* (annual rabbits foot grass), *Nasturtium officinale* (watercress), and *Artemisia biennis* (biennial wormwood). These taxa may be the most important species to watch moving forward into Phase 2 and 3 as the park manages UUI.

An improved wetland condition from lower ungulate use, all else being equal, should lead to lower nonnative species richness. In raw form, sites that move into a WCI best rating will likely have nonnative richness below two or three species. Worst sites might have over twice this number, with some sites invaded by up to seven nonnative species.

Interestingly, this metric did not have environmental adjustment (i.e., all coefficients were zero in the WCI adjustment process). Nonnative species are common on the GRSA sand sheet and may be less sensitive to variation in environmental gradients across UMP sites. Alternatively, we may not have the right environmental variables for these taxa or the data we do include were insufficiently precise. However, adjustment can still matter in complex statistical ways given internal relationships or interactions in the model. This is evident in the slightly improved correlation between adjusted nonnative species richness and UUI vs. the raw correlation.

Finally, given the management importance of nonnative species, it is of note that we actively attempted to develop a stand-alone HP metric focused on nativity or invasiveness. However, no relevant metric in isolation, even when adjusted for environmental gradients, performed adequately. Only when included in a multivariate way as part of a WCI do we see an interpretable nativity/invasiveness response. This may be in part because of the higher presence of nonnatives across the sand sheet in general, which reduces variance in nativity/invasiveness metrics.

Hand-picked metrics for woody wetlands

Analysis of our baseline data suggests that with lower ungulate use, we expect reduced density of browsed willows and cottonwoods (also an important component metric in the woody WCI) and increased wetland affinity. These two changes should also reflect movement of sites into improved wetland conditions (higher WCI). Our expectations are based on the environmentally adjusted versions of these metrics.

As noted above, our HP and WCI component metrics are often based on species with complex ecology with many long lived perennials. Our models suggest patterns can be linked to ungulate use but it is likely that additional actions by park resource management beyond reducing use are needed to affect change in these aspects of the park's wetlands.

Density of browsed willows and cottonwoods

Density of browsed willows and cottonwoods is the second of two (the first being cover of iris and silverweed) more diagnostic responses (Figure 31 and Figure 32) we include in this report. It has the strongest univariate correlation with UUI of any of our metrics (still not as good as the WCI, however). It is included as a component metric in the woody WCI. Importantly, we use this metric as an indicator of wetland condition (sensu Rowland and Lovelock 2024), not of ungulate browse itself, and thus it is not redundant with UUI. Browsed cottonwood and willow density is expected to be higher in lower condition wetlands. Highly browsed wetlands often have degraded conditions that include lost biodiversity, impaired physical structure, and impacted (i.e., compacted, heavily eroded, etc.) soils—all because of heavy use (Lodge et al. 1998; Baker et al. 2005; Schweiger et al. 2016; Zeigenfuss and Schoenecker 2021; Skovlin 2021).



Figure 31. Extensively browsed low condition willow stand along Sand Creek (site 212), Great Sand Dunes National Park and Preserve. The two images have near identical orientation. In 2010 (top), when we first sampled this site, it was heavily browsed but had a notably higher density of stems in comparison to 2018 (bottom). NPS / B. SCHWEIGER



Figure 32. Unbrowsed higher condition willow stand inside an exclosure along Sand Creek (site 401), Great Sand Dunes National Park and Preserve. The site had a higher density of shorter willow stems and even some recruiting cottonwood (addressing multiple component metrics in the woody WCI).
NPS / B. SCHWEIGER

This metric combines browse and density of willow and cottonwood plants (see Methods for our concept of what we mean by "plant"). Browse and willow density at UMP woody sites are both notably low relative to other systems. It is difficult to support this with fully comparable data and metrics based on the same methods. However, using identical methods (not UMPs), Schoenecker (2012) shows mean willow offtake (as a proxy of browse) in GRSA sand sheet sites was 0.21 while in ROMO it was, on average, 0.35 (and ranged as high as 0.60; Zeigenfuss et al. 2011). While different (but somewhat comparable) methods were used, 2018 willow densities from unexclosed sites in ROMO averaged 1.5 plants/m^2 (L. Zeigenfuss, unpublished data). In GRSA, the mean willow density in unexclosed sites across the baseline (which includes 2018) was 0.33 plants/m^2, or roughly 20% of what we see in ROMO.

The lower density of willow and cottonwood at UMP sites on the sand sheet may be a relatively recent phenomenon, with most willow stands degrading over the last decade or two (see Figure 31). Many areas of the sand sheet are likely marginal habitat for willow. Some decadent tall cottonwood stands remain intact on the sand sheet (Figure 33). Outside of uncommon or manipulated contexts

(like exclosures) however, willow has largely collapsed. This suggests that there may be “nowhere to go but up” and reduced UUI might be a key part of a meaningful recovery of willow on the sand sheet. Cooper et al. (2024) show that ungulate use is the likely central driver in the collapse of willow systems on the west side of Rocky Mountain National Park. However, recovery will require more than just a reduction of ungulate use; restoration of ground water is also needed, especially as climate change increases drought impacts (Wurster et al. 2003; Thoma et al. 2020). Nevertheless, we provide the same sort of UUI-specific expectations for this metric as we do others.



Figure 33. Cottonwood dominated wetland on the higher elevation eastern side of the sand sheet (site 413) along Sand Creek, Great Sand Dunes National Park and Preserve, 2021. Elevation can have an important control on wetland condition. NPS / K. ZYBKO

An improved wetland condition from lower ungulate use, all else being equal, should lead to a reduced density of browsed willow and cottonwood. Degraded willow stands also often lead to lower ungulate use as they are less attractive browse, suggesting use likely has a non-linear relationship with low condition stands (Cooper et al. 2025). In raw form, sites transitioning into a best category because of the park’s reduction in UUI will likely have a maximum density of around 0.12 browsed stems/m^2 (the range in the baseline across all sites is 0 to 0.9 browsed stems/m^2). If sites instead

move into a worst condition class, the maximum density is likely to be higher, at around 0.9 browsed stems/m^2.

Adjustment of the density of browsed willows and cottonwoods metric includes four environmental gradients, suggesting the controls on this process were complex. Higher ground water (or wetter) conditions reduced the density of browsed plants. This is an interesting pattern and we likely need more data to offer more than conjecture as an explanation. It may reflect higher production in wetter sites with plants better able to recover from browse. Higher water tables may also allow plants to better defend chemically. While the final results were somewhat inconclusive, Singer et al. (1994) found that heavily browsed willow had lower chemical defenses in more xeric growth conditions. Browsed willow and cottonwood density also increased with elevation, growing degree days, and soil moisture. All three of these may also be proxies for enhanced production that may allow plants to recover quicker.

Wetland affinity (woody)

We presented wetland affinity as a component metric in the herbaceous WCI model above and some of the following narrative is therefore abbreviated. We selected wetland affinity as an HP metric for woody systems given guidance from GRSA and an intuitive relationship with woody wetland condition. It has an acceptable statistical relationship with UUI (see Table 6 and Table 7) for it to be interpretable as the park changes UUI—but not strong enough for it to appear in the woody WCI.

The basis for and interpretation of wetland affinity in woody wetlands is generally the same as in herbaceous sites. Remember that sites with higher wetland affinity include more wetland obligates or facultative wetland species. This likely reflects a higher (wetter) and/or, more importantly, a stable and wetter water table, which we assume reflects a better condition. Note that important wetland obligate taxa in woody systems do not necessarily need to be woody themselves. Cottonwood and willow are the most important wetland facultative taxa in woody systems, although, given their ubiquitousness on the sand sheet, they occur in both best and worst condition sites. Likewise, several herbaceous taxa, including *Equisetum laevigatum* (smooth horsetail), *Carex praegracilis,* and *Juncus arcticus*, are important wetland facultative taxa, although these taxa do not have clear patterns across best and worst condition sites. The rush and horsetail are often associated with poorer condition sites (or are so ubiquitous that they have no clear association with a condition state).

An improved wetland condition from lower ungulate use, all else being equal, should lead to increased wetland affinity in woody sites. In raw form, best sites could have wetland affinity scores up to around 5, indicating a high level of obligate wetland taxa at sites. This is out of a range of 0 to 5, with higher scores for "wetter" communities of species. In worst sites this might fall to a score under 4.0, with more facultative wetland or even upland taxa. The abbreviated range in metric values from best to worst sites is likely because wetland affinity varies across a relatively small numeric range across the UUI gradient, and because UMP sites are wetlands with even degraded scores on the high side. Adjustment for wetland affinity in woody sites included a negative effect of litter cover, with higher affinity where there is less litter. Wetter sites tend to have lower litter cover as saturated

soils or standing water likely replaces litter cover or facilitates quicker decomposition and breakdown of litter (Gingerich et al. 2014; Zhou et al. 2023).

WCI component metrics for woody wetlands

An improved woody wetland condition will likely be characterized by the following changes in WCI component metrics (see Table 5). With lower ungulate use, we expect a decrease in browsed density of willow and cottonwood (also an HP metric, see above for its interpretation), a decreased percentage of rabbitbrush in a 0.5 to 1 m height class, a decreased salt intolerant species cover, and a decreased density of sandbar willow less than 1.0 m in height. We would expect increased cover of willows and cottonwood (as a ratio to all woody cover). We omit interpretation of a species dominance component metric given its very small correlation with UUI. It is relevant in the WCI but primarily in support of the other component metrics.

Percentage of rabbitbrush, 0.5 to 1.0 m tall

Rabbitbrush (*Ericameria*) are woody shrubs that are characteristic dominants of much of the GRSA sand sheet upland habitat. They occur on the edges of wetlands in transitional areas or as wetlands dry out over time (Kray et al. 2012).

An improved wetland condition from lower ungulate use should, all else being equal, decrease the percentage of rabbitbrush in the 50–100 cm height class (relative to other height classes). Rabbitbrush is generally considered to be a browsing resilient species (Tirmenstein 1999) and we therefore expect that the positive relationship we see in our baseline data with ungulate use (more rabbitbrush with higher ungulate use) is indirect. While speculative, an increase in willow and cottonwood cover (see "Ratio of willow and cottonwood cover to all woody cover" below) coincident with a decline in UUI will likely crowd out shorter more recently established rabbitbrush that may have gotten a foothold under conditions of high browsing and declining water tables.

One environmental gradient, litter cover, was important in the adjustment of this component metric. The percentage of rabbitbrush between 0.5 and 1.0 m increased with increased litter cover. It is unclear if more rabbitbrush creates the higher litter or is because of the elevated litter (i.e., via a mulching effect). Nevertheless, as with other metrics, adjustment increased the strength of the positive correlation between the metric and UUI. Controlling for these variables in future applications will be important.

Cover of salt intolerant species (woody)

Cover of salt intolerant species is a similar component metric in the herbaceous model as described above for woody sites and some of the following narrative is therefore abbreviated. Salt tolerant, or halophytic species, are plants that thrive in environments with high salinity, such as many UMP sites (even woody ones). We assume that higher salt tolerance (as higher halophytic species cover) is a generally desirable aspect of woody wetland vegetation on the sand sheet. The component metric form in the herbaceous and woody models is for salt intolerance (the inverse of the response of halophytes to salt levels). Our interpretation of the ecology behind these metrics is from the more intuitive halophyte perspective.

An improved woody wetland condition from lower ungulate use should, all else being equal, lower the cover of salt intolerants. In raw data form, mean total absolute salt intolerant cover may drop to around 1% (the baseline range was 0 to 26%), with a decrease in ungulate use. If sites instead remain, or move into a worst condition class, salt intolerant cover might be higher at around an average of 5%, with lower halophyte cover. Most halophytes in woody sites are understory herbaceous species, although cottonwood displays moderate tolerance for higher salinity levels (Carpenter 1970; Chen and Polle 2010). Important halophyte species in woody sites include some of the same species we see at herbaceous sites, like scratch grass. Other halophyte species in woody sites include *Pascopyrum smithii* (western wheatgrass) and *Chenopodium rubrum* (red goosefoot). These species might increase in cover as UUI is decreased and WCI increases in woody sites.

Adjustment for cover of salt intolerant species includes three environmental gradients: positive effects of sodium absorption ratio (SAR) and soil moisture, and a negative effect of growing degree days (GDD, as a proxy for air temperature). The strong and positive role of SAR is intuitive for a salt tolerance response. The strength and direction of the adjustment for SAR (coefficient of 7.3) is likely why the correlation with UUI in raw form changes from a small and slightly negative value to a moderate/strong positive correlation with UUI when adjusted (raw: −0.01, adjusted: 0.57, see Table 5). The negative relationship with GDD and positive for soil moisture may reflect the preference for the salt intolerant taxa at woody sites to prefer cooler and wetter conditions and/or that salt flats are less common at higher elevations.

Ratio of willow and cottonwood cover to all woody cover

Willow and cottonwood are important components of sand sheet woody wetlands. They define the physical structure of sites and thus influence many other species. They are critical forage for elk (to a lesser degree—but see Rose and Cooper 2016) and bison and are well supported indicators of wetland condition. The browsed density HP and WCI component metric integrates a measure of the condition of willow and cottonwood plants by integrating browse with the density of these species in a site. The importance of these species is further reinforced via the inclusion of this component metric that estimates the ratio of willow and cottonwood cover to all woody cover in a site.

An improved woody wetland condition from lower ungulate use should, all else being equal, increase the ratio of cover of willow and cottonwood to all woody cover. In raw data form, the ratio of cover of willow and cottonwood to all wood might increase to around 44% in best condition sites. Should the park not decrease UUI, typical baseline ratios in worst sites of around 31% might be more typical (the range across all sites was 24 to 45%). Reduction of ungulate use should allow willow and cottonwood plants to grow to heights beyond the reach of elk browsing. This might then allow recruitment of willow and cottonwood to the tree canopy, increasing overall canopy size and cover. Decreased elk use in ROMO led to increases in willow cover (Gage et al. 2023). Zeigenfuss and Schoenecker (2021) found that removal of all ungulate herbivory led to taller and denser cottonwood suckers in GRSA, and higher density of cottonwood would contribute to higher cover of Salicaceae. Beschta and Ripple (2015) observed increased cottonwood recruitment when elk densities declined as long as an area did not have high concentration of bison use in Yellowstone National Park.

Adjustment for the ratio of cover of willow and cottonwood to all woody cover includes two environmental gradients, both with negative effects: sodium absorption ratio (SAR) and litter cover. Higher litter cover might reflect reduced bare substrates needed for cottonwood recruitment (Auble and Scott 1998; Cooper et al. 1999). Tiebel et al. (2023) show lower seedling germination of *Salix* with more litter cover (although this study used a species, pussy willow, not found at GRSA, and was in a controlled mesocosm). The SAR response is less interpretable, but it may be that most willow species and cottonwood in our samples were more salt intolerant than tolerant.

Density of sandbar willow, 0.5 to 1.0 m tall

We continue to see the importance of willow in UMP woody wetlands with this last component metric in the woody WCI: the density of *Salix exigua* between 0.5 to 1.0 m tall. Sandbar willow is the most common woody plant overall in our woody sites, accounting for 76% of all records. This suggests much of the response we see in other willow- and cottonwood-focused metrics (see above) is embedded at least in part in the patterns and relationships of this species.

An improved woody wetland condition from lower ungulate use should, all else being equal, increase the density of sandbar willow, 0.5 to 1.0 m tall. In raw data form, in best condition sites this might increase to around 0.41 plants/m^2. Should the park not decrease UUI, typical densities might be around 0.36 plants/m^2 (these densities also bound the range of this metric in our baseline data). Currently, the highest densities of sandbar willow are in the <50 cm tall size class. A reduction in ungulate use would be expected to allow these "browse-suppressed" willows to increase in height, and under low enough ungulate use, to move into the taller height classes (>1 m). Decreases in elk browsing in Yellowstone National Park led to development of thickets of sandbar willow in areas where the species either had not been found during periods when elk densities were high or where heavy browsing kept sandbar willow plants at a height of less than 1 m (Painter and Tercek 2020). These authors point out that as sandbar willows grow tall, they spread through root sprout. This likely would also account for increased density of sandbar willow in shorter size classes as existing stems are released from their suppression by browsing and begin to sprout new stems nearby. A caution, however: Painter and Tercek (2020) observed a horizontally suppressed condition in areas of the greatest bison concentrations, where willows had escaped browsing vertically but were constricted horizontally by bison browsing and horning (often destructive rubbing of horns on woody vegetation).

Adjustment for the density of sandbar willow metric includes two environmental gradients: a positive effect of sodium absorption ratio and a negative effect of productivity. Interestingly, this is the only component metric that plays an important role in a WCI where adjustment reduces the correlation with UUI (from 0.33 in raw form to 0.18 in adjusted form see Table 5). This may be because of the weak role of UUI in the adjustment model—no other important metric in either WCI had a lower coefficient value for UUI (relative to any gradient, see Table 5). While we do not use raw versions of metrics to assess status and trend, it may mean that future analyses need not worry so much about how the included gradients influence this response.

Management recommendations

At the request of GRSA resource management, we provide several recommendations for ongoing and possible future ungulate-related actions as the park transitions into Phase 2 and 3 of the UMP. We stress that the park is the final decision-maker on these matters. We recommend that decisions made by the park be adaptive, since management actions other than changing ungulate use may be needed to affect change.

Analyzing for and assessing success

We recommend GRSA resource management staff, working with the Rocky Mountain Network, use UUIs (Ungulate Use Indices), WCIs (Wetland Condition Indices) and HP (hand-picked) metrics to characterize future ungulate use and wetland condition. Changes in these metrics relative to the baselines presented in this report provide a quantitative assessment that may be linked to the park's management actions.

The simplest and most integrative future test of an improved wetland condition will be to look for changes in WCI scores relative to the baseline. WCI models are designed to distill the complex ecology within condition estimates down to a single value—the park can focus on WCI, much like one does when reading the morning paper and checking out the Dow Jones Industrial Index. We further simplify WCI interpretation by classifying WCI scores into the three park-supported condition categories (turning continuous WCI scores into a categorical response)—this often is described as an assessment "green/yellow/red stop light."

If ungulate use (as estimated by UUI) is reduced in the future, and other appropriate actions are taken as needed, WCI scores should increase "back up the WCI curve," or from a red/worst condition class to an improved yellow/intermediate or green/best condition (see Figure 17 and Figure 18). For example, with reduced UUI, more herbaceous sites than the baseline 22% should be in a best class and/or the mean herbaceous WCI score should increase above its baseline of 5.24. The percentage of woody sites in the best class should increase above 18% and/or the mean should be higher than 5.39. With a full resample, we should be able to detect a minimum change in a mean WCI of less than 2% for herbaceous sites and around 3.5% for woody. These minimum detectable changes are at the population scale and apply to means across all sites.

To develop future WCI, UUI, and HP metrics, we will need to resample field data (vegetation and dung/collar/camera UUI) and the 10 environmental gradients. Baseline work allows targeting of future efforts to these core components. We then recalculate and adjust the vegetation metrics, isolate each HP metric and develop new WCI values. The network has code that integrates UUI, the gradients, and the environmentally adjusted component metrics and outputs new WCI results. We then test for a change in these responses. We can do this with a single year of Phase 2 sample events, but we will not approach the minimum detectable difference our power models suggested until we obtain around 30 woody sites and 50 herbaceous events (probably in 2027 or 2028). The statistical model type to do these comparisons will need to be determined but we intend it to be as simple as possible to allow it to be easily interpretable.

In the following sections we highlight some key considerations for how the park might maximize the chance that management actions, especially to reduce ungulate use, could lead to improvements in wetland condition.

Where should the park target ungulate management actions?

We recognize that unavoidable legal and operational constraints exist for where ungulate management can occur. However, the closer it occurs to UMP wetland sites, the better our modeling can assess its effects on wetland condition. This also reduces the likelihood of other factors being the causes of any change in wetland condition. It is the best way to connect the two major links in the UMP causal chain (UUI response to park management actions followed by wetland condition response to changed UUI). There may be some diffuse effect across the range from managing elk many kilometers from wetland sample sites, but this separation introduces many unknowns.

Coordinating on both the location and outcomes of ungulate management action will improve our modeling. To date, elk hazing/culling has occurred across the sand sheet (2020 and 2021 actions are shown in Figure 34). These have been undertaken in a somewhat spatially inconsistent way with respect to the monitoring sites where data are collected on the effects of these actions. Some park actions are coincident with UMP sample sites while others are not. There is a general lack of management action inside the bison pasture near important wetland sites along Big and Little Spring Creeks. Management of elk (and indirectly bison) does occur inside the bison pasture in the form of Zapata Partners elk hunts; however, spatially explicit data on the timing and outcome of these hunts is not available for our modeling.

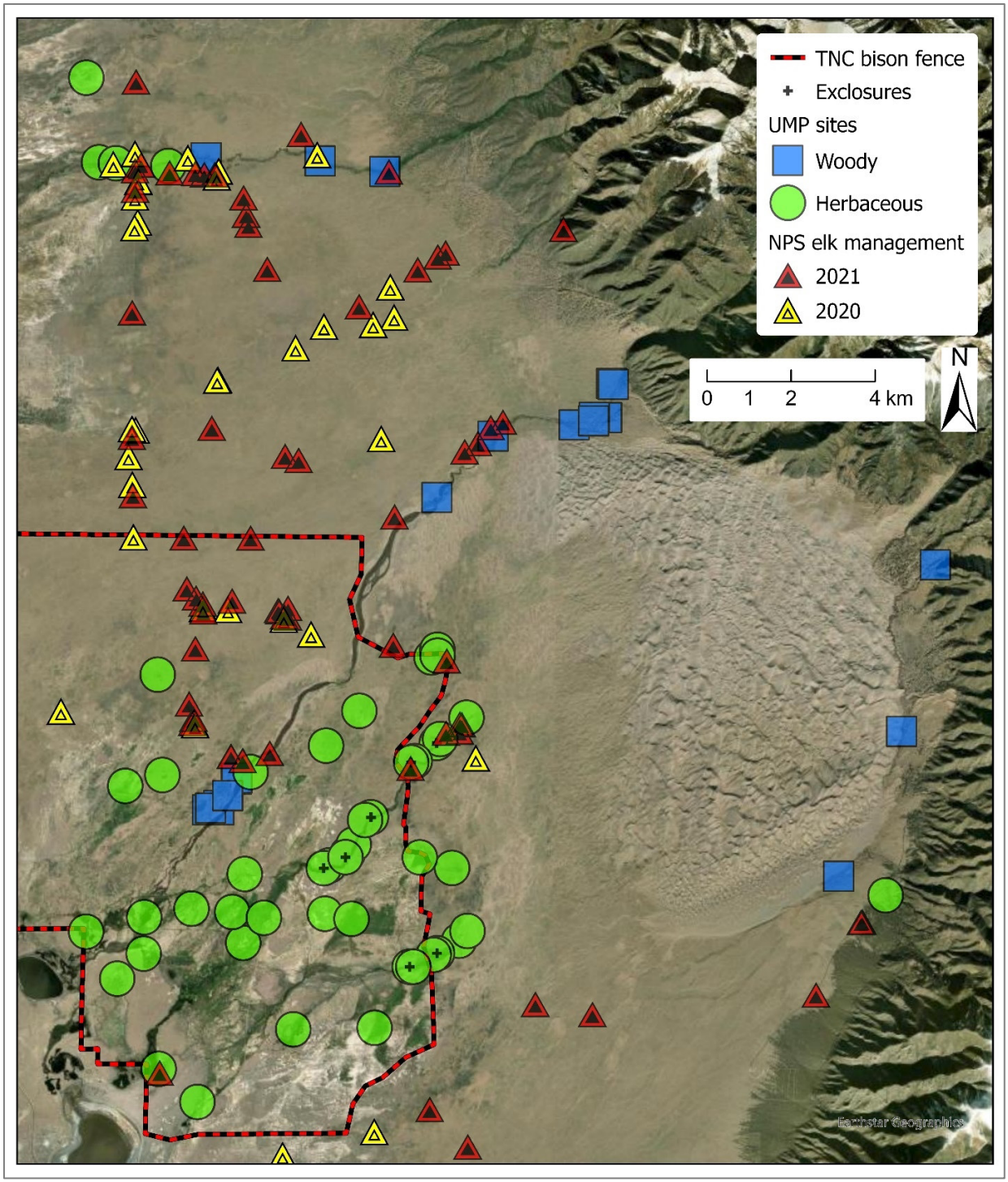


Figure 34. Ungulate Management Plan (UMP) sample sites and the location of park elk management actions, such hazing and culling, in 2020 and 2021, Great Sand Dunes National Park and Preserve. NPS

It is unclear what a minimum threshold of spatial overlap between actions and our wetland sites might be. But if it is possible for more of this to be near or at UMP sites, this seems useful. It will reduce the likelihood of other factors being the causes of any change in wetland condition. We

realize that actions will be done elsewhere because of various logistical constraints but if we can more cleanly document their effect at UMP sites it will be easier to show the effects at non-monitored sites.

Well-defined areas of concentrated best condition UMP sites could be prioritized for protection actions to prevent degradation (see Figure 20 and Figure 22). For herbaceous sites, these tend to be just outside the bison fence and on lower Deadman Creek. Little Spring Creek headwaters, Elk Springs and Indian Springs also seem higher quality. Woody best sites are concentrated along upper Sand Creek and between the main dune field and the mountain front (near park headquarters). This approach is conceptually similar to possible future exclosures the park might construct as further discussed below. Ideally, ease of access will not take priority over choosing high value wetlands for exclosures (because they retain high condition or because they are degraded and at risk).

Bison are the dominant ungulate stressor on wetlands inside and near the fence. Until the park can control bison use, influence over wetland condition inside the fence will be more uncertain. Elk and bison readily habituate to human activity and effective hazing will require a lot of effort and variety. Elk may learn to avoid hazing and culling outside the fence by spending more time inside the bison fence, increasing use on these already heavily used wetlands. Zeigenfuss and Schoenecker (2021) found that elk in GRSA consumed cottonwood at a much higher rate than did bison, and Schoenecker et al. (2015) observed that bison avoided willow and cottonwood areas (i.e., our woody wetland type) in most seasons. As the park begins to actively manage bison, there may be important implications for elk habitat use that will require close monitoring and fast action as bison use decreases. Elk habitat use may be "released" with the removal of the strong competition from bison. Park resource management staff should be ready for this. This will likely be one of the more interesting challenges during Phase 3 of the UMP.

Exclosures

One of the more surprising patterns we found in the baseline data was a lack of a spatially explicit exclosure effect. This is an interesting contrast to work in ROMO, where exclosure effects on responses like willow stem height are often dramatic and consistent across most exclosures. They were also notable at ROMO through time, with taller willow inside exclosures after only a few years of no elk or moose browse (Cooper et al. 2025). With UMP sites at GRSA, there were no statistically significant or, we feel, ecologically meaningful differences in responses inside vs. outside exclosures. This includes each WCI, all component metrics, and all HP metrics in this report. Only UUI in woody sites had a statistical difference in our tests, but this is due to ungulate use in sites spatially far removed from exclosures when compared to sites just adjacent to exclosures (see box plots for the woody UUI in Appendix E). This difference is not related to an exclosure effect, but rather it is driven by sites along the mountain front having little to no ungulate use at all. These exclosure results are for the baseline sample as a whole. There are select examples of individual exclosures having notable differences in responses (e.g., willow and cottonwood cover or litter biomass; Figure 35) when compared to paired sampled areas just outside the exclosure; however, these may be anecdotal or site specific.



Figure 35. Fence line in an herbaceous wetland exclosure along Big Spring Creek, Great Sand Dunes National Park and Preserve, 2018. The left side of the image is inside the exclosure. This is a case specific example showing more litter inside the exclosure and evidence of ungulate use outside the exclosure; however, in general there is not a difference in most measures across exclosures.
NPS / B. SCHWEIGER

Though we did not find an exclosure effect during 2016–2019, some differences were immediately apparent when the exclosures were first constructed. Original work with the exclosures by GRSA and

USGS, soon after their construction, found that removing ungulates did result in reduced herbaceous production and herbaceous nitrogen yield, taller and denser cottonwood suckers, and taller willows with larger canopies (Schoenecker 2012; Zeigenfuss and Schoenecker 2021; Schoenecker et al. 2022). We do not measure site level production and our methods for woody plants differ from this earlier work. This work was conducted within four years of exclosure construction, whereas the UMP exclosure data spans a period of 11–15 years after ungulate removal.

In general, these exclosures are too small and may create not so much a "use free zone" but rather some complex fence effect with no real interior where ecological processes could play out in some interpretable way (but without ungulate use effects). A good argument can be made that fully excluding use is not the natural state. These systems evolved with ungulates and in many ways depend on them. Perhaps their most important contribution is to inform the design of the next iteration of exclosures the park is planning. These should be much larger (several dozen acres would be ideal—see ROMO—Gage et al. 2023), and the fences would need to be well-maintained to prevent ungulate trespass. The park has initiated planning for a new design like this and the network assisted with recommendations for their locations.

When should the park target management actions?

Time of day considerations

Zeigenfuss et al. (2024) show with camera traps that the primary use of wetland sites by both elk and bison was during the day. However, relative nocturnal use was greater for elk than bison especially during the summer months. Differences across woody or herbaceous types in day vs. night use were minor. Elk are often described as crepuscular and bison diurnal (Foca and Boyce 2022). This may be why more elk use in our camera dataset is classified as nocturnal, as we do not differentiate nighttime use by the hour, and early dawn and late dusk use are treated as nocturnal. While we recognize that the timing of park management actions, such as hazing, is controlled by many factors, park resource management may want to consider extending timing to include early morning and early evening hours. Park managers should be cautious when implementing ungulate management strategies developed only from a diurnal perspective (Beyer and Haufler 1994).

Seasonal considerations

Zeigenfuss et al. (2024) also present seasonal patterns in bison and elk use based on telemetry data. Bison use patterns across season inside the park were fairly consistent, with the productive herbaceous wetlands on and between Big and Little Spring Creeks in the central portion of the pasture having the highest use, especially in spring and summer. Use outside the park varied with season, shifting to the west onto the Baca National Wildlife Refuge, where the Fish and Wildlife Service (FWS) is responsible for ungulate management in winter. Also, the far northwest corner (again outside the park) was notably lower in bison use in summer versus other seasons. Bison movements are, of course, also influenced by seasonal ranching operations (i.e., moving animals for round up, stock tanks, irrigation activities). Elk use inside the park in summer and fall was highest in woody wetlands around Sand Creek in the bison pasture. During spring, elk used herbaceous wetlands most heavily near Dollar Lake in the southwest corner of the bison pasture and in the southeast corner of the bison pasture both inside and outside the fence. Elk use of the area north of

the bison pasture up to and including Deadman Creek was highest in winter (Figure 36). Similar to bison, elk use also shifted towards the Baca National Wildlife Refuge in the winter. In general, seasonal patterns in ungulate use of habitat are well described for many systems, with habitat productivity the most typical driver (Seigle-Ferrand et al. 2021).



Figure 36. Large elk herd on an herbaceous wetland (site 204) in early winter at Great Sand Dunes National Park and Preserve. NPS / B. SCHWEIGER

We recognize that the seasonal timing of park management actions, such as hazing, is controlled by many factors. However, park resource management might want to consider targeting actions to the elk or bison specific seasonal patterns described above. In general, the most important time to focus actions is likely during the growing season (late spring through early fall) when plants are trying to establish, grow, and reproduce. Specifically, the park could target elk actions at UMP sites in the spring to the southeast and southwest areas of the bison pasture and in the summer to the Sand Creek area. Objectives in the UMP EIS also include reducing the wintering elk population inside the park, and this might require management activity outside the growing season focused on the Deadman Creek area.

In general, the timing of actions both on a daily and seasonal basis will need to be an adaptive decision made by the park. Because both elk and bison can use areas seasonally outside the park proper, actions should be closely coordinated with the FWS on the Baca National Wildlife Refuge.

Annual variation

Temporal patterns may transcend daily or seasonal dynamics as discussed above and can vary across longer time steps, such as years. However, most UMP responses were stable across the years within the four-year baseline period, suggesting there may be fewer management considerations in terms of scheduling actions across years. This is, of course, dependent on the duration and years included in the baseline period.

A lack of an annual effect (differences driven by year of the sample) in most UMP data is important as it allows us to use all years of the baseline data as a single sample. Only UUI and WCI in herbaceous sites varied across baseline years (see herbaceous UUI and WCI box plots in relation to "year" in Appendix E). When we perform comparisons of Phase 2 and 3 with the baseline, we likely need to include a year term in the models of these responses. Note that we have yet to test for a trend across years in any UMP data. When we have Phase 2 and Phase 3 data, we can test for trend using mixed model quantile regressions (Schweiger et al. 2023).

Preliminary results: park management of ungulates

We do not include any final results in this report from GRSA resource staff's management of elk, which began in 2020 and has continued each year since. We recognize that results on the success of ungulate management in improving wetland condition are very important. We will work to produce interim products (visualizers, briefs, and other summaries; Figure 37) that present timely data showing the possible effects of park ungulate management. Initially these will focus on ungulate use, and eventually they will also include wetland condition response.

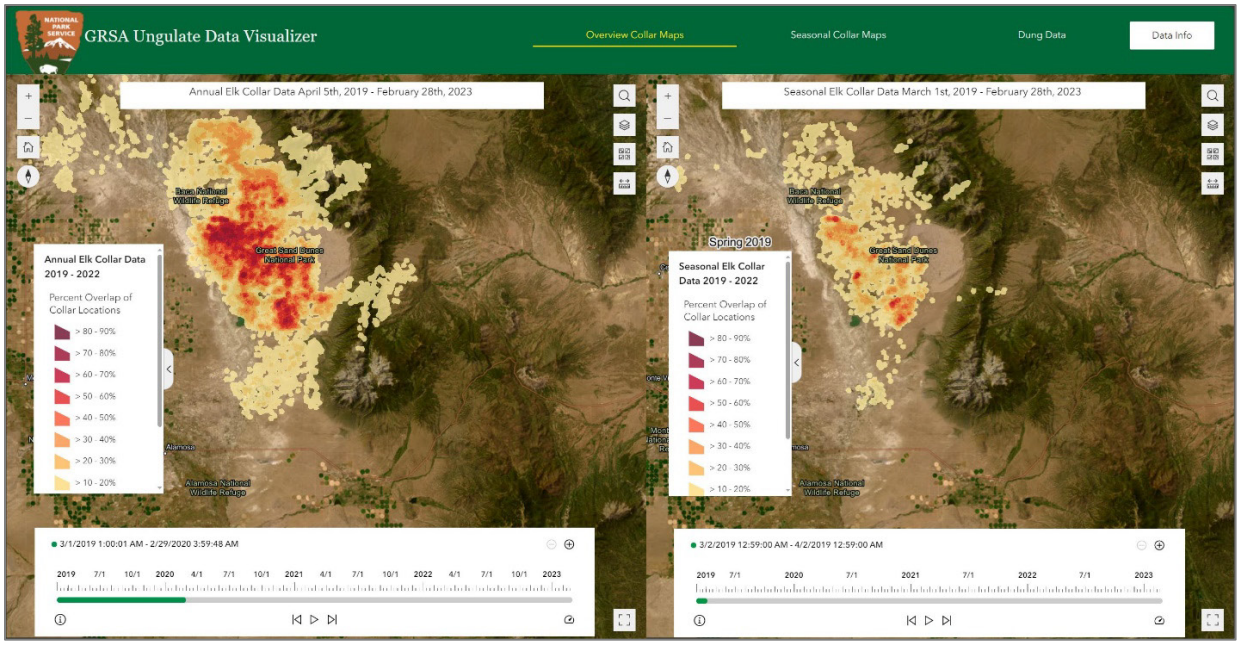


Figure 37. Example screen capture from a draft web-based visualizer (Great Sand Dunes National Park and Preserve data visualizer) showing winter and annual elk spatial patterns at GRSA from 2023 collar data. As of publication of this report, the data visualizer was not yet a public facing tool. NPS

In preliminary analyses of post-hazing collar data in comparison to 2019 (when there was no hazing or culling) we do see some shifts in elk distributions (L. Zeigenfuss, unpublished data). Areas of more intense elk use shifted north away from the bison pasture towards Deadman Creek. Across all of 2020, there were fewer areas of high elk use relative to 2019. Mean annual elk use was lower by 2022–2023, and the drop was greater in areas outside the bison fence.

Interesting patterns across seasons were also seen. In particular, when data are examined by growing season (perhaps most important for possible wetland condition impacts) instead of at the annual scale, there were still areas of concentrated high elk use, even after three years of hazing activities. These shifts could be due to the park's hazing and culling but we cannot rule out other drivers. The park's actions were very unlikely to have influenced bison use, but we don't have any current collar data to confirm this. Finally, preliminary analyses of 2021–2022 dung and vegetation data are inconclusive as to whether park elk management improved wetland condition at our sites. More careful and complete analyses of the full Phase 2 dataset will be needed to ascertain this in future UMP reports.

Summary

This report develops several indices that estimate ungulate use (UUI) at both herbaceous and woody wetlands. We modeled how wetland condition, through a wetland condition index (WCI), responds to this ungulate use, controlling for environmental covariates. With park input, we hand-picked a small set of individual metrics (HP metrics) that may have direct management utility. For each of these, we estimated baseline values, classified into park-derived condition classes. These baseline condition values provide a point of comparison for the park to assess the effectiveness of management actions into the future. These results are well-suited to meet the objectives of the UMP, and as the park contemplates ungulate management (Figure 38), we hope this report provides useful support.



Figure 38. Park resource staff examine a heavily used willow on the sand sheet at Great Sand Dunes National Park and Preserve, 2016. Will the park's management of ungulates reduce heavy browse like this and return wetlands to a better condition? NPS / B. SCHWEIGER

Literature Cited

Ackerfield, J. 2015. Flora of Colorado. Botanical Research Institute of Texas (BRIT) Press, Fort Worth, Texas.

Anderson, K. L., and D. J. Leopold. 2002. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York State. Journal of the Torrey Botanical Society 129:238–250.

Auble, G. T., and M. L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. Wetlands 18:546–556.

Baker, B. W., H. C. Ducharme, D. C. Mitchell, T. R. Stanley, and H. R. Peinetti. 2005. Interaction of beaver and elk herbivory reduces standing crop of willow. Ecological Applications 15(1):110–118.

Barbour, M. T., W. F. Swietlik, S. K. Jackson, D. L. Courtemanch, S. P. Davies, and C. O. Yoder. 2000. Measuring the attainment of biological integrity in the USA: A critical element of ecological integrity. Hydrobiologia 422:453–464.

Battaglia, L. L., and R. R. Sharitz. 2006. Responses of floodplain forest species to spatially condensed gradients: a test of the flood–shade tolerance tradeoff hypothesis. Oecologia 147:108–118.

Bennetts, R. E., J. E. Gross, K. Cahill, C. McIntyre, B. B. Bingham, A. Hubbard, L. Cameron, and S. L. Carter. 2007. Linking monitoring to management and planning: Assessment points as a generalized approach. The George Wright Forum 24:59–77.

Beschta, R. L., and W. J. Ripple. 2015. Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone, USA. Ecohydrology 8(1):58–66.

Beyer Jr, E., and J. B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. The Journal of Wildlife Management 58:178–180.

Blocksom, K. A. 2003. A performance comparison of metric scoring methods for a multimetric index for mid-Atlantic highlands streams. Environmental Management 31:670–682.

Bryant, L., W. Burkhardt, T. Burton, W. Clary, R. Henderson, D. Nelson, and R. Wiley. 2006. Using stubble height to monitor riparian vegetation. Rangelands, 28(1):23–28.

Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. Conservation Biology 16:630–640.

Cairns, J. 1977. Quantification of biological integrity. Pp. 171–187 in *The Integrity of Water*, R. K. Ballentine and L.J. Guarraia, eds. U.S. Environmental Protection Agency, Office of Water and Hazardous Materials, Washington, D.C.

Carpenter, E. D. 1970. Salt tolerance of ornamental plants. American Nurseryman 131(2):12–71.

Cary, M. 1911. A biological survey of Colorado. N. Am. Fauna 33:1–256, https://doi.org/10.3996/nafa.33.0001

Chen, S., and A. Polle. 2010. Salinity tolerance of Populus. Plant Biology 12(2):317–333.

Chesson, P. 2000. General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58(3):211–237.

Christian, J. M., and S. D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. Ecology 80:2397–2407.

Colorado Department of Public Health and Environment (CDPHE). 2012. Integrated water quality monitoring and assessment report: State of Colorado. Section 303(d) and Section 305(b) 2012 update to the 2010 305(b) report. Colorado Department of Public Health and Environment, Water Quality Control Division, Denver, Colorado.

Colorado Division of Wildlife. 2010. Sand Dunes elk herd. https://static.huntscore.com/data/co/docs/management/E11_DAUplan_SandDunesElkHerd.pdf

Colorado Natural Heritage Program (CNHP). 2021. Landscape disturbance index layer for Colorado. Raster digital data set. Colorado State University, Colorado Natural Heritage Program, Fort Collins, Colorado.

Colorado Parks and Wildlife (CPW). 2005–2020. Elk hunting statistics. Data online at: https://cpw.state.co.us/thingstodo/Pages/Statistics-Elk.aspx (accessed October 5, 2020).

Cooper, D. J., D. M. Merritt, D. C. Andersen, and R. A. Chimner. 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management 15(5):419–440.

Cooper, D. J, E. W. Schweiger, J. R. Shaw, C. Westbrook, K. Kaczynski, S. Esser, K. Nydick, H. Abouelezz, I. de Silva, and R. Chimner. 2025 (*accepted pending revisions*). Riparian ecosystem collapse in Rocky Mountain National Park. Conservation Biology.

Croke, B. F., F. Andrews, A. J. Jakeman, S. Cuddy, and A. Luddy. 2005. Redesign of the IHACRES rainfall-runoff model. Pp. 21–23 In 29th Hydrology and Water Resources Symposium, February 2005, Water Capital, Engineers Australia, Canberra.

Cuassolo, F., V. Díaz Villanueva, and B. Modenutti. 2020. Litter decomposition of the invasive *Potentilla anserina* in an invaded and non-invaded freshwater environment of North Patagonia. Biological Invasions 22(3):1055–1065.

Daubenmire, R. 1968. Soil moisture in relation to vegetation distribution in the mountains of Northern Idaho. Ecology 49:431–438.

De Lange, H. J., M. P. C. P. Paulissen, and P. A. Slim. 2013. 'Halophyte filters': the potential of constructed wetlands for application in saline aquaculture. International Journal of Phytoremediation 15(4):352–364.

De'ath, G. 1999. Extended dissimilarity: a method of robust estimation of ecological distances from high beta diversity data. Plant Ecology 144:191–199.

Dee, L. E., P. J. Ferraro, C. N. Severen, K. A. Kimmel, E. T. Borer, J. E. Byrnes, A. T. Clark, Y. Hautier, A. Hector, X. Raynaud, and P. B. Reich. 2023. Clarifying the effect of biodiversity on productivity in natural ecosystems with longitudinal data and methods for causal inference. Nature Communications 14:2607.

DeWine, J. M., and D. J. Cooper. 2008. Canopy shade and the successional replacement of tamarisk by native box elder. Journal of Applied Ecology 45:505–514.

Dobrowski, S. Z. 2011. A climatic basis for microrefugia: the influence of terrain on climate. Global Change Biology 17:1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x

Eckert, R. E. Jr., A. D. Bruner, G. J. Klomp, and F. P. Peterson. 1973. Control of Rocky Mountain iris and vegetative response on mountain meadows. J. Range Manage. 26:352–355.

Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6:503–523.

Ervin, G. N., B. D. Herman, J. T. Bried, and D. C. Holly. 2006. Evaluating non-native species and wetland indicator status as components of wetlands floristic assessment. Wetlands 26(4):1114–1129.

Faber-Langendoen, D., J. Lemly, W. Nichols, J. Rocchio, K. Walz, and R. Smyth. 2019. Development and evaluation of NatureServe's multi-metric ecological integrity assessment method for wetland ecosystems. Ecological Indicators 104:764–775.

Farzi, A., S. M. Borghei, and M. Vossoughi. 2017. The use of halophytic plants for salt phytoremediation in constructed wetlands. Int. J. Phytoremediation 19:643–650. https://doi.org/10.1080/15226514.2016.1278423

Fertig, W. 2011. Determining the nativity of plant species. Newsletter of the Utah Native Plant Society. https://www.unps.org/segolily/Sego2011SepOct.pdf

Foca, J. M., and M. S. Boyce. 2022. Bison and elk spatiotemporal interactions in Elk Island National Park. Frontiers in Conservation Science 3:937203.

Frank, D. A., R. L. Wallen, and P. J. White. 2016. Ungulate control of grassland production: grazing intensity and ungulate species composition in Yellowstone Park. Ecosphere 7(11):p.e01603.

Fridley, J. D., J. J. Stachowicz, S. Naeem, D. F. Sax, E. W. Seabloom, M. D. Smith, T. J. Stohlgren, D. Tilman, and B. Von Holle. 2007. The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17.

Gage, E. A., D. J. Cooper, B. Bultema, C. McKernan, and R. Lichvar. 2016. Developing a field-tested wetland indicator rating for blue spruce (*Picea pungens*) in the Southern Rocky Mountains. Wetlands 36:111–120.

Gage, E. A., L. C. Zeigenfuss, H. G. Abouelezz, A. J. Konkowski, D. J. Cooper, and T. L. Johnson. 2023. Vegetation response to Rocky Mountain National Park's elk and vegetation management plan: Analysis of 2008–2018 data. Natural Resource Report NPS/ROMO/NRR—2023/2537. National Park Service, Fort Collins, Colorado. https://doi.org/10.36967/2299264

Gingerich, R. T., G. Merovich, and J. T. Anderson. 2014. Influence of environmental parameters on litter decomposition in wetlands in West Virginia, USA. Journal of Freshwater Ecology 29(4):535–549.

Grace, J. B. 2024. An integrative paradigm for building causal knowledge. Ecological Monographs. https://doi.org/10.1002/ecm.1628

Grace, J. B., T. M. Anderson, E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, Y. Hautier, H. Hillebrand, E. M. Lind, M. Pärtel, and J. D. Bakker. 2016. Integrative modelling reveals mechanisms linking productivity and plant species richness. Nature 529(7586):390–393.

Grace, J. B., N. Huntington-Klein, E. W. Schweiger, M. Martinez, N. Enwright, M. Osland, L. Feher, B. Chivoiu, D. Johnson, G. Guntenspergen, and K. Thorne. 2024. Causal effects vs causal mechanisms: Two traditions with different requirements and contributions towards causal understanding. Accepted Ecology Letters.

Grace, J. B., D. R. Schoolmaster Jr., J. Pearl, G. R. Guntenspergen, A. M. Little, B. R. Mitchell, K. M. Miller, and E. W. Schweiger. 2012. Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere 3:73.

Gray, S. T., and G. J. McCabe. 2010. A combined water balance and tree ring approach to understanding the potential hydrologic effects of climate change in the central Rocky Mountain region. Water Resources Research 46(5).

Herman, K. D., L. A. Masters, M. R. Penskar, A. A. Reznicek, G. S. Wilhelm, W. R. Brodowicz, 1997. Floristic quality assessment: development and application in the state of Michigan (USA). Natural Areas Journal 17:265–279.

Hock, R. 2003. Temperature index melt modelling in mountain areas. Journal of Hydrology 282(1–4):104–115.

Holden, Z. A., A. Swanson, C. H. Luce, W. M. Jolly, M. Maneta, J. W. Oyler, D. A. Warren, R. Parsons, and D. Affleck. 2018. Decreasing fire season precipitation increased recent western US forest wildfire activity. Proceedings of the National Academy of Sciences 115:E8349–E8357. https://doi.org/10.1073/pnas.1802316115

Hostetler, S. W., and J. W. Alder. 2016. Implementation and evaluation of a monthly water balance model over the US on an 800m grid. Water Resources Research 52:1729–1745. https://doi.org/10.1002/2016WR018665

Jennings, K. S., T. S. Winchell, B. Livneh, and N. P. Molotch, 2018. Spatial variation of the rain-snow temperature threshold across the Northern Hemisphere. Nature Communications 9:1–9.

Johnston, D. B., D. J. Cooper, and N. T. Hobbs. 2007. Elk browsing increases aboveground growth of water-stressed willows by modifying plant architecture. Oecologia 154:467–478.

Jones, J. D., K. M. Proffitt, J. T. Paterson, E. S. Almberg, J. A. Cunningham, and K. M. Loveless. 2021. Elk responses to management hunting and hazing. The Journal of Wildlife Management 85(8):1721–1738.

Jones, W. M. 2005. A vegetation index of biotic integrity for small-order streams in southwest Montana and a floristic quality assessment for western Montana wetlands. Montana Natural Heritage Program, Helena.

Karr, J. R. 1991. Biological integrity - a long-neglected aspect of water-resource management. Ecological Applications 1:66–84.

Kauffman, J. B., D. L. Cummings, C. Kauffman, R. L. Beschta, J. Brooks, K. MacNeill, and W. J. Ripple. 2023. Bison influences on composition and diversity of riparian plant communities in Yellowstone National Park. Ecosphere 14(2):p.e4406.

Keddy, P. A. 1989. Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. Canadian Journal of Botany 67:708–716.

Keddy, P. A., H. T. Lee, and I. C. Wisheu. 2020. Choosing indicators of ecosystem integrity: wetlands as a model system. Pp. 61–79 In Ecological integrity and the management of ecosystems. CRC Press.

Kloppers, E. L., C. C. St. Clair, and T. E. Hurd. 2005. Predator-resembling aversive conditioning for managing habituated wildlife. Ecology and Society 10(1).

Koerner, S. E., M. D. Smith, D. E. Burkepile, N. P. Hanan, M. L. Avolio, S. L. Collins, A. K. Knapp, N. P. Lemoine, E. J. Forrestel, S. Eby, and D. I. Thompson. 2018. Change in dominance determines herbivore effects on plant biodiversity. Nature Ecology & Evolution 2(12):1925–1932.

Kray, J. A., D. J. Cooper, and J. S. Sanderson. 2012. Groundwater use by native plants in response to changes in precipitation in an intermountain basin. Journal of Arid Environments 83:25–34.

Kutcher, T. E., and G. E. Forrester. 2018. Evaluating how variants of floristic quality assessment indicate wetland condition. Journal of Environmental Management 217:231–239.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. The American Naturalist 147(5):784–812.

Lemly, J. M., and J. Rocchio. 2009. Vegetation index of biotic integrity (VIBI) for headwater wetlands in the southern Rocky Mountains: Version 2.0: Calibration of selected VIBI models. Colorado State University, Colorado Natural Heritage Program, Fort Collins.

Levine, J. M., M. Vilà, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. Proceedings of the Royal Society of London: Biological Sciences 270:775–781.

Li, W., F. P. Tian, Z. W. Ren, H. Z. Huang, and Z. N. Zhang. 2013. Effects of grazing and fertilization on the relationship between species abundance and functional traits in an alpine meadow community on the Tibetan Plateau. Nordic Journal of Botany 31(2):247–255.

Littell, J. S., D. L. Peterson, and M. Tjoelker. 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. Ecological Monographs 78:1–20.

Lodge, D. M., G. Cronin, E. van Donk, and A. J. Froelich. 1998. Impact of herbivory on plant standing crop: comparisons among biomes, between vascular and nonvascular plants, and among freshwater herbivore taxa. Pp. 149–174 In The structuring role of submerged macrophytes in lakes. Springer, New York.

Loheide, S. P., and S. M. Gorelick. 2007. Riparian hydroecology: A coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. Water Resources Research 43:W07414. https://doi.org/10.1029/2006WR005233

Lou, Y., Y. Pan, C. Gao, M. Jiang, X. Lu, and Y. J. Xu. 2016. Response of plant height, species richness and aboveground biomass to flooding gradient along vegetation zones in floodplain wetlands, Northeast China. Plos One 11(4):p.e0153972.

Lutz, J. A., J. W. van Wagtendonk, and J. F. Franklin. 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. Journal of Biogeography 37:936–950. https://doi.org/10.1111/j.1365-2699.2009.02268.x

Mabry, C., M. E. G. Golay, D. Lock, and J. R. Thompson. 2018. Validating the use of coefficients of conservatism to assess forest herbaceous layer quality in upland mesic forests. Natural Areas Journal 38(1):6–14.

Mack, J. J. 2007. Developing a wetland IBI with statewide application after multiple testing iterations. Ecological Indicators 7(4):864–881.

Magee, T. K., K. A. Blocksom, and M. S. Fennessy. 2019. A national-scale vegetation multimetric index (VMMI) as an indicator of wetland condition across the conterminous United States. Environmental Monitoring and Assessment 191(Suppl 1):322.

Magee, T. K., and M. E. Kentula. 2005. Response of wetland plant species to hydrologic conditions. Wetlands Ecology and Management 13:163–181.

Marshall, S., and J. Lemly. 2020 Colorado Wetland Program Plan: 2020–2024. Colorado Natural Heritage Program, Colorado State University, Fort Collins, Colorado. https://cnhp.colostate.edu/download/documents/2020/Colorado-Wetland-Program-Plan-2020-2024.pdf

Matthews, J. W., G. Spyreas, and C. M. Long. 2015. A null model test of Floristic Quality Assessment: Are plant species' Coefficients of Conservatism valid? Ecological Indicators 52:1–7.

Meaney, C. A., and D. Van Vuren. 1993. Recent distribution of bison in Colorado west of the Great Plains: Proceedings of the Denver Museum of Natural History Series 3, v. 4, p. 1–10, https://www.dropbox.com/scl/fi/mwlu9xhq5uuwy7gbrtu7r/PSeries3-4.pdf?rlkey=c4a0xyg68zdkivicnlp3g1gaq&e=1&dl=0

Meiners, S. J., S. A. Pickett, and M. L. Cadenasso. 2001. Effects of plant invasions on the species richness of abandoned agricultural land. Ecography 24:633–644.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments: Ecological Archives M063-001. Ecological Monographs 63(4):327–366.

Miller, K. M., B. R. Mitchell, and B. J. McGill. 2016. Constructing multimetric indices and testing ability of landscape metrics to assess condition of freshwater wetlands in the Northeastern US. Ecological Indicators 66:143–152.

Miller, K. M., S. J. Perles, J. P. Schmit, E. R. Matthews, A. S. Weed, J. A. Comiskey, M. R. Marshall, P. Nelson, and N. A. Fisichelli. 2023. Overabundant deer and invasive plants drive widespread regeneration debt in eastern United States national parks. Ecological Applications 33(4):p.e2837.

Mollard, F. P., A. L. Foote, M. J. Wilson, V. Crisfield, and S. E. Bayley. 2013. Monitoring and assessment of wetland condition using plant morphologic and physiologic indicators. Wetlands 33:939–947.

Morse, L. E., J. M. Randall, N. Benton, R. Hiebert, and S. Lu. 2004. An invasive species assessment protocol: evaluating non-native plants for their impact on biodiversity. Version 1. U.S. Government Documents, Utah Regional Depository.

Munson, S. M., R. H. Webb, D. C. Housman, K. E. Veblen. K. E. Nussear, E. A. Beever, K. B. Hartney, M. N. Miriti, S. L. Phillips, R. E. Fulton, N. G. Tallent, L. Susan, R. E. Fulton, and N. G. Tallent. 2015. Long-term plant responses to climate are moderated by biophysical attributes in a North American desert. Journal of Ecology 103:657–668. https://doi.org/10.1111/1365-2745.12381

National Park Service (NPS). 2007. Final General Management Plan / Wilderness Study / Environmental Impact Statement; Great Sand Dunes National Park and Preserve. Alamosa and Saguache Counties, Colorado. National Park Service, Mosca, Colorado.

National Park Service (NPS). 2018. Draft Great Sand Dunes National Park and Preserve Ungulate Management Plan and Environmental Impact Statement April 2018. National Park Service. Accessed online October 19, 2020, at https://parkplanning.nps.gov/document.cfm?parkID=67&projectID=25517&documentID=87067

Natural Resources Conservation Service (NRCS). 2021. Soil Survey Geographic (SSURGO) Database. Available online at https://sdmdataaccess.sc.egov.usda.gov

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4(4):355–364.

Otfinowski, R., and V. Coffey. 2022. Grazing effects on the composition, diversity, and function of wet meadow grasslands in Manitoba, Canada. Rangeland Ecology & Management 80:78–86.

Painter, L. E., and M. T. Tercek. 2020. Tall willow thickets return to northern Yellowstone. Ecosphere 11(5):e03115.

Panjabi, S. S., K. Decker, G. Doyle, and D. G. Anderson. 2004. Great Sand Dunes National Monument and Preserve 2003 vascular plant inventory. Colorado State University, Colorado Natural Heritage Program, Fort Collins, Colorado.

Poggenburg, C., U. Nopp-Mayr, J. Coppes, and F. Sachser. 2018. Shit happens … and persists: decay dynamics of capercaillie (*Tetrao urogallus* L.) droppings under natural and artificial conditions. European Journal of Wildlife Research 64:1–16.

Pritekel, C., A. Whittemore-Olson, N. Snow, and J. C. Moore. 2006. Impacts from invasive plant species and their control on the plant community and belowground ecosystem at Rocky Mountain National Park, USA. Applied Soil Ecology 32(1):132–141.

Pysek, P., D. M. Richardson, M. Rejmanek, G. L. Webster, M. Williamson, and J. Kirschner. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon 53:131–143.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Ratajczak, Z., S. L. Collins, J. M. Blair, S. E. Koerner, A. M. Louthan, M. D. Smith, J. H. Taylor, and J. B. Nippert. 2022. Reintroducing bison results in long-running and resilient increases in grassland diversity. Proceedings of the National Academy of Sciences 119(36):p.e2210433119.

Rhodes, A. C., R. T. Larsen, and S. B. St Clair. 2018. Differential effects of cattle, mule deer, and elk herbivory on aspen forest regeneration and recruitment. For Ecol Manag 422:273–280.

Rocchio, J. 2007a. Assessing ecological condition of headwater wetlands in the Southern Rocky Mountains using a vegetation index of biotic integrity (Version 1.0). Colorado Natural Heritage Program, Colorado State University, Fort Collins.

Rocchio, J. 2007b. Floristic quality assessment indices for Colorado plant communities. Report prepared for the Colorado Department of Natural Resources and U.S. EPA Region 8. Colorado State University, Colorado Natural Heritage Program, Fort Collins.

Rodhouse, T. J., C. J. Sergeant, and E. W. Schweiger. 2016. Ecological monitoring and evidence-based decision-making in America's National Parks: highlights of the Special Feature. Ecosphere 7(11):p.e01608.

Rose, J. R., and D. J. Cooper. 2016. The influence of floods and herbivory on cottonwood establishment and growth in a multi-herbivore system. Ecohydrology https://doi.org/10.1002/eco.1768

Rowland, P. I., and C. E. Lovelock. 2024. Global impacts of introduced ungulates on wetland carbon and biodiversity: A review. Biological Conservation 290:110432.

Sabo, A. E., J. A. Forrester, E. L. Kruger, and D. J. Mladenoff. 2023. Herbaceous plant height is an early indicator of groundlayer response to an experimental manipulation of forest structure and deer pressure. Forest Ecology and Management 536:120902.

Salas, D. E., J. Stevens, K. Schulz, M. Artmann, B. Friesen, S. Blauer, E. W. Schweiger, and A. Valdez. 2010. Vegetation classification and mapping project report: Great Sand Dunes National Park and Preserve. Natural Resource Report NPS/Network/NRR—2010/179. National Park Service, Fort Collins, Colorado.

Schoenecker, K. A. 2012. Ecology of bison, elk, and vegetation in an arid ecosystem. Ph.D. dissertation, Colo. State Univ., Fort Collins.

Schoenecker, K. A., S. E. Nielsen, L. C. Zeigenfuss, and C. A. Pague. 2015. Selection of vegetation types and density of bison in an arid ecosystem. The Journal of Wildlife Management 79:1117–1128. https://doi:10.1002/jwmg.940

Schoenecker, K. A., L. C. Zeigenfuss, and D. J. Augustine. 2022. Can grazing by elk and bison stimulate herbaceous plant productivity in semi-arid ecosystems. Ecosphere v. 13 (4) e4025. https://doi.org/10.1002/ecs2.4025

Schoolmaster, D. R. Jr., J. B. Grace, and E. W. Schweiger. 2012. A general theory of multimetric indices and their properties. Methods in Ecology and Evolution 3:773–781.

Schoolmaster, D. R. Jr., J. B. Grace, E. W. Schweiger, G. R. Guntenspergen, B. R. Mitchell, K. M. Miller, and A. M Little. 2013. An algorithmic and information-theoretic approach to multimetric index construction. Ecological Indicators 26:14–23.

Schoolmaster, D. R. Jr., J. B. Grace, E. W. Schweiger, B. R. Mitchell, and G. R. Guntenspergen. 2013. A causal examination of the effects of confounding factors on multimetric indices. Ecological Indicators 29:411–419.

Schweiger, E. W., M. Britten, E. Borgman, and K. Sherrill. 2018. Glacier National Park stream ecological integrity: 2007–2009 status report. Natural Resource Report NPS/ROMN/NRR—2018/1699. National Park Service, Fort Collins, Colorado.

Schweiger, E. W., M. Britten, and J. Jones. 2017. Great Sand Dunes National Park and Preserve wetland ecological integrity: 2010–2014 status and trend report. Natural Resource Report NPS/ROMN/NRR—2017/1569. National Park Service, Fort Collins, Colorado.

Schweiger, E. W., E. Gage, K. Driver, D. Cooper, L. O'Gan, and M. Britten. 2015. Rocky Mountain Network wetland ecological integrity monitoring protocol: Narrative, version 1.0. Natural Resource Report NPS/Network/NRR—2015/991. National Park Service, Fort Collins, Colorado.

Schweiger E. W., E. Gage, K. M. Haynes, E. Borgman, L. O'Gan, D. Shorrock, D. Cooper, and M. Britten. 2015. Rocky Mountain Network wetland ecological integrity monitoring protocol: Standard operating procedures, version 1.0. Natural Resource Report. NPS/ROMN/NRR—2015/992. Fort Collins, Colorado.

Schweiger, E. W., J. B. Grace, D. Cooper, B. Bobowski, and M. Britten. 2016. Using structural equation modeling to link human activities to wetland ecological integrity. Ecosphere 7(11):e01548. https://doi:10.1002/ecs2.1548

Schweiger, E. W., J. Lemly, D. Witwicki, K. Sherrill, R. Whittington, L. Messner, E. Cubley, and K. Haynes. 2023. Florissant Fossil Beds National Monument wetland ecological integrity: 2009–2019 synthesis report. Natural Resource Report NPS/ROMN/NRR—2023/2577. National Park Service, Fort Collins, Colorado. https://doi.org/10.36967/2300778

Schweiger, E. W., K. Sherrill, M. Bozek, D. Witwicki, and S. Esser. 2024. Glacier National Park stream ecological integrity: 2007–2019 trend synthesis report. Natural Resource Report NPS/ROMN/NRR—2024/2631. National Park Service, Fort Collins, Colorado. https://doi.org/10.36967/2302379

Seigle-Ferrand, J., K. Atmeh, J. M. Gaillard, V. Ronget, N. Morellet, M. Garel, A. Loison, and G. Yannic. 2021. A systematic review of within-population variation in the size of home range across ungulates: what do we know after 50 years of telemetry studies?. Frontiers in Ecology and Evolution 8:555429.

Singer, F. J., L. C. Mack, and R. C. Cates. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management 47:435–443.

Skovlin, J. M. 2021. Impacts of grazing on wetlands and riparian habitat: A review of our knowledge. Pp. 1001–1104 In Developing strategies for rangeland management. CRC Press.

Smith, P., G. Doyle, and J. Lemly. 2020. Revision of Colorado's Floristic Quality Assessment Indices. Colorado State University, Colorado Natural Heritage Program, Fort Collins, Colorado.

Spackman Panjabi, S., K. Decker, G. Doyle, and D.G. Anderson. 2004. Great Sand Dunes National Monument and Preserve 2003 Vascular Plant Inventory. Colorado State University, Colorado Natural Heritage Program, Fort Collins, Colorado.

Stephenson, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25:855–870. https://doi.org/10.1046/j.1365-2699.1998.00233.x

Stoddard, J. L., A. T. Herlihy, D. V. Peck, R. M. Hughes, T. R. Whittier, and E. Tarquinio. 2008. A process for creating multimetric indices for large-scale aquatic surveys. Journal of the North American Benthological Society 27:878–891.

Stoddard, J. L., D. P. Larsen, C. P. Hawkins, R. K. Johnson, and R. H. Norris. 2006. Setting expectations for the ecological condition of streams: The concept of reference condition. Ecological Applications 16:1267–1276.

Suplee, M., R. S. de Suplee, D. Feldman, and T. Laidlaw. 2005. Identification and assessment of Montana reference streams: A follow-up and expansion of the 1992 benchmark biology study. Montana Dept. of Environmental Quality, Helena.

Swift, L.W. 1945. A partial history of the elk herds of Colorado. Journal of Mammalogy 26(2):114–119.

Terborgh, J. W. 2015. Toward a trophic theory of species diversity. Proceedings of the National Academy of Sciences 112(37):11415–11422.

Thoma, D. P., M. T. Tercek, E. W. Schweiger, S. M. Munson, J. E. Gross, and S. T. Olliff. 2020. Water balance as an indicator of natural resource condition: Case studies from Great Sand Dunes National Park and Preserve. Global Ecology and Conservation 24:e01300.

Thornton, M. M., R. Shrestha, Y. Wei, P. E. Thornton, S. Kao, and B. E. Wilson. 2020. Daymet: daily surface weather data on a 1-km grid for North America, Version 4. ORNL DAAC, Oak Ridge, Tennessee. https://doi.org/10.3334/ORNLDAAC/1840

Tiebel, K., A. Karge, and S. Wagner. 2023. Does shading and ground cover of moss and litter improve germination and establishment of *Betula pendula* Roth, *Salix caprea* L. and *Populus tremula* L. seedlings during drought stress in climate change?–A greenhouse study. Forest Ecology and Management 544:121212.

Tiner, R. W. 2012. Defining hydrophytes for wetland identification and delineation. ERCD/CRREL CR-12-1. U.S. Army Corps of Engineers, Engineer Research and Development Center, Washington, D. C.

Tirmenstein, D. A. 1999. *Chrysothamnus nauseosus*, in Fire Sciences Laboratory, Producer, Fire Effects Information System, [Online]: Fort Collins, Colo., U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, accessed June 26, 2015 at https://www.fs.usda.gov/database/feis/plants/shrub/erinau/all.html

U.S. Department of Agriculture. 2014. The PLANTS Database: Greensboro, N. C., U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Team, accessed June 26, 2015, at http://plants.usda.gov

U.S. Department of Agriculture, NRCS. 2024. The PLANTS Database (http://plants.usda.gov, 06/25/2024). National Plant Data Team, Greensboro, North Carolina.

U.S. Fish and Wildlife Service (USFWS). 1991. National wetlands inventory map report of San Luis Valley for the 1:100,000 map units of: Pueblo SW, Montrose SE, Durango NE, Durango SE, Trinidad NW and Trinidad SW Denver, Colorado, USA. U.S. Fish and Wildlife Service, Denver, Colorado.

U.S. Environmental Protection Agency (US EPA). 2016. National wetland condition assessment: 2011 Technical Report. EPA-843-R-15-006. US Environmental Protection Agency, Washington, D.C.

Warren, E. R. 1910. The mammals of Colorado. The Knickerbocker Press, New York.

Wellek, S., 2017. A critical evaluation of the current "p-value controversy". Biometrical Journal 59(5):854–872.

Wilhelm, G., and D. Ladd. 1988. Natural area assessment in the Chicago region. Transactions of the North American Wildlife and Natural Resources Conference 53:361–375.

Williams. 2003. Past and current practices of winter maintenance at the Montana Department of Transportation (MDT). Prepared by Dan Williams, MDT Maintenance Engineering Officer, Montana Department of Transportation, December 18, 2001, updated December 31, 2003. Accessed from the web on 12/27/2021 at https://www.mdt.mt.gov/publications/docs/brochures/winter-maint/wintmaint-whitepaper.pdf

Wockner, G., R. Boone, K. A. Schoenecker, and L. C. Zeigenfuss. 2015. Modeling elk and bison carrying capacity for Great Sand Dunes National Park, Baca National Wildlife Refuge, and The Nature Conservancy's Medano Ranch, Colorado. U.S. Geological Survey Open-File Report 2014–1200. http://dx.doi.org/10.3133/ofR20141200

Wurster, F. C., D. J. Cooper, and W. E. Sanford. 2003. Stream/aquifer interactions at Great Sand Dunes National Monument, Colorado: influences on interdunal wetland disappearance. Journal of Hydrology 271(1–4):77–100.

Yilmaz, K. T., E. Akca, H. Cakan, Y. Ünlükaplan, and S. Kapur. 2020. Relation between soil salinity and species composition of halophytic plant communities: A baseline data inventory for wetland monitoring. Turkish Journal of Botany 44(5):493–508.

Zeigenfuss, L., and T. L. Johnson. 2015. Monitoring of vegetation response to elk population and habitat management in Rocky Mountain National Park, 2008–14 (No. 2015-1216). US Geological Survey. https://doi.org/10.3133/ofr20151216

Zeigenfuss, L. C., T. L. Johnson, and Z. Wiebe. 2011. Monitoring plan for vegetation responses to elk management in Rocky Mountain National Park. US Department of the Interior, US Geological Survey. https://pubs.usgs.gov/of/2011/1013/

Zeigenfuss, L.C. and Schoenecker, K.A., 2021. Effects of elk and bison herbivory on narrowleaf cottonwood. Western North American Naturalist 81(1):97–112.

Zeigenfuss, L. C., E. W. Schweiger, and K. Sherrill. 2024. Wetland habitat use by elk and bison in Great Sand Dunes National Park. National Park Service report, Fort Collins, Colorado. https://irma.nps.gov/DataStore/Reference/Profile/2307232

Zhou, X., K. Dong, Y. Tang, H. Huang, G. Peng, and D. Wang. 2023. Research progress on the decomposition process of plant litter in wetlands: A review. Water 15(18):3246.

Appendix A: Ungulate Use Indices, Select Vegetation Metrics, and Wetland Condition Indices

Appendix A provides additional methods for Ungulate Use Indices (UUI), select vegetation metrics, and Wetland Condition Indices (WCI). For a full treatment of UUI methods, see also Zeigenfuss et al. (2024).

Ungulate Use Indices

Ungulate use data from categorical crew observations, dung counts, collars, and camera traps were developed into site scale UUIs that estimate the intensity of use by elk and/or bison of wetland habitat. Brief summaries of these methods are below but see Zeigenfuss et al. (2024) for a full treatment of methods.

Qualitative

Categorical or qualitative crew observation data were summarized into site level UUIs as medians, means, or various estimates of variation of these data (across plots within a site). These methods and metric details originated with the 2010 survey as presented in Schweiger et al. (2017).

Dung

Dung counts were developed into two types of UUI and calculated for elk, bison, or elk and bison. First, a simple dung pellet group density was derived from physical counts of total (old and new) dung in an event and then divided by the total area surveyed. Second, we estimated a more derived dung index by scaling the dung pellet group density in two ways. One was by a disappearance time (see "Dung disappearance" section below) for dung pellets, which is the amount of time it takes for dung to either decay, scatter, or otherwise disappear. The other was by scaling dung pellet group density by a species-specific defecation rate (based on data from the literature but that had to include assumptions about the ecology of these two species in the unique sand sheet system).

In 2018–2019, we implemented procedures to improve dung data using within event and across year blind resampling to test the accuracy of dung age assignment and overall counts. Resample data also added to our understanding of seasonal ungulate use and fecal accumulation rates. In 2021–2023, we established an additional 10 plots in existing sites and monitored the disappearance rate of 10 marked dung piles in each over three years. Analysis of these data allowed estimates of habitat and species-specific dung disappearance rates to correct fecal standing crop counts and better reflect ungulate use. Disappearance rate includes both decay of dung and the ability for crews to relocate dung (i.e., the detectability of any given dung pile). See Zeigenfuss et al. (2024) for additional details on dung disappearance methods and analyses.

Dung disappearance

Initial dung counts from exclosures suggested that dung piles likely persisted for long periods and thus unadjusted counts likely confounded an unknown history of ungulate defecation levels and accumulation of dung on a site. Lacking any relevant information in the literature for how long elk or bison dung persists in a place like the GRSA sand sheet, we developed UMP specific estimates. The

rate of dung disappearance includes both decay of dung and the ability for crews to relocate dung, which is influenced by the detectability of any given dung pile. The rate was calculated as the proportion of marked dung piles that disappeared divided by the mean interval between dung creation and recorded disappearance. We also estimated the number of days for dung to disappear as the inverse of the rate.

Collar

Collar-based UUIs were developed using estimates of spatial and temporal distribution of elk and bison from radio and GPS collars. As noted above, we had to use bison collar data from 2005 to 2007. While not ideal, the bison pasture fence and ranch management operations effectively constrain bison use to a limited area that is same in our baseline period as during 2005–2007. Strong correlations between (old) bison collar, current camera-based UUIs, and current dung-based UUIs were also used to support our assumptions and use of old bison collar data. We created "concentrated use" range maps for each collared animal by buffering each location to several distances—100 m, 200 m, 300 m, 500 m, 1000 m. We tested each buffer size for best fit with camera and dung data. Through this process we determined a 500 m buffer had the best correlation with other UUI types. We then converted these 500 m concentrated use maps to grid-based maps with a 100 m cell size (1 ha) and summed the maps for each individual collared animal to create a continuous grid of total overlapping individual use grid-based maps. Collar UUI values were derived because the proportion of all collared individuals that used each cell in the raster was calculated with separate maps for each year and seasons. UUI values for each species, year, and season were extracted from this collar UUI surface for each UMP site using bilinear interpolation of all adjacent cell values to the cell containing the site.

Camera trap

Three site-specific camera-based UUIs were developed to describe ungulate use at the 10 UMP wetland sites with camera traps for elk, bison, and elk and bison. These metrics were based on those commonly found in the literature. As with collars, we were able to split these into annual, seasonal, and growing season versions. Cameras also allowed an interesting look at day vs. night use.

The simplest camera-based metric was a daily presence index that calculated the proportion of days (out of the total camera deployment time) when a species was present at a site. We also estimated slightly more involved relative indices of activity based on the total number of photos capturing a species at a site, standardized by the number of days of camera deployment at a site. Weighted variants on relative indices of activity used the total number of individuals counted in all the photos or both the number of photos and the number of animals. These indices treat cumulative number of photos as an indicator of the amount of animal activity under the presumption that larger numbers and longer visit duration to a site will result in a greater number of photos. In contrast, the third camera-based index accounts for lack of independence of individual photos by using "capture events" that we assume subset data into independent sets of animals at a site. It then uses the total number of these events to estimate ungulate activity (again standardized by the number of days of camera deployment and with weighted variants using mean, median, and maximum group size in the

photos). The distribution of interval length between the time since last photo suggested a minimum length between events of roughly five minutes.

Selecting final UUI

Given little *a priori* knowledge about how UUIs would perform, we purposefully estimated a large number (over 300) of UUI variants based on calculation details (such as weighting for body mass or not), and different seasonal or annual subsetting. All UUIs are available from the Rocky Mountain Network. To then select final or "best" UUIs, we estimated correlations between each UUI and all possible vegetation metrics. We then rank ordered UUIs based on mean absolute correlation coefficients. Next, we evaluated high ranked UUIs by estimating Wetland Condition Indices. UUIs that produced the highest quality and most interpretable WCIs were identified as the most useful UUIs to focus on.

Camera-like Ungulate Use Indices

We developed a camera-like UUI form that sought to integrate the strengths of dung-, collar-, and camera-based approaches (Figure 39). Camera-based UUIs were only possible at the 10 sites where cameras were deployed. However, as the most information rich approach to estimating ungulate use, we developed models to extrapolate camera UUIs to all UMP sites.

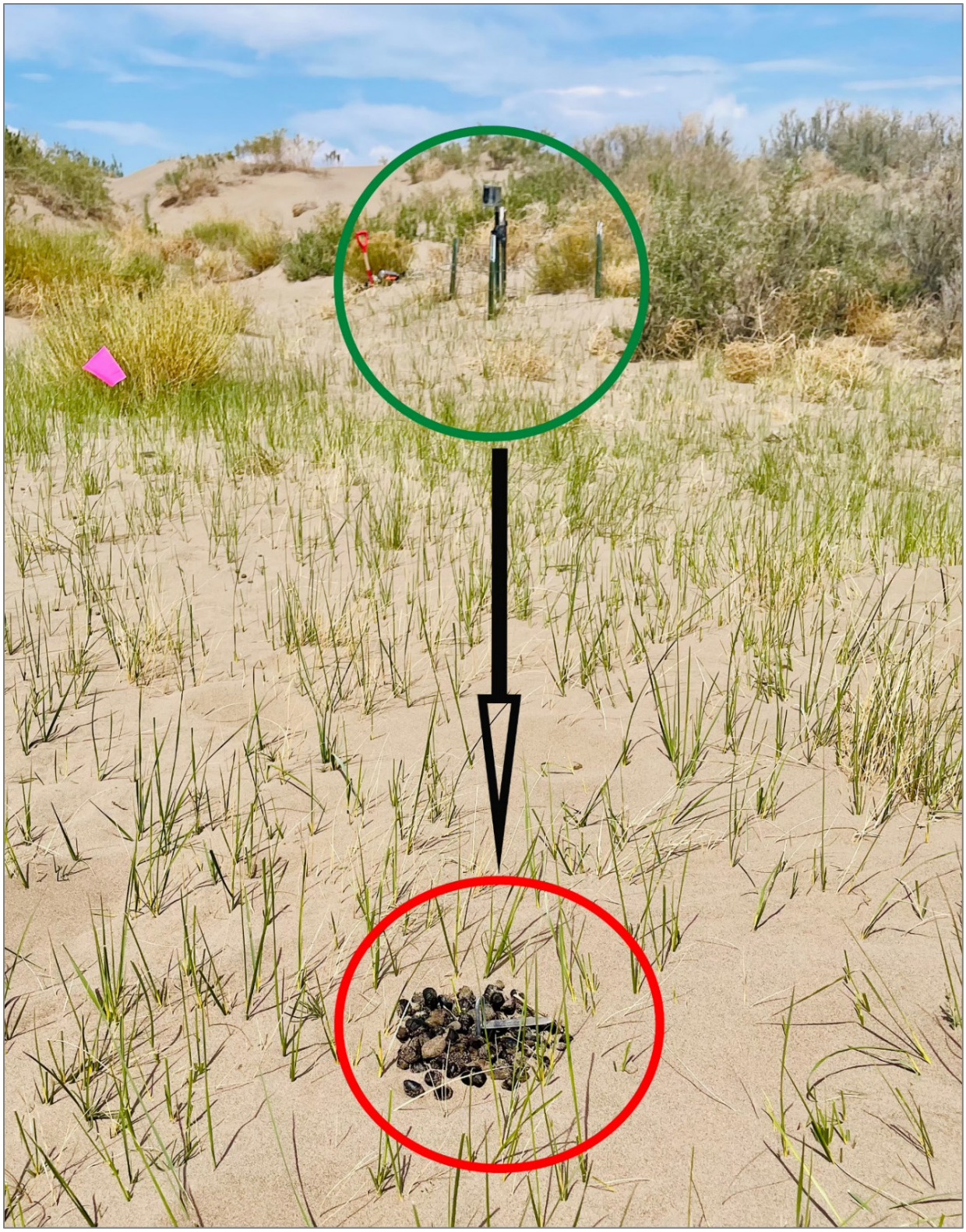


Figure 39. Wetland site with a camera and elk dung pile at Great Sand Dunes National Park and Preserve, 2019. Green and red connected circles illustrate a conceptual relationship between these two sources of ungulate use information that are used to construct the camera-like Ungulate Use Indices. NPS / B. SCHWEIGER

Given sample size constraints we purposefully kept these models simple. In summary, we estimated both linear regression and general additive non-linear models (GAM) using camera UUIs as the response and dung and collar indices as predictors. We stepped through many combinations of single and double predictors using patterns in correlations to focus on the likely best choices. All collar UUIs were adjusted for an exclosure effect. No other predictors were included to avoid overfitting the models. We also chose to not transform or rescale any variable to reduce level of derivation in these analyses and not fix them in time to the baseline distribution of each component. Partial plots were utilized to visualize the form of fitted relationships among camera-, dung- and collar-based UUIs. We chose final models based on Akaike information criterion (AIC) or adjusted R^2 to choose between linear and GAM where AIC based comparisons were not appropriate. We then used these final best models to predict a camera-like UUI from dung and collar UUIs at all sites. Predicted values for all sample events were our final camera-like UUIs. For both elk (woody sites) and elk and bison (herbaceous sites), the final best model form was linear.

Vegetation metrics

R code snippets for each of the metrics in this report are given in Table 8. Complete R code for all metrics is available from the Rocky Mountain Network on request.

Table 8. Derivation of select component and hand-picked (HP) vegetation metrics for ungulate use modeling at Great Sand Dunes National Park and Preserve. H = herbaceous wetland. W = woody wetland.

HP metric (wetland type)	R code snippet
Density of willow and cottonwood with browse, adjusted, index (W)	wd.SalPop.LiveBrowsedAll <- d.SalPop.All.Dens * x.SalPop.LiveBrowsedAll d.SalPop.All.Dens = sum(d.SalPop.Short.Dens + d.SalPop.Tall.Dens) d.SalPop.Short.Dens=sum(d$Count[(d$Genus=='Salix' | d$Genus=='Populus') & d$HeightClass < 4]) / d$UMPEvent_PlotAreaSubplot[1] d.SalPop.Tall.Dens=sum(d$Count[(d$Genus=='Salix' \| d$Genus=='Populus') & d$HeightClass >= 4]) / d$UMPEvent_PlotAreaWhole[1] x.SalPop.LiveBrowsedAll <- mean(d$LiveBrowsed_Prcnt[(d$Genus=='Salix' | d$Genus=='Populus')], na.rm=T)/100
Conservatism graminoids cover weighted, index (H)	c.C.CWM.Mean.graminoid=weighted_mean((ds$CNHP_FQA_C.Value2020_Numeric[ds$CNHP_FQA_Family=='Poaceae' | ds$CNHP_FQA_Family=='Cyperaceae']), ds$RelativeCoverSpecies[ds$CNHP_FQA_Family=='Poaceae' \| ds$CNHP_FQA_Family=='Cyperaceae'], na.rm = T)
Iris & silverweed absolute cover, index (H)	t.Abs.sumcov.IrisSilver=sum(ds$AbsoluteCover[ds$FinalTaxaName=='Iris missouriensis' | ds$FinalTaxaName=='Potentilla anserina'],na.rm=T)
Wetland affinity, cover weighted (W)	ws.WetAff.Mean.relcov.CW.Score.All=weighted.mean(WetAff,dplyr::coalesce(ds$AbsoluteCover,0), na.rm = T)
Woody species richness (H)	r.Richness.Woody=sum(d$CNHP_USDA_GrowthHabitSimple=='Tree' \| d$CNHP_USDA_GrowthHabitSimple=='Shrub')
Relative cover of salt intolerants (H)	s.Rel.sumcov.NoSalt=sum(ds$RelativeCoverSpecies[ds$ROMN_SalinityTolerance=='None'],na.rm=T)

Table 8 (continued). Derivation of select component and hand-picked (HP) vegetation metrics for ungulate use modeling at Great Sand Dunes National Park and Preserve. H = herbaceous wetland. W = woody wetland.

HP metric (wetland type)	R code snippet
Total height of sedges (H)	h.height.total.Carex=sum(d$TotalHeight[d$CNHP_FQA_Genus=='Carex'],na.rm = any(!is.na(d$TotalHeight)))
Non-native species richness (H)	n.cnhp.Inv.Richness=sum(d$CNHP_FQA_NativeStatus=='Non-native',na.rm=T)
Percentage of rabbit brush 0.5 to 1.0 m tall (%) (W)	p.Rabbit.PercentHt2=(d.Rabbit.2.Dens / d.Rabbit.All.Dens) *100 d.Rabbit.2.Dens=sum(d$Count[(d$Genus=='Ericameria' | d$Genus=='Chrysothamnus') & d$HeightClass==2]) / d$UMPEvent_PlotAreaSubplot[1] d.Rabbit.All.Dens = sum(d.Rabbit.Short.Dens + d.Rabbit.Tall.Dens) d.Rabbit.Short.Dens=sum(d$Count[(d$Genus=='Ericameria' \| d$Genus=='Chrysothamnus') & d$HeightClass < 4]) / d$UMPEvent_PlotAreaSubplot[1 d.Rabbit.Tall.Dens=sum(d$Count[(d$Genus=='Ericameria' | d$Genus=='Chrysothamnus') & d$HeightClass >= 4]) / d$UMPEvent_PlotAreaWhole[1]
Total cover of salt intolerant species (%) (W)	s.Abs.sumcov.NoSalt=sum(ds$AbsoluteCover[ds$ROMN_SalinityTolerance=='None'],na.rm=T)
Ratio of cover of willows and cottonwood to all woody cover (index) (W)	t.cov.Salicaceae.Woody = t.Abs.sumcov.Salicaceae / (t.Abs.sumcov.Salicaceae + lf.Abs.sumcov.Woody)
Density of sandbar willow 0.5 to 1.0 m tall (plants/m^2) (W)	d.Exigua.2.Dens=sum(d$Count[d$Species=='Salix exigua' & d$HeightClass==2]) / d$UMPEvent_PlotAreaSubplot[1]

Wetland Condition Index: detailed method summary

The following summarizes our WCI methods in more detail than in the main narrative—see also Schoolmaster et al. (2012), Schoolmaster, Grace, Schweiger, Mitchell et al. (2013), and Schoolmaster Grace, Schweiger, Guntenspergen et al. (2013).

Bioassessment is, generally speaking, the use of biologically based response measures to assess and monitor natural systems (Barbour et al. 2000). We use a multimetric index (WCI; classically known as an index of biotic integrity or IBI) as our primary way of estimating ecological integrity. WCIs synthesize data from multiple levels of biological organization with the goal of deriving a single index that reflects the overall effects of disturbance on wetland integrity. Importantly, at GRSA we use ungulate disturbance (Ungulate Use Index, UUI) to create corresponding WCIs.

Schoolmaster et al. (2012), Schoolmaster, Grace, Schweiger, Mitchell et al. (2013), and Schoolmaster Grace, Schweiger, Guntenspergen et al. (2013) refine the theory behind WCI models and develop the approach we apply to UMP data. Key statistical features of our approach include:

1. control of potentially confounding influences of environmental covariates using a strategy based on causal graphical models (key for ecosystems like wetlands where condition can vary markedly along natural gradients),
2. use of all data to adjust for environmental gradients, simultaneously considering the effects of disturbance and environmental covariates on metrics in a single model, not a series of residualized adjustments as in other methods that require an *a priori* classification of sites into reference and non-reference,
3. developing a statistically optimal number of metrics in a final WCI, accounting for correlations among candidate component metrics and their impacts on the performance of the WCI,
4. incorporation of metrics in the final WCI only if they improve the performance of the model—this process depends nonlinearly on the signal of the disturbance gradient, the noise (error) of the metric, and the correlation of the metric errors, and
5. use of an information-theoretic model selection approach to assemble and select the final WCI—this evaluates all possible combinations of component metrics and guarantees a statistically best model for any empirical dataset.

Overall, this modeling approach requires fewer assumptions and is more efficient with the given information than classic methods; thus, it represents an important advance for creating synthetic bioassessments of system response.

We construct WCIs from candidate vegetation metrics, UUIs, and a suite of environmental covariates following Schoolmaster et al. (2012), Schoolmaster, Grace, Schweiger, Mitchell et al. (2013), and Schoolmaster Grace, Schweiger, Guntenspergen et al. (2013). Our models assume that ungulate use at GRSA has a complex, multivariate effect on park wetlands and that therefore it is the multivariate relationship with disturbance that needs to be evaluated and incorporated into index construction. In practice, this means selecting sets of metrics based on how they respond to disturbance as a group, as opposed to how each metric responds individually, as is done in more classic bioassessments. Schoolmaster, Grace, Schweiger, Mitchell et al. (2013) and Schoolmaster Grace, Schweiger, Guntenspergen et al. (2013) showed that the characteristics of metrics that will combine to produce the most sensitive WCI cannot be deduced from the bivariate relationships between the metrics and disturbance. Instead, whether a candidate metric improves the sensitivity of a WCI (or not) depends on the strength of the disturbance signal in the candidate metric and its unique explanatory power within the set of candidate metrics. We therefore incorporate the way that metrics combine to convey information about disturbance into the construction of WCIs for GRSA's wetlands.

A summary of the steps used to create a WCI follows (Figure 40; Schoolmaster et al. 2012; Schoolmaster, Grace, Schweiger, Mitchell et al. 2013; Schoolmaster Grace, Schweiger, Guntenspergen et al. 2013). R code for estimating a WCI is available from the network on request.

1. Develop conceptual graphical model of the relationships among disturbances and responses, and identify important environmental covariates. These can be based on ecological knowledge and/or other models of patterns in the data.
2. Assemble disturbance indices (i.e., UUIs).
3. Assemble a set of candidate vegetation metrics.
4. Evaluate all possible vegetation metrics for interpretability (expert opinion), completeness (remove any with missing and/or 0 values below a threshold of 25%), and multicollinearity (remove one from pairs with an $r > 0.95$, choosing those that are more interpretable).
5. Construct WCI:
    a. Reflect metrics that are positively numerically correlated with disturbance to ensure each metric (and final WCI) is negatively correlated with disturbance.
        i. Note this is not the same as our focus on the decreasing condition effect of UUI. Our WCI methods evaluate all candidate metrics fed into the algorithm, carefully accounting for multivariate correlation and outputting the statistically best and smallest set based on the correlation with UUI. Our methods drop candidate metrics without a meaningful response. However, including both negative condition response metrics (decreaser metrics) and positive condition response metrics (increasers metrics) in the same WCI model proved to be problematic, with metrics essentially "canceling each other out." Therefore, in consultation with the park, we elected to focus our WCI only on a decreaser effect. We identified all metrics that were indicators of an increasing wetland condition and removed them from the modelling process.
    b. Adjust metrics for important covariates using an approach that uses all available data to model metrics as a function of known gradients and disturbance simultaneously.
    c. Scale metrics from 1 to 10 (Blocksom 2003).
    d. Select an initial metric (m_1) to include in the WCI. This selection can be made arbitrarily since all metrics will eventually be used as an initial metric.
    e. Add m_1 to each of the rest of the metrics, m_j, site-by-site.
    f. For each m_j, find which combination $m_1 + m_j$ has the strongest negative correlation with disturbance. Select that one.
    g. Record the correlation (or other statistic) of the relationship between the assembled index with disturbance.
    h. Add the index to each of the remaining metrics m_j, site-by-site.
    i. Find the combination of index + m_j that has the strongest negative correlation with disturbance. Select this as a WCI based on AIC scores.

j. Near equivalent (statistically the same) models are reported, such that final selection may also be based on the metrics included in each.

k. A model averaging approach is also used that creates a WCI as a matrix product of all equivalent WCI and their AIC scores as weights. Component metrics within this model are the combined list from all near equivalent WCIs.

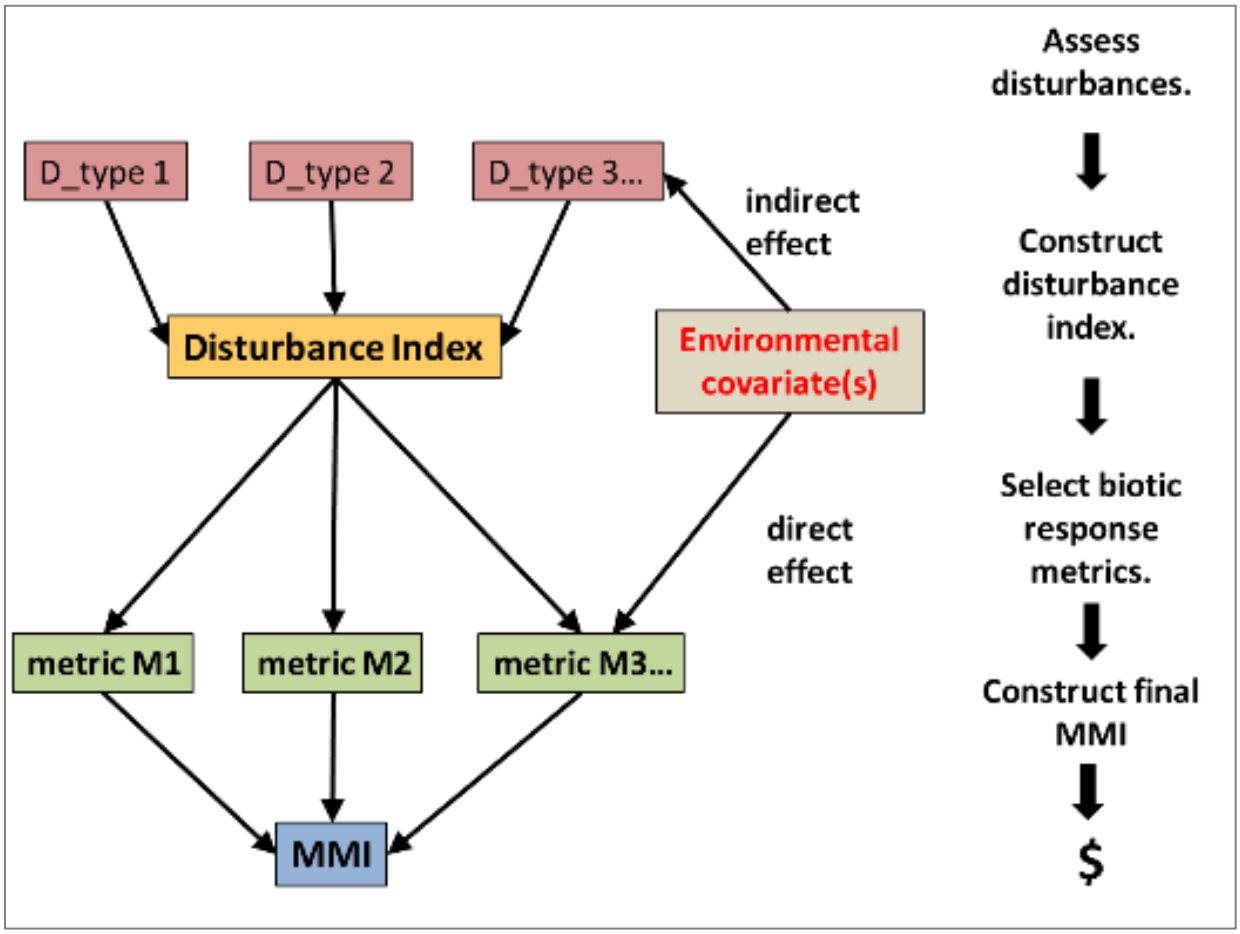


Figure 40. General flowchart for creating a Wetland Condition Index from a disturbance index, like ungulate use, with statistical control of confounded environmental covariates. We use "$" to denote success! NPS

Selection and validation of Wetland Condition Indices

Our WCI methods estimate the statistically best combination of component metrics to create a WCI given an input dataset. However, there can be viable competing approaches to arrive at the same place (a WCI). For example, in the UMP we had several UUIs that could all be considered to create a WCI. We could have also explored alternate suites of environmental variables for a given UUI–WCI combination.

We used our experience coupled with exploratory analyses (i.e., ordination) of patterns to examine these choices. This was used to identify a suite of comprehensive environmental covariates for all

WCIs (see Table 1). By assuming these were the default, this eliminated a black hole of considering all possible covariates. It is, however, a large assumption that we have the most useful set of environmental gradients in our modelling. Likewise, an important, if somewhat subjective, method used to select a final model was the interpretability of the component metrics in each model. While a WCI stands alone, it is a much better management tool if its component metrics support its interpretation. Every WCI presented in this report has been evaluated in this regard, with several alternates that were otherwise statistically valid models not chosen because their component metrics were less informative.

We also used several statistical model selection and validation methods to choose among WCIs based on different UUIs (all using the same covariates and candidate vegetation component metrics). First, for each candidate model constructed from a UUI–WCI pair, we estimate a simple linear model of the final WCI vs. its UUI (for example, see Figure 17). Standard statistics (r, adjusted r^2, RMSE) of the quality of this model are used to help determine if it is the "best." Second, we performed more explicit validation using semi-independent calibration and validation datasets. Where sample sizes permitted, we subsetted events into first samples as a calibration dataset and revisits and quality assurance / quality control (QAQC) events as validation data. We estimated iterations of the same WCI using these two datasets. We built linear models of each against its UUI and then tested the two slopes of these models and the interaction between calibration and validation events (Frost 2022). A significant interaction term suggests that validation data did not reproduce the same relationship as seen with calibration data and the model is less likely to be predictive when applied to comparisons between the baseline and Phase 2 or 3 data. Figure 41 shows these validations for the camera-like UUI-based and the dung-only UUI-based WCI models. The camera-like model validates better than the dung-only ($p = 0.17$ suggesting no difference between the two versions vs. $p = 0.024$ suggesting a potentially meaningful difference). However, both of these models are far superior to a model using only a qualitative UUI that shows a poor validation of the model ($p < 0.001$) with likely far lower predictive capabilities.

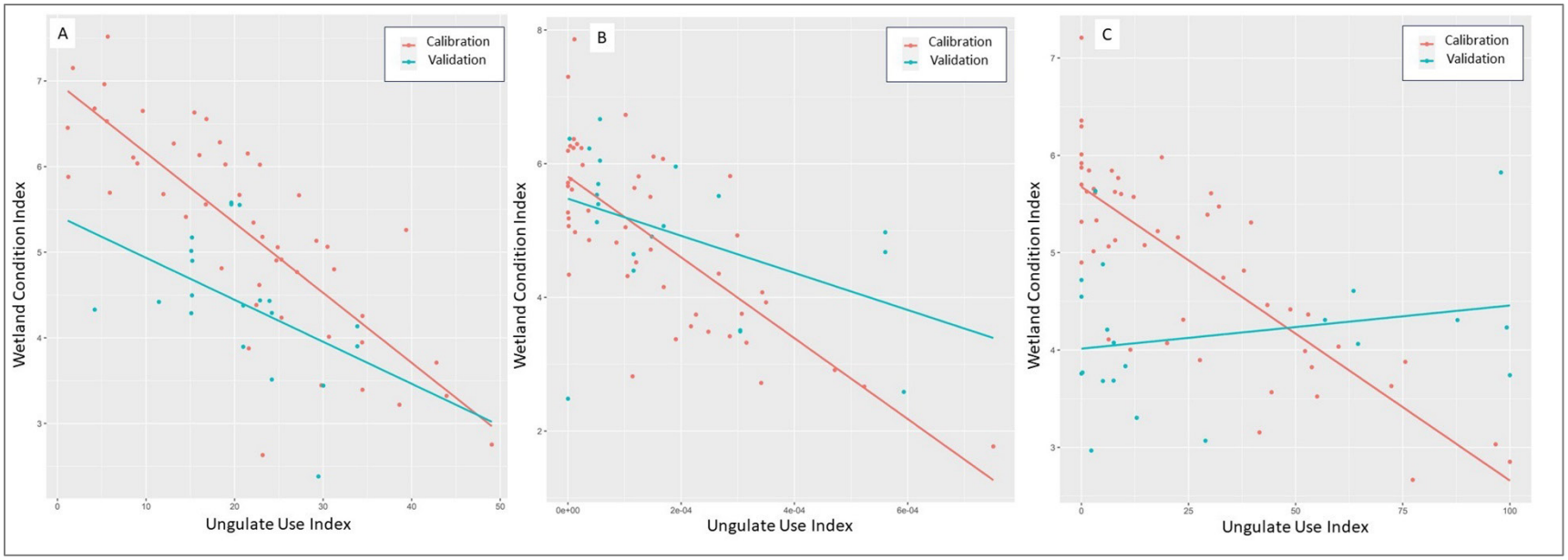


Figure 41. Comparison of validations of an herbaceous Wetland Condition Index (WCI) from three different Ungulate Use Indices (UUIs). (A) camera-like UUI (this is the final WCI model presented in the main narrative); (B) dung-only UUI (this is presented in more detail in Appendix D); (C) qualitative UUI. Comparisons with more similar slopes are better validated WCI models. NPS

Third, where we do not have sufficient sample sizes to perform the formal validation described above, we randomly subsample (i.e., 1000 times) all sample events available (creating UUI, vegetation metrics, and covariate datasets). We then re-estimate the WCI model using each of these random subsets of samples and compare the slopes and interaction with the original model. We average each of the interaction term p-values and treat this as an approximation to the method described above. This is the main method available for woody model validation. Comparisons become a matter of degree with this method, as, given the sample size limitations, most mean interaction p-values are above 0.10. This mean p-value was highest (suggesting it was the "most nonsignificant") for the camera-like UUI WCI ($p = 0.85$). The dung-only WCI was slightly lower ($p = 0.67$), while a qualitative UUI was still lower ($p = 0.56$). This method and results are not ideal and we also rely on evaluation of model quality (r, adjusted r^2, RMSE) and component metrics as stated above.

Appendix B: Environmental Data and Adjustment

Appendix B summarizes key select environmental data used in Ungulate Management Plan (UMP) baseline analyses, including any additional modeling of variables used in this report.

Climate and water balance

Although temperature and precipitation are often used to characterize the climatic context of a study area, water balance (WB) or water cycle variables have been shown to be stronger indicators of ecological processes than temperature and precipitation alone. Water balance variables incorporate the interaction of temperature and precipitation with topographic and edaphic (i.e., soil-related) properties that control temporal water availability in wetlands (Dobrowski 2011; Munson et al., 2015; Thoma et al. 2020). For example, stream flow in much of western North America is controlled by the abundance and timing of snow melt that occurs months after winter precipitation (Hostetler and Alder 2016); vegetation growth is closely linked to soil moisture and water deficit (Daubenmire 1968; Littell et al. 2008; Stephenson 1998), and fire is more closely related to aridity than precipitation (Littell et al. 2016; Williams et al. 2015), although wetting events diminish fire potential (Holden et al. 2018).

The water cycle within a watershed or a wetland site has several intuitive connections to groundwater depths. This is most obvious in wetlands with a surface water-driven hydrology strongly influenced by input from adjacent streams or rivers. It is less obvious in groundwater dominated wetland systems. However, groundwater input to a wetland also ultimately originates from the water cycle in a watershed, with likely complex spatial and temporal lags in these connections. For example, groundwater takes more time to move through a watershed through shallow aquifers or via soil moisture dynamics. Therefore, water balance parameters from a previous period may be more relevant to a current day depth to water (DTW) for groundwater dominated sites.

We estimate the components of the water cycle (Figure 42, Table 9) using equations outlined by Lutz (2010) as implemented in Thoma et al. (2020). We first derive precipitation and temperature from DAYMET version 4 (Thornton et al. 2018) in the 1 km^2 grid cell that included each site. The WB model partitions precipitation (P) falling on this cell into rain or snow, following Jennings et al. (2018), the latter of which accumulates until temperatures become warm enough to melt (Hock 2003). Subsequent steps in the WB process treat the movement of water from this grid cell into the wetland sentinel site.

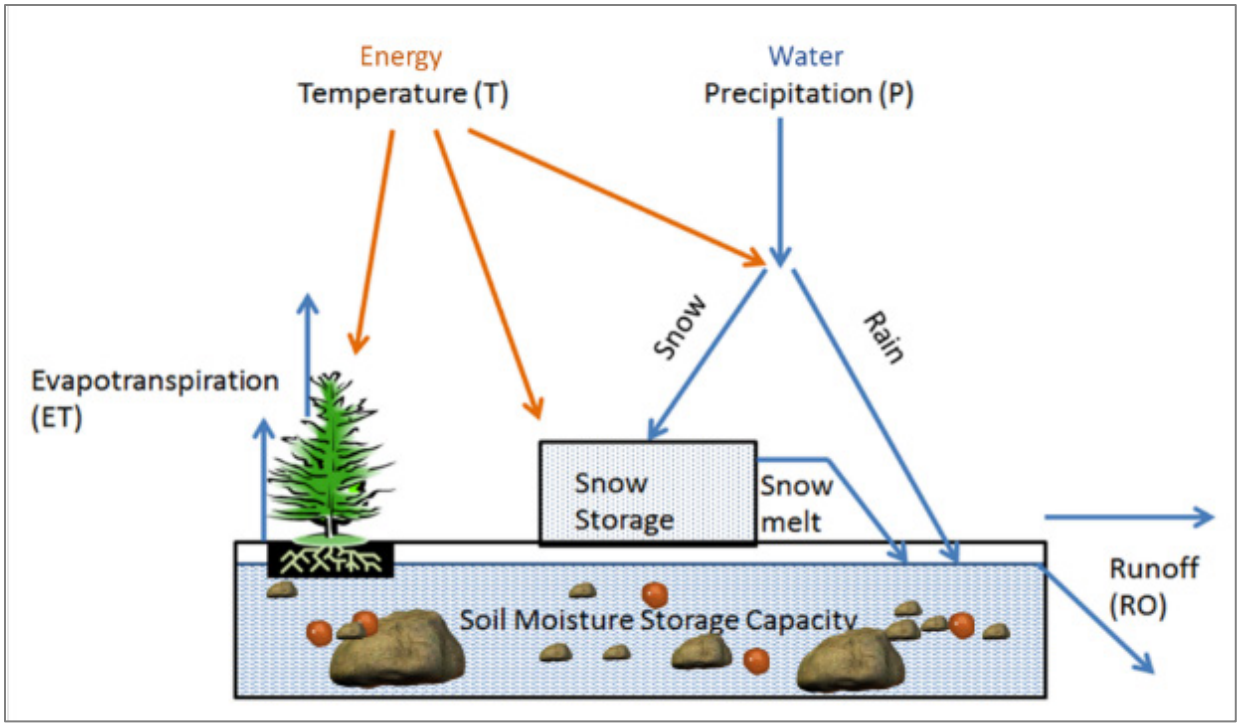


Figure 42. Water balance schematic adapted from Gray and McCabe (2010). NPS

Table 9. Summary of water balance variables used in the Rocky Mountain Network's wetland ecological integrity protocol at Great Sand Dunes National Park and Preserve, Colorado.

Water balance variable (units)	**Description**
Evapotranspiration (actual ([ET] and potential [PET]) (mm)	Evapotranspiration (ET) is the movement (loss) of water from both plant transpiration and soil evapotranspiration. PET is the "conceptual maximum" water loss from a large homogeneous vegetation-covered area that never lacks water and represents the climatic demand for water relative to the available energy. AET is the realized loss of water from soil via evaporation and transpiration.
Runoff (mm)	The amount of water that leaves a system exceeding water use by plants and storage in soils. It is estimated as the daily change in soil water, minus AET, plus direct runoff (i.e., from impervious surfaces).
Drainage (mm)	Runoff accumulated across days via base ("slow") and event-based ("fast") runoff.
Climatic water deficit (mm)	Unmet evaporative demand for water; what vegetation would use but does not have; estimated as PET−AET.
Soil moisture (mm)	Water stored in soil (mm) given idealized loss from soil via PET.
Growing degree days (degree C)	Amount of energy available in a day for plant growth; estimates the accumulation of heat units required for plant growth and development or temperature above a base temperature threshold that is necessary for plant growth.

Several parameters in the WB model come from readily available GIS data, such as slope or aspect, or field data, such as vegetative cover—these scale the relatively coarse climate variables (T and P; temperature and precipitation) from DAYMET to more localized edaphic conditions and improve WB data. We also conduct a series of model calibrations to improve WB output relating drainage or other water balance variables to depth to water. Trial work has suggested that direct runoff and water holding capacity parameters are most sensitive within this calibration. We optimize bivariate fits of these terms to response(s) by iterating these parameters singly and as pairs across a range of values, maximizing adjusted R^2. We then do the same for the "quick" and "slow" drainage coefficient to calibrate drainage—these coefficients can have a strong effect on how well drainage fits a response. This calibration may be done in a relatively simple heads-up method using initial conditions that we have seen work well for typical Rocky Mountain Network park wetlands. It may also be done using an optimization routine that steps through all possible combinations of parameters, checking for the best relationship between drainage parameters and depth to water.

We estimate an initial direct runoff parameter, or the portion of any precipitation that does not enter the water cycle but instead leaves the system, via a USDA Natural Resources Conservation Service (NRCS) curve number (CN) from vegetation type and hydric soil class and methods developed in NRCS (2017). The WB model then calculates a potential evapotranspiration following Oudin et al. (2010) as the amount of water that could be evaporated and transpired with available energy if water was unlimited. Potential evapotranspiration uses slope and aspect summarized across the catchment as derived from a 10-m digital elevation model to better estimate a heat load from solar radiation. We use an estimate of soil water holding capacity as the quantity of water stored in the top meter of soil as defined by NRCS (2021). The model then runs for each day in the period of record using this soil water to estimate actual evapotranspiration, weighted by shade cover estimated from Rocky Mountain Network wetland ecological integrity (WEI) monitoring plots. Daily climatic water deficit is estimated as the amount of additional water vegetation would use if available, calculated as the difference between actual and potential evapotranspiration (Stephenson 1998). Water that exceeds soil storage capacity after evapotranspiration creates runoff. Finally, runoff values are used to accumulate a "drainage" term across time following Croke et al. (2005). Drainage is built as a unit hydrograph with coefficients for "quick," or event-based flow, and "slow," or base flow, that are used as weights on the runoff value for each day.

Productivity

Productivity was estimated by a Normalized Difference Vegetation Index (NDVI) model adjusted from cage-based offtake data. The NDVI uses satellite data and the reflectance of vegetation to estimate productivity as a "greenness" index. We developed NDVI for all locations in a 2005–2008 clip plot data from Schoenecker et al. (2012, 2015). We then estimated a general additive model (GAM) that accounted for non-linear relationship and select covariates (ungulate use zones, whether a site was in an exclosure or not, and wetland type). The GAM model was highly significant and explained most of the variation in the data (adjusted $r^2 = 0.79$). This model was then used to predict a clip plot like production at all UMP sites from 2016 to 2019.

Environmental adjustment

Adjusting response variables for confounded effects of environmental gradients is a central part of UMP analysis. Adjustment is embedded in the WCI algorithms as it assures that the component metrics in a WCI are included because of their response to ungulate use, not some extraneous driver of less interest to park management. Likewise, hand-picked (HP) metrics must be adjusted. These both use an identical method. R code for each step is available from the Rocky Mountain Network on request.

Why is this needed? As a simple example, elevation influences wetland vegetation (i.e., growing season length). If we do not remove the elevation signal from measures of vegetation condition, we cannot know if changes in vegetation given park management of ungulates are due to a site's elevation or differential ungulate use along the elevation gradient. Our WCI and HP metrics include adjustment for each of these environmental variables as measured at each baseline and future sample event.

Our 10 environmental variables were chosen because of statistical patterns and relationships with ungulate use and wetland condition. We include depth to ground water (DTW) as a master wetland variable fundamentally driving vegetation type and condition—wetlands are not wetlands without sufficient and persistent ground water. Sodium absorption ratio (SAR) is a measure of soil salinity and controls for GRSA's important saline soils. Humans set the environmental template for wetlands and directly control ungulate use (i.e., fences). We use a remotely sensed cumulative measure of human use in and around a site called the Landscape Disturbance Index (CNHP 2021). We include both litter and bare ground as small-scale indicators of the physical nature of ground cover that can have strong control on plant germination. As noted, elevation has fundamental direct and indirect controls on wetland condition and how ungulates use wetlands. Production has well-documented (i.e., Grace et al. 2016) relationships with vegetation species richness and composition and may be stimulated by ungulate use of vegetation (Frank et al. 2016). We found that a five-year mean production response modeled from remotely sensed greenness data and USGS clip plot data was most predictive. Finally, we include three climate or water balance variables given clear connections between climate or the water cycle, vegetation, and ungulate use. Soil moisture from a water balance model at each site was best correlated as a five-year average. Another water balance variable, climatic deficit or the unmet evaporative water demand was best as a three-year lagged term. Temperature was strongly related as growing degree days, again averaged over a five-year window.

Our adjustment methods use linear multiple regression-based approaches as described in Schoolmaster et al. (2012), Schoolmaster, Grace, Schweiger, Mitchell et al. (2013), and Schoolmaster Grace, Schweiger, Guntenspergen et al. (2013). We first find the environmental variables out of the 10 we determined were likely most important to control for in the UMP that, along with UUI, have an effect on a response (either a potential component or an identified HP metric). This is done via model selection and a custom approach (similar to p-value based stepwise regression using lm() and step() in R) that results in an intercept and set of coefficients for UUI and any environmental variables included by the process (which can be none). We then apply these sets of coefficients to raw data and predict adjusted values (again in a custom function that is similar to

predict() in R). Finally, we scale the predicted values to range from 0 to 10 following Blocksom (2003). This allows metrics with naturally often very different ranges to be treated in a consistent way, enhances model stability, and reduces multicollinearity.

Using the density of browsed willow and cottonwood, the UUI, and our 10 environmental variables, we estimate a final model as in Table 7. This model has an adjusted r^2 of 0.52 and all variables in it have p-values well below 0.05. To further understand a particular adjustment, we can estimate partial residuals and the importance of each predictor. Figure 43a–e shows partial residual plots of the five non-zero coefficient valued predictors for density of browsed willow and cottonwood. Partial plots show the effect of each predictor given a unit change in the predictor. Density of browsed willow and cottonwood increases with UUI, decreases with ground water depth (DTW; site getting wetter), increases with elevation, increases with growing degree days (air temperature), and increases with soil moisture. These are all intuitive except for DTW. Perhaps wetter sites may be more productive, allowing *Salicaceae* to recover faster from browsing and thus show it less. Or where water tables are lower, root systems may be more developed, leading to plants that are able to sustain browsing and rebrowsing for a longer time. Plants that have continuous heavy browsing end up with a lot of decadent parts, leading them to "look" more browsed than plants that have a shorter history of browsing or less dieback (due to better water conditions) due to browsing. Figure 43f shows a bar plot of the importance as a proportion of the five non-zero coefficient valued predictors for density of browsed willow and cottonwood. Soil moisture is the most important predictor (by about 2x) of browsed density. This may be again because of productivity effects. These results show the implications of failing to adjust for environmental covariates in understanding the effects of UUI on a metric like the density of browsed willow and cottonwood.

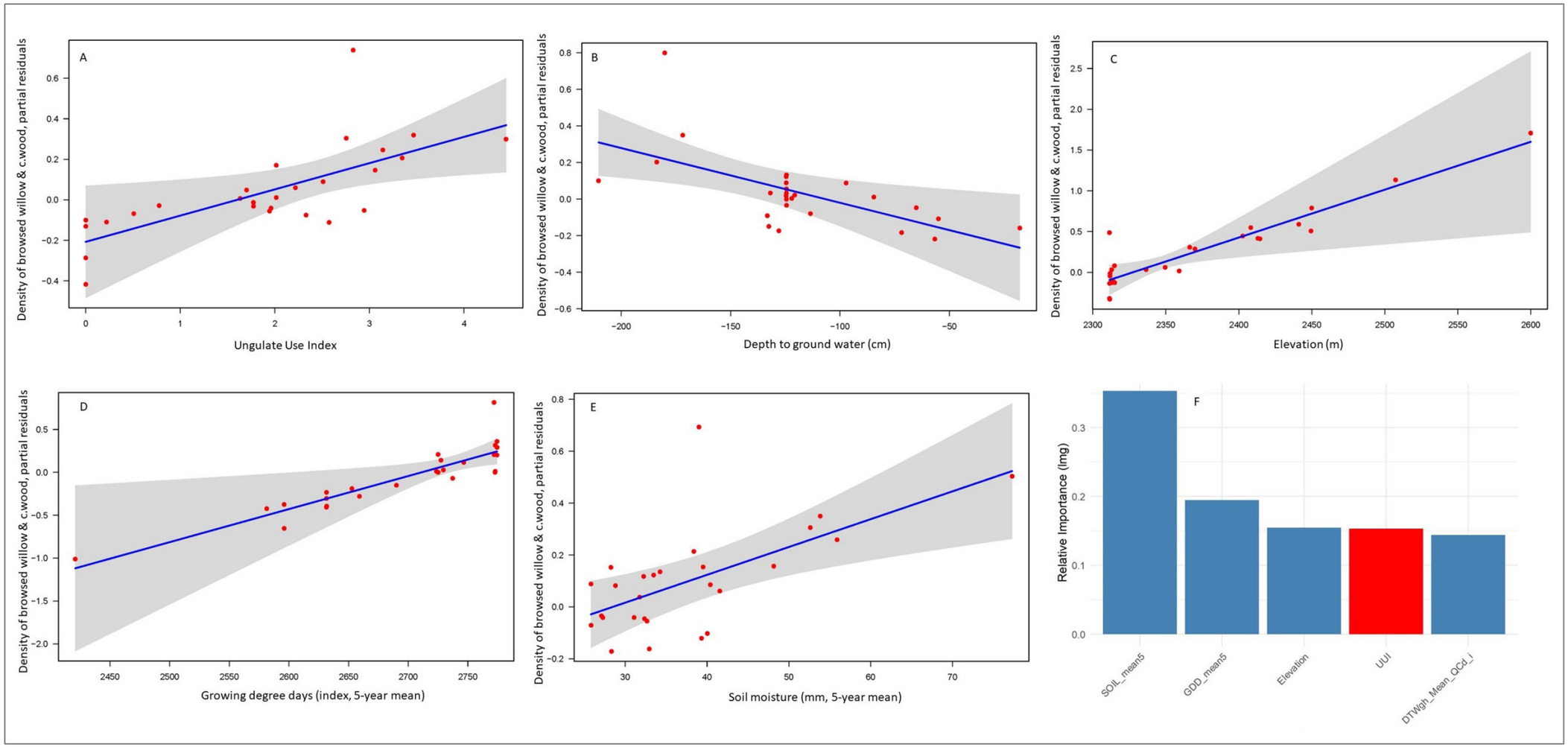


Figure 43. Example of an environmental adjustment of the metric, density of browsed willow and cottonwood. Partial residual plots of (A) UUI, (B) ground water depth, (C) elevation, (D) growing degree days, and (E) soil moisture. Panel (F) shows that UUI is only the fourth most important, which shows the need for this adjustment. Labels in panel F are as follows: “SOIL_mean5” = soil moisture, GDD_mean5 = growing degree days, and DTWgh_Mean_QCd = ground water depth. NPS

Appendix C: Vegetation Species List

Table 10 lists vascular plants documented during wetland monitoring at sentinel sites in Great Sand Dunes National Park and Preserve from 2016 to 2019.

Table 10. Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Alismataceae	*Sagittaria cuneata*	SACU	arumleaf arrowhead	6	Native	1	–	–	5	0.50	0.50	0.19	0.42
Alliaceae	*Allium cernuum*	ALCE2	nodding onion	5	Native	4	–	–	4	0.50	0.50	0.31	0.38
Alliaceae	*Allium geyeri*	ALGE	Geyer's onion	5	Native	4	–	–	6	0.69	1.67	0.87	3.79
Anacardiaceae	*Rhus trilobata*	RHTR	skunkbush sumac	5	Native	5	–	–	2	1.50	2.50	3.92	7.50
Anacardiaceae	*Rhus trilobata* var. *trilobata*	RHTRT	skunkbush sumac	5	Native	5	–	–	6	2.72	9.33	3.45	9.82
Apiaceae	*Berula erecta*	BEER	cutleaf waterparsnip	5	Native	1	2	–	4	1.21	2.00	0.41	0.96
Apiaceae	*Conioselinum scopulorum*	COSC2	Rocky Mountain hemlockparsley	7	Native	2	–	–	1	1.00	1.00	0.13	0.13
Apocynaceae	*Asclepias speciosa*	ASSP	showy milkweed	3	Native	3	–	–	3	0.50	0.50	0.36	0.61
Araceae	*Lemna minor*	LEMI3	common duckweed	2	Native	1	–	–	9	1.54	5.00	0.45	1.13
Asteraceae	*Achillea millefolium*	ACMI2	common yarrow	4	Native	4	–	–	15	1.77	13.43	1.54	12.12
Asteraceae	*Acroptilon repens*	ACRE3	hardheads	0	Nonnative	–	4	8	1	0.50	0.50	2.42	2.42
Asteraceae	*Almutaster pauciflorus*	ALPA14	alkali marsh aster	4	Native	2	–	–	23	0.76	1.94	1.12	5.28
Asteraceae	*Ambrosia acanthicarpa*	AMAC2	flatspine bur ragweed	4	Native	–	–	–	10	0.53	0.67	1.41	3.76
Asteraceae	*Ambrosia tomentosa*	AMTO3	skeletonleaf bur ragweed	3	Native	–	–	–	1	0.50	0.50	0.13	0.13
Asteraceae	*Antennaria microphylla*	ANMI3	littleleaf pussytoes	5	Native	–	–	–	1	0.50	0.50	0.26	0.26

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Asteraceae	*Artemisia biennis* var. *biennis*	ARBIB	biennial wormwood	0	Nonnative	2	2	–	2	1.42	2.33	1.02	1.77
Asteraceae	*Artemisia campestris*	ARCA12	field sagewort	5	Native	4	–	–	3	0.50	0.50	0.74	1.27
Asteraceae	*Artemisia cana* ssp. *cana*	ARCAC5	silver sagebrush	5	Native	4	–	–	3	0.67	1.00	0.44	0.58
Asteraceae	*Artemisia carruthii*	ARCA14	Carruth's sagewort	5	Native	–	–	–	2	0.50	0.50	0.45	0.61
Asteraceae	*Artemisia dracunculus*	ARDR4	tarragon	3	Native	4	–	–	6	2.45	4.88	4.13	14.77
Asteraceae	*Artemisia frigida*	ARFR4	prairie sagewort	4	Native	–	–	–	10	1.35	3.10	1.39	4.70
Asteraceae	*Artemisia ludoviciana*	ARLU	white sagebrush	4	Native	4	–	–	11	1.39	5.00	1.17	4.14
Asteraceae	*Bidens cernua*	BICE	nodding beggartick	5	Native	1	2	–	1	2.00	2.00	1.29	1.29
Asteraceae	*Chrysothamnus linifolius*	CHLI3	spearleaf rabbitbrush	6	Native	3	–	–	1	0.00	0.00	0.00	0.00
Asteraceae	*Cirsium arvense*	CIAR4	Canada thistle	0	Nonnative	3	4	8	46	2.29	13.50	3.52	35.69
Asteraceae	*Cirsium canescens*	CICA11	prairie thistle	6	Native	–	–	–	1	2.50	2.50	3.08	3.08
Asteraceae	*Conyza canadensis*	COCA5	Canadian horseweed	1	Native	4	3	–	17	0.54	0.75	0.69	2.69
Asteraceae	*Crepis runcinata* ssp. *runcinata*	CRRUR	fiddleleaf hawksbeard	6	Native	4	–	–	38	3.65	25.00	6.08	44.20
Asteraceae	*Ericameria nauseosa*	ERNA10	rubber rabbitbrush	3	Native	–	–	–	58	3.00	18.00	3.87	37.31
Asteraceae	*Erigeron flagellaris*	ERFL	trailing fleabane	3	Native	4	–	–	5	0.50	0.50	0.55	1.08
Asteraceae	*Erigeron glabellus*	ERGL2	streamside fleabane	6	Native	3	–	–	1	0.50	0.50	0.43	0.43
Asteraceae	*Erigeron lonchophyllus*	ERLO	shortray fleabane	5	Native	2	–	–	5	0.77	1.83	0.50	1.09
Asteraceae	*Gnaphalium palustre*	GNPA	western marsh cudweed	5	Native	2	–	–	1	0.50	0.50	0.15	0.15
Asteraceae	*Helianthus petiolaris*	HEPE	prairie sunflower	2	Native	–	–	–	1	0.50	0.50	0.07	0.07

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Asteraceae	*Heterotheca villosa*	HEVI4	hairy false goldenaster	3	Native	–	–	–	10	1.15	4.00	1.99	6.00
Asteraceae	*Hymenopappus filifolius*	HYFI	fineleaf hymenopappus	6	Native	–	–	–	1	0.50	0.50	0.50	0.50
Asteraceae	*Iva axillaris*	IVAX	povertyweed	2	Native	4	–	–	1	20.00	20.00	8.60	8.60
Asteraceae	*Lactuca serriola*	LASE	prickly lettuce	0	Nonnative	4	3	2	5	2.90	11.83	2.21	9.40
Asteraceae	*Lactuca tatarica* var. *pulchella*	LATAP	blue lettuce	3	Native	3	–	–	14	2.18	8.00	2.00	8.12
Asteraceae	*Lygodesmia juncea*	LYJU	rush skeletonplant	4	Native	–	–	–	2	0.50	0.50	0.70	0.78
Asteraceae	*Nothocalais cuspidata*	NOCU	prairie false dandelion	4	Native	–	–	–	7	0.51	0.56	0.74	2.36
Asteraceae	*Packera fendleri*	PAFE4	Fendler's ragwort	4	Native	–	–	–	1	0.50	0.50	0.17	0.17
Asteraceae	*Packera multilobata*	PAMU11	lobeleaf groundsel	5	Native	–	–	–	1	0.50	0.50	0.61	0.61
Asteraceae	*Packera paupercula*	PAPA20	balsam groundsel	7	Native	2	–	–	2	0.85	1.08	4.09	6.50
Asteraceae	*Packera pseudaurea* var. *flavula*	PAPSF	falsegold groundsel	7	Native	2	–	–	1	2.00	2.00	2.09	2.09
Asteraceae	*Packera tridenticulata*	PATR7	threetooth ragwort	7	Native	–	–	–	19	0.63	1.25	0.87	3.13
Asteraceae	*Pyrrocoma lanceolata* var. *lanceolata*	PYLAL	lanceleaf goldenweed	8	Native	3	–	–	8	1.05	2.83	1.95	12.14
Asteraceae	*Rudbeckia laciniata* var. *ampla*	RULAA	cutleaf coneflower	6	Native	3	–	–	1	0.75	0.75	0.25	0.25
Asteraceae	*Senecio multicapitatus*	SEMU2	–	6	Native	–	–	–	5	0.51	0.57	1.80	4.30
Asteraceae	*Senecio spartioides*	SESP3	broom-like ragwort	5	Native	–	–	–	3	1.25	2.75	0.90	2.13
Asteraceae	*Solidago canadensis*	SOCA6	Canada goldenrod	5	Native	4	–	–	1	1.25	1.25	1.18	1.18
Asteraceae	*Sonchus oleraceus*	SOOL	common sowthistle	0	Nonnative	5	3	–	3	6.42	10.00	3.18	4.44
Asteraceae	*Sonchus uliginosus*	SOUL5	–	0	Nonnative	4	–	–	2	3.50	6.50	0.63	1.20

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Asteraceae	*Stephanomeria pauciflora*	STPA4	brownplume wirelettuce	5	Native	–	–	–	3	0.67	1.00	0.71	1.84
Asteraceae	*Symphyotrichum ascendens*	SYAS3	western aster	5	Native	4	–	–	2	0.63	0.75	0.15	0.22
Asteraceae	*Symphyotrichum ciliatum*	SYCI2	rayless alkali aster	7	Native	2	–	–	1	0.50	0.50	0.72	0.72
Asteraceae	*Symphyotrichum falcatum*	SYFA	white prairie aster	4	Native	4	–	–	1	1.07	1.07	3.23	3.23
Asteraceae	*Symphyotrichum lanceolatum* ssp. *hesperium*	SYLAH	white panicle aster	5	Native	1	–	–	12	0.63	1.17	1.12	5.04
Asteraceae	*Taraxacum officinale*	TAOF	common dandelion	0	Nonnative	4	3	–	12	0.51	0.60	0.60	1.88
Asteraceae	*Tragopogon dubius*	TRDU	yellow salsify	0	Nonnative	–	2	4	9	0.50	0.50	0.43	1.05
Betulaceae	*Alnus incana* ssp. *tenuifolia*	ALINT	thinleaf alder	6	Native	2	–	–	2	16.00	30.00	6.74	8.47
Boraginaceae	*Cryptantha crassisepala* var. *elachantha*	CRCRE	thicksepal cryptantha	1	Native	–	–	–	1	0.50	0.50	0.33	0.33
Boraginaceae	*Cryptantha fendleri*	CRFE3	sanddune cryptantha	3	Native	–	–	–	9	0.72	1.50	0.56	1.27
Boraginaceae	*Lappula occidentalis*	LAOC3	flatspine stickseed	2	Native	–	–	–	1	0.50	0.50	1.36	1.36
Boraginaceae	*Oreocarya pustulosa*	ORPU14	–	8	Native	–	–	–	3	0.50	0.50	0.26	0.33
Boraginaceae	*Plagiobothrys scouleri* var. *hispidulus*	PLSCH	sleeping popcornflower	3	Native	2	–	–	1	2.83	2.83	2.15	2.15
Brassicaceae	*Cardamine breweri*	CABR6	Brewer’s bittercress	7	Native	2	–	–	1	5.00	5.00	0.61	0.61
Brassicaceae	*Cardamine pensylvanica*	CAPE3	Pennsylvania bittercress	9	Native	2	–	–	1	20.00	20.00	2.58	2.58

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Brassicaceae	*Descurainia californica*	DECA6	Sierra tansymustard	3	Native	–	–	–	2	0.50	0.50	0.07	0.07
Brassicaceae	*Descurainia incisa*	DEIN13	–	2	Native	–	–	–	2	0.50	0.50	1.14	1.37
Brassicaceae	*Descurainia pinnata* ssp. *brachycarpa*	DEPIB	western tansymustard	2	Native	–	–	–	3	0.50	0.50	0.36	0.61
Brassicaceae	*Erysimum capitatum*	ERCA14	sanddune wallflower	5	Native	–	–	–	2	0.50	0.50	0.42	0.50
Brassicaceae	*Lepidium alyssoides*	LEAL4	mesa pepperwort	3	Native	–	–	–	1	0.50	0.50	0.50	0.50
Brassicaceae	*Lepidium densiflorum*	LEDE	common pepperweed	0	Nonnative	4	3	–	3	0.50	0.50	0.08	0.11
Brassicaceae	*Lepidium latifolium*	LELA2	broadleaved pepperweed	0	Nonnative	3	4	9	4	7.54	20.94	27.65	62.27
Brassicaceae	*Lepidium montanum*	LEMO2	mountain pepperweed	5	Native	–	–	–	1	0.50	0.50	1.96	1.96
Brassicaceae	*Nasturtium officinale*	NAOF	watercress	0	Nonnative	1	–	4	4	0.75	1.00	0.28	0.45
Brassicaceae	*Rorippa sinuata*	ROSI2	spreading yellowcress	4	Native	3	–	–	1	0.50	0.50	0.54	0.54
Brassicaceae	*Thelypodium integrifolium*	THIN	entireleaved thelypody	6	Native	2	–	–	4	0.88	2.00	0.16	0.19
Cactaceae	*Opuntia polyacantha*	OPPO	plains pricklypear	5	Native	–	–	–	5	0.60	1.00	0.40	0.61
Campanulaceae	*Campanula parryi* var. *parryi*	CAPAP2	Parry's bellflower	7	Native	3	–	–	1	0.50	0.50	0.15	0.15
Cannabaceae	*Humulus lupulus* var. *neomexicanus*	HULUN	common hop	5	Native	4	–	–	1	0.50	0.50	0.08	0.08
Capparaceae	*Cleome multicaulis*	CLMU	slender spiderflower	4	Native	2	–	–	29	1.83	18.00	1.50	7.29
Capparaceae	*Cleome serrulata*	CLSE	Rocky Mountain beeplant	2	Native	4	–	–	30	0.66	2.00	0.43	2.15
Capparaceae	*Cleomella angustifolia*	CLAN	narrowleaf rhombopod	6	Native	3	–	–	1	1.00	1.00	0.13	0.13
Caryophyllaceae	*Moehringia lateriflora*	MOLA6	bluntleaf sandwort	8	Native	3	–	–	1	1.00	1.00	0.17	0.17

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Caryophyllaceae	*Stellaria crassifolia*	STCR	fleshy starwort	7	Native	2	–	–	1	0.75	0.75	0.18	0.18
Caryophyllaceae	*Stellaria longifolia*	STLO	longleaf starwort	7	Native	2	–	–	2	0.85	1.20	0.91	1.05
Caryophyllaceae	*Stellaria longipes*	STLO2	longstalk starwort	8	Native	2	–	–	9	0.61	1.17	0.58	1.26
Chenopodiaceae	*Chenopodium berlandieri* var. *zschackii*	CHBEZ	Zschack's goosefoot	2	Native	–	–	–	2	0.50	0.50	0.24	0.33
Chenopodiaceae	*Chenopodium fremontii*	CHFR3	Fremont's goosefoot	6	Native	4	–	–	6	0.46	0.50	0.45	1.23
Chenopodiaceae	*Chenopodium leptophyllum*	CHLE4	narrowleaf goosefoot	5	Native	4	–	–	10	0.54	0.75	1.02	3.50
Chenopodiaceae	*Chenopodium pratericola*	CHPR5	desert goosefoot	4	Native	–	–	–	4	0.50	0.50	0.45	0.87
Chenopodiaceae	*Chenopodium rubrum*	CHRU	red goosefoot	2	Native	2	–	–	5	0.50	0.50	0.61	2.15
Chenopodiaceae	*Kochia scoparia*	KOSC	–	0	Nonnative	3	4	3	1	0.50	0.50	0.15	0.15
Chenopodiaceae	*Salsola tragus*	SATR12	prickly Russian thistle	0	Nonnative	4	4	–	18	0.50	0.50	1.13	7.46
Chenopodiaceae	*Sarcobatus vermiculatus*	SAVE4	greasewood	4	Native	4	–	–	16	4.55	20.25	6.02	41.18
Chenopodiaceae	*Suaeda calceoliformis*	SUCA2	Pursh seepweed	3	Native	2	–	–	19	0.69	1.60	0.64	2.70
Cupressaceae	*Juniperus scopulorum*	JUSC2	Rocky Mountain juniper	5	Native	–	–	–	7	4.48	7.17	4.94	14.46
Cyperaceae	*Amphiscirpus nevadensis*	AMNE3	Nevada bulrush	7	Native	1	–	–	13	5.19	31.43	5.80	48.40
Cyperaceae	*Carex aquatilis*	CAAQ	water sedge	6	Native	1	–	–	13	5.06	26.00	5.33	31.73
Cyperaceae	*Carex athrostachya*	CAAT3	slenderbeak sedge	7	Native	2	–	–	1	0.50	0.50	0.25	0.25
Cyperaceae	*Carex bebbii*	CABE2	Bebb's sedge	7	Native	1	–	–	2	0.50	0.50	0.20	0.31
Cyperaceae	*Carex ebenea*	CAEB	ebony sedge	4	Native	–	–	–	1	3.50	3.50	2.44	2.44

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Cyperaceae	*Carex inops* ssp. *heliophila*	CAINH2	sun sedge	7	Native	–	–	–	1	0.50	0.50	0.15	0.15
Cyperaceae	*Carex nebrascensis*	CANE2	Nebraska sedge	5	Native	1	–	–	27	19.31	85.00	15.15	70.79
Cyperaceae	*Carex pellita*	CAPE42	woolly sedge	6	Native	1	–	–	9	4.87	23.14	13.25	70.90
Cyperaceae	*Carex praegracilis*	CAPR5	clustered field sedge	5	Native	2	–	–	54	4.02	25.83	6.36	28.70
Cyperaceae	*Carex simulata*	CASI2	analogue sedge	6	Native	1	–	–	34	9.82	75.00	14.39	94.44
Cyperaceae	*Carex utriculata*	CAUT	Northwest Territory sedge	5	Native	1	–	–	19	18.14	72.14	14.68	80.93
Cyperaceae	*Eleocharis acicularis*	ELAC	needle spikerush	5	Native	1	–	–	1	0.83	0.83	0.91	0.91
Cyperaceae	*Eleocharis palustris*	ELPA3	common spikerush	3	Native	1	–	–	18	9.11	71.31	11.52	59.52
Cyperaceae	*Eleocharis pauciflora*	ELPA6	–	8	Native	1	–	–	7	8.32	20.00	1.68	3.25
Cyperaceae	*Schoenoplectus acutus*	SCAC3	hardstem bulrush	3	Native	1	–	–	10	1.33	5.00	0.59	3.11
Cyperaceae	*Schoenoplectus americanus*	SCAM6	chairmaker’s bulrush	4	Native	1	–	–	1	1.13	1.13	1.65	1.65
Cyperaceae	*Schoenoplectus pungens*	SCPU10	common threesquare	4	Native	1	–	–	25	10.21	55.00	12.37	53.68
Cyperaceae	*Scirpus microcarpus*	SCMI2	panicled bulrush	5	Native	1	–	–	1	1.40	1.40	1.17	1.17
Equisetaceae	*Equisetum arvense*	EQAR	field horsetail	4	Native	3	–	–	4	0.50	0.50	0.48	0.69
Equisetaceae	*Equisetum laevigatum*	EQLA	smooth horsetail	4	Native	2	–	–	32	0.71	5.00	1.02	7.75
Equisetaceae	*Equisetum variegatum* var. *variegatum*	EQVAV	variegated scouringrush	5	Native	2	–	–	3	0.50	0.50	1.23	2.70
Euphorbiaceae	*Chamaesyce fendleri*	CHFE3	Fendler’s sandmat	5	Native	–	–	–	1	0.50	0.50	0.07	0.07
Euphorbiaceae	*Chamaesyce serpyllifolia*	CHSE6	thymeleaf sandmat	2	Native	–	2	–	1	#DIV/0!	0.00	#DIV/0!	0.00

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Euphorbiaceae	*Euphorbia brachycera*	EUBR	horned spurge	6	Native	–	–	–	1	0.50	0.50	0.58	0.58
Fabaceae	*Astragalus bodinii*	ASBO	Bodin's milkvetch	8	Native	2	–	–	6	2.22	6.00	3.95	13.46
Fabaceae	*Astragalus ceramicus*	ASCE	painted milkvetch	7	Native	–	–	–	3	0.50	0.50	0.33	0.78
Fabaceae	*Astragalus eucosmus*	ASEU2	elegant milkvetch	7	Native	4	–	–	1	0.50	0.50	0.52	0.52
Fabaceae	*Astragalus hallii* var. *hallii*	ASHAH	Hall's milkvetch	4	Native	–	–	–	1	3.00	3.00	0.71	0.71
Fabaceae	*Glycyrrhiza lepidota*	GLLE3	American licorice	3	Native	3	–	–	1	0.50	0.50	0.14	0.14
Fabaceae	*Psoralidium lanceolatum*	PSLA3	lemon scurfpea	5	Native	–	–	–	20	1.41	3.00	2.67	14.02
Fabaceae	*Sphaerophysa salsula*	SPSA3	alkali swainsonpea	0	Nonnative	5	–	–	2	1.00	1.00	0.31	0.32
Fabaceae	*Thermopsis rhombifolia*	THRH	prairie thermopsis	5	Native	4	–	–	5	2.85	6.00	3.34	9.23
Fabaceae	*Trifolium repens*	TRRE3	white clover	0	Nonnative	3	3	4	12	1.39	6.63	1.65	9.60
Grossulariaceae	*Ribes cereum*	RICE	wax currant	6	Native	–	–	–	4	1.13	2.00	0.68	1.23
Grossulariaceae	*Ribes inerme*	RIIN2	whitestem gooseberry	5	Native	3	–	–	3	1.04	1.88	0.64	1.25
Hydrophyllaceae	*Phacelia bakeri*	PHBA3	Baker's phacelia	7	Native	–	–	–	2	0.50	0.50	0.22	0.29
Iridaceae	*Iris missouriensis*	IRMI	Rocky Mountain iris	4	Native	2	–	–	36	4.14	35.00	4.31	33.65
Iridaceae	*Sisyrinchium demissum*	SIDE4	stiff blue-eyed grass	7	Native	1	–	–	3	0.67	1.00	0.16	0.18
Iridaceae	*Sisyrinchium montanum* var. *montanum*	SIMOM	strict blue-eyed grass	6	Native	3	–	–	1	0.50	0.50	0.32	0.32
Juncaceae	*Juncus arcticus* var. *balticus*	JUARB5	–	4	Native	2	–	–	94	12.17	80.00	20.30	82.47
Juncaceae	*Juncus bufonius*	JUBU	toad rush	3	Native	2	–	–	1	0.50	0.50	0.15	0.15
Juncaceae	*Juncus confusus*	JUCO2	Colorado rush	5	Native	3	–	–	3	0.50	0.50	0.52	1.08

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Juncaceae	*Juncus drummondii*	JUDR	Drummond's rush	6	Native	2	–	–	1	0.75	0.75	0.37	0.37
Juncaceae	*Juncus longistylis*	JULO	longstyle rush	6	Native	2	–	–	3	6.26	13.17	3.74	9.76
Juncaginaceae	*Triglochin maritima*	TRMA20	seaside arrowgrass	6	Native	1	–	–	19	0.65	1.22	0.66	2.70
Juncaginaceae	*Triglochin palustris*	TRPA28	marsh arrowgrass	7	Native	1	–	–	7	0.60	1.19	0.23	0.81
Lamiaceae	*Lycopus asper*	LYAS	rough bugleweed	5	Native	1	–	–	1	3.25	3.25	2.80	2.80
Lamiaceae	*Mentha ×piperita*	MEPI	peppermint	0	Nonnative	2	1	–	1	0.50	0.50	0.12	0.12
Lamiaceae	*Mentha arvensis*	MEAR4	wild mint	4	Native	2	–	–	14	1.05	4.50	0.83	3.16
Lamiaceae	*Stachys palustris* var. *pilosa*	STPAP6	–	6	Native	2	–	–	2	1.63	2.25	1.98	3.29
Malvaceae	*Sidalcea neomexicana*	SINE3	salt spring checkerbloom	5	Native	2	–	–	11	2.46	7.10	3.12	11.74
Montiaceae	*Montia chamissoi*	MOCH	water minerslettuce	8	Native	1	–	–	1	0.50	0.50	0.50	0.50
Myrsinaceae	*Glaux maritima*	GLMA	sea milkwort	7	Native	1	–	–	23	3.67	34.50	3.28	29.72
Nyctaginaceae	*Mirabilis linearis*	MILI3	narrowleaf four o'clock	5	Native	–	–	–	1	0.50	0.50	0.50	0.50
Nyctaginaceae	*Tripterocalyx micranthus*	TRMI6	smallflower sandverbena	6	Native	–	–	–	2	0.50	0.50	0.45	0.78
Onagraceae	*Epilobium brachycarpum*	EPBR3	tall annual willowherb	2	Native	3	–	–	1	0.50	0.50	0.31	0.31
Onagraceae	*Epilobium ciliatum* ssp. *ciliatum*	EPCIC	fringed willowherb	3	Native	2	–	–	21	1.17	5.93	1.60	17.47
Onagraceae	*Epilobium hornemannii*	EPHO	Hornemann's willowherb	6	Native	2	–	–	4	0.50	0.50	0.15	0.24
Onagraceae	*Epilobium lactiflorum*	EPLA3	milkflower willowherb	7	Native	2	–	–	1	0.50	0.50	0.05	0.05
Onagraceae	*Epilobium palustre*	EPPA	marsh willowherb	8	Native	1	–	–	3	0.50	0.50	0.64	1.05

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Onagraceae	*Oenothera coronopifolia*	OECO2	crownleaf evening primrose	4	Native	–	–	–	6	1.17	3.00	1.11	3.88
Onagraceae	*Oenothera pallida*	OEPA	pale evening primrose	4	Native	–	–	–	13	0.50	0.50	0.70	3.16
Orchidaceae	*Platanthera aquilonis*	PLAQ2	northern green orchid	7	Native	2	–	–	1	0.50	0.50	0.26	0.26
Orobanchaceae	*Orthocarpus luteus*	ORLU2	yellow owl's-clover	6	Native	4	–	–	9	0.67	1.00	1.03	3.93
Phrymaceae	*Mimulus floribundus*	MIFL2	manyflowered monkeyflower	10	Native	1	–	–	1	0.50	0.50	0.08	0.08
Phrymaceae	*Mimulus glabratus*	MIGL	roundleaf monkeyflower	5	Native	1	–	–	3	2.17	5.00	0.33	0.45
Phrymaceae	*Mimulus guttatus*	MIGU	seep monkeyflower	8	Native	1	–	–	5	0.83	1.17	0.28	0.61
Phrymaceae	*Mimulus tilingii*	MITI	Tiling's monkeyflower	10	Native	1	–	–	2	0.75	1.00	0.17	0.17
Plantaginaceae	*Hippuris vulgaris*	HIVU2	common mare's-tail	6	Native	1	–	–	5	1.00	3.00	0.18	0.40
Plantaginaceae	*Penstemon barbatus*	PEBA2	beardlip penstemon	7	Native	–	–	–	3	0.50	0.50	0.15	0.17
Plantaginaceae	*Plantago eriopoda*	PLER	redwool plantain	5	Native	2	–	–	9	2.40	6.71	5.16	21.36
Plantaginaceae	*Plantago major*	PLMA2	common plantain	0	Nonnative	3	3	–	8	0.75	2.00	0.69	3.00
Plantaginaceae	*Veronica americana*	VEAM2	American speedwell	6	Native	1	–	–	5	1.43	2.00	0.39	0.77
Plantaginaceae	*Veronica anagallis-aquatica*	VEAN2	water speedwell	1	Native	1	–	–	7	2.02	5.25	0.82	1.28
Plantaginaceae	*Veronica peregrina* ssp. *xalapensis*	VEPEX2	hairy purslane speedwell	2	Native	2	–	–	1	0.50	0.50	1.48	1.48
Plantaginaceae	*Veronica serpyllifolia* var. *humifusa*	VESEH4	–	6	Native	3	–	–	5	0.66	1.00	0.54	1.49
Poaceae	*Achnatherum hymenoides*	ACHY	Indian ricegrass	5	Native	5	–	–	30	1.19	5.00	1.56	6.39
Poaceae	*Agrostis gigantea*	AGGI2	redtop	0	Nonnative	3	3	4	7	1.46	7.20	2.32	15.52

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Poaceae	*Agrostis idahoensis*	AGID	Idaho bentgrass	7	Native	2	–	–	1	0.60	0.60	1.09	1.09
Poaceae	*Agrostis scabra*	AGSC5	rough bentgrass	4	Native	3	–	–	5	1.15	2.00	0.78	2.12
Poaceae	*Agrostis variabilis*	AGVA	mountain bentgrass	4	Native	–	–	–	1	0.50	0.50	0.31	0.31
Poaceae	*Alopecurus aequalis*	ALAE	shortawn foxtail	4	Native	1	–	–	2	0.50	0.50	0.29	0.37
Poaceae	*Beckmannia syzigachne*	BESY	American sloughgrass	4	Native	1	–	–	1	0.88	0.88	1.28	1.28
Poaceae	*Bouteloua gracilis*	BOGR2	blue grama	4	Native	–	–	–	1	1.00	1.00	0.62	0.62
Poaceae	*Calamagrostis canadensis*	CACA4	bluejoint	6	Native	2	–	–	4	3.54	5.00	3.65	6.57
Poaceae	*Calamagrostis stricta*	CAST36	slimstem reedgrass	7	Native	2	–	–	13	2.85	20.00	4.90	28.67
Poaceae	*Calamovilfa longifolia*	CALO	prairie sandreed	7	Native	–	–	–	3	0.75	1.00	0.79	1.56
Poaceae	*Catabrosa aquatica*	CAAQ3	water whorlgrass	7	Native	1	–	–	8	0.91	2.00	0.28	0.45
Poaceae	*Deschampsia cespitosa*	DECE	tufted hairgrass	4	Native	2	–	–	4	1.15	2.58	1.37	4.97
Poaceae	*Distichlis stricta*	DIST3	–	4	Native	2	–	–	35	5.02	32.86	6.60	73.87
Poaceae	*Elymus elymoides*	ELEL5	squirreltail	4	Native	4	–	–	3	0.67	1.00	0.32	0.50
Poaceae	*Elymus glaucus* ssp. *glaucus*	ELGLG	blue wildrye	7	Native	4	–	–	2	6.06	10.00	3.75	4.45
Poaceae	*Elymus repens*	ELRE4	quackgrass	0	Nonnative	3	4	8	3	0.67	1.00	0.74	1.08
Poaceae	*Elymus trachycaulus*	ELTR7	slender wheatgrass	4	Native	3	–	–	34	4.64	35.00	4.40	34.26
Poaceae	*Glyceria grandis*	GLGR	American mannagrass	6	Native	1	–	–	3	0.78	1.33	0.34	0.70
Poaceae	*Glyceria striata*	GLST	fowl mannagrass	5	Native	1	–	–	1	1.00	1.00	0.17	0.17
Poaceae	*Hesperostipa comata*	HECO26	needle and thread	6	Native	–	–	–	12	2.14	10.00	2.54	9.00
Poaceae	*Hordeum jubatum*	HOJU	foxtail barley	2	Native	3	–	–	55	2.68	16.63	3.25	23.19

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Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Poaceae	*Koeleria macrantha*	KOMA	prairie Junegrass	6	Native	–	–	–	8	0.74	1.43	0.88	3.21
Poaceae	*Leymus triticoides*	LETR5	beardless wildrye	5	Native	3	–	–	2	10.42	20.00	1.21	2.09
Poaceae	*Muhlenbergia asperifolia*	MUAS	scratchgrass	4	Native	2	–	–	58	4.74	23.33	8.33	28.33
Poaceae	*Muhlenbergia richardsonis*	MURI	mat muhly	8	Native	3	–	–	14	2.00	8.00	1.32	4.88
Poaceae	*Panicum capillare*	PACA6	witchgrass	1	Native	3	2	–	1	8.40	8.40	4.38	4.38
Poaceae	*Pascopyrum smithii*	PASM	western wheatgrass	5	Native	4	–	–	50	3.35	30.40	6.58	46.06
Poaceae	*Phragmites australis*	PHAU7	common reed	1	Cryptogenic	2	–	9	1	5.00	5.00	0.83	0.83
Poaceae	*Poa arida*	POAR3	plains bluegrass	5	Native	5	–	–	17	1.47	9.00	2.50	12.14
Poaceae	*Poa fendleriana* ssp. *longiligula*	POFEL	muttongrass	7	Native	–	–	–	2	3.69	6.75	2.81	4.71
Poaceae	*Poa palustris*	POPA2	fowl bluegrass	6	Native	3	–	–	6	0.89	2.86	0.74	3.33
Poaceae	*Poa pratensis*	POPR	Kentucky bluegrass	0	Nonnative	3	4	6	16	2.27	6.71	3.42	17.80
Poaceae	*Poa secunda*	POSE	Sandberg bluegrass	6	Native	4	–	–	6	0.98	3.38	2.02	10.23
Poaceae	*Polypogon monspeliensis*	POMO5	annual rabbitsfoot grass	0	Nonnative	2	3	7	5	1.56	2.50	1.22	2.76
Poaceae	*Puccinellia distans*	PUDI	weeping alkaligrass	0	Nonnative	2	–	–	1	1.00	1.00	0.39	0.39
Poaceae	*Puccinellia nuttalliana*	PUNU2	Nuttall's alkaligrass	6	Native	2	–	–	13	1.07	3.20	0.92	3.80
Poaceae	*Redfieldia flexuosa*	REFL	blowout grass	8	Native	–	–	–	5	6.97	18.33	3.85	7.82
Poaceae	*Spartina gracilis*	SPGR	alkali cordgrass	7	Native	2	–	–	11	0.59	1.00	2.70	23.53
Poaceae	*Spartina pectinata*	SPPE	prairie cordgrass	7	Native	1	–	–	1	1.00	1.00	0.17	0.17
Poaceae	*Sphenopholis obtusata*	SPOB	prairie wedgescale	5	Native	3	–	–	14	0.71	2.00	0.76	2.52

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Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Poaceae	*Sporobolus airoides*	SPAI	alkali sacaton	5	Native	3	–	–	21	4.01	37.83	6.19	38.22
Poaceae	*Sporobolus cryptandrus*	SPCR	sand dropseed	2	Native	4	–	–	6	0.56	0.88	0.94	2.33
Polemoniaceae	*Aliciella pinnatifida*	ALPI2	sticky gilia	5	Native	3	–	–	2	0.50	0.50	0.58	0.87
Polemoniaceae	*Ipomopsis aggregata*	IPAG	scarlet gilia	5	Native	–	–	–	2	0.75	1.00	0.38	0.50
Polemoniaceae	*Ipomopsis longiflora*	IPLO2	flaxflowered ipomopsis	7	Native	–	–	–	1	0.50	0.50	0.35	0.35
Polygonaceae	*Persicaria amphibia*	PEAM8	–	4	Native	1	–	–	6	4.16	11.00	1.50	5.39
Polygonaceae	*Persicaria maculosa*	PEMA24	–	0	Nonnative	2	4	–	11	3.01	10.60	3.26	14.52
Polygonaceae	*Persicaria pensylvanica*	PEPE19	–	1	Native	2	–	–	2	10.00	19.00	6.20	12.26
Polygonaceae	*Polygonum aviculare*	POAV	prostrate knotweed	0	Nonnative	3	3	3	2	11.50	22.50	7.23	14.08
Polygonaceae	*Polygonum kelloggii* ssp. *kelloggii*	ZZ_POKEK50	–	7	Native	2	–	–	1	1.00	1.00	0.13	0.13
Polygonaceae	*Rumex crispus*	RUCR	curly dock	0	Nonnative	3	3	2	1	0.50	0.50	0.22	0.22
Polygonaceae	*Rumex fueginus*	RUFU3	–	4	Native	2	–	–	2	0.50	0.50	0.16	0.18
Polygonaceae	*Rumex triangulivalvis*	RUTR3	–	4	Native	3	–	–	1	0.50	0.50	0.07	0.07
Portulacaceae	*Portulaca oleracea*	POOL	little hogweed	0	Nonnative	3	3	–	3	0.50	0.50	0.54	0.78
Potamogetonaceae	*Potamogeton natans*	PONA4	floating pondweed	4	Native	1	–	–	1	1.00	1.00	0.28	0.28
Ranunculaceae	*Clematis ligusticifolia*	CLLI2	western white clematis	4	Native	3	–	–	11	0.79	2.00	0.92	4.62
Ranunculaceae	*Ranunculus aquatilis* var. *diffusus*	RAAQD	–	3	Native	1	–	–	2	0.50	0.50	0.07	0.10
Ranunculaceae	*Ranunculus cardiophyllus*	RACA4	heartleaf buttercup	8	Native	2	–	–	1	1.43	1.43	1.22	1.22
Ranunculaceae	*Ranunculus cymbalaria*	RACY	alkali buttercup	4	Native	1	–	–	38	1.68	20.00	1.72	9.30
Ranunculaceae	*Ranunculus macounii*	RAMA2	Macoun’s buttercup	7	Native	1	–	–	1	0.50	0.50	0.29	0.29

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Ranunculaceae	*Ranunculus sceleratus* var. *multifidus*	RASCM	cursed buttercup	1	Native	1	–	–	2	0.50	0.50	0.19	0.21
Ranunculaceae	*Thalictrum fendleri*	THFE	Fendler's meadow-rue	6	Native	3	–	–	1	0.50	0.50	0.24	0.24
Rosaceae	*Fragaria virginiana*	FRVI	Virginia strawberry	5	Native	4	–	–	1	0.50	0.50	0.08	0.08
Rosaceae	*Geum rivale*	GERI2	purple avens	5	Native	2	–	–	1	0.50	0.50	0.42	0.42
Rosaceae	*Potentilla anserina*	POAN5	–	3	Native	1	–	–	50	5.76	42.14	7.07	46.96
Rosaceae	*Potentilla norvegica*	PONO3	Norwegian cinquefoil	1	Native	3	3	–	2	1.25	2.00	0.26	0.26
Rosaceae	*Potentilla plattensis*	POPL	Platte River cinquefoil	7	Native	2	–	–	12	0.68	1.64	1.32	3.72
Rosaceae	*Rosa acicularis* ssp. *sayi*	ROACS	prickly rose	5	Native	4	–	–	5	1.08	1.88	1.69	6.00
Rosaceae	*Rosa arkansana*	ROAR3	prairie rose	5	Native	4	–	–	1	0.50	0.50	0.29	0.29
Rosaceae	*Rosa woodsii*	ROWO	Woods' rose	5	Native	4	–	–	3	3.88	8.75	3.74	10.12
Rosaceae	*Rubus idaeus* var. *strigosus*	RUIDS3	–	5	Native	4	–	–	2	1.25	2.00	0.88	1.50
Rubiaceae	*Galium trifidum* ssp. *subbiflorum*	GATRS2	threepetal bedstraw	7	Native	2	–	–	3	0.60	0.80	0.36	0.48
Ruscaceae	*Maianthemum stellatum*	MAST4	starry false lily of the valley	7	Native	3	–	–	3	1.42	3.25	0.63	1.54
Salicaceae	*Populus angustifolia*	POAN3	narrowleaf cottonwood	5	Native	2	–	–	16	19.87	60.00	27.98	77.52
Salicaceae	*Populus tremuloides*	POTR5	quaking aspen	5	Native	4	–	–	1	0.50	0.50	0.15	0.15
Salicaceae	*Salix bebbiana*	SABE2	Bebb willow	6	Native	2	–	–	3	14.50	42.00	9.57	27.98
Salicaceae	*Salix eriocephala*	SAER	Missouri River willow	6	Native	–	–	–	3	0.38	0.50	0.43	0.44
Salicaceae	*Salix exigua*	SAEX	sandbar willow	3	Native	2	–	–	24	10.84	60.00	17.40	84.63

Table 10 (continued). Complete list of vascular taxa documented in wetland monitoring sentinel sites at Great Sand Dunes National Park and Preserve, Colorado, from 2016 to 2019. For an explanation of C-score (coefficients of conservatism) and invasiveness (I-rank scores), see main narrative. I-rank scores are a categorical ranking of the invasiveness of a taxa following Morse et al. (2004) as modified by Smith et al. (202). Nomenclature follows Ackerfield (2015).

Family	Species	Code	Common name	C-score	Nativity	Wetland affinity	Invasive-ness	I-rank score	Frequency	Mean absolute cover (%)	Maximum absolute cover (%)	Mean relative cover (%)	Maximum relative cover (%)
Salicaceae	*Salix exigua*	SAEX	sandbar willow	3	Native	2	–	–	24	10.84	60.00	17.40	84.63
Salicaceae	*Salix lasiandra* var. *caudata*	SALAC	–	7	Native	2	–	–	4	3.75	6.00	6.94	16.10
Salicaceae	*Salix lasiandra* var. *lasiandra*	ZZ_SALAL50	–	6	Native	2	–	–	–	10.50	18.00	5.28	8.99
Salicaceae	*Salix monticola*	SAMO2	park willow	6	Native	1	–	–	2	10.33	20.00	2.51	3.33
Salicaceae	*Salix planifolia*	SAPL2	diamondleaf willow	7	Native	1	–	–	1	10.00	10.00	1.67	1.67
Scrophulariaceae	*Scrophularia lanceolata*	SCLA	lanceleaf figwort	5	Native	3	–	–	1	0.50	0.50	0.08	0.08
Scrophulariaceae	*Verbascum thapsus*	VETH	common mullein	0	Nonnative	4	4	6	1	0.50	0.50	0.31	0.31
Typhaceae	*Typha latifolia*	TYLA	broadleaf cattail	4	Native	1	–	–	1	0.50	0.50	0.42	0.42
Urticaceae	*Urtica dioica*	URDI	stinging nettle	3	Native	3	–	–	2	0.75	1.00	0.46	0.75
Valerianaceae	*Valeriana edulis*	VAED	tobacco root	7	Native	3	–	–	1	0.50	0.50	0.38	0.38
Verbenaceae	*Verbena hastata*	VEHA2	swamp verbena	4	Native	3	–	–	1	1.00	1.00	0.09	0.09
Violaceae	*Viola palustris*	VIPA4	marsh violet	7	Native	1	–	–	1	0.50	0.50	0.31	0.31
Zannichelliaceae	*Zannichellia palustris*	ZAPA	horned pondweed	2	Native	1	–	–	1	1.00	1.00	0.90	0.90

Appendix D: Wetland Condition Indices from a Dung-Only Ungulate Use Index

In this report's main narrative, we develop and focus on camera-like UUIs. Given potential future application of dung-only based UUIs and associated WCIs, we present alternate UUI and WCI models developed from a dung-only UUI here.

Summary dung-only UUI statistics, including park-supported baseline assessment points (APs), are presented in Table 11. Dung-only UUIs in both wetland types have lower power than the camera-like version and may only be able to detect an 8 to 10% difference for herbaceous and woody sites, respectively, in a mean UUI comparison with Phase 2 and 3 results. The camera-like UUI can likely detect a 4 and 8% difference for herbaceous and woody sites (respectively)—up to twice the power of the dung-only version. Dung-only WCI do not validate as well as the camera-like WCI (see "Selection and validation of Wetland Condition Indices" section). Nevertheless, they may be more efficient than the camera-like WCI and a possible alternative in the future.

Table 11. Summary of dung-only Ungulate Use Indices in woody (W) and herbaceous (H) wetland sites at Great Sand Dunes National Park and Preserve. The r^2 is from a linear model of an adjusted Wetland Condition Index and Ungulate Use Index (UUI) and is the explained variation, adjusted for the number of predictors in the model. AP: park-based assessment points; SD: standard deviation; CV: coefficient of variation. Minimum (Min.) detectable difference (statistical power) is the smallest percent change resolvable when comparisons are made between baseline and Phase 2 or 3 means for each UUI.

UUI metric, (wetland type)	Best baseline condition AP	Worst baseline condition AP	Mean	Median	SD	CV (%)	Min. detectable difference (%)
UUI dung-only (H)	≤ 1.05 [A]	≥ 20.8 [A]	14.84	11.41	16.28	109.69	7.90
UUI dung-only (W)	≤ 0.22 [A]	≥ 0.28 [A]	0.35	0.27	0.31	88.33	10.08

[A] AP estimated using median.

Summary statistics for WCIs created from these dung-only UUIs, including park-supported baseline APs, are presented in Table 12. The WCI in each wetland type will likely have a useful minimally detectable difference, with a relatively small change of 1.9 to 2.5% in the mean WCI statistically resolvable when comparisons are made to Phase 2 and 3 results. This is comparable to the camera-like WCI.

Table 12. Summary of dung-only Wetland Condition Indices (WCIs) in woody (W) and herbaceous (H) wetland sites at Great Sand Dunes National Park and Preserve. The r^2 is from a linear model of adjusted WCIs and UUIs and is the explained variation, adjusted for the number of predictors in the model. AP: park-based assessment points; Corr.: correlation; SD: standard deviation; CV: coefficient of variation. Minimum (Min.) detectable difference (statistical power) is the smallest percent change resolvable when comparisons are made between baseline and Phase 2 or 3 means for each WCI.

WCI (wetland type)	Best baseline condition AP	Worst baseline condition AP	Corr. with UUI	r^2 (adj.) with UUI	Mean	Median	SD	CV (%)	Min. detectable difference (%)
WCI dung-only (H)	≥ 5.32 [A]	≤ 4.11 [A]	−0.75	0.55	4.91	5.05	1.32	26.80	1.93
WCI dung-only (W)	≥ 5.28 [B]	≤ 4.45 [B]	−0.87	0.75	5.09	5.18	1.12	21.92	2.50

[A] AP estimated using mean.

[B] AP estimated using median.

Relationships between wetland condition and ungulate use; dung-based

Final herbaceous and woody dung-based WCIs are presented relative to the UUI gradient on which they are based in Figure 44 and Figure 45. Both of these relationships are strong, with adjusted r^2 of 0.55 and 0.76 for herbaceous and woody. These are lower than the camera-like equivalents but still acceptable. Each model had a strong negative linear correlation with UUI, reflecting our "by definition focus" on the negative consequences of UUI to wetland condition. An important difference in the camera-like and dung-only based WCI is in the validation of the herbaceous models using a largely independent sample (see Figure 41 in Appendix A). The camera-like model validated better ($p = 0.43$), while the dung-only model was less well validated ($p = 0.024$). We lack the sample size to do a full independent validation with the woody model. Our approximate randomized subsetting method (see Appendix A) was generally equitable for the dung and camera-like woody model.

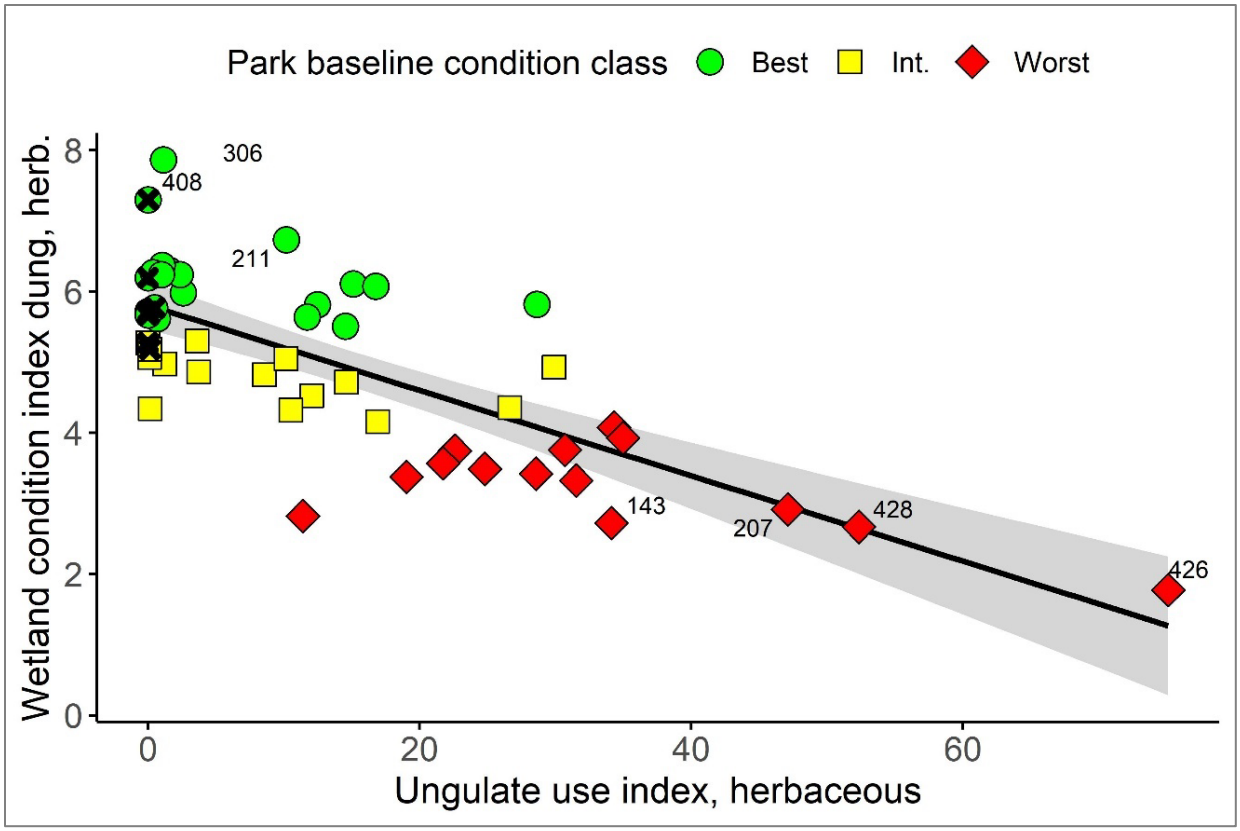


Figure 44. Relationship of dung-only Wetland Condition Index (WCI) and Ungulate Use Index (UUI) for herbaceous wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Linear fit and its 95% confidence interval are shown with the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition, with green circles for "best available," yellow squares for "intermediate (int.)," and red diamonds for "worst" condition classes. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst WCI and/or UUI ranges are labeled with their site number. NPS

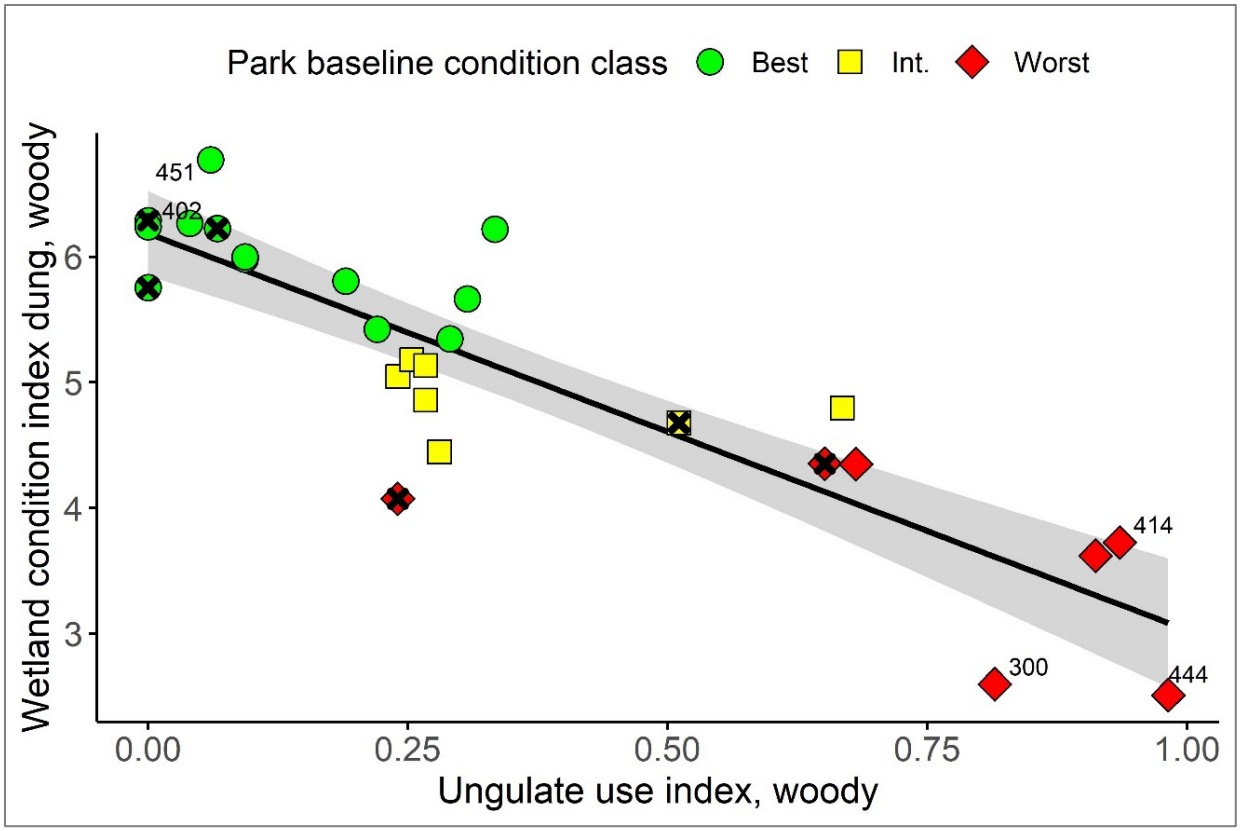


Figure 45. Relationship of dung-only Wetland Condition Index (WCI) and Ungulate Use Index (UUI) for woody wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Linear fit and its 95% confidence interval are shown by the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition with green circles for "best," yellow squares for "intermediate (int.)," and red diamonds for "worst" condition classes. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst WCI and/or UUI ranges are labeled with their site number. NPS

Component metrics

Component metrics in the dung-based herbaceous model were generally interpretable (Table 13), all decreasing with increasing UUI: mean grass height, Simpson diversity, woody richness, sedge to grass cover, wetland affinity, and mean conservatism. Component metrics in the dung-based woody model were also generally interpretable (Table 14). Components decreasing with increasing UUI were hydrophyte richness, percent short willow, relative importance natives, and total cover willow. The one component increasing with increasing UUI was browsed cover of all wood.

Table 13. Final component metrics of dung-only Wetland Condition Index (WCI) for herbaceous wetland sites, Great Sand Dunes National Park and Preserve, 2016–2019. Correlation (corr.) with ungulate use (UUI) is given before (raw) and after (adjusted, Adj.) adjustment and scaling by 10 environmental covariates listed in the table. Each component variable's model intercept and coefficients for the environmental covariates are shown. Human disturbance (LDI); Depth to ground water (DTW); Sodium absorption ratio (SAR); Bare ground (BRE); Litter cover (LIT); Elevation (ELEV); Production, 5-year mean (PROD); Temperature as growing degree days, 5-year mean (GDD); Climatic deficit, lagged 3 years (D); Soil moisture, 5-year mean (SOIL). For units of measure and other details of the environmental variables, see Table 1.

Metric name, (units)	Adj. corr. with UUI	Raw corr. with UUI	Adj. model int.	UUI	LDI	DTW	SAR	BRE	LIT	ELEV	PROD	GDD	D	SOIL
Mean grass height (cm)	−0.388	−0.448	6.286	−2516.431	0	0	0	−0.025	−0.020	0	0	0	−0.018	−0.024
Simpson diversity (index)	−0.385	−0.335	0.809	−128.158	0	0	0	0	0	0	0	0	0.000	0.000
Woody richness (count)	−0.379	−0.273	−36.140	−2561.474	0	−0.010	0	0	0.014	0.016	0	0	0.000	0.000
Sedge to grass cover (index)	−0.342	−0.466	0.758	−667.511	0	0.002	0	0	0	0	0	0	0.000	0.000
Wetland affinity (index)	−0.283	−0.176	17.555	−776.889	0	0.006	0	0	0	−0.005	0	0	−0.005	−0.011
Mean conservatism (index)	−0.188	−0.156	4.149	−396.790	0	0	0	0.005	0	0.000	0	0	0.000	0.006

Table 14. Final component metrics of dung-only Wetland Condition Index (WCI) for woody wetland sites, Great Sand Dunes National Park and Preserve, 2016–2019. Correlation (corr.) with ungulate use (UUI) is given before (raw) and after (adjusted, Adj.) adjustment and scaling by 10 environmental covariates listed in the table. Each component variable's model intercept and coefficients for the environmental covariates are shown. Human disturbance (LDI); Depth to ground water (DTW); Sodium absorption ratio (SAR); Bare ground (BRE); Litter cover (LIT); Elevation (ELEV); Production, 5-year mean (PROD); Temperature as growing degree days, 5-year mean (GDD); Climatic deficit, lagged 3 years (D); Soil moisture, 5-year mean (SOIL). For units of measure and other details of the environmental variables, see Table 1.

Metric name, (units)	Adj. corr. with UUI	Raw corr. with UUI	Adj. model intercept	UUI	LDI	DTW	SAR	BRE	LIT	ELEV	PROD	GDD	D	SOIL
Hydrophyte richness	−0.477	−0.306	−39.611	−475197.107	0	0.054	0.000	0	0	0.022	0	0	0	0
Percent willow 0–0.50 m tall	−0.395	−0.211	936.117	−3663744.407	0	0	41.410	0	−0.450	−0.366	0	0	0	0
Cover of browsed wood	0.323	0.289	6.516	1249939.185	0	0	0	0	0	0	0	0	0	0
Relative importance natives	−0.254	−0.180	44.603	−479109.297	0	0	0	0.119	0	0	−0.033	0	0	0
Total cover willow	−0.132	−0.117	5.156	−12440.349	0	0	0	0.006	0	0	0	−0.002	0	0

Patterns across baseline condition classes

Figure 46 and Figure 47 show patterns in the herbaceous dung-only WCI across park management defined condition classes by group and spatially. Across all herbaceous sites, 41% were in a baseline best condition and 28% were in a baseline worst condition. This is a notably higher proportion of sites in a best condition class and correspondingly lower value for the proportion of sites in a baseline worse condition relative to the camera only model. This may suggest a meaningful difference in the two models, with the dung-only UUI potentially not capturing some of the subtlety in ungulate use—this needs more investigation. While the majority of herbaceous sites are inside the bison fence (elk and bison use zone), and we have a less reliable sample of herbaceous wetland outside the bison pasture, there is a clear pattern for lower WCI where both species impact herbaceous sites (inside the bison fence). WCI increases as sites are further from the bison pasture. However, this pattern is also less pronounced with the dung-only WCI.

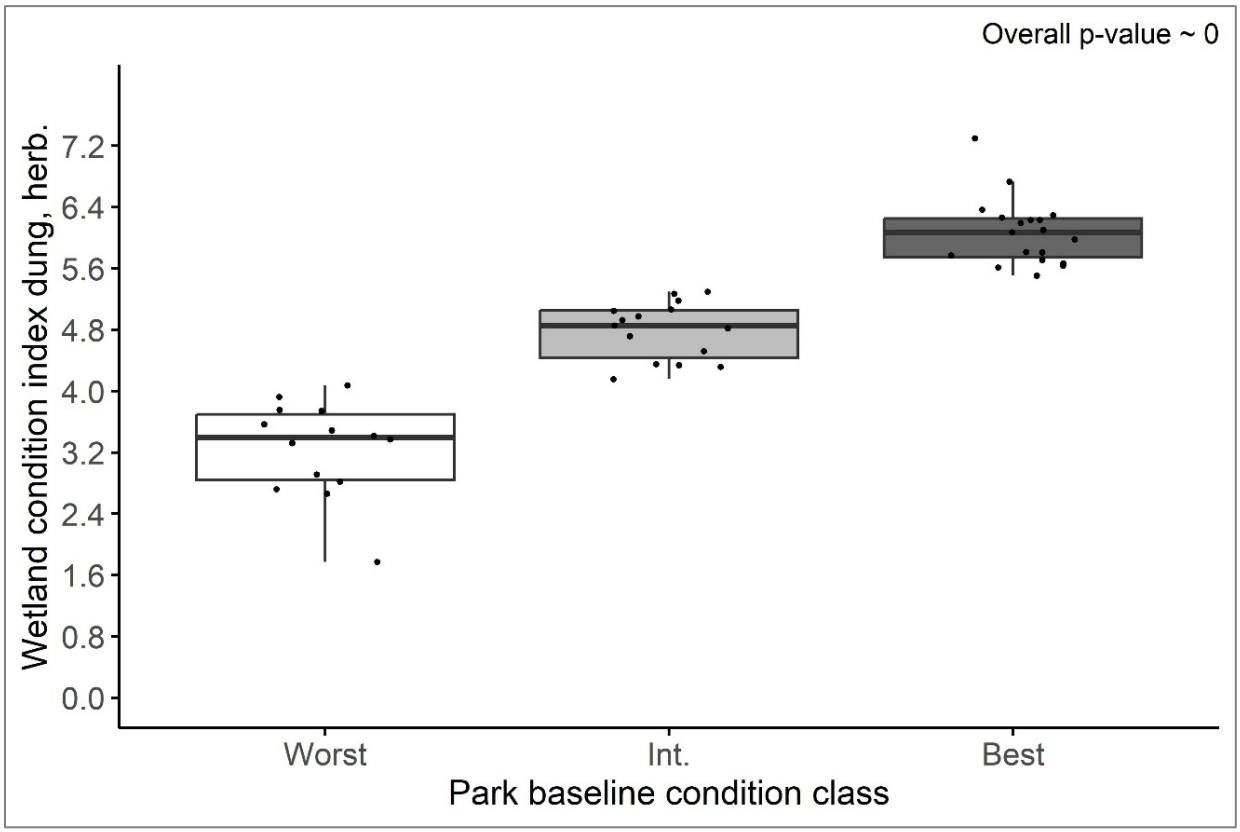


Figure 46. Dung-only Wetland Condition Index for herbaceous wetland sites across park-supported condition classes at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test with "p-value ~ 0" indicating a vanishingly small probability. Select individual paired comparison p-values are reported in text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

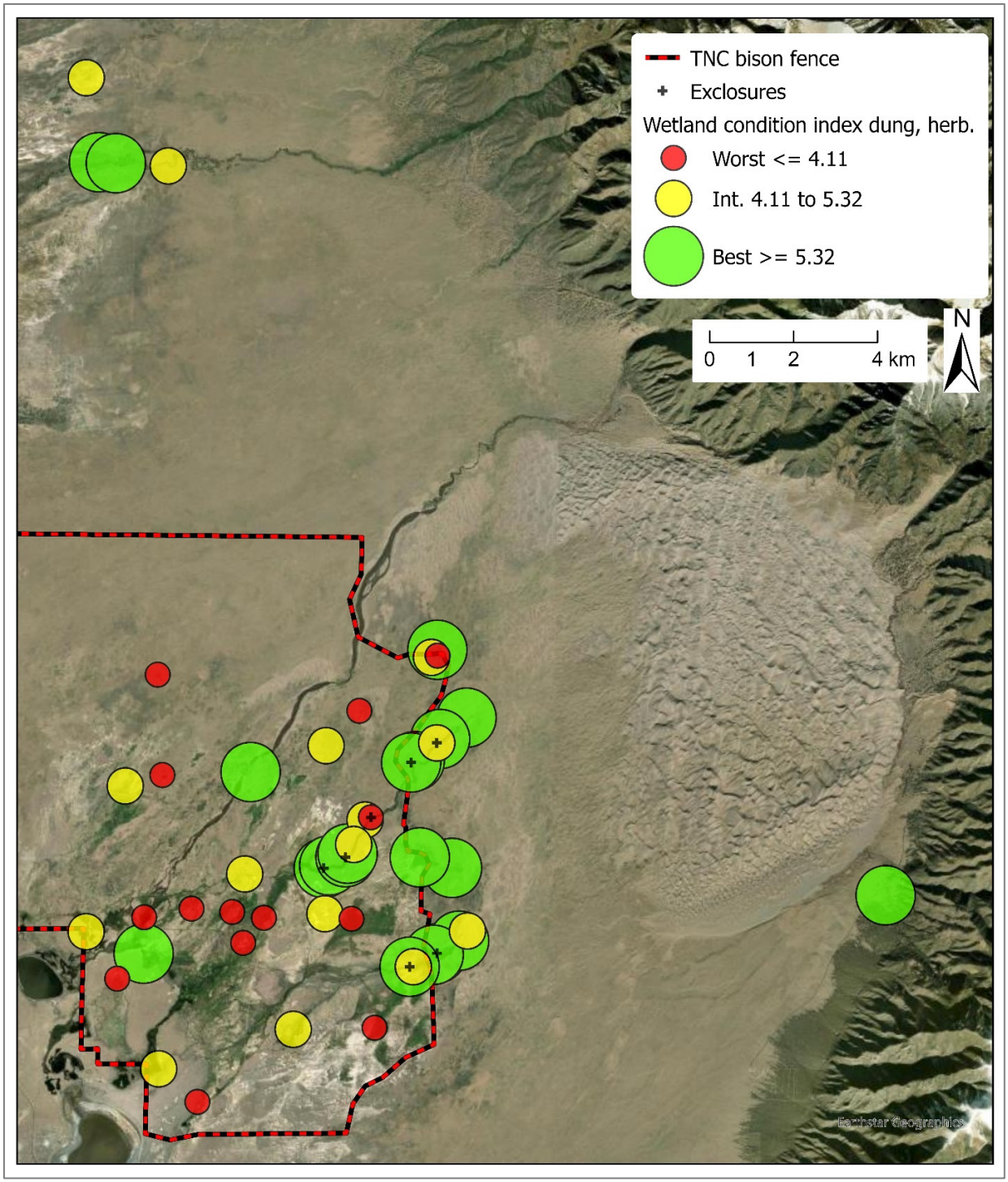


Figure 47. Dung-only Wetland Condition Index in herbaceous wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Only the first visit is shown at sites with more than one sample. Point colors and size are based on condition classes as defined by park staff, with larger green points for a best available condition, yellow medium sized points for an intermediate (“Int.”) condition, and smaller red points for a worst condition state. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. NPS

Figure 48 and Figure 49 show patterns in a baseline woody dung-only WCI across park management defined condition classes by group and spatially. Baseline woody dung-only WCI had a similar general pattern as with the camera-like WCI, with 28% in a baseline best condition and 48% in a baseline worst class. However, the distribution of these sites was different than the camera-like model as not all woody sites inside the bison fence (elk and bison use zone) were in the worst condition class; rather, many worst condition sites were along Sand Creek outside the bison fence.

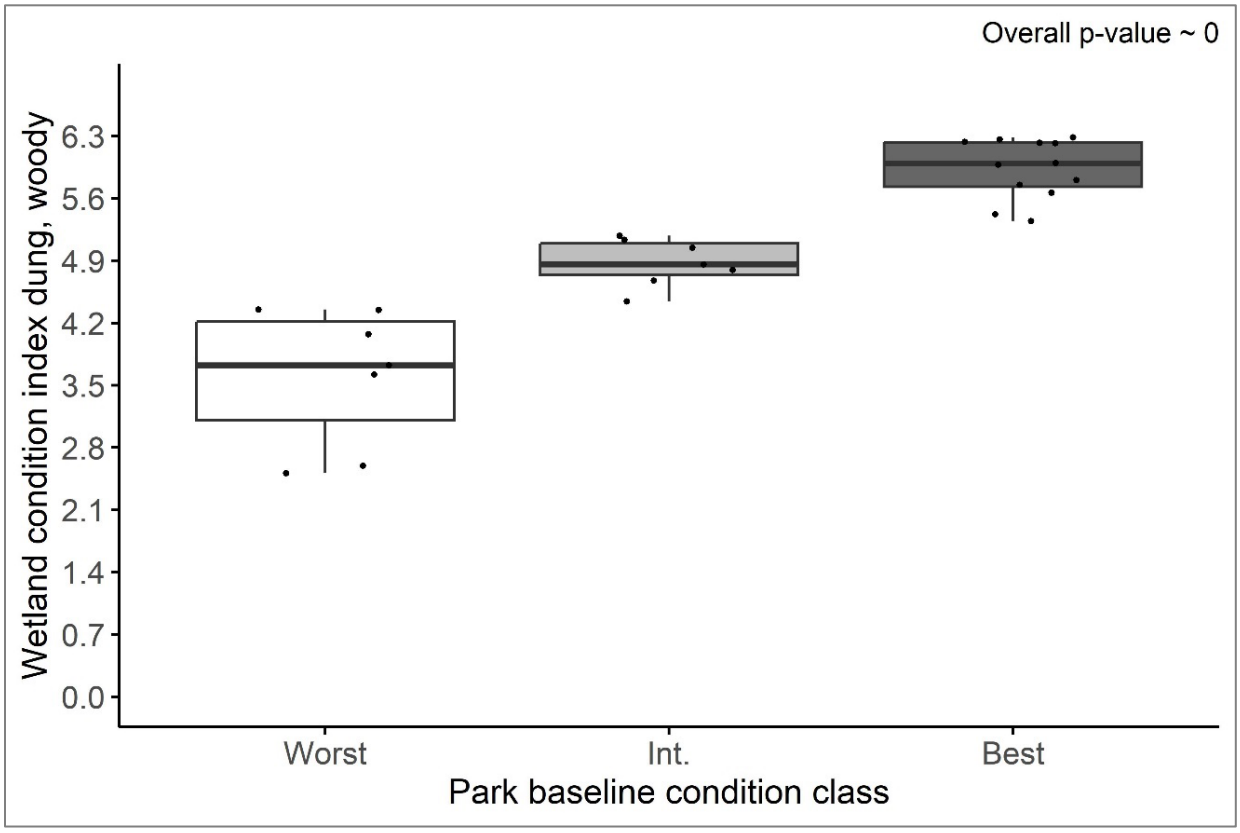


Figure 48. Dung-only Wetland Condition Index for woody wetland sites across park-supported condition classes at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test with "p-value ~ 0" indicating a vanishingly small probability. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

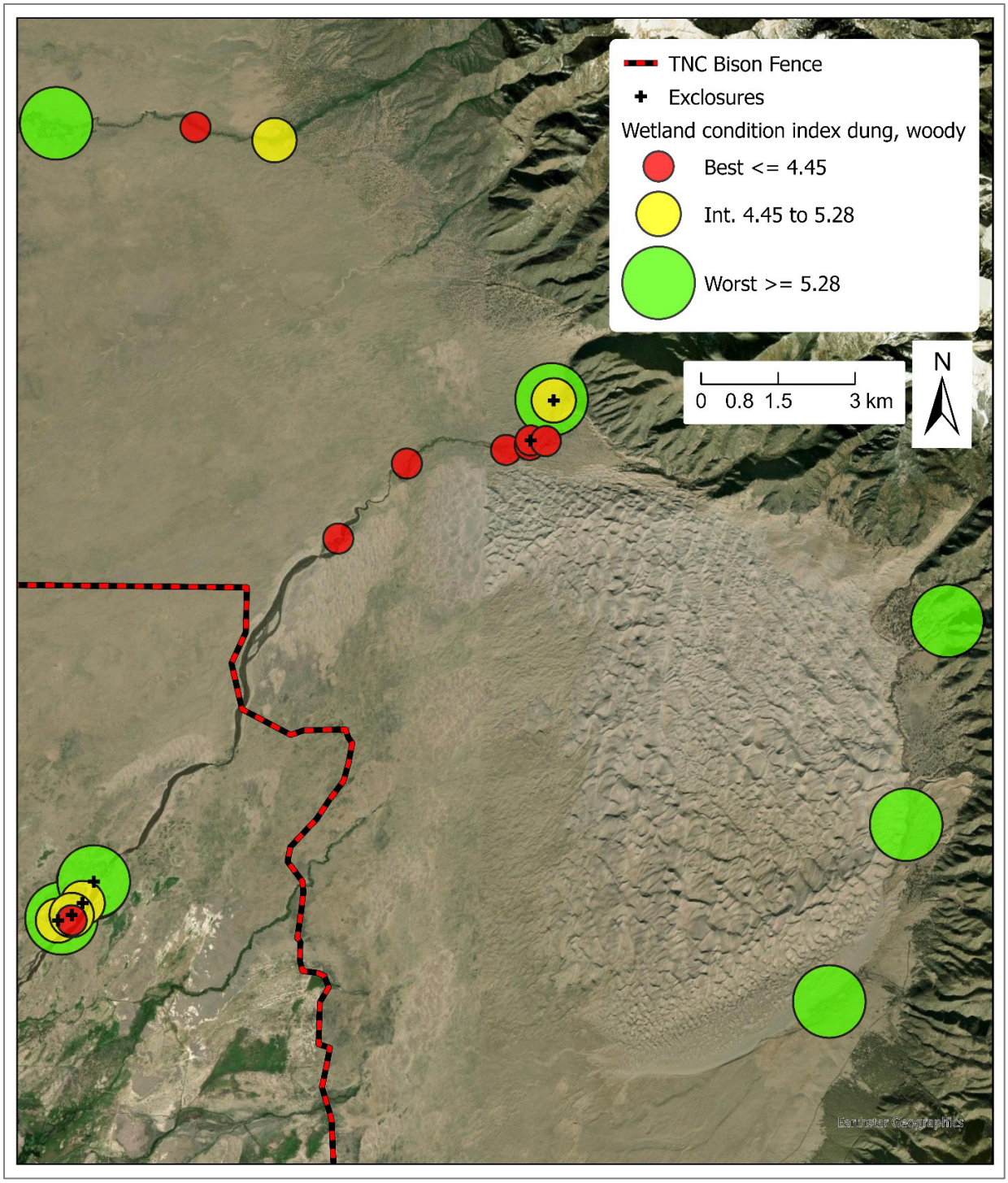


Figure 49. Dung-only Wetland Condition Index at woody wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Only the first visit is shown at sites with more than one sample. Point colors and size are based on condition classes as defined by park staff, with larger green points for a best available condition, yellow medium size points for an intermediate (“Int.”) condition, and smaller red points for a worst condition state. Points with black crosses are sites inside an ungulate exclosure. NPS

Patterns across important management variables

Patterns across exclosures, years, ungulate use type, and habitat types in WCIs derived from dung-only based UUIs in herbaceous (Figure 50) and woody (Figure 51) wetlands were similar to those seen in the camera-like WCIs presented in the main narrative. Overall, the herbaceous WCI differed across each of these four comparisons. However, there was not really an exclosure effect as the difference was due to contrasts with sites far from exclosure-unexclosed pairs. There was a year effect, with condition decreasing across the four baseline years. The ungulate use type effect was due to lower condition where both elk and bison used sites. Finally, condition was lower in salt flat wetland types. Overall woody WCI condition did not differ statistically across each of these four comparisons, although there were some notable patterns. There was no exclosure effect or year effect across the four baseline years. There was a marginal ungulate use type effect, with lower condition where both elk and bison used sites. Finally, condition was marginally lower in cottonwood wetland types.

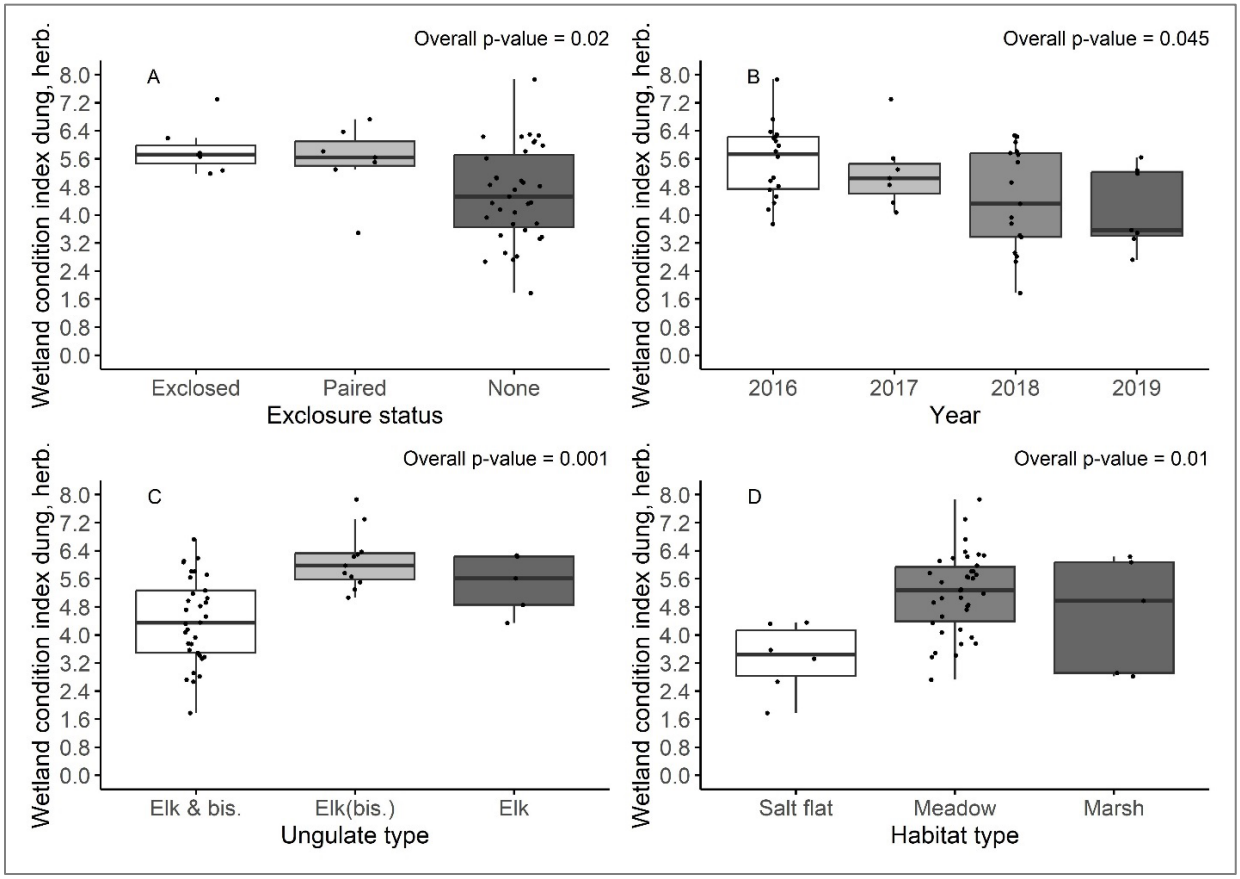


Figure 50. Dung-only Wetland Condition Index at herbaceous wetland sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, elk and some bison, and elk only) and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

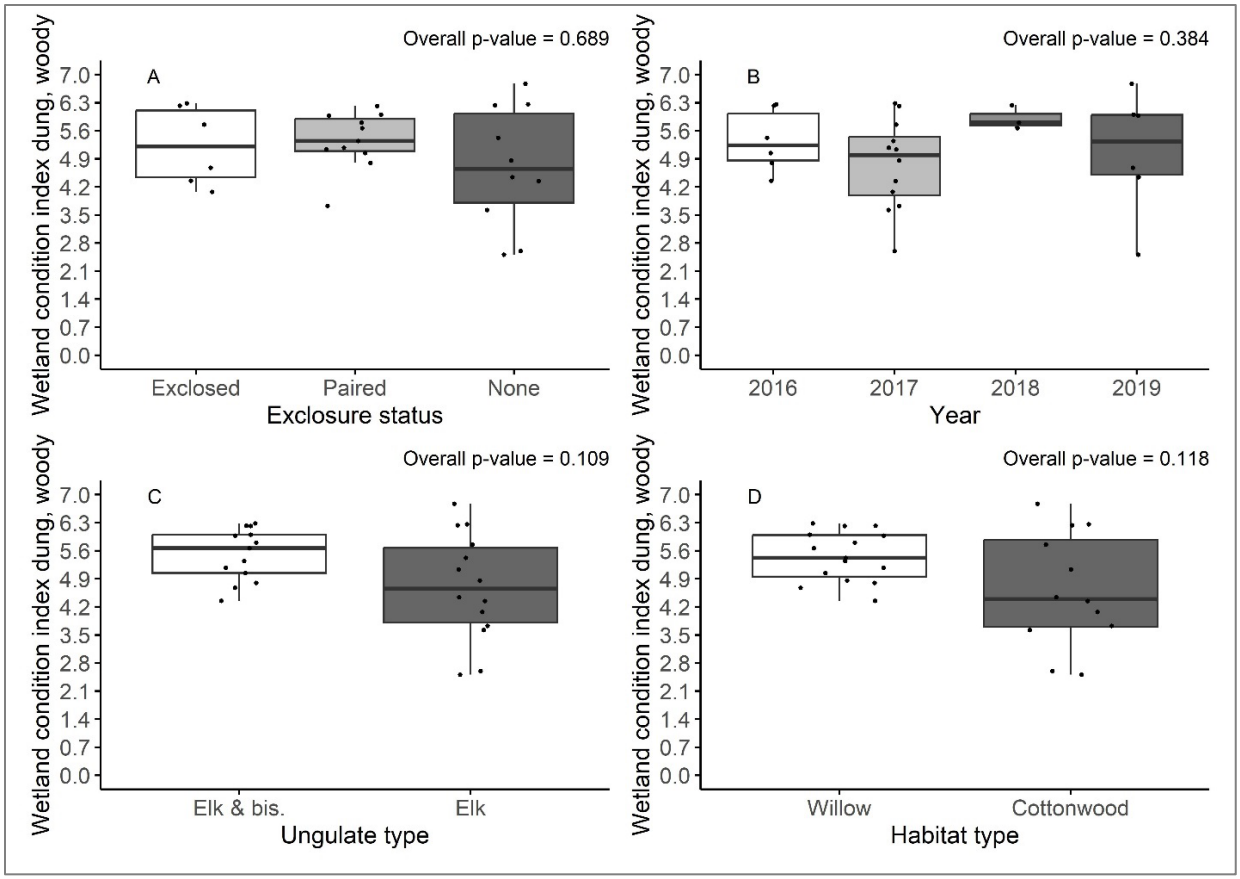


Figure 51. Dung-only Wetland Condition Index at woody wetland sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

Appendix E: Additional Results for Ungulate Use Indices, Wetland Condition Indices, and Hand-Picked Metrics

Appendix E provides additional results for Ungulate Use Indices (UUI), Wetland Condition Indices (WCI), and hand-picked (HP) metrics. All WCIs are for a camera-like UUI based model.

Ungulate Use Indices

Ungulate use in both herbaceous and woody wetlands had complex patterns across variables important to park management, such as exclosures, years, use by elk only or elk and bison, and wetland type. Figure 52 and Figure 53 show box plots of these patterns as interpreted in the main narrative in the *Patterns across important management variables* section of *Ungulate Use Indices*.

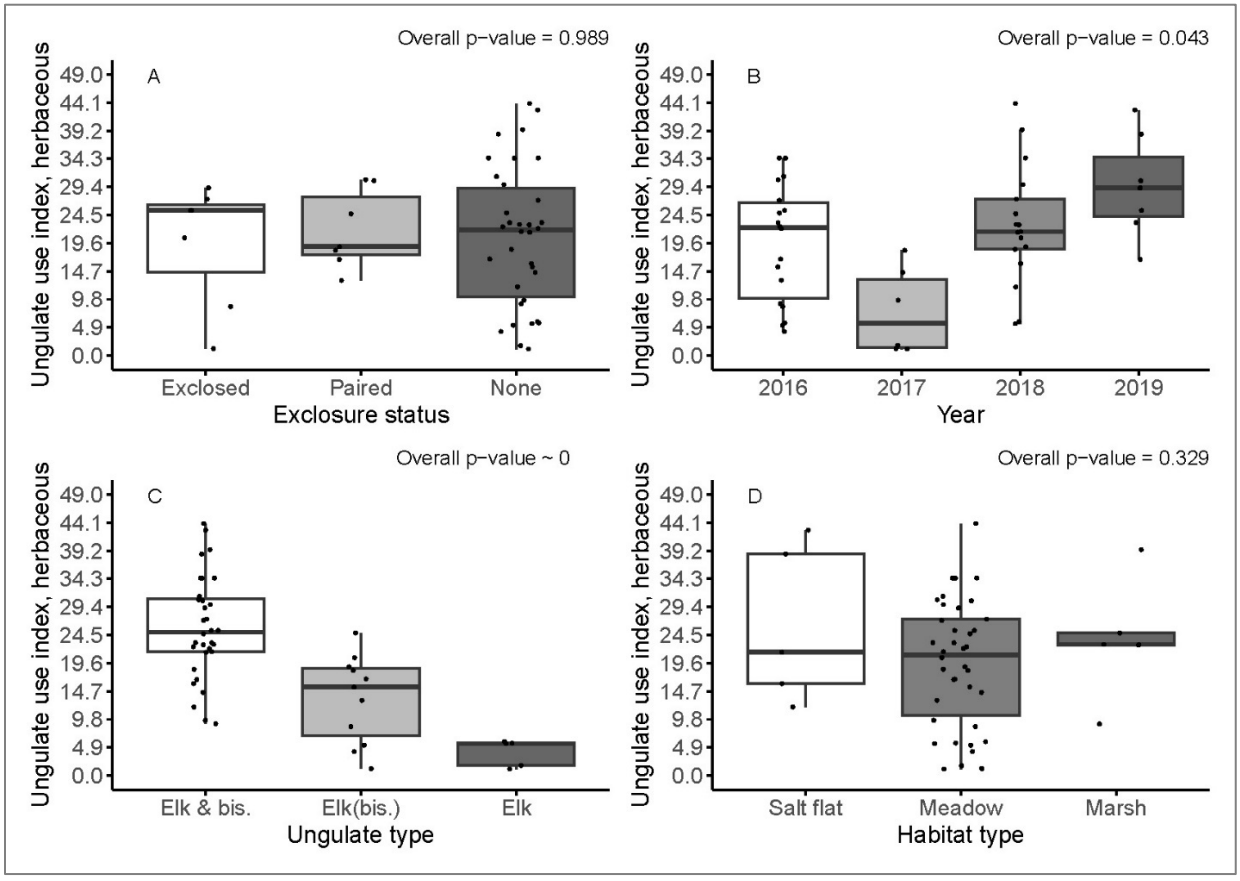


Figure 52. Ungulate Use Index at herbaceous wetland sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, elk and some bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test, with "p-value ~ 0" indicating a vanishingly small probability. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

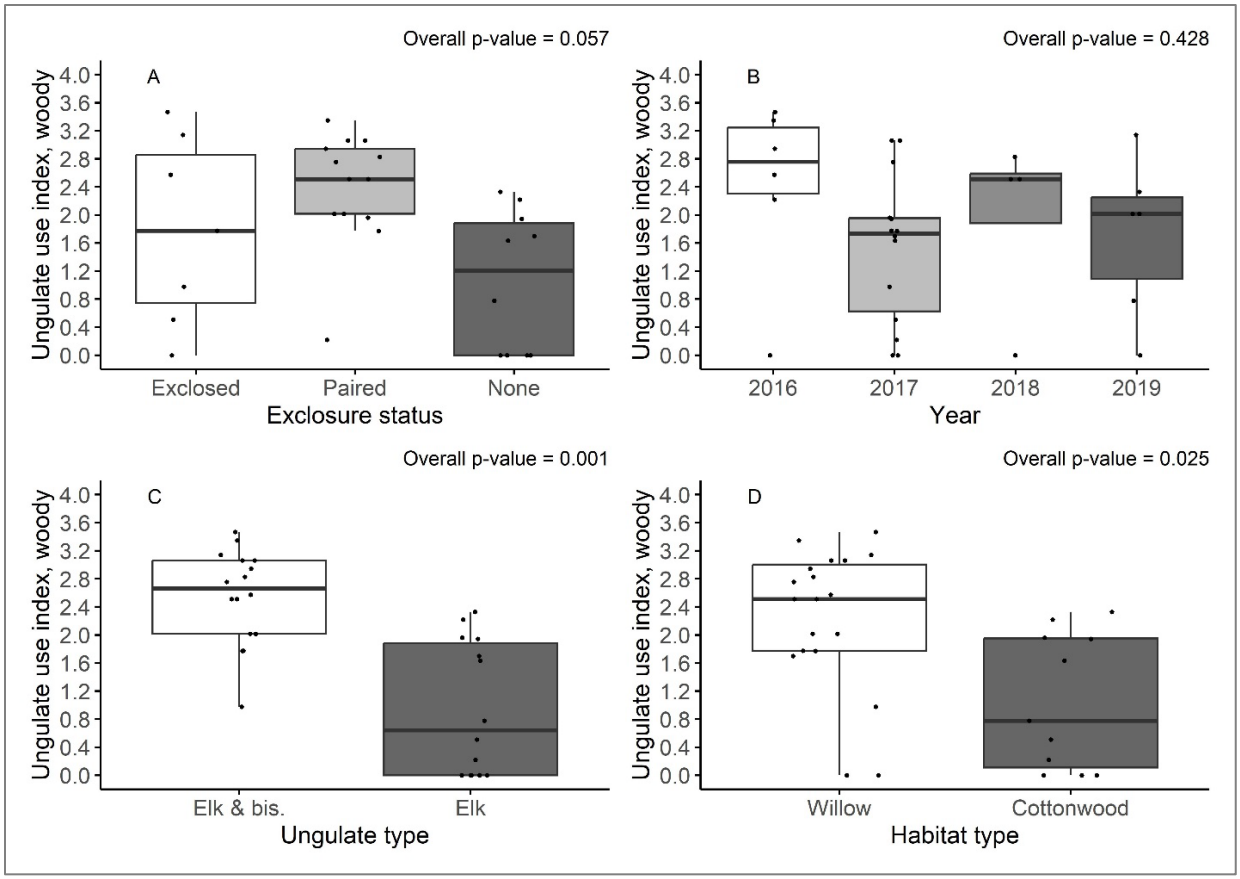


Figure 53. Ungulate Use Index at woody wetland sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

Wetland Condition Indices

Given the strong relationships between the UUIs and WCIs in woody and herbaceous sites, many of the patterns summarized here for WCI are similar to those presented above for UUIs. Figure 54 and Figure 55 show box plots of these patterns as interpreted in the main narrative in the *Patterns across important management variables* section of *Wetland Condition Indices*.

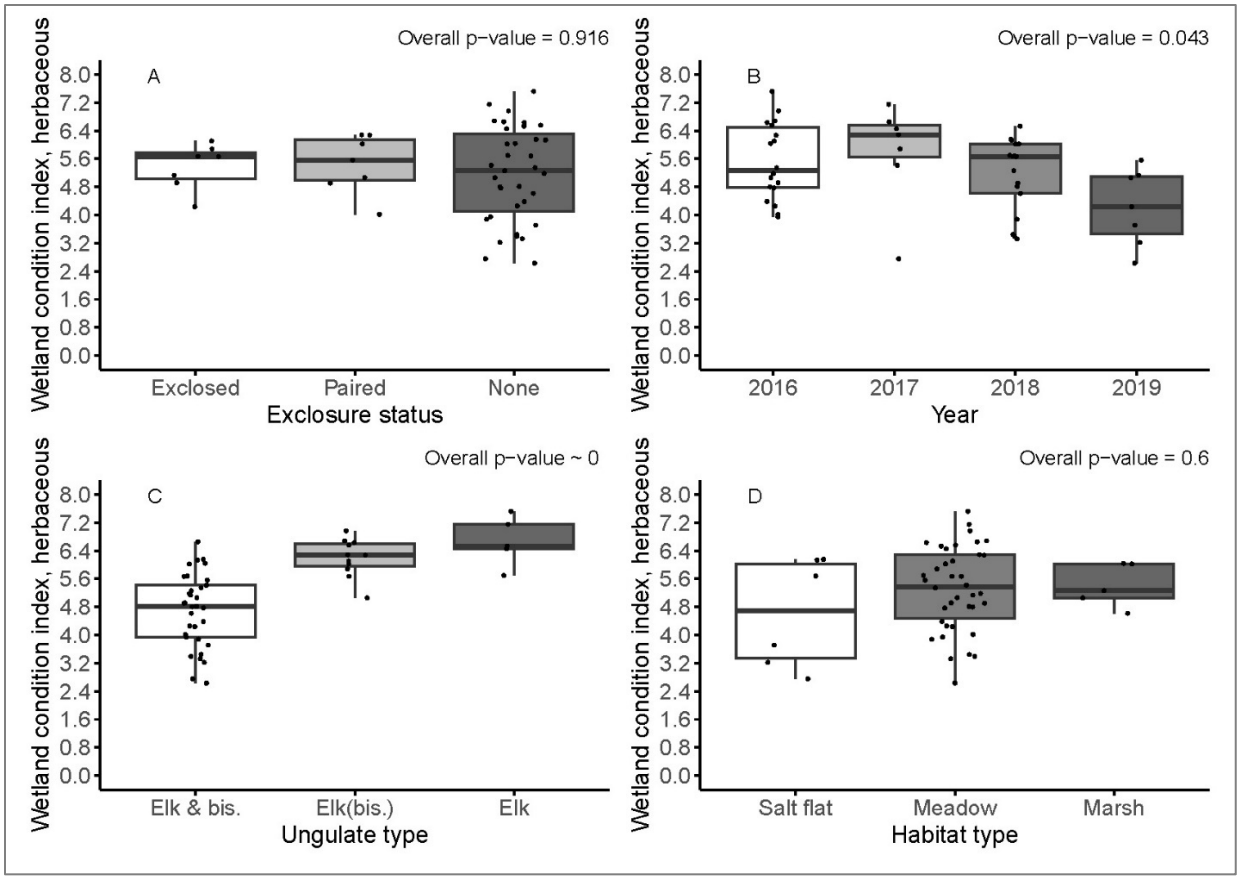


Figure 54. Wetland Condition Index at herbaceous wetland sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, elk and some bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test, with “p-value ~ 0” indicating a vanishingly small probability. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

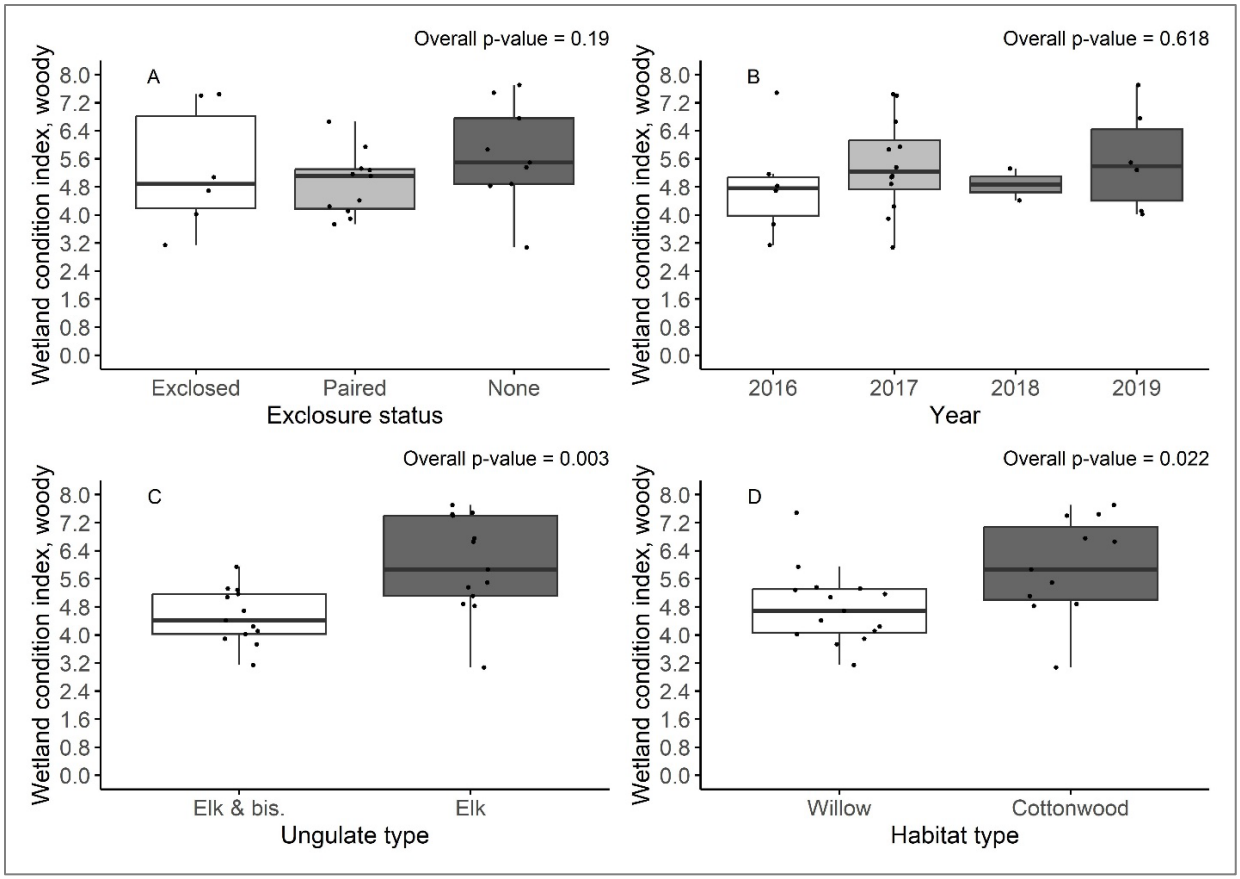


Figure 55. Wetland Condition Index at woody wetland sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

Hand-picked metrics (HP)

Density of Salicaceae with browse (woody)

Figure 56 gives linear models of adjusted and raw density of browsed willows and cottonwood relative to UUI. Adjustment for environmental gradients increased (relative to the raw data) the correlation with UUI and the amount of variation explained. This figure supplements discussion of results in the main text for the *Hand-picked metrics* section.

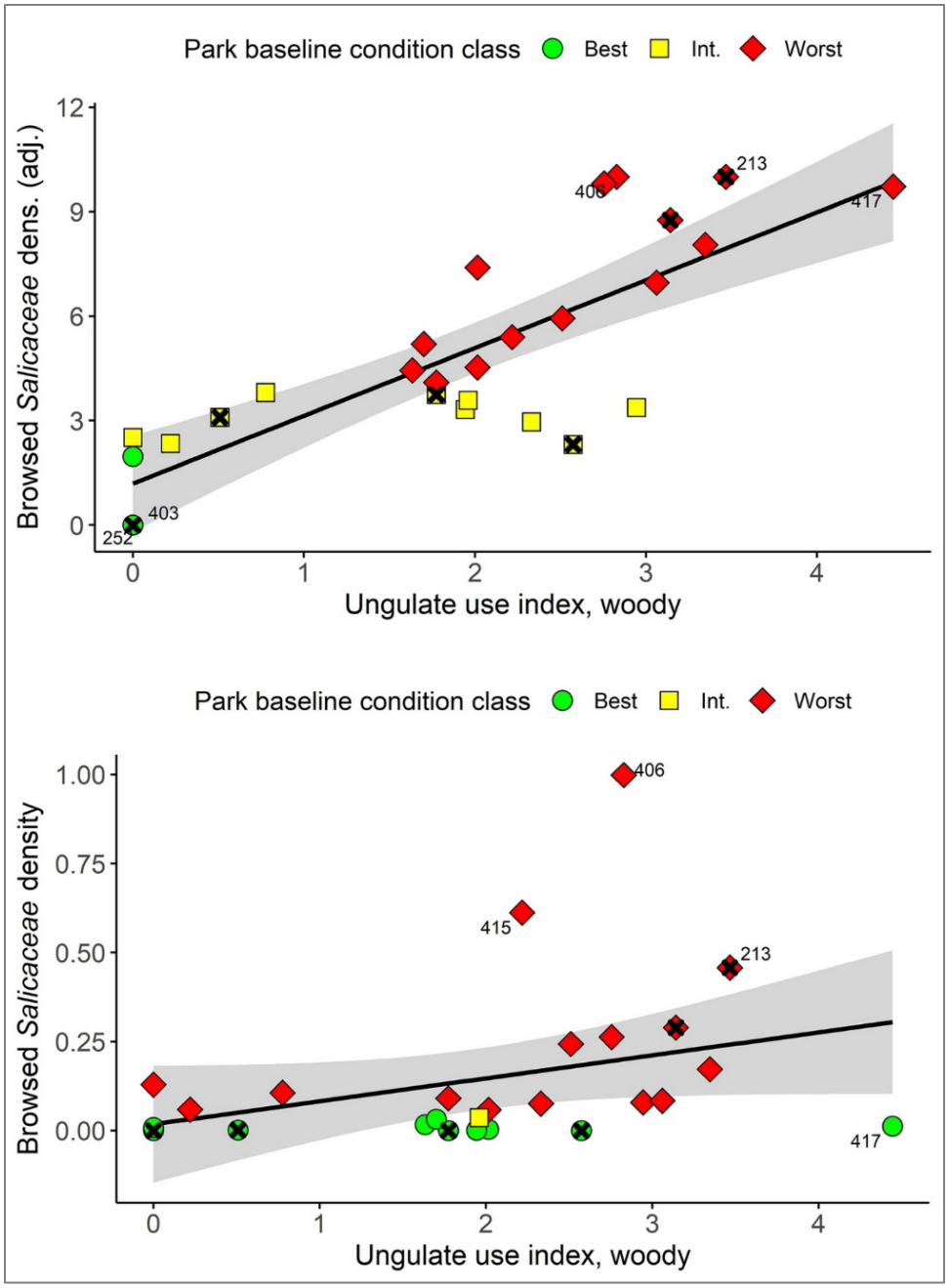


Figure 56. Relationship of (top) adjusted and (bottom) raw density of browsed Salicaceae with Ungulate Use Index (UUI) for woody wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Adjustment is by a linear model with 10 environmental gradients. Linear fit and its 95% confidence interval are shown with the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition, with green circles for "best available" condition, yellow squares for "intermediate" (Int.) condition, and red diamonds for "worst" condition class. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst density of browsed Salicaceae and/or UUI ranges are labeled with their site number. NPS

Density of browsed willows and cottonwood in woody wetlands had complex patterns across variables important to park management, such as exclosures, years, use by elk only or elk and bison, and wetland type. Figure 57 shows box plots of these patterns as interpreted in the main narrative *Hand-picked metrics* section.

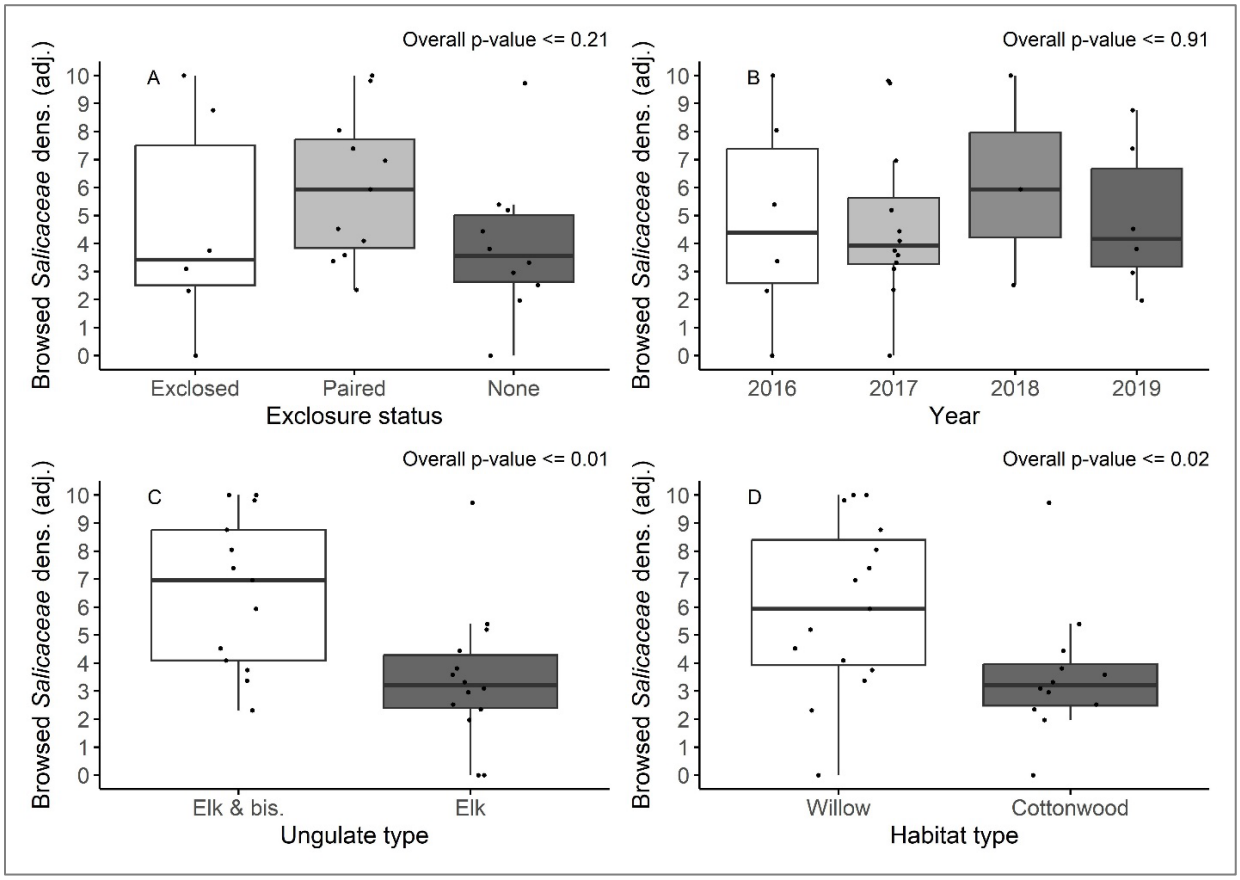


Figure 57. Density of browsed *Salicaceae* (adjusted) in woody sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

Mean graminoid conservatism

Figure 58 gives linear models of adjusted and raw mean graminoid conservatism relative to UUI. Adjustment for environmental gradients increased (relative to the raw data) the correlation with UUI and the amount of variation explained.

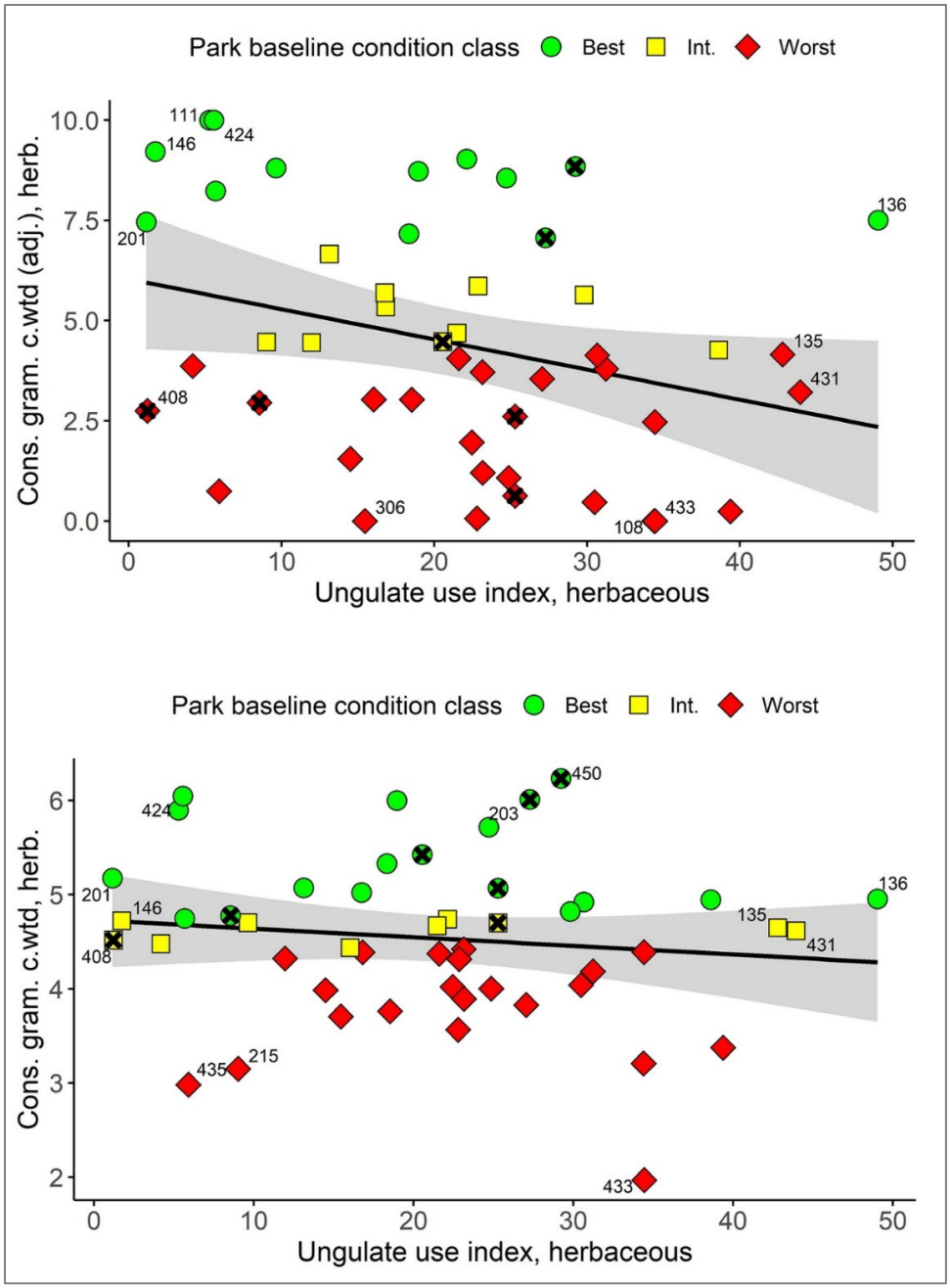


Figure 58. Relationship of (top) adjusted and (bottom) raw mean graminoid conservatism (weighted by cover) with Ungulate Use Index (UUI) for herbaceous wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Adjustment is by a linear model with 10 environmental gradients. Linear fit and its 95% confidence interval are shown with the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition, with green circles for "best available," yellow squares for "intermediate" (Int.), and red diamonds for "worst" condition classes. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst mean graminoid conservatism and/or UUI ranges are labeled with their site number. NPS

Mean graminoid conservatism in herbaceous wetlands had complex patterns across variables important to park management such as exclosures, years, use by elk only or elk and bison, and wetland type. Figure 59 shows box plots of these patterns as interpreted in the main narrative *Hand-picked metrics* section.

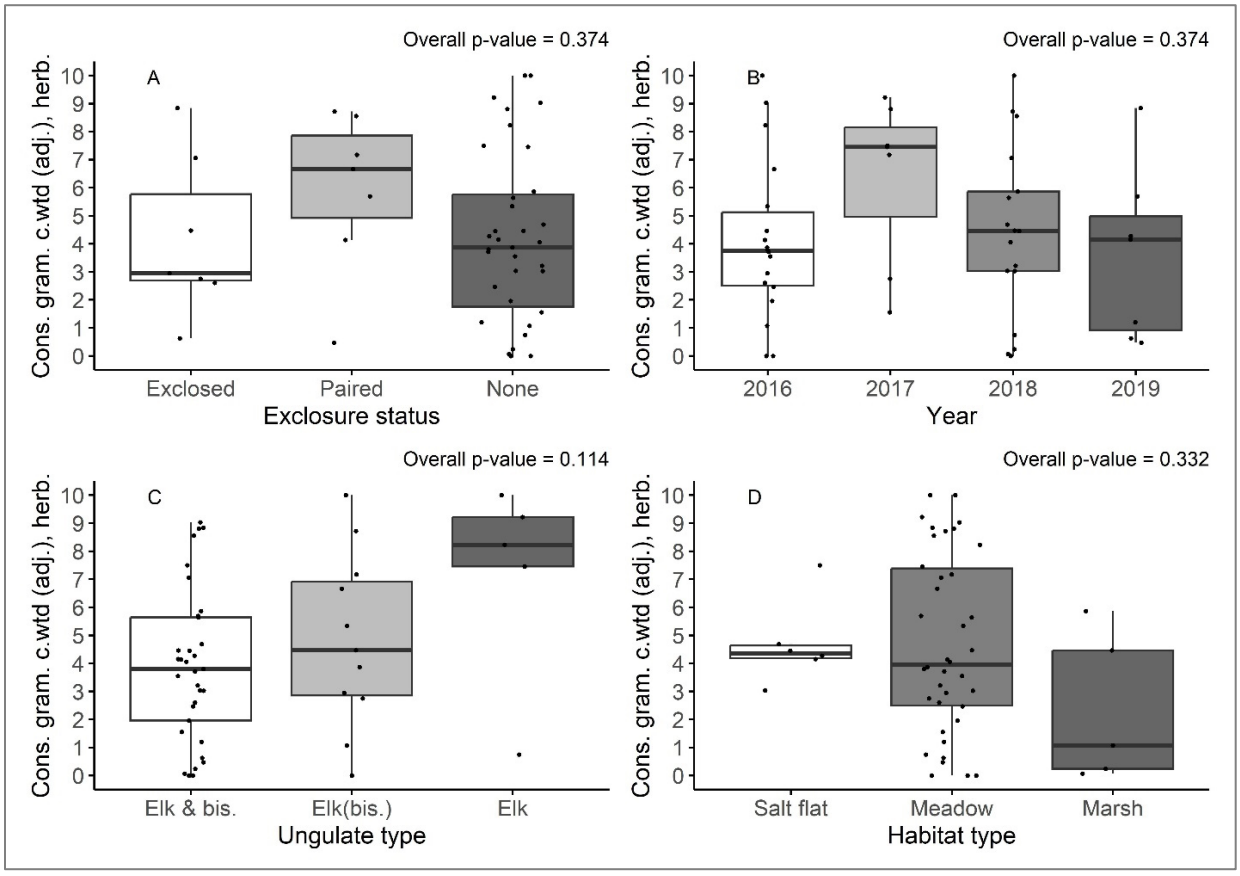


Figure 59. Adjusted mean conservative graminoids (weighted by cover) in herbaceous sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, elk and some bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019 An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

Iris and silverweed absolute cover

Figure 60 gives linear models of adjusted and raw iris and silverweed absolute cover relative to UUI. Adjustment for environmental gradients increased (relative to the raw data) the correlation with UUI and the amount of variation explained.

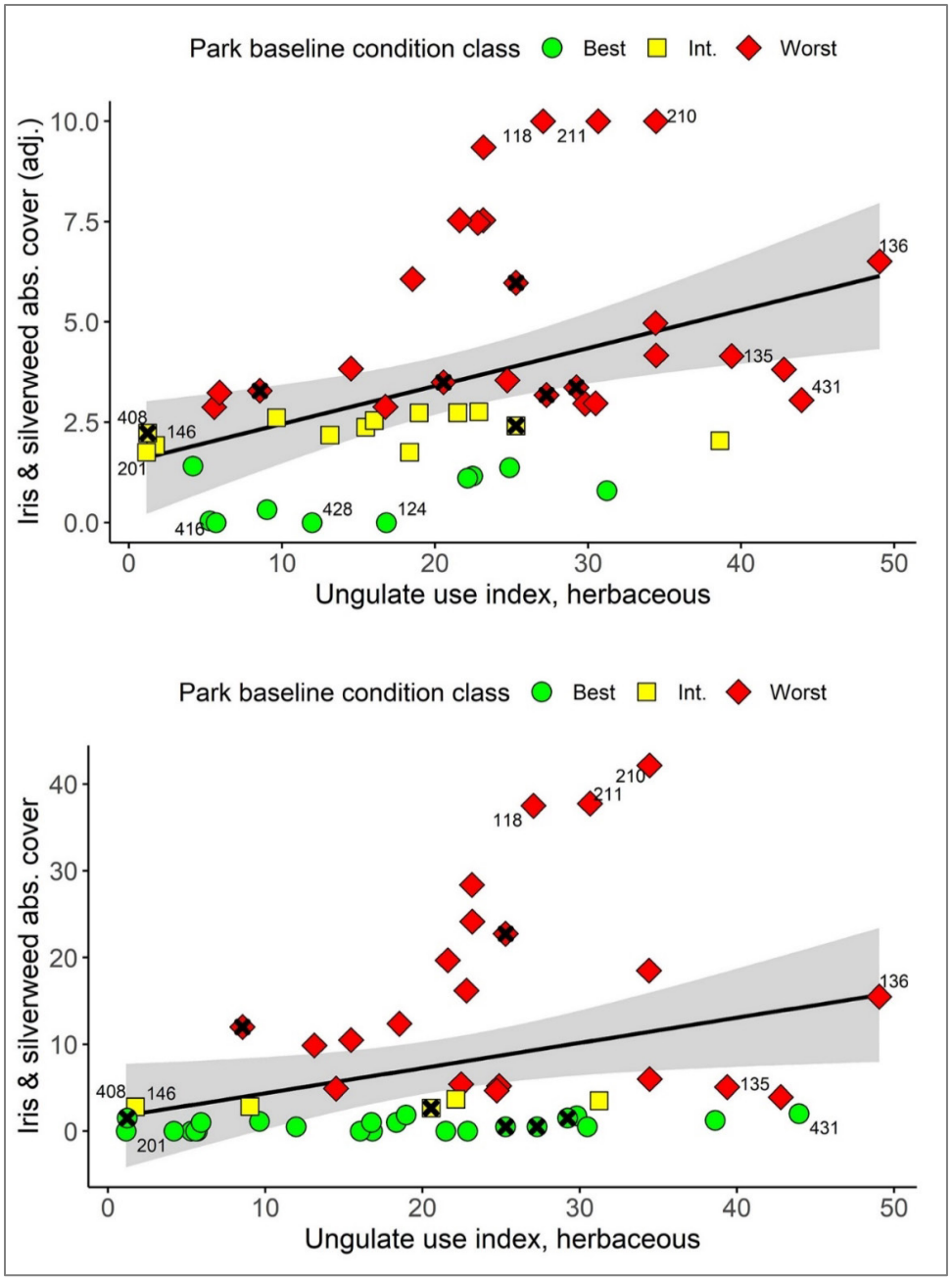


Figure 60. Relationship of (top) adjusted and (bottom) raw iris and silverweed absolute cover with Ungulate Use Index (UUI) for herbaceous wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Adjustment is by a linear model with 10 environmental gradients. Linear fit and its 95% confidence interval are shown with the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition, with green circles for "best available," yellow squares for "intermediate" (Int.), and red diamonds for "worst" condition classes. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst iris and silverweed absolute cover and/or UUI ranges are labeled with their site number. NPS

Iris and silverweed absolute cover in herbaceous wetlands had complex patterns across variables important to park management such as exclosures, years, use by elk only or elk and bison, and wetland type. Figure 61 shows box plots of these patterns as interpreted in the main narrative *Hand-picked metrics* section.

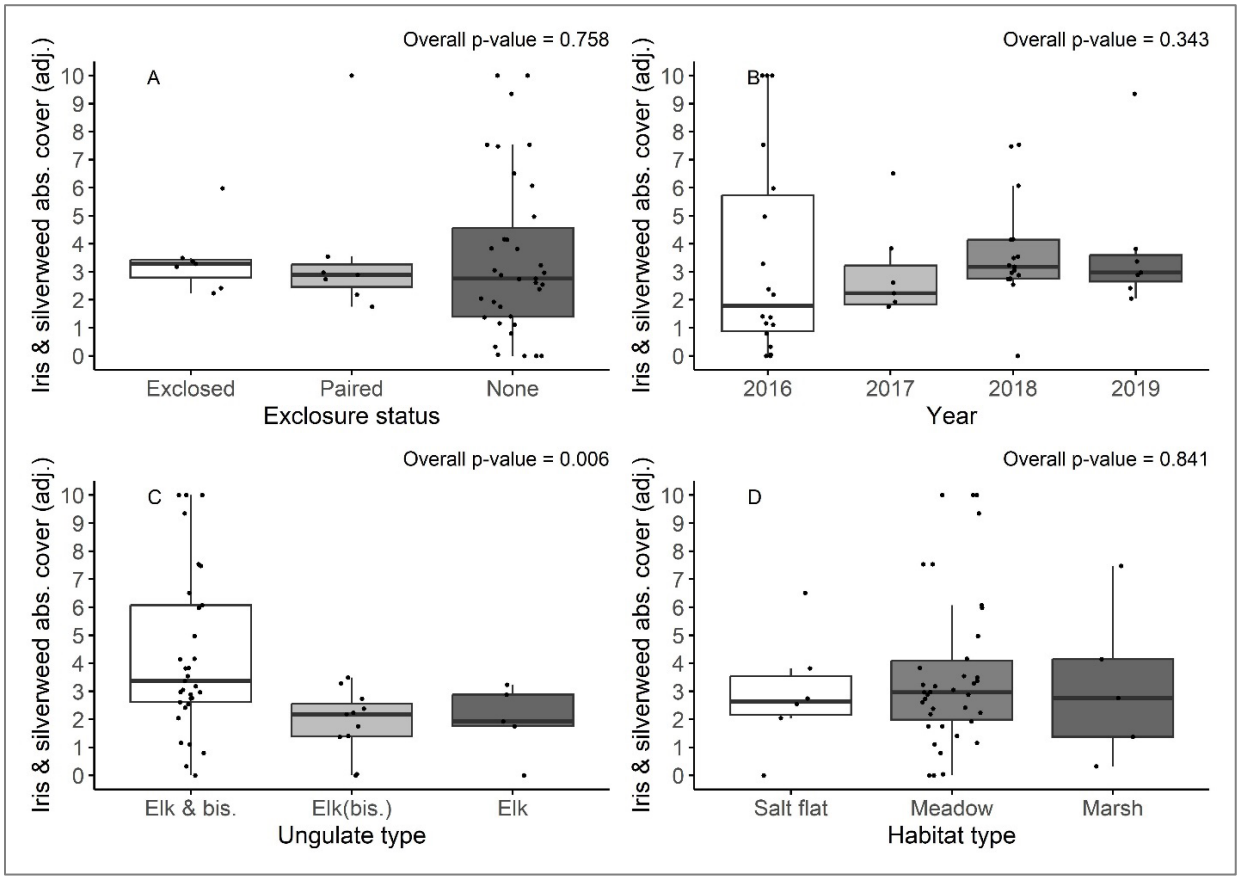


Figure 61. Iris and silverweed absolute cover in herbaceous sites across (A) exclosure status, (B) year, (C) ungulate use type (elk and bison, elk and some bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

Wetland affinity (woody)

Figure 62 gives linear models of adjusted and raw wetland affinity in woody sites relative to UUI. Adjustment for environmental gradients increased (relative to the raw data) the correlation with UUI and the amount of variation explained.

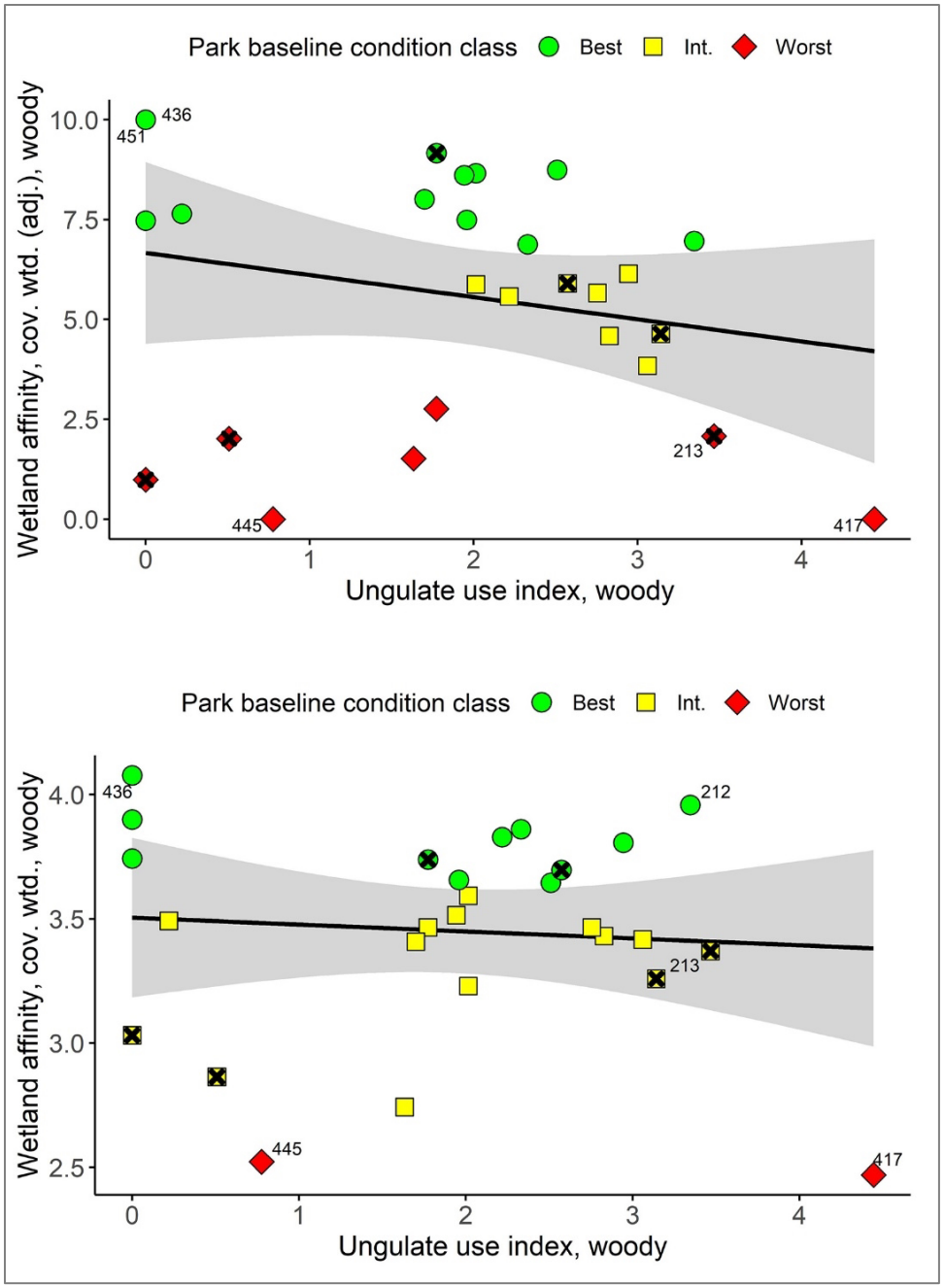


Figure 62. Relationship of (A) adjusted and (B) raw wetland affinity (weighted by cover) and Ungulate Use Index (UUI) for woody wetland sites at Great Sand Dunes National Park and Preserve, 2016–2019. Adjustment is by a linear model with 10 environmental gradients. Linear fit and its 95% confidence interval are shown with the black solid line and gray shaded areas. Point symbology indicates park-based baseline condition with green circles for "best available," yellow squares for "intermediate" (Int.), and red diamonds for "worst" condition classes. Points with black crosses are sites inside an ungulate exclosure. Not all sites are visible given overlapping points. A subset of points that fall in the upper or lower 5th percentile limits of the best/worst wetland affinity and/or UUI ranges are labeled with their site number. NPS

Wetland affinity in woody wetlands had complex patterns across variables important to park management such as exclosures, years, use by elk only or elk and bison, and wetland type. Figure 63 shows box plots of these patterns as interpreted in the main narrative *Hand-picked metrics* section.

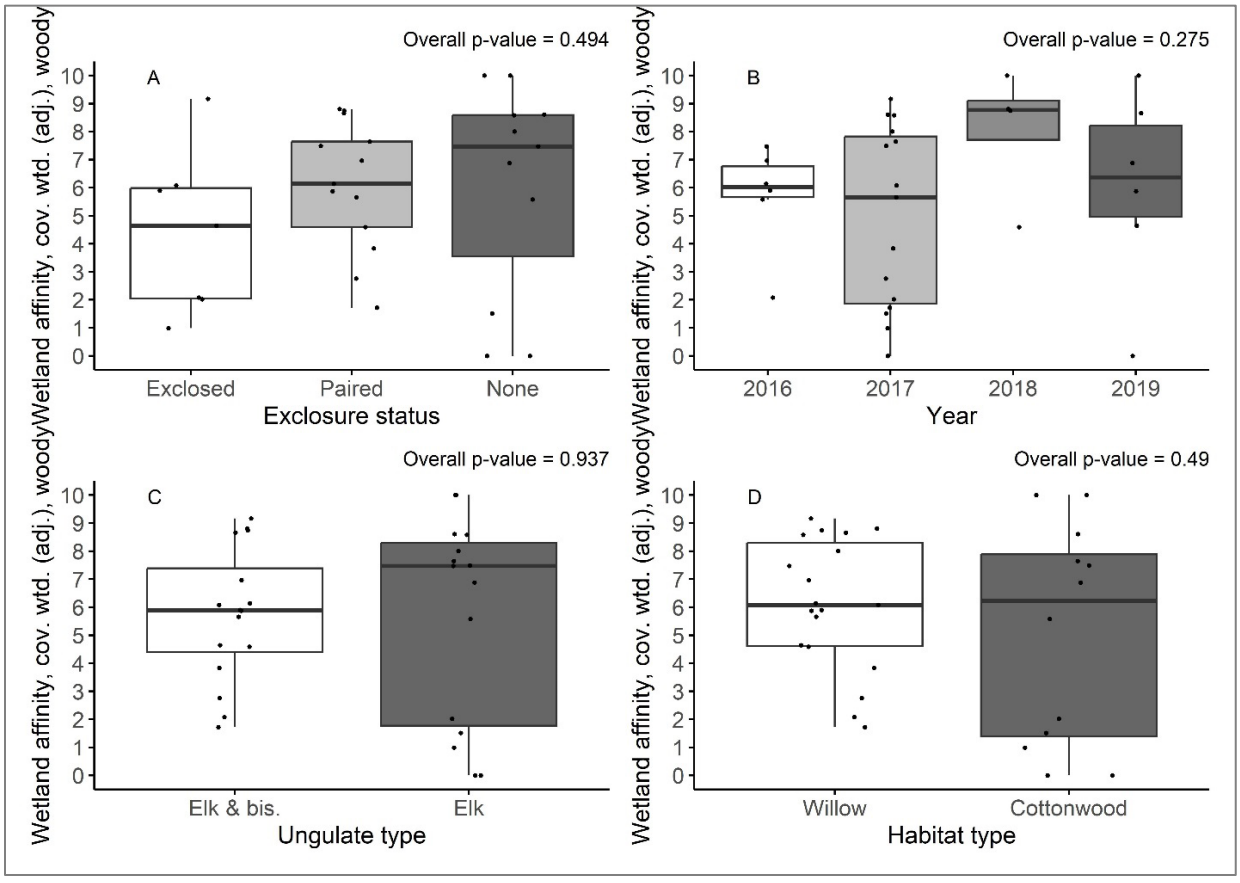


Figure 63. Wetland affinity in woody sites across (A) exclosures, (B) year, (C) ungulate use type (elk and bison, and elk only), and (D) wetland subtype at Great Sand Dunes National Park and Preserve, 2016–2019. An overall p-value is shown from a Wilcox nonparametric test. Select individual paired comparison p-values are reported in the text. Points are individual results. Horizontal lines in boxes are medians. Boxes span the interquartile range and whiskers include any outliers. NPS

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