Title: Quantifying ecological variation across jurisdictional boundaries in a management mosaic landscape

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STRUCTURED ABSTRACT:

Context:

Large landscapes exhibit natural heterogeneity. Land management can impose additional variation, altering ecosystem patterns. Habitat characteristics may reflect these management factors, potentially resulting in habitat differences that manifest along jurisdictional boundaries.

Objectives:

We characterized the patchwork of habitats across a case study landscape, the Grand Canyon Protected Area-Centered Ecosystem. We asked: how do ecological conditions vary across different types of jurisdictional boundaries on public lands? We hypothesized that differences in fire and grazing, because they respond to differences in management over time, contribute to ecological differences by jurisdiction.

Methods:

We collected plot-scale vegetation and soils data along boundaries between public lands units surrounding the Grand Canyon. We compared locations across boundaries of units managed differently, accounting for vegetation type and elevation differences that pre-date management unit designations. We used generalized mixed effects models to evaluate differences in disturbance and ecology across boundaries.

Results:

Jurisdictions varied in evidence of grazing and fire. After accounting for these differences, some measured vegetation and soil properties also differed among jurisdictions. The greatest differences were between US Forest Service wilderness and Bureau of Land Management units. For most measured variables, US Forest Service non-wilderness units and National Park Service units were intermediate.

Conclusions:

In this study, several ecological properties tracked jurisdictional boundaries, forming a predictable patchwork of habitats. These patterns likely reflect site differences that pre-date jurisdictions as well as those resulting from different management histories. Understanding how ecosystem differences manifest at jurisdictional boundaries can inform resource management, conservation, and cross-boundary collaborations.

Keywords:

Cross-boundary management; Ground cover; Management mandates; Management mosaic; Soil stability; Tree species richness

Introduction:

The structure and function of ecosystems are determined by the interaction of natural and anthropogenic factors. Climate, geology, topography, and other abiotic factors interact with organisms to define ecosystem properties, from nutrient cycling to biodiversity. Natural disturbances influence these properties, resulting in heterogeneous landscapes that are patchworks of habitat types and successional stages. Humans further alter the complexity of such patchworks, actively changing land cover for different land uses (Haddad et al. 2015). When these anthropogenic pressures increase fragmentation in ecological communities across the landscape (Kerby et al. 2007; Fuhlendorf et al. 2009), they can reduce gene flow (Dixo et al. 2009) and cause population declines in remnant fragments (Haddad and Baum 1999).

Classic fragmentation studies focus on stark boundaries defining remnant habitat islands surrounded by a matrix of non-habitat (Cushman et al. 2012). Fragmentation can reduce the resources available to individuals in isolated patches and drive local extinctions (Virgós et al. 2002). Additionally, fragmentation can generate edge effects where habitat quality near the edge of isolated habitat patches is altered due to stress, invasion, and disturbance (Fahrig 2003). Through these effects, even without complete habitat transformation (Fischer and Lindenmayer 2007; Måren et al. 2018), disturbance and other processes that drive fragmentation can create subtle changes in ecosystem properties and habitat quality (e.g., groundcover, water availability, presence of native species). For human-managed ecosystems, different management practices (so-called management mosaic landscapes; sensu Epanchin-Niell et al. 2010) may also impose subtle or slow-developing differences across jurisdictional boundaries (Fischer and Lindenmayer 2007; Dorrough et al. 2007). Divergence between neighboring jurisdictions can emerge over time from differences in the type, duration, and intensity of management actions (e.g., Knight et al. 1998; Landres et al. 1998; Holcomb et al. 2011; Kulakowski et al. 2017).

Natural and human-driven ecological heterogeneity can contrast in temporal or spatial scale. Natural ecological transitions (i.e., ecotones) often track topographic features, such as mountains and waterways, while anthropogenic transitions may more closely track jurisdictional boundaries (Aslan et al. 2020). Understanding when and how management influences the characteristics of habitat patchworks is thus essential to predicting ecological processes across landscapes. Furthermore, this understanding is central to key current research priorities in conservation. Since ongoing global climate change operates at large, multi-jurisdictional landscape scales and will influence species range shifts, migration, population connectivity, interspecific interactions, and ecosystem services (e.g., Pearson 2006; Brooker et al. 2007), predicting how habitats and resources vary at a landscape scale is a major research focus (e.g., Bedford et al. 2012; Breed et al. 2013; Kalle et al. 2018; Senner et al. 2018). Such predictions facilitate cross-boundary collaboration, which can bolster the efficiency of conservation efforts at a landscape scale by aligning management directions, permitting coordination of resources and timing, and sharing knowledge and expertise (Kark et al. 2015; Prager et al. 2018; Doyle-Capitman et al. 2018; Cyphers and Schultz 2019; Bothwell 2019). As a result, such collaborative efforts are another active research area in current conservation literature (e.g., Prager et al. 2018; Cyphers and Schultz 2019).

In the United States, four agencies manage more than 90% of federal public lands (~600 million acres) and their management differences may promote ecological divergence at their jurisdictional boundaries. These agencies have different mandates and include the National Park Service (NPS), US Fish & Wildlife Service (USFWS), and Bureau of Land Management (BLM), all part of the US Department of Interior, and the US Forest Service (USFS), which is part of the US Department of Agriculture. While the NPS prioritizes conservation and recreation, BLM and USFS prioritize resource exploitation (primarily grazing and logging); USFWS spans these priority areas (Gorte et al. 2012). Management units within jurisdictions include multiple districts as well as “wilderness” and “non-wilderness” areas, where wilderness areas are managed to preserve their “natural” condition and non-wilderness areas permit some resource extraction and active resource management (USGS 2020).

Disturbances are a primary way in which differences in management mandates, philosophies, resources, and missions become evident across jurisdictional boudaries. As a natural disturbance type, fire is a key process managed differently across federal agencies. For example, natural fires are usually allowed to burn in wilderness areas, and prescribed burning is used to control fuels buildup in some NPS and USFS units (van Wagtendonk 2007; Quinn-Davidson and Varner 2012). Accidental human-ignited fires are usually suppressed as “non-natural,” and suppression techniques in some jurisdictions require tools (e.g., chainsaw use) that may not be permitted in other jurisdictions (Ostergren 2006). Managed resources may be impacted by fire, and thus managers balance the need to protect resources with the need to reduce the risk of high-severity wildfires (Parsons and Landres 1996; Lueck and Yoder 2015).

Livestock grazing, an anthropogenic disturbance, also varies according to jurisdiction, with consequences for vegetation community structure and composition. Across the U.S., the USFS and BLM lease 49% and 63% of their land area, respectively, for grazing (fs.fed.us and blm.gov). Although wilderness areas are managed to minimize human influence (Holmes et al. 2015), grazing is permitted in USFS and BLM wilderness areas as long as it was initiated prior to 1964 (McClaran 1990; Squillace 2014). Grazing is also found on a piecemeal basis in national parks, often due to grandfather clauses (Pinto 2014). Livestock grazing reduces plant biomass, compacts and erodes soils, disturbs water sources, and selects for grazing-tolerant plants, altering ecosystem structure, function, and composition (Stamati et al. 2011; Canals et al. 2011; Herbst et al. 2012; Taboada et al. 2015; Aryal et al. 2015). Grazing can also suppress non-native plants and boost overall plant diversity (e.g., Souther et al. 2019). Effects are influenced by stocking rates and practices (Aubault et al. 2015; Souther et al. 2019). Grazing effects on landscapes and plant communities can last many decades after grazing cessation or reduction (Browning and Archer 2011; Monger et al. 2015).

Here we test whether ecological patterns at jurisdictional boundaries surrounding Grand Canyon, Arizona, are consistent with differences in mandates and objectives of adjacent management units. Grand Canyon National Park is at the center of a patchwork of protected areas, comprising multiple different management units (Fig. 1). Differences in management among these units may create ecological differences at boundaries. For example, NPS and USFS management practices appear to drive divergence in forest structure (Holcomb et al. 2011). The entire area can be viewed as a Protected Area-Centered Ecosystem (hereafter PACE), delineated by mapping habitats and ecological flows influencing Grand Canyon NP as the focal protected area (sensu Hansen et al. 2011). As PACEs illustrate, all protected areas exist within broader landscapes within which human activities across a range of jurisdictions can affect the species and ecosystem properties of the protected area. Little work, however, has explored patterns in ecological factors across multiple boundary types within PACEs. We used our general knowledge of differences in fire and grazing management among agencies to make predictions about ecological differences of adjacent management units (Table 1). We then collected field data on fire and grazing evidence as well as vegetation and soils, to compare adjacent management units. For each measured factor, we tested predictions (Table 1) for pairs of adjoining jurisdictions while accounting for vegetation type and landscape elements that may contribute to pre-existing ecological differences. Our results elucidate key ecological differences across jurisdictional boundaries, several of which are consistent with differences in management practices among units.

Methods:

Study area

To examine how ecological patterns vary across jurisdictional boundaries, we characterized the habitat patchwork within the Grand Canyon PACE as a case study system. The Grand Canyon PACE encompasses 133,260 square kilometers managed by the National Park Service (NPS), the Bureau of Land Management (BLM), the United States Forest Service (USFS), Tribal, state, and private individuals (Fig. 1). Due to access limitations, our samples were restricted to USFS wilderness, USFS non-wilderness, BLM, and NPS, which together account for 83.2% of the PACE (USGS 2020). We use the term “jurisdiction” to refer to sampled management unit types. Elevations across the PACE range from 121 to 3849 m, with high topographic variation, and precipitation ranges from 104.42 to 1161.45 mm/year (1981-2010 average annual precipitation) with most of the landscape considered semiarid (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu). Historic activities impacting current land cover include mining (for uranium, asbestos, bat guano, lead, zinc, copper, and gold), Native American traditional management, logging, livestock grazing, and commercial tourism (Stortz et al. 2018). Today, the region is visited by increasing numbers of recreationists including hikers, campers, hunters, off-highway vehicle enthusiasts, and canyoneers (Stortz et al.

2018). Eleven American Indian tribes are traditionally associated with the Grand Canyon itself: the Havasupai Tribe, Hopi Tribe, Hualapai Tribe, Kaibab Band of Paiute Indians, Las Vegas Band of Paiute Indians, Moapa Band of Paiute Indians, Navajo Nation, Paiute Indian Tribe of Utah, San Juan Southern Paiute Tribe, Yavapai-Apache Nation, and Zuni Tribe (Stortz et al. 2018).

Jurisdictions we sampled are managed for resource extraction, conservation of natural and cultural resources, recreation, and livestock grazing. Grand Canyon National Park, the center of this PACE, was established in 1919 (99 years before our data collection) (Stortz et al. 2018), and replaced the former Grand Canyon National Monument. National Forest tracts surrounding the park were first delineated in 1891 by the Forest Reserve Act, while areas that would become BLM tracts were largely designated in 1934 through the Taylor Grazing Act (Steen 1991; Koontz and Bodine 2008). Historical delineations of jurisdiction did not track clearly evident differences between habitats: for example, each jurisdiction we sampled spans wide elevational gradients and contains diverse vegetation types, and individual habitats occur across multiple jurisdictions (for example, sagebrush steppe, pinyon-juniper, and ponderosa pine can all be found in all sampled jurisdiction types).

Combined, this management mosaic across the Grand Canyon PACE presents an ideal opportunity to compare the ecological properties of adjacent management units that differ in jurisdiction. Current conditions in each unit represent the combined influence of natural patterns such as broad vegetation type, elevation, slope, and aspect, as well as decades of differences in management goals, priorities, and practices. This complexity of factors is likely to generate enormous heterogeneity at multiple scales. However, we hypothesize that differences in management objectives have generated consistent and significant pressures that result at boundaries in distinct ecological patterns that are detectable after accounting for natural heterogeneity. A better understanding of how management differences may manifest ecologically could inform landscape ecology and cross-boundary collaboration and coordination within coupled natural-human systems.

Focal disturbances across the study area

Fire is a dominant natural disturbance in the Grand Canyon PACE, which includes ponderosa pine (*Pinus ponderosa*) forests, high desert sagebrush, pinyon-juniper woodland, and mixed conifer forest (LANDFIRE 2014) (Fig. 1S). The natural fire return interval varies by vegetation type: ponderosa pine forests' estimated natural fire return interval ranges from 2 to 8 years (Fulé et al. 1997) while mixed conifer forests ranges from 4 to 11 years (Wolf and Mast 1998). Decades of fire suppression around the Grand Canyon, however, have lengthened fire intervals considerably in many areas (e.g., to 75 years in mixed conifer; Wolf and Mast 1998; and to more than a century in ponderosa pine; Fulé et al. 1997). The estimated natural fire return interval in juniper stands range broadly, from 26 to 100 years (Huffman et al. 2008). Sagebrush in the broader Great Basin has an estimated natural fire return interval of nearly 200 years, but invasion by cheatgrass (*Bromus tectorum*) has shortened that interval to 78 years (Balch et al. 2013). Heterogeneous vegetation types, fire management, and wildfires have produced a mosaic of fire recovery across the region, including sites which vary in fire severity, extent, and recovery time (Fulé et al. 2000).

Apart from fires on the landscape, livestock grazing is another consistent disturbance that can vary based on management unit. Current livestock grazing densities within the Grand Canyon PACE are low (largely ranging from 0.2-3.3 Animal Unit Months/ha, Souther et al.

2019) and restricted to USFS, BLM, state, and private lands. However, grazing in this region was historically high intensity (likely 2-3 times the current rate, Abruzzi 1995), and effects from that historic grazing are still present (Abruzzi 1995). Cattle are the primary livestock in the PACE, with bison managed as a game species (Reimondo 2012).

Despite broad knowledge on grazing and fire history for the region, we lack detailed historical information that would allow us to perfectly differentiate the ecological effects of management differences from pre-existing patterns at boundaries. However, consistent differences in samples taken just across adjacent unit boundaries can suggest an ecologically-meaningful role of management history, when vegetation type and elevation are held constant to minimize natural differences. Since we cannot know how similar adjacent jurisdictions were prior to the initiation of current management, we adopted a clustered sampling approach that held constant elevation, dominant vegetation type, parent soil material, and topography among contrast points. This sampling approach reduced underlying biophysical variation to increase our ability to detect management-driven differences across jurisdictional boundaries. We then used a two-part approach to address whether differences in fire and grazing management give rise to ecological differences at jurisdictional boundaries. In our first analysis, we asked whether the occurrence of grazing and/or fire evidence differ by jurisdiction type. In our second analysis, we asked whether plant and soil characteristics within sites were related to these disturbance signs and, more broadly, whether these disturbance-relevant plant and soil variables vary systematically across different types of jurisdictional boundaries.

Data collection

We compared current ecological condition across sites varying in jurisdiction, using clustered sampling to minimize natural ecological variation among contrasted data collection locations. Field data collection locations were chosen using a randomization process in ArcGIS. We generated a set of 92,080 random points located 100 m from jurisdictional boundaries between federal units, with a distance of ≧200m between each point. We extracted the subset of points within the following landform classes, to maximize field sampling efficiency: lower slope, lower slope (cool, warm & flat), upper slope, upper slope (cool, warm & flat), valley, valley (narrow); based on Theobald et al. (2015). Out of the reduced set of points, we randomly selected 15 sampling sites to contrast locations across boundaries for each of the following management pairs: NPS and USFS non-wilderness areas; NPS and USFS wilderness areas; NPS and BLM; BLM and USFS non-wilderness; BLM and USFS wilderness; and USFS wilderness and USFS non-wilderness. When access was attempted, some sites could not be reached, usually because no route without cliffs could be found; a minimum of eight sites and a maximum of 15 per contrast were sampled. Each randomly-generated GIS point served as the first of four sampling locations per sampling site. Sampling locations were established in a square array, 200 m on each side, such that two locations were sampled on each side of the jurisdictional boundary (Fig. 2). At each of these locations, two 50-m transects were placed at a 90-degree angle from one another, extending away from the boundary (Fig. 2). Transects were thus spatially nested within locations, which were nested within sampling sites for a maximum of 60 locations and 120 transects per management unit contrast. This design allowed comparison of ecological characteristics blocked by site, to determine whether locations on the same side of the boundary were more similar than locations across the boundary. The design also allowed us to compare ecological conditions between locations in different management tracts while holding constant site factors such as elevation, broad vegetation type, parent soil material, and topography.

Transects were surveyed for percent ground cover by type using a line-point intercept method in which a surveyor dropped a pin every 0.5 m and recorded the first cover type encountered (below waist height) as bare ground, rock, litter, lichen, moss, biocrust, forb, grass, shrub, or tree. Evidence of disturbance (e.g., fire scar, livestock scat, digging, human trail) was recorded using the transects as midlines of 6x50m belt transects, with disturbance types quantified as presence/absence within each 1-m interval of the central transect. Nine soil samples were collected along each transect (at 5m intervals from meters 5-45) and a soil slake test kit was used to quantify stability of the samples. Three soil cores were taken from meters 15, 30, and 45 along each transect, and the depths of the cores were recorded. The three cores were homogenized and placed on ice for later chemical analysis. Finally, a 10x10m quadrat was established, centered along each transect and extending from meters 20-30. Within this quadrat, all trees greater than 10cm DBH were recorded by species and DBH, and counts of all seedlings and saplings <10cm DBH were recorded by species (Fig. 2). These data allowed calculation of tree species richness, seedling/sapling density, and average size for each transect.

Soil chemical analyses were conducted at the Kansas State University Soil Testing Laboratory. Field soils were homogenized and pooled for each transect, then subsampled and analyzed for total C, total N, and Mehlich-3 P. Total carbon and nitrogen were analyzed on a LECO TruSpec CN Carbon/Nitrogen combustion analyser (LECO Corporation, St. Joseph, USA). Available nitrogen was calculated as the sum of ammonium and nitrate. Total phosphorus content was measured using the Mehlich-3 method on a Lachat Quickchem 8000 (Lachet Instruments, Loveland, USA).

Data analysis

Our stepwise analyses examined (1) the relationship between disturbance and jurisdiction and (2) the relationship between measured ecological characteristics and both jurisdiction and evidence of disturbance. In both analyses, we controlled for elevation and vegetation type. The inference associated with Analysis 1 examined whether the intensity of various disturbances is meaningfully different among jurisdictions. The inference associated with Analysis 2 spanned two parts: (Part 2A) assessing whether disturbance is predictive of ecological characteristics; and (Part 2B) estimating the differences between jurisdictions after controlling for presence of disturbance. In Analysis 1, jurisdiction type and elevation were fixed effects and the best fitting model was the beta binomial. In Analysis 2, fixed effects included jurisdiction type, evidence of grazing (i.e., presence/absence of grazing sign), evidence of fire (i.e., presence/absence of evidence of fire or fuel disturbance, including chainsaw marks, charring, or fallen logs), and elevation. We included both jurisdiction and observed signs of disturbance in these models because we expected ecological differences between jurisdictions to be driven by the combined effects of intrinsic site-to-site heterogeneity and varying management trajectories; we wished to quantify ecological differences discernible between jurisdictions even after accounting for observed disturbance.

Responses were observed along each segment or intercept of transects, and covariates were observed at the transect level. Each model also included a random intercept term for sampling site to accommodate the blocking structure created by the sampling design and to account for variation among sites that is not captured by the fixed effects in our model. The random intercept term allowed the site-level means to vary around an overall mean. We also allowed site-level variances to vary (i.e., to arise from an underlying distribution of site-level variances). In cases where estimates of both intercepts and variances did not converge, we made the simplifying assumption that variances were the same for observations at all locations across the PACE. We did not include a nested random intercept for sampling locations within sites because the sampling design blocked locations by site to minimize variation.

We used a Bayesian statistical framework to fit generalized linear mixed models (GLMM) (Table 2). This approach allows us to account for the nested structure of the field sampling design (i.e., observations collected at sampling locations nested within sites, the blocking factor) as described above. Also, Bayesian models are highly flexible, accommodating many different types of observations represented in our field data (Table 1S), including counts and 0 to 1 data, among others. Bayesian models can also be mixed to account for zero inflation (Min and Agresti 2005).

We used Markov chain Monte Carlo (MCMC) for parameter estimation. We used the algorithm implemented in JAGS (Plummer 2003), making all calls to fit and summarize models in the R programming language (R-Core-Team, 2017). Covariates in responses were standardized to reduce autocorrelation in the MCMC chain, to support comparison of the relative influence of model coefficients, and to aid in the interpretation of model predictions. Convergence was checked by visual inspection of trace plots and by the diagnostic of Rubin (1992). Model fit was evaluated using posterior predictive checks (Gelman et al. 2013).

Model inference on ecological differences across jurisdictional boundaries was based on the mean predicted response for each jurisdiction in the PACE, after accounting for elevation, fire sign, and grazing sign. We contrasted the means for each pair of jurisdiction types as differences (e.g., mean grass cover in Jurisdiction A minus mean grass cover for Jurisdiction B).

Results:

Analysis 1: Relationship between jurisdiction and evidence of disturbance

Our disturbance occurrence models found differences by jurisdiction in field-collected evidence of our focal disturbance types, consistent with the premise that these signs of disturbance reflect jurisdictional mandates and practices. In general, presence of livestock evidence was most associated with BLM sampling locations and least with USFS wilderness, and presence of cattle scat was highest in BLM sampling locations and lowest in USFS wilderness sampling locations (Fig. 3). Evidence of fire and fuels management was highest in USFS nonwilderness and NPS sampling locations and lowest in USFS wilderness (Fig. 3). Specifically, evidence of chainsaw use was lowest in USFS wilderness sampling locations and highest in USFS non-wilderness sampling locations. Presence of charring was lowest in USFS wilderness sampling locations and highest in NPS sampling locations. Fallen log presence was lowest in BLM sampling locations and highest in USFS wilderness sampling locations.

Analysis 2a: Relationship between disturbance evidence and measured ecological variables

Disturbance that varied by jurisdiction was related to measured ecological variables. In our field sampling plots, after accounting for elevation, field evidence of fire, and jurisdiction and holding constant broad vegetation type, topography, and soil parent material, our models indicated that percent cover of bare ground and grass, as well as tree species richness and tree DBH, tended to be higher where signs of grazing were present. For edaphic properties, total soil nitrogen, total soil carbon, soil stability, and phosphorus were generally lower when signs of grazing were present (Fig. 2S). However, there were no discernible relationships between signs of grazing and sapling density, tree cover, soil available nitrogen, or cover of shrubs or forbs (Fig. 2S).

Where signs of fire were present, our models indicated that percent cover of bare ground and grass, as well as tree DBH and sapling density tended to be lower than in locations with no evidence of fire. By contrast, cover of trees and forbs, as well as soil stability and soil carbon, were each higher where fire evidence occurred. We found no discernible relationships between signs of fire and total soil nitrogen, phosphorus, soil C:N ratio, soil available nitrogen, tree species richness, or cover of shrubs (Fig. 2S).

Analysis 2b: Jurisdictional contrasts in measured ecological variables

After accounting for observed fire and grazing disturbances at site locations and comparing adjacent jurisdictions sampled just 200 m apart, we identified those jurisdictional contrasts for which two criteria hold: 1) the modeled probability of difference between jurisdictions exceeded 90%, which we considered strong evidence for a difference between jurisdictions; and 2) the model predicted a median difference between jurisdictions that is at least 10% of the median value of the variable across all sites, a threshold we selected to indicate biologically meaningful contrasts among jurisdictions (Table 3). Based on these criteria, we found several notable patterns observable directly across jurisdictional boundaries even when elevation and broad vegetation type were held constant. BLM sampling locations had relatively lower soil stability, lower tree species richness and tree cover, and higher bare ground and shrub occurrence than, in each case, at least one contrast jurisdiction (Table 3). USFS wilderness sampling locations had higher soil stability, higher total soil carbon, higher tree species richness and tree cover, and lower occurrence of grass and bare ground than at least one contrast jurisdiction (Table 3). USFS non-wilderness locations had more grass cover than BLM or USFS wilderness, less bare ground and shrubs than BLM or NPS, and lower soil stability and tree cover than USFS wilderness (Table 3). NPS locations also had more grass cover than BLM or USFS wilderness, and more bare ground than USFS wilderness or USFS non-wilderness (Table 3). No contrasts between jurisdictions exceeded the 10% threshold in forb cover, sapling density, average DBH of non-sapling trees, or soil nitrogen or phosphorus (Fig. 3S).

Discussion:

Adjacent jurisdictions in the Grand Canyon PACE show consistent differences in recent disturbance and ecological variables. Analysis 1 revealed that, as predicted, jurisdictions showed clear differences in recent fire and grazing evidence, with the greatest differences between areas managed by the Bureau of Land Management and by the US Forest Service as wilderness. Moreover, Analysis 2 revealed that these jurisdictional differences were repeated in vegetation (e.g., cover and tree diversity) and edaphic factors (soil stability and carbon), several of which were directly linked to recent fire and grazing evidence at the sites. These ecological factors that differ between jurisdictions are critical to forage, habitat availability, erosion, and carbon storage (e.g., Schuman et al. 2002; Klaus et al. 2005; Ware et al. 2014; Hessburg et al. 2019). While only visible evidence of disturbances was observable in the field, sampled locations surely have experienced grazing and fire disturbances, over the decades since jurisdictions were assigned, for which evidence is no longer visible. Absence of disturbance evidence does not confirm the absence of disturbance. Nevertheless, our findings are consistent with differing management practices and mandates among agencies. For example, BLM has a mandate for multiple resource use compared to “untrammeled wilderness” for USFS wilderness. These differences exemplify how management choices may increase complexity in the ecological mosaic (Epanchin-Niell et al. 2010) within and surrounding protected areas.

Some predicted ecological differences between jurisdictions were not observed in field data (Tables 1 and 3). Differences in groundcover (e.g., grass and bare ground) differed among multiple jurisdiction pairs, a pattern consistent with the known effects of fire (Balch et al. 2013) and grazing (Best and Arcese 2009; D'Odorico et al. 2012). Tree saplings and tree age (i.e. DBH) were not consistently different among jurisdictions, even though we had predicted that stand age and post-disturbance recruitment would play greater roles in particular jurisdictions (e.g. USFS-nonwilderness vs USFS wilderness; Table 1). Since tree diversity differed between adjacent jurisdictions, we cannot rule out that the lack of other patterns in trees were obscured by changing species. Like tree diversity, soil carbon and soil stability were highest in USFS Wilderness, yet jurisdictional differences were not evident in soil nutrients, including nitrogen and phosphorus. Grazing can alter many of these soil properties, although these grazing effects often depending on precipitation (Piñeiro et al. 2010) and so may have been obscured by the broad precipitation gradient across the Grand Canyon PACE. Nutrients deposited by cattle (and other grazers) through feces and urine may be too localized to produce consistent differences between jurisdictions (Augustine and Frank 2001), particularly because we pooled soils along each transect. Fire effects on soil nutrients are also well-known (Certini 2005), but like grazing may be spatially heterogeneous (and severity dependent) such that they did not manifest as consistent nutrient differences between jurisdictional pairs. Our work was suited to isolate any predictable patterns in these variables by contrasting jurisdictions at samples clustered around the boundary (200m) and stratified (experimentally and statistically) to account for natural heterogeneity throughout the Grand Canyon PACE. That natural heterogeneity likely swamped the effects of some differences in disturbance management among agencies and jurisdictions, an important finding for our growing understanding of how ecosystems and habitats vary over management mosaics.

Landscape ecology quantifies the drivers and consequences of habitat patchiness and heterogeneity stemming from disturbance as well as other factors (Turner & Gardner 2015). Classic ecology models identify disturbance as a critical determinant of community structure and diversity (e.g., Connell 1978; Tilman 2004; Vanschoenwinkel et al. 2013). Fires, for example, create heterogeneity (i.e., pyrodiversity) that can maintain species diversity and drive evolutionary diversification (Pausas and Ribeiro 2017; He et al. 2019). Our work suggests that subdivision of landscapes among anthropogenic jurisdictions can contribute in predictable ways to landscape heterogeneity (Allouche et al. 2012), likely at least in part because they differ in disturbance management. Research aiming to predict global change, including wildfires, increasingly recognizes that ecological factors must be integrated with human decisions to explain land cover and disturbance patterns worldwide (Turner 2010; Pechony and Shindell 2010; Bowman et al. 2011). While decision-making frameworks are multi-faceted, our findings indicate that jurisdiction may help predict specific ecological variables and be useful to incorporate in landscape-scale habitat models. These integrated models may better account for disturbance management trajectories, guide vulnerability assessments, and foster collaborative planning.

Causes and effects in jurisdictional and ecological patterns:

Differences in ecological variables between jurisdictions may be both a product of and contributor to differences in management. Because our work cannot contrast perfectly similar areas that differ only in one disturbance, the differences observed between units may be products of other factors that control both management regimes and ecological variables. Our study design controlled for natural heterogeneity among contrasting samples. Nevertheless, ecological variables differing among units may have played a role in their original jurisdictional designation. For example, more bare ground in BLM units (as compared to USFS) may both have contributed to BLM jurisdictional boundary establishment and be a consequence of decades of management differences between the two agencies. Decision-making processes to designate jurisdictional boundaries (nearly a century ago) are poorly catalogued; we have found no information at the fine scale (within 200 m) indicating clear ecological drivers underlying boundary designations within our sampled areas. Instead, our approach was intended to evaluate whether present-day ecological differences between units are consistent with those differences we anticipate, based on our knowledge of various management strategies in various jurisdictions and their likely effects on localized ecological variables. As researchers continue to explore feedbacks between ecology and management and how they affect habitats over time, disturbance management is a promising focal area. For example, ecosystems maintained with recurrent fires may be key focal study systems to further our understanding. In many such locations, prescribed fires maintain vegetation which, in turn, creates fuels that "engineer" fire spread and intensity, resulting in a feedback (Beckage et al. 2009). Just as ecological differences may manifest between jurisdictions, so too may management actions in specific jurisdictions may be shaped by differences in ecology.

Variation in the intensity of disturbances like grazing and fire may further contribute to management differences at boundaries and ultimately landscape heterogeneity. Based on vegetation cover, two grazed units may make different management decisions about livestock type, grazing intensity, seasonality, duration, and frequency, all of which in turn influence groundcover and soil carbon and stability. Our results are consistent with the hypothesis that, in the Grand Canyon PACE, heterogeneity in grazing sign is related to variable ecological conditions across the landscape, particularly cover of bare ground and grass, soil chemistry, soil stability, and tree species richness. Along similar lines, differences in fire severity and frequency between adjacent jurisdictions may arise from management histories leading to different quantities and connectivity of fuels on either side of the boundary. In the Grand Canyon PACE, we found that heterogeneity in fire evidence was related to variable groundcover by functional group, as well as tree DBH, sapling density, soil stability, and soil carbon.

The patchwork of habitats across the landscape, which we show is partly related to jurisdictional differences in grazing and fire management, may impact ecological communities and biodiversity. For example, species requiring mature, mixed tree-species forests (e.g., northern goshawk) or bare ground (e.g., some native bee species) for nesting may occur at higher densities in USFS wilderness and BLM/NPS jurisdictions respectively (Stortz et al. 2018; Potts et al. 2005), as a result of increased availability of these resources in those jurisdictions. Spread of fire or biological invaders is also influenced by factors like groundcover type (Balch et al. 2013; Le Maitre et al. 2014). The habitat patchwork described here should produce corresponding patchiness in their spread, some of which may predictably track jurisdictional boundaries. In contrast, the movement of generalist species with broad forage and cover requirements (e.g., Kaibab mule deer or mountain lion) may exhibit little relationship to jurisdiction (Stortz et al. 2018; Dickson et al. 2013). Future work that connects species traits and habitat requirements with the ecosystem elements altered by differences in specific management will be necessary for predicting whether jurisdictional boundaries may act as barriers for species to respond to global change.

Conclusion:

This study finds evidence that ecological conditions vary systematically by jurisdiction across the management mosaic of this landscape. Our analyses found that evidence of fire and grazing varied by jurisdiction and were linked to ecological variables, resulting in ecological differences among jurisdictions. Specifically, evidence of fire and grazing varied across focal jurisdictions, as did ecological variables including percent cover of grass, shrubs, trees, and bare ground; tree diversity; and soil stability and carbon. However, forb cover, tree size and sapling density, and soil nitrogen and phosphorus did not vary across jurisdictions. Overall, the largest differences were found between Bureau of Land Management and US Forest Service wilderness sites. This finding is consistent with their differing management and mandates: multiple resource use for the BLM and untrammeled wilderness for USFS wilderness.

Social science engagement with land managers could enable future researchers to identify specific social drivers of the differences observed here and in similar landscapes, by investigating current and past differences in management practices. Economic resources (e.g., Kachergis et al. 2014), organizational hierarchies (e.g., Cundill and Fabricius 2010), and game theory (e.g., Martin and Bender 1999) all may provide important insights into decisions that, if sustained through time, drive ecological divergence on the landscape. In the meantime, cross-boundary ecological differences should be incorporated into modeling and prediction of species assemblages and fire risk across the region. These differences may be of increasing importance as species and communities change in response to landscape-scale drivers such as climate change. Jurisdictional boundaries that manifest as ecological thresholds could hinder or alter species' range shifts and movements if important habitat elements change across those boundaries.

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Literature Cited

Abruzzi WS (1995) The social and ecological consequences of early cattle ranching in the Little Colorado River Basin. Human Ecology 23:75–98.

Allouche O, Kalyuzhny M, Moreno-Rueda G, et al (2012) Area–heterogeneity tradeoff and the diversity of ecological communities. Proceedings of the National Academy of Sciences 109:17495–17500.

Aryal S, Cockfield G, Maraseni TN (2015) Effect of summer livestock grazing on plant species richness and composition in the Himalayan rangelands. The Rangeland Journal 37:309–321.

Aslan CE, Brunson MW, Sikes BA, Epanchin-Niell RS, Veloz S, Theobald DM, Dickson BG (In review) Feedbacks between ecological and management connectivity across administrative boundaries in undeveloped landscapes. Ecosphere.

Aubault H, Webb NP, Strong CL, et al (2015) Grazing impacts on the susceptibility of rangelands to wind erosion: The effects of stocking rate, stocking strategy and land condition. Aeolian Research 17:89–99.

Augustine DJ, Booth DT, Cox SE, Derner JD (2012) Grazing intensity and spatial heterogeneity in bare soil in a grazing-resistant grassland. Rangeland Ecology & Management 65:39–46.

Augustine DJ, Frank DA (2001) Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. Ecology 82:3149–3162.

Balch JK, Bradley BA, D'Antonio CM, Gómez-Dans J (2013) Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology 19:173–183.

Beckage B, Platt WJ, Gross LJ (2009) Vegetation, Fire, and Feedbacks: A disturbance-mediated model of savannas. The American Naturalist 174:805–818.

Bedford FE, Whittaker RJ, Kerr JT (2012) Systemic range shift lags among a pollinator species assemblage following rapid climate change1This article is part of a Special Issue entitled "Pollination biology research in Canada: Perspectives on a mutualism at different scales". Botany 90:587–597.

Best RJ, Arcese P (2009) Exotic herbivores directly facilitate the exotic grasses they graze: mechanisms for an unexpected positive feedback between invaders. Oecologia 159:139–150.

Bothwell KN (2019) Practicing collaborative natural resource management with federal agencies: keys to success across partnership structures. Journal of Forestry 117:226–233.

Bowman DMJS, Balch J, Artaxo P, et al (2011) The human dimension of fire regimes on Earth. Journal of Biogeography 38:2223–2236.

Breed GA, Stichter S, Crone EE (2013) Climate-driven changes in northeastern US butterfly communities. Nature Climate Change 3:142–145.

Brooker RW, Travis JMJ, Clark EJ, Dytham C (2007) Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change. Journal of Theoretical Biology 245:59–65.

Browning DM, Archer SR (2011) Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing. Ecological Applications 21:1629–1642.

Canals RM, Ferrer V, Iriarte A, et al (2011) Emerging conflicts for the environmental use of water in high-valuable rangelands. Can livestock water ponds be managed as artificial wetlands for amphibians? Ecological Engineering 37:1443–1452.

Certini G (2005) Effects of fire on properties of forest soils: a review. Oecologia 143:1–10

Cundill G, Fabricius C (2010) Monitoring the governance dimension of natural resource co-management. Ecology and Society 15:1.

Cushman SA, Shirk A, Landguth EL (2012) Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. Landscape Ecology 27:369–380.

Cyphers LA, Schultz CA (2019) Policy design to support cross-boundary land management: The example of the Joint Chiefs Landscape Restoration Partnership. Land Use Policy 80:362–369.

Dickson BG, Roemer GW, McRae BH, Rundall JM (2013) Models of regional habitat quality and connectivity for Pumas (Puma concolor) in the Southwestern United States. PLoS ONE 8:e81898.

Dixo M, Metzger JP, Morgante JS, Zamudio KR (2009) Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. Biological Conservation 142:1560–1569.

D'Odorico P, Okin GS, Bestelmeyer BT (2012) A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. Ecohydrology 5:520–530.

Dorrough JW, Ash JE, Bruce S, McIntyre S (2007) From plant neighbourhood to landscape scales: how grazing modifies native and exotic plant species richness in grassland. Plant Ecology 191:185–198.

Doyle-Capitman CE, Decker DJ, Jacobson CA (2018) Toward a model for local stakeholder participation in landscape-level wildlife conservation. Human Dimensions of Wildlife 23:375–390.

Epanchin-Niell RS, Hufford MB, Aslan CE, et al (2010) Controlling invasive species in complex social landscapes. Frontiers in Ecology and the Environment 8:210–216.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265–280.

Fuhlendorf SD, Engle DM, Kerby J, Hamilton R (2009) Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. Conservation Biology 23:588–598.

Fulé PZ, Covington WW, Moore MM (1997) Determining reference conditions for ecosystem management of Southwestern ponderosa pine forests. Ecological Applications 7:895–908. ht

Fulé PZ, Heinlein TA, Covington WW, Moore MM (2000) Continuing fire regimes in remote forests of Grand Canyon National Park. In: Proceedings: Wilderness Science in a Time of Change. Proc. RMRS-P-15. USA Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah, USA. pp 242–248

Fulé PZ, Laughlin DC, Covington WW (2005) Pine-oak forest dynamics five years after ecological restoration treatments, Arizona, USA. Forest Ecology and Management 218:129–145.

Gelman A, Carlin JB, Stern HS, et al (2013) Bayesian Data Analysis, Third Edition. CRC Press.

Gorte RW, Vincent CH, Hanson LA, Rosenblum MR (2012) Federal land ownership: overview and data. Congressional Research Service Washington, DC.

Haddad NM, Baum KA (1999) An experimental test of corridor effects on butterfly densities. Ecological Applications 9:623–633.

Haddad NM, Brudvig LA, Clobert J, et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances 1:e1500052.

Hansen AJ, Davis CR, Piekielek N, et al (2011) Delineating the ecosystems containing protected areas for monitoring and management. BioScience 61:363–373.

Hawkins BA, Field R, Cornell HV, et al (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117.

Herbst DB, Bogan MT, Roll SK, Safford HD (2012) Effects of livestock exclusion on in-stream habitat and benthic invertebrate assemblages in montane streams. Freshwater Biology 57:204–217.

Hessburg PF, Miller CL, Parks SA, et al (2019) Climate, environment, and disturbance history govern resilience of western North American Forests. Front Ecol Evol 7:239.

Hilbe JM (2014) Modeling Count Data. In: Cambridge Core.

Holcomb CM, Sisk TD, Dickson BD, Sesnie SE, Aumack EN (2011) Administrative boundaries and ecological divergence: the divided history and coordinated future of land management on the Kaibab Plateau, Arizona, USA. Pages 1–20 in Van Riper III C, Villareal ML, van Riper CR, Johnson MJ, eds. The Colorado Plateau V: Research, Environmental Planning, and Management for Collaborative Conservation. University of Arizona Press, Tucson, Arizona.

Huffman DW, Fulé PZ, Pearson KM, Crouse JE (2008) Fire history of pinyon–juniper woodlands at upper ecotones with ponderosa pine forests in Arizona and New Mexico. Canadian Journal of Forest Research 38:2097–2108.

Huffman DW, Moore MM (2004) Responses of *Fendler ceanothus* to overstory thinning, prescribed fire, and drought in an Arizona ponderosa pine forest. Forest Ecology and Management 198:105–115.

Jimenez Aguilar A, Huber-Sannwald E, Belnap J, et al (2009) Biological soil crusts exhibit a dynamic response to seasonal rain and release from grazing with implications for soil stability. Journal of Arid Environments 73:1158–1169.

Kachergis E, Derner JD, Cutts BB, et al (2014) Increasing flexibility in rangeland management during drought. Ecosphere 5:art77.

Kalle R, Ramesh T, Downs CT (2018) When and where to move: Dynamic occupancy models explain the range dynamics of a food nomadic bird under climate and land cover change. Global Change Biology 24:e27–e39.

Kark S, Tulloch A, Gordon A, et al (2015) Cross-boundary collaboration: key to the conservation puzzle. Current Opinion in Environmental Sustainability 12:12–24.

Kerby JD, Fuhlendorf SD, Engle DM (2007) Landscape heterogeneity and fire behavior: scale-dependent feedback between fire and grazing processes. Landscape Ecology 22:507–516.

Klaus NA, Buehler DA, Saxton AM (2005) Forest management alternatives and songbird breeding habitat on the Cherokee National Forest, Tennessee. The Journal of Wildlife Management 69:222–234.

Knight RL, Knight RL, Landres P (1998) Stewardship Across Boundaries. Island Press.

Koontz TM, Bodine J (2008) Implementing ecosystem management in public agencies: lessons from the U.S. Bureau of Land Management and the Forest Service. Conservation Biology 22:60–69.

Kutiel P, Shaviv A (1989) Effect of simulated forest fire on the availability of N and P in mediterranean soils. Plant Soil 120:57–63.

Landres PB, Knight RL, Pickett ST, Cadenasso ML (1998) Ecological effects of administrative boundaries. Pages 39-64 in Knight RL, Landres PB (editors), Stewardship Across Boundaries.

Le Maitre DC, Kotzee IM, O’Farrell PJ (2014) Impacts of land-cover change on the water flow regulation ecosystem service: Invasive alien plants, fire and their policy implications. Land Use Policy 36:171–181.

Lueck D, Yoder J (2015) The economic foundations of firefighting organizations and institutions. j for 113:291–297.

Manley JT, Schuman GE, Reeder JD, Hart RH (1995) Rangeland soil carbon and nitrogen responses to grazing. Journal of Soil and Water Conservation 50:294–298.

Måren IE, Kapfer J, Aarrestad PA, et al (2018) Changing contributions of stochastic and deterministic processes in community assembly over a successional gradient. Ecology 99:148–157.

Martin WE, Bender HW (1999) Modelling public land-use decisions as a cooperative game. International Journal of Environment and Pollution 12:217–231.

McClaran MP (1990) Livestock in wilderness: a review and forecast. Environmental Law 20:857–890.

Min Y, Agresti A (2005) Random effect models for repeated measures of zero-inflated count data. Statistical Modelling 5:1–19.

Monger C, Sala OE, Duniway MC, et al (2015) Legacy effects in linked ecological–soil–geomorphic systems of drylands. Frontiers in Ecology and the Environment 13:13–19.

Neff JC, Reynolds RL, Belnap J, Lamothe P (2005) Multi-decadal impacts of grazing on soil physical and biogeochemical properties in Southeast Utah. Ecological Applications 15:87–95.

Parsons DJ, Landres PB (1996) Restoring natural fire to wilderness: how are we doing? Rocky Mountain Research Station.

Pearson RG (2006) Climate change and the migration capacity of species. Trends in Ecology & Evolution 21:111–113.

Pechony O, Shindell DT (2010) Driving forces of global wildfires over the past millennium and the forthcoming century. PNAS 107:19167–19170.

Pellegrini AFA, Ahlström A, Hobbie SE, et al (2018) Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. Nature 553:194–198.

Piñeiro G, Paruelo JM, Oesterheld M, Jobbágy EG (2010) Pathways of grazing effects on soil organic carbon and nitrogen. Rangeland Ecology & Management 63:109–119.

Pinto RL (2014) Cattle grazing in the national parks: Historical development and history of management in three Southern Arizona parks. Ph.D., The University of Arizona

Prager K, Lorenzo-Arribas A, Bull H, et al (2018) Social constraints in cross-boundary collaborative deer management. Ecology and Society 23:4.

Kulakowski D, Seidl R, Holeksa J, et al (2017) A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. Forest Ecology and Management 388:120–131.

Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Working Papers 8.

Potts SG, Vulliamy B, Roberts S, et al (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology 30:78–85

Quinn-Davidson LN, Varner JM (2012) Impediments to prescribed fire across agency, landscape and manager: an example from northern California. International Journal of Wildland Fire 21:210–218.

Ricklefs RE, He F (2016) Region effects influence local tree species diversity. Proceedings of the National Academy of Sciences 113:674–679.

Rubin DB (1992) Computational aspects of analysing random effects/longitudinal models. Statistics in Medicine 11:1809–1821.

Saiz H, Alados CL (2012) Changes in semi-arid plant species associations along a livestock grazing gradient. PLoS ONE 7:e40551.

Schuman GE, Janzen HH, Herrick JE (2002) Soil carbon dynamics and potential carbon sequestration by rangelands. Environmental Pollution 116:391–396.

Senner NR, Stager M, Cheviron ZA (2018) Spatial and temporal heterogeneity in climate change limits species' dispersal capabilities and adaptive potential. Ecography 41:1428–1440.

Souther S, Loeser M, Crews TE, Sisk T (2019) Complex response of vegetation to grazing suggests need for coordinated, landscape-level approaches to grazing management. Global Ecology and Conservation 20:e00770.

Squillace M (2014) Grazing in wilderness areas. Environmental Law 44:415–445.

Stamati FE, Nikolaidis NP, Venieri D, et al (2011) Dissolved organic nitrogen as an indicator of livestock impacts on soil biochemical quality. Applied Geochemistry 26:S340–S343.

Steen HK (1991) The Beginning of the National Forest System. U.S. Department of Agriculture, Forest Service.

Stortz SD, Aslan CE, Sisk TD, Chaudhry T, Rundall JM, Palumbo J, Zachmann L, Dickson B (2018) The Greater Grand Canyon Landscape Assessment: A resource condition assessment of Grand Canyon National Park and surrounding region. Natural Resource Technical Report. NPS, Ft. Collins, CO.

Taboada MA, Rubio G, Chaneton EJ (2015) Grazing impacts on soil physical, chemical, and ecological properties in forage production systems. In: Soil Management: Building a Stable Base for Agriculture. John Wiley & Sons, Ltd, pp 301–320.

Theobald DM, Harrison-Atlas D, Monahan WB, Albano CM (2015) Ecologically-relevant maps of landforms and physiographic diversity for climate adaptation planning. PLoS ONE 10:e0143619.

Turner MG (2010) Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

U.S. Forest Service. 2007. Forest Service manual FSM 2300 – Recreation, wilderness, and related resource management. US Forest Service, Washington, DC.

U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 20180930, Protected Areas Database of the United States (PAD-US): PAD-US Version 2.0, U.S. Geological Survey (USGS), https://usgs.gov/gapanalysis/PAD-US/, downloaded January 2020.

van Wagtendonk JW (2007) The history and evolution of wildland fire use. Fire Ecology 3:3–17.

Verma S, Jayakumar S (2012) Impact of forest fire on physical, chemical and biological properties of soil: a review. Proceedings of the International Academy of Ecology and Environmental Sciences 2:168-176.

Virgós E, Tellería JL, Santos T (2002) A comparison on the response to forest fragmentation by medium-sized Iberian carnivores in central Spain. Biodiversity and Conservation 11:1063–1079.

Ware IM, Terletzky P, Adler PB (2014) Conflicting management objectives on the Colorado Plateau: Understanding the effects of bison and cattle grazing on plant community composition. Journal for Nature Conservation 22:293–301.

Weber GE, Jeltsch F, Rooyen NV, Milton SJ (1998) Simulated long-term vegetation response to grazing heterogeneity in semi-arid rangelands. Journal of Applied Ecology 35:687–699.

Wolf JJ, Mast JN (1998) Fire history of mixed-conifer forests on the North Rim, Grand Canyon National Park, Arizona. Physical Geography 19:1–14.

Tables

Table 1. Conceptual framework and predicted ecological differences among jurisdictions across the focal Grand Canyon Protected Area-Centered Ecosystem. Due to combined fire and grazing management (mechanisms discussed in the text), we hypothesized that different jurisdictions will exhibit systematic differences in measured ecological variables, when sources of natural heterogeneity were held constant. For each measured variable, higher expected values are indicated by more stars. BLM = Bureau of Land Management. USFS = United States Forest Service. NPS = National Park Service. Nonwild = nonwilderness. Wild = wilderness.

Response variable	**Predicted jurisdictional difference**	**Rationale**	**Citations**
Groundcover			
Grass	BLM > USFS-nonwild > NPS > USFS-wild	Due to competition and succession, grass cover is higher where trees are rare, in post-fire systems, and where grazing is frequent.	Best and Arcese 2009; D'Odorico et al. 2012; Balch et al. 2013
Forbs	USFS-nonwild > NPS > BLM > USFS-wild	Due to competition and succession, forb cover is higher where trees are rare, in post-fire systems, and where grazing is frequent.	Best and Arcese 2009; D'Odorico et al. 2012; Balch et al. 2013
Shrubs	BLM ≈ USFS-nonwild > NPS > USFS-wild	Due to competition and succession, shrub cover is higher where trees are rare, in post-fire systems, and where grazing is frequent.	Best and Arcese 2009; D'Odorico et al. 2012; Balch et al. 2013
Trees	USFS-wild > NPS > USFS-nonwild > BLM	Tree cover is likely lowest in BLM sites as a consequence of high long-term grazing pressure. Disturbances including prescribed fire likely limit tree cover in USFS nonwilderness and NPS sites	Best and Arcese 2009
Bare ground	BLM > USFS-nonwild > NPS > USFS-wild	Bare ground is likely highest where over-grazing and other localized disturbances are common.	D'Odorico et al. 2012
Trees			

	No. saplings	USFS-nonwild ≈ NPS > BLM ≈ USFS-wild	Post-disturbance tree regeneration likely increases sapling densities in USFS nonwilderness and NPS sites.	USFS 2007
	Size/age	USFS-wild > NPS > USFS-nonwild > BLM	Historical logging, prescribed burning, and fuels management likely result in reduced tree sizes and ages in USFS nonwilderness and NPS sites.	Stortz et al. 2018
	Richness	USFS-wild > NPS > USFS-nonwild > BLM	Tree diversity is likely to be highest where management interventions are lightest and thus allow for diverse tree functional groups	USFS 2007
Soil				
	Stability	USFS-wild ≈ NPS > USFS-nonwild > BLM	Soil stability can be promoted by well-established vegetation cover and intact soil biocrust and reduced by livestock movements and loss of vegetation.	Neff et al. 2005; Jimenez Aguilar et al. 2009
	C:N ratio	BLM ≈ USFS-nonwild > NPS ≈ USFS-wild	Grazing generally increases carbon:nitrogen (C:N) ratios. Fire has historically been thought to increase C:N ratios, because N volatilizes at lower temperatures, but recent work has found that repeated fires over longer periods decrease N and C equally, since reduced N in the short term results in decreased C fixation in the longer term.	Manley et al. 1995; Piñeiro et al. 2010; Verma and Jayakumar 2012; Pellegrini et al. 2018
	Phosphorus	USFS-nonwild ≈ NPS > BLM ≈ USFS-wild	Fire generally liberates phosphorus (P) from plants, increasing available P in soils.	Kutiel and Shaviv 1989

Table 2. Summary of selected inferential models for each response.

Response	Probability distribution	Deterministic model	Variance type	p mean	p SD	Gelman diagonal
Ammonium PPM	lognormal	log-linear	fixed	0.54	0.6	1.01
Available nitrogen	lognormal	log-linear	hier	0.33	0.12	1.01
Available nitrogen	lognormal	log-linear	hier	0.33	0.12	1.01
Bare ground cover	beta-binomial	inverse-logit	hier	0.52	0.67	1.04
Carbon to nitrogen ratio	lognormal	log-linear	hier	0.81	0.83	1.01
Forb cover	beta-binomial	inverse-logit	hier	0.52	0.6	1.17
Grass cover	beta-binomial	inverse-logit	hier	0.5	0.65	1.05
Nitrate PPM	lognormal	log-linear	hier	0.16	0.2	1.01
Number of saplings	negative-binomial	linear	fixed	0.19	0.1	1.02
Phosphorus PPM	lognormal	log-linear	fixed	0.78	0.95	1
Shrub cover	beta-binomial	inverse-logit	hier	0.51	0.78	1.02
Soil stability	ordinal-latent-normal	linear	fixed	0.88	0.78	2.16
Total carbon	beta	inverse-logit	hier	0.69	0.69	1.04
Total nitrogen	beta	inverse-logit	hier	0.46	0.6	1.01
Tree cover	beta-binomial	inverse-logit	fixed	0.5	0.69	1.02
Tree DBH	lognormal	log-linear	hier	0.73	0.83	1.01
Tree species richness	gen-pois	zero-trick	fixed	0.5	0.25	1.13

Table 3. Effect sizes of contrasts among jurisdictions across the focal Grand Canyon Protected Area-Centered Ecosystem. Where modeled probability of differences between jurisdictions was high, we examined the median difference in values for the contrast. To focus on differences likely to be biologically meaningful, we here identify for discussion only those contrasts with **both** high (≥90%) probability of some difference and for which the model predicted a median difference between jurisdictions that is at least 10% of the median value of the variable across all sites. Note that median groundcover differences in the table below refer to percentage point differences. BLM = Bureau of Land Management. USFS nonwild = United States Forest Service non-wilderness. USFS wild = United States Forest Service wilderness. NPS = National Park Service.

Variable	**Jurisdictional contrast**	**Probability of difference**	**Median difference/ Overall median**
Groundcover			
Grass	USFS nonwild > USFS wild	1.000	0.521
	NPS > USFS wild	0.998	0.380
	USFS nonwild > BLM	1.000	0.352
	NPS > BLM	0.982	0.202
	BLM > USFS wild	0.935	0.134
Forbs	<none>		
Shrubs	BLM > USFS nonwild	0.982	0.229
	NPS > USFS nonwild	0.992	0.215
Trees	USFS wild > BLM	0.925	0.371

	USFS wild > USFS nonwild	0.961	0.383
Bare ground	BLM > USFS wild	0.976	0.347
	BLM > USFS nonwild	0.999	0.276
	NPS > USFS wild	0.993	0.255
	NPS > USFS nonwild	0.982	0.173
Trees			
No. saplings	<none>		
DBH	<none>		
Richness	USFS wild > BLM	1.000	0.137
Soil			
Stability	USFS wild > BLM	0.971	0.196
	USFS wild > USFS nonwild	0.934	0.130
Total carbon	USFS wild > NPS	0.995	0.191
	USFS wild > BLM	0.983	0.176
	USFS wild > USFS nonwild	0.982	0.145
Available nitrogen	<none>		
Total nitrogen	<none>		
C:N ratio	<none>		
Phosphorus	<none>		

Figures

Figure 1. For this case study, we focused on the management mosaic in the Grand Canyon Protected Area-Centered Ecosystem (PACE). (a) Map of the study area with management boundaries obscured. (b) Map of the study area, which is defined by natural ecosystem boundaries, displaying management unit boundaries across the landscape. Jurisdiction abbreviations: BLM = Bureau of Land Management; NPS = National Park Service; USFS = United States Forest Service.

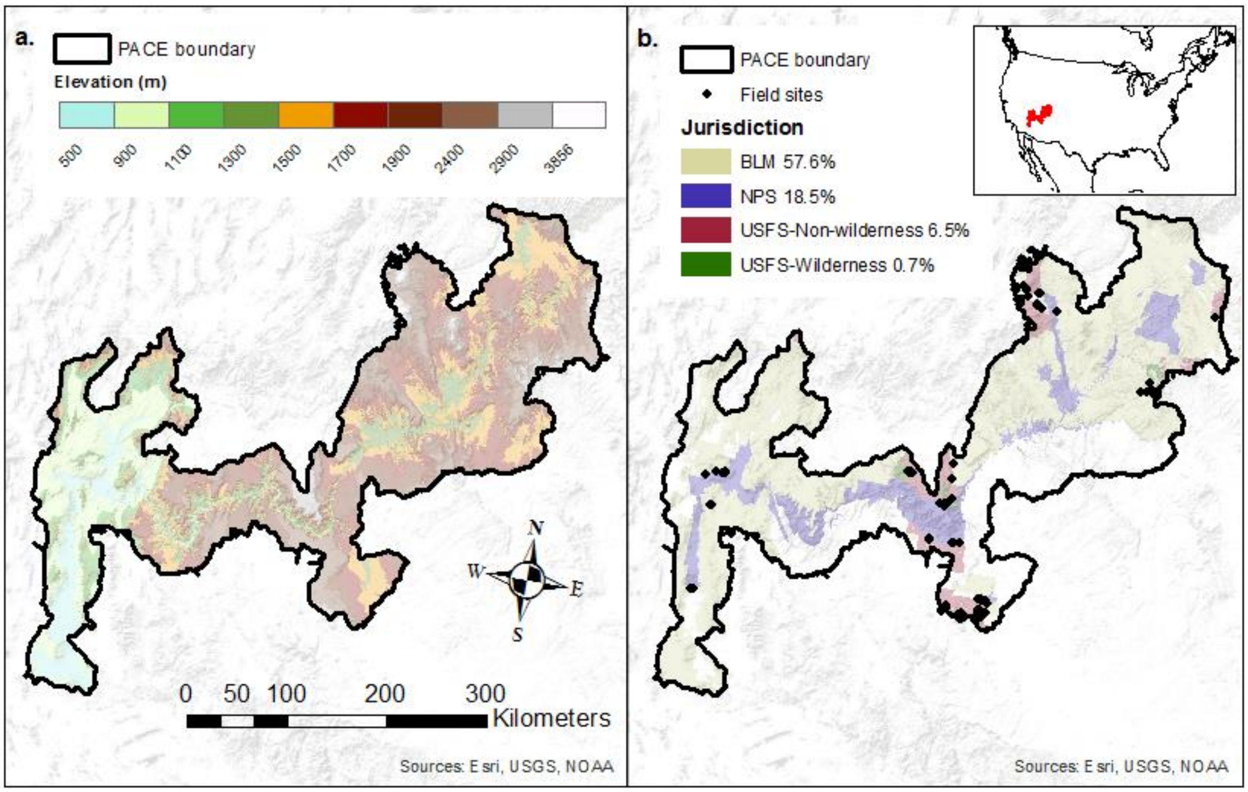


Figure 2. Field data were collected on either side of management unit boundaries by generating random sampling points (i.e. sites) and establishing four sampling locations at each site, two on either side of the boundary. Two sampling transects were established at each location, as described in the text.

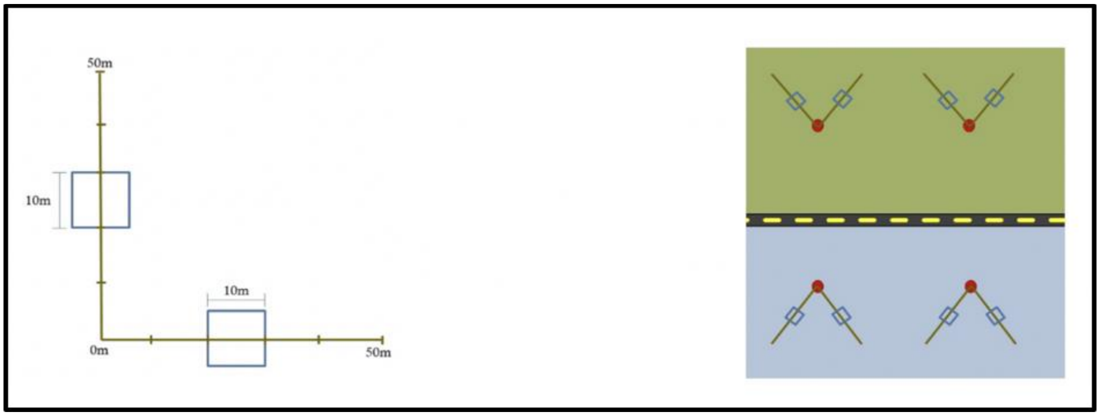
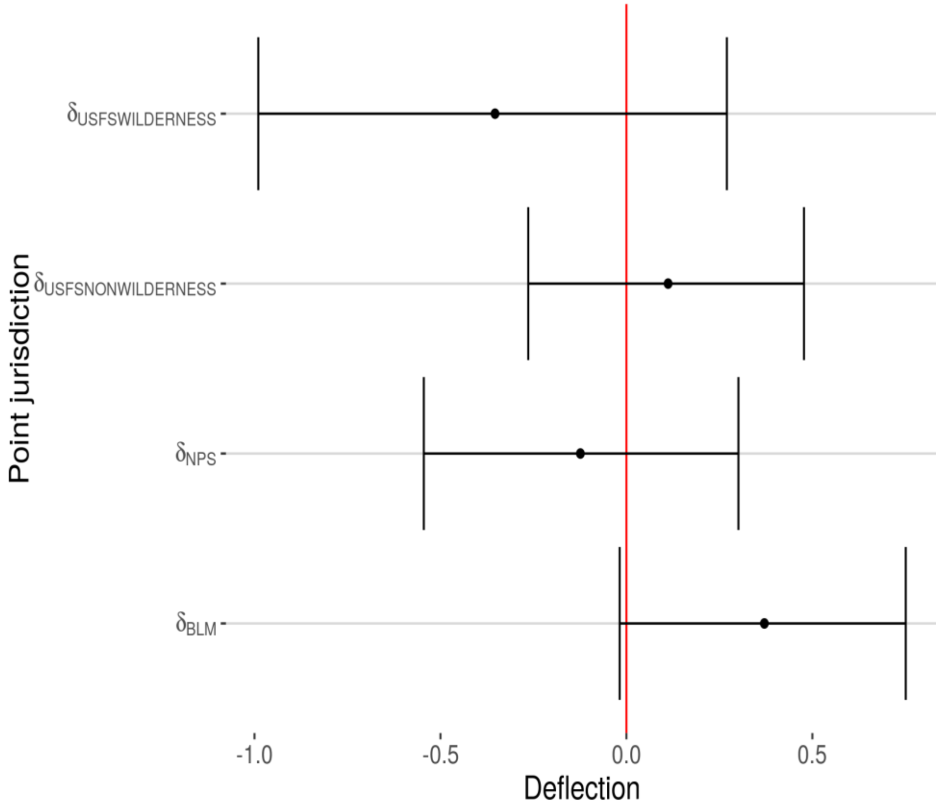
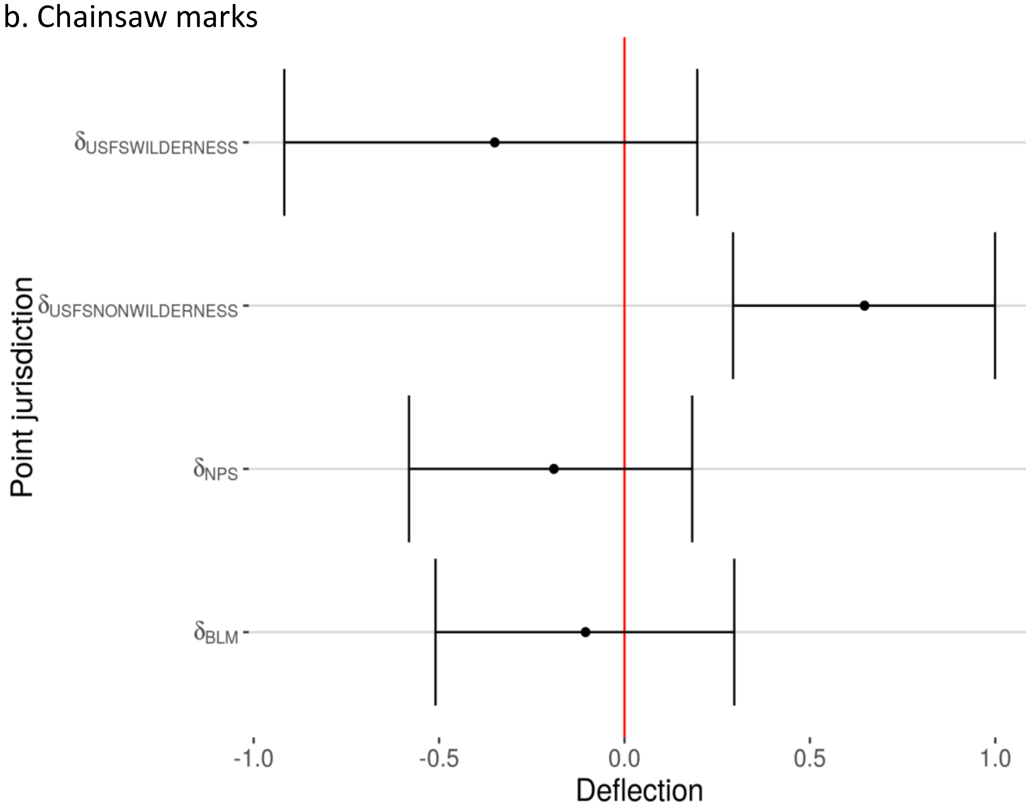


Figure 3. Coefficients (± 95% credible intervals) for the effect-coded jurisdiction variables included in the beta binomial models of disturbance. Results suggest there is evidence of disturbance by jurisdiction in field sampling data. Specifically, (a) BLM sampling locations exhibited the highest presence of cattle scat, with lowest occurrence in USFS wilderness. (b-d) Presence of fire and fuel disturbance evidence recorded on the ground included chainsaw marks, charring, and fallen logs. (b) Presence of chainsaw marks was lowest in USFS wilderness and highest in USFS non-wilderness. (c) Charring presence was lowest in USFS wilderness and highest in NPS. (d) Fallen log presence was lowest in BLM and highest in USFS wilderness.

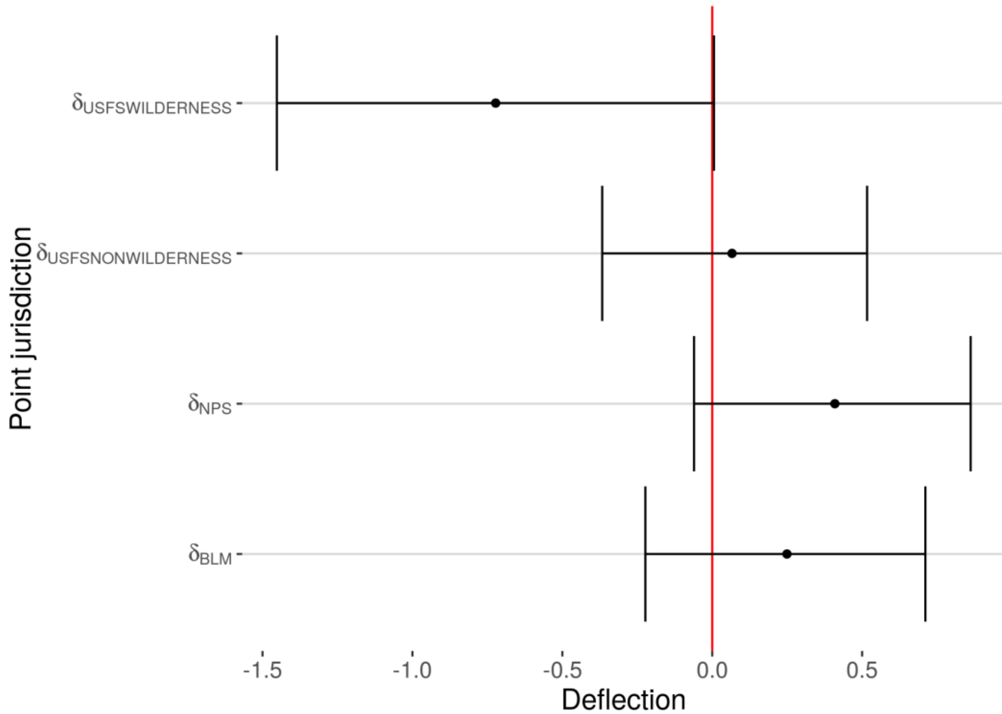
a. Cattle scat



b. Chainsaw marks



c. Charring



d. Fallen log presence