frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 23 December 2022
DOI 10.3389/fevo.2022.1053548

OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Biogeography and Macroecology, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 25 September 2022
ACCEPTED 02 December 2022
PUBLISHED 23 December 2022

CITATION
Aslan CE, Zachmann L, Epanchin-Niell RS, Brunson MW, Veloz S and Sikes BA (2022) Soil characteristics and bare ground cover differ among jurisdictions and disturbance histories in Western US protected area-centered ecosystems.
Front. Ecol. Evol. 10:1053548.
doi: 10.3389/fevo.2022.1053548

Soil characteristics and bare ground cover differ among jurisdictions and disturbance histories in Western US protected area-centered ecosystems

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Introduction: Ecological conditions at a given site are driven by factors including resource availability, habitat connectivity, and disturbance history. Land managers can influence disturbance history at a site by harvesting resources, creating transportation pathways, introducing new species, and altering the frequency and severity of events such as fires and floods. As a result, locations with different land management histories have also likely experienced different disturbance trajectories that, over time, are likely to result in different ecological characteristics.

Methods: To understand how the presence of different management histories may shape ecological conditions across large landscapes, we examined plant and soil characteristics at matched sampling points across jurisdictional boundaries within four Protected Area-Centered Ecosystems (PACEs) in the western US. We employed Bayesian modeling to explore 1) the extent to which specific ecological variables are linked to disturbance and jurisdiction both among and within individual PACEs, and 2) whether disturbance evidence differs among jurisdictions within each PACE.

Results: Across all jurisdictions we found that disturbances were associated with ecologically meaningful shifts in percent cover of bare ground, forbs, grass, shrubs, and trees, as well as in tree species richness, soil stability, and total carbon. However, the magnitude of shifts varied by PACE. Within PACEs, there were also meaningful associations between some ecological variables and jurisdiction type; the most consistent of these were in soil stability and soil carbon:nitrogen ratios. Disturbance evidence within each PACE was relatively similar across jurisdictions, with strong differences detected between contrast jurisdictions only for the Lassen Volcanic National Park PACE (LAVO).

Discussion: These findings suggest an interaction between management history and geography, such that ecotones appear to manifest at jurisdictional boundaries within some, but not all, contexts of disturbance and location. Additionally, we detected numerous differences between PACEs in the size of disturbance effects on ecological variables, suggesting that while the interplay between disturbance and management explored here appears influential, there remains a large amount of unexplained variance in these landscapes. As continued global change elevates the importance of large landscape habitat connectivity, unaligned management activities among neighboring jurisdictions are likely to influence existing ecological conditions and connectivity, conservation planning, and desired outcomes.

KEYWORDS

anthropogenic disturbance, coupled natural-human systems, cross-boundary management, ecological variability, fire, forest management, grazing, groundcover

1. Introduction

The ecosystem at any given location is driven in part by history of disturbance and stress (e.g., Pierce et al., 2007; Miller et al., 2011). Events and processes that add, reduce, or rearrange resources are key influences on the diversity and function of species assemblages (Powell et al., 2011; Trivellone et al., 2017; Zhang et al., 2019). Human activity shapes these patterns, even in large undeveloped landscapes. Human management type and activity at a given site can affect resources through harvest, restoration, biological invasion, and other processes (Lampert et al., 2014; Goldmann et al., 2015; Innes et al., 2019). Management also affects the types, intensity, and frequency of disturbance, such as through fire suppression, damming and diversion of water, or grazing (Führer, 2000; Alkemade et al., 2013; Schmutz and Moog, 2018). As a result, sites with similar environmental conditions but different management histories may exhibit different biodiversity, function, and adaptive capacity (Bengtsson et al., 2000; Fischer et al., 2006; Levin et al., 2006; Floren et al., 2014; Nicotra et al., 2015; Teague and Barnes, 2017; Huang et al., 2020). Understanding how management may drive such differences among sites is particularly important in light of global change, the emergence of novel ecosystems, and an increasing need for planners and managers to tailor solutions to changing conditions across landscapes (Hobbs et al., 2006).

If management processes shape ecological patterns, over time ecological similarities between jurisdictions may be predicted by similarities in management history (Aslan et al., 2021a). Conversely, initially intact ecosystems that are subjected to unique management histories across jurisdictional boundaries may, over time, diverge to be ecologically distinct even with similar climate, geology, and geography. A primary mechanism driving these management-driven shifts is likely consistent differences between jurisdictions in anthropogenic disturbance. Sites that have been managed primarily for resource extraction such as logging and mining, for example, will exhibit high occurrence of surface disturbance, resource transportation roads, younger forests on average, and possibly active restoration following extraction (DeLong et al., 2004; Zollner et al., 2005; Andrés and Mateos, 2006; Hartmann et al., 2012; Huang et al., 2015; Nelson et al., 2019). Sites managed for recreation, by contrast, may exhibit disturbances clustered in accessible areas such as campgrounds or attractions, passenger car roads and trails, and active restoration such as revegetation projects (Brown et al., 2008; Marzano and Dandy, 2012; Monz et al., 2013; Gutzwiller et al., 2017). Residential sites, including rangelands or forests with subsistence farms, ranches, or private inholdings, may exhibit disturbances that are clustered around built structures, with surrounding undeveloped areas containing trails and further disturbance through off-road vehicle use, harvesting of non-timber forest products, or firewood collection (Maestas et al., 2001; Havlick, 2002; Hansen et al., 2005; Ponstingel, 2020; Gonçalves et al., 2021). Adjacent sites managed for different goals likely provide a key indicator of the potential for management-driven ecological divergence.

Conservation relies on understanding how differing management on the two sides of a boundary may create discontinuities between protected and adjacent areas. These effects may differ across scales. Conservation planning often relies on large, connected landscapes protected from development. In North America, examples include Paseo Pantera: the Path of the Panther (for jaguar movement between Mexico and the United States) and the Yellowstone to Yukon initiative (protecting large mammal migration between Canada and the United States) (Rabinowitz, 2014; Chester, 2015). Smaller, more numerous efforts seek to preserve local habitat connectivity across multi-jurisdictional landscapes through coordinated restorations, watershed, or fire management (e.g., Schultz et al., 2012; Koontz and Newig, 2014; Schultz and Moseley, 2019). Connected landscapes, in turn, allow for dispersal of individuals, gene flow, seasonal migration, recolonization of sites following disturbance, and distributional shifts of populations as a result of climate change (Rudnick et al., 2012; Baguette et al., 2013). However, large landscapes that are divided into multiple distinct management units—as a result of historical events and decisions, distribution of economically-valuable resources, funding allocations, grandfathered practices, and other drivers—are subject to an assortment of internal decisions that result in a patchwork of management practices (Huggard, 2004; Andrew et al., 2012; Aslan et al., 2021a). The result is a management mosaic (*sensu* Epanchin-Niell et al., 2010) that can manifest as an ecological mosaic.

In undeveloped landscapes, management mosaics likely maintain some commonalities that span jurisdictions—for example, broad vegetation type responds to elevation, latitude, and topography and is unlikely to shift across boundaries in response to management except where disturbance has removed all vegetation such as at a mine or quarry. By contrast, changes in plant composition and vegetation pattern and disturbance evidence may respond at smaller spatial and temporal scales to varying management activities, tracking the management mosaic. This mix of factors and scales likely generates an ecological continuum between adjacent management units (Duinker et al., 2010; Andrew et al., 2012; Wiersma et al., 2015). Within that continuum, our aim was to understand how ecological conditions vary as a function of the jurisdictional mosaic within landscape-scale ecosystems.

We placed our study in the landscapes containing four large national parks in the western US: Sequoia-Kings Canyon National Park (SEKI), Lassen Volcanic National Park (LAVO), Grand Canyon National Park and protected areas encompassed in the same ecosystem along the Colorado River (CORI), and Rocky Mountain National Park (ROMO). We selected these case study ecosystems to inform our ongoing conversations with land managers in each park regarding the influences of cross-boundary management challenges. We used field-based data collection to measure ecological characteristics and disturbance evidence across jurisdictional boundaries and employed a Bayesian framework to analyze and understand the resulting patterns, in order to determine whether jurisdiction is predictive of certain ecological characteristics within these large landscapes. We hypothesized that variation in disturbance management is a likely mechanism driving such relationships, so we also analyzed first the relationship between disturbance and ecological variables, then the relationship between disturbance and jurisdiction, and finally the relationship between jurisdiction and measured ecological variables. We piloted the methods used here in the CORI landscape (Aslan et al., 2021b) and in this study refined analyses and extended them across all four landscapes to enable comparison among different geographies. Our findings thus enable us to discuss possible social-ecological influences on ecological conditions within and among landscapes.

With this study, we aimed to examine differences in ecological variables at a point in time that are reflective of mechanisms that span temporal and spatial scales. Knowing that the vegetation and soils at a sampling location are reflective of broad biogeographical influences, geology, historical events, and days to decades to centuries of species interactions and biological processes, we aimed to investigate whether differences in management can manifest in a consistent way detectable in spite of such broad natural variability.

2. Materials and methods

2.1. Study areas

We collected ecological data across jurisdictional boundaries within four focal Protected Area-Centered Ecosystems (PACEs), which served as case study systems for this work. All four PACEs are located in the western US. ROMO occupies a section of the eastern slope and high elevations of the Rocky Mountains in Colorado, spanning vegetation types including oak grasslands, coniferous forests, and tundra. CORI occurs in northern Arizona, southern Utah, and southeastern Nevada and includes sagebrush desert, oak and pinyon-juniper woodlands, and coniferous forests. SEKI occupies a stretch of ridgeline and both western and eastern slopes of the Sierra Nevada in south-central California, ranging from mesic oak grasslands to tundra to high desert. LAVO occurs in temperate coniferous forest in northern California.

2.2. Framework and hypothesis development

Our field sampling protocols and analyses were guided by an *a priori* set of hypotheses linking ecological variables to disturbance and disturbance to jurisdiction (Table 1; Figure 1). At our field sites, we examined the frequency of evidence of disturbance in the form of fire, forest management, grazing, and general human presence. We predicted that vegetation structure would respond to these disturbances. Specifically, we hypothesized that disturbances would be associated with diminished tree cover, and, due to increased light penetration, would be associated with increasing cover of bare ground, grasses, forbs, and, over time, shrubs (Goosem, 2007; Shatford et al., 2007; Schwilk et al., 2009; Stephens et al., 2012; Crotteau et al., 2013; Miller et al., 2014). We also hypothesized that disturbances would reduce soil stability and alter soil chemistry (Kutiel and Shaviv, 1989; Manley et al., 1995; Neff et al., 2005; James et al., 2021). Our detailed hypotheses are presented in Table 1.

We hypothesized that disturbances would vary in frequency and severity across different jurisdictional types (National Park Service-NPS, US Forest Service-USFS-Wilderness and Nonwilderness, and Bureau of Land Management-BLM) in our case study landscapes. Wilderness areas in the US are managed to be “untrammeled,” with as little human disturbance as possible (Parsons and Landres, 1996; Zellmer, 2014); as a result, general forest management activities are rare, as are prescribed burns, although natural wildfires may be particularly frequent and extensive. With their dual missions of conservation and recreation, national parks may employ burns and forest management to restore biodiversity or reduce fire hazard, but also aim to support natural processes and patterns, likely resulting in an intermediate level of fire and forest management in such units. National forests are managed to produce the nation’s timber crop and thus most likely to use intensive management techniques. Grazing occurs in all sites if

TABLE 1 Conceptual framework and predicted ecological differences among jurisdictions.

Disturbance Type	Response variables affected	Rationale	Citations
Fire	Tree percent cover; shrub percent cover; bare ground percent cover; adult tree density; sapling density; soil carbon; soil phosphorus; soil stability; tree richness	Fire of high enough intensity decreases percent cover of woody plants, particularly trees, initially. Bare ground cover can increase and trees decrease with fire. In the longer term, fire often facilitates shrub and sapling regeneration, resulting in increased densities of those woody plants following fire. Fire can release both carbon and phosphorus from plants into the soil. By removing dominant trees and initiating successional processes, fire can increase tree diversity.	Kutiel and Shaviv (1989), Shatford et al. (2007), Verma and Jayakumar (2012), Crotteau et al. (2013), Miller et al. (2014), Pellegrini et al. (2018)
Forest management	Tree percent cover; grass percent cover; forb percent cover; bare ground percent cover; adult tree density; sapling density; soil carbon; soil stability; adult tree dbh	Forest management consists of chainsaw work and tree/log removal. This reduces cover of trees and allows light penetration, increasing grass and forb and bare ground percent cover. Thinning efforts reduce density of both adult trees and saplings but often leave the largest trees in place, increasing overall average tree size. Soil carbon is released by tree removal and management activities, and soil stability can be reduced by management activities.	Schwilk et al. (2009), Stephens et al. (2012), James et al. (2021)
Human activity	Tree percent cover; grass percent cover; forb percent cover; bare ground percent cover; adult tree density; sapling density; soil carbon; soil stability	Human activity includes forest management work as well as trails and roads. These activities reduce cover of trees and allows light penetration, increasing grass and forb and bare ground percent cover. Such activities also facilitate invasion of non-native grasses and forbs. Soil carbon is released by tree removal and vegetation disturbance, and soil stability can be reduced by vegetation disturbance.	DiTomaso (2000), Pocock and Lawrence (2005), Goosem (2007), Schwilk et al. (2009), Stephens et al., 2012, James et al. (2021)
Grazing	Tree percent cover; shrub percent cover; grass percent cover; forb percent cover; bare ground percent cover; adult tree density; soil carbon; soil stability; C:N ratios	Tree cover and density are diminished where grazing occurs. Grasses and forbs may be facilitated by grazing, although overgrazing can lead to increased shrub cover and increased bare ground cover. Grazing can increase carbon: nitrogen ratios and soil carbon and decrease soil stability.	Manley et al. (1995), Teague et al. (2004), Neff et al. (2005), Best and Arcese (2009), Augustine et al. (2012), D'Odorico et al. (2012), Taboada et al., 2015, Souther et al. (2019), Zheng et al. (2020)

We hypothesized that ecological factors would vary over multijurisdictional landscapes due to systematic differences in frequency and severity of disturbances including fire, grazing management, forest management, and human activity.

grandfathered into NPS or USFS Wilderness (Pinto, 2014; Squillace, 2014), but is excluded from such units if not practiced prior to their protection. Grazing is a primary land use in BLM and USFS Nonwilderness areas. General human presence is likely to be particularly high in those areas as well, since they are considered multiuse (Havlick, 2002; Koontz and Bodine, 2008; Monz et al., 2013; Theobald, 2013; Payne, 2016). In our analytical methods, described below, we examined the strength of relationships between disturbance variables and ecological responses and identified instances in which ecological responses and disturbance evidence contrasted between jurisdictional units within the focal landscapes.

2.3. Field data collection

In 2017, 2018, and 2019 data were collected from public lands under different jurisdictions in all four PACEs. Data were collected from randomly selected sites near jurisdictional boundaries and, at each site, from clustered points such that two points lay on each side of the boundary and points formed a square with sides of 200 m (Supplementary Figure S1). Distance between points was selected to minimize natural differences in elevation and general vegetation type between the points within each square, in order to hold constant sources of natural variation as much as possible. At each point, researchers established two 50 m-long, 6 m-wide belt transects directed away from the jurisdictional boundary and angled 45 and 135 degrees from the boundary line (Supplementary Figure S1). Disturbance was recorded as present/absent within 1-m intervals along each belt transect. Groundcover was recorded by line-point intercept at 0.5-m intervals along the midline of the two transects. Abundance, size, and species richness of adult and sapling trees were recorded within a $100 m^2$ quadrat established between 20 m and 30 m along each transect and centered on the transect's 25 m mark. Soil stability was assessed at 5-m intervals along each of the transects, using a field soil slake test kit (Herrick et al., 2001). Soil cores to 20 cm depth

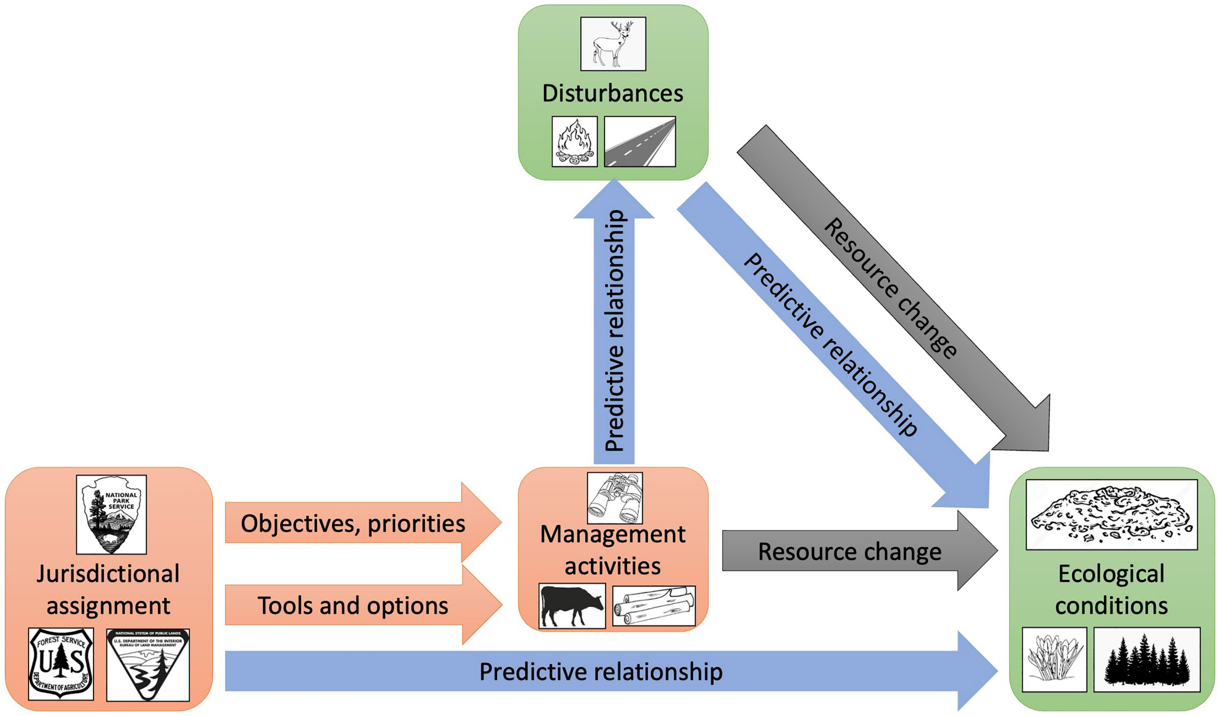

FIGURE 1
Experimental design and analytical flow. Green boxes=measured empirically during this study. Orange boxes and arrows=inferred from established policy and documents; drivers of hypotheses. Gray arrows=hypothesized mechanisms for relationships. Blue arrows=analyzed relationships.

were collected from three locations per transect and homogenized to allow later lab-based chemical and physical analysis (after Aslan et al., 2021b).

We aimed to sample 15 sites (90 points) from each of the following contrasts within each PACE: NPS/USFS Wilderness; NPS/USFS Nonwilderness; NPS/BLM; USFS Wilderness/USFS Nonwilderness; USFS Nonwilderness/BLM; and USFS Wilderness/BLM. In practice, not all contrasts occur within all PACEs, and due to access issues, we were not able to reach the full 15 sites for each contrast. Nevertheless, all management types and at least four contrasts were sampled in each PACE and our final set of sampled sites included 28 (112 points; 224 transects) in ROMO (4 contrasts), 50 (200 points; 400 transects) in LAVO (5 contrasts), 51 (204 points; 416 transects) in SEKI (4 contrasts), and 64 (256 points; 512 transects) in CORI (6 contrasts) (Figure 2).

2.4. Overall modeling and data analysis

To examine the relationships between disturbance and ecological variables (Table 1), disturbance and jurisdiction, and jurisdiction and ecological variables, we modeled data from sites within each PACE using a general, hierarchical formulation for the posterior and joint distribution of unobserved quantities:

$$\mu_{ij} = g\left(\alpha_j + x_{ij}'\beta + w_{ij}'\gamma\right) \quad (1)$$

$$\left[\alpha,\ \beta,\ \gamma,\ \sigma^2,\ \mu_\propto,\ \sigma_\propto^2,\ y_j\right] \propto \prod_{i=1}^{n_j}\prod_{j=1}^{J}\left[y_{ij} \mid h\left(\mu_{ij},\sigma_j^2\right)\right]\left[\alpha \mid, \mu_\alpha \mid, \sigma_\alpha^2\right] \quad (2)$$

$$\times[\beta][\gamma]\left[\sigma^2\right][\mu_\alpha]\left[\sigma_\alpha^2\right]$$

Bracket notation (Gelfand and Smith, 1990), $[a \mid b,c]$, reads the probability of a conditional on b and c and implies that any distribution appropriate for the support of the random variable y_{ij} could be used (Supplementary Table S1). Generality in notation is achieved using the moment matching function $h()$ that returns the parameters of a distribution given its first and second central moments (Hobbs and Hooten, 2015). The subscript $i = 1, 2, n_j$ indexes observations within site j; $j = 1, 2, J$ indexes sites within the PACE. The observations come from either of two transects at each of two points in each jurisdiction at a site (Supplementary Figure S1).

Observations were modeled with site-level intercept and, usually, site-specific variance terms. Intercepts for each site, α_j,

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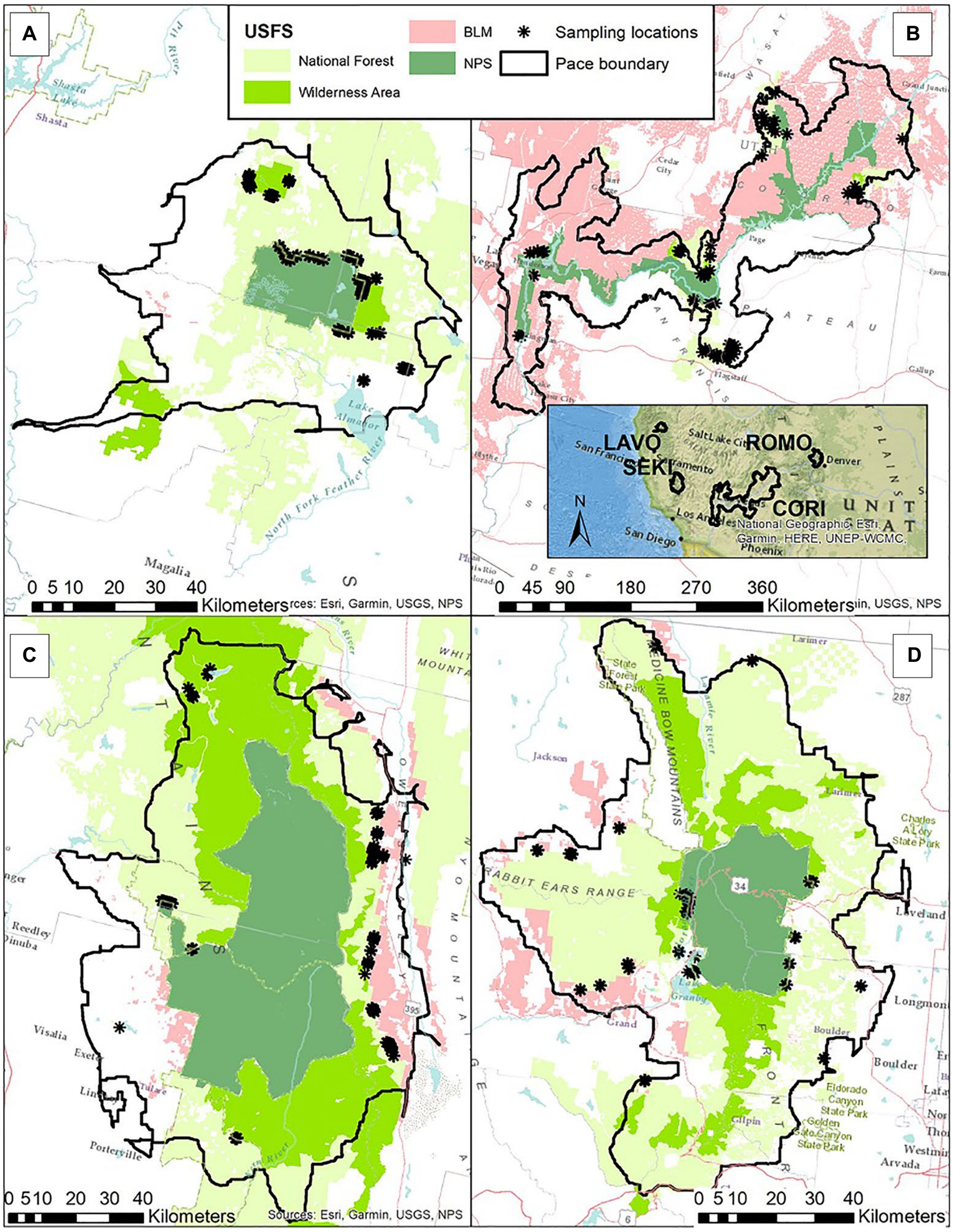

FIGURE 2
Map showing the four protected area centered ecosystems (PACEs) where we collected field samples; **(A)** Lassen LAVO, **(B)** Grand Canyon CORI, **(C)** Sequoia Kings Canyon SEKI, and **(D)** Rocky Mountain ROMO. Colors in the map indicate the different jurisdictions we examined; United States Fish and Wildlife Service (USFWS) wilderness and non-wilderness areas, Bureau of Land Management (BLM) and National Park Service (NPS). The solid black line indicates the boundary of each PACE.

were modeled as a random variable arising from a normal distribution with mean μ_α and variance $\sigma_\alpha^2 : \alpha_j \sim \mathrm{N}(\mu_\alpha,\ \sigma_\alpha^2)$. Site-level variances, σ_j^2, were modeled as a random variable arising from a gamma distribution with parameters matched to moments μ_{σ^2} and $\varsigma_{\alpha^2}^2$: $\sigma_j^2 \sim \mathrm{gamma}(\mu_{\alpha^2}^2 / \varsigma_{\alpha^2}^2,\ \mu_{\sigma^2} / \varsigma_{\alpha^2}^2)$. We also considered models with.

a simple fixed error term, σ^2, for observations. $\boldsymbol{\beta}$ are jurisdictional effects, and $\boldsymbol{\gamma}$ are other disturbance effects in a generalized linear model (linear, exponential, or logit^{-1}) appropriate for the data, notated by the link function $g()$ (Supplementary Table S1).

The model described above assumes that jurisdictional effects are fixed at the scale of the PACE. Although simple and sensible, such a model does not allow for the possibility that jurisdictional effects are random, and may co-vary with other terms (the intercept, for instance). For example, the influence of jurisdiction in a model of bare ground cover may depend on the proportion of bare ground cover at a site, with more barren sites exhibiting different jurisdictional effects than highly vegetated sites. Thus, we also considered models in which jurisdictional effects were treated as random using random slope terms, $\boldsymbol{\beta}_j$. In this case, α_j and $\boldsymbol{\beta}_j$ are distributed multivariate normal. Their covariance was modeled using the scaled inverse-Wishart distribution with degree of freedom parameter set to $L+1$ to induce a uniform prior distribution on parameter correlations (Gelman and Hill, 2006). L is the dimension of the covariance matrix.

The covariate vector $\boldsymbol{x}_{ij}$ encodes the jurisdiction within which each sample falls. Specifically, jurisdiction was "effect coded." Effect coding uses ones, zeros, and minus ones to convey group membership (BLM, NPS, USFS non-wilderness, or USFS wilderness). With $k = 1, 2, K$ groups there are $K - 1$ effect-coded variables. The K^{th} effect variable is not needed because the other $K - 1$ variables contain all of the information needed to determine the group into which an observation falls. With effect coding, the intercept, α_j, is equal to the overall mean at site j. It is the grand mean of all observations at site j holding all other covariates (disturbance variables, $\mathbf{w}_{ij}$) at their means. The coefficients, $\boldsymbol{\beta}$, are equal to the difference between the mean of the jurisdiction and the overall mean at the site (α_j). The coefficient for the K^{th} variable can be computed as a derived quantity using - $\sum_{k=1}^{K-1} \beta$.

The covariates, $\mathbf{w}_{ij}$, were chosen to explain spatial variation in the response as a result of disturbance factors, including fire, human disturbance, forest management, and grazing. Disturbance factors varied by transect and were defined as the number of point intercepts at which a given disturbance sign was detected. Such sign included indicators of fire (ash, charring, etc.), human disturbance (trail, chainsaw, trash, etc.), forest management (chainsaw, other cutting, etc.), and grazing (cattle prints, scat, etc.; included only for models of CORI and ROMO). Additional covariates in $\mathbf{w}_{ij}$ were derived using remotely sensed or gridded data products, including elevation, and typically varied by point within site according to the spatial resolution of the product from which it was came.

The models of disturbances are meant to reveal whether the frequency/intensity of disturbances is more pronounced on specific jurisdictions. Because disturbance factors are the focus here (appearing on the lefthand side of the model equation) we simplified the model in Eq. 1 by removing $\mathbf{w}'_{ij}\boldsymbol{\gamma}$ and removed all references to $\boldsymbol{\gamma}$ in the expression for the posterior and joint distribution (Eq. 2).

Priors on all parameters were specified to be vague. Priors on model coefficients were normal centered on zero. Variance of these priors was set to assure that dispersion of the prior was much larger than the dispersion of the marginal posterior of the coefficients, except in the case of inverse logit models, where the variance was set to assure a flat distribution of the prediction of proportions (Hobbs and Hooten, 2015). Priors on variances were broad uniform or gamma distributions. Analysis of sensitivity to priors revealed no meaningful effects of priors on marginal posterior distributions of model parameters.

2.5. Model checking and selection

We selected only models that converged using statistics of Brooks and Gelman (1988) and used posterior predictive checks to remove models that were not capable of generating the observed data (Hobbs and Hooten, 2015). We used the minimum posterior predictive loss approach (Gelfand and Ghosh, 1998) to select among the remaining candidate models for each response variable in each PACE.

2.6. Inference

We used the posterior distribution of the coefficients in each model to test our hypotheses about jurisdictional effects and the influence of disturbance factors on each of our ecological variables. Effects were considered positive if estimates of the posterior distributions of their corresponding coefficients had probability density > 0.75 to the right of zero and negative if their coefficients had probability density > 0.75 left of zero.

Contrasts between jurisdictions were computed in the following way. First, at each Markov chain Monte Carlo (MCMC) iteration, m, we make a draw for the intercept term for hypothetical, out-of-sample site $\tilde{j}$ from the underlying distribution of intercepts–e.g., $\alpha_{\tilde{j}}^{m} \sim$ normal (μ_α, σ_α^2). In the model invoking random point jurisdiction effects, draws for the intercept and jurisdiction effects were made concurrently using the multivariate normal. In this case, the intercept and jurisdictional effects will co-vary according to the covariance matrix, Σ. Next, we computed the expected value of the response, $\hat{y}_{\tilde{j}}^{m}$, for each jurisdiction, holding elevation and all disturbance variables at their respective means. Contrasts are formed by computing the difference, $z_{\tilde{j}}^{m}$, in the means between two jurisdictions at each MCMC iteration. For instance, $z_{\tilde{j},BLM-NPS}^{m} = \hat{y}_{\tilde{j},BLM}^{m} - \hat{y}_{\tilde{j},NPS}^{m}$. We summarize the differences between jurisdictions using all M samples in the converged output of the MCMC algorithm. We implemented the algorithm in JAGS (Plummer, 2003), using the R programming language (R Core Team, 2017) to fit all models.

3. Results

Our analysis examined, first, whether field-collected evidence of focal disturbance types was associated with measured ecological groundcover, tree, and soil characteristics across all PACEs; second, whether disturbance evidence varied by jurisdiction and where; and third, whether ecological variables varied by jurisdiction and where. In combination, these outputs allowed us to evaluate the contexts in which jurisdiction was predictive of ecological condition across our focal landscapes, and whether these patterns were consistent with our hypotheses surrounding disturbance variability by management type. We considered relationships to have ecological meaning if a disturbance or jurisdiction type was associated with at least a 75% probability of a shift in an ecological or disturbance variable, and if the magnitude of that shift was at least 10% of the range of that variable, excluding the most extreme observations (Table 2; Supplementary Figures S2, S3).

3.1. Relationships between focal disturbance types and ecological variables

Consistent with our hypotheses (Table 1), we found that each focal disturbance type was related to shifts in groundcover type, soil stability, and soil carbon. However, the magnitude of these relationships varied strongly by PACE. Fire evidence was related to increases in bare ground cover in ROMO, LAVO, and SEKI and a decrease in bare ground in CORI; decreases in soil stability in ROMO and LAVO; increased forb cover in SEKI; and increased shrub cover, decreased tree cover, and decreased tree species richness in ROMO (Table 2). Evidence of forest management (e.g., chainsaw scars) was related to decreased bare ground cover in ROMO and SEKI; increased soil stability in ROMO, SEKI, and CORI; decreased grass cover in ROMO; and decreased shrub cover in SEKI (Table 2). Grazing was associated with both increased bare ground cover and forb cover in ROMO and CORI (Table 2). Finally, evidence of human activity in general (e.g., roads, trails, and disturbance from active forest management) was associated with increased cover of bare ground in CORI, ROMO, and LAVO; decreased soil stability in ROMO and LAVO; increased grass cover in SEKI and LAVO; decreased shrub cover in ROMO; and soil carbon in SEKI (Table 2).

3.2. Relationships between focal disturbance type and jurisdiction

Our analysis detected differences in the occurrence of disturbance evidence between jurisdictional contrasts only for forest management overall and only in LAVO (Table 3).

3.3. Relationships between jurisdiction and ecological variables

We compared pairs of adjacent jurisdictions within each PACE for meaningful differences in ecological variables. Two ecological variables, soil stability and soil carbon: nitrogen ratios, differed between jurisdictions in multiple contrast pairs. Soil stability differed between USFS Wilderness and USFS Nonwilderness in LAVO and SEKI, between NPS and USFS Wilderness in ROMO, and between NPS and USFS Nonwilderness in ROMO and LAVO (Table 4). Carbon: nitrogen ratios differed between BLM and USFS Nonwilderness in LAVO and between NPS and both USFS Nonwilderness and USFS Wilderness in LAVO.

4. Discussion

This study detected two scales of ecological patterns (plant community structure and soil properties) that were predicted by the evidence of disturbances and by the site's jurisdiction. Disturbance was linked to a site's ecological variables, including groundcover type, soil stability, and soil carbon, although these relationships differed among systems. Jurisdictional relationships with soil stability were clear, with additional but less consistent relationships emerging between jurisdiction and soil carbon: nitrogen ratios, bare ground cover, and tree diameter at breast height. Two take-home messages emerge from our findings: first, relationships between ecological variables and disturbance and between ecological variables and jurisdiction varied by PACE. This finding suggests that context is important, with ecotones manifesting at jurisdictional boundaries in certain environmental settings but not in others. Secondly, soil properties showed the strongest and most consistent patterns, both to jurisdiction type and disturbance. Interestingly, then, the signals of jurisdictional boundaries on ecological properties across large landscapes were strongest at the finest spatial scale examined.

Although all disturbance types were linked to ecological responses, no such link was consistent across all the examined PACEs. The greatest number of meaningful shifts in ecological variables associated with disturbance occurred in ROMO, where effects were detected in cover of bare ground, grass, shrubs, and trees, as well as in soil stability. Spanning the continental divide with a national park established in 1915, the ROMO PACE includes wide variation in temperature and precipitation as well as wide variation in human population density, land use, and recreation impacts (Maestas et al., 2001; Kumar et al., 2009; Hansen et al., 2011). From historic cattle ranches to amenity migrants, a blend of human occupants can be found across the Rocky Mountain region (Riebsame et al., 1996; Gosnell and Travis, 2005; Hansen et al., 2014). Furthermore, with a large metropolitan area nearby and steady growth in visitation (national park records report 4 million visitors per year since 2015), it may be that the ecosystems of the ROMO PACE are particularly subject to a relatively constant diversity of anthropogenic disturbances. On the other end of the spectrum, few links between disturbance and ecological responses were observed in the CORI PACE. Although the park itself (established in 1919) receives the highest visitation of those we examined (the National Park Service reported 6.4 million visitors in 2018), visitation is concentrated into a small area and CORI PACE as a whole has low human population density. The large majority of the landscape has been subject to a century and a half of intensive grazing. Fires and forest management are mainly restricted to the forested portions of the PACE, with current forest

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TABLE 2 Hypothesized relationships between disturbance types and ecological measures.

Disturbance	Ecological variable	Hypothesis	CORI	ROMO	LAVO	SEKI
Fire	Bare ground cover	(+)	(−) 11.4	(+) 13.1	(+) 12.2	(+) 10.3
Forest management	Bare ground cover	(+)	(−) 9.5	(−) 10.3	(−) 7.6	(−) 20.6
Grazing	Bare ground cover	(+)	(+) 18.7	(+) 19.0		
Human activity	Bare ground cover	(+)	(+) 53.7	(+) 64.7	(+) 44.8	() 9.1
Fire	Carbon-to-nitrogen ratio	(+)	() NA	() 7.6	(−) 21.2	() NA
Forest management	Carbon-to-nitrogen ratio	(+)	(+) NA	(+) 5.5	(+) 7.1	(+) NA
Grazing	Carbon-to-nitrogen ratio	(+)	(−) NA	(+) 10.3		
Human activity	Carbon-to-nitrogen ratio	(+)	(−) NA	(+) 8.1	() 4.8	() NA
Fire	Soil stability	(−)	() 2.9	(−) 27.3	(−) 16.4	() 0.2
Forest management	Soil stability	(−)	(+) 14.7	(+) 21.6	(+) 4.2	(+) 19.3
Grazing	Soil stability	(−)	(−) 4.5	() 2.3		
Human activity	Soil stability	(−)	() 1.0	(−) 26.3	(−) 19.1	() 2.4
Fire	Diameter at breast height	(+)		() NA	(+) NA	(+) NA
Forest management	Diameter at breast height	(+)		(−) NA	(−) NA	(+) NA
Grazing	Diameter at breast height	(−)		(−) NA		
Human activity	Diameter at breast height	(+)		(+) NA	() NA	(−) NA
Fire	Forb cover	(+)	(+) 1.0	(−) 9.0	(+) 3.9	(+) 33.5
Forest management	Forb cover	(+)	(+) 0.9	() 2.9	(−) 1.0	(−) 9.5
Grazing	Forb cover	(−)	() 0.3	(+) 12.7		
Human activity	Forb cover	(−)	(+) 1.4	(+) 8.5	(+) 5.7	() 6.7
Fire	Grass cover	(+)	(+) 8.2	(+) 38.4	(+) 3.1	(+) 5.9
Forest management	Grass cover	(+)	(−) 5.7	(−) 11.9	(−) 1.0	(−) 7.9
Grazing	Grass cover	(+)	(−) 2.4	() 3.5		
Human activity	Grass cover	(+)	(−) 5.3	() 3.4	(+) 12.0	(+) 41.3
Fire	Number of saplings	(+)	(+) NA	() NA		(−) NA
Forest management	Number of saplings	(−)	() NA	(−) NA		(+) NA
Grazing	Number of saplings	(−)	(+) NA	(−) NA		
Human activity	Number of saplings	(−)	(+) NA	(+) NA		(+) NA
Fire	Phosphorus PPM	(+)	(+) NA	(+) NA		(+) NA
Forest management	Phosphorus PPM	()	(+) NA	(−) NA		(−) NA
Grazing	Phosphorus PPM	()	(−) NA	(+) NA		
Human activity	Phosphorus PPM	()	(−) NA	() NA		() NA
Fire	Shrub cover	(+)	(−) 3.0	(+) 19.3	(+) 7.8	() 2.6
Forest management	Shrub cover	(−)	(−) 3.8	() 3.5	(−) 6.6	(−) 40.1
Grazing	Shrub cover	(−)	(+) 5.2	() 1.4		
Human activity	Shrub cover	(+)	(−) 9.7	(−) 16.2	() 4.1	() 5.3
Fire	Total carbon	(+)	(−) 2.2	(+) NA	(−) 7.8	() 1.3
Forest management	Total carbon	(+)	(+) 8.4	(+) NA	(+) 2.8	(+) 5.5
Grazing	Total carbon	(+)	(−) 7.8	(+) NA		
Human activity	Total carbon	(+)	(−) 4.2	() NA	(−) 2.9	(−) 18.8
Fire	Tree cover	(−)	(−) 1.5	(−) 10.3	() 2.0	
Forest management	Tree cover	(−)	(+) 2.1	(+) 8.1	(+) 2.8	

(Continued)

TABLE 2 (Continued)

Disturbance	Ecological variable	Hypothesis	CORI	ROMO	LAVO	SEKI
Grazing	Tree cover	(−)	(−) 3.3	() 6.4		
Human activity	Tree cover	(−)	(−) 2.2	() 1.0	() 1.6	
Fire	Tree species richness	(+)	(+) 2.5	(−) 12.6	(−) NA	
Forest management	Tree species richness	(+)	(+) 4.3	() 0.2	(+) NA	
Grazing	Tree species richness	(−)	() 1.9	(−) 3.5		
Human activity	Tree species richness	(+)	(−) 8.8	(−) 2.7	() NA	

Directionality is indicated parenthetically. A test of each hypothesis is obtained by evaluating the density of the posterior distribution of each coefficient left or right of zero. Negative (−) or positive (+) effects have at least 75% density on either side of zero. Less influential effects are left blank (). An indication of the magnitude of each effect is given next to the sign of each coefficient. This effect size measure is calculated by evaluating the influence of a given covariate (l) on the mean of the response, $\hat{y}$, over its observed range from min(w_l) to max(w_l). Because the size of a given effect depends on the native range of the data, we use $\left|\hat{y}^{\max(w_l)} - \hat{y}^{\min(w_l)}\right| \Big/ \left(q(y,0.975) - q(y,0.025)\right) \times 100$, where the denominator represents the range of the data, excluding the most extreme observations.

TABLE 3 Contrast results for forest management.

PACE	Contrast	median(z)	P(z<0)	P(z>0)	$\frac{\lvert \text{median}(z) \rvert}{q(y,0.975)-q(y,0.025)} \times 100$
LAVO	BLM–USFSNONWILDERNESS	−0.031	0.81	0.19	6.3
LAVO	NPS–USFSNONWILDERNESS	0.073	0.01	0.99	14.5
LAVO	NPS–USFSWILDERNESS	0.055	0.07	0.93	11.1
SEKI	NPS–USFSNONWILDERNESS	0	0.17	0.83	0.1
SEKI	USFSNONWILDERNESS–USFSWILDERNESS	0	0.19	0.81	0

We present the median of the expected difference, z, in forest management between each jurisdiction shown. We also present the probability that z is left or right of zero. A value of zero corresponds to no difference. Only contrasts with probability density > 0.75 to either side of zero are included. The final column provides an indication of the magnitude of the difference on the scale of the data. $q(y,p)$ returns the quantile of y at probability p. Thus, the denominator in the expression in the final column corresponds to the range of the data, omitting the most extreme values. For example, a value of 5 would correspond to a median difference between two jurisdictions that is 5% of the range of forest management observations in the corresponding PACE. These results are based on coefficients presented in Supplementary Figure S2.

management trying to mimic the historic fire regime (Holcomb et al., 2011). As a whole, the PACE is arid within only a few high moisture pockets (on the Kaibab Plateau). Aridity as a common environmental stress may play a homogenizing role in the ecology of all jurisdictions across the PACE. That is, the small number of ecological responses to disturbance and jurisdictions likely reflects a consistent effect of low water availability. Fire and grazing have been a consistent part of the landscape so long and may have interacted with water stress to apply strong selective pressures on vegetation communities, such that grazing-intolerant and fire-intolerant species are no longer common in any jurisdiction on the landscape (Moore et al., 1999; Simpson, 2020). A lack of jurisdictional responses may be consistent in areas where disturbance adaptation is consistent across habitat types, including grasslands and savannas (Bowman et al., 2009).

Pre-existing ecological differences among jurisdictions are an important confounding variable that may obscure the relationships we aimed to examine here. The historical assignment of management units to specific jurisdictions was driven by their characteristics—for example, BLM lands are generally rangelands with high forage incidence, and forested landscapes are generally managed by the USFS. Differences in grass or tree cover, therefore, may have driven the assignment of jurisdiction, rather than the other way around. This study, however, was designed with the expectation that both are true—that regions with certain characteristics are indeed more likely to be assigned to certain jurisdictions, but also that the management differences can reinforce divergence of neighboring parcels, such that ecotones may also be products of management itself. Jurisdictional boundaries, drawn on a map at coarse scale, are unlikely to precisely track natural ecotones such as shifts from forests to woodlands to grasslands. By sampling very close to boundaries, at sites matched by elevation and vegetation type, we aimed to keep sources of natural variation as constant as possible in order to discern any divergence emerging at fine scale and directly at the boundary, and thus possibly as a result of management, if it occurs. Our findings that some ecological characteristics do vary in some cases by jurisdiction, but also by PACE, suggest an interplay between the social construct of jurisdictions, the response time of individual ecological characteristics, and the biophysical and geographical characteristics across and between landscapes.

Importantly, we observed relationships between disturbances and ecological variables at the level of full PACEs, as well as between jurisdictions and ecological variables. Our methods only detected disturbances recent enough to leave

TABLE 4 Contrast results for soil stability and carbon-to-nitrogen ratio.

Ecological variable	PACE	Contrast	Median (z)	$P(z<0)$	$P(z>0)$	$\frac{\lvert \text{median}(z) \rvert}{q(y,0.975)-q(y,0.025)} \times 100$
Soil stability						
	CORI	BLM–USFSWILDERNESS	−0.432	0.9	0.1	8.6
	CORI	NPS–USFSWILDERNESS	−0.317	0.81	0.19	6.3
	CORI	USFSNONWILDERNESS–USFSWILDERNESS	−0.373	0.9	0.1	7.5
	ROMO	NPS–USFSNONWILDERNESS	1.219	0.04	0.96	24.4
	ROMO	NPS–USFSWILDERNESS	0.745	0.19	0.81	14.9
	LAVO	NPS–USFSNONWILDERNESS	0.499	0.07	0.93	10
	LAVO	USFSNONWILDERNESS–USFSWILDERNESS	−0.631	0.96	0.04	12.6
	SEKI	BLM–USFSNONWILDERNESS	−0.213	0.83	0.17	4.3
	SEKI	BLM–USFSWILDERNESS	0.322	0.07	0.93	6.4
	SEKI	NPS–USFSNONWILDERNESS	0.379	0.11	0.89	7.6
	SEKI	USFSNONWILDERNESS–USFSWILDERNESS	0.536	0.01	0.99	10.7
Carbon-to-nitrogen ratio						
	CORI	BLM–NPS	1.12	0.13	0.87	2.6
	CORI	BLM–USFSNONWILDERNESS	−0.817	0.82	0.18	1.9
	CORI	BLM–USFSWILDERNESS	−2.325	0.98	0.02	5.4
	CORI	NPS–USFSNONWILDERNESS	−1.928	0.99	0.01	4.5
	CORI	NPS–USFSWILDERNESS	−3.424	1	0	7.9
	CORI	USFSNONWILDERNESS–USFSWILDERNESS	−1.511	0.95	0.04	3.5
	ROMO	BLM–USFSNONWILDERNESS	1.749	0.08	0.92	4.4
	LAVO	BLM–USFSNONWILDERNESS	−2.514	0.99	0.01	11.9
	LAVO	NPS–USFSNONWILDERNESS	−1.598	0.99	0.01	7.5
	LAVO	NPS–USFSWILDERNESS	−2.233	1	0	10.5

We present the median of the expected difference, z, in soil stability or carbon-to-nitrogen ratio between each jurisdiction shown. We also present the probability that z is left or right of zero. A value of zero corresponds to no difference. Only contrasts with probability density > 0.75 to either side of zero are included. The final column provides an indication of the magnitude of the difference on the scale of the data. $q(y,p)$ returns the quantile of y at probability p. Thus, the denominator in the expression in the final column corresponds to the range of the data, omitting the most extreme values. For example, a value of 5 would correspond to a median difference between two jurisdictions that is 5% of the range of soil stability or carbon-to-nitrogen observations in the corresponding PACE. These results are based on coefficients presented in Supplementary Figures S3, S4.

visible traces on the landscape – i.e., charred or downed wood, chainsaw cuts, cattle scat and prints, trails and campsites, etc. High incidences of a disturbance may indicate recent disturbance, but a lack of visible disturbance may indicate either no disturbance or a past disturbance that is simply no longer visible. Future research in which investigations such as these are performed in collaboration with environmental historians might enable longer-term or historical drivers of current conditions to be elucidated, perhaps deepening our understanding of ecological heterogeneity across management mosaics. Furthermore, because we were interested in the degree to which administrative boundaries manifested as ecological boundaries, our empirical data collection took place within 100 m of each jurisdictional boundary. Some disturbance types likely track boundaries closely; for example, livestock grazing in a fenced unit is likely to exert maximum impact immediately along and up to the fenceline and to be absent across the boundary. However, some disturbances (e.g., recreation or fire) and management activities (e.g., fuels or invasives management) may be more spatially diffuse and may become more visible at greater distances from those boundaries. Most of the administrative boundaries we observed in our sampling areas are unmarked or are designated only with rare signage or bits of unmaintained fencing, suggesting that management activities and disturbance effects may not respond to sharp barriers but may instead dissipate more diffusely as they near or cross a boundary. Thus, the temporal persistence and spatial heterogeneity of management effects and disturbance evidence vary in ways that may additionally impede detection of the relationships we examined.

Soil properties, and soil stability particularly, showed the most consistent and well-supported relationships to disturbance or jurisdiction. Soil properties can vary over short distances, due to a combination of parent material, vegetation type, and disturbance (Manley et al., 1995; Lamarche et al., 2004; Neff et al., 2005; Hartmann et al., 2012; Verma and Jayakumar, 2012; Pellegrini et al., 2018). As such, soil properties represent ecological variables at the smallest spatial scale we examined for this study. Soil changes, particularly those in response to disturbances, may be relatively long-lived (Neff et al., 2005; Hartmann et al., 2012; Kuske et al., 2012; Pellegrini et al., 2018), such that their "recovery" may well outlast visible evidence of disturbance. Combined, these facets may make soils the most durable ecological indicators of disturbance and jurisdictional differences. Given their foundational role in ecosystems, divergence in soil properties may have indirect effects that affect the resilience of other components over longer time scales. Different soil properties, however, varied in their responsiveness to the factors investigated here. Despite well-known effects of fire, grazing, and forestry on soil chemistry (Kutiel and Shaviv, 1989; Manley et al., 1995; Neff et al., 2005; Verma and Jayakumar, 2012; Pellegrini et al., 2018), total soil C and N were not related to evidence of these disturbances in our PACEs. In contrast, soil stability was linked to both fire and forest management evidence, and often coincided with changes in ground cover. Soil stability is directly reduced by disturbances that remove plant cover (Belnap, 1995; Duchicela et al., 2012; Chandler et al., 2019) so these patterns are almost certainly mechanistically linked and soil stability changes may continue even after vegetation recovers (Duchicela et al., 2012; Pohl et al., 2012). The broader jurisdictional differences in both soil chemistry and stability may reflect either (1) the gap between visible disturbance sign and past management impacts, (2) soil differences that contributed to different land uses and jurisdictional designations, or (3) a combination of both. Ultimately, though, jurisdictional differences in soil stability and soil fertility (C: N ratio) may impact erosion, hydrology, and vegetation representing both livestock forage and fuels for fire. Better understanding these jurisdictional differences in soils can help with conservation planning and predicting ecosystem resilience.

Large landscape conservation is an ongoing challenge in light of global change drivers, which impact large areas and drive rapid shifts in species composition and distribution, biological invasions, and large-scale disturbances such as megafires and floods (Rudnick et al., 2012; Baldwin et al., 2018). However, such landscapes inevitably encompass multiple jurisdictions, requiring planning and predictions that incorporate cross-boundary effects and multijurisdictional decision-making (Locke, 2011; Bixler et al., 2016; Imperial et al., 2016; Scarlett and McKinney, 2016). Understanding how differing management approaches may lead to ecological differences and thus ecotones, and the scale and context of these effects, will be critical for identifying areas of collaboration and prioritization for cross-boundary decision-making. Our work suggests that anthropogenic disturbances are structuring forces across landscapes, but that their legacies may present in unexpected ways and unequally in different regions. As managers and policymakers aim to support resilient landscapes, it will be important to incorporate history, social landscapes, and the interplay of ecological stress and disturbance into truly interdisciplinary planning, going forward.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

CA, RE-N, MB, SV, and BS designed the study and received the funding. LZ analyzed the data. CA led the manuscript writing. CA, LZ, RE-N, MB, SV, and BS contributed to manuscript revisions. All authors contributed to the article and approved the submitted version.

Funding

Funding for this work was provided by National Science Foundation Award #1617309.

Acknowledgments

We thank the National Park Service, US Forest Service, and Bureau of Land Management personnel who provided permits, guidance, and feedback in each of the sampled protected area-centered ecosystems. We are deeply grateful for the hard work of our tireless field crewmembers, including: M. Sample, B. Tiffany, S. Sterner, M. Sotelo, G. Conley, M. Barasha, M. Andrews, J. Collier, M. Bannard, R. Lee, S. Lehman, B. Oxford, and W. Topete.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1053548/full#supplementary-material

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