

Pando's Pulse: Vital Signs Signal Course Correction at World-Renowned Aspen Forest

Paul C. Rogers (✉ p.rogers@usu.edu)

Utah State University

Research Article

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Abstract

Upland aspen (*Populus spp.*) forests contribute significantly to biodiversity in their circumboreal role as keystone species. As aspen ecosystems flourish or diminish, myriad dependent species follow suit. The 43-hectare Pando aspen (*Populus tremuloides* Michx.) clone in Utah, USA, is thought to be the largest living organism on earth, but is faltering due to chronic herbivory. Long-term resilience in aspen communities, including Pando, rests on successful recruitment of vegetative suckers that are nutritiously desirable to browsing ungulates. Here, I evaluate aspen reproduction alongside numerous vital indicators of Pando's status in the first trend assessment of this embattled iconic forest. I measured 64 plots using 19 indicators to determine current conditions. Findings show that the genetically uniform Pando is "breaking up" because of herbivory and fencing. Initial successes within fenced zones are tempered by nearly half of Pando that remains unprotected from chronic wild and domestic herbivory. I propose a strategy of process-based stewardship informed by adaptive monitoring to restore this famed 'one-tree forest.' Lessons from Pando include linkages to struggling, often species rich, aspen systems facing similar challenges globally.

Introduction

Upland *Populus spp.*, commonly called "aspen," play a circumboreal role in facilitating biodiversity [1]. Collectively, the six world aspens, as foundational species, are experiencing mixed rates of decline from land clearing, fire suppression, climate change/drought, commercially driven tree conversions, and herbivory [2,3,4,5]. As these ecosystems falter, commensurate trajectories affect dependent flora and fauna [6,7]. To address such complex multi-causal and interdisciplinary conservation issues, adaptive monitoring strategies show great promise where evidence-driven prescriptions may be incrementally adjusted to ensure long-term resilience [8,9].

In North America, the 43 ha Pando clone is the most well-known specimen of aspen (*P. tremuloides* Michx.) and putatively the world's largest organism by dry weight mass [10,11,12]. This iconic aspen clone, however, has experienced persistent browsing over in recent decades by mule deer (*Odocoileus hemionus* Raf.) and cattle (*Bos Taurus* L.) such that it is slowly dying; a once-dense canopy is thinning out while vegetative offspring (regenerating suckers) fail to reach maturity [13,14]. Pando's increasing notoriety via international media [15,16] has paralleled the steady decline of the clone (e.g., *Nature* 2018; Dykes 2022). Fences have been erected to mitigate herbivory at Pando (Figure 1), but such visual and ecological intrusions potentially bring additional problems, such as creating aesthetic impairments and novel floristic pathways [17] at this natural wonder.

Aspen forests, whether monotypic aspen such as at Pando or as a successional component, are considered disturbance dependent [18,19]. Thus, a key element in resilience stewardship is to ensure post-disturbance juvenile suckers attain recruitment stature [9,20]. Conventional aspen management worldwide has focused on asexual stand replacement [1], though we now know regeneration from seed plays some undetermined ecological role, too [21,22]. Monitoring efforts commonly assess sucker

regeneration (i.e., < 2 m ht.) and browse intensity, while neglecting the next developmental stage of recruitment (> 2 m, < mature). Where ungulate herbivory exceeds sustainable aspen levels [23,24], herbivore stunted regeneration may not reach recruitment height [25]. Thus, adequate recruitment is a vital indicator of resilience monitoring in aspen [4,9,26]. Long-term recruitment failure—signaling ability to replace short-lived mature stems—in aspen systems may have cascading effects on hundreds of dependent species [27,28]. Despite active management [13] and piecemeal fencing since 2013, widespread growth above the vulnerable regeneration stage has fallen short [14].

The present study has three aims: 1) To gain a comprehensive understanding of Pando's fitness by examining patterns across treatment/fencing groups; 2) To perform critical analyses of the condition and roles of regeneration and recruitment throughout the clone; 3) To address key practices as they affect conservation efforts at Pando, which carry important linkages to aspen's biodiversity functions internationally. Findings here will contribute to developing necessary strategies for reversing the break-up already underway at Pando. Further, this high-profile forest may act as both a proving ground and blueprint for adaptive management in keystone aspen systems worldwide [1,7].

Results

Descriptive Statistics of Four-Year Change

Most sampled indicators showed no significant change since the previous full measure of Pando [14]. Table 1 displays an array of descriptive statistics, by treatment groups, of change between 2017 and 2021, with areas shaded where measured change is greater than variance (SD). This initial look indicates declines in canopy cover in all groups, increases in regeneration and decreases in browse within the No Fence and 2014 Fence zones, a strong increase in recruitment and modest decrease in basal area inside the 2013 Fence, and a decline in standing dead tree basal area in the 2013 and 2014 Fenced areas.

Exploratory Analysis for Discerning Key Variables

Ordination analysis produced a three-dimensional solution on a matrix of 64 stands by 19 variables. Non-metric multidimensional scaling (NMS) ordination is displayed as a joint plot where the most highly correlated ($r^2 \geq 0.3$) results are displayed as an overlay (Figure 2). The final NMS solution produced a stress value of 7.61 with an instability of 0.00. A Monte Carlo test of 250 random data runs versus the real data set verified a significant NMS outcome ($p = 0.004$). The three-axis result described about 95% of ordination variance (axis 1: $r^2 = 0.588$, axis 2: $r^2 = 0.255$, axis 3: $r^2 = 0.109$; orthogonality = 98.1; Table 2). Table 2 presents all NMS results by axes for environmental variables. Because axis 3 contributes relatively little to the overall dataset explanation, further results will focus only on axes 1 and 2. Length and direction of robust vectors ($r^2 \geq 0.3$) in Figure 2 correspond to variable strength and relationship to the two-dimensional plot-data space. As the stronger of the two dimensions represented here, axis 1 describes a gradient of recruitment abundance negatively correlated to deer and cattle presence, plus browse level (Figure 2). Axis 2 displays no negative elements, though a positive gradient is evident in the

data set with regeneration ha^{-1} . Protection status (fence) and recruitment as a percent of live trees ha^{-1} also correlated positively with axis 1 (Table 2), though just below criteria for joint plot display.

Testing for Group Differences Using All Variables

The Multi-Response Permutation Procedures (MRPP) results express stronger within group agreement (validation) than between groups for all three pairwise alignments (Table 3). All comparisons were highly significant (< 0.001). Greater negative T values indicate stronger between group differences. The relatively large negative T value in the No Fence vs. 2013, alongside very similar results in the other two comparison groups, suggest a “distance” factor in overall plot values based on treatment groups.

Treatment Effects in Regeneration, Recruitment, and Browsing

Figure 3 presents an array of non-parametric test results—Kruskal-Wallis test for three-way and Mann-Whitney-U test for two-way comparisons—to discern status of regeneration (3a-b), recruitment (3c-d), and browsing (3e-f). The regeneration response yielded a significant statistical finding identical to the 2017 baseline measurement of Pando (Figure 3a; $\chi^2 = 37.10$, $p < 0.0001$). An unusually high regeneration count of the shortest height class (S1), however, warranted another look at supposed parity between No Fence and 2014 Fence regeneration. When the < 0.5 m height class (likely current year emergence) were removed from all plots, a significant difference resulted between No Fence and 2014 Fence areas (Figure 3b; $\chi^2 = 5.86$, $p = 0.015$).

Recruitment between treatment groups initially indicated no overall group difference (Figure 3c; $\chi^2 = 3.68$, $p = 0.158$), though further examination of *recent* recruitment after removing six sample plots within the old 1992 fence—29-year old aspen stems, many growing into the canopy class—highlighted a 2013 Fence area with significantly higher levels of recruitment than the other two groups (Figure 3d; $\chi^2 = 12.42$, $p = 0.002$).

Tests between groups for browse levels focused only on the No Fence and 2014 Fence areas because the 2013 Fence area recorded almost no browsing. The resulting two-way test for browse differences was insignificant (Figure 3e; $\chi^2 = 3.19$, $p = 0.076$); however, when the anomalous smallest size class was removed (S1), a significant pattern of much higher browse was found in the No Fence area (Figure 3f; $\chi^2 = 4.15$, $p = 0.035$). This suggests short suckers in the No Fence area (S1) are not yet being browsed to the extent of taller, presumably older, regeneration.

Discussion

The overarching message from this first remeasurement of the Pando aspen clone is one of limited stem recruitment resulting from persistent browsing (Figure 2). Mule deer browsing is the main factor affecting recruitment success, with domestic cattle also have significant impacts (Table 2). This conclusion is supported by significant ordinal relationships in axis 1 (Figure 2) between herbivore presence, browse level, surviving recruitment, and protection status (i.e., “fence”). A promising finding here is that many

aspen stems within the 2013 fence have moved into the recruitment class, though recruitment is lagging in the 2014 Fence (Table 1, Figure 3d), likely related to the permeable condition of the 2014 enclosure prior to 2019 fortification. Overall, more than 80% of Pando's 43 ha area has inadequate recruitment. A secondary finding here was that regeneration counts (ha^{-1}) define a distinct gradient within the study area, explaining ~25% variance. The relationship between regeneration (axis 2) and recruitment (axis 1) is explored further below.

The present assessment at Pando indicates protection regimes (treatments) are driving this genetically uniform forest toward divergent ecological pathways based on an array of tree and herbivore measures (Table 3). This divergence was supported by previous work at Pando where dissimilar vegetation assemblages track the same protection regimes [17]. Evidently past management—limiting or allowing herbivores differentially—is driving observed understory and overstorey departures from a relatively consistent forest overstorey. Fencing to limit herbivory is a logical first-step after decades of failed recruitment, although barriers appear to be having unintended consequences.

This study suggests that regeneration and recruitment success are not equivalent, and that recruitment is a more meaningful indicator of long-term resilience [29,30]. The NMS ordination (Figure 2) indicates deviating gradients of recruitment, browse, and ungulate presence (axis 1) from regeneration (axis 2) where we would expect covariance in these factors. In self-replacing aspen, a predictable rate of attrition occurs in juvenile stems based on resource availability [31]. However, aspen affected by chronic herbivory in the Rocky Mountains commonly have plentiful regeneration (< 2 m ht.) with few suckers attaining recruitment (>2 m ht.) size [25]. This pattern seems to hold here.

In this study, direct and indirect human influences complicated initial result interpretations (Table 1). For instance, increased regeneration in unfenced areas of Pando defied expectations based on previous studies [13,14]. Further investigation found most of that unprotected regeneration was in the smallest height class (< 0.5 m), suggesting newly emerged unbrowsed suckers disproportionately influenced counts (S1). Successful regeneration-to-recruitment development has been absent outside fenced areas at Pando for decades [14]. Thus, I was curious to investigate whether taller stems were surviving or whether this was simply a case of new regeneration that had gone unbrowsed in first-year emergence. After removing the smallest height class the No Fence and 2014 Fence treatments displayed significant differences in regeneration success and reduced browse (Figure 3b, 3e-f), contrasting with baseline results [14] and suggesting the 2019 fence reinforcement (2014 Fence) is showing positive effects (Figure 3b, 3f).

If regeneration success in protected areas progresses at Pando, we would expect signs of burgeoning recruitment. While long-term aspen recruitment may be episodic based on disturbance, climate, or other human factors [32,33], the decadal dearth of recruitment at Pando suggests recent management is driving successes and failures [14]. A deeper examination was required. Viewing only recruitment, the older 1992 enclosure (Figure 1) seemed to have an undue influence on initial findings. This parcel, within the 2014 Fence, contains six plots where many recruitment stems have grown into the “mature tree”

class, erroneously implying a loss of the recruitment here (Table 1). Though there were differences in recruitment overall, most of that consists of the large gap between fenced and unfenced groups (Figure 3c). Rerunning the analysis with the subgroup of six 1992 clearfell plots removed presents a different outcome; No Fence and 2014 Fence areas contain almost no *recent* recruitment (Figure 3d). Twenty-nine-year-old recruitment confounds our understanding of restoration success in the full Pando data set. When accounting for that in the context of regeneration shortfalls (Figure 3b), a stubborn trend of marginal stand replacement at Pando persists, particularly in the sizable unfenced zone. This conclusion leaves us with nagging questions regarding a path forward and whether recovery solely dependent on fencing is appropriate.

Aspen forests worldwide support outsized biodiversity [6,7,34], but at Pando overabundant browsers are usurping resilience with expected spiraling (or diverging) diversity outcomes. Results here bolster evidence of a faltering recovery when protection from herbivores is absent (Figure 3c-d). The dominant ecological gradient among 19 system indicators was an inverse relationship between recruitment success and browse pressure (Figure 2, Table 2). A secondary gradient of regeneration fecundity suggests the importance of this variable, though regeneration alone is a poor predictor of system resilience [25]. Moreover, Pando is affectively “breaking up,” as evidence here shows distinct forests within the clone by protection status (Table 3) and previously by plant communities [17].

Excessive herbivory is present on a much larger landscape surrounding Pando and, in fact, is a major pressure on aspen communities regionally [35]. Caretakers at Pando will need to address herbivory to ensure long-term system sustenance. Primarily mule deer, but also domestic cattle, are responsible for insufficient recruitment. This conclusion is reached by mule deer’s stronger linkages to browse (Figure 2). Additionally, there are unfenced areas of Pando off-limits to cattle during their brief annual occupancy (e.g., campground, near recreational cabins), though these areas still experience browse-induced aspen suppression. This should not suggest, however, that cattle have no impact on aspen recruitment (Figure 2); additionally, cattle are influencing broader floral diversity within Pando [17].

Pando is paradoxical: putatively earth’s largest organism, it is small as conservation challenges go. As an exemplar, however, it portends pathways for aspen diversity and resilience globally. In turn, circumboreal aspen forests contain ‘mega-conservation’ potential as these keystone forests support hundreds of dependent species [1]. Given that ungulate populations, and to a degree movement, are controlled by land- and wildlife- managers, policy changes are needed to sustain Pando as well as aspen writ large. With high biodiversity value and visibility, wise choices backed by credible monitoring are required.

Current short-term strategies favor system control over more lasting process-based restoration [8,36]. Aesthetically, visitors may be disappointed to see an illustrious native forest fenced; perhaps symbolizing nature in captivity or managerial expediency over ecological integrity. Temporary secession of livestock grazing and iterative mule deer culling and/or dispersal will require multiagency coordination—no small request, but necessary for prioritizing long-term process-, rather than control-, based conservation. Current browsing pressure, alongside increasing human traffic, forecasts a bleak future for Pando. An adaptive

monitoring approach [9] paired with greater stewardship agility offers a robust framework for a resilient Pando. Such recommended actions are not only needed for prolonging Pando's status as the 'World's Largest Organism,' but this prescription has implications for conservation writ large; lessons here may inform aspen resilience and biodiversity globally.

Methods

The Pando aspen clone is located in Utah on the Fishlake National Forest (UTM 434701 E, 4264266 N). Vegetation here consists of a sparse cover of native and invasive species, punctuated by plentiful volcanic boulders. Common juniper (*Juniperus communis* L.) occurring in dense patches is the dominant forest floor vegetative component. Annual precipitation totals 466 mm, largely accumulated as winter snow. A more detailed site description, and summary of recent human activities at Pando, can be found in Rogers & McAvoy [14].

Sampling layout and methods were replicated from an earlier study [14] to ensure consistency and ultimately attain data trends. Briefly, I randomly selected 65 sample sites (plots) from a 50 x 50 m grid within Pando's 43 ha genetically defined boundary [11,13]. One plot was dropped due to inaccurate relocation, reducing the sample to 64 plots across three broad management regimes (treatment groups; Figure 1). The No Fence area remains unprotected from browsers (21 ha), the 2013 Fence consists of a 2.5 m high mesh fence (7 ha), and the 2014 Fence was built around a 1992 enclosure in disrepair (15 ha). Rogers & McAvoy [14] found that 2014 Fence allowed routine access by mule deer, thus in 2019 this fencing was reinforced and heightened to 2.5 m. The former 1992 fence was dismantled in 2020. A legacy of this 1992 fence is a subsection of Pando with even-aged dense stems now ~8-9 m tall and 8-15 cm diameter at breast height (Figure 1).

Sampling took place in both 2017 and 2021 early in the growing season (June). Fixed-area sample plots consisted two "belt transects" arranged perpendicular to each other totaling 120 m². At each plot, an array of variables was measured capturing data on site conditions, stand attributes (stem counts by aspen diameter/height classes), mature tree status (live/dead), juniper and aspen cover, percent regeneration browsed, and ungulate type/use. Domestic livestock scat was tallied per individual dropping. Visitations by wild ungulates were considered distinct if pellet groupings included at least three individual pieces [37]. All area-based data were summed, by plot, to the ha⁻¹ level via an expansion factor of 83.33. See Rogers & McAvoy [14] for detailed sampling method descriptions.

Data analysis may be outlined in four steps (replicated and detailed in [14]): 1) descriptive statistic compilation and change assessment, 2) exploratory analysis to discern key variables, 3) testing for overall group differences, and 4) determination treatment effects using key variables. All analytical tests employed non-parametric assumptions due to uneven data variances and large numbers of zero values [38,39]. We used PC-ORD[®] v. 7.0 software [40] for statistical analyses in the first two steps, then the SAS[®] statistical package (SAS Institute Inc.) to test group differences. Summary data describes broad changes since the 2017 baseline Pando assessment using means bound by standard deviations.

Non-metric multidimensional scaling (NMS) ordination is an exploratory technique for parsing and correlating this study's matrix of 64 plots by 19 response variables for the purpose of highlighting key variables while extracting the strongest ecological gradients (axes) within the total "data landscape" [41]. The lowest stress solution was derived from 250 runs with real plot data. "Stress" is a quantitative assessment final NMS solution monotonicity, a measure of how well real data fit the ordination [39,42]. The lowest stress solution was subjected to a Monte Carlo test of an additional 250 randomized iterations to evaluate the probability of the final NMS solution being greater than chance occurrence (i.e., provides a *p*-value). Orthogonal rotation of the final ordination was used to maximize correlations between the strongest environmental variables (i.e., Pearson *r* values) and the major ordination axes. The lowest number of dimensions (axes) was selected when adding another dimension would have decreased the final stress by <5 [39].

Overall group differences were assessed using Multi-Response Permutation Procedures (MRPP), a technique for describing within group agreement of variables in contrast to *a priori* data groups [43]. We selected MRPP using the Sørensen distance measure because it is less inclined to exaggeration based on outliers and zero values [42]. MRPP produces a T score indicating the degree of difference between group pairs, an A-value which is the chance-corrected within group agreement (effect size), as well as a *p*-value establishing level of test significance [39].

Tests of group differences based on key response variables from the exploratory ordination (NMS) were conducted using Wilcoxon–Mann–Whitney *U* (two-group) and Kruskal–Wallis (three-group) tests following Zar [38]. All tests in this study used a 95% confidence level ($p \leq 0.05$) to determine significance.

Declarations

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Conflict of Interest Author declares no conflict of interests within this study.

Author Contributions Paul C. Rogers conceived, acquired funding for, analyzed data, and wrote the manuscript for this study.

Ethics Statement Not Applicable

Data Accessibility Statement: All study data will be made publicly available through Utah State University's Digital Commons data repository.

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Tables

Table 1: Summary change statistics between 2017-2021 for all locations by treatment group. All values represent group means (SD), followed by four-year change (+/-), except for number of plots. Regeneration are young aspen stems ≤ 2 m in height. Percent browse measures are only taken from regeneration stems. Recruitment are stems > 2 m in height and < 8 cm diameter at breast height. Gray highlight indicates measure changes beyond the standard deviation (SD) or gross variability.

Treatment	Number sample plots	Percent juniper cover	Percent aspen cover	Aspen regeneration ha ⁻¹	Percent browse	Aspen recruitment ha ⁻¹	Live trees ha ⁻¹	Basal area live trees m ² ha ⁻¹	Dead BA as percent of total BA
No Fence	21	23(17), +1	12(8), -11	1996(1431), +1697	27(26), -28	24(75), +8	353(319), -63	18(14), +5	11(13), -19
2013 Fence (Treatment-No Treatment)	21	21(20), -3	9(4), -8	1873(1212), +175	1(3), +1	1805(1230), +1745	250(137), -75	12(7), -11	14(18), -23
2014 Fence (No Treatment)	22	34(10), -1	16(7), -12	1561(113), +1410	1(3), -23	765(1174), -439	723(738), +253	24(13), +6	15(19), -9

Table 2: Pearson's coefficients (r) between environmental variables and primary NMS ordination axes. The strongest response variables for Axes 1 & 2 are highlighted in bold type, where $r > 0.5$ or $r < -0.5$.

Variable Name	r - value		
	Axis 1	Axis 2	Axis 3
Elevation	-0.155	-0.246	-0.516
Treatment	0.476	-0.165	-0.189
Fence	0.505	-0.249	-0.100
Layers	-0.155	0.011	0.091
Condition	-0.151	-0.301	0.233
Juniper Cover	0.123	-0.390	-0.173
Aspen Cover	0.248	-0.207	-0.687
Regeneration ha ⁻¹	0.126	0.919	-0.116
Browse Level	-0.552	0.013	-0.026
Recruitment ha ⁻¹	0.789	0.356	0.278
Recruitment % Live TPH	0.541	0.237	0.606
Trees ha ⁻¹	0.472	0.041	-0.718
Live Trees ha ⁻¹	0.459	0.021	-0.675
Basal Area Live	0.154	-0.150	-0.754
Basal Area Dead	-0.006	0.084	-0.253
Percent Basal Area Dead	0.035	0.097	-0.028
Basal Area Total	0.133	-0.102	-0.746
Cattle	-0.575	0.080	0.042
Deer	-0.650	0.388	0.008
Variance Explained by Axes (r^2)	0.588	0.255	0.109
Cumulative Variance	0.588	0.843	0.952

Table 3. Multi-Response Permutation Procedures (MRPP) test results for differences in cumulative scores for all variables between treatment groups. “T” is the MRPP test statistic which calculates the difference between observed and expected delta. “A” is the chance-corrected within-group agreement.

Treatment Group	T	A	p
No Fence vs. 2013 Fence	-19.31	0.30	<0.001
No Fence vs. 2014 Fence	-9.48	0.13	<0.001
2013 Fence vs. 2014 Fence	-9.19	0.14	<0.001

Figures

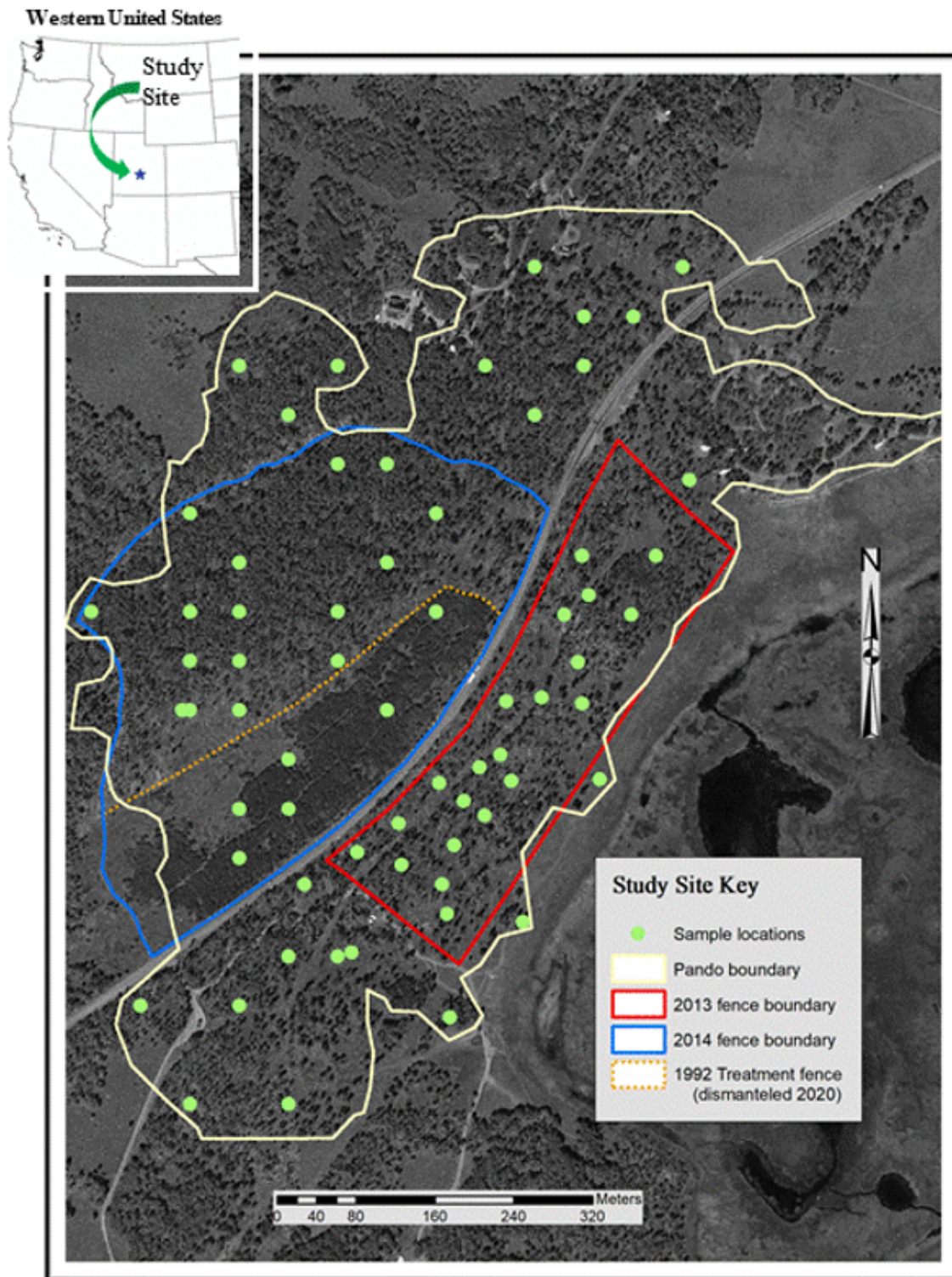


Figure 1

Pando aspen clone study site projected over National Agriculture Imagery Program aerial photography backdrop, Utah, USA. Sixty-four sample plots were randomly distributed across the study area, with near-equal portions located within No Fence, 2013 Fence, and 2014 Fence management regimes. A low-volume paved road bisects the clone; a campground is in the northeast portion and small cabins are located in the northcentral portions of the study area.

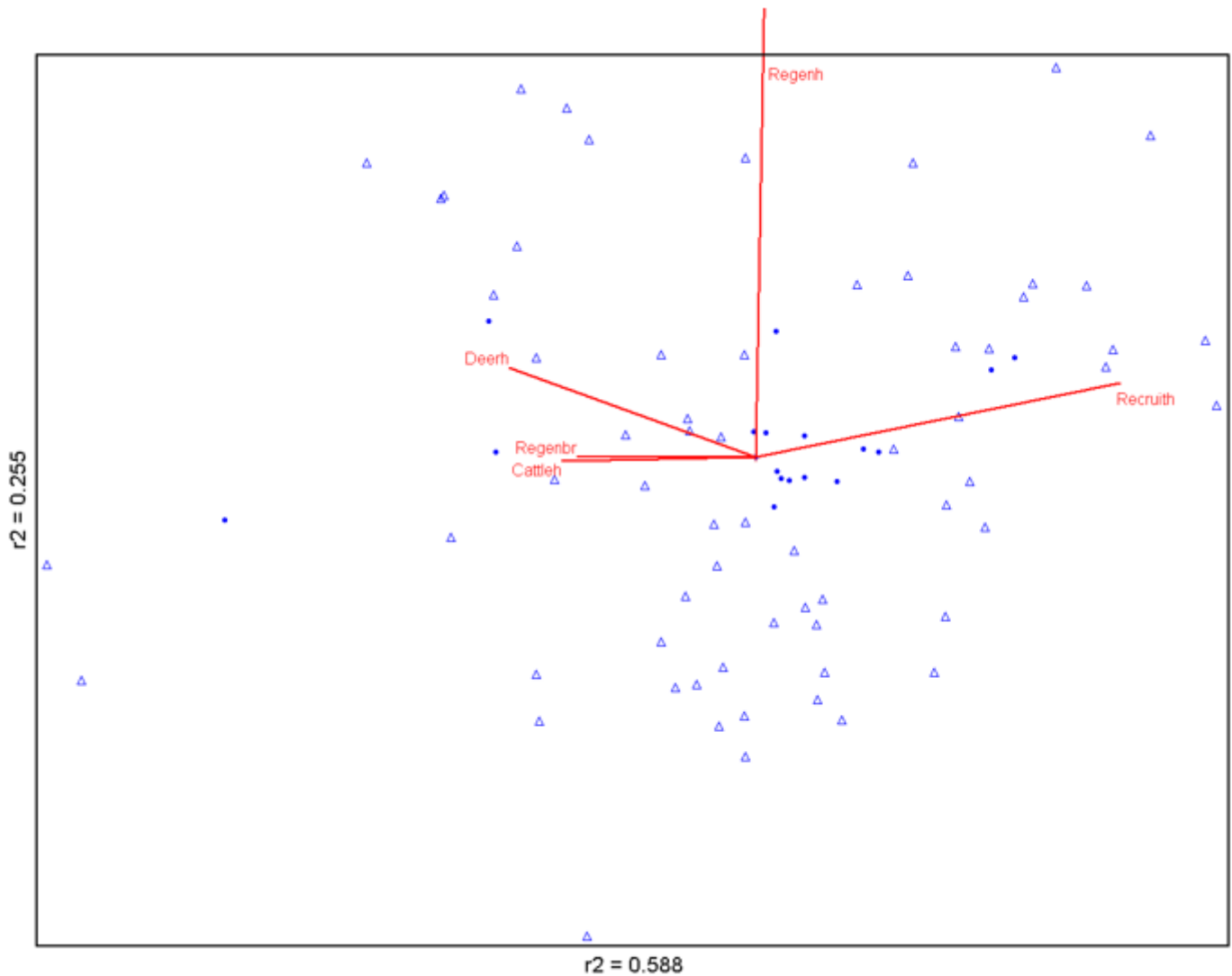


Figure 2

A joint plot depicts the results of nonmetric multidimensional scaling (NMS) ordination on a matrix of 64 plots by 19 monitoring variables. Highly correlated environmental variables ($r^2 \geq 0.3$) are overlaid on the ordination to show relationships to primary axes. Vectors explain direction and strength (length) of factors in the ordination space as defined by cumulative plot values of all variables. Variables shown (from left): cattle scat ha^{-1} (Cattleh), percent of regeneration browsed (Regenbr), deer pellet groups ha^{-1} (Deerh), aspen regeneration stems ha^{-1} (Regenh), and aspen recruitment stems ha^{-1} (Recruith). Hollow triangles show locations of plot scores and solid circles represent overall variable scores in “data space” within the NMS ordination.

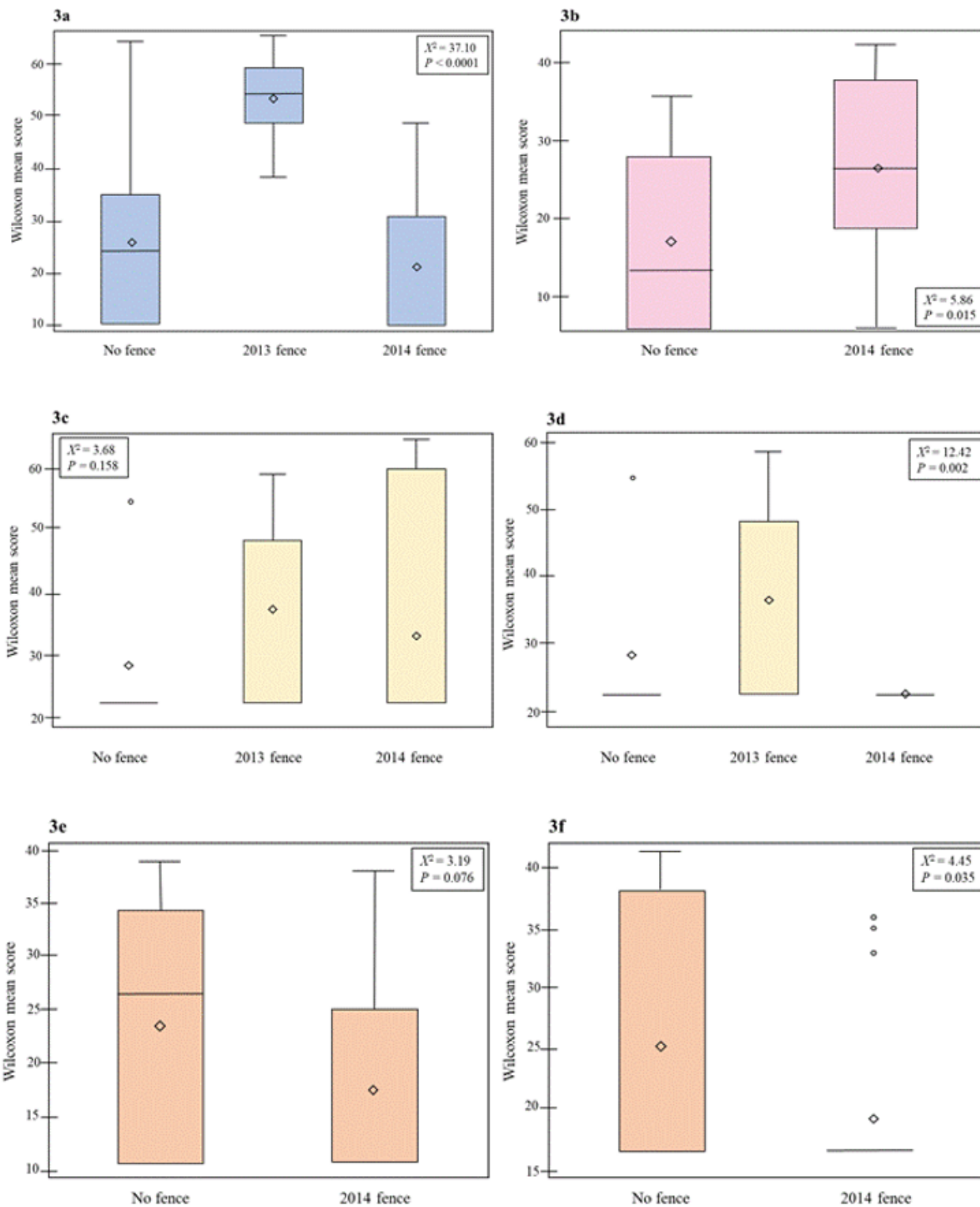


Figure 3

Box plots of nonparametric tests describe study site patterns of regeneration, recruitment, and browsing impacts by protection management groups. Analyses graphics are as follows: a) significant difference between regeneration ha⁻¹ for all regeneration height classes; b) significant difference between regeneration ha⁻¹ comparing No Fence and 2014 Fence groups with the shortest regeneration height class (< 0.5 m) removed; c) significant difference in recruitment ha⁻¹ for all study plots; d) significant difference

in recruitment ha^{-1} with five 1992 fenced area plots removed; e) browse level (percent regeneration browsed) nonsignificant difference between No Fence and 2014 Fence groups; and f) browse level significant difference between No Fence and 2014 Fence groups with the shortest regeneration height class ($< 0.5 \text{ m}$) removed. Kruskal-Wallis test results are shown for differences between three groups and the Wilcoxon–Mann–Whitney U test for comparison of two groups. The x-axis shows protection/fence groups and the y-axis reports Wilcoxon mean scores (SAS®). Results are significant when a Monte Carlo-simulated chi-square test using 10,000 runs produced an estimated p -value of < 0.05 . Output from Kruskal–Wallis test Whiskers show minimum and maximum values, open circles are outliers, boxes represent 25–75% data ranges, horizontal lines within boxes are medians (no line indicates Wilcoxon score of zero), and diamond symbols are means.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [S1RegenerationChangebyClasswithcaption.docx](#)