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## **Quaking Aspen Clonal Expansion in the Greater Yellowstone Ecosystem**

Running footer: Aspen Clonal Expansion

2 tables, 3 figures, 1 supplementary table, 1 supplementary figure

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## **Abstract**

Quaking aspen is a widely distributed tree that provides valuable ecosystem services in Western landscapes, including forage for ungulates. It forms multi-shoot clones that can cover large areas and live for centuries. Although individual shoots die back, stands are maintained through asexual reproduction. Current threats include drought, ungulate browsing, and conifer competition. Owing to its ecological importance and sensitivity to disturbance, aspen has been the subject of a 34-year monitoring effort in the Custer-Gallatin National Forest in the Greater Yellowstone Ecosystem. To assess aspen status on this landscape, we used remote sensing to monitor changes in stand area from 1990–2023 and related the increase in 60% of the stands to long-term changes in stand size-class composition, browsing, and conifer encroachment. Stand area in 2023 was associated with more intermediate-sized shoots and absence of encroaching conifers 18 years prior. Larger stands also tended to have more mature trees and experience less contemporaneous browsing. However, higher past browsing was associated with larger and faster-growing stands, indicating that browsing may have complex and conditional effects on aspen stand growth. Other site factors including slope, aspect, and elevation did not have detectable effects. Our results suggest that management promoting intermediate size classes and removing conifer competition could be important for the long-term health of aspen. Browsing affected stand area and structure but was not necessarily harmful. We hypothesize that intermediate browsing may benefit stands by stimulating suckering, provided browsing it does not prevent regeneration of mid-sized shoots which appear vital for long-term stand health.

## **Key Points**

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- Aspen stands are threatened by climate change, over-browsing, and conifer encroachment.
- Aspen stands have expanded by a median value of approximately 200 m<sup>2</sup> per stand (roughly 10%) from 1991–2023.
- Stand area and growth are associated with high numbers of medium-sized stems 18 years prior and absence of encroaching conifers, but effects of browsing were complex.

**Keywords:** Aspen population health; Greater Yellowstone Ecosystem; Ungulate browsing; Western forest health; Woody plant encroachment

## Introduction

Quaking aspen (*Populus tremuloides* Michx.) is the most widely distributed deciduous tree species in North America (Rogers et al., 2014, Krasnow and Stephens, 2015). Aspen is a clonal species that reproduces primarily through vegetative suckering and less commonly by seed. It grows primarily as large, long-lived (up to 120 years for individual shoots, but sometimes thousands of years for the entire genet; Kimble et al., 2011b) multi-shoot clones, also known as ‘stands’ (Šenfeldr et al., 2024). Aspen stands provide habitat for many small animals (Oaten and Larsen, 2008, Earnst et al., 2012) and forage for ungulates such as deer (*Odocoileus* spp.), elk (*Cervus canadensis*), and moose (*Alces alces*; Kimble et al., 2011a, Rhodes et al., 2017, Rhodes et al., 2018). Wild (particularly elk) and domestic ungulates (e.g., cattle, *Bos* spp.) forage on aspen suckers as they are highly palatable, nutritious, and accessible during the winter season (Kimble et al., 2011b, Rhodes et al., 2018). However, herbivory targets small size classes and can impair recruitment (Refsland and Cushman, 2021, Reikowski et al., 2022). Aspen stands

are utilized by herbivores due to their high nutritional content, cover for thermoregulation, and seasonal availability (Rhodes et al., 2017, Rhodes et al., 2018, Reikowski et al., 2022). Light to moderate browsing encourages recruitment, but over-browsing can occur when browsing rates exceed the ability of the stand to recover (Rhodes et al., 2017, Reikowski et al., 2022).

Aspen stands are widely recognized as biodiversity hotspots, even in regions where they are the minority species, such as boreal forests (McCullough et al., 2012, Rogers et al., 2020). Stable stands can function as a fire break due to their high moisture content (Krasnow and Stephens, 2015, Carter et al., 2017, Harris et al., 2025) and can sequester water and carbon (Woldeselassie et al., 2012, Boča and Miegroet, 2017). Aspen stands provide aesthetic value to outdoor recreators (*i.e.*: hunting, fishing, skiing, photography), bolstering local and state economies (Roger, 2017).

Combined effects of climate change, conifer encroachment, and excessive browsing by ungulates can affect the survival of individual aspen stands or have negative effects at a landscape scale (Seager et al., 2013, Wan et al., 2014, Carter et al., 2017). Water availability has been found to be the most influential factor in aspen stand health, especially prolonged droughts (Krasnow and Stephens, 2015, Chen et al., 2017, Ayres et al., 2025). Droughts, as well as wildfires, which are more severe and frequent due to anthropogenic disturbance (Liu and Biondi, 2021), can reduce growth or induce root mortality (Krasnow and Stephens, 2015, Chen et al., 2017). Additionally, drought can increase the frequency of invasive insects and diseases, which in other regions of the United States are becoming more prevalent (Couture and Lindroth, 2012, Crouch et al., 2021, Ruess et al., 2021). In the southwestern U.S., an insect known as oystershell scale (*Lepidosaphes ulmi* L.) induces diebacks and mortality of aspen stands (Grady, 2017, Crouch et al., 2021). These threats are situationally nuanced and interacting. For example,

drought can lead to fire, which has been found to increase the regeneration rate of aspen, as it is an early-successional species (Carter et al, 2017, Harris et al., 2025). Fire can also offset the threats associated with conifer encroachment in boreal forests by increasing sunlight, soil moisture, and soil temperature (McCullough et al., 2012, Krasnow and Stephens, 2015). Furthermore, aspen stands face direct competition with other trees. Conifer encroachment into aspen stands causes stand loss due to shading and crowding (McCullough et al., 2012). Conversion of aspen stands to coniferous forest can lead to a decrease in understory plant diversity, and influence soil temperature, moisture retention, and seed germination (Krasnow and Stephens, 2015, Berrill et al., 2024).

Aspen stands occupy about ~1.4% of the Greater Yellowstone Ecosystem (Brown et al., 2006). Because of the ecological importance of aspen, its role in the natural heritage of the region, and stakeholder awareness of the various threats to aspen in the region, significant efforts are being made to retain aspen stands throughout the North American west. Pursuant to this, in 1990 St. John established a long-term, observational study of aspen stands ( $n = 342$ ) in the Custer Gallatin National Forest. Surveys of the established stands were conducted in 1990–1991 (St. John, 1995) and then again in 2005–2006 (Kimble et al., 2011a, Kimble et al., 2011b) and 2023–2024 (Keller, 2025) to monitor the recruitment, regeneration, and changes in stand structure related to browsing in the Greater Yellowstone Ecosystem. In 1990, stands located within scree fields had the highest rates of recruitment of small size-class shoots, most likely attributed to the exclusion of ungulates. Stands within 500 m of main roads and human habitations yielded higher recruitment than those stands outside of the 500 m range, which St. John postulated was because of the negative effect of human activity on elk distribution (St. John, 1995). By 2006, overstory stems were declining at a faster rate than replacement. This was

attributed primarily to elk consumption, but also conifer encroachment and cattle grazing (Kimble et al., 2011b). Recently, the health of many stands has improved, as lower size classes that escaped browsing, have matured into large, competitive, and browse-resistant trees (Keller, 2025). While the efforts by St. John, Kimble, and Keller measured shoot size classes and density, the total stand area was not recorded during these respective sampling efforts due to logistical and technological limitations at the time.

The objective of this study is to remotely measure changes between 1991 and 2023 in the land area cover of selected aspen stands in the Custer Gallatin National Forest, Montana, USA, located directly north of Yellowstone National Park (YNP). We relate stand size and change in size over time to habitat conditions and stand stage structure. This study tested two hypotheses: 1) expansion occurs in stands with active recruitment; and 2) stand expansion and contraction depends on habitat characteristics such as aspect, slope, elevation, spring precipitation, winter snow water, and distance to YNP.

## **Methods**

### *Study Area*

The study area (Fig. 1) is in south-central Montana, primarily in the Gardiner Ranger District of the Custer Gallatin National Forest. The whole of the Custer Gallatin National Forest occupies over three million acres covering several mountain ranges in southwest Montana, USA. The Gardiner Ranger District occupies the portions of the Absaroka and Beartooth mountain ranges directly to the north of YNP and contains the southwest portions of the Absaroka-Beartooth Wilderness. The elevation of the study area ranges from 1521 m to 3896 m (ArcGIS PRO, version 3.3.2). The mean (1990–2023) annual precipitation is 537 mm, ranging from 442

to 842 mm, and the temperature ranges from -36.61 °C to 34.64 °C with a mean of 4.42 °C (Thornton et al., 2022). In lower elevations, meadows containing big sagebrush (*Artemisia tridentata*) and grasses (e.g. *Pseudoroegneria spicata*, *Festuca idahoensis*) are common, with quaking aspen (*Populus tremuloides*), willows (e.g. *Salix bebbiana*, *S. geyeriana*), alder (*Alnus incana*) and cottonwoods (*Populus deltoides*) occupying wetter areas (Runyon et al., 2014). Mid-elevation forests consist of species such as lodgepole pine (*Pinus contorta*), Engleman pine (*Picea engelmannii*), and Douglas fir (*Pseudotsuga menziesii*), while high elevation regions include sub-alpine fir (*Abies lasiocarpa*) and whitebark pine (*Pinus albicaulis*) (Kimble et al., 2011a, Kimble et al., 2011b). Our study area includes the portion of the Northern Yellowstone elk winter range that is located outside of YNP (approximately 40% of the total winter range for that herd—the remainder being within YNP), as well as the Upper Yellowstone West elk herd that utilizes winter range in Tom Miner Basin and Paradise Valley (St. John, 1995, Kimble et al., 2011b). The region provides vital seasonal habitat for these herds to maintain them through the winter.

### *Sampling Methods Overview*

The stands monitored in this study were taken as a subset of a large, multi-decade monitoring effort initiated by the Custer Gallatin National Forest. Aspen stands were first mapped throughout the entire district in 1990 using 1:15,840 aerial photos. Of the ~1400 mapped stands, roughly every fourth stand (342) was selected for long-term monitoring. These 342 stands were selected as representative of the entire landscape, and as such were evenly distributed relative to the total identified stands (St. John, 1995). Recruitment data were collected every decade to monitor changes in stand size class composition. These surveys were established

by St. John 1990–1991 ( $n = 342$ ; St. John 1995), resampled by Kimble from 2005–2006 ( $n = 315$ ; Kimble et al., 2011a, Kimble et al., 2011b), and most recently completed by Keller from 2023–2024 ( $n = 302$ ; Keller, 2025). During each sample effort some stands could not be relocated with confidence, either because the stand was damaged by fire or beaver activity; because the stand was no longer accessible or because a living stand was found more than several tens of meters from the recorded coordinates, a marking stake could not be found, and the stand could not be re-identified with confidence. Detailed investigation of 34-year changes in stage structure are the subject of another study (Keller 2025). In this study, we measured changes in individual stand area over time and related these to changes in stage structure. Stand area was estimated on a subset of 170 of the 302 continuously monitored stands due to imagery restraints such as image clarity or convolution of stand perimeter due to coniferous encroachment. Historical satellite imagery was collected during the monitoring period (1990–2023; Google Earth Pro, 2024).

#### *Recruitment and Other Environmental Data*

Plots were established with a permanent stake driven into the interior of each stand, marking the center of a 202.3 m<sup>2</sup> circular plot. In the first survey the number of shoots greater than 2 m high were counted and sorted into two size classes: recruitment ( $< 5$  cm diameter at breast height [DBH]) and non-recruitment ( $> 5$  cm DBH). In the second and third surveys the size classes were expanded to five: sprouts ( $< 1$  m tall), saplings (1–2 m tall), recruiting stems ( $> 2$  m tall and  $< 5$  cm DBH), poles ( $> 2$  m tall and 5–10 cm DBH), and mature ( $> 2$  m tall and  $> 10$  cm DBHr). The proportion of ungulate-browsed sprouts and saplings in each category was counted. Geographical coordinates, slope, aspect, elevation, and presence of coniferous

encroachment were recorded at each plot center. A plot was considered encroached upon if it had at least 10% estimated canopy cover of reproductive conifers.

### *Climate Data*

Snow water equivalent (SWE) has been shown to be a primary driver of winter movement and behavior of elk (Proffitt et al., 2011, Brice et al., 2024) and was acquired for each stand via the NASA Daily Surface Weather and Climatological Summaries (DAYMET) at 1 km<sup>2</sup> spatial resolution (Thornton et al., 2022). We downloaded SWE from November 1<sup>st</sup> to April 30<sup>th</sup> to capture the period when elk would be browsing aspen (Proffitt et al., 2011, Brice et al., 2024). We also downloaded spring precipitation from April 1<sup>st</sup> to July 31<sup>st</sup>. To account for variation between years, we averaged winter SWE and spring precipitation 10 years prior to each period of interest (study onset: 1980–1990, current time: 2013–2023).

### *Expansion Data*

We estimated stand area in each study period using satellite imagery (Google Earth Pro, 2024). Images were considered viable if aspen could be clearly differentiated from surrounding vegetation and stand borders could be located. A total of 170 stands had viable images that satisfied our selection criteria of having between four and six valid images, each six or fewer years apart, starting in September 1991 or August 1994, and ending in September 2019 or September 2023. It was not possible to restrict analysis to sites with a more constrained set of images, because that would have created both a loss in sample size and a spatial bias in sample representation. Image resolutions differed among photographs. Every stand had a photo from July 2014 and the most common other imagery dates were September 1991 (90 stands), August

2005 (142 stands), November 2011 (131 stands), and September 2019 (142 stands). The majority of images were captured in spring, summer, or fall during the aspens “leaf on” season. Images in which leaves were not visible and it was not possible to identify stand outlines to a tolerance of ~1 m were not used. Perimeter polygons drawn (Supplementary Figure S1) around each stand in Google Earth were exported to ArcGIS Pro (version 3.3.2) to calculate stand area (m<sup>2</sup>). To account for error in area estimation and for the fact that not all stands had the same survey dates, we did not measure stand area change by comparing our oldest and most recent stand area estimates. Instead, for each stand we regressed stand area against time and projected those regressions to two time points: 1990 and 2023. Stand area difference was calculated by subtracting the 2023 values from 1990. We used both linear and quadratic regression, but these returned similar interpolated estimates and so we chose the simpler linear regressions for the final estimations.

### *Analysis*

We analyzed two sets of models: 1) ‘current-time’ models with natural log-transformed 2023 stand area as the response variable, and 2) ‘change-over-time’ models with the difference between 2023 and 1990 stand area as the response variable. Because the number of possible predictors was large, we used corrected Aikake Information Criterion (AICc) to select a final model for analysis from a full set of candidate predictors (Table 1). These candidate predictors included hill slope (degrees from Earth surface), elevation, aspect (eight categories corresponding to the nearest cardinal or intercardinal direction), distance to nearest border of YNP, 10-year average SWE (ton), 10-year average precipitation (cm), change in 10-year average SWE (2023 10-year average minus 1990 10-year average), change in 10-year average

precipitation (2023 minus 1990), number of shoots in each measured size class for each decadal survey per 202.3 m plot (all square-root transformed), number of browsed shoots per 202.3 m plot for decadal surveys two and three (square-root transformed), proportion of shoots browsed in the same time periods (arcsine-square-root transformed), and the absence/presence of competing conifers in surveys two and three. For the current-time models, present and past values of all predictors were used, but change in SWE and precipitation was not. For the change-over-time models, only past values of predictors were used, along with change in SWE and precipitation (Table 1). We identified correlated covariates and excluded subset models that contained predictors with  $|r| > 0.6$  to other variables in the model (Supplementary Fig. S2). We also excluded models that contained both proportional and raw browse variables (*i.e.* a model that contained 2023 proportional browse as a predictor could not also contain number of browsed shoots in either 2006 or 2023). The model with the lowest AICc score was chosen for each of the two response variables (Supplementary Table S1). Assumptions of linearity and normality of variables were evaluated by analyzing model residuals. Variables were transformed as described above to better conform to model assumptions. We used a Moran I test to check for evidence of spatial auto-correlation of the residuals and found no significant correlation ( $p > 0.068$ ), so we excluded spatial terms from the final model. All statistical analyses were completed in R version 4.2.3 (R Core Team, 2025).

## Results

The median stand in 2023 was 0.19 hectares and expanded by 0.02 hectares since 1990. Stand area depended upon both abiotic and biotic factors. Among the 170 aspen stands assessed, 104 (61.1%) expanded in area from 1990–2023 (Supplementary Figure S3). Stand area changes

ranged from a decrease of 0.54 hectare to a growth of 1.17 hectare. The percentage change ranged from a contraction of -88.73% to an expansion of 9,618.81%, with the median stand contracting by -14.0%, which equates to -0.42% per year.

The final model for 2023 stand area included distance to YNP; 1991 number of recruitment stems; 2006 number of saplings, number of browsed shoots, and conifer presence; and 2023 number of poles, mature, and browsed shoots. Stand area in 2023 was greatest in stands that were farther from YNP and that had more saplings, recruits, and mature trees in earlier time periods. Stand area was lower in stands with conifer encroachment in 2006, and, contrary to predictions, with more poles in 2023. Stands with heavy browsing in 2023 had smaller stand areas in 2023, but those with heavy browsing in 2006 had larger stand areas in 2023 (Table 2, Fig. 2).

The final model for change in stand area over time included number of sprouts, saplings, mature, and browsed trees in 2006. Stands with more area growth had more saplings and mature trees in 2006, but fewer sprouts. As with the 2023 stand area model, heavy browsing in 2006 was associated with stand area increases over time (Table 2, Fig. 3).

## Discussion

We found that ~60% of aspen stands in the National Forest lands north of Yellowstone National Park (YNP) have expanded their area size since 1990. Stands farthest from the park were largest, but no other environmental variables—including elevation, aspect, hillslope, stand recruitment, spring precipitation, and winter SWE—covaried significantly with stand area. Instead, the most important covariates with stand area and/or stand growth were related to the past stage structure of the aspen stand. In general, larger stands in 2023 were those that in the

past had more saplings (1–2 m tall), more ‘recruitment’ stems (>2 m tall and < 5 cm DBH), and possibly more mature trees (> 2 m tall and > 10 cm DBH). Large area stands are also associated with high density of mature trees and low density of trees in the ‘pole’ category (> 2 m tall and between 5 and 10 cm DBH). These findings are important because they mean that the shoot stage structure of aspen stands may serve both as an indicator of stand health and potential stand growth. To the degree that stand area is an element of stand health—*e.g.*, if smaller stands are more likely to die off—a better understanding of the processes that affect changes in stand area could be vital for the management of aspen in the GYE.

Because the different elements of stand structure are correlated with one another—and with other site factors—it is difficult to know definitively what stand characteristics were the most important drivers of stand size and stand expansion. Nonetheless, we found that a high density of young, established shoots in intermediate size classes, with heights greater than 1 m and diameters less than 5 cm, may be important indicators of stand area growth in the coming decades. In contrast, stands with large densities of sprouts, less than 1 m tall, lost area over the study period, perhaps because these stands lacked the larger size classes needed to compete for resources. These large size classes seem to be important; the largest and fastest-growing stands had high densities of mature trees at present. Based upon these findings, we recommend that management for future aspen health prioritize promoting and preserving intermediate-sized shoots with potential to grow into mature shoots 10–20 years into the future. Of particular concern is protecting stands with only small size classes, which may be vulnerable to decline until intermediate-sized shoots are able to grow (Keller, 2025). These findings reinforce both the need to promote size class diversity and to consider long-term processes affecting aspen stand growth.

One way to protect intermediate size classes is to limit browsing on subordinate classes. Browsing effects on aspen recruitment increase with ungulate population density (Kimble et al., 2011a, Endress et al., 2012, Brice et al., 2024). Our results paint a complex picture of possible effects of browsing on stand growth. In 2023, the largest stands had the least contemporaneous browsing, but the largest and fastest-growing stands had a legacy of high browsing in 2006. It is not clear why heavy browsing should lead to eventual stand growth almost 20 years later. In previous studies, stands with high-intensity, chronic consumption of regenerative shoots have been documented to decrease in density and structure (Rhodes et al., 2017), although moderate consumption on stands that have not been affected by high-stress episodes (*i.e.* wildfire) have been found to positively benefit from browsing (Endress et al., 2012). It may be that browsing weakened the smallest shoots, releasing intermediate and large shoots from competition with smaller shoots. It may also be that past browsing was not an important driver of future growth, but was instead correlated with other, more important drivers, although none of those observed in this project stood out as likely candidates. Past browsing was associated with drier, shallower, sites with more sprouts and fewer large trees, none of which are associated with growth potential.

The study area contains critical winter habitat for major elk herds in the region: the Northern Yellowstone elk winter range and the Upper Yellowstone West elk winter range. More distant regions of the study area from YNP may have been less accessible to the Northern Yellowstone elk herd (Keller, 2025), perhaps explaining why stands were larger farther from the park. The Custer Gallatin National Forest also facilitates Forest Service livestock allotments in the study area, thus the aspen shoots in our study region face domestic browsing pressures at various times throughout the year. Livestock has a similar relation to ungulates but will primarily feed on aspen shoots in the late growing season (late August–mid September) (Jones et al.,

2011). Browsing pressures in the region are highly dynamic and may be a significant factor in affecting aspen stand size dynamics over decadal time scales.

More clear than effects of browsing was the inhibitory role of conifers. Stands with encroaching conifers in 2006 had only 54% the median area in 2023 as those without (0.32 ha compared to 0.17 ha). Many studies have determined that encroachment has a negative impact against aspen trees and has been shown to induce a decline in mature trees (McCullough et al., 2012). Stands with conifer encroachment also have been observed to have lower herbaceous understory biodiversity and richness, as well as an increased depth of the soil O horizon (McCullough et al., 2012). Conifers can eventually outcompete aspen by shading, which in turn eliminates both the aspen stand and herbaceous understory (Kuhn et al., 2011). This study provides further evidence that conifer encroachment, in addition to its plot-scale effects, can cause major long-term inhibition of aspen stand growth.

Additionally, stand dynamics may have been affected by unmeasured variables. For example, our analysis did not include changing temperatures or impacts of wildfire. Increases in summer temperatures and droughts have been linked to a decline in annual aspen growth, which suggests this is the primary factor making aspen more susceptible to other mortality factors (Chen et al., 2017). It has also been suggested that fluctuations in and out of the frost-thaw cycle during winter and early spring can have a negative impact by dehydrating sprouts in warm periods and leaving them vulnerable to frost in cold periods (Worrall et al., 2013, Chen et al., 2017). As an early successional species, aspen rebounds from wildfire exceptionally fast when ideal requirements are met. However, with decreases in available water (Turner et al., 2022) and increases in herbivory (Rhodes et al., 2018), aspen stands are not always able to access resources before they get outcompeted by other vegetation or browsed, post-wildfire (Wan et al., 2014,

Krasnow and Stephens, 2015). Another possible concern is that stand declines may have been worse than detected, because our analysis excludes some stands lost between 1991 and 2023. Of these 40 stands, reasons for loss included: fire; inundation by beavers; loss of access; and excessive distance between a found, living stand and the recorded plot coordinate. Therefore, our study may underestimate aspen declines due to sporadic, extreme events such as fire and beaver activity. However, there is no evidence that our sample was biased with respect to the processes we specifically investigated with this study: conifer encroachment, ungulate browsing, or climate.

## Summary

The aim of this study was to determine whether aspen stands in the Custer Gallatin National Forest have grown or shrunk in size since 1990. We found that 60% of stands have increased in area size since 1990, with stand growth related to current and past shoot stage structure, ungulate browsing, and encroachment by conifers, but not elevation, aspect, slope, or precipitation. Successful management of these aspen stands and the resources they provide will require attention to forest structure, with management prioritizing intermediate size classes that will, in 10–20 years grow into mature trees within large stands. Attention should also be paid to the long-term harm caused by conifer competition. The role of browsing is less clear. Effects on stand area may be positive or negative, perhaps depending upon timing, site conditions, intensity of browsing, and stand stage structure. Future studies are needed to measure the severity of concern associated with each of these threats and to explore more effective management strategies.

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## **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.

## **Animal Care and Use**

No permits or Animal Care Committee compliance were necessary.

## **Data Availability Statement**

All data and R scripts are included as supplements to this manuscript.

## **Supplementary Materials**

Supplementary materials, if cited in the text and accepted through peer review, can be hosted with the published article on BioOne.

## **Author Contributions**

AK and DT designed the field methods, adapted from prior studies begun by DT and others, with input from DA. HH, AK, and DT conducted the field studies, and HH, AK, and DA analyzed the data. All authors contributed to the writing of this manuscript.

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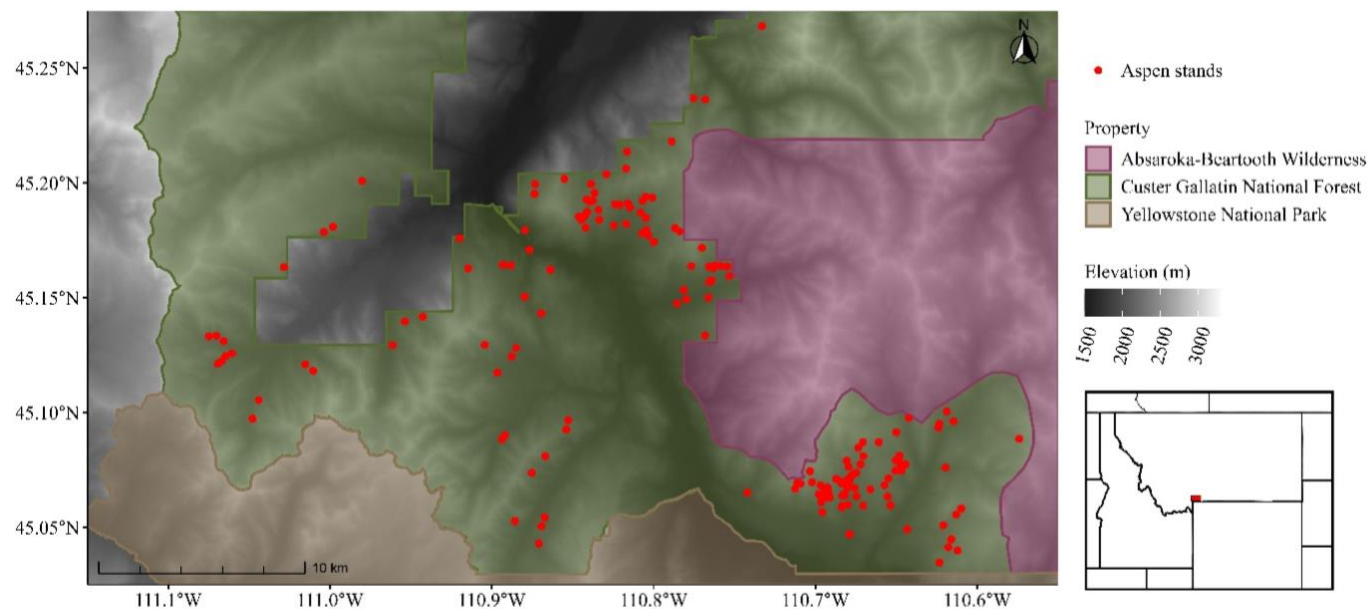
## Figure Captions

**Figure 1.** Map of study area and aspen stands used in analysis.

**Figure 2.** Results of the final model of 2023 stand area. Raw data are shown along with a trendline showing the model-predicted relationship with 95% confidence intervals.

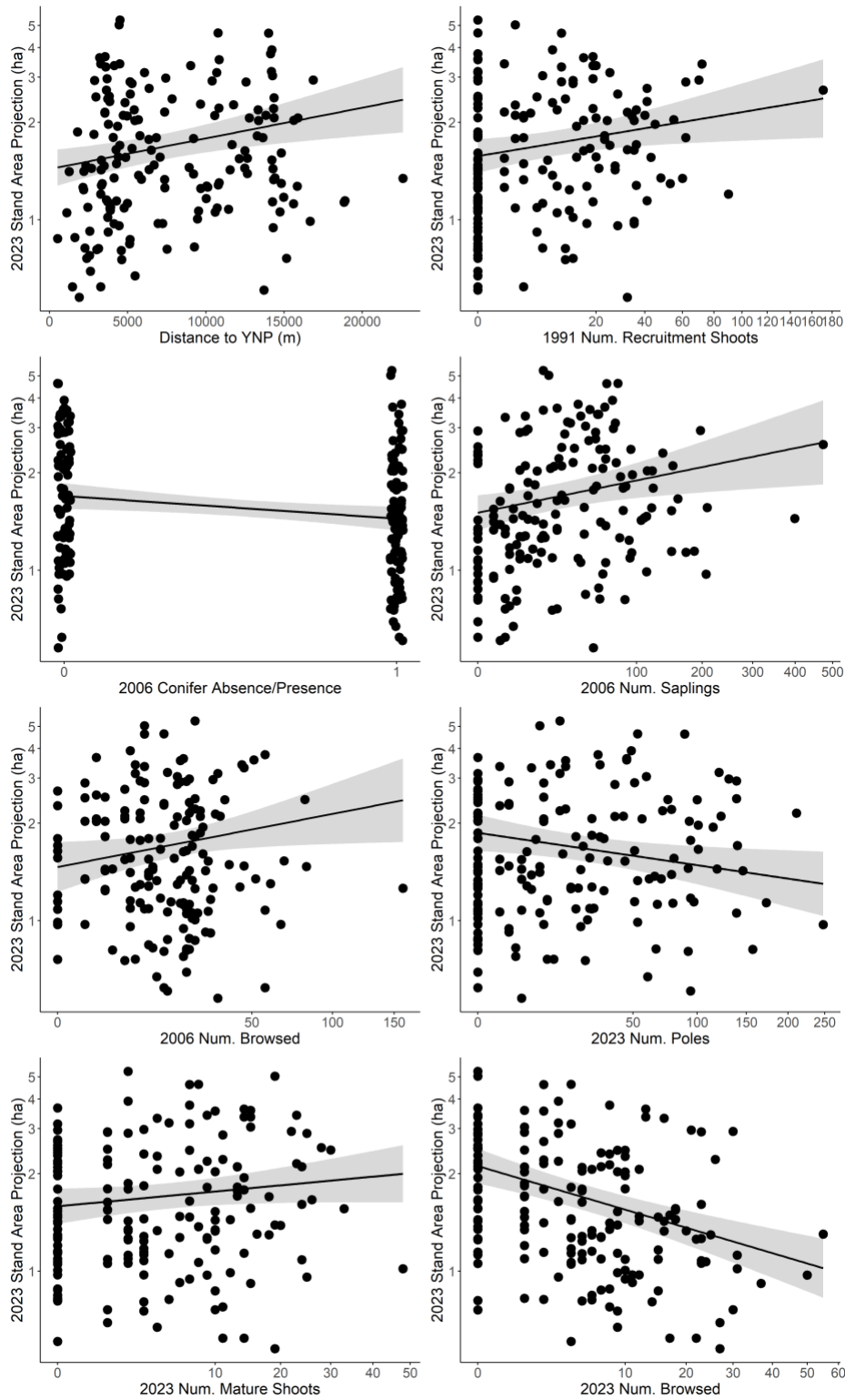
**Figure 3.** Results of the final model of change in stand area from 1990 to 2023. Raw data are shown along with a trendline showing the model-predicted relationship with 95% confidence intervals.

**Fig. 1.**



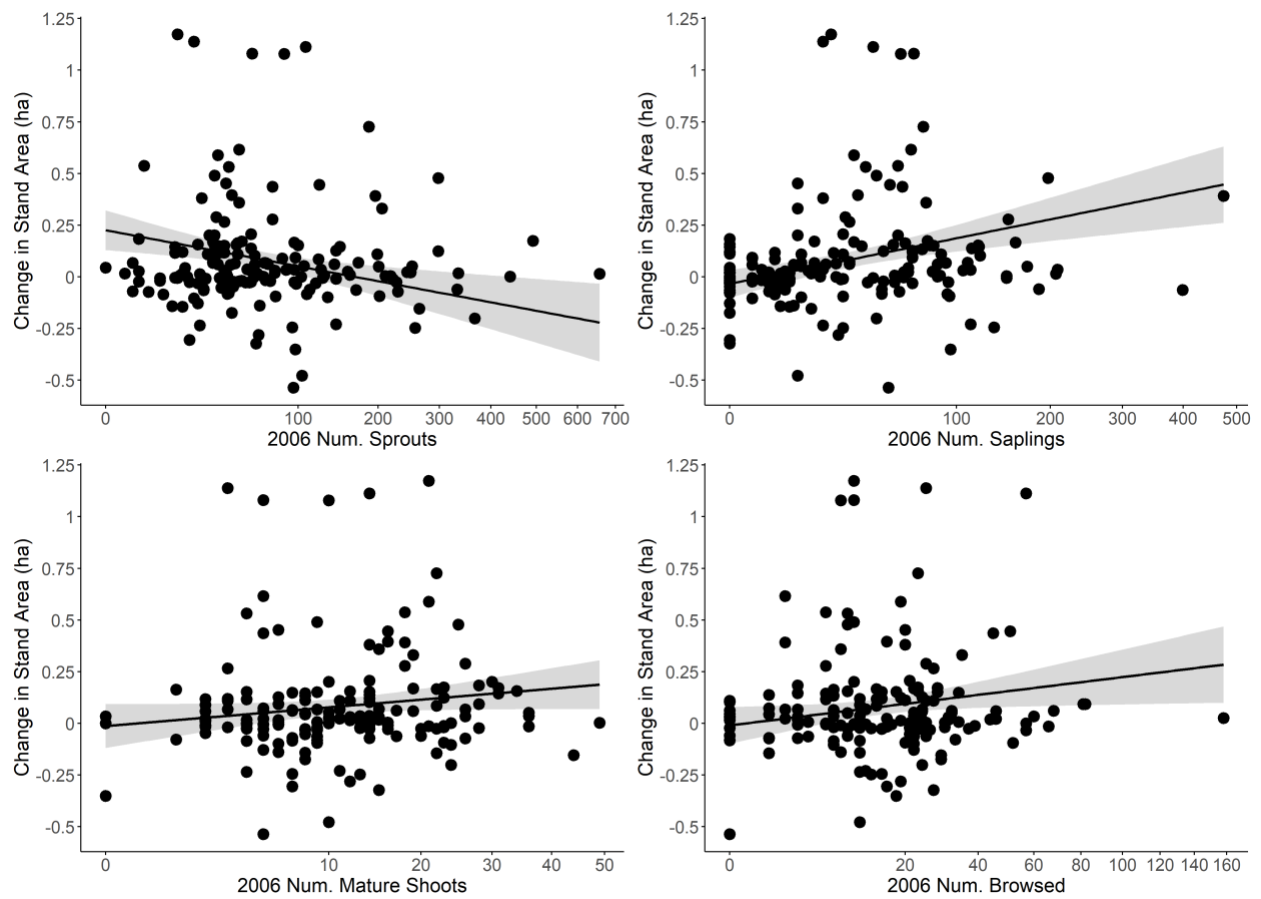
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**Fig. 2**



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**Fig. 3**



Accepted

## Tables

**Table 1.** Variables used in candidate models and in the final chosen model (based upon AICc).

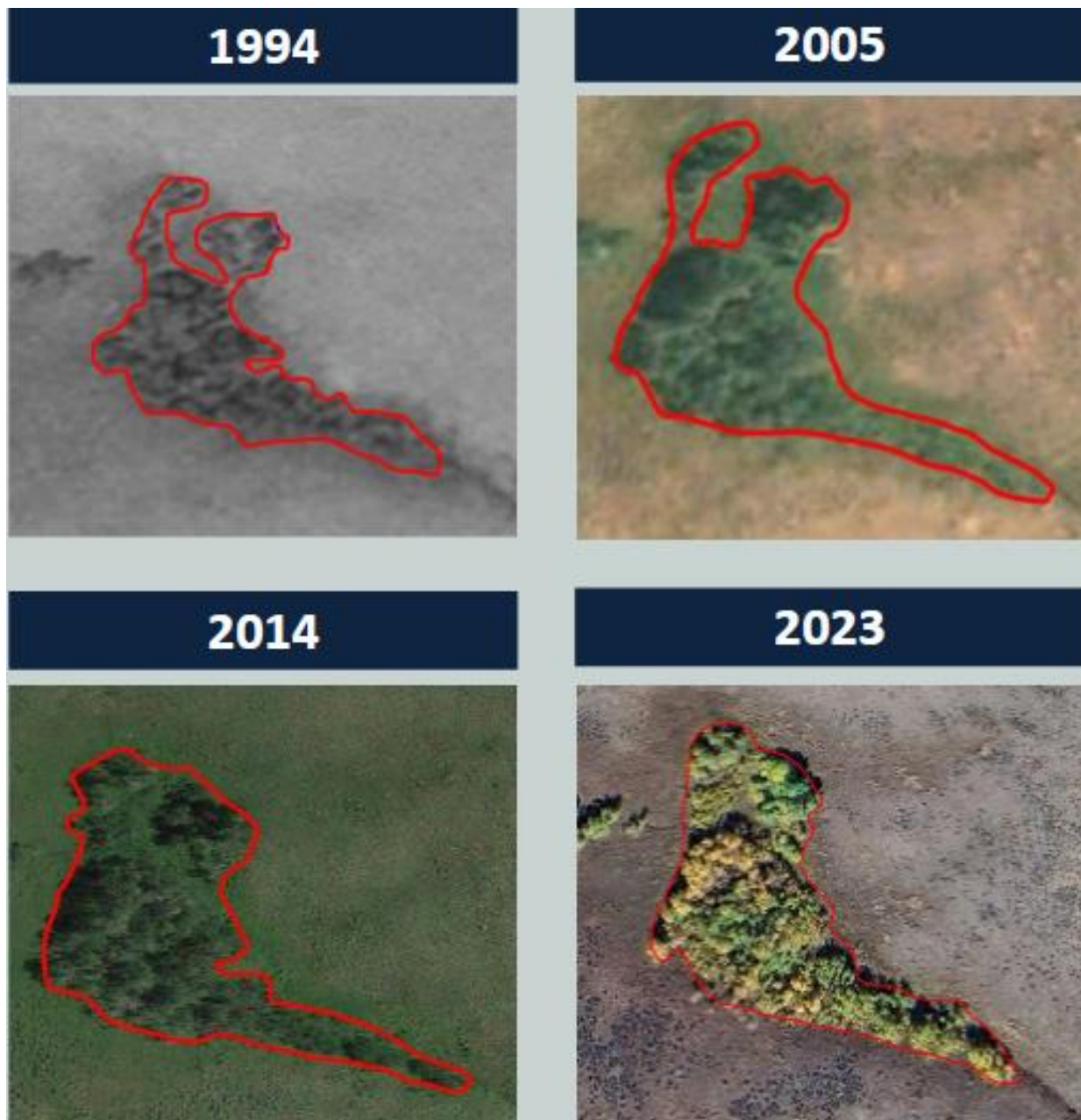
	Transformation	Current-Time		Change Over Time	
		Candidate	Final Model	Candidate	Final Model
Hillslope	none	X		X	
Elevation	none	X		X	
Distance to YNP	none	X	X	X	
Aspect	factor: 8 directions	X		X	
2023 SWE	none	X			
2023 Precipitation	none	X			
Change in SWE	none			X	
Change in Precipitation	none			X	
1991 Num. Recruitment Stems	square root	X	X	X	
2006 Num. Sprouts	square root	X		X	X
2006 Num. Saplings	square root	X	X	X	X
2006 Num. Recruitment Stems	square root	X		X	
2006 Num. Poles	square root	X		X	
2006 Num. Mature Stems	square root	X		X	X
2006 Num. Browsed Sprouts & Saplings	square root	X	X	X	X
2006 Prop. Browsed Sprouts & Saplings	arcsine-square root	X		X	
2006 Conifer Present in Plot	factor: yes/no	X	X	X	
2023 Num. Sprouts	square root	X			
2023 Num. Saplings	square root	X			
2023 Num. Recruitment Stems	square root	X			
2023 Num. Poles	square root	X	X		
2023 Num. Mature Stems	square root	X	X		
2023 Num. Browsed Sprouts & Saplings	square root	X	X		
2023 Prop. Browsed Sprouts & Saplings	arcsine-square root	X			
2023 Conifer Present in Plot	factor: yes/no	X			

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**Table 2.** Results of top models. Shoot count of saplings: height 1–2 m; recruits: height > 2 m and DBH < 5 cm; poles: height > 2 m and DBH 5–10 cm; mature: height > 2m and DBH > 10 cm.

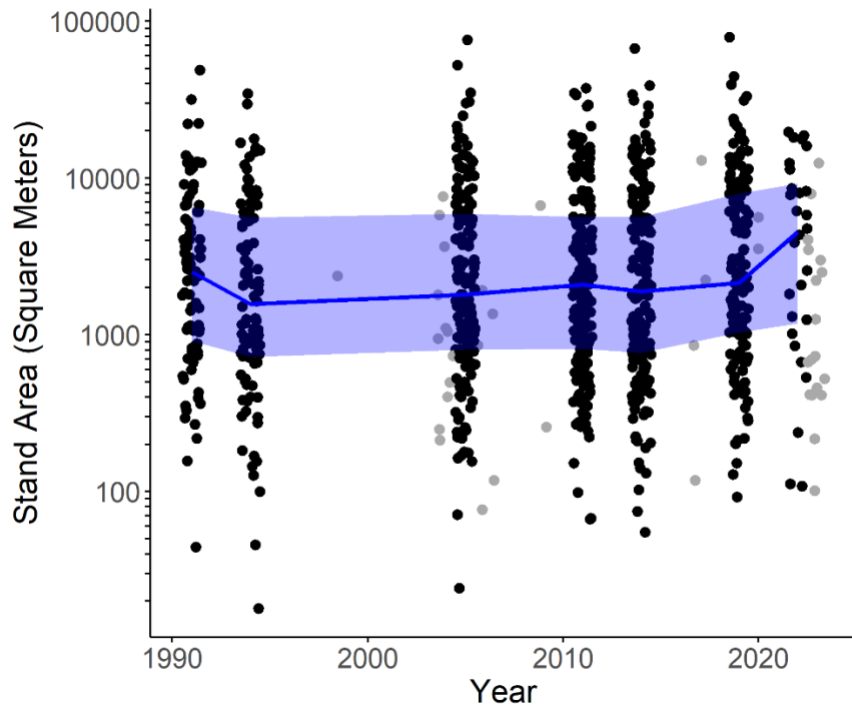
	Variable	Std. Effect ( $\beta$ )	SS	$t$ ( $df$ )	$P$
log-2023 Stand Area	Distance to YNP	0.233 ± 0.074	7.442	3.133 (160)	0.002
	1991 Num. Recruits <sup>1/2</sup>	0.188 ± 0.080	4.204	2.354 (160)	0.020
	2006 Num. Saplings <sup>1/2</sup>	0.215 ± 0.080	5.426	2.675 (160)	0.008
	2006 Num. Browsed <sup>1/2</sup>	0.173 ± 0.080	3.507	2.150 (160)	0.033
	2006 Conifers	-0.360 ± 0.147	4.546	-2.448 (160)	0.015
	2023 Num. Poles <sup>1/2</sup>	-0.205 ± 0.086	4.280	-2.376 (160)	0.019
	2023 Num. Mature <sup>1/2</sup>	0.125 ± 0.073	2.191	1.700 (160)	0.091
	2023 Num. Browsed <sup>1/2</sup>	-0.380 ± 0.072	21.081	-5.272 (160)	< 0.001
Change in Stand Area	2006 Num. Sprouts <sup>1/2</sup>	-0.297 ± 0.092	9.575	-3.232 (164)	0.001
	2006 Num. Saplings <sup>1/2</sup>	0.356 ± 0.089	14.609	3.993 (164)	< 0.001
	2006 Num. Mature <sup>1/2</sup>	0.144 ± 0.077	3.223	1.875 (164)	0.063
	2006 Num. Browsed <sup>1/2</sup>	0.185 ± 0.083	4.522	2.221 (164)	0.028

**Supplemental Material**



**Figure S1.** Satellite imagery outlining the process of collecting the perimeter stand area data.





**Figure S3.** Line plot illustrating the average stand size ( $\text{m}^2$ ) stand per year collected.

**Table S1.** Top 20 models ranked by AICc for each candidate set. Hillslope: degrees of slope; Dist. To YNP: distance to YNP in km; Elevation: site elevation in m; Precip.: spring total precipitation average over prior 10 years; SWE: snow-water-equivalent season average, averaged over prior 10 years; Precip. change: change in spring precipitation (2023–2006); SWE change: change in snow-water-equivalent (2023–2006); Sprout: number of shoots with height < 1 m; Saplings: height 1–2 m; Recruit: height > 2 m and DBH < 5 cm; Pole: height > 2 m and DBH 5–10 cm; Mature: height > 2 m and DBH > 10 cm. Numbers preceding each age category indicate the year of observation. Degrees of freedom, log-likelihood ratio, AICc, and difference in AICc between indicated model and top model are also shown. The top model (lowest AICc) for each response variable (2023 area and change in area) was selected for analysis.

	Intercept	Hillslope	Dist. to YNP	Elevation	24 Precip.	24 SWE	Precip. Change	SWE Change	91 Recruit	06 Sapling	06 Sprout	06 Mature	06 Browse	06 Conifer	24 Sapling	24 Pole	24 Mature	24 Browse	df	logLik	AICc	Delta AICc
2023 Area	0.19		0.23						0.19	0.21			0.17	-0.36					10	-211.8	445.0	0.0
	0.21		0.24						0.19	0.19			0.17	-0.39					9	-213.3	445.8	0.8
	0.18		0.21	-0.08					0.20	0.23			0.16	-0.34			0.11	-0.36	11	-211.2	446.2	1.1
	0.19		0.20	-0.10					0.20	0.21			0.16	-0.36				-0.35	10	-212.4	446.3	1.3
	0.18		0.23						0.17	0.20	0.09	0.16	-0.34					-0.38	10	-212.5	446.3	1.3
	0.16		0.18	-0.11					0.18	0.22	0.11	0.14	-0.29					-0.35	11	-211.3	446.3	1.3
	0.18		0.27		-0.08				0.19	0.22			0.16	-0.33			0.12	-0.37	11	-211.4	446.4	1.4
	0.19		0.23						0.20	0.25	-0.08		0.20	-0.36			0.12	-0.35	11	-211.4	446.5	1.4
	0.18		0.21			-0.07			0.20	0.22			0.16	-0.33			0.11	-0.37	11	-211.4	446.5	1.5
	0.18		0.23						0.18	0.22	0.06	0.16	-0.33				0.10	-0.38	11	-211.5	446.7	1.7

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0.17	0.21			0.19	0.26	-0.13	0.11	0.20	-0.32	-0.13	-0.33	11	-211.5	446.7	1.7		
0.19	0.21		-0.09	0.21	0.20			0.16	-0.36	-0.16	-0.36	10	-212.7	446.7	1.7		
0.15	0.17			0.20	0.22	-0.16	0.12	0.20	-0.27		-0.30	10	-212.7	446.8	1.8		
0.21	0.23			0.21	0.23	-0.10		0.21	-0.39	-0.14	-0.34	10	-212.7	446.9	1.9		
0.19	0.28		-0.09	0.20	0.20			0.16	-0.35	-0.15	-0.36	10	-212.7	446.9	1.9		
0.18	0.15	-0.13		0.13	0.22		0.13		-0.33	-0.13	-0.33	10	-212.8	447.0	1.9		
0.13	0.14	-0.13		0.19	0.17		0.11	0.12	-0.23		-0.33	10	-212.8	447.0	2.0		
0.20	0.23			0.20	0.20			0.17	-0.38	-0.08	-0.14	-0.33	10	-212.8	447.1	2.0	
0.19	0.23			0.19	0.22			0.17	-0.36	-0.04	-0.19	0.11	-0.36	11	-211.7	447.1	2.1
0.16	0.16	-0.12		0.21	0.16			0.15	-0.30		-0.32		9	-214.0	447.1	2.1	
Change in Area	0.00				0.36	-0.30	0.14	0.19					6	-229.9	472.3	0.0	
	0.00				-0.08	0.37	-0.29	0.16	0.15				7	-229.5	473.7	1.4	
	0.00				0.33	-0.26		0.19					5	-231.7	473.7	1.4	
	0.00			0.06	0.36	-0.28	0.14	0.16					7	-229.6	474.0	1.7	
	0.00	-0.04			0.36	-0.28	0.14	0.17					7	-229.8	474.2	1.9	
	0.00				-0.13	0.33	-0.23	0.17					6	-230.9	474.4	2.1	
	0.00	0.02			0.35	-0.30	0.14	0.19					7	-229.9	474.4	2.1	
	0.00			-0.01	0.36	-0.30	0.14	0.18					7	-229.9	474.5	2.2	
	0.00				0.36	-0.30	0.15	0.19	+				7	-229.9	474.5	2.2	
	0.00	0.00			0.36	-0.30	0.14	0.19					7	-229.9	474.5	2.2	
	0.00			0.09	-0.12	0.34	-0.21	0.17					7	-230.2	475.1	2.8	
	0.00				0.28	-0.22	0.15						5	-232.4	475.2	2.9	
	0.00			0.11		0.30	-0.20	0.15					6	-231.4	475.3	3.0	
	0.00			0.06	-0.08	0.37	-0.27	0.16	0.13				8	-229.2	475.3	3.0	
	0.00			0.06		0.33	-0.24		0.17				6	-231.4	475.3	3.0	
	0.04				0.33	-0.26		0.18	+				6	-231.6	475.6	3.3	
	0.00	-0.04			0.33	-0.25		0.18					6	-231.6	475.6	3.3	
	0.00			-0.04	0.34	-0.26		0.18					6	-231.6	475.6	3.3	
	0.00	-0.03			-0.07	0.37	-0.28	0.16	0.15				8	-229.4	475.7	3.4	
	0.00		-0.03		-0.09	0.37	-0.29	0.16	0.14				8	-229.4	475.7	3.4	

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