WASHINGTON NATURAL HERITAGE PROGRAM

2023 status and conservation assessment of golden paintbrush (*Castilleja levisecta*) in Washington

Prepared by
Jesse E. D. Miller and Adam Martin
July 18, 2024

Natural Heritage
Report 2024-10

WASHINGTON STATE DEPARTMENT OF NATURAL RESOURCES

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ON THE COVER: Golden paintbrush blooms at the Glacial Heritage Preserve in Thurston County, Washington. Photograph by Jesse E. D. Miller

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Introduction

Golden paintbrush (*Castilleja levisecta*) is a yellow-flowered perennial herb in the broomrape family (Orobancaceae) that is restricted to remnant prairie sites in the San Juan Islands, Puget Trough, and Willamette Valley in Washington and Oregon, USA, and in British Columbia, Canada. Golden paintbrush has been a species of conservation concern for several decades, following the loss of most of its prairie habitat and subsequent population declines. Golden paintbrush was listed as Threatened under the Endangered Species Act (ESA) in 1997. Subsequently the abundance and number of populations increased significantly due to a reintroduction program coordinated by the US Fish and Wildlife Service (USFWS) and partner organizations in state government and the private sector. However, wild (unaugmented) populations have continued to decline.

Since the mid-1990s, annual monitoring has taken place at most native and introduced golden paintbrush occurrences. Monitoring data are critical for estimating population numbers, trends, and whether recovery objectives are being reached (Fertig 2021). Based on monitoring data and other targets in the 2007 five-year review (USFWS 2007), the US Fish and Wildlife Service (USFWS) removed golden paintbrush from the federal Endangered Species List in 2023. Following delisting, post-delisting monitoring began in 2023 (with subsequent monitoring planned in 2025 and 2027). Post-delisting monitoring is required under the ESA to ensure the species remains secure from the risk of extinction and does not require being restored to the Endangered species list (USFWS 2020).

The specific mechanisms underpinning the decline of wild populations of golden paintbrush remain incompletely understood but appear to be linked to competition from invasive species, loss of native plant associates, and poor seed production (Lawrence and Kaye 2009). Golden paintbrush relies primarily on outcrossing to produce seeds, suggesting that pollination limitation could be one factor in its decline (Lawrence and Kaye 2003). There is some research suggesting that inbreeding depression is not a major factor in the decline of golden paintbrush; even small populations have been found to be genetically robust (Godt et al. 2003). However, numerous small populations of golden paintbrush have been extirpated in recent decades, highlighting the need for further research on how population size relates to viability. Further research is also needed into other potential threats to golden paintbrush such as herbivory.

Here, we present the results of 2023 golden paintbrush monitoring across Washington and the range of golden paintbrush more broadly. To explore how population size relates to population persistence, we analyze how seed capsule production varies with population size (e.g., number of plants). We also analyze the degree to which herbivory appears to be affecting golden paintbrush populations. Finally, we provide detailed descriptions of several study sites and discuss the outcomes of past management efforts.

Methods

2023 monitoring of Washington golden paintbrush populations was performed from May 31 to June 9, when phenology had progressed to the point that seed pod production could be assessed in the field, but while flowering stems were still colorful and readily visible. Monitoring began with more southerly sites and progressed north to sites on the San Juan Islands and on Whidbey Island (Figures A1 and A2). All extant Washington populations were monitored in 2023 by personnel from the Ecostudies Institute, the Washington Natural Heritage Program, the US Fish and Wildlife Service, the Natural Areas Program, and local site stewards and volunteers. Maps of study site locations are included in Appendix A.

Monitoring methods varied among sites depending on population sizes. At sites with populations under 5,000 plants, all individual golden paintbrush plants were counted. At sites with larger populations, subsets of the population were sampled using two-meter-wide band transects. At these sites, transect routes were digitally recorded using the ArcGIS Online Field Maps application on mobile phones so that area surveyed could be calculated. In all cases, only flowering plants were counted, since detecting vegetative plants at broad spatial scales is difficult. A detailed description of sampling methods is given in Appendix B.

While all golden paintbrush sites that are believed to be extant in Washington were visited in 2023, not all sites were visited in most previous survey years. To account for missing values, we interpolated count data to estimate total population sizes following methods used by Fertig (2021). To interpolate missing values, we assumed linear change between measured data points, and the nearest measured value was extended forward or backwards in cases of missing data points at the beginning or end of the time series. From 2015-2022, interpolated population estimates represented only 2% or less of total estimated number of plants in all years except in 2021, when several of the largest populations were not surveyed, and interpolated population estimates represented 83% of the total estimated number of plants.

To better understand factors underpinning declining seed capsule production in golden paintbrush, we collected data on seed capsule production at 10 of the Washington sites during monitoring visits. We assessed seed capsule production on 15-61 arbitrarily selected plants that were dispersed across the population at each site. The number of plants sampled at each site depended on personnel availability.

For each plant selected for seed capsule study, we counted the number of flowering stems, the number of stems that were browsed, and the number of capsules produced by the whole plant. For browsed plants we also assessed if browse was due to ungulates (plant stems ripped, no 45-degree angle cut), rabbits (45-degree angle cuts, plants browsed low on stem), or voles (45-degree angle cuts, browse in close proximity to vole tunnels, cut low to ground).

A power analysis indicated that seed capsule production needs to be sampled on at least 56 plants per site to have 90% confidence and a margin of error no more than 20%. The power analysis was based off of the average standard deviation of estimated capsule production with no browse across all the monitored sites. Sample size was then rounded to the nearest half. The standard deviation for number of capsules across all sites was 24.25, the average 20% confidence interval range across all sites was 5.34, and the 90% confidence Z-score was 1.6. The following equation was used to determine sample size:

$$[(1.65*24.25)/5.34)].$$

Seed capsule production on an individual plant could be counted in ~ 30 seconds or less, so the overall additional burden for monitoring capsules in future years would be about 30 minutes per site. We analyzed variation in capsule production among sites and the effects of browsing on and population size on seed capsule production. All analysis was completed using Bayesian inference in R. We provide R^2 values for each model (Gelman et al. 2018), and associated effect sizes for parameters of interest following the sequential effect existence and significance testing framework elaborated by Makowski et al. (2019).

Results And Discussion

Overview of 2023 population trends

In Washington and rangewide, golden paintbrush numbers remain substantially higher than they were before outplanting efforts began, though populations declined from an estimated s 600,000 plants rangewide in 2022 to about 400,000 plants rangewide in 2023 (Figure 1), and from an estimated 400,000 plants in Washington in 2022 to about 200,000 plants in Washington in 2023 (Figure 2, Table 1, Figure A3). Because seeds were sown at high densities at outplanting sites, the decrease observed from 2022 to 2023 probably represents a reversion towards more stable plant densities, and will likely continue in future years, at least at some sites.

Wild populations of golden paintbrush reached all-time lows in 2023 (Figures 1 and 2), and extinction of remaining wild, unaugmented populations now appears to be all but inevitable. The drop from 2022 to 2023 was precipitous at some sites, such as Rocky Prairie Natural Area Preserve, the only remaining unaugmented wild population in the South Puget Sound region (Figure 3; discussed in detail below).

At individual sites, population trends from 2022 to 2023 varied from positive to negative, suggesting that 2023 population trends were not strongly driven by regional climate trends or other broad-scale conditions. In some previous years, drought is believed to have negatively impacted populations rangewide.

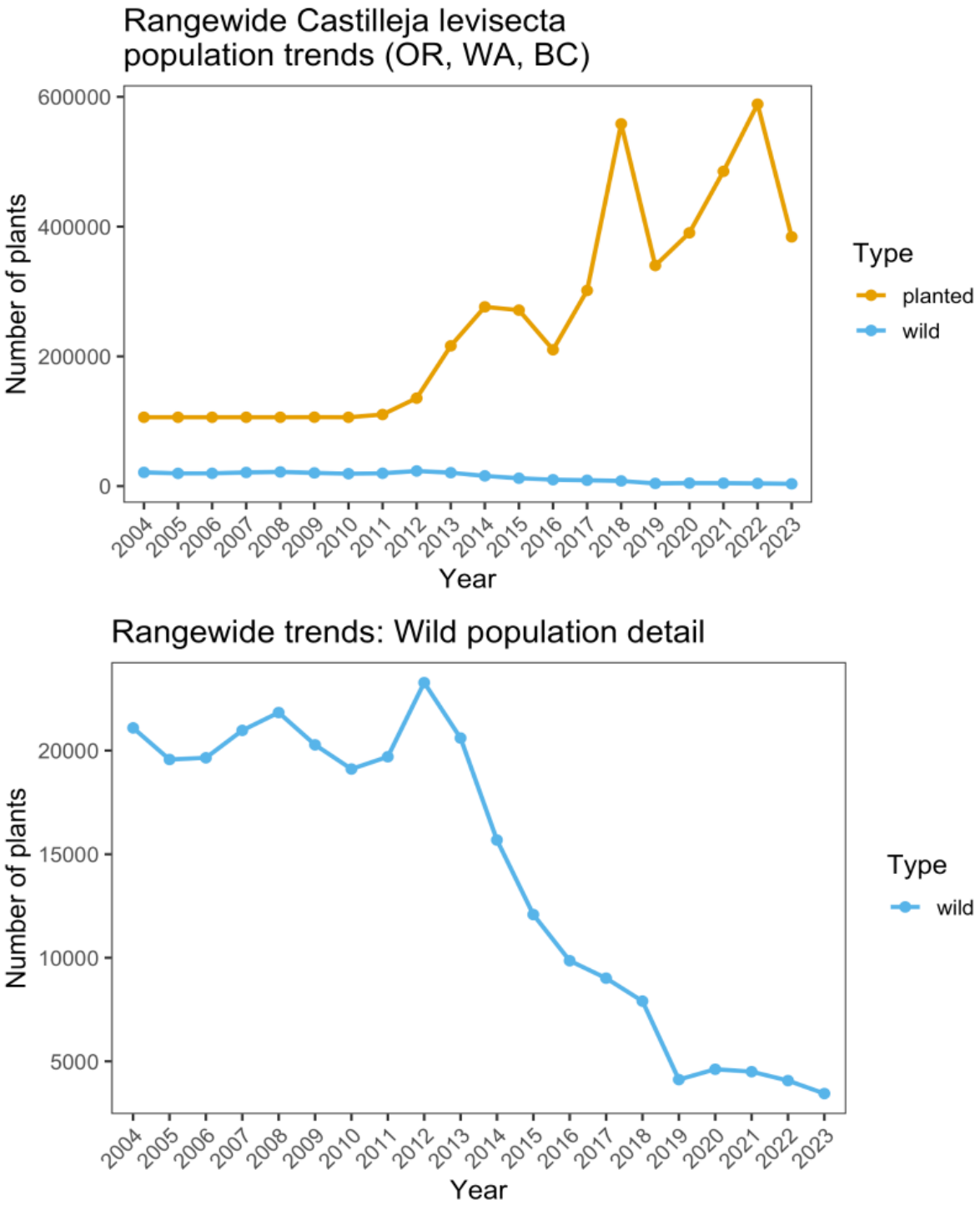

Figure 1. Rangewide golden paintbrush population trends are shown for outplanted and wild plants (top panel) and wild plants only (bottom panel). Because we use interpolated data for years where individual sites were not surveyed, these population estimates are not exact, and actual population sizes could be slightly higher or lower. A description of data interpolation is given in the Methods section. Sites that contain both wild and outplanted plants are considered wild populations here, so strictly speaking, wild population numbers are slightly lower than shown here.

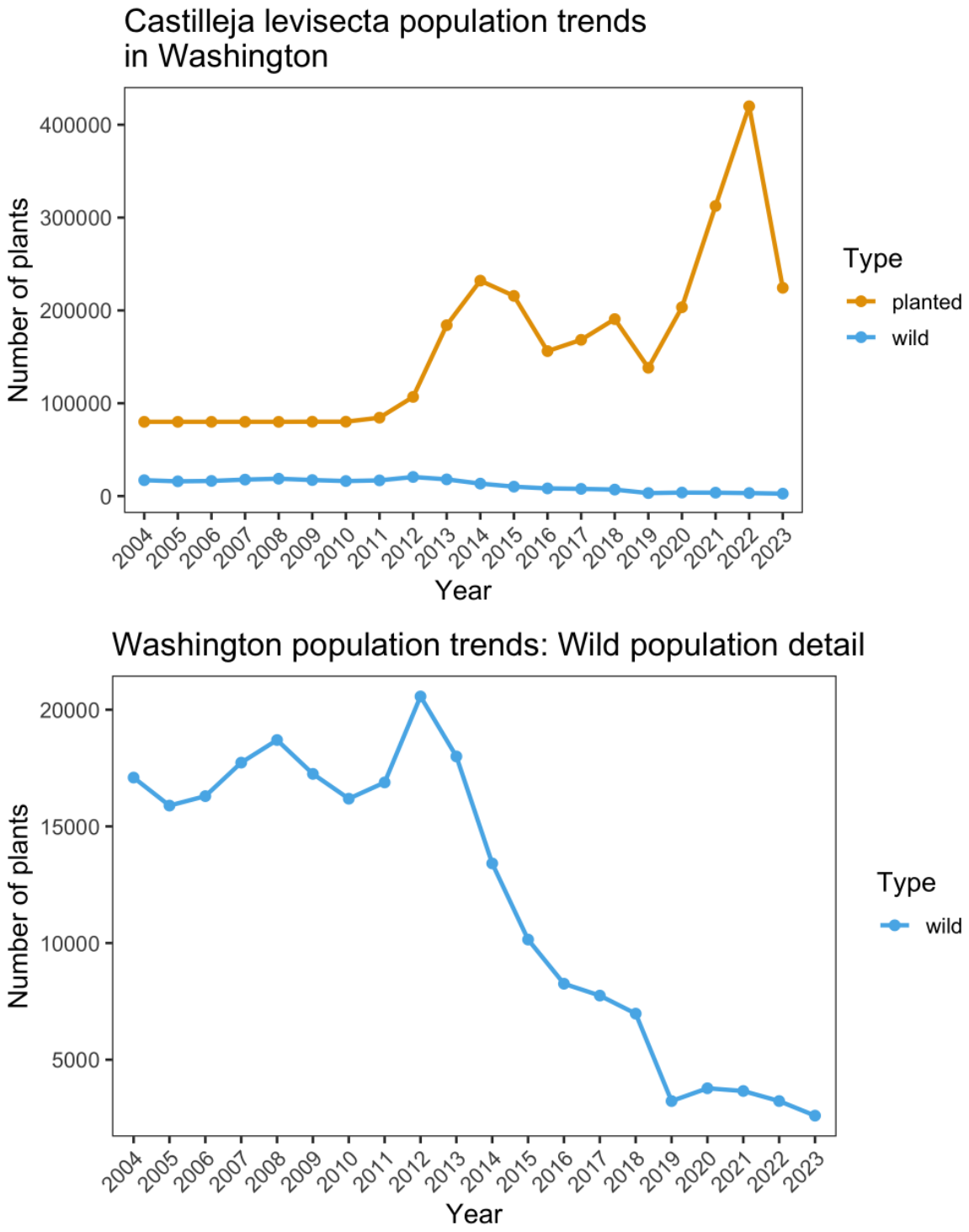

Figure 2. Golden paintbrush population trends in Washington State are shown. Because we use interpolated data for years where individual sites were not surveyed, these population estimates are not exact, and actual population sizes could be slightly higher or lower. A description of data interpolation is given in the Methods section. Sites that contain both wild and outplanted plants are considered wild populations here, so strictly speaking, wild population numbers are slightly lower than shown here.

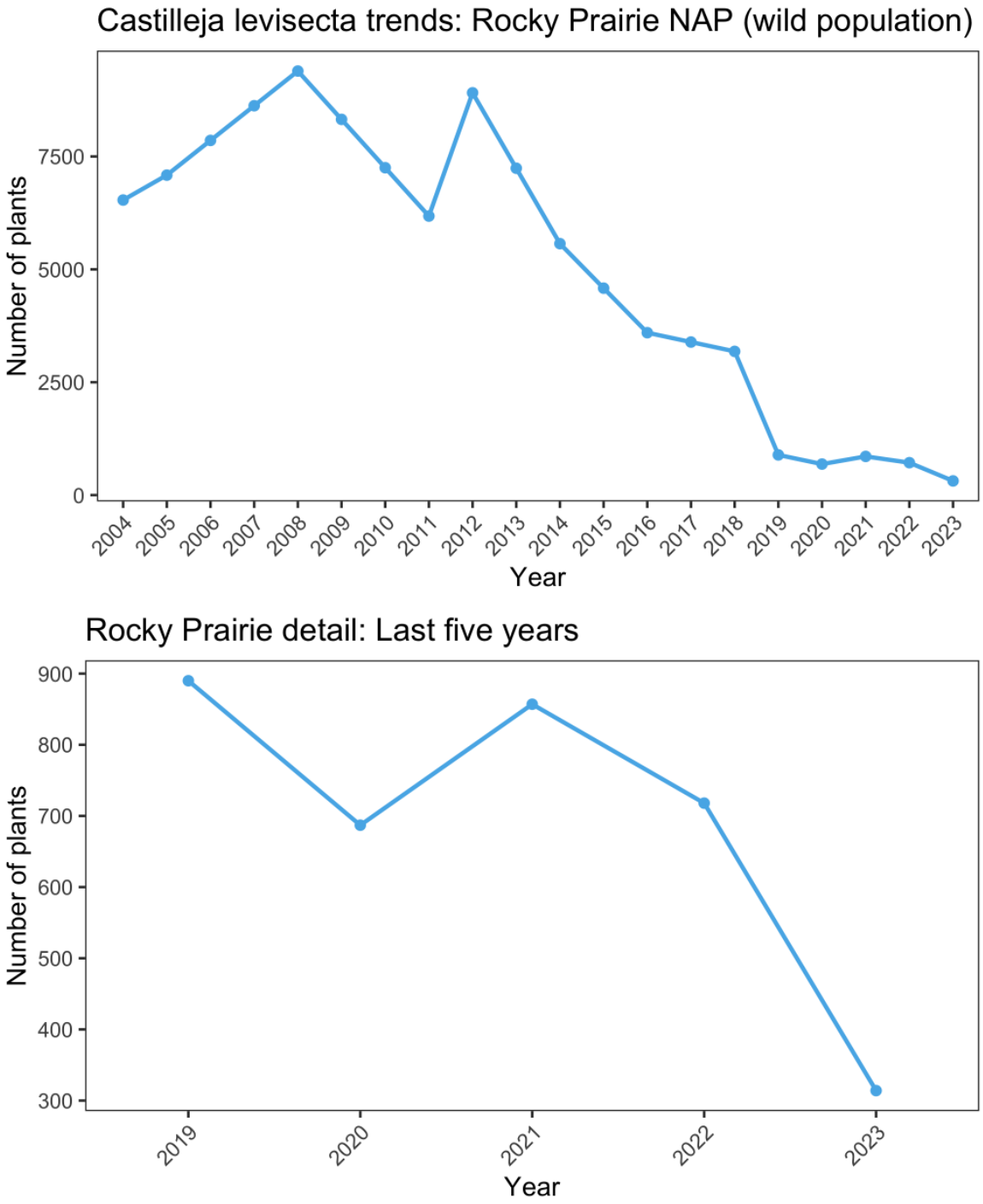

Figure 3. Golden paintbrush population trends at Rocky Prairie Natural Area Preserve, the last wild population in the South Puget Sound region. The upper figure shows trends over the last 20 years; the bottom figure shows trends over the last five years, highlighting the precipitous decline that occurred in 2023.

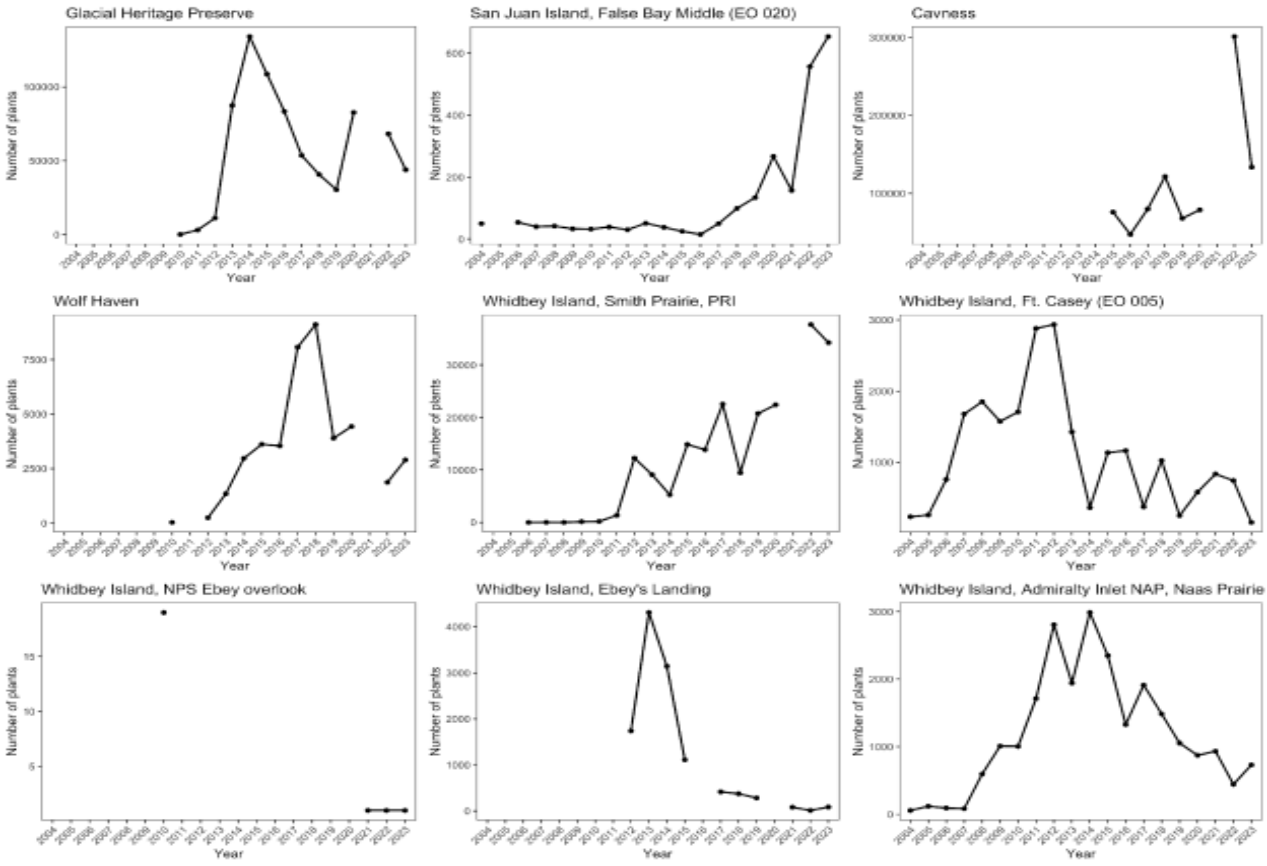

Figure 4. Population trends in selected outplanted golden paintbrush populations in Washington using measured data only (without interpolation). Some of these populations also contain wild plants, which are included in these counts. Confidence intervals for large populations that were estimated using subsampling are shown in figure A3.

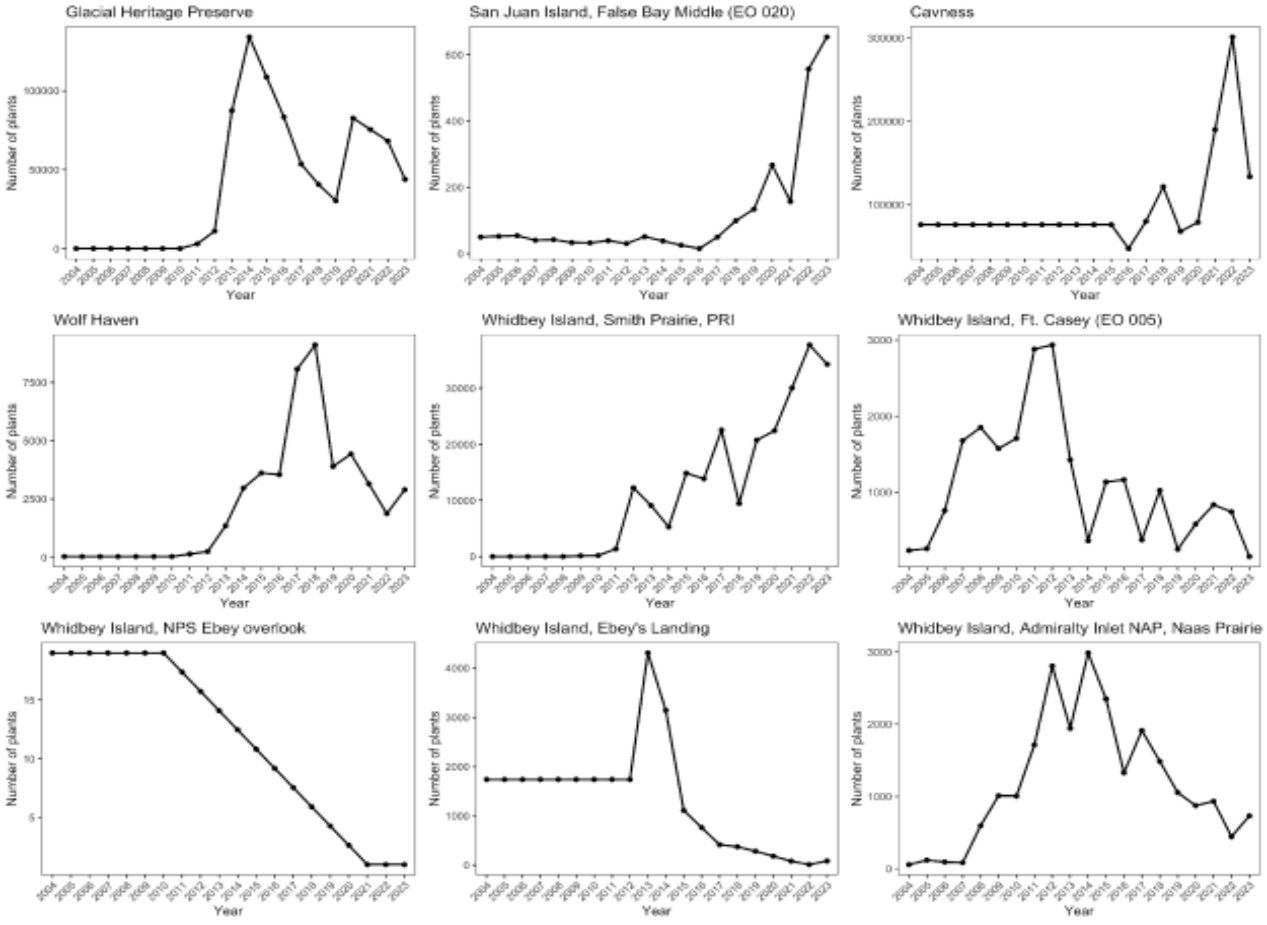

Figure 5. Population trends in selected outplanted golden paintbrush populations in Washington using interpolation for missing data points. Some of these populations also contain wild plants, which are included in these counts. Confidence intervals for large populations that were estimated using subsampling are shown in figure A3.

Table 1. Summary of golden paintbrush population counts, estimates, and interpolated values for sites visited in 2023. Cells with grey backgrounds represent interpolated values; cells with white backgrounds represent counts (for populations with fewer than 5,000 plants) or population estimates based on subsampling (for populations with more than 5,000 plants). The bottom row shows the percentage of the estimated total population count that was based on counts or estimates rather than interpolation.

Site	Wild	Out-planted	Year								
			2015	2016	2017	2018	2019	2020	2021	2022	2023
Cavness		x	75,985	47,334	79,910	121,550	67,978	78,736	190,003	301,269	133,623
Glacial Heritage Preserve		x	108,647	83,355	53,614	40,724	30,396	82,692	193,959	68,231	43,871
Whidbey Island, Smith Prairie, PRI		x	14,854	13,865	22,544	9,458	20,747	22,421	24,848	37,708	34,248
Mima Mounds Natural Area Preserve		x	992	817	801	6,314	9,936	10,233	9,309	6,413	5,325
Wolf Haven		x	3,616	3,546	8,075	9,112	3,898	4,431	1,872	1,872	2,900
Protection Island		x	66	194	71	325	579	833	1,087	1,341	1,595
USFWS Headquarters, Dungeness		x	1,304	1,304	1,304	1,304	2,962	2,485	2,033	1,785	1,537
Whidbey Island, Admiralty Inlet NAP, Naas Prairie Unit (EO 009a)	x	x	2,350	1,329	1,913	1,487	1,055	874	935	445	732
San Juan Island, False Bay Middle (EO 020)	x	x	25	15	50	99	134	267	157	557	654
Rocky Prairie NAP (EO 011)	x			3,597		3,183	890	687	857	718	314
Morgan/ Tenalquot		x	1,974	297	720						289
Whidbey Island, Admiralty Inlet NAP, Bluff (EO 009b)	x	x	94	310	406	415	297	550	429	261	257

Site	Wild	Out-planted	Year								
			2015	2016	2017	2018	2019	2020	2021	2022	2023
Whidbey Island, Ft. Casey (EO 005)	x	x	1,136	1,165	375	1,025	251	582	836	744	156
Whidbey Island, Hill Road - Ebeys Landing (EO 21)	x		883	766	687		32	213	21	80	135
Whidbey Island, Forbes Point (EO 016)	x	x	168	95	111	94	96	128	68	80	92
Whidbey Island, Ebey's Landing		x	1,112	764	416	373	283	182	81	12	85
San Juan Island, San Juan Valley (no EO #)	x		477	664	466	96	217	289	177	164	84
Whidbey Island, NPS Ebey overlook		x	10	9	7	5	3	2	1	1	1
Total counted or estimated plants			214,394	159,365	172,176	197,252	141,191	206,608	41,773	420,497	227,921
Total interpolated plants			1,314	1,789	1,311	330	582	1,017	198,939	3,206	0
Percent of plants counted or estimated			99.4%	98.9%	99.2%	99.8%	99.6%	99.5%	17.4%	99.2%	100%

Seed capsule production

Seed capsule production varied substantially between sites and ranged from two seed capsules per plant at San Juan Valley to 23 capsules per plant at Pacific Rim Institute (Table 2). Herbivory appears to have had strong effects on seed capsule production; at sites where more than 5% of plants have been partially eaten, herbivory may be reducing overall seed capsule production. Within sites, there is some evidence that plants with more flowering stems are more likely to be browsed ($R^2 = 0.62$, 90% confidence interval = [0.56, 0.67]; Figures 6 and 7). This was particularly true at Cavness Ranch, where herbivore pressure is high and plants with 10 or more stems had a probability of > 80% of being eaten.

Seed capsule production increased with an increasing number of plants ($R^2 = 0.23$, 90% confidence interval = [0.17,0.25]), and populations with >1000 stems were the most likely to make enough capsules to potentially replace themselves each year (Figure 8). This is a promising result since it aligns with the initial recommendations of the golden paintbrush technical team regarding population targets. Nonetheless, the influence of flowering plant population size on seed capsule production was not as strong as the influence of herbivory.

Table 2. Summary of golden paintbrush capsule monitoring at 10 sites in Washington. Estimated Capsule production is based off of the average number of capsules per stem at each site. Site Codes: SJV = San Juan Valley, San Juan Island; Pratt = Pratt Preserve, Whidbey Island; PRI = Pacific Rim Institute, Whidbey Island, Naas = Admiralty Inlet Preserve, Whidbey Island; FCSP = Fort Casey State Park, Whidbey Island, Tenalquot = Tenalquot Preserve, Thurston County; Cavness = Cavness Ranch Preserve, Thurston County; GHP = Glacial Heritage Preserve, Thurston County; WHI = Wolf Haven International, Thurston County; Rocky = Rocky Prairie Natural Area Preserve, Thurston County.

			Flowering Stems			Capsule Production			Estimated Capsule Production (no browse)			
Site	Pop Size	*n*	mean(sd)	median (Q1,Q3)	Max	mean(sd)	median (Q1,Q3)	Max	mean(sd)	median (Q1,Q3)	Max	*p.* browse
CVP	133,623	49	9(8)	8(3,12)	43	6(5)	5(3,9)	21	38(40)	27(12,49)	198	0.73
GHP	43,871	52	5(4)	4(2,7)	20	24(22)	15(10,34)	127				
PRI	34,248	23	5(4)	4(2,7)	16	35(33)	23(16,45)	169				
WHI	2,900	26	3(2)	2(2,3)	14	16(13)	14(6,22)	67				
Naas	732	01	4(3)	3(2,4)	10	25(16)	19(14,34)	63				
Rocky	310	55	3(4)	2(1,3)	25	6(10)	3(1,7)	59				0.02
TQ	289	46	3(2)	2(1,4)	13	10(9)	8(4,14)	54				
FCSP	156	12	4(6)	2(1,4)	29	14(14)	10(3,20)	54	39(84)	14(6,24)	367	0.15
Pratt	85	05	5(5)	3(2,7)	30	21(22)	17(6,28)	123	27(35)	17(6,31)	205	0.07
SJV	84	82	3(2)	3(2,4)	7	4(5)	2(1,6)	19	5(5)	3(1,7)		0.09

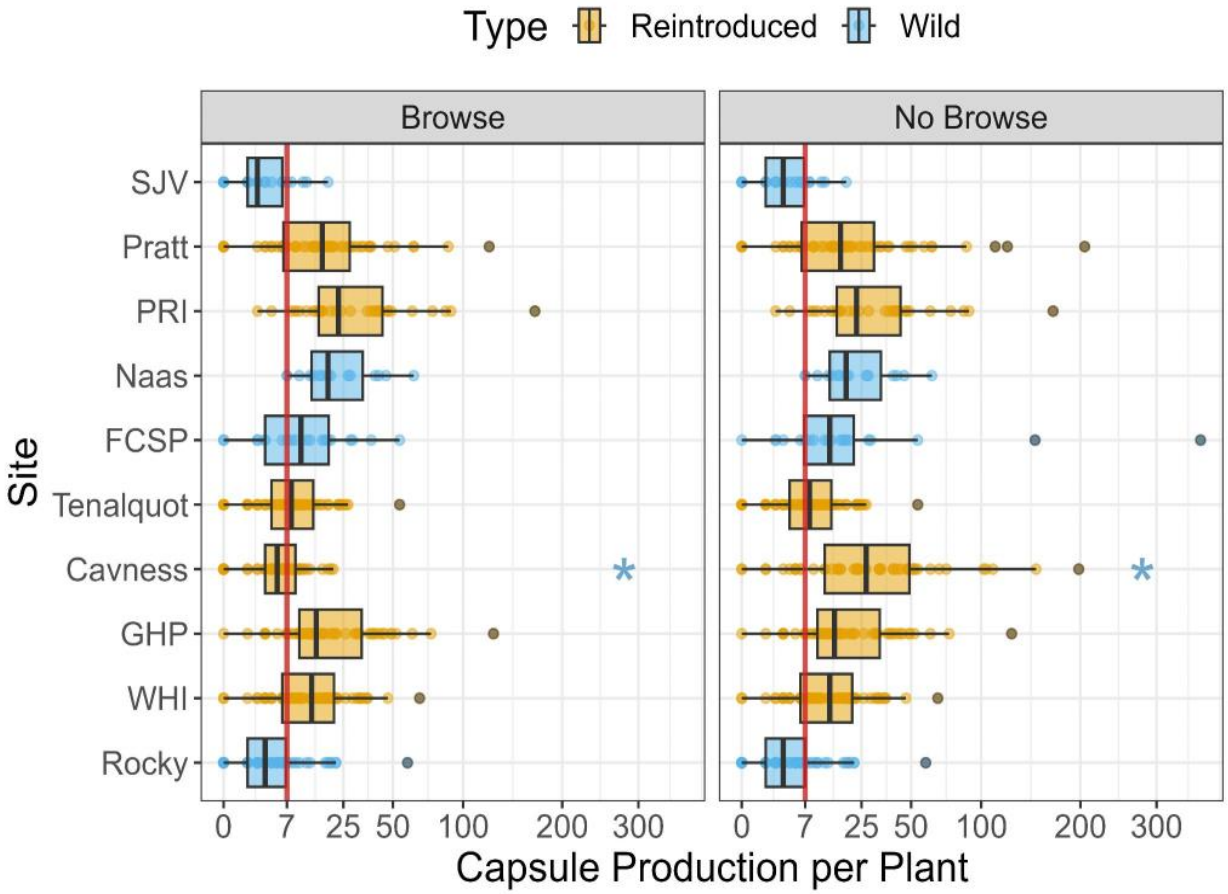

Figure 6. The distribution of capsule production per flowering plant across 10 monitored populations of golden paintbrush in Washington with and without browsing pressure. Capsule production per plant for *No Browse* is based on the average capsules per flowering stem of unbrowsed plants at given site and then extrapolated based on the number of browsed stems for each site. The asterisk (*) denotes an ecologically and statistically significant effect of browse on capsule production. The *X-axis* scale is square root transformed to reduce skewness and ease interpretation. The red line denotes 7 capsules, the average number of capsules needed to produce one new established recruit (unpublished data, R. Martin). *Site Codes*: SJV = San Juan Valley, San Juan Island; Pratt = Pratt Preserve, Whidbey Island; PRI = Pacific Rim Institute, Whidbey Island, Naas = Admiralty Inlet Preserve, Whidbey Island; FCSP = Fort Casey State Park, Whidbey Island, Tenalquot = Tenalquot Preserve, Thurston County; Cavness = Cavness Ranch Preserve, Thurston County; GHP = Glacial Heritage Preserve, Thurston County; WHI = Wolf Haven International, Thurston County; Rocky = Rocky Praire Natural Area Preserve, Thurston County. *Model fit*: (R^2 = 0.23, CI_{90} = [0.13, 0.30]), probability of effect = 1.0, probability of large effect = 1.0).

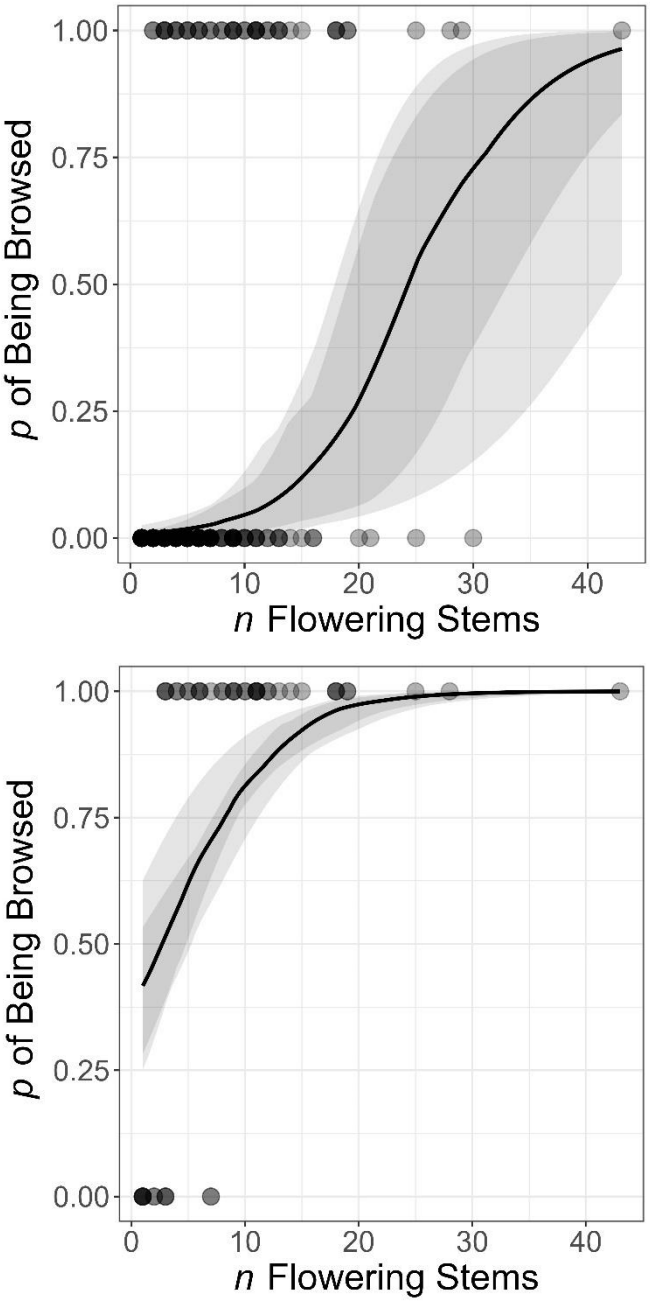

Figure 7. *Top*: The probability of being browsed as a function of the number of flowering stems per plant across all Washington golden paintbrush populations. *Bottom*: The probability of being browsed based upon the number of flowering stems per plant at Cavness Ranch, where there was the greatest herbivory pressure. Dark grey denotes a 1 SD credible interval, and light grey denotes a 90% credible interval. *Model fit for all sites*: (R^2 = 0.62, CI_{90} = [0.56, 0.67]), probability of effect = 1.0, probability of large effect = 0.0)

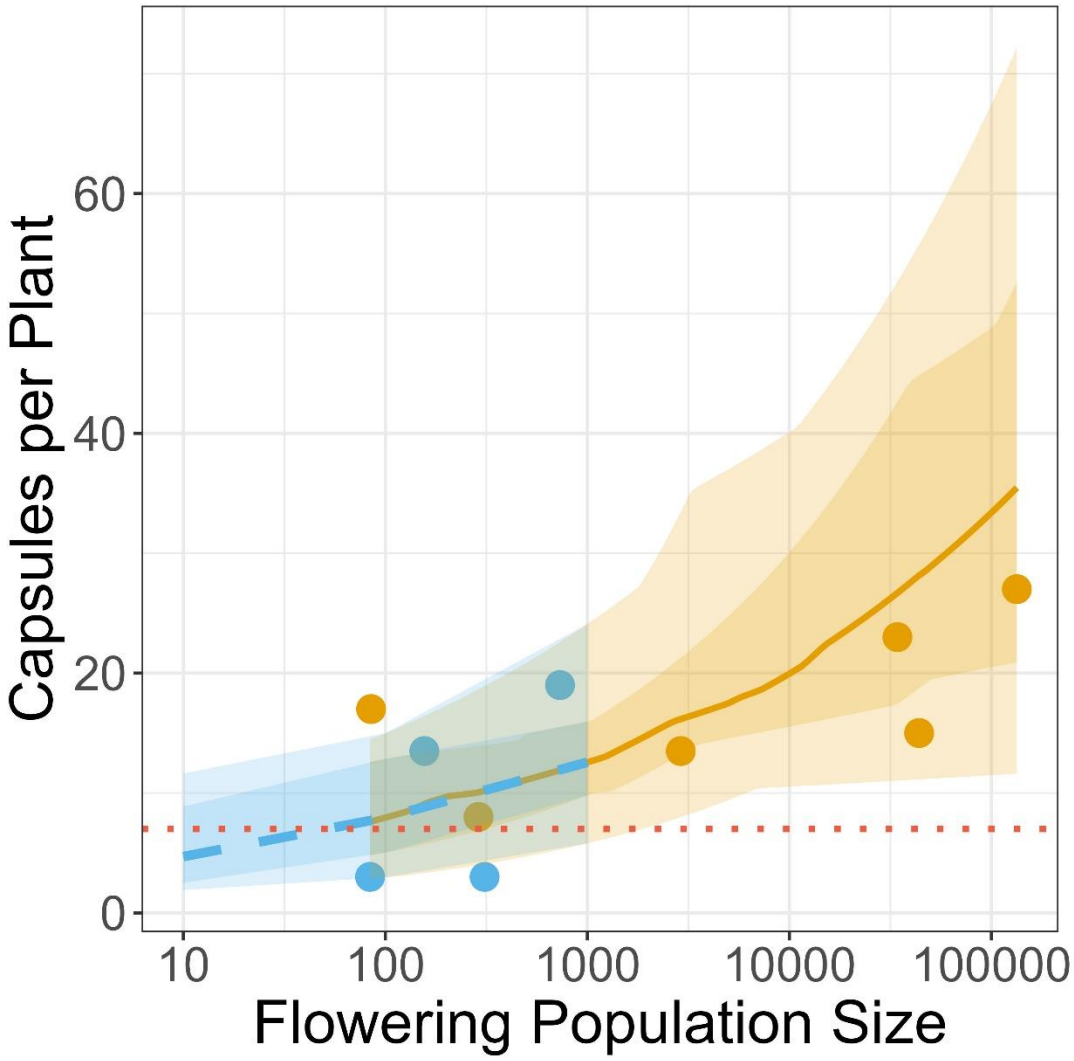

Figure 8. The influence of flowering golden paintbrush population size on the number seed capsules produced per plant. The red dotted line denotes 7 capsules, the average number of capsules needed to produce one new established recruit (unpublished data, R. Martin). Points represent the median number of seed capsules per plant at each site. The *X-axis* is on a $\log^{10}$ scale to ease interpretation. Dark blue or orange denotes a 1 SD credible interval, and light blue or orange denotes a 90% credible interval. The model for including both wild and planted populations had moderate explanatory fit (R^2 0.23, CI_{90} = [0.17,0.25]). *Model fit:* The influence of population size on seed capsules produced per plant had a probability of effect = 0.95, probability of large effect = 0.3; Reintroduced populations had a probability of effect = 0.85, probability of large effect = 0.65; and wild populations had a probability of effect = 1.0, probability of large effect = 0.75).

Washington State Site Summaries

North Salish Sea – San Juan Islands

Orca Dreams - Mar Vista, False Bay Middle (EO 020)

This site is on private land without a conservation easement and is managed by the landowner in conjunction with help from private contractors (Figure 9). The site was first censused in 1995, when 128 plants were found along the steep exposed southern facing bluff growing among snowberry and sparse remnant coastal meadowland. Besides a few failed augmentation attempts between 2007-2009, little management occurred at the site prior to 2014.

In 2014 the site was sold to a different private owner. Since that time the new landowner has provided considerable funds to establish a larger population in a fenced area in conjunction with overall coastal meadow restoration. The small handful of wild golden paintbrush were caged to protect them from deer browse, though the wild population has never rebounded and is likely effectively extirpated.

Beginning in 2014, the augmented golden paintbrush population was established with a mixture of plugging and seed sowing. Management includes regular mowing, intermittent spraying, and in the winter of 2023 the first prescribed burn occurred. A considerable increase in flowering plants in 2023 was likely caused by the prescribed burn. A census by Peter Dunwidde estimated the 2023 population at 654 flowering plants, a substantial increase since 2016, when the effects of restoration were not yet evident and only 15 flowering plants were counted at the site. This population is now the largest in the San Juan Islands and is a demonstration of the power of engaged landowners in protection of rare species.

Figure 9. ***Top Left*****: Wild plants were caged in 2016 in an attempt to reduce herbivory and potentially increase seed set.** ***Top Right*****: The view of the habitat where the remnant wild population was primarily located (Photo from November 2018).** ***Bottom Left*** **The location of the fenced augmented population where thousands of plugs of native coastal meadow species, including golden paintbrush were planted (photo from November 2016).** ***Bottom Center*****: seed of native annuals, golden paintbrush, and perennial forbs sown in 2016.** ***Bottom Right:*** **Fenced augmentation area demonstrating restoration success (Spring 2017).**

San Juan Valley (Paintbrush Prairie)

Figure 10. ***Left Photo:*** **A typical flowering golden paintbrush at San Juan Valley, most plants had a single stem and few made capsules.** ***Center Photo*****: abundant chaff of several potential host species for golden paintbrush, including Oregon sunshine and selfheal.** ***Right Photo*****: Fence construction to exclude the horse and deer from experimentally seeded and plugged golden paintbrush.**

The San Juan Valley / Paintbrush Prairie site is on private land that has been placed under a conservation easement managed by the San Juan Preservation Trust (Figure 10). The golden paintbrush population occurs within a grazed pasture with remnant prairie vegetation. Currently a single horse grazes the pasture, though at one time there were several horses and a llama.

Over several years prior to 2023 there has been a steady decline in the number of flowering plants, despite efforts to cage plants. Seed production at the site has been low, and over the past several years, we noticed a concerning decline in capsule production at the site. The reasons for the population decline are unclear, but are likely related to several interacting factors, a story similar at most other wild populations in the state.

There is some evidence that capsule production in individuals is associated with the overall size of the flowering plant population; populations of less than 1000 plants, and especially populations of less than 100 plants, experience dramatically lower capsule production per plant. We monitored capsule production in 2023; this population had the lowest incidence of capsule production and the lowest average capsules per plant of any site monitored in Washington. The flowering plant population was also the smallest of all monitored populations in the state at 84 flowering plants, down from a high of 7,528 in 2003.

The small population size could decrease the probability of effective pollination and pollinator visitation (Dauber et al., 2010), given that plant density and population size are extremely low. The low population size could also be causing low seed viability. Determining the primary influences and mechanisms impacting capsule production will be key for managing large and small paintbrush populations.

Golden paintbrush plant persistence and establishment is strongly associated with native perennial forb cover and richness (Dunwiddie & Martin 2016). However, the site is currently

dominated by tall pasture grasses, primarily tall fescue (*Schedonorus arundinaceus*), which has made a thick thatch layer across much of the footprint of the remnant population. Thus, forb cover and localized richness are low and likely not suitable for paintbrush persistence since golden paintbrush is believed to depend on native forb associates, which it partially parasitizes. A concerted effort to restore native forbs would likely be needed to restore the *golden paintbrush* population.

Given the status of decline at the site, and the uncertainties surrounding the population decline, the San Juan Preservation Trust and Ecostudies, with the support of USFWS, have begun an adaptive management study to assess how grass-specific herbicide, mowing, and fencing in conjunction with population augmentation using seeds and plugs improve the establishment and persistence of golden paintbrush at the site. In March 2023, Ecostudies performed two large grass-specific herbicide treatments adjacent to the current extant population. In September 2023, we sowed 62 grams (425,816 seeds) of *golden paintbrush* seed sourced from the Ebey's Hill road population and grown by the Pacific Rim Institute, and 25 grams (171,700 seeds) of seed is grown by the Salish Seeds Project from plants from Paintbrush Prairie. Both seed provenances were combined before putting out in the footprints sourced of the herbicide treatments.

We also seeded known paintbrush hosts in conjunction, including Oregon sunshine (*Eriophyllum lanatum*), yarrow (*Achillea millefolium*), and self-heal (*Prunella vulgare*). This seeding density equates to ~370 paintbrush seeds per square meter. In November 2023, we planted 294 golden paintbrush plugs systematically within each herbicide footprint. Monitoring, including assessment of plug survivorship, will occur in Spring 2024, and the most successful restoration treatments will be expanded upon the following year.

North Salish Sea – Whidbey Island

Pratt Preserve

This site is managed and owned by The Nature Conservancy, and the small remaining out-planted population was established between 2010-2012 by Eric Delvin as part of his Ph.D. research at the University of Washington (Figure 11). This research explored the effectiveness of various combinations of herbicide, burning, solarization, and seeding for establishing prairie vegetation including golden paintbrush. The out-planting site is a small fragment of the large historic grassland that comprised what is now Ebey's Landing and the Coupeville area.

Figure 11. Remnant golden paintbrush in a small patch of established native forbs from experimental seeding that occurred in 2010-2012.

The golden paintbrush population peaked at this site in 2014, several years after the first seeded out-planting, to 4,308 individuals. It then steadily declined to the 2023 count of 85 flowering plants. During counts in 2023, we recorded all native species present in the planting area, as well as the most common and dominant weeds. For the 58 flowering golden paintbrush plants that we counted seed capsules on, we also listed all the native species within 10cm of the plant. Assessing these three things lets us rapidly determine which species from the original planting effort are persisting after a decade and, of those species, which species are associated with golden paintbrush persistence.

Of the 19 species originally sown during Delvin's research, there are 10 still present at the site, and seven are associated with golden paintbrush (Table 3). Of the seven associates, Oregon sunshine (*Eriophyllum lanatum*), field chickweed (*Cerastium arvense*), western buttercup (*Ranunculus occidentalis*), and Roemer's fescue (*Festuca Roemer)* were the most frequently co-occurring with flowering paintbrush. The most dominant weeds at the site are the pasture grasses tall fescue (*Schedonorus arundinaceus*), orchard grass (*Dactylis glomerata*), and Kentucky bluegrass (*Poa pratensis*), followed by two weedy annual bromes (*Bromus diandrus* and *B. hordeaceus*), and the weedy annual forb corn salad (*Valerianella locusta*). Much of the vegetation at the site is heavily thatched, and golden paintbrush plants are clumped in the scattered old plots of established native forbs. Many of the native forb islands are being rapidly invaded with pasture grasses.

This site has extremely high potential for supporting golden paintbrush in a larger capacity given some management to control the weeds. Despite many years of minimal management, both native forbs and golden paintbrush continue to persist, and the remaining golden paintbrush plants are producing sufficient capsules despite the small population size. There have been preliminary discussions with TNC about reviving management at the site and potentially expanding into adjacent land on the property.

Table 3. List of sown prairie species from the UW Experiment and whether they are still present in 2023, and the frequency with which they co-occur with flowering golden paintbrush (n=58). "Paintbrush associate" represents the proportion of flowering golden paintbrush plants with which the species occurred within a 10cm radius.

Species Sown	Present	Paintbrush Associate
Achillea millefolium	X	0.28
Allium acuminatum		
Allium cernuum		
Armeria martima		
Camassia quamash	X	
Cerastium arvense	X	0.53
Delphinium nuttallii		
Erigeron speciosus		
Eriophyllum lanatum	X	0.71
Lomatium nudicale	X	0.14
Lomatium utriculatum	X	0.09
Lupinus albicaulis	X	
Lupinus bicolor		
Lupinus littoralis		
Plectritis congesta		
Ranunculus occidentalis	X	0.5
Solidago simplex	X	
Danthonia californica		
Festuca roemeri	X	0.43

Ebey's Hill Rd.

This is a small wild population of golden paintbrush in a small patch of remnant coastal meadow found on an eroding bluff off Ebey's Hill Road on Whidbey Island near Coupeville (Figure 12). It is owned and managed by The Nature Conservancy. The site was first censused in 1993 and was the largest population on Whidbey Island at the time. Seed collected from this site was used to establish the multi-source seed mix used to establish plants across the region and is the source locality for seed used at the Pratt Preserve and at Pacific Rim Institute. The population was largest in 2000, when 7,627 plants were censused, but began declining after a wildfire caused by fireworks in the early 2000s and fell to a low of 214 plants before again rising back into the thousands (4,612 plants in 2013). However, after 2013, there was a rapid decline when the population more than halved to 687 flowering plants in 2017 and then collapsed to a low of 21 plants in 2021. The causes of this decline are unknown, but extended droughts in conjunction with abundant annual grasses at the site likely played a significant role.

Given the precipitous decline, Ecostudies worked with TNC to augment the population with golden paintbrush seed and host plants from seed grown at Pacific Rim Institute. In November 2021, we seeded 14 grams of golden paintbrush seed (~97,500 seeds), along with several host plant species – common yarrow (*Achillea millefolium*, 8 grams) and Oregon sunshine (*Eriophyllum lanatum*, 8 grams), and this was repeated in 2022 and fall 2023.

Figure 12. *Top Photo*: Flowering golden paintbrush and remnant native coastal meadow plants being rapidly invaded by annual bromes. *Bottom Photo*: landscape view from the beach looking up at the extant habitat of the golden paintbrush population on Ebey's Hill Road.

Despite the small area occupied by golden paintbrush and its location on an eroding bluff, there is still room for the population to expand northwards along the bluff, where remnant coastal meadow communities continue. This strategy could mitigate some of the risks of erosion. Given the modest increase in the number of flowering plants, the current minimal management strategy seems to be increasing the population. Despite being located on an eroding bluff, population augmenting should continue, given the paucity of extant wild sites in the North Sound and their tenuous population numbers. Also, because the Pacific Rim Institute golden paintbrush was sourced from this population, it is an opportunity to rapidly increase the seed bank size without bringing in genetics from a faraway locality.

Pacific Rim Institute

Figure 13. *Left Photo*: Dense population of flowering golden paintbrush in remnant coastal prairie at Pacific Rim Institute. *Right Photo:* Extensive population of sickle-keel lupine established as part of prairie restoration.

The Pacific Rim Institute (PRI) is a nonprofit conservation organization located just south of the town of Coupeville (Figure 13). It supports one of the larger remaining patches of coastal prairie left on Whidbey Island. Golden paintbrush recovery began in 2006 when the site was first outplanted with golden paintbrush plugs with seed sourced from the Ebey's Hill Road population. Recovery efforts again increased in intensity after the 2009-2012 period when PRI was a site of Eric Delvin's PhD research. Several acres of the site were sown with golden paintbrush seed sourced again from the Ebey's Hill Road population. PRI is one of the most successful reintroduction sites in Washington, and rapidly crossed the 1,000 flowering stem threshold in 2011, and has steadily increased since then. Since 2019, the population has remained stable, and there are more than 20,000 flowering plants. Several new areas on the site were sown this past fall, and the long-term trajectory for this site remains extremely promising.

The primary threats to the site are extensive herbivory from deer and rabbits, and the encroachment and expansion of invasive grasses, primarily annual fescues (*Vulpia spp.*) and sweet vernal grass (*A. odoratum*). To mitigate the browsing pressure, PRI invested in fencing an area comprising most of the remnant intact coastal prairie, and a section of restored prairie within the footprint of the University of Washington experimental plots. To mitigate grass cover, PRI has invested in several prescribed fires across the site, and regular herbicide treatments. The newest emerging threat to the site is a rapid expansion of sickle-keel lupine, which was successfully established as part of the UW experimental plots. However, the population has rapidly expanded, and there is some evidence it is negatively impacting flowering plant numbers. Where sickle lupine is dense, there was 60% fewer flowering paintbrush on average (n = 3,069) than where lupine was sparse or not present (n = 8,038).

Admiralty Inlet

Figure 14. *Left Photo*: Primarily extant population of golden paintbrush in the upland meadow habitat of Admiralty Inlet Preserve. *Right Photo:* Habitat view of the Admiralty Bluff golden paintbrush population (the Pratt Preserve bluff can be seen in the far distance).

Admiralty Inlet (also known as Naas) is a wild population on Whidbey Island, just south of the Ebey's Hill Rd. wild population, and just north of the Fort Casey State Park population (Figure 11). The population was discovered in 1984 with a population size of around 1,200 flowering plants. The first annual monitoring occurred in 1993, and at that time, the flowering population had collapsed to 273 flowering plants (a 77% decline in a decade), probably because of tree and shrub encroachment into the open meadow habitat.

The population increased into the thousands again, with a population high of 2,987 plants in 2014, after restoration efforts controlled shrubs, trees, and invasive grasses, and population augmentation using nursery-grown plugs began again by Whidbey Camano Land Trust, which currently monitors the site. Since then, the site has been regularly burned every few years, and weed management and native species augmentation have occurred. However, since the population peaked in 2014, the golden paintbrush population has steadily declined and has remained below 1,000 flowering stems since 2020; the reasons for the decline are unclear.

In addition to the primary population in the upland meadow habitat, a second wild population of golden paintbrush occurs along the bluffs just west of the meadow. This second population has been monitored since 2010, when it was first discovered and contained 80 flowering plants. The population was augmented in 2015 and rose to 550 flowering plants in 2020 but has declined by nearly half (47%) to 257 plants in 2023. The precise reasons for population decline are unknown.

Fort Casey

Figure 15. Top Left Photo: patchy distribution of remaining golden paintbrush within fenced area at Fort Casey State Park, Whidbey Island. Red pin flags denote flowering plants. Note association with forbs, and extensive invasion of annual bromes. Top Right Photo: Difference in grass cover due to march herbicide treatment. Lower Left Photo: Restoration plot prior to march grass herbicide treatment. Lower Right Photo: Restoration plot after march grass herbicide treatment.

Just south of the Admiralty Inlet population is the Fort Casey State Park golden paintbrush population, a remnant wild population (Figure 15). This population is found in a small remnant coastal meadow just west of the old concrete military structures on the state park along the edge of the coastal bluff. The population was first censused at 400 flowering plants in 1980. The population stayed at less than 1,000 flowering plants until 2006, when focused shrub management was initiated.

After shrub management began, the population grew and stabilized above 1,000 flowering plants except for two years of significant rabbit browse (2014 and 2017). These significant browse years were the impetus for installing a fenced area around the primary population, and the population again rebounded above 1,000 flowering plants in 2018. However, the population again crashed in 2019, and has continued to decline and stay below 1,000 plants to a population low of 156 plants in 2023. Despite the construction of the fence, the high winds at the site take a toll on it, and parts of the fence are regularly damaged and down, and the regular detection of recent herbivory and herbivore sign within the fenced area (scats of deer, rabbit, and voles and their sign on vegetation) suggest that it is not consistently inhibiting herbivores. Seed capsule monitoring in 2023 detected 15% of plants within the fenced area had been browsed at some capacity, primarily by rabbits.

The population crash over the last several years is likely due to several factors in addition to herbivory, including change in site vegetation. In 2020, Peter Dunwiddie and Adam Martin re-monitored 23 vegetation plots within the core population center of golden paintbrush at Fort Casey that had been monitored in 2008. Since 2008, there has been a dramatic increase in the frequency of two invasive annual grasses, annual bromes *Bromus hordeaceus* and *B. sterilis*) and annual fescues (*Vulpia myuros* and *V. bromoidies*). While annual brome cover has slightly declined from an average of 11% to 6% cover at sites where it is present, its frequency has increased from 78% to 100%. More dramatically, annual fescue frequency has more than doubled from 30% to74%, and the average cover where it is present has increased from an average of 4% cover in 2008 to 10% cover in 2020.

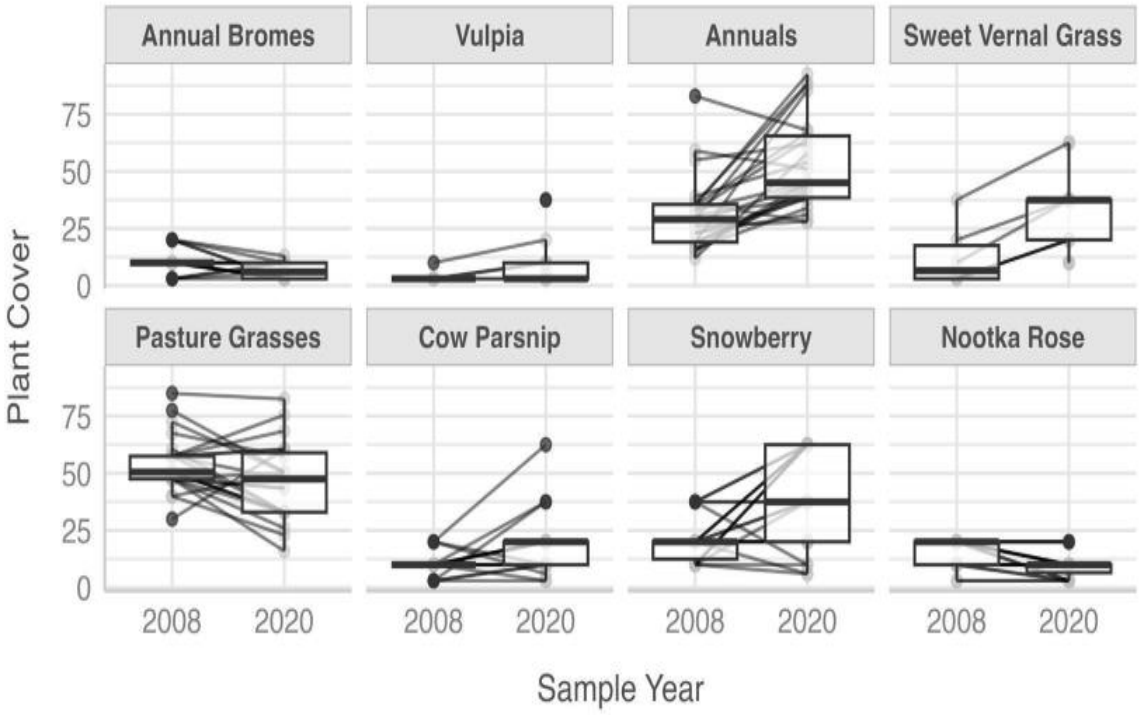

Figure 16. Changes in key vegetation components in 23-100m^2 vegetation plots that comprise the core population of golden paintbrush at Fort Casey; results from 2008 and 2020 sampling are shown.

Annual plant cover has nearly doubled from an average of 31% cover in 2008 to 54% cover in 2020. While overall pasture grass cover has not significantly changed (average of 51% in 2008, 48% in 2020), the cover of the allelopathic sweet vernal grass (*Anthoxanthum odoratum*) has dramatically increased in frequency and cover. Since 2008, the frequency of sweet vernal grass more than tripled from 26% to 100%, and when it is present, its cover has increased from 3.3% to 32% (Figure 16). These increases in annual plants are concerning because annuals are generally associated with poor paintbrush habitat, and golden paintbrush is dependent on perennial host plants (Dunwiddie and Martin 2016).

At Fort Casey, indicator species analysis suggested that within the fenced and mowed area, snowberry is generally positively associated with paintbrush presence (Indicator value = 47.8, $p = 0.002$), Nootka rose and Canada goldenrod are neutrally associated (N. rose: Indicator Value = 46.4, $p = 0.41$, C. golden rod: Indicator Value =43.5, $p = 0.21$). Compared to woody shrubs, even when small in stature, the large palmate leaves of cow parsnip likely create too much shading, and cow parsnip continues to be negatively associated within the mowed area of golden paintbrush (Indicator Value = 50.3, $p = 0.03$; Martin, *unpublished data*). It's hypothesized that short-statured woody shrub cover, especially when dominated by rose, may inhibit browse and may also protect against drought due to shading and potential hydraulic lift (Callaway & Pugnaire, 2007). In grasslands, shrub cover from species like snowberry can inhibit the presence of grass cover (Köchy & Wilson, 2000), and this may make mowed shrub-covered areas more resistant to grass invasion, increasing their suitability for paintbrush. This latter point is worth further examination because if there is strong evidence for it, it would suggest a consistent causal mechanism for facilitation that negates the need to control shrubs with herbicide.

Starting in 2019, the Ecostudies Institute began a small restoration effort within the fenced population, controlling grasses and shrubs using herbicide and adding in forbs and native grasses with seed and plugs; golden paintbrush was also planted (Figure 13, lower panels). This effort was expanded in 2022 after continued decline of golden paintbrush plants had been observed; the population had remained below 1000 flowering plants for several years, while invasive grasses had increased (Figure 13, upper panels). Ecostudies worked with State Parks to increase the population by controlling both sweet vernal grass and annual grasses using a March clethodim treatment in spring 2023 over a little less than half of the fenced area and augmenting the population with golden paintbrush seed from Pacific Rim Institute. This represents the first effort at augmenting the population at the site. Expanded grass treatments across the entire fenced area were planned for spring 2024, and additional golden paintbrush may be seeded in fall 2024.

South Salish Sea

Wolf Haven International

This out-planted golden paintbrush population is on a small, mounded prairie remnant in Thurston County only a few km from the sole extant golden paintbrush site at Rocky Prairie Natural Area Preserve (NAP). Both Wolf Haven and Rocky Prairie NAP are fragments of a single larger prairie (Rocky Prairie; Figure 17). Wolf Haven is primarily a wolf sanctuary, and the entire property is well fenced; thus, there is no herbivory pressure from ungulates. Golden paintbrush was first established at Wolf Haven in 2007, where yearly plug out-plantings occurred until 2013, when direct-seeding became the primary augmentation method. Wolf Haven is actively managed cooperatively with the Center for Natural Lands Management, and combinations of prescribed fires, native plant seeding enhancements, manual control of shrubs, and herbicide treatments occur yearly at the site.

Intensive seeding and out-planting efforts tapered dramatically by 2016, when the population had reached 3,546 flowering plants; the population then peaked at 9,112 flowering plants in 2018. However, the population subsequently declined to 3,898 plants in 2019, and has oscillated between 1,800-4,400 plants yearly since then. In 2023 the flowering plant population was 2,900 plants, a 54% increase from 2022 (1,872 plants).

The Wolf Haven population has been one of the most stable populations in the South Sound, and it appears that regular management is likely a major factor in this pattern. However, besides spring and summer drought, which are likely impacting all paintbrush populations to some degree, the main threat at the site is the rapid invasion of invasive annual grasses (Figure 17). Golden paintbrush has contracted spatially to the most productive Mima mounds that generally have the highest density of native perennials. Much of the interstitial areas, and some of the drier Mima mounds, have been invaded by annual fescues (*Vulpia* spp.) and to a lesser degree the annual bromes (primarily *Bromus hordaecous*).

Figure 17. A Mima Mound at Wolf Haven International that once had abundant golden paintbrush several years ago is now dominated by annual fescue.

Cavness Ranch

Cavness Ranch is managed by the Center for Natural Lands Management and is a historical Christmas tree farm that is being converted to upland prairie habitat. The outplanted golden paintbrush population was first established in 2014 with broadcast seeding on 37.6 acres. By 2015, Cavness had the largest golden paintbrush population in Washington (85,403 plants). Since that time the population has remained > 40,000 flowering plants, with several years above 100,000 plants (2018, 2022, 2023). While there were other out-planting efforts with seed at that site since 2014, none established until a 2021 broadcast seeding on another 9.1 acres at Cavness.

The primary threat to the Cavness golden paintbrush population is herbivory from elk and rabbits. In 2023, 78% of plants that we studied for seed capsule production had been browsed. This is an increase in browsing pressure from 2018, when it was estimated 64% of plants had browsed. Fencing would be the most straightforward solution, and even fencing part of the population would be useful. A lesser threat at the site is the lack of native perennial forbs. There is a large population of paintbrush, despite the low richness and cover of native perennial forbs, likely due to the legacy of productive soils from the tree farm.

Figure 18. Dense population of golden paintbrush at Cavness Ranch.

Glacial Heritage Preserve

The Glacial Heritage Preserve is owned by Thurston County and managed by The Center for Natural Lands Management (Figure 19). It was first outplanted with plugs in 2005. The population first crossed the 1,000 flowering plant threshold in 2011 and has stayed above 30,000 flowering plants since 2013. The population is spread across the site in many small subpopulations across ~200 acres of the main remnant upland prairie. Like Cavness Ranch and Wolf Haven, Glacial Heritage is actively managed with combinations of prescribed fires, seeding enhancements, and manual control of shrubs. Herbicide treatments also occur yearly at the site. The primary threats at the site are invasive grasses – both annual fescues and annual bromes, as well as sweet vernal grass – and hybridization of golden paintbrush with harsh paintbrush (*Castilleja hispida*) to a lesser degree. The Center for Natural Lands Management actively removes all suspected hybrids, and there are fewer presumed hybrid plants than there were in the mid 2010s.

Figure 19. Sparse golden paintbrush in an area rapidly being invaded by annual grasses (tan vegetation).

Rocky Prairie Natural Area Preserve

Rocky Prairie Natural Area Preserve is the only extant wild population of golden paintbrush in the South Sound (Figure 20). It is a small, triangle-shaped prairie fragment isolated between a road and railway and is managed and monitored by the Washington Department of Natural Resources. The site has had several small, prescribed burns, and invasive weeds and grasses are regularly managed at the site. The population was first censused in 1983 and 15,634 flowering plants were found. The population has declined continuously since then, with a notable decrease from 3,183 plants in 2018 to 890 in 2019. Since then, it has declined yearly and is now down to 314 flowering plants as of 2023.

The causes of the population decline at Rocky Prairie remain incompletely understood, but several factors are likely in play. First, low seed set on golden paintbrush plants has been anecdotally reported in recent years, and in 2023, focused capsule monitoring confirmed this observation. Next, vegetation has steadily changed over recent decades. A comparison of a site assessment performed in 2020 by Peter Dunwiddie and Adam Martin to a site assessment from 1983 reveals several interesting patterns. First, of the 36 perennials with high fidelity to native prairies found at the site in 1983, 12 taxa were not detected in 2020 (33%). Another 19 taxa (53%) declined in cover by 2020, including Oregon sunshine (*Eriophyllum lanatum*), one of the most important host species for golden paintbrush (Martin and Dunwiddie, unpublished data). Concurrently, sweet vernal grass has greatly increased in cover, from being only occasionally present in 1983 to being abundant in 2020 (Figure 17). Further, several other invasive annual grasses are present along road edges and other ruderal areas in low abundances, though they have yet to invade into the remnant prairie fully.

Figure 20. Golden paintbrush at Rocky Prairie surrounded by sweet vernal grass.

Conclusions

There are significantly more golden paintbrush plants in Washington State today than there were in the late 1990s following the outplanting of new populations throughout western Washington. Plants were seeded much more densely than they occur in nature at these sites, so it is not surprising that the number of golden paintbrush plants decreased in 2023 at outplanted sites; it will likely continue to decrease until it reaches equilibrium with site conditions. However, the long-term sustainability of outplanted populations remains unknown since it is unclear whether outplanted populations are successfully reproducing.

In contrast to the relative success of outplanted populations, wild populations have been declining since 2011, and reached critically low numbers in 2023. The complete loss of all wild (unaugmented) populations of golden paintbrush throughout the range of the species now seems likely, and golden paintbrush may already be functionally extinct in the wild. In particular, the southernmost (Rocky Prairie NAP) and northernmost (San Juan Valley) wild populations are at risk of imminent extirpation. The DNR Natural Areas Program is now considering augmenting the Rocky prairie population with seed from other populations.

The primary threats to golden paintbrush are believed to be invasive species, loss of native plant associates, herbivory, poor seed set, and drought worsened by climate change. Across all sites, exotic grasses are increasing in cover, and native perennial forbs, which are critical to the hemiparasitic lifecycle of golden paintbrush, appear to be declining in cover and richness. Management at Pacific Rim Institute, Fort Casey and in the South Sound has demonstrated that March treatments can effectively control sweet vernal grass and annual bromes, and winter treatments can effectively control annual grasses. In this study, we documented the importance of several specific native plant species as associates of golden paintbrush (Table 3), highlighting that native plant community restoration, and not just weed control alone, may be necessary to maintain golden paintbrush populations.

We found that larger populations of golden paintbrush set seed capsules at higher rates per plant; seed capsule set was an order of magnitude higher at the largest populations than at smallest populations. A minimum population size of at least a few hundred plants appears to be necessary to maintain a stable (e.g., self-replacing) population. This suggests that large populations established through outplantings may be likely to set sufficient seed. However, the underlying causes of the relationship between population size and seed set relationship remain incompletely understood. Pollination limitation may be one factor at play; because golden paintbrush is a near-obligate outcrosser (Lawrence and Kaye 2003), even large populations will not be able produce sufficient seeds if sufficient pollinators do not persist on the landscape. Anecdotal observations suggest that there may be insufficient pollinators for golden paintbrush in the contemporary, fragmented prairie landscape, and further study of golden paintbrush pollination is needed.

While herbivory is not strongly affecting golden paintbrush populations at most sites, it is an issue at Cavness and Fort Casey, which contribute substantially to augmented and wild plant populations, respectively. Herbivory is more prevalent on plants that have more flowering stems, and since these plants produce disproportionate numbers of capsules, this may have negative implications for the long-term trajectory of golden paintbrush populations. Successful fencing efforts at places like Mar Vista on San Juan Island, Pacific Rim Institute on Whidbey Island, or Wolf Haven in Thurston County (which was fenced prior to augmentation) demonstrate that fences can effectively decrease herbivore pressure.

Overall, golden paintbrush is doing better at sites with active and continual management compared to sites with little or no management, suggesting that with coordinated efforts, some of the declines seen in wild populations could be reversed. Nonetheless, some challenges, such as the increasing prevalence of drought, may be difficult to mitigate; supplementary watering may be one useful approach (Dunwiddie et al. 2013).

Just three sites--Cavness Ranch, the Glacial Heritage Preserve, and the Pacific Rim Institute--collectively contain 94% of all golden paintbrush plants in the state. The population at Cavness Ranch alone comprises 59% of all plants in the state. Because the great majority of golden paintbrush plants in Washington occur in just three populations spread across just two counties, a substantial proportion of Washington's golden paintbrush population could be lost in a single chance disturbance event. Golden paintbrush remains one of the rarest plants in Washington, and it remains a high priority for monitoring, research, and conservation.

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Walter Fertig, former WNHP botanist, initiated this project and provided useful guidance. We would like to thank Whidbey Camano Land Trust, San Juan Preservation Trust, Pacific Rim Institute, Center for Natural Lands Management, Washington Department of Natural Resources, The Nature Conservancy, Wolf Haven International, and private land owners for site access, help with monitoring golden paintbrush, and the continued management and focused care they have taken with managing this species. We would also like to thank US Fish and Wildlife Service for dedicated funding to recover the species and the many volunteers who have helped establish and count golden paintbrushes throughout the years. We are particularly grateful to Peter Dunwiddie, whose legacy of dedication, collaboration, comradery, stewardship, and scientific inquiry was key to the restoration success golden paintbrush has experienced to date.

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Appendix A: Field survey locations for golden paintbrush in Washington

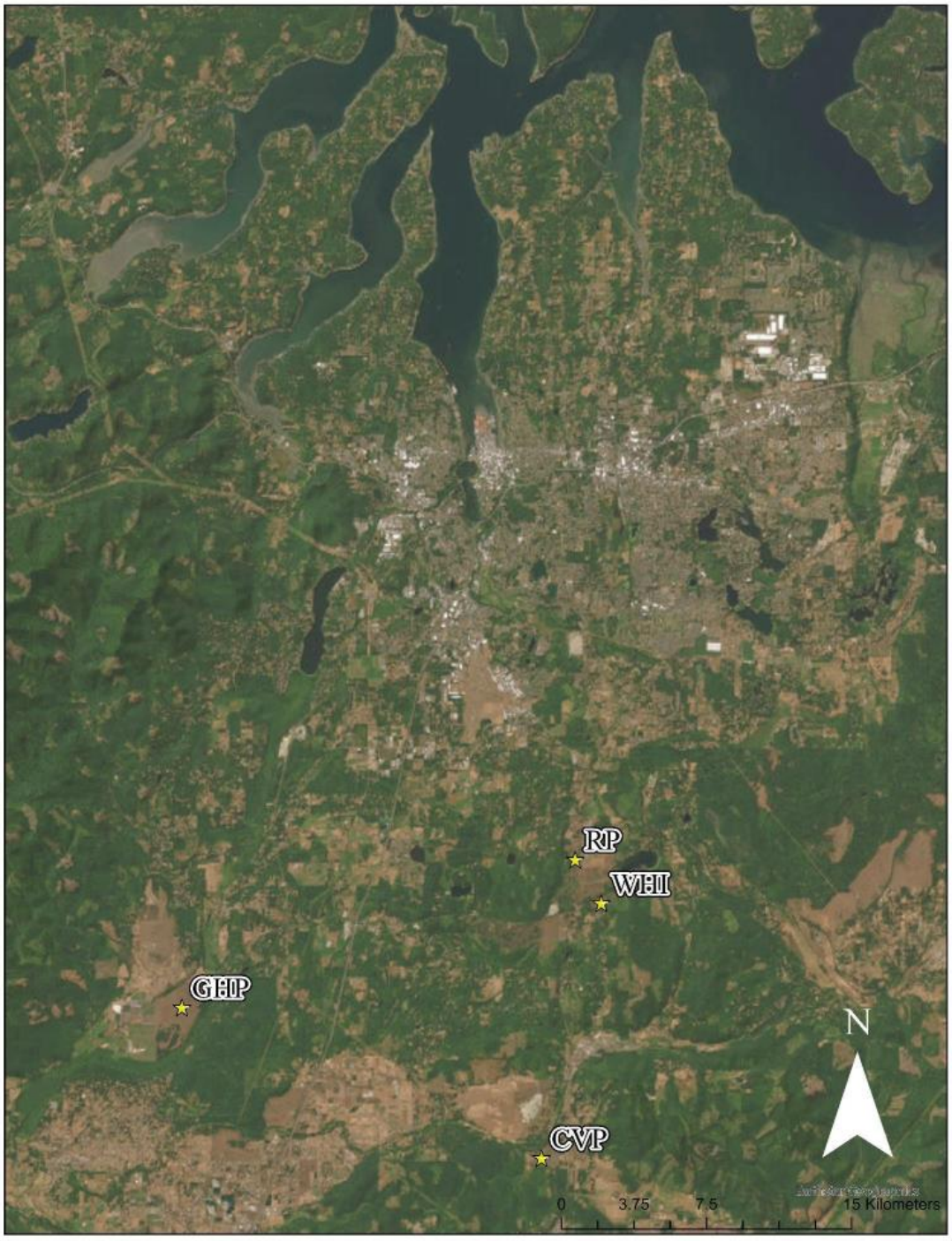

Figure A1. South Salish Sea golden paintbrush Site locations. GHP = Glacial Heritage Preserve; RP = Rocky Prairie NAP; WHI = Wolf Haven International; CVP = Cavness Ranch Preserve.

Figure A2. North Salish Sea golden paintbrush Site locations. FCSP= Fort Casey State Park; AI = Admiralty Inlet; EB = Ebey's Hill Road Bluff; Pratt = Pratt Preserve; PRI = Pacific Rim Institute.

Appendix B: Field survey protocol for monitoring flowering golden paintbrush populations

This is a broad decision framework that has generally been used for determining which strategy was the most effective and efficient for monitoring golden paintbrush in the Washington sites.

1. Is population <1000 plants?
    a. Yes; use pin flags to mark flowering individuals in effort to census entire flowering population at a site. If needed, break site into subunits using landmarks within a site, or using meter tapes to partition sites into more manageable areas to look for plants and mark. Once all flowering plants are marked. Recollect flags, and when a flag is removed, record number of flowering stems.**[1]
    b. No; go to 2.
2. Is population >1000 plants
    a. Is population in distinct areas on a site with known planting history?
        i. Yes; is sub population <1000 plants?
            1. Yes; follow protocol in 1a. for each subpopulation <1000 plants
        ii. No; is the sub-population ~>5000 plants
            1. Yes; for each sub-population consider using belt transects to estimate flowering plant number if population is too dense to discern using meter tapes to partition into more manageable counting transects. Use at least 3, but preferably ≥ 5 belt transects to estimate flowering plants. Belt transects are typically 2m wide, and a 2m PVC tube is used to facilitate counting. To make a population estimate from belt transect, divide the flowering plant count by area of belt transect (2m * length of transect) to get an estimated number of flowering plants per meter, multiply this value by the total area of the planting area to get an estimate of total population.
            2. No; follow protocol in 1a. to get census of individuals, using meter tapes or landmarks to break population up into manageable counting chunks.

[1] If time allows, also recording the number of capsules per plant is extremely valuable to estimate seed production and population trajectory for a subset of individuals (25 – 50 plants). If using pin flags, randomly select flowering plants to count capsules on. This can be done by either counting capsules on individual flowering stems per plant and then summing up, or counting across flowering stems (while noting the number of flowering stems). Knowing both the number of flowering stems and number of capsules is separately useful, since it allows one to assess the potential capsule production of a plant given the effort it put into flowering.

[2.] Counting the number of placed flags is a useful double-check for the number of flowering individuals found at a site. Recording the number of flowering stems per plant has not been done every year at every site, but is more frequently done in the smaller populations. Using the pin flags is an effective way of looking for and marking plants when populations are really sparse, or when the risk of double-counting is higher.

Appendix C: Population estimates for large golden paintbrush populations

Figure A3. Population estimates for three large, outplanted golden paintbrush populations (Cavness, Glacial Heritage, and the Pacific Rim Institute [PRI]) that were estimated based on sampling, with error regions representing 90% confidence intervals.