

Article

Whitebark Pine Prevalence and Ecological Function in Treeline Communities of the Greater Yellowstone Ecosystem, U.S.A.: Potential Disruption by White Pine Blister Rust

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Abstract: In the northern Rocky Mountains of the U.S. and Canada, whitebark pine (*Pinus albicaulis* Engelm.) is a functionally important species in treeline communities. The introduced fungal pathogen *Cronartium ribicola*, which causes white pine blister rust, has led to extensive whitebark pine mortality nearly rangewide. We examined four treeline communities within the Greater Yellowstone Ecosystem (GYE) to assess structure and composition, whitebark pine prevalence and functional role, differences in growing season mesoclimate among study areas, and blister rust infection incidence. We found that (1) whitebark pine frequently serves as the majority overall, solitary, and leeward tree island conifer; (2) the prevalence of different tree species in the windward position in tree islands, and thus their potential as tree island initiators, may be predicted from their relative abundance as solitary trees; and (3) white pine blister rust infection incidence ranged from 0.6% to 18.0% across study areas. White pine blister rust poses a threat to treeline development and structure and the provision of ecosystem services in the GYE. Increasing blister rust resistance in nearby subalpine whitebark pine communities through seedling planting or direct seeding projects should eventually result in higher levels of blister rust resistance in whitebark pine in treeline communities.

Keywords: *Pinus albicaulis* Engelm.; alpine-treeline ecotone; treeline; tree islands; Greater Yellowstone Ecosystem; *Cronartium ribicola*; white pine blister rust; climate; ecosystem services; community structure; ecological function

1. Introduction

Conifer communities in temperate zone alpine-treeline ecotones—the transition between open subalpine forest and alpine tundra, hereafter, “treeline” [1]—provide important ecosystem services such as snow retention, soil stabilization [2,3], and wildlife habitat (e.g., [4]). Across the Rocky Mountains in locations not limited by geomorphology or topography, treeline community distribution and composition reflect the relationship between the physiological limits of constituent conifer species [5,6] and the harsh environmental conditions that characterize these ecotones, including extreme winds [7], cold and variable temperatures [8], moisture deficiency [9], and high solar radiation [10]. Community structure and composition at treeline have been assessed in many locations, and differences exist within and across regions, mainly in response to topographic and climatic variation, but also in response to subalpine species distribution, seed sources, site suitability, and snow deposition (e.g., [11–14]).

Treeline conifer community development often relies on ecological facilitation both during the initial establishment of solitary individuals and subsequent establishment of other trees leeward of solitary individuals [15]. Facilitation, defined as a positive interaction between an individual of the same or different plant species or between a protective (“nurse”) object and a plant (e.g., [16]), often shapes plant community spatial structure in stressful environments [17–19]. At treeline, solitary trees frequently establish leeward of protective objects, such as rocks or plants, or in micro-topographic depressions (small hollows), which facilitate seed and seedling survival (Figure 1) [20–22]. Once established, these trees ameliorate wind [23,24], reduce exposure to solar radiation [25], decrease soil temperature variation [26], and improve water availability [27] in leeward microsites. Tree islands form when the initiator facilitates the establishment of conifers in its lee [7].



Figure 1. Facilitation at treeline. Whitebark pine (*Pinus albicaulis*) established in the lee of a rock on Tibbs Butte, Shoshone National Forest, Wyoming. Photo credit: Elizabeth R. Pansing.

The structure and composition of treeline communities in some geographic regions of western North America are not well known. In the greater Yellowstone Ecosystem (GYE), the predominant subalpine conifers include whitebark pine (*Pinus albicaulis* Engelm.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) [28], which suggests that these species might also predominate in treeline communities. Previous studies from the Beartooth Plateau in the northeastern GYE indicate that whitebark pine, Engelmann spruce, and subalpine fir form treeline communities east of the Continental Divide, but vary in relative abundance [14,15,29]. In the Line Creek Plateau Research Natural Area (RNA), Custer Gallatin and Shoshone National Forests, whitebark pine was the most frequent windward conifer in tree islands, providing protection through facilitation interactions for species established in its lee [3,12]. Information about the structure and composition of treeline communities in most other regions of the GYE is lacking.

Whitebark pine functions as an important subalpine and treeline conifer and tree island initiator in the Rocky Mountains of the U.S.A. and Canada [14,30]. Moderately shade-intolerant and slow-growing, whitebark pine is out-competed by faster-growing conifers at productive sites [31]. However, a

comparatively high water-use efficiency and carbon gain relative to other treeline conifers, hardy seedlings, and efficient seed dispersal allow it to tolerate arid, windy conditions and poor soils [3,5,26]. Whitebark pine relies on Clark's nutcracker (*Nucifraga columbiana* Wilson) for seed dispersal. In late summer and fall, nutcrackers bury caches of ripe pine seeds for future retrieval throughout the montane landscape, as far as ~30 km from parent trees, often in recently burned and high elevation terrain, including treeline and tundra [32–35]. Unretrieved seeds may germinate following snowmelt or rain, leading to regeneration. Moreover, nutcrackers often cache seeds near nurse objects [36]; placement in micro-topographic depressions or leeward of rocks or other nurse objects or vegetation improves survival at treeline [15,20,24].

Throughout much of whitebark pine's range, the disease white pine blister rust—resulting from infection by the exotic fungal pathogen, *Cronartium ribicola* J.C. Fisher—has caused extensive mortality [37–39]. Blister rust can kill whitebark pine at all life stages and reduce cone production by damaging tree canopies [37]. Due to significant declines in many regions from white pine blister rust and other threats, whitebark pine is a candidate for listing under the U.S. Endangered Species Act [40] and listed in Canada under the Species at Risk Act [41]. Because the establishment of whitebark pine at treeline depends on seed dispersal from subalpine communities, and the ecological function of whitebark pine at treeline depends on the occurrence of healthy trees, white pine blister rust may limit the development of treeline communities in some areas. In the GYE, subalpine whitebark pine blister rust incidences ranged from 20% to 30% [42]. A recent, detailed survey at Line Creek Plateau RNA estimated blister rust infection incidence to be 19.2% [43].

Previous assessments of whitebark pine's ecological role in treeline community development have been conducted from approximately 42° N to 54° N in the Rocky Mountains [14], including preliminary data from the GYE. Tomback et al. [14] indicated that the relative occurrence of whitebark pine as a solitary tree at treeline predicted its prevalence as a tree island initiator, and studies further suggested that whitebark pine's occurrence and functional role are possibly both topographically and climatically related [12,14]. They established whitebark pine as an important species in treeline communities in the Central and Northern Rocky Mountains of the U.S.A. and Canada, and they documented the presence of blister rust in many regions [12,14]. However, there is little information on treeline communities in the GYE, which represents the southernmost distribution of whitebark pine in the Rocky Mountains.

Here, we examined four treeline communities both east and west of the Continental Divide within the GYE. Our objectives were as follows: (1) describe community structure and composition, (2) assess the ecological role of whitebark pine (solitary, leeward, initiator), (3) explore the relationship between solitary conifer abundance and tree island initiation, (4) examine nurse object associations with solitary tree and tree island initiator establishment, (5) determine how differences in mesoclimate among the study areas might account for variation in community structure and composition, and (6) evaluate the incidence of white pine blister rust and the potential benefit of restoration.

2. Materials and Methods

2.1. Study Areas

We performed community composition and climatic assessments for four treeline communities in the GYE (Figure 2, Table 1). Our criteria for study area selection were geographic diversity across the GYE and logistical feasibility. The areas selected span the latitudinal range of the ecosystem and encompass both sides of the Continental Divide. The Paintbrush Divide study area, Grand Teton National Park, is at the upper end of Paintbrush Canyon and characterized by rockfall debris and talus deposits. Hurricane Pass, also in Grand Teton National Park, is proximal to the terminal moraine of the Schoolroom Glacier and is similarly comprised of rocky terrain from talus deposits and rock falls. Our study area at Tibbs Butte, Shoshone National Forest, which is a prominent topographic feature situated approximately 3.7 km southeast of the Beartooth Pass summit, comprises vegetated terrain with few exposed rocks. At Christina Mountain, Shoshone National Forest, one of the southernmost

peaks in the Wind River Range, the terrain consists primarily of a rock field with scattered patches supporting little-developed soils.

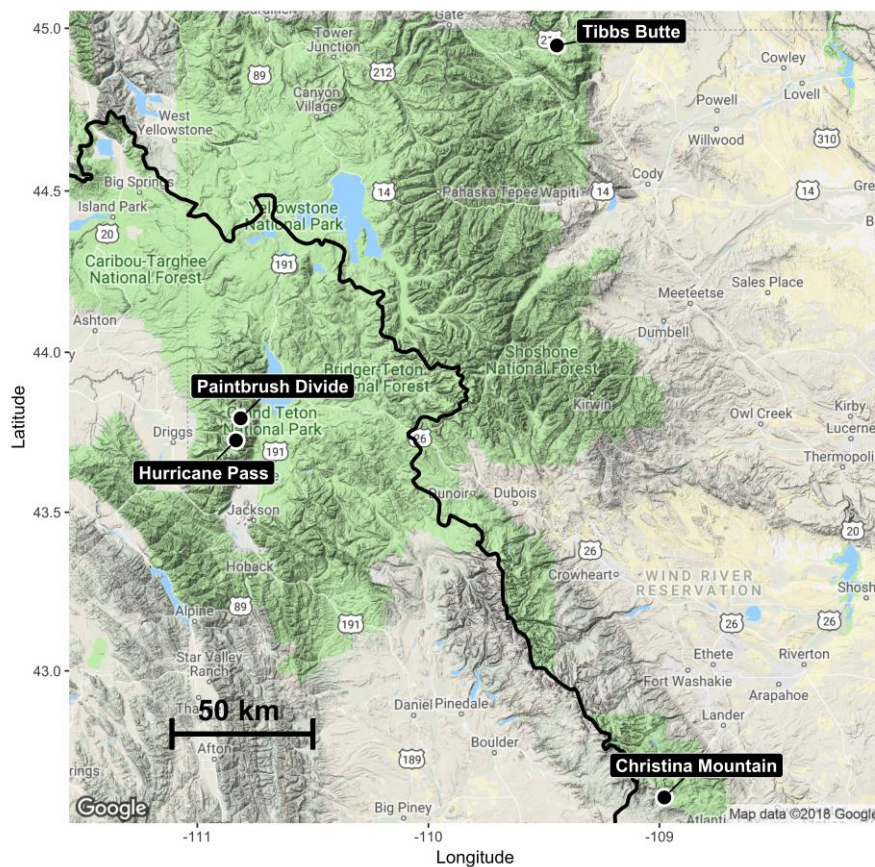


Figure 2. Study area geographic locations. The geographic location of study areas within the GYE. The black line traces the Continental Divide. Map courtesy of Google [44]. Figure created using the ggmap (version 2.6.1, Waco, TX, USA.) [45], ggplot2 (version 3.0.0, Houston, TX, USA.) [46], and ggrepel (version 0.8.0, Cambridge, MA, USA.) [47] packages in R (version 3.5.1, Vienna, Austria) [48].

Table 1. Study area characteristics.

Study Area	Area (ha)	Elevation (m)	Aspects	Parent Material	Vegetation
Paintbrush Divide	121	3055–3289	NE NW SW	Early Proterozoic granite ^a Quaternary sedimentary deposits ^a	<i>Arctostaphylos uva-ursi</i> (L.) Spreng <i>Myosotis asiatica</i> (Vestergr.) Schischk. & Serg. <i>Silene acaulis</i> (L.) Jacq.
Hurricane Pass	92	3045–3078	NE SE SW	Middle Cambrian limestone ^a Early Proterozoic granite ^a Quaternary sedimentary deposits ^a	<i>Dryas octopetala</i> L. <i>Silene acaulis</i> Graminoids
Tibbs Butte	4	2983–3238	NE	Precambrian granite ^b	<i>Geum rossii</i> (R.Br.) Ser. <i>Potentilla diversifolia</i> Lehm. <i>Saxifraga</i> spp.
Christina Mountain	117	3200–3400	NE SE SW	Precambrian granite ^c Granodiorite ^c Porphyritic quartz monzonite ^c Magmatic gneiss ^c	<i>Geum rossii</i> <i>Pteryxia hendersonii</i> (J.M. Coult & Rose) Mathias & Constance <i>Phlox pulvinata</i> (Wherry) Cronquist <i>Silene acaulis</i>

^a: ref. [49]; ^b: ref. [50]; ^c: ref. [51].

2.2. Community Assessments

In July 2014 and 2015, we established 225 m² assessment plots at each study area as follows: Paintbrush Divide ($n = 20$, circular: $r = 8.46$ m), Hurricane Pass ($n = 20$, circular: $r = 8.46$ m), Tibbs Butte ($n = 12$, square: 15 m × 15 m), and Christina Mountain ($n = 30$, square: 15 m × 15 m). In previous

work, this plot area has been found to encompass enough of the community to determine structure and composition (e.g., [43]), while ensuring that all conifers within the plot experience relatively uniform environmental conditions. We generated random points for plot placement using ArcGIS (version 10.2.2, Redlands, CA, USA; Paintbrush Divide and Hurricane Pass) [52] or the *splancs* package (version 2.01-40, Bergen, Norway) in R (version 3.1.0, Vienna, Austria; Tibbs Butte and Christina Mountain) [48,53]. If a random position was located outside of the treeline (i.e., in subalpine forest or alpine tundra), we moved the position to the nearest area of krummholz growth.

For each plot, we classified conifers by tree island membership (i.e., solitary tree or tree island component), ecological role (i.e., tree island initiator, leeward tree island conifer, or solitary tree), and species. We defined a 'tree island' as two or more contiguous conifers with spatially overlapping foliage. The windward conifer of each tree island was designated as the initiator if integrated within the tree island (i.e., not a separate, younger tree), and all other trees within the same tree island were categorized as leeward. To determine the prevailing wind direction, we examined the flagged branches of conifers within the plot or in the immediate vicinity. Trees spatially isolated from other conifers (i.e., having canopies that did not overlap with any other conifers) were classified as solitary. In some cases, distinct whitebark pine stems arise from a single nutcracker seed cache, creating a multi-genet stem cluster at a single site [15,19,54]. Additionally, some Engelmann spruce and subalpine fir have multiple stems of the same genotype due to clonal reproduction [7,55]. Following the methods of Resler and Tomback [15], we characterized multi-stem growth forms as a single individual.

We also categorized tree island initiators and solitary conifers based on windward nurse object type (i.e., rocks, micro-topographic depressions, and woody plants). We defined 'nurse objects' as potentially protective objects or micro-topography directly windward of solitary trees or tree island initiators. We designated conifers with the apparent absence of a nurse object (or no protective micro-topography) as 'unprotected'. Finally, we evaluated each whitebark pine for blister rust infection by thoroughly examining stems and canopies. The criteria for classifying a stem as infected were at least one active canker, or three of five symptoms from the following list: (1) inactive canker, (2) stem swelling, (3) branch flagging (i.e., dead foliage), (4) rodent gnawing, and (5) oozing sap (e.g., [56]).

2.3. Mesoclimate Assessments

To assess mesoclimate, we obtained 30 years (1985–2015) of mean daily temperature and precipitation data using open-source Precipitation Elevation Regressions on Independent Slopes Model (PRISM) information (PRISM Climate Group, 2015). For each study area and year, we only retained the growing season data, which we defined as the temporal period between mean daily air temperatures of $>5\text{ }^{\circ}\text{C}$ for >5 consecutive days and mean daily air temperatures of $<5\text{ }^{\circ}\text{C}$ for >5 consecutive days [57]. Although literature definitions of growing season length differ, a global study by Körner and Paulsen [8] determined the lower limit for plant tissue growth at treeline to be $5\text{ }^{\circ}\text{C}$. This temperature is also the threshold at which tissue growth is interrupted in cold-adapted trees [58].

2.4. Data Analysis

Conifers observed within the same plot are not spatially-independent and therefore cannot serve as statistical replicates. For this reason, we considered the plot to be the sampling unit and converted raw counts to raw relative abundances for all assessment plots. We conducted all statistical analyses using R (version 3.4.2, Vienna, Austria) [48].

2.4.1. Community Analysis

We estimated relative abundance parameters (e.g., relative species abundances) and their corresponding precision as follows: For each study area, we bootstrapped the per-plot relative abundance data—that is, we sampled randomly with replacement over the size of the sample (e.g., 20 plots on Paintbrush Divide) and calculated the mean for each of 5000 iterations. This process generated a sampling distribution of mean relative abundances for each variable of interest. We then

calculated the mean of each sampling distribution to identify the percent relative abundance parameter estimate (\hat{p}). Finally, we used the 2.5% and 97.5% quantiles of each sampling distribution to determine the lower and upper boundary, respectively, of the 95% confidence interval (CI; [59]).

After calculating raw per-plot relative abundances, we derived pairwise mean-difference-in-relative-abundance variables for each assessment plot. To consider differences in species relative abundances, for example, we calculated the difference in per-plot relative abundance between whitebark pine and Engelmann spruce, whitebark pine and subalpine fir, and Engelmann spruce and subalpine fir. We repeated this general process for comparisons of tree island membership status (i.e., tree island, solitary), ecological role (i.e., initiator, leeward, solitary), nurse object type (i.e., rocks, micro-topographic depressions, woody plants, and unprotected), and white pine blister rust infection status (i.e., present, absent). We also determined per-plot differences in relative abundance between tree island initiators and solitary trees within species to test the association between solitary conifer relative availability and tree island initiation.

We bootstrapped each mean-difference-in-relative-abundance variable (5000 iterations) to generate its sampling distribution. We then calculated the mean of each sampling distribution to identify the mean-difference-in-percent-relative-abundance parameter estimate ($\hat{p}_{difference}$). We made Bonferroni adjustments based on the number of pairwise comparisons to determine which sampling distribution quantiles to use as the CI lower and upper boundaries. The formula for these adjustments is: $CI = \alpha/n$, where n is the number of pairwise comparisons; our α for all analyses in this study was 0.05. For three pairwise comparisons (i.e., species and ecological role comparisons), we estimated the 98.3% CI by calculating the 0.83% and 99.17% quantiles of each sampling distribution. For six pairwise comparisons (i.e., nurse object type comparisons), we estimated the 99.17% CI by calculating the 0.42% and 99.58% quantiles of each sampling distribution as the lower and upper boundary, respectively. For all pairwise difference estimates, we concluded that relative abundances did not differ if the estimated CI included zero.

2.4.2. Mesoclimate Analysis

We bootstrapped the PRISM growing season data (5000 iterations) to generate sampling distributions for mean growing season length, temperature, and precipitation. We calculated the mean of each sampling distribution to estimate the average growing season length (\hat{L}), temperature (\hat{T}), and precipitation (\hat{P}) for each study area. Finally, we estimated the 95% CI by calculating the 2.5% and 97.5% quantiles of each sampling distribution as the lower and upper boundary, respectively.

Once the sampling distributions for mean daily growing season length, temperature, and precipitation had been generated, we derived pairwise difference-in-mean sampling distributions for mean growing season length, temperature, and precipitation between study areas by subtracting one area's sampling distribution from the sampling distribution of the other study areas in a pairwise fashion. We then calculated the mean of each difference-in-mean-growing-season length ($\hat{L}_{difference}$), temperature ($\hat{T}_{difference}$), and precipitation ($\hat{P}_{difference}$) sampling distribution to identify its parameter estimate. For six pairwise comparisons, we estimated the 99.17% CI by calculating the 0.42% and 99.58% quantiles of each sampling distribution as the lower and upper boundary, respectively. For all pairwise difference estimates, we concluded that climatic conditions did not differ by study area if the estimated CI included zero.

3. Results

3.1. Community Structure, Composition, and Ecological Roles

We found that there were more solitary conifers relative to tree island conifers at both study areas east of the Continental Divide, Tibbs Butte, and Christina Mountain (Table 2). At those two locations, solitary conifers comprised 95.5% (95% CI: 88.0%, 100.0%) and 74.5% (95% CI: 61.5%, 85.9%), respectively, of all conifers assessed. We did not detect any differences in the relative abundance of

solitary conifers and tree island conifers at the study areas located west of the Continental Divide, Paintbrush Divide, and Hurricane Pass.

Table 2. Community structure parameter estimates.

Study Area	$\hat{p}_{\text{solitary}}$ (95% CI)	$\hat{p}_{\text{tree island}}$ (95% CI)	$\hat{p}_{\text{solitary-tree island}}$ (95% CI)
Paintbrush Divide	62.0% (48.2%, 75.0%)	38.0% (25.0%, 51.8%)	24.1% (−3.6%, 49.9%)
Hurricane Pass	53.8% (40.8%, 67.6%)	46.2% (32.4%, 59.2%)	7.6% (−18.4%, 35.1%)
Tibbs Butte	95.5% (88.0%, 100.0%)	4.5% (0.0%, 12.0%)	91.0% * (76.0%, 100.0%)
Christina Mountain	74.5% (61.5%, 85.9%)	25.5% (14.1%, 38.5%)	48.9% * (23.0%, 71.8%)

Parameter estimates and CIs for solitary and tree island conifer relative abundance, and mean differences in relative abundance between solitary and tree island conifers, by study area. Significant differences are denoted by asterisks.

Species comprising the treeline communities at all four study areas included whitebark pine, Engelmann spruce, and subalpine fir; we observed no other conifer species at any location (Figure S1A). Our community composition analysis revealed that the relative abundance of whitebark pine was significantly greater than that of Engelmann spruce and subalpine fir at three of the four study areas: Paintbrush Divide, Tibbs Butte, and Christina Mountain (Table 3). At these locations, respectively, whitebark pine comprised 57.9% (95% CI: 43.8%, 70.3%), 91.3% (95% CI: 84.3%, 97.5%), and 90.3% (95% CI: 85.6%, 94.5%) of all conifers assessed (Table 4 and Figure 3). At the fourth study area, Hurricane Pass, we did not observe a majority conifer species.

Table 3. Overall community composition mean difference parameter estimates.

Study Area	$\hat{p}_{\text{whitebark pine-subalpine fir}}$ (98.3% CI)	$\hat{p}_{\text{whitebark pine-Engelmann spruce}}$ (98.3% CI)	$\hat{p}_{\text{subalpine fir-Engelmann spruce}}$ (98.3% CI)
Paintbrush Divide	43.4% * (19.1%, 64.0%)	30.1% * (0.2%, 56.4%)	−13.3% (−31.3%, 3.1%)
Hurricane Pass	16.6% (−4.5%, 38.8%)	9.4% (−15.0%, 32.7%)	−7.2% (−25.3%, 9.5%)
Tibbs Butte	90.2% * (81.0%, 98.1%)	83.7% * (65.9%, 97.5%)	−6.6% (−16.1%, 1.7%)
Christina Mountain	83.9% * (72.6%, 92.8%)	87.1% * (80.4%, 93.2%)	3.3% (−1.7%, 9.7%)

Parameter estimates and CIs for pairwise mean differences in species relative abundance by study area. Significant differences are denoted by asterisks.

Table 4. Overall community composition parameter estimates.

Study Area	$\hat{p}_{\text{whitebark pine}}$ (95% CI)	$\hat{p}_{\text{subalpine fir}}$ (95% CI)	$\hat{p}_{\text{Engelmann spruce}}$ (95% CI)
Paintbrush Divide	57.9% (43.8%, 70.3%)	14.4% (7.2%, 22.8%)	27.7% (17.4%, 39.5%)
Hurricane Pass	42.0% (30.4%, 54.4%)	25.4% (17.1%, 34.1%)	32.6% (23.3%, 43.1%)
Tibbs Butte	91.3% (84.3%, 97.5%)	1.1% (0.0%, 3.1%)	7.6% (1.4%, 15.0%)
Christina Mountain	90.3% (85.6%, 94.5%)	6.5% (2.8%, 10.9%)	3.2% (1.5%, 5.2%)

Parameter estimates and CIs for species relative abundance by study area.

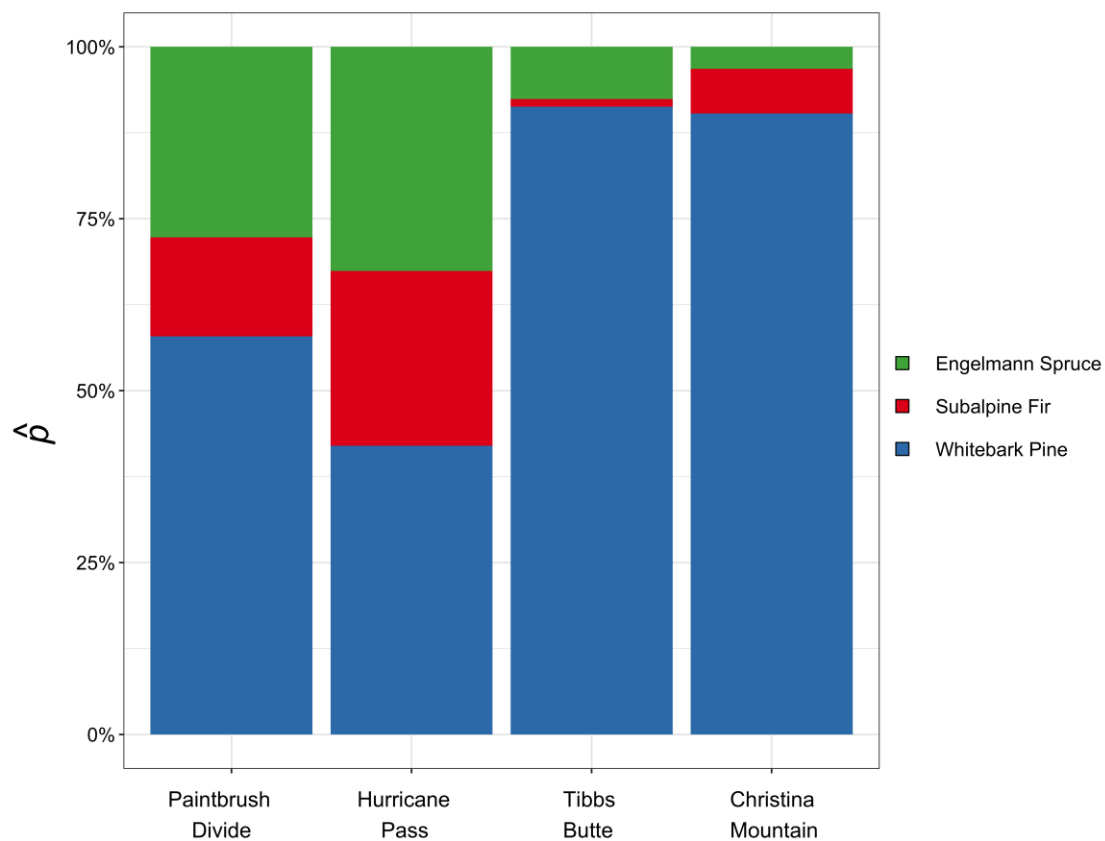


Figure 3. Overall community composition parameter estimates. Parameter estimates for species relative abundance by study area. The variability (i.e., 95% CIs) associated with each parameter estimate is provided in Table 4.

Our analysis of community composition by ecological role revealed that whitebark pine was the most abundant solitary and leeward conifer at three of the four study areas: Paintbrush Divide, Tibbs Butte, and Christina Mountain (Figure 4A). At those locations, respectively, whitebark pine comprised 64.5% (95% CI: 52.1%, 75.3%), 92.6% (95% CI: 85.2%, 98.8%), and 92.3% (95% CI: 88.2%, 96.1%) of all solitary conifers; it comprised 66.3% (95% CI: 46.8%, 83.4%), 77.5% (95% CI: 75.0%, 80.0%), and 95.4% (95% CI: 89.7%, 99.5%) of all leeward conifers (Figure 4B). At Hurricane Pass, we did not observe a majority solitary or leeward conifer species. Additionally, we found that Engelmann spruce was more abundant than subalpine fir as a solitary conifer at Paintbrush Divide.

Our analysis did not reveal any species as a majority tree island initiator at any study area. However, we did find significantly more whitebark pine tree island initiators relative to Engelmann spruce at Christina Mountain ($\hat{p}_{\text{whitebark pine-Engelmann spruce}} = 58.5\%$; 95% CI: 28.0%, 88.9%).

We found that whitebark pine's relative abundance as a tree island initiator did not differ from its relative abundance as a solitary tree at any study area (Table 5), with the exception of Hurricane Pass. There, we observed fewer whitebark pine tree island initiators than expected given its relative solitary tree abundance. Subalpine fir at Hurricane Pass served as a tree island initiator more than expected given its relative abundance as a solitary tree.

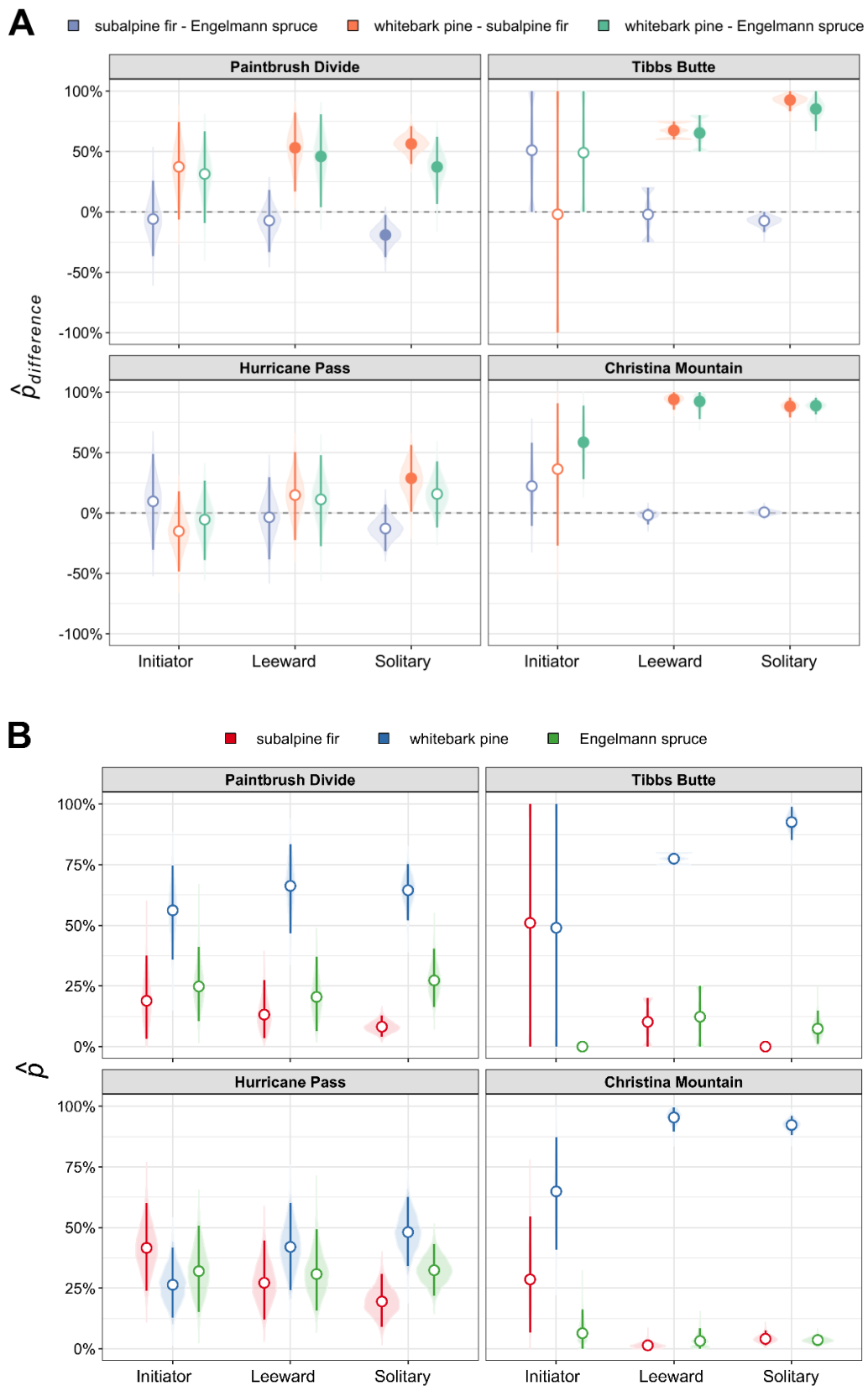


Figure 4. Parameter estimates for community composition by ecological role. **(A)** Pairwise mean differences in relative abundance among species, by ecological role. **(B)** Conifer species relative abundance by ecological role. Shaded centers delineate sampling distributions, circles indicate parameter estimates, and vertical lines delineate 98.3% CIs **(A)** or 95% CIs **(B)**. Closed circles in **(A)** denote significant differences.

Table 5. Mean difference between tree island initiator and solitary conifer relative abundance by species parameter estimates.

Study Area	Whitebark Pine $\hat{p}_{\text{initiator-solitary}}$ (95% CI)	Subalpine Fir $\hat{p}_{\text{initiator-solitary}}$ (95% CI)	Engelmann Spruce $\hat{p}_{\text{initiator-solitary}}$ (95% CI)
Paintbrush Divide	−1.3% (−23.9%, 20.1%)	4.1% (−5.3%, 16.7%)	−2.8% (−19.2%, 15.9%)
Hurricane Pass	−20.9% (−39.9%, −3.1%) *	17.6% (2.5%, 32.8%) *	3.3% (−16.7%, 24.5%)
Tibbs Butte	−51.0% (−100.0%, 0.0%)	51.0% (0.0%, 100.0%)	0.0% (0.0%, 0.0%)
Christina Mountain	−15.3% (−38.2%, 4.3%)	12.4% (−5.6%, 36.8%)	3.0% (−5.6%, 13.4%)

Parameter estimates and CIs for mean differences between tree island initiator and solitary conifer relative abundance by species for each study area. Significant differences are denoted by asterisks.

3.2. Facilitation by Nurse Objects and Blister Rust Assessments

Nurse objects varied in relative abundance by type across study areas, and included rocks, micro-topographic depressions, woody plants, and no nurse object (i.e., unprotected; Figure S1B). We found differences in the relative abundance of unprotected conifers (i.e., conifers with ‘no nurse object’) based on location with respect to the Continental Divide. In the study areas west of the Continental Divide, unprotected conifers were at least as common as those protected by any other nurse object type (Figure 5A). Conversely, east of the Continental Divide, the relative abundance of unprotected conifers was never as common as conifers facilitated by rocks or woody plants, and only exceeded that of conifers in micro-topographic depressions at Christina Mountain.

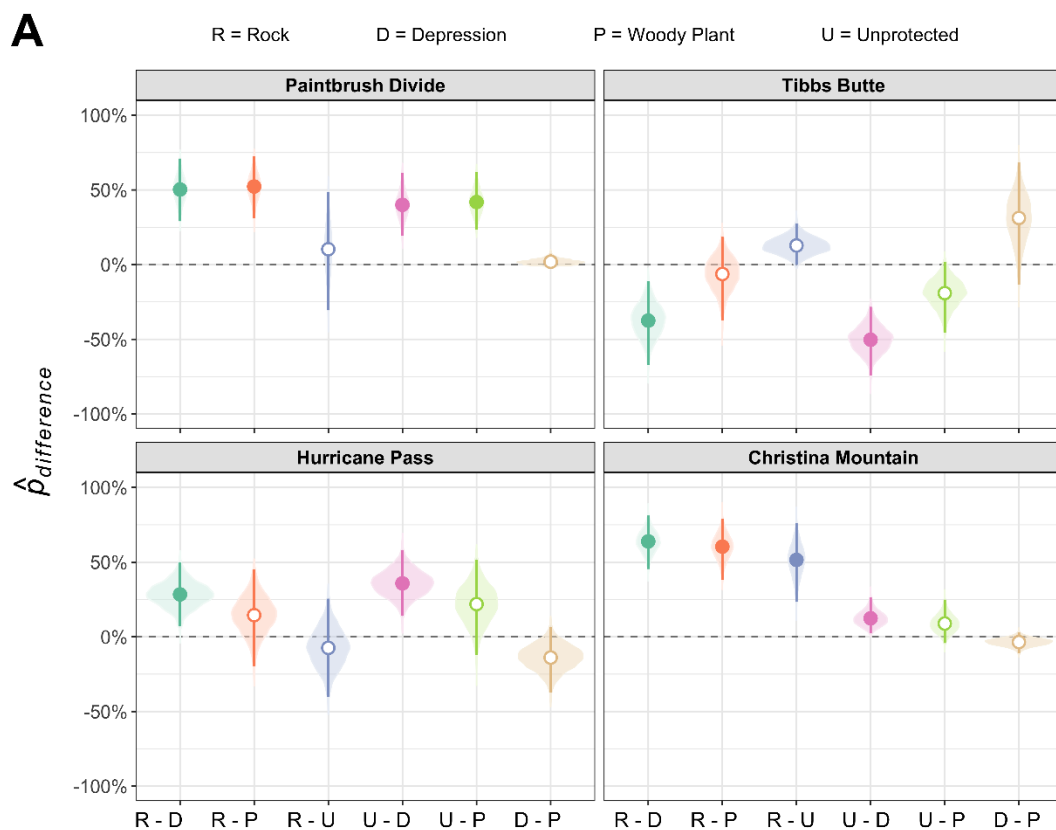


Figure 5. Cont.

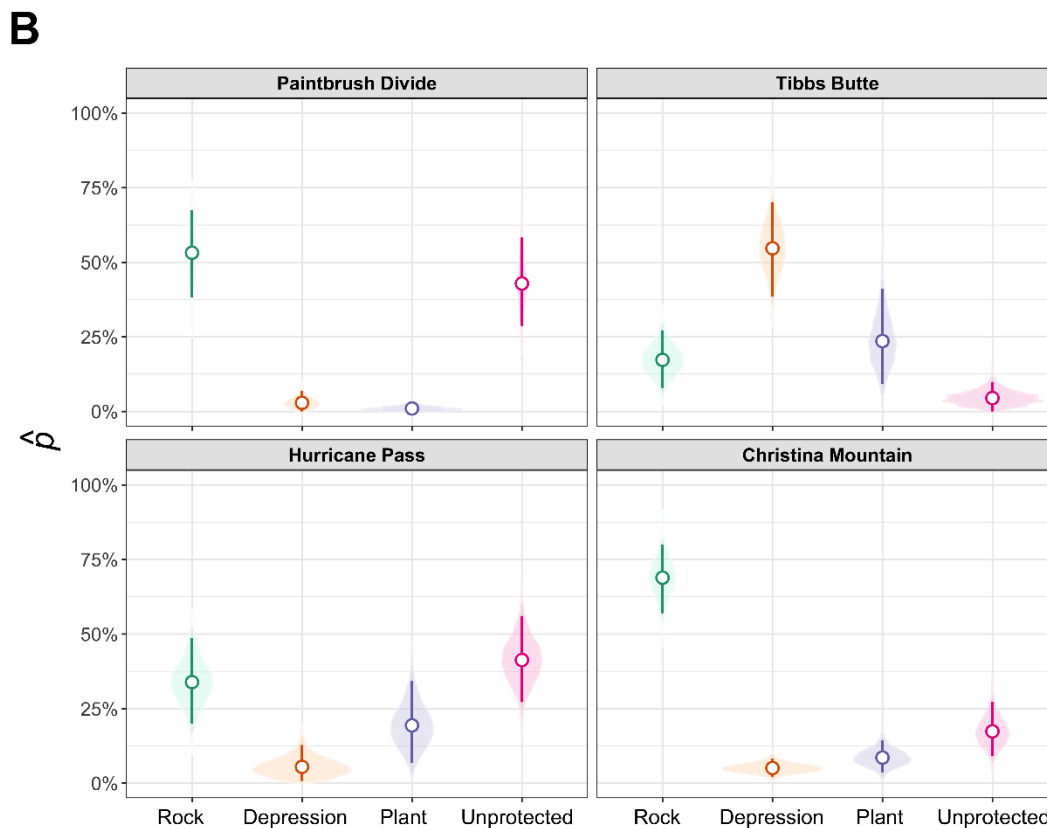


Figure 5. Parameter estimates for nurse object facilitation. (A) Pairwise mean differences in relative abundance between nurse objects. (B) Nurse object relative abundances. Shaded curves delineate sampling distributions, circles indicate parameter estimates, and vertical lines delineate 99.2% CIs (A) or 95% CIs (B). Closed circles in (A) denote significant differences.

The relative abundance of conifers facilitated by rocks exceeded (1) micro-topographic depressions and woody plants at Paintbrush Divide, (2) micro-topographic depressions at Hurricane Pass, and (3) all other nurse object types at Christina Mountain. Indeed, at Christina Mountain, rocks comprised 68.9% (95% CI: 57.0%, 80.0%) of all nurse objects (Figure 5B). Tibbs Butte was the only study area at which the relative abundance of another nurse object type—micro-topographic depressions—was greater than that of rocks. Across all four study areas, woody plants never facilitated a greater proportion of solitary conifers and tree island initiators relative to any other nurse object.

We found that the mean white pine blister rust infection incidence was highest for the two study areas west of the Continental Divide: 18.0% (95% CI: 9.8%, 27.4%) at Paintbrush Divide and 14.4% (95% CI: 6.2%, 23.9%) at Hurricane Pass. The infection incidence for the two study areas east of the Divide was 0.6% (95% CI: 0.0%, 1.8%) at Tibbs Butte, and 2.0% (95% CI: 0.5%, 3.8%) at Christina Mountain.

3.3. Mesoclimate Assessments

From 1985 to 2015, mean growing season lengths varied by study area, ranging from 115 days (95% CI: 107 days, 123 days) at Tibbs Butte to 136 days (95% CI: 129 days, 143 days) at Christina Mountain (Table 6). We found that the mean growing season length at Tibbs Butte was 21 days shorter than the growing season lengths at both Paintbrush Divide (95% CI: 6 days, 34 days) and Christina Mountain (95% CI: 6 days, 35 days; Table 7).

Table 6. Mesoclimate parameter estimates.

Study Area	\hat{L} (95% CI)	\hat{T} (95% CI)	\hat{P} (95% CI)
Paintbrush Divide	136 days (129 days, 142 days)	9.9 °C (9.5 °C, 10.3 °C)	27.6 cm (23.8 cm, 31.5 cm)
Hurricane Pass	128 days (120 days, 136 days)	9.0 °C (8.5 °C, 9.4 °C)	28.1 cm (23.4 cm, 33.0 cm)
Tibbs Butte	115 days (107 days, 123 days)	8.7 °C (8.3 °C, 9.2 °C)	19.2 cm (16.3 cm, 22.1 cm)
Christina Mountain	136 days (129 days, 143 days)	9.1 °C (8.7 °C, 9.5 °C)	19.4 cm (16.3 cm, 22.5 cm)

Parameter estimates and CIs for mean annual growing season length (\hat{L}), mean daily growing season temperature (\hat{T}), and mean annual growing season precipitation (\hat{P}) from 1985 to 2015, by study area.

Table 7. Mesoclimate pairwise difference parameter estimates.

Comparison	$\hat{L}_{difference}$ (99.2% CI)	$\hat{T}_{difference}$ (99.2% CI)	$\hat{P}_{difference}$ (99.2% CI)
PD-HP	8 days (−6 days, 21 days)	1.0 °C * (0.1 °C, 1.8 °C)	−0.5 cm (−9.1 cm, 7.5 cm)
PD-TB	21 days * (6 days, 34 days)	1.2 °C * (0.4 °C, 1.9 °C)	8.5 cm * (2.2 cm, 15.1 cm)
PD-CM	0 days (−13 days, 13 days)	0.8 °C (0.0 °C, 1.5 °C)	8.3 cm * (1.7 cm, 14.9 cm)
CM-HP	8 days (−6 days, 22 days)	0.2 °C (−0.6 °C, 1.0 °C)	−8.8 cm * (−16.8 cm, −1.4 cm)
CM-TB	21 days * (6 days, 35 days)	0.4 °C (−0.4 °C, 1.2 °C)	0.2 cm (−5.3 cm, 5.7 cm)
HP-TB	13 days (−2 days, 28 days)	0.2 °C (−0.6 °C, 1.0 °C)	8.9 cm * (1.7 cm, 16.5 cm)

Parameter estimates and CIs for pairwise differences in mean annual growing season length ($\hat{L}_{difference}$), mean daily growing season temperature ($\hat{T}_{difference}$), and mean annual growing season precipitation ($\hat{P}_{difference}$) between study areas from 1985 to 2015. Significant differences are denoted by asterisks. PD = Paintbrush Divide, HP = Hurricane Pass, TB = Tibbs Butte, and CM = Christina Mountain.

Estimates for mean growing season temperature (1985 to 2015) ranged from 8.7 °C (95% CI: 8.3 °C, 9.2 °C) at Tibbs Butte to 9.9 °C (95% CI: 9.5 °C, 10.3 °C) at Paintbrush Divide. Pairwise differences in mean growing season temperature between study areas from 1985 to 2015 revealed that Paintbrush Divide was, on average, 1.0 °C (99.2% CI: 0.1 °C, 1.8 °C) warmer than Hurricane Pass and 1.2 °C (99.2% CI: 0.4 °C, 1.9 °C) warmer than Tibbs Butte.

For mean growing season precipitation from 1985 to 2015, estimates ranged from 19.2 cm (95% CI: 16.3 cm, 22.1 cm) for Tibbs Butte to 28.1 cm (95% CI: 23.5 cm, 33.0 cm) for Hurricane Pass. We found that study areas west of the Continental Divide had higher mean growing season precipitation estimates relative to those east of the Continental Divide. Paintbrush Divide received an average of 8.5 cm (99.2% CI: 2.2 cm, 15.1 cm) and 8.3 cm (99.2% CI: 1.7 cm, 14.9 cm) more growing season precipitation than Tibbs Butte and Christina Mountain, respectively. In addition, Hurricane Pass received an average 8.9 cm (99.2% CI: 1.7 cm, 16.5 cm) and 8.8 cm (99.2% CI: 1.4 cm, 16.8 cm) more growing season precipitation than Christina Mountain and Tibbs Butte, respectively.

4. Discussion

4.1. Community Structure and Composition

The principal objective of this study was to describe the structure and composition of four treeline communities within the GYE. We found that whitebark pine is locally abundant, regionally common, and frequently serves as the majority conifer in the GYE treeline communities we sampled. Our results also show that solitary whitebark pine define much of the treeline community structure and composition east of the Continental Divide.

The general abundance of whitebark pine at treeline within the GYE is consistent with studies conducted across the Central and Northern Rocky Mountains, which establish it as a prevalent treeline conifer (e.g., [14,30]). Whitebark pine's prevalence at treeline results from a combination of factors described in detail in Tomback et al. [3] and summarized briefly here. First, whitebark pine, which tolerates poor seedbeds and harsh sites [31], has been classified as a stress-tolerant conifer (e.g., [60]). It has a number of physiological characteristics that promote efficient water and carbon use, and greater carbon gain relative to other treeline species in both seedling and mature life stages, as well as tolerance of solar radiation and freezing stress [5,26,61]. Seed dispersal by Clark's nutcracker to protected treeline cache sites (e.g., [34,36]) may further contribute to seedling establishment and tree survival. Pansing et al. [20] concluded that the odds of whitebark pine seedling survival are increased near protective objects at treeline.

Whitebark pine's high relative abundance relative to other treeline species east of the Continental Divide underscores its ability to survive harsh conditions. Continental climates that shape these treeline landscapes impose greater annual temperature variation [62], aridity [63], and downslope winds [64] relative to climates with maritime influence. Complex, and mostly downslope, winds also highlight the importance of "directed" upslope nutcracker seed dispersal. Other treeline conifers depend on wind for seed dispersal from subalpine forests to treeline, which has a higher element of chance, particularly with respect to seeds ending up in treeline "safe sites" [1].

4.2. Tree Island Initiation and the Relationship to Species Relative Abundance among Solitary Trees

We examined whether whitebark pine was the most common windward tree among tree islands, and thus most likely to serve the ecological role of "tree island initiator" in the GYE. Although whitebark pine has been found to serve this role within several treeline communities across the Central and Northern Rocky Mountains [14], we found that it was not the majority tree island initiator at any study area, despite serving as a majority solitary and leeward conifer in three of four of the communities assessed.

We examined the possible association between solitary tree relative abundance and tree island initiator relative abundance by species. In other words, if tree island initiation is random with respect to species—that is, if solitary whitebark pine, Engelmann spruce, and subalpine fir are equally likely to have conifers establish in their lee—then we would expect tree island initiator relative abundance for a given species to be similar to solitary tree relative abundance for that species. Our results revealed that the relative abundance of solitary trees by species was similar to the relative abundance of tree island initiators by species at three of the four study areas. This finding is consistent with a meta-analysis by Tomback et al. [14], which showed that the abundance of solitary whitebark pine and subalpine fir predicted their tree island initiator abundance across the Central and Northern Rocky Mountains. Further, Pyatt et al. [26] measured biophysical conditions leeward of treeline conifers and found that species-specific differences in protection were not strongly evident. Tree island initiation appears to be related to the relative abundance of solitary trees at a landscape-scale and not necessarily better microclimate amelioration. By this logic, it follows that whitebark pine's importance in community structure and composition is likely abundance-based (i.e., more opportunities to facilitate tree island development). Understanding the processes leading to whitebark pine's high abundance clarifies its dominant role in community structure and composition.

4.3. Retrospective Evaluation of the Sampling Strategy

There is one caveat concerning the assessment of the role of whitebark pine as a tree island initiator, or assessing the ecological roles of the different treeline species in general: Our use of assessment plots as replicates (i.e., sampling units) resulted in the aggregation of multiple tree islands into one sampling unit, which could have decreased the precision of our estimates to a degree that precluded our ability to detect mean differences in tree island initiator or leeward relative abundance among species.

Previous treeline conifer community studies have analyzed transect- or plot-based sampling strategies by combining totals across replicates (e.g., [15,30]), thereby using individual conifers as sampling units. The method used here, however, presents an improvement because it accounts for the lack of spatial independence in plot-based sampling, thus avoiding pseudoreplication [65]. In future examinations of ecological roles by species, and especially in evaluating the role of tree island initiation, we recommend sampling designs that forego assessment plots and transects (i.e., ensure the tree or tree island is the sampling unit).

4.4. Differences in Nurse Object Facilitation

Differences in the facilitation of solitary trees and tree island initiators by windward nurse object type may reflect variation in microsite availability and/or mesoclimatic conditions among study areas. For the former, the availability of some microsites may reflect surface roughness elements (e.g., rocks) or the result of fine-scale geomorphic processes (e.g., micro-topographic depressions). The occurrence of relatively fewer trees in unprotected microsites (i.e., no nurse object) relative to protected microsites (i.e., rocks, micro-topographic depressions, or woody plants) may reflect a harsher climate, and especially a continental climate (east of the Continental Divide) vs. climates with maritime influence (west of the Continental Divide).

When examining solitary tree and tree island initiator facilitation by nurse object type, we in fact found differences that may be based on community location relative to the Continental Divide. At Tibbs Butte and Christina Mountain, which are both east of the Divide, our results show that the relative abundance of solitary conifers and tree island initiators in unprotected microsites was lower than that in protected microsites (i.e., micro-topographic depressions at Tibbs Butte and rocks at Christina Mountain). In a previous study at Tibbs Butte by Tomback et al. using a different sampling protocol, rocks were found to predominate as facilitative microsites rather than micro-topographic depressions, which may reflect local differences within a study area [30].

Conversely, our results from the communities west of the Continental Divide at Paintbrush Divide and Hurricane Pass show that the relative abundance of solitary trees and tree island initiators in unprotected microsites was never lower than any other nurse object type. The occurrence of relatively fewer trees in unprotected microsites relative to protected microsites east of the Continental Divide may reflect the harsher continental climate and represent evidence of establishment and/or survival limitations in continental climates where nurse object protection may be essential for recruitment.

4.5. The Effects of Mesoclimate on Tree Island Composition

Previously, Resler et al. [12] found temperature and surface convexity to be important predictors of the frequency of whitebark pine's occurrence windward in tree islands, and thus as a tree island initiator. Here, we examined whether differences in mesoclimate alone corresponded to differences in whitebark pine's ecological function at treeline. At Hurricane Pass, which is west of the Continental Divide, we found that whitebark pine was not a majority conifer, and initiated fewer tree islands than expected given its relative abundance as a solitary tree, whereas subalpine fir initiated more tree islands than expected. These results may be explained by climatic trends coupled with physiological differences between whitebark pine and subalpine fir. Griggs [64] noted that subalpine fir survives better in moist, snowy environments relative to other treeline species. Little [66] found subalpine fir establishment

and survival to be limited by low soil moisture, especially on southern aspects—conditions tolerated by whitebark pine.

Our examination of mesoclimates among study areas confirmed that both study areas west of the Continental Divide received higher mean growing season precipitation relative to both study areas east of the Continental Divide. These findings suggest that mesoclimatic conditions, particularly mean growing season precipitation, may influence the structure and composition of treeline communities in the GYE, and particularly the relative occurrence of solitary trees vs. tree islands.

4.6. The Level and Impact of *C. ribicola* Infection: Management Implications

Although *C. ribicola* infection incidence has been widely surveyed in subalpine stands within the GYE (e.g., [42,67]), this is the first study to specifically assess and consider the ramifications of infection in treeline communities across the GYE. Our results revealed that treeline white pine blister rust infection ranged from 0.6% to 18.0% and was highest west of the Continental Divide (14.4% to 18.0%) relative to sites east of the Continental Divide (0.6% to 2.0%).

The incidence of blister rust infection at treeline may reflect both its occurrence in nearby subalpine forests and the mesoclimatic conditions suitable for its spread. Several studies at larger geographic scales have demonstrated an increase in blister rust infection levels along a continental east to west gradient (e.g., [68,69]), and suggest that climates with a maritime influence (i.e., moderate temperatures and high relative humidity) may be more favorable for spore transmission (e.g., [37,70]). Our finding that white pine blister rust was highest west of the Continental Divide supports those results. For our study areas east of the Continental Divide, Christina Mountain, and Tibbs Butte, arid or otherwise harsh conditions (such as variable temperatures and complex, downslope winds) may have slowed spore development and/or transmission. However, communities east of the Continental Divide are not protected from blister rust. Two previous assessments of blister rust infection levels in treeline communities east of the Continental Divide at Line Creek Plateau RNA in the GYE and on the east slope of Glacier National Park showed infection levels at 19.2% and 23.6%, respectively [43].

Given that whitebark pine was the most abundant conifer in three of our four treeline study areas and comprised between 42.0% and 91.3% of the total trees per plot across all study areas, the spread of *C. ribicola* has the potential to significantly reduce overall conifer abundance at treeline and thereby alter community structure and composition. This disturbance to the GYE's extensive treeline whitebark pine population could disrupt the ecosystem services that treeline conifers provide, including substrate stabilization against erosion [71], snow retention, and regulation of downstream flows, as a result of reduced whitebark pine occurrence [14].

Management actions that increase the number of trees resistant to white pine blister rust in subalpine whitebark pine communities near treeline communities should eventually lead to higher numbers of resistant whitebark pine at treeline. Increasing the prevalence of population resistance to blister rust would ensure the continuity of seed dispersal from subalpine forest communities to treeline, and at treeline, maintain community structure and continuity of ecosystem services. Planting seedlings or sowing seeds from parent trees with confirmed resistance to white pine blister rust is one of the major strategies for reversing the rapid decline in whitebark pine populations [38,39,72]. Tomback et al. [14] discussed how either planting seedlings or sowing seeds from known trees with genetic resistance to blister rust in both the nearby subalpine forest zone and also within appropriate treeline communities may help counter the expected decline in whitebark pine from infection. Restoration work directly at treeline, however, would greatly reduce the time between treeline community decline and treeline community recovery, and thus the recovery of ecosystem services. The relatively high incidence of blister rust in the two treeline study areas west of the Continental Divide, Paintbrush Divide, and Hurricane Pass, suggests the need for timely management intervention.

5. Conclusions

Our results indicated that whitebark pine is locally abundant, regionally common, and frequently serves as the majority conifer in the GYE treeline communities we sampled. Our results also show that solitary whitebark pine define much of the community structure and composition east of the Continental Divide. West of the Divide, whitebark pine is more variable in its prevalence and ecological role, but still well-represented in treeline communities.

We found that the prevalence of whitebark pine as the windward tree island species, and thus as a potential tree island initiator, may be predicted from its relative abundance as a solitary tree. Thus, whitebark pine's importance in community structure and composition is likely abundance-based (i.e., it has more opportunities to facilitate tree island development) rather than a result of better microclimate amelioration relative to other species. White pine blister rust infection incidence ranged from 0.6% to 18.0% across study areas, and west of the Continental Divide currently poses a threat to some treeline communities and their provision of ecosystem services. Increasing the genetic resistance to white pine blister rust in subalpine whitebark pine communities through seedling planting or direct seed sowing should eventually increase the numbers of whitebark pine with resistance to blister rust at treeline. Direct planting or sowing at treeline, particular in communities with a higher blister rust infection incidence, would speed up the recovery of treeline communities and the ecosystem services that they provide.

Supplementary Materials: The following are available online at <http://www.mdpi.com/1999-4907/9/10/635/s1>, Figure S1: (A) Total conifer counts by species for each study area. (B) Total nurse object and unprotected site counts.

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