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Relative Abundance and Functional Role of Whitebark Pine at Treeline in the Northern Rocky Mountains

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Abstract

Facilitative interactions among plant species enable plant community development under stressful environmental conditions. Previous studies in two treeline communities within the alpine-treeline ecotone on the Rocky Mountain Front in northwestern Montana, U.S.A., indicated that whitebark pine (*Pinus albicaulis*) serves as the majority tree island initiator, thus facilitating the development of tree islands (Resler and Tomback, 2008). However, 33.7% of whitebark pine at these treeline study sites were infected by the introduced pathogen *Cronartium ribicola*, which causes white pine blister rust. We examined the prevalence of whitebark pine, its ecological role, and the incidence of blister rust within two study sites, Tibbs Butte and Wyoming Creek, to the south on the Beartooth Plateau, and within two study sites, Stanley Glacier and Gibbon Pass, to the north in Kootenay and Banff National Parks, for comparison with information from the Rocky Mountain Front (Resler and Tomback, 2008). We found that whitebark pine was an important component of treeline communities in both the southern and northern study areas, although its abundance and ecological role varied with study site. Nearly half the solitary trees sampled overall in the northern and southern study areas were whitebark pine. Whitebark pine was also the most frequently occurring conifer species among tree islands at three of the four study sites. Across all study sites, whitebark pine served as tree island initiator for 29.4% of the tree islands sampled, but was a more frequent initiator within two study sites. Blister rust incidence for the Wyoming Creek study site in the southern study area was 7.7%, and for the Stanley Glacier study site in the northern study area, 16.2%. Damage and mortality over time from *Cronartium ribicola* will diminish the current ecological role of whitebark pine as a facilitator of landscape vegetation pattern development and may confound predictions of upward movement of treeline in response to climate warming.

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Introduction

Environmental conditions at alpine treeline are not favorable for tree growth and survival, and facilitative interactions, both between nurse objects (such as rocks) and plants and among plants, are important for vegetation establishment (Bertness and Callaway, 1994; Brooker et al., 2007; Callaway et al., 2002; Resler, 2006; Smith et al., 2009). With climate warming trends and the anticipated upward movement of alpine treeline (Bartlein et al., 1997; Kullman, 1998, 2002; Moen et al., 2004), we predict that processes currently involved in solitary tree and tree island establishment will be important at the migrating upper limits of treeline.

Whitebark pine (*Pinus albicaulis*, Family Pinaceae, Subgenus *Strobus*) inhabits upper subalpine and treeline communities throughout its distribution in the western United States and Canada (Arno and Hammerly, 1984; Arno and Hoff, 1990). Clark's nutcrackers (*Nucifraga columbiana*, Family Corvidae) are the primary dispersers for whitebark pine, scatterhoarding the large, wingless seeds in late summer and early fall (Hutchins and Lanner, 1982; Tomback, 1978, 1982) over a broad elevational gradient from lower treeline to alpine communities above upper treeline (Tomback, 1986; Baud, 1993; see overviews in Tomback, 2001, 2005). Nutcrackers often place their seed caches near trees, rocks, vegetation, and other objects, which may increase seedling survival (Tomback, 1978; Vander Wall, 1982; Tomback 2001). Whitebark pine seeds maintain viability within a soil seed bank and germinate under favorable moisture conditions (Tomback et al., 2001a; Tillman-Sutela et al., 2008). Whitebark pine seedlings are morphologically robust and tolerant of arid, windy conditions (Arno and Hoff, 1990; McCaughey and Tomback, 2001; Tillman-Sutela et al., 2008).

Previous studies in the alpine-treeline ecotone along the Rocky Mountain eastern Front, northwestern Montana, indicated that whitebark pine serves as the majority tree island initiator in this region (Resler and Tomback, 2008). Initiation entails that a whitebark pine becomes established, often within a protective microsite, and over time other conifers establish leeward of the whitebark pine, which moderates wind exposure. Similarly, Habeck (1969) noted that whitebark pine east of the Continental Divide in Glacier National Park was the first tree to invade alpine meadows, leading to the establishment of subalpine fir (*Abies lasiocarpa*), which grew into large tree islands. Initial tree establishment in this region is facilitated by microtopography (e.g., Resler et al., 2005), but tree island development on some harsh sites frequently requires more protection than microtopography, with whitebark pine or other conifers serving that functional role.

The invasive fungal pathogen *Cronartium ribicola* (Division Basidiomycota, Order Uredinales) causes white pine blister rust,

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a disease that damages and kills five-needle white pines (Geils et al., 2010). *Cronartium ribicola* now occurs nearly rangewide in whitebark pine, leading to widespread decline (Tomback and Achuff, 2010; Schwandt et al., 2010). Furthermore, recent large-scale outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) have killed high proportions of mature, cone-bearing whitebark pine, particularly in the Rocky Mountains (Gibson et al., 2008; Logan et al., 2010; Schwandt et al., 2010).

In the United States, whitebark pine is a candidate species for federal listing as endangered or threatened (U.S. Fish and Wildlife Service, 2011), and it was recently declared endangered in Canada under the Species at Risk Act (Government of Canada, 2012). Whitebark pine functions as a foundation and keystone species of western high mountain ecosystems (Tomback et al., 2001b; Ellison et al., 2005). As whitebark pine declines, the ecosystem services it provides, including the production of large, nutritious seeds as wildlife food, soil stabilization, protracted snowmelt, which moderates downstream flows, and community development after disturbance through facilitation interactions, are also diminished (Tomback et al., 2001b, 2011; Tomback and Achuff, 2010).

On the Rocky Mountain Front in the alpine-treeline ecotone (ATE), Resler and Tomback (2008) found that 33.7% of whitebark pine sampled were infected by *Cronartium ribicola*, and dead krummholz trees often had multiple blister rust cankers. An assessment of treeline sites in Glacier National Park east of the Continental Divide indicated that, overall, 47% of the sampled whitebark pine were infected with blister rust (Smith et al., 2011). Whitebark pine initiating tree islands in northern Montana is an important ecological function currently being disrupted by blister rust. As the initiating whitebark pine in many tree islands die, there is a wave of tree mortality through some tree islands as a result of high wind exposure. With global climate warming trends, recent bioclimatic models predict distributional changes in forest trees involving latitudinal shifts from south to north and to higher elevations (e.g., Hamann and Wang, 2006; McKenney et al., 2007; Schrag et al., 2008). Tomback and Resler (2007) predicted that the loss of whitebark pine to blister rust in treeline communities could delay or diminish the expansion of ATE communities above current treeline as temperatures warm.

In the Rocky Mountains, whitebark pine is distributed from southwestern Wyoming north through Montana and through the Canadian Rocky Mountains of Alberta and British Columbia, north to about 54°N latitude (McCaughey and Schmidt, 2001). Here, in an exploratory study, we examined the distribution and role of whitebark pine in treeline communities to the north and south of the Rocky Mountain Front of Montana, in order to assess the ecological importance of whitebark pine at treeline and potential for disruption by white pine blister rust. We asked specifically: (1) Is there geographic variation in the occurrence of whitebark pine at treeline north and south of the northwestern Montana Rocky Mountain Front? (2) Does whitebark pine occur as solitary trees in these northern and southern areas? If so, what proportion of solitary trees is whitebark pine, and how does that vary geographically? (3) Is whitebark pine a component of tree islands? If so, what proportion of tree islands includes whitebark pine, and how does that vary geographically? (4) Is whitebark pine the majority tree island initiator in these regions to the north and south, as it is on the Rocky Mountain Front? (5) Given the prevalence of white pine blister rust in the Rocky Mountain Front study areas (Resler and Tomback, 2008; Smith et al., 2011), what is the infection level to the north and south? We compare data from new study areas with re-analyzed and/or unpublished data previously collected from the Rocky Mountain Front (Resler and Tomback, 2008).

Methods

STUDY AREAS

Our study was conducted in the alpine-treeline ecotone (ATE), which we define as the upper transition zone between subalpine forest and alpine tundra. In the ATE, trees are distributed both as solitary individuals and as tree patches or "tree islands," often interspersed with woody shrubs (Marr, 1977). Tree islands are multi-tree associations, typically comprised of more than one species. Both solitary trees and those in tree islands are generally in dwarfed or "krummholz" growth forms, sometimes with erect stems or branches "flagged" by strong winds. Many solitary trees and tree islands grow leeward of protective features, such as large rocks, microtopographic hollows, and dense, woody vegetation (e.g., *Salix* spp.). These microsite shelters enable the solitary tree or initiating conifer of a tree island to become established (e.g., Resler et al., 2005; Resler and Tomback, 2008). Within tree islands, different conifer species are contiguous or intertwined in associations not typically found in subalpine forests. Working in two different study areas, and in two study sites within each study area, we sampled on dominant aspects and in representative communities in the upper ATE. Hiking time and accessibility restricted our sampling locations. Study sites occurred east of the Continental Divide with the exception of Stanley Glacier in Kootenay National Park.

NORTHERN AND SOUTHERN STUDY AREAS

Treeline communities were sampled in the south on the Beartooth Plateau, just northeast of Yellowstone National Park, U.S.A., at ~45°N, and in the north in Kootenay and Banff National Parks, British Columbia and Alberta, Canada, respectively, at ~51°N (Table 1, Fig. 1). The two southern study sites on the Beartooth Plateau were Tibbs Butte, Shoshone National Forest, Wyoming, and above the Wyoming Creek drainage, designated as the "Wyoming Creek" study site, Custer National Forest, Montana. In the northern study area, we sampled at Stanley Glacier, Kootenay National Park, and at Gibbon Pass, Banff National Park, east of the Stanley Glacier drainage. Access to Gibbon Pass was by helicopter.

The elevation of treeline communities diminished with latitude and varied with topography (Table 1). Aspect also varied with study site: The two southern study sites, Tibbs Butte and Wyoming Creek, had northwest and northeast exposures, respectively; the northern study site, Stanley Glacier, varied from southwest to westerly; and the northern Gibbon Pass study site, on a ridgetop, had both southern and northeastern exposures. Wind direction was determined by observing tree growth and flagging patterns. The prevailing winds for the southern study sites and Gibbon Pass were from the west or northwest, and at the Stanley Glacier study site from the northeast (Table 1). The Stanley Glacier study site had the steepest slopes. There, geomorphology appeared to limit the elevation of treeline, whereas at other study sites, treeline appeared to be climatically determined.

ROCKY MOUNTAIN FRONT STUDY AREA

For comparison with results from the northern and southern study areas, we used data previously sampled by Resler and Tomback (2008) from treeline communities in two study sites east of the Continental Divide (Table 1, Fig. 1; see Resler and Tomback, 2008, for details). Lee Ridge is just within the eastern boundary of Glacier National Park, and Divide Mountain (referred

TABLE 1

Characteristics of study sites in the southern study area (Beartooth Plateau), and the northern study area (Kootenay and Banff National Parks). The study sites in the Rocky Mountain Front study area, previously sampled by Resler and Tomback (2008), are described here for comparison.

Study area	Beartooth Plateau				Rocky Mountain Front		Kootenay/Banff National Parks				
Study site	Tibbs Butte		Wyoming Creek		Divide Mtn.	Lee Ridge	Stanley Glacier		Gibbon Pass		
Latitude	44°56′N		45°02′N		48°40′N	48°55′N	51°11′N		51°11′N		
Longitude	109°27′W		109°24′W		113°02′W	113°39′W	116°03′W		115°56′W		
Transect	1	2	1	2	1–5	1–5	1	2	1	2	3
Elevation (m)	3156	3049	3001	2997	2097–2127	2136–2168	1997	1969	2415	2389	2430
Aspect	340°	340°	60°	59°	45°	337°	204°	280°	177°	178°	58°
Steepness	17°	14°	8.5°	4°, 8.5°	1–13°	0–3°	25°	15°	11°, 16°	7°	4°, 11°
Wind origin	270°	270°	300°	270°	variable	270°	55°	55°	290°	290°	300°

to as Divide Peak; Resler and Tomback, 2008) straddles the eastern park boundary and the western boundary of the Blackfeet Indian Reservation, Montana. Both study sites feature patterned ground, which provides protective microsites for tree establishment (Butler and Malanson, 1989, 1999; Resler et al., 2005).

SAMPLING SOLITARY TREES AND TREE ISLANDS

Solitary trees and tree islands were sampled during July 2007 in study sites within the northern and southern study areas. We examined the conifer species composition of solitary trees, the frequency of occurrence of whitebark pine and other conifers among tree islands, and the most windward conifer of each tree island, which putatively had acted as a tree island initiator. Total numbers of each species were not possible to assess in tree islands because of the multi-stem nature of krummholz growth forms and the large size of many tree islands. Instead, we assessed the presence (≥1 stem) of conifer species within tree islands.

We sampled two 50 m long × 10 m wide belt transects or plots within each study site with two exceptions: we sampled three transects on Gibbon Pass, which had two major slope aspects; and Transect 2 at Stanley Glacier was only 25 m long because of high tree density. We determined transect starting position by blind toss of a transect pin or rock. On the Beartooth Plateau, transects were on elevation isoclines. For the northern study sites, we established vertically oriented transects with the long axis within stringers of tree islands. Slope steepness, slope aspect, transect heading, geospatial location (NAD 83), and elevation were recorded at the starting and end points of each transect. We recorded the species of each solitary conifer within each transect. For each tree island, we noted the following: the windward shelter source, the initiating species, the presence of each species within each tree island but not by count, and the length and width of each tree island sampled within transects. However, we did not take these latter tree island measurements on Transect 1 at the Stanley Glacier study site, because of slope steepness (Table 1), and insecure footing from loose shale.

For comparison, we present data from Resler and Tomback (2008) on solitary trees and tree islands from the two Rocky Mountain Front study sites. Our current sampling protocols were similar to those of Resler and Tomback (2008), except they established five belt transects rather than two, and they placed these transects along elevational isoclines in each study site. The belt transects at Lee Ridge were 10 m × 75 m rather than 10 m × 50 m because of low tree island density.

In the northern and southern study areas, we examined each whitebark pine stem that occurred within a given transect for blister rust cankers, which are indicated by fusiform swellings of branches and/or eruption of aecial sacs (which contain aeciospores) from branches and stems (McDonald and Hoff, 2001). We classified cankers as potential (branch swelling but no signs of past or present sporulation), inactive (old cankers with dead and roughened bark from previous aecial sac eruptions), and active (cankers with fresh or old aecial sacs) (Hoff, 1992). Additional symptoms noted include canopy kill, rodent gnawing, and recently dead branches (Resler and Tomback, 2008). The following categories were used to classify canopy kill: 1 (0%), 2 (1 to 5%), 3 (6 to 25%), 4 (26 to 50%), 5 (51 to 75%), 6 (76 to 95%), and 7 (96 to 100%). This protocol was previously used by Resler and Tomback (2008) to assess whitebark pine for blister rust in the two Rocky Mountain Front study sites.

DATA ANALYSIS

We examined data at multiple scales, from individual transect to study site to study area, and across regions, and include data from Resler and Tomback (2008) in tables and figures for comparison. We did not adjust data for departures from 500 m^2 in sampling area for Stanley Glacier Transect 2 or for the five Lee Ridge transects, because the alteration in sampling was initially intended to compensate for differences in tree density.

We used the Binomial Distribution (Sokal and Rohlf, 1981) function in Microsoft Excel (2010, Microsoft Office, Microsoft Corporation) to calculate the probability of occurrence of a given proportion of whitebark pine among solitary trees, tree islands, and among conifer species initiating tree islands. The function takes the form BINOM.DIST (number_s, trials, probability_s, cumulative), but we designated *false* for cumulative to calculate the mass probability function. We computed the exact probability of observing the proportion of whitebark pine, or the conifer species in question, if the theoretical proportion, which varied by transect and study site, reflected an equally probable distribution among the most common conifer species. If only one conifer species occurred within a study site or study area in addition to whitebark pine, the theoretical proportion was 0.5. If three conifer species occurred commonly, the theoretical distribution was 0.333, and if four, 0.250. The proportional occurrence of each conifer species within tree islands could be as great as 1.00 at the same time, because the presence of one species does not preclude the presence of others, but we compared prevalence

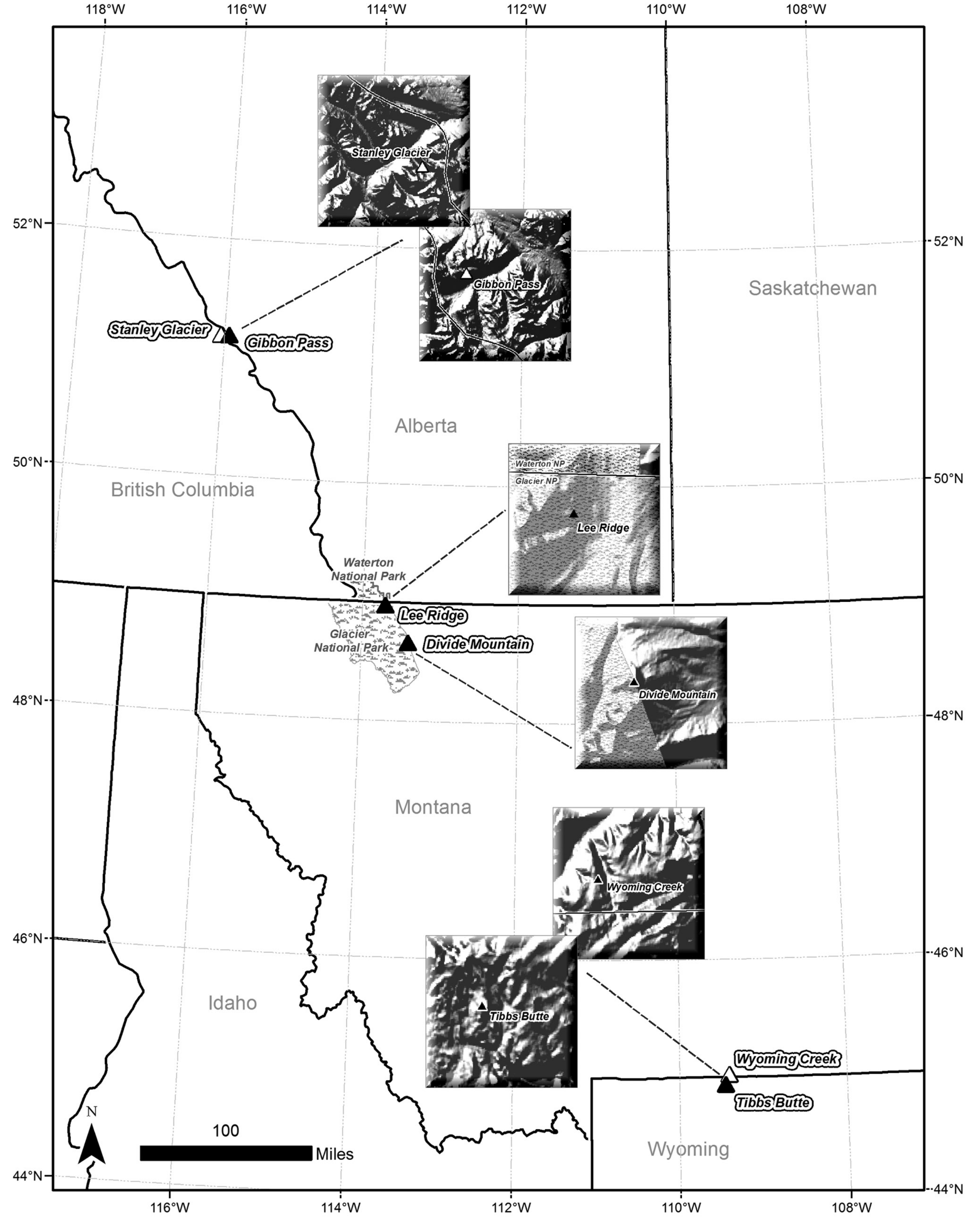

FIGURE 1. Map of study sites sampled within study areas designated "northern," which includes Banff and Kootenay National Parks; "Rocky Mountain Front," which includes Glacier National Park and the Blackfeet Indian Reservation, previously sampled by Resler and Tomback (2008); and, "southern," which comprises the Beartooth Plateau.

among conifer species by assuming they would add up to 1.00 . Thus, the use of the Binomial Distribution for this analysis must be interpreted cautiously.

The lengths of tree islands could be normalized by log transformations, but variances were not equal; thus, lengths were compared among the three study regions by means of Kruskal-Wallis One Way ANOVA (Statistix 9, Analytical Software, Tallahassee, Florida). For all statistical tests, we used $\alpha = 0.05$.

Results

SOLITARY TREE AND TREE ISLAND NUMBER, DENSITY, SPECIES RICHNESS, AND INITIATING MICROSITE SHELTER

Across the southern and northern study areas, the number of solitary trees per transect ranged from 6 to 88 and generally outnumbered the number of tree islands per transect (Table 2). Solitary trees ranged in density from 0.012 to 0.176 trees m^{-2} per transect. The southern study area transects had the most consistent numbers, and thus densities, of solitary trees per transect., The three transects from the Gibbon Pass study site in the northern study area varied the most in solitary tree number within a study site. Data from Resler and Tomback (2008) indicated considerable variation in solitary tree number among transects from their Divide Mountain study site in the Rocky Mountain Front study area (Table 2).

Most transects across the southern and northern study areas supported from 3 to 5 tree islands each, with the density of tree islands ranging from 0.004 to 0.020 m^{-2} (Table 2). Transect 2 at Stanley Glacier had the highest tree island density of all, but under-represented the potential number of tree islands because of its shorter length. The five transects sampled by Resler and Tomback (2008) in the Lee Ridge study site on the Rocky Mountain Front also showed high variation in tree island number from transect to transect (Table 2).

Whitebark pine, Engelmann spruce (*Picea engelmannii*), and subalpine fir occurred in all northern and southern study areas (Fig. 2, Tables 3 and 4). Several conifer species were sampled in only one study site: lodgepole pine (*Pinus contorta*) (Wyoming Creek), alpine larch (*Larix lyallii*) (Gibbon Pass), and common juniper (*Juniperus communis*) (Stanley Glacier).

The Rocky Mountain Front study sites sampled by Resler and Tomback (2008) included whitebark pine and six other conifer species comprising solitary trees and tree islands (lodgepole pine, limber pine [*Pinus flexilis*], Engelmann spruce, subalpine

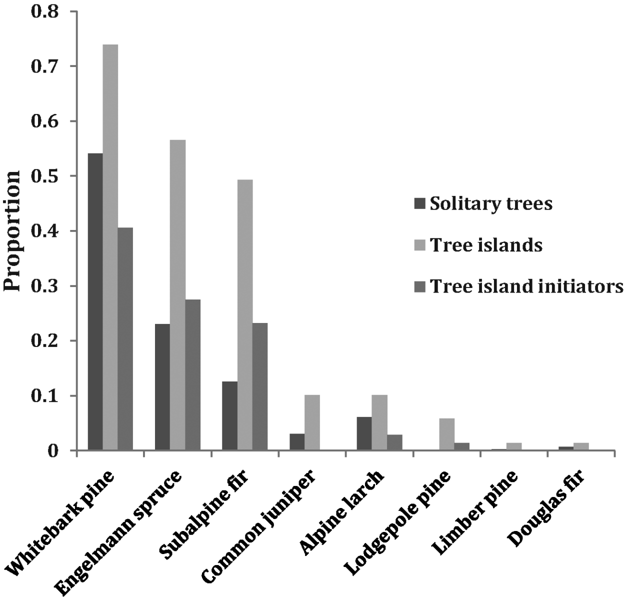

FIGURE 2. The overall proportional occurrence of conifer species among solitary conifers, tree islands, and among tree island initiating conifers, sampled across all study sites including the Rocky Mountain Front (Resler and Tomback, 2008). For solitary trees and conifers initiating tree islands, the proportional occurrence was based on the summed number across study sites. For conifer occurrence across tree islands, the proportion was based on the occurrence of one or more stems of that conifer (counting as one occurrence) within the tree island, so proportions are independent among conifers.

TABLE 2

The most frequent microsite shelter, numbers of solitary trees and tree islands per transect, and density in numbers per m^2. Two 500 m^2 transects were sampled in each study site, with the following exceptions: Stanley Glacier Transect 2, 250 m^2; Lee Ridge, five transects, 750 m^2 each; Divide Mountain, five transects, 500 m^2 each (Resler and Tomback, 2008).

Study area	Southern: Beartooth Plateau				Northern: Kootenay NP/Banff NP					Rocky Mountain Front	
Study site	Tibbs Butte		Wyoming Creek		Stanley Glacier		Gibbon Pass			Divide Mtn.	Lee Ridge
Transect	1	2	1	2	1	2	1	2	3	Range, $\bar{x} \pm SD$	Range, $\bar{x} \pm SD$
No. and density of solitary trees	21 0.042	20 0.040	26 0.052	19 0.038	12 0.024	30 0.12	9 0.018	6 0.012	88 0.176	6–39, 24.2 ± 13.9 Total = 121 0.048	14–27, 21.6 ± 5.2 Total = 108 0.029
No. and density of tree islands	3 0.006	4 0.008	5 0.010	2 0.004	3 0.006	5 0.020	3 0.006	4 0.008	5 0.010	1–4, 2.6 ± 1.1 Total = 13 0.005	0–8, 4.4 ± 3.3 Total = 22 0.006
Total solitary trees and tree islands	24	24	31	21	15	35	12	10	93	7–42, 26.8 ± 14.4 Total = 134	14–32, 26.8 ± 7.0 Total = 130
Micro-site shelter	Rocks	Rocks	Shrubs	Topo[1]	Rocks	Rocks	Shale	Shale	Rocks, topo[1]	Topo[1]	Topo[1]

[1] Topo = topographic feature, such as a depression or patterned ground.

TABLE 3

Species composition by number and proportion among solitary trees across all treeline study sites and study areas in the southern study area (Beartooth Plateau), Rocky Mountain Front study area (sampled by Resler and Tomback, 2008), and northern study area (Kootenay/Banff National Parks). Study area proportions calculated from total trees of each species. Sampling based on five 750 m² transects for Lee Ridge, five 500 m² transects for Divide Mountain, and two 500 m² transects for all other study sites, except for Transect 2, Stanley Glacier (250 m²). The probability of obtaining a given number of whitebark pine out of total solitary trees at each spatial scale is calculated from the Binomial Distribution function. See text for explanation.

Study Area	Southern: Beartooth Plateau				Northern: Kootenay NP/Banff NP					Rocky Mountain Front	
Study Site	Tibbs Butte		Wyoming Creek		Stanley Glacier		Gibbon Pass			Divide Mtn.	Lee Ridge
Transect	1	2	1	2	1	2	1	2	3	Range, x̄ ± SD	Range, x̄ ± SD
Whitebark pine	8	16	18	13	6	14	6	2	16	3–28	10–17
	0.381	0.800	0.692	0.684	0.500	0.467	0.667	0.333	0.182	15.4 ± 9.30	14.6 ± 2.8
	0.585		0.698		0.476		0.233			0.636	0.676
	0.640				0.303					0.655	
Limber pine	0	0	0	0	0	0	0	0	0	0	0–1
	0	0	0	0	0	0	0	0	0	0	0 0.2 ± 0.4
	0		0		0		0			0	0.009
	0				0					0.004	
Engelmann spruce	13	4	8	3	5	6	0	0	39	1–9	1–4
	0.619	0.200	0.308	0.158	0.417	0.200	0	0	0.443	3.4 ± 3.4	2.4 ± 1.1
	0.415		0.244		0.262		0.379			0.140	0.102
	0.326				0.345					0.122	
Subalpine fir	0	0	0	3	1	0	2	4	6	1–10	0–8
	0	0	0	0.158	0.083	0	0.222	0.667	0.068	4.8 ± 4.4	3.6 ± 3.4
	0		0.067		0.024		0.117			0.198	0.167
	0.035				0.090					0.183	
Douglas-fir	0	0	0	0	0	0	0	0	0	0–1	0–1
	0	0	0	0	0	0	0	0	0	0.2 ± 0.4	0.4 ± 0.5
	0		0		0		0			0.008	0.019
	0				0					0.013	
Alpine larch	0	0	0	0	0	0	1	0	27	0	0
	0	0	0	0	0	0	0.111	0	0.307	0	0
	0		0		0		0.272			0	0
	0				0.193					0	
Common juniper	0	0	0	0	0	10	0	0	0	0–1	0–1
	0	0	0	0	0	0.333	0	0	0	0.4 ± 0.5	0.2 ± 0.4
	0		0		0.238		0			0.017	0.019
	0				0.069					0.017	
Binomial distribution probability for whitebark pine occurrence	0.381	0.800	0.692	0.684	0.500	0.467	0.667	0.333	0.182	0.636	0.676
	0.0970[2]	*0.0046*[2]*	*0.0233*[2]*	*0.0015*[1]*	*0.1109*[1]	*0.0460*[1]*	*0.0340*[1]*	*0.2344*[2]	*0.0007*[1]* (lower)	*0.0000*[1]*	*0.0000*[1]*
	0.585		0.689		0.476		0.233				
	0.0689[2]		*0.0047*[2]		*0.0195*[1]*		*0.0079*[1]* (lower)				
	0.640				0.303					0.655	
	0.0030[2]*				0.0538[1]					*0.0000*[1]*	

Notes: [1]Theoretical proportion of whitebark pine as 0.333. [2]Theoretical proportion of whitebark pine as 0.500. *Statistical significance set at α = 0.05.

TABLE 4

Proportion of tree islands with each conifer species across study sites in the southern and northern study areas, with data collected from the Rocky Mountain Front by Resler and Tomback (2008) for comparison. The exact probability of the occurrence of whitebark pine across tree islands is calculated from the binomial distribution function; see text for description.

Study area	Southern: Beartooth Plateau				Northern: Kootenay NP, Banff NP					Rocky Mountain Front	
Study site	Tibbs Butte		Wyoming Creek		Stanley Glacier		Gibbon Pass			Divide Mtn.	Lee Ridge
Transect	1	2	1	2	1	2	1	2	3	Range, overall	Range, overall
Whitebark Pine	1.00	0.750	0.600	1.00	1.00	0.800	0.330	0	0.200	0.67–1.0 0.923	0.5–1.0 0.864
Limber pine	0	0	0	0	0	0	0	0	0.	0	0–0.12 0.045
Lodgepole pine	0	0	0.400	0	0	0	0	0	0	0–0.333 0.154	0
Engelmann spruce	1.00	1.00	1.00	0	0	0.200	1.00	0.500	0.800	0–1.0 0.615	0.17–1.0 0.409
Subalpine fir	0	0	0	0	0	0.400	1.00	1.00	0.200	0.5–1.0 0.846	0–0.75 0.591
Douglas fir	0	0	0	0	0	0	0	0	0	0	0–0.17 0.045
Alpine larch	0	0	0	0	0	0	0.330	0.500	0.800	0	0
Common juniper	0	0	0	0	0	0.400	0	0	0	0–0.67 0.385	0
Overall prop whitebark pine, *P*	0.857, *0.0547*[2]		0.714, *0.0383*[1] *		0.875, *0.0024*[1]*		0.167, *0.2323*[3]			0.886, *0.0000*[1] *	
	0.786, *0.0222*[2] *				0.450, *0.0983*[1]						

Notes: Theoretical proportion of whitebark pine 0.333[1] and 0.500[2], 0.250[3]. Statistical significance set at $\alpha = 0.05$*. The italics are all statistical probability values associated with the binomial distribution. The non-italicized values are proportions of whitebark pine.

fir, Douglas-fir [*Pseudotsuga menziesii*, and common juniper]) (Fig. 2, Tables 3 and 4). These study sites had greater conifer species richness than the northern study area with five species (Tables 3 and 4).

The most frequent microsite shelter initiating tree islands for the southern and northern study areas was rocky material, which varied with the parent bedrock. For example, in the northern study area weathered shale predominated (Table 2). For the Rocky Mountain Front, however, Resler and Tomback (2008) found that small topographic features, such as depressions or patterned ground, most frequently sheltered the initiating conifer.

SOLITARY TREE COMPOSITION AND WHITEBARK PINE PREVALENCE

Across the northern and southern study areas, whitebark pine comprised 0.428 of the solitary trees sampled, and the next most common conifer, Engelmann spruce, comprised 0.338. In the southern study area alone, more than half of the solitary trees were whitebark pine with spruce again the next most common conifer (Fig. 2, Table 3).

For the northern study area, the solitary trees sampled included five conifer species. Whitebark pine and Engelmann spruce were the two most common conifer species among solitary trees, but varied in occurrence with study site and transect (Fig. 2, Table 3). Subalpine fir, juniper, and alpine larch accounted for small proportions of the solitary trees. On the Stanley Glacier transects, nearly half the solitary trees were comprised of whitebark pine, followed in relative abundance by Engelmann spruce and juniper, with only one subalpine fir. At Gibbon Pass, whitebark pine prevalence varied among the three transects, but represented only about a quarter of the solitary trees overall. Subalpine fir and alpine larch occurred as well on these transects. Transect 3, the only transect in the northern study area with a northeastern aspect, had the greatest number of solitary trees, the smallest relative proportion of solitary whitebark pine, and supported the only Engelmann spruce sampled at Gibbon Pass, but also had the highest number and proportion of alpine larch.

The solitary trees sampled on the Rocky Mountain Front by Resler and Tomback (2008) were the most diverse of all study areas, with six species represented (Table 3). Overall, whitebark pine was the most abundant conifer among the solitary trees, and showed the highest relative abundance of all study areas. Whitebark pine was most abundant on Lee Ridge, exceeded in prevalence only at Wyoming Creek in the southern study area.

Calculated across all study areas, including the Rocky Mountain Front (Resler and Tomback, 2008), more than half the solitary trees sampled on transects were whitebark pine, followed in occurrence by Engelmann spruce, and subalpine fir (Table 3, Fig. 2). Reflecting this trend, the overall proportional occurrence of whitebark pine among solitary trees per study area was 0.541. Assuming three dominant conifer species across the study areas, with a theoretical probability of occurrence of 0.333, the proportional occurrence of whitebark pine was highly statistically significant ($P = 0.0000$).

Binomial tests comparing the relative proportion of dominant conifers among solitary trees indicated that whitebark pine was significantly prevalent in the southern study area, but not on Tibbs Butte, and significantly prevalent on the Rocky Mountain Front, based on the data from Resler and Tomback (2008) (Table 3). Whitebark pine showed a trend in prevalence overall in the northern study area, but not on Gibbon Pass, where it was under-represented.

TREE ISLAND SIZE, COMPOSITION, AND WHITEBARK PINE PREVALENCE

Whitebark pine occurred in 0.588 of all tree islands sampled across the southern and northern study areas, and Engelmann spruce occurred in 0.647 of the tree islands (Table 4, Fig. 3). Whitebark pine had high prevalence among tree islands in all study sites that we sampled except for Gibbon Pass (Fig. 3, Table 4). Whitebark pine prevalence within tree islands sampled on the Rocky Mountain Front was highest overall, followed by subalpine fir and Engelmann spruce (Resler and Tomback 2008) (Table 4). Of the 69 tree islands examined in the three study areas combined, whitebark pine was by far the most prevalent of all species (Fig. 3). The next most frequent conifer species among tree islands overall were Engelmann spruce and subalpine fir. Other conifers occurred within only about a tenth or fewer of the tree islands (Fig. 3).

Between the southern and northern study areas, the longest tree islands occurred in the northern study area, and particularly at Gibbon Pass (Table 5). However, tree island lengths collected from the Rocky Mountain Front (Resler and Tomback, 2008) were greater overall, but the differences were not statistically significant (Kruskal-Wallis One-Way ANOVA, KW = 1.787, $P = 0.4091$).

TREE ISLAND INITIATORS AND WHITE PINE BLISTER RUST

Of the 34 tree islands that we sampled across the southern and northern study areas, whitebark pine served as the windward conifer, or likely initiator, for 10 tree islands or 29.4% (Binomial Distribution, theoretical probability = 0.333, $P = 0.1322$), which was not statistically significant. For the 35 tree islands in the Rocky Mountain Front study area examined by Resler and Tomback (2008), our reanalysis indicated that whitebark pine was the windward initiator for 18 or 51.4%, which was statistically significant (Binomial Distribution, theoretical probability = 0.333, $P = 0.0118$). Combining the tree islands sampled across all three study areas, we determined that whitebark pine served as the windward conifer, or likely tree island initiator, for 28 or 0.406 of these multi-tree tree islands (Fig. 2). Engelmann spruce and subalpine fir were next most frequent in occurrence as initiators across study areas, and lodgepole pine, alpine larch, and dead tree stems (whitebark pine) were rarely the windward conifers. Given a total of three major conifers as common tree island initiators, the greater occurrence of whitebark pine was statistically significant for this overall sample (Binomial Distribution, theoretical probability 0.333, $P = 0.0439$); but because of the higher number of tree islands on the Rocky Mountain Front, these results must be interpreted cautiously.

In the southern study area, Engelmann spruce occurred more frequently (0.714) as an initiator than whitebark pine (0.285) but not significantly so (Binomial test, theoretical probability = 0.500, $P = 0.061$). At the Wyoming Creek study site, however, whitebark pine (0.429) and Engelmann spruce (0.571) were both frequent initiators, differing in prevalence by only one tree island. In the northern study area, subalpine fir was the most frequent tree island initiator (0.400) followed by whitebark pine (0.300), Engelmann spruce (0.200), and alpine larch (0.100). Whitebark pine, however, was the most frequent tree island initiator at the Stanley Glacier study site (0.750) (theoretical probability = 0.333, $P = 0.0170$). At Gibbon Pass, whitebark pine was absent as an initiator among sampled transects.

In the southern study area, we did not detect blister rust within the Tibbs Butte transects. However, we noticed a whitebark pine with an active canker outside one transect. At the Wyoming Creek study site, cankered trees occurred on both transects: two trees had one inactive canker each and one tree had two active cankers for a total of three infected trees. Based on estimated numbers of whitebark pine on both transects, the incidence was about 3 out of

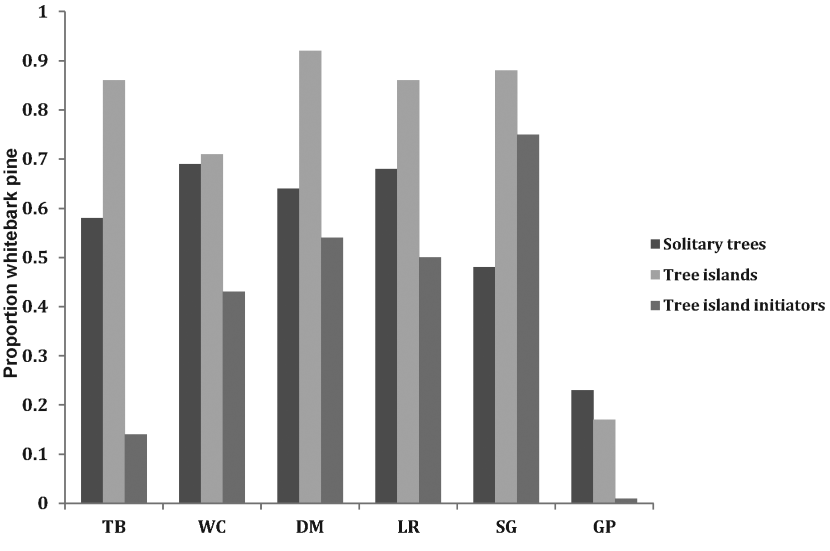

FIGURE 3. Proportional occurrence of whitebark pine among solitary conifers, among tree islands, and among initiating conifers of tree islands per study site (TB = Tibbs Butte, WC = Wyoming Creek, DM = Divide Mountain, LR = Lee Ridge, SG = Stanley Glacier, GP = Gibbon Pass). For solitary trees and tree island initiating conifers, the proportional occurrence was based on the summed number within each study site. For conifer occurrence across tree islands, the proportion was based on the occurrence of one or more stems of that conifer in any given tree island within, so proportions are independent among conifers. Previously sampled data from the Rocky Mountain Front study sites (Resler and Tomback, 2008) were included for comparison.

TABLE 5

Longest dimension (m) of tree islands sampled for all study sites in the southern and northern study areas. Data from the Rocky Mountain Front are provided for comparison (Resler and Tomback, 2008).

Study area	Study site	Range	Mean	S.D.
Southern	Tibbs Butte	2.40–9.67	4.10	2.64
	Wyoming Creek	1.82–5.08	3.50	1.07
Rocky Mtn. Front	Divide Mtn.	0.82–35.00+	8.22	9.94
	Lee Ridge	0.29–35.00+	7.52	11.56
Northern	Stanley Glacier	1.00–7.35	5.23	3.66
	Gibbon Pass	0.65–11.06	5.36	3.45

39 trees or 7.7%. Canopy kill class for infected trees ranged from 3 to 4, indicating loss of up to 50%.

In the northern study area, no blister rust was recorded on the Gibbon Pass plots, but we found blister rust on Transect 1 at the Stanley Glacier study site. Six trees were infected with a total of 10 cankers, for an average of 1.7 cankers per tree, distributed as follows: 5 probable cankers, 2 inactive cankers, and 3 active cankers. The active cankers occurred on three different trees, and an inactive canker on one additional tree. Based on an estimated 37 total whitebark pine on both Stanley Glacier transects, the incidence of infected trees was 6 out of 37 trees or 16.2% for all cankers, or 10.8% for only active and inactive cankers. Canopy kill class was 2 or 3 for infected trees, indicating a range of canopy loss from about 1% to 25%. Several trees without identifiable cankers in all of our study areas were found to have symptoms of blister rust, including rodent gnawing of stems and branches, dead foliage, and canopy kill. However, we considered the presence of cankers to be the definitive indicator of infection.

As previously reported by Resler and Tomback (2008), blister rust incidence in whitebark pine assessed for the Rocky Mountain Front transects overall was 33.7%, including all categories of blister rust cankers—active, inactive, and potential. Based on the more conservative categories of active and inactive cankers only, overall 24.3% of the sampled whitebark pine were infected.

Discussion

Our objectives for this exploratory study were to examine the distribution and role of whitebark pine and incidence of blister rust, in regions north and south of the Rocky Mountain Front, and to compare the results with Resler and Tomback (2008). We found that whitebark pine, which was present on all transects, comprised an important component of treeline communities in both the southern and northern study areas, although its abundance and ecological role varied with study site. Nearly half the solitary trees sampled across the northern and southern study areas were whitebark pine. Whitebark pine was also the most prevalent conifer species among tree islands at three of the four study sites. Across both study areas, whitebark pine served as tree island initiator for 29.4% overall of the tree islands sampled, but was more prevalent as an initiator within two study sites. We found white pine blister rust in both the southern and northern study areas, but at lower infection rates than within the Rocky Mountain Front study sites (Resler and Tomback 2008). Overall, however, the Rocky Mountain Front study area had a higher proportion of whitebark pine among solitary trees, a higher prevalence of whitebark pine among tree islands, and a higher proportion of tree islands initiated by whitebark pine than did the northern and southern study areas combined (Resler and Tomback, 2008).

Whitebark pine was more prevalent among solitary trees in the southern study area than in the northern study area, with the greatest abundance in the Wyoming Creek study site; although less prevalent across the northern study area, it was present among solitary trees on every transect sampled. Its dominance among solitary trees in the southern study area was similar to its occurrence in the Rocky Mountain Front study area (Resler and Tomback, 2008). Although whitebark pine occurred widely among tree islands, except for one transect at Gibbon Pass, our results indicated that Engelmann spruce was slightly more prevalent among tree islands overall, because of its abundance in the Gibbon Pass study site.

Whitebark pine was most prevalent as a tree island initiator within the Stanley Glacier study site, even exceeding its occurrence as initiator in the Rocky Mountain Front study area (Resler and Tomback, 2008). Whitebark pine and Engelmann spruce had nearly equal prevalence as initiators within the sampled transects at the Wyoming Creek study site, but recent, intensive sampling over a much wider area (Smith-McKenna et al., unpublished data) indicated that whitebark pine is the majority tree island initiator there, suggesting some limitations to our exploratory sampling. In fact, we had placed the original transects on the northeast-facing slope in an atypical area of late-lying snowpack, characterized by a high density of willow (*Salix* spp.) clumps. These clumps provided shelter for initiator establishment, as indicated for Transect 1 in Table 2, and may have enabled tree island development without a lead whitebark pine in several instances.

Slope aspect alone did not predict whitebark pine prevalence or its role as a tree island initiator. For example, the prevalence and role of whitebark pine varied across northeast aspects. Whitebark pine was least prevalent as a treeline species and tree island initiator at Gibbon Pass and particularly on Transect 3, which had a northeast exposure. Alpine larch and Engelmann spruce both comprised most of the solitary trees on this transect and were the main components of tree islands for this study site, although alpine larch at Gibbon Pass was near its northernmost distributional limit. Alpine larch is most abundant on cool, snowy, north-facing slopes (Arno, 1990), whereas whitebark pine at more northern latitudes tends to be less abundant on colder aspects and patchier in occurrence (Arno and Hoff, 1990).

Solitary trees likely serve as initiating conifers for tree islands, potentially offering a protected microsite on their leeward side. Tree islands may start when a nutcracker caches whitebark pine seeds leeward of a solitary tree or wind-blown seeds germinate in substrate leeward of a solitary tree (Malanson et al., 2007). The established solitary tree may offer leeward protection from solar radiation, wind, and extreme temperatures, or provide moister soil or a nutrient-rich environment, thus facilitating the survival and growth of the next conifer (Maher et al., 2005). The combined protection from two or more conifers may then lead to development over time of a larger tree island. Solitary trees potentially lead to development of treeline vegetation at a landscape scale, particularly as climate warms and the elevation of treeline rises. By extrapolation from its prevalence, whitebark pine plays an important ecological role in developing landscape vegetation (Tomback and Resler, 2007; Resler and Tomback, 2008).

Is whitebark pine a majority tree island initiator in some locations because nutcrackers place it in sheltered locations, it has superior hardiness, or it offers greater microsite protection than other conifer species? All factors may contribute, including adaptive physiology (e.g., Maher et al., 2005; Bansal et al., 2011). Regardless of mechanism, the role of whitebark pine as a widespread treeline component and tree island initiator extends the list of ecological functions and ecosystem services provided by this high elevation species (Callaway, 1998; Tomback et al., 2001b; Tomback and Achuff, 2010).

Both of these ecological roles are threatened by white pine blister rust. The spread of blister rust to treeline communities was considered unlikely (e.g., Campbell and Antos, 2000), given that some stages of the *Cronartium ribicola* life cycle require high humidity and moderate temperatures (e.g., McDonald and Hoff, 2001; Geils et al., 2010). The Yellowstone Plateau was previously described as a low hazard region because of a principally cold, dry climate, but blister rust infection levels in this region have increased steeply within the last decade (Jean et al. 2011; Bockino and Tinker, 2012). Here, we show that *Cronartium ribicola* is infecting treeline whitebark pine across at least 6° latitude, and that some areas, such as the Rocky Mountain Front, are experiencing tree damage and mortality and potential disruption of whitebark pine's ecological function. Climate warming trends may be accelerating the spread of blister rust to treeline communities as well as increasing infection rates in upper subalpine communities. Climate trends in western Montana over the last century show fewer days of extreme cold, an increase in extremely hot days, and a lengthening of the number of days during which warm temperatures occur each year (Pederson et al., 2010).

The highest blister rust infection levels for whitebark pine at subalpine elevations within its entire North American range are reported for the Northern Divide of the Rocky Mountains. Glacier National Park, the Blackfeet Indian Reservation, and the contiguous Waterton Lakes National Park, Alberta, Canada, support overall infection levels of 73% and as high as 100% on individual plots (Kendall and Keane, 2001; Smith et al., 2008). Assessing six other treeline sites in Glacier National Park, Smith et al. (2011) found blister rust infection levels ranging from 33 to 96%, suggesting that treeline along the Rocky Mountain Front actually has a lower infection level, possibly because of the cool, dry, and windy conditions found east of the Continental Divide (Finklin, 1986; Walsh et al., 1992).

Given the current prevalence of blister rust in the Glacier National Park and Rocky Mountain Front communities, a large-scale decline of whitebark pine at treeline appears imminent. The loss of whitebark pine could change the dynamics of tree island establishment, especially under harsh conditions where facilitation appears most important; this could inhibit the response of treeline to warming temperatures. Tomback and Resler (2007) presented a conceptual model illustrating the steps in this process that potentially reduce whitebark pine's facilitative role in tree island development: First, whitebark pine populations decline at treeline as damage and mortality from blister rust reduces whitebark pine seed production in the upper subalpine and as blister rust kills established treeline whitebark pine. Next, with fewer whitebark pine at upper treeline, fewer tree islands may be initiated through facilitation, despite warming trends. Consequently, treeline may be slow to respond to climate warming. The impact of these events on regional treeline will depend on the local prevalence and importance of whitebark pine.

As whitebark pine declines from blister rust and other threats, the ecosystem services it provides will also decline (Tomback and Achuff, 2010; Tomback et al., 2011), including its facilitative role at upper treeline. We encourage restoration projects for whitebark pine that include planting blister rust–resistant seedlings at treeline in protective microsites and also in upper subalpine forests contiguous with treeline to provide future seed sources (e.g., Tomback and Achuff, 2010; Schwandt et al., 2010; Keane et al., 2012).

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