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Climatic Correlates of White Pine Blister Rust Infection in Whitebark Pine in the Greater Yellowstone Ecosystem

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Abstract: Whitebark pine, a foundation species at tree line in the Western U.S. and Canada, has declined due to native mountain pine beetle epidemics, wildfire, and white pine blister rust. These declines are concerning for the multitude of ecosystem and human benefits provided by this species. An understanding of the climatic correlates associated with spread is needed to successfully manage impacts from forest pathogens. Since 2000 mountain pine beetles have killed 75% of the mature cone-bearing trees in the Greater Yellowstone Ecosystem, and 40.9% of monitored trees have been infected with white pine blister rust. We identified models of white pine blister rust infection which indicated that an August and September interaction between relative humidity and temperature are better predictors of white pine blister rust infection in whitebark pine than location and site characteristics in the Greater Yellowstone Ecosystem. The climate conditions conducive to white pine blister rust occur throughout the ecosystem, but larger trees in relatively warm and humid conditions were more likely to be infected between 2000 and 2018. We mapped the infection probability over the past two decades to identify coarse-scale patterns of climate conditions associated with white pine blister rust infection in whitebark pine.

Keywords: white pine blister rust; *Cronartium ribicola*; whitebark pine; *Pinus albicaulis*; Greater Yellowstone Ecosystem; relative humidity

1. Introduction

Forest pathogens are a significant contributor to global forest decline [1–3] and non-native pathogens can decimate naïve host species, leading to significant disruption in ecosystem structure and function (e.g., Chestnut blight [4]). Live plant imports are a major vector for the introduction of many non-native pathogens [5], including white pine blister rust, caused by the fungus *Cronartium ribicola.* White pine blister rust was introduced to both coasts of North America on European nursery stock in the early 1900s [5,6], and has since become one of the most detrimental exotic pathogens, affecting all species of North American white pines [7,8]. Though not as commercially valuable as other white pine species, whitebark pine (*Pinus albicaulis*) is a primary contributor to the biodiversity and productivity of high-elevation forests and alpine communities in the interior Pacific Northwest, northern Rocky Mountains, and northern Sierra Nevadas [9]. In the western U.S., white pine blister rust affects whitebark pine, limber pine (*Pinus flexilis*), and western white pine (*Pinus monticola*). White pine blister rust was first observed in the Greater Yellowstone Ecosystem (GYE) in 1937 [10].

Recent declines in whitebark pine have been recorded throughout its range, as a result of biotic and abiotic drivers, including white pine blister rust, native mountain pine beetle (*Dendroctonus ponderosae*), wildland fire, and drought [11–15]. The mountain pine beetle outbreak in the GYE from the early 2000s to around 2010 killed approximately 75% of mature, canopy-occupying trees [16,17] when warmer than normal temperatures induced faster growth and synchronous emergence of the beetles [15,18]. Because mountain pine beetles attack large-diameter trees [19], a climate-induced shift to smaller size class trees has occurred region-wide since 2000 [15]. Historically, epidemic outbreaks of mountain pine beetle have occurred during periods of unusual warmth, such as in the 1930s. These types of periodic outbreaks have abated with cooler temperatures, but continued warming will maintain the susceptibility of whitebark pine to attack [20,21]. While mountain pine beetles selectively attack large-diameter trees, white pine blister rust, now persistent and pervasive in the GYE, infects and kills trees of all sizes and is currently considered the pathogen of greatest concern in GYE whitebark pine forests [15]. White pine blister rust infection is more imminently lethal in smaller diameter trees than in larger trees, because it has less distance to travel from needle to bole, where it girdles and kills trees [22]. However, in larger trees, it can limit the reproductive potential through top-kill, where cone production is greatest even if larger trees survive longer. Larger diameter trees are more likely to be infected due to a greater leaf surface area, which can intercept airborne spores [23–25]. With the loss of cone-producing, mature trees, altered fire regimes, and the presence of a pathogen that kills trees of all size classes, the fate of whitebark pine in the GYE is uncertain [26].

The life cycle of white pine blister rust is linked to the biophysical conditions under which spores germinate and disseminate between intermediary hosts including white pines, *Ribes* spp., *Pedicularis* spp., and *Castillija* spp. [27,28]. Each of the five stages of sporulation (spermatia, aeciospore, urediniospore, teliospore, basidiospore) require a unique suite of temperature, moisture, and time criterion in order to advance in development [29–32]. While each stage is critical for the successful completion of the life cycle, the basidiospore phase produces the inoculum responsible for white pine blister rust infection in whitebark pine [7]. In the GYE, the dispersal of inoculum takes place from August through to September, and is considered the most limiting developmental phase for white pine blister rust in this region [6,33]. Under optimal conditions for transmission, rapid expansion into new locations and an intensification of the infection can occur in a given area, which is referred to as a wave event [29]. Wave year conditions are marked by multiple periods of high relative humidity in the summer and fall that lead to new or increased infection [30]. Once infected, it takes two to four years for a white pine blister rust canker to become visible [11,33,34].

Tree diameter at breast height (DBH) is positively correlated with infection probability [25,35,36] and studies have also described relationships between white pine blister rust and topographic and climatic variables, specifically summer rain and elevation [25,36–38]. Recent studies in the Western U.S. linked white pine blister rust infection to regional weather [24] and latitude in the whitebark pine range in British Columbia [23]. However, finer scale relationships between white pine blister rust and climate were established in the 1950s from studies in the Great Lakes region, where infection was related to distance from shore, wind currents, solar radiation, and humidity [30,31]. Similar to early work near the Great Lakes, proximity to streams and wet landscape positions increased infection rates [24], as did fine-scale microclimates mediated by topography and landscape position [39]. Thus, weather on short time scales, from hours to weeks, and persistent regional climate patterns are linked to white pine blister rust geography and prevalence. Prior to the recent advent of high-resolution climate data sets, it has been difficult to characterize mountain climates at fine spatial scales in a large, complex region like the GYE.

In the GYE, environmental conditions throughout the region are compatible with the spread of white pine blister rust, as evidenced by its region-wide presence. This suggests it is possible that the spatial distribution of whitebark pine in combination with time may be the best indicator of the historic and future dispersal of white pine blister rust infection. Alternatively, white pine blister rust patterns in the GYE today may be linked to persistent climate patterns that are generally drier in the southeast and wetter in the northwest regions of the ecosystem [40]. Such persistent climate patterns may result in a wave year frequency that also varies by region. That is, wave years may occur more frequently in the northwest region. The wide range in climate conditions in whitebark pine habitat across the GYE presents an opportunity to determine if climate conditions or merely a regional pattern of infection best explain white pine blister rust distribution. Understanding dominant environmental drivers or spatial patterns of white pine blister rust can indicate where it may be most damaging in the future. Such information could be used to select locations for restoration and bolster already strong cross-boundary collaborations in the GYE, which include multiple management jurisdictions with different management paradigms [26].

In combination with gridded climate data, we used repeat observations of tagged whitebark pine trees throughout the GYE to determine if spatial location was a more reliable indicator of the probability of white pine blister rust infection than biologically meaningful climate variables. Specifically, at the tree level, we assessed if selected climate variables averaged over time at each location were more effective at determining the presence of white pine blister rust infection than location alone.

2. Materials and Methods

2.1. Study Area

The study area encompassed the GYE, which includes five national forests (NF), two national parks (NP), and state and private lands in portions of Wyoming, Montana, and Idaho (Figure 1). Geographically, the GYE is comprised of the Yellowstone Plateau volcanic fields and 14 surrounding mountain ranges above 2130 m [41]. In this region, whitebark pine stands occupy over 800,000 hectares [42].

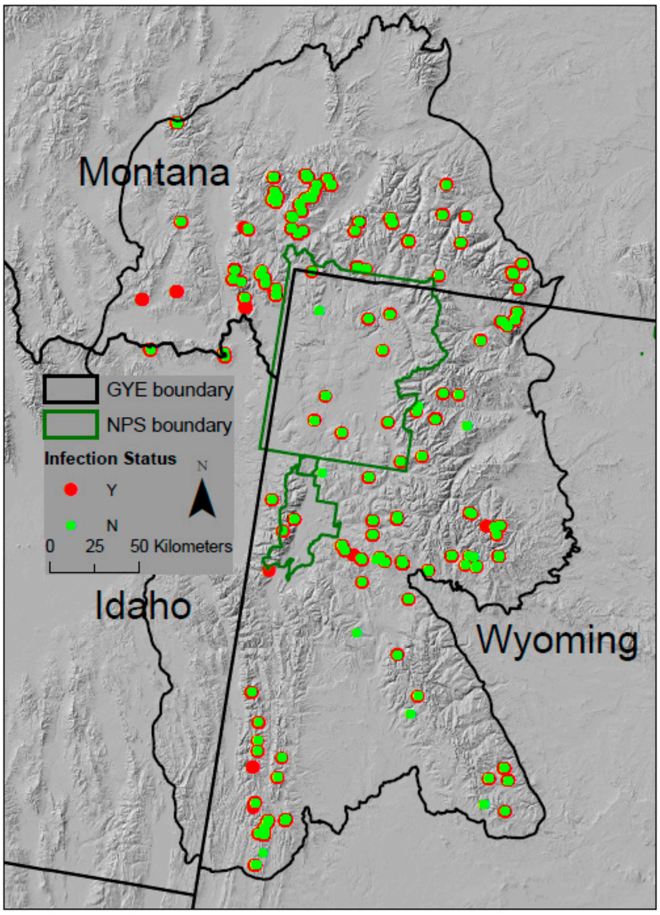


Figure 1. Location of 176 long-term monitoring transects in the Greater Yellowstone Ecosystem (GYE) and distribution of white pine blister rust infected and uninfected transects monitored between 2004 and 2018. Infection status is mapped with different sized symbols, such that overlapping points representing infected (Y) and uninfected (N) trees in the same transect can be seen.

2.2. Field Sampling for Infection Status

We monitored 5138 trees between 2004 and 2018 on a four-year revisit schedule to determine if trees were infected at any time during the study period or remained uninfected during the study. We established 176 permanent 10 × 50 m transects in randomly selected stands of pure and mixed whitebark pine ≥2.0 ha ([42], Figure 1) between 2400–3172 m in elevation. All live whitebark >1.4 m tall within the transect boundaries were permanently marked and biometrics, including DBH and signs of white pine blister rust infection (aecia or three of five white pine blister rust indicators; flagging, rodent chewing, swelling, roughened bark, oozing sap), were recorded. Each tree was revisited at four-year intervals through 2018 because the determination of infection status at the first visit, if not obvious, required a subsequent visit four years later due to the latency between initial infection and visible expression of white pine blister rust indicators. This latency made it impossible to determine the exact year of infection in our revisit design. Our inability to identify a nascent infection on a first visit, if visible clues were not present, resulted in the exclusion of 17 seedlings visited only once between 2014 and 2018, which grew to be >1.4 m tall. Thus, for our analysis we included only trees visited at least twice and used the following rules to classify the infection status from data collected on multiple visits. Trees that were recorded as infected, but at subsequent visits displayed no signs of infection because infected branches may have been removed by wind, snow, "self-pruning", or rodent chewing, were placed in the infected category. This decision was based on our interest in climate correlates with infection rather than tree survival. Trees that eventually died from any cause, including fire or mountain pine beetle, after they were determined to have been infected were also placed in the infected category. Trees that were never observed with white pine blister rust were categorized as uninfected. Using these rules, we classified each tree as infected or uninfected through the sampling period and thus collapsed the multi-visit status assessment into two infection classes: yes = infected, and no = uninfected.

2.3. Climate and Location Variables

We evaluated the relative contribution of location (latitude, longitude, elevation, slope, aspect) versus climate as determinants of infection. Climate variables were a parsimonious set identified in earlier studies as biologically relevant metrics that could be derived from 1 km daily Daymet climate grids [42]. We derived other biophysical measures of climate from Daymet via a water balance model [43,44]. Relative humidity was derived from Daymet via Allen [45],

$$RH = \frac{Vp}{Svp}, \tag{1}$$

where Vp is vapor pressure (Pa) and Svp is saturation vapor pressure (Pa).

Daily saturation vapor pressure is,

$$Svp = 610.8 * 10^{\frac{17.27 * Tavg}{237.3 + Tavg}}, \tag{2}$$

where $Tavg$ is daily average temperature (°C).

Because it can take four years for indicators of infection to be observable, the climate four years prior to survey initiation was relevant. For this reason, climate data were summarized for the period 2000–2018, which spans the period four years prior to beginning the survey through to the most recent revisit. We summarized climate data annually in the period August to September, the seasonal window when basidiospores infect whitebark pine in the GYE before October frosts [33]. We screened a large suite of climate variables (Table S1) through pair-wise correlation and retained the variable more relevant to basidiospore transmission reported in the literature when correlation was greater than 0.7. This resulted in a small set of biologically relevant climate variables, which included maximum annual snow water equivalent (aPACK mm); August through September relative humidity (asRH %); August through September average temperature (asTEMP °C); and August through September cumulative rain (asRAIN mm).

2.4. Data Analysis

We modeled the probability of white pine blister rust infection (i.e., response variable was infected or not infected) using generalized linear mixed-effects models with a binomial logit-link function. To understand tree-level characteristics that impacted the probability of infection, we used the function glmer from the glmer package [46]. A random intercept was included for each transect to account for the cluster sample design [47] and the potential correlation of trees within a transect [48]. Due to the importance of DBH noted in previous studies [15,35], we included the most recent measurement of DBH in all models except one to demonstrate the importance of DBH in our study region (Table 1). We established two general classes of a priori model sets for white pine blister rust infection that tested the support for attributes of location or climate factors as determinants of infection. In our modeling framework we kept spatial location and climate variables separate because of the strong relationships between elevation and regional patterns of climate in our study region [24,40]. All spatial and climate variables were centered and scaled before model fitting, so that we could compare model coefficients for variables measured on different scales (relative humidity, temperature). We compared the non-nested spatial and climate models using Akaike information criterion (AIC) [49] and within the spatial and climate classes, we evaluated nested patterns using evidence ratios to identify the most influential variables.

Table 1. Delta AIC (ΔAIC) and adjusted R^2 for models of white pine blister rust infection of whitebark pine trees in the Greater Yellowstone Ecosystem. All models included a random intercept for transect. The marginal R^2 is the proportion of variance explained by the fixed factors (climate or location variables), while the conditional R^2 is the proportion of variance explained by both fixed (climate variables or location variables) and random (transect) intercept.

Class	Model	(Intercept)	Recent DBH (cm)	Elev. (m)	Longitude	Latitude	Aspect	Slope	asRAIN	asRH	asTEMP	aPACK	asRH: asTEMP	df	logLik	AICc	ΔAIC	Weight	R^2 Conditional	R^2 Marginal
climate	m17	−1.459	0.062							0.738	0.541		−0.435	6	−2888	5789	0.0	1.00	0.20	0.40
climate	m15	−1.275	0.062							0.641	0.448			5	−2900	5810	21.0	0.00	0.16	0.41
climate	m10	−1.286	0.062							0.656	0.452	0.071		6	−2900	5811	22.5	0.00	0.16	0.41
climate	m8	−1.284	0.062						−0.110	0.733	0.490	0.120		7	−2899	5812	23.8	0.00	0.17	0.41
climate	m9	−1.284	0.062						−0.110	0.733	0.490	0.120		7	−2899	5812	23.8	0.00	0.17	0.41
location	m3	−1.325	0.063	−0.335	−0.303									5	−2901	5813	24.3	0.00	0.15	0.40
location	m4	−1.304	0.063	−0.291	−0.287	0.114								6	−2901	5814	25.3	0.00	0.15	0.40
location	m6	−1.303	0.063	−0.290	−0.283	0.088	0.035	0.111						8	−2900	5817	28.2	0.00	0.15	0.41
location	m2	−1.329	0.063	−0.498										4	−2905	5817	28.4	0.00	0.13	0.40
location	m13	−1.306	0.063		−0.511									4	−2906	5820	30.8	0.00	0.14	0.42
climate	m19	−1.229	0.063							0.433				4	−2910	5828	39.2	0.00	0.13	0.42
climate	m11	−1.236	0.063							0.442		0.046		5	−2910	5830	41.1	0.00	0.13	0.42
climate	m21	−1.307	0.063						0.292					4	−2914	5836	46.9	0.00	0.11	0.42
climate	m20	−1.329	0.063								0.230			4	−2915	5837	48.6	0.00	0.11	0.43
climate	m1	−1.289	0.063											3	−2917	5841	52.1	0.00	0.10	0.43
climate	m12	−1.286	0.063									−0.020		4	−2917	5843	54.1	0.00	0.10	0.43
location	m14	−0.341		−0.427										3	−3084	6174	385.5	0.00	0.04	0.30

3. Results

3.1. Patterns of Infection and Climate in the GYE

White pine blister rust in the GYE occurs at all elevations and in trees of all sizes, with 40.9% of 5138 trees visited between 2004 and 2018 showing signs of infection. This includes trees that died from any cause but showed signs of infection before death and live trees that once showed signs of infection and, at subsequent visits, no longer show signs of infection due to the loss of infected limbs. Although pervasive and variable in intensity across the region, infection was more common in the northern (Figure 2a) and western (Figure 2b) zones, and mid elevations (Figure 2c) of the study area. While trees in all size classes were infected, the smallest trees were least likely to be infected. The right skew indicated that most infection occurred in middle size classes, but larger trees were also infected (Figure 2d). All of the climate variables used to model blister rust infection were inversely related to elevation across the monitored transects (Figure 3).

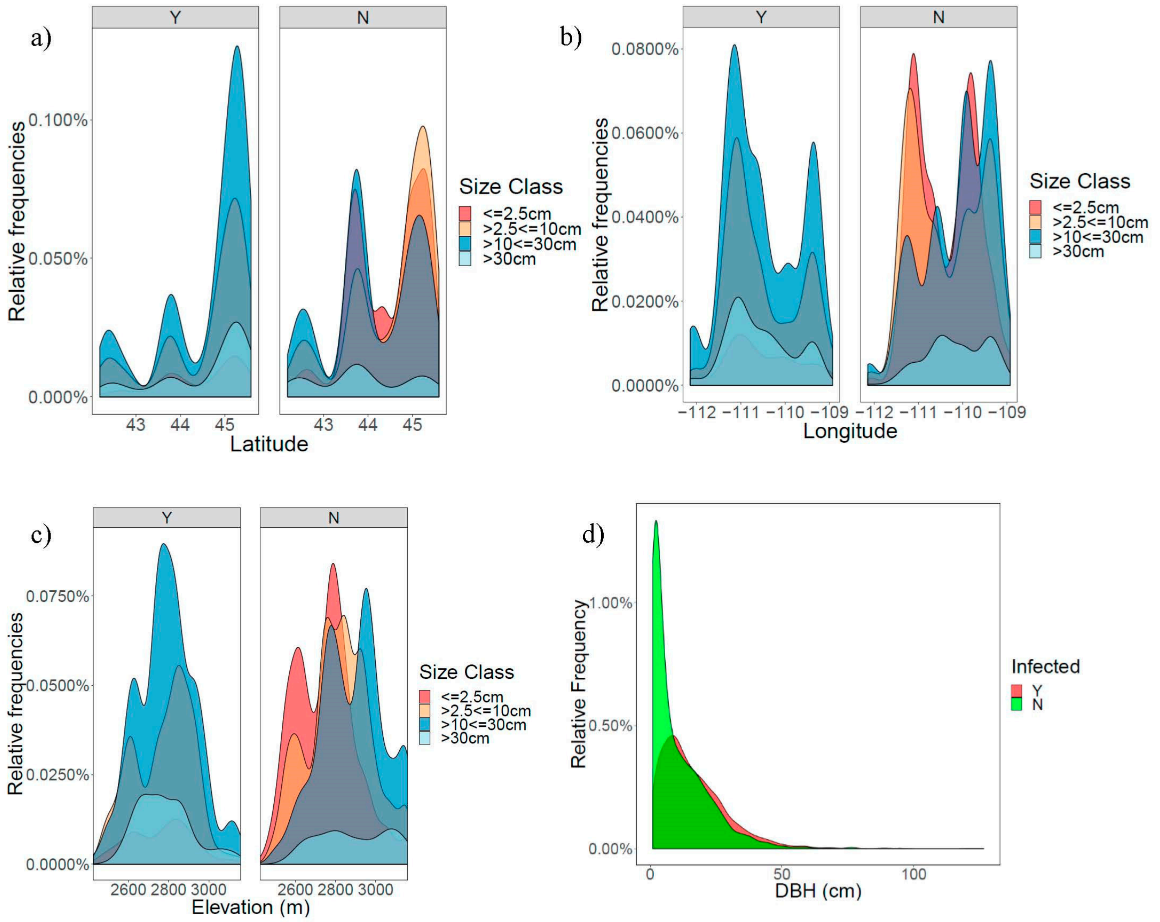


Figure 2. Proportion of white pine blister rust infected (Y) and uninfected (N) trees by (**a**) latitude, (**b**) longitude, (**c**) elevation, and (**d**) the proportion of infected and uninfected trees by DBH (cm).

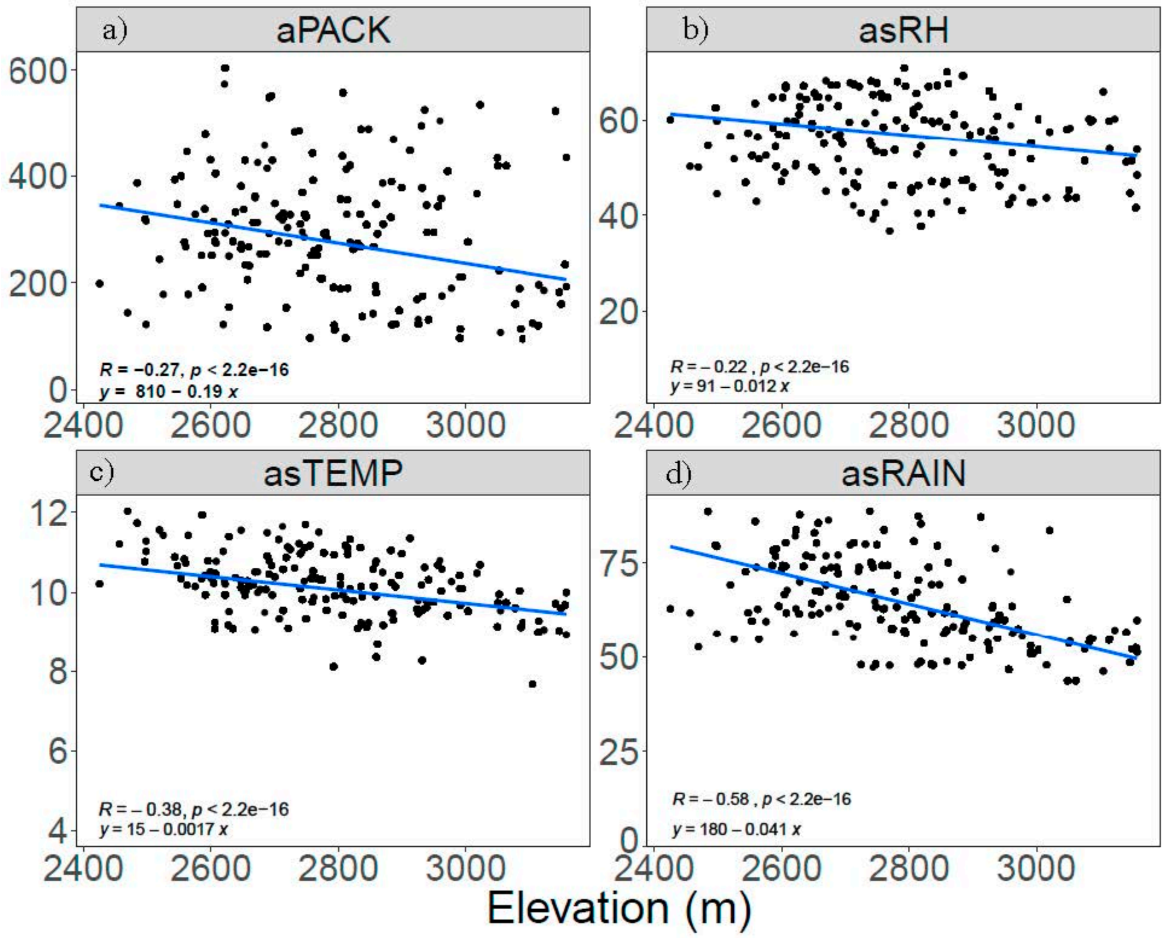
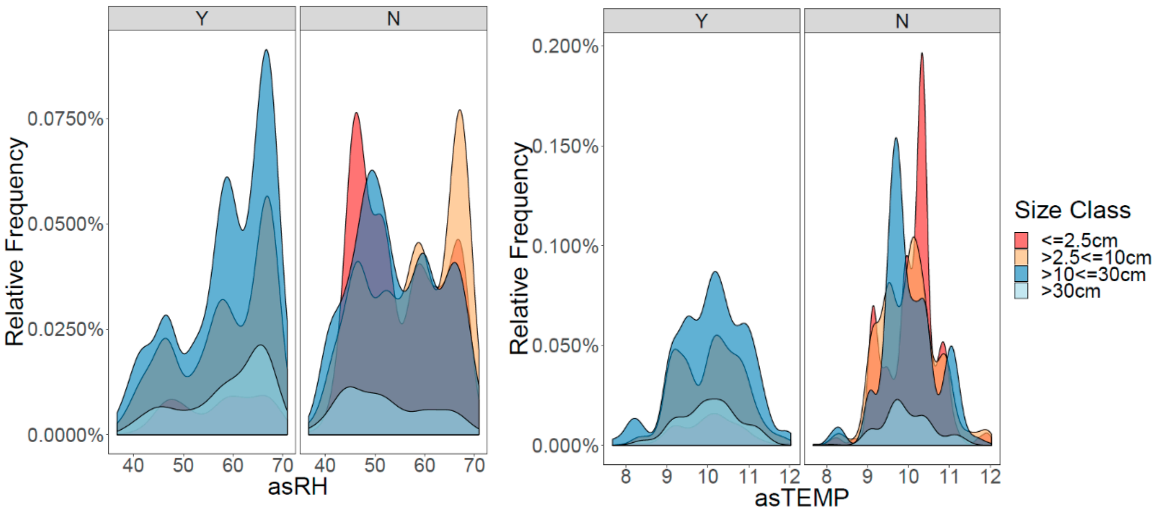


Figure 3. Relationships at monitored whitebark pine stands between elevation and climate variables (**a**) maximum annual snowpack snow water equivalent, aPACK (mm); (**b**) August–September mean relative humidity, asRH (%); (**c**) August–September mean temperature, asTEMP (°C); (**d**) August–September cumulative rain, asRAIN (mm) used in the climate class of models of white pine blister rust infection in the GYE.

3.2. Climatic Correlates of White Pine Blister Rust Infection

The class of models that included only climate variables outperformed the location class of models in all cases (Table 1). Accounting for tree DBH, the model with the most support included asRH, asTEMP, and their interaction. None of the other climate models that included aPACK or asRAIN were competitive. Due to our parsimonious selection of climate variables, the large ΔAIC values between the top model and other models, and the top model including only two climate variables, there was no need to identify a reduced model. Based on model ranks (m20 versus m19) and the coefficient of asRH being greater than asTEMP when evaluated independently, we conclude that asRH was more influential than asTEMP as a determinant of white pine blister rust infection. The model without DBH (m14) was the least competitive, demonstrating the important effect of DBH. The model with elevation and DBH was not competitive either, suggesting elevation did not add information.

The average relative humidity and temperature in August and September were the most important climate correlates of white pine blister rust (Table 1, Figure 4). The prevalence of infection was highest where August–September relative humidity and temperature were above 65% and between 9 and 11 °C, respectively.



(**a**) (**b**)

Figure 4. Proportion of whitebark pine trees infected and uninfected by white pine blister rust relative to (**a**) August and September average relative humidity, and (**b**) August and September average temperature (°C).

3.3. Climate Limits on White Pine Blister Rust Infection

After accounting for the association with tree size and random intercept for transect, we found evidence of temperature and humidity limitations on white pine blister rust infection (Figure 5). At locations with a mean August–September temperature of 7 °C, the probability of infection did not increase until average relative humidity increased above 50%, whereas at increasingly warmer temperatures the probability of infection increased until 11 °C, where the probability of infection sharply decreased with higher temperature. We used the top model (m17) to map the spatial pattern of white pine blister rust infection in the GYE (Figure 6).

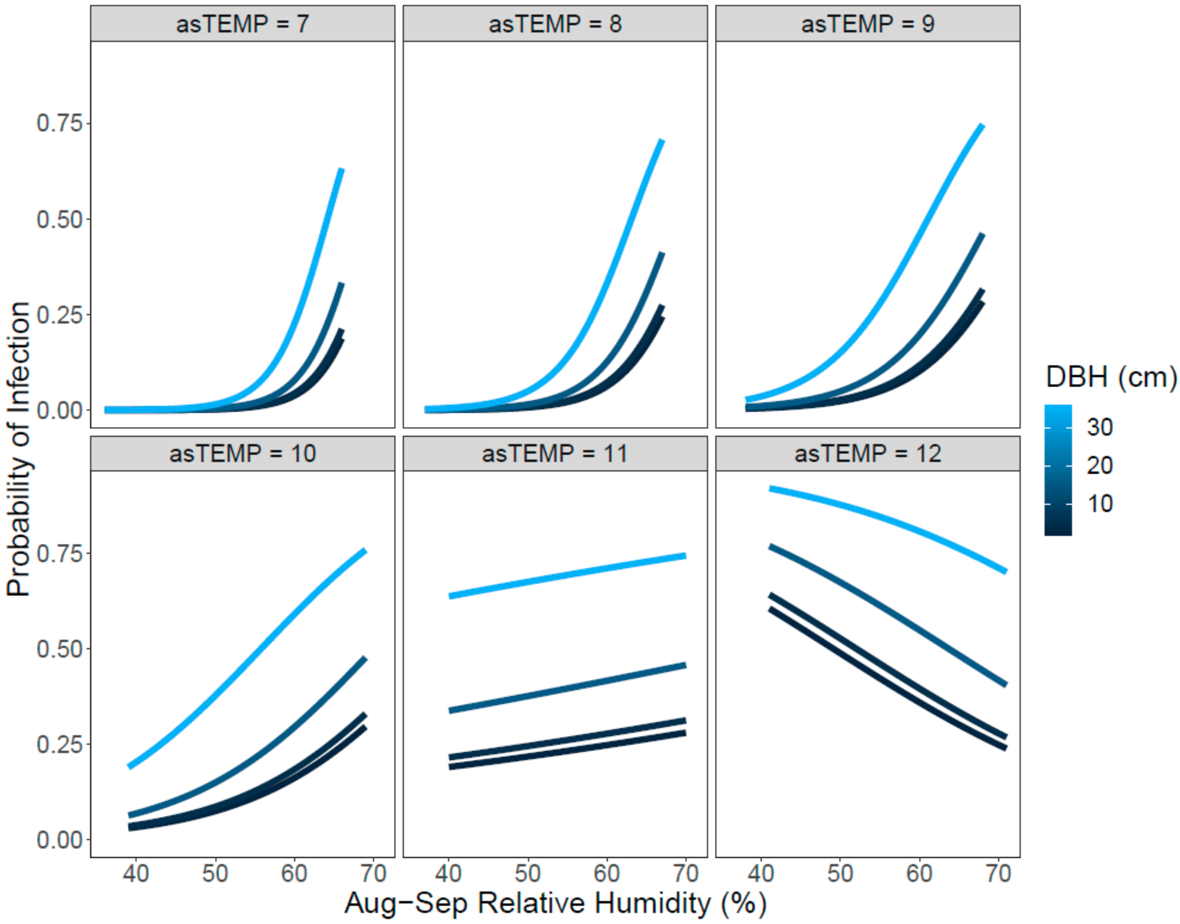


Figure 5. Probability of white pine blister rust infection by diameter at breast height (DBH) of whitebark pine trees as a function of average August–September relative humidity (asRH) for six levels of average August–September temperature (asTEMP). The panel labels indicate scenarios of average temperature (°C) that span the range of the average August–September temperature at monitored stands.

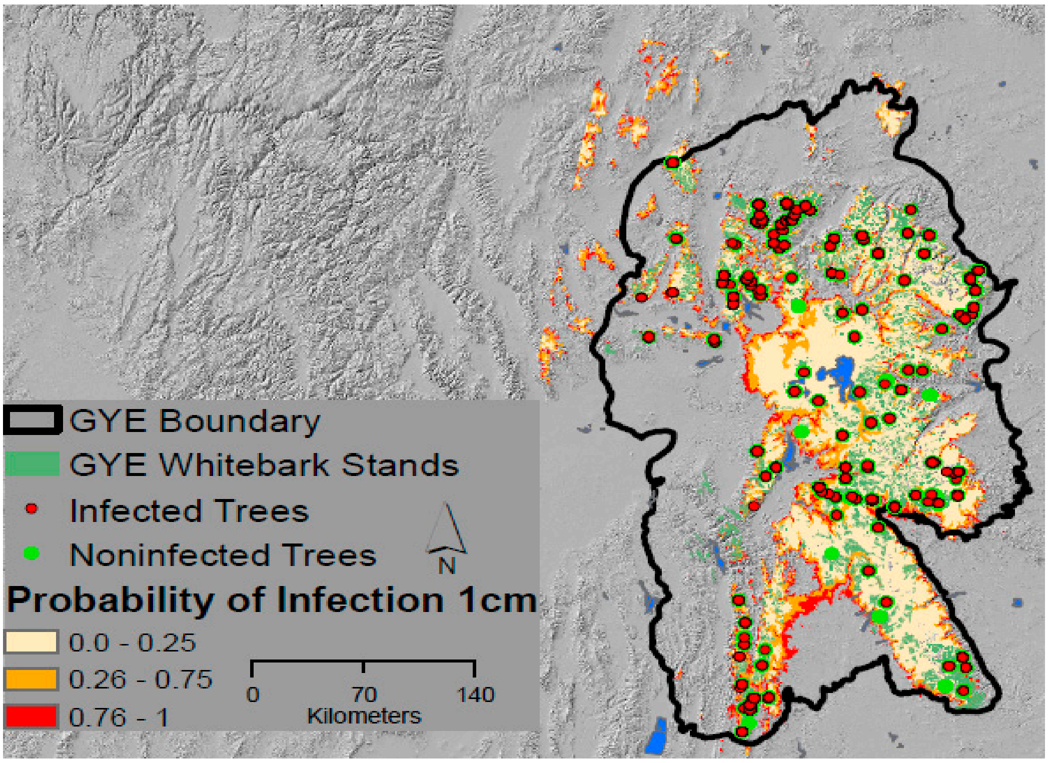


Figure 6. Probability of white pine blister rust infection in whitebark pine in the Greater Yellowstone Ecosystem created using the top model (m17) from Table 1. Probability is based on the interaction between August and September relative humidity (asRH) and temperature (asTEMP), modeled for a 1 cm DBH tree. The extent of modeled probability was limited to locations with mean August–September temperatures between 7.67 and 12.03 °C, the range of asTEMP from Daymet at the monitored stands.

4. Discussion

4.1. Climate and Scale

Collectively, fine scale processes operating under the broader influence of regional climates resulted in the current pattern of infection, which will continue to influence patterns of infection and prevalence in the future. Our findings align with studies showing white pine blister rust is often concentrated in areas within larger regions [23], and are also aligned with well-documented white pine blister rust life stages affected by climate, that operate at fine spatial scales [24,28]. Understanding fine-scale patterns is useful for recognizing local controls on infection, which are determined by distance to and density of alternate hosts [32,36,37], while identifying regional climate drivers provides insight for a potential intensification of infection levels and the geography of infection. For instance, infection rates are higher under climates ideally suited to the pathogen in northwestern Montana, which has moderate summer temperatures and high summer rain [50,51] reviewed in Mahalovich [33]. Although white pine blister rust likely spread from isolated points of introduction, we found that white pine blister rust prevalence in the GYE today is ubiquitous, which is not surprising given that spores can easily be transported locally within stands and up to 27 km under favorable conditions [31]. Such conditions are generally cool summer nights when soil moisture and relative humidity are high, and downslope winds carry spores to new hosts [31]. Our findings support the timing of climate conditions (late summer) and the link between attributes of climate (temperature and humidity) and infection mechanisms described by these earlier studies. The existing pattern of white pine blister rust prevalence and our model results suggest that regional climate controls are important determinants of existing patterns of infection in the GYE, and prevalence in the future will be strongly influenced by regional climate now that white pine blister rust is firmly established in the ecosystem. Indeed, this was recognized implicitly in 1978 when *Ribes* eradication efforts were halted in GYE, with studies indicating the efforts were largely ineffective, presumably because the climate was conducive and there were sufficient populations of alternate hosts to sustain or increase white pine blister rust spread, in spite of control efforts [10].

4.2. Climate Influence

Our study confirmed that conditions in August and September, when basidiospores infect whitebark pine [33], were reasonably good predictors of infection, while others found spring conditions were better predictors of white pine blister rust prevalence in limber pine in Colorado and Wyoming [24]. Although our approach differed from theirs due to our interest in climate relations with the basidiospore inoculum, we also found that temperature and relative humidity were important determinants of white pine blister rust incidence, but we found relative humidity was the more influential variable. This suggests that low asRH was more limiting than temperature in the GYE and may explain why the rate of white pine blister rust spread in the GYE has been slow compared to the spread in other white pine populations in more humid regions of its range as indicated by previous studies [6,25,50]. Drier conditions inhibit the survival and transfer of the basidiospore inoculum to whitebark pine [30], because this transmission requires extended periods of time during late summer and early autumn, with cool nighttime temperatures and free moisture on the needle surfaces [25,29]. At least two consecutive days of these favorable conditions are required for the infection of pines [30]. However, in our study the influence of dew formation (count of days when dew formation occurred) and count of days above 80% relative humidity were not supported.

4.3. Regional Patterns

Elevation is often used as a proxy for climate due to the strong elevation gradients in temperature and precipitation on mountain slopes [52], and studies have found relationships between white pine blister rust prevalence and elevation in mountain environments. Specifically, Smith and Hoffman [25] found decreasing incidence of white pine blister rust at lower elevations in western Wyoming and southern Idaho, and noted a report (cited therein as Berg et al.) that also found white pine blister rust infection decreased at lower elevations in the GYE. However, other studies reviewed by Burns et al. [53] found relationships with elevation were latitude dependent and recommended white pine blister rust hazard ratings use climate rather than elevation in hazard models. Based on interpretations from our findings, the relationship with elevation described by earlier studies is likely due to higher temperature and lower relative humidity at lower altitude. Although we explicitly kept climate and location variables separate in our modeling framework, we found ad hoc that a model with DBH, asRAIN, and elevation, which was similar to the best model found by Smith and Hoffman [25] that included DBH, summer rain, and elevation, was not competitive (ΔAIC 30.4) with our top climate model. In our study, regional patterns of temperature followed the expected decrease in temperature with increasing elevation. However, regional patterns were stronger than local elevation effects on precipitation and relative humidity. That is, precipitation and relative humidity generally increase with elevation on an individual mountain slope, however, across the GYE the expectation of increasing aPACK, asRH, and asRAIN with elevation was confounded by even stronger regional climate patterns. These regional patterns explain why elevation was not as informative at the ecosystem scale and why local climate at the transect level that accounted for regional effects was most informative of white pine blister rust infection.

The regional patterns of the probability of white pine blister rust infection were very similar to those reviewed by Mahalovich [33], which were constructed by Helmbrecht [51]. We also found a higher probability of infection in the northwestern region of GYE and lower probability of infection in the southwestern region. There were also elevation-dependent patterns in maps from both studies. Although we make a case for using climate data rather than elevation as a proxy for climate, elevation still performs well in some regions. This is because of strong relationships between elevation, temperature, and relative humidity, due to the physical lapse rates in mountain environments. Since Smith and Hoffman [25] included summer rain in their model, they effectively captured the important regional variation in humidity and elevation served as a good proxy for temperature. In contrast with the Helmbrecht map [51], ours suggests a higher probability of infection over a larger area. This may be due to a difference in the ground-based measurements that informed the two studies, or could be the result of an intensification in the presence of white pine blister rust throughout the GYE during the time (2007 and 2018) between the two studies.

The mountain pine beetle epidemic that killed approximately 75% of the largest trees over the course of our study had the potential to impact our estimate of the proportion of trees infected with white pine blister rust in the GYE. However, we found that the death of 29% (1502) of the originally tagged trees did not affect the rate of infection in the GYE, nor did the addition of 447, predominantly uninfected, new trees that grew up into our minimum height for monitoring (>1.4 m). The greatest difference between any of the scenarios was no greater than 4% and not statistically significant [54].

4.4. Limitations and Opportunities

The limitations of our study include averaging climate through time at stand locations, which relies on an assumed relationship between average conditions and wave event frequencies. That is, researchers have previously described white pine blister rust infection occurring in "wave years", when conditions are particularly well suited to basidiospore long distance transport over broad areas [31], resulting in new infections. Temporal averaging, combined with our repeat visits at four-year intervals, made it difficult to determine when infection occurred and what the environmental conditions were at that time. However, canker length could be used to approximate time since infection [55], which could be coupled with wave year analysis. Our study could be strengthened by including distance to streams or wet landscape positions with high *Ribes* density, which are large sources of inoculum [24,37].

4.5. Management Relevance

Our findings that relative humidity and temperature are related to regional white pine blister rust presence provide a better understanding of climate–pathogen interactions, which could be used to model the future geography of white pine blister rust in the GYE. These include identifying the geography of "climate escapes" [56] that are unsuitable for white pine blister rust because they are too warm, too cold, or too dry. Because our model was climate-based rather than based on elevation, as a proxy for climate, future efforts could identify the geography of refugia from white pine blister rust using climate projections. The union of such refugia with projections of suitable bioclimate for whitebark pine in the future [57] could map potential planting locations for white pine blister rust-resistant stock. Identifying planting locations that can sustain whitebark pine and provide some protection from white pine blister rust is important due to the expense associated with raising and planting genetically resistant stock and the limited number of seedlings relative to the expansive landscapes that may need treatment to sustain this iconic species.

5. Conclusions

White pine blister rust infection, which results in the loss of large cone-producing trees and heightened lethality in smaller trees, is a double jeopardy for whitebark pine. White pine blister rust-resistant seedling planting programs are the best hope for sustaining whitebark pine [33], and could consider planting locations, with respect to regional climate, which minimize the likelihood and intensity of the infection that may build over time. Here, we presented information consistent with findings from other studies but specific to the GYE, that suggests regional climate patterns can be used with information about local conditions and alternate host densities to inform restoration efforts. Specifically, if planting targets include areas outside the temperature and humidity range identified as ideal for infection, the probability of infection may be temporarily reduced, thus buying time for growth to cone-producing age.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/8/666/s1, Table S1: Correlation matrix for selecting climate variables considered for analysis with blister rust incidence.

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