

University of Nevada, Reno

**Host size and distance to infested stands predicts defoliation of aspen by non-native  
white satin moth**

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requirements for the degree of Master of Science in  
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## Abstract

Forest decline and tree mortality events often result from simultaneous stressors and can be amplified by novel climatic conditions and the introduction of invasive pests and pathogens. The potential compounding effects of these novel disturbances pose a risk of cascading impacts if they affect species with outsized ecological influence, such as foundation species like quaking aspen (*Populus tremuloides* Michx.). Quaking aspen is limited in extent in the Sierra Nevada and Sierra Front forests, making the relatively recent introduction of the invasive aspen defoliator, white satin moth (*Leucoma salicis*), especially concerning. To understand current aspen stand conditions and the extent of white satin moth in the region, we assessed the impacts of a multi-year satin moth defoliation event on quaking aspen stand composition and dynamics. A conditional random forest model was used to narrow predictor variables prior to evaluating drivers of defoliation and aspen regeneration with generalized linear models. We found that defoliation rates were strongly influenced by the availability of aspen host trees and the distance to the nearest stand infested by white satin moth, while aspen regeneration was most strongly influenced by heat load index as warmer soil temperatures are more likely to promote aspen root sucker initiation. White satin moth may lead to declines in regional aspen stands yet may concurrently promote regeneration through more favorable establishment conditions. Our findings indicate that the occurrence of white satin moth is likely to spread throughout the Carson Range, but further monitoring is necessary to better understand its impacts on aspen stand composition, particularly regeneration and potential declines.

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## 1. Introduction

Anthropogenically-driven climate change is creating novel climatic and disturbance conditions in forests worldwide (Hammond et al., 2022) and is, increasingly, amplifying the extent and severity of forest decline and tree mortality events (Allen et al., 2015; Anderegg et al., 2019; Berner et al., 2017). In many cases, the causal driver of tree stress and mortality is not a single disturbance agent but instead multiple agents that interact to overwhelm tree defense mechanisms (i.e., compounding disturbance; Raffa et al., 2008; Wermelinger et al., 2008). Hotter or prolonged drought may, for instance, compound a bark beetle attack by weakening trees and allowing an endemic mortality agent to reach epidemic levels (Raffa et al., 2008; Breshears et al., 2009). Climate sensitive disturbances, such as bark beetle outbreaks, may also compound upon themselves via repeated or successive disturbance events that create climate conditions more favorable to the disturbance agent and allow population numbers to surge (Jactel et al., 2012). Novel conditions and outcomes following compound disturbance can then alter the rates or trajectories of recovery in forests (Buma, 2015; Fensham et al., 2015; Johnstone et al. 2016), making forests more vulnerable to stress and increasing risk of decline or extirpation under ongoing climate change (Allen et al., 2015).

Decline or extirpation is particularly concerning for tree species of high ecological, economic, or social value, as losses have cascading ecological impacts. Aspen (*Populus*. section *Populus* (syn. *Leuce*)), a group of keystone species of global importance (Rogers et al. 2020), has experienced widespread decline across its North American range over the last two decades (Hanna & Kulakowski, 2012; Worrall et al., 2013). Here, quaking aspen (*Populus tremuloides* Michx.) decline is a complex

phenomenon attributed to multiple agents that drive canopy loss, tree defoliation, physiological stress, and mortality – known collectively as sudden aspen decline (SAD, Huang & Anderegg, 2012; Singer et al. 2019). Although climatic stress is a key driver of decline (Worrall et al., 2013; Anderegg et al., 2019), SAD is more common when pests and pathogens, both native and non-native, compound physiological or drought stress (Singer et al., 2019). These biotic agents tend to be the proximate causal agents of mortality that push stressed individuals beyond a critical threshold (Kulakowski et al., 2013; Barker Plotkin et al., 2021). This multi-decadal mortality event has been of critical concern due to the disproportionate impact quaking aspen, as a keystone species, has on both ecosystems and ecosystem services (Shinneman et al., 2013, Rogers et al. 2020). Ecologically, quaking aspen facilitates compositional biodiversity by supporting a greater number of plant and animal species compared to neighboring forest types (Stohlgren et al., 1997; Shepperd et al., 2006; Berrill et al., 2017). Socially and economically, aspen is highly valued due to the aesthetic and recreational values it provides (Shepperd et al., 2006; Worrall et al., 2015). It is thus increasingly important to understand how stressing agents influence aspen forests and affect their ability to persist on the landscape.

Quaking aspen persistence is of particular concern in the Sierra Nevada Mountains of California and Nevada, where it is limited in extent (<1% of the landscape, Shepperd et al., 2006) yet plays a disproportionate role in supporting high levels of biodiversity and providing critical wildlife habitat and water-holding capacity as compared to more dominant regional forest types (Mueggler, 1985, Rogers et al., 2007; Brewen et al., 2021). Widespread and sudden decline has thus far been limited in this region (Shepperd et al., 2006; Rogers et al. 2007, Morelli et al., 2009); however, many

Sierra Nevada aspen stands are advanced in age following a century of fire exclusion and at increasing risk of loss or decline due to age-related senescence, disease, and decay (Potter, 1998; Shepperd et al., 2006). Specifically, the stage is set for a potential reduction in aspen cover in the region, particularly in stands mixed with or adjacent to conifers due to successional processes that allow a shift in forest composition to other species (Berrill, 2014).

The recent introduction of an invasive insect defoliator, the white satin moth (*Leucoma salicis*, hereafter: satin moth), poses an additional challenge for aspen stands across the region and may compound existing climatic and biotic stressors to threaten Sierra Nevada aspen persistence. Satin moth was introduced to North America in the early 1900s (Burgess, 1921; Wagner & Leonard, 1980), yet little research has investigated its ecology and much of the existing knowledge draws on impacts in eastern North America forests (e.g., Wagner & Leonard, 1979a; Wagner & Leonard, 1979b; Wagner & Leonard, 1980). Satin moth belongs to the same subfamily (Lymantriinae) as the well-known spongy moth (*Lymantria dispar*), which has defoliated deciduous North American forests for more than a century, causing reduced growth, dieback, and mortality in repeatedly defoliated trees (Davidson et al. 1999). *Salix* and *Populus* species are vulnerable to satin moth attack (Burgess, 1921) and, although it was initially regarded as a pest of ornamental trees, it has defoliated thousands of hectares of forests across North America, including the western portion of the continent (Humphreys, 1996). Little is known about satin moth's westward spread, and it is unclear if it has the potential to cause similar widespread, catastrophic damage as spongy moth to the West's limited deciduous forests. Given aspen's notable ecological importance and its vulnerability in

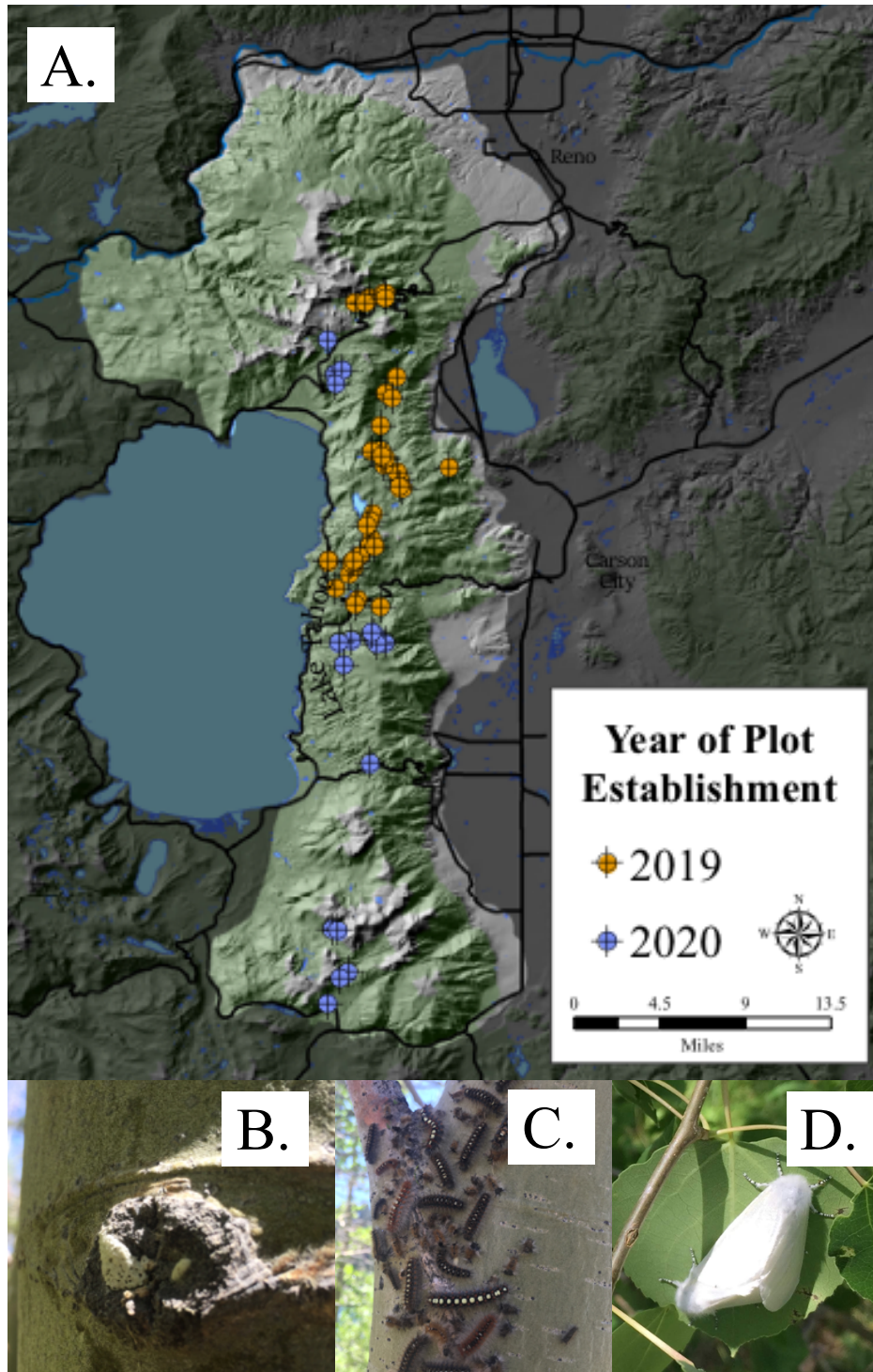
the region, understanding how this invasive defoliator may influence aspen stand conditions and persistence is critical.

In this study, we quantify the impacts of a multi-year satin moth defoliation event that has affected quaking aspen stands since 2017 along the eastern rim of the Lake Tahoe Basin, Nevada (Roland Shaw, personal communication, 2017). Our primary objective was to assess quaking aspen stand composition and structure following repeated defoliation by this non-native insect as well as identify the potential topoclimatic characteristics driving defoliation. We specifically asked: 1) What are the current stand conditions, and what proportion of stands are affected by satin moth? and 2) How do stand characteristics influence rates of defoliation, and do defoliation rates or stand characteristics in turn influence aspen regeneration densities? Given other pest-host plant interactions (Raffa et al., 2008; Davidson et al., 2001; Anderegg et al., 2015), we hypothesized that the severity of defoliation in aspen stands is largely influenced by stand structural conditions, specifically those related to sizes and densities of mature aspen trees in the infested stand. We additionally hypothesized that the density of overstory trees will influence the density of aspen seedlings and saplings in the regeneration class given the primary role of asexual reproduction (i.e., suckering) in aspen regeneration. Local climate or topographic conditions may further influence defoliation by reducing or bolstering plant defenses through alteration of available moisture and temperature. This study represents the first regional assessment of satin moth impacts and will provide much needed insight on how this novel defoliator may compound existing stressors and improve our understanding of the impacts and drivers of satin moth defoliation in aspen stands across the region.

## 2. Methods

*2.1 Site Selection* – To assess regional satin moth defoliation, plots were established in aspen stands in the Carson Range along the eastern edge of the Lake Tahoe Basin in California and Nevada, USA (Fig. 1). Plot locations were selected using a spatially balanced, random sampling design overlaid across the region's mapped aspen forest type (USDA Forest Service, 2004), and forest cover was confirmed via aerial imagery prior to visiting plots on the ground. In 2018, 11 plots were established in North Canyon and around Marlette Lake in the Lake Tahoe Nevada State Park, Nevada. In 2019, 19 additional plots were established from Spooner Summit (US Highway 50) to Mount Rose Summit (NV-SR 431). In 2020, 8 additional plots were established from Spooner Summit to Mount Rose Summit, and 17 plots were established south from Spooner Summit to Luther Pass. Plots were established successively each field season and remeasured for satin moth defoliation activity in each subsequent year after plot establishment.

*2.2 Field Sampling*- At each plot location, we installed nested, fixed-radius plots and sampled each year from 2018 to 2020. During the year of plot establishment, all trees (>7.6cm diameter) were inventoried in a 0.1 ha circular plot (17.8m radius), while all seedlings (<1.37m in height) and saplings (>1.37m height and < 7.6cm diameter) were measured in a nested 0.02 ha subplot (8m radius). The following data were collected: species, diameter at breast height (DBH; 1.37 m height, excluding seedlings), satin moth occurrence (0/1), satin moth defoliation damage, mortality status (dead or alive), and tree Dieback. Satin moth occurrence was determined by the presence of hibernacula, larvae, adult moth, cocoon, and egg masses (Humphreys, 1996; Fig. 1). Defoliation was assessed visually and qualitatively scored as the following: crown defoliation absent (0%), light



**Figure 1.** A: Map of monitoring plots examining the effect of the novel, invasive white satin moth (*Leucoma salicis*) on quaking aspen (*Populus tremuloides*) stands in the Carson Range of California and Nevada, USA. B: A white satin moth egg mass on a quaking aspen stem. C: An aggregate of white satin moth caterpillars on a quaking aspen stem. D: An adult white satin moth on a quaking aspen leaf.

defoliation (<15% crown loss), moderate defoliation (15% to 90% crown loss), heavy defoliation (>90% crown loss), and dead (no sign of leafing out during the given year). Tree dieback was scored as the following: healthy (0-10% crown dieback), light to moderate decline (11-50% crown dieback), severe decline (greater than 50% crown dieback), and dead (100% crown dieback).

Defoliation was assessed each year during the month of July using a streamlined protocol that permitted rapid remeasurement. This allowed new plots to be established in June and August, and defoliation to be consistently measured at its peak. To accomplish this, we conducted the measurements described above on a subset of 12 trees, saplings, and seedlings at 5 m intervals on 17.8m long N-S and E-W oriented transects radiating from plot center. Height and the presence of other pests and pathogens (e.g., mistletoe, rusts, cankers, galls, leaf miners, other defoliators, woodpecker damage, etc.) were also recorded for all focal individuals. Subsampling individuals in this way enabled remeasurement of an increasing number of plots each year during the period of peak defoliation while also establishing new plots to bolster our sample size and the inferences we were able to draw from the dataset.

*2.3 Data Analysis & Processing-* A hierarchical cluster analysis with plot latitude and longitude data was used to group plots geographically into regions. Geographic names were assigned to groups of plots corresponding to the following regions: Mount Rose – Slide Mountain, Hobart Reservoir, Marlette Lake – North Canyon, Genoa Peak, and Luther Pass. Tree measurement and count data from fixed area inventory plots were used to compute live and dead tree density per hectare (stems/ha), basal area per hectare (BA/ha), quadratic mean diameter (QMD), and live seedling and sapling stems/ha for

both aspen and conifer species separately. Aspen seedling and sapling stems per hectare (hereafter aspen regeneration stems/ha) were pooled for this analysis. To ensure that comparisons could be drawn between years, the proportion of aspen trees exhibiting satin moth defoliation (hereafter, proportion of defoliated aspen tree stems/ha) as well as mean satin moth crown defoliation were quantified using the twelve seedlings, saplings, and trees, respectively, that were subsampled during peak defoliation in July each year. Two metrics were calculated to assess the proximity of satin moth occurrence within and among geographic regions, which were computed as (1) the distance from each plot to the nearest satin moth plot (hereafter nearest neighbor distance) and (2) the average distance from each plot to the nearest three plots with satin moth (hereafter mean neighbor distance). Topographic variables were computed for each plot location using a digital elevation model via the ArcGIS ‘Geomorphometry and Gradient Metrics Toolbox’ tool (Evans et al. 2014), and historic climate variables (1981-2010) were extracted as scale-free point estimates using plot coordinates in ClimateNA v6.00 software (Wang et al. 2016).

Current stand conditions were assessed by computing summary statistics for stand structure variables such as live and dead aspen and conifer BA/ha, stems/ha, and QMD. The change in aspen regeneration stems/ha between sampling years was assessed by a Welch’s two sample t-test. The impact of satin moth was assessed by evaluating the mean proportion of crown defoliation and the proportion of individuals affected by defoliation in the stand for seedling, sapling, and tree life stages.

*2.3.1 Defoliation Analysis-* To investigate the influence of stand structure and landscape characteristics on defoliation, we parameterized a model using the following steps: (1)

Define response variable and candidate predictor variables, and assess correlations between candidate predictors, (2) Narrow predictor variables and evaluate their correlation with the response variable, (3) Examine predictor importance and further reduce predictor variables using a conditional random forest model (hereafter RF), and (4) Assemble hierarchical generalized linear mixed models (GLMMs) to examine the strength of the predictors ascertained from the RF process.

The response variable in this analysis was the proportion of defoliated aspen tree stems/ha and predictor variables were selected based on hypothesized relationships and the results of previous analysis of the dataset (Nelson & Bisbing, 2021). A correlation matrix with all potential predictor variables was used to initially reduce predictors by excluding correlations  $\geq |0.6|$ . The resulting predictor variables included live aspen tree BA/ha, live aspen tree stems/ha, live conifer BA/ha, nearest neighbor distance, heat load index (HLI), compound topographic index (CTI), and climatic moisture deficit (CMD). These predictors were plotted against the response variable and Pearson's correlation and its significance ( $\alpha = 0.95$ ) were calculated for each.

The RF model was used to identify influential predictor variables by assessing their permutation importance. Model tuning parameters were optimized to reduce root mean square error (RMSE) and predictor variable selection was further narrowed using a repeated cross-validation method. The final variables retained were nearest neighbor distance, live aspen tree BA/ha, and live conifer tree BA/ha. This reduction in the number of predictor variables required the 'mtry' parameter to be reduced to the number of predictors supplied to the model ( $n = 3$ ). Finally, marginal effects plots were created for each of the predictor variables retained in the final model to allow prediction of the

response variable across a range of values for that predictor variable. Analysis was conducted using the R Statistical Software (v4.2.2; R Core Team 2022) and the *party* package in R (Hothron et al., 2006; Strobl et al., 2007; Strobl et al., 2008) was utilized for the RF process. Model tuning and feature elimination was accomplished with the *caret* package (Kuhn 2022) and the *pdp* package (Greenwell, 2017) was used to create the marginal effects plots.

The GLMMs were used to examine predictor strength and account for the random effect of measurement year on defoliation. Two GLMMs were built with the random effect of measurement year; the first utilized all the predictor variables identified by the extensive RF process (nearest neighbor distance, live aspen BA/ha, and live conifer BA/ha) while the second used only nearest neighbor distance and live aspen BA/ha for full model comparison against a simpler model. Predictor variables were centered and scaled prior to analysis. The models were compared using analysis of variance (ANOVA) and corrected Akaike information criterion (AICc) scores were calculated for all models using the *AICc* function from the *AICc* package. This method was used in place of the standard AIC scores calculated by the *glmer* function due to the small sample size of the dataset. GLMMs were constructed with the *lme4* package in r (Bates et al., 2015) and AICc was calculated using the *MuMIn* package in r (Bartoń, 2023).

**2.3.2 Regeneration Analysis-** The same model parameterization and RF process described above was utilized to select predictor variables influencing the regeneration of aspen. The response variable for this analysis was the aspen regeneration stems/ha sampled during the initial year of plot establishment. A generalized linear model (GLM) was used in this analysis, so the response variable was square root transformed prior to the RF process to

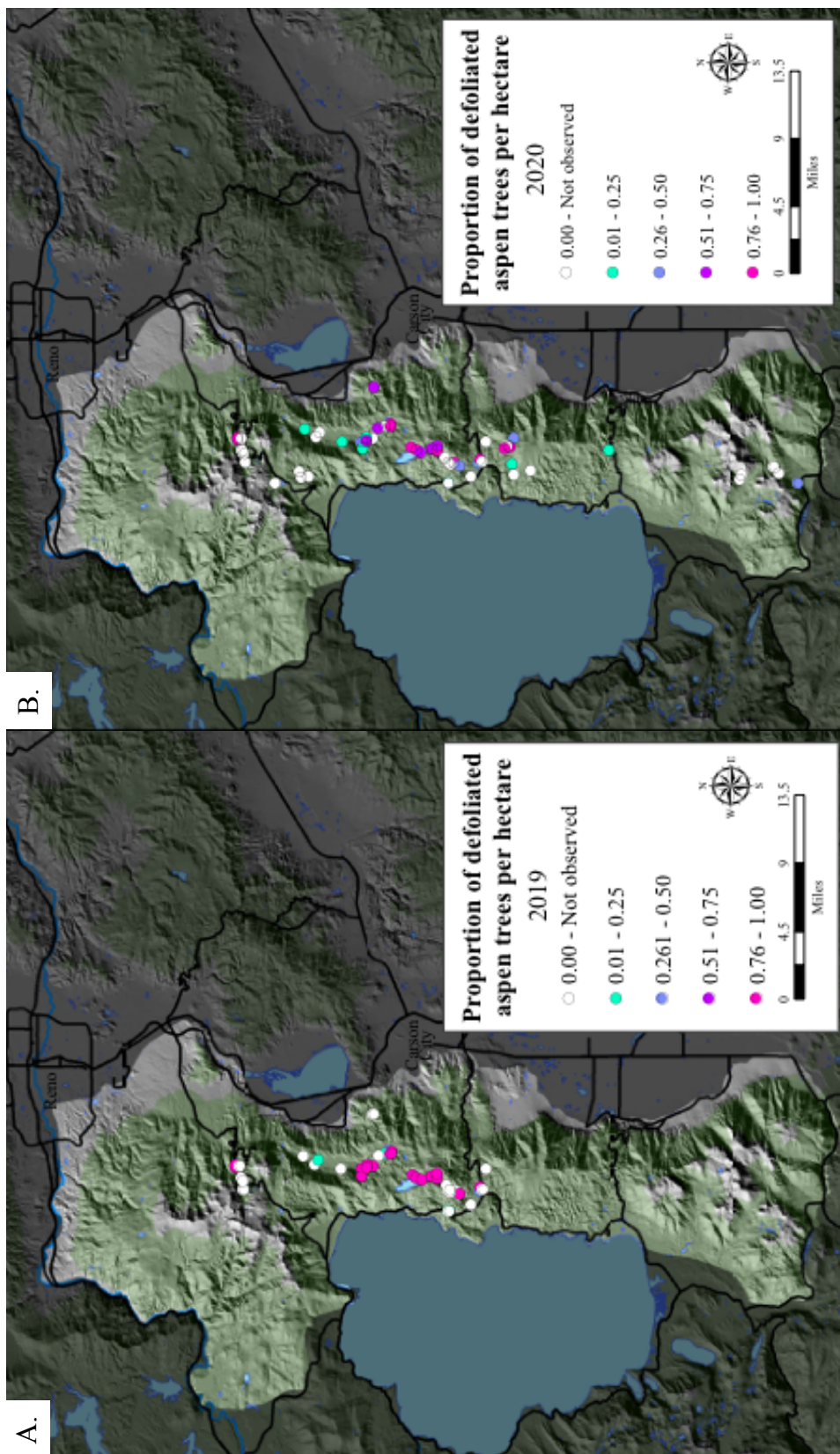
obtain a normal distribution. The correlation matrix for this analysis narrowed predictor variables to live aspen tree BA/ha, live aspen tree stems/ha, dead aspen tree BA/ha, live conifer BA/ha, conifer regeneration stems/ha, proportion of defoliated aspen tree stems/ha, nearest neighbor distance, HLI, CTI, and CMD. To illustrate the relationship of individual predictor variables with the response variable, each predictor was plotted against the response and Pearson's correlation calculated. The *rfe* function retained HLI, live conifer tree BA/ha, CMD, and proportion of defoliated aspen tree stems/ha for the predictor variables and marginal effects plots were created for each. A total of three hierarchical GLMs were then built with the predictor variables selected by the RF process and AICc was used to select the best fitting model.

### **3. Results**

*3.1 Aspen Stand Conditions-* Aspen composed greater than 50% of the trees in 93% of our sample plots stands and greater than 90% of the trees in 69% of the plots. The mean percentage of dead aspen tree stems/ha was relatively low ( $14.3 \pm 1.69\%$ ), and only 10 stands had greater than 25% mortality. The mean percentage of live aspen trees experiencing light to severe canopy dieback was also low ( $23.8 \pm 2.68\%$ ), with only 7 stands experiencing dieback in greater than 50% of the aspen trees. Pests and pathogens other than satin moth were common in aspen trees throughout the stands, and more than 90% of the sampled trees were affected by one or more non-satin-moth-related mortality agents in both 2019 and 2020 (Fig. S1). Although the mean aspen regeneration stems/ha did not differ between years ( $p = 0.455$ ), aspen regeneration stems/ha was more variable between regions in 2019 than 2020 (Fig. S2).

*3.2 Satin Moth Extent & Effects-* Satin moth occurrence did not change significantly between 2019 and 2020, with 54% of sampling plots infested in 2019 and 52% in 2020. Stands that lacked satin moth in both sampling years were bordered by areas of moderate to high proportions of defoliated aspen tree stems/ha (Fig. 2). In 2019, the mean percentage of canopy defoliation on infested aspen trees was  $15.9 \pm 3.88\%$  and only 3 plots had a mean canopy defoliation greater than 25%. The mean percentage increased slightly in 2020 to  $17.1 \pm 2.64\%$ ; however, the number of plots with a mean canopy defoliation greater than 25% nearly tripled. The mean percentage of defoliated aspen trees stems/ha in 2019 was  $46.6 \pm 8.09\%$  but this percentage decreased in 2020 to  $31.8 \pm 5.25\%$ . The mean nearest neighbor distance to known infested plot was  $1.99\text{km} \pm 0.295\text{km}$ . The maximum nearest neighbor distance was 20.4km.

*3.3 Drivers of White Satin Moth Defoliation-* The only significant Pearson's correlations of predictors with defoliation measures were nearest neighbor distance and live aspen tree BA/ha (Fig. S3); however, nearest neighbor distance was negatively correlated ( $R = -0.30$ ) while live aspen BA/ha had a slightly stronger, positive correlation ( $R = 0.41$ ). The variable permutation importance from the RF process was highest for nearest neighbor distance and lowest for live conifer BA/ha (Fig. S4). The marginal effects plot for nearest neighbor distance showed a sudden decline in the predicted proportion of defoliated aspen tree stems/ha while changes in predicted values for live conifer BA/ha was more gradually negative (Fig. S5). The marginal effects plot for live aspen BA/ha showed a positive effect on the predicted proportion of defoliated aspen tree stems/ha (Fig. S5). For the GLMM, nearest neighbor distance and live aspen tree BA/ha best explained the proportion of defoliated aspen tree stems/ha ( $p < 0.01$ ; Table 1), explaining a large

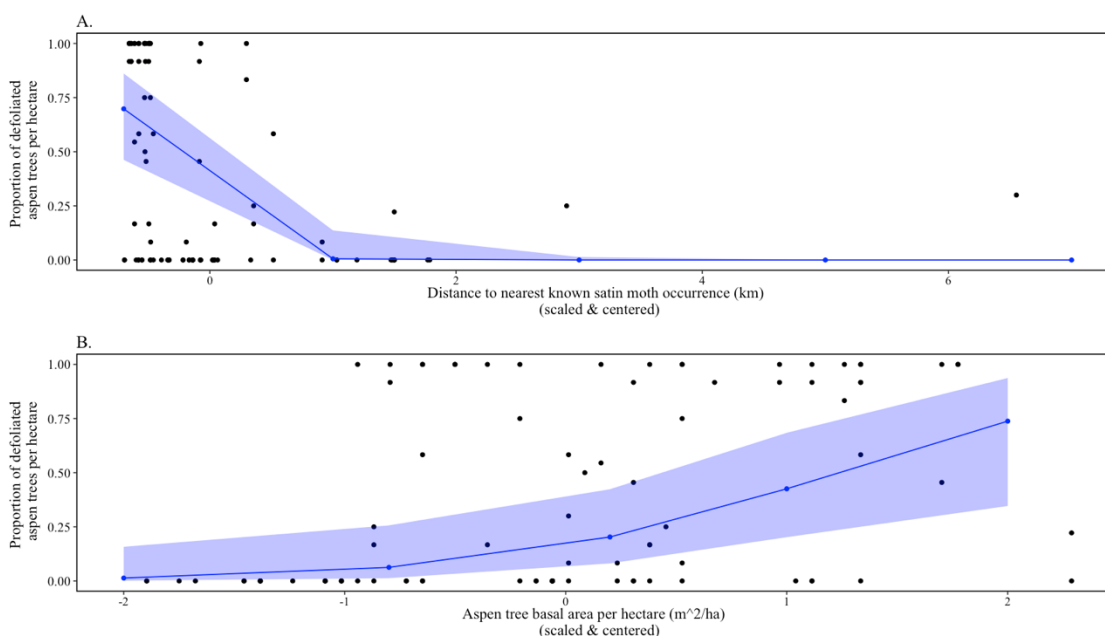


**Figure 2.** A. The proportion of quaking aspen (*Populus tremulooides*) trees defoliated by the novel, invasive white satin moth (*Leucoma salicis*) in each sampling plot across the Carson Range of California and Nevada, USA. A: The proportion of defoliated aspen trees in 2019. B: The proportion of defoliated aspen trees in 2020.

**Table 1.** Summary of fixed effects from best fitting generalized linear mixed model examining the proportion of quaking aspen (*Populus tremuloides*) trees per hectare defoliated by the invasive white satin moth (*Leucoma salicis*) with the random effect of plot in the Carson Range of California and Nevada, USA. ( $p < 0.05$ )

Fixed Effects	Estimate	Std. Error	z value	Pr(> z )
Intercept	-1.6353	0.5807	-2.8161	0.0049
Distance to Nearest Known Satin Moth Plot	-3.5339	1.1943	-2.9590	0.0031
Live Aspen Tree Basal Area per Hectare	1.3356	0.4815	2.7738	0.0055

portion of variation (marginal  $r^2 = 0.740$ ) with only a small portion of the variation explained by measurement year (Conditional  $r^2 = 0.784$ ). The effect of nearest neighbor distance was negative while live aspen tree BA/ha had a positive influence on the proportion of defoliated aspen tree stems/ha (Fig. 3).



**Figure 3.** The effects plots for each of the predictor variables in the best-fit generalized linear mixed model evaluating the drivers of quaking aspen (*Populus tremuloides*) tree defoliation by the invasive white satin moth (*Leucoma salicis*) in the Carson Range of California and Nevada, USA. The response variable (y-axis) for all plots is the proportion of defoliated aspen trees per hectare. A: The distance to the nearest known plot with satin moth occurrence (km), which has been scaled and centered. B: The live aspen tree basal areas (m<sup>2</sup>/ha), which has been scaled and centered.

**3.4 Drivers of Aspen Regeneration-** The only significant ( $p < 0.05$ ) Pearson's correlation were HLI and proportion of defoliated aspen tree stems/ha, and both had a positive

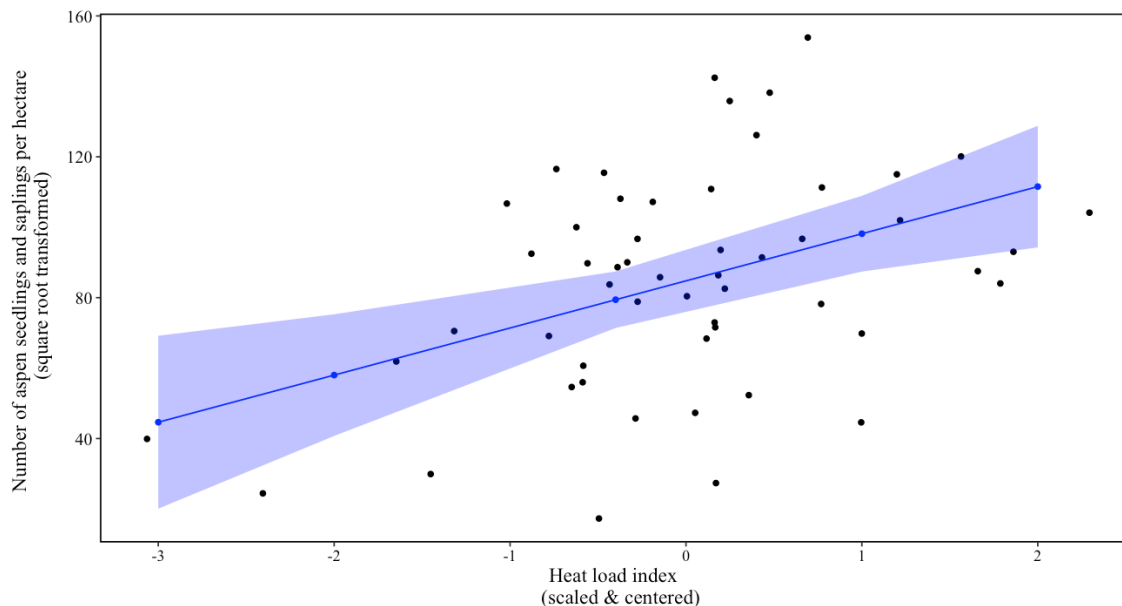
correlation with the aspen regeneration stems/ha (Fig. S6). The variable permutation importance from the RF process was highest for HLI and lowest for live conifer BA/ha (Fig. S7). The marginal effects plots showed all predictor variables having a positive influence on the aspen regeneration stems/ha except for live conifer BA/ha (Fig. S8). For the GLM, HLI best explained the aspen regeneration stems/ha ( $p < 0.05$ ; Table 2), explaining a modest portion of variation (McFadden's pseudo  $r^2 = 0.291$ ). The influence of HLI on aspen regeneration stems/ha was positive (Fig. 4).

**Table 2.** Summary of coefficients from best fitting generalized linear model examining the density of quaking aspen (*Populus tremuloides*) seedlings and saplings per hectare within the Carson Range of California and Nevada, USA. ( $p < 0.05$ )

Coefficients	Estimate	Std. Error	t value	Pr(> t )
Intercept	84.777	3.744	22.642	0.000
HLI	11.966	3.855	3.104	0.001
Proportion of defoliated aspen trees per hectare	6.820	4.092	1.667	0.102
Live Conifer Basal Area per Hectare	-6.627	4.032	-1.643	0.327
CMD	7.960	3.972	2.004	0.152

#### 4. Discussion

Non-native satin moth is a little-known disturbance agent with the potential to lead to reduced growth and dieback in quaking aspen, one of North America's most ecologically and socially important tree species. These impacts are of particular concern in regions, such as the Sierra Nevada, where aspen is limited in extent but plays a disproportionate ecosystem role, though findings of impacts of this non-native insect have continental implications given aspen's widespread distribution. In this study, we surveyed a multi-year satin moth infestation in quaking aspen of the east Tahoe Basin in



**Figure 4.** The effects plot for heat load index, the only significant predictor variable in the best-fit generalized linear model evaluating the drivers of quaking aspen (*Populus tremuloides*) regeneration in the Carson Range of California and Nevada, USA. The response variable (y-axis), number of aspen seedling and saplings per hectare, is square root transformed. The predictor variable (x-axis) is scaled and centered.

order to quantify the potential implications of white satin moth defoliation, providing the first assessment of this non-native disturbance agent in western forests. Rates of defoliation varied both spatially and temporally, and the stand and landscape factors best explaining defoliation rates were the availability of host trees (i.e., basal area of mature aspen) and the distance to the nearest neighboring infested stand. Although these findings do not provide implications for direct management and control of this non-native insect, they do suggest that containing the spread of satin moth among the scattered aspen of the Sierra Nevada may provide the strongest mitigation in limiting further infestation in an ecosystem where aspen is highly valued yet limited in extent.

*4.1 Stand Condition & Satin Moth Extent-* The level and variable nature of defoliation in Sierra Nevada aspen is consistent with findings in the Acadian forests of eastern North America, where spongy moth defoliation was more uniform in areas of higher defoliation

(Hennigar et al., 2007). Defoliation was widespread across our region, but many of the stands experiencing the greatest proportion of defoliated aspen tree stems/ha were concentrated in the central portion of the Carson range. This may reflect the initial introduction point of satin moth in the region, especially given that others observed satin moth in this area much earlier than the 2019/2020 defoliation events (Roland Shaw, Nevada Division of Forestry, *personal communication*).

Although human movement was likely the initial vector of satin moth into the region, as was the case with spongy moth in eastern North America (Liebhold et al., 1992; Bigsby et al., 2011), future spread between stands will likely result from life cycle conditions or host tree abundances that favor satin moth population growth. Similar to spongy moth in invaded Siberian forests (Ananko & Kolosov, 2021), years with increased snow cover may allow for greater winter survival of satin moth egg masses. Although the Sierra Nevada is expected to receive less precipitation as snowfall under projected climate scenarios (Das et al., 2011), occasional winters with abundant snowpack may allow satin moth populations to erupt. Furthermore, satin moth may reach epidemic levels if those high snowpack years are preceded by multiple years of climatic conditions that favor increased host tree population abundance or growth, as was shown with spongy moth in eastern North American forests (Haynes et al., 2022).

Conversely, climatic conditions may increase physiological stress in host trees and reduce plant defenses, as with other forest pests (Breshears et al., 2009; Haynes et al., 2022). For example, aspen mortality in western North America from SAD is a result of prolonged drought stress (Worrall et al., 2013; Anderegg et al., 2019) in concert with concurrent pest or pathogen infestations (Worrall et al., 2008; Marchetti et al., 2011;

Singer et al., 2019). Similarly, given the prevalence of other pests and pathogens on aspen in our study region and the increased risk of future severe droughts in California (AghaKouchak et al., 2014; Das et al., 2022), we may expect increased infestations when drought diminishes host tree vigor, especially if such conditions persist over multiple years.

Although many of our plots currently lack satin moth, we anticipate infestation in the near term given their proximity to infested stands, the abundance of host trees, and likelihood for future climatic conditions that reduce host tree vigor or promote satin moth population growth. The infestation of new stands will likely be greatest when climatic conditions favor aspen tree growth and high snowpack increase satin moth larvae survival followed by prolonged periods of drought that diminish aspen defenses. The relatively healthy aspen stands in our study area may experience increased canopy dieback or stand decline from the compounding stress of drought and defoliation, as has been observed with other aspen pests in western North America (Worrall et al., 2013). However, it is too early in the invasion process for such impacts to be observed and further monitoring of aspen stand health is necessary to attribute such declines to satin moth.

*4.2 Drivers of Defoliation-* As pest-host biology would predict (e.g., Liebhold et al., 1995), the availability of aspen host trees as well as the local populations of this non-native insect were the strongest determinants of defoliation rates. The strong influence of nearest neighbor distance indicates that dispersal is subject to both density dependence and distance limitations. Female satin moths tend to oviposit their first and largest egg masses prior to flight (Wagner & Leonard, 1987b), which likely contributes to the strong influence of distance. Given this and accounts of poor flight capabilities (Brown &

Rodstrom, 2017), we hypothesize that baseline rate of satin moth dispersal to new aspen stands will be relatively slow given the short distances they are capable of traveling.

While satin moth was only observed on aspen in our study region, it is known to infest a variety of *Populus* and *Salix* species throughout North America (Burgess, 1921; Humphreys, 1996; Spears, 2018) and has been observed simultaneously infesting aspen and *Salix* species in other parts of the West (K. Nelson, personal communication).

Therefore, dispersal between noncontiguous aspen stands could be facilitated by other host species should satin moth in the region exhibit more generalist host selection. Such broadening of host selection has been observed at high population densities for other herbivorous insects (Wallin & Raffa, 2004; Castagneyrol et al., 2006). Additionally, increased levels of intraspecific competition have been shown for other herbivorous insects at greater population densities (e.g., Craig et al., 1990; Denno & Roderick, 1990; Anderbrant et al., 1985), thus we would also expect behavior favoring dispersal to be more prominent when satin moth populations are denser. Therefore, dispersal to uninfested sites may be more likely to occur during future population eruptions leading to potential expansion of satin moth to other aspen stands in the Carson range, particularly those adjacent to areas with high abundances of other host species.

Our finding of a positive relationship between defoliation and aspen basal area is consistent with that of spongy moth (Davidson et al., 2001, Haynes et al., 2022) as we may expect being that they are in the same subfamily. However, others have found stand density of susceptible host trees to explain greater variance in defoliation (Foster et al., 2013). Considering that larger trees account for a greater portion of basal area per hectare relative to small trees, the importance of basal area over stem density may be a result of

larger diameter trees supporting larger crowns and leaf area, thus providing more forage to satin moths. This may also mean that the basal area metric is capturing a diameter preference by satin moth, which is integral to basal area and important in host tree selection for other forest pests (Boone et al., 2011; Dodds et al., 2011). The close proximity of currently uninfested stands to those of moderate to high defoliation and the similar range of basal areas between these stands further indicates that uninfested stands are vulnerable to satin moth invasion in the near term.

*4.3 Regeneration and Defoliation-* Aspen regeneration is often stimulated by disturbances, such as wildfire, that increase resource availability (Jones & DeByle, 1985) and stimulate root suckering (Brown & DeByle, 1987). However, aspen regeneration via root suckering can persist in the absence of disturbance when climatic conditions are adequate for stimulation (Kurzel et al., 2007). Therefore, the strong influence of HLI on regeneration in our stands aligns with other findings demonstrating warmer soil temperatures promote root sucker initiation (Fraser et al., 2002; Hungerford 1988; Schier et al. 1985). Although defoliation had a nearly significant, positive influence on regeneration, we cannot attribute this disturbance to changes in light availability or stimulation of suckering given the regeneration class included saplings and many seedlings that would have established well before the 2018-2020 defoliation events. Therefore, an unexamined topoclimatic variable may underlie the correlation between defoliation and regeneration.

One potential explanation for the correlation between defoliation and regeneration is CMD. Although it was not significant, CMD was positively correlated with regeneration in this analysis. The higher soil temperatures resulting from greater solar

insolation would increase CMD (Stephenson, 1998) and stimulate root sucker initiation. However, increased CMD concomitantly reduces aspen tree vigor and may result in decline (Anderegg et al., 2013; Anderegg et al., 2015). These declines may be exacerbated by compounding disturbances as is the case in aspen stands affected by SAD, where higher CMD values led to greater declines (Worrall et al., 2010; Anderegg et al., 2012). Stands affected by SAD also have lower soil moisture levels and higher soil temperatures, potentially creating positive feedbacks that increase stressors and leave aspen stands vulnerable to further decline (Korb et al., 2014). Therefore, climatic conditions, such as CMD, may reduce overstory aspen tree vigor and render stands vulnerable to future defoliation while simultaneously generating microclimatic conditions in the understory that favor regeneration. While this may be the underlying correlation between defoliation and regeneration found in this study, further monitoring of future satin moth defoliation events and more detailed evaluations of the aspen regeneration class are necessary to expand on this relationship.

## **5. Conclusions**

The occurrence of satin moth is likely to spread throughout the Carson Range due to the local abundance of suitable host trees and the insect's current wide distribution across the range. The establishment of new infestations should be expected in host stands that are in close proximity to those currently infested and the impacts of satin moth are likely to be the most pronounced in stands with high aspen tree BA/ha. Given satin moth's broader host selection in other regions of North America, we expect dispersal between noncontiguous aspen stands to occur in part through the infestation of other host species, especially if host selection becomes broader at high satin moth population

densities. However, there is little research on satin moth ecology and its dispersal, particularly in western forests, so further studies are necessary to understand its invasion potential more fully.

Aspen regeneration is abundant in the region and is strongly tied to stand climatic conditions and greater densities of seedlings and sapling should be expected in stands with high HLI (i.e., southwest-facing slopes). While the effect of defoliation on regeneration cannot be explained by this study, it is plausible that topoclimatic stand conditions create favorable circumstances for both increased aspen regeneration and increased aspen tree susceptibility to satin moth. Our findings indicate that stand improvement actions which reduce aspen tree basal area may slow the rate of satin moth dispersal, particularly in uninfested stands immediately adjacent to current infestations. However, given how little is known about satin moth dispersal and its invasion potential, further research is needed to better inform such management actions. Therefore, we recommend current management priorities focus on improving the public's awareness of satin moth to increase its identification across the landscape and prevent the spread of potentially contaminated plant material, such as leaves or firewood, to other stands in the region and throughout the Sierra Nevada. Improving our understanding of this novel, invasive pest while preventing its unintentional spread, to the degree possible, provides a stronger recognition of satin moth's impacts on quaking aspen and how those may be mitigated to protect the ecologically valuable, yet spatially limited stands of the Sierra Nevada.

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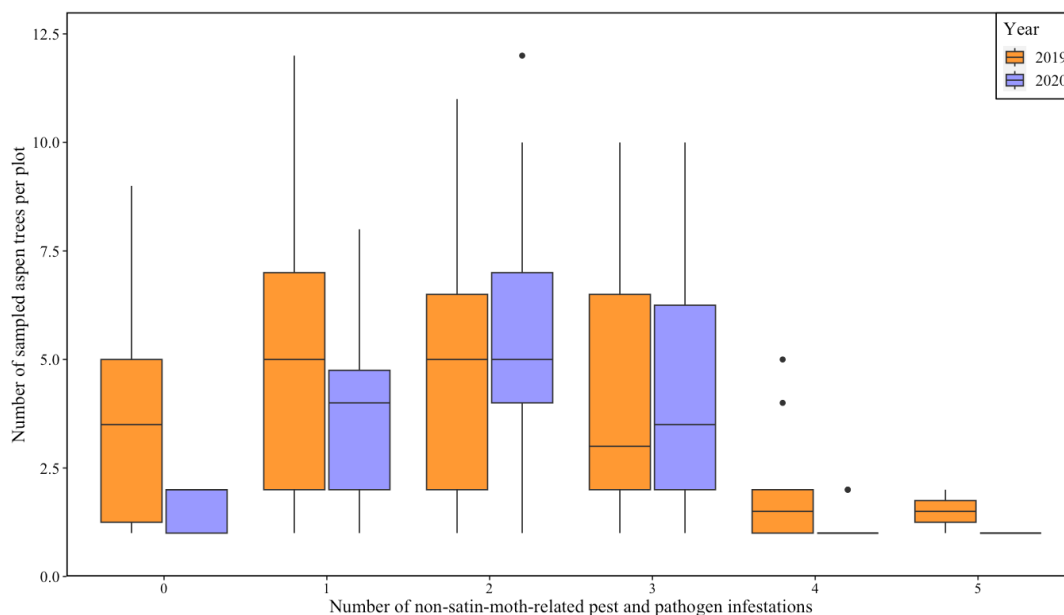
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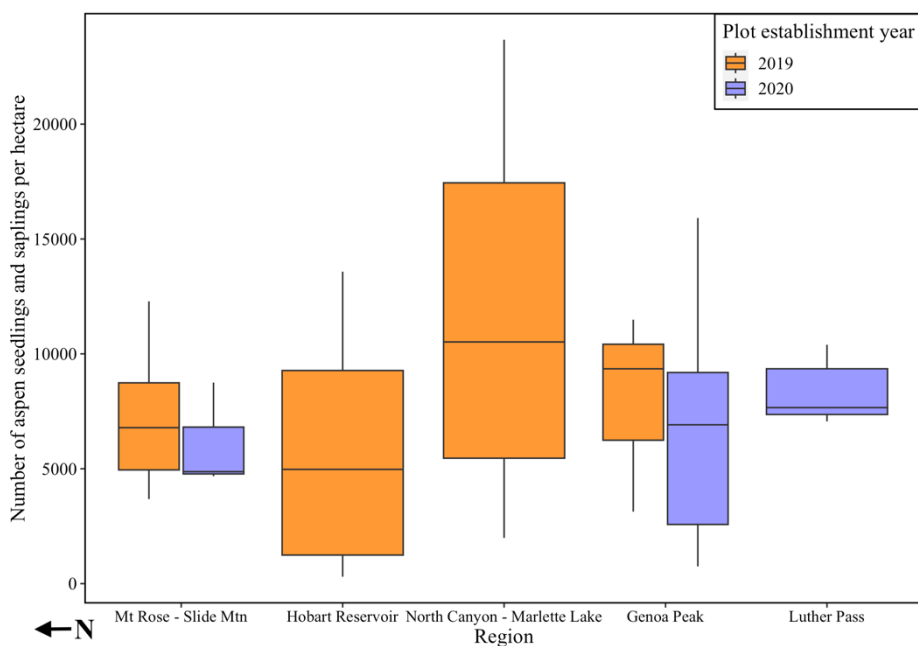
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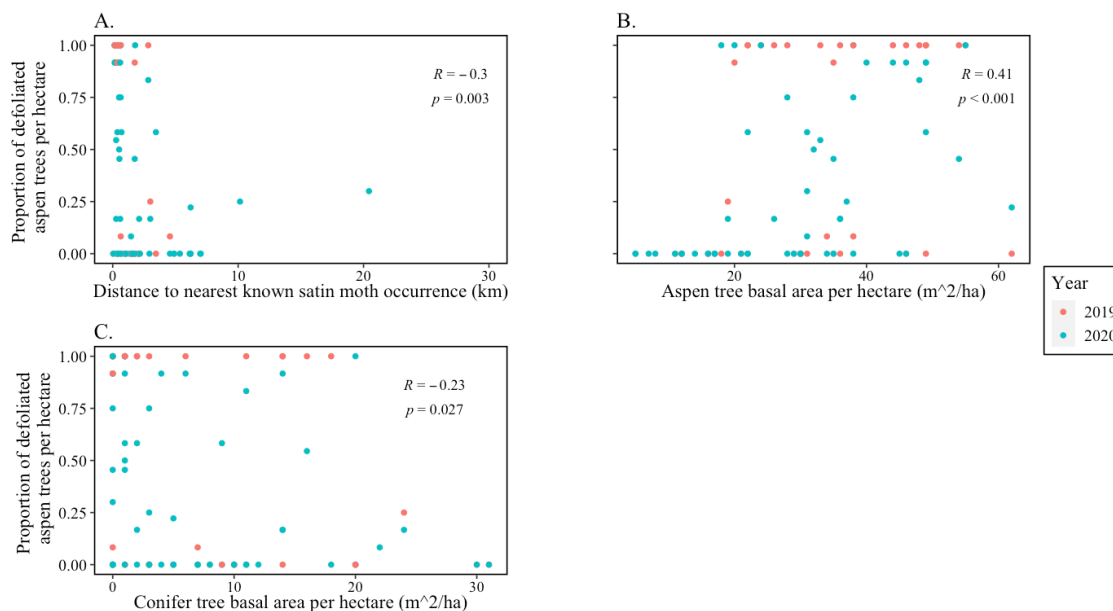
## Appendix A: Supplemental figures



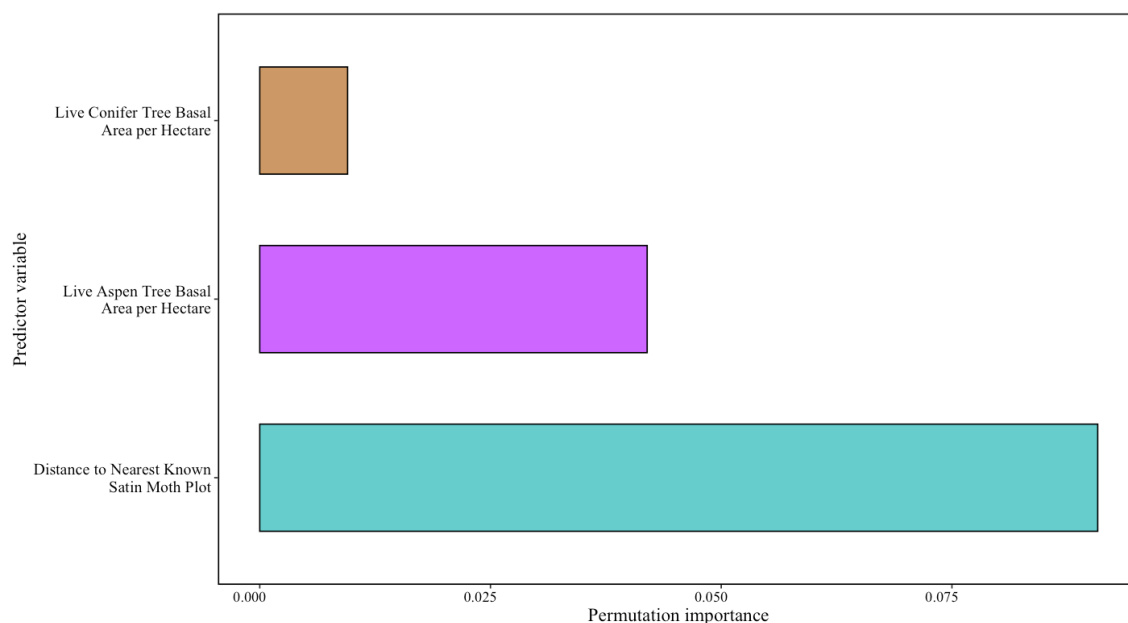
**Figure S1.** The number of sampled quaking aspen (*Populus tremuloides*) trees per plot ( $n = 12$ ) affected by the number of pest and pathogen infestations other than white satin moth (*Leucoma salicis*) from 37 study plots in 2019 and 55 plots in 2020 across the Carson Range of California Nevada, USA.



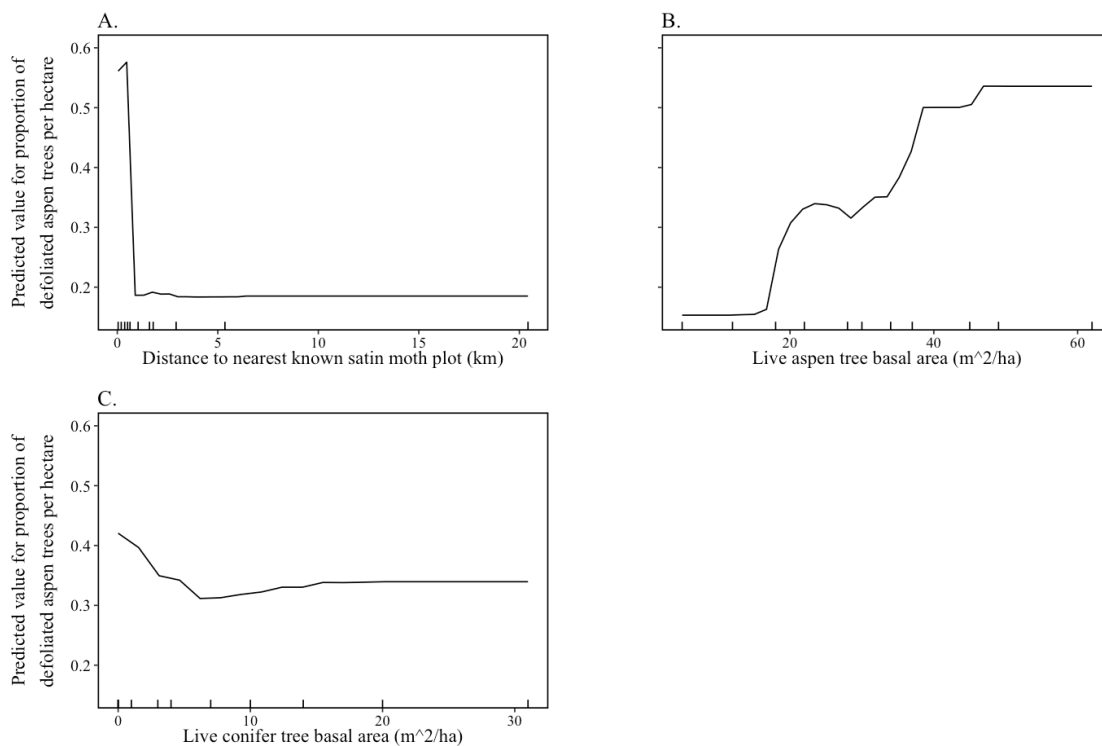
**Figure S2.** The number of quaking aspen (*Populus tremuloides*) seedlings and saplings by region from the year of plot establishment in the Carson Range of California and Nevada, USA. Regions are arranged from north to south.



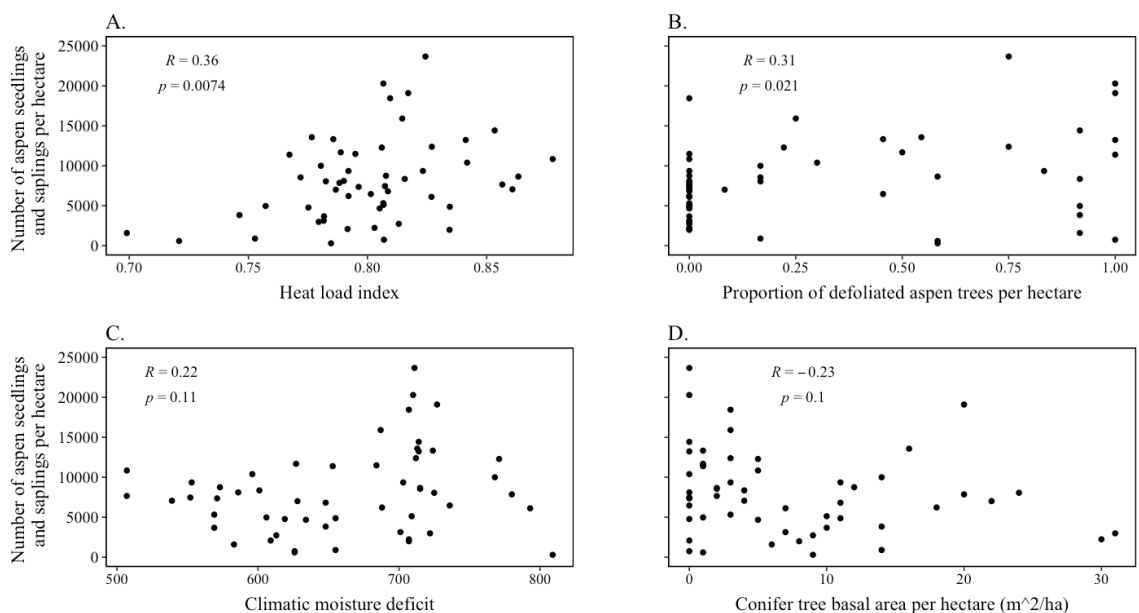
**Figure S3.** Correlation plots for a subset of potential predictor variables in the conditional random forest model evaluating the drivers of quaking aspen (*Populus tremuloides*) tree defoliation by the invasive white satin moth (*Leucoma salicis*) in the Carson Range of California and Nevada, USA. The response variable (y-axis) for all plots is the proportion of defoliated aspen trees per hectare. The value for  $R$  is the Pearson's correlation coefficient and  $p$  is the p-value. A: The correlation of distance to the nearest known plot with white satin moth occurrence with the response variable. B: The correlation of live aspen tree basal area per hectare ( $m^2/ha$ ) with the response variable. C: The correlation of live conifer tree basal area per hectare ( $m^2/ha$ ) with the response variable. Note differences in x-axis scales.



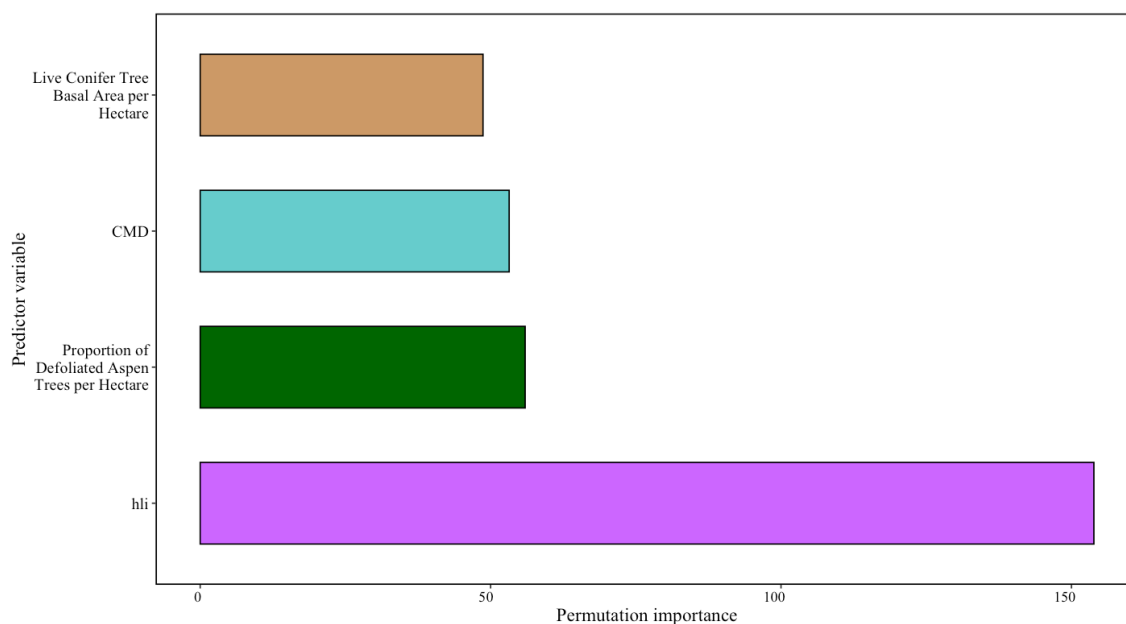
**Figure S4.** The variable permutation importance for the final three predictor variables used in the conditional inference random forest model analyzing the drivers of white satin moth (*Leucoma salicis*) defoliation on quaking aspen (*Populus tremuloides*) in the Carson Range of California and Nevada, USA.



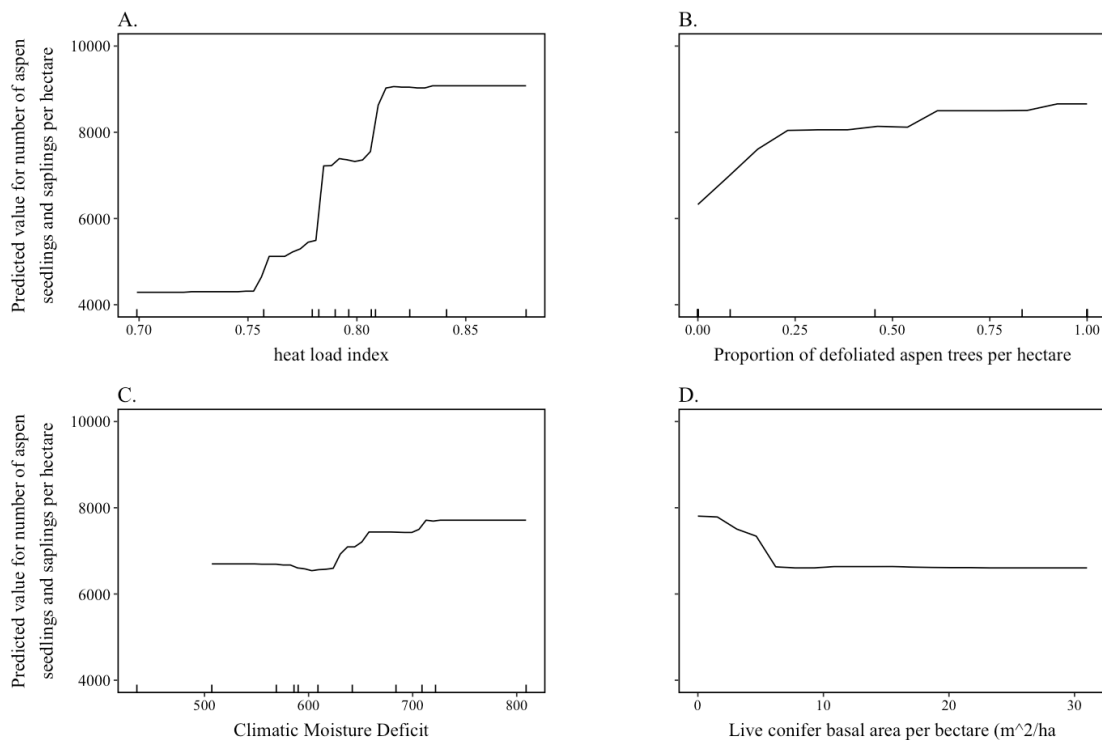
**Figure S5.** Marginal effects plots for each of the predictor variables in the conditional random forest model evaluating the drivers of quaking aspen (*Populus tremuloides*) tree defoliation by the invasive white satin moth (*Leucoma salicis*) in the Carson Range of California and Nevada, USA. The response variable (y-axis) for all plots is the proportion of defoliated aspen trees per hectare. A: The predicted proportion of defoliated aspen trees across a range of distances to the nearest known plot with satin moth occurrence. B: The predicted proportion of defoliated aspen trees across a range of live aspen tree basal areas (m<sup>2</sup>/ha). C: The predicted proportion of defoliated aspen trees across a range of live conifer tree basal areas (m<sup>2</sup>/ha). Note differences in x-axis scales.



**Figure S6.** Correlation plots for a subset of potential predictor variables in the conditional random forest model evaluating the drivers of quaking aspen (*Populus tremuloides*) regeneration in the Carson Range of California and Nevada, USA. The response variable (y-axis) for all plots is the number of aspen seedlings and saplings per hectare. The value for  $R$  is the Pearson's correlation coefficient and  $p$  is the p-value. A: The correlation of heat load index with the response variable. B: The correlation of the proportion of aspen trees per hectare defoliated by the invasive white satin moth (*Leucoma salicis*) with the response variable. C: The correlation of climatic moisture deficit with the response variable. D: The correlation of live conifer tree basal area per hectare ( $m^2/ha$ ) with the response variable. Note differences in x-axis scales.



**Figure S7.** The variable permutation importance for the final three predictor variables used in the conditional inference random forest model analyzing the drivers of quaking aspen (*Populus tremuloides*) regeneration in the Carson Range of California and Nevada, USA.



**Figure S8.** Marginal effects plots for each of the predictor variables in the conditional random forest model evaluating the drivers of quaking aspen (*Populus tremuloides*) regeneration in the Carson Range of California and Nevada, USA. The response variable (y-axis) for all plots is number of aspen seedlings and saplings per hectare (hereafter regeneration stems/ha). A: The predicted regeneration stems/ha across a range of heat load index values. B; The predicted regeneration stems/ha across a range of proportions of defoliated aspen trees per hectare. C: The predicted regeneration stems/ha across a range of climatic moisture deficit values. D; The predicted regeneration stems/ha across a range of live conifer tree basal areas ( $m^2/ha$ ). Note differences in x-axis scales.