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Species climatic suitability explains insect-host dynamics in the Southern Rocky Mountains, USA

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Manuscript highlights:

- Widespread outbreak patterns are determined by host climatic suitability.
- Suitable climatic conditions for the insect promote outbreak initiation and spread.
- Forest structure mediates the influence of climatic suitability on outbreak patterns.

Abstract

Recent extreme events of drought and heat have been associated with insect-driven tree mortality. However, there is substantial uncertainty about the impact of climate variability and extreme climatic episodes on insect-host dynamics, especially over species biogeographical ranges. Here, we use climatic suitability indices derived from Species Distribution Models to analyze the spruce beetle (*Dendroctonus rufipennis*) outbreak dynamics in spruce-fir forests across the Southern Rocky Mountains (USA) during a warm and dry episode (2000-2013). We estimated the historical climatic suitability of the host tree (1969-1998), its interannual variability, and the climatic suitability during the 2000-2013 episode for both beetle and host tree. Overall, outbreak was more like to occur in host tree populations inhabiting areas with historically suitable climatic conditions that were also characterized by loss of suitability during the episode. Specifically, the outbreak initiation was located in areas with suitable climatic conditions for the beetle and high historical suitability for the host. However, the year-to-year analysis revealed that low-moderate amounts of outbreak initiation and spread were also determined by high host historical climatic suitability, with high historical interannual variability, and a modest reduction of suitability during the episode. Years with high amounts of outbreak initiation and spread mostly occurred in dense forests with large trees, and were promoted by suitable climate conditions for the beetle. This study highlights the importance of considering the climatic suitability of the insect-host system to understand and anticipate outbreak dynamics at different temporal scales.

Keywords: *Dendroctonus rufipennis*, host susceptibility, outbreak initiation, outbreak spread, *Picea engelmannii*, Species Distribution Models.

INTRODUCTION

Extreme episodes of dry and warm conditions have led to increased forest mortality from fire, extreme drought, and insect disturbances worldwide (Seidl and others 2017; Sommerfeld and others 2018). In particular, bark beetles have emerged as an important biotic disturbance in recent decades (Raffa and others 2008; Anderegg and others 2015). Unprecedented outbreaks and the expansion of beetle species distribution into new areas are altering insect-host interactions (Bentz and others 2010; Sommerfeld and others 2020). Furthermore, tree populations are responding differently to abiotic and biotic disturbances throughout their distributional ranges (Camarero and others 2015; Cavin and Jump 2017). This underscores many uncertainties about the effects of climate on insect and host tree populations, especially in the context of climate change, which may bring more frequent and intense episodes of climatic extremes (Kolb and others 2016; Mezei and others 2017; Biedermann and others 2019).

The bark beetle-host system is sensitive to climatic variability because warming may accelerate insect development, while drought stress may reduce host tree defenses (Bentz and others 2010; Raffa and others 2016). Habitat conditions such as tree characteristics, stand structure, and landscape-level patterns of tree populations are also known to influence insect populations' capacity to grow and spread (Bakaj and others 2016; Aoki and others 2018). Variable responses of tree populations to drought and insect disturbances may also be explained by the climatic suitability experienced across species' geographic ranges (Cavin and Jump 2017; Lloret and Kitzberger 2018; Jaime and others 2019; Margalef-Marrase and others 2020). On the one hand, the occurrence and severity of disturbances may be more evident near the edge of a species' distribution due to higher limitations on population performance (Abeli and others 2014). Alternatively, locally adapted populations living under less suitable environmental conditions may be more resistant to drought due to plastic responses or directional selection (Vilà-Cabrera and others 2019). Likewise, tree populations inhabiting areas with historically suitable environmental conditions may show greater sensitivity and lower resistance to extreme drought events (Lloret and Kitzberger 2018; Margalef-Marrase and others 2020), likely due to acclimation to favorable conditions, and higher susceptibility to biotic disturbances, especially when these sites are also suitable for insects (Jaime and others 2019).

Species Distribution Models (SDMs) are commonly used to obtain estimates of climatic suitability for assessing ecological processes - such as mortality, decline, establishment, and insect outbreaks - related to short-term climatic events (Evans and Lyons 2013; Lloret and Kitzberger 2018; Pérez Navarro and others 2018). Unlike process-based models that incorporate mechanistic relationships, SDMs are correlative statistical approaches that are used to characterize a species' environmental niche (Franklin 2010). Concerning climate, SDMs quantify the probability of species occurrence under a set of climate conditions that characterize a given location. Such probabilities can be interpreted as a species-specific index of climatic suitability experienced by a population living at a given site (Soberón and Peterson 2005). Generally, SDMs are parameterized with current species distribution and historical climatic conditions to predict past or future distribution changes in relation to altered climates (Elith and Graham 2009). SDMs can also be used to quantify a populations' climatic suitability during an adverse climatic episode, as a measure of the episode's magnitude, and to consider the inter-annual variability in historical climatic conditions, as a measure of site environmental stability. Such stability is a key element to ecosystem vulnerability to extreme climatic events (Gutschick and BassiriRad 2003), for instance, because structural overshoot during favorable periods can lead to a mismatch between water demand and availability during drought (Jump and others 2017).

Across the Southern Rocky Mountain Ecoregion, USA (SRME; U.S. EPA, 2011), populations of Engelmann spruce (*Picea engelmannii*) have recently experienced widespread and severe spruce beetle (*Dendroctonus rufipennis*) outbreaks concurrent with warm and dry conditions. Specifically, the initiation of recent (i.e., post-2000) spruce beetle outbreaks in the SRME has been driven by summer, winter, and multi-year drought, whereas the proximity and the extent of the nearest affected forest drove the spread (Hart and others 2017). The presence of vast areas of susceptible habitat (e.g., stands with a high basal area and high density of spruce; (Schmid and Hinds 1974; Jenkins and others 2014) and suitable climatic conditions for the beetle may also be responsible for the recent broad-scale outbreaks (DeRose and Long 2012; DeRose and others 2013; Pettit and others 2020). Despite the evidence that the dynamics of spruce beetle outbreaks are functionally associated with climate, it remains unknown how site-specific host-beetle climatic suitability influences outbreak patterns.

Using annual time series of climatic data, we developed SDMs for both the host tree (i.e., Engelmann spruce) and spruce beetle to analyze outbreak dynamics in the SRME during the warm-dry 2000-2013 episode. To better understand how both host and beetle climatic suitability influence outbreaks, we defined the following suitability indices: 1) the average historical, or long-term, climatic suitability for the host (HCS_{host}; period 1969-1998); 2) the standard deviation of the historical climatic suitability for the host ($HCS\text{-}SD_{host}$), as a measure of the inter-annual variability; and 3) the average and yearly episode climatic suitability of the host and beetle for the 2000-2013 period (ECS_{host} and ECS_{beetle}). A negative or positive effect of HCS_{host} on beetle outbreak would indicate a higher infestation in host populations living close to their climatic limit of tolerance or their climatic optimum, respectively. Whereas, a positive effect of $HCS\text{-}SD_{host}$ on beetle outbreak would indicate increased amounts of infestation in environments with greater variability in historical climate conditions. Finally, a negative or positive effect of ECS_{host} on beetle outbreak would suggest that infestation is lower or higher, respectively, under less suitable climatic conditions for the host during the episode. Similarly, a positive effect of ECS_{beetle} on outbreak would indicate that high climatic suitability for the beetle is associated with greater infestation amounts. To understand the roles of climatic suitability, together with forest attributes, in driving spruce beetle outbreaks, we analyzed their effects in the response of outbreak dynamics at three spatiotemporal approaches: 1) cumulative outbreak occurrence during the 2000-2013 episode, 2) Locations of outbreak initiation and spread, 3) Year-to-year patterns of outbreak initiation and spread.

STUDY AREA

Our study area was constrained to spruce-fir forests in the SRME, extending from southern Wyoming to northern New Mexico, USA (Fig. 1). Within this region, spruce-fir forests range from 2,500 to 3,700 m in elevation. From December to March, average temperatures were –8.6 ± 1.5 °C and total precipitation was 138.4 ± 50.7 mm; from June to August, mean temperatures were 10.3 ± 2.1 °C and mean total precipitation was 138.1 ± 37.8 mm (1969-1999, CHELSA, Karger and others 2017). During the study period (2000-2013), the climate in SRME became increasingly warm and dry, with an increase of mean temperatures of 1 ± 0.2 °C from June to August and of 0.1 ± 0.3 °C from December to March. Likewise, a decrease of mean total precipitation of 29.5 ± 9.7 mm from June to August and 30.1 ± 20.2 mm from December to March (2000-2013, CHELSA, Karger and others 2017). Specifically, two severe drought events occurred in 2000-2003 and 2012-2013 across the region (Lukas and others 2014). The dominant tree species in spruce-fir forests of the SRME are Engelmann spruce and subalpine fir (*Abies lasiocarpa*), with some lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), and trembling aspen (*Populus tremuloides*).

DATA AND METHODS

Maps of spruce beetle outbreaks

To analyze the spatiotemporal dynamics of spruce beetle outbreaks in the SRME, we used annual maps describing the Engelmann spruce mortality attributed to spruce beetles at 30 × 30 m resolution (Hart and Veblen 2015; Hart and others 2017). These maps were developed using Landsat imagery from 2000-2014, in which gray-stage outbreak was identified within spruce-fir forests using multi-temporal trends in vegetation indices sensitive to tree mortality (Hart and Veblen 2015). Because beetle infestation precedes tree mortality's spectral signal (Meddens and Hicke 2014), we subtracted one year from the Landsat-derived detection year to identify the timing of the outbreaks (i.e., from 2000-2014 to 1999-2013). The 1999 map, which included prior spruce beetle-caused tree mortality, was used as a reference point for identifying newly outbreak pixels in subsequent years. From the spruce beetle outbreak maps, we removed burned, harvested, and blowndown areas that occurred 0-10 years before the outbreak period (Appendix S1, Table S1).

Because tree mortality identified using remotely-sensed vegetation indices may also be due to other factors besides spruce beetle, we overlaid the Landsat-based maps of bark beetle outbreak with a map of the cumulative spruce beetle damage from 1997-2014 period, derived from Aerial Detection Survey (ADS) data (McConnell and others 2000). Only areas included in both datasets were identified as affected by spruce beetle outbreak. Finally, we aggregated the 30 × 30 m grids of outbreak occurrence to 1 × 1 km pixels to match the scale of the available climatic predictors, while still retaining a spatial resolution fine enough to differentiate the initiation and spread processes of spruce beetle outbreaks. This pixel size selection is supported by mark and recapture studies showing that most spruce beetle dispersal occurs within 90-1600 m (Schmid 1970; Werner and Holsten H. 1997; Lindemann and Baker 2001).

Forest attributes

Given that the susceptibility of spruce-fir stands to beetle outbreak increases with average tree size and stand density (Schmid and Hinds 1974; Schmid and Frye 1977; Jenkins and others 2014), we obtained spatially-extensive proxies for each of these variables. To estimate stand density, we obtained Landsat-based maps of percent tree cover in 2000 (Sexton and others 2013) and calculated the percentage of tree cover within each 1 × 1 km pixel over the study region. To characterize dominant tree size, we used maps of stand structure (USFS 2003) to calculate the proportion of each 1 × 1 km pixel dominated by large trees (diameter at breast height >22 cm) (Appendix S1, Table S1). Though the relative proportion of host tree vs non-host tree may also influence stand–scale infestation (Schmid and Frye 1977), we did not have this geospatial information for spruce-fir forests and therefore this could not be included in our analysis.

Host–Beetle historical and episode climatic suitability

We used SDMs to estimate climatic suitability indices for the host tree and the bark beetle species. To build SDMs, we obtained 2,965 occurrence locations of Engelmann spruce from the ForeCASTS Project Tree Atlas V5 (2014) spanning the species' distribution in western North America (Appendix S1, Table S1). For the spruce beetle, we extracted the infestation occurrence from the ADS of the US Forest Service (McConnell and others 2000) and the Aerial Overview Survey (AOS) of the Canadian Forest Service (Koot 1997) (Appendix S1, Table S1). These datasets contain polygons derived from aerial surveys that delineate spruce beetle infestation and other forest disturbances at an annual timestep. We obtained polygons affected by spruce beetle from 2001-2014 collected in the Conterminous United States, Alaska, British Columbia, and Yukon territory. Within these polygons, we generated point locations using a stratified random sample to obtain annual infestation occurrence records of spruce beetle. Because infestation precedes visible effects of tree mortality, we assigned the year of spruce beetle infestation to the year before the recorded year in aerial surveys (i.e., from 2001-2014 to 2000-2013). To build SDMs, we also generated 10,000 pseudoabsences for the Engelmann spruce and 30,000 for the spruce beetle, based on the number of occurrences. To limit the influence of spatial autocorrelation (Veloz 2009) and match the resolution with the climate data, we filtered all the records by a minimum distance of 1 × 1 km.

Climate data were obtained from the CHELSA climate database v.1.2 and CHELSAcruts (Karger and others 2017) with 1 × 1 km resolution from 1969 to 2013. Over this period, we calculated 19 standard bioclimatic variables from monthly rainfall and maximum and minimum temperatures data, which represent annual trends, seasonality, and extreme or limiting environmental factors, using the 'dismo' package in R (Hijmans and others 2012). To limit multicollinearity, we filtered bioclimatic variables using a Variance Inflation Factor (VIF) <10 as a critical threshold (Quinn and Keough 2002) and a cluster dissimilarity value <0.8. From this filtered subset, we selected six variables with the lowest correlation among them. These final variables, describing temperature and precipitation regimes, helped to characterize environmental limitations for the host tree and beetle (see variables in Appendix S1, Table S1).

We used four different algorithms – GLM (generalized linear models), GAM (generalized additive models), Random Forest, and MaxEnt (maximum entropy) – to obtain robust estimates of climatic suitability for Engelmann spruce and spruce beetle. We evaluated each model's predictive accuracy by comparing model predictions with test sets in cross-validation using the area under the receiver operating characteristic curve (AUC) (mean AUC values range from 0.85 ± 0.001 to 0.96 ± 0.001; Appendix S2, details and Table S1). Then, we combined individual model predictions into an ensemble prediction using a weighted mean value, with individual weights proportional to AUC scores (Araújo and New 2007). We used the 'biomod2' package in R (Thuiller and others 2019) to build all SDMs and develop predictions.

To develop SDMs for Engelmann spruce, we used 30-year historical climate data (1969-1998) of the six selected climatic variables. For spruce beetle SDMs, we used annual climate variables from the year of infestation (*t*) and two years before infestation (*t*-2) in the warm-dry 2000-2013 episode to account for temporal lags in the response of infestation occurrence associated with climate variability, as well as the time (1 to 3 yr) required for beetle reproduction (Schmid and Frye 1977). Finally, we projected both host tree and beetle SDMs to obtain the following suitability indices throughout the SRME: 1) the averaged historical climatic suitability for the host tree (HCS_{host}) from 1969 to 1998, 2) the inter-annual variability in historical climatic suitability for the host tree ($HCS\text{-}SD_{host}$), corresponding to the standard deviation of annual suitability values from 1969 to 1998, and 3) the averaged episode climatic suitability for both the host tree and the beetle ($aECS_{host}$ and $aECS_{beetle}$) and the year-specific ($yECS_{host}$ and $yECS_{beetle}$) values during the 2000 to 2013 episode.

Outbreak initiation and spread

To explore the factors that determine the emergence and maintenance of outbreaks, we classified spruce beetle-occurrence pixels in the annual Landsat-derived maps as 'outbreak initiation'/'non-initiation' and 'outbreak spread'/'non-spread'. Most spruce beetle dispersal occurs at distances of 90 m to 1.6 km (Schmid 1970; Werner and Holsten H. 1997; Lindemann and Baker 2001). Thus, a pixel was classified as 'outbreak spread' for a given year if it was within a radius of 1.5 km of any pixels affected by outbreak in the previous year. Alternatively, the 'non-spread' category was assigned to unaffected pixels within 1.5 km of any previously affected pixel. We defined 'outbreak initiation' as affected pixels further than 1.5 km from any pixels considered affected by outbreak in the previous year. Finally, the ‘non-initiation’ category during a given year was assigned to all unaffected pixels further than 1.5 km from any outbreak initiation or outbreak spread pixels in the previous year.

Modeling the development of spruce beetle outbreak

To assess how the climatic suitability of both host and beetle, as well as forest attributes, influenced the spatiotemporal dynamics of spruce beetle outbreak from 2000 to 2013, we used three modeling approaches to analyze 1) the likelihood of any outbreak occurrence based on the cumulative infestation during the 2000-2013 episode, 2) the locations of outbreak initiation and spread as individual responses during the episode, and 3) the annual patterns of outbreak initiation and spread related to year-to-year climatic variability. Because spruce beetle outbreaks result in clustered patterns of affected pixels, typical of contagious processes, we addressed spatial autocorrelation in each analysis approach using different methods depending on the database size and the available computational capacity. The use of replicates with subsets of randomly selected pixels without incorporating spatial dependence terms allowed the inclusion of bivariate interactions in the models, while autoregressive methods allowed more accurate control of spatial dependence but prevented such interactions because of high computational demand.

First, we used GLMs with a logit-link function and binomial error structure to model the occurrence/absence of cumulative (2000-2013) spruce beetle outbreak as a function of $\mathrm{HCS}_{\mathrm{host}}$ (1969-1998), $\mathrm{HCS\text{-}SD}_{\mathrm{host}}$, $\mathrm{aECS}_{\mathrm{host}}$ (average 2000-2013), $\mathrm{aECS}_{\mathrm{beetle}}$ (average 2000-2013), proportion of large trees, and tree cover. While the estimation of regression coefficients may be sensitive to multicollinearity, none of our predictor variables were strongly correlated (correlation coefficient $(|r|) < 0.7$; Appendix S3, Table S1) supporting their inclusion into the models (Dormann and others 2013). We also included bivariate interactions between predictors of climatic suitability.

Because spatial autocorrelation was present in residuals when using a GLM with the full dataset, we ran 100 replicates of the final model with subsets of randomly selected pixels with a minimum spacing of 10 km.

Second, we used Generalized Linear Mixed-effects Models with a logit-link function and binomial error structure (GLMMs; 'lme4' R package, Bates and others 2015) to model outbreak initiation and spread locations as a function of HCS_{host} (1969-1998), $HCS\text{-}SD_{host}$, $yECS_{host}$ (year-specific values 2000-2013), $yECS_{beetle}$ (year-specific values 2000-2013), and forest attributes. Bivariate interactions between predictors were also included. We considered the 'outbreak initiation' *vs* 'non-initiation' and the 'outbreak spread' *vs* 'non-spread' pixel categories from 2000 to 2013 as response variables in two separate analyses. We fit GLMMs by Laplace approximation and included 'year' as a random intercept term to account for individual variation among years related to the locations of outbreak initiation and spread. Given the extreme imbalance in the number of observations per year, we only used years with more than ten outbreak pixels. Thus, for the outbreak initiation model, we included data from 2000, 2001, and 2011; for the outbreak spread model, we included all years except 2002. We ran 100 replicates for each final model with subsets of randomly selected pixels with a minimum spacing of 2 km, accommodating the beetle's dispersal distance to limit spatial autocorrelation effects.

Third, we developed conditional autoregressive models (CARs) using the 'R-INLA' package (Rue and others 2009) to evaluate the annual responses of outbreak initiation and spread from 2000 to 2013 as a function of HCS_{host} (average 1969-1998), $HCS\text{-}SD_{host}$, $yECS_{host}$ (year-specific values 2000-2013), $yECS_{beetle}$ (year-specific values 2000-2013), and forest attributes. In CARs, spatial dependence is incorporated using a matrix of spatial neighborhood weights (Fletcher and Fortin 2018). We considered the 'outbreak initiation' *vs* 'non-initiation' and the 'outbreak spread' *vs* 'non-spread' as response variables in separate analyses for each year. CAR annual models added information at finer spatio-temporal scale to our GLM and GLMM-based analysis.

To improve model stability and permit a direct comparison of effect sizes, we rescaled explanatory variables in each statistical model using the series-wide means and standard deviations (i.e., z-score transformation). For GLM and GLMM, we selected the most parsimonious models by minimizing the Akaike Information Criterion (AIC) from an initial full model, including the individual effects of forest attributes and the individual and interaction between climatic suitability indices for the host tree and the beetle. We tested for spatial correlation in all model residuals using correlograms (Appendix S4). All the statistical analyses were performed in R, version 3.5.2 (R Core Team 2017).

RESULTS

Across the SRME, approximately 33% of the total area of spruce-fir forests was affected by spruce beetle outbreaks from 2000 to 2013 (Fig. 1). Specifically, 78 % of the spruce-fir affected forest was situated in areas with suitable historical climatic conditions for the host tree (HCS_{host} values > 0.7, Fig. 2A). However, during the 2000-2013 episode, the host's climatic suitability declined by 44.8 % (± 13.3 SD), and 66 % out of the total affected area experienced unsuitable climatic conditions ($aECS_{host}$ values < 0.5, Fig. 2B). For comparison, almost 95% of the affected area of spruce-fir forests was found in areas with highly favorable climatic conditions for the spruce beetle during the 2000-2013 episode ($aECS_{beetle}$ values > 0.7, Fig. 2C).

The GLM of outbreak likelihood (i.e., cumulative infestation) from 2000 to 2013 (Table 1) indicated that outbreak occurrence was promoted by suitable climatic conditions for the spruce beetle, a high proportion of large trees, and the interaction between $aECS_{host}$ and HCS_{host}, where the likelihood of an outbreak tended to increase under the combination of high values of both

HCS_{host} (average 1969-1998) and $aECS_{host}$ (average 2000-2013). This HCS_{host}-$aECS_{host}$ interaction was driven by sites with high historical suitability that experienced a lower average reduction of climatic suitability over the 2000-2013 episode (Appendix S3, Fig. S1).

Individual GLMMs of the locations of (1) outbreak initiation and (2) spread over the study period (2000-2013) revealed that outbreak initiation typically occurred where year-specific suitable climatic conditions for the spruce beetle aligned with a high historical climatic suitability for the host tree, as reflected by a significant positive interaction between $yECS_{beetle}$ and $HCS_{host.}$ (Table 2). In contrast, none of the considered predictors explained patterns of outbreak spread. There was substantial variability in both initiation and spread models' temporal components, reflected by the variance explained by 'year' as a random effect (*R conditional*).

Annual maps showed that the initiation and spread of spruce beetle outbreaks primarily occurred in 2000, 2001, and 2010 at the square kilometer scale (Fig. 3); 33 % of the cumulative outbreak area experienced initiation and spread in 2000-2001 and 60 % in 2010. Host climatic suitability ($yECS_{host}$) was low throughout the study area during these years. A very small percentage of spruce-fir forest was affected by outbreak initiation or spread in the rest of the years (~7%), even though host climatic suitability was low in several years, such as 2007, 2011, 2012, and climate conditions were suitable for the spruce beetle ($yECS_{beetle}$) from 2000 to 2013. (Appendix S3, Fig. S2). CAR models provided additional insight into annual responses of outbreak initiation and spread (Fig. 4). These models demonstrated that in years with low amounts of newly-affected forest (2003-2009 and 2011-2013), small proportion of large trees, high suitable historical climatic conditions (HCS_{host}), and a decline in year-specific host suitability ($yECS_{host}$) were positively associated with outbreak spread. In 2010, the year with the highest amount of newly-affected forest, both initiation and spread emerged in areas with a high proportion of large spruce-fir trees and high tree cover. Additionally, in 2010, sites affected by spread showed favorable year-specific climatic conditions for the spruce beetle ($\text{yECS}_{\text{beetle}}$) and had higher variability in host-tree climatic suitability in the historical period ($\text{HCS-SD}_{\text{host}}$). In years with moderate amounts of initiation and spread (2000 and 2001), newly-affected areas were found in sites with favorable historical conditions for the host tree (HCS_{host}), which in 2001 was combined with high inter-annual historical variability ($\text{HCS-SD}_{\text{host}}$), and a higher year-specific suitability for the host tree ($\text{yECS}_{\text{host}}$).

DISCUSSION

Climatic suitability of both the host tree and the beetle, as well as forest cover and tree size, strongly influenced outbreak patterns during the warm and dry 2000-2013 episode in the SRME. The integration of Landsat-based data of Engelmann spruce mortality driven by spruce beetle with indices of climatic suitability obtained by Species Distribution Models improves our understanding of complex outbreak dynamics at a regional scale. In addition, the combination of three approaches to analyze the outbreak, from the general response for the whole episode to the yearly pattern of outbreak initiation and spread, revealed the importance of processes operating at different temporal scales.

Outbreak likelihood

The positive association of high historic and episodic climatic suitability for the host with the spruce beetle outbreak occurrence over the 2000-2013 period agrees with studies in other regions that observed a greater susceptibility of tree populations living near their climatic optimum to drought episodes (Cavin and Jump 2017; Margalef-Marrase and others 2020), bark beetle infestation (Jaime and others 2019), or the combination of both (Lloret and Kitzberger 2018). Notably, our results showed that an extreme loss of host climatic suitability during a warm and dry episode was not strictly necessary to increase the likelihood of outbreak occurrence. The direct effects of drought and heat on host trees may be less important than climate impact on bark beetle life cycle and outbreak likelihood (Pettit et al., 2020). Historically favorable growing conditions for the host may result in dense stands with high tree competition, especially during episodes of reduced water availability (Jump and others 2017), leading to successful beetle colonization due to greater availability of stressed hosts (Schmid and Hinds 1974; Schmid and Frye 1977). In addition, in areas with climatic conditions historically suitable for host trees, favorable conditions for beetles during the episode could promote insect population development rates and thus the infestation of larger and more vigorous trees, despite their stronger defenses (Krokene 2015).

Location of outbreak initiation and spread

Outbreaks were most likely to initiate in regions historically suitable for host trees when the year-specific climatic conditions were also suitable for the beetles. This aligns with the idea that favorable climatic conditions for beetle development may be more determinant than decreased host climatic suitability for the initiation of spruce beetle outbreaks (Hart and others 2017; Pettit and others 2020). In contrast, the lack of association between the overall pattern of outbreak spread with host and beetle climatic suitability may reflect an amplifying mechanism in which, once the outbreak is initiated, large beetle populations can colonize nearby healthy trees and, consequently, the size of the beetle population governs subsequent propagation of the outbreak (Raffa and others 2016). As such, when climatic conditions do not adversely affect insect survival, beetle pressure and the proximity to previously affected sites may be stronger predictors of outbreak spread (Preisler and others 2012; Hart and others 2017) than the climatic suitability of individual components of the host-beetle system.

Annual patterns of spruce beetle outbreak initiation and spread

Year-to-year climatic variability determines the patterns of outbreak initiation and spread. Low to moderate amounts of outbreak activity were observed in years with moderately warm and dry conditions, as indicated by year-specific host climatic suitability. During these years, initiation was scarce and spread mostly occurred in sites with historically favorable conditions and high inter-annual variability for the host. High climatic variability involving multiple past dry and heat episodes can have cumulative effects on tree vigor (Lloret and others 2004) and enhance the likelihood of outbreak due to the presence of more stressed trees (Hart and others 2014). Repeated, unfavorable year-specific climatic conditions leading to drought stress may affect tree vigor by compromising essential physiological processes, like photosynthesis, gas flux, resin production, and absorption of water and ions (Anderegg and others 2015). However, during years with moderate water stress, the increase of tree resistance may also contribute to maintaining low and moderate amounts of initiation and spread if tree growth is more constrained than the production of defense compounds (Kolb and others 2016).

A high amount of outbreak initiation and spread, and therefore years in which vast areas of forests were newly-affected, was associated with highly favorable conditions for the beetle but not with extreme conditions for the host (i.e., severe reduction of year-specific climatic suitability). This further supports the idea that outbreak dynamics are linked with unfavorable climatic conditions for the host that develop over multiple years (e.g., warming trends, frequent extreme events; Bigler and others 2007; Hebertson and Jenkins 2008; Hart and others 2014). Indeed, the two years in which outbreak initiation and spread were most common (2000 and 2010) were preceded by a year with favorable climatic conditions for the host after several years of unfavorable conditions (Huberty and Denno 2004). In turn, the substantial initiation and spread of new outbreaks in 2010 were preceded by three years of highly suitable conditions for the beetle.

Importantly, these suitable climatic conditions captured mild winter and warm summer temperatures, which might have increased the survival rates of overwintering beetles (Schmid and Frye 1977; Miller and Werner 1987) and accelerated beetle population growth (Hansen and Bentz 2003), facilitating a mass attack or spread to neighboring areas (Raffa and others 2016).

Forest attributes mediated the influence of host and beetle climatic suitability on outbreak patterns. In years with low to moderate amounts of new infestation, initiation and spread mainly occurred in areas of high tree density dominated by small trees. On the contrary, in the year with the highest amount of new infestation, the outbreaks emerged and propagated in areas dominated by large trees. Small tree size can play an important role in constraining spruce beetle activity when previous outbreaks mostly kill large trees (Hart and others 2015; Bakaj and others 2016) and also in areas affected by stand-replacing fires, in which the regenerating small tree-sized forests are buffered from regional-scale outbreaks (Bebi and others 2003; Kulakowski and others 2016). However, our results suggest that in areas dominated by small trees, infested hosts could operate as reservoirs of beetles (Logan and others 2010), helping to maintain outbreak activity in years when conditions are not optimal for the beetle. Eventually, the occurrence of highly suitable climatic conditions for the beetle may promote expansion into areas dominated by large trees, which along with the growth of endemic populations, may allow for the emergence of widespread and severe outbreaks in areas of old spruce-fir forests (DeRose and Long 2012).

This study improves our knowledge of how insect-host climatic suitability, together with forest attributes, modulates the outbreak pattern during episodes of warm and dry conditions. Particularly, it highlights the need to integrate the different components of the insect-host system to understand the processes driving the outbreak dynamics at different temporal scales. Overall, the observed regional insect-host dynamics suggest that tree populations situated closer to the species' climatic optimum can be affected by outbreaks under future warmer and drier conditions (Lloret and Kitzberger 2018; Jaime and others 2019). By contrast, in populations closer to the species' climatic edge, drought stress itself may play a limited role in determining the outbreak dynamics (Pettit and others 2020). Specifically, the combination of suitable drought-stressed trees, that experienced suitable historical conditions, with favorable climate for the insect may predispose forests to a rapid emergence of outbreaks with widespread tree mortality. This may lead to shifts in forest structure, carbon pools, and other forest ecosystem functions at broad spatial scales (Hart and others 2015; Biedermann and others 2019). Understanding the spatiotemporal variability of this changing disturbance regime provides opportunities to apply site-specific management actions. For instance, this variability can contribute to understand the limited role of thinning and shelterwood on bark beetle control, while being effective to enhance resilience following outbreaks (Temperli and others 2014) Also, this approach can be used to elaborate risk maps summarizing regional host-insect suitability under future climate scenarios, in order to maintain spruce-fir forests in the Southern Rocky Mountains while climate becomes more favorable to spruce beetle outbreaks.

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Table 1. Generalized linear model (GLM) results of the occurrence of cumulative spruce beetle outbreak in relation to insect-host climatic suitability and forest attributes during the 2000-2013 episode. Coefficient and p-value estimates are the mean values from 100 replicates of 600 pixels (300 affected and 300 unaffected), corresponding to randomly selected pixels within each 10 × 10 km cell over the study region. The models were carried out with outbreak occurrence/absence as binary response variable and seven predictor variables (including one 2-way interaction).

Table 2. Generalized linear mixed models (GLMM) results of the outbreak initiation and spread locations in relation to insect-host climatic suitability and forest attributes during the 2000-2013 episode. Coefficient and p-value estimates are the mean values from 100 replicates of 600 pixels (300 of initiation/spread and 300 non-initiation/non-spread), corresponding to randomly selected pixels within each 2 × 2 km cell over the study region. The models were carried out with initiation and spread as binary response variables (outbreak initiation/non-initiation, outbreak spread/non-spread), seven fixed predictor variables (including one 2-way interaction), and 'year' as random effect.

Table 1

Random pixels – 100 km^2				
Term	Coefficient	*SD**	*SE*	p
Intercept	–0.114	0.035	0.097	0.272
HCS_{host}	0.337	0.165	0.260	0.266
$\text{HCS–SD}_{\text{host}}$	0.208	0.143	0.206	0.379
$\text{aECS}_{\text{host}}$	0.275	0.157	0.257	0.335
$\text{aECS}_{\text{beetle}}$	**0.700**	**0.181**	**0.246**	**0.018**
$\text{aECS}_{\text{host}} \times \text{HCS}_{\text{host}}$	**0.727**	**0.209**	**0.302**	**0.044**
Large trees	**0.559**	**0.185**	**0.186**	**0.029**
Tree cover	0.254	0.137	0.196	0.255
R^2	0.10 ± 0.02			

Abbreviations: HCS_{host}, historical climatic suitability for the host; $\text{HCS-SD}_{\text{host}}$, inter-annual variability in historical climatic suitability for the host; $\text{aECS}_{\text{host}}$, averaged episode climatic suitability for the host; $\text{aECS}_{\text{beetle}}$, averaged episode climatic suitability for the beetle. Standard deviation (SD*) from the 100 replicates and standard error (SE) of model estimates. *Notes*: In bold, significant effects ($p < 0.05$).

Table 2

	Initiation				Spread			
Term	Coefficient	SD *	SE	p	Coefficient	SD *	SE	p
Intercept	-0.590	0.061	0.690	0.393	–1.296	0.498	0.054	0.133
HCS_{host}	**0.860**	**0.239**	**0.263**	**0.011**	0.347	0.319	0.019	0.359
$\text{HCS–SD}_{\text{host}}$	0.371	0.188	0.224	0.185	0.128	0.268	0.012	0.483
$\text{yECS}_{\text{host}}$	0.024	0.196	0.219	0.534	0.144	0.277	0.010	0.446
$\text{yECS}_{\text{beetle}}$	0.383	0.255	0.245	0.252	0.328	0.372	0.025	0.400
$\text{yECS}_{\text{beetle}} \times \text{HCS}_{\text{host}}$	**0.850**	**0.300**	**0.326**	**0.049**	-0.035	0.435	0.073	0.510
Large trees	0.360	0.213	0.209	0.205	-0.530	0.538	0.032	0.404
Tree cover	–0.061	0.176	0.205	0.554	-0.354	0.813	0.034	0.490
R marginal	0.05 ± 0.02				0.02 ± 0.01			
R conditional	0.29 ± 0.03				0.48 ± 0.05			

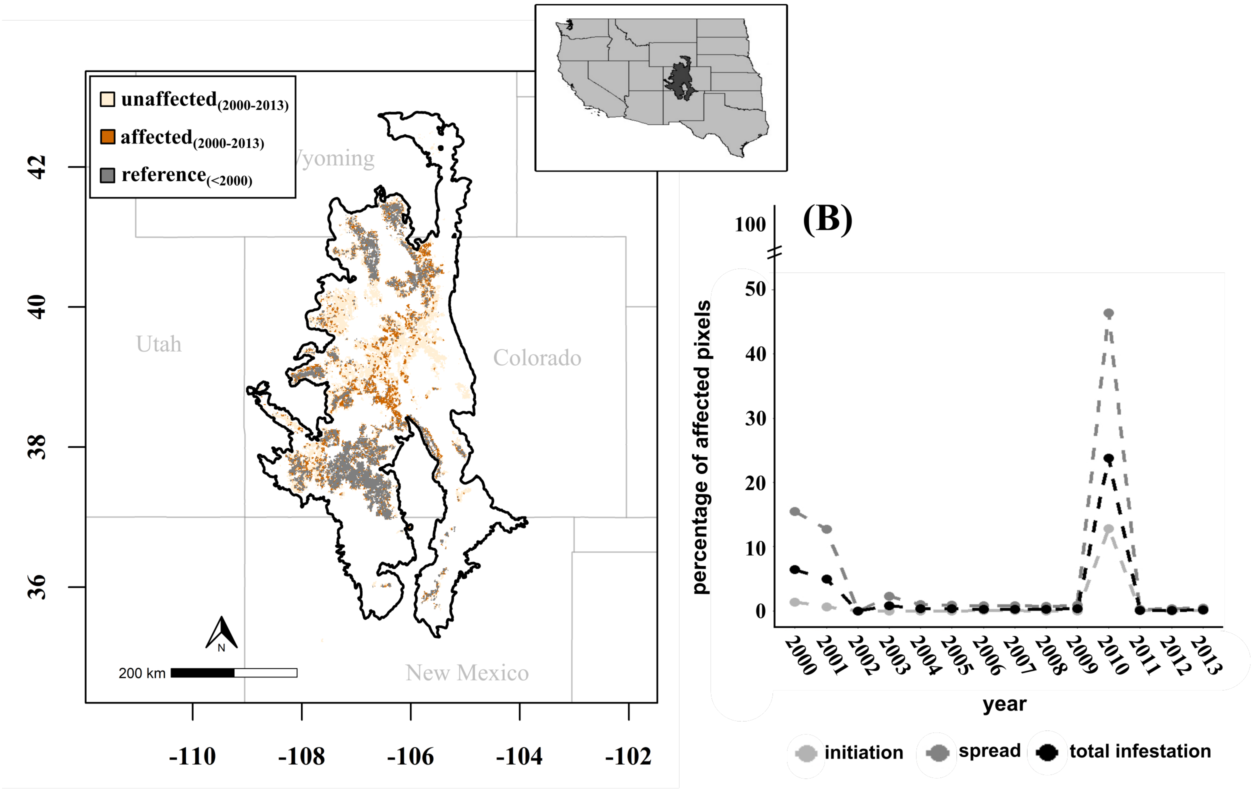
Abbreviations: HCS_{host}, historical climatic suitability for the host; $\text{HCS-SD}_{\text{host}}$, inter-annual variability in historical climatic suitability for the host; $\text{yECS}_{\text{host}}$, yearly episode climatic suitability for the host; $\text{yECS}_{\text{beetle}}$, yearly episode climatic suitability for the beetle. Standard deviation (SD*) from the 100 replicates and standard error (SE) of model estimates. *Notes*: In bold, significant fixed effects (p <0.05).

Figure 1. (A) Map of the Southern Rocky Mountain Ecoregion (SRME) displaying the total affected (N = 6,712) and unaffected pixels (N =13,414) of spruce-fir forest by spruce beetle outbreak during the 2000-2013 episode. Data were obtained from Landsat annual maps describing the Engelmann spruce mortality attributed to spruce beetles. The reference area encompassed the forest affected in previous years and was considered the baseline to account for new outbreak points over the 2000-2013 period. (B) Percentage of affected pixels from the available ones susceptible to be affected each year, thus reflecting the evolution of the total infestation, outbreak initiation, and outbreak spread during the 2000-2013 episode.

Figure 2. (A) Historical (1969-1998) climatic suitability (HCS_{host}) for the host tree in the SRME (67 px < 0.5; 1407 px ~ 0.5-0.7; 5238 px > 0.7 suitability values); (B) Episode (average 2000-2013) climatic suitability ($aECS_{host}$) for the host tree in the SRME (4449 px < 0.5; 2263 px ~ 0.5-0.7; 0 px > 0.7 suitability values); (C) Episode (average 2000-2013) climatic suitability ($aECS_{beetle}$) for the bark beetle in the SRME (7 px < 0.5; 336 px ~ 0.5-0.7; 6369 px > 0.7 suitability values). Black dots show pixels affected by spruce beetle infestation during the 2000-2013 episode. Brown to dark blue colors indicate low to high values of climatic suitability, respectively.

Figure 3. Newly-affected pixels by year in relation to the climatic suitability of the host tree during the 2000-2013 episode. The year 1999 was taken as reference to the previously affected area (grey dots) to create a baseline for the newly affected pixels in the following years. Black dots indicate outbreak spread pixels and red dots the outbreak initiation pixels. Brown to dark blue colors show low to high climatic suitability values. Number of new pixels by year (initiation/spread): 2000 (170/1115); 2001 (73/863); 2002 (0/0); 2003 (0/134); 2004 (1/57); 2005 (1/49); 2006 (2/43); 2007 (2/41); 2008 (1/38); 2009 (1/50); 2010 (1465/2565); 2011 (1/12); 2012 (0/9); 2013 (2/13).

Figure 4. Summary of coefficient estimates obtained in the conditional autoregressive models (CAR) performed for each year, describing: (A) outbreak initiation *vs* non-initiation and (B) outbreak spread *vs* non-spread of spruce beetle in relation to climatic suitability and forest attributes in each year of the 2000-2013 episode. Abbreviations: HCS_{host}, historical climatic suitability for the host; $HCS\text{-}SD_{host}$, inter-annual variability in historical climatic suitability for the host; $yECS_{host}$, yearly episode climatic suitability for the host; $yECS_{beetle}$, yearly episode climatic suitability for the beetle. Only years with more than ten affected pixels were included: 2000, 2001, and 2010 for initiation; and all years except 2002 for spread. '*' indicates significance ($p < 0.05$).



unaffected(2000-2013)
affected(2000-2013)
reference(<2000)
Wyoming
Utah
Colorado
New Mexico
42
40
38
36
-110
-108
-106
-104
-102
N
200 km
(B)
100
50
40
30
20
10
0
percentage of affected pixels
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
year
initiation
spread
total infestation

Figure 1

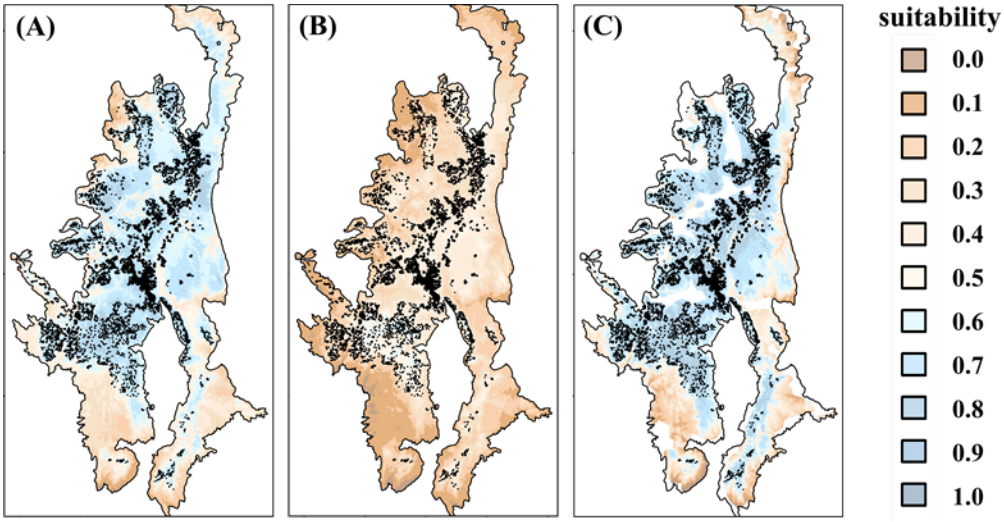


Figure 2

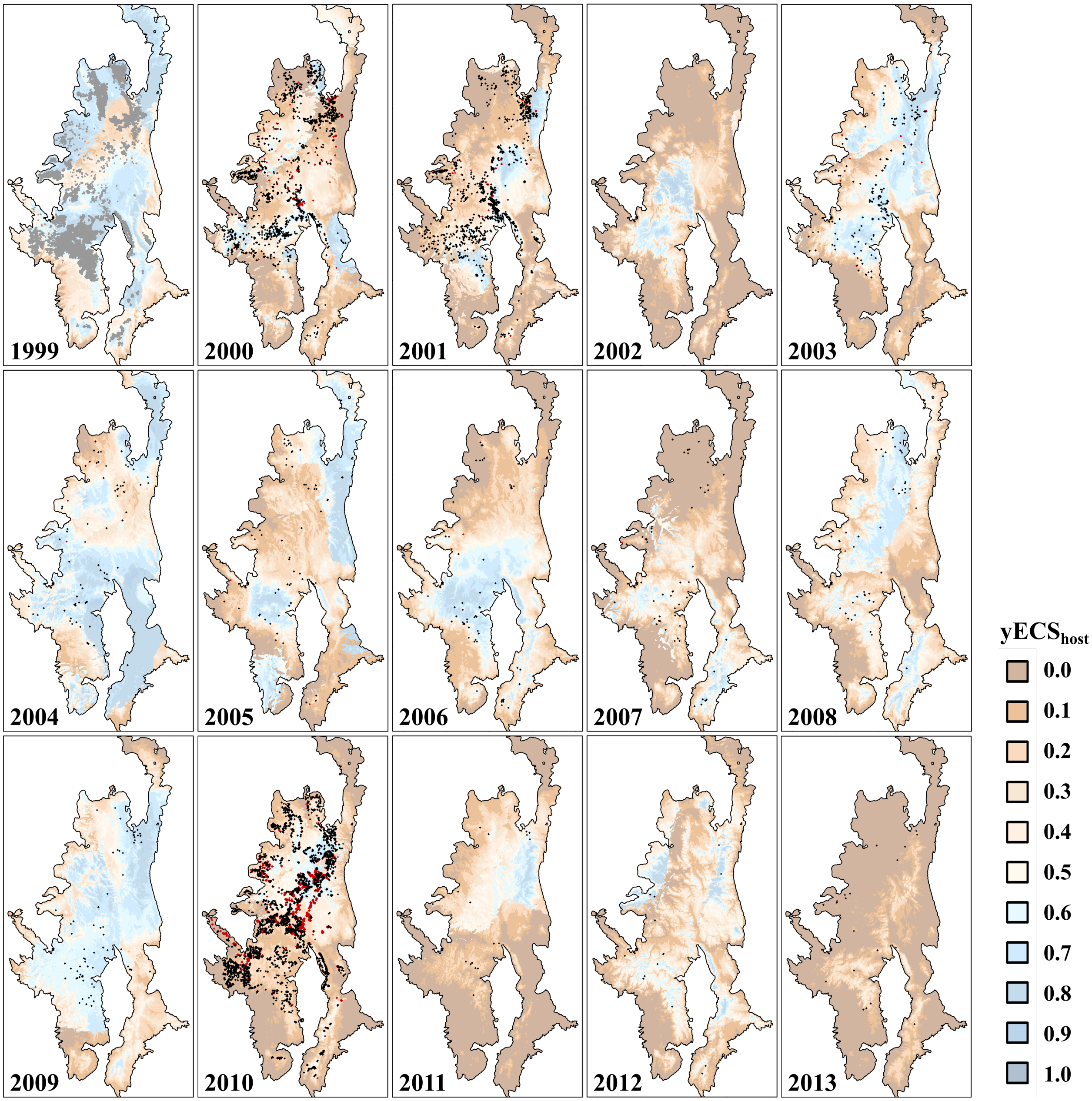

1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
yECS$_{host}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

Figure 3

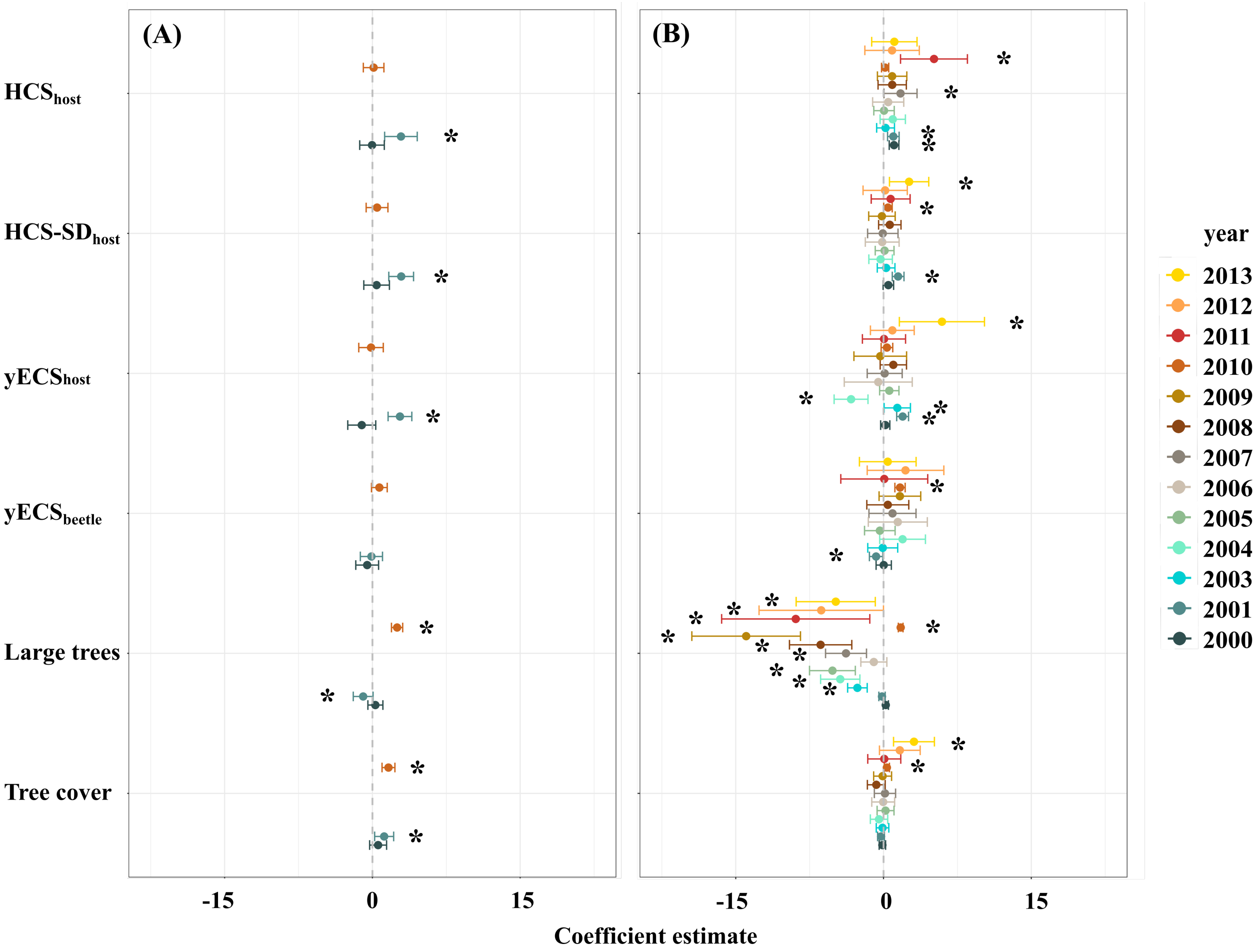

(A)
(B)
HCS$_{host}$
HCS-SD$_{host}$
yECS$_{host}$
yECS$_{beetle}$
Large trees
Tree cover
-15
0
15
-15
0
15
Coefficient estimate
year
2013
2012
2011
2010
2009
2008
2007
2006
2005
2004
2003
2001
2000

Figure 4