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ORIGINAL PAPER

Host-environment mismatches associated with subalpine fir decline in Colorado

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Abstract Subalpine fir decline (SFD) has killed more trees in Colorado's high elevation forests than any other insect or disease problem. The widespread nature of this disorder suggests that the cause involves climatic factors. We examined the influence of varying combinations of average annual temperature and precipitation on the incidence and distribution of SFD. Climatic transition matrices generated in this study indicate that most healthy trees are found in climatic zones with moderate to low temperatures and high precipitation; whereas, SFD occurs mostly in zones of moderate temperatures and moderate precipitation. The contrasting distributions define an environmental mismatch. Forests matched with favorable climatic conditions thrive; those that are mismatched can become vulnerable to decline disease.

Keywords Abiotic disorder · Climate stress · High elevation forests · Forest disease · Subalpine fir

Introduction

Mortality of subalpine fir (*Abies lasiocarpa*) associated with decline symptoms (Sinclair 1965) was first noted in high elevation forests of Colorado in the early 1990s (Geils *pers. com*). This condition was coined "subalpine fir decline" (SFD). Since then, SFD has contributed to the death of more trees in Colorado's high elevation forests than any other insect or disease problem (Colorado State Forest Service 2011, 2013). Yet published studies of SFD, other than what has appeared in annual assessments by federal and state agencies, are lacking.

Subalpine fir decline has been found over a large geographical region. The widespread nature of this disorder suggests that the cause involves climatic factors like temperature and precipitation. These factors, by themselves, seldom cause trees to die (Marchetti et al. 2011). Insect pests or diseases or both are usually the proximal cause of death. In this regard, SFD is thought to be caused primarily by western balsam bark beetle (*Dryocoetes confusus*) (Stock 1991; Molnar 1965; Furniss and Carolin 1977; McMillin et al. 2003; Bleiker et al. 2003; Lane and Goheen 1979; Negrón and Popp 2009), often in combination with a pathogenic canker causing fungus, *Ceratocystis dryocoetidis* (Molnar 1965; Furniss and Carolin 1977; Negrón and Popp 2009; Mcmillin et al. 2003; Stock 1991), or root disease fungi (*Armillaria ostoyae*) and fir-annosus (*Heterobasidion* sp.) (Lane and Goheen 1979; James and Goheen 1981; McMillin et al. 2003; Negrón and Popp 2009), or fir engraver beetles (*Scolytus ventralis*). The different roles of these causal agents are not well understood (e.g., Harris et al. 2001; Harris 2003). Although the symptom syndrome of SFD has not been well-described, the most obvious symptom is tree mortality. Tree mortality in subalpine fir in high elevation forests of the central Rocky Mountains is commonly attributed to SFD.

Limited information exists regarding the influence of climatic conditions on the physiology of the host and the dynamics of the various stress agents associated with SFD. Interactions between biotic agents and abiotic stresses can be complex, difficult to define, and commonly vary

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spatially. A critical method to describe these interactions would be useful. In this study, we hypothesized that mortality attributed to tree disorders, like SFD, is more common and/or more severe in climate zones where host trees encounter abiotic stress conditions that are marginal for host growth. We used Climate Transition Matrices (CTMs) with spatially-explicit climatic data to describe these kinds of host tree-climate relationships. In CTMs, data are summarized in a table where the rows correspond to predefined temperature zones and the columns to predefined precipitation zones. The use of climate zones provides an opportunity to examine the influence of temperature and precipitation on the large scale spatial dynamics of SFD. Climate zones similar to the ones developed for this study have been used to define strata in an inventory and monitoring program in Jalisco, Mexico (Reich et al. 2008a, 2010), describe the influence of climate on forest tree species richness (Reich et al. 2008b), model soil texture (Pongpattananurak et al. 2012) and characterize forest stand structure (Reich et al. 2011) and the influence of climate on the abundance and severity of forest insects in Alaska (Reich et al. 2013, 2014).

In this study, we use CTMs to identify and characterize environmental mismatches that have resulted in or contributed to mortality attributed to SFD in Colorado. In this regard, this study addressed three questions: (1) How do varying climatic conditions influence the distribution of spruce-fir forests and subalpine fir mortality in the state? (2) How do varying climatic conditions influence the level of subalpine fir mortality over large geographic areas? (3) How can the current spatial distribution of subalpine fir mortality influence the future distribution of that tree species in the state?

Materials and methods

Establishing statewide climate zones for Colorado

GIS raster layers representing 50 year average monthly temperatures (°C) and precipitation (mm) for the state of Colorado were obtained from previous work at a 30 m resolution (Aguirre-Bravo and Reich 2006). These layers were used to define six temperature zones and six precipitation zones, which in combination, defined 36 unique climatic zones in the western part of Colorado (Figs. 1, 2). The climate zones were based on a histogram equalization approach that produced a uniform distribution of temperatures and precipitations across the state of Colorado (Acharya and Ray 2005). This produces a somewhat linear relationship between the average temperature and precipitation associated with a given climate zone and the classes used to denote the climate zones. Zonal statistics were used to summarize the variability in temperatures and precipitation in each zone (Table 1).

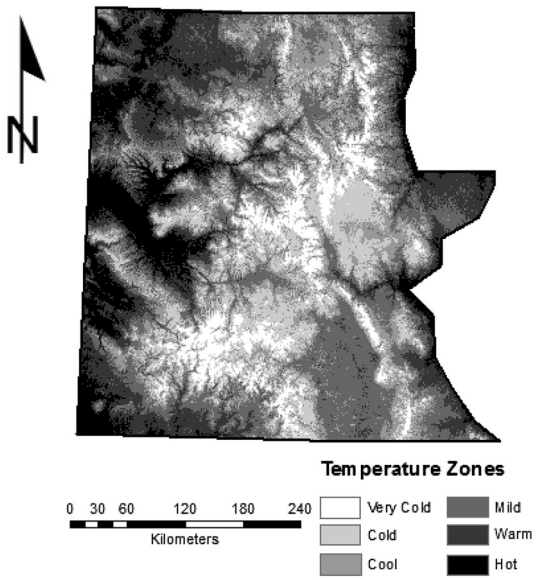

Fig. 1 Temperature zones of Colorado (Longitude: 102°W to 109°W; Latitude: 37°N to 41°N)

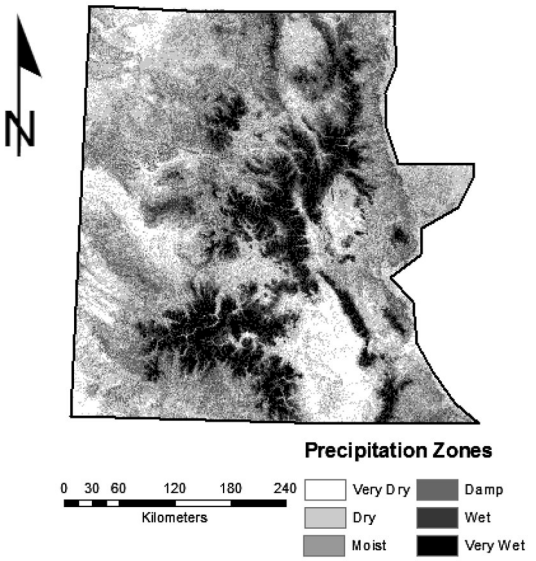

Fig. 2 Precipitation zones of Colorado (Longitude: 102°W to 109°W; Latitude: 37°N to 41°N)

Presence of spruce-fir forests in Colorado

Thirty meter raster layers of the major vegetation types were obtained from the Colorado Division of Wildlife as part of the Gap Analysis Program (http://ndis1.nrel.colostate.edu/cogap/cogaphome.html). The raster layer of vegetation types was converted to binary surfaces representing

Table 1 Summary statistics for the average annual temperature and precipitation associated with the temperature (T) and precipitation (P) zones identified in Colorado

Zone	Min	Mean	Max	CV %
Precipitation (mm)				
P1—Very dry	4.8	27.0	30.4	9.9
P2—Dry	30.4	33.9	36.7	5.2
P3—Moist	36.7	39.5	42.7	4.3
P4—Damp	42.7	46.0	50.7	4.8
P5—Wet	50.7	55.5	60.6	5.2
P6—Very wet	60.6	65.6	83.7	5.2
Temperature (°C)				
T1—Very cold	−5.7	−1.7	−0.3	55.1
T2—Cold	−0.3	1.3	2.4	54.7
T3—Cool	2.4	3.5	4.4	16.6
T4—Mild	4.4	5.3	6.3	10.0
T5—Warm	6.3	7.4	8.4	8.0
T6—Hot	8.4	9.4	13.9	8.3

the presence and absence of spruce-fir forests in Colorado. The binary maps were intersected with the raster layers representing the climate zones described above to obtain estimates of the probability of observing spruce-fir forests in each climate zone. Following the classical interpretation of probabilities, the probability of observing spruce-fir forests in a given climate zone, P (S|C), was defined as the ratio of the number of raster cells classified as spruce-fir, A(S), divided by the total number of raster cells in the climate zone A(C). This information was summarized as a 6 × 6 Climate Transition Matrix (CTM) where the rows represent the six temperature zones and the columns represent the six precipitation zones in the state (Reich et al. 2013).

Probability of mortality associated with SFD in Colorado

GIS layers of the Colorado aerial pest survey maps developed by Region 2 Forest Health Protection of the USDA Forest Service from 1994 through 2009 were obtained from the U.S. Forest Service (http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=stelprdb5348787). Georeferenced data were displayed as distribution maps in which visible patches associated with SFD mortality were delineated. The polygons mapped during the aerial detection surveys represent the spatial extent of the SFD mortality in a given area and not the area of mortality. Subalpine fir mortality occurs as individual trees or small clumps of trees scattered throughout the spruce dominated forests. In the interior of British Columbia, Parish et al. (1999) observed that the spatial distribution of both live and dead subalpine fir trees were significantly aggregated with most clusters having a radius less than 5 m. Given the scattered nature of the mortality and the speed at which the plane is flying (160 km h^{-1}) sketchmappers and photo-interpreters commonly use a tactic known as "lumping" in which spots of SFD mortality are lumped into large polygons (Johnson and Ross 2008). Both the USDA Forest Service (2014) and Colorado State Forest Service (CSFS 2013) define these polygons as having active mortality.

Layers for individual years were joined to obtain estimates of the cumulate area of active mortality from 1994 to 2009. The polygons representing active mortality were then converted to a raster with a 30 m spatial resolution using ArcGIS 10 (ESRI 2011). The software used the dominant method in converting vector to raster, so each cell was assigned the value of the polygon that occupied the largest amount of cell area. While Wade et al. (2003) observed no significant differences in landscape metrics based on the conversion of polygons to raster layers or raster layers to polygons, some details may be lost when converting the polygons representing the spatial extent of SFD mortality to a 30 m binary raster. Using a 30 m spatial resolution, the smallest feature that can be accurately delineated is one acre (0.4 ha) (Herold 2011), the minimum mapping unit of the aerial forest health survey (Johnson and Ross 2008). Thus, the conversion of polygons of active SFD mortality to a binary raster was not considered a major source of error in this study.

The binary raster layer representing the presence-absence of active SFD mortality was intersected with the climate raster layer to obtain estimates of the probability of observing active mortality within each climate zone, P (D|C). This probability was defined as the ratio of the number of raster cells classified as having active mortality, A (D), divided by the total number of raster cells in the climate zone, A(C). The probability of observing mortality given the presence of spruce-fir forests in a given climate zone were also computed. This conditional probability, P(D|S), was defined as the ratio of the number of raster cells classified as having active mortality, A (D), divided by the number of raster cells associated with the host species in the climate zone, A (S).

Influence of climate on distribution of spruce-fir forests and subalpine fir decline in Colorado

Linear and polynomial regression analyses were applied to patterns in the probabilities of observing both the host species and active SFD mortality on the CTMs as a function of the temperature (T = 1, 2, 3, 4, 5 or 6) and precipitation (P = 1, 2, 3, 4, 5 or 6) zones. A natural logarithm

transformation was used to stabilize the variability in the probabilities across climate zones, while the integers (1, 2, 3, 4, 5) were used to identify the temperature and precipitation zones in the model. The forms of the regression models were chosen based on the assumption that a species response to environmental factors generally follows either a linear (Reich et al. 2010) or curvilinear relationship (Grime 1979). The linear relationship between the integers representing the temperature and precipitation zones and the average temperature and precipitation is a property of the histogram equalization technique used in defining the climate zones (Table 1) (Acharya and Ray 2005). To account for the spatial structure in the probability data among the CMTs, a spatial autoregressive model was used to estimate the parameters of the model (Upton and Fingleton 1985):

$$\begin{aligned} y &= X\beta + \varepsilon \\ \varepsilon &= \lambda W\varepsilon + \eta \end{aligned} \tag{1}$$

where y is the dependent variable, X is a design matrix of independent variables, β are the regression coefficients, W is a binary spatial weights matrix used to define the joins of the 6 × 6 CTM following the chess move for a rook (up, down, left, right), $-1 < \lambda > 1$ is a measure of the degree of spatial correlation, ε are spatially correlated errors and $\eta \sim N(0, \sigma^2)$ spatially independent errors. A step AIC was used to select the subset of climate variables (temperature and precipitation zones) to include in the models. A likelihood ratio test was used to test the null hypothesis that the spatial models are an improvement over ordinary least squares (OLS), which assumes that the errors are spatially independent (H_o: $\lambda = 0$). Moran's I was used to test the residuals for spatial autocorrelations. p values were calculated under the randomization assumption (Upton and Fingleton 1985).

The fitted models were used to create a set of CTMs of the expected probability of observing active mortality, P (D|C), the expected probability of observing active mortality given the host, P (D|S), and the expected probability of observing the host, P (S|C). The CTMs based on the regression models were used to develop raster layers of the expected probabilities of observing spruce-fir forests and the probability of observing active mortality given the host.

Differential effects of climate on mortality associated with SFD

To assess the influence of climate on the probability of observing active SFD mortality an index is proposed to measure the differential effects of climate on the probability of mortality. The null hypothesis underlying this index assumes that the damage in terms of the area of active mortality is proportional to the availability of the host (i.e., area) and independence of climatic conditions. The distribution of the host, however, may be influenced by the climatic conditions. Expressed in terms of probabilities, the conditional probability of active mortality given the presence of the host P(D|S) in climate zone i ($i = 1,2,\ldots,C$) is proportional to the probability of observing the host P(S):

$$P_i(D|S) = \alpha P_i(S) \tag{2}$$

where α may be thought of as the intrinsic rate of increase. Next, probability values on both sides of the equation are normalized by dividing the individual probabilities in a given CTM by the maximum probability observed in the CTM. Following from (2)

$$P_{Max}(D|S) = \alpha P_{Max}(S) \tag{3}$$

where $P_{\text{Max}}()$ represents the maximum observed probability among the climate zones. Normalizing (2) using the relationship in (3) we get:

$$\frac{P_i(D|S)}{P_{Max}(D|S)} = \frac{\alpha P_i(S)}{\alpha P_{Max}(S)} \tag{4}$$

The rate α cancels out providing a simple expression for evaluating the effects of climate on the probability of active mortality:

$$P_{Ri}(D|S) = P_{Ri}(S) \tag{5}$$

where P_{Ri}(D|S) represents the normalized or relative probability in climate zone i. Under the null hypothesis this is a strict equality. If the null hypothesis is not true, the probability on the right side of the equation will not equal the probability on the left side of the equation. To account for any deviations from the null hypothesis a variable (Δ_i) specific to each climate zone is added to (5) to ensure this equality between the two sets of probabilities is satisfied:

$$P_{Ri}(D|S) = \Delta_i + P_{Ri}(S) \tag{6}$$

Rearranging (6) and solving for Δ_i we get

$$\Delta_i = P_{Ri}(D|S) - P_{Ri}(S), \tag{7}$$

a measure of the differential effect climate has on the probability of active mortality. This measure ranges over the interval $-1 \leq \Delta_i \leq 1$. If $\Delta_i = 0$ the probability of active mortality meets expectations under the null hypothesis, while positive values indicate probabilities of mortality higher than expectations; negative values represent probabilities of mortality lower than expectation. In the former case, the SFD insect-disease complex has a competitive advantage over the host, while the latter case represents situations in which the host has a competitive advantage over the SFD insect-disease complex.

To assess the potential impact of SFD mortality on the distribution and abundance of subalpine fir forests in Colorado, spatial representations of the CTMs for the rescaled probability of observing spruce-fir forests, the rescaled probability of active mortality given the presence of the host and their difference (Δ_is) were created using the regression equations developed for the individual CTMs. The difference layer was intersected with the binary layer associated with the presence-absence of spruce-fir forests to obtain area estimates associated with four levels of mortality in which the host had a competitive advantage over the SFD insect-disease complex: (a) high: $\Delta_i < -0.7$, (b) medium: $-0.7 \leq \Delta_i < -0.4$, (c) low: $-0.4 \leq \Delta_i < -0.15$ and (d) very little: $-0.15 \leq \Delta_i < 0$, and four classes in which the SFD insect-disease complex had a competitive advantage over the host: (e) very little: $0 \leq \Delta_i < 0.15$, (f) low: $0.15 \leq \Delta_i < 0.4$, (g) medium: $0.4 \leq \Delta_i < 0.7$ and (h) high: $\Delta_i > 0.7$. The classes were based on natural breaks in the distribution of differential effects of climate on the probability of active mortality.

Results

Influence of temperature and precipitation on the distribution of spruce-fir forest type

The spruce-fir forest type is a major component of the high elevation forests in Colorado (Fig. 3a). The spruce-fir forest type occurred in 32 of the 36 climate zones covering an area of more than 2.1 million ha (Table 2). A second degree polynomial was used to describe the relationship between the temperature and precipitation zones and the log of the rescaled probability of observing spruce-fir forests (Table 3). The spatial autoregressive model and a model based on ordinary least squares (OLS) accounted for

Table 2 Probability of observing spruce-fir forests in Colorado

Temperature zone	Precipitation zone					
	1	2	3	4	5	6
1			0.03	0.43	0.37	0.28
2	0.00	0.03	0.12	0.40	0.68	0.82
3	0.00	0.01	0.09	0.31	0.84	1.00
4	0.00	0.00	0.02	0.16	0.45	0.89
5	0.00	0.00	0.00	0.01	0.02	
6	0.00	0.00	0.00	0.00	0.01	

Probabilities are rescaled so the maximum probability is equal to one (max prob = 0.7929)

98 % of the variability observed in the rescaled probabilities of observing spruce-fir forests in a given climate zone (Table 3). Since the residuals from the OLS model were spatially independent (Moran's $I = -0.10$, p value = 0.486), the spatial autoregressive model did not significantly improve the overall fit of the model (Likelihood ratio, $LR = 0.569$, p value = 0.451). The probability of observing spruce-fir forests was highest throughout the central region of the mountains in western Colorado (Fig. 3a). This region represents a climate with moderate to high levels of precipitation (P = 4, 5 and 6) and very cold to mild temperatures (T = 1, 2, 3 and 4). The highest probability of observing spruce-fir forests was in the cool-very wet (T = 3, P = 6) region of the state. The probability of observing spruce-fir forests was lowest in the very driest (P = 1) and hottest (T = 6) regions of the state. This forest type did not occur in the coldest-driest and the hottest-wettest regions of the state.

Subalpine fir mortality

Subalpine fir mortality occurred in small to large patches scattered throughout the spruce-fir forest (Fig. 3b). The

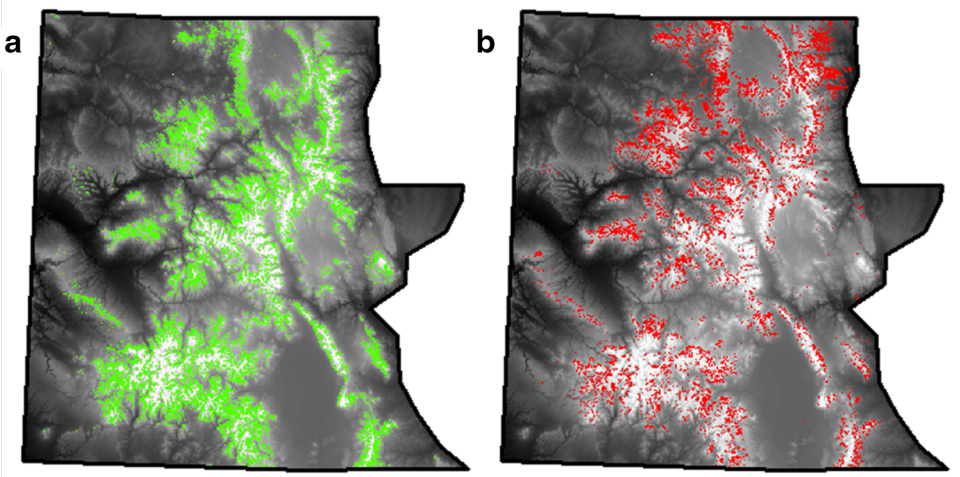

Fig. 3 **a** Spruce-fir forests (*green*) in western Colorado. **b** Spatial extent of subalpine fir decline (*red*) for the years 1994–2009 in western Colorado. Developed from ADS survey data (USDA Forest Service; http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/?cid=fsbdev3_041629)

Table 3 Comparison of ordinary least squares model with a spatial autoregressive model for the natural logarithm of the rescaled probability of observing spruce-fire forests in the mountains of Colorado as a function of the temperature and precipitation zones

Variable	Ordinary least squares		Spatial autoregressive model[a]	
	Coefficient	Standard error	Spatial autoregressive model[a]	Standard error
Intercept	−8.9075	1.1141	−35.6912	0.9067
T	1.0364	0.4002	10.7640	0.3248
P	2.4236	0.3894	9.5614	0.3158
T2	−0.3776	0.0434	−1.3210	0.0351
P2	−0.2236	0.0434	−0.8993	0.0351
TP	0.1494	0.0452	−0.6862	0.0364
Λ			−0.1778	0.2152
R^2	0.9791		0.9938	
FIT[b]	0.9791		0.9797	
AICC	61.1		60.6	
Likelihood ratio[c]			0.5686	0.4508)
Moran's I for residuals[d]	−0.0986	0.4858)	−0.0136	0.8878)

[a] Full Model: $\ln(Prob) = \beta_0 + \beta_1 T + \beta_2 P + \beta_3 T^2 + \beta_4 P^2 + \beta_0 TP + \varepsilon$, where $\varepsilon = \lambda W\varepsilon + U$; Prob = probability of observing spruce-fir forests; T = temperature zone (T = 1, 2, …, 6); P = precipitation zone (P = 1, 2, …, 6); W = binary spatial weights matrix based on the rook's move; $-1 < \lambda < 1$, measure of spatial correlation in the residuals; ε = spatially correlated errors from the regression model, U ∼ N(0,1) spatially independent errors

[b] The correlation between the observed and predicted values squared. This may be more reliable estimate of model fit than R^2 for the spatial models

[c] Testing the hypothesis that the spatial model is an improvement over the OLS model. The *p* value associated with the test statistic is given in parentheses

[d] Testing the hypothesis that the residuals are spatially independent. The *p* value associated with the test statistic is given in parentheses

probability of observing mortality followed patterns similar to the probability of observing spruce-fir forests in a given climate zone (Table 4). Subalpine fir mortality occurred in 32 of the 36 climate zones. A second degree polynomial was used to describe the relationship between the temperature and precipitation zones and the log of the rescaled probability of observing active subalpine fir morality. The spatial autoregressive and OLS models accounted for 97 % of the variability observed in the rescaled probabilities of observing mortality in a given climate zone (Table 5). The spatial autoregressive model did not significantly improve the overall fit of the model (LR = 2.206, *p* value = 0.138) since the residuals from the OLS model were spatially independent (Moran's I = −0.19, *p* value = 0.410).

Table 4 Probability of observing subalpine fir decline in Colorado. Probabilities are rescaled so the maximum probability is equal to one (max prob = 0.3158)

Temperature zone	Precipitation zone					
	1	2	3	4	5	6
1			0.04	0.37	0.19	0.11
2	0.00	0.04	0.16	0.36	0.59	0.58
3	0.00	0.04	0.17	0.42	0.97	1.00
4	0.00	0.02	0.07	0.26	0.60	0.31
5	0.00	0.00	0.01	0.02	0.02	
6	0.00	0.00	0.00	0.00	0.02	

Conditioning on the presence of the spruce-fir forests it becomes evident that the spruce-fir forests are being severely impacted by mortality in certain climatic regions (Table 6). These climate zones define a temperature-precipitation gradient that forms a diagonal through the CTM. It starts in the upper left corner of the CTM which represents a cool-dry climate (T = 3, P = 2) and stretches to the lower right corner of the CTM representing a hot-wet climate (T = 6, P = 5). In four climate zones along this diagonal, the spatial extent of active mortality covered 100 % of the spruce-fir forests. A spatial autoregressive model consisting of components of a third degree polynomial accounted for 84 % of the variability observed in the probability of observing active mortality given the presence of spruce-fir forests in a given climate zone (Table 7). A cosine of the temperature zones was introduced in the model to help model temperature-precipitation gradient that formed a diagonal through the CTM. The spatial autoregressive model was a significant improvement over the OLS model (LR = 11.791, *p* value <0.001)

Table 5 Comparison of ordinary least squares model with a spatial autoregressive model for the natural logarithm of the rescaled probability of observing active subalpine fir mortality in the mountains of Colorado as a function of the temperature and precipitation zones

Variable	Ordinary least squares		Spatial autoregressive model[a]	
	Coefficient	Standard error	Spatial autoregressive model[a]	Standard error
Intercept	−11.3473	1.6253	−11.4135	1.1715
T	2.3142	0.5838	2.3762	0.4187
P	3.1449	0.5680	3.1516	0.4069
T2	−0.6199	0.0633	−0.6263	0.0450
P2	−0.3618	0.0633	−0.3615	0.0450
TP	0.2306	0.0660	0.2236	0.0466
Λ			−0.3532	0.1982
R^2	0.9670		0.9920	
FIT[b]	0.9670		0.9704	
AICC	85.3		83.1	
Likelihood ratio[c]			2.2057	0.1375)
Moran's I for residuals[d]	−0.1858	0.410)	−0.0319	0.9979)

[a] Full Model: $\ln(Prob) = \beta_0 + \beta_1 T + \beta_2 P + \beta_3 T^2 + \beta_4 P^2 + \beta_0 TP + \varepsilon$, where $\varepsilon = \lambda W\varepsilon + U$; Prob = probability of observing active SFD mortality; T = temperature zone (T = 1, 2, …, 6); P = precipitation zone (P = 1, 2, …, 6); W = binary spatial weights matrix based on the rook's move; $-1 < \lambda < 1$, measure of spatial correlation in the residuals; ε = spatially correlated errors from the regression model, U ~ N0,1) spatially independent errors

[b] The correlation between the observed and predicted values squared. This may be more reliable estimate of model fit than R^2 for the spatial models

[c] Testing the hypothesis that the spatial model is an improvement over the OLS model. The *p* value associated with the test statistic is given in parentheses

[d] Testing the hypothesis that the residuals are spatially independent. The *p* value associated with the test statistic is given in parentheses

Table 6 Probability of observing subalpine fir decline given the presence of spruce-fir forests in Colorado

Temperature zone	Precipitation zone					
	1	2	3	4	5	6
1			0.50	0.34	0.21	0.16
2	0.10	0.55	0.53	0.36	0.35	0.28
3	0.34	1.00	0.77	0.54	0.46	0.40
4	0.58	1.00	1.00	0.65	0.53	0.14
5	0.46	0.73	0.75	0.63	0.42	
6	0.00	0.02	0.03	0.14	1.00	

Probabilities are rescaled so the maximum probability is equal to one (max prob = 1.0)

even though the residuals from the OLS model exhibited no spatial autocorrelation (I = −0.270, *p* value = 0.290).

Using the fitted regression models, the negative association between the rescaled probability of observing active mortality given the host and the rescaled probability of observing the host is displayed in Fig. 4. The symbols in this figure represent the climate zone in which the probability of observing spruce-fir forests (circle) and mortality (triangle) are at a maximum. The highest probability of observing spruce-fir forests occurred in a cool-very wet climate (T = 3, P = 6) while the highest probability of observing mortality given the presence of the host occurred in a cool-dry climate (T = 3, P = 2). This shift represents an increase of 1.3 °C in the average monthly temperature from 2.5 to 3.1 °C and a decrease of 27.5 mm in the average monthly precipitation from 60.4 to 34.8 mm. The differences in climatic conditions optimal for the presence of spruce-fir forests and mortality may reduce the overall impact the insect-disease complex is having on the subalpine fir population.

Differential effect of climate on the probability of subalpine fir mortality

Subtracting the rescaled CTM for the probability of spruce-fir forests from the rescaled CTM for the probability of mortality conditioned on the presence of the host developed using the fitted regression models provides a measure of the differential effect of climate on the probabilities of active mortality (Fig. 5). Positive values indicate a differential increase in probability of mortality above expectations, while negative numbers indicate a differential decrease in the probability of mortality. A value of zero would indicate that the level of mortality is proportional to

Table 7 Comparison of ordinary least squares model with a spatial autoregressive model for the natural logarithm of the rescaled probability of observing active SFD mortality give the presence of spruce-fir forests in the mountains of Colorado as a function of the temperature and precipitation zones

Variable	Ordinary least squares		Spatial autoregressive model[a]	
	Coefficient	Standard error	Spatial autoregressive model[a]	Standard error
Intercept	−152.2229	70.5521	−128.5861	45.2580
P	9.6814	2.9096	8.4711	1.7846
T2	25.1264	11.8627	21.2005	7.6100
P2	−1.9681	0.8812	−1.7039	0.5410
TP	−2.1052	0.5094	−1.8547	0.3107
T3	−2.9441	1.3419	−2.4911	0.8609
P3	0.1627	0.0844	0.1408	0.0520
T2P	0.3493	0.0695	0.3072	0.0421
Cos(πT/6)	136.0394	67.2253	114.2092	43.0896
λ			−0.5454	0.1660
R^2	0.7841		0.9137	
FIT[b]	0.7841		0.8418	
AICC	133.1		126.9	
Likelihood ratio[c]			11.7911	<0.0001)
Moran's I for residuals[d]	−0.2704	(0.2895)	−0.1010	0.5913)

[a] Full Model: $\ln(Prob) = \beta_0 + \beta_1 P + \beta_2 T^2 + \beta_3 P^2 + \beta_4 TP + \beta_5 T^3 + \beta_6 P^3 + \beta_7 T^2 P + \beta_8 cos(\pi T/6) + \varepsilon$, where $\varepsilon = \lambda W\varepsilon + U$; Prob = probability of observing spruce-fir forests; T = temperature zone (T = 1, 2, …, 6); P = precipitation zone (P = 1, 2, …, 6); W = binary spatial weights matrix based on the rook's move; $-1 < \lambda < 1$, measure of spatial correlation in the residuals; ε = spatially correlated errors from the regression model, U ~ N0,1) spatially independent errors

[b] The correlation between the observed and predicted values squared. This may be more reliable estimate of model fit than R^2 for the spatial models

[c] Testing the hypothesis that the spatial model is an improvement over the OLS model. The *p* value associated with the test statistic is given in parentheses

[d] Testing the hypothesis that the residuals are spatially independent. The *p* value associated with the test statistic is given in parentheses

the area associated with the host. This may be thought of as a baseline condition that exists across the landscape. The climate zones that satisfy this condition form a line running through four temperature zones (very cold to mild) and three precipitation zones (damp to very wet); {T:P}: {1.4}, {2:4}, {3:4}, {4, 0.5}, and {4.6}. Only in the coldest and wettest regions of the state are the probabilities of mortality lower than expected. Higher than average probabilities of mortality are associated with climate zones with cool (T = 3) temperatures and low (P = 2) to moderate (P = 3) amounts of precipitation.

Spatial representations of the rescaled CTMs for the probability of observing spruce-fir forest, the rescaled probability of SFD mortality given the presence of the host and their difference were developed using the fitted regression models. The difference layer was intersected with the binary layer associated with the presence-absence of spruce-fir forests to obtain area estimates associated with classes developed to characterize the differential effect of temperature and precipitation on the probability SFD mortality (Table 8). Approximately 12 % or 263,805 ha of spruce-fir forests had probabilities of mortality associated subalpine fir close to the expectations ($\Delta_i \pm 0.15$) (red areas in Fig. 6. Thirty-three percent of the spruce fir forests (703,436 ha) had probabilities of mortality higher than expectations ($\Delta_i > 0.15$) (yellow areas in Fig. 6) and 54 % (1,156,861 ha) had probabilities of mortality lower than expectations ($\Delta_i < -0.15$) (blue areas in Fig. 6). Only 8 % (169,234 ha) of the spruce-fir forests had probabilities of mortality greater than 70 % of the expectations. Spruce-fir forests with the highest positive differential in the probability of mortality generally occurred in the northwestern (e.g., Route National Forest) and the southwestern (e,g., Uncomphagre National Forest) parts of the state and at lower elevations where temperatures were higher and amounts of precipitation were lower. In contrast, stands with the lowest probability of mortality occurred at the highest elevations where temperatures were cooler and amounts of precipitation higher.

Discussion

Although SFD is one of the most prevalent disorders in high elevation forests of the Rocky Mountains (e.g., Harris 2003; Colorado State Forest Service 2011, 2013), there are

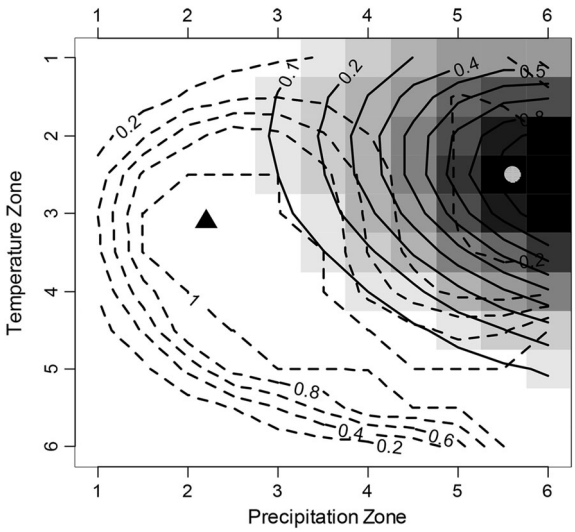

Fig. 4 Spatial association between the probability of observing spruce-fir forests (*gray-scale* image and *solid contour lines*) and the probability of observing subalpine fir decline given the presence of spruce-fir forests (*dashed contour lines*). The symbols represent the maximum probabilities (*white circle*—spruce-fir forests, *black triangle*—subalpine fir decline). The probability surfaces were modeled using a second degree trend surface

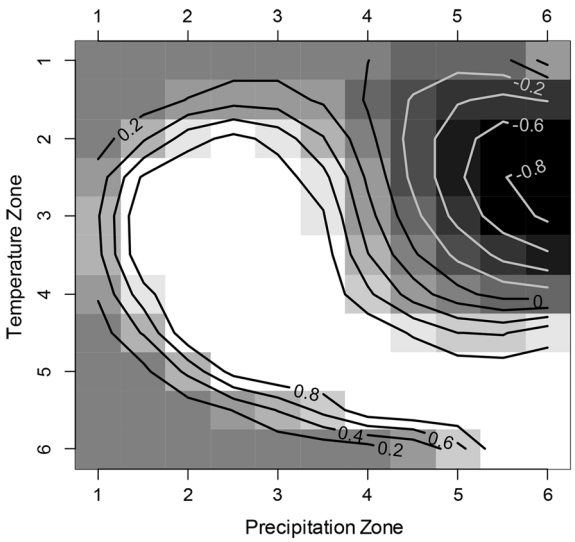

Fig. 5 Risk map for subalpine fir decline. High values (*white*) indicate climatic regions where the probability of mortality is greater than expected, while low or negative values (*darker areas*) indicate areas where the probability of mortality is lower than expected

many questions about its causes and impacts. The results of this study suggest that the abiotic environment is at least part of its etiology. Many different environmental factors can play significant roles in determining the distribution across forest landscapes of tree species and the various biotic disturbances that attack trees (Allen et al. 2010; Breshears et al. 2005; Hanson and Weltzin 2000; Rennenberg et al. 2006). The methods developed here aim at characterizing the differential effects of temperature and precipitation on the mortality associated with SFD. They indicate that subalpine fir forests matched with favorable climatic conditions thrive; those that are mismatched with their environment are vulnerable to mortality causing agents. More specifically, results show that healthy trees are found mostly in climatic zones with moderate to low temperatures and high precipitation; whereas, the probability of finding mortality is greatest in zones where trees grow under relatively moderate temperatures and moderate amounts of precipitation relative to host trees.

The importance of temperature or precipitation can be measured directly by measuring the spatial correlations and associations of the distributional patterns of forest conditions. In this study, methods are presented to quantify the influence of temperature and precipitation on the probability of observing active mortality given the presence of the host. Under the null hypothesis the model assumes that mortality is proportional to the amount of available host independent of climatic conditions. Deviations from the null hypothesis indicate that temperature and/or precipitation is having either a positive or negative influence on the probabilities of mortality. The models generated in this study indicate that subalpine fir is found mostly (i.e., it grows optimally) in climatic zones with cold to moderate temperatures and high precipitation. Tree mortality is greatest where it is relatively warm and relatively dry and outside of the optimal zones of growth for spruce-fir. We refer to this as an environment/host "mismatch" and the sites on which these trees grow as "marginal". Trees growing on these marginal sites experience varying levels of stress. Ayres (1984) defines stress as an "environmental factor that reduces the growth rate of a plant below the maximal level for its age and genotype…"

Temperature and precipitation interact directly or indirectly with many or most physiological processes that enable a tree to function optimally (Huberty and Denno 2004). Extreme temperature or drought alone can cause mortality in forest communities, but this is rare (Wargo 1981). More commonly, secondary biotic agents are the proximate causes of tree death. Western balsam bark beetle (*Dryocoetes confuses* (Swaine) [Coleoptera: Curculionidae: Scolytinae]), root diseases caused by *Armillaria* spp. and *Heterobasdion parviporum*, and other insects and pathogens have been associated with mortality attributed to SFD. It is well-known that temperature and precipitation play dominant roles in the life histories and the phenologies of these disturbance agents (Angilletta 2009). Although the connection between temperature and precipitation, insects and/or pathogens, and the occurrence of trees killed by SFD is unclear, three types of possible interactions resulting from environmental mismatches can be defined (Sturrock et al. 2011):

Table 8 Area estimates associated with differential effects climate on the probability of active SFD mortality in the spruce-fir forests of Colorado

Differential effect of climate on the probability of active subalpine fir mortality ($\Delta \times 100$)	Area (ha)	Percent by type of risk	Percent of grand total
Advantage of host—probability of mortality lower than expectations			
High (<−70 %)	386,306	31.7	18.3
Medium (−70 to −40 %)	760,555	62.5	36.0
Low (−40 to −15 %)	0	0	0
Very little (−15 to 0 %)	70,667	5.8	3.3
Total	1,217,528	100	57.6
Risk to host—probability of mortality higher than expectations			
Very little (0–15 %)	193,138	21.5	9.1
Low (15–40 %)	428,671	47.8	20.3
Medium (40–70 %)	105,530	11.8	5.0
High (>70 %)	169,234	18.9	8.0
Total	896,574	100	42.4

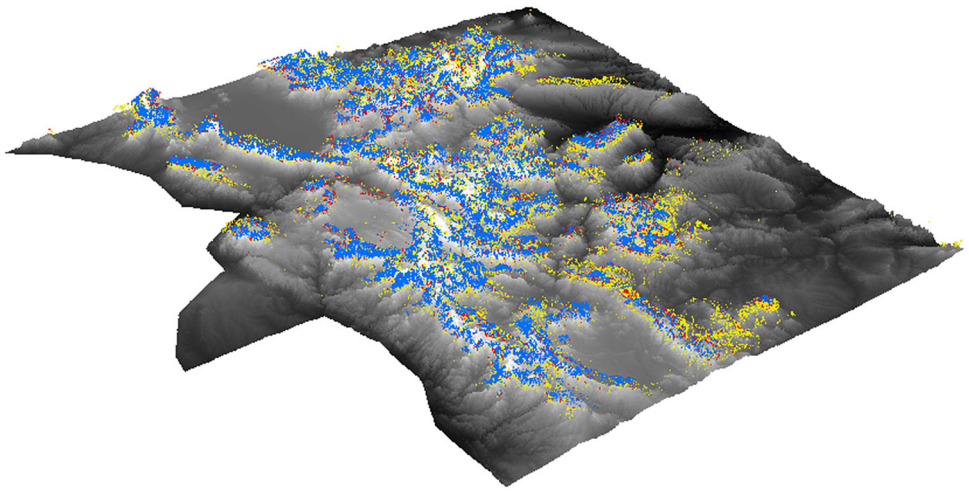

Fig. 6 Perspective plot displaying the differential effect of climate on the probability of active SFD mortality in the spruce-fir forest of Colorado as viewed from the northeast. *Yellow* represents stands with a probability of mortality from subalpine fir decline greater than expectations (i.e., insect-disease complex has a competitive advantage over the host); *red* represents stands with probabilities of mortality equal to expectations (i.e., area of mortality is proportional to area of the host), and *blue* represents stands with probabilities of mortality lower than expectations (i.e., host has a competitive advantage over the insect-disease complex)

(1) Mismatches could increase host vulnerability. Abiotic stresses influence tree vigor making forested stands more vulnerable to pathogen or insect pests. For example, the Plant Stress Hypothesis (PSH) states trees under stress generate higher concentrations of amino acids that provide a more palatable food source for nitrogen-limited agents (White 1993; Mattson and Haack 1987) and decreased ability to synthesize defensive secondary chemicals (Rhoades 1983), causing plants to become more susceptible to biotic stresses. The PSH has been difficult to prove (Larsson 1989).

(2) Mismatches could increase host vulnerability AND enhance pest and/or pathogen aggressiveness. Biotic disturbance populations can be directly affected by climate. Temperature and precipitation play dominant roles in the life histories and population dynamics of insect pests and pathogens (Bale et al. 2002; Huberty and Denno 2004, Furniss and Carolin 1977). The Climate Release Hypothesis (CRH), for example, states that impacts depend on not only the indirect effects of abiotic factors on the condition of the host as described by the PSH, but also the direct effects of abiotic factors on the population dynamics

of the insects (Price 1991). Palatability and quantity of host trees are generally enhanced by stresses in ways that indirectly impact the rates of growth and replication/multiplication, and aggressiveness of co-occurring secondary insect pests (Mattson and Addy 1975), onset of flight, rate and length of development and number of generations, extent of winter mortality, level of activity, activity and behavior of biological enemies, presence and composition of neighboring insect assemblages, and population dynamics of natural symbionts (Six and Bentz 2007; Lombardero et al. 2003). According to the CRH, insect populations respond to conditions within marginal areas by altered assemblage composition, range extension and contraction, changes in ecological roles and interactions, changing phenological timing of life history events and other ways that enhance or diminish their aggressiveness or virulence (Danks 1992; Weed et al. 2013).

(3) Mismatches could cause emergent disorders, like declines. Less is known about the relationship between climatic factors and complex disorders, like declines (Weed et al. 2013). In fact, the basis for calling SFD a decline is not clear, and whether this disorder is actually a decline disease needs more clarification. Ciesla and Donaubauer (1994) define decline as "an episodic event characterized by premature, progressive loss of tree and stand vigor and health over a given period without obvious evidence of a single clearly identifiable causal factor such as physical disturbance or attack by an aggressive disease or insect." Sinclair (1965) was the first to decipher the etiology of decline disease and developed the "chain reaction theory of causal factors" to explain it. According to this theory, decline diseases proceed in a characteristic sequence involving predisposing factors (factors that weaken trees and reduce their ability to tolerate adverse conditions), inciting factors (factors that trigger the decline event), and contributing factors (factors that intensify and perpetuate the disorder). Sinclair and Hudler (1988) later expanded this theory to include four primary symptoms: (1) persistent irritation by one factor, (2) injury co-occurring with a secondary stress, (3) predisposing and contributing factors acting interchangeably, and (4) synchronous cohort senescence. Manion (1991) proposed a decline disease spiral model that suggests that the three factors in Sinclair's chain reaction model interact. A number of other theories have been proposed to explain decline disease (Houston 1992; Huettl and Mueller-Dombois 1993; Jurskis 2005). Forest decline diseases are fairly common worldwide (Ciesla and Donaubauer 1994; Sturrock et al. 2011). Where this type of disorder has been studied, climatic stresses have usually been associated with the symptom syndrome (Manion 1991).

The causal relationship between abiotic stressors and insect infestations or pathogen epidemics can be complex (Huberty and Denno 2004). Schweiger et al. (2008) note that little is known about how the optimal environmental conditions of interacting species become mismatched, but appearance of mismatches can cause unexpected outcomes. Insects and diseases commonly facilitate large scale changes that result in host species shifts and compositional changes over long time scales, and thus play a major role in the appearance of what Hobbs et al. (2009) refer to as "novel ecosystems". By leading to complex disorders, like SFD, environmental mismatches can impact stand structure, species composition, mortality rates, and ultimately the patterns across the forest landscape that lead to novel ecosystems. One of the biggest challenges faced by natural resource managers is how to manage for vital ecosystem goods and services under the emerging conditions driven by changing patterns of temperature and precipitation. Declines and other complex disorders associated with landscapes made marginal by these changes are predicted to become increasingly common, especially in high elevations like those in subalpine fir forests of Colorado. Although little or nothing can be done to mediate the impacts of these disorders at landscape scales, natural resource decision makers need to at least understand what is going on, where impacts will occur, and what would be the consequences.

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