Tree Rings, Ecological Theory, and the Distribution of North American Spruce: A Biogeographical Analysis

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ABSTRACT: Classic ecological theory postulates that species will find more favorable conditions near the center of their range, hence grow better, than at the edges, where conditions are more fickle and growth, as a result, is more variable. Dendrochronological techniques, coupled with a determined effort to collect and archive tree-ring data in the International Tree-Ring Data Bank, now allow a direct test of theoretical predictions in tree species growing in their natural environments. I analyze the climate-growth relationships of five native North American spruce species (Engelmann spruce, *Picea engelmannii*; white spruce, *P. glauca*; black spruce, *P. mariana*; red spruce, *P. rubens*; and Sitka spruce, *P. sitchensis*) across their geographic range in North America. Quadratic regression is used to model the climate response in the form of three ring-width variables—mean width, standard deviation and first-order autocorrelation—of these five species as a function of the following geographic variables: latitude, longitude, elevation,

and continentality. In addition, I analyze the relationships among climate variables and the mapped distribution of these five species, along with blue spruce (*P. pungens*), using maximum entropy modeling.

INTRODUCTION

In the more than 160 years since Justus von Liebig proposed his "law" of the minimum—that growth of a plant would be limited by the nutrient that is least available (Liebig 1840)—ecologists have been expanding its application far beyond the nutrient relations of agricultural plants that Liebig originally envisioned. Victor Shelford built upon F.F. Blackman's recognition of upper limits, in other words, an organism can have too much of a good thing as well in addition to too little (Blackman 1905), and that environmental factors often act together rather than alone, proposed a theory of tolerance (Shelford 1911, 1913, Good 1931, 1947). Shelford's suggestion was that organisms were able to survive and reproduce within a limited range of environmental conditions: the boundary of that range was called the limits of tolerance (Figure 1a). Several principles could be inferred from the tolerance theory (Odum 1970): 1) that the breadth of an organism's range of tolerance for one factor was independent of the breadth of tolerance of other factors; 2) organisms with a wide range of tolerance for all factors are likely to be widely distributed; 3) when one factor is limiting, the organism's range of tolerance for other factors may be restricted; 4) organisms frequently do not live within their optimum range with respect to a particular factor; and 5) environmental factors are most likely to be limiting during the reproductive stage of an organism's life cycle.

Limiting factors form the basis of an important principle of the science of tree-ring dating, or dendrochronology (Fritts 1976). Tree rings can be dated only if one or more environmental factors become sufficiently limiting, persistent and widespread so that the effects can be demonstrated in a large number of trees. The percentage of variance in a tree-ring series accounted for by climate generally increases as from the center of a species' distribution toward the edges (Figure 1b). The principle of limiting factors leads to another important concept of dendrochronology, that of ecological amplitude (Fritts 1976). According to the concept of ecological amplitude, a tree species near the center of its geographic range is often found on a wide variety of sites, but its distribution becomes more restricted toward the edges of its distribution as climatic factors place more severe limits on physiological processes.

A third concept of dendrochronology is relevant to this project, that of modeling growth-environment relationships (Fritts 1976). Fritts defines a model as "a statement, equation, or diagram which represents a basic set of facts and their interrelationships," and suggests that models may serve as hypotheses which can be tested against data obtained from observations.

North American spruce (*Picea* spp.) are an excellent group of species with which to test the relationship between climate and plant distributions. Eight species are resident to North America: Brewer, *P. breweriana*; Chihuahua, *P. chihuahuana*; Englemann, *P. englemannii*; white *P. glauca*; black, *P. mariana*; red, *P. rubens*; and Sitka, *P. sitchensis* (Gordon 1968, Little 1971). Two species, white spruce (Figure 2a)[1] and black spruce (Figure 2b), largely share a widespread distribution across the North American continent, their range largely bounded by the Arctic, Atlantic, and Pacific oceans and extending south into the Northern Rocky Mountain and Great Lakes states (Nienstaedt and Zasada 1990, Viereck and Johnston 1990). Three species occur primarily in subalpine environments: Engelmann spruce (Figure 2c) occurs in the Rocky Mountains and the Cascades and Coast Ranges in the western United States and Canada

[1] Given my personal priority for updating the literature review, I did not update the maps. That won't take too much work, but I did not feel it was worth the time for now.

(Alexander and Shepperd 1990); blue spruce (Figure 2d) is largely restricted to the Rocky Mountains (Fechner 1990); and red spruce (Figure 2e) occurs in the Appalachian Mountains of the western United States and Canada, though it also occurs in lowland areas in the Saint Lawrence valley and coastal New England and Canada's Maritime Provinces (Blum 1990). Sitka spruce (Figure 2f) occurs in both montane and coastal environments along the Pacific coast from Alaska to Northern California (Harris 1990). The remaining two species, Chihuahua spruce and Brewer's spruce, have restricted distributions. Chihuahua spruce occurs in isolated areas in Mexico's Sierra Madre, and Brewer's spruce occurs primarily in the Siskiyou Mountains of Oregon and California (Gordon 1968, Thornburgh 1990). While the distributions of Brewer's and Chihuahua spruce are too restricted for much meaningful analysis, the other six occupy such a wide range of geographic, topographic, and climatic conditions to test a number of interesting biogeographic hypotheses.

METHODS

Overall Approach

This study employs a two-pronged approach. The first is a direct test of climate-growth relationships using regression modeling with tree-ring measurements as the dependent variable. The second is to model the relationship between species' distributions and climate using maximum entropy (MaxEnt) modeling (Phillips et al. 2006).

Tree Rings: Conceptual Models

Ed Cook's linear aggregate model of tree rings (Cook 1985, 1987, 1990) provides a theoretical foundation for describing the relationship between environmental factors and tree growth:

$$R_t = A_t + C_t + D1_t + D2_t + E_t$$

where: R_t = the observed tree-ring series; A_t = the age-related growth trend; C_t = the climate-related environmental signal; $D1_t$ = local endogenous disturbances; $D2_t$ = stand-wide exogenous disturbances; and E_t = unexplained variability. Tree-ring scientists, in the effort to develop annual chronologies based on ring characteristics, typically try to partition the variance in R_t according to each of the sources. The proposed analysis, however, is concerned solely with analyzing the relationship between large-scale climate parameters (C_t) and ring variables (R_t). I envision the climate response as a function of several climatic complex-gradients (Whittaker 1954, 1956). With a nod to Hans Jenny (Jenny 1941), I offer the model below:

$$C = f(\phi, \lambda, z, k, s)$$

where: C = climate response; ϕ = latitude; λ = longitude; z = elevation; k = continentality; and s = site factors (aspect, slope, soil, etc.) not otherwise accounted for in this analysis.

ϕ – Latitude

Latitude is inversely correlated with the amount of solar radiation reaching the surface of the earth, and therefore with ambient temperature and the amount of energy available for both physical and physiological processes.

λ – Longitude

At a given latitude, longitude has relationships with moisture gradients and the mean position of major features of the atmospheric circulation at certain times of the year. The base elevation of the landscape also varies with longitude.

z – Elevation

A number of atmospheric variables vary along elevation gradients, such as temperature, precipitation, pressure (including partial pressures of physiologically-important gases), and the intensity and spectral composition of incoming solar radiation.

k – Continentality

Due to the high specific heat of water, temperature ranges are damped near large bodies of water and increase with increasing distance from moisture sources. *Continental* climates, as opposed to *maritime* climates, are characterized by large annual ranges of temperature.

s – Site factors

A number of site factors may affect the climate response of trees. *Aspect*, *slope* and *exposure* all may affect the amount of radiation reaching a site. Slope also affects drainage, while exposure, or the lack thereof, may influence the temperature ranges experienced by vegetation on a site. *Soil* affects both site moisture and nutrient balance characteristics, with nutrient-poor sites making plants more sensitive to environmental fluctuations.

Tree Rings: Data

Tree-ring data

Tree-ring data were available from the following sources: the International Tree-Ring Data Bank, or ITRDB (Contributors to the International Tree-Ring Data Bank 2012); the FOrest Responses to Anthropogenic STress (FORAST) project (McLaughlin et al. 1986); data from tree-ring samples I obtained during the Boreal Ecosystem-Atmosphere Study (BOREAS) in Manitoba and Saskatchewan; data from samples I have collected from the central Appalachian Mountains; and additional data from samples collected by other investigators which have yet to be donated to the ITRDB.

Three tree-ring characteristics were used in the analysis: ring width, maximum latewood density and minimum earlywood density. Ring width is an especially useful parameter—as a measure of annual growth it averages (or integrates) the effects of a host of factors acting upon the tree, from external influences such as long- and short-term fluctuations in climate to small-scale disturbances, to internal influences such as genetic potential and physiological vigor (Fritts 1976). Ring width is also the tree-ring characteristic most commonly measured. Maximum density is highly correlated with a number of climate variables (Parker and Henoch 1971, Schweingruber et al. 1978). Minimum density does not consistently correlate with climate (Schweingruber et al. 1978) but has at time been found to be useful in studies of the relationships between tree growth and climate (Polge 1970, Schweingruber et al. 1978). Only three species—black, white, and Engelmann spruce—have sufficient density collections to warrant analyses of these data.

Three summary statistics will be calculated for each tree-ring characteristic. The mean will be used to estimate the "typical" measurement for a series of tree rings. First-order autocorrelation is a measure of the year-to-year variability within a tree ring series, while standard deviation is a measure of the total variability within a tree-ring series.

Climate data

In order to base the analyses on a consistent time period, Canadian or U.S. monthly temperature normals for the period 1971-2000 (National Climate Data and Information Archive 2012, National Climatic Data Center 2012) were used to calculate the Conrad Index (Conrad 1946), a measure of continentality and the sole climate variable used in the analysis of the tree-ring data. The formula for the Conrad Index is:

$$k = [1.7T/(\sin\phi + 10)] - 14$$

where k = the Conrad index, T = average annual range of temperature (i.e., the difference of the highest mean monthly temperature and lowest mean monthly temperature), and ϕ = latitude.

Tree Rings: Statistical analyses

Regression models

Quadratic regression was first used to analyze the relationship between tree growth (or growth variability) and climate. Quadratic regression takes the form:

$$y = \beta_0 + \beta_1 x + \beta_2 x^2$$

where: y = tree-ring variable; x = the environmental variable; β_0 = the intercept term; and β_1 and β_2 are slope terms

Quadratic regression may not be valid in cases where samples have not been obtained from an adequate range of environments inhabited by a species. This is most likely to occur in subalpine species (*P. engelmannii, P. rubens*) as most tree-ring sampling in the subalpine zone tends to be biased towards sites near the upper distributional limits. Therefore linear regressions of the form:

$$y = \beta_0 + \beta_1 x$$

will be also be run as a benchmark with which to evaluate quadratic regression results. All regression analyses will be carried out using SYSTAT (Wilkinson 1988).

In order to test the fit of the quadratic regression, the regression results were subjected to a *post-hoc* analysis of variance (ANOVA) to determine whether addition of the second-order term significantly increases predictive power as compared to the linear model. Procedures for conducting the *post-hoc* ANOVA are described in Kleinbaum et al. (1998).

Because of the large number of comparisons involved (4 climate variables multiplied by 3 statistics for each tree-ring characteristic), a Bonferroni correction was applied in order to reduce Type I error (the likelihood of rejecting the null hypothesis when it is true). In the case of these analyses, the traditional alpha value of 0.05 is divided by 12; regression probabilities must be equal to or less that the adjusted value before the null hypothesis will be rejected.

Hypotheses

Mean ring width and maximum density (Figure 3a) will be highest near the center of a species' distribution along an environmental gradient and will taper off more or less evenly towards the edges of the range. This follows from the "law" of limiting factors and the theory of tolerance (Figure 1a).

Because of the inconsistent response of minimum density (Polge 1970, Schweingruber et al. 1978, Schweingruber et al. 1979) it is difficult to determine whether the minimum density should be greatest near the center of a species' distribution along an environmental gradient and taper off toward the edges or vice versa. Nevertheless, a quadratic relationship is expected even though no prediction can be made with respect to the direction of the curve.

Variability in measurements of ring width and density will be least near the center of the range and increase toward the edges (Figure 3b). First-order autocorrelation of ring width and density will be greatest near the center of the range and decrease toward the edges (Figure 3c).

Assumptions

Two assumptions underlie the proposed hypothesis tests. The first is that species' distributions are at equilibrium with climate. Species at equilibrium with climate should in turn have a Gaussian (bell-shaped) response along environmental gradients. The second is that tree species' response to environmental factors can be measured by total ring width, maximum latewood density and possibly minimum earlywood density.[2]

Implications

Skewed or truncated ring-width and density responses should indicate that other factors, in addition to climate, limit the distribution of the species. Such factors could include competition with other species, disturbance regimes, geographic barriers to migration, or insufficient time to reach equilibrium with climate. Multi-modal responses may indicate different populations or sub-populations with a species, each adapted to regional conditions.

If the relationships between climate and ring width and density prove more complex than enumerated in the expectations, different populations or sub-populations may likewise be indicated. Otherwise, such results may reveal that several rules-of-thumb explaining the relationship between climate and the distribution of tree species should be reconsidered.

MaxEnt: Data

Digitized range maps of spruce distributions were obtained from the U.S. Geological Survey (2006). The shapefiles were converted into raster data based on a 10 minute grid size[3] using the Spatial Analysis in Macroecology, or SAM, software (Rangel et al. 2006, 2010a, b). Bioclimatic data were obtained from the WorldClim dataset (Hijmans et al. 2005a, b).

MaxEnt: Statistics

The combined spruce distribution/bioclimatic data were subsequently analyzed in SYSTAT for exploratory data analysis—box plots were used to identify bioclimatic variables that were

[2] With the exception of the Engelmann spruce data already analyzed, only ring-width variables are evaluated in this report. Densitometric variables for other species will be included in the analysis later once I figure out what to do about the missing value bug I found last week. (Only three Engelmann spruce chronologies are affected.)

[3] The grid, which only includes land areas, spans 52 degrees of latitude (74° N to 22° N), 120 degrees of longitude (51° W to 171° W), and contains nearly 104,000 cells.

likely to influence spruce distributions. Spruce presence data were imported into MaxEnt for maximum entropy modeling, with 20 percent of each species' dataset randomly selected and withheld for model training purposes.

RESULTS

Tree-Rings

Only five species had sufficient tree-ring data for the regression analysis: white, black, Englemann, red, and Sitka spruce. Of those, the Sitka spruce data set suffers from a lack of available chronologies in the southern part of its range. Three remaining tree species—blue, Brewer's, and Chihuahua spruce—have either no archived tree-ring collections, or just one in the case of blue spruce. The number of chronologies available for and preferred geographic zones occupied by the eight species are given in Table 1.

Regression Results: White Spruce

Statistically significant quadratic regressions were obtained for mean ring width and longitude (Table 2a; Figure 4), standard deviation of ring width and longitude (Table 2b; Figure 5), and serial autocorrelation of ring width and continentality (Table 2c; Figure 6). Statistically significant linear regressions were obtained for mean ring width and latitude (Table 2d; Figure 7), standard deviation of ring width and latitude (Table 2e; Figure 8), and standard deviation of ring width and continentality (Table 2f; Figure 9).

Regression Results: Black Spruce

No statistically significant regressions were obtained for black spruce.

Regression Results: Engelmann Spruce

Statistically significant quadratic regressions were obtained for mean ring width and latitude (Table 3a; Figure 10) and standard deviation of ring width and latitude (Table 3b; Figure 11).

Statistically significant linear regressions were obtained for mean maximum density and elevation (Table 3c; Figure 12), standard deviation of maximum density and latitude (Table 3d; Figure 13), standard deviation of maximum density and longitude (Table 3e; Figure 14), standard deviation of maximum density and elevation (Table 3f; Figure 15), serial autocorrelation of maximum density and latitude (Table 3g; Figure 16), autocorrelation of maximum density and longitude (Table 3h; Figure 17), and autocorrelation of maximum density and elevation (Table 3i; Figure 18). No statistically significant correlations were obtained for any of the Engelmann spruce minimum density variable.

Regression Results: Red Spruce

Statistically significant quadratic regressions were obtained for standard deviation of ring width and latitude (Table 4a; Figure 19) and standard deviation of ring width and longitude (Table 4b; Figure 20). Statistically significant linear regressions were obtained for mean ring width and latitude (Table 4c; Figure 21) and mean ring width and longitude (Table 4d; Figure 22).

Regression Results: Sitka Spruce

No statistically significant regressions were obtained for Sitka spruce.

MaxEnt

While distribution data was available for all eight North American spruce, two were too locally restricted to include in the MaxEnt analysis: Out of the nearly 104,000 grid cells available, Chihuahua spruce was present in only 11 cells and Brewer’s spruce was present in just two. The ability of MaxEnt to adequately model the climatic envelope of the six other species was mixed. MaxEnt performed rather poorly for white and black spruce, with 60 percent receiver operating characteristic (ROC) success rates. For the remaining species—Engelmann, blue, red and Sitka spruce—ROC success rates were 94 percent or more.

For the two predominantly lowland species—white and black spruce—the primary bioclimatic variable influencing species' distribution (i.e., with either a percent contribution or permutation importance greater than 5 percent for one or both species) were mean annual temperature. Other influential variables include minimum temperature of coldest month, annual temperature range, mean temperature of warmest quarter, precipitation seasonality, mean temperature of wettest quarter, and temperature seasonality (Table 5a).

For the three predominantly subalpine or montane species—Engelmann, blue, and red spruce—the primary bioclimatic variables influencing species' distributions were again mean annual temperature, along with mean temperature of coldest quarter, mean temperature of wettest quarter, mean diurnal temperature range, temperature seasonality, precipitation seasonality, isothermality, annual temperature range, and precipitation of driest month (Table 5b).

Sitka spruce was rather idiosyncratic in terms of bioclimatic variables that influence its distribution. The primary variables of bioclimatic influence were mean temperature of wettest quarter, mean temperature of coldest quarter, minimum temperature of coldest month, precipitation of coldest quarter, mean temperature of driest quarter, and mean temperature of warmest quarter (Table 5b).

Maps showing MaxEnt predictions of suitable geographic ranges are presented for white spruce (Figure 23a), black spruce (Figure 23b), Engelmann spruce (Figure 23c), blue spruce (Figure 23d), red spruce (Figure 23f), and Sitka spruce (Figure 23g).

DISCUSSION

The tree-ring data reveal variable climate-growth responses among the five species analyzed. To some extent, it is little surprise that no significant regressions were found for either black or Sitka spruce. Black spruce tends to be found moist sites (Viereck and Johnston 1990, Wirth et al. 2008). Sitka spruce tends to be found in areas with mild winters, warm summers, and abundant precipitation (Hopkins 1959, Harris 1990). Such sites are typically considered “complacent” (Fritts 1976), i.e., not ideal for producing datable tree-ring series much less series with a strong environmental signal.

The statistically significant quadratic regressions for white spruce mean ring width and longitude (Figure 4), standard deviation of ring width and longitude (Figure 5), and serial autocorrelation of ring width and continentality (Figure 6) are likely all related, as white spruce spans the continent longitudinally from the Atlantic to the Pacific, thus spans the full spectrum of climate variation from maritime conditions to highly continental ones. The linear relationship between ring width standard deviation and continentality (Figure 9) should not be surprising, either: ring width standard deviation increases as continentality, hence climate variability, increases. This relationship might explain why the form of the quadratic curve in Figure 5 is opposite the expectation presented in Figure 2b, as the edges of the species’ longitudinal range correspond with more maritime conditions while the center corresponds with the most continental conditions. The significant linear regressions for mean ring width and latitude (Figure 7) and standard deviation of ring width and longitude (Figure 8) suggest that the latitudinal limits of white spruce are not in equilibrium with climate as both mean ring width and standard deviation of ring width are highest at white spruce’s current southern limits.[4]

[4] It will be interesting to see what analysis of the x-ray data will reveal. I’m leaving this as a placeholder for when I get the x-ray data analyzed.

The quadratic regression model does a good job of modeling Engelmann spruce ring width response along latitudinal gradients, but the direction of the mean ring width curve (Figure 10) in opposite the expectations presented in Figure 1a. This suggests other factors, such as a possible interaction effect with elevation, confound the relationship. The upper altitudinal limit, or treeline, for alpine forests generally decreases in elevation as one moves from the tropics to the poles (Daubenmire 1954, Peet 1988, Cogbill and White 1991). Treelines are also lower on isolated mountains than they are on large mountain ranges at comparable latitudes (Grubb 1971, Richardson and Friedland 2009). This phenomenon, called the *Massenerhebung* effect, may be a significant factor to consider in the southern part of Engelmann spruce's range where isolated mountains are much more prevalent (such as in the Basin and Range Province). Indeed, a statistically significant quadratic regression (Figure 24) suggests the *Massenerhebung* effect may be relevant. It may be that growth conditions are more favorable for the species at the lower elevations, but that other factors—such as competition, regeneration, or lack of suitable habitat—limits its distribution in the northern and southern portions of its range. The significant regression of mean maximum density versus elevation (Figure 12) likewise suggests more favorable growth conditions at lower elevations. Nevertheless, the results of the standard deviation (Figure 15) and serial autocorrelation (Figure 18) regressions suggest more variability at lower elevations, too.

Both the standard deviation (Figure 13) and serial autocorrelation (Figure 16) of maximum density linear regressions suggest more variable growth conditions at higher latitudes—this may represent the effect of annual fluctuations in growing season climate or growing season length. Likewise, the linear regression results of both density characteristics (Figures 14 and 17) suggest more variable growth in the western portion of Engelmann spruce's range than in the eastern portion. Given that the eastern portion represents the eastern rampart of the Rocky Mountains, it may be that a readily available moisture supply from the Gulf of Mexico ensures adequate moisture in most years or that warmer winter conditions result in longer growing seasons (Borchert 1950, Adams 1997, Gray et al. 2003).

The red spruce regression results are more difficult to interpret as the tree is a significant break in its distribution in the central Appalachians. Whereas the quadratic regression results for ring width standard deviation versus latitude (Figure 19) and longitude (Figure 20) are significant, the shape of the regression curve is opposite what was expected (Figure 1b). The linear regression results for mean ring width versus latitude (Figure 21) and longitude (Figure 22) show a decrease toward the northern and eastern portion of its range. It is reasonable to conclude that the distribution of red spruce is limited more by lack of suitable environments, competition, or other factors, than by climate.

MaxEnt results suggest that the suitable climatic envelope for both white (Figure 23a) and black (Figure 23b) spruce is much broader than their current distributions indicate. Suitable climate conditions—based on the suite of bioclimatic variables used—occur both to the north and south of each species' range. At the northern and upper extremes, snowpack depth, wind abrasion and dessication, an other factors may limit growth (Baker 1944, Daubenmire 1954, Smith et al. 2003, Bekker and Malanson 2008, Barbeito et al. 2011). The finding that suitable environments exist to the south of the species' current range seems to conflict with prior claims that temperature or radiation controls the boundaries of the boreal forest biome in which the species are found (Larsen 1980, Elliott-Fisk 1988). It is likely that the picture is quite complex, with competition, disturbance, and dispersal also playing a role in restricting both species' expansion to warmer environments. The MaxEnt results suggest both species could have a circumboreal distribution, not a surprising finding given that closely related species—primarily Norway spruce, *P. abies*; Jezo spruce, *P. ajanensis*; and Siberian spruce, *P. obovata* (Nikolov and Helmisaari 1992).

The climate envelope for the three western spruce species—Engelmann (Figure 23c), blue (Figure 23d), and Sitka (Figure 23f)—overlap somewhat, suggesting that congeneric competition plays a role in restricting their distributions. Engelmann spruce has the broadest envelope of the three. It already occupies all of the blue spruce's current range and has the potential of occurring anywhere Sitka spruce currently occurs. Both blue and Sitka spruce grow better in more humid conditions (Fechner 1990, Harris 1990), which may give those two species an advantage where they are now found.

Red spruce (Figure 23e) already occupies much of what the MaxEnt suggest is its environmental envelope. The species has potential for expansion westward into the Great Lakes region and northeastward into Newfoundland and Labrador. Competition with other species—including white and black spruce—likely prevent a westward expansion. Water barriers, in particular the Gulf of St. Lawrence, probably prevent dispersal to the east and north.

CONCLUSIONS

The results of the regression analyses suggest that most of the species are not at equilibrium with climate. In all but a few cases in which statistically significant regression results were obtained, either: either the form of the quadratic regression was asymmetric, or the linear regression and not the quadratic regression proved significant. This suggests that environments suitable for the species' growth exists beyond the boundaries of their current geographic range. This finding is supported by the results of the MaxEnt analyses. Only two of the montane species, Sitka and Engelmann spruce, occupy a significant portion of their potential bioclimatic range. For the two predominantly lowland species, white and black spruce, most of the suitable bioclimatic envelope is to the south of their current range, which suggests that, under a warming climate, their range would either largely remain the same or their southern boundaries migrate northward. A suitable climate envelope exists for the other two montane spruces, blue and red, to expand their range the north and west of where they are found today.

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Table 1. Number of available chronologies for and preferred geographic zones occupied by the eight species of North American spruce.

Species	Number of Chronologies	Preferred Geographic Zones
Black spruce	46	Subarctic; Continental Lowlands
Blue spruce	1	Subalpine
Brewer's spruce	0	Subalpine
Chihuahua spruce	0	Subalpine
Engelmann spruce	79	Subalpine
Red spruce	100	Subalpine; Coastal Lowlands
Sitka spruce	34	Coastal Lowlands; Subalpine
White spruce	168	Subarctic; Continental Lowlands

Table 2a. Results of ANOVA test for statistical significance of quadratic regression of white spruce mean ring width and longitude. The quadratic regression is statistically significant (critical value of F: 3.901, p < 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	1.42076	26.44531	1	1.42076	8.54219	0.00398
Regression (X^2)	5.32034	22.54573	2	2.66017	18.66017	0.00000
Regression (X^2|X)	3.89958		1	3.89958	27.32817	
Residual	22.54573		158	0.14269		
Total	27.86607		160			

Table 2b. Results of ANOVA test for statistical significance of quadratic regression of white spruce standard deviation of ring width and longitude. The quadratic regression is statistically significant (critical value of F: 3.901, p < 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.19666	7.63219	1	0.19666	4.09705	0.04463
Regression (X^2)	1.34699	6.48186	2	0.67350	16.41695	0.00000
Regression (X^2|X)	1.15033		1	1.15033	28.04012	
Residual	6.48186		158	0.04102		
Total	7.82885		160			

Table 2c. Results of ANOVA test for statistical significance of quadratic regression of white spruce standard deviation of ring width and continentality. The quadratic regression is statistically significant (critical value of F: 3.901, p = 0.00273).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.00168	0.41345	1	0.00168	0.64719	0.42232
Regression (X^2)	0.02990	0.03852	2	0.01495	6.13122	0.00273
Regression (X^2|X)	0.02822		1	0.02822	11.57428	
Residual	0.38523		158	0.00244		
Total	0.41513		160			

Table 2d. Results of ANOVA test for statistical significance of quadratic regression of white spruce mean ring width and latitude. The linear regression is statistically significant (critical value of F: 3.901, p < 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	3.96177	23.90430	1	3.96177	26.35183	0.00000
Regression (X^2)	4.05549	23.81059	2	2.02775	13.45550	0.00000
Regression (X^2|X)	0.09372		1	0.09372	0.62190	
Residual	23.81058		158	0.15070		
Total	27.86607		160			

Table 2e. Results of ANOVA test for statistical significance of quadratic regression of white spruce standard deviation of ring width and latitude. The linear regression is statistically significant (critical value of F: 3.901, p = 0.00021).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.64880	7.18006	1	0.64880	14.36740	0.00021
Regression (X^2)	0.71528	7.11358	2	0.35764	7.94350	0.00052
Regression (X^2|X)	0.06648		1	0.06648	1.47659	
Residual	7.11358		158	0.04502		
Total	7.82886		160			

Table 2f. Results of ANOVA test for statistical significance of quadratic regression of white spruce standard deviation of ring width and continentality. The linear regression is statistically significant (critical value of F: 3.901, p = 0.00277).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.43000	7.39886	1	0.43000	9.24058	0.00277
Regression (X^2)	0.43291	7.39595	2	0.21646	4.62410	0.01118
Regression (X^2|X)	0.00291		1	0.00291	0.06217	
Residual	7.39595		158	0.04681		
Total	7.82886		160			

Table 3a. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce mean ring width and latitude. The quadratic regression is statistically significant (critical value of F: 3.967, p = 0.00006).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.41135	21.71698	1	0.41135	1.45849	0.23087
Regression (X^2)	5.03162	17.09672	2	2.51581	11.18352	0.00006
Regression (X^2|X)	4.62027		1	4.62027	20.53848	
Residual	17.09671		76	0.22496		
Total	22.12833		78			

Table 3b. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce standard deviation of ring width and latitude. The quadratic regression is statistically significant (critical value of F: 3.967, p < 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.34977	4.77356	1	0.34977	5.64198	0.02002
Regression (X^2)	1.60669	3.51664	2	0.80335	17.36151	0.00000
Regression (X^2|X)	1.25692		1	1.25692	27.16397	
Residual	3.51664		76	0.04627		
Total	5.12333		78			

Table 3c. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce mean maximum density and elevation. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00291).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.07601	0.27658	1	0.07601	10.16844	0.00291
Regression (X^2)	0.07739	0.27520	2	0.03870	5.06167	0.01156
Regression (X^2|X)	0.00138		1	0.00138	0.18052	
Residual	0.27520		36	0.00764		
Total	0.35259		38			

Table 3d. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce standard deviation of maximum density and latitude. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00036).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.00553	0.01323	1	0.00553	15.46796	0.00036
Regression (X^2)	0.00680	0.01197	2	0.00340	10.22301	0.00030
Regression (X^2|X)	0.00127		1	0.00127	3.82274	
Residual	0.01196		36	0.00033		
Total	0.01876		38			

Table 3e. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce standard deviation of maximum density and longitude. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.00813	0.01064	1	0.00813	28.27661	0.00001
Regression (X^2)	0.00902	0.00975	2	0.00451	16.64265	0.00001
Regression (X^2|X)	0.00089		1	0.00089	3.28615	
Residual	0.00975		36	0.00027		
Total	0.01877		38			

Table 3f. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce standard deviation of maximum density and elevation. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00022).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.00584	0.01293	1	0.00584	16.72267	0.00022
Regression (X^2)	0.00642	0.01235	2	0.00321	9.36231	0.00053
Regression (X^2|X)	0.00058		1	0.00058	1.69069	
Residual	0.01235		36	0.00034		
Total	0.01877		38			

Table 3g. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce serial autocorrelation of maximum density and latitude. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00141).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.06523	0.20262	1	0.06523	11.91152	0.00141
Regression (X^2)	0.06788	0.19996	2	0.03394	6.11064	0.00519
Regression (X^2|X)	0.00265		1	0.00265	0.47707	
Residual	0.19997		36	0.00555		
Total	0.26785		38			

Table 3h. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce serial autocorrelation of maximum density and longitude. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00082).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.07076	0.19709	1	0.07076	13.28456	0.00082
Regression (X^2)	0.07109	0.19676	2	0.03555	6.50632	0.00388
Regression (X^2|X)	0.00033		1	0.00033	0.06038	
Residual	0.19676		36	0.00547		
Total	0.26785		38			

Table 3i. Results of ANOVA test for statistical significance of quadratic regression of Engelmann spruce serial autocorrelation of maximum density and elevation. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00047).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	0.07623	0.19162	1	0.07623	14.72010	0.00047
Regression (X^2)	0.07830	0.18955	2	0.03915	7.43551	0.00198
Regression (X^2|X)	0.00207		1	0.00207	0.39314	
Residual	0.18955		36	0.00527		
Total	0.26785		38			

Table 4a. Results of ANOVA test for statistical significance of quadratic regression of red spruce standard deviation of ring width and latitude. The quadratic regression is statistically significant (critical value of F: 3.939, p = 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	1.29729	6.47578	1	1.29729	19.63235	0.00002
Regression (X^2)	1.71944	6.05363	2	0.85972	13.77569	0.00001
Regression (X^2|X)	0.42215		1	0.42215	6.76430	
Residual	6.05363		97	0.06241		
Total	7.77307		99			

Table 4b. Results of ANOVA test for statistical significance of quadratic regression of red spruce standard deviation of ring width and longitude. The quadratic regression is statistically significant (critical value of F: 3.939, p < 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	1.41852	6.35455	1	1.41852	21.87650	0.00001
Regression (X^2)	1.82103	5.95204	2	0.91052	14.83861	0.00000
Regression (X^2|X)	0.40251		1	0.40251	6.55968	
Residual	5.95204		97	0.06136		
Total	7.77307		99			

Table 4c. Results of ANOVA test for statistical significance of quadratic regression of red spruce mean ring width and latitude. The linear regression is statistically significant (critical value of F: 3.939, p = 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	7.49802	32.83280	1	7.49802	22.38023	0.00001
Regression (X^2)	8.76875	31.56207	2	4.38438	13.47454	0.00001
Regression (X^2|X)	1.27073		1	1.27073	3.90535	
Residual	31.56207		97	0.32538		
Total	40.33082		99			

Table 4d. Results of ANOVA test for statistical significance of quadratic regression of red spruce mean ring width and longitude. The linear regression is statistically significant (critical value of F: 3.939, p = 0.00001).

Source	SSreg	SSres	df	MS	F	P
Regression (X)	7.88288	32.44794	1	7.88288	23.80805	0.00000
Regression (X^2)	8.46583	31.89499	2	4.23292	12.88539	0.00001
Regression (X^2|X)	0.58295		1	0.58295	1.77455	
Residual	31.86499		97	0.32851		
Total	40.33082		99			

Table 5a. Analysis of bioclimatic variable contributions for white and black spruce.

	White spruce		Black spruce	
Variable	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Annual Mean Temperature	87.8	55.8	82.4	54.8
Min Temperature of Coldest Month	3	0	7	0
Temperature Annual Range	2.6	11.5	1.4	17.2
Max Temperature of Warmest Month	1.8	0	0	0
Mean Temperature of Warmest Quarter	1.6	11.7	2.2	11
Precipitation Seasonality	1.4	7.2	1.8	9.1
Mean Temperature of Wettest Quarter	0.9	5.1	1	4.9
Temperature Seasonality	0.7	6.8	0.6	2.4
Mean Temperature of Driest Quarter	0.1	1.9	0	0
Isothermality	0	0	2.9	0
Mean Temperature of Coldest Quarter	0	0	0.6	0.1
Mean Diurnal Range	0	0	0	0
Precipitation of Warmest Quarter	0	0	0	0
Precipitation of Driest Month	0	0	0	0
Annual Precipitation	0	0	0	0
Precipitation of Wettest Quarter	0	0	0	0
Precipitation of Coldest Quarter	0	0	0	0
Precipitation of Wettest Month	0	0	0	0
Precipitation of Driest Quarter	0	0	0	0.5

Table 5b. Analysis of bioclimatic variable contributions for Engelmann, blue, red, and Sitka spruce.

	Engelmann spruce		Blue spruce		Red spruce		Sitka spruce	
Variable	Percent contribution	Permutation importance	Percent contribution	Permutation importance	Percent contribution	Permutation importance	Percent contribution	Permutation importance
Annual Mean Temperature	55.7	46.1	33.7	55.9	30.4	5.1	3.1	0.5
Min Temperature of Coldest Month	0.1	1.1	0	1.3	0.1	0	8.3	0
Temperature Annual Range	0	0	1.4	4.1	3.8	14	4.6	2.8
Max Temperature of Warmest Month	0	0.3	0	0	0	4.8	0	0.2
Mean Temperature of Warmest Quarter	1.2	0.6	1	0	0.5	0	0.1	8.4
Precipitation Seasonality	2.9	2.7	17.7	3.1	42	23.8	0.2	0.9
Mean Temperature of Wettest Quarter	10.7	0	1.3	0.5	0.4	0.3	49.7	46.7
Temperature Seasonality	4.1	22.9	2.7	0.1	0	0	0.5	0
Mean Temperature of Driest Quarter	1.5	0.7	0.9	0	1.2	0	1.4	34.9
Isothermality	0.4	11.9	0.7	2.7	0.7	5.1	0	2
Mean Temperature of Coldest Quarter	15.7	0	0.8	0	11.6	44	20	0
Mean Diurnal Range	7.4	13	39.8	32.3	1	0.2	2.3	1
Precipitation of Warmest Quarter	0.2	0	0	0	0	0	0.1	0
Precipitation of Driest Month	0	0.1	0	0	7.3	2.3	0.3	0
Annual Precipitation	0	0	0	0	0.8	0.1	3.2	0.2
Precipitation of Wettest Quarter	0	0	0	0	0.2	0.1	0	2.4
Precipitation of Coldest Quarter	0	0.5	0	0	0	0	5.2	0
Precipitation of Wettest Month	0	0	0	0	0	0	0.8	0
Precipitation of Driest Quarter	0	0	0	0	0	0	0	0

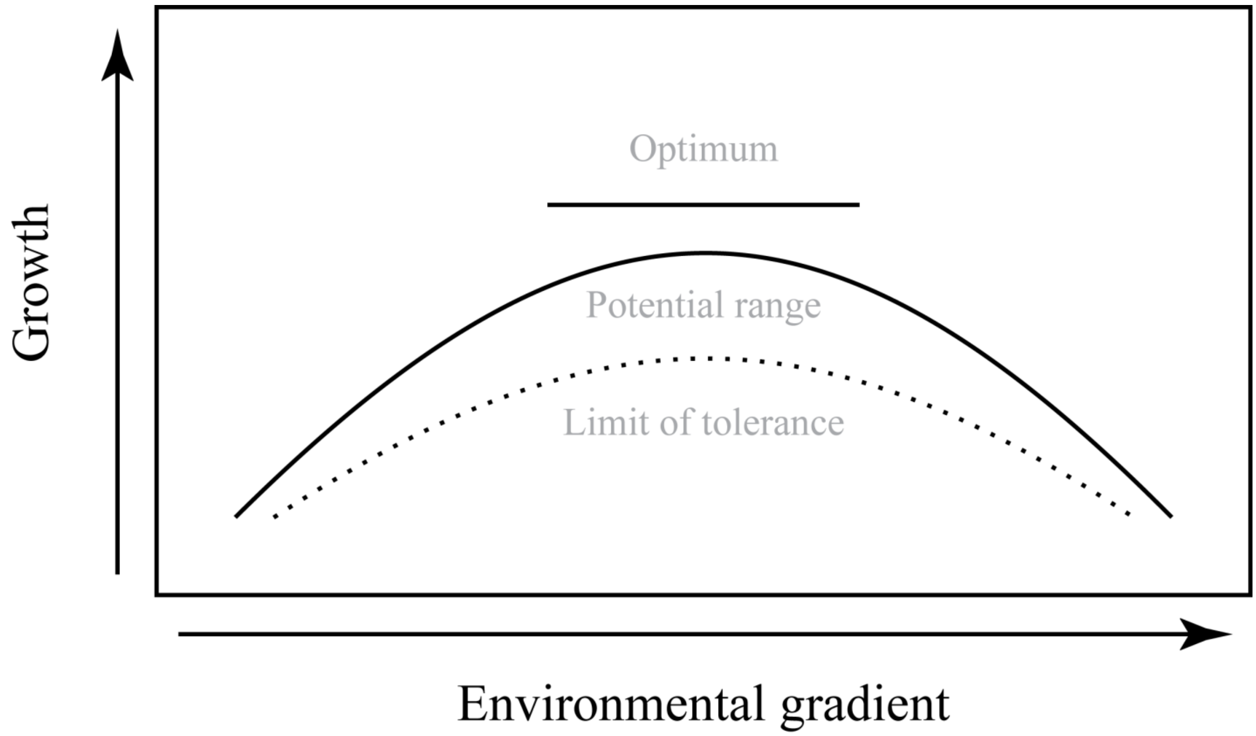

Figure 1a1**.** Some implication of Shelford's theory of tolerance. The potential physiological range (solid curve) is more extensive than the actual limit of tolerance (dotted curve). In the absence of competition, as shown above, a species' optimal distribution falls somewhere near the middle of the limit of tolerance.

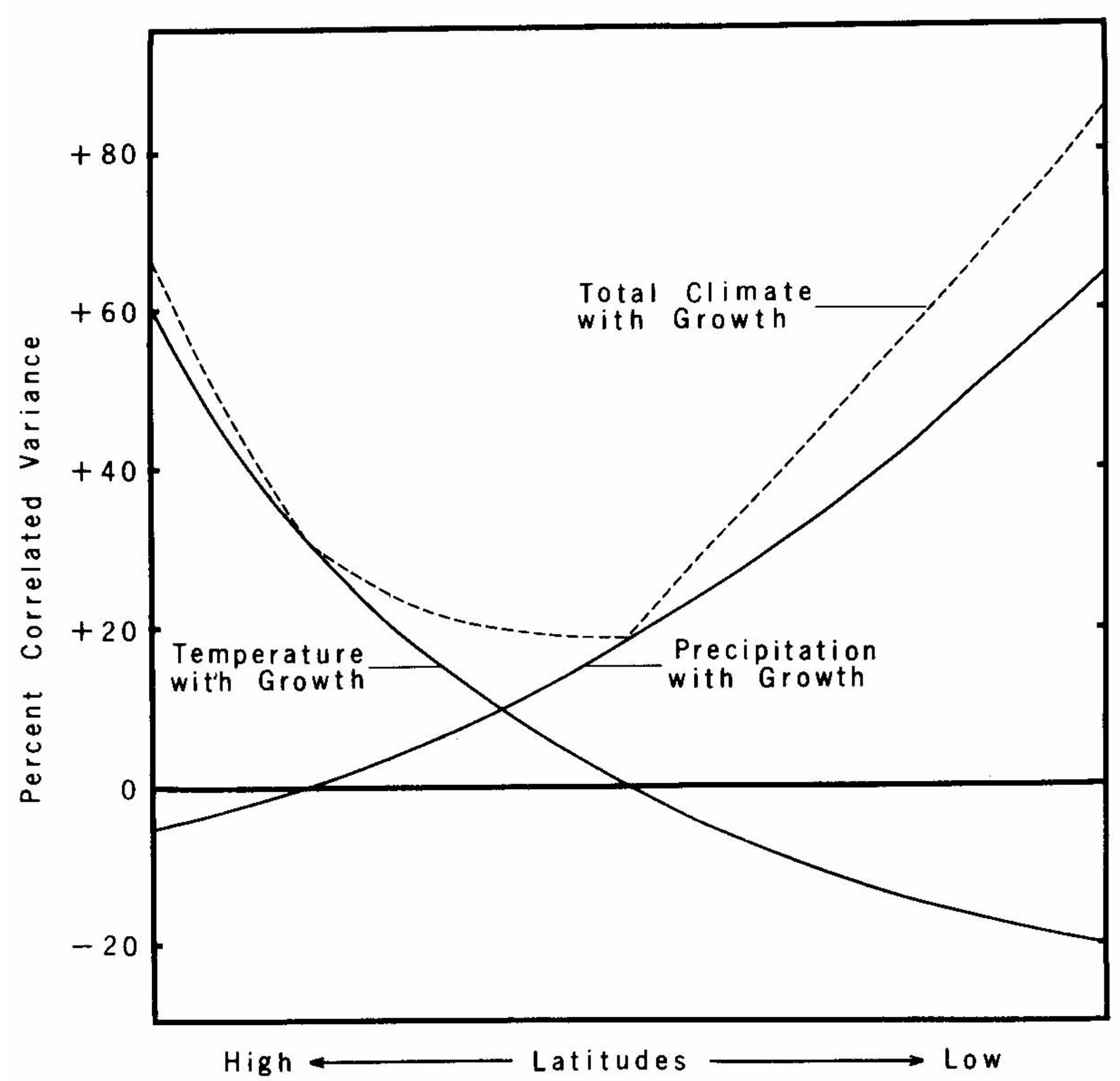

Figure 1b. A model demonstrating how the correlation between ring width and either temperature or precipitation changes as a function of latitude. Solid lines indicate the sign and strength of the correlations, while the dashed line indicates the total amount of ring width variation accounted for by both climate variables. (From Fritts 1976).

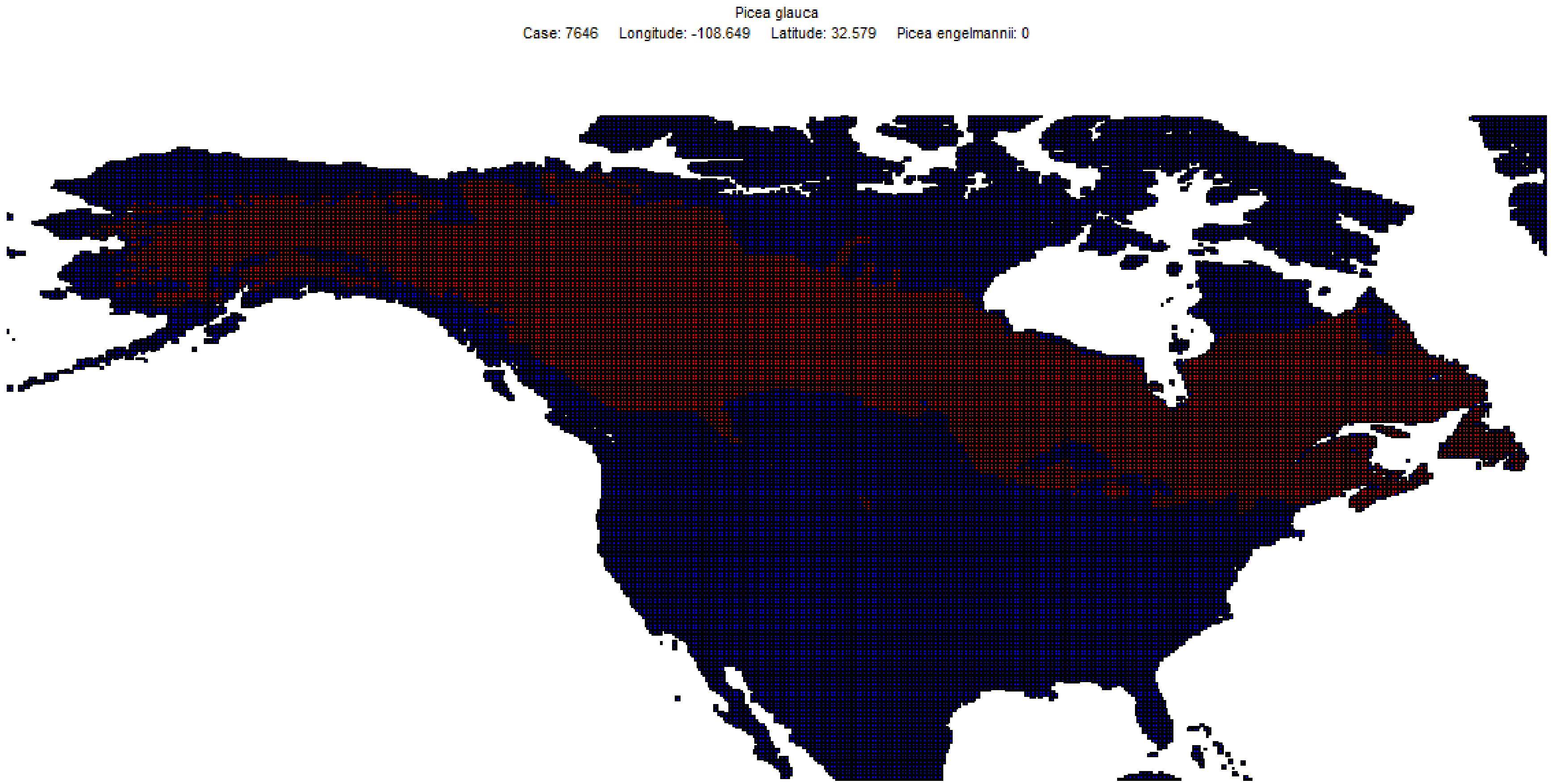

Figure 2a. Distribution of white spruce (*Picea glauca*).

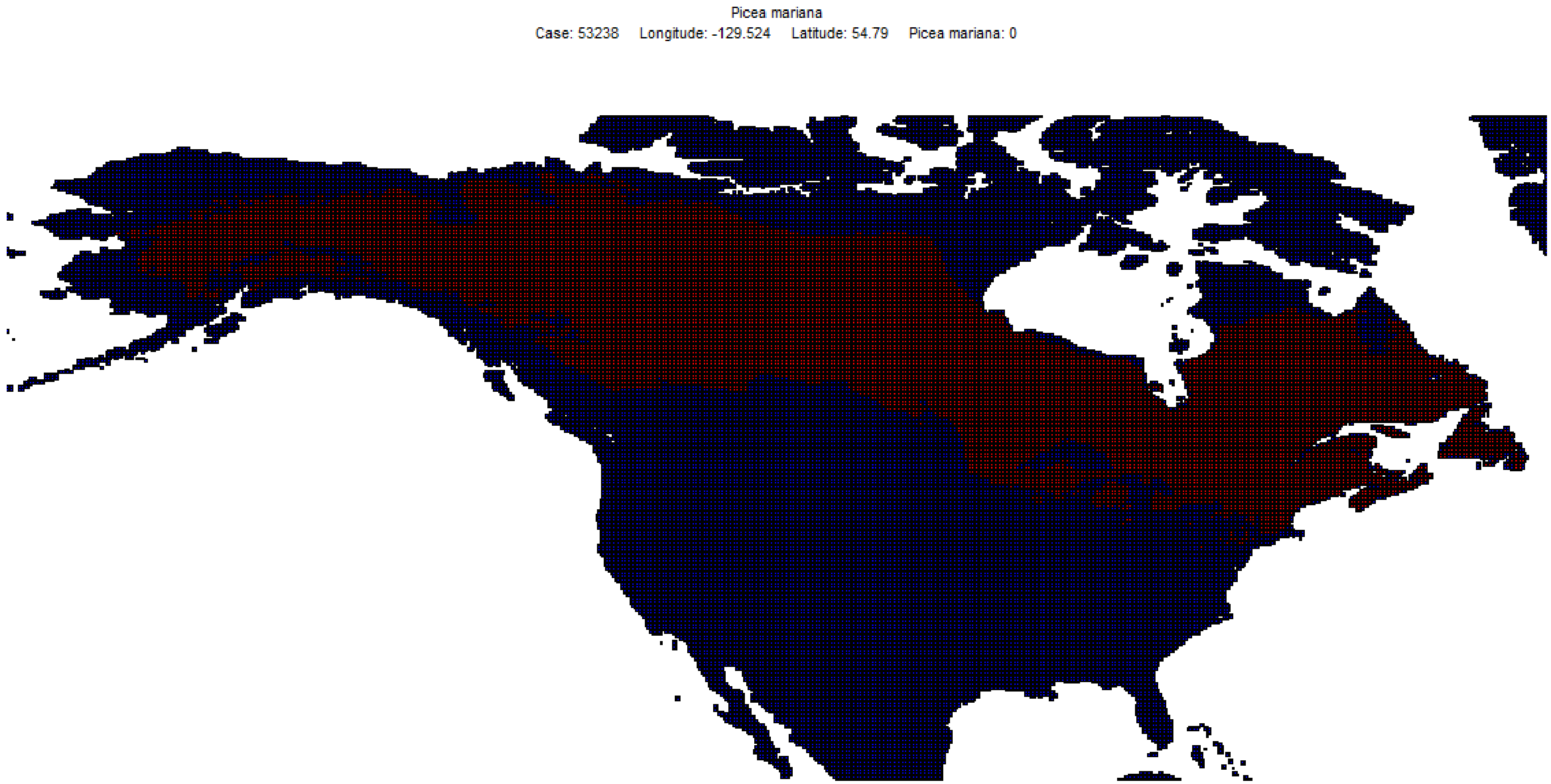

Figure 2b. Distribution of black spruce (*Picea mariana*).

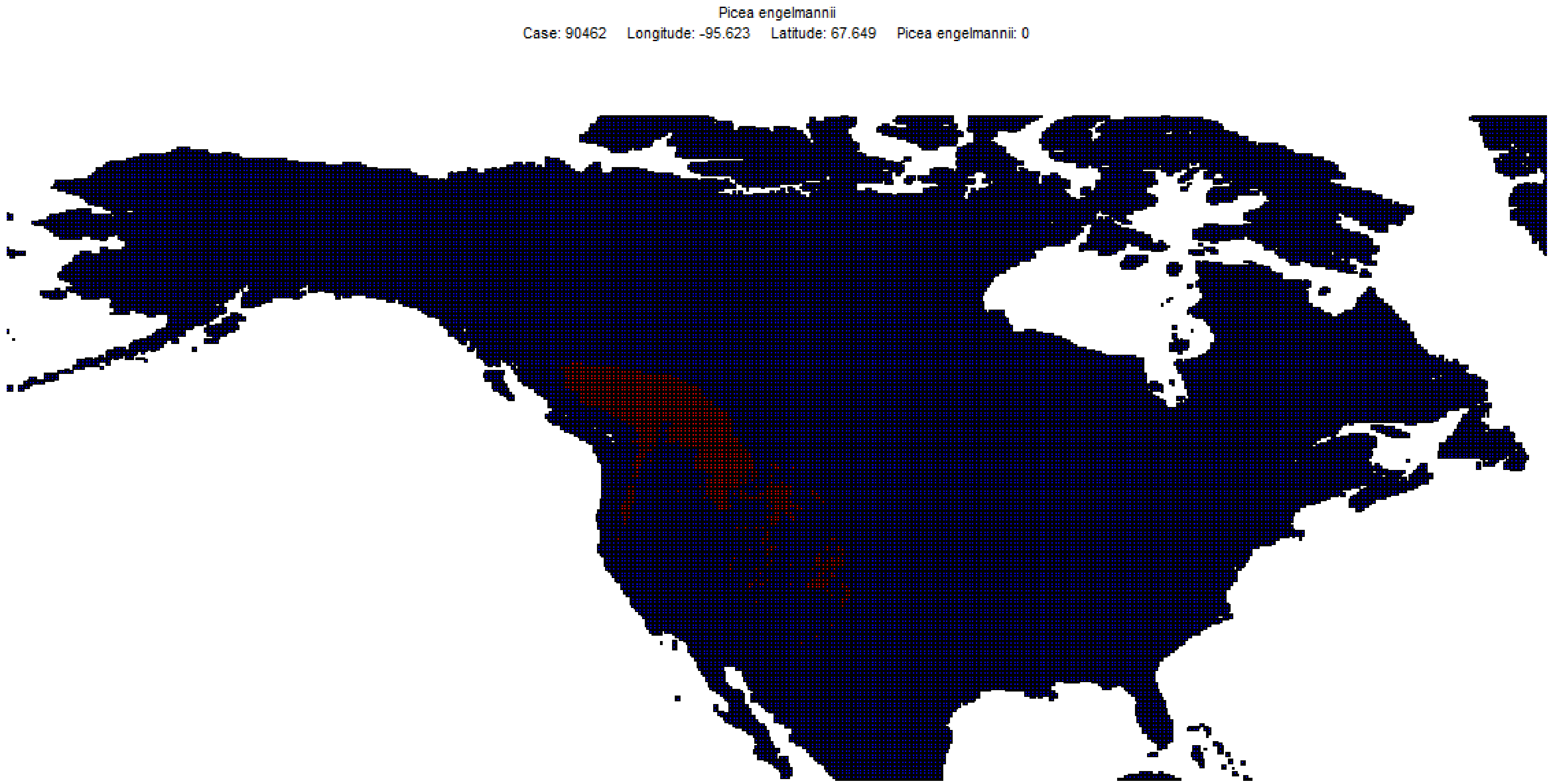

Figure 2c. Distribution of Engelmann spruce (*Picea engelmannii*).

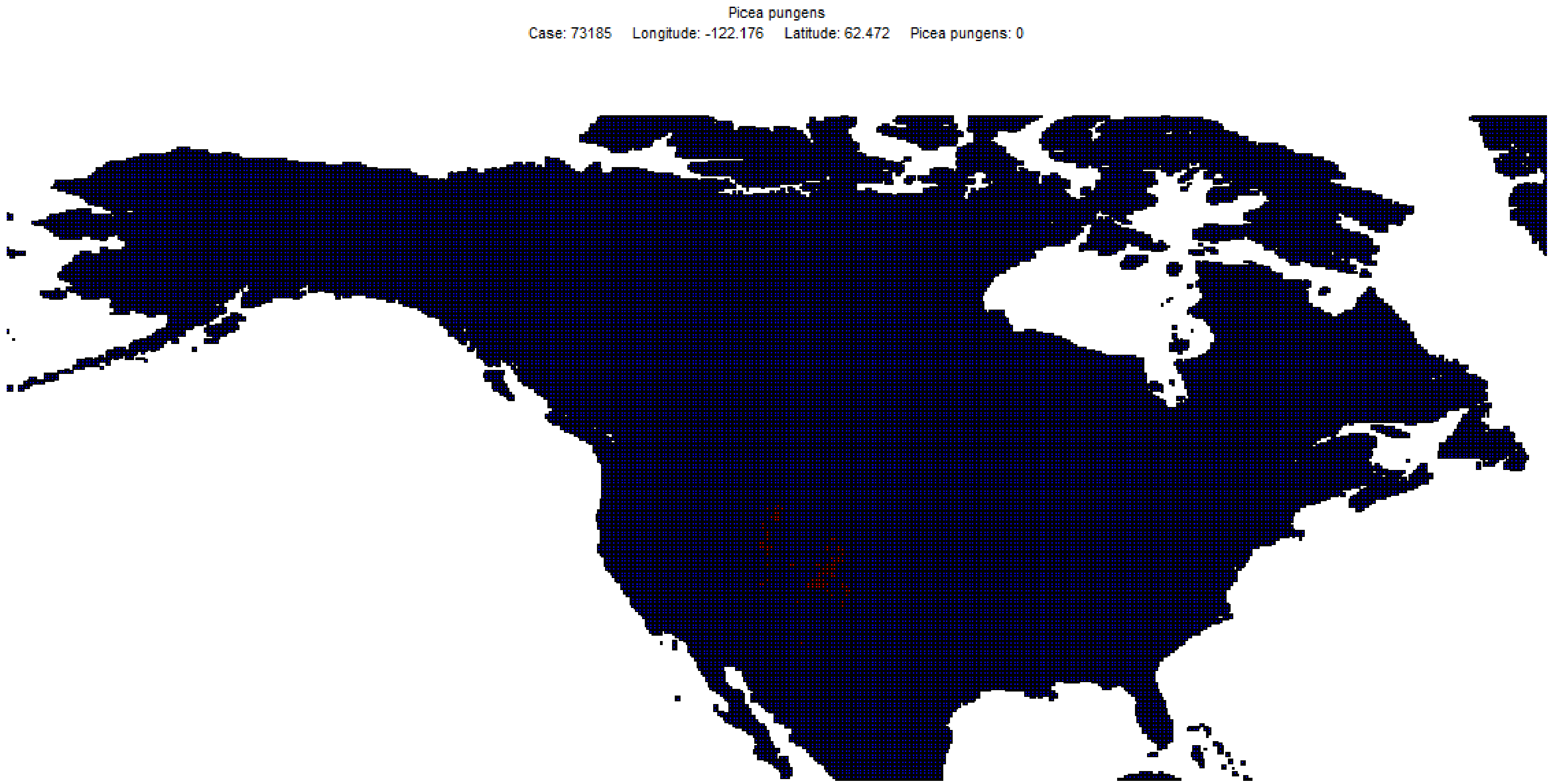

Figure 2d. Distribution of blue spruce (*Picea pungens*).

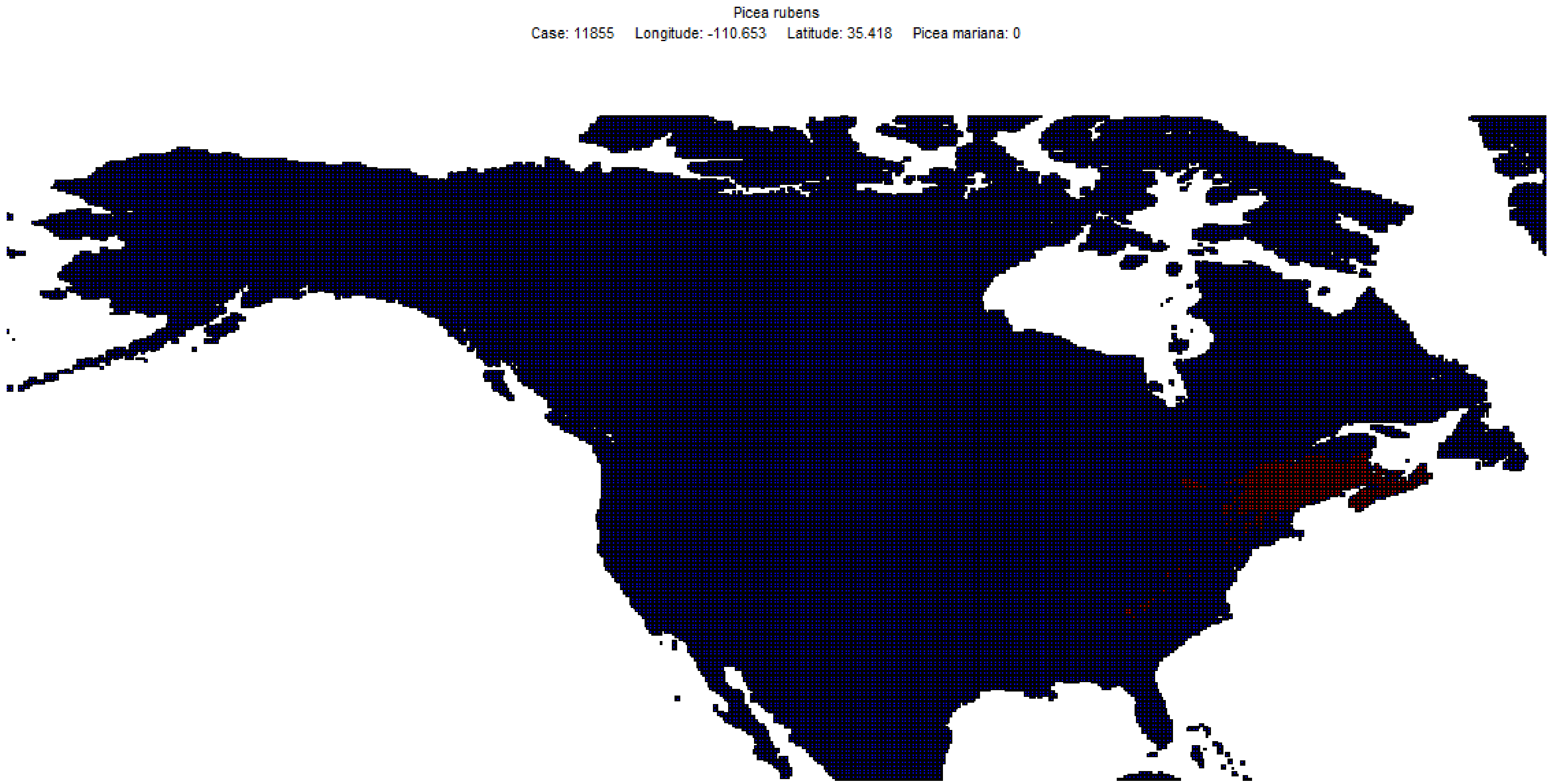

Figure 2e. Distribution of red spruce (*Picea rubens*).

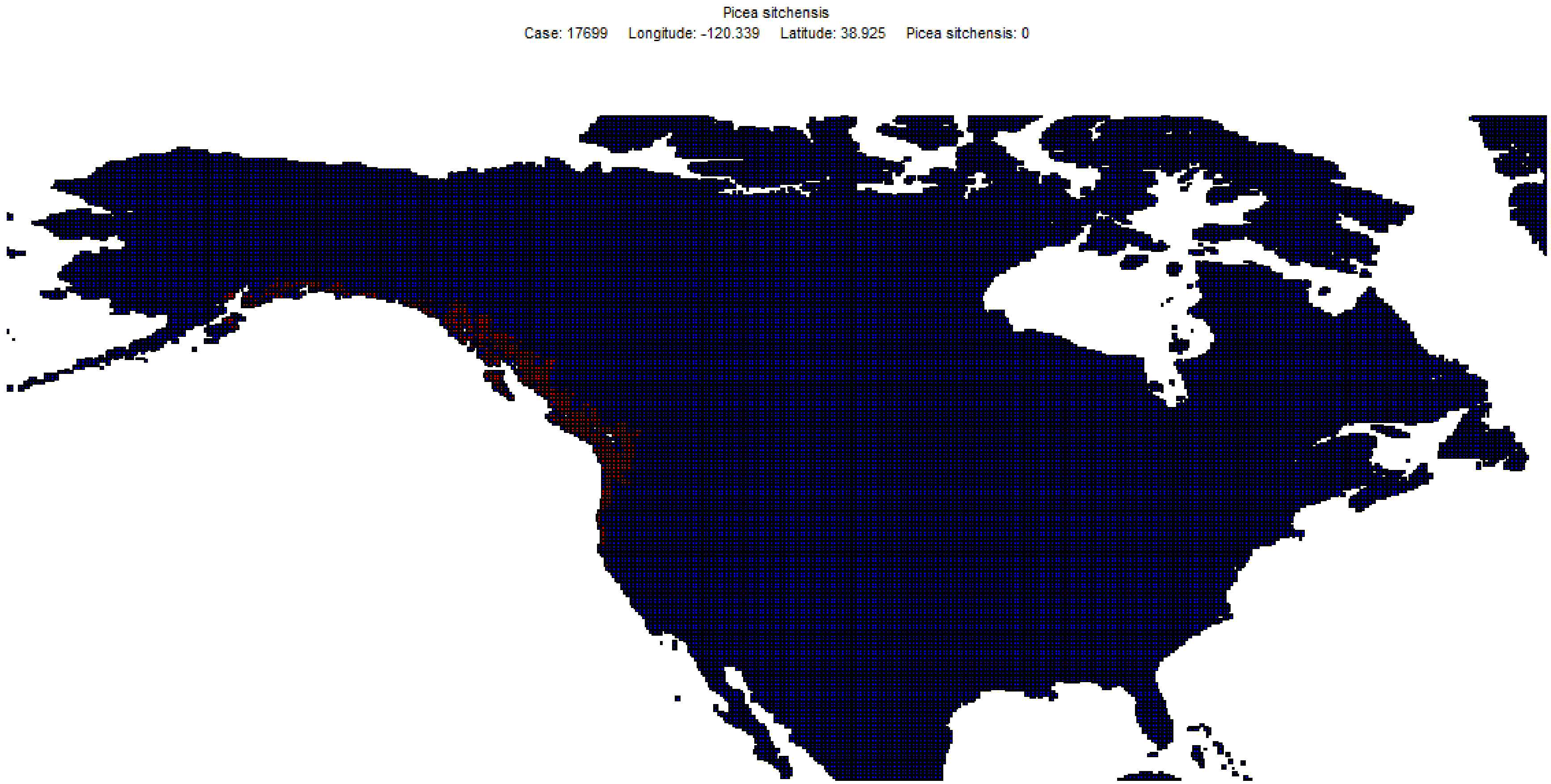

Figure 2f. Distribution of Sitka spruce (*Picea sitchensis*).

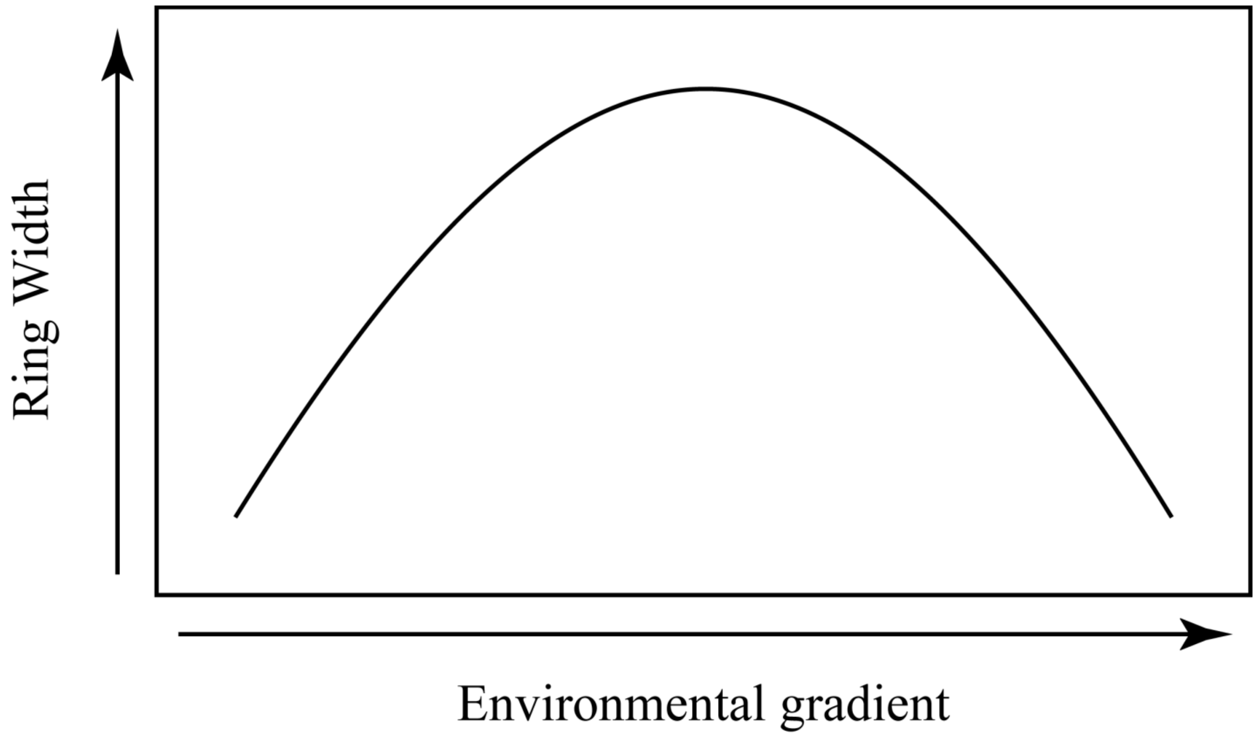

Figure 3a. The expected response trend or mean ring width along an environmental gradient. The response trend of maximum density should follow a similar pattern.

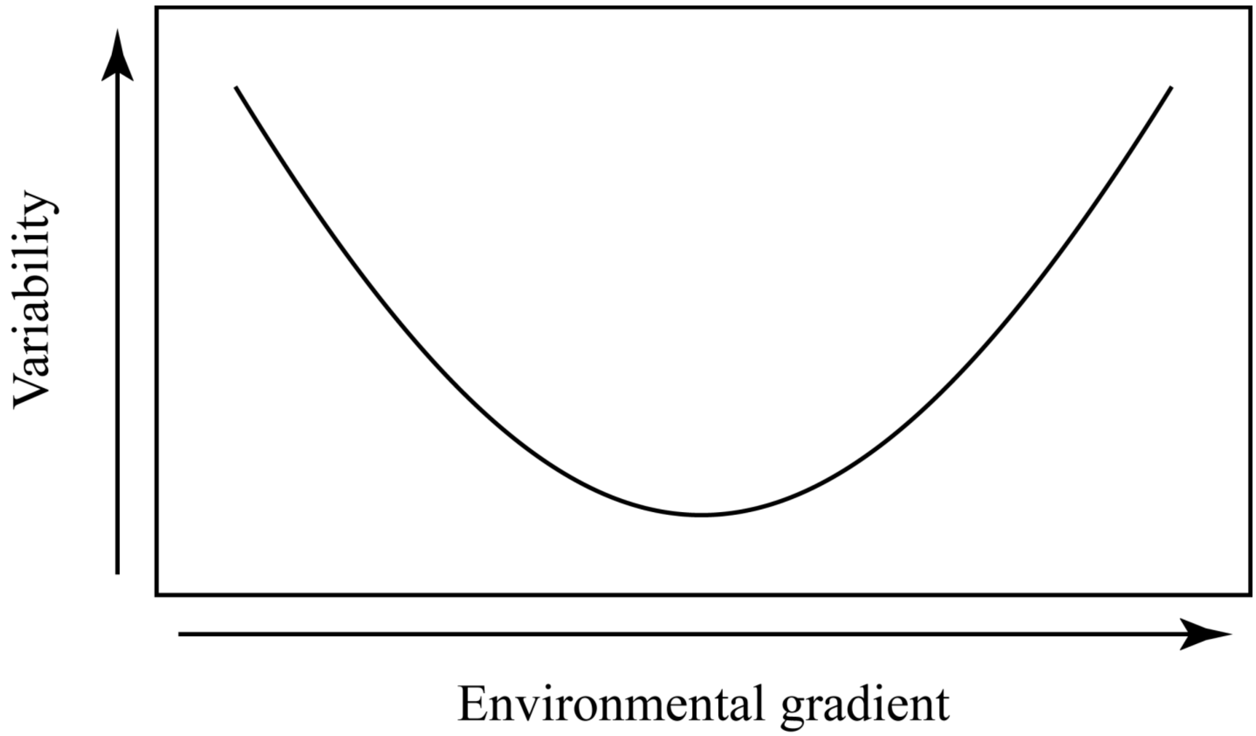

Figure 3b. The expected response trend of the variability in ring-width characteristics (as measured by the standard deviation) along an environmental gradient.

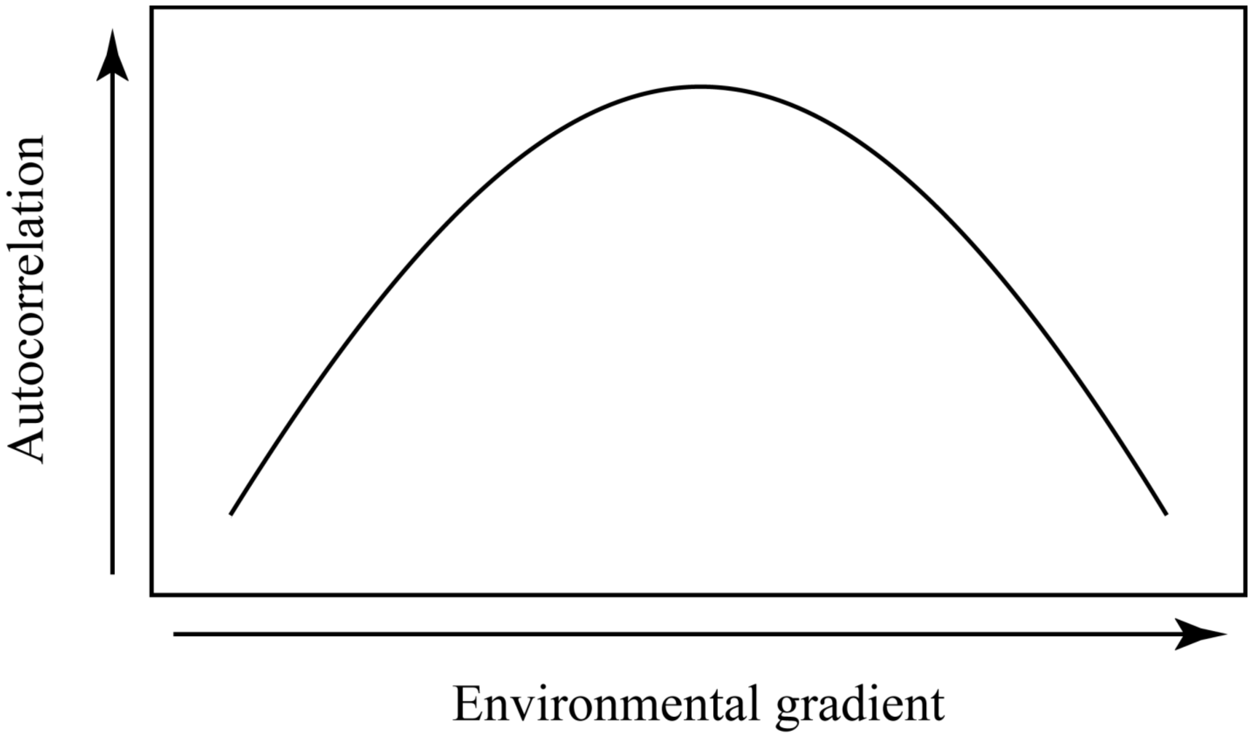

Figure 3c. The expected response of the first-order autocorrelation of tree-ring characteristics along an environmental gradient.

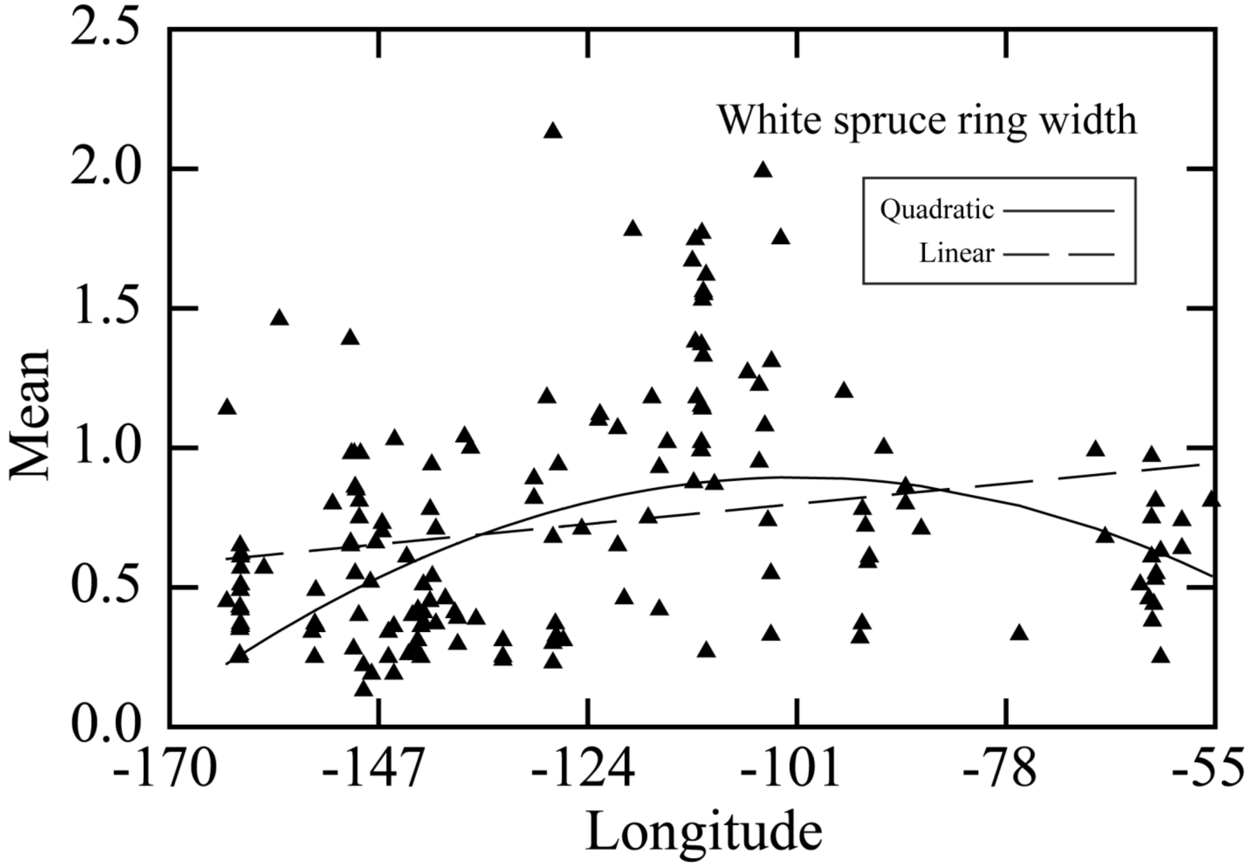

Figure 4. Plot of white spruce mean ring width versus longitude with fitted quadratic and linear regression lines. The quadratic regression is statistically significant (critical value of F: 3.901, p < 0.00001).

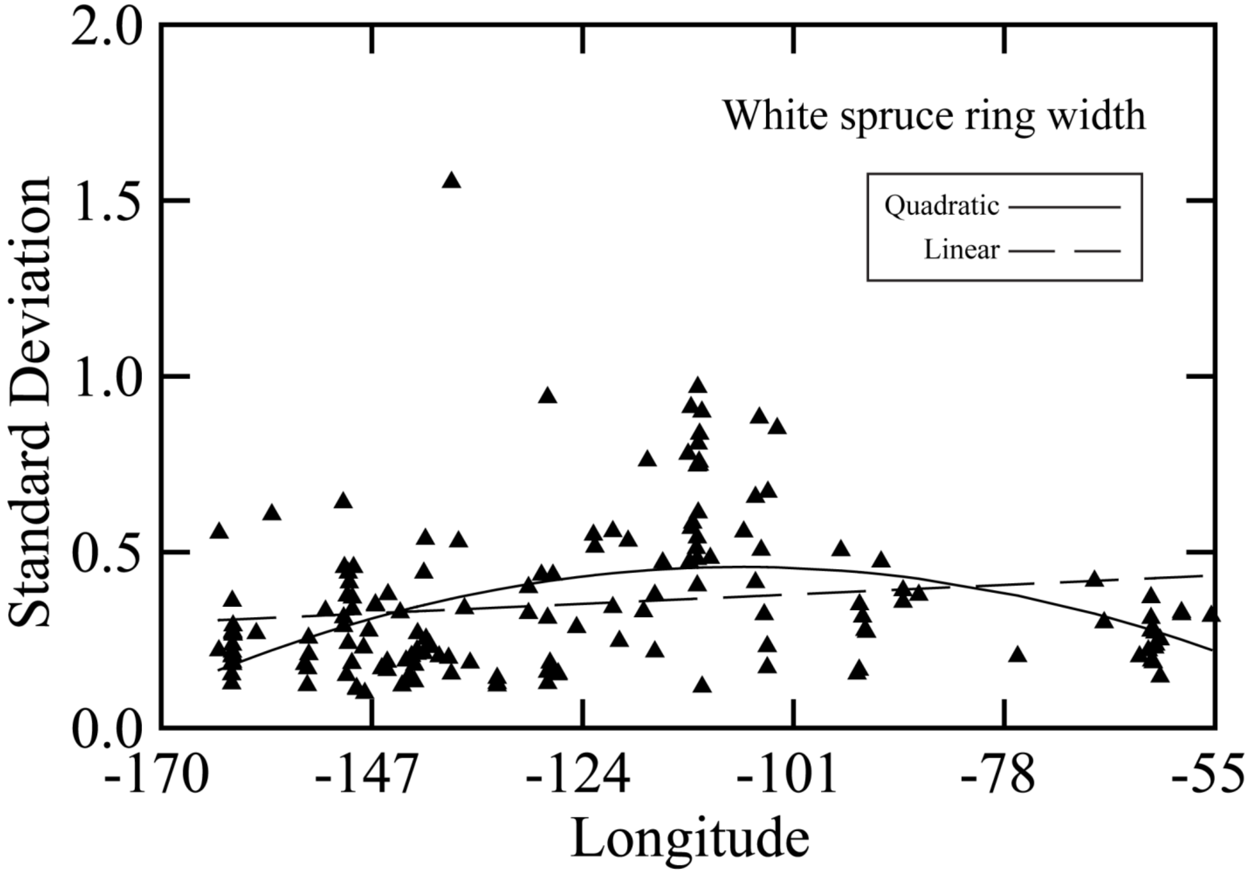

Figure 5. Plot of white spruce standard deviation of ring width versus longitude with fitted quadratic and linear regression lines. The quadratic regression is statistically significant (critical value of F: 3.901, $p < 0.00001$).

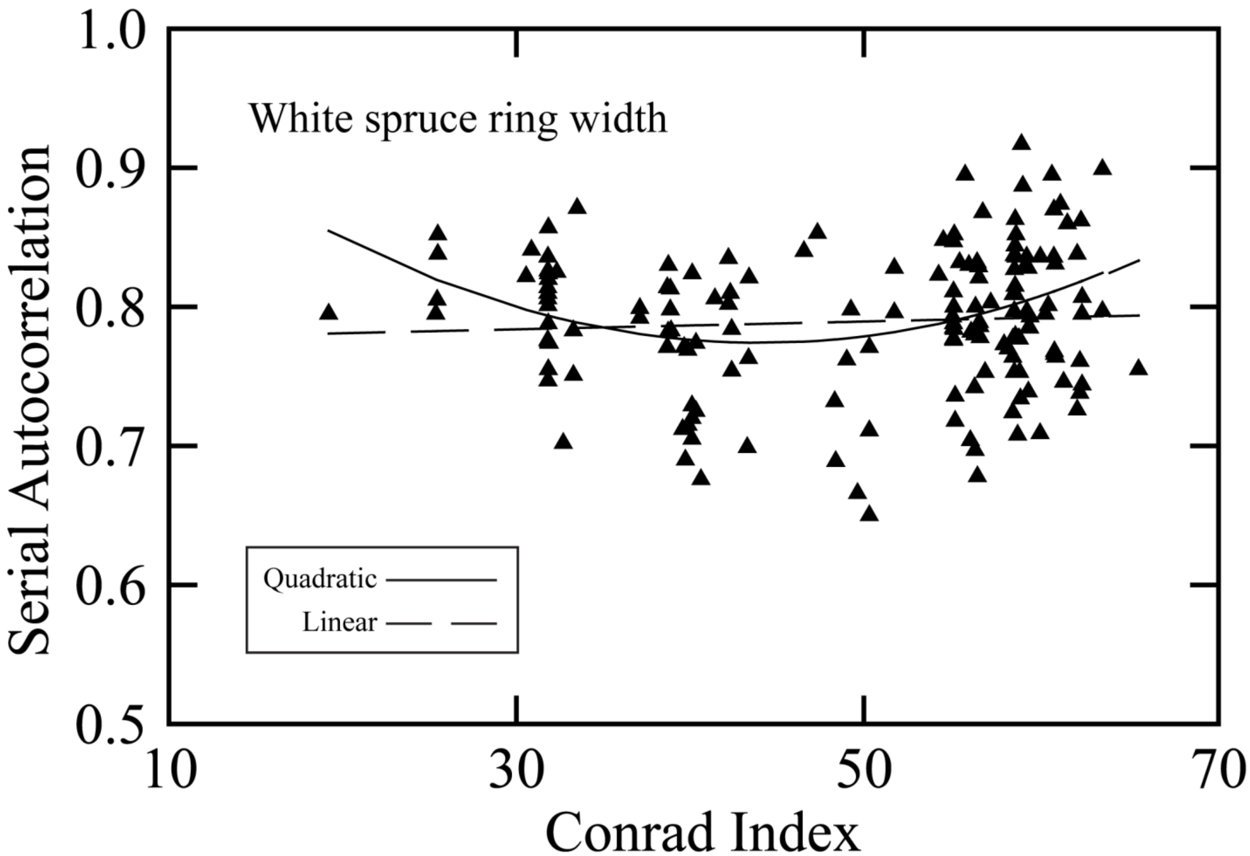

Figure 6. Plot of white spruce serial autocorrelation of ring width versus continentality (Conrad Index) with fitted quadratic and linear regression lines. The quadratic regression is statistically significant (critical value of F: 3.901, p = 0.00273).

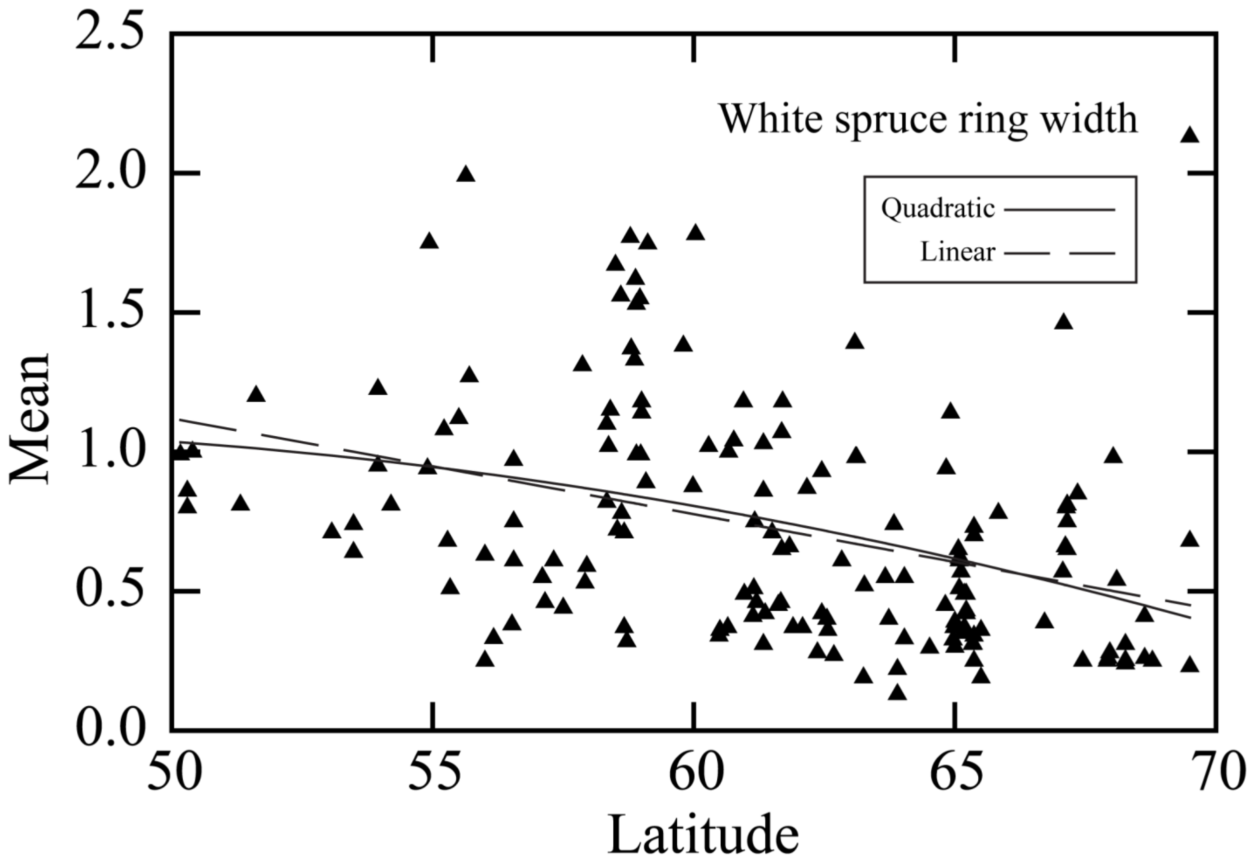

Figure 7. Plot of white spruce mean ring width versus latitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 3.901, $p < 0.00001$).

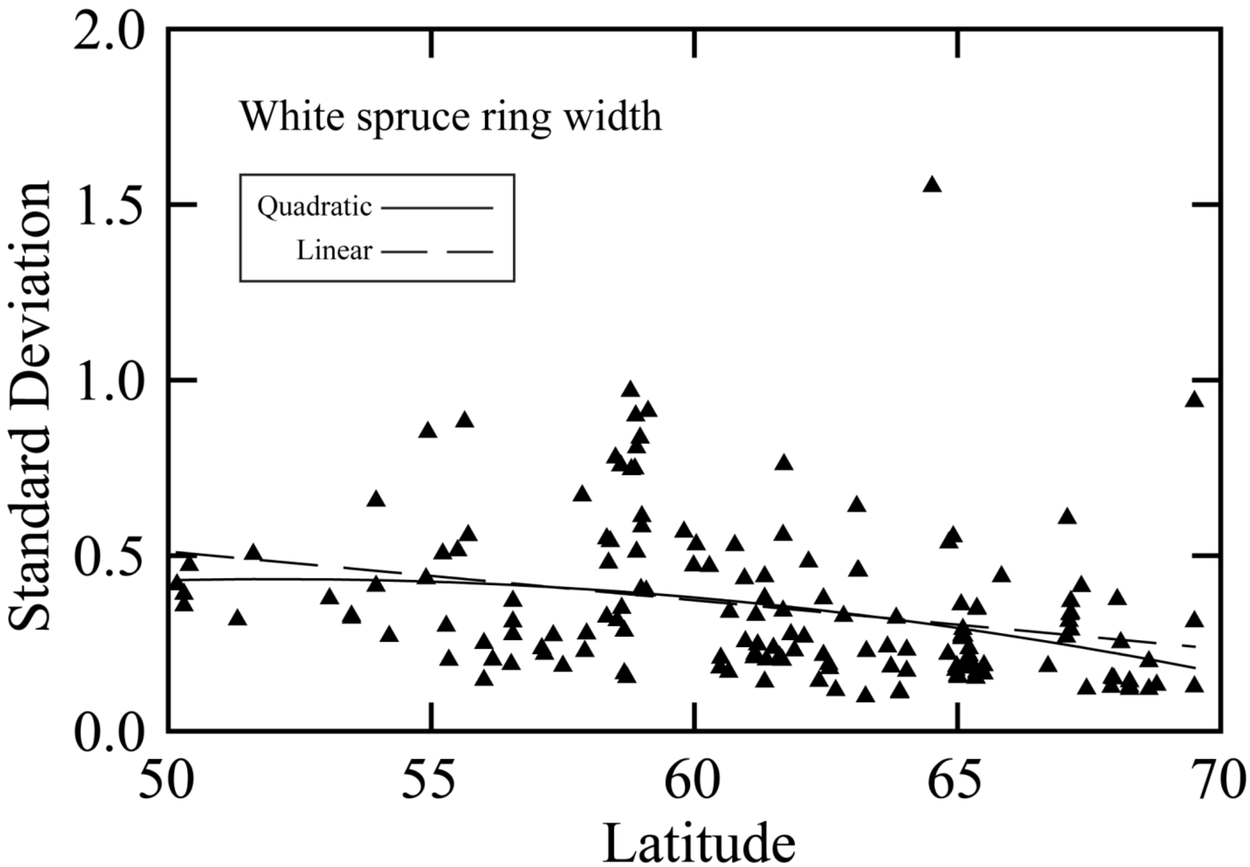

Figure 8. Plot of white spruce standard deviation of ring width versus latitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 3.901, p = 0.00021).

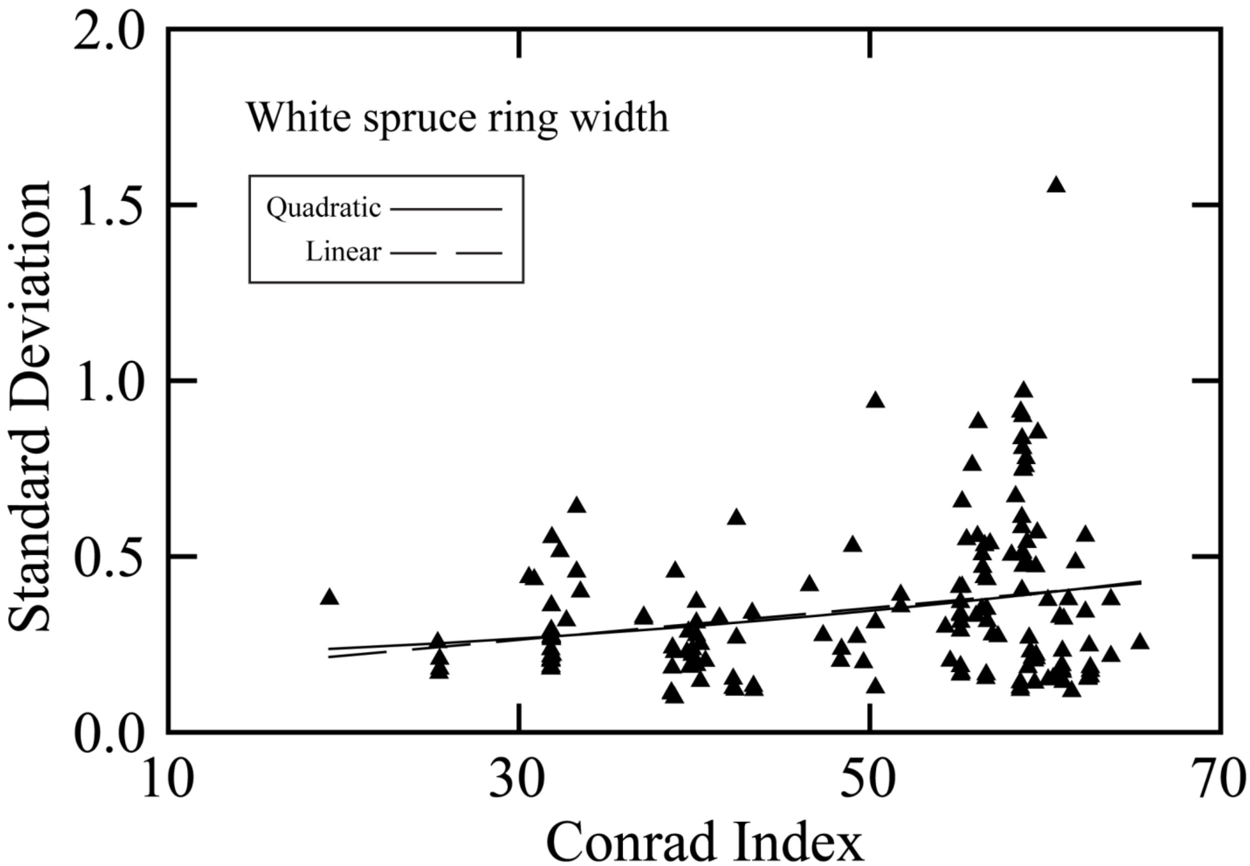

Figure 9. Plot of white spruce standard deviation of ring width versus continentality (Conrad Index) with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 3.901, p = 0.00277).

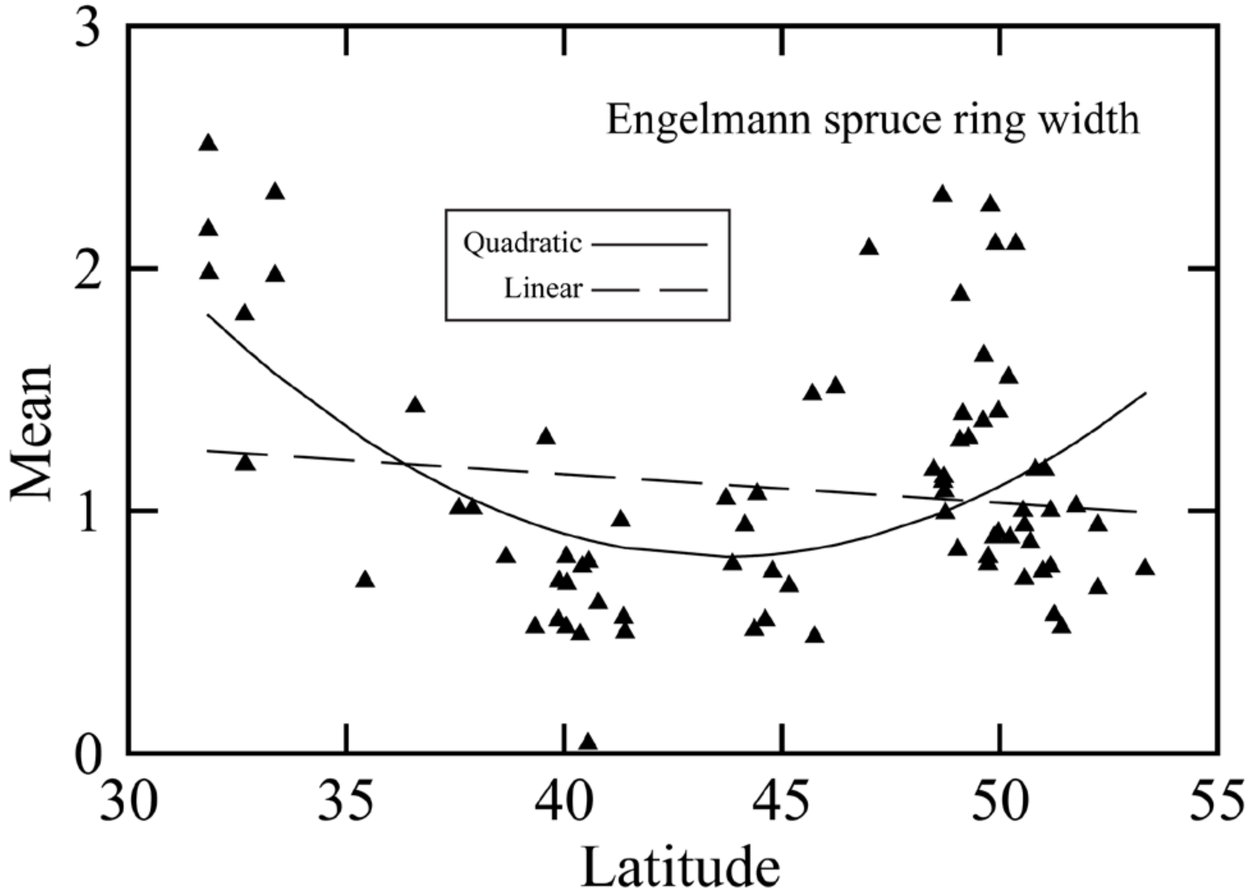

Figure 10. Plot of Engelmann spruce mean ring width versus latitude with fitted quadratic and linear regression lines. The quadratic regression is statistically significant (critical value of F: 3.967, $p = 0.00006$).

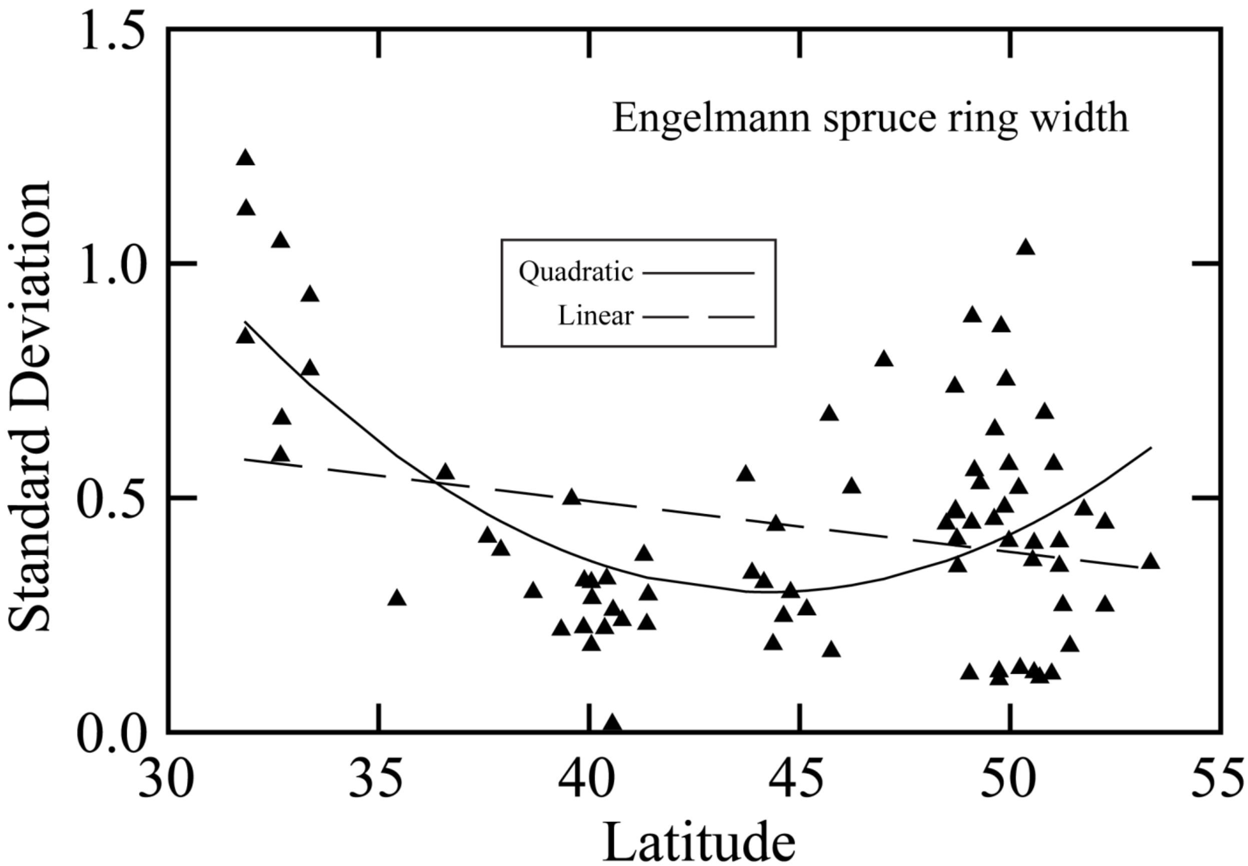

Figure 11. Plot of Engelmann spruce standard deviation of ring width versus latitude with fitted quadratic and linear regression lines. The quadratic regression is statistically significant (critical value of F: 3.967, $p < 0.00001$).

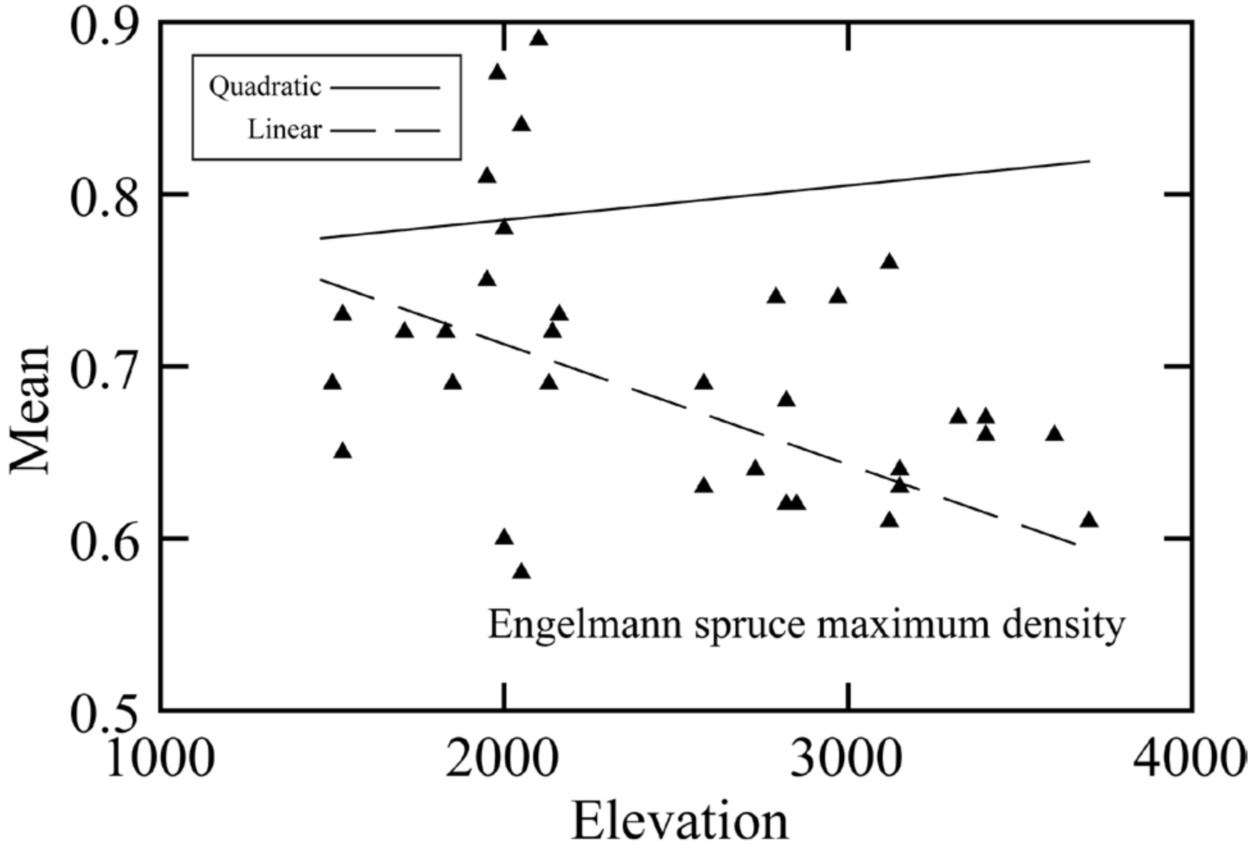

Figure 12. Plot of Engelmann spruce mean maximum density versus elevation with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00291).

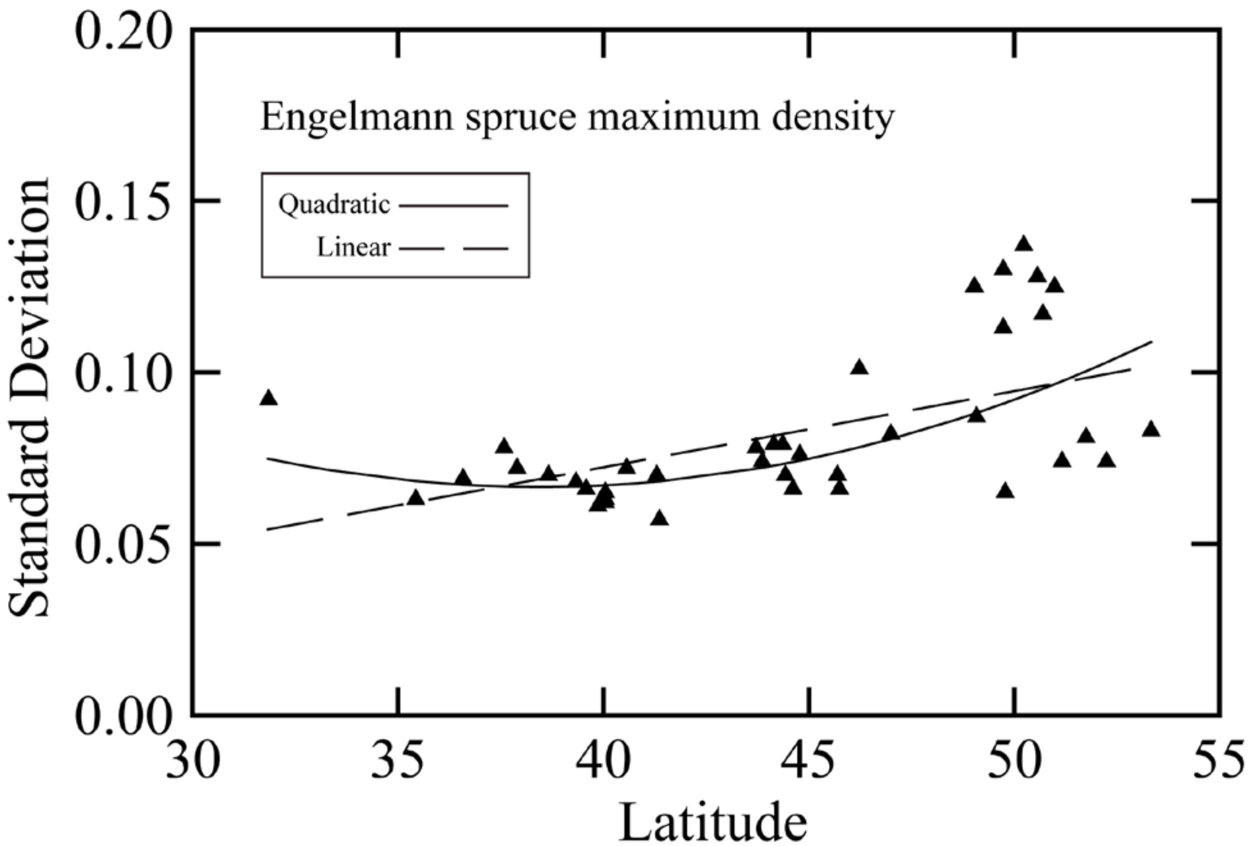

Figure 13. Plot of Engelmann spruce standard deviation of maximum density versus latitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00036).

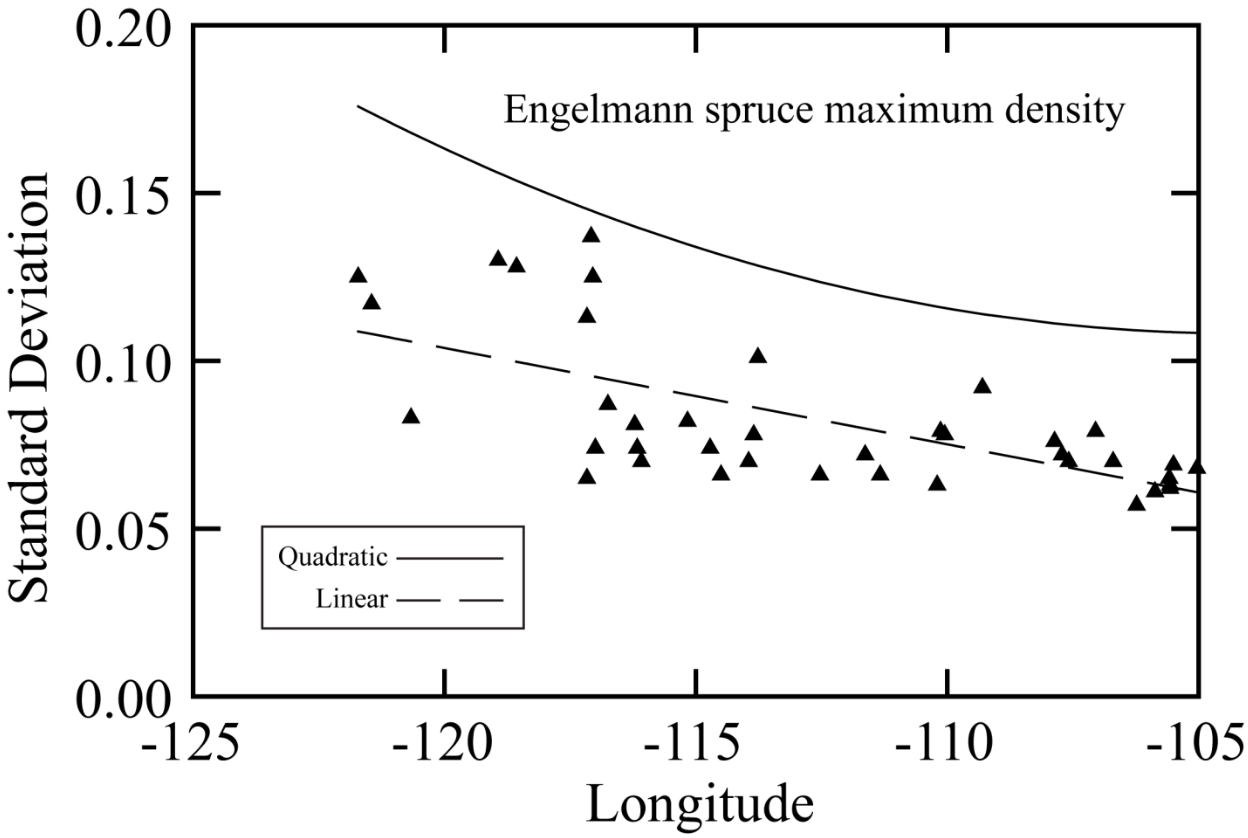

Figure 14. Plot of Engelmann spruce standard deviation of maximum density versus longitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00001).

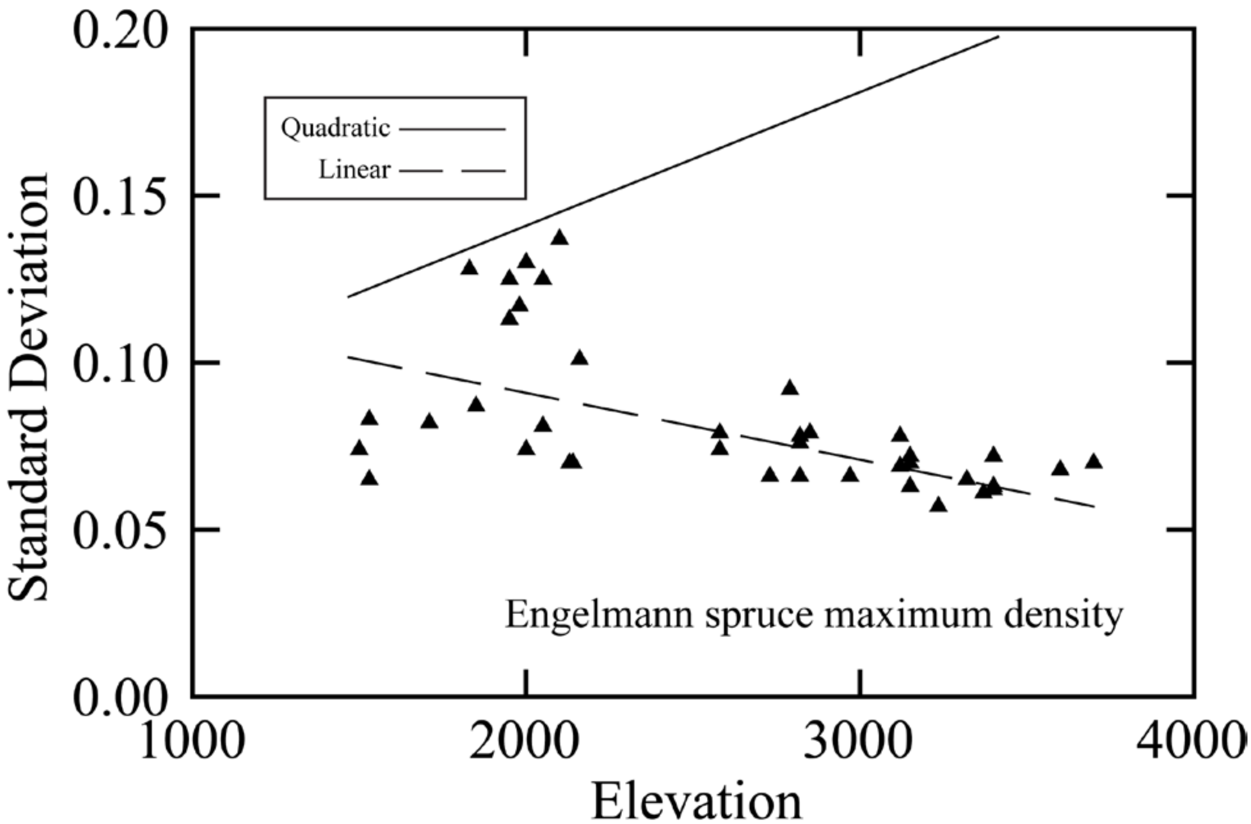

Figure 15. Plot of Engelmann spruce standard deviation of maximum density versus elevation with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00022).

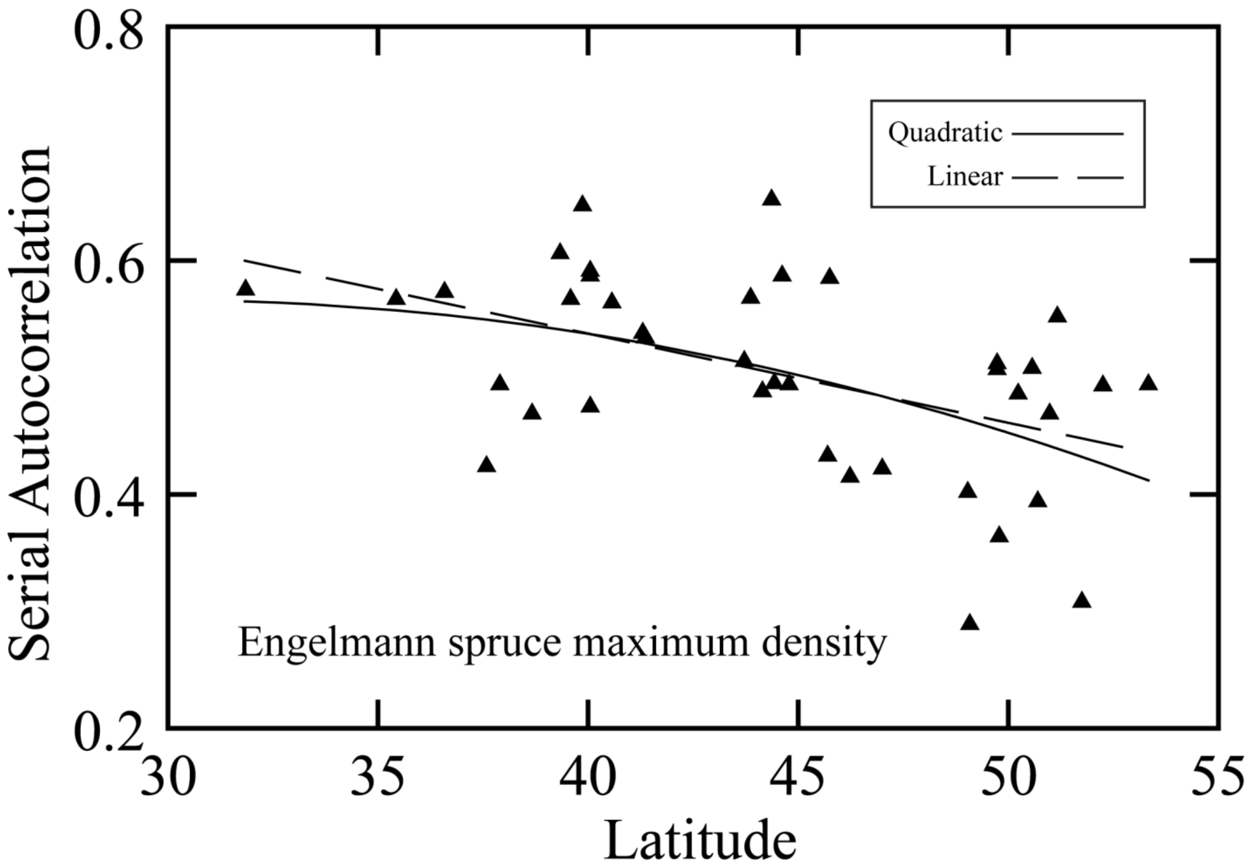

Figure 16. Plot of Engelmann spruce serial autocorrelation of maximum density versus latitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00141).

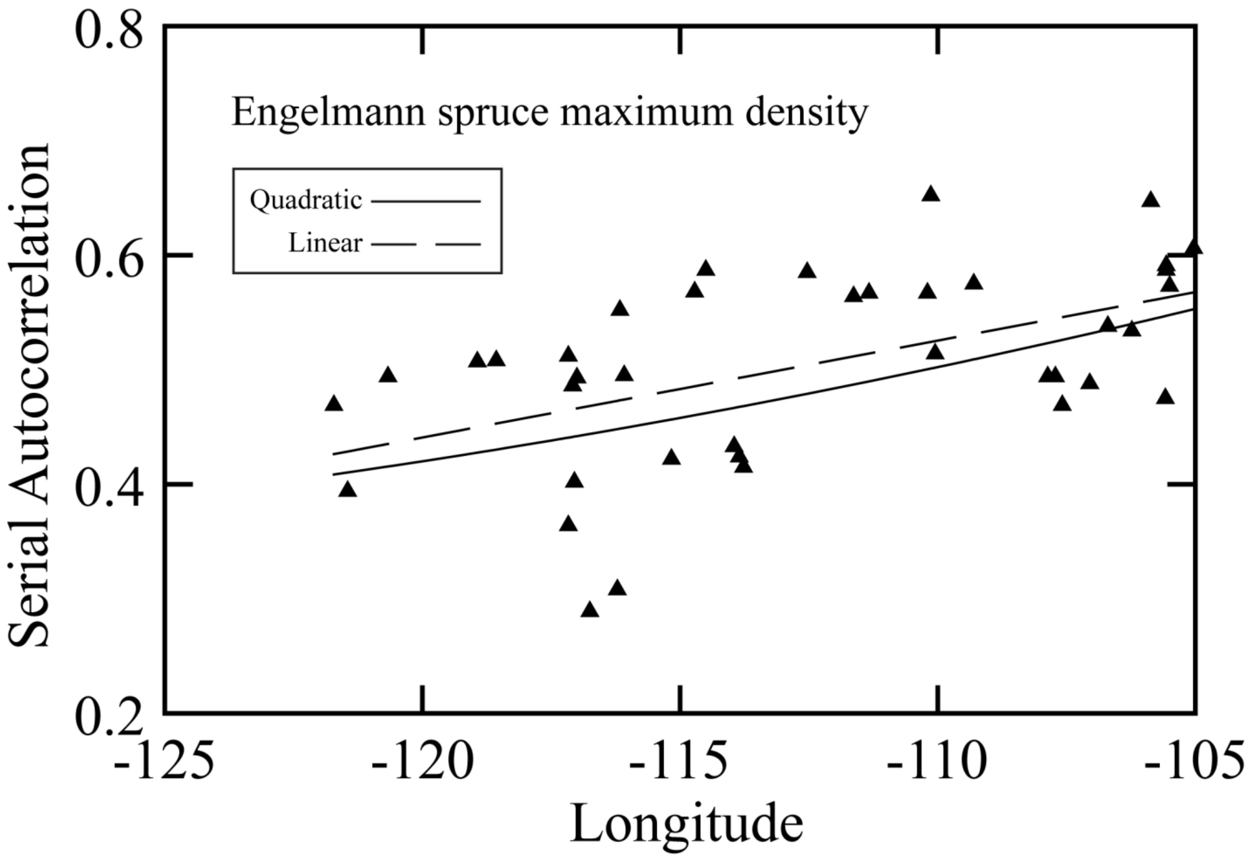

Figure 17. Plot of Engelmann spruce serial autocorrelation of maximum density versus longitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00082).

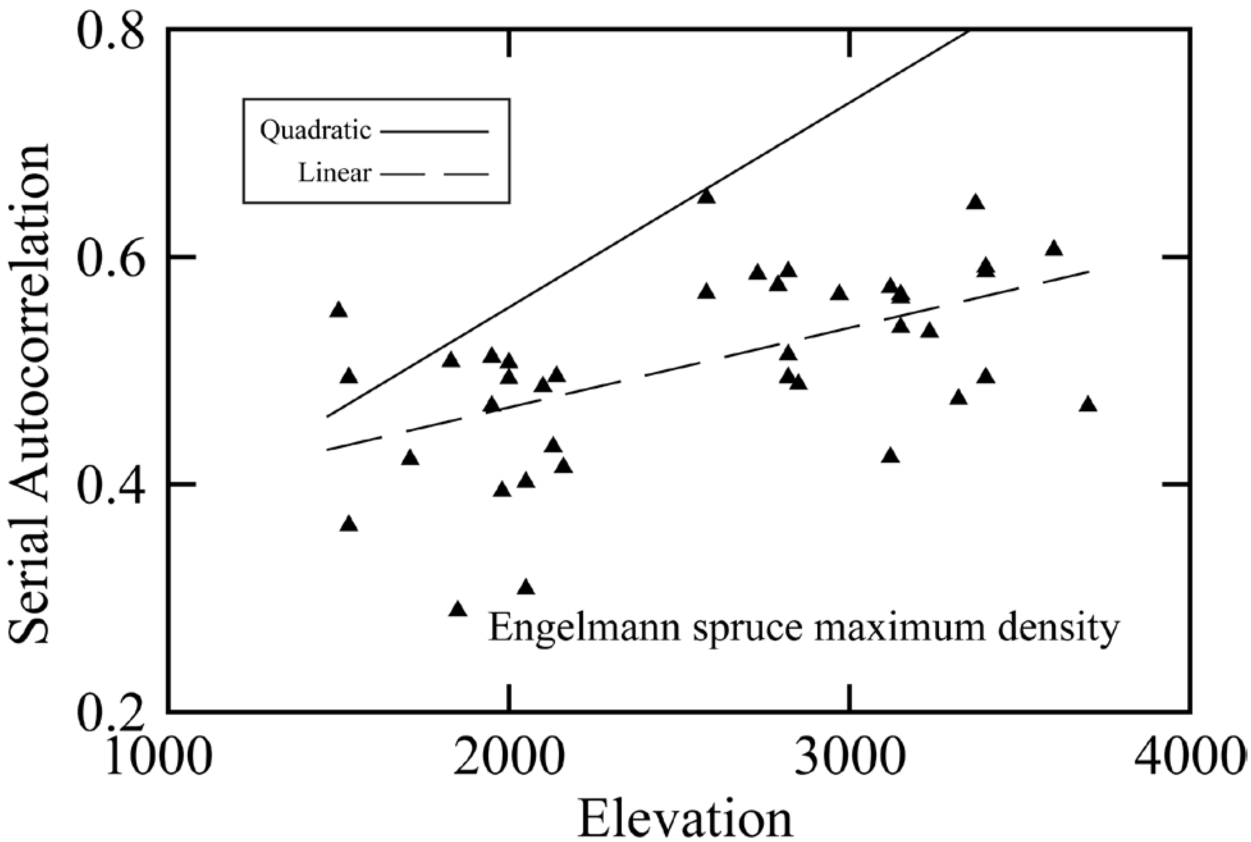

Figure 18. Plot of Engelmann spruce serial autocorrelation of maximum density versus elevation with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 4.113, p = 0.00047).

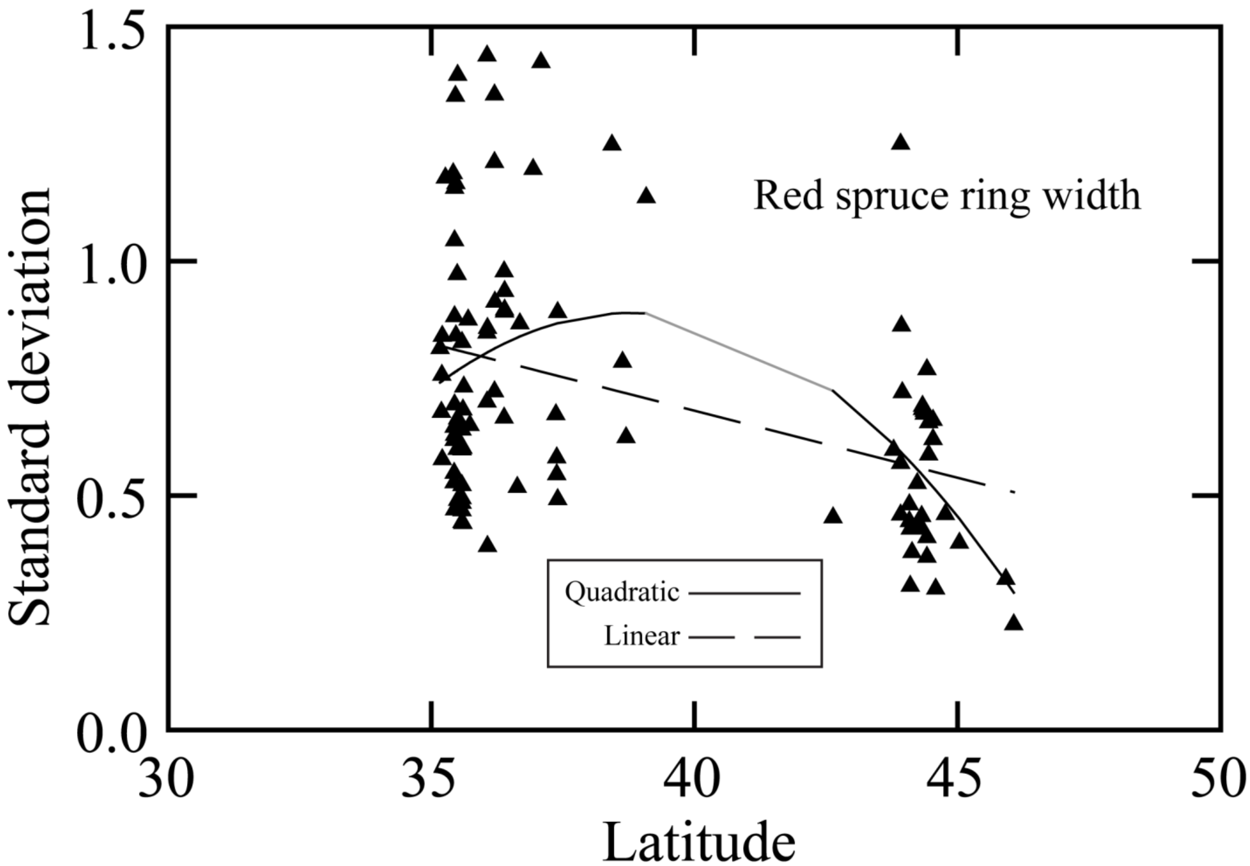

Figure 19. Plot of red spruce standard deviation of ring width versus latitude with fitted quadratic and linear regression lines. The quadratic regression is statistically significant (critical value of F: 3.939, p = 0.00001). Gray-shaded area in quadratic regression curve marks break in red spruce distributions between northern and southern portions of red spruce's range.

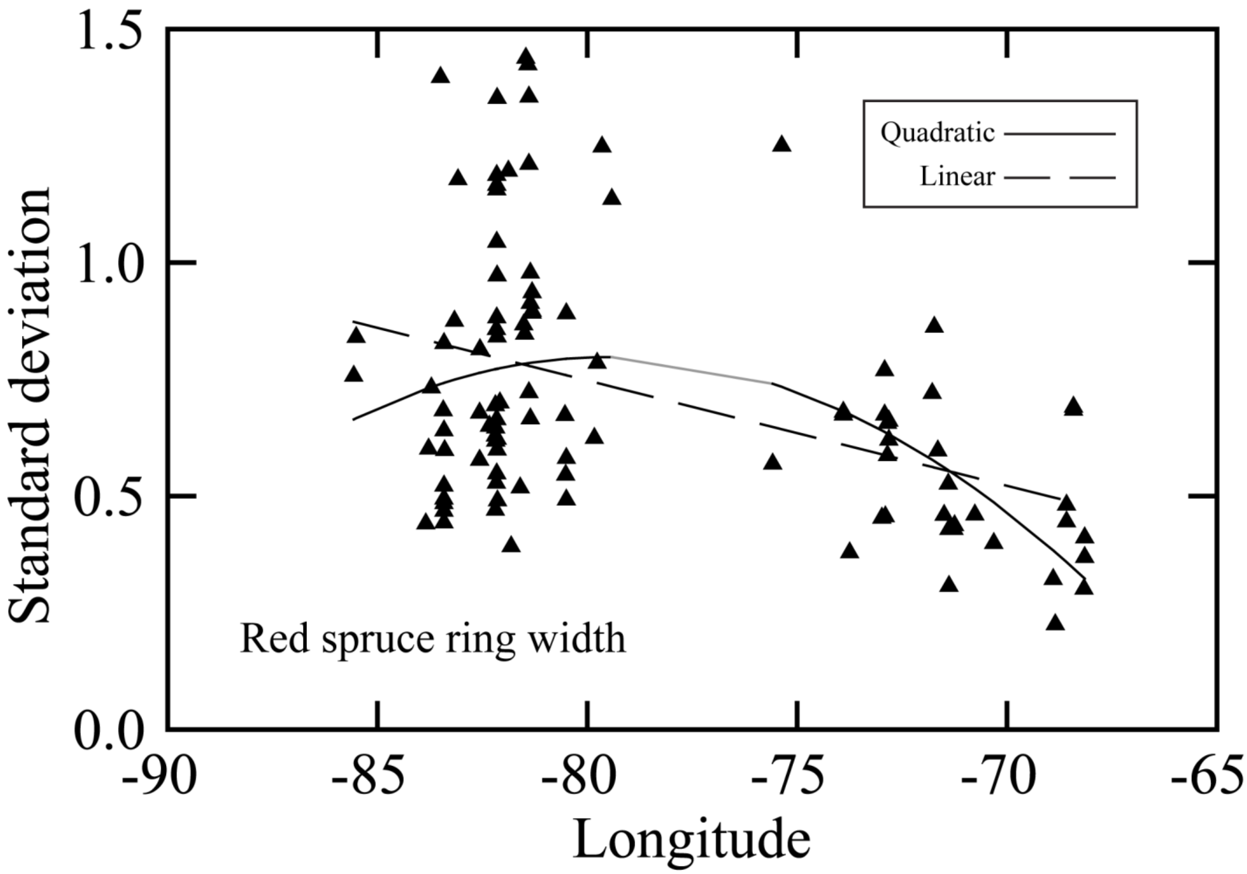

Figure 20. Plot of red spruce standard deviation of ring width versus longitude with fitted quadratic and linear regression lines. The quadratic regression is statistically significant (critical value of F: 3.939, $p < 0.00001$). Gray-shaded area in quadratic regression curve marks break in red spruce distributions between northern and southern portions of red spruce's range.

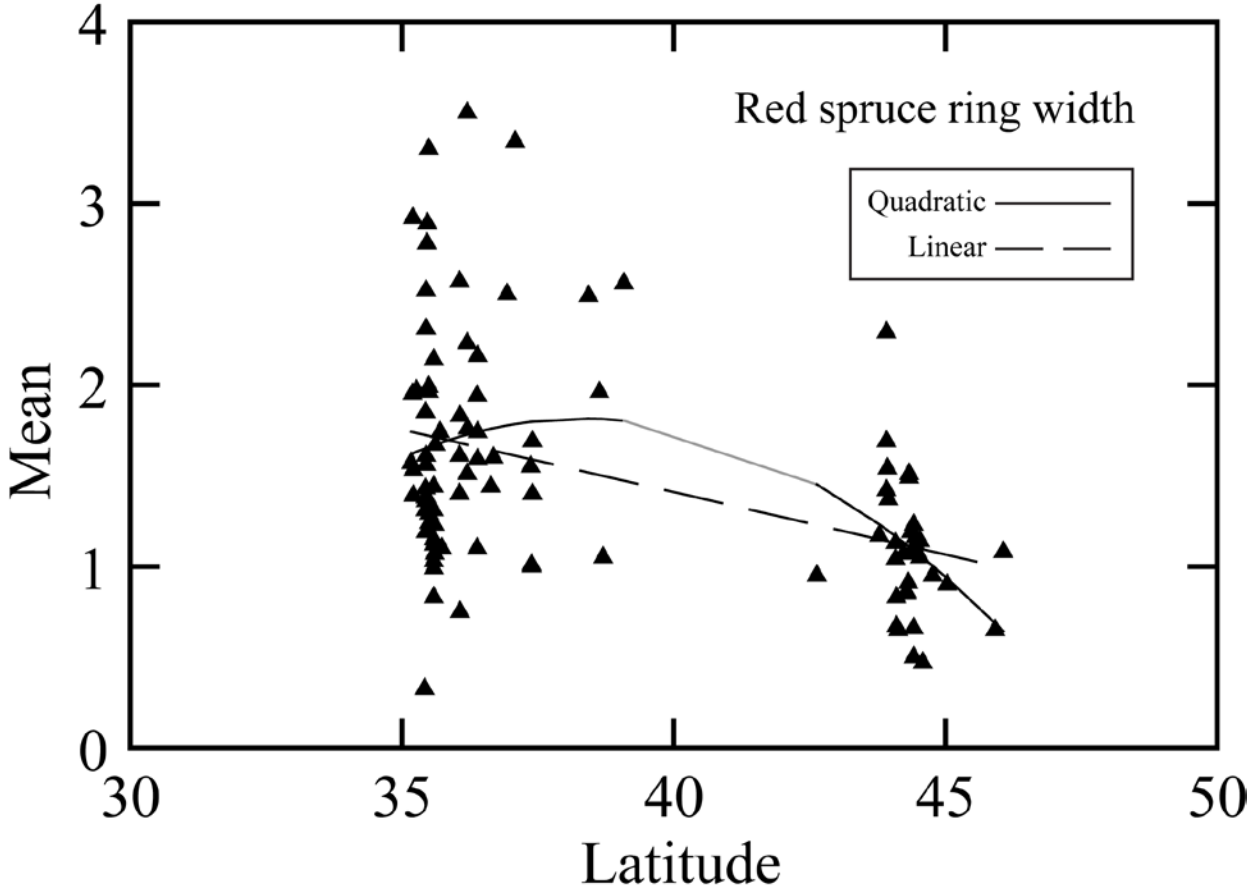

Figure 21. Plot of red spruce mean ring width versus latitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 3.939, p = 0.00001). Gray-shaded area in quadratic regression curve marks break in red spruce distributions between northern and southern portions of red spruce's range.

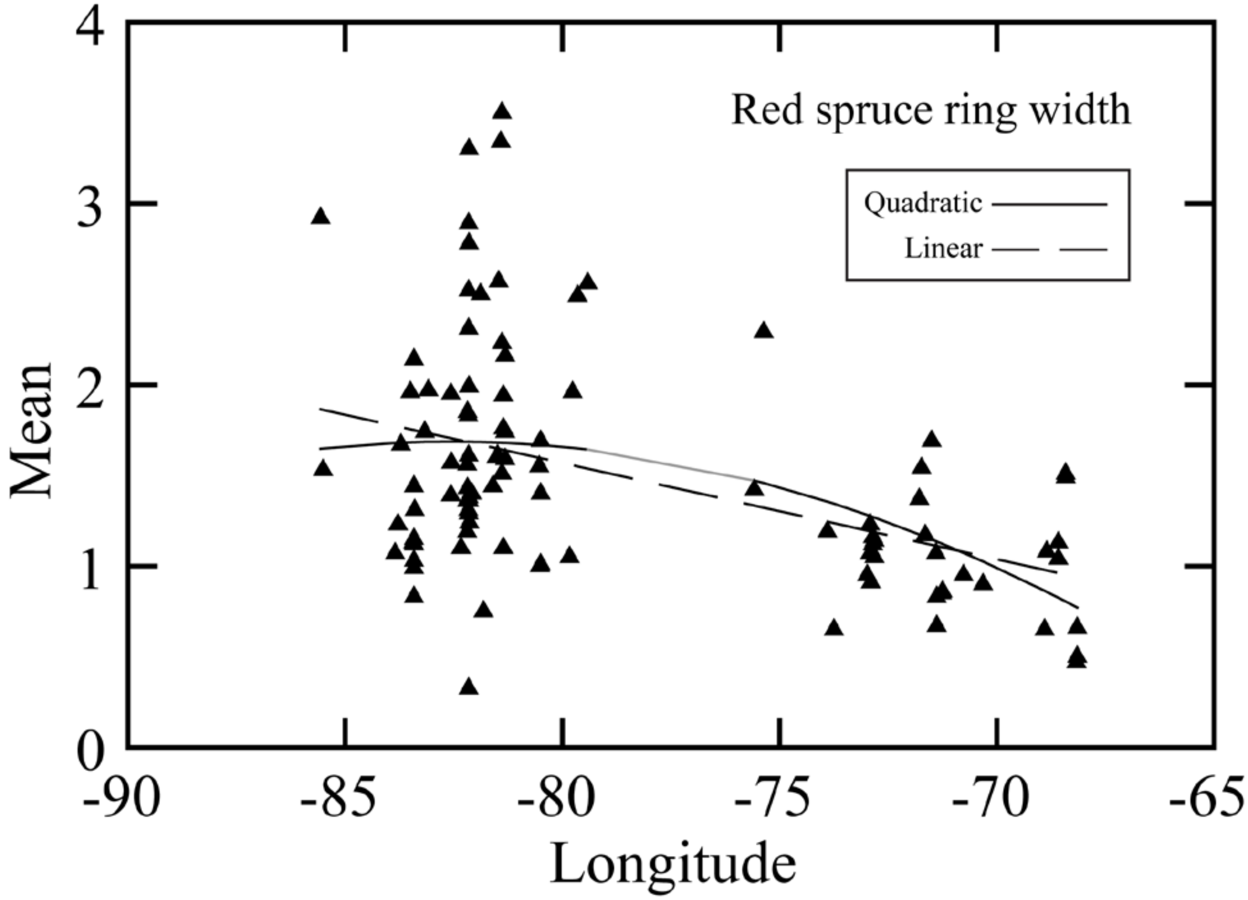

Figure 22. Plot of red spruce mean ring width versus longitude with fitted quadratic and linear regression lines. The linear regression is statistically significant (critical value of F: 3.939, p = 0.00001). Gray-shaded area in quadratic regression curve marks break in red spruce distributions between northern and southern portions of red spruce's range.

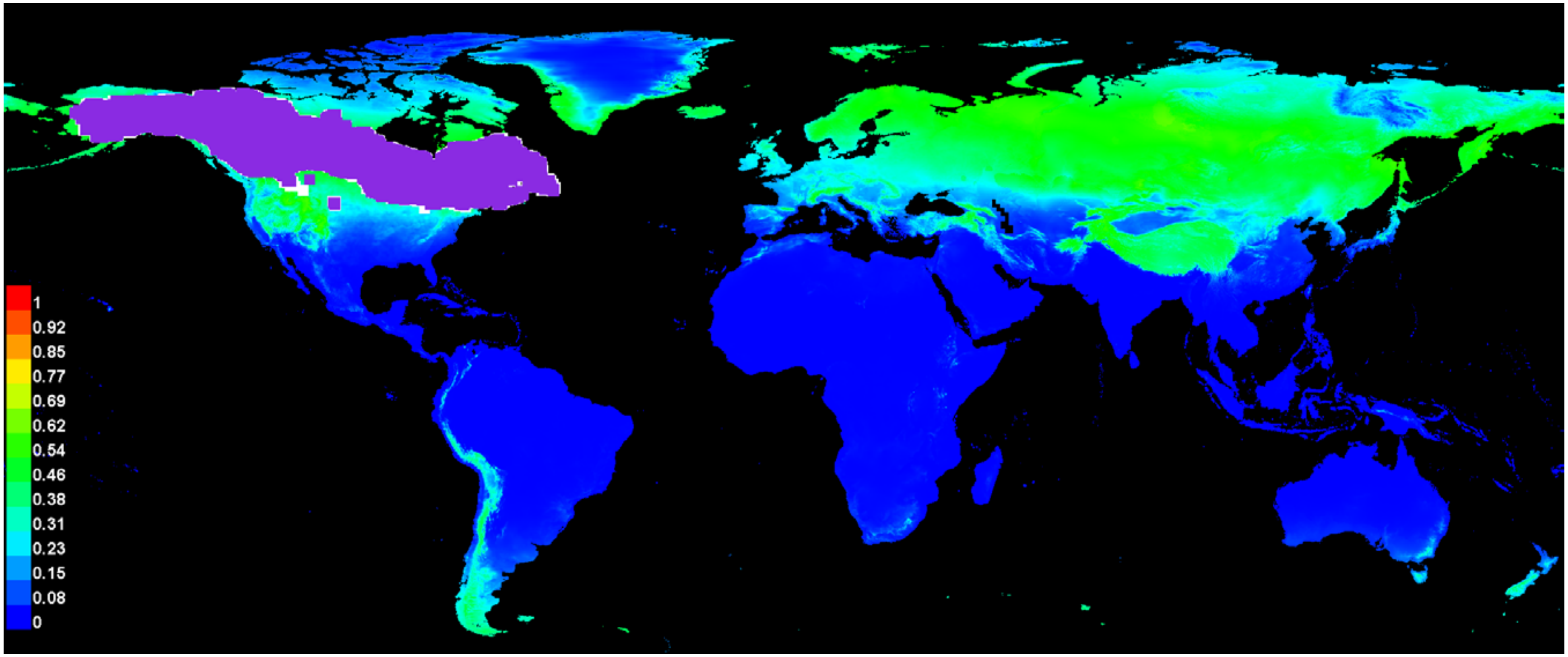

Figure 23a. MaxEnt predictions of suitable geographic ranges for white spruce.

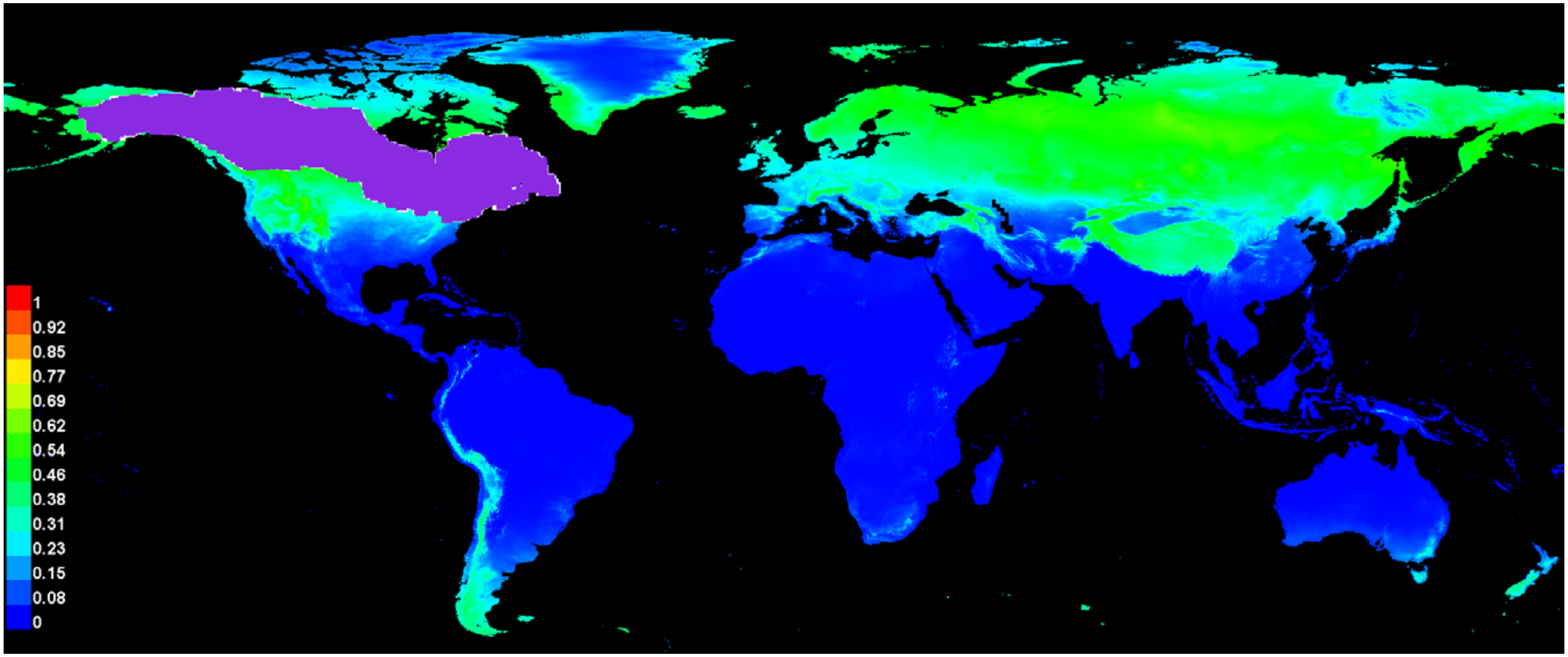

Figure 23b. MaxEnt predictions of suitable geographic ranges for black spruce.

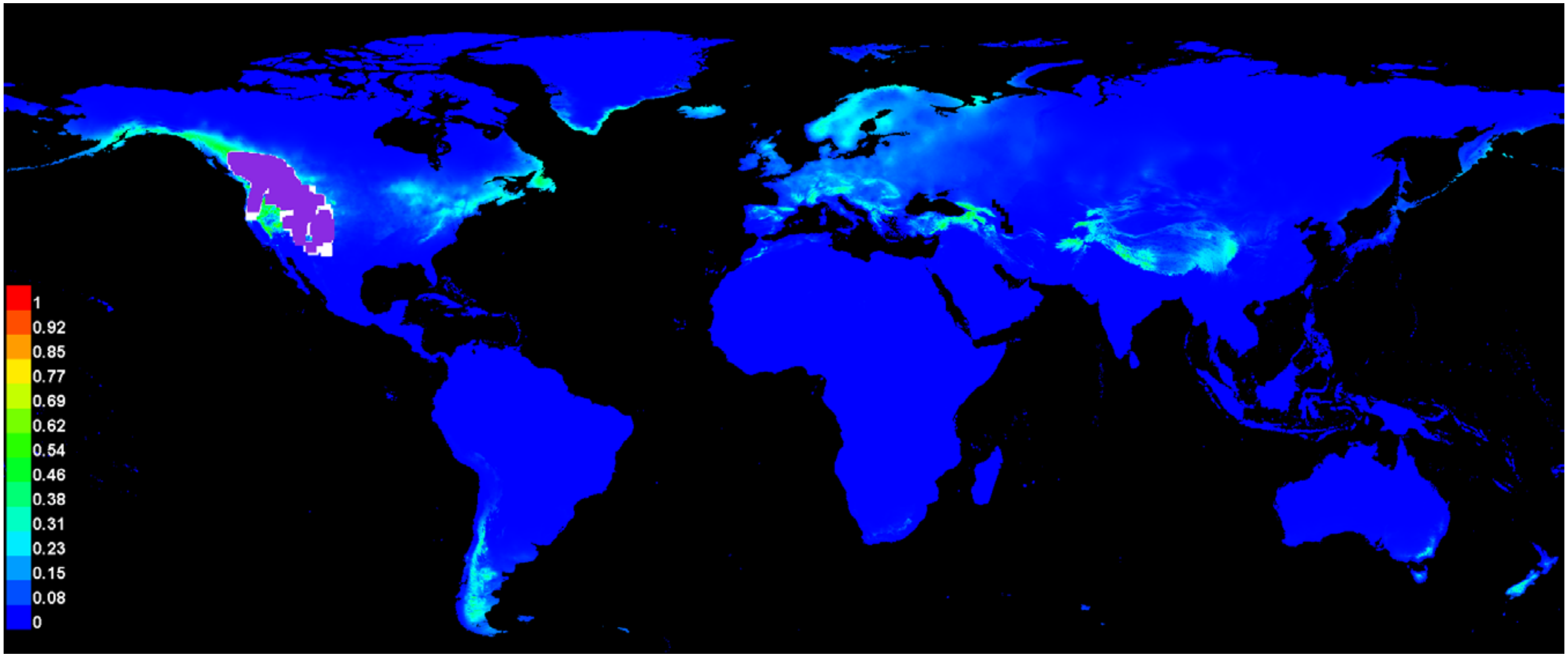

Figure 23c. MaxEnt predictions of suitable geographic ranges for Engelmann spruce

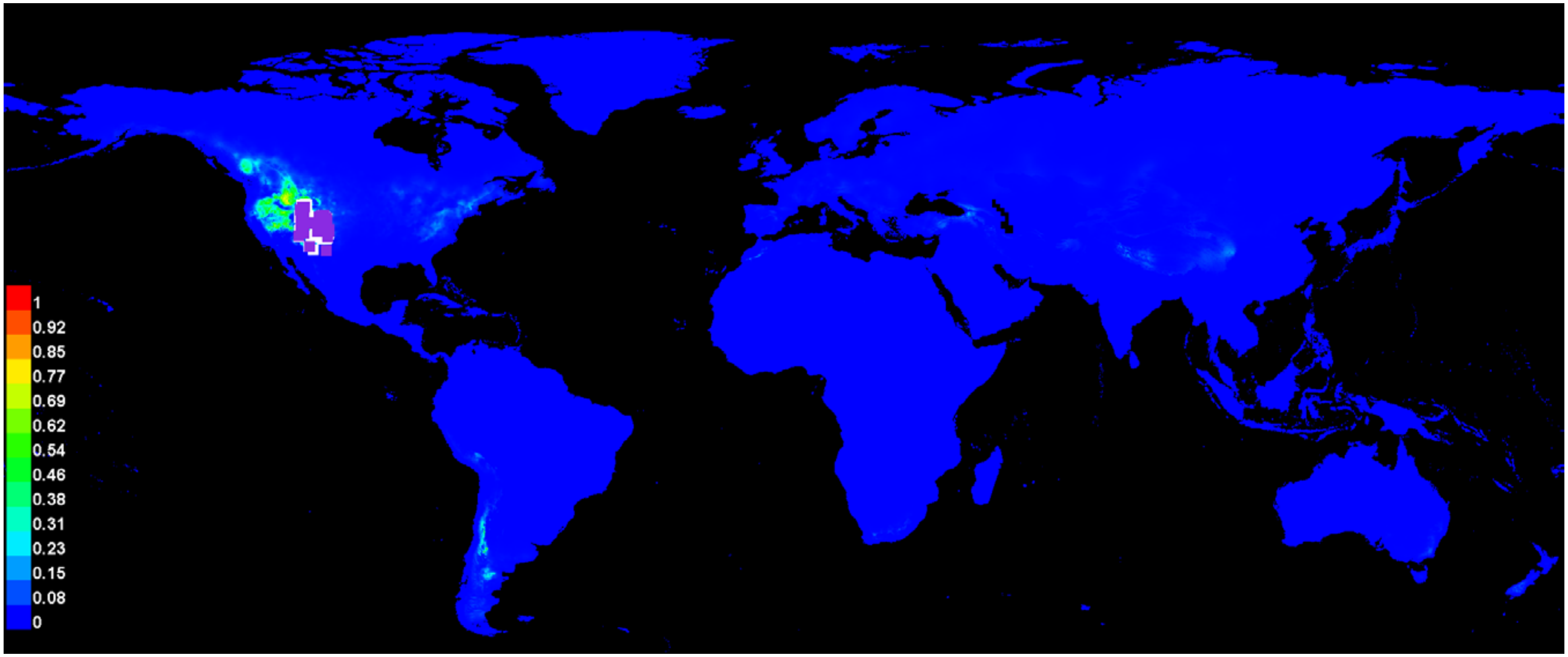

Figure 23d. MaxEnt predictions of suitable geographic ranges for blue spruce

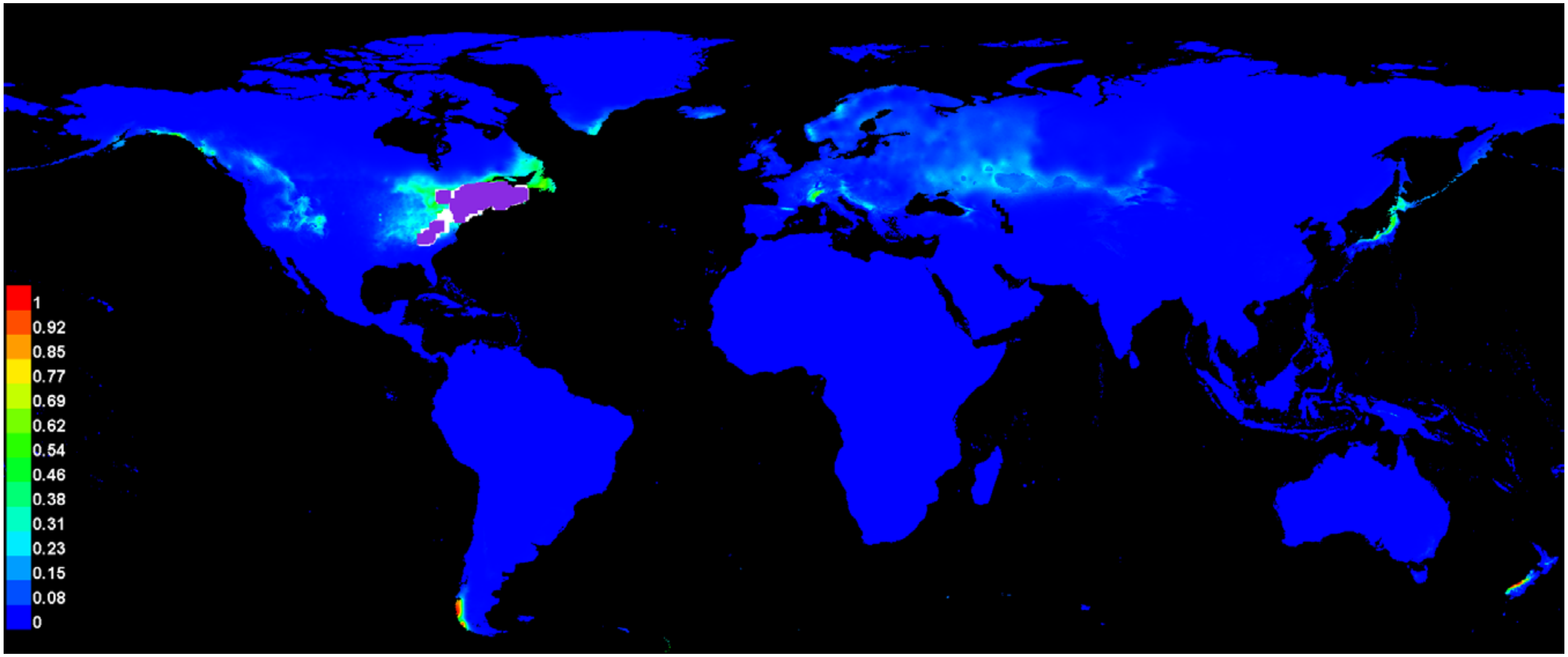

Figure 23e. MaxEnt predictions of suitable geographic ranges for red spruce

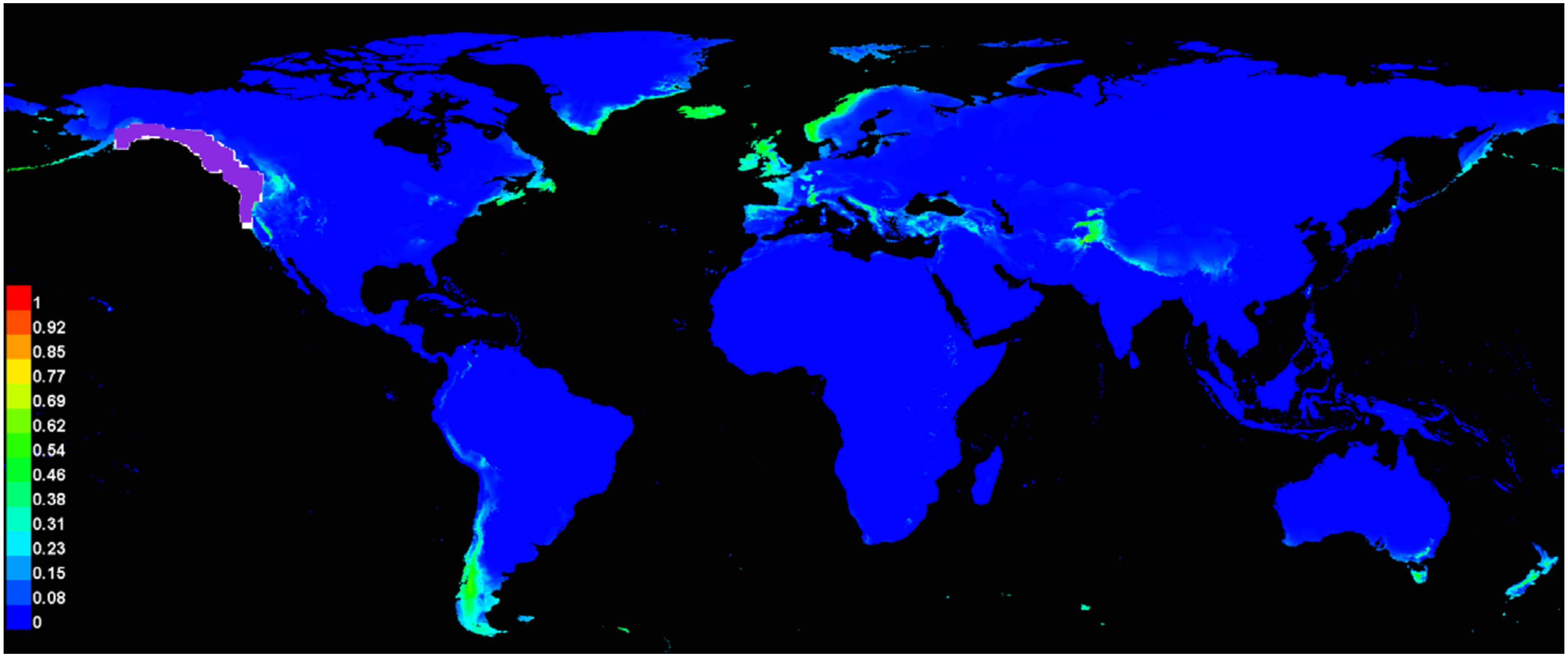

Figure 23f. MaxEnt predictions of suitable geographic ranges for Sitka spruce

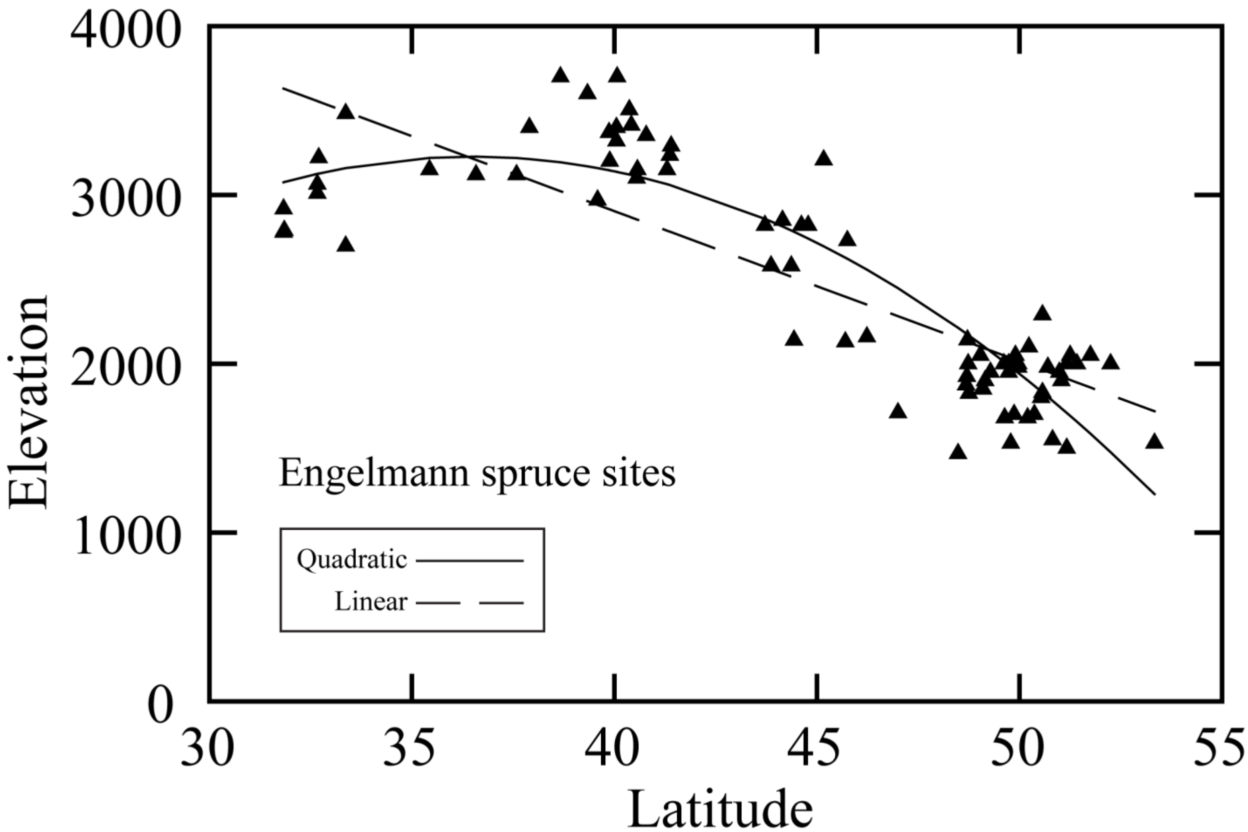

Figure 24. Elevation of Engelmann spruce sites by latitude.