

“Community Assembly Rules in Southern Appalachian Oak Forests”

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Abstract

Conservation efforts depend in part on adequate understanding of how ecological communities are assembled, and yet there is much about community assembly that is unknown. This study is an attempt to test whether oak subgenera follow a type of assembly rule known as niche partitioning. Niche partitioning is a process by which competition between more ecologically similar species selectively favors the co-dominance of ecologically less similar species. Two null models were constructed to predict the frequency of “co-dominance” in 9 oak species in Southern Appalachian forests if species were distributed randomly. The first null model found evidence that niche partitioning was taking place because there was a greater than expected frequency of co-dominance. This result could have been caused by niche partitioning at the local scale, or environmental differences at larger scales. The second null model failed to account for the occurrence of pure red and pure white oak stands in plots of high abundance. Environmental gradient analysis indicated that red oak was the dominant subgenus across all environmental factors. Conclusive evidence for niche partitioning was not found for the two subgenera of oaks, but the methods developed in this study could grant insight into co-occurrence patterns of other plant species that are known to overlap in distribution. This type of research has the potential to increase our understanding of how evolution is implicated in the macro ecological patterns in plant communities, knowledge that can be used to better manage and preserve forest communities.

Introduction:**Assembly rules:**

In order to effectively manage our plant communities, ecologists work to develop a good understanding of how these communities are assembled from the local species pool (Weiher and Keddy, 1999). The species pool is considered to be the group of potential members to a local assemblage of species. Wilson (1999) recognized two types of community assembly processes in ecological communities: environmental processes that form correlations between species due to their shared or opposite response to the physical environment, and assembly rule processes which result from biotic interactions between species. Both of these processes likely operate in a community such that species must pass through an environmental filter followed by a biotic filter. Ecologists interested in assembly rules generally focus on non-random patterns associated with species co-occurrence (Kelt and Brown, 1999; Gotelli and Graves, 1996). However, it is difficult to prove that various species interactions are responsible for these patterns; to overcome this obstacle many ecologists have attempted the usage of null models.

A simple definition of a null model is a model that generates the pattern that is expected to occur in a community in the absence of a particular mechanism. The expected communities can then be compared statistically to the real communities, and any differences can be related back to the missing mechanism and our theoretical understanding of community ecology (Gotelli and Graves, 1996). Studies interested in co-occurrence patterns of species within a community often create a null model that randomizes a species incidence (presence or absence) matrix using a particular algorithm (Gotelli and Graves, 1996; Peres-Neto, 2001). The species incidence matrix is a matrix in which each species is a row, and

each site is a column, and the cells within the matrix indicate presence (1) or absence (0). The algorithm shuffles the incident matrix in such a way as to maintain the original structure of the community only without the particular mechanism of interest. The structure of the community or the pattern of co-occurrence is quantified for the matrix using a test statistic that is calculated after each shuffling event (Stone and Roberts, 1990).

The importance of null model analysis was first made widely evident for ecologists by Conner and Simberloff (1979) who investigated Diamond's (1975) proposed assembly rules for avian communities in the tropics. Diamond asserted that interspecific competition between various species (the process) had resulted in distinct species assemblages (the pattern) on the Bismarck islands. However, Conner and Simberloff found that the same non-random patterns could be recreated by using a null model that statistically randomized the distribution of species across the islands. The literature has built upon these early attempts at constructing null models to test for non-random co-occurrence patterns through the usage of new test statistics and randomization algorithms (Stone and Roberts, 1990; Sanderson et. al., 1998; Gotelli and Entsminger, 2001).

Oak co-occurrence:

Niche partitioning refers to a process by which competition between more similar species selectively favors the co-occurrence of ecologically less similar species (i.e. similar species are more likely to competitively exclude each other). A few of the types of the differences between species that might facilitate co-occurrence include: differences in phenology, depth and placement of roots, response to microtopography, response along soil moisture gradients, regeneration requirements, nutrient requirements, and response to water depth (Aarsen, 1983). MacArthur and Levins (1967) established the basis for the concept of

niche partitioning when they investigated the theoretical limit of similarity of coexisting species. MacArthur (1972) also applied the concept of limited niche similarity between coexisting species to large geographic scales in which competitive exclusion between similar species should be visible in the present species compositions of islands and continents (Gotelli and Graves, 1996). The concept that competition structures a community's composition represented a dominant paradigm in ecology, and it was first seriously challenged by Conner and Simberloff (1979) in their critique of Diamond's paper using null models.

The purpose of my study was to develop null models to investigate a specific assembly rule, niche partitioning, that may determine the co-occurrence pattern of subgenera of oaks, white oak (*Leucobalanus*) and red oak (*Erythrobalanus*), in southern Appalachian forests. This is a difficult task because it requires that the effects of a biotic process that determines the co-occurrence pattern at the local site be differentiated from the effects of large-scale segregation of species along environmental gradients. The importance of environmental gradients has been well established by Whittaker (1956) in his analysis of the vegetation of the Great Smokey Mountains. Racine (1971) recognized the importance of these environmental gradients to the population dynamics of oak species in the southern Appalachians, and he also noted that oak species overlap in environmental tolerance; however, they do not always co-occur because of differences in competitive abilities. Currently it is recognized that ecological differences between red and white oaks exist; however, which of these differences are most important and if they can explain the patterns of co-occurrence of the different oak subgenera that are observed in the southern Appalachians is not fully known. Mohler (1990) considered the differences in the

regeneration niche of red and whites to be the most important in regards to co-existence of different oak species. There are two ways in which the subgenera differ with respect to their regeneration niche: 1) the timing of acorn fruiting, and 2) the behavior of seed predators and dispersers. White oak acorns germinate in fall and red oak acorns germinate in the spring (Mohler, 1990). Timing of mast years is highly correlated between species of the same subgenus rather than different subgenus. This temporal variability in seed release between the subgenera would favor more complexity in the overstory trees because competition for an opening in the canopy would be less intense between the groups. One subgenus would be more likely to take advantage of a gap opening at a given point in time (Grubb, 1977). White and red acorns differ in their lipid and tannin concentrations and because they germinate at different times of the year they are susceptible to different pests and predators (Bourdeau, 1954). Fluctuations in pest populations have the potential to introduce fluctuation into the competitive balance between the two subgenera from one year to the next that could promote co-occurrence (Mohler, 1990).

It has also been cited that the general trends in populations of *Q. alba* and *Q. rubra* are linked to the difference in disturbance regime between pre- and post European settlement (Crow, 1988; Abrams et. al., 1995; Abrams, 2003). White oaks are generally considered more fire resistant than red oaks. The change in disturbance regimes and difference in resistance to fire may affect the co-occurrence patterns of oaks that overlap broadly in environmental tolerance.

I have two specific questions that I would like to address in this study: 1) do different subgenera of oaks co-occur more often than expected by null models as the most dominant species of oak in a plot regardless of their location on environmental gradients, and 2) do the

subgenera that differ widely in their environmental tolerances and how is this linked to the local site patterns that exist. A study conducted by Mohler (1990) addressed very similar questions with regard to co-occurrence pattern of the subgenera of oaks. He used a binomial null model to find evidence of niche partitioning, but he did not have access to environmental data. I used Mohler's binomial model as a basis for developing my own null models to answer my first hypothesized question. In addition, I have had access to an exceptionally large dataset that includes abiotic characteristics which allows me to examine my second question: how environment is effecting niche partitioning.

Methods:

For this study I used plots gathered by the Carolina Vegetation Survey (archived by the North Carolina Botanical Garden, Chapel Hill, NC, USA). The focus was narrowed to only data pertaining to montane upland forest of the southern Appalachians at a spatial scale of 1000 m². Plots were selected using the criteria that the plots must have a total oak cover value equal to or greater than 25%. This was done because I wanted to focus my study on only plots in which oak was a dominant or subdominant part of the vegetation. The plots selected contained some combination of nine species: *Quercus alba*, *montana*, *stellata*, *muelenbergii*, *rubra*, *coccinea*, *falcata*, *marilandica*, and *velutina*. The statistical analysis of the data was broken up into two phases. In the first phase I used Mohler's (1990) null model as a basis to build my own null models designed to find evidence of niche partitioning in oaks. The second phase was used to investigate patterns in environmental distributions of the various oak species.

Phase 1: Null Model Approach

I created two null models that were both based on the binomial distribution. A binomial distribution is the expected probability distribution in a random sample of "events" that can only have one of two outcomes (Sokal and Rohlf, 1995). In my usage of the binomial distribution each "event" could be thought of as the occurrence in a plot of a white oak or red oak. There are two main assumptions that are key to understanding why the binomial model is a good choice as a null model for testing the co-occurrence pattern of oaks:

- 1) the probability of an "event" in each trial (p) is constant, and
- 2) the trials are independent of each other.

I wanted to test if oaks were assembling randomly regardless of subgenus. So in each independent plot I predict the occurrence of co-dominance based solely on the fixed overall probability of occurrence of a given subgenera (p). This prediction was then compared to the observed data. Sokal and Rolf (1995) note in models of biological phenomena we often have no preconceived notion of the magnitude of p , and therefore it is common to calculate p from the observed value. If this is preformed we can test whether the samples are random and if the events (white oak or red oak) are independent. Mohler (1990) theorized that if the oaks were randomly distributed across the landscape that there should be equal proportions of same and different subgenera species combinations. Therefore he used the preconceived value of $p = 0.5$ as the null hypothesis of a binomial proportion which he tested against his observed frequency. I did not use a preconceived value for p and I instead calculated it from the observed data for the two models that I tested. This effectively enabled me to test if the occurrence of red and white oaks is independent and random.

For the first null model I grouped all plots based on oak diversity, and calculated the expected probability that the two most dominant species in a plot would be co-dominant (from different subgenera). The value of p was calculated individually for each diversity group. The expected frequency of co-dominance was compared to the observed frequency of co-dominance and a significance level was calculated for each diversity group. The significance level described the probability that the expected frequency of co-dominance would be greater then or equal to the expected frequency of co-dominance. These separate significance levels were weighted relative to the number of plots occurring in each diversity group and were summed to get a overall test significance level. If the overall test significance level was less than 0.05 then I would conclude that red and white oaks were

occurring together significantly more often than expected by chance which could be thought of as evidence for niche partitioning. The dominance of a species was quantified by counting the number of stems of a species in the entire 1000 m² plot with diameter at breast height (dbh) ≥ 10 cm. This dbh criteria was used because I only wanted to consider adult oak species that had fully established themselves on a plot, and were more likely to show evidence of niche partitioning.

This null model had two observed parameters: plot diversity and proportion of red oaks at a given plot diversity (I could have used the proportion of white oaks just as easily). The following is an explanatory example to demonstrate my method for testing the null model for plots with a diversity of two. The first step is to group the plots by oak diversity, and to calculate the proportion of red oaks and white oaks within those diversity groups.

Thus,

$$p = \frac{\text{number of red occurrences in a plot diversity of 2}}{\text{total number of trees in plot diversity of 2}}$$

$$q = 1-p$$

where,

$$p = \text{proportion of red oaks}$$

$$q = \text{proportion of white oaks}$$

The next step was to calculate the probability of co-occurrence by a red and a white oak given the plot diversity and the proportion that each subgenus occurs at (*p and q*).

Possible species combinations in a two species plot

Species	Binomial probability of occurrence
rr	p^2
rw	pq
wr	pq
ww	q^2

$$\left. \begin{array}{l} \\ \\ \end{array} \right\} pq + pq = 2pq = \hat{p}$$

\hat{p} = probability of co-dominance

Table 1. The calculated probability of co-dominance is simply the sum of the probabilities that a species combination has red and white species as the two most dominant species.

Once the \hat{p} value for a diversity group was calculated it was used to generate the expected frequency of co-occurrence using a binomial model.

Thus,

$$X_i \sim \text{Binomial}(N_i, \hat{p}_i)$$

where,

$$\begin{aligned} N_i &= \text{number of plots with } (i) \text{ species} \\ X_i &= \text{expected frequency of co-dominance} \end{aligned}$$

Finally the probability that the expected frequency of co-dominance was larger than or equal to the observed frequency of co-dominance was calculated. This probability was weighted with respect to the number of plots in that diversity group, and then these weighted probabilities were summed to calculate the overall test significance level.

Thus,

$$pvalue = \sum_{i=2}^m \frac{N_i}{N_T} P(X_i \geq x_i),$$

where,

$$\begin{aligned} N_T &= \text{total number of plots with at least two species} \\ N_i &= \text{number of plots with } (i) \text{ species} \\ m &= \text{maximum number of species in a plot} \end{aligned}$$

X_i = expected frequency of co-dominance
 x_i = observed frequency of co-dominance

The second null model that I designed was also based on a binomial distribution, and it was used to model the frequency of co-dominance and pure dominance for each abundance group. The abundance group was simply all the plots that had the same number of oak stems. The fit of the model to the observed data was assessed using a Pearson chi-square test. If the model fit the observed data I would conclude that the co-occurrence pattern was random and that there is no evidence for niche partitioning between the subgenera. If the model does not fit then I would calculate weighted residual values to assess where the model was misestimating the observed values, and I would speculate as to why that might have occurred. This model was based on two observed values: the oak stem density of a plot and the proportion of red oaks (this could have just as easily been proportion of white oaks). Three important characteristics differentiate this model from the first: 1) that data on all the species in a plot were incorporated into the model and not just data on the two most dominant species 2) the plots were grouped based on oak stem density and not oak diversity, and 3) an overall proportion of red oaks was calculated for all the plots instead of calculating a separate proportion of red oaks each diversity or abundance group. Once again, the goal of this null model was to test if the frequency of plots with one and two subgenera could be modeled simply by using observed oak abundance and proportion of red oak trees.

The first step that was taken in this modeling process was to calculate the proportion of red and white oaks.

Thus:

$$p = \frac{\text{number of red oak stem}}{\text{total number of oak stems}}$$

total number of oak stems

$$q = 1-p$$

where,

p = probability of a red oak

q = probability of a white oak

Once the proportions of the subgenera were calculated the probabilities that a plot of oak stem density (i) would contain species from different subgenera $P(C_i)$ and from the same subgenera $P(P_i)$ were calculated using the binomial model.

Thus:

$$P(C_i) = 1 - (p^i + q^i), \text{ and}$$

$$P(P_i) = (p^i + q^i)$$

where:

$P(C_i)$ = probability that a plot of oak stem density (i) will be co-dominant

$P(P_i)$ = probability that a plot of oak stem density (i) will be pure dominant

These calculated probabilities were multiplied by the number of plots with oak stem density (i) to calculate the expected frequency of co-dominance and the expected frequency of pure dominance.

Thus:

$$E_{ci} = N_i * P(C_i) \text{ and } E_{pi} = N_i * P(P_i)$$

where:

E_{ci} = expected frequency of co-dominant plots in a plot size (i)

E_{pi} = expected frequency of pure dominant plots in a plot size (i)

To aid in understanding the modeling process up to this point, Table 2 and 3 were created to lay out the models components and demonstrate how each component of the model relates.

# oaks per plot (i)	# of plots with (i) oaks	Prob. of co-dom.	Exp. co-dom.	Obs. co-dom.
1	N_1	$P(C_1) = 1 - (p + q)$	$E_{C_1} = N_1 * P(C_1)$	0
2	N_2	$P(C_2) = 1 - (p^2 + q^2)$	$E_{C_2} = N_2 * P(C_2)$	2
3	N_3	$P(C_3) = 1 - (p^3 + q^3)$	$E_{C_3} = N_3 * P(C_3)$	5
...
i	N_i	$P(C_i) = 1 - (p^i + q^i)$	$E_{C_i} = N_i * P(C_i)$	O_{C_i}

Table 2. This table demonstrates how the expected frequency of co-dominance was calculated (Prob. = probability, Exp. = expected, Obs. = observed).

# trees per plot (i)	# plots with (i) oaks	Prob. of pure dom.	Exp. pure dom.	Obs. Pure dom.
1	N_1	$P(P_1) = p + q$	$E_{P_1} = N_1 * P(P_1)$	34
2	N_2	$P(P_2) = p^2 + q^2$	$E_{P_2} = N_2 * P(P_2)$	16
3	N_3	$P(P_3) = p^3 + q^3$	$E_{P_3} = N_3 * P(P_3)$	21
...
i	N_i	$P(P_i) = p^i + q^i$	$E_{P_i} = N_i * P(P_i)$	O_{P_i}

Table 3. This table demonstrates how the expected frequency of pure dominance was calculated (Prob. = probability, Exp. = expected, Obs. = observed).

Once the expected frequency of co-dominance and the expected frequency of pure dominance was calculated it was compared to the actual observed values using a Pearson chi-square goodness of fit test. Note that although plots with an oak stem density of one are included in Table 2 and 3, they were not included in the Pearson chi-square test. This was done because a plot with a stem density of one will always be a pure plot and the model has nothing to predict in this case. Also before the test was implemented the expected frequencies were binned so that each bin contained a value ≥ 5 to meet the standard

requirement for chi-square tests. The observed frequencies were binned in the same manner as the expected frequencies.

The actual chi-square value was calculated separately for the expectations of the frequency of co-dominance and the expectations for the frequency of pure dominance. In each case the observed frequency was subtracted from the expected frequency. This difference was squared and divided by the expected frequency. The resulting quotient was summed with the other calculated quotients for each oak density bin. The two chi-square values were then summed to calculate the total chi-square value for the model.

Thus:

$$X_C^2 = \sum_{i=1}^m \frac{(O_{Ci} - E_{Ci})^2}{E_{Ci}}$$

$$X_P^2 = \sum_{i=1}^m \frac{(O_{Pi} - E_{Pi})^2}{E_{Pi}}$$

$$X_T^2 = X_C^2 + X_P^2$$

where:

m = the number of bins used for the goodness of fit test

X_C^2 = the chi-square value for the co-dominance prediction of the null model

X_P^2 = the chi-square value for the pure dominance prediction of the null model

X_T^2 = the chi-square value for the entire test.

Each calculated chi-square value has a certain number of degrees of freedom associated with it. The degrees of freedom are equal to the number of bins used in the test minus one because of the estimate of p used in the model. A significance value was then calculated using the chi-square value and the degrees of freedom.

Phase 2: Large scale environmental gradients

The goal of this phase of the investigation was to determine if the oak subgenera differentiate along environmental gradients, and whether or not these patterns are shaping the results that were generated by the null model. Environmental data on elevation, soil calcium, soil manganese, and a calculated estimate of potential annual direct solar radiation were used in this analysis. The soil mineral data was log transformed because these variables have positively skewed distributions (Quinn and Keough, 2002). An algorithm was used to calculate the potential annual solar radiation using three observed variables: latitude, slope, and aspect (McCune and Keon, 2002).

I calculated plot frequency of species and subgenera per 1000 m² plot for sets of 10 contiguous plots along an environmental gradient. Ten plots were set at regular intervals along the plot sequence so as to assign equal numbers of plots to each gradient segment. The plots were binned in this way because of the non-uniform distribution of plot frequency along each observed environmental gradient. Lowess lines were fit to the observed scatter plots to indicate what general trends the species and subgenera were showing. A lowess line is a smoothed line that is created by estimating ordinary least squares regression lines for a small range of x-values many times until the entire range of x-values has been covered. (Quinn and Keough, 2002).

Results:

Phase 1:

The result from the first null model indicated that a probability of 0.01 existed that the expected frequency of co-dominance was greater than or equal to the observed frequency of co-dominance. This indicates that the two most dominant oaks in a plot were from different subgenera a significant amount of time which is similar to what Mohler found in his study. Table 4 shows the significance levels for the binomial models using Mohler's 0.5:0.5 null hypothesis and using my observed proportions for each diversity group as the null hypothesis.

	Binomial test 0.5 as null	Binomial test with observed proportions as null
p-value	$<10^{-40}$	0.01

Table 4. Both models yielded a significant result but the model that incorporated group diversity calculated proportions of red oaks generated a more realistic result for this dataset.

The proportion of red oak out of the total population was 0.93 in my entire dataset which explains why Mohler's null hypothesis of 0.5:0.5 was insufficient.

The results of the second null model indicated that it did not fit to the observed frequency of co-dominance and pure dominance, and therefore I cannot conclude the co-occurrence pattern is necessarily random. After conducting a Pearson chi-square goodness of fit test, I rejected the null model ($X^2 = 13006$, $df = 11$, $p\text{-value} < 10^{-30}$). This is an extremely large chi-square value and is evidence of a very poor fit. A plot of the weighted residuals was generated in order to observe where the largest difference between the modeled frequencies and the observed frequencies was occurring.

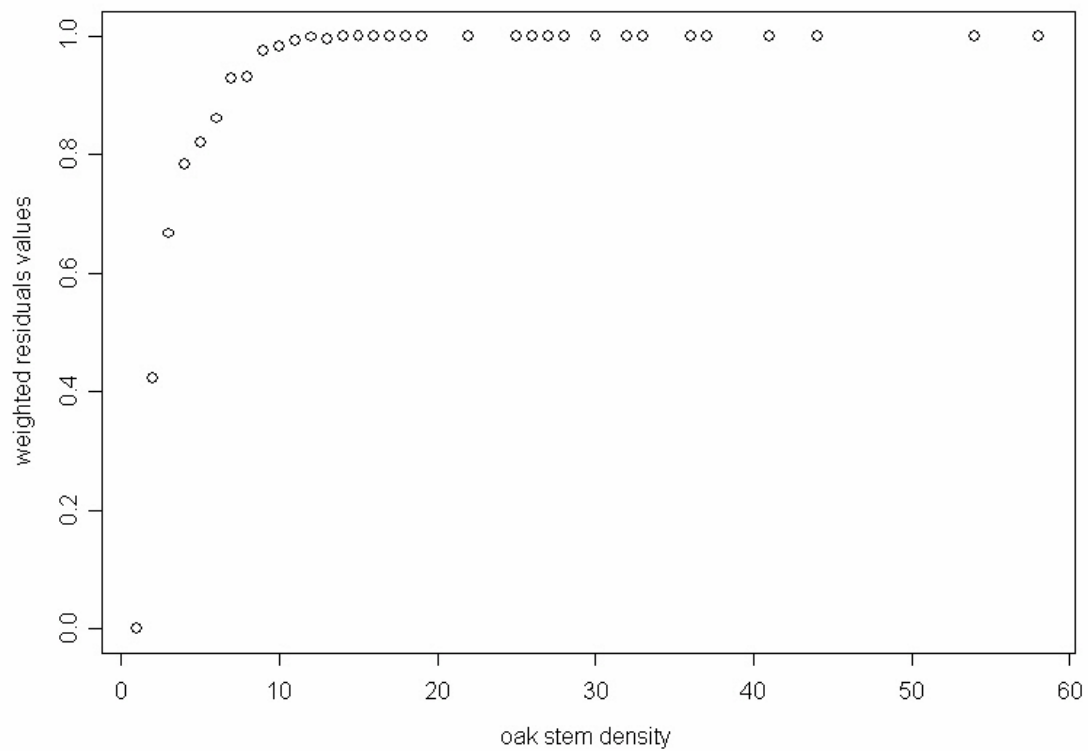


Fig 1. The weighted residual values for the expected and observed frequencies of pure plots.

As Fig. 1 shows, at larger plot sizes the null model poorly estimates the observed frequency of pure dominance plots. This is a logical result because the model expects the probability of encountering a pure plot to tail off rapidly as plot size is increased based simply on probabilities of occurrence, however, this not does not appear to always be true in nature.

Phase 2:

The results of the gradient analysis indicate that across the entire range of each environmental variable that red oaks are more dominant than white oaks (Fig 2,4,6, and 8). This dominance is driven mostly by the high frequency of two red oak species, *Q. rubra* and *Q. coccinea*. Plots of the six most abundant species indicate that *Q. rubra* is dominant across the majority of every environmental variable (Fig 3,5,8, and 9). Along the elevational gradient it appears that the red oak subgenus is especially dominant at high elevations, but this signal is driven completely by *Q. rubra* which occurs in almost pure stands above 1200 m (Fig 2 and 3) . White and red oak seem equally well adapted to low calcium sites, but red oak also does well in high calcium sites where as white oaks decrease in frequency (Fig 4 and 5). Here again this signal seems completely driven by a high frequency of *Q. rubra* at high calcium sites. Oak distributional dominance does not seem dependent on potential annual solar irradiance (Fig 6 and 7) or soil manganese (Fig 8 and 9) because total frequency per 10 plot segments does change appreciably across these environmental gradients.

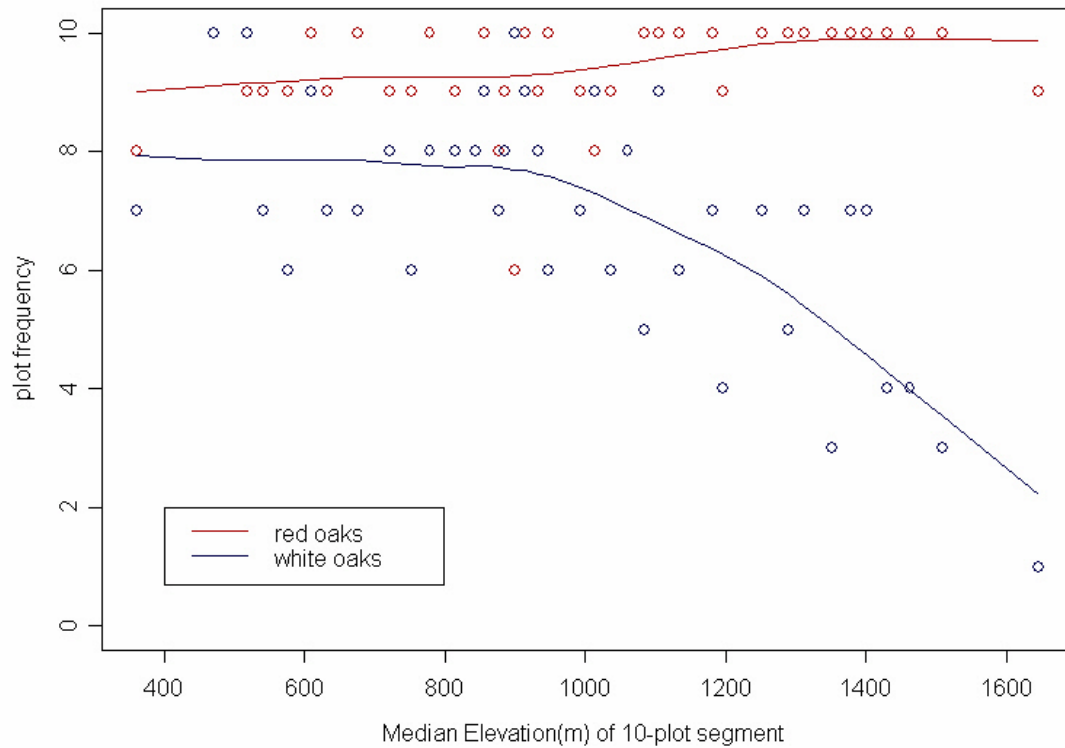


Fig 2. The distribution of the two subgenera along an elevational gradient. Lowess lines have been fit to the scatter plot in order to show a smoothed trend.

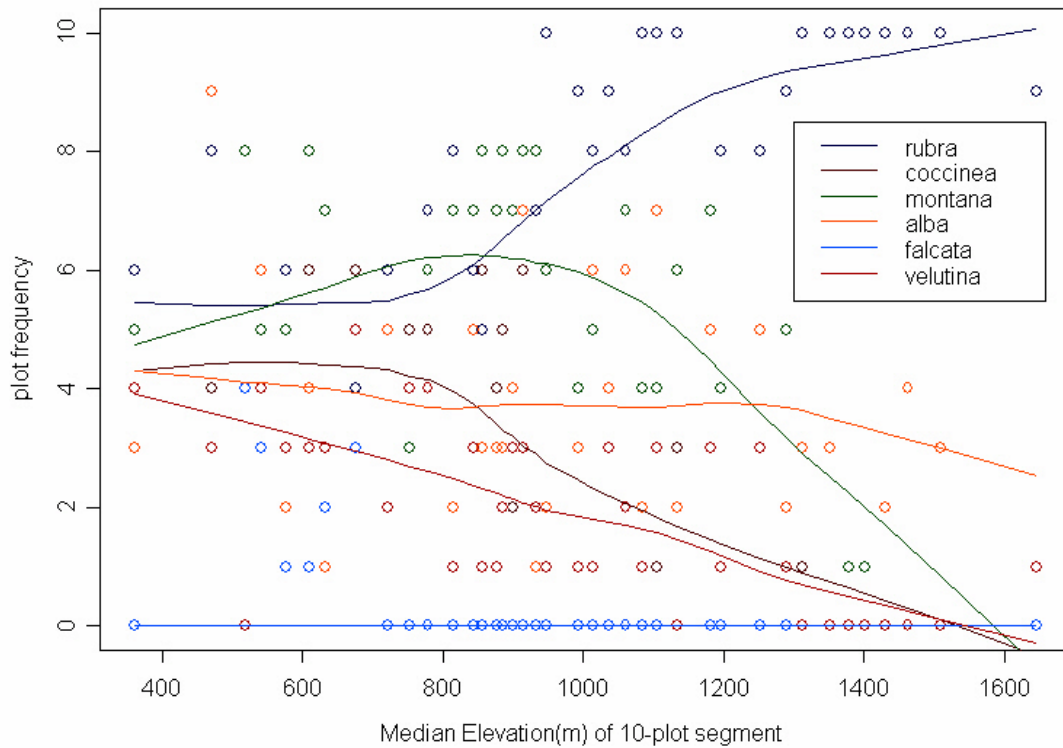


Fig 3. The distribution of the six most abundant species along an elevational gradient. Note that *Q. rubra* is the most dominant species across most of the gradient

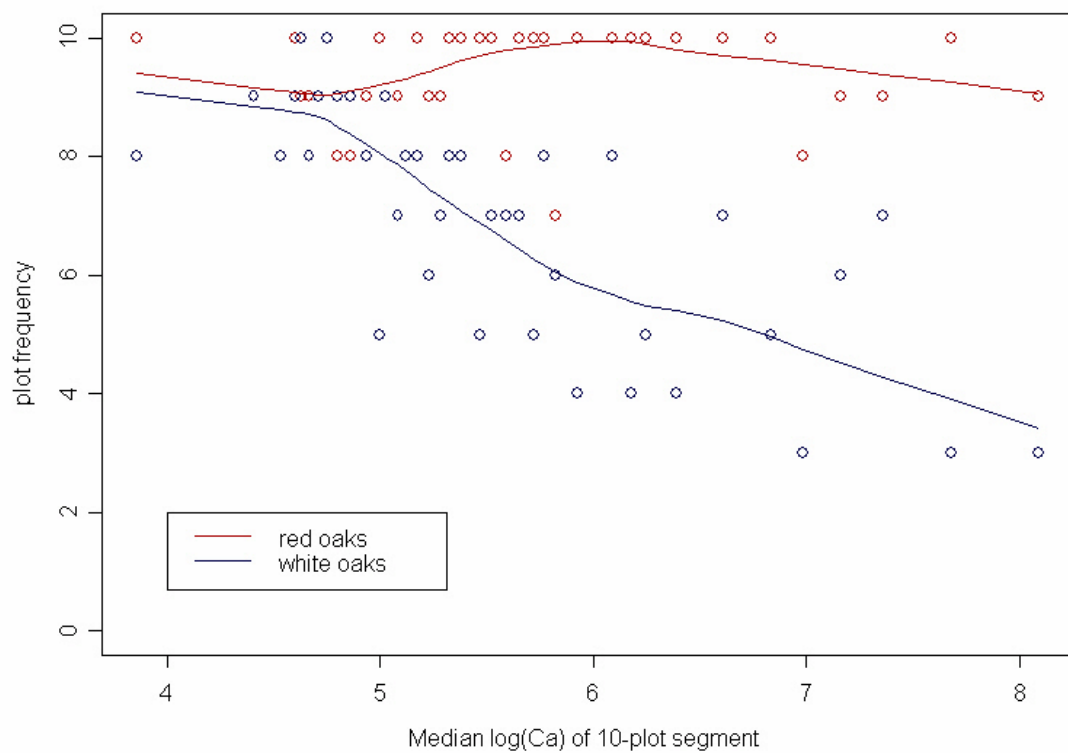


Fig 4. The distribution of the two subgenera along a log calcium gradient.

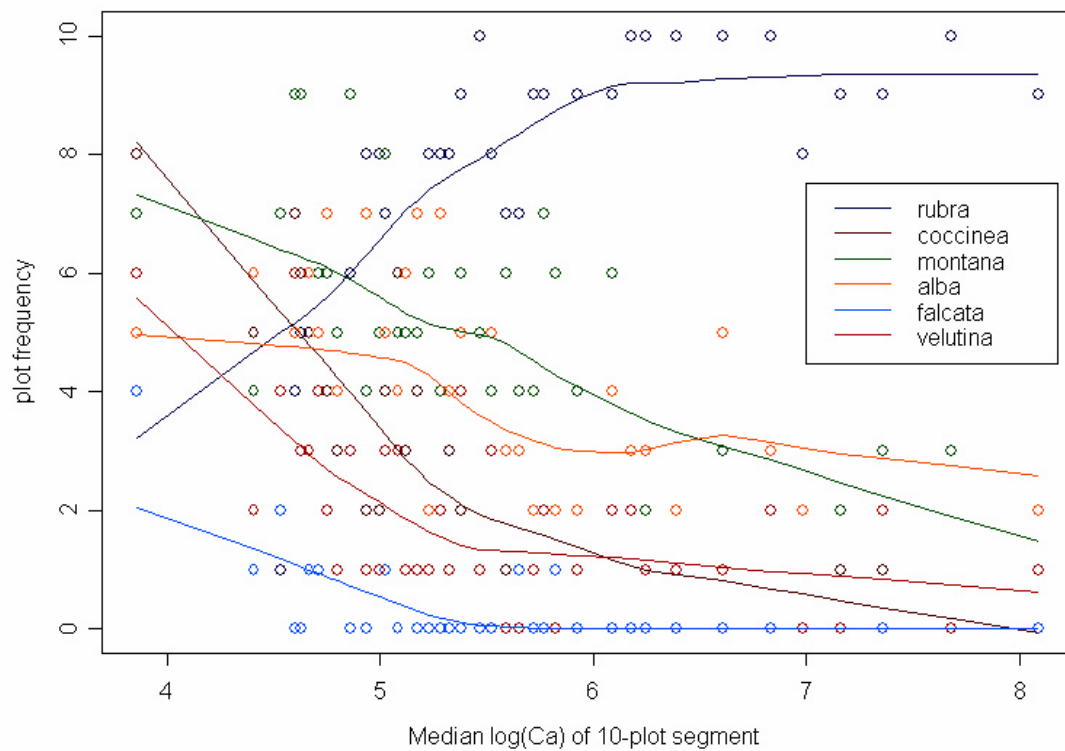


Fig 5. The distribution of the six most abundant species along a log calcium gradient.

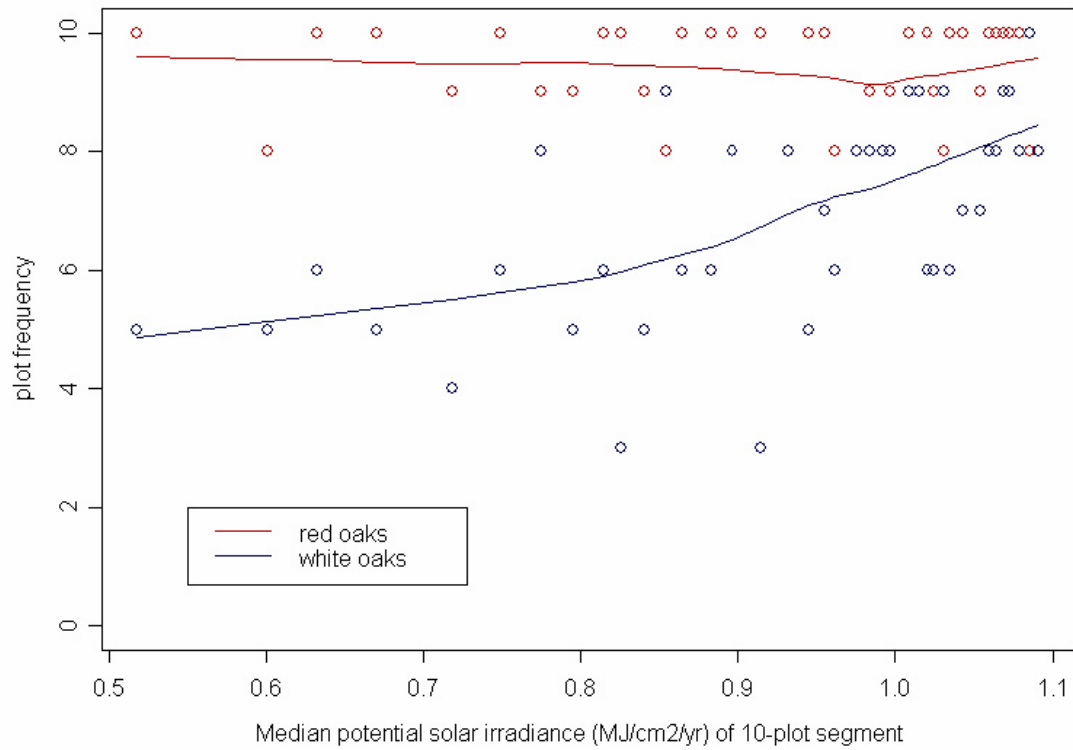


Fig 6. The distribution of the two subgenera along a potential annual solar irradiance gradient.

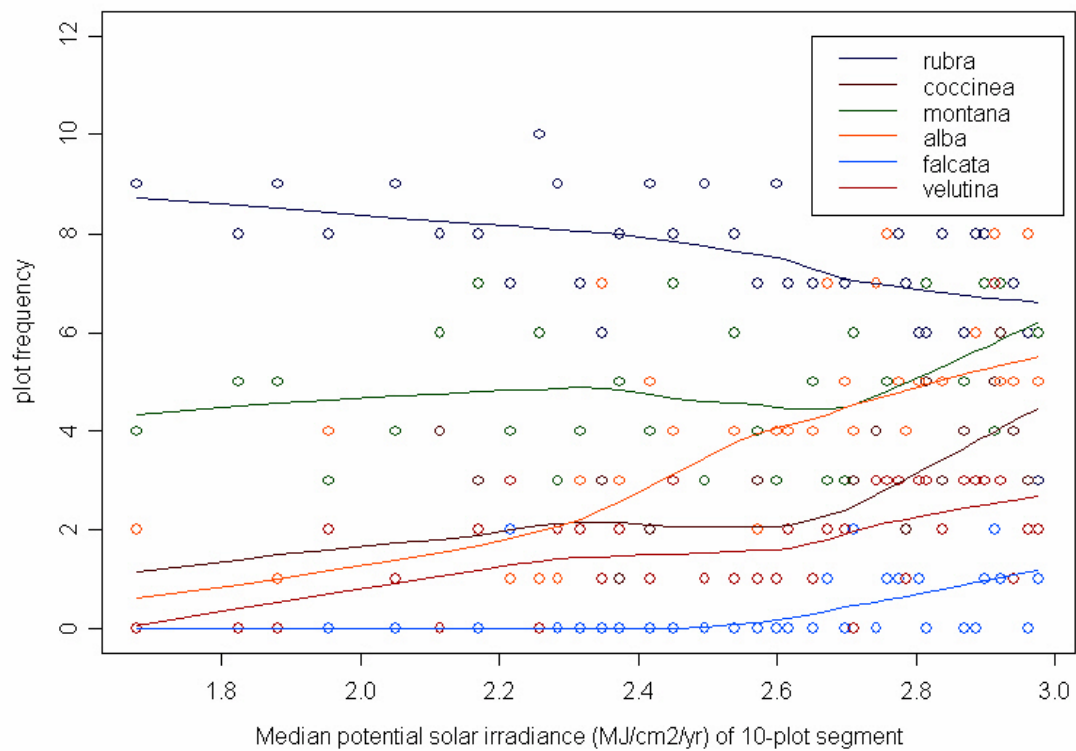


Fig 7. The distribution of the six most abundant species along a potential solar irradiance gradient.

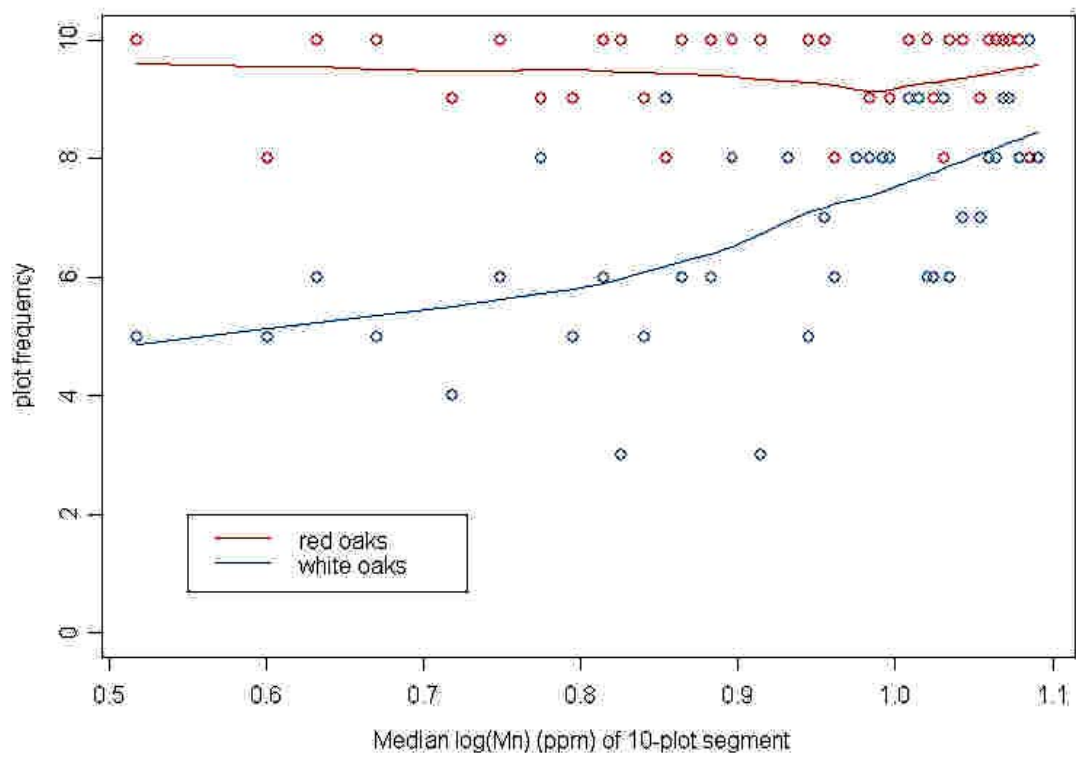


Fig 8. The distribution of the two subgenera along a log manganese gradient.

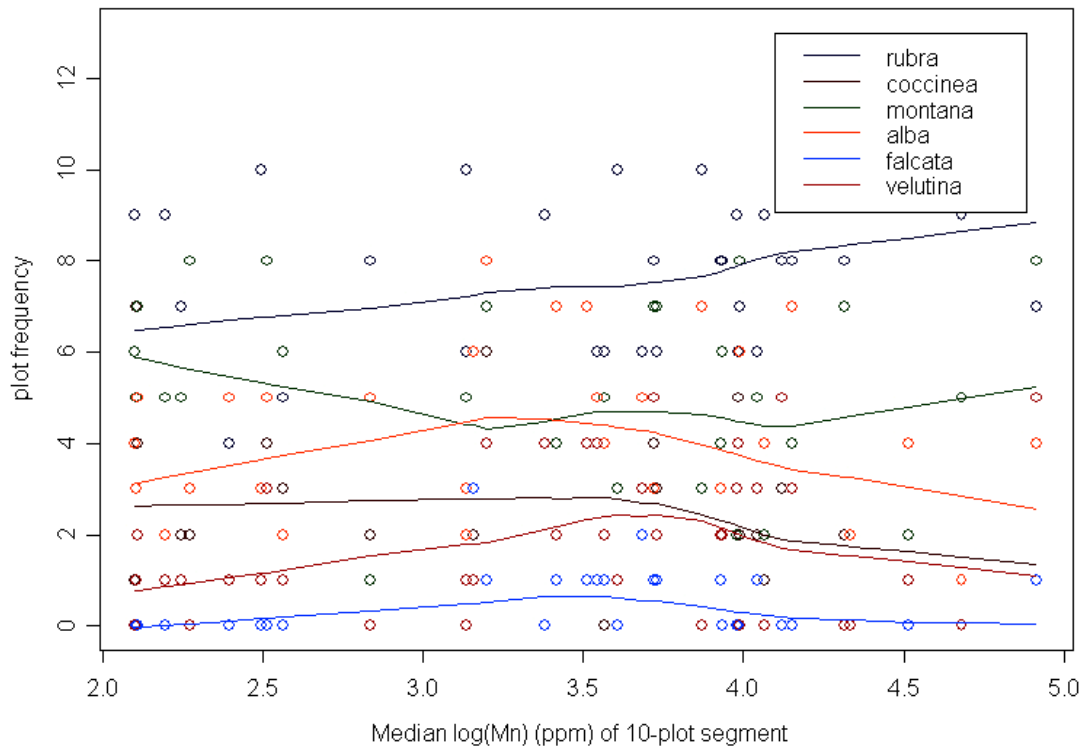


Fig 9. The distribution of the six most abundant species along a log manganese gradient.

Discussion:

It is difficult to conclude with any certainty whether or not niche partitioning between white and red oaks exists. The null model analysis indicates that at the local site the two most dominant species in a plot tend to be from different subgenera a significant amount of the time. This occurs despite the fact that red oaks have a larger distribution and tend to be more abundant than white oaks. The environmental analysis indicates that along the environmental gradients red oak is always the dominant subgenus, which is evidence that the oaks are not demonstrating large-scale “differentiation” with respect to their environmental tolerances.

The finding that the two most dominant species in a plot tend to be from different subgenera is consistent with what Racine (1971) hypothesized and Mohler (1990) concluded to be true. The second null model in which the plots were grouped according to oak stem density did not fit the observed frequency of co-dominance and pure dominance because it under predicted the frequency of pure plots of red oak that occurred at high stem density. This null model could be improved if plots were grouped based on spatial proximity rather than by equal oak abundance. Without a spatial component the null model is assuming that plots with the same oak abundance should display a similar frequency of co-dominance and pure-dominance; however, it is more likely that plots that are spatially more proximate to each other are more similar in composition. The pure subgenus plots may be all clustered together or near other plots with high proportions of that same subgenus, therefore, spatial information could make the prediction of these pure plots more accurate.

The fact that red oaks were dominant over the entire range of each environmental gradient was not expected. Whittaker (1969) found that along an elevational gradient in the

Santa Catalina Mountains that red and white oak species alternated in dominance.

Furthermore, Racine (1971) found that the three species of oak that he studied in the southern Appalachians: *Q. rubra*, *Q. prinus*, and *Q. coccinea* all differed strongly in terms of elevation, slope, aspect, and soil moisture. In my study it appeared as though only one species, *Q. rubra*, was driving the pattern of red oak dominance across the environmental gradients. Another direction to take this study would be to look at co-occurrence patterns between specific species pairs. Kernel density curves of the four most abundant oak species, that included two white oaks and two red oaks, indicated that co-dominant species pairs share similar elevational distributions (Fig 10). Kernel density curves can be used as a relative display of dominance at a particular place on an environmental gradient because the area under every curve is equal to one.

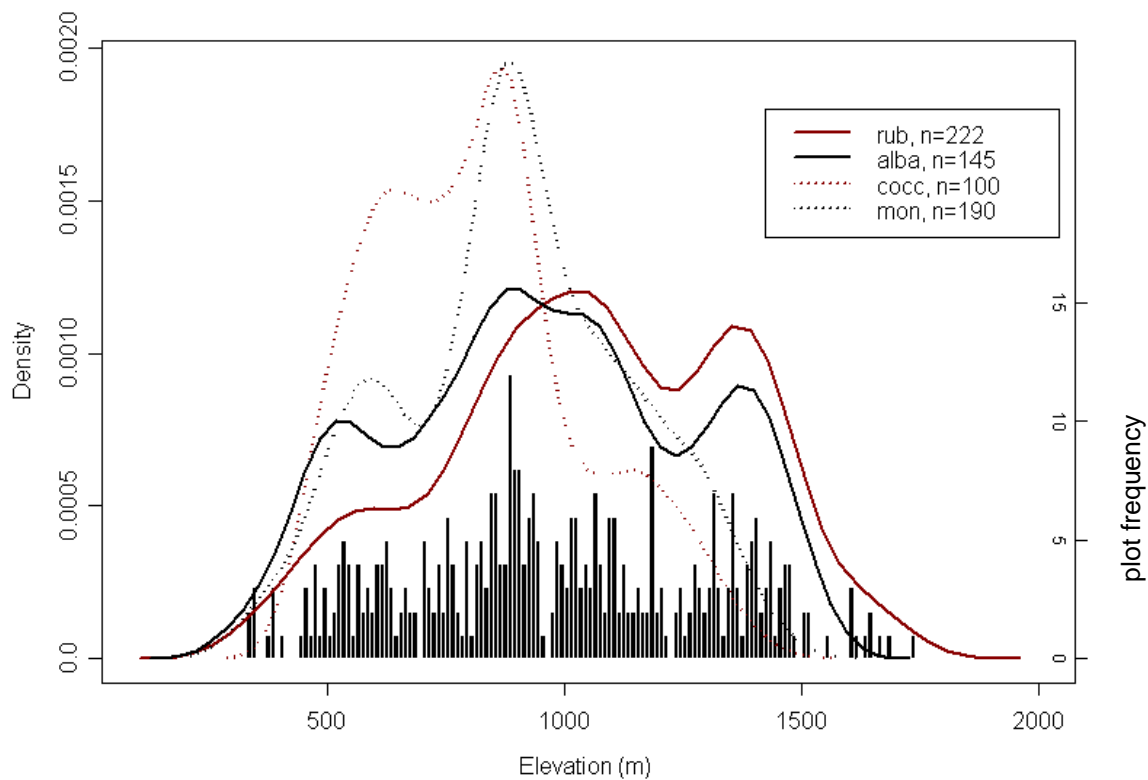


Fig 10. Kernel density curves of the four most abundant oak species. The histogram corresponds with the axis labeled plot frequency on the right. In the legend, the n-value is the species's total plot frequency. (species names: rub = rubra, cocc = coccinea, mon = montana)

A null model could be created that uses a product Bernoulli model to calculate the probability of a specific assembly of the nine oak species based on estimates of species proportion. The expected frequencies of an assemblage of a certain number of red and white oaks could be compared to observed data using a contingency table.

Further study will be needed to conclude whether or not oaks are showing a local co-occurrence pattern consistent with the concept of niche partitioning at the subgeneric level. Incorporating a spatial component into a null model and investigation of particular species assemblages may lead to further understanding of how these oak species are assembling at the local site. The analysis performed in this study could also be applied to other related species that are known to overlap in environmental distribution. This type of research has the potential to increase our understanding of large-scale macroecological processes which is important for effective management of these natural systems.

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