# AN APPRAISAL OF THE CLASSIC FOREST SUCCESSION PARADIGM WITH THE SHADE TOLERANCE INDEX

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**Abstract—** We revisit the classic theory of forest succession that relates shade tolerance and species replacement and assess its validity to understand patch-mosaic patterns of forested ecosystems of the USA. We introduce a macroscopic parameter called the "shade tolerance index" and compare it to the classic continuum index in southern Wisconsin forests. We exemplify shade tolerance driven succession in White Pine–Eastern Hemlock forests using computer simulations and analyzing approximated chronosequence data from the USDA FIA forest inventory. We describe this parameter across the last 50 years in the ecoregions of mainland USA, and demonstrate that it does not correlate with the usual macroscopic characteristics of stand age, biomass, basal area, and biodiversity measures. We characterize the dynamics of shade tolerance index using transition matrices and delimit geographical areas based on the relevance of shade tolerance to explain forest succession. We conclude that shade tolerance driven succession is linked to climatic variables and can be considered as a primary driving factor of forest dynamics mostly in central-north and northeastern areas in the USA. Overall, the shade tolerance index constitutes a new quantitative approach that can be used to understand and predict succession of forested ecosystems and biogeographic patterns.

## INTRODUCTION

The classic succession paradigm has been formulated based on observations of temperate forest patterns in Wisconsin, Michigan and New England (e.g., Cowles, 1911, Curtis and McIntosh, 1951) and in northern and Central Europe. In this type of forest the gap dynamics and shade tolerance driven succession are most noticeable and easy to observe. In a broad range of plant ecology literature, including in major textbooks, shade tolerance is considered as a primary factor underlying forest successional dynamics. North-American tree species can also independently be classified as early and late successional species based on their life history and physiological traits (Niinemets and Valladares, 2006). In the classic shade tolerance succession paradigm, species that are shade intolerant and tolerant are analogous to early and late successional species, respectively. The goal of our research is to develop a quantitative approach that can be used to appraise succession of forested ecosystems.

## METHODS

According to the classic paradigm, the proportion of shade tolerant versus intolerant trees is linked to the forest succession stage. We propose a quantitative parameter, the shade tolerance index, $\delta$ , to characterize stand successional stages as follows:

1. The shade tolerance of every tree species is quantified by a number from an interval $\rho$ in [0,1] where the range spans very intolerant to tolerant species. We will call the number $\rho$ the shade tolerance rank of a tree species. Specifically, we quantify the species as following: very intolerant = 0, intolerant = 0.25, intermediate = 0.5, tolerant = 0.75, and very tolerant = 1, according to [29, 36, 50].

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2. The shade tolerance index of the stand, δ, is defined as a weighted sum of the species abundance on their shade tolerance ranks defined as:

$$\delta = \sum_{j=1}^{k} \rho_j \alpha_j$$

In this formula $\alpha_j$ is a measure of relative abundance of a species *j* in the stand, is a shade tolerance rank of the species *j*, and the index *j* runs through all *k* tree species present in the stand. The relative abundance parameter $\alpha_j$ is estimated using the formula:

$$\alpha_j = \frac{\Omega_j}{\sum_{i=1}^{k} \Omega_i}$$

where $\Omega_j$ is a measure of abundance of the tree species in the stand. The shade tolerance index δ, is a number from [0, 1]. Specifically, δ is equal to 0 if all the trees in the stand are very shade intolerant and equal to 1 if all trees are shade tolerant.

## RESULTS

### Comparison with the forest continuum index

The classic forest succession paradigm was historically developed under a strong influence of the studies conducted in the Lake States (MI, WI and MN). In particular, Curtis and McIntosh (1951) have developed the classic continuum index to describe successional patterns in southern Wisconsin, in a collection of 95 forest stands. Using tree dominance data, these stands were positioned along the continuum line representing a forest succession sequence. According to this continuum index axis, Curtis and McIntosh (1951) assigned numerical values to the tree species within the stands called the climax adaptation numbers.

The original data used in this classic study is not available, and we reproduced a similar analysis using the FIA data. We have calculated the same statistical characteristics using a sample of 7017 FIA plots on mesic soils corresponding to the same geographic area as the original article. Our extension of the analysis of Curtis and McIntosh (1951) to a wider range of plots resulted in a much more diverse species composition. Despite this, our results are in good agreement with the original results (Figure 1 here vs Figures 5, 6, 7 in Curtis in McIntosh, 1951). Our results are also in agreement with the work of Rogers et al. (2008) who re-sampled the same sites as Curtis and McIntosh (1951) some 50 years later. In particular, we notice that the relative importance value of red oak (*Quercus rubra*), black oak (*Quercus velutina*) and secondarily white oak (*Quercus alba*) have decreased compared to sugar maple (*Acer saccharum*). Overall, our analysis shows that the successional pattern observed in Southern Wisconsin can be measured with the shade tolerance index. In addition, our study shows that these patterns did not change substantially over the several decades, and that the original plot sampling restrictions did not affect them substantially (Lienard et al., 2015a).

### Successional dynamics

The forest stand dynamics theory states that after a major disturbance stand development follows four consecutive stages: initiation, stem exclusion, understory reinitiation, and old-growth. The stand initiation stage marks the onset of succession by regeneration of open space from seed, sprouts and advance regeneration, and lasts until the canopy closes. Different disturbances leave various types of biological legacies providing highly variable initial species composition. In the second stage of stem exclusion, the light-driven competition becomes the major determinant of survival, resulting in a domination of fast-growing early successional species. The third stage, understory reinitiation, is characterized by the selective recruitment of understory trees in the canopy through gap-dynamics. The final stage, the old-growth corresponds to the climax state of the forest, where the species composition is stable.

We compared the results of computer simulations with the statistical analysis of White Pine – Eastern Hemlock forest stands from the FIA database,

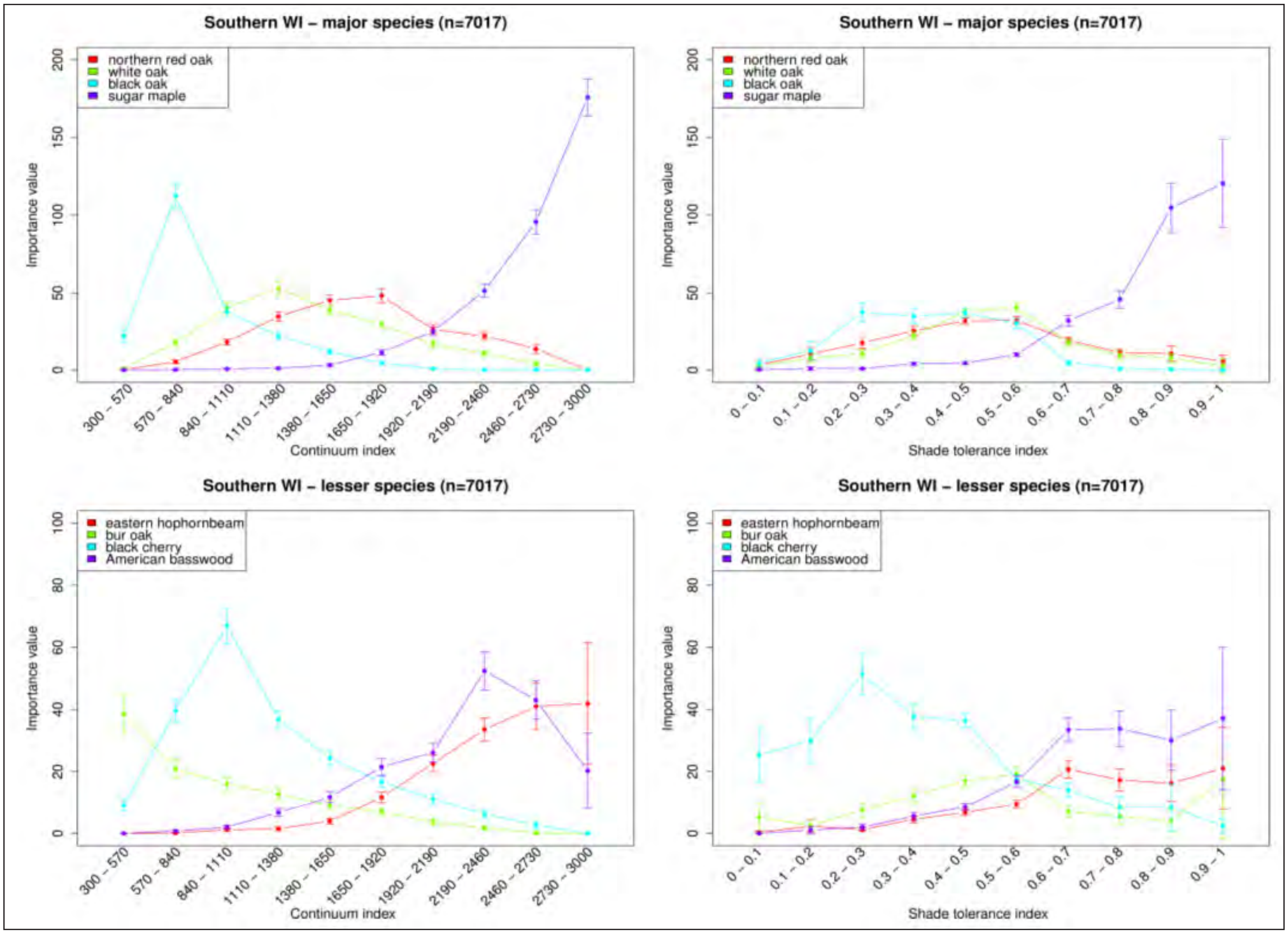


Figure 1—Comparison of the continuum index (left) and shade tolerance index (right) in southern Wisconsin. Similarly to the original study of Curtis and McIntosh (1951), the species were split in two groups: major (top) and lesser (bottom) species. Bars indicate the standard error of the mean.

using the shade tolerance index. We consider here approximate chronosequences, as the plots are ordinated relatively to the average age of trees, the time since last disturbance being not available (Strigul et al., 2012). The stands are observed throughout northeastern parts of the US. We isolated all plots in the database with more than 75% of cumulative basal area composed by these two species, resulting in a pool of 1375 plots. The comparison of these with computer simulations reveal striking qualitative similarities. Specifically, the initial distribution of seedling shade tolerance index decreases in the early years as the faster growing pioneering species start to dominate the canopy. The shade tolerance index then reaches high values as shade tolerant species eventually dominate the early successional species. These trends observed both in FIA database and in the computer simulations demonstrate the capacity of the shade tolerance index to model temporal dynamics of forest succession.

## Spatiotemporal patterns of US forests

We analyzed forest stand mosaic in the whole mainland US, using the FIA dataset. Our goal is to understand statistical relationships between forest characteristics and patch mosaic patterns related to shade tolerance. The analysis of correlation patterns indicates that the shade tolerance index displays weak correlations in the range of 0.12—0.26 with the other macroscopic characteristics studied:

biomass, basal area, Gini-Simpson diversity index, species richness and average age of trees (Figure 2). However, some of the other measures are correlated: biomass with basal area (confirming the previous study by Strigul et al., 2012), and Gini-Simpson diversity with species richness. Correlation matrices have been further calculated separately for all provinces in mainland USA and all inventory years with more than 500 plots recorded from 1968 to 2012. Correlations between different variables were virtually identical for all the inventory years and different ecoregions. This result is similar to what we obtained by analyzing another dataset for Eastern Canada forests (Lienard et al., 2015b). The fact that shade tolerance index has been repeatedly shown to be uncorrelated with other macroscopic characteristics demonstrates its usefulness in the statistical description of the mosaic of forest patches.

## DISCUSSION

The shade tolerance index introduced in this work is designed as a quantitative measure of forest succession according to the classic theory based on gap dynamics and replacement of shade intolerant by shade tolerant species. This study shows that this index can be utilized to understand the forest stand dynamics in ecoregions where the classic theory is validated, as it represents forest succession scale. In particular, our results demonstrate that this index is in agreement with the continuum index developed by Curtis and McIntosh (1951) as well as with gap model simulation (Strigul et al., 2008). Applications of the shade tolerance index include statistical analyses of the relationship between shade tolerance and soil moisture (Lienard and Strigul, 2015), data-intensive modeling of forested ecosystems (Lienard et al., 2015b), and the classification of U.S. ecoregions with respect to the temporal dynamics of their shade tolerance index (Lienard et al., 2015a).

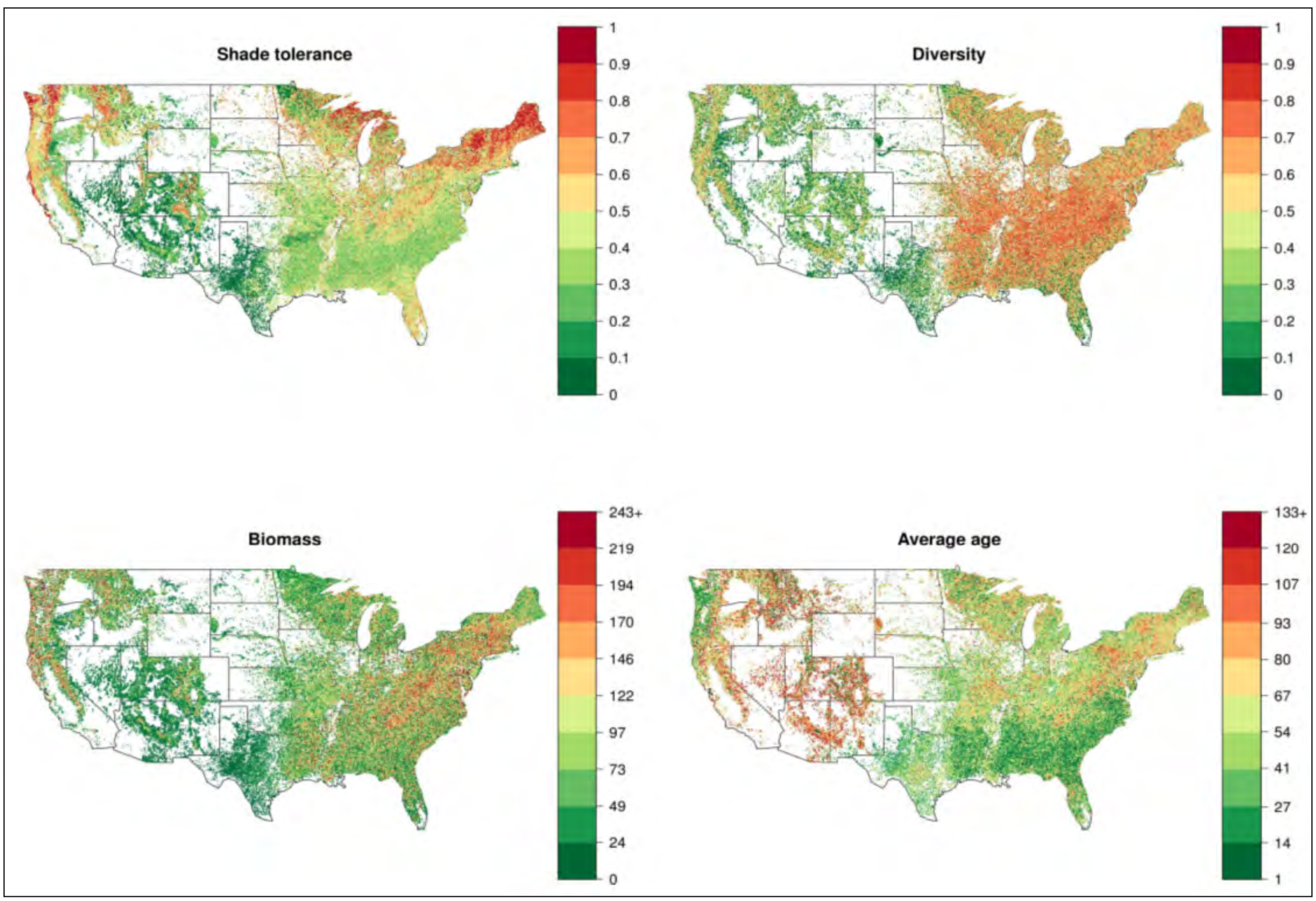


Figure 2—The stand-level characteristics of plots for all years demonstrate very heterogeneous forest types in the US, with no obvious common distribution pattern between indicators.

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