

Trees are rarely most abundant where they grow best

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Abstract

Aims

A common assumption in ecology is that where a species is found to be most abundant must correspond to the environmental context in which the species performs the best (i.e. optimal niche space). This assumption is central to common conservation and management tools such as habitat suitability assessment and species distribution modeling. I test this hypothesis.

Methods

I use the US Forest Inventory Assessment data for the abundance of trees across eastern North America. I use the FORAST tree-ring dataset for ontogenetic growth rate (tree-ring increment), a measure of niche performance and correlated with intrinsic rate of increase, r .

Important Findings

I find that across 15 species, there are significantly more negative correlations than expected by chance. This negative correlation between abundance and performance across space contradicts common assumptions but is consistent with an inclusive niche structuring of the community.

Keywords: tree rings • biogeography • inclusive niche • climate change

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INTRODUCTION

A central, although often implicit, assumption in ecology is that where a species is most common matches the conditions that are optimal for the population dynamics of the species. This intuitively appealing idea extends on the idea of Hutchinson (1957) that any point in space can be conceptualized as mapping to a point in n -dimensional physiological niche space, and so if a species is found in a location, that location must match to a point within the fundamental physiological niche of the species. Birch (1953) extended this by showing that, under laboratory conditions for *Tribolium* flour beetles, the intrinsic rate of population increase, r , and the equilibrium population size, N^* , were positively correlated across different physiological conditions. Under Hutchinson's concept of mapping between space and physiological niche, this would imply that r and N are correlated in space as well.

It is worth briefly distinguishing the topic of interest here: studies of performance versus abundance across environmental gradients from the rather different topic of looking at performance as a function of abundance itself at smaller scales. The latter topic is the study of density dependence, where the individuals are assumed to interact with each other through some

fashion and influence each other's growth rates. A large number of studies have been performed that look at r versus N when the environmental conditions were assumed constant (or just noise) and the focus was on gradients in N (Dennis *et al.* 1994; Hassell 1975; Sibly *et al.* 2005). In contrast, this paper is focused across large spatial scales where no interactions between individuals are conceived, and rather it is assumed the environment is the important variability.

Within this context, beyond Birch's study, I know of only a handful of studies that have empirically explored the relationship between r and N^* across environmental gradients (e.g. Bell 1990; Underwood 2007). These studies were all conducted on a single species and small-scale environmental variation and typically found r and N^* to be uncorrelated. Despite these studies, it continues to be commonly assumed that r and N^* are positively correlated with each other. Holt *et al.* (1997) assume this in a model of geographic species ranges. Lawton (1993) also suggested that N^* and r should covary across a species range. The most common model of single-species density-dependent growth, the logistic equation, has two parameters r and K that are completely independent of each other. This has caused several authors to suggest that the logistic equation is a suboptimal model for assuming these two factors to be independent (Kuno

1991; Williamson 1972). In contrast, the alternative Ricker model has $N^* = r/c$, where c is the density-dependent parameter, suggesting that there should be a positive correlation.

Regardless of its accuracy, the assumption that a high equilibrium population N^* at a point in space is indicative of a high r and more generally of “good conditions” for a species is extremely convenient. It allows for a quick assessment of optimal conditions for species for applied purposes—there is no need to bring a species into controlled laboratory conditions and measure preferences—just find the species and observe the surroundings. This is a central assumption to the practice of species distribution modeling (SDM) also known as niche modeling (Guisan and Thuiller 2005; Guisan and Zimmerman 2000) and an important tool in planning for mitigation of climate change in natural systems (Araujo and Rahbek 2006). This assumption is also pivotal to the similar but smaller scale practice of habitat modeling found in wildlife conservation (Verner *et al.* 1986).

Because r is difficult to measure in trees with long generation times, I use ontogenetic growth rate as a surrogate for r . This directly tests the general concept that places of high abundance provide good conditions where organisms of the target species perform well. Additionally, ontogenetic growth is typically found to be positively correlated with population growth rate (Lampert and Trubetskova 1996; Silvertown *et al.* 1993). Thus, the use of growth rate as a surrogate for overall population fitness is common and reasonable.

Here, I test whether ontogenetic growth rate and abundance are correlated for trees of eastern North America across 15 species.

METHODS

Data

To measure the abundance, I used a database derived from the US Forest Inventory Analysis (USFIA) (US Department of Agriculture Forest Service 2010) by Iverson and Prasad (1998; Prasad and Iverson 2003). This product aggregates individual plots to a 20 × 20 km pixel. This avoids the fact that the exact locations of individual plots are not legally available and is a more appropriate spatial scale for this analysis in any case. There are a number of different measures for abundance used in indeterminate growers with widely varying individual body sizes such as trees (Morlon *et al.* 2009; Wilson 1991) including density (number of individuals), biomass and percent cover. There is no one correct measure and a choice must be made based on the question. Here, I adopt the concept of an importance value (IV), which is the standard value used by the US Forest Service. It is a mixture of density and percent basal area. In the USFIA, at each pixel for each species, an IV is calculated. The IV is given by percent of total basal area occupied by target species plus percent of total stem count occupied by target species. Thus, IV ranges from 0 when a species is absent to 200 when the target species is grown in monoculture. IV is a mixture of biomass and abundance measures of frequency that is

a reasonable way to measure population size in trees. Prasad and Iverson (2003) calculated IV across an equal area grid covering eastern North America for 134 species of trees.

To measure ontogenetic growth rates, I use the FORAST database of tree-ring increments (McLaughlin and Boden 1986). I downloaded this data from the NOAA Paleoclimate Web site. Unlike most tree-ring data that are collected intentionally in marginal environments to explore time series of deviations that can be attributed to climate, the FORAST data were collected with an intention of comparing and contrasting ontogenetic growth rates between sites. The FORAST data were collected by coring mature healthy trees of ~100 years of age for a total of >7,000 trees at 168 undisturbed sites spanning 17 states in eastern North America. The tree-ring width for each year was recorded in units of 0.01 mm. Thirty-six species were sampled.

Analysis

Of the 36 species in FORAST (listed only by common name), 27 could be matched unequivocally to a species in the USFIA data (Latin binomial and common name given). Nine could not be clearly assigned a one-to-one match (e.g. FORAST’s ‘red oak’). For the 27 overlapping species, all FORAST records were pulled (Table 1).

For each FORAST site, and for each tree of the target species in that site, the mean tree-ring width for the years 1940–86 was taken. The year 1986 is when the FORAST data were collected and thus all cores ended in that year. Although climate can vary between sites, at least all tree rings in this study were controlled to come from the same years. The mean was chosen as the simplest representation of average growth rate. In tree-ring analysis, it is common to fit an exponential growth model (Fritts 1976), but no exponential growth was detected in the data I analyzed. Data plots suggested that ring width was constant over 1940–86. This is probably due to the fact that the trees were already mature full-grown trees by 1940. Thus, the mean is an appropriate measure. Also, since the trees were selected to be roughly equally aged, even if there were a slight exponential growth, roughly the same portion of the growth curve was sampled for all trees, again making comparison of means across trees and sites appropriate.

Only ~10% of the trees were duplicates within a site, so to avoid pseudoreplication, one tree at each site was chosen randomly to be retained and duplicate trees at a site were removed from the analysis. For each FORAST site, the latitude and longitude were given in the FORAST database. This was used to lookup an IV in the USFIA data. Thus, a mean growth increment and an IV were available for each site. Number of sites per species varied from 1 to 75 (Table 1).

A Pearson correlation statistic, r , was calculated for each species. To analyze the overall pattern of correlations, two analyses were performed. First, a t -test was used to see if the correlations across species were significantly different from a distribution with a mean of 0. Second, a binomial test was used to assess the probability of getting the number of negative

Table 1: list of species

Species	Common name	Pearson r	P	No. of sites
<i>Quercus alba</i>	White oak	-0.23	0.02	75
<i>Picea rubens</i>	Red spruce	-0.33	0.04	28
<i>Liriodendron tulipifera</i>	Yellow poplar	-0.13	0.26	27
<i>Quercus velutina</i>	Black oak	-0.24	0.15	22
<i>Pinus strobus</i>	Eastern white pine	+0.24	0.86	22
<i>Quercus prinus</i>	Chestnut oak	-0.14	0.29	17
<i>Pinus rigida</i>	Pitch pine	-0.40	0.07	16
<i>Acer rubrum</i>	Red maple	-0.34	0.10	16
<i>Tsuga canadensis</i>	Eastern hemlock	-0.47	0.06	12
<i>Pinus echinata</i>	Shortleaf pine	-0.29	0.19	12
<i>Fagus grandifolia</i>	American beech	-0.13	0.35	12
<i>Fraxinus americana</i>	White ash	-0.14	0.40	6
<i>Betula alleghaniensis</i>	Yellow birch	-0.82	0.05	5
<i>Quercus stellata</i>	Post oak	+0.33	0.68	5
<i>Acer saccharum</i>	Sugar maple	+0.39	0.72	5
<i>Pinus taeda</i>	Loblolly pine	-0.91	0.07	4
<i>Prunus serotina</i>	Black cherry	+0.21	0.59	4
<i>Pinus virginiana</i>	Virginia pine	+0.28	0.61	4
<i>Quercus falcata</i> var. <i>falcata</i>	Southern red oak	+0.86	0.90	4
<i>Quercus michauxii</i>	Swamp chestnut oak	—	—	3
<i>Juniperus virginiana</i>	Eastern redcedar	-1.00	—	2
<i>Liquidambar styraciflua</i>	Sweetgum	—	—	2
<i>Quercus phellos</i>	Willow oak	—	—	2
<i>Carya ovata</i>	Shagbark hickory	+1.00	—	2
<i>Quercus coccinea</i>	Scarlet oak	—	—	1
<i>Tilia americana</i>	American basswood	—	—	1
<i>Chamaecyparis thyoides</i>	Atlantic white cedar	—	—	1

This table shows the species that were identified in both the FORAST and FIA data. Species found in one dataset but not the other or without a clear one-to-one mapping are omitted. The Pearson correlation value, r , between IV and tree-ring size (growth increment) across sites within a species is shown. The significance or P value and the number of sites (number of points in the correlation) are also shown. No r value can be calculated for $n = 1$. An r value but not a P value can be calculated for $n = 2$. Several species with only 2 or 3 or three sites had IV values that were the same at all sites (usually IV = 0) and thus did not have r or P values.

correlations observed if positive and negative correlations were equally likely.

RESULTS

Eight species had FORAST data for only one site (making a correlation impossible to calculate) or two sites (making a P value impossible to calculate) or had three sites but identical IV values across all sites (making a correlation value impossible to calculate). Correlation values for the 19 species with 4 or more sites were examined (Table 1).

On the whole, correlations between IV and growth increment were negative. Across all species with four or more sites, correlation between IV and growth increment tended to have a negative correlation with the average Pearson $r = -0.12$. Significance tests for the 19 species including the very noisy species with only 4 sites were not significant (t -test $P = 0.24$) or borderline significant (binomial $P = 0.06$). Successively higher cutoffs on number of sites showed successively stronger results (Fig. 2). Namely, for the 15 species found at at least five sites, the distribution of correlations showed mean $r = -0.18$, t -test $P = 0.044$ and binomial test $P = 0.007$, while for the 11 species found at at least 10 sites, results showed mean $r = -0.22$, t -test $P = 0.003$ and binomial $P = 0.00098$. Cutoffs of six, seven, eight and nine sites also showed correlations that were significantly less than zero with $P < 0.05$ for both the t -test and binomial test. The correlations with only 4 sites are so noisy that there is not enough power to quite attain significance for a test of correlations being different from zero, but for any other cutoff including the natural cutoffs of 5 and 10 sites, there is clear evidence that there are more correlations less than 0 than possible by chance (for $\alpha = 0.05$) and the evidence gets stronger as fewer species (i.e. better species with more sites) are used.

DISCUSSION

This paper presents a rare test of the common assumption that performance and abundance, N^* (here measured as IV), are correlated across large environmental gradients. Indeed, this is the first multi-species test (focused on environmental gradients) I am aware of since Birch's original work (Birch 1953). Surprisingly, it appears that there is actually a negative correlation between ontogenetic growth rate, a proxy for r , and N^* . This is contrary to a commonly held assumption that is central to many tools used in conservation such as habitat suitability modeling and SDM.

The main limitation in these results is the available data at the spatial scale of interest (i.e. across large environmental gradients). Specifically, the use of a 20×20 km pixel from the USFIA is probably an appropriate grain size for comparisons across extents of thousands of kilometer. But it would be nice to be able to contrast with population growth rates, r , at the same 20×20 km resolution. However, such data do not exist and probably never will. To enable the analysis, two compromises were made. First, I used ontogenetic growth rate, which clearly is a measure of performance (*Sensu* McGill *et al.* 2006), and is usually strongly correlated with r , but is not in fact r . Calculating r for populations of trees that live hundreds of years is prohibitive and rarely done. However, many of the motivations for examining this question (e.g. the use of wildlife habitat modeling) apply equally to the use of performance as r . Second, I use data from single individuals. This is in part necessitated by the focus on performance rather than r . However, the net statistical effect of using performance for a single individual rather than averaged over all individuals in a 20×20 km area (again data that will not exist any time soon) is to greatly increase the variance and decrease the power, thus

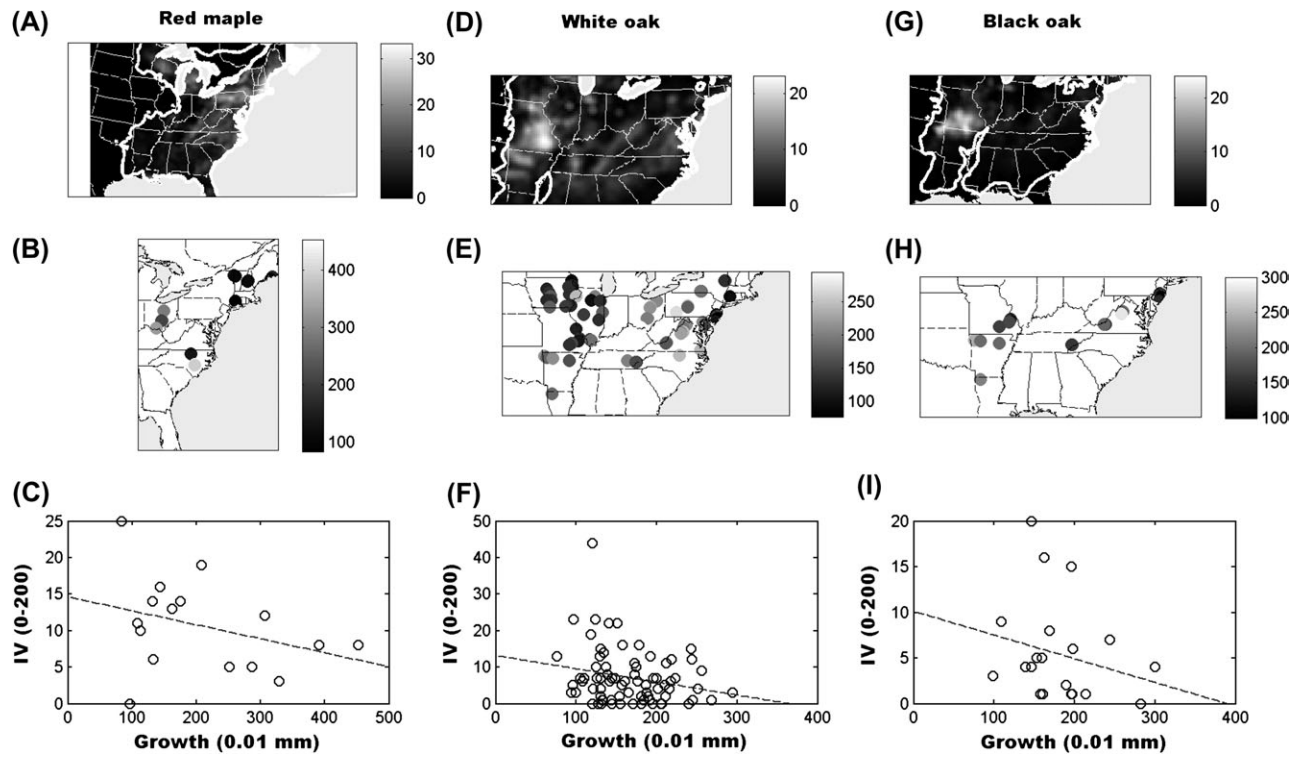


Figure 1: plot of IV (IVs are a measure of abundance) (A, D, G), average ring width (in 0.01 mm) (B, E, H) and their correlation (C, F, I). Left column is for Red maple (*Acer rubrum*) that is most common in the northeastern USA (Pennsylvania to Maine) but grows best on the southern and southwestern edges of where it is abundant. Central column is for White oak (*Quercus alba*) that grows best in the southeast portion of its range but is most abundant on the western portion of its range. Right column is Black oak (*Quercus velutina*) that grows fastest south of where it is most abundant.

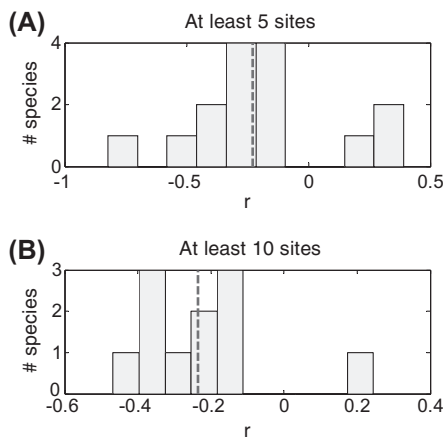


Figure 2: histogram of Pearson r values for different species. (A) All species with at least 5 sites, and (B) all species with at least 10 sites. Dashed lines indicate median value. The top figure has three outlying species above zero and one outlying species at -0.8 . All but one of these outliers (*Pinus strobus*) disappear when at least 10 sites are required. Excepting these outliers, the Pearson r correlations are tightly clustered around $r = -0.1$ to -0.4 .

making tests conservative. Finding such a strong signal despite this noise is indicative of a strong pattern. Despite these limitations, I have used the FORAST dataset (and trees more

generally) because the FORAST dataset is one of the only datasets I know of that has a reliable measure of varying performance within a species across large geographic areas. Thus, using these two datasets enables an analysis of an important question at a scale at which data availability is very limited. It would also be interesting and important to verify these results as other datasets examining performance across large environmental gradients become available.

There is a well-established theory that predicts my finding that performance and abundance are negatively related across large environmental gradients. Traditional niche theory has focused on exclusive niches (Grant and Grant 1989; MacArthur 1958, 1968)—each species in a guild has its optimum at a different location in niche space. This exclusive niche structure is often assumed to be the only possible organization. However, an alternative niche structure known as inclusive niches is also possible (Colwell and Fuentes 1975). In inclusive niches, all species have optimum performance (r or here growth increment) under the same environmental conditions. However, there is a trade-off between competitive ability and environmental tolerance (Loehle 1998; Rosenzweig 1981, 1987, 1989). As a result, the most competitively able species can dominate numerically at the shared optimal location in niche space. However, the competitively dominant species is not able to tolerate poorer environmental conditions. This allows a

competitively weaker species that is more environmentally tolerant to live elsewhere in poorer conditions without having to compete with the dominant. This scenario can be repeated with additional species that are even less competitively able but more environmentally tolerant (McGill *et al.* 2006). In this scenario, only the competitively dominant species is living at its performance optimum. A meta-analysis of the literature has shown that inclusive niches are far more common than exclusive niches (Wisheu 1998) and that this is especially true in plants.

The results found in this paper are certainly not compatible with the idea of exclusive niches (each species most common at its performance optimum in niche space). The results found in this paper are consistent with the idea of inclusive niche organization of eastern North American trees, although an unknown third alternative community organization cannot be ruled out. An anecdotal examination of the data in this paper strongly suggests inclusive niches and a competitive dominance/environmental trade-off may be operating. The only species with a large sample and a positive correlation between IV and growth is the eastern white pine (*Pinus strobus*). This species is famously one of the tallest trees in eastern North America and certainly the tallest in New England where it is most common. Although it is a leap, it is not hard to imagine that the tallest tree could be competitively dominant for light competition. Figure 1 also is suggestive. Red maple is most common in the northern-most portions of the USA, but it grows best in the southern and southwest portions of its range that are presumably warmer, equally as wet and probably overall more favorable conditions. This suggests that Red maple has its niche optimum in the warm moist area around Virginia and Ohio, but is competitively excluded and thus is most common in colder climates. White oak has a similar story (also growing best around Virginia) but being most common in the western, driest portions of its range.

In short, this paper shows that in trees of eastern North America, a species usually shows a negative correlation between where it is most common (IV) and grows the best (growth increment). This result is in contradiction to the assumption usually made in conservation tools that seek to identify optimal habitat for species. This result also contradicts an exclusive niche organization for trees. However, it is consistent with an inclusive niche community structure.

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