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Monitoring succession from space: A case study from the North Carolina Piedmont

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Abstract

Question: Is the successional transition from pine to hardwood, which has been inferred from chronosequence plots in previous studies, validated through a time line of satellite imagery?

Location: Durham, North Carolina, USA.

Methods: We examined successional trends in a time-series of winter-summer pairs of Thematic Mapper imagery from 1986 to 2000. We calculated the normalized difference of vegetation index (NDVI) for winter and summer, as well as the difference between summer and winter NDVI (i.e., summer increment NDVI). A set of approximately 50 forest stands of known age and phenology were used to interpret patterns in winter and summer increment NDVI over successional time, and a continuum was found to exist between pine-dominance and hardwood-dominance. We fitted a series of linear regressions that modeled the change in winter and summer increment NDVI as a function of initial winter and summer increment NDVI, and additional explanatory variables.

Results: All regressions were highly significant ($P < 0.0001$, R^2 = ca. 0.3). Predicted dynamics are in accord with successional theory, with pixels moving from evergreen dominance to deciduous dominance along a line of fairly constant summer NDVI. A large disturbance event that occurred over the course of this study, Hurricane Fran, appeared to slow rates of succession in the short term (1-3 years), but increase the rate of conversion to hardwoods over longer time spans.

Conclusions: We conclude that temporal sequences of remote sensing images provide an excellent opportunity for broad-scale monitoring of successional processes, and that continuous metrics of that change are essential to accurate monitoring.

Keywords: Chronosequence; Conditional auto-regression; Dark Object Subtraction; Deforestation; Duke Forest; Edge Effect; Loblolly Pine; NDVI; *Pinus taeda*; Self-thinning; Thematic Mapper.

Abbreviations: CAR = Conditional Autoregression Framework; NDVI = Normalized Difference of Vegetation Index.

Introduction

One important subject in plant ecology has been post-disturbance succession (cf. Connell & Slatyer 1977; Peet & Christensen 1980; Tilman 1985; Huston & Smith 1987). Most studies of succession are based on the examination of chronosequences, a set of sites of varying time since disturbance that are presumed to be similar in other relevant characteristics. However, some studies (e.g. Pickett 1989) have criticized this space-for-time substitution (i.e. ergodic assumption), pointing out that sites are likely to vary in environmental characteristics, and that the abiotic and biotic conditions that determine establishment (e.g. seed dispersal from surrounding areas) will vary over time (Mast et al. 1998). In addition, community ecology studies necessarily take place at fine spatial scales, leading some to worry about the general applicability of successional studies to broader regions (cf. Levin 1992). As one examines sites that are increasingly different from the conditions that occurred in a given studied chronosequence, the process of extrapolation becomes increasingly difficult (Pickett 1989).

The widespread availability of satellite imagery raises new possibilities for plant ecology, and particularly for the study of plant succession (e.g. Lawrence & Ripple 2000). The broad spatial scales that can be covered by satellite imagery, and the full coverage of a particular region obtained in an image, enable a more thorough examination of many processes in plant ecology. Moreover, many remote sensing platforms have been in place long enough to obtain a consistent time series of imagery for close to 20 years, long enough for successional processes to be detected. In cases where different successional states can be determined from imagery, there is thus a potential for using satellite imagery to examine the process of succession, and plant species dynamics more generally (e.g. Price & Jakubauskas 1998). Changes in forests potentially could be monitored over broad spatial scales, mapping out the response of vegetation to anthropogenic disturbances quickly enough to be of use to policy makers.

The focus of many studies of plant community succession has been on the autogenic component of plant dynamics. However, we hypothesize that an analysis at broader spatial scales will increase the importance of allogenic factors in determining the successional trajectory, as the frame of analysis incorporates more and more variation in environmental conditions and biotic surroundings into the analysis. Furthermore, there is significant spatial autocorrelation in many of the potential explanatory variables, from edaphic conditions to human management decisions. We hypothesize that this spatial autocorrelation in driving variables, as well as inherent autocorrelation in the processes of forest change (e.g. gap dynamics), will lead to significant spatial autocorrelation in the rate of change along a successional trajectory. Finally, edge effects have a significant effect on growth rates in the North Carolina Piedmont (McDonald & Urban 2004), where this study is directed, and one thus might expect them to effect successional trajectories within some finite distance of an edge where edge effects are important (cf. Cadenasso et al. 2003a, b). Thus an analysis of successional trends from satellite imagery will highlight the importance of edge effects. More particularly, we hypothesize that increased light near forest edges will tend to delay transition from early-successional, shade-intolerant species, to late-successional, shade-tolerant species.

Here we examine spatial patterns in a transition from early-successional pine to later-successional hardwood for the area around the Raleigh-Durham metropolitan region, using a 16-year time series of Thematic Mapper imagery. This may be a case study of the potential utility of monitoring succession at broad spatial scales using continuous state variables (cf. Price & Jakubauskas 1998), in contrast to many previous remote sensing works on succession that have used categorical state variables (e.g. Hall et al. 1991; Pan et al. 2001), with the notable exception of Song & Woodcock (2002). Our approach is similar to the literature on change vector analysis (e.g. Lambin & Strahler 1994; Johnson & Kasischke 1998). 1.We model successional trends over time for each change interval, to determine if they are consistent with previous work in this system based on fine-scale plots. 2. We examine the relative importance of autogenic vs. allogenic factors in a linear regression framework. For the purposes of this study, autogenic factors are taken to be biotic, and are represented by the cover of the deciduous and evergreen forest fractions. Allogenic factors are taken to be abiotic, and are represented by environmental variables incorporated into our regression analysis. 3. We measure the scale of autocorrelation in the process of successional change. 4. We test whether edge effects play an important role in this particular successional transition.

Methods

Study site

This study is located in the North Carolina Piedmont (Fig. 1). Temperature for the region ranges from a mean daily maximum of 10.1 °C in January to 31.5°C in July. Precipitation falls evenly throughout the year, with a mean annual precipitation of 1052 mm (Anon. 2003). Topography is usually gentle, with rolling hills. Soils vary from sandy, sediment-derived soils to highly plastic clay soils on the uplands (Bain 1966). Due to the low available water holding capacity of many soils and the high summer temperatures, evapotranspirative demand often exceeds available water (cf. Bormann 1953).

Humans have heavily altered the forests of the region since the time of European settlement. Much of the area that was fairly flat and with good soil properties was cleared for agriculture in the 19th century (Trimble 1974). These old agricultural fields were abandoned in the early 20th century, and are dominated by a canopy of *Pinus taeda*, an early-successional pioneer species in this area with a typical maximum lifespan of 80-100 years (Oosting 1942). Deciduous trees grow in the shade of *Pinus taeda* and dominate the understory of these forests, and it appears likely that when the pine canopy dies these hardwoods will mature into the canopy (Christensen & Peet 1984). Areas of the landscape that were never cleared for agriculture, usually rocky sites or sites within floodplains, have retained a hardwood canopy, typically dominated by *Quercus* spp. and *Carya* spp., although other hardwoods such as *Acer rubrum* have increased recently (Lorimer 1984; Abrams 1998; McDonald et al. 2002, 2003).

Data handling

We obtained a set of winter-summer (i.e. December and May/June) pairs of 30 m resolution Thematic Mapper (TM) Imagery from four years: 1986 (12/14/1986 and 5/4/1986), 1990 (12/9/1990 and 5/2/1991), 1997 (12/28/1997 and 5/18/1997), and 2000 (12/20/2000 and 5/26/2000). No ETM+ Imagery was used. Images from each season were obtained on anniversary dates whenever possible, to minimize differences in solar zenith angles and phenology among images taken in the same season. In all summer images, leaf expansion and growth had finished. We recognize that the 30 m resolution of TM Imagery may limit our ability to detect edge effects on successional dynamics (see below), but it is the only type of imagery available in our study area over a long enough period to analyse succession. The images were geometrically rectified, with a root mean square error of less than 8 m, using ERDAS Imagine software. The

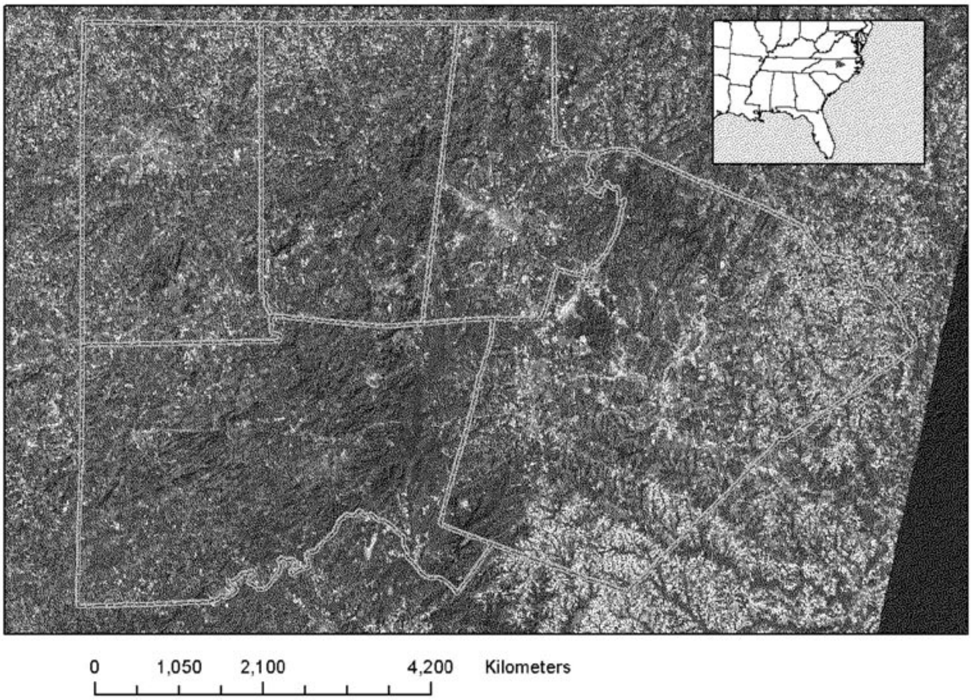

Fig. 1. Map of five-county study area. The black and white color scheme of the landscape is band 4 of a Thematic Mapper Image of the region from May 2000. Forests appear as dark gray or black in the image, while non-forested areas appear white or light gray. The inset map in the corner shows the location of these five counties within the southeastern United States.

1986 winter image was geometrically rectified to a set of ground control points (e.g. intersections of major roads) whose geo-coordinates were known very precisely, and all remaining TM images were geo-rectified to this image. Small portions of the landscape (< 1% of the total study area) with snow, smoke, or clouds were masked out of the analysis. To minimize atmospheric variation between images, we used dark-object subtraction on digital numbers (e.g. Chavez 1988), which offers an appealing blend of effectiveness and ease of parameter estimation (Song et al. 2001). Dark-object subtraction was performed independently on each image, as is consistent with the theoretical justification behind the approach, although the total atmospheric variation between images may not be fully removed by this technique.

The Normalized Difference of Vegetation Index (NDVI) was calculated for all summer and winter images (Tucker 1979), which reflect the total and evergreen fractions of vegetation, respectively. As a measure of the deciduous fraction of vegetation, the difference between summer NDVI and winter NDVI, henceforth referred to as 'summer increment NDVI', was also calculated. As our purpose for this study was to study forest dynamics (and not patterns of anthropogenic land-cover change), we wished to only examine forest dynamics within pixels that stayed forested over the 16-year interval. Accordingly, we used high-resolution aerial photographs to define a training dataset for a five-class land-cover classification scheme (sediment-laden water, deep water, sparse vegetation, forested, and developed). The spectral signatures for each class (with information from both summer and winter TM images, excluding band 6) were used in a maximum likelihood classification (Legendre & Legendre 1998) to classify each pixel in each year. Only pixels that were forest in all time steps were retained for the following analysis, removing much of the effect of anthropogenic disturbance. This effectively limits our analysis to closed-canopy forests, the dominant forest structure in the NC Piedmont, so different shadow lengths between different seasons or stand phenologies are of little concern, as the spectral characteristics of the pixels are a function of the canopy characteristics.

While many studies have shown a nonlinear but monotonic relationship between NDVI values and leaf area index (LAI), with some saturation at high values of LAI (cf. Gobron et al. 1997), we wanted to see how patterns of winter NDVI and summer increment NDVI related to the successional states (pine versus hardwood dominance) of the forest (cf. Kasischke & French 1997; Kasischke et al. 2000). The Duke Forest (Durham, NC) maintains good geospatial records, with polygons delineating forest stands and quantifying their age and management history going back to the 1930s, and is thus an excellent source of data for verification that the NDVI values observed relate to successional state. We selected a broad set of forest stands in each of 6 age classes: 0-20 years since disturbance (pine-dominated), 20-40 years (pine-dominated), 40-60 years (pine-dominated), 60-80 years (pine-dominated), 80-100 years (mixed), and uneven-aged (hardwood-dominated). For all pixels within these various classes, the mean and distribution of winter NDVI and summer increment NDVI were graphically examined over time.

Hardwood forests in this region, barring disturbance, will tend to retain fairly constant leaf area (cf. Oosting 1942; Riley & Jones 2003), and so we expected pixels from this age class to have a relatively invariant distribution of winter and summer increment NDVI. However, examination of the data revealed that these pixels underwent a slight linear shift in different images (<0.05 units of NDVI in all cases). This shift could be due to differing atmospheric and soil conditions, or due to interannual variability in leaf area due to climatic variability. As these linear shifts of many relatively constant hardwood pixels seemed unlikely to have meaning for the successional process we are trying to study, we subtracted the difference in median values between pairs of images of the same season to normalize to the arbitrary year 1990. The results reported below are from this corrected dataset, although the results are similar (but slightly more noisy) with the uncorrected data.

The relationship between winter NDVI and summer increment NDVI for all time periods was graphically examined for a set of 10 000 sample pixels drawn randomly from the landscape. We examined a set of 10,000 pixels rather than all pixels in the scene partially for computational reasons, and partially to avoid the increased problems with spatial autocorrelation and interpretation of P-values that can occur with very large raster maps (see McDonald & Urban 2006 for more discussion). Changes in winter NDVI and summer increment NDVI for each time interval (i.e., 1986 to 1990, 1990 to 1997, and 1997 to 2000) were plotted as vectors in this state space by dividing the space into regions and calculating mean change vectors for each region. The empirical patterns displayed informed our choice of the functional form for our statistical analysis below. In particular, there is a correlation between winter NDVI and summer increment NDVI for most pixels (shown below). We believe that this correlation is of ecological interest, and thus present an analysis of both terms separately, despite the statistical issue of independence the correlation presents.

Spatial regression

The average annual (normalized) change in winter NDVI and summer increment NDVI over *n* years was calculated as:

$$\mathrm{norm}\Delta NDVI = \frac{NDVI_{t+n} - NDVI_t}{n} .$$

Normalized changes in either winter or summer increment NDVI (henceforth referred to simply as ‘change in winter or summer increment NDVI’) was modeled in a linear regression framework with a system of two equations:

$$\begin{aligned}\mathrm{norm}\Delta NDVI_{winter} = {} & \beta_{0,w} + \beta_{1,w} NDVI_{winter} + \beta_{2,w} NDVI_{summerincr} \\ & + \beta_{3,w} NDVI_{winter} NDVI_{summerincr} + ?_w \mathbf{X} + \varepsilon_w\end{aligned}$$

$$\begin{aligned}\mathrm{norm}\Delta NDVI_{summerincr} = {} & \beta_{0,s} + \beta_{1,s} NDVI_{winter} + \beta_{2,s} NDVI_{summerincr} \\ & + \beta_{3,s} NDVI_{winter} NDVI_{summerincr} + ?_s \mathbf{X} + \varepsilon_w .\end{aligned}$$

where **X** is a vector of other explanatory variables (and summer increment is abbreviated as *summerincr*). These included the distance to a non-forested pixel, calculated from the land-cover maps described above, to account for possible edge effects on successional dynamics. Using a digital elevation model (ca. 30 m resolution) from the SRTM dataset (Anon. 2004), we calculated Beer’s transformed aspect, a measure of the amount of sunlight available on a slope facet (Beers et al. 1966). Topographic convergence index (TCI, Beven & Kirkby 1979) was also calculated as an index for hydrologic inflow of water, as a proxy for topographically-derived soil moisture. Finally, information on edaphic conditions was extracted from digitized soil survey maps from the SSURGO dataset (Anon. 2004) for the percent clay in the A and B soil horizons, the soil plasticity index for the B-horizon, and soil pH. SSURGO data have variable minimum mapping units depending on the county utilized- see online metadata for details. All explanatory variables were converted to 30-m resolution raster grids using a nearest-neighbor resampling rule in ArcInfo, as is appropriate for our categorical datasets (e.g. SSURGO).

This system of two equations was fit separately for each time interval, to understand how forest dynamics may have varied over time, using data from the same 10 000 sample pixels described above. We used a system of two equations to explicitly examine how both winter and summer increment NDVI change over time. The error terms e_w and e_s are weakly correlated; this would often be remedied using the Seemingly Unrelated Regression (SUR) framework. However, in this particular case as the explanatory variables are identical between the two equations there is no gain in efficiency using the SUR framework and parameter estimates remain unbiased (Pindyck & Rubinfeld 1998). To address concerns that *e* would be spatially autocorrelated (i.e. pixels close to one another in space would have similar residuals), we used the Conditional Autoregression Framework (CAR) with the strength of autocorrelation (i.e. edge weights) assumed to be proportional to the inverse distance between points (Keitt et al. 2002).

To visualize further the extent and magnitude of spatial autocorrelation in the process of forest change, we calculated a correlogram of the residuals. The correlogram was calculated first with residuals from the above system of two equations fit with ordinary least squares regression, and then with residuals from the system of equations fit with CAR. The results gave a graphical picture of how well the CAR framework does at factoring out spatial autocorrelation.

A small subset of pixels had a lower summer NDVI than other pixels. As this may imply a lower total leaf area, perhaps due to disturbance or a mixed pixel, we were interested in examining the spatial patterns of these pixels. Accordingly, we mapped pixels with values less than 0.75 in total summer NDVI for each year to visualize patterns. This threshold was picked because it was below the variation in 99% of the forest pixels, which were between 0.75 and 0.85 in summer NDVI. In particular, to examine the effects of Hurricane Fran (1996), a large disturbance event in the North Carolina Piedmont, we mapped pixels with less than 0.75 summer NDVI in 1997 that had values of summer NDVI above 0.75 in all other years (i.e., returned to approximately full forest cover in 2000). Hurricane Fran toppled forest stands in a variety of patch sizes along river corridors in the Duke Forest, where the soil had become waterlogged due to the excessive rain during the hurricane (Carpino 1998), and so we hypothesized that our selected pixels would reflect this pattern.

Results

Hardwood and pine-dominated forests show consistent and interpretable patterns in winter and summer increment NDVI (Fig. 2). Note that pixels are arrayed upon a line, implying a summer NDVI of between 0.75 and 0.85 regardless of successional state. We chose to display the pine-dominated pixels with a single symbol, rather than denoting each age class separately, because there is very little pattern in differences between age classes. Hardwood-dominated pixels are separable from pine-dominated pixels, although there appears to be a continuum between the two states with some pixels having intermediate levels of winter NDVI and summer increment NDVI.

Trends for the larger set of 10 000 sample points are similar (Fig. 3a.), with points arrayed along a line that implies a relatively constant summer NDVI of around 0.85. Presumably, the relative position along the line reflects the degree of deciduous (i.e. summer increment NDVI) versus evergreen (i.e. winter NDVI) dominance. This interpretation is also consistent with changes over time in winter and summer increment NDVI (Fig. 3b.), where any increase in summer increment NDVI is accompanied by a corresponding decrease in winter NDVI. Patterns for the other two intervals are similar, with summer increment NDVI on average increasing and winter NDVI on average decreasing. Note also that in Fig. 3a a small subset of pixels fall below the horizon of summer NDVI equals 0.85, and these same pixels tend to be the ones that are above the line in Fig. 3b, indicating an increase in both winter and summer increment NDVI.

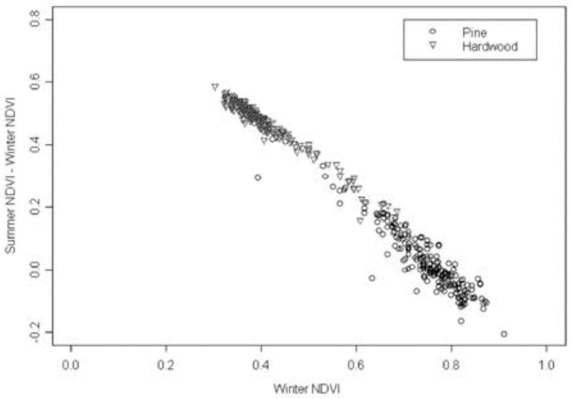

Fig. 2. Plot of winter NDVI versus the difference between the winter and summer NDVI for 1986; all other years show identical patterns. Triangles denote training pixels that are known to be within hardwood stands in Duke Forest, while circles denote training pixels known to be within pine-dominated stands.

All three regressions of change in winter NDVI (e.g. Table 1) are highly significant ($P < 0.0001$, R^2 ca. 0.27), with the most significant explanatory variables being winter and summer increment NDVI, as well as the interaction between them, the parameters of which have negative signs in all three intervals. Similarly, all three regressions of change in summer increment NDVI (e.g. Table 2) are highly significant ($P < 0.0001$, R^2 ca. 0.22), with the most significant explanatory variables being winter and summer increment NDVI (negative sign for all intervals), and the interaction (positive sign for all intervals). For both classes of regressions, distance from edge, TCI, and transformed aspect are nonsignificant in all cases. However, for both classes of regressions edaphic variables, with the exception of pH, are highly significant for all intervals, although the effect size is quite small (partial R^2 ca. 0.02 for each edaphic variable). High levels of clay tend to increase the change in summer increment NDVI and make more negative the change in winter NDVI, while soil plasticity has the opposite effect. Given the low R^2, these trends need to be treated with extreme caution, and may simply reflect correlations between soil conditions and NDVI.

The regression equations exemplified in Tables 1 and 2 imply a trajectory in winter and summer increment NDVI that is consistent over time (Fig. 4). There is a combination of winter and summer increment NDVI (an 'attractor point') towards which all other points tend to move over time. For all three intervals, this attractor point lies near the location of the cluster of hardwood points

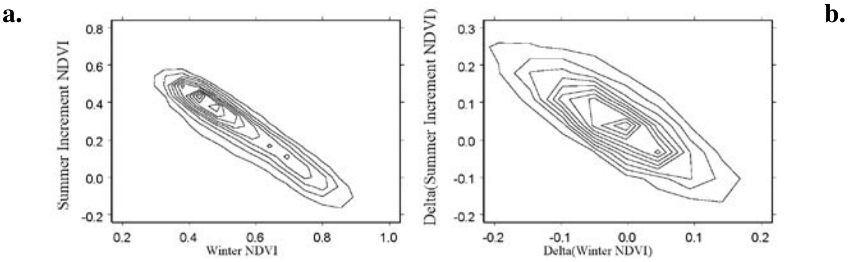

Fig. 3. a. Winter NDVI vs. the difference between the winter and summer NDVI for 1986 for 10 000 sample points used in the regression analysis. Contour lines are the density of points, estimated using kernel density estimation. Density is at its highest around (0.4, 0.4). Note that most points fall along a line that implies a relatively invariant summer NDVI ca. 0.85. **b.** Change in winter NDVI versus the change in the difference between the winter and summer NDVI, from the interval 1986 to 1990. Contour lines are the density of points, with density is at its highest around (0.0, 0.03).

in Fig. 2, although it is slightly lower for the interval from 1990 to 1997. The trajectories for each interval show that points with low winter and summer increment NDVI tend to increase in both measures over time, while points on the 'line' of relatively constant summer NDVI move up toward the hardwood attractor (i.e. decrease in winter NDVI and increase in summer increment NDVI). There is significant spatial autocorrelation in residuals in changes in winter and summer increment NDVI (e.g. Fig. 5) at scales below 600 m. The problem is particularly evident when one assumes an independent error term. Using a CAR framework, the autocorrelation of residuals is much reduced, although there is still a slight tendency for sample points close to one another to have similar residuals. Therefore, any predictions of future mean changes in CAR will have some spatial structure in their (unknown) residuals, and the *P*-values in Tables 1 and 2 are likely to be slightly lower than the true probability under the null hypothesis.

An analysis of the spatial locations of forested pixels (not shown) that fall below the 'line' of summer NDVI of 0.75 suggests that some of these pixels are disturbance events, and appear to be distributed randomly throughout forested areas. However, the majority of these forested pixels with values of summer NDVI below 0.75 appear to be mixed pixels (i.e., pixels that record spectral data from both forest canopy cover and other land-cover types), and tend to cluster near the edges of forested patches. These mixed pixels stay low in summer NDVI over time, suggesting that only a portion of the cell remains vegetated.

The spatial patterns of forested pixels that were below 0.75 summer NDVI in 1997 only (i.e., those pixels that underwent some disturbance event, like Hurricane Fran, before returning to normal summer NDVI) is shown in Fig. 6 for one small region in the Triangle. Note that areas of disturbance tend to cluster spatially, and are most intense in the upper reaches of New Hope Creek, the stream shown in this picture, consistent with the pattern of hurricane damage described by Carpino (1998). A graphical analysis of these disturbed pixels over time suggests that any loss in summer NDVI during the interval from 1990 to 1997 was balanced by an increase in summer increment NDVI from 1997 to 2000, with winter NDVI showing no change from 1997 levels.

Discussion

Table 1. Regression parameters of winter NDVI for the interval 1986 to 1990.

Variables	Parameters	*t*-value	*P*-value
Intercept	1.02E-1	25.6294	<0.0001
Winter NDVI	-1.45E-2	-39.2310	<0.0001
Summer increment NDVI	-3.24E-2	-6.3405	<0.0001
Distance to edge	1.28E-6	0.4209	0.6738
TCI	-1.67E-4	-1.9329	0.0533
Transformed aspect	2.22E-5	0.0721	0.9425
Clay in A horizon	-4.30E-4	-7.9758	<0.0001
Clay in B horizon	-1.75E-4	-5.2068	<0.0001
Soil plasticity	1.85E-4	6.3025	<0.0001
pH	-3.64E-4	-0.6772	0.4983
Winter:Summer increment NDVI	-5.40E-2	-7.1454	<0.0001

Table 2. Regression parameters of summer increment NDVI for the interval 1986 to 1990

Variables	Parameters	*t*-value	*P*-value
Intercept	3.83E-2	8.4933	<0.0001
Winter NDVI	-2.10E-2	-5.0430	<0.0001
Summer increment NDVI	-1.32E-1	-22.8566	<0.0001
Distance to Edge	2.29E-6	0.6661	0.5054
TCI	2.34E-6	0.0239	0.9809
Transformed aspect	-1.32E-4	-0.3789	0.7047
Clay in A horizon	4.27E-4	6.9897	<0.0001
Clay in B horizon	1.88E-4	4.9370	<0.0001
Soil plasticity	-2.45E-4	-7.3706	<0.0001
pH	-1.93E-4	-0.3173	0.7510
Winter:Summer increment NDVI	8.61E-2	10.0677	<0.0001

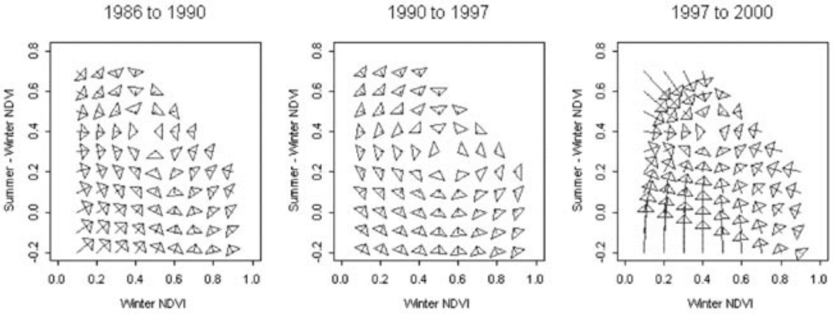

Fig. 4. Predicted change vectors from the linear regression analysis for three intervals: 1986 to 1990, 1990 to 1997, and 1997 to 2000. The direction of arrow represents the average direction of change for that point of the state space, while the length of the arrow represents the average magnitude of change. Note that predicted change vectors are not shown in the portion of the space in which there are no pixels present (i.e. summer NDVI > 1).

Our results are in accord with previous studies of succession in the region, but put the successional trajectory in more perspective. We find a fairly constant summer NDVI for nearly all forested pixels, regardless of successional state. If one assumes a monotonic relationship between NDVI and LAI, then this finding is consistent with reported trends in LAI, which find that early-successional pine stands quickly (< 5 years) reach a stable LAI ca. 4-6, and that LAI remains fairly constant over the rest of succession (cf. Adegbidi et al. 2002; Riley & Jones 2003). Pixels tend to decrease over time in winter NDVI and increase by a similar amount in summer increment NDVI, which implies a shift from evergreen dominance to deciduous dominance. The physiological explanation for this phenomenon may simply be that a decrease in evergreen leaf area tends to be followed quickly by an increase in deciduous leaf area. This phenomenon, as visualized in the 900-m2 pixels used in this study, appears continuous, and there are many pixels that have fairly equal proportions of evergreen and deciduous leaf area. Such a continuum between evergreen and deciduous dominance is consistent with gradual stand replacement of individual trees in the canopy, rather than the more synchronized successional transition envisioned by Oosting (1942).

Contrary to our hypothesis, autogenic factors such as the phenology at the site appear far more important in determining the rate of transition from pine to hardwood than allogenic factors like soil texture and pH. Regression coefficients for the autogenic factors have a much higher partial R^2 in all cases than the coefficients corresponding to the allogenic factors. One potential reason for this result is that the taxonomic groups used in our study (i.e., evergreen vs. deciduous) are very broad. We speculate that a study that had a finer taxonomic resolution would find more effects of abiotic factors, since, for example, many hardwood species that may look the same spectrally to a satellite have very different edaphic preferences. Our results might also have been different if we had used a different scheme for defining pixels as forested. For example, it is possible that some pixels that were severely denuded by Hurricane Fran, which struck the North Carolina Piedmont in 1996, were classified as

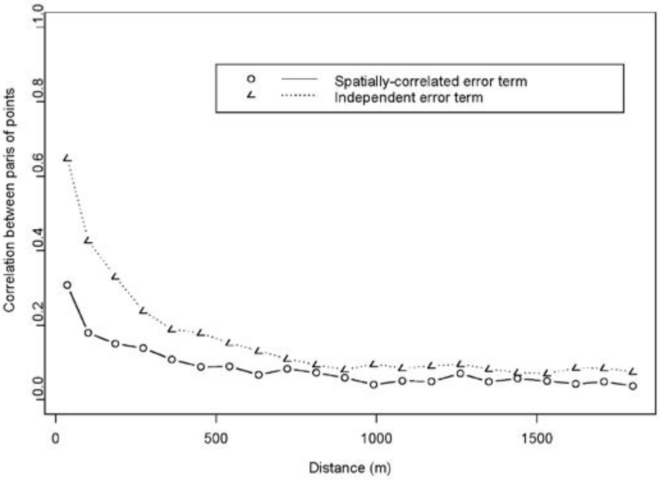

Fig. 5. Correlogram for residuals from the linear regression analysis from the prediction of change in winter NDVI for the interval 1986 to 1990; other regressions show similar trends. Triangles are the correlation between the residuals of the linear model with an independent error term for pairs of points in various distance classes. Circles are the correlation between the residuals of the linear model using a conditional autoregression error term, which reduces the extent of spatial autocorrelation in residuals.

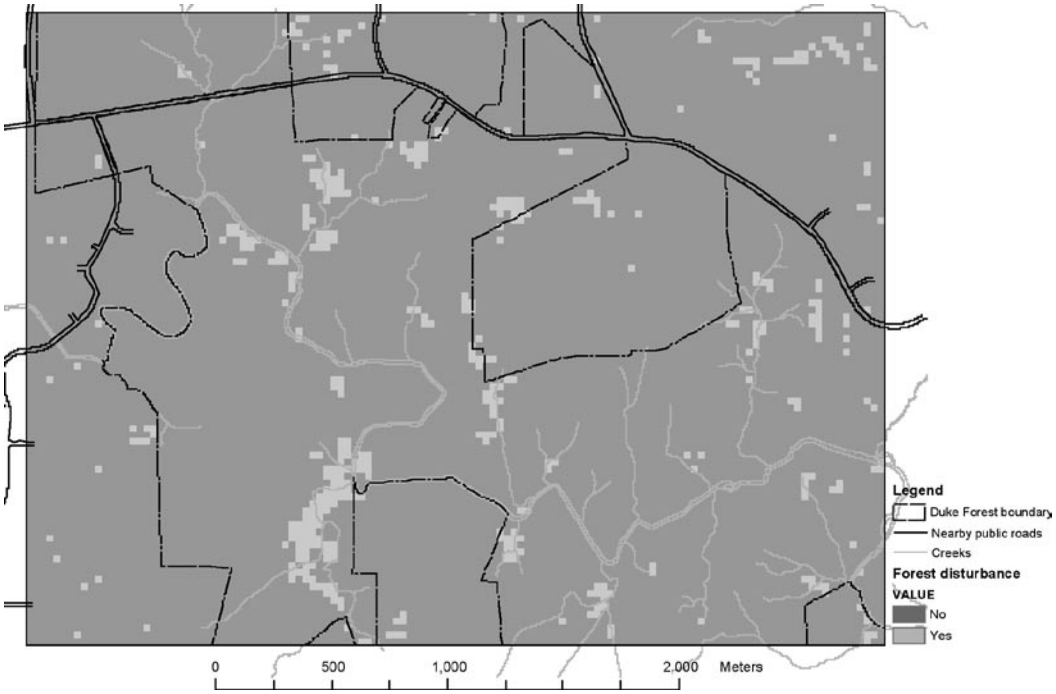

Fig. 6. The spatial location of pixels that have undergone a presumed disturbance (see text for details) for one region of the Duke Forest (North Carolina) near Mount Sinai Road in the Korstian Division. Note that disturbed pixels cluster closely, and are concentrated in the upper reaches of the New Hope Creek, which flows through the forest.

non-forest, and thus excluded from this analysis. This would tend to mask the affects of the hurricane, and the correlations between hurricane damage and abiotic factors like TCI (cf. Carpino 1998). Human management in the forest, and particularly the conversion from forest to other land-cover types, is similarly excluded from our analysis, and has been show to have significant correlations with abiotic factors (e.g. Trimble 1974).

The net effect of Hurricane Fran, a particularly large disturbance event in the North Carolina Piedmont (Pasch & Avila 1999), seems to be to temporarily slow the average rate of the successional transition from pine to hardwood, as leaf area decreases, followed by a shift toward greater hardwood dominance. Change vectors from the period 1990 to 1997 are often half in magnitude that of the change vectors from the period 1986-1990. The variance in direction and magnitude of change vectors overall was higher during the interval from 1990 to 1997 than in either of the other intervals. This suggests that the effect of Hurricane Fran was highly variable between pixels, and that some pixels were relatively unaffected by the hurricane and continued on the normal successional trajectory, while others were disturbed and generally moved towards lower total leaf area. The subset of pixels that were likely disturbed (Fig. 6) was lower in total summer NDVI in 1997, but moved quickly toward 'saturating' NDVI of ca. 0.85 in 2000, with the increase mostly due to an increase in summer increment NDVI in 2000. It should be noted that there are potential anthropogenic interactions with Hurricane Fran, for many hardwood-dominated stands that were severely affected were salvaged-logged and replanted with loblolly pine. It should also be noted that other factors that have changed over time, such as changes in the climate regime, may also be explaining part of this pattern.

The set of regressions fit in this study have a generally low R^2, around 0.3 in all cases. This low explanatory power may be due to measurement error. For example, the dark object subtraction technique (and subsequent correction of NDVI values) may not have adequately removed variation in atmospheric conditions. Moreover, NDVI is imperfect for measuring changes in evergreen and deciduous leaf area, as it incorporates information about not just leaf area but other spectral characteristics of the site. More advanced techniques such as those in Song and Woodcock (2002) may achieve higher greater explanatory power. However, we believe that the low explanatory power of our regressions may also represent a real biological phenomenon. Much of the interactions at the scale of 900 m^2, the resolution of Landsat Thematic Mapper Imagery, are fundamentally stochastic (e.g. gap dynamics). For instance, the predictions of individual-based forest models find deterministic successional trajectories at broad scales but little trend at fine spatial scales (Smith & Urban 1988). Similarly, the transition from pine to hardwood may be very predictable at broader spatial scales, but be patchy and seemingly random at scales near the canopy size of one tree.

Distance to a non-forest edge did not significantly affect the rate of successional change in any of our regressions. This result seems to contrast with McDonald & Urban (2004), who found increased growth rates for loblolly trees near forest edges, as one would expect a factor that affect growth rates of the principal evergreen species in the region to have some effect on forest dynamics and hence successional trajectories. It seems likely, however, that much of the effects of edges may have been masked due to the difficulty in classifying edge pixels as forest and the relatively coarse spatial scale of TM imagery. Only pixels that were classified as forest in all time periods were included in the analysis, which potential excluded some mixed pixels near forest edges that may have been erroneously classified as non-forest in one interval. Moreover, pixels near edges that were classified as forest in all intervals presented a challenge to model if they showed low values of summer NDVI, potentially implying they were only partially forested. Any change in NDVI in such a mixed pixel could then be due to a change in the areal extent of forest or to a change in leaf area index within the forested region.

The rate of successional change from evergreen to hardwood was autocorrelated, as hypothesized. Interestingly, the scale of significant autocorrelation extends up to 900-m^2 well beyond the size of the interactions that make up gap dynamics and species composition. This suggests that a spatially-autocorrelated unmeasured factor (or factors) affect the rate of successional change. One of the broader-scale spatially-autocorrelated unmeasured factors might be human management decisions, which undoubtedly affect NDVI and can occur in management units that are up to a km in size. For example, McDonald & Urban (2006) found similar scales of spatial autocorrelation in the process of deforestation in the North Carolina Piedmont.

Overall, our results suggest the potential for satellite image-based monitoring of forest dynamics (e.g. Asner & Vitousek 2005). The greater spatial extent and coverage of imagery allows testing of predictions of successional trajectories based on fine-scale community ecology studies or modeling efforts. Moreover, broad-scale assessments of forest compositional change, even with coarse taxonomic resolution as in this study, allow for real time analysis of the response of vegetation to global climate change. Many of the methodological difficulties that this project faced may be overcome through enhanced remote sensing images in the near future. As time series of data from remote sensing platforms with greater spatial resolution become more available, spatial effects such as edge effects may become easier to detect, as the 'mixed' pixel problem becomes less commonplace. Similarly, as time series of images from remote sensing platforms with greater spectral resolution become more commonplace, increased taxonomic resolution may be possible, which may allow for more elucidation of the importance of abiotic, allogenic factors in succession (Song & Woodcock 2002). Future studies such as these are crucial for scaling-up the wealth of knowledge from fine-scale studies of succession to landscape scales, and in the process providing information on the response of vegetation to anthropogenic disturbances.

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References

Anon. 2003. *RDU Climate Normals*. North Carolina Climate Office, North Carolina State University, Durham, NC, US.

Abrams, M.D. 1998. The red maple paradox. *Bioscience* 48: 355-364.

Adegbidi, H.G., Jokela, E.J., Comerford, N.B. & Barros, N.F. 2002. Biomass development for intensively managed loblolly pine plantations growing on Spodosols in the southeastern USA. *For. Ecol. Manage.* 167: 91-102.

Asner, G. & Vitousek, P. 2005. Remote analysis of biological invasion and biogeochemical change. *Proc. Natl. Acad. Sci.* 102: 4383-4386.

Bain, G.L. 1966. *Geology and ground-water in the Durham area, North Carolina*. United State Geological Survey, Raleigh, NC, US.

Beers, T.W., Dress, P.E. & Wensel, L.C. 1966. Aspect transformation in site productivity research. *J. For.* 64: 691-692.

Beven, K.J. & Kirkby, M.J. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrol. Sci. Bull.* 24: 43-69.

Bormann, F. H. 1953. Factors determining the role of loblolly pine and sweet gum in early old-field succession in the Piedmont of North Carolina. *Ecol. Monogr.* 23: 339-358.

Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C., Bell, S.S., Benning, T.L., Carreiro, M.M. & Dawson, T.E. 2003a. An interdisciplinary and synthetic approach to ecological Boundaries. *Bioscience* 53: 717-722.

Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C. & Jones, G.C. 2003b. A framework for a theory of ecological boundaries. *Bioscience* 53: 750-758.

Carpino, E.A. 1998. Ecological Determinants of Hurricane Damage in a Southeastern Piedmont Forest. M.E.M. Thesis.

Duke University, Durham, NC, US.

Chavez, P.S. 1988. An improved dark-object subtraction technique for atmospheric correction of multispectral data. *Remote Sens. Environ.* 24: 459-479.

Christensen, N.L. & Peet, R.K. 1984. Convergence during secondary forest succession. *J. Ecol.* 72: 25-36.

Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.

Gobron, N., Pinty, B. & Verstraete, M.M. 1997. Theoretical limits to the estimation of the leaf area index on the basis of visible and near-infrared remote sensing data. *IEEE Trans. Geosci. Remote Sens.* 35: 1438-1445.

Hall, F.G., Botkin, D.B., Strebel, D.E., Woods, K.D. & Goetz, S.J. 1991. Large-scale patterns of forest succession as determined by remote-sensing. *Ecology* 72: 628-640.

Huston, M. & Smith, T. 1987. Plant succession – Life-history and competition. *Am. Nat.* 130: 168-198.

Johnson, R. & Kasischke, E.S. 1998. Change vector analysis: a technique for the multispectral monitoring of land cover and condition. *Int. J. Remote Sens.* 19: 411-426.

Kasischke, E.S. & French, N.H. 1997. Constraints on using AVHRR composite index imagery to study patterns of vegetation cover in boreal forests. *Int. J. Remote Sens.* 18: 2403-2426.

Kasischke, E.S., French, N.H. & Bourgeau-Chavez, L.L. 2000. Using satellite data to monitor fire-related processes in boreal forests. In: Kasischke, E.S. & Stocks, B.J. (eds.) *Fire, climate, and carbon cycling in the boreal forest,* pp. 406-422. Springer-Verlag, New York, NY, US.

Keitt, T., Bjørnstad, O.N., Dixon, P.M. & Citron-Pousty, S. 2002. Accounting for spatial pattern when modeling organism-environment interactions. *Ecography* 25: 616-625.

Lambin, E. & Strahler, A. 1994. Change-vector analysis in multitemporal space: a tool to detect and categorize land-cover change processes using high temporal-resolution data. *Remote Sens. Environ.* 48: 231-244.

Lawrence, R.L. & Ripple, W.J. 2000. Fifteen years of revegetation of Mount St. Helens: A landscape-scale analysis. *Ecology* 81: 2742-2752.

Legendre, P. & Legendre, L. 1998. *Numerical ecology,* 2nd. ed. Elsevier Science, Amsterdam, NL.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.

Lorimer, C.G. 1984. Development of the red maple understory in northeastern oak forests. *For. Sci.* 30:3-22.

Mast, J., Veblen, T. & Linhart, Y. 1998. Disturbance and climatic influences on age structure of ponderosa pine at the pine/grassland ecotone, Colorado Front Range. *J. Biogeogr.* 25: 743-755.

McDonald, R.I. & Urban, D.L. 2004. Forest edges and tree growth rates in the North Carolina Piedmont. *Ecology* 85: 2258-2265.

McDonald, R.I. & Urban, D.L. 2006. Spatially varying rules of land-cover change: lessons from a case study. *J. Landsc. Urban Plann.* 74: 7-20.

McDonald, R.I., Peet, R.K. & Urban, D.L. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea* 67: 84-95.

McDonald, R.I., Peet, R.K. & Urban, D.L. 2003. Spatial pattern of oak regeneration limitation in a complex forest environment. *J. Veg. Sci.* 14: 441-450.

Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *Am. Midl. Nat.* 28: 1-126.

Pan, D., Domon, G., Marceau, D. & Bouchard, A. 2001. Spatial pattern of coniferous and deciduous forest patches in an Eastern North American agricultural landscape: The influence of land use and physical attributes. *Landscape Ecol.* 16: 99-110.

Pasch, R.J. & Avila, L.A. 1999. Atlantic hurricane season of 1996. *Month. Weather Rev.* 127: 581-610.

Peet, R.K. & Christensen, N.L. 1980. Succession: A population process. *Vegetatio* 43: 131-140.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (ed.) *Long-term studies in ecology: Approaches and alternatives*, pp. 110-135. Springer-Verlag, New York, NY, US.

Pindyck, R.S. & Rubinfeld, D.L. 1998. *Econometric models, economic forecasts*. Irwin, McGraw-Hill, New York, NY, US.

Price, K. & Jakubauskas, M. 1998. Spectral retrogression and insect damage in lodgepole pine successional forests. *Int. J. Remote Sens.* 19: 1627-1632.

Riley, J.M. & Jones, R.H. 2003. Factors limiting regeneration of *Quercus alba* and *Cornus florida* in formerly cultivated coastal plain sites, South Carolina. *For. Ecol. Manage.* 177: 571-586.

Smith, T.M. & Urban, D.L. 1988. Scale and resolution of forest structural pattern. *Vegetatio* 74: 143-150.

Song, C. & Woodcock, C.E. 2002. The spatial manifestation of forest succession in optical imagery: The potential for multiresolution imagery. *Remote Sens. Environ.* 82: 271-284.

Song, C., Woodcock, C.E., Seto, K.C., Lenney, M.P. &Macomber, S.A. 2001. Classification and change detection using landsat TM Data: When and how to correct atmospheric effects? *Remote Sens. Environ.* 75: 230-244.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. *Am. Nat.* 125: 827-852.

Trimble, S.W. 1974. *Man-induced soil erosion on the southern Piedmont.* Soil Conservation Society of America, Ankeny, IA, US.

Tucker, C.J. 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sens. Environ.* 8: 127-150.

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