

Seeing the forest for the heterogeneous trees: stand-scale resource distributions emerge from tree-scale structure

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Abstract. Forest ecosystem processes depend on local interactions that are modified by the spatial pattern of trees and resources. Effects of resource supplies on processes such as regeneration are increasingly well understood, yet we have few tools to compare resource heterogeneity among forests that differ in structural complexity. We used a neighborhood approach to examine understory light and nutrient availability in a well-replicated and large-scale variable-retention harvesting experiment in a red pine forest in Minnesota, USA. The experiment included an unharvested control and three harvesting treatments with similar tree abundance but different patterns of retention (evenly dispersed as well as aggregated retention achieved by cutting 0.1- or 0.3-ha gaps). We measured light and soil nutrients across all treatments and mapped trees around each sample point to develop an index of neighborhood effects (NI). Field data and simulation modeling were used to test hypotheses that the mean and heterogeneity of resource availability would increase with patchiness because of greater variation in competitive environments. Our treatments dramatically altered the types and abundances of competitive neighborhoods (NI) in each stand and resulted in significantly nonlinear relationships of light, nitrogen and phosphorus availability to NI. Hence, the distribution of neighborhoods in each treatment had a significant impact on resource availability and heterogeneity. In dense control stands, neighborhood variation had little impact on resource availability, whereas in more open stands (retention treatments), it had large effects on light and modest effects on soil nutrients. Our results demonstrate that tree spatial pattern can affect resource availability and heterogeneity in explainable and predictable ways, and that neighborhood models provide a useful tool for scaling heterogeneity from the individual tree to the stand. These insights are needed to anticipate the outcomes of silvicultural manipulations and should become more holistically integrated into both basic ecological and management science.

Key words: aggregate retention silviculture; competition; dispersal patterns; forest structure; gap size; heterogeneity; light; likelihood modeling; neighborhood index; nutrients; *Pinus resinosa*; variable-retention harvesting.

INTRODUCTION

Forests are complex, adaptive systems that vary in time and space (Puettmann et al. 2008). Variation in the spatial patterning of trees and the resulting distribution of soil and light resources drives community and ecosystem dynamics, from regeneration and growth (Dovciak et al. 2001, Palik et al. 2003, Zou et al. 2005) to maintenance of species diversity (Halpern and Spies 1995). Ecologists have long recognized the importance of heterogeneity in ecosystem structure as a regulator of composition and function, yet forest management has been slow to incorporate an appreciation of heterogeneity into management approaches (Puettmann et al.

2008). Instead, forests have largely been managed as “homogeneous” units (i.e., stands); managers have ignored heterogeneity or more often have manipulated stands to maximize homogeneity. This approach arose from application of an agricultural production paradigm, in which trees were considered the only productive component of a forest and other biotic components of the ecosystem were manipulated to concentrate productivity on trees. As alternative ecosystem management objectives, such as resiliency and adaptability, maintenance of ecosystem diversity, and provision of ecosystem services, become more prevalent, a new paradigm that recognizes heterogeneity and manages for complexity is emerging (Puettmann et al. 2008).

A number of large-scale silvicultural experiments have begun to explore strategies to incorporate heterogeneity into forest management. Often, these take the form of variable-retention harvesting experiments (VRH) that

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manipulate the type, amount, and spatial pattern of structures (e.g., live trees, dead wood) retained during harvest (Aubry et al. 2004, Palik et al. 2005, Seymour et al. 2006). VRH approaches have their origin in an appreciation of the structural legacies and heterogeneity created by natural disturbance. Rarely are organic structures completely consumed or removed by natural disturbances, such that often there remains a rich legacy of the previous forest that influences ecosystem recovery and development (Franklin et al. 2002). Mature trees are the primary legacy structure on which VRH approaches focus. The spatial configuration of those trees and canopy gaps directly influence patterns of resource availability in the forest understory (Battaglia et al. 2002, Coates et al. 2003, Sprugel et al. 2009).

Understanding how the spatial pattern of trees drives heterogeneity of understory light and soil resources is a critical step for understanding responses of regeneration (i.e., tree seedlings) to overstory structure, because resource availability and competition are likely to be the primary drivers of seedling growth and survival (Coates et al. 2003, Kobe 2006). However, the influence of structural heterogeneity on resource availability at different spatial scales remains poorly understood. One model posits that the overall level of resource availability at any point in a forest is a nonlinear function of competitor abundance and influence in the immediate tree neighborhood (Goldberg 1987, Palik et al. 2003). In this resource response model (sensu Goldberg 1987), resources should be low across a wide range of competitor abundance, increasing rapidly only at low levels of competition (Palik et al. 2003). Changes in forest canopy structure that result from natural disturbances or harvesting can alter the pattern of competitors in a stand, and therefore alter resource distributions (Battaglia et al. 2002, Coates et al. 2003, Sprugel et al. 2009). However, stand-scale effects of tree pattern on resource availability have rarely been demonstrated in long-term experimental studies (Coates et al. 2003, Palik et al. 2003). Understanding such relationships is needed if forest managers are to predict regeneration responses in forests managed for increased structural complexity.

Our objective was to determine the effects of tree spatial pattern on the neighborhood-scale heterogeneity of resources within stands, and the average availability of resources across stands. We did this in two complementary ways. First, we used field data to estimate average stand-level resource supplies, and then developed empirical resource response curves for both soil and light resources as a function of the structure (e.g., density and spatial arrangement) of the surrounding tree neighborhood. Second, we used these empirical relationships to predict the resource distributions for simulated stands with different spatial patterns. This approach is based on our assumption that neighborhood-scale processes are most important for determining local resource supplies and individual tree performance; hence a forest stand is most appropriately

viewed as a collection of unique neighborhoods. Stand-level processes should therefore depend on the types and distribution of neighborhoods that the stand contains.

Our study uses a VRH experiment implemented in a *Pinus resinosa* (red pine) ecosystem in north-central Minnesota, USA (Palik and Zasada 2003), in which spatial pattern of overstory retention varied while residual tree abundance was held relatively constant. Our experiment included three overstory treatments (partial harvest with residual trees dispersed evenly throughout the stand and patch cutting that created either 0.1- or 0.3-ha gaps in a forest matrix) and an unharvested control. We measured light and soil nitrogen and phosphorus availability over time. Based on the expected nonlinear relationship between competitor abundance and resource availability, we hypothesized that forests with equivalent average basal area would have higher stand-level resource availability in patchy vs. uniform stands due to differences in the distribution (types and abundances) of competitive neighborhoods. Furthermore, we expected that spatial variation in resource availability would be greater in patchy forests because of greater heterogeneity in competitive environments across a stand. We tested these hypotheses empirically, using field-collected data, and in the abstract, using modeled data for simulated forest stands.

METHODS

Study area

We conducted the experiment in largely single-cohort, monotypic red pine forests in the Chippewa National Forest in north-central Minnesota, USA. The site has a cold-temperate climate with mean annual temperatures of 3.9°C and mean annual precipitation of 70.0 cm. The study area contains outwash and ice contact landforms characterized by deep-sand parent materials. Soils are excessively to well-drained, nutrient-poor loamy sands. This ecosystem is dominated by red pine in the overstory (90% of total basal area), with smaller amounts of *Pinus strobus* (eastern white pine), *Acer rubrum* (red maple), *Populus tremuloides* (trembling aspen), *Populus grandidentata* (bigtooth aspen), *Betula papyrifera* (paper birch), *Abies balsamea* (balsam fir), *Picea glauca* (white spruce), *Quercus rubra* (northern red oak), and *Quercus macrocarpa* (bur oak). The understory is dominated by *Corylus cornuta* (beaked hazel) and *Amelanchier* spp. (serviceberry). Stands were estimated to be ~85 years old at the time of treatments, broadly even-aged, and naturally regenerated after early 20th century logging and wildfires.

Experimental design

Our study was implemented as a randomized-block split-plot design replicated four times. It included three retention harvest treatments and an unharvested control (Fig. 1), split by two understory removal treatments (woody shrubs removed, control). Each block was ~64

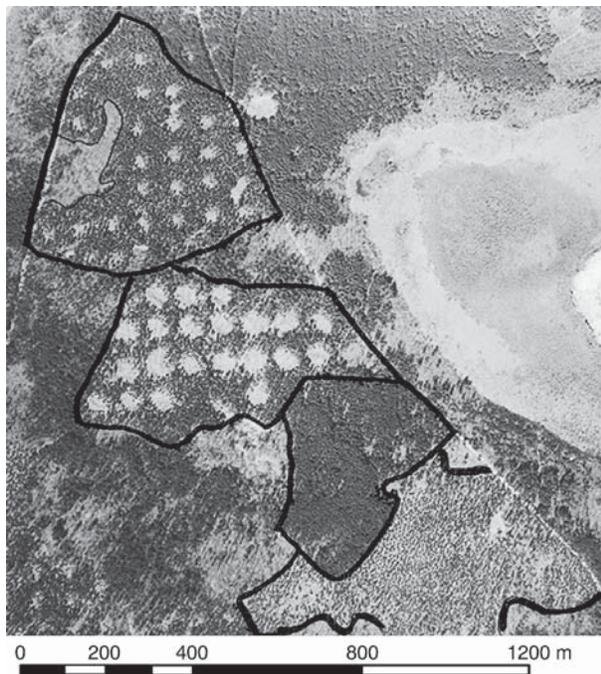


FIG. 1. Aerial photograph of a single experimental block in the study area in red pine (*Pinus resinosa*) forest in the Chippewa National Forest, north-central Minnesota, USA. Overstory treatments (outlined polygons) from top to bottom are: aggregate retention small gap, aggregate retention large gap, control, and dispersed retention. Blocks were replicated four times on the landscape.

ha with four ~16-ha treatment stands. Blocking (rather than random treatment allocation) was used due to the large spatial extent of the study (blocks were separated by up to 7 km). Although the forest type was the same in each block, and structural and compositional conditions were very similar, there probably still was natural variation in environmental and forest conditions across such a large geographic region. Stands were logged in winter 2002/2003 (Palik et al. 2003, Atwell et al. 2008). The overstory treatments included a partial harvest with residual trees dispersed evenly throughout the stand (dispersed) and two aggregated treatments created through patch cutting of 0.1-ha gaps (small gap) or 0.3-ha gaps (large gap) in a forest matrix. The control forest had an average basal area of 36 m²/ha, and ~55% was removed in the harvest, leaving a near-constant residual basal area (~16 m²/ha) in the three harvest treatments. In the aggregate retention treatments, all trees were removed from the gaps, and ~36% of the basal area was removed from the forest matrix to achieve similar basal area across harvest treatments (Appendix A: Table A1). Thinning across all treatments was spread randomly among tree size classes. Not surprisingly, given the scale of these experimental treatments, modest differences in residual basal area occurred among the three cut retention treatments (Appendix A: Table A1). On half of each overstory treatment, understory shrubs and aspen suckers were cut

annually (from 2002 to 2008) using brush saws. Other species of regenerating trees were not removed during brushing. Here, we limit our analysis to stands with woody shrubs removed, thereby reducing variation in resource availability due to understory vegetation. Although shrub effects on resource supplies are important (e.g., Montgomery et al. 2010) and will be addressed elsewhere (R. Montgomery, S. Boyden, P. B. Palik, and P. B. Reich, *unpublished manuscript*), isolation of canopy impacts is necessary to test the influence of tree pattern on resource availability and heterogeneity (Palik et al. 2003).

Neighborhood mapping

Before implementing the overstory treatments, we randomly located 10 permanent sample points within each overstory treatment (4 overstory × 4 replicate blocks × 10 point = 160 points). We mapped and measured the diameter at breast height (1.3 m) of all trees >10 cm dbh in a 16.1 m radius (1/5 acre) around each point (average canopy tree height was 14.9 m). After harvesting was completed, 2–7 new sample points were established in each of the aggregate retention treatments to adequately capture the range and distribution of structural variation created. This resulted in a total of 192 permanent sample points.

Resource availability

To evaluate the effects of experimental treatments on resource availability, we measured light and nutrient availability at each of our sample points. We measured light availability during the 2004, 2005, 2007, and 2008 growing season (June–August) using a LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, Nebraska, USA) or a sunfleck ceptometer (Decagon Devices, Pullman, Washington, USA). Sensors were used in paired mode, with one sensor located in an open clearing serving as the above-canopy sensor and another sensor taking readings at individual plots. Measurements were made on uniformly overcast days or at dawn and dusk at 1 m above the forest floor. Four measurements taken in each cardinal direction were averaged at each point during every sampling year. This approach allowed calculation of percentage transmittance of light. Instantaneous measures of percentage diffuse transmittance are effective estimates of seasonal light environment (Parent and Messier 1996, Machado and Reich 1999) and are especially relevant to juvenile tree growth and survival (Kobe and Hogarth 2007, Tobin and Reich 2009).

Nutrient availability was assessed using ion exchange resins. Resins exchange NO₃⁻, PO₄⁻, and NH₄⁺, providing an index of inorganic nutrient availability. We enclosed ~3 g of mixed-bed resin in a small bag made of nylon stocking and placed two bags ~2 m on either side of our sample points in the mineral soil layer (~5 cm depth). Resin bags were installed in the field in May and removed in late September/early October of 2007. In the lab, resin bags were rinsed in deionized

water and air-dried. The resin beads were removed from their bags, weighed, and extracted with 2 mol/L NaCl in 0.1 mol/L HCl. Extractant was analyzed on a Lachat QuikChem 800 Automated Ion Analyzer (Hach, Loveland, Colorado, USA) at the analytical lab of the USDA Forest Service, Northern Research Station, Grand Rapids, Minnesota, USA. This approach yields nutrients on a per gram resin basis. Our resin bag nutrient assay is reflective of both supply and demand: greater nutrients may reflect reduced demand or enhanced supply. Because we do not know the exact mechanism, we consider our assay to be a measure of potential nutrient availability to the roots of a seedling.

Statistical analysis: stand scale

We analyzed average percentage transmittance data (2004, 2005, 2007, 2008) and total resin-available N and P in 2007 using a mixed-model ANOVA for block (r), overstory treatment (i), and plot (k). The form of the model was

$$Y_{r(ik)} = \mu + \alpha_i + \eta_{r(i)} + \varepsilon_{r(ik)}$$

$$\eta_{r(i)} \sim \mathcal{N}(0, \sigma_{\text{block}}^2)$$

$$\varepsilon_{r(ik)} \sim \mathcal{N}(0, \sigma_{\text{error}}^2).$$

We used orthogonal contrasts to compare uncut with cut, dispersed with aggregate retention, and small with large gaps. We used Tukey's post hoc tests to compare all pairwise differences. Data were transformed when necessary to meet assumptions of parametric statistical tests.

Statistical analysis: neighborhood scale

Resource response models.—We modeled average percentage light transmittance data (2004, 2005, 2007, 2008) and total resin-available N and P in 2007 as a function of the neighborhood structure surrounding the measurement point. This approach assumes that resource supply depends on both the size and spatial arrangement of neighboring trees, calculated with a neighborhood index (NI; described in *Neighborhood effects*). We used our field data to test four candidate models that represent a range of biologically realistic responses of resource supplies to resource demand: a linear model ($y = \text{Max} + C \times \text{NI}$); a quadratic model ($y = \text{Max} + (C \times \text{NI}) + (D \times \text{NI}^2)$); a decay curve ($y = \text{Max} / (1 + C \times \text{NI})$); and an exponential model ($y = \text{Max} \times \exp(-C \times \text{NI})$). Max is the maximum resource level in the absence of any trees, or the y -intercept, C and D are slope or shape parameters, and NI is the neighborhood index, which is a unique index parameterized separately for each of the measured resources. We parameterized and compared NI and the four candidate resource models as described in *Parameter estimation and model selection*.

Neighborhood effects

We quantified neighborhood effects (NI) around sampling points as a function of the size and proximity of surrounding trees. We used a simple, distance-dependent summation equation that has been effectively applied in various forms to predict individual tree growth (Bella 1971, Stoll et al. 1994, Canham et al. 2004, Uriarte et al. 2004). For $i = 1$ to n neighbors within a given radius (r), the neighborhood index (NI) for a given point is given by

$$\text{NI}_r = \sum_{i=1}^n \frac{\text{dbh}_i^\alpha}{d^\beta}. \quad (1)$$

This equation assumes that a neighbor's competitive impact increases as a direct function of its diameter (dbh), and as an inverse function of the distance from the focal tree (d). The shape, or importance, of these size and distance effects is controlled by the parameters α and β .

Neighborhood calculations have traditionally used arbitrarily fixed values for scaling and shaping parameters as well as neighborhood radius, yet these parameters potentially have a large impact on model performance and there is no theoretical basis for assuming that they should be equivalent across different ecological systems (Silander and Pacala 1985, Canham et al. 2004, Uriarte et al. 2004). We therefore estimated optimal parameter values for light (NI_L), nitrogen (NI_N), and phosphorus (NI_P) separately, as described in the next section.

Parameter estimation and model selection.—We used simulated annealing to find the best parameter values for our three neighborhood indexes and to select the best resource response models. This is a global optimization procedure (Goffe et al. 1994) that simultaneously converges, over a minimum of 100 000 iterations, on a set of parameter values that maximize the log likelihood. Unlike least squares estimation, maximum likelihood estimation approximates the likelihood of observing the actual data, given each of the candidate models. The program was written and provided by Charles Canham and was run in the R language (R Foundation for Statistical Computing, Vienna, Austria). Alternative resource response models were compared using Akaike's Information Criterion adjusted for small sample sizes (AIC_c). AIC_c entails calculating the expected value of the information lost when using a model to approximate the truth; using the principle of parsimony, models are penalized for having more parameters. Lower AIC_c values indicate stronger model performance (Burnham and Anderson 1998). The strength of evidence for the best model relative to the full set of candidate models was calculated using Akaike weights. The weight of each model is the ratio of the likelihood of the model to the sum of the likelihoods for the full set of models that were compared. A weight can be thought of as the probability

TABLE 1. Light availability (transmittance, mean and confidence intervals) and resin-available inorganic phosphorus and total inorganic nitrogen (means and confidence intervals) for four overstory treatments in red pine forest, Chippewa National Forest, Minnesota, USA.

Treatment	Light transmittance, T (%)		PO_4^- availability (mg/g resin)		$\text{NH}_4^+ + \text{NO}_3^-$ availability (mg/g resin)	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
Control	13.7 ^a	12.3–15	0.097 ^a	0.75–0.125	0.099 ^a	0.081–0.120
Dispersed	50.6 ^b	47.8–53.5	0.190 ^{ab}	0.152–0.238	0.174 ^{ab}	0.139–0.219
Small gap	46.1 ^b	41.7–50.5	0.176 ^{ab}	0.135–0.229	0.180 ^{ab}	0.143–0.227
Large gap	58.3 ^c	53.9–62.7	0.235 ^b	0.194–0.286	0.204 ^b	0.166–0.251

Note: Means with different lowercase letters are significantly different in Tukey's post hoc tests ($P < 0.05$).

of selecting that model, from the available set of candidate models, given the data.

Light modeling in simulated stands.—We simulated three 16-ha forest stands with identical average neighborhood index values ($\text{NI}_L = 0.25$) that represented idealized versions of our aggregate (small- and large-gap) and dispersed-retention treatments. Using the relationship between light and NI_L parameterized with our field data, we predicted light availability at 60 random points and then generated means and standard deviations for light availability in each simulated stand (methods are described in more detail in Appendix B).

RESULTS

Stand scale

Overstory treatments differed significantly in all measures of resource availability (Table 1). The large-gap treatment had highest mean light, N, and P availability and the uncut treatment had the lowest, with the small-gap and dispersed treatments intermediate. The dispersed and small-gap treatments did not differ significantly for any of the measures and were significantly greater than the uncut control treatment only for light availability (Table 1). In contrast, the large-gap treatment had significantly greater mean resource availability than the uncut treatment for all measures, and significantly greater mean light availability than the dispersed and small-gap treatments.

Neighborhood scale

The resource response curve for light shows the relationship between neighborhood structure (NI_L) and light availability (Fig. 2). The density, size, and distance of trees up to 14.7 m from our resource measurement points explained 75% of the variation in light (Tables 2 and 3). The low values of the α and β parameters indicated that neighbor density is more important than neighbor size (scaled by distance). The support intervals did not straddle zero, however, supporting a model that does include both size and distance. As theory predicted, neighborhood effects on light availability were strongly nonlinear (Fig. 2). The exponential shape of the resource response curve supported the hypothesis that (moving along curves from right to left) small removals of BA initially result in more modest increases in light

availability than subsequent removals of similar magnitude. Individual retention treatments created a limited range of competitive neighborhoods, and therefore only captured one portion of the resource response curve. Although the control had the largest range of neighborhoods, they all fell along the asymptote, and therefore created little variation in light. Conversely, the aggregate retention treatments captured the rapidly changing part of the response curve and therefore had larger variation in light environments. Only the combination of all four treatments captured the full range of light environments from 5% to 100% light transmittance.

Frequency diagrams more clearly show how variation in neighborhood structure affected the mean and heterogeneity of light resources differently across the overstory treatments (Fig. 3, Table 1). Uncut stands had more than twice the spatial variation in competitive neighborhoods (NI_L) than all three of the retention treatments ($\text{SD} = 0.21$ vs. ≤ 0.1 ; Fig. 3A–D), but lower light levels (13.7% T , on average) and little variation in light availability (Fig. 3H). Although the aggregate retention stands had less variation in NI_L than the uncut stands, they had much greater variation in light.

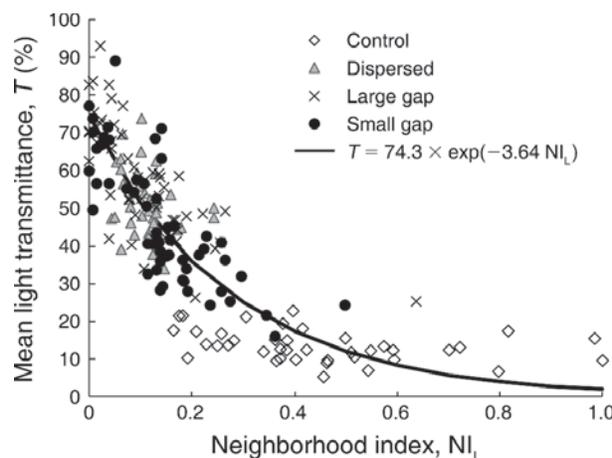


FIG. 2. Exponential relationship between the optimized neighborhood index for light (NI_L) and mean light availability (T , percentage transmittance). Data points are plotted separately by overstory treatment. Lines represent the best-fit relationship based on maximum likelihood (see Table 2).

TABLE 2. Goodness of fit (r^2) and Akaike weights for the best-fitting resource models.

Response variable	Model	r^2	ΔAIC_c	Akaike weight, w
Light	exponential	0.75	44	1
Nitrogen	decay	0.15	8	0.99
Phosphorus	decay	0.20	54	1

Notes: Results of only the best model are shown. ΔAIC_c is the difference in AIC_c between the given model and the next best model (not shown). Akaike weights can be viewed as the probability that the model would be selected as the best model, given the data (Burnham and Anderson 1998).

Although the aggregate retention treatments appear visually to have similar distributions of neighborhoods in Fig. 3, the large-gap treatment actually had many more low-competition neighborhoods: 54% of the stand fell below an NI_L of 0.1 (Fig. 3C), compared to 28% for the small gap (Fig. 3B). This translates into more “very” high light environments in the large gap (10% of the large-gap treatment had $>80\%$ light, vs. $<2\%$ for the small-gap treatment). There was an 80% loss of heterogeneity in the neighborhood structure from the uncut to dispersed cut ($SD = 0.21$ and 0.04 , respectively), yet the dispersed cut had more than twice the variation in light availability (Fig. 3E, H).

Effects of neighborhood spatial patterns on N and P availability followed the same nonlinear pattern as for light availability, but in a much more muted fashion. In contrast to results for light, the relationships of N and P availability to NI_N and NI_P were shallowly nonlinear, with a large amount of scatter and low model r^2 values (Fig. 4, Table 2). Nonlinear models did have stronger support in the data than their linear counterparts, as evidenced by the ΔAIC values >7 (Burnham and Anderson 1998). Soil resources were responsive to the size and distance of neighbors, as with light, but only up to 8–9 m away (Table 3). The flatter relationships mean that although treatments have distinct clusters on the x -axis, there is little separation of treatments along the y -axis (Fig. 4), and modest effects of treatment on soil resource supplies (Table 2). At low levels of competition there is tremendous scatter and soil resources can be very low or high, whereas at high values for NI, there is less variation and soil resources are consistently low. This is in contrast to light availability (Fig. 3), which shows similar amounts of variation at both low and high levels of competition.

Simulation models

Random sampling of the simulated forests generated NI_L distributions that differed greatly from one another (Appendix B: Fig. B1). The simulated structures had distributions broadly similar to our actual data (Fig. 3), but differed in their spread and in the abundance of open and very dense plots as a result of absence of thinning in the matrix. Light predictions based on these distributions revealed large treatment differences (Appendix B: Fig. B1D–F). The aggregate retention treatments had more light, on average, and more variable light environments than the dispersed cut. The small- and large-gap treatments had 22% and 41% more average light, respectively, than the dispersed cut. The simulated dispersed treatment had a narrower distribution than the experimental data, and the simulated large-gap treatment had more high- and low-light neighborhoods than the experimental data.

DISCUSSION

As a general rule, resource availability influences tree growth, regeneration, and forest ecosystem processes, and resource supplies are in turn modified by the plant community. Varying the spatial pattern of residual trees across space, while maintaining the same stand-level basal area, substantially altered the types and abundances of competitive neighborhoods across our treatments. Structural changes significantly but modestly impacted the availability of soil resources and markedly altered both the availability and heterogeneity of light resources, presumably as a result of changes in the amount of competition and resource use at the neighborhood scale. To our knowledge, neighborhood indexes have been used almost exclusively to directly

TABLE 3. Maximum-likelihood parameter estimates and 95% asymptotic support intervals (in parentheses) for the best-fitting resource models and neighborhood indexes.

Response	Resource model		Neighborhood index, NI		
	C	Max	Radius	α	β
Light	3.6 (3.4–3.9)	74.3 (72.1–76.5)	14.7 (14.3–14.8)	0.13 (0.09–0.15)	0.0013 (0.0001–0.053)
Nitrogen	7.2 (5.2–9.0)	0.42 (0.37–0.47)	10.0 (8.0–10.8)	0.7 (0.5–0.8)	0.3 (0.1–0.6)
Phosphorus	7.8 (7.5–8.0)	0.46 (0.45–0.47)	9.0 (8.8–9.4)	0.006 (0.001–0.060)	0.62 (0.50–0.72)

Notes: C is a shape parameter that controls the steepness of the declining function; Max is the y -intercept, or the maximum resource level in the absence of any trees; Radius defines the optimal radius (in meters) of the area around each focal tree used to calculate NI; and α and β are scaling parameters that control the effect of tree neighbor size and distance, respectively, on resource availability. All models were distance dependent (Eq. 1) because β was estimated to be >0 . Asymptotic support intervals are measures of support for parameter estimates based on profile likelihood and are roughly analogous to 95% confidence intervals. Equations are described in detail in *Methods*.

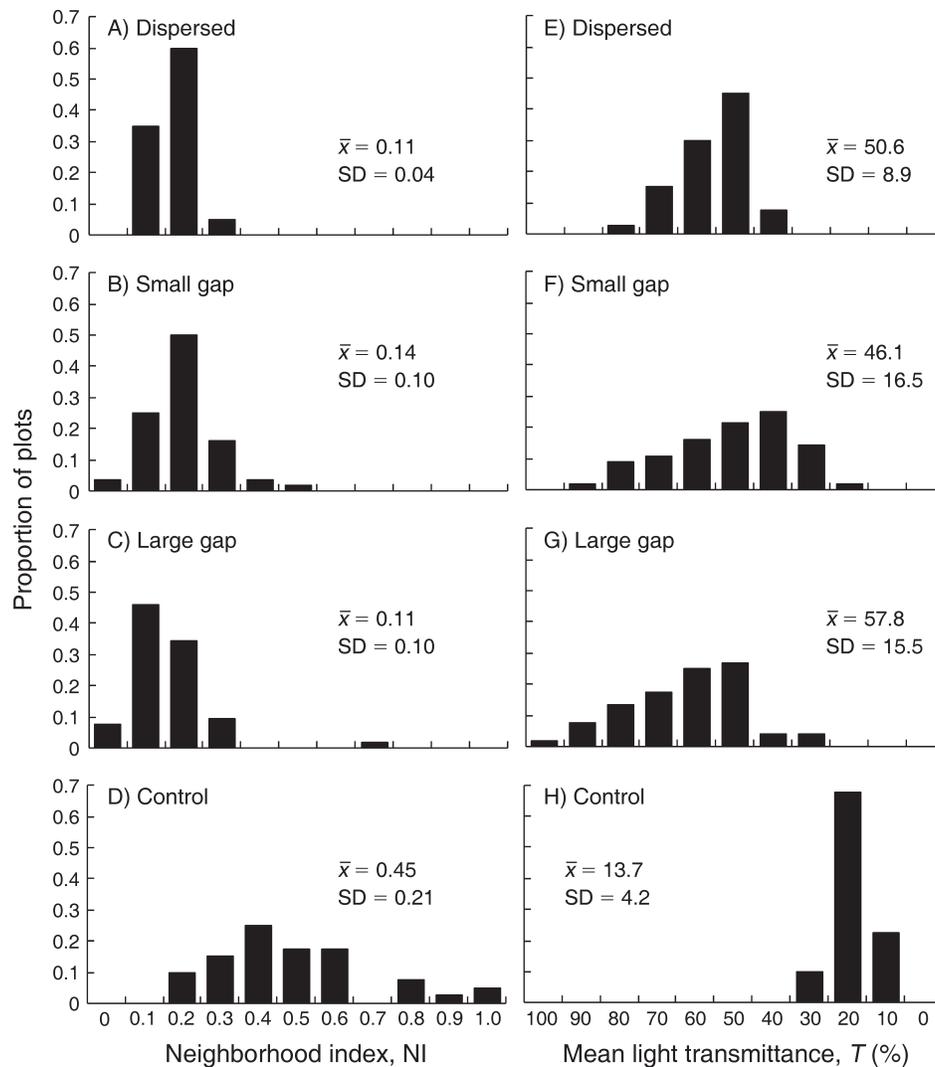


FIG. 3. Frequency distributions (proportion of plots) for the optimized neighborhood index for light (NI_L , left-hand panels) and mean light transmittance (T , right-hand panels) across the four overstorey treatments. The zero bin in all panels contains only values = 0; the remaining bins include values less than or equal to the value shown. Mean and standard deviation for each distribution are shown. See Table 3 for the parameters of NI_L .

model competitive effects on growth, survival, or other metrics of tree performance. Directly modeling the effects of neighborhood structure, or plant demand, on resource availability more closely approximates the mechanisms of tree interactions.

Mechanisms that determine resource response curves

The shapes of the relationships between the neighborhood index and resource supplies are ecologically significant and provide some insight into patterns of resource availability. We observed that at low levels of competition, light levels were consistently high but soil resources could be either high or low, supporting the idea that nutrients are inherently patchy at small spatial scales. High levels of competition, however, consistently depleted soil resources as well as light.

Light availability declined exponentially with increasing neighborhood competition (NI_L), conforming to the Beer-Lambert law, which describes light absorption through a substance. Multiple forms of the original equation have been used to describe light transmission through a forest canopy, by substituting leaf area index (LAI) or basal area (BA) for the original terms describing path length and the density of absorbing particles. In this study, we replaced these commonly used descriptors of structure with the neighborhood index (NI_L). The exponential relationship means that in open parts of a stand, small increases in vegetation have a larger effect on light availability than comparable increases in a dense stand, because in the latter the majority of the light has been preempted at even intermediate tree densities. This pattern has important

consequences for resource distributions and forest stand dynamics.

Consequences of resource response curves

The distribution of neighborhoods within a stand, and where they are positioned along the resource response curve, determines resource heterogeneity in the stand. Our light data (both empirical and modeled) clearly demonstrate that any structural variation in high-light environments creates heterogeneous light conditions (e.g., dispersed cut), whereas structural variation in low-light conditions creates little variation in light availability (e.g., control). The large change in light per unit shift in NI_L at low NI_L values means that two stands with similar average structures can have different average resource environments as a result of the distribution of neighborhoods across each stand. For instance, in the aggregate retention treatments, we found higher average light levels in the large-gap than the small-gap treatment, despite similar mean structures. Conversely, if a stand contains all neighborhoods above a certain threshold of NI_L , any changes in structure or increases in competition would not significantly alter light supplies because they are mostly depleted, which results in very little stand-level resource heterogeneity under these conditions. The overall loss of variation in neighborhood structure with both aggregate and dispersed retention may be surprising, given the generally held assumption that gaps increase forest heterogeneity. However, natural disturbance elsewhere in Minnesota that led to decreased basal area also made forest structure less, not more, heterogeneous: tree basal area losses ranging from 30% to 60% decreased heterogeneity in 12 m radius neighborhoods (Rich et al. 2010). Our red pine data indicate that when gap creation is accompanied by thinning in the matrix between gaps, a forest may ultimately have less diverse neighborhood structures depending upon the initial conditions. However, gap creation still increases resource variation due to the presence of low-competition neighborhoods.

Modeling light heterogeneity

Our experimental data supported our hypothesis that aggregate retention would increase mean light availability and heterogeneity relative to dispersed retention, due to greater variation in competitive environments. However, this was only apparent in large-gap vs. dispersed treatments. Light levels in the small-gap and dispersed treatments did not differ significantly, which may partly be attributable to the irregularities in cutting among treatments. The simulated retention treatments eliminated those irregularities and reduced the level of thinning, creating significantly different light distributions as a result. Despite identical average neighborhood structure, the three simulated stands had very different light environments due to their structural heterogeneity. Patchy tree distributions increased the average light and the spatial heterogeneity of light reaching the forest

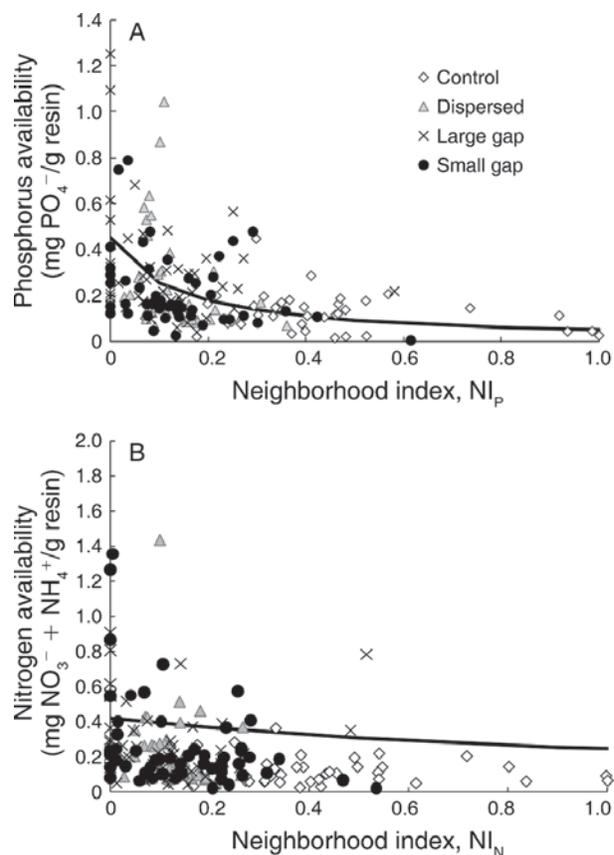


FIG. 4. Relationship between the neighborhood index and (A) available soil phosphorus and (B) available soil nitrogen. Data points are plotted separately by overstory treatment. Lines represent the best-fit relationship based on maximum likelihood (see Table 1).

understory, and this effect was magnified as the gap size increased. There was a 41% increase in light from the dispersed to the large-gap treatment, a considerable difference in mean resource supply for two stands with similar mean structural conditions. Both our experimental and simulation results support and extend prior modeling studies on the immediate effects of silvicultural treatments on light regimes (Coates et al. 2003, Sprugel et al. 2009). Clearly, looking beyond average conditions enriches our understanding of complex forest ecosystems.

Our empirical modeling and simulation demonstrate how neighborhood-scale structural distributions can be used to understand and predict stand-level resource patterns once a resource response curve is generated. This approach effectively scales from the individual tree neighborhood to the landscape. We present a generalized resource response model (Fig. 5) for illustration. The ability to accurately scale to the stand scale depends on knowing the shape of the resource response curve for the specific resource and forest type of interest. In this study the curve applies primarily to light resources, secondarily to phosphorus, and only minimally to nitrogen availability; but more generally could be

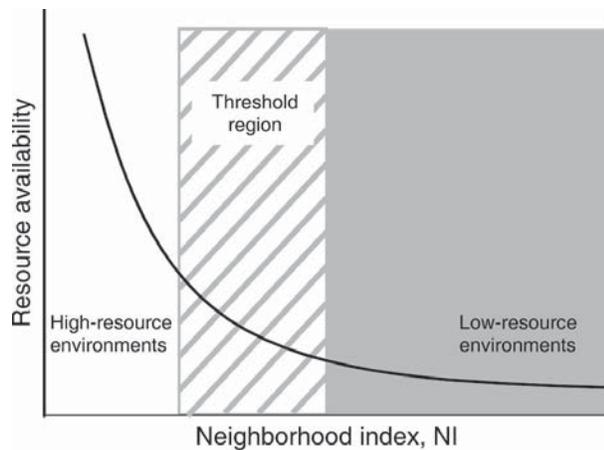


FIG. 5. Nonlinear resource response model. The threshold region represents values of the neighborhood index above which resources are largely unchanging and depleted, and below which resource levels are high and change rapidly with small changes in structure. The threshold is represented as a region because the shape of the resource response curve will depend on species composition and the type of resource being modeled.

applicable to any process that has a strong and curvilinear response to competition.

In our resource response model (Fig. 5), the structural threshold, below which resources show little variation and above which they increase rapidly, will depend strongly on the nature of resource competition (i.e., symmetric vs. asymmetric), as well as physical properties of the vegetation itself. For light, tree species with high leaf area indexes and broad crown shapes will have a threshold that occurs at lower stand densities because light will be preempted more efficiently, whereas species with narrower architecture and lower leaf area will have a threshold that is shifted right, toward higher NI_L values. The threshold region represents a highly interesting ecological feature in any forest; although large changes in neighborhood structure create little variation in resource supplies in this region, even small changes in resources may lead to large changes in growth and survival, because tree growth tends to increase most rapidly at low resource levels and plateau at higher resource levels (Walters and Reich 2000, Montgomery and Chazdon 2001). Our model potentially applies to any ecological process that has a nonlinear response to structural heterogeneity, such as seed dispersal (Nathan and Mueller-Landau 2000), patterns of mycorrhizal infection (Dickie and Reich 2005), or species-specific impacts on litterfall and soil chemistry (Gomez-Aparicio and Canham 2008). Meaningful changes in these processes could be expected to occur only within certain ranges of neighborhood structure where there is high sensitivity of the response variable (at or above the threshold region).

Many closed-canopy forests may fall largely in the high- NI_L or low-resource portion of the curve (e.g., Parent and Messier 1996, Machado and Reich 1999,

Tobin and Reich 2009). In such forests, resource models based on structural indexes may appear ineffective, at least during periods of low disturbance severity or frequency. For example, BA is normally a strong predictor of light availability in the understory, but many studies have noted that the relationship does not hold in mature or dense forests because there is low transmittance regardless of basal area (Mitchell and Popovich 1997, Comeau 2001, Parker et al. 2002, Hale 2009). This is often discussed as a weakness in building light models using basal area, without noting that the pattern is not a flaw in the choice of predictor, but rather an inevitable consequence of the shape of the light response curve. In these forest types, even small differences in structure that place a given neighborhood in the threshold region can have ecologically significant consequences for resource supplies and understory vegetation (Kobe and Hogarth 2007, Tobin and Reich 2009).

Application

It is clear from our results that neighborhood heterogeneity resulting from differing spatial patterns of retained trees can affect the mean and variation of resource availability in ways that are mechanistically explainable and quantifiable, yet are not predictable based on average structural conditions. The implications for forest management, whether it is variable-retention harvesting approaches, old-growth restoration, or fire management, are far-reaching. The goal of VRH prescriptions, in many applications, is to deliberately create greater heterogeneity in the structural conditions left after harvest. The uncertain consequences of doing this for resource supplies, regeneration dynamics, and wood productivity are widespread. Understanding how structural heterogeneity affects resource supply has particular application to management of mixed-species stands, where those species differ in tolerance of low-resource conditions. For example, the three native pine species in our study ecosystem, *Pinus strobus*, *P. resinosa*, and *P. banksiana* (jack pine), differ in shade tolerance: from mid-tolerant, to intolerant, to very intolerant, respectively. Using information derived from our work, managers could deliberately manipulate the structural heterogeneity of stands to shift the distribution of neighborhoods along the light response curve, favoring different species in different locations, while still maintaining structural complexity. Similarly, managers interested in maximizing productivity of a regenerating cohort of trees could manipulate the spatial pattern of residual trees to shift the neighborhood distribution to higher light environments, thereby favoring growth of faster growing intolerant species, while at the same time maintaining structural complexity of the stand through retention.

Such insight is needed to better anticipate the probable outcomes of silvicultural manipulations in similar forest types and should become more holistically

integrated into both basic ecological and management science. Because of the difficulty with incorporating direct light readings into stand prescriptions, a structure-based light transmittance model, like the one presented here, may be a useful tool for forest management. Equally important, as management increasingly focuses on alternative goals, such as restoring old-growth structure or mimicking natural disturbance regimes, understanding resource outcomes of heterogeneity, as well as average stand conditions, will provide more meaningful and effective strategies for managing complex forest stands.

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SUPPLEMENTAL MATERIAL

Appendix A

Treatment averages and standard deviations for residual basal areas remaining following tree removal (*Ecological Archives* A022-083-A1).

Appendix B

A comparison of neighborhood and light distributions for three simulated forest stands with different overstory patterns (*Ecological Archives* A022-083-A2).