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ARTICLE

Interspecific competition limits the realized niche of *Fraxinus nigra* along a waterlogging gradient

Christopher E. Looney, Anthony W. D'Amato, Shawn Fraver, Brian J. Palik, and Lee E. Frelich

Abstract: Gradient studies of wetland forests have inferred that competition from upland tree species confines waterlogging-tolerant tree species to hydric environments. Little is known, however, about competition effects on individual-tree growth along stress gradients in wetland forests. We investigated tree growth and competition in mixed-species stands representing a waterlogging stress gradient in *Fraxinus nigra* Marsh. (black ash) forests in Minnesota, USA. Using competition indices, we examined how *F. nigra* basal area increment (BAI) responded to competition along the gradient and whether competition was size-asymmetric (as for light) or size-symmetric (as for soil resources). We modeled spatial distributions of *F. nigra* and associated tree species to assess how variation in species mixtures influenced competition. We found that although *F. nigra* BAI did not significantly differ with variations in site moisture, the importance of competition decreased as waterlogging stress increased. Competition across the gradient was primarily size-asymmetric (for light). Variation in species mixtures along the gradient was an important influence on competition. Some segregation of tree species occurred at all but the most upland site, where waterlogging stress was lowest and evidence of competition was greatest, confirming that competition from upland tree species confines *F. nigra* and potentially other waterlogging-tolerant species to hydric environments.

Key words: environmental stress gradient, black ash wetlands, size symmetry, species interactions, point pattern analysis.

Résumé : Les études sur les gradients dans les forêts de milieux humides ont conclu que la concurrence provenant d'espèces d'arbres des hautes terres confinait les espèces d'arbres tolérantes à l'engorgement des sols aux environnements hydriques. Cependant, on en sait peu sur les effets de la concurrence sur la croissance des arbres individuels le long des gradients de stress dans les forêts des milieux humides. Nous avons étudié la croissance et la concurrence des arbres dans des peuplements mixtes situés le long d'un gradient de stress lié à l'engorgement des sols dans les forêts de *Fraxinus nigra* Marsh. (frêne noir) du Minnesota, aux États-Unis. À l'aide d'indices de compétition, nous avons examiné comment l'accroissement en surface terrière (AST) de *F. nigra* réagissait à la compétition le long du gradient et si la compétition était asymétrique à la taille (comme pour la lumière) ou symétrique à la taille (comme pour les ressources du sol). Nous avons modélisé la distribution spatiale de *F. nigra* et des espèces d'arbres associées pour évaluer de quelle façon la variation des mélanges d'espèces influençait la concurrence. Nous avons constaté que même si l'AST de *F. nigra* ne variait pas significativement en fonction de l'humidité de la station, l'importance de la concurrence diminuait avec une augmentation du stress lié à l'engorgement du sol. La concurrence le long du gradient était principalement asymétrique à la taille (pour la lumière). La variation du mélange d'espèces le long du gradient influençait fortement la concurrence. Une certaine ségrégation des espèces d'arbres s'est produite sur toutes les stations à l'exception des plus hautes terres où le stress lié à l'engorgement du sol était le plus faible et la concurrence semblait la plus forte. Ceci confirme que la concurrence des espèces d'arbres des hautes terres confine *F. nigra* aux environnements hydriques, ce qui est aussi potentiellement le cas d'autres espèces tolérantes à l'engorgement des sols. [Traduit par la Rédaction]

Mots-clés : gradient de stress environnemental, frêne noir des milieux humides, symétrie due à la taille, interactions interspécifiques, analyse d'agrégat spatial.

Introduction

Variations in resource availability across a given landscape can strongly influence plant–plant interactions, affecting the growth, composition, size, and spatial distributions of plant populations (Keddy 2001). In forest ecosystems, topographic variation in soil moisture can create stress gradients with implications for tree growth and forest composition (Dymond et al. 2016). This effect may be especially dramatic in wetland forests where relatively minor topographic changes can alter tree exposure to waterlogging stress, reflecting the magnitude, timing, and duration of soil saturation (Dudek et al. 1998).

In upland forests, topographic variation can influence the nature of tree–tree competition and may even shift tree–tree interactions along an abiotic stress gradient from competition to facilitation (Callaway 2007). Topographic variation is also theorized to shift tree–tree competition from size-asymmetric (as for light) to size-symmetric (as for soil resources) with increasing stress (Coomes and Grubb 2000), a pattern that has been observed along a topographic gradient in New Zealand *Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole (mountain beech) forests (Coomes and Allen 2007). Species traits may interact with variations in abiotic stress to influence the growth response to competition, as

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evidenced by increased growth of *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) in stands with poor soils and two-species combinations, as opposed to pure stands, along a Dutch soil fertility gradient (Lu et al. 2018).

Gradient studies of wetland forests have focused on the longer term population-level outcomes of competition (e.g., Denneler et al. 2000), rather than on the shorter term influence of competition on individual-tree growth (sensu Keddy 2001). Denneler et al. (2000) observed that abiotic factors alone failed to account for the confinement of boreal wetland tree species to hydric sites along a flood gradient in Quebec and suggested that competition may play an additional role. In a gradient study of mixed-species floodplain forests in Florida before and after dam construction, Smith et al. (2013) inferred from changes in forest composition that competition from upland tree species confines less productive, waterlogging-tolerant tree species to hydric environments.

Fraxinus nigra Marsh. (black ash) is a waterlogging-tolerant tree species that ranges from southeastern Canada to the western Great Lakes region of the USA (Wright and Rauscher 1990). In the postglacial topographic setting of northern Minnesota, USA, *F. nigra* occurs within an environmental gradient between mesic uplands and wet peat-influenced bottomlands (Minnesota Department of Natural Resources (MNDNR) 2003). At the mesic upland margins of the gradient, *F. nigra* occurs with hardwoods such as *Acer saccharum* Marsh. (sugar maple) and *Tilia americana* L. (American basswood), *Populus tremuloides* Michx. (quaking aspen), and *Betula* (birch) spp. (MNDNR 2003). At the wet bottomland margins of the gradient, *F. nigra* is most often associated with the coniferous species *Thuja occidentalis* L. (northern white-cedar; MNDNR 2003). Variation in the traits of these *F. nigra* associated species suggests that differences in waterlogging stress may account for the dominance of *F. nigra* at the center of the gradient, where *F. nigra* helps regulate spring–summer water-table rise through evapotranspiration (Slesak et al. 2014). Anoxic soil conditions associated with waterlogging from water-table rise negatively impact the growth and survival of many species (Kozlowski 1997), and *F. nigra* may aid in the survival of less waterlogging-tolerant species on the moister sites where it is dominant (Davis et al. 2017). On sites subject to lower waterlogging stress, the intermediate shade tolerance of *F. nigra* is expected to render this species at a competitive disadvantage relative to shade-tolerant upland species such as *Acer saccharum* (Keddy and MacLellan 1990).

Previous studies of competition effects on individual-tree growth in *F. nigra* forests have focused largely on monospecific stands (Looney et al. 2016), with conflicting results (Benedict and Frelich 2008). Based on a simple measure of stand density, Benedict and Frelich (2008) found that *F. nigra* growth was higher at upland sites but that tree competition had little influence on the growth of the species at either upland or lowland sites. A subsequent study that included local variation in stand density, as well as the relative size and distance of neighboring trees, found that size-asymmetric competition limited *F. nigra* growth at the center of its moisture niche, with the effect weaker on slightly wetter sites, raising the possibility that tree–tree interactions may vary among *F. nigra* stands (Looney et al. 2016). Little is known about the influence of competition on *F. nigra* growth in the mixed-species stands at the upland and bottomland margins of its moisture niche.

To fill this knowledge gap and test the theory that competition from upland tree species confines *F. nigra* to hydric environments, we investigated the *F. nigra* growth response to competition in mixed-species stands representing a gradient of waterlogging stress at the margins of *F. nigra* forests in Minnesota, USA. Our research objectives were to determine (*i*) how the *F. nigra* growth response to competition, measured as basal area increment (BAI), varied along the gradient of waterlogging stress, (*ii*) whether *F. nigra* competition along the gradient shifted from size-asymmetric (as for light) to size-symmetric (as for soil resources) with increasing stress, and (*iii*) how variations in species mixtures reflected in tree spatial distributions influenced *F. nigra* competition along the gradient. Because *F. nigra* forests are threatened by the invasive insect emerald ash borer (EAB; *Agrilus planipennis* Fairmaire, 1888; Costanza et al. 2017), the overarching goal of our research was to better inform management strategies to maintain post-EAB forest function.

Methods

Site description

The study took place in six mixed-species *F. nigra* stands on the Chippewa National Forest in northern Minnesota, USA (Fig. 1). The climate is continental, with most precipitation occurring from May through September. Mean 1981–2010 temperatures for January and July were –13.7 and 16.5 °C, respectively, while mean precipitation totaled 742 mm·year^{-1} (PRISM Climate Group 2015).

Using the U.S. Forest Service FSVeg Database (https://www.fs.fed.us/nrm/fsveg, accessed 21 May 2014) and the Minnesota native plant community classification system (MNDNR 2003), we identified potential sites at the *F. nigra* forest margins representing a range of moisture conditions and containing a minimum of 30 trees each of *F. nigra* and at least one associated tree species with a diameter at breast height (DBH) ≥ 10 cm. We selected six sites for sampling: Wilderness Lake, Round Lake, Third River, Kupcho Run, Pigeon Lake, and Virgin Lake (Fig. 1). The Kupcho Run site was located within a multi-aged stand dating to the pre-settlement era (A.W. D'Amato and M.R. Reinikainen, unpublished data). We observed isolated treefall gaps and snags but no evidence of extensive tree mortality at any site, suggesting that the stands had experienced only minor disturbances in recent decades. Major tree and understory plant indicator species varied among sites (Table 1). The Wilderness Lake and Round Lake sites were located within 30 m of lakes, whereas no other site was located near a lake, river, or stream. Based on Soil Survey Staff (2016) data and observed site drainage features described below, water table rise above the soil surface occurs annually on all but the Wilderness Lake site. We did not note evidence of present or past beaver activity that would have altered site hydrology.

Soil type, duration of observed ponding, and depth to the water table varied by site (Table 1). In early June 2014, we observed no ponding at Wilderness Lake, which was elevated on a gently downward-sloping bluff with minimal variation in its flat surface topography. We observed vernal pooling in topographic depressions that persisted into mid-June at Round Lake, mid-July at Third River, and mid-July at Kupcho Run. The Round Lake and Third River sites were slightly sloping, whereas Kupcho Run had minimal slope. At Pigeon Lake and Virgin Lake, which were bottomland floodplain sites with large areas of topographic depression, we observed extensive ponding with minor stream flows into mid-August. To better characterize variation in depth to the water table both within and between sites, in August 2014, we used a hand trowel to sample for the presence of standing or shallow soil water (≤10 cm depth of soil surface), using a grid of 48 points with 10 m spacing (Table 1; Supplementary Fig. S1[1]). Based on soil type, observed ponding, and depth to the water table, sites increased in waterlogging stress in the following order: Wilderness Lake, Round Lake, Third River, Kupcho Run, Virgin Lake, and Pigeon Lake (Table 1).

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2018-0023.

Fig. 1. Study site locations in the Chippewa National Forest, Minnesota, USA.

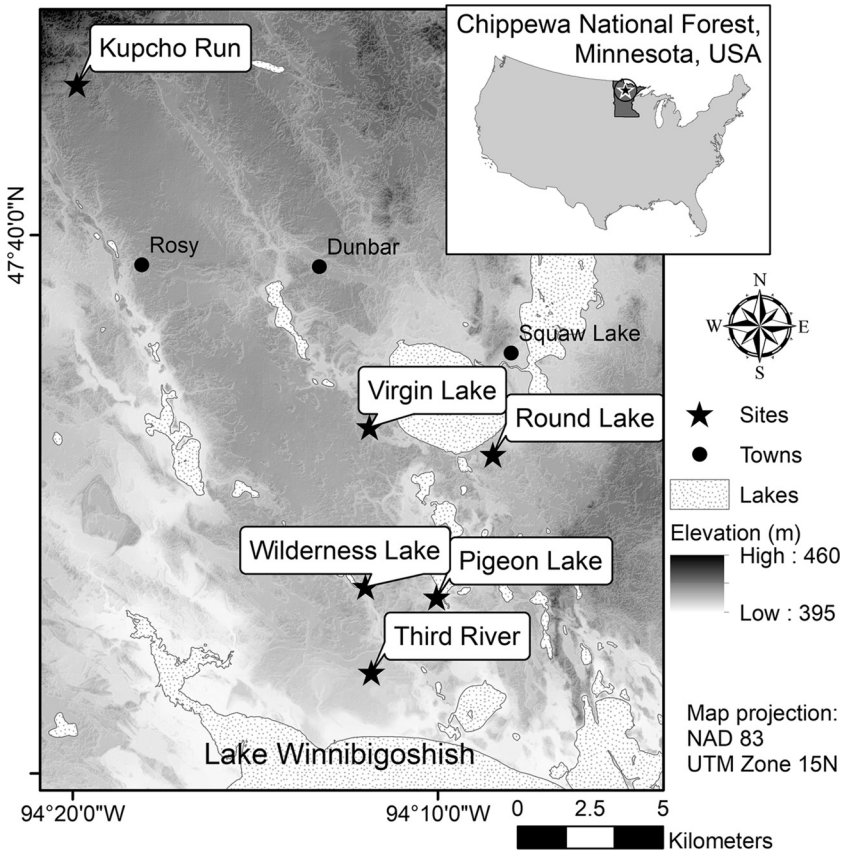


Table 1. Summary of stand and physical characteristics for six sites located in *Fraxinus nigra* forest in northern Minnesota, USA.

	Site					
	Wilderness Lake	Round Lake	Third River	Kupcho Run	Pigeon Lake	Virgin Lake
Density (trees·ha^{-1})						
ACSA	149	111	0	0	0	0
BEAL	40	34	0	0	11	83
FRNI	217	151	320	346	326	497
FRPE	57	106	80	114	6	0
POTR	6	29	183	226	0	0
THOC	3	0	0	0	117	343
TIAM	166	149	0	54	0	0
Other	66	66	23	37	66	37
Total	703	646	606	777	526	960
Total BA (m^2·ha^{-1})	34.0	28.9	21.8	31.7	39.7	54.5
FRNI % BA	25.5	15.4	38.1	26.5	69.3	47.8
QMD (cm)	21.5	17.4	28.3	20.8	41.0	25.2
Understory plants	CAPE6, COCO6	CAPE6, GLST	CACA4, ALINR	CACA4, STROC	ONOCL, CAPAP6	CAPAP6, GLST
Soil	Aquic Glossudalf	Mollic Psammaquent	Histic Humaquept	Histic Humaquept	Typic Haplosaprist	Typic Haplosaprist
Ponding	None	Mid-June	Mid-July	Mid-July	Mid-August	Mid-August
Soil water (% site)	0.0	20.8	22.9	35.4	56.2	60.4

Note: Tree species abbreviations: ACSA, *Acer saccharum*; BEAL, *Betula alleghaniensis*; FRNI, *Fraxinus nigra*; FRPE, *Fraxinus pennsylvanica*; POTR, *Populus tremuloides*; THOC, *Thuja occidentalis*; TIAM, *Tilia americana*; Other, minor species. BA, basal area. QMD, quadratic mean diameter. Plant symbols: CAPE6, *Carex pensylvanica*; COCO6, *Corylus cornuta*; GLST, *Glyceria striata*; CACA4, *Calamagrostis canadensis*; ALINR, *Alnus incana*; STROC, *Streptopus roseus*; ONOCL, *Onoclea sensibilis*; CAPAP6, *Caltha palustrus*. Ponding, observed duration of ponding in spring–summer 2014. Soil water, % of site with water at or ≤10 cm below soil surface. Sites are arranged from left to right to represent the gradient of waterlogging stress.

Field data collection

We used using QGIS software (Quantum GIS Development Team 2014) to randomly generated a single initial sampling point per stand on which we established the southwest plot corner. In summer 2014, we installed one 50 × 70 m (0.35 ha) plot per stand. We assessed all live trees ≥10 cm DBH within each plot for species, DBH, stem Cartesian (*x* and *y*) coordinates, and crown class (Oliver and Larson 1996). Trees were sampled if their bases were located within plot boundaries, regardless of lean. Each plot was divided along the *y* axis into seven 10 × 50 m transects to facilitate increment core sampling. Within each transect, we sampled every third tree by collecting a single increment core at 1.37 m above ground level, to pith when possible. To avoid directional bias, we systematically cored trees from the four cardinal directions,

Table 2. Summary of diameter-based competition indices.

Index	Type	Size symmetry	Equation	Source
CI-1	Distance independent	Symmetric	$CI_i = \sum_{j=1}^{n} d_j$	Author adapted*
CI-2	Distance independent	Asymmetric	$CI_i = \sum_{j=1}^{n} \frac{d_j}{d_i}$	Lorimer (1983)
CI-3	Distance independent	Asymmetric	$CI_i = \sum_{j=1}^{n} \left(\frac{d_j}{d_i}\right)^2$	Author adapted*
CI-4	Distance dependent	Symmetric	$CI_i = \sum_{j=1}^{n} \frac{d_j}{L_{ij}}$	Rouvinen and Kuuluvainen (1997)
CI-5	Distance dependent	Asymmetric	$CI_i = \sum_{j=1}^{n} \frac{(d_j/d_i)}{L_{ij}}$	Hegyi (1974)
CI-6	Distance dependent	Asymmetric	$CI_i = \sum_{j=1}^{n} \frac{(d_j/d_i)^2}{L_{ij}}$	Rouvinen and Kuuluvainen (1997)

Note: "Type" and "size symmetry" indicate, respectively, whether competitors are weighted by distance and treated as symmetric or asymmetric in terms of diameter, equations, and in original publications where applicable. Symbols: CI_i, competition index for the individual target tree i; d_j, diameter of a given competitor j; d_i, diameter of target tree i; L_{ij}, distance (L) between target i and competitor j. Indices are calculated for $j = 1$ where $j \neq i$.

*Adapted by authors based on indices in Rouvinen and Kuuluvainen (1997).

beginning on the north side of the stem for the first tree sampled and rotating the direction of coring 90° clockwise for each subsequent tree. We sampled *F. nigra* on all sites to assess growth. We sampled *A. saccharum*, *F. pennsylvanica*, and *T. americana* at Round Lake, *A. saccharum* and *T. americana* at Wilderness Lake, *P. tremuloides* and *F. pennsylvanica* at Third River and Kupcho Run, and *T. occidentalis* at Pigeon Lake and Virgin Lake. We relocated sampling points within stands when the initial point fell within an area lacking target tree species and randomly selected additional trees for coring in GIS when sampling yielded fewer than 30 trees of a target species. For trees selected for coring in GIS, the direction of core sampling was determined by randomly assigning trees to one of the four cardinal directions prior to collection. Increment coring of leaning trees, which were rare in species other than *T. occidentalis* and *T. americana*, was performed at the slope distance equivalent of breast height.

Sample preparation

We prepared increment cores for analysis by drying, mounting, and progressively sanding to a fineness of up to 1500 grit (Speer 2010). We scanned the prepared cores on an Epson V600 flatbed scanner to a resolution of 945 dots·cm^{-2} and measured annual ring widths using Cybis CooRecorder image analysis software (version 7.8, Cybis Electronik, Stockholm, Sweden). We cross-dated *F. nigra* cores using the marker-year method (Speer 2010). Notably narrow *Fraxinus nigra* tree rings served as marker years across all sites and corresponded with droughts (e.g., 1911, 1931, 1976–1977, and 1987–1988), as indicated by the Palmer drought severity index (National Oceanic and Atmospheric Administration (NOAA) 2015). We further verified cross-dating using the COFECHA program (Holmes 1983) and calculated interseries correlations based on 32-year spline-detrended ring-width series. For increment cores with missing piths, we estimated distance and age to pith using the Applequist pith locator method (Applequist 1958), as implemented in CooRecorder 7.8 (Larsson 2014). Pith was not estimable for a percentage of increment cores due to lack of ring curvature or extensive rot (Table 3).

We calculated annual basal area increments (BAI) inward from the most recent year of growth using a regional bark thickness equation (Dixon and Keyser 2008) to estimate inside-bark radius. We used the dplR (Bunn 2008) package for R to calculate BAI. Because our focus was on the *F. nigra* growth response to competition, associated tree species were excluded from tree-ring analysis.

Statistical analysis

Growth and competition

To help characterize the nature of inter- and intra-specific *F. nigra* competition along the waterlogging stress gradient, we selected both distance-independent and distance-dependent neighborhood competition indices (Larocque et al. 2013). Because we were particularly interested in whether competition symmetry varied along the gradient, we chose competition indices ranging from size-symmetric to highly size-asymmetric. Size-symmetric indices consider the absolute size of the competitor trees and assume that growth responds proportionally, as with competition for soil resources (Larocque et al. 2013). Size-asymmetric indices consider the size of competitor trees relative to target tree size and assume that larger trees disproportionately influence growth of smaller trees, as with competition for light (Larocque et al. 2013). We tested three distance-independent indices, CI-1, CI-2, and CI-3 (Table 2). CI-1 is the sum of neighbor stem diameters within a given radius and models competition as size-symmetric. CI-2 divides individual neighbor diameter by the diameter of the target tree and models competition as size-asymmetric. CI-3 squares the size ratio of CI-2 and, thus, models competition as more highly size-asymmetric. CI-1 and CI-3 were adapted from indices numbered CI-4 and CI-6, respectively, in Rouvinen and Kuuluvainen (1997), while CI-2 corresponds with Lorimer's (1983) index. We also tested distance-dependent versions of these indices, CI-4, CI-5, and CI-6, in which the ratio of tree sizes is divided by the intertree distance (Table 2), thereby downweighting neighbors according to distance. CI-4 models competition as size-symmetric, CI-5 as size asymmetric, and CI-6 as more highly size-asymmetric. CI-4 and CI-6 were adapted from distance-dependent indices numbered CI-9 and CI-12, respectively, in Rouvinen and Kuuluvainen (1997), while CI-5 corresponds to Hegyi's (1974) index.

We modeled the effects of competition on *F. nigra* growth using linear modeling. We used 20-year average BAI (1994–2013) as the response variable, based on the results of previous studies that found this window to be most effective in eliminating the short-term variability in growth that may be associated with climate and stand dynamics (Aakala et al. 2013). We did not examine longer periodic averages, as ingrowth and mortality would have created increasing disparities between present (2014) tree neighborhoods and past conditions. We developed a set of candidate growth models ranging from bivariate to multivariate, which included the main effects of neighborhood CI, target *F. nigra* DBH,

and a nominal site variable. Neighborhood CI was our main explanatory variable of interest. Target *F. nigra* DBH was included to control for size-related variation in *F. nigra* growth, while a nominal site variable was included to examine *F. nigra* BAI across the waterlogging gradient. In addition to these three main effects, we also examined the DBH × CI, DBH × site, and CI × site interactions, as previous research suggests that these interactions may influence the growth of *F. nigra* as much or more than the main effects of neighborhood CI or target *F. nigra* DBH (Looney et al. 2016). We included a target *F. nigra* DBH-only null model to assess whether tree size and spatial autocorrelation alone provided a plausible explanation for observed growth patterns.

We used the information-theoretic approach to evaluate the strength of evidence for each model using corrected Akaike's information criterion (AICc; Burnham and Anderson 2002) rather than using stepwise selection methods. To simplify the analysis and avoid model overfitting given the limited number of sites, models did not simultaneously contain both the DBH × site and CI × site interactions. Given the large number of candidate models, we did not present models with limited AICc support (ΔAICc > 7; Burnham and Anderson 2002). We used a significance level of $\alpha = 0.05$ for all growth-competition models but restricted the use of significance testing to description rather than inference. To meet model assumptions, BAI was log-transformed. We also applied log transformations to DBH and CI to meet the assumption of constant variance. After applying the transformations, we converted BAI, DBH, and CI to *Z* scores to compare the effects of predictors on a common scale. Multicollinearity, as indicated by variance inflation factors (VIF), was low to moderate for all models with substantial support (VIF < 5) and did not exceed tolerable levels (VIF < 10; Quinn and Keough 2003) for any model.

Adjacent trees may show similar growth as a result of shared disturbance histories or microsite characteristics, so we controlled for this by fitting an exponential variogram to each model to model spatial autocorrelation (Aakala et al. 2013). We confirmed that this autocorrelation structure was appropriate through AICc comparisons with alternative structures and by examining semivariogram plots. We used generalized least-squares modeling in the nlme package for R (Pinheiro et al. 2016), offsetting coordinates by site geographic location to stratify autocorrelation estimates. We used the lsmeans package (Lenth 2016) to investigate interaction effects where present.

We used mapped tree coordinates to define fixed-radius neighborhoods around each target tree sampled for competition analysis. We selected neighborhood size by evaluating the relative performance of the candidate models at neighborhood radii ranging from 5 to 10 m at 1 m intervals, with the top-performing models assumed to include the radii most appropriate for assessing competition in our heterogeneous stands (Fraver et al. 2014). Top model fit as indicated by ΔAICc was achieved at the 5 m radius, with model fit consistently poorer in neighborhoods with radii larger than 5 m (data not shown). Neighborhoods with radii smaller than 5 m were not investigated because preliminary analysis found that they contained target trees with no competitors. The mean number of competing trees in the 5 m radius neighborhoods ranged from 5.0 ± 0.3 at Pigeon Lake to 8.1 ± 0.3 at Virgin Lake, indicating that the 5 m radius was well adjusted to the mean tree size and density of forests in the study area as recommended by Lorimer (1983).

Tree neighborhoods were defined using buffering and intersection operations in QGIS. Within neighborhoods, we calculated six competition indices (CI; detailed below) for each target tree. We did not exclude sampled trees from plot edges, as this would have greatly reduced the number of trees available for study. Instead, we used the linear expansion method to correct for edge bias (Martin et al. 1977), dividing the total measured CI of each edge tree by the proportion of its neighborhood falling within the stem map. For example, a target tree on a plot corner would have 25% of its neighborhood falling within the plot, with the adjustment equal to the sum of measured CI/0.25.

Tree spatial relationships

We examined the spatial relationships of *F. nigra* and associated tree species to determine whether *F. nigra* competition at each site was predominantly inter- or intra-specific. In preliminary quadrat tests of complete spatial randomness (Baddeley et al. 2015), *F. nigra* spatial distributions showed significant deviation from homogeneity (or stationarity) at most sites. Therefore, for each site, we constructed candidate sets of *F. nigra* in homogeneous point pattern models, which permit generalized linear modeling of nonstationary Poisson point patterns (Baddeley and Turner 2000). Modeling the intensity (in our study, local *F. nigra* density) of the response point pattern as a log-linear function of spatial covariates or marked factors allowed us to evaluate the influence on spatial point patterns of multiple covariates, in this case, the density of more than one competing species, alongside alternatives in a multimodel framework (Wiegand and Moloney 2013). Intraspecific interactions among *F. nigra* can be examined through the residual Ripley's $K(t)$ function. This function indicates whether the fitted model deviates from complete spatial randomness, which should not be the case if the points are independent Poisson and the fitted model is valid (Baddeley et al. 2015). In the event that *F. nigra* spatial point patterns displayed intraspecific clustering or dispersion, we modeled these intraspecific interactions using an area-interaction term to account for stochastic clustering between points (Baddeley et al. 2015). Residual *F. nigra* clustering suggests higher intensity of intraspecific competition (Fraver et al. 2014). We used maximum pseudo-likelihood to achieve model fit (Baddeley and Turner 2000), which permitted the use of AICc for multimodel inference. The null hypothesis was that the density of the response *F. nigra* point pattern did not vary with respect to associated species density.

Within each site, we examined relationships between the density of common (≥100 trees·ha^{-1}) associated tree species and the spatial distribution of *F. nigra* (Table 1; Fig. 2). Because a prerequisite of point pattern analysis is that the local density of spatial covariates must be estimated at each point of the response pattern (Baddeley et al. 2015), we estimated local density of each major associated species through kernel smoothing using a 5 m bandwidth corresponding with growth model CI neighborhood radii. We used Diggle's (2010) method for edge correction. Partial residual plots suggested log-quadratic interspecific relationships were potentially present; therefore, we included quadratic polynomial terms of spatial covariates in our analyses. We did not investigate higher order polynomial terms as these were difficult to justify ecologically and may have resulted in overfitting. We also fitted an intercept-only null hypothesis model for each site, in which *F. nigra* density was modeled as a stationary process. We evaluated point pattern models in terms of AICc using the information-theoretic approach, as per growth modeling (Burnham and Anderson 2002).

We used four-panel diagnostic residual plots to evaluate models and partial residual plots to better examine relationships between *F. nigra* density and density of associated tree species (Baddeley et al. 2015). In the event that the residual $K(t)$ function indicated intraspecific spatial interactions among *F. nigra*, we determined optimal disc radius for the area interaction term at each site using profile AIC to find the radius minimizing AIC (Baddeley et al. 2015). We performed Poisson point pattern modeling (ppm) and diagnostics using the spatstat package for R (Baddeley and Turner 2005).

Fig. 2. Mapped locations of live trees ≥10 cm DBH of major species for six study sites. Plots are oriented so that the *y* axis broadly follows the major gradient of within-site moisture, with waterlogging decreasing with increasing *y* coordinates. Major species defined as having ≥100 trees·ha^{-1}. Species abbreviations: ACSA, *Acer saccharum*; BEAL, *Betula alleghaniensis*; FRNI, *Fraxinus nigra*; FRPE, *Fraxinus pennsylvanica*; POTR, *Populus tremuloides*; TIAM, *Tilia americana*; Other spp, pooled minor species.

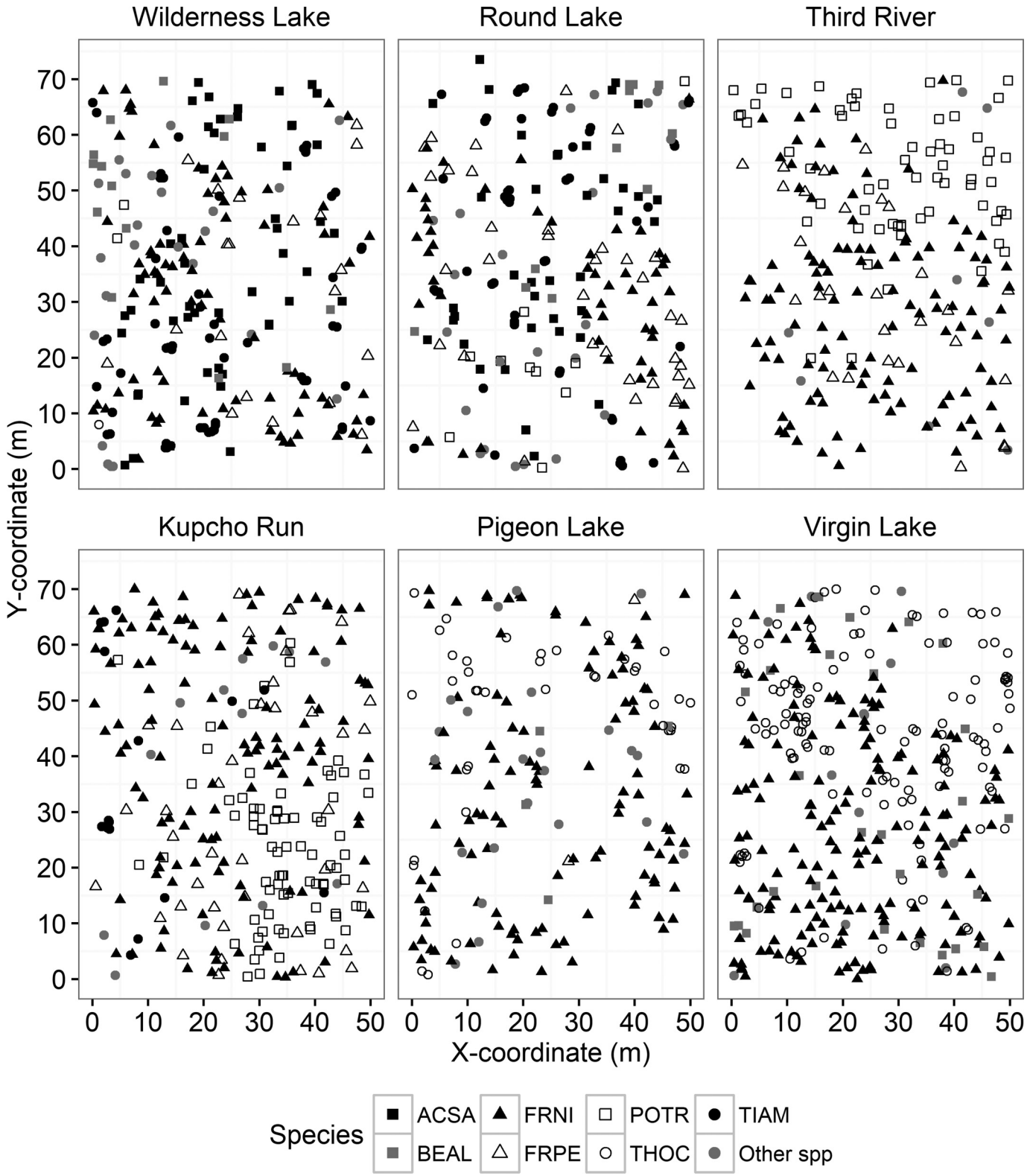


Table 3. Selected characteristics of *Fraxinus nigra* tree-ring series by site, as used in basal area increment (BAI) models.

Site	No. of trees cored	DBH (cm)	BAI ($cm^2 \cdot year^{-1}$)	Mean age (years)	Age range (years)	Missing age data (%)*	Interseries correlation†
Wilderness Lake	27	20.5±1.1	6.4±0.8	65.7±4.1	26–84	11	0.42
Round Lake	26	20.3±1.4	7.3±1.0	90.2±2.9	35–121	23	0.51
Third River	33	17.2±1.4	5.1±1.0	73.5±3.4	24–116	3	0.44
Kupcho Run	39	16.7±1.2	3.7±0.5	68.0±3.3	28–106	16	0.59
Pigeon Lake	26	28.6±2.2	8.1±1.5	115.2±6.9	48–170	37	0.46
Virgin Lake	30	22.0±1.5	5.7±0.7	85.5±3.4	35–144	11	0.49

Note: DBH, diameter at breast height; BAI, basal area increment. Means ± standard errors are provided for DBH and BAI.
*Percent of *F. nigra* for which age to pith could not be determined.
†The mean correlation of an individual-tree ring series with the master chronology.

Results

Growth and competition

Over the 1994–2013 period, mean *F. nigra* basal area increment (BAI) ranged from 8.1 ± 1.3 $cm^2 \cdot year^{-1}$ for 26 trees at Pigeon Lake to 3.6 ± 0.4 $cm^2 \cdot year^{-1}$ for 39 trees at Kupcho Run (Table 3). The best-supported BAI growth model for *F. nigra* across the waterlogging gradient included the main effects of DBH, highly size-asymmetric, distance-dependent CI-6, and site, as well as the interaction between CI-6 and site (Supplementary Table S1).[1] The second most supported model was equivalent to the first, with the addition of the DBH × CI interaction term (ΔAICc = 0.9). The third model with substantial AICc support (ΔAICc = 1.1) was equivalent to the first but used the highly size-asymmetric, distance-independent CI-3. The fourth-ranked model (ΔAICc = 2.2) also used CI-3 but added the DBH × CI interaction. Less supported models used the size-asymmetric, distance-independent CI-2 (ΔAICc = 4.1) and the size-asymmetric, distance-dependent CI-5 (ΔAICc = 6.0). All other models had minimal support, including the null DBH-only model (ΔAICc > 7).

Based on the best-supported model, increasing competition appeared to have the most negative effect on *F. nigra* BAI at Wilderness Lake, followed by Round Lake (Fig. 3). Competition had a weak effect at Third River and Virgin Lake and no discernable effect at Kupcho Run or Pigeon Lake (Fig. 3). However, when modeling the growth of *F. nigra* at the study-wide mean of CI, mean *F. nigra* BAI did not appear to vary significantly by site (Fig. 3). Tree diameter had a stronger influence on BAI than CI or site, with growth increasing with tree size. Models including the DBH × CI term indicated a weakly positive, nonsignificant interaction effect such that large trees were slightly less responsive to competition than small trees.

Spatial point pattern models

We found support for spatial point pattern models of *F. nigra* density as a function of the density of associated species at all sites except Wilderness Lake (Supplementary Table S2).[1] Based on residual $K(t)$ diagnostics, we found evidence of significant spatial clustering of *F. nigra* at Wilderness Lake, which we modeled using an area-interaction term. Once we accounted for residual intraspecific clustering, Wilderness Lake models including *A. saccharum* and *T. americana* density terms did not improve AICc over the model containing only the *F. nigra* area interaction term, indicating that the density of *F. nigra* did not vary spatially with the density of *A. saccharum* and *T. americana* (i.e., *F. nigra* occurred in mixtures with these species, irrespective of interspecific density).

In the best-supported model for Round Lake, density of *F. nigra* varied log-quadratically with density of *F. pennsylvanica*, indicating that the highest *F. nigra* densities were associated with moderate densities of *F. pennsylvanica* (Fig. 4). The density of *F. nigra* also decreased log-linearly with the densities of *A. saccharum* and *T. americana*, indicating that *F. nigra* was spatially segregated from these species. A competing model in which *F. nigra* density varied log-quadratically with density of *T. americana* also had considerable support (ΔAICc = 0.4), with *F. nigra* density declining at low to moderate *T. americana* densities and increasing slightly at higher *T. americana* densities.

At Third River, density of *F. nigra* varied log-quadratically with density of *P. tremuloides*, indicating that *F. nigra* density slightly increased at low to moderate *P. tremuloides* densities but declined at higher *P. tremuloides* densities (Fig. 4). At Kupcho Run, the best-supported model similarly showed a log-quadratic relationship between *F. nigra* density and *P. tremuloides* density, with *F. nigra* density increasing slightly at low to moderate *P. tremuloides* densities and decreasing at higher *P. tremuloides* densities. A substantially supported competing model (ΔAICc = 0.73) at Kupcho Run additionally included a negative log-linear effect of *F. pennsylvanica* density, indicating that *F. nigra* density declined in association with *F. pennsylvanica* density.

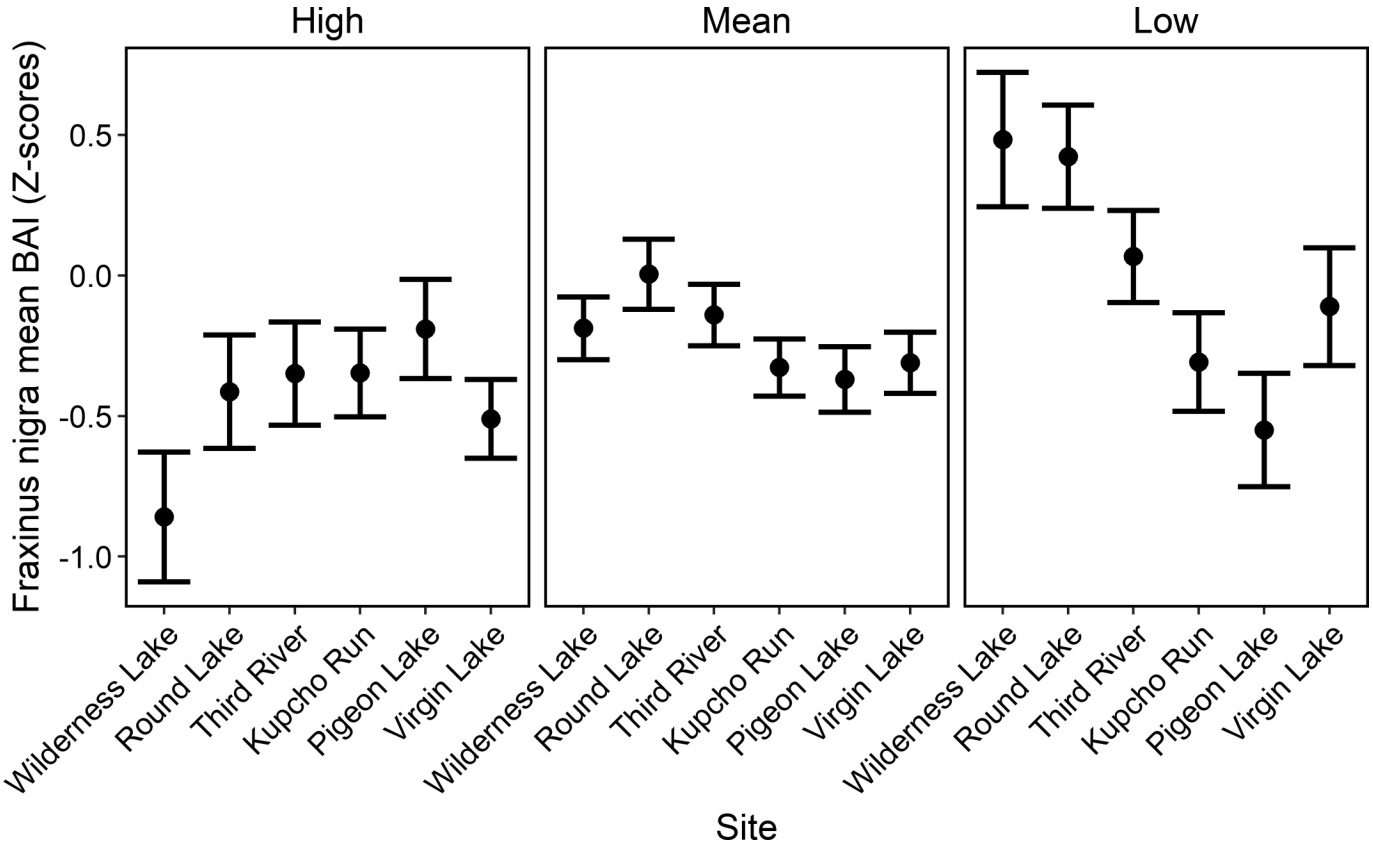
At Pigeon Lake, we found greatest support for a model describing *F. nigra* density as a negative log-linear function of *T. occidentalis* density, indicating that *F. nigra* density declined with increasing *T. occidentalis* density (Fig. 4). The null, stationary model for Pigeon Lake also had high support (ΔAICc = 0.6). At the Virgin Lake site, there was high support for a log-linear decrease in *F. nigra* density with increased density of *T. occidentalis*. Density of *F. nigra* declined more steeply with increasing *T. occidentalis* density at Virgin Lake than at Pigeon Lake. We also found substantial support for a log-quadratic relationship (ΔAICc = 1.5) between *F. nigra* density and *T. occidentalis* density.

Discussion

In temperate forests, growth of a given tree species generally increases with site moisture in the absence of competition (Canham et al. 2006) but diminishes as the duration of waterlogging stress from soil saturation increases (Megonigal et al. 1997). In our growth modeling, we found that *F. nigra* BAI did not significantly differ with site moisture conditions, when controlling for the influences of tree size and competition. It should be noted, however, that because no stand histories were available for our sites, we were unable to distinguish seed-origin trees from sprout-origin trees, which typically grow more rapidly and follow major disturbances (Tardif and Bergeron 1999). Although mean *F. nigra* growth did not vary by moisture condition, the influence of competition appeared to shift from important on the sites with low to moderate waterlogging stress to unimportant on sites with high waterlogging stress, a finding that will be discussed in depth for the individual sites below.

Tree competition is theorized to shift from size-asymmetric for light to size-symmetric for soil resources with increasing stress (Coomes and Grubb 2000), a pattern that has been confirmed for upland forests (Coomes and Allen 2007). At our wetland forest sites, however, multimodel comparisons revealed greatest support for highly size-asymmetric CI-6 across the gradient of waterlogging stress. Not only was support lacking for *F. nigra* models using less asymmetric CI, but the best-supported models that incorporated less asymmetric CI such as CI-5 showed equivalent patterns of tree response to competition across sites (data not

Fig. 3. Interaction plot illustrating the varying effects of competition on *Fraxinus nigra* growth (basal area increment, BAI) at six study sites in Minnesota, USA, based on the best-supported model, which used competition index 6 (CI-6). The *y* axis represents least-squares mean estimates of BAI (*Z* scores ± standard errors). The *x* axis shows study sites, arranged from left to right according to inferred waterlogging stress from most mesic (Wilderness Lake, top left) to wettest (Virgin Lake). To graphically interpret the interaction between CI and the study site, the continuous CI is set at three contrasting levels, with BAI modeled at study-wide high (1.5), mean (0), and low (–1.5) values within the range of the data at each site.

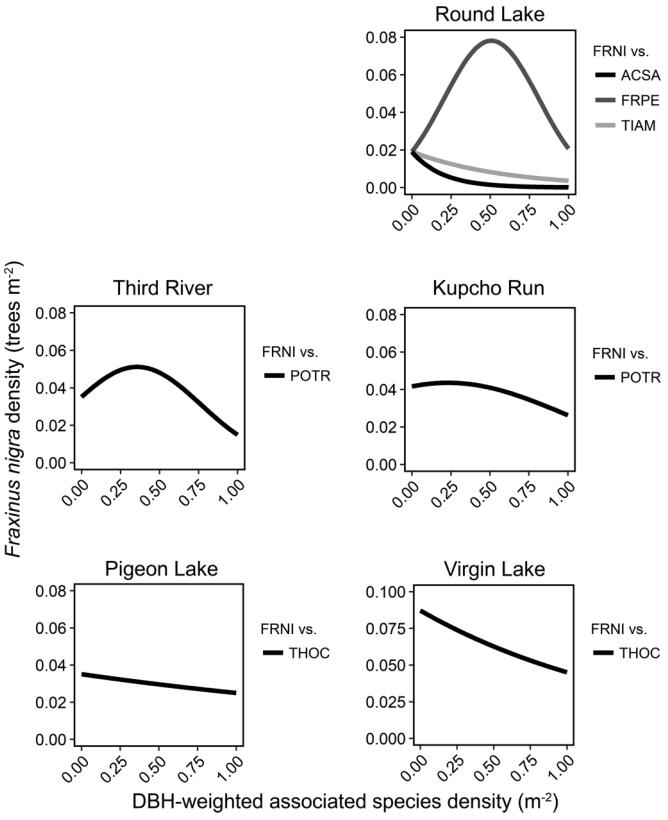


shown). This finding suggests that *F. nigra* competes predominantly for light across the waterlogging stress gradient (Larocque et al. 2013). We found greater evidence of size asymmetry at our mixed-species sites than in a previous study of tree–tree interactions in nearly pure, multi-age stands at the center of *F. nigra*'s moisture niche (Looney et al. 2016). Our study sites were generally younger than those in the earlier study (Looney et al. 2016), and size-asymmetric competition is hypothesized to be more important under the higher leaf areas of young stands (Binkley et al. 2006). In British Columbia, Canada, a study of tree species along a soil fertility gradient found that although resource limitation influences competition symmetry, the response is species-specific and may be contingent on the species composition of competitor trees (Coates et al. 2013).

Variation in species composition, rather than in competition symmetry, may better account for differences in the *F. nigra* BAI response to competition along the waterlogging stress gradient. At the driest site, Wilderness Lake, where growth in BAI showed a strong negative response to competition, *F. nigra* spatial patterns displayed residual clustering, suggesting increased intensity of intraspecific competition compared with other sites (Fraver et al. 2014). At the same time, we found evidence that *F. nigra* was spatially integrated with the associated species *T. americana* and *A. saccharum*. Taken together, the two results are consistent with the inferred findings of previous studies that competition from upland tree species may confine waterlogging-tolerant species such as *F. nigra* to more hydric sites (Denneler et al. 2000; Smith et al. 2013). Once established in stands, *A. saccharum*, a co-dominant tree species at Wilderness Lake, is noted for excluding neighboring species through a combination of high light interception and shade-tolerant seedlings (Frelich 2002). Alternatively, the occurrence of adult *F. nigra* alongside shade-tolerant competitors, despite our finding of reduced *F. nigra* growth in response to competition, could suggest that competition with mesic upland species may reduce *F. nigra* growth without necessarily resulting in *F. nigra* mortality and competitive exclusion.

At Round Lake, the *F. nigra* BAI responded negatively to competition, but the response was less strong than at Wilderness Lake, despite similarity of species composition between the two sites. Spatial analysis indicated that *F. nigra* at Round Lake grew in association with *F. pennsylvanica*, with which it frequently co-occurs (MNDNR 2003). This finding suggests that *F. nigra* was concentrated on more heavily inundated microsites, and in fact, we observed that *F. nigra* at this site was concentrated within vernal pools that persisted into early July. This spatial arrangement limited *F. nigra*'s interaction with less moisture tolerant *A. saccharum* and *T. americana*. As a result, the slightly weaker negative response of *F. nigra* BAI to competition at Round Lake compared with Wilderness Lake appears to reflect predominantly intrageneric competition, the intensity of which can be dramatically altered by differences in species traits such as leaf area and phenology (Forrester and Pretzsch 2015). Both *F. nigra* and *F. pennsylvanica* have among the most limited leaf-on periods of northern Minnesota tree species (Ahlgren 1957), and nearly pure stands of *F. nigra* have notably low leaf area (Looney et al. 2017). In contrast, *Acer* spp. are noted for both longer leaf-on periods (Ahlgren 1957) and stand leaf areas (Kassnacht and Gower 1997), subjecting moderately shade-tolerant *F. nigra* to heavy shade throughout its grow-

Fig. 4. Predicted *Fraxinus nigra* (FRNI) density (trees·m^{-2}) as a function of major associated species density (trees·m^{-2} weighted by associated species DBH) for five study sites. Relationships are based on the most plausible point process model for each site. Species abbreviations: ACSA, *Acer saccharum*; FRPE, *Fraxinus pennsylvanica*; TIAM, *Tilia americana*; POTR, *Populus tremuloides*; THOC, *Thuja occidentalis*. Wilderness Lake was omitted because no spatial relationships were found between *F. nigra* and major tree species.



ing season. In upland stands such as Round Lake, wet microsites may provide *F. nigra* with opportunities to escape competition with more upland and shade-tolerant species.

Competition had a moderately negative influence on *F. nigra* BAI at Third River and a neutral influence at Kupcho Run, the two sites with moderate waterlogging stress. We found nuanced spatial relationships between *F. nigra* at these sites and the major associated species, *P. tremuloides*. The negative influence of competition on *F. nigra* BAI was more pronounced at Kupcho Run, where both waterlogging stress and density of *P. tremuloides* were higher. Previous research suggests that facilitation or neutralism may be common between overstory *P. tremuloides* and more shade-tolerant tree species (Stadt et al. 2007). While we found separate populations of the two species in some areas, with *F. nigra* presumably occupying inundated microsites and *P. tremuloides* occupying more upland sites, the abundance of *F. nigra* did not consistently decrease with *P. tremuloides* density. In fact, *F. nigra* abundance was highest in areas with low to moderate *P. tremuloides* density, suggesting that the two species may co-occur in transitional areas between *F. nigra* dominated vernal pools and *P. tremuloides* dominated uplands. These transitional areas may allow *F. nigra* to escape more severe waterlogging stress, while simultaneously providing more reliable summer soil moisture for *P. tremuloides*, whose growth appears to be limited by early growing season drought (Dymond et al. 2016).

Fraxinus nigra showed no response to competition at wet Pigeon Lake and a very weak negative response at Virgin Lake, where waterlogging stress was highest. At both sites, we found evidence of weak spatial segregation between *F. nigra* and *T. occidentalis*, indicating reduced interspecific competition. Erdmann et al. (1987) observed that *T. occidentalis* often succeeds *F. nigra* on stands in bog sites, and the spatial distributions of these species could be driven by variations in water chemistry. However, high deer browse pressure has resulted in low recruitment of *T. occidentalis* in northern Minnesota since the beginning of the 20th century (Hofmeyer et al. 2009), limiting succession towards stands of this species. At both sites, we also noted that *T. occidentalis* was predominantly confined to intermediate and suppressed crown classes (C.E. Looney, unpublished data). Light partitioning between *F. nigra* and shorter statured *T. occidentalis* could potentially reduce interspecific competition impacts on *F. nigra* BAI (Forrester and Pretzsch 2015). The low responsiveness of *F. nigra* growth to competition at these sites may also reflect faster tree growth on more optimal microsites, a phenomenon reported in other wetland forest systems (MacDonald and Yin 1999).

In conclusion, it should be noted that our study represents only a preliminary investigation into the process of competition in six stands within one *F. nigra* forest system. As such, additional research is needed to more fully describe the competition dynamics of *F. nigra* forests. In particular, the growth-competition response of *F. nigra* associated tree species should be examined, as well as the longer term impacts of competition on forest tree community composition, to better predict how associated species along the gradient will respond to canopy gaps created by EAB invasion. Furthermore, our analysis was limited to static assessments of conditions during the most recent 20 years and did not examine the potential influence of disturbance on tree growth and spatial distributions. Detailed reconstructions of stand history could be especially useful in elucidating longer term stand dynamics, including succession, while clarifying the extent to which the spatial distribution of *F. nigra* in relation to *P. tremuloides* and *T. occidentalis* reflects past competitive exclusion (Connell 1980) or the effects of past disturbance (Stadt et al. 2007).

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References

Aakala, T., Fraver, S., D'Amato, A.W., and Palik, B.J. 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. For. Ecol. Manage. **308**: 128–135. doi:10.1016/j.foreco.2013.07.057.

Ahlgren, C.E. 1957. Phenological observations of nineteen native tree species in northeastern Minnesota. Ecology, **38**: 622–628. doi:10.2307/1943128.

Applequist, M.B. 1958. A simple pith locator for use with off-center increment cores. J. For. **56**: 138–143.

Baddeley, A., and Turner, R. 2000. Practical maximum pseudolikelihood for spatial point patterns. Aust. N. Z. J. Stat. **42**: 283–322. doi:10.1111/1467-842X.00128.

Baddeley, A., and Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. J. Stat. Softw. **12**: 1–42. doi:10.18637/jss.v012.i06.

Baddeley, A., Rubak, E., and Turner, R. 2015. Spatial point patterns: methodology and applications with R. CRC Press, Boca Raton, Fla.

Benedict, M.A., and Frelich, L.E. 2008. Site factors affecting black ash ring growth in northern Minnesota. For. Ecol. Manage. **255**: 3489–3493. doi:10.1016/j.foreco.2008.02.029.

Binkley, D., Kashian, D.M., Boyden, S., Kaye, M.W., Bradford, J.B., Arthur, M.A., Fornwalt, P.J., and Ryan, M.G. 2006. Patterns of growth dominance in forests of the Rocky Mountains, USA. For. Ecol. Manage. **236**: 193–201. doi:10.1016/j.foreco.2006.09.001.

Bunn, A.G. 2008. A dendrochronology program library in R (dplR). Dendrochronologia, **26**: 115–124. doi:10.1016/j.dendro.2008.01.002.
Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York. doi:10.1007/b97636.
Callaway, R.M. 2007. Interaction between competition and facilitation. *In* Positive interactions and interdependence in plant communities. Springer, Dordrecht, Netherlands. pp. 179–254. doi:10.1007/978-1-4020-6224-7_4.
Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., and Twery, M.J. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol. Appl. **16**: 540–554. doi:10.1890/1051-0761(2006)016[0540:NAOCTC]2.0.CO;2. PMID:16711043.
Coates, K.D., Lilles, E.B., and Astrup, R. 2013. Competitive interactions across a soil fertility gradient in a multispecies forest. J. Ecol. **101**: 806–818. doi:10.1111/1365-2745.12072.
Connell, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos, **35**: 131–138. doi:10.2307/3544421.
Coomes, D.A., and Allen, R.B. 2007. Effects of size, competition and altitude on tree growth. J. Ecol. **95**: 1084–1097. doi:10.1111/j.1365-2745.2007.01280.x.
Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. **70**: 171–207. doi:10.1890/0012-9615(2000)070[0171:IORCIF]2.0.CO;2.
Costanza, K.K.L., Livingston, W.H., Kashian, D.M., Slesak, R.A., Tardif, J.C., Dech, J.P., Diamond, A.K., Daigle, J.J., Ranco, D.J., Neptune, J.S., Benedict, L., Fraver, S.R., Reinikainen, M., and Siegert, N.W. 2017. The precarious state of a cultural keystone species: tribal and biological assessments of the role and future of black ash. J. For. **115**: 435–446. doi:10.5849/jof.2016-034R1.
Davis, J.C., Shannon, J.P., Bolton, N.W., Kolka, R.K., and Pypker, T.G. 2017. Vegetation responses to simulated emerald ash borer infestation in *Fraxinus nigra* dominated wetlands of Upper Michigan, USA. Can. J. For. Res. **47**(3): 319–330. doi:10.1139/cjfr-2016-0105.
Denneler, B., Bergeron, Y., and Bégin, Y. 2000. An attempt to explain the distribution of the tree species composing the riparian forests of Lake Duparquet, southern boreal region of Quebec, Canada. Can. J. Bot. **77**(12): 1744–1755. doi:10.1139/b99-147.
Diggle, P. 2010. Nonparametric methods. *In* Handbook of spatial statistics. *Edited by* A.E. Gelfand, P. Diggle, M. Fuentes, and P. Guttorp. CRC Press, Boca Raton, Fla. pp. 299–337.
Dixon, G.E., and Keyser, C.E. (*Compilers*). 2008. Lake States (LS) variant overview: Forest Vegetation Simulator. USDA Forest Service, Forest Management Service Center, Fort Collins, Colorado, Int. Rep.
Dudek, D.M., McClenahen, J.R., and Mitsch, W.J. 1998. Tree growth responses of *Populus deltoides* and *Juglans nigra* to streamflow and climate in a bottomland hardwood forest in central Ohio. Am. Midl. Nat. **140**: 233–244. doi:10.1674/0003-0031(1998)140[0233:TGROPD]2.0.CO;2.
Dymond, S.F., D'Amato, A.W., Kolka, R.K., Bolstad, P.V., Sebestyen, S.D., and Bradford, J.B. 2016. Growth–climate relationships across topographic gradients in the northern Great Lakes. Ecohydrology, **9**: 918–929. doi:10.1002/eco.1700.
Erdmann, G.G., Crow, T.R., Peterson, R.M., Jr., and Wilson, C.D. 1987. Managing black ash in the Lake States. USDA Forest Service, North Central Forest Experimental Station, St. Paul, Minn, Gen. Tech. Rep. NC-115.
Forrester, D.I., and Pretzsch, H. 2015. Tamm review: on the strength of evidence when comparing ecosystem functions of mixtures with monocultures. For. Ecol. Manage. **356**: 41–53. doi:10.1016/j.foreco.2015.08.016.
Fraver, S., D'Amato, A.W., Bradford, J.B., Jonsson, B.G., Jönsson, M., and Esseen, P.-A. 2014. Tree growth and competition in an old-growth *Picea abies* forest of boreal Sweden: influence of tree spatial patterning. J. Veg. Sci. **25**: 374–385. doi:10.1111/jvs.12096.
Frelich, L.E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen–deciduous forests. Cambridge University Press, Cambridge, UK.
Hegyi, F. 1974. A simulation model for managing jack-pine stands. *In* Growth models for tree and stand simulation. Royal College of Forestry, Stockholm, Sweden. Research Note No. 30. pp. 74–90.
Hofmeyer, P.V., Kenefic, L.S., and Seymour, R.S. 2009. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: a synthesis of knowledge. North. J. Appl. For. **26**: 21–27.
Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. **43**: 69–78.
Kassnacht, K.S., and Gower, S.T. 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Can. J. For. Res. **27**(7): 1058–1067. doi:10.1139/x97-058.
Keddy, P.A. 2001. Competition. 2nd ed. Springer, Dordrecht, Netherlands. doi:10.1007/978-94-010-0694-1.
Keddy, P.A., and MacLellan, P. 1990. Centrifugal organization in forests. Oikos, **59**: 75–84. doi:10.2307/3545125.
Kozlowski, T.T. 1997. Responses of woody plants to flooding and salinity. Tree Physiol. **17**: 490. doi:10.1093/treephys/17.7.490.
Larocque, G.R., Luckai, N., Adhikary, S.N., Groot, A., Bell, F.W., and Sharma, M. 2013. Competition theory — science and application in mixed forest stands: review of experimental and modelling methods and suggestions for future research. Environ. Rev. **21**(2): 71–84. doi:10.1139/er-2012-0033.
Larsson, L.A. 2014. CooRecorder and Cdendro programs of the CooRecorder/Cdendro package. Cybis Elektronik, Saltsjöbaden, Sweden.
Lenth, R.V. 2016. Least-squares means: the R package lsmeans. J. Stat. Softw. **69**: 1–33. doi:10.18637/jss.v069.i01.
Looney, C.E., D'Amato, A.W., Fraver, S., Palik, B.J., and Reinikainen, M.R. 2016. Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands. For. Ecol. Manage. **375**: 238–248. doi:10.1016/j.foreco.2016.05.050.
Looney, C.E., D'Amato, A.W., Palik, B.J., and Slesak, R.A. 2017. Canopy treatment influences growth of replacement tree species in *Fraxinus nigra* forests threatened by the emerald ash borer in Minnesota, USA. Can. J. For. Res. **47**(2): 183–192. doi:10.1139/cjfr-2016-0369.
Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. **6**: 343–360. doi:10.1016/0378-1127(83)90042-7.
Lu, H., Condés, S., del Río, M., Goudiaby, V., den Ouden, J., Mohren, G.M.J., Schelhaas, M.-J., de Waal, R., and Sterck, F.J. 2018. Species and soil effects on overyielding of tree species mixtures in the Netherlands. For. Ecol. Manage. **409**: 105–118. doi:10.1016/j.foreco.2017.11.010.
MacDonald, S.E., and Yin, F. 1999. Factors influencing size inequality in peatland black spruce and tamarack: evidence from post-drainage release growth. J. Ecol. **87**: 404–412. doi:10.1046/j.1365-2745.1999.00370.x.
Martin, G.L., Ek, A.R., and Monserud, R.A. 1977. Control of plot edge bias in forest stand growth simulation models. Can. J. For. Res. **7**(1): 100–105. doi:10.1139/x77-014.
Megonigal, J.P., Conner, W.H., Kroeger, S., and Sharitz, R.R. 1997. Aboveground production in southeastern floodplain forests: a test of the subsidy–stress hypothesis. Ecology, **78**: 370–384. doi:10.1890/0012-9658(1997)078[0370:APISFF]2.0.CO;2.
Minnesota Department of Natural Resources (MNDNR). 2003. Field guide to the native plant communities of Minnesota: the Laurentian mixed forest province. Minnesota Department of Natural Resources, St. Paul, Minn.
National Oceanic and Atmospheric Administration (NOAA). 2015. National Climatic Data Center: Minnesota Climate Division 2 [online]. Available from http://www1.ncdc.noaa.gov/pub/data/cirs/ [accessed 10 July 2015].
Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics: updated edition. John Wiley & Sons, New York.
Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D. 2016. nlme: linear and nonlinear mixed effects models [online]. Available from https://CRAN.R-project.org/package=nlme [accessed 5 March 2016].
PRISM Climate Group. 2015. PRISM climate data [online]. Northwest Alliance for Computational Science and Engineering. Available from http://www.prism.oregonstate.edu/recent/ [accessed 11 January 2015].
Quantum GIS Development Team. 2014. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available from http://qgis.osgeo.org.
Quinn, G.P., and Keough, M.J. 2003. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, U.K.
Rouvinen, S., and Kuuluvainen, T. 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. **27**(6): 890–902. doi:10.1139/x97-012.
Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., and Palik, B.J. 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. **44**(8): 961–968. doi:10.1139/cjfr-2014-0111.
Smith, M.C., Stallins, J.A., Maxwell, J.T., and Van Dyke, C. 2013. Hydrological shifts and tree growth responses to river modification along the Apalachicola River, Florida. Phys. Geogr. **34**: 491–511.
Soil Survey Staff. 2016. Web soil survey [online]. Natural Resources Conservation Service, U.S. Department of Agriculture. Available from http://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/soils/home/?cid=nrcs142p2_053587 [accessed 30 December 2016].
Speer, J.H. 2010. Fundamentals of tree-ring research. University of Arizona Press, Phoenix, Ariz.
Stadt, K.J., Huston, C., Coates, K.D., Feng, Z., Dale, M.R.T., and Lieffers, V.J. 2007. Evaluation of competition and light estimation indices for predicting diameter growth in mature boreal mixed forests. Ann. For. Sci. **64**: 477–490. doi:10.1051/forest:2007025.
Tardif, J., and Bergeron, Y. 1999. Population dynamics of *Fraxinus nigra* in response to flood-level variations, in northwestern Quebec. Ecol. Monogr. **69**: 107–125. doi:10.1890/0012-9615(1999)069[0107:PDOFNI]2.0.CO;2.
Wiegand, T., and Moloney, K.A. 2013. Handbook of spatial point-pattern analysis in ecology. CRC Press, Boca Raton, Fla.
Wright, J.W., and Rauscher, H.M. 1990. Black ash. *In* Silvics of North America, Volume 2: hardwoods. *Edited by* R.M. Burns and B.H. Honkala. USDA Forest Service, Washington D.C., Agric. Handb. 654.