Environmental context alters the magnitude of conspecific negative density dependence in a temperate forest

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Abstract. Conspecific negative density dependence (CNDD) is an important driver of stand-level tree diversity in temperate forests. CNDD can occur via two main processes. First, soil pathogens and herbivores form a halo of high enemy density surrounding established trees at local spatial scales. As a result, seedlings and saplings residing within this halo experience reduced growth and survival. Second, intraspecific competition can lead to local depletion of resources, reducing the performance of conspecific seedlings and saplings, and encouraging spatial mixing of tree species. While seedlings and saplings respond to nearby conspecific adults, they are simultaneously responding to local environmental conditions. Solar radiation, soil moisture, and soil nutrients can all influence tree recruitment patterns. Furthermore, these environmental factors can influence densities and activities of soil pathogens, as well as seedling and sapling carbon balance. As a result, we expect small-scale variation in the abiotic environment to influence the magnitude of CNDD, although this expectation has thus far received little attention. We combined tree stem and environmental data from a mapped oak-hickory forest plot to evaluate whether the local environment modulates the direction or magnitude of negative density dependence. We tested for the interaction between conspecific and heterospecific basal area within a sapling’s neighborhood and each of five environmental covariates: index of canopy gaps, soil organic matter, soil cations, topographic curvature, and topographic slope/aspect. We found that increasing local conspecific and heterospecific basal areas reduced sapling growth and that the conspecific basal area reduced sapling growth more so than did heterospecific basal area. Furthermore, we observed significant interactions between adult tree density and all environmental covariates that differed depending on the category of nearby adults (i.e., conspecific vs. heterospecific), and this effect was most important with variations in soil organic matter, soil cations, and topographic slope/aspect. We conclude that tree basal area not only interacts with environmental conditions to influence sapling growth, but more importantly, that small-scale environmental conditions interact with the density of nearby conspecifics to modulate sapling growth. Thus, if this result proves general, a central mechanism underlying the maintenance of diversity can be modified by small-scale environmental conditions.

Key words: environmental heterogeneity; Janzen-Connell effect; sapling growth; soil fertility; tree recruitment.

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INTRODUCTION

Ecosystems maintain diversity through a variety of natural mechanisms that have been the focus of ecological studies for decades. Notable examples include Janzen’s (1970) and Connell’s (1971) studies on the role of plant enemies in driving the maintenance of tree diversity in tropical forests. Specialist enemies can drive diversity maintenance by reducing growth or survivorship
of seeds and seedlings in locations dense with conspecifics (i.e., conspecific negative density dependence, or CNDD), which leads to spatial mixing of plant species (Bever 2003, Bagchi et al. 2014, Johnson et al. 2014). CNDD can also result from intraspecific competition as a consequence of local depletion of critical resources by neighboring conspecific adults (Lekberg et al. 2018, Germany et al. 2019). Additionally, seedling growth and survival vary as a function of small-scale (i.e., local) environmental conditions through spatial variation in light availability, soil nutrient content, and soil moisture. However, questions remain about the interaction between the abiotic and biotic environment in driving patterns of plant recruitment (LaManna et al. 2016). For example, how might the abiotic environment modify the direction or magnitude of biotic processes such as CNDD?

Only a few papers on CNDD have addressed how environmental context may affect the strength and direction of CNDD in forests. For example, McCarthy-Neumann and Ibanez (2013) found that for three of four tree seedling species experiencing CNDD, CNDD was only observed under low light conditions. Light may have varying effects on tree carbon allocation and soil microbe communities, both of which may then influence the magnitude or direction of CNDD. Light access can indirectly influence the soil microbe community by affecting soil temperature and moisture. Light access might also affect tree susceptibility to enemies by changing how trees allocate carbon resources in terms of a growth-defense trade-off (Kitajima 1994). These findings imply that heterogeneity of light levels across a forest may lead to variation in the level of tissue defense of individual trees.

Along with spatially patchy light availability, forests contain heterogeneity in soil resources that may influence patterns of CNDD through effects on tree leaf nitrogen content and soil pathogen populations. LaManna et al. (2016) found that higher levels of soil nutrients and moisture can lead to an increase in the magnitude of CNDD in seedlings and saplings. This pattern could mean that resource-rich environments lead to higher densities of soil pathogens (Fierer and Jackson 2006). Additionally, it is possible that high levels of soil nutrients lead to enhanced plant allocation of carbon to growth rather than tissue defense (Dudt and Shure 1994). This effect may particularly influence species that have high potential growth rates (Zhu et al. 2018) such that young stems in resource-rich environments shunt carbon to growth rather than tissue defense, rendering the tissues of new growth more vulnerable to infection or herbivory (Kardol et al. 2006, García-Guzmán and Heil 2014). Furthermore, trees in high soil resource environments often have higher leaf nitrogen content, thereby attracting higher densities of herbivores (Campo and Dirzo 2002). Additionally, higher soil temperature and moisture levels may increase pathogen abundance (Martin and Loper 1999) and virulence (Velásquez et al. 2018). Because of the paucity of studies focusing on how the abiotic context modulates CNDD, it remains unclear the extent to which environmental conditions affect small-scale spatial patterns in tree recruitment.

To better understand whether and how abiotic processes modulate biotic effects and drive patterns of CNDD in temperate forests, we posed the following questions: (1) Does the abiotic environment interact with the biotic neighborhood, including conspecific, heterospecific, and total tree density, to affect sapling growth and survival? And (2) if so, does the abiotic environment interact with observed patterns of CNDD?

To our knowledge, no study has previously evaluated how local abiotic environments modify the magnitude or direction of CNDD on tree sapling growth rate and survival. To address this question, we paired spatial patterns of sapling growth and survival over 8 yr with environmental measurements related to soil resources and light availability in a mapped forest plot in central North Carolina, USA. We then examined the relative importance of conspecific and heterospecific effects and environmental conditions in driving spatial patterns of sapling growth and survival.

**METHODS**

**Data collection**

Stem data were collected from a 6.55-ha mapped forest plot located in Duke Forest (Orange County, North Carolina, USA) on the North Carolina Piedmont. Duke Forest includes over 2800 ha managed by Duke University for research, education, and recreation (Lynch 2006).
The plot contains mixed hardwoods that have never been clear-cut and have been left unmanaged since the forest was established in 1931. Although most of the plot is considered upland, a section of the plot slopes into a lower-elevation area near a stream. Elevation varies by about 8 m across the plot (Fig. 1). We used survey data taken from the years 1990 and 1998, where recorded stem density (for stems at least 2 cm diameter at breast height) was 1365–1536 stems per ha (respectively).

Each tree stem at least 2 cm in diameter at breast height (DBH) was mapped to the nearest 0.1 m, along with species identity and DBH. During resurveys, stems recorded from the previous survey were located, re-measured, and assigned a condition code indicating whether the stem was alive, damaged, dead, or missing. Between 1998 and 2014 (the most recent survey), elevated deer browsing may have been the cause of an observed increase in sapling death. Thus, we selected the two earlier survey years, 1990 and 1998, because the effects of elevated deer browsing were likely not as important in sapling growth or survival rates (data not shown).

Soil samples were collected on a regular grid across the 256 × 256 m plot at 16-m intervals, resulting in a total of 289 samples. Each sample was collected by the same person, who removed soil from the A horizon after removing undecomposed organic litter from the soil surface. Samples were oven-dried to remove moisture before shipping to Brookside Laboratories (New Knoxville, Ohio, USA) for soil nutrient and texture analysis (for more details, see Reed et al. 1993, Palmer et al. 2007).

**Data preparation**

To determine the response of small stems to established trees within their neighborhood, we separated stems into two size classes: saplings (2–12.7 cm) and trees (≥12.7 cm), following the Forest Inventory and Analysis size-class designations (U.S Forest Service 2011). The magnitude of CNDD is a function of distance to nearest conspecific and density of conspecifics within the neighborhood. Thus, we calculated the basal area of conspecific and heterospecific trees surrounding each sapling at four different spatial scales: 5, 10, 15, and 20 m. It is important to distinguish conspecific effects from other effects unrelated to species identity (e.g., competition with heterospecifics). Therefore, we evaluated the conspecific vs. heterospecific effects separately to detect patterns of CNDD. This approach resulted in eight measurements: conspecific tree basal area and heterospecific tree basal area of all trees within 5, 10, 15, and 20-m scales. Finally, we removed saplings from the dataset found within 20 m of plot boundaries to avoid problems with edge bias (i.e., where stems near plot boundaries would falsely appear to have fewer stems in the neighborhood, only because stems outside plot boundaries were not surveyed).

We evaluated the contribution of five environmental measurements in our models based on either their direct effect on tree survival and growth or their ability to act as a proxy for some other important measurement that was not directly collected. First, we calculated a soil fertility indicator. We performed principal component analysis (PCA) on four soil measurements related to cation availability: levels of soil calcium, magnesium, and potassium (in ppm) and soil pH. We used the first PCA axis as a proxy for soil cation availability. We used the vegan package in R to perform PCA (Oksanen et al. 2019).

We included percent soil organic matter in the analysis because this measurement may act as an indicator of site productivity and soil fertility. Additionally, higher levels of organic matter can better retain moisture in the soil for plant access. Thus, soil organic matter represents an indicator of areas that may be more fertile and/or have higher soil moisture levels.

As our measures of cations and soil organic matter were collected every 16 m across the plot, we were able to interpolate those values to create a continuous surface for each measurement (Fig. 1). To accomplish this, we fitted empirical variograms to the data and selected the best-fit model. We used this model to interpolate values across the entire plot, allowing us to extract a single value for each soil measurement for each sapling. We used the gstat and sp packages in R for interpolation (Pebesma 2004, Pebesma and Bivand 2005, R Development Core Team 2018).

Next, we calculated a proxy for the size of recently emerged canopy gaps based on known locations of large stem deaths. We located trees (≥12.7 cm DBH) that had died during the period between the two surveys used for this study (1990
We used spatial smoothing on the tree diameters of the dead stems to estimate the size of canopy gaps across the plot (Fig. 1). Soil organic matter values (%) are estimated based on soil sampling and laboratory analysis performed on a 16 × 16 m regular grid across the plot and then kriged on top of stem locations. Soil cations represent the first axis of the principal component analysis constructed on four soil measurements (calcium, magnesium, and potassium measures [ppm] and soil pH). Topographic curvature and slope/aspect were constructed from an elevation raster, which was created by kriging elevation measures collected across a 16 × 16 m regular grid. Low values of curvature indicate areas that are laterally concave, while higher values indicate areas that are laterally (upwardly) convex. High values of topographic slope/aspect indicate locations that face north; values close to 0 indicate topographically flat areas; and low values indicate locations that face south.

Fig. 1. Environmental conditions across the 6.5-ha plot, where each dot on the map represents the magnitude of the environmental value associated with each stem. Light gray dots represent low values of the measurement, and dark gray dots represent higher values. Canopy gap measure is a spatial smoothing of diameters (in cm) of adult trees (trees > 12.6 cm DBH) that died between surveys (1990–1998). Soil organic matter values (%) are estimated based on soil sampling and laboratory analysis performed on a 16 × 16 m regular grid across the plot and then kriged on top of stem locations. Soil cations represent the first axis of the principal component analysis constructed on four soil measurements (calcium, magnesium, and potassium measures [ppm] and soil pH). Topographic curvature and slope/aspect were constructed from an elevation raster, which was created by kriging elevation measures collected across a 16 × 16 m regular grid. Low values of curvature indicate areas that are laterally concave, while higher values indicate areas that are laterally (upwardly) convex. High values of topographic slope/aspect indicate locations that face north; values close to 0 indicate topographically flat areas; and low values indicate locations that face south.
Finally, we included surface curvature and a slope/aspect value as topographic environmental covariates because these measurements may correlate with soil moisture. We calculated curvature and slope/aspect from a continuous elevation surface. We created the elevation surface using the same interpolation approach as described for soil organic matter and soil cations. We then used the curvature function in the spatialEco package in R to calculate topographic curvature for each sapling stem (Evans 2020). Low values of curvature indicate areas that are upwardly (i.e., laterally) concave, whereas higher values indicate areas that are upwardly convex. We used the slopeaspdf function in the landsat package in R to calculate the angle of the slope and the aspect for each sapling stem (Goslee 2011) and used the sa.trans function in the spatialEco package to cosine-transform the two variables into a slope/aspect measure (i.e., slope × cos(aspect)). Slope/aspect values close to +1 indicate north-facing slopes, values close to −1 indicate south-facing slopes, and values closer to 0 indicate flat areas. Results indicating an important effect of curvature or slope/aspect on sapling growth or survival we interpret as a likely a response to soil moisture.

**Model description**

We used two response variables, sapling growth and sapling survival, to test the effects of abiotic and biotic neighborhoods on saplings.

To evaluate the sapling survival response, we constructed generalized linear mixed-effects models using a binary response, which indicated whether the sapling survived or died during the 8-year time interval between surveys. We constructed five competing models for each combination of environmental covariate and spatial scale to determine whether competition (total basal area) or conspecific effects (conspecific basal area) are more important in determining sapling survival, and whether the environmental context modulates the adult basal area effect (by using interactions between environment and adult basal area; Table 1). We performed model selection using AIC value comparison. If there were multiple high-performing models that did not show a difference in performance (i.e., AIC values with difference of <2), we selected the simplest of the competing models.

The five environmental covariates included an index of canopy gaps, soil cations, soil organic matter, and topographic curvature and slope, where basal area covariates included total adult, conspecific adult, and heterospecific adult basal areas. We included species as a random effect for all models, which accounts for the differing life history strategies for recruitment across species (i.e., that we expected overall sapling survival to differ between species). While we are aware that CNDD patterns can vary across species, we did not have a sample size adequate for including these random slopes. We included sapling diameter as a covariate in all models to account for differential growth and survival rates of saplings of different sizes. We constructed a series of models and performed model selection separately for

| Environmental contribution | Neighborhood adult density contribution | Log(growth rate) or Log odds of survival |
|----------------------------|----------------------------------------|-----------------------------------------|
| Additive                   | None                                   | $\alpha_s + \beta_1 \times \text{DIAM} + \beta_2 \times \text{ENV}$ |
|                            | Total                                   | $\alpha_s + \beta_1 \times \text{DIAM} + \beta_2 \times \text{ENV} + \beta_3 \times \text{BACON} + \beta_4 \times \text{BACON}$ |
|                            | Conspecific vs. heterospecific Total    | $\alpha_s + \beta_1 \times \text{DIAM} + \beta_2 \times \text{ENV} + \beta_4 \times \text{BACON} + \beta_5 \times \text{BAHET}$ |
| Interactive with adult density | Conspecific vs. heterospecific Total    | $\alpha_s + \beta_1 \times \text{DIAM} + \beta_7 \times \text{ENV} + \beta_8 \times \text{BACON} + \beta_9 \times \text{BAHET}$ |

**Notes:** The models are compared for each of five environmental covariates (canopy gaps, soil organic matter, soil cations, and topographic curvature and slope/aspect), and within each environmental covariate at four spatial scales (5, 10, 15, 20 m). Model terms include initial sapling diameter (DIAM), one of five environmental variables (ENV), total adult basal area within a specific spatial scale (BACON), conspecific adult basal area within a specific spatial scale (BACON), and heterospecific adult basal area within a specific spatial scale (BAHET). We allowed species to vary in their intercepts for all models, as represented by the parameter $\alpha_s$. 

Table 1. Five mixed-effects models evaluating the contribution of neighboring adult tree density and the environmental contribution to two sapling responses—growth and survival.
each of the five environmental covariates. Within each series of models for each environmental covariate, we constructed models at 5, 10, 15, and 20 m spatial scales and performed model selection separately for each.

To evaluate the sapling growth response, we modeled the log-transformed growth rate against the same series of covariates and random effect used for the survival analysis. Growth rates were calculated as the difference in diameter between survey years divided by the number of years between measurements. The three highest growth rates were removed due to possible measurement error, and negative growth rates were assigned a growth rate of zero. We performed model selection using the same approach as for the survival analysis. We performed all analyses using the lme4 package in R (Bates et al. 2015, R Development Core Team 2018).

When plotting the results from best-performing models, we specifically looked for instances where the interactive environmental effect differed between conspecific and heterospecific basal area because these situations suggest that the abiotic neighborhood can alter the magnitude or direction of conspecific density dependence in temperate forests.

**Results**

We found that the abiotic and biotic neighborhoods of saplings were associated with changes in sapling growth and survival, and these patterns varied across spatial scales and between the two response types (i.e., growth and survival; Fig. 2). The separate effects of conspecific and heterospecific basal area consistently outperformed the effect of total basal area on sapling growth, indicating that it is important to consider conspecific and heterospecific basal areas independently as they may affect saplings in different ways. Furthermore, the main effect of conspecific basal area was almost always associated with reduced growth in contrast to that of heterospecific basal area (Fig. 3, Appendix S1), a pattern indicative of CNDD. However, sapling survival was generally not contingent on the biotic neighborhood at any scale (with just one exception; Fig. 2, Appendix S2), indicating sapling growth may be a better indicator of CNDD than sapling survival.

In terms of sapling growth, we detected interactions between the environment and the biotic neighborhood occurring with both conspecific and heterospecific basal area. This indicates that differing levels of soil resources, topography, and light availability may either enhance or counteract the negative effect that conspecific and heterospecific basal area have on sapling growth. All five environmental variables (canopy gaps, soil organic matter, soil cations, curvature, and slope) revealed a significant interaction with adult basal area for at least one spatial scale (Fig. 2; Appendix S1).

At the 5-m scale, the interaction between conspecific basal area and canopy gaps was slightly lower than that of heterospecific basal area for sapling growth (interaction parameter estimates for conspecific and heterospecific effects: 0.0005 and 0.0023; Appendix S2). But upon further investigation of the effect size (seen in Fig. 4A), we were not able to distinguish an important difference between conspecific and heterospecific effects. What is apparent is that while the effect of increasing heterospecific basal area is less negative in areas with a greater influence of canopy gaps, the standard error in the sapling response to increasing adult conspecific basal area becomes very large.

We found a somewhat more negative relationship between heterospecific basal area and soil organic matter than that of conspecific basal area and organic matter. Upon investigating effect size (Fig. 4B), we observed a more negative growth response to conspecifics compared to heterospecifics, but only when organic matter levels were low; at high levels the effects of increasing conspecific and heterospecific density became undistinguishable. This result implies that CNDD occurs in locations with low levels of soil organic matter, but not in areas with high levels of organic matter.

We found a greater decrease in sapling growth as conspecific density increases relative to heterospecific density, but only when soil cation levels were low (Fig. 4C, Appendix S1). At high soil cation levels, the conspecific and heterospecific effects were similar.

Topographic curvature had a statistically significant interaction with adult conspecific and heterospecific basal area in terms of sapling growth. However, when examining effect size,
the sapling response to increasing conspecifics vs. heterospecifics under low vs. high levels of curvature did not reveal an obvious pattern (i.e., the confidence intervals overlap; Fig. 4D).

Topographic slope/aspect interacted with conspecific and heterospecific basal area in different ways, revealing a stronger negative effect of increasing conspecifics on sapling growth in areas with high slope values (i.e., north-facing slopes; Fig. 4E). Although the effect appeared less important, the same pattern was found for sapling survival (Fig. 5). In fact, topographic slope was the only environmental variable to significantly interact with conspecific and heterospecific adult basal area in different ways in terms of sapling survival (Fig. 2).

**DISCUSSION**

We found that the environmental context can modify the effect that the biotic neighborhood has on sapling growth and survival. All environmental covariates interacted with conspecific basal area in different ways than heterospecific basal area to influence sapling growth (Fig. 4), indicating a potential modulation of CNDD based on the environmental context. This finding has implications for the detection of CNDD because it introduces environmental factors that play into the presence and magnitude of CNDD that have not yet been explored deeply.

**Main effects and CNDD**

We observed a reduction in sapling growth under increasing levels of conspecific basal area more so than heterospecific basal area (Fig. 3). Our finding that conspecifics have more of a negative effect on sapling growth than heterospecifics is in line with the body of literature on CNDD (e.g., McCarthy-Neumann and Kobe...
Fig. 4. Model-estimated sapling growth response (in log-transformed cm/year) to increasing conspecific (gray ribbons) and heterospecific (white ribbons) basal area (in cm²) depending on low and high levels of each of the five environmental variables—canopy gaps (A), soil organic matter (B), soil cations (C), topographic curvature (D), and topographic slope/aspect (E). Low and high variable levels are based on the minimum and maximum values (respectively) of the raw data. For illustration purposes, canopy gap, soil organic matter, and curvature variables are shown at the 5-m spatial scale, and soil cation and slope variables are shown at the 15-m scale.
2010, Johnson et al. 2014, LaManna et al. 2016, Ramage et al. 2017). Saplings located near high densities of conspecifics may experience greater herbivory or a higher pathogen load. Infection by specialist pathogens, coinfection by multiple generalist pathogens, or interspecific susceptibility to generalist pathogens (Hersh et al. 2012, Benítez et al. 2013) can lead to a spatial signature of CNDD. It is also possible that strong intraspecific competition leads to CNDD, although studies suggest that plant enemies are more important in causing patterns of CNDD than intraspecific competition (Bever 2003, Mangan et al. 2010).

We modeled both sapling growth and survival because CNDD can affect multiple tree vital rates, and the extent to which CNDD affects tree recruits can change with ontogeny (Johnson et al. 2014, Zhu et al. 2015, LaManna et al. 2016). In experimental work, the focus is on the early seedling stages (from germination to 2–3 months old), and seedling survival is a commonly used response variable (Ramage et al. 2017). Seedling survival is a reliable measure of CNDD or other biotic processes because seedlings are more vulnerable to suboptimal environmental conditions, competition, and plant enemies than older stems (Johnson et al. 2014). Once seedlings have survived the vulnerable early stages, we see less mortality as recruits move into larger life stages (Zhu et al. 2018). This is consistent with our finding that sapling growth responded more dramatically to the biotic neighborhood than sapling survival.

**Interactive effects and CNDD: environmental context**

We found a large amount of variation in how sapling growth responds to increasing conspecific density when saplings are within or near canopy gaps. In low-gap areas, sapling growth consistently decreases with increasing conspecific density. However, in high-gap areas, saplings may respond positively or negatively (or not at all) to increasing conspecific density (Fig. 4A). This result indicates that CNDD may be more difficult to identify in areas with patchy canopies, such as areas that have been recently disturbed. Indeed, a study in tropical forests found that high light conditions can induce positive or negative conspecific density dependence, depending on the life stage (seedling vs. adult) of neighboring conspecifics (Inman-Narahari et al. 2016).

When soil organic matter levels were low, saplings showed a decrease in growth under increasing levels of conspecific (but not heterospecific) density (Fig. 4B). In other words, we only observed CNDD in places where there was less organic matter. This pattern disappears when there is more soil organic matter, because in these circumstances sapling growth responds negatively to both conspecific and heterospecific basal areas. This indicates that CNDD may not be at play in these environments, but rather we are...
seeing an effect of increased competition due to high total adult basal area. The level of soil organic matter may be correlated with plant productivity: Areas with low productivity may have less leaf production and thus low levels of soil organic matter, and lower nutrient access may explain the presence of such areas in our plot. In support of this hypothesis, soil cation levels showed the same interactive effect on CNDD, revealing enhanced CNDD only in areas with low soil cation levels (i.e., low fertility).

We observed a counteractive effect of high soil cations and soil organic matter on sapling growth under increasing levels of conspecific basal area (Fig. 4B, 4C), implying that increases in soil cations and soil organic matter may reduce the magnitude of CNDD in lieu of a non-species-specific competitive effect. It is possible that saplings with greater resource availability may divert these resources to secondary metabolism (i.e., tissue defense), rendering them better able to resist the negative effects of CNDD. However, this finding contradicts a body of literature that argues that soil fertilization typically leads to higher plant growth at the expense of secondary metabolism (Herms 2002). LaManna et al. (2016) found that higher soil resources led to more dramatic effects of CNDD, supporting the idea that higher soil nutrient levels can lead to reduced tissue defense. They argue that when provided with greater soil resources, plants may allocate those resources to build more photosynthetic machinery within their leaves, leading to higher leaf nitrogen content in high soil resource areas. Herbivores are attracted to plant tissues with higher nutritional quality or lower secondary metabolite concentrations (Herms 2002). Consequently, some have found that higher soil nutrient availability may lead to a greater impact of herbivory and CNDD in saplings (Campo and Dirzo 2002, LaManna et al. 2016), contradicting our findings.

There are two possible reasons why our results differ from those of LaManna et al.’s (2016) work. One reason may be that CNDD responses do not vary linearly with abiotic conditions, instead showing a unimodal peak in CNDD magnitude under specific environmental conditions. This is consistent with the growth-differentiation balance hypothesis, which predicts a parabolic response of secondary metabolite production to differences in soil nutrient resources (Herms and Mattson 1992). Based on this framework, in areas with low nutrient resources, fertilizing the soil may initially benefit plant growth (and reduce the effects of CNDD). Continuing to increase nutrient resources to even higher levels may result in greater pathogen infection or herbivory of saplings (and enhanced effects of CNDD) as plant nitrogen levels increase. LaManna et al.’s (2016) study plot may represent a sample of temperate forests under different environmental conditions than those of the current study, so our opposing results may reflect the non-linear nature of the trade-off between growth and tissue protection. To test this idea, it is necessary to conduct observational and experimental studies on differential CNDD across a wider range of abiotic conditions while considering the complex nature of the growth vs. tissue defense trade-off. A second potential reason for ours and LaManna's differing results stem from the relative novelty of our research questions. The literature has not yet fully addressed how the trade-off between tree growth and tissue defense in terms of CNDD plays out in natural forest systems. There are many factors that likely contribute to CNDD susceptibility, all of which may be interacting in complex ways that the literature has not yet defined. For example, even if higher soil resources lead to increased herbivory, those resources may also help trees to replace damaged or consumed structures more quickly, rendering it less important to invest in tissue defense.

We included topographic characteristics in this analysis, because variation in solar radiation and soil moisture can modify allocation of plant resources to tissues (Kitajima 1994, Canham et al. 1996), which could lead to changes in sapling growth and survival patterns. Higher curvature values indicate locations that are upwardly convex (e.g., on top of a hill), which are often associated with lower soil moisture. There appeared to be an overall more negative growth response to both increasing conspecific and heterospecific basal areas on upwardly convex areas as compared to more concave areas (Fig. 4D). Reduced water availability may have led to lower sapling growth rates overall, with a more dramatic effect with increased competition for resources (i.e., with increasing adult basal area). The model that considered adult
conspecific vs. heterospecific basal areas performed better than the model using total adult basal area, indicating a different effect with increasing conspecifics than that of heterospecifics; however, the effect size appears small, so we hesitate to interpret those differences as indicating a modulating CNDD effect.

Along with topographic curvature, we included a slope value that considers a combination of the steepness of the slope and the aspect, where positive values indicate more north-facing, steeper slopes, while negative values indicate south-facing, steeper slopes (flatter areas have values close to zero). In the northern hemisphere, north-facing slopes receive less solar radiation, leading to cooler, wetter conditions. We observed sapling growth rates indicative of CNDD on north-facing, but not south-facing, slopes (Fig. 4E). We also observed this effect on sapling survival, albeit to a much lesser degree (Fig. 5). This implies that saplings are more negatively affected by conspecifics when located in cooler, wetter areas. In fact, our data imply that when heterospecific basal area increases on north-facing slopes, sapling growth may actually increase; while increasing conspecific basal area in these same areas reduces sapling growth. One possible explanation for these patterns comes from pathogen-mediated CNDD literature, which often ascribes cool, wet soil conditions as encouraging pathogen reproduction and dispersal (Martin and Loper 1999, Velásquez et al. 2018). If the north-facing slopes on our site contain higher pathogen densities or virulence, this could explain reduced sapling growth (and perhaps survival) as conspecific (but not heterospecific) density increases.

While our results indicate a modulating effect of the environment on CNDD, our study site is contained within a relatively narrow spectrum of environmental conditions, limiting our ability to generalize the results. Nonetheless, our results suggest that CNDD can vary across small-scale landscapes, a phenomenon that has not yet been thoroughly investigated. Future CNDD studies should take environmental variation into consideration.

Conclusions
In summary, we found evidence that the biotic and abiotic environments of saplings interact to modify sapling growth and (perhaps) survival. Our results indicate that the direction and magnitude of negative density dependence can shift based on small-scale (plot-level) environmental conditions, and in our case, the environmental variables driving that modulating effect occurred most importantly with soil organic matter, soil cations, and topographic slope/aspect. Our results provide a rationale for further investigation of the role of environmental conditions in driving variation in the magnitude of CNDD at local scales.

CNDD literature has just begun to focus its attention to more nuanced patterns of differential CNDD patterns that vary across species, along environmental gradients, or between geographic regions. Uncovering these patterns will result in a better understanding of how abiotic and biotic neighborhoods interact to affect tree recruitment patterns, forest structure and composition, and the maintenance of tree diversity.

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DATA AVAILABILITY

Raw data are publicly available (https://cdr.lib.unc.edu/record/uuid:eff38f72-3244-47a1-9175-cfc66d4a3407). R scripts are publicly available on GitHub (https://github.com/alissab) and structured (analysis-ready) data available on Figshare (https://figshare.com/authors/Alissa_Brown/2603275).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3406/full