Prevalence and strength of density-dependent tree recruitment

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Abstract. Density dependence could maintain diversity in forests, but studies continue to disagree on its role. Part of the disagreement results from the fact that different studies have evaluated different responses (survival, recruitment, or growth) of different stages (seeds, seedlings, or adults) to different inputs (density of seedlings, density or distance to adults). Most studies are conducted on a single site and thus are difficult to generalize. Using USDA Forest Service's Forest Inventory and Analysis data, we analyzed over a million seedling-to-sapling recruitment observations of 50 species from the eastern United States, controlling for the effects of climate. We focused on the per-seedling recruitment rate, because it is most likely to promote diversity and to be identified in observational or experimental data. To understand the prevalence of density dependence, we quantified the number of species with significant positive or negative effects. To understand the strength of density dependence, we determined the magnitude of effects among con- and heterospecifics, and how it changes with overall species abundance. We found that density dependence is pervasive among the 50 species, as the majority of them have significant effects and mostly negative. Density-dependence effects are stronger from conspecific than heterospecfic adult neighbors, consistent with the predictions of the Janzen-Connell hypothesis. Contrary to recent reports, density-dependence effects are more negative for common than rare species, suggesting disproportionately stronger population regulation in common species. We conclude that density dependence is pervasive, and it is strongest from conspecific neighbors of common species. Our analysis provides direct evidence that density dependence regulates population dynamics of tree species in eastern U.S. forests.

Key words: demography; density dependence; diversity maintenance; Forest Inventory and Analysis; Janzen-Connell hypothesis; population dynamics; recruitment; temperate forest.

Introduction

Density dependence (DD) has long been viewed as one of the mechanisms that maintains species diversity (MacArthur and Levins 1967, Antonovics and Levin 1980, Chesson 2000, HilleRisLambers et al. 2012), but studies continue to disagree on its role (Harms et al. 2000, HilleRisLambers et al. 2002, Comita et al. 2010, Johnson et al. 2012, Bagchi et al. 2014). Diversity may be promoted when competition is concentrated within the species, a demographic penalty suffered by species that become locally abundant (Clark 2010). At least part of the disagreement could result from the fact that studies evaluate effects of different predictors, including adult distance or seedling density, on different responses, including juvenile densities or one of several demographic rates (Herrando-Perez et al. 2012). Furthermore, it is difficult to generalize DD effects on diversity, because most DD studies are conducted on a single site, and the few large-scale studies are contra-

dictory (HilleRisLambers et al. 2002, Johnson et al. 2012). In this study, we investigated both the prevalence and strength of DD effects by introducing a more inclusive perspective that recognizes the different predictor–response combinations. We evaluated them using a forest inventory data set across the eastern United States.

We begin by clarifying how analyses of DD in the literature relate to one another. The three life stages that are typically involved in DD studies include seedlings, saplings, and trees, defined on the basis of size and/or age. These three stages can be represented by a system of equations

$$\frac{dx_1}{dt} = f(t) - m_1 x_1(t) - r x_1(t)$$

$$\frac{dx_2}{dt} = r x_1(t) - m_2 x_2(t) - g x_2(t)$$
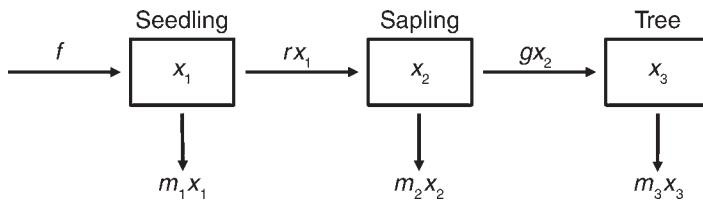
$$\frac{dx_3}{dt} = g x_2(t) - m_3 x_3(t) \qquad (1)$$

FIG. 1. Simplified life cycle graph for a size-structured tree population. Seedlings (x_1), saplings (x_2), and trees (x_3) are classified by a continuum of diameter at breast height (dbh). Demographic transitions include fecundity (f), recruitment (r), growth (g), mortality for seedlings (m_1), saplings (m_2), and trees (m_3).

and a life cycle graph (Fig. 1). Seedling abundance x_1 changes due to fecundity f, seedling mortality m_1, and growth from seedlings to saplings $r(t; z(t))$, which depends on covariates $z(t)$, including DD and other environmental variables. Recruitment to the sapling class $r(t; z(t))$ is a per capita rate; in most studies defined on a per-seedling basis. Sapling abundance x_2 changes due to recruitment r, sapling mortality m_2, and growth to the tree class g. Tree abundance x_3 changes due to growth g and tree mortality m_3.

Part of the disagreement in the literature is caused by the fact that the definition of DD can refer to different terms in this simple model. For example, to test the Janzen-Connell hypothesis (Connell 1970, Janzen 1970), most studies focus on seedling mortality (m_1) (Webb and Peart 1999, HilleRisLambers et al. 2002, Queenborough et al. 2007, Comita and Hubbell 2009, Bagchi et al. 2010, Chen et al. 2010, Comita et al. 2010, Metz et al. 2010, Kobe and Vriesendorp 2011, Bai et al. 2012, Lin et al. 2012, Paine et al. 2012, Piao et al. 2013, Gripenberg et al. 2014, Johnson et al. 2014, Lebrija-Trejos et al. 2014); while others quantify sapling and tree mortality (m_2 and m_3) (He and Duncan 2000, Hubbell et al. 2001, Peters 2003), growth rate (g) (Uriarte et al. 2004, Newbery and Stoll 2013), or seedling abundance (x_1) (Johnson et al. 2012, Sheffer et al. 2013). Direct tests of DD effects on recruitment (r) mostly come from a single site: Barro Colorado Island (BCI). Yet, even at BCI, there is disagreement: Conclusions vary from limited DD effects on a few common species (Hubbell et al. 1990, Condit et al. 1992, 1994), to strong DD effects on the majority of species (Wills et al. 1997, Wills and Condit 1999, Harms et al. 2000).

The stage assumed to predict DD likewise varies among studies, sometimes seedling density, other times adult density, and with different ways of treating distance. Here we argue that the most efficacious DD, in terms of promoting diversity, occurs when there is a negative relationship between adult density (x_3) and recruitment (r). Recruitment represents the most important response to DD, because it could increase population size (Bagchi et al. 2014). In contrast, seedling growth need not affect population growth, and survival responses only affect population growth if they result in increased recruitment rates. The life stage of responses to DD is likewise important: They can be offset and even result from high seed production and germination rates. For example, DD effects of seedling density (x_1) or adult density (x_3) on seedling mortality risk (m_1) can have limited diagnostic value because seedling densities and demographics can fluctuate dramatically in space and time without having large effects on population growth rates. In other words, seedling mortality may be loosely coupled with population dynamics and diversity.

Not only has the relative importance of species-specific DD been the subject of debate, but also whether the strength of DD is greatest for rare species (Comita et al. 2010, Johnson et al. 2012) or not (Kobe and Vriesendorp 2011, Bagchi et al. 2014). We note that a species that is rare everywhere should have the weakest evidence of DD for two reasons that are different from those previously suggested. First, rare species have the smallest sample sizes and rarely co-occur with conspecific neighbors, making it difficult to identify significant relationships. In one of the recent analyses finding that DD is strongest in rare species, one-third of the 180 species had <10 individuals across 20 000 plots, and seven species were singletons (Comita et al. 2010). The requirement for inference, that all species occur at a range of con- and heterospecific densities, cannot be satisfied for rare species. Second, continuing strong negative DD in the rarest species is unlikely to be a mechanism that promotes diversity or stabilizes coexistence. If it exists, it is at most transient; otherwise populations are increasingly at risk of extinction the smaller they become, which is to the contrary to the coexistence of rare and common species. A more careful analysis of species with a range of con- and hetero-specific neighbors could add insight to this debate.

Beyond clarifying the important stages for DD, there is a need to test effects across biogeographical scales and to include a large number of species. In this regard, forest inventory data provide unique opportunities to complement the understandings already gained from local sites (e.g., BCI). Johnson et al. (2012) provide a first analysis of DD in forest inventory data, finding that seedling abundance (x_1) tends to be negatively correlated with conspecific tree abundance (x_3), consistent with negative DD. Another study on a single species found a hump-shaped DD relationship between seedling abundance (x_1) and tree abundance (x_3) (Sheffer et al. 2013). In both cases, the use of seedling abundance (x_1) as a surrogate for recruitment (r) could influence the results. Seedlings can be abundant because fecundity (f) is high, seedling mortality (m_1) is low, or recruitment (r) is low (Eq. 1, Fig. 1). A dense, long-lived seedling bank does not necessarily mean that recruitment is high. For a number of reasons, tests of DD effects using seedling abundance are indirect. A reexamination of the recruit-

ment rates from forest inventory data could provide new insights for a broad region.

In this study, we examined both the prevalence and strength of DD effects on per capita recruitment and its relationship with tree species abundance in eastern U.S. forests. Specifically, we asked the following questions: (1) Concerning prevalence, do the majority of species have DD effects in per capita recruitment (r), and are these DD effects mostly negative? (2) Concerning strength, do conspecifics have stronger DD effects than heterospecifics and how does the strength of DD effects vary with overall species abundance (e.g., rare species advantage)?

To answer these questions, we used data from the Forest Inventory and Analysis (FIA) program of the USDA Forest Service, with over one million stem observations. For a range of tree species, we developed statistical models to examine the relationships between per capita recruitment and neighboring densities through life stages, controlling for climate variation at biogeographic scales. Our approach differs from previous studies in using seedling-to-sapling recruitment, rather than seedling abundance, to analyze DD patterns in recruitment. To understand the prevalence of DD, we quantified the proportion of species with significant positive or negative effects. To understand the strength of DD, we determined the magnitude of effects among con- and heterospecifics, and how it changes with overall species abundance.

Methods

Data

The USDA Forest Service's FIA program is the primary source for information about the extent, condition, status, and trends of forest resources in the United States (Smith et al. 2009). FIA applies a nationally consistent sampling protocol using a quasi-systematic design across the United States, resulting in a national sample intensity of one plot per 2428 ha (Bechtold and Patterson 2005). Classified satellite imagery is used to identify forested land, which is defined as areas with at least 10% forest cover, at least 0.4 ha in size, and at least 36.6 m wide. In forest land, FIA inventory plots consist of four, 7.2-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (Bechtold and Patterson 2005). All trees (standing live and dead) with a diameter at breast height (dbh) of at least 12.7 cm are inventoried on forested subplots. Within each subplot, a 2.07 m radius microplot offset 3.66 m from subplot center is established where only live trees with a dbh between 2.5 and 12.7 cm are inventoried. Within each microplot, all live tree seedlings are tallied according to species. Conifer seedlings must be at least 15.2 cm in height with a diameter <2.5 cm. Hardwood seedlings must be at least 30.5 cm in height with a diameter <2.5 cm. Note that they are often well-established stems, typically not first-year seedlings.

In this analysis, FIA data were extracted from 21 201 fully forested natural plots (non-plantation and non-disturbance) with two censuses (1996–2011) in 31 eastern states from the FIA data base (FIADB) version 5.1 on May 5, 2012 (*available online*).[7] We restricted analysis to 50 species with sufficient sample sizes (>1000 plots). We followed the FIA sampling design to divide the data into three size classes: seedling (dbh < 2.5 cm; x_1 in Fig. 1), sapling (2.5 cm $\leq$ dbh < 12.7 cm; x_2 in Fig. 1), and tree (dbh $\geq$ 12.7 cm; x_3 in Fig. 1). For each species, we used seedling-to-sapling recruitment (x_1 to x_2), rather than seedling abundance (x_1), as the basis for interpretation of recruitment. Individual stems were tracked for saplings and trees between the two censuses available from these sites, completed at an average interval of 5 yr. We defined total seedling-to-sapling recruitment as the number of new saplings that appeared for the first time in the second census. We defined per capita recruitment as per-seedling recruitment (annual per conspecific seedling count recruitment rate, seedlings/yr; r in Eq. 1). Since FIA plots record each stem with species identity, we defined con- and heterospecific neighboring trees in two ways: tree density (trees/ha), or tree basal area (m²/ha) in the first census. In other words, we used per-seedling recruitment as the response and neighboring tree densities or basal areas as the predictors.

In addition, we controlled for effects of climate variation on DD at biogeographic scales. Climate data in this study were extracted from the 800-m resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) data set (*available online*).[8] Recognized as a high-quality spatial climate data set in the United States, PRISM is an interpolation of meteorological station data to produce continuous, digital grid estimates of climatic parameters, with consideration of location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly et al. 2008). We used long-term average climate data (1990–2010) corresponding to each FIA plot as the climate covariates. We extracted annual mean temperature (°C), ranging from 0°C to 25°C, and annual precipitation (mm), ranging from 550 mm to 1650 mm.

Since the actual FIA plot coordinates are not publicly available, the longitude and latitude of plot locations have been perturbed in an unbiased direction not exceeding 1.67 km, and typically within a 0.8 km radius of the actual plot location, so as to facilitate study repeatability without introducing bias (McRoberts et al. 2005). The spatial resolution of PRISM data is similar to that of the FIA perturbed plot locations. We therefore used the publicly available perturbed plot coordinates to match the FIA plot location with the PRISM climate data.

[7] http://fia.fs.fed.us/
[8] http://prism.nacse.org/

Analysis

We applied a zero-inflated Poisson (ZIP) distribution (Lambert 1992) to model recruitment, rather than seedling abundance, in a single synthetic analysis for each species across the entire data set. For each species, we analyzed plots where seedlings are present to focus on dynamics within the geographic range of the species (e.g., *Liriodendron tulipifera* in Fig. 2). Recruitment is likely to be zero where seedlings are absent; DD effect of adult on recruitment is only relevant when seedlings occur. We used a zero-inflated model because recruitment can be absent due to strong DD effects. Neighboring tree densities were used as predictors to determine the strength of DD effects on recruitment. Climate variables helped account for occurrence at biogeographic scales. Climate variables were not used to predict recruitment because they showed limited relationships, as suggested by our previous FIA analysis (Zhu et al. 2012, 2014).

Recruitment was analyzed on the basis of repeated censuses of the same plot. New recruits are the numbers of new saplings in plot i that appear for the first time in the second census y_i, modeled as a two-stage process: presence with probability θ_i, and abundance conditional on presence with a Poisson distribution

$$y_i \sim \begin{cases} \text{Poisson}(A_i \Delta t_i \lambda_i) & \text{with probability } \theta_i \\ 0 & \text{with probability } 1 - \theta_i \end{cases} \quad (2)$$

where A_i is plot area (ha), Δt_i is the interval between censuses (yr), and λ_i is total recruitment (individuals·m^{-2}·yr^{-1}). Per capita recruitment is expressed as $r_i = \lambda_i/x_{1c,i}$, where $x_{1c,i}$ is the conspecific seedling density in the first census (seedlings/m^2). The sub-model for per capita recruitment is

$$\log r_i = \beta_0 + \beta_{3c} x_{3c,i} + \beta_{3h} x_{3h,i} \quad (3)$$

where $x_{3c,i}$ is the conspecific tree density (trees/ha) and $x_{3h,i}$ is the heterospecific tree density (trees/ha). A negative DD effect is interpreted as a negative coefficient (β_{3c}, β_{3h}): Per capita recruitment is reduced by neighboring densities. In contrast, a positive DD effect is interpreted as a positive coefficient (β_{3c}, β_{3h}): Per capita recruitment is enhanced by neighboring densities. In a second analysis, we quantified the effects of tree basal area (m^2/ha), instead of tree density (trees/ha), as an alternative measure of tree abundance. In addition, climate covariates were limited to the presence portion of the model because inclusion in both results in overfitting (Zhu et al. 2014). The sub-model for presence is

$$\text{logit}\,\theta_i = \gamma_0 + \gamma_T T_i + \gamma_P P_i + \gamma_{T^2} T_i^2 + \gamma_{P^2} P_i^2 + \gamma_{TP} T_i P_i \quad (4)$$

where T_i is temperature (°C), P_i is precipitation (mm), and with quadratic and interaction terms (T_i^2, P_i^2, $T_i P_i$). The functional forms of climate variables were suggested by our previous FIA analysis (Zhu et al. 2014).

For each species, we implemented a two-step model selection procedure to determine the *prevalence* of DD from different predictors. We conducted this in two steps because of the large number of possible variable combinations. First, we used logistic regression to choose climate variables based on the best fitting model for occurrence (0 or 1). For each species we chose the best four out of 32 models (five climate covariates; 2^5 combinations) based on the Akaike information criterion (AIC). We chose climate variables first because they determine the presence/absence of recruitment within species range. Second, we fitted these four models using the full ZIP model for recruitment. For each species we chose the best model with neighboring densities based on the deviance information criterion (DIC) in the Bayesian framework. In this way only important DD effects were included in the final model, so as to understand how prevalent DD is among different species. Within these important DD effects, we quantified their *strength* from different predictors as DD coefficients (β's).

All covariates were centered and scaled to unit standard deviation to fit the model, but coefficients were transformed back to their original scales to interpret DD effects. For the Bayesian model, non-informative priors β_j, $\gamma_j \sim N(0, 10^2)$ were used. Posterior distributions were simulated using Markov chain Monte Carlo (MCMC). Convergence was checked by both visually assessing trace plots and Geweke diagnostics after 10 000 iterations for each species. All analyses were performed in R version 3.0.0 (R Development Core Team 2013).

Results

DD effects on recruitment were *pervasive*, dominated by the negative relationship between per capita recruitment and neighboring density. In Fig. 3, we included species for which neighboring densities (con- and heterospecific tree densities) were chosen by model selection. Of the 50 species examined, DD effects were significant (chosen by model selection) for 34 species from conspecific trees; and 35 species from heterospecific trees. These significant DD effects were mostly negative. Fig. 3 shows DD effects from con- and heterospecific neighboring densities (β_{3c} and β_{3h} in Eq. 3), where a negative coefficient indicates that the per-seedling recruitment rate (r) is reduced by neighboring tree density (x_{3c} and x_{3h}): a negative DD effect. Of the species chosen by model selection, 22 species had negative DD effects from conspecific trees (β_{3c}; Fig. 3a); and 29 species had negative DD effects from heterospecific trees (β_{3h}; Fig. 3b). In other words, many species had significant negative DD effects on per-seedling recruitment rate (r).

Conspecific effects were *stronger* than heterospecific effects, and the conspecific effects were negatively related to species abundance. On average, species experienced three times greater DD effects from
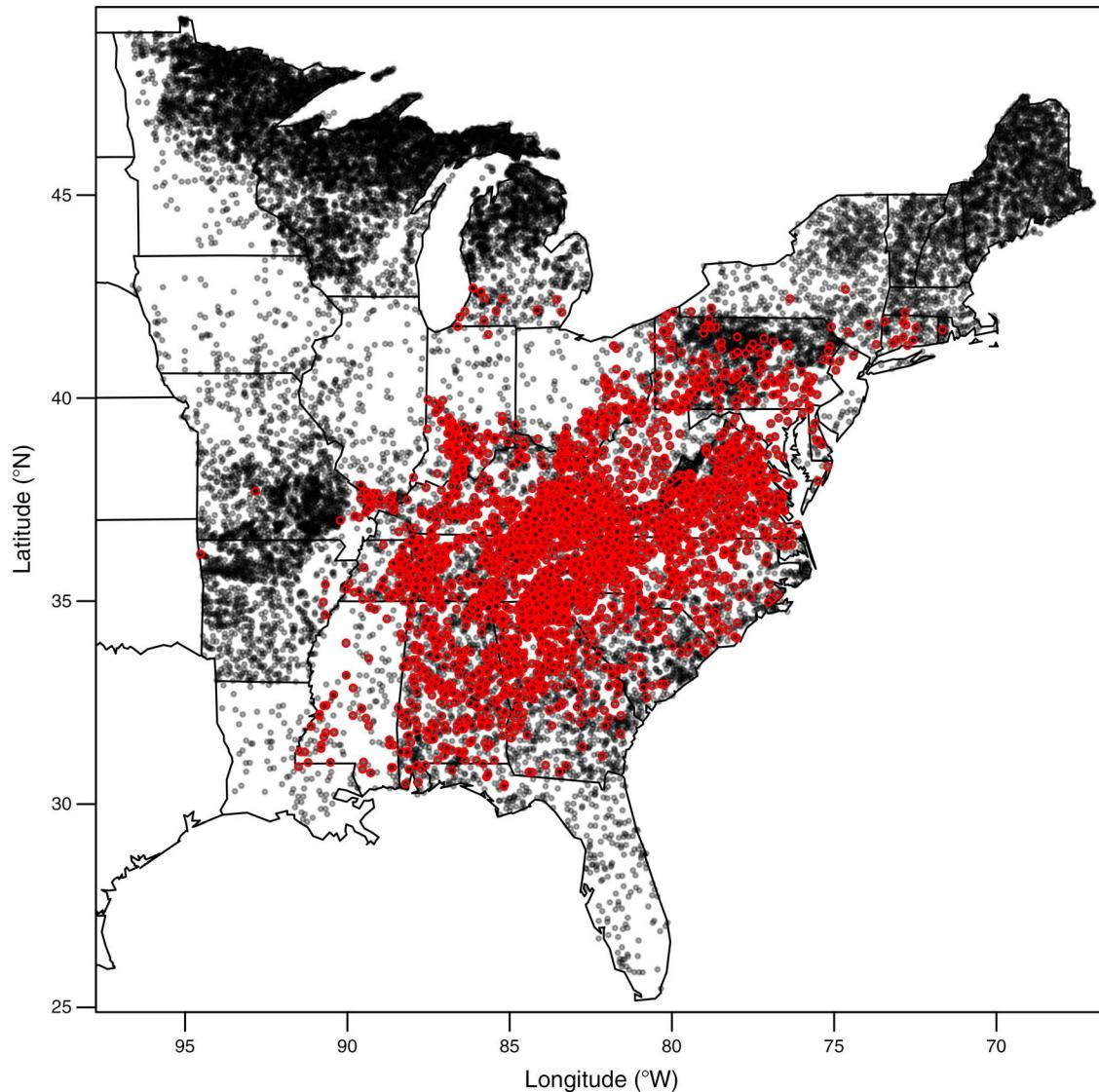
FIG. 2. USDA Forest Service Forest Inventory and Analysis (FIA) plot locations (gray/black points) and occurrence of an example species *Liriodendron tulipifera* (red circles) in the eastern United States.

conspecific (β_{3c}; Fig. 3a) than heterospecific trees (β_{3h}; Fig. 3b). Furthermore, we ranked DD effects by species abundance, defined as the average sapling and tree basal areas (m^2/ha) in all 21 201 plots (Fig. 3). It takes into account both regional occurrence and local abundance. Note that it is not the tree densities used in model fitting (to avoid circularity). This abundance gradient spanned more than three orders of magnitude, from common species (e.g., *Acer rubrum* 1.668 m^2/ha, *Pinus taeda* 1.503 m^2/ha) to rare species (e.g., *Cercis canadensis* 0.005 m^2/ha, *Persea borbonia* 0.010 m^2/ha). Along this gradient, common species experienced stronger conspecific negative effects than rare species (β_{3c}; Fig. 3a). Some of the rare species even experienced positive DD effects. This linear relationship (fitted by weighting the inverse of standard deviation) was significant ($R^2 = 0.41$, $P <$

0.01). There was no significant relationship from heterospecific trees (β_{3h}; Fig. 3b). In other words, per capita recruitment experienced the strongest negative DD effects from conspecific neighbors of common species.

Evaluating DD effects based on tree basal area (x_{3c} and x_{3h}) led to qualitatively similar results: Most species had significant negative effects, and they were strongest from conspecific neighbors of common species (Fig. 4). DD effects were significant for 31 species from conspecific trees; and 35 species from heterospecific trees. Among these significant relationships, 21 species had negative DD effects from conspecific trees (Fig. 4a); and 28 species had negative DD effects from heterospecific trees (Fig. 4b). On average, the conspecific effect was twice that of heterospecifics (compare Fig. 4a and
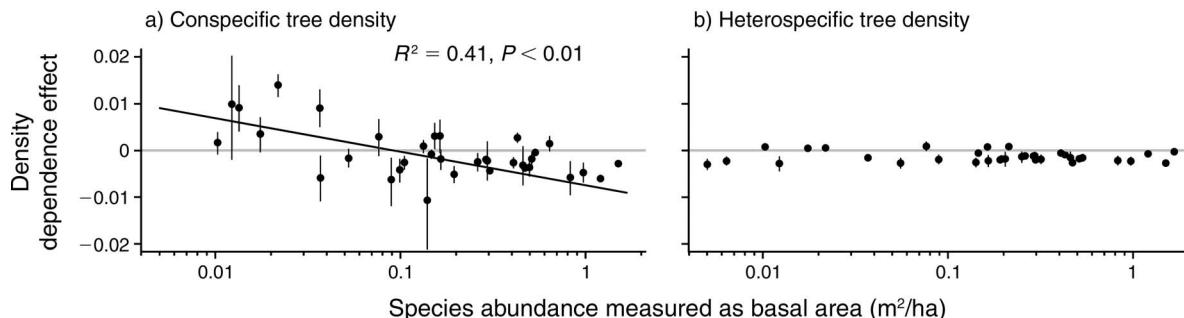
Fig. 3. Density dependence (DD) effects of per-seedling recruitment from neighboring tree densities, ranked by species abundance measured as basal area. Each species is summarized by a posterior mean (point) and 95% credible interval (vertical line) for variables included in the selected model. Negative coefficients indicate species for which per capita recruitment is reduced by neighboring densities. A trend line is included if the relationship between DD effect and species abundance is significant by linear regression, summarized by the statistics on the top.

Fig. 4b). Along the species abundance gradient, common species experienced significantly stronger negative effect than rare species from conspecific trees ($R^2 = 0.71$, $P < 0.01$; Fig. 4a). On the contrary, rare species experienced strong positive effect from conspecific trees. There was no significant relationship from heterospecific trees (Fig. 4b). In summary, recruitment mostly had stronger negative DD effects from conspecific neighbors of common species.

Climate effects were much less important than DD effects, with balanced negative and positive coefficients. We included all coefficients and species abundance in the Supplement.

DISCUSSION

Our analysis of adult effects on recruitment provides direct evidence that DD regulates population dynamics of tree species in eastern U.S. forests. DD effects are pervasive, mostly negative, stronger from con- than heterospecific neighbors, and more negative for common than rare species. The pervasive evidence reported here relied on the dynamics of recruitment from seedling to sapling, rather than correlations involving densities. These negative effects from adult to recruitment can result from canopy shading, moisture depletion, seed predation, and pathogen that inhibit understory recruit-

ment by reducing light, moisture, and seed source. The fact that most conspecifics have stronger DD effects than heterospecifics is consistent with the host-specific predictions of the Janzen-Connell hypothesis (pathogen, natural enemies, etc.). The negative relationship between the strength of DD effect and species abundance suggests disproportionate reduction of recruitment in common species, an important feature of population regulation.

To answer our first question on prevalence, we provide strong support for pervasive DD effects in tree recruitment, suggesting that it could be as efficacious in temperate forests as in the tropics. Most of these effects are negative, except for some of the rare species (Figs. 3a and 4a). Using 50-ha plot tree census data in BCI, Wills et al. (1997) found recruitment has negative DD effects from conspecific trees for the majority of the 84 most common species. Likewise, Wills and Condit (1999) found negative correlation between recruitment and conspecific tree density in two 50-ha rain forest plots, one in BCI and the other in Pasoh, Malaysia. Per capita recruitment likewise experience pervasive DD effects from conspecific neighbors in tropical forests in BCI (Harms et al. 2000) and Belize (Bagchi et al. 2014). All these are consistent with our findings that common
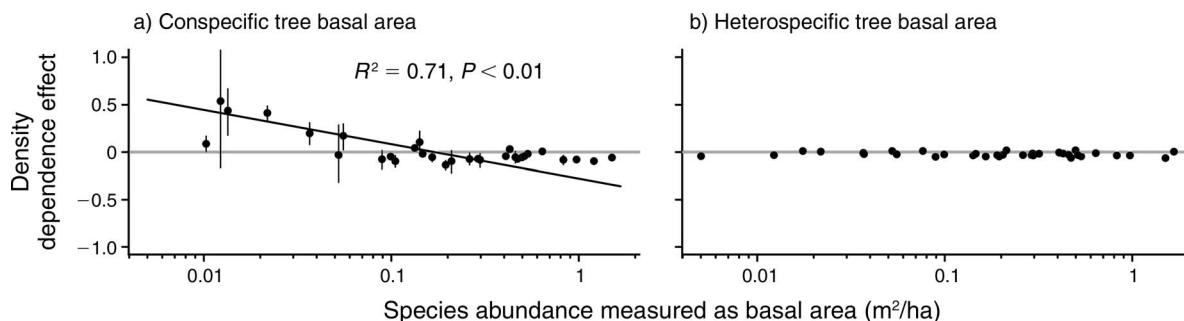

Fig. 4. Density dependence (DD) effects of per-seedling recruitment from neighboring tree basal areas, ranked by species abundance measured as basal area. Symbols follow Fig. 3.

conspecific trees have strong negative DD effects on recruitment.

To answer our second question on strength, we found that DD effects from conspecifics exceed that from heterospecifics, that is, for the same amount of change in neighboring densities, conspecifics lead to greater change in per capita recruitment than heterospecifics. This pattern could be caused by specialized natural enemies and pathogen, as predicted by the Janzen-Connell hypothesis (Terborgh 2012). Our result is consistent with the finding that conspecifics have stronger effects than heterospecifics on seedling mortality (Comita et al. 2010), but it provides a more comprehensive assessment at the overall population level by focusing on recruitment.

Furthermore, our results suggest that across this subcontinental scale, DD effects, mostly negative, are greatest for abundant species. Two processes could influence density relationships between juveniles and adults: (1) localized dispersal, which can concentrate juveniles near adults, showing a positive correlation between them, and (2) competition or mortality from enemies, where adults draw down resources (light, moisture, nutrients, et cetera) and offspring survivorship, showing a negative correlation. Our results demonstrate transitions from positive to negative conspecific DD effects along the species abundance gradient (Figs. 3a and 4a). This finding suggests that when a species is rare (low density), localized dispersal overrides competition or mortality from enemies, causing positive DD; when a species is abundant (high density), competition or mortality from enemies dominates, causing negative DD, as pointed out by Sheffer et al. (2013). At the community level, DD could benefit rare species by reducing recruitment of common species disproportionately. Our result supports the positive relationship between negative DD and species abundance found in a tropical forest experiment on recruitment (Bagchi et al. 2014). It does not support the findings that rare species suffer stronger conspecific negative DD than common species (Comita et al. 2010, Johnson et al. 2012).

Just as the interpretation of DD can be complicated by different methods and definitions (Fig. 1), the question of how it might vary with species abundance is complicated by methods of analysis. Comita et al. (2010) reported that rare species suffer the highest negative DD effects in seedling survival at BCI. Using FIA data in eastern U.S. forests, Johnson et al. (2012) likewise reported that DD was highest in rare species in a study limited to correlations between seedling and adults rather than dynamic recruitment. By contrast, more limited studies of Kobe and Vriesendorp (2011) and Bagchi et al. (2014) suggest agreement with our result, that DD is not disproportionately strong in rare species. Bagchi et al. (2014) have the advantage of controlled manipulation, but included only a few species at a single site. Our study has the advantage of focusing

directly on seedling-to-sapling recruitment at a subcontinental scale. However, apparent disagreement on how DD varies with abundance is partly methodological.

The BCI analysis (Comita et al. 2010) arguing that DD was strongest for rare species treated species as random effects in a logistic regression and assumed that coefficients for rare vs. abundant species are directly comparable. There are three minimal requirements for learning about DD in logistic regression, which are not satisfied in studies of this type. First, there must be sufficient observations of both survivors and deaths. Second, a species must occur over a range of con- and heterospecific densities. Third, a coefficient in logistic regression can only be estimated if the range of con- and heterospecifics overlaps for survivors and deaths. These requirements cannot be met for species that are rare everywhere. The rarest species contain no information on DD: They have few conspecific neighbors on all plots (some have none). Furthermore, when there are one or a few individuals, there will be no overlap in the level of DD for survivors and deaths, in which case the estimate of DD strength is undefined. The lack of information is obscured by the treatment of species as a random effect. When species is a random effect, and when there is a large range of abundances, estimates for rare species are driven by common species. Thus, it is surprising to conclude that rare species experience the strongest DD from a model where results have to be dominated by common species. These issues are avoided by treating species as fixed effects or by fitting them separately, as in our analysis, recognizing of course that there is no information on the rarest species.

The other FIA study (Johnson et al. 2012) reporting stronger DD for rare species reflects their treatment of zero-inflated data (Dickie et al. 2012). The apparent negative relationship between juvenile and adult is likely to be biased, as shown by Dickie et al. (2012). It also contrasts with the finding that juvenile and adult abundances are positively correlated in forest plots in New Zealand (Dickie et al. 2012), Spain (Vayreda et al. 2013), and the United States (Zhu et al. 2014). In addition, Johnson et al. (2012) report regression coefficients on regression coefficients, estimated independently for con- and heterospecific effects for every 2°-latitude–longitude cell. This approach cannot provide confidence intervals for a synthetic analysis. Our method uses a zero-inflated distribution to explicitly separate per capita recruitment and species occurrence, taking advantage of climate variations along biogeographic gradients. Our analysis provides a coherent synthesis of DD effect in tree recruitment.

Our analysis comes with several caveats. The DD patterns we found might be influenced by the fact that nearly all eastern U.S. forests are successional. Early successional species tend not to occur beneath adults of any species, so a negative correlation with adults is expected. We examined results for species by shade-tolerance classes, yet we did not find a tendency for

effects to vary between these groups. Our finding that DD is much stronger for con- than heterospecific adults still supports the importance of DD for maintaining diversity. Because FIA plots are small (0.067 ha), we were unable to conduct a spatial analysis of local neighborhood effects, which could be important in DD studies. Finally, we recognize that the FIA diameter threshold might affect our results for some species. Our recruitment is defined as stems achieving a dbh of 2.5 cm, which could have different biological meanings for canopy species (e.g., *Liriodendron tulipifera*) or subcanopy species (e.g., *Cercis canadensis*). DD effect through life stages is a knowledge gap that warrants future examination.

Despite caveats, we found pervasive DD effects, strongest from conspecific adults of common species, on the per capita recruitment rate. By explicitly focusing on seedling-to-sapling recruitment across over 20 000 plots spanning a continental scale, our results provide the most direct evidence that DD effects are regulating population dynamics, especially for common species. Our comparison between con- and heterospecific adults is consistent with the Janzen-Connell hypothesis, with stronger controls from con- than heterospecific neighbors. Our comparison among a range of species suggests that this negative regulation of population dynamics is stronger in common than rare species.

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