

Measuring the demographic impact of conspecific negative density dependence

Evan C. Fricke¹ · S. Joseph Wright²

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Abstract Rare plant species often suffer stronger conspecific negative density dependence (CNDD) in studies that assess the impact of local conspecific density on individual survival. All else equal, this causes a relative disadvantage among rare species that appears inconsistent with the role of CNDD in coexistence. The resolution to this apparent paradox is for lower species abundance to decrease the frequency of conspecific interactions sufficiently to outweigh the disadvantage of stronger CNDD. Whether this occurs in natural systems is untested because existing metrics do not isolate demographic impacts of CNDD, and it is also uncertain for tropical forest trees because the greater spatial aggregation observed in rare species could cause higher frequency of conspecific interactions despite lower abundance on the landscape. We develop a new metric, effective density-dependent mortality (EDDM), to quantify the proportion of individuals that are killed by density-dependent effects. We apply EDDM to a long-term study of seed fall and recruitment at Barro Colorado Island, Panama. Rare species had stronger CNDD but lower conspecific densities, and EDDM increased with abundance. Lower abundance, thus, reduces the frequency of conspecific interaction and,

consequently, mortality associated with CNDD. This mechanism allows rare species to avoid a disadvantage-when-rare that would, all else equal, result from stronger CNDD in rare species. Our work provides empirical support for a resolution to the apparently paradoxical findings that rare species experience stronger CNDD and may help reconcile contrasting findings for the relationship between the CNDD strength and abundance.

Keywords Advantage-when-rare · Coexistence · Community compensatory trend · Janzen–Connell hypothesis · Seed dispersal

Introduction

The mechanisms that maintain diversity and determine species abundance are fundamental to ecology. Conspecific negative density dependence (CNDD) appears to play a key role in both, particularly among tropical forest trees (Wright 2002; Comita et al. 2010; Mangan et al. 2010). CNDD among plants in tropical forests is typically attributed to density- or distance-responsive predators and pathogens (Janzen 1970; Connell 1971; Bell et al. 2006; Fricke et al. 2014; Bagchi et al. 2014; Bever et al. 2015). In theory, CNDD gives locally rare species an advantage that enables their persistence and thereby facilitates coexistence (Chesson 2000). Yet field studies from grasslands and temperate and tropical forests have shown that rare plant species suffer stronger CNDD, suggesting that stronger CNDD among rare species causes their lower abundance (Klironomos 2002; Comita et al. 2010; Mangan et al. 2010; Johnson et al. 2012). This suggests a possible paradox. If greater CNDD strength were to cause more negative demographic impacts among rare species, CNDD might impose

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✉ Evan C. Fricke
ecfricke@iastate.edu

¹ Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA

² Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panama

a disadvantage on rare species that would limit rather than facilitate species coexistence (Zhu et al. 2015).

Recent simulations help resolve this apparent paradox (Chisholm and Muller-Landau 2011; Yenni et al. 2012, Mack and Bever 2014). In these simulations, each species has an intrinsic CNDD strength that determines the degree to which it self-limits, meaning that species with stronger CNDD stabilize at lower abundances than species with weaker CNDD (Chisholm and Muller-Landau 2011; Mack and Bever 2014). Stronger CNDD also facilitates coexistence by strongly stabilizing rare species toward their equilibrium abundances when stochastic population fluctuations would otherwise cause extinction (Yenni et al. 2012). These studies suggest how the apparent paradox is avoided. Because the demographic effect of CNDD depends both on the strength of CNDD (or strength of self-limitation) and on the frequency of conspecific interaction, a species with stronger CNDD may avoid a demographic “disadvantage-when-rare” through infrequent conspecific interaction. However, the spatially implicit simulations assume population-level abundance controls the responses of individuals to conspecific density (Chisholm and Muller-Landau 2011; Yenni et al. 2012). Among tropical forest trees, strong interactions are restricted to local scales defined by immediate neighbors (Harms et al. 2000; Comita et al. 2010; Uriarte et al. 2010; Lebrija-Trejos et al. 2014) and there is a strong inverse relationship between spatial aggregation and population-level abundance (Condit et al. 2000). Greater aggregation—likely caused by factors involving niche differentiation and dispersal (Detto and Muller-Landau 2013, 2016)—will increase local conspecific density experienced by the average individual and intensify the demographic impact of CNDD. How the counteracting impacts of greater spatial aggregation and lower population-level abundance influence local conspecific densities will determine how the demographic impact of CNDD varies with abundance.

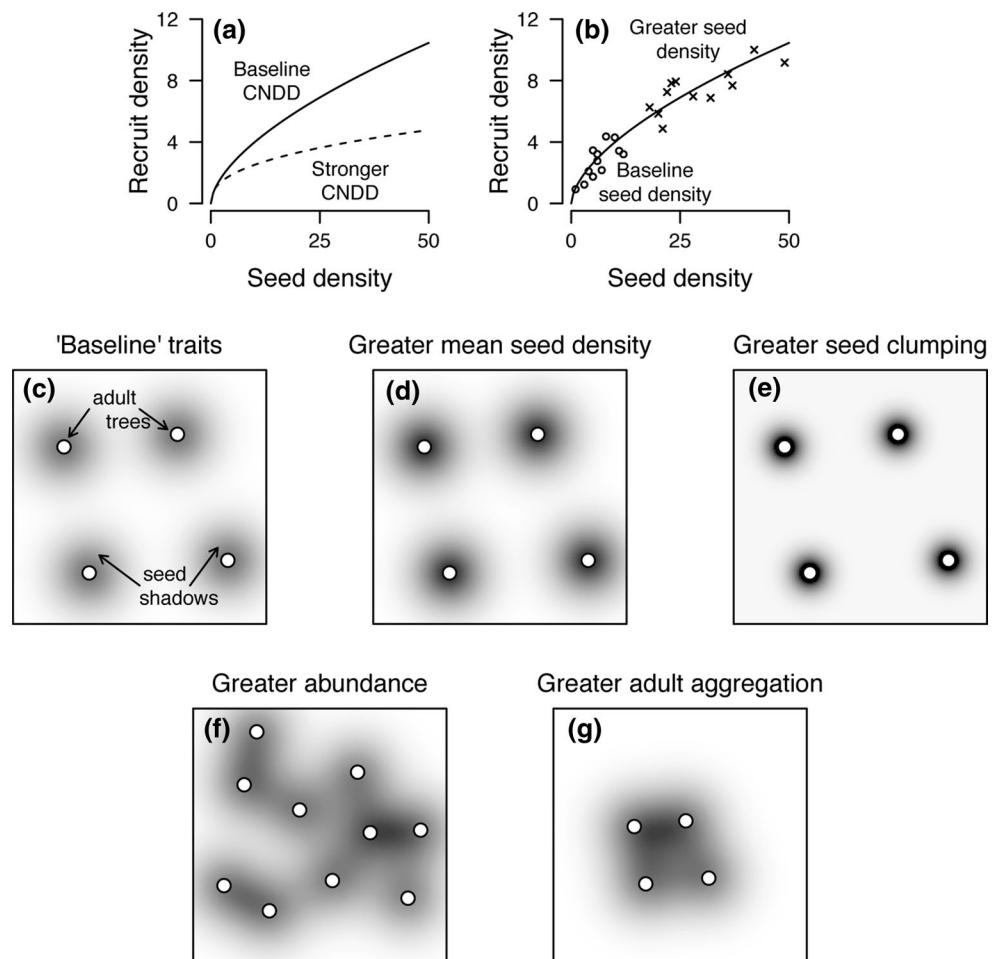
Existing metrics do not measure the population-level consequences of CNDD. For tropical forests, community-level tests of a rare species advantage have focused on a ‘community compensatory trend’, predicting that individuals of rare species should have greater survival probabilities (Connell et al. 1984; Webb and Peart 1999; Queenborough et al. 2007; Comita and Hubbell 2009; Chen et al. 2010). In contrast, studies that relate the strength of density dependence to abundance extract a CNDD strength parameter from the relationship between density at one life stage and survival to a subsequent stage (Klironomos 2002; Comita et al. 2010; Mangan et al. 2010; Johnson et al. 2012; Bagchi et al. 2014). Neither metric directly quantifies how CNDD itself influences demography. The survival probabilities used to test for a community compensatory trend do not isolate the impact of CNDD from other density-independent influences on

survival. Likewise, CNDD strength does not provide information on interspecific differences in the frequency of conspecific interaction that determine how CNDD acting among immediate neighbors scales up to population-level demographic outcomes. A new metric that isolates the demographic impact of CNDD, assessing the net effect of potentially counteracting impacts of CNDD strength and local conspecific densities, is needed.

To improve our ability to quantify the demographic impact of CNDD on populations, we develop a metric that estimates the proportion of deaths attributable to density-dependent effects. The new metric, effective density-dependent mortality (EDDM), compares the number of individuals who actually survive (i.e., that recruit from the seed to the seedling stage) to the number of individuals estimated to survive under a density-independent scenario (see “Effective density dependent mortality” section). To introduce this metric and explore its implications empirically, we focus on demographic impacts of CNDD at the seed-to-seedling transition. The seed-to-seedling transition has been a major focus of research on CNDD (e.g., Harms et al. 2000; HilleRisLambers et al. 2002; Bagchi et al. 2014) and the dynamics of such early life stages are thought to have a disproportionately large influence on diversifying processes within forests (Green et al. 2014). Although we will focus on this life stage transition and on the influence of conspecifics on survival alone, our approach can be extended to other vital rates and life stages and accommodate more detailed models of density-dependent dynamics. Figure 1 illustrates how EDDM over the seed-to-seedling transition increases with stronger CNDD (more strongly saturating relationships between seed and recruit density) and higher local conspecific densities (in our case, shown as greater mean seed densities and more clumped seed distributions). Population-level factors such as adult spatial aggregation and abundance could influence EDDM by affecting local conspecific density. The increase in EDDM caused by higher abundance (and, inversely, lower EDDM caused by lower abundance; compare Fig. 1c, f) constitutes the “advantage-when-rare” outcome of CNDD as a stabilizing mechanism.

Here, we use data from a long-term study of seed fall and recruitment on Barro Colorado Island, Panama to measure the demographic impact of CNDD at the seed-to-seedling transition, determine the factors that influence its severity, and test whether stronger CNDD leads to greater EDDM in rare species. Specifically, we assess how CNDD strength and local conspecific seed densities influence EDDM, how species abundance and spatial aggregation influence CNDD strength and local conspecific densities, and finally how EDDM is related to species abundance and spatial aggregation. To compare to one previous approach for measuring population-scale demographic impacts of

Fig. 1 Factors that directly determine the demographic impact of conspecific negative density dependence (CNDD) over the seed-to-seedling transition include **a** the strength of CNDD and **b** local seed density; there are fewer recruits per seed with stronger CNDD and higher local seed density and, hence, greater effective density dependent mortality (EDDM). Relative to **c** a hypothetical ‘baseline’ population of four adults (*circles*) and their seed shadows (*shading*), otherwise equivalent populations with **d** greater mean seed density, **e** greater seed clumping, **f** greater adult abundance, and **g** greater adult aggregation have greater EDDM



CNDD, we also test for a community compensatory trend in survival across the seed-to-seedling transition.

Materials and methods

Effective density-dependent mortality

To demonstrate how to calculate EDDM, we focus on the seed-to-seedling transition and use a model of density-dependent recruitment where local recruit density (R) is related to local seed density (S) as $R = a S^b$ (Harms et al. 2000; Wright et al. 2005a; Bagchi et al. 2014). The a -value is per-capita survival at low conspecific density and the b -value is the CNDD strength term, with $b = 1$ and $b < 1$ indicating density independence and CNDD, respectively. To estimate density-independent recruitment, we set b to 1 and use the same fitted a -value; this allows us to calculate recruitment expected if density-dependent processes did not influence survival. Finally, we compare this estimate of density-independent recruitment to density-dependent recruitment using the fitted

a - and b -values (although observed recruitment could be used instead). In practice, we measure the local density of conspecific seeds and recruits across locations (j) and estimate the number of recruits for density-dependent (R_{dd}) and density-independent (R_{di}) scenarios and EDDM as follows:

$$R_{dd} = \sum_j a S_j^b$$

$$R_{di} = \sum_j a S_j^1$$

$$EDDM = (R_{di} - R_{dd})/R_{di} = 1 - \frac{\sum_j S_j^b}{\sum_j S_j^1}$$

Note that the a -values, which are equal, cancel from the summation. This removes the impact of species-specific, density-independent recruitment probabilities that would otherwise complicate interspecific comparisons. As a result, EDDM isolates the demographic impact of CNDD on the population and can be compared among species. EDDM increases with stronger CNDD (smaller

b), higher mean seed density (\bar{S}_j), and more clumped seed distributions (greater variation in S_j) (Fig. 1c–e).

Seed production and seedling recruitment

Our seed production and seedling recruitment data are from censuses conducted in the 50-ha Forest Dynamics Plot at Barro Colorado Island, Panama (Wright et al. 2005a). Weekly censuses recorded the number of seeds of each species in 200 0.5-m² seed traps. Annual censuses recorded the number of seedling recruits in 600 1-m² plots located 2 m from three sides of each seed trap. We refer to each seed trap and its associated seedling plots as a station. We summed seeds and the resulting recruits for each year and station, associating recruits with the appropriate year of seed production by incorporating species-specific germination lags (Garwood 1983). We include 16 tree species with more than 100 recruits recorded over the study period (1995 through 2011 inclusive).

Recruitment model

We used maximum likelihood estimation in the R package *bbmle* (Bolker and R Development Core Team 2014) to model the relationship between seeds and recruits per square meter as $R = a S^b$ with a negative binomial error distribution (Wright et al. 2005a). We also fitted a linear model ($R = a S$) and used likelihood ratio tests to compare this linear model with the power law model to determine significance of the *b*-value. Station-years with $R = S = 0$ do not affect this analysis because the negative binomial likelihood is one. Station-years with $S < R$ present a problem, however, because the negative binomial likelihood is undefined. To avoid this problem in a similar analysis, HilleRisLambers et al. (2002) increased *S* to equal *R* and assessed the impact of this approach by repeating analyses after excluding cases with $S < R$. We adopt this approach and, after excluding station-years where $S < R$, we find qualitatively consistent results among species in which the power law model provides a better fit than a linear model (Fig. S1 in Supporting Information).

A second potential bias could result from space limitation. Rarely, a trap captured more seeds than could possibly recruit due to simple spatial constraints. We, therefore, repeated our analyses excluding station-years that had conspecific seed densities above the maximum observed conspecific seedling density of 71 seedlings m⁻² (Harms et al. 2000). The results were qualitatively similar, suggesting that our conclusions are not simply the result of space limitation.

Abundance, aggregation, and conspecific seed densities

As measures of adult abundance, we used basal area (m² ha⁻¹) and population density (total number of individuals ha⁻¹) calculated using all individuals ≥ 1 cm dbh (Condit 1998; Hubbell et al. 1999; Hubbell et al. 2005). To measure adult spatial aggregation, we calculated Ω_{0-10} for adults of each species (Condit et al. 2000). The Ω_{0-10} index standardizes the density of adult conspecifics located within 10 m of an adult by the overall adult density observed for the 50-ha plot. To determine whether individuals were adults, we used species-specific estimates of the dbh threshold at which individuals are reproductive (Wright et al. 2005b; Visser et al. 2016).

For each species, we describe the local conspecific seed densities that seeds of each species experience by fitting negative binomial distributions to seed density data using only those station-year combinations that received seeds. By omitting station-year combinations with zero seeds and subtracting 1 from the number of seeds, we captured the relevant distribution of conspecific seed densities experienced by focal seeds. The negative binomial parameters are mean conspecific density (μ) and the clumping parameter (κ). We used the *glm.nb* function in the MASS package to fit negative binomial distributions (Venables and Ripley 2002).

Measuring effective density-dependent mortality

We used the seed density data from each of the 3400 station-year combinations and the species-specific parameter indicating survival at low density (*a*-value) from the power law model to estimate recruitment in the density-independent scenario (summed across stations as R_{di} , as described in the “Effective density-dependent mortality” section). For recruitment with density dependence, we used observed seedling density data (summed across station-years *j* as R_{obs}). The use of observed recruit density data in place of R_{dd} differs slightly from the description of EDDM above, where fitted parameters were used to calculate R_{dd} . Results are consistent whether R_{dd} or R_{obs} is used. For each species *i*, we calculated effective density-dependent mortality as $EDDM = (R_{di} - R_{obs})/R_{di}$.

Analyses of EDDM

As a proof of concept to assess whether the factors hypothesized to influence EDDM directly (Fig. 1a–e) do so when these factors are fitted from field data, we first analyzed relationships between EDDM and mean seed density (μ), the clumping parameter (κ), and CNDD strength (*b*). The

logit transformation of EDDM (Warton and Hui 2011) was the dependent variable in a multiple regression model with μ , κ and b as independent variables.

The factors hypothesized to influence EDDM directly (μ , κ and b) may in turn be influenced by population-level factors, including abundance and adult spatial aggregation. In three separate multiple regression models, we use μ , κ or b as the dependent variable and aggregation (Ω_{0-10}) and abundance as independent variables.

Finally, abundance and adult spatial aggregation might influence EDDM indirectly through their direct effects on μ , κ and b . To evaluate this possibility, we use a multiple regression model with EDDM as the dependent variable and abundance and adult spatial aggregation as independent variables.

In each analysis with abundance as an independent variable, we performed separate analyses using basal area or population density as the measure of abundance. We assume that each effect is present and interpret estimates and their standard errors from full models (Bolker et al. 2009).

Analyses of the community compensatory trend

We tested for the existence of a community compensatory trend in the relationship between abundance and the logit transformation of the recruit-to-seed ratio. For each species, we calculated the recruit-to-seed ratio (1) as the mean value of R_j/S_j over all station-year combinations and (2) as R_j summed across all station-years to S_j summed across all station-years.

Results

Our analysis of 16 tree species included 185,773 seeds and 21 299 recruits. A density-dependent recruitment model strongly improved model fit over a linear model for 13 of the 16 species ($P < 0.001$, Table S1). The three exceptions were extreme heliophiles, with the three smallest a -values ($a \leq 0.008$, meaning that 1000 seeds generated 8 or fewer first-year seedling recruits) and recruitment limited to tree fall gaps (SJW, unpublished data) (Table S1). Parameter estimates for these three species are dominated by spatial variation in light availability and do not reflect density-dependent recruitment dynamics, and thus we remove them from further analysis. Negative binomial distributions provided good fits describing the distribution of conspecific seed densities experienced by seeds (Table S1).

The dynamics illustrated in Fig. 1a–e, showing the factors hypothesized to influence EDDM directly, were strongly supported by the data. EDDM increased with greater mean conspecific seed density (larger values of

μ ; 0.040 ± 0.007 ; multiple regression coefficient estimate ± 1 S.E.), more clumped distributions of conspecific seed density (smaller values of κ ; -2.0 ± 0.5), and stronger CNDD (smaller values of b ; -1.7 ± 0.5).

Species abundance influenced two of the factors that directly influence EDDM. CNDD strength was positively related to abundance (0.12 ± 0.06 ; multiple regression coefficient estimate ± 1 SE; Fig. 2a), indicating stronger CNDD among less abundant species. Mean seed density was also positively related to abundance (15 ± 3.0 ; Fig. 2b). The clumping parameter was unrelated to abundance (-0.095 ± 0.078). CNDD strength, mean seed density and the clumping parameter were also unrelated to adult spatial aggregation (0.0031 ± 0.0034 , 0.070 ± 0.17 and -0.0024 ± 0.0043 , respectively).

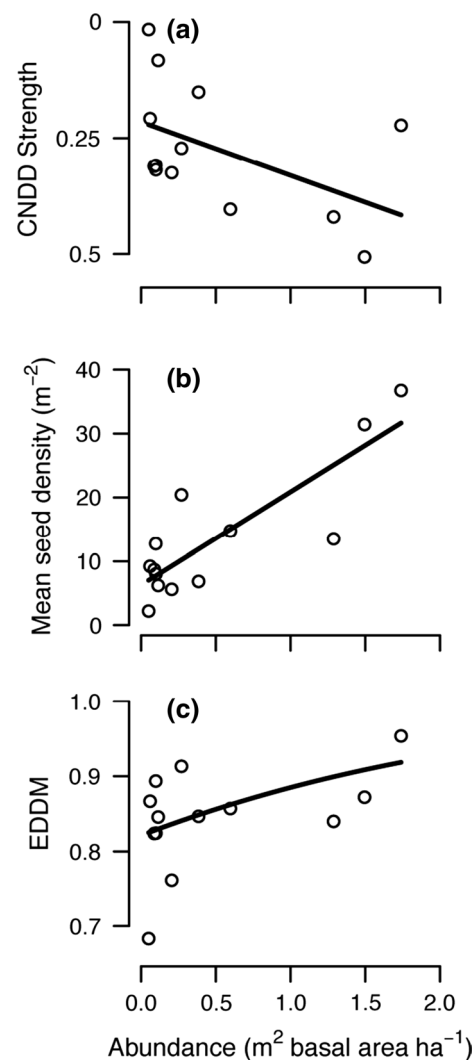


Fig. 2 Relationships between **a** species abundance and CNDD strength, **b** mean seed density, and **c** effective density dependent mortality (EDDM). Note the inverted b -value scale for CNDD strength, which is negatively related to b -values. Each panel uses mean values for the remaining independent variables

Species abundance indirectly influenced EDDM via its impact on CNDD strength and local conspecific seed densities. EDDM was positively related to abundance (0.52 ± 0.24 ; multiple regression coefficient estimate ± 1 SE; Fig. 2c) but was unrelated to adult spatial aggregation (0.009 ± 0.013). Each result was qualitatively similar when abundance was measured as population density (Tables S2, S3).

There was no evidence for a community compensatory trend. When measured as the mean value, over all station-year combinations, of recruit density divided by seed density, the recruit-to-seed ratio was not related to basal area (linear regression, $R^2 = 0.05$, $P = 0.48$; Fig. S2a) or to population density ($R^2 = 0.02$, $P = 0.64$; Fig. S2b). When measured as the sum of recruit density across all station-years to sum of seed density across all station-years, the recruit-to-seed ratio was not related to basal area ($R^2 = 0.14$, $P = 0.20$; Fig. S2c) or to population density ($R^2 < 0.01$, $P = 0.99$; Fig. S2d).

Discussion

We developed a new metric, effective density-dependent mortality (EDDM), to measure the demographic impact of conspecific negative density dependence (CNDD) using field data. EDDM estimates the portion of individual deaths associated with conspecific density-dependent effects. EDDM should increase with greater local conspecific densities and with stronger CNDD. Interspecific differences in these characteristics should cause variation in EDDM among species within a community. We measured EDDM at the seed-to-seedling transition for 13 tree species at Barro Colorado Island, Panama. We found that locally rare species had stronger CNDD, but because their individuals experienced lower local conspecific densities, rare species had lower EDDM. Our findings help reconcile conflicting theoretical expectations for the impact of CNDD on diversity maintenance and on species abundance, as well as conflicting empirical results regarding the relationship between CNDD strength and species abundance.

An apparent paradox exists between the diversity-maintaining and abundance-determining roles of CNDD. To achieve its role in determining abundance, CNDD is thought to cause rare species to suffer more from conspecifics (Comita et al. 2010; Mangan et al. 2010). All else equal, this would cause a demographic disadvantage among rare species that would be inconsistent with the diversity-maintaining role of CNDD (Chesson 2000). EDDM allows us to address this paradox by estimating the demographic impact of CNDD empirically. We found evidence contrary to the “all else equal” assumption that underlies the paradox. The local conspecific densities that individuals experience

increase as species abundance increases and, in turn, EDDM increases with abundance. When acting on individual populations, this constitutes the stabilizing mechanism necessary for diversity maintenance (Chesson 2000). This advantage of rarity was present despite heterogeneity in local conspecific density and was not outweighed by effects of adult spatial aggregation on local conspecific seed density. These results provide empirical support for a mechanism that allows rare species to avoid a disadvantage that would otherwise result from the stronger CNDD they experience, and, thus, for the resolution to the paradox.

We found no evidence of a community compensatory trend (CCT) in survival probabilities among these species. For two reasons, we question whether the CCT can provide a strong test of the demographic rare species advantage hypothesized to be necessary for diversity maintenance (Connell et al. 1984). First, the survival probabilities used to test the CCT are shaped by confounded density-dependent and density-independent influences. This should increase variability around the predicted CCT relationship or, if density-independent influences are correlated with abundance, can cause spurious CCTs (Wright 2002). Second, we question whether the CCT is necessary for the diversity-maintaining outcome of CNDD. The CCT should tend to make rare species increase in abundance and common species decrease (Connell et al. 1984). Unless other factors correlated with abundance balance this effect, all species should stabilize toward the same abundance (Wright 2002). If any processes do stabilize species at different abundances, it seems unlikely that species abundance alone would strongly predict whether a species is currently above or below its stable abundance, and therefore unlikely that a CCT would be evident. Metrics such as EDDM that isolate the demographic impact of CNDD from density-independent influences on survival are better suited than simple vital rates for quantifying the diversity-maintaining outcome of CNDD.

We did find a rare species advantage to the extent that rare species tended to have lower EDDM (Fig. 2c). Whether this positive relationship between EDDM and abundance is necessary for diversity maintenance is not resolved by this study. On first principles, it may be more appropriate to expect the lack of a relationship between abundance and EDDM among species; perhaps species should stabilize toward abundances that result in similar EDDM across species. Alternatively, lower EDDM in rare species could be necessary to balance species-level fitness inequalities that exist across rare and common species (Chesson 2000).

One previous approach incorporates information on the frequency of conspecific interaction to better quantify demographic impacts of CNDD. Kobe and Vriesendorp (2011) and Lin et al. (2012) quantify ‘potential NDD’ for each species by multiplying CNDD strength by the

maximum conspecific density at which seedlings of a species were observed in the field. This index is proportional to the maximum potential demographic impact of CNDD on a population, but may not be a strong measure of the actual demographic impact if a species exhibits variation in local conspecific density. We suggest that approaches like EDDM that account for heterogeneity in local conspecific density, incorporating densities recorded across all measured plots to make demographic predictions, provide a stronger ability to link local, heterogeneous survival dynamics to community-scale outcomes of CNDD. Applying such approaches across other life stages and vital rates would broaden understanding of the full demographic influence of CNDD on plant populations and may reveal contrasting patterns across life stages (LaManna et al. 2016) or tradeoffs that operate across different aspects of plant performance.

EDDM may reconcile contrasting findings for the relationship between the strength of CNDD and species abundance (Klironomos 2002; Comita et al. 2010; Mangan et al. 2010; Kobe and Vriesendorp 2011; Johnson et al. 2012; Bagchi et al. 2014, Zhu et al. 2015; LaManna et al. 2016). For example, Zhu et al. (2015) showed that rare species experienced weaker density-dependent effects, contrasting with the results of an earlier study using data from the same forest inventory (Johnson et al. 2012). This calls into question other existing research showing stronger CNDD in rare species. However, studies of CNDD have used widely differing approaches and scales (Zhu et al. 2015). Our work suggests that the spatial scale of analysis influences the relationship between abundance and apparent CNDD; rare species can exhibit stronger negative impacts of local conspecific density on individual survival (stronger CNDD) and at the same time have a smaller demographic impact of CNDD when sampled at the 50-ha scale (lower EDDM). Studies sampling at scales larger than the scales at which conspecific density-dependent effects operate could underestimate the effect of strongly negative local conspecific interactions that in rare species are infrequent on the landscape and overemphasize the effect of individually weak interactions that occur frequently in common species. This suggests that findings of weaker demographic impacts of density dependence in rare species at larger spatial scales may not be evidence against the existence of stronger CNDD in rare species or the abundance-determining outcome of CNDD. We hope that this study highlights the need for careful consideration of the distinction between the degree of self-limitation (CNDD strength) and the demographic impact of that self-limitation given a population's current state (EDDM).

We have structured our discussion of CNDD as though there are two distinct outcomes of CNDD, as existing research has generally focused on either the

abundance-determining or diversity-maintaining outcomes separately, employing distinct predictions and metrics to test each. Yet as our empirical results and previous simulation studies (Chisholm and Muller-Landau 2011; Yenni et al. 2012; Mack and Bever 2014) demonstrate, it may be more appropriate to consider both outcomes to be the result of the single role of CNDD as a stabilizing mechanism. By stabilizing species abundance, CNDD facilitates diversity maintenance, and because the strength of this stabilization varies, CNDD determines species abundance. Effective density-dependent mortality provides an approach to measure how CNDD influences demography to achieve both outcomes.

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Author contribution statement ECF conceived of the study. SJW collected field data. ECF and SJW designed the analysis and wrote the manuscript.

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