

TECHNICAL RESPONSE

FOREST ECOLOGY

Response to Comment on “Plant diversity increases with the strength of negative density dependence at the global scale”

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Hülsmann and Hartig suggest that ecological mechanisms other than specialized natural enemies or intraspecific competition contribute to our estimates of conspecific negative density dependence (CNDD). To address their concern, we show that our results are not the result of a methodological artifact and present a null-model analysis that demonstrates that our original findings—(i) stronger CNDD at tropical relative to temperate latitudes and (ii) a latitudinal shift in the relationship between CNDD and species abundance—persist even after controlling for other processes that might influence spatial relationships between adults and recruits.

To explore potential bias in our estimates of conspecific negative density dependence (CNDD) (1), Hülsmann and Hartig (2) present simulations that vary several processes, including dispersal, habitat specificity, adult/recruit ratios, and species richness.

Some of these simulations produce spuriously strong CNDD for rare species, leading them to suggest that our methods might be biased. If this were correct, then our estimates of CNDD would be biased toward stronger effects for rare species at any latitude. However, this was not the case,

because our original estimates of CNDD varied substantially among rare species when matched for abundance [figure 2D in (1)]. Furthermore, median CNDD for rare species differed across latitudes, with rare species having stronger median CNDD in tropical than in temperate forests [figure 2C in (1)].

The strong negative biases in CNDD that Hülsmann and Hartig observe for rare species are erroneously generated because their simulation models assume that a certain proportion of recruits are globally dispersed across an entire 50-ha forest plot on Barro Colorado Island (BCI). This assumption is biologically unrealistic because the vast majority of species at BCI exhibit dispersal limitation (3), spatially clumped distributions (4, 5), and an average mean dispersal distance of 28 m (6). Although such distances allow some recruits to disperse quite far from parent trees, recruit density is still greatest around the parent (7, 8). That is why analyses that assume global dispersal, as in Hülsmann and Hartig, underestimate or fail to detect CNDD when it is actually present (8) (Fig. 1). Moreover, the assumption of global dispersal results in recruits of rare species being farther from adults than recruits of common species ($r = -0.43$, $P < 0.0001$, $N = 187$ species in the BCI data set), mimicking the same pattern that would be produced if CNDD were stronger for rare species. Even where Hülsmann and Hartig relax the assumption of completely global dispersal, a large proportion of recruits are still randomly dispersed across the entire plot (e.g., 50% directly under parent tree, 50% globally dispersed; Fig. 1). Moreover, these empirically unjustifiable assumptions about dispersal permeate their simulations of other processes (i.e., the authors use some degree of global dispersal for all other panels in their figure 1). Thus, the unrealistic assumption of global dispersal largely generates the biases that Hülsmann and Hartig claim to observe.

Hülsmann and Hartig suggest that our use of an offset value introduced bias in our CNDD estimates. We applied an offset value to retain recruits located in 20 m × 20 m quadrats without a conspecific adult in the calculation of CNDD (1). Retention of all recruits was important because, in many cases, recruits in quadrats without adults

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likely came from adults in adjacent quadrats. The mean distance ($\pm$ SE) between recruits in these quadrats and the nearest conspecific adult was 26.95 ± 0.04 m (24.16 ± 0.19 m and 27.08 ± 0.04 m for temperate and tropical trees, respectively), and 80% were within 36 m of a conspecific adult (31 and 36 m for temperate and tropical trees, respectively). These distances are well within average dispersal kernels for tree species (6, 9). Therefore, we applied an offset value to quadrats with recruits but no conspecific adults, so as to ensure that these recruits remained in the calculation of CNDD and to avoid bias that results from excluding these recruits (1, 10, 11). However, adding the offset value to all quadrats did not qualitatively change either the relationship between species rarefied richness and CNDD across latitudes ($r = -0.877$, $P < 0.001$) or the latitudinal shift in the relationship between CNDD and species abundance ($r = -0.552$, $P = 0.006$). Moreover, these findings persisted when we used an alternative distance-weighted approach to estimate CNDD that avoids the use of an offset altogether (11). Therefore, the main findings of our original paper are robust to the statistical approach used to estimate CNDD.

To further verify that our results reflect changes in CNDD across species and latitudes, we used a null model similar to the model used by Hülsmann

and Hartig that simply modifies the assumption of global dispersal. The model, recommended by Wiegand and Moloney (12), fixes adult locations and disperses recruits away from adults given some dispersal kernel. Instead of globally dispersing all or a fraction of recruits (as done by Hülsmann and Hartig), we use the best-fitting model for seed dispersal across tropical and temperate forests (Clark's 2dT dispersal kernel) (6, 7, 9, 12). As in Hülsmann and Hartig's model, our null model also preserves habitat specificity (adult locations), adult/recruit ratios, and abundances for each species to test whether these processes could have generated artificial CNDD patterns. As suggested by Wiegand and Moloney, we also modeled immigration by treating each forest plot as a torus, allowing recruits dispersing off the plot to immigrate back into the plot from the other side (12). We performed two versions of this null model: (i) with every species having a fixed mean dispersal distance of 30 m [approximating the mean across >60 tropical and temperate species (6, 7)] and (ii) with species having allometrically scaled dispersal distances that incorporate intraspecific variation. For the allometric-dispersal model, we modeled inter- and intraspecific variation in dispersal using a recent meta-analysis, which showed that more than half of the total variation in mean dis-

persal distance across >200 plant species scaled allometrically with their maximum height (9). We used this relationship, along with observed variation around this relationship, to simulate a wide range of empirical dispersal distances for each species given its maximum height and to calculate null-expected values of CNDD for each species in our data set (12).

The results of this null-model analysis using the distance-weighted measure of adult abundance [described briefly above and presented in detail in (11)] are shown in Figs. 2 and 3. The expected values of CNDD were near zero and did not show evidence of strong bias across rare and common species. Results from these null-model analyses supported the conclusions from our original paper (1). Moreover, similar results were obtained when we applied the same null-model analysis using the Ricker model with offset approach presented in (1). Therefore, although we acknowledge that other processes such as dispersal and habitat specificity may contribute to our estimates of CNDD, null-model results strongly suggest that these processes alone cannot account for observed patterns in CNDD across latitudes and species. Instead, our results are consistent with the idea that density dependence, caused by specialized natural enemies and/or intraspecific competition, strongly contributes to the latitudinal diversity gradient.

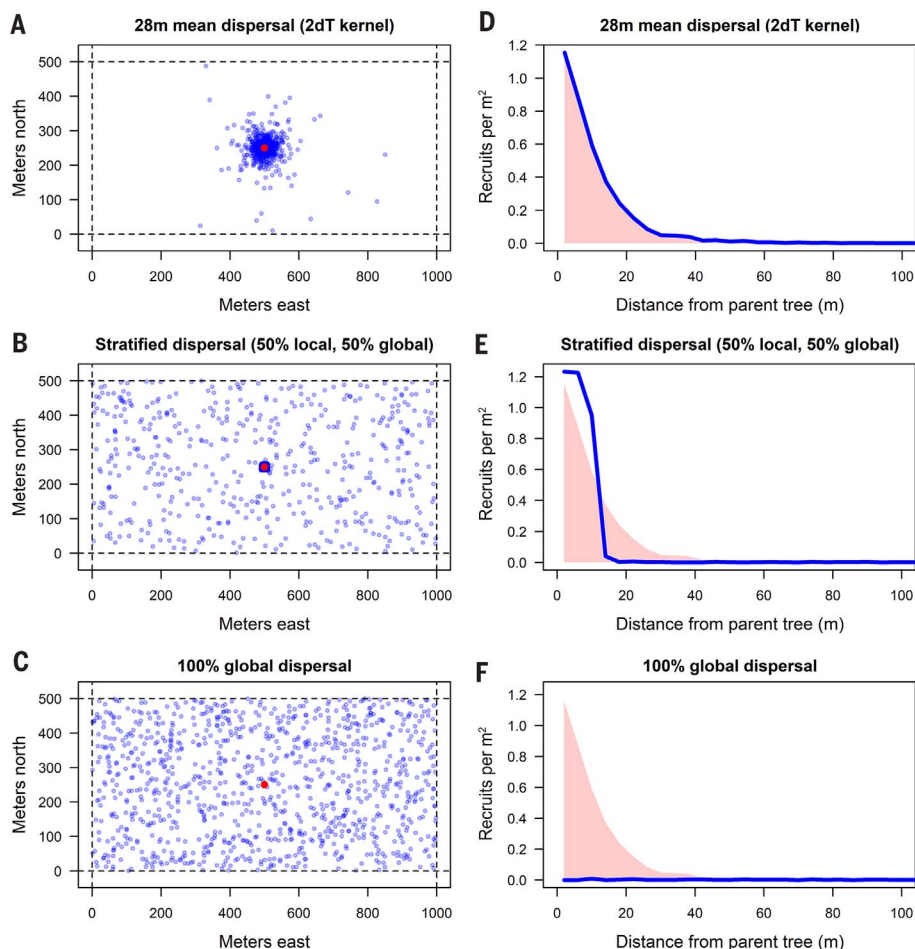


Fig. 1. Simulated spatial patterns of dispersal.

(A to C) Simulated spatial patterns of 1000 recruits (blue points) relative to a parent tree (red point) in a 50-ha plot the same size as the plot at BCI. (D to F) Recruits per m^2 as a function of distance from the parent. Dispersal patterns were produced by Clark's 2dT dispersal kernel (7) at the average observed mean dispersal distance across more than 60 tropical and temperate species (6, 7) [(A) and (D)], by stratified dispersal (used in Hülsmann and Hartig) whereby a certain proportion of recruits are dispersed into the same quadrat as the adult and the rest are globally dispersed across the entire forest plot [(B) and (E)], and by complete global dispersal [(C) and (F)]. Blue lines in (D) to (F) show the expected recruit density for each dispersal kernel [(D), observed mean dispersal from the literature; (E), stratified; (F), global]. The pink shaded areas show the expected recruit density using the observed mean dispersal from the literature [same as in (D)] (6, 7). The assumption of global dispersal is inappropriate because it vastly underestimates expected recruit density near the parent tree [compare blue lines with pink shaded areas in (E) and (F)] and produces a pattern identical to that expected under strong CNDD (8). Even stratified dispersal (E) underestimates the density of recruits between 10 and 30 m. Recruits dispersing off the plot were retained by treating the plot as a torus (12).

Fig. 2. Results from a null model that incorporates empirically supported values of dispersal and preserves habitat specificity, adult/recruit ratios, and abundances for each species. The null model, recommended by Wiegand and Moloney (12), fixes adult locations to preserve habitat specificity of a species and then disperses recruits away from adults. This is the same model used by Hülsmann and Hartig, except that it incorporates empirically supported dispersal values. In this version of the null model, all species were given the same mean dispersal distance of 30 m, based on empirical estimates for more than 60 tropical and temperate species (6, 7). **(A to F)** A distance-weighted measure of adult abundance was used to calculate both observed [(A) to (C)] and simulated values [(D) to (F)] of CNDD (11). Observed and simulated values are presented on the same scale for comparison. The analysis was performed at the 20 m × 20 m scale. **(G to I)** Standardized effect sizes are the observed value minus the mean simulated value from 100 iterations of the null model divided by the standard deviation of the simulated values. These results support the main results in our original paper [figures 1 and 2 in (1)]. Colors reflect distance from the equator [see legend of figures 1 and 2 in (1)]. Linear fits are shown, along with Spearman rank correlation coefficients and their *P* values. Gray dashed lines represent a median CNDD of zero [(A), (C), (D), (F), (G), and (I)] or a zero slope between CNDD and species abundance [(B), (E), and (H)].

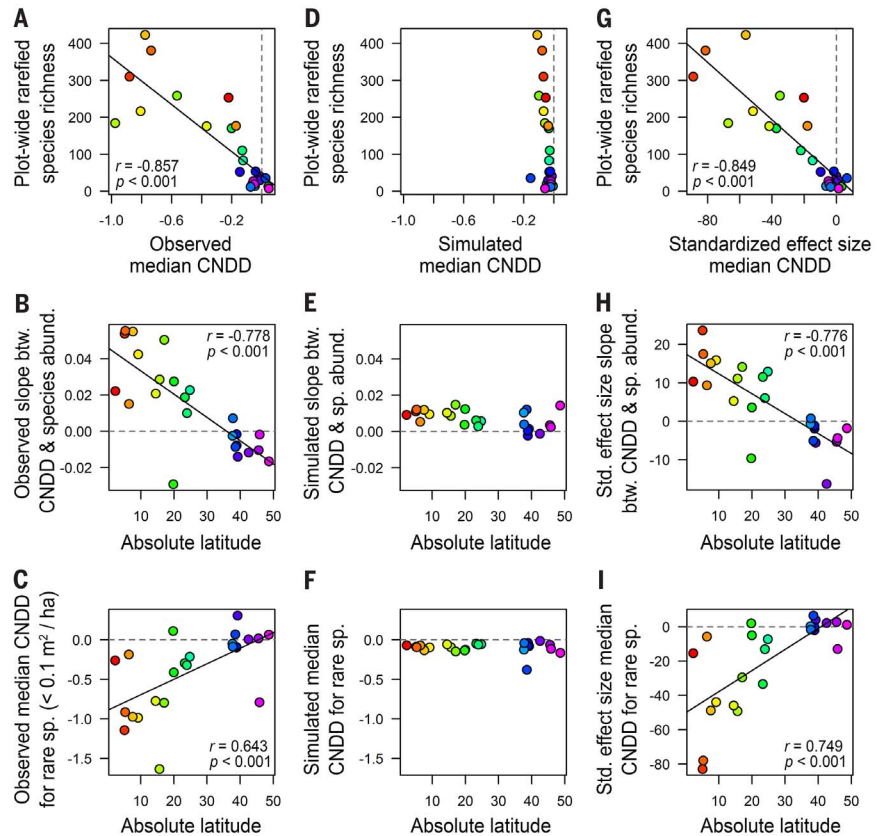
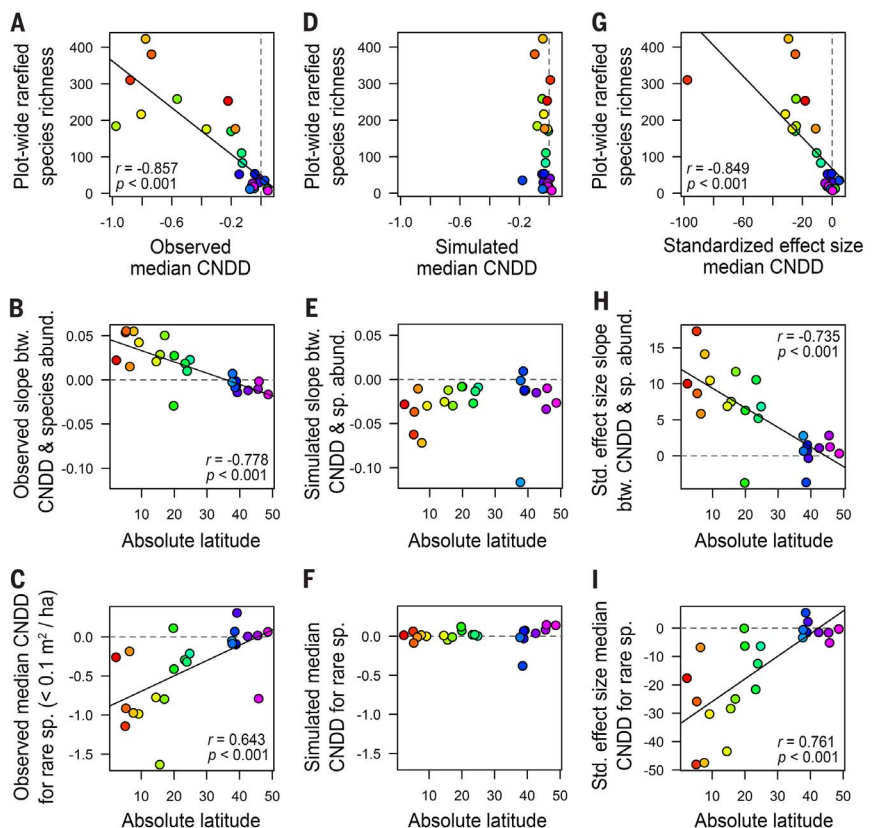


Fig. 3. Results from a null model that incorporates empirically supported interspecific differences in dispersal and preserves habitat specificity, adult/recruit ratios, and abundances for each species. The null model is the same as the model shown in Fig. 2, except that all species are given a mean dispersal distance that scales allometrically with their maximum height and incorporates variation in dispersal within species (9).



The null-model results we report here support the main conclusions of our original paper: CNDD was (i) stronger in tropical than in temperate forests and (ii) stronger for rare species than for common species in the tropics, but equivalent or weaker for rare species than for common species in temperate latitudes (1). The latter finding is supported by both observational and experimental studies of tropical seedling growth and survival as well as temperate sapling recruitment (13–15). Hülsmann and Hartig raise the common misconception that strong negative density dependence for rare species should always increase their likelihood of local extinction. This is true if stabilizing forces such as CNDD are lacking in rare species. However, theory shows that strong CNDD can promote the persistence of rare species in communities, even when CNDD is relatively weaker for common species (16), as we observed in tropical forests (1). Under these conditions, rare species that are strongly stabilized by interactions with specialized natural enemies or

other conspecifics (i.e., strong CNDD) should be less susceptible to local extinction from ecological drift than rare species that are not stabilized (1, 16). Our results not only are consistent with this idea, they suggest fundamental differences in the nature of local stabilizing interactions that contribute to the maintenance of species diversity across temperate and tropical latitudes.

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