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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Chisholm and Fung claim that our method of estimating conspecific negative density dependence (CNDD) in recruitment is systematically biased, and present an alternative method that shows no latitudinal pattern in CNDD. We demonstrate that their approach produces strongly biased estimates of CNDD, explaining why they do not detect a latitudinal pattern. We also address their methodological concerns using an alternative distance-weighted approach, which supports our original findings of a latitudinal gradient in CNDD and a latitudinal shift in the relationship between CNDD and species abundance.

Chisholm and Fung (1) claim that our statistical approach (2) produces CNDD estimates that are systematically biased, causing rare species to always exhibit strong CNDD. In particular, they argue that our CNDD estimates for rare species are biased because an offset value was added to retain recruits ($y > 0$ sapling density) located in 20 m × 20 m quadrats without a conspecific adult ($x = 0$ adult density). Retention of all recruits was important because our data demonstrate that recruits in quadrats without adults likely came from adults in adjacent quadrats (3). To avoid bias that results from excluding these recruits (4), we therefore added a minimum adult density of 0.1 (offset value) to quadrats containing recruits but no conspecific adults. This approach allowed us to include all quadrats and meet the assumptions of a conventional Ricker model that fixes the intercept at the origin (5). This is what Chisholm and Fung refer to as "selective data transformation."

Three lines of evidence refute Chisholm and Fung's claim. First, if their claim is correct, then our approach should have always produced strong estimates of CNDD for rare species regardless of their latitude. Yet our estimates of CNDD vary substantially among rare species when they are matched for abundance [figure 2D in (2); see below]. Moreover, median CNDD for rare species differed across latitudes, with rare tropical species having stronger median CNDD than rare temperate species [figure 2C in (2)]. Second, adding the offset value to all quadrats does 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 ($r = -0.552$, $P = 0.006$). Third, these findings persist using an alternative distance-weighted approach to estimate CNDD that avoids the use of an offset altogether (described in detail below).

In contrast, Chisholm and Fung offer an alternative approach to retain all recruits by including an additional additive intercept in the Ricker model (Fig. 1). However, their modification of the Ricker model and inferences made from it are flawed for two reasons. First, the extra intercept in Chisholm and Fung's model is confounded with the CNDD parameter (and recruitment parameter, or r) such that the same reduction in recruitment with increasing adult densities (i.e., CNDD) can be described by a wide range of CNDD-parameter values (Fig. 1C). This problem is similar to another flawed attempt to add a third parameter to the Ricker model, which has been demonstrated to produce strongly biased estimates of CNDD (6). Second, the Ricker model already has an intercept that measures density-independent recruitment (r) (Fig. 1B). The addition of a second intercept removes a constant proportion of recruits from the calculation of the CNDD parameter in the Ricker model, thereby assuming that these recruits are immune to the influence of neighboring adults. This assumption is flawed because all recruits (even those that immigrate from outside the forest plot) are subject to potential effects from intraspecific competition and shared natural enemies associated with neighboring adult trees (7, 8). Thus, the addition of an extra-intercept parameter suggested by Chisholm and Fung fundamentally alters the Ricker model so that it no longer measures the biological process of interest: CNDD.

Benchmark tests, which quantify a model's ability to recover known parameter values, further demonstrate that Chisholm and Fung's extra-intercept Ricker model produces severely biased estimates of CNDD. Building on benchmark tests provided in our original paper (2), we simulated data with known values of CNDD across the range of recruitment and mean adult abundances observed in the data while incorporating uncertainty due to immigration and random error (2, 9). We then tested the ability of the extra-intercept model to recover these known CNDD values. CNDD estimates from the extra-intercept model were severely biased, imprecise, and centered at zero, regardless of the known CNDD value (Fig. 2, A and C). Indeed, Chisholm and Fung state that their approach resulted in CNDD being generally weak across species, which contradicts previous experimental demonstrations of strong CNDD for several tropical and temperate species in our study (10–12). This explains why they show no patterns in CNDD across species or latitudes. Moreover, estimated values of Chisholm and Fung's extra-intercept parameter were not associated with known values of immigration in the benchmark tests ($r = 0.010$, $P = 0.089$), which suggests that the extra intercept does not reflect immigration as they claim.

Inspired by Chisholm and Fung's concern, we used an alternative approach to estimate CNDD that avoids the use of an offset. This approach yields relationships between CNDD and latitude, and between CNDD and species abundance, nearly identical to those in our original paper. This approach uses a distance-weighted measure of adult abundance for each quadrat, heavily weighting the number of conspecific adults in that quadrat but also incorporating (with lesser weights) the number of conspecific adults in neighboring quadrats (Fig. 3). To weight adult abundances, we used Clark's 2dT dispersal kernel because it is well supported in previous studies of seed dispersal and reflects the probability that a sapling recruit in a focal quadrat came from an

adult at a given distance (13, 14). This kernel also reflects the decreasing influence with distance that an adult may have on recruits in a focal quadrat via intraspecific competition or shared natural enemies (7, 8). We used a mean dispersal-distance parameter of 30 m for the 2dT kernel, which is the mean dispersal distance estimated across more than 60 species in two of the largest studies of seed dispersal in tropical and temperate forests (13, 14) (Fig. 3A). The distance-weighted approach yields only nonzero values of adult abundance, reflecting the nonzero probability that recruits from any adult can potentially disperse to any quadrat in these 4- to 50-ha forest plots, and thus negates the need for an offset value. Moreover, because there are only nonzero values of adult abundance (no

data at $x = 0$), this approach meets the assumptions of a conventional Ricker model that fixes the intercept at the origin (5).

Results using this distance-weighted approach support our original conclusions that CNDD is stronger in tropical than in temperate forests and that the relationship between CNDD and species abundance changes with latitude (Fig. 4). Null-model analyses conducted using the distance-weighted approach further demonstrate that these results are robust to the influence of other processes that might affect the spatial distribution of recruits relative to adults (e.g., habitat specificity, adult/recruit ratios, species abundances) (3). Moreover, benchmark tests that incorporate uncertainty due to immigration and random error (described above) demonstrate

that the distance-weighted approach accurately recovers known values of CNDD (Fig. 2, B and D). In summary, regardless of whether we use (i) the distance-weighted approach (which requires no offset value), (ii) the Ricker model with an offset applied to quadrats with recruits but no adults (2), (iii) the Ricker model with an offset applied to all quadrats (described above), or (iv) an offset-power model (2), we find the same qualitative results as those presented in our original paper (2).

In conclusion, we demonstrate that our key findings are not an artifact of systematic bias. We also demonstrate that the alternative approach proposed by Chisholm and Fung fundamentally alters the Ricker model so that it no longer measures CNDD accurately or precisely, explaining
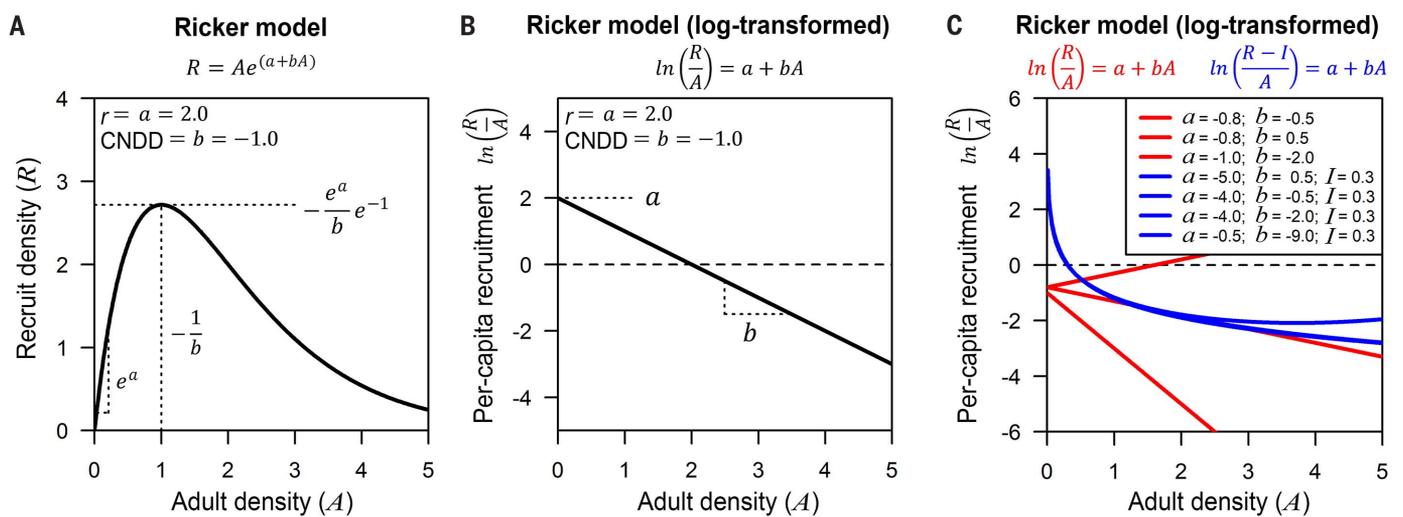
Fig. 1. Basic parameterization of the Ricker model and comparison to the model proposed by Chisholm and Fung. (**A** and **B**) The Ricker model measures linear changes in log-transformed per capita recruitment with increasing adult densities (5). The intercept, a, measures density-independent per capita recruitment (r), and the slope, b, measures density-dependent recruitment (CNDD). (**C**) Comparison of the Ricker model (red) to the model suggested by Chisholm and Fung (blue), which adds an intercept, I, to the right side of the equation in (A). I is mathematically confounded with a and b, similar to other attempts that add a third parameter to the Ricker model (6), such that a wide range values of a and b can describe the same density dependence in recruitment. Hence, the five overlapping blue curves shown in (C) can be described by a wide range of a and b values. That is not the case with the conventional Ricker model (red lines).

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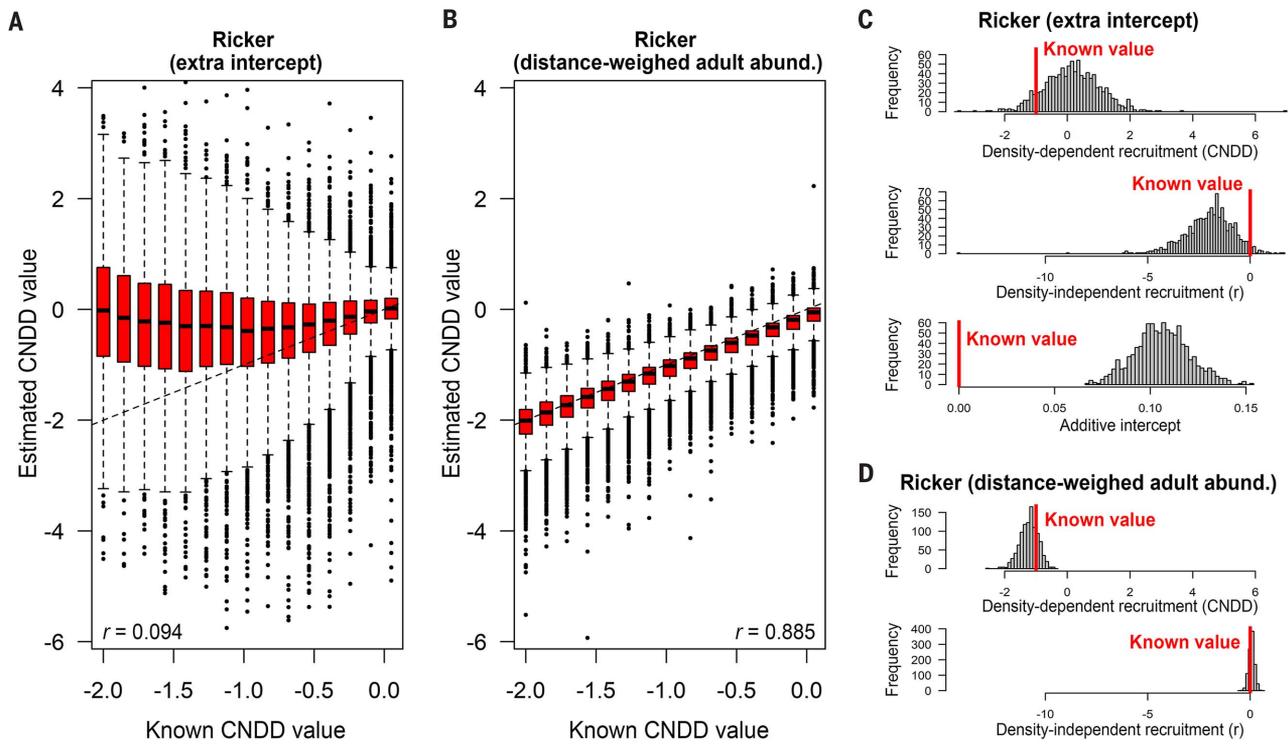
Fig. 2. Benchmark tests that attempt to recover known values of CNDD from simulated data with error. (**A** and **B**) Tests of the ability of the extra-intercept approach proposed by Chisholm and Fung (A) and the distance-weighted adult abundance approach (B) to recover known values of CNDD across a wide range of CNDD, *r*, mean adult abundance, random error, and immigration values. An unbiased approach should produce estimates that fall on the identity line (diagonal black dashed lines). The greater spread of estimated values in (A) relative to (B) reflects the confounded nature of the CNDD and extra-intercept parameters in the model proposed by Chisholm and Fung. (**C** and **D**) One thousand iterations of the same benchmark test at one set of known parameter values (i.e., known values in red). Histograms show the distribution of estimated values from the Ricker model using the extra-intercept approach (C) and the distance-weighted approach (D). The distribution of estimated values should fall around the known value if the model is not biased. The extra-intercept model tends to bias CNDD weak (i.e., closer to zero) and tends to bias *r* low. The extra-intercept model also estimates a wide range of nonzero intercepts, even though these simulated data were generated without an intercept.
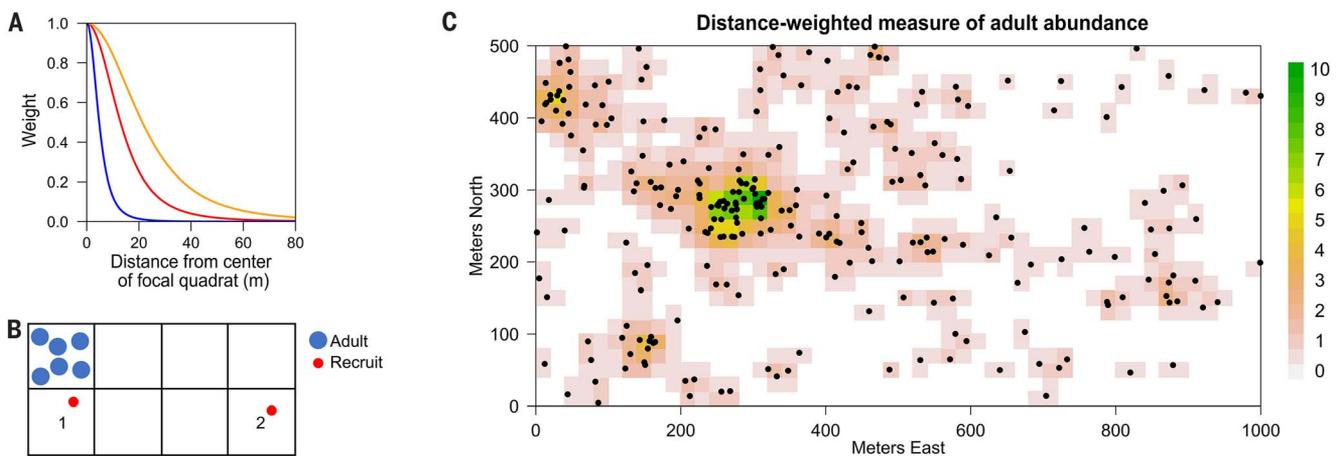
Fig. 3. Distance-weighted measure of adult abundance. (**A**) Distance kernel used to weight adult abundances as a function of distance from a focal quadrat. We used the mean dispersal distance (30 m, red curve) across more than 60 tropical and temperate species estimated from Clark's 2dT kernel (*13, 14*), but inferences were similar using more extreme values [i.e., 10 m (blue curve), 60 m (orange curve)]. (**B**) The distance-weighted approach is advantageous because it provides information on adults in neighboring quadrats. Whereas both quadrats 1 and 2 have naïve adult abundances of zero, the distance-weighted adult abundance of quadrat 1 would be greater than quadrat 2 because of the presence of six adults in the neighboring quadrat. (**C**) Example of distance-weighted adult abundance values (color scale) for *Cassipourea elliptica* at Barro Colorado Island, Panama (range of distance-weighted adult abundance values is 0.003 to 10.48). Black dots are adult individuals of this species.
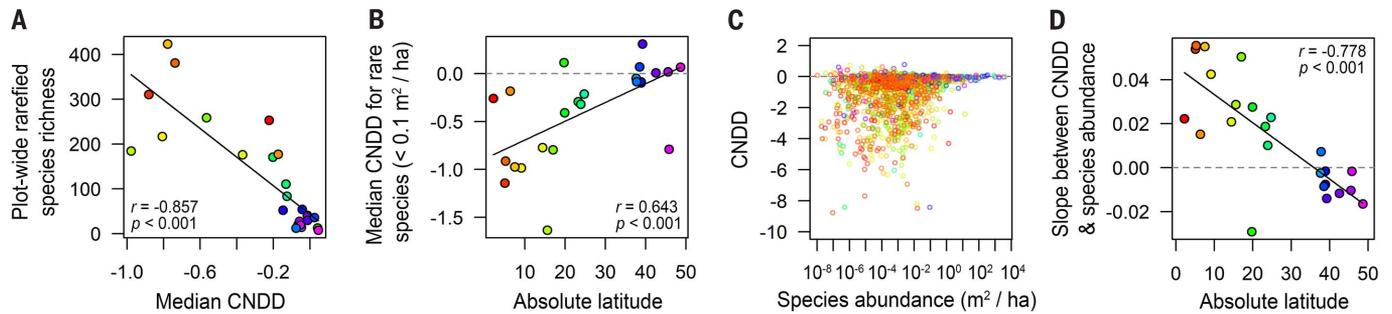
Fig. 4. Results using the Ricker model with distance-weighted measure of adult abundance. (**A**) Species rarefied richness increased with the median strength of CNDD across tropical and temperate forest plots. (**B**) Median CNDD was stronger for rare species in tropical than in temperate forests. (**C**) Estimates of CNDD plotted against species abundance for all species and forests (tropical species in red/orange; temperate species in blue/purple; mid-latitude species in green). (**D**) The slope between CNDD and species abundance decreased with increasing latitude. These results support the main results in our original paper [figures 1 and 2 in (*2*)]. Colors reflect distance from the equator [see captions of figures 1 and 2 in (*2*)]. Results are shown at the 20 m × 20 m scale. Linear fits are shown, along with Spearman rank correlation coefficients and their *P* values.

why their method shows no latitudinal pattern in CNDD. Finally, we show that our key findings— (i) tree species diversity increases with the strength of CNDD across temperate and tropical forests, and (ii) there is a latitudinal shift in the relationship between CNDD and species abundance— are supported using a distance-weighted approach that addresses the methodological concerns raised by Chisholm and Fung.

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