TECHNICAL COMMENT

FOREST ECOLOGY

Comment on "Plant diversity increases with the strength of negative density dependence at the global scale"

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LaManna *et al.* (Reports, 30 June 2017, p. 1389) found higher conspecific negative density dependence in tree communities at lower latitudes, yielding a possible mechanistic explanation for the latitudinal diversity gradient. We show that their results are artifacts of a selective data transformation and a forced zero intercept in their fitted model. A corrected analysis shows no latitudinal trend.

I n ecological systems, conspecific negative density dependence (CNDD) occurs when individuals are more negatively affected by neighboring conspecific individuals than by neighboring heterospecific individuals (*1–4*). Communities with stronger CNDD should, all else equal, have higher diversity, because CNDD prevents any one species from becoming too abundant. Accordingly, it is theoretically possible that global variation in CNDD drives global variation in diversity (*5*). In particular, the latitudinal diversity gradient, whereby diversity decreases with increasing latitude, could be driven by a concomitant weakening in CNDD with increasing latitude. Thus, there is scientific interest in testing the hypothesis that species in tropical high-diversity sites are more susceptible to conspecific competition than are their temperate counterparts.

LaManna *et al.* (*6*) tested this hypothesis by analyzing the relationship between sapling density and adult density for nearly 2.4 million trees of more than 3000 species across 24 forest plots worldwide. For each species at each site, they fitted the Ricker population dynamics model (*7*) to static counts of adults and saplings within 10 m × 10 m or 20 m × 20 m quadrats. They found that the fitted CNDD parameter of the Ricker model was, on average, substantially more negative in high-diversity, low-latitude forests, providing apparent support for the hypothesis that CNDD explains high tropical tree diversity.

However, the analysis of LaManna *et al.* has two flaws. First, they transformed a subset of their data prior to analysis while leaving the remainder of the data untransformed, which biased the model results. For each species, they added +0.1 to the adult abundance in any quadrat that had nonzero sapling abundance and zero adult abundance, but did not transform adult abundance values in other quadrats. The problem LaManna *et al.* were trying to address with this selective transformation was that the Ricker model has a zero intercept and therefore cannot account for observations that have nonzero sapling abundance and zero adult abundance. However, the selective transformation they used is not valid (and renders goodness-of-fit statistics meaningless). Indeed, we cannot think of any circumstances under which it is valid to transform only a subset of data prior to analysis.

How did the selective transformation used by LaManna *et al.* introduce a specific bias toward

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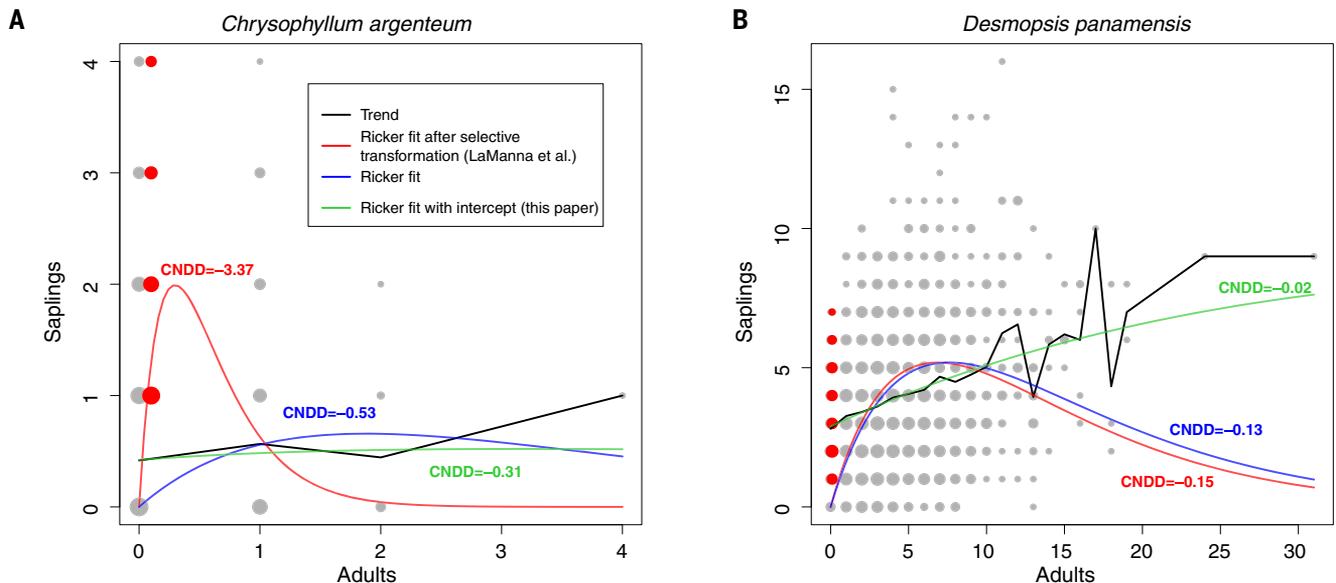*Corresponding author. Email: ryan.chis@gmail.com

Fig. 1. The selective transformation and forced zero intercept used by LaManna *et al.* inflate CNDD, especially for rare species. (**A** and **B**) Sapling abundance versus adult abundance for two illustrative species at the Barro Colorado Island plot in Panama, *Chrysophyllum argenteum* (a rare species) and *Desmopsis panamensis* (a common species), across quadrats [gray points, with sizes proportional to log(number of quadrats + 1)]. The selective transformation applied by LaManna *et al.* (red points) leads to a fitted model (red curves) that has an inflated intrinsic growth rate and inflated CNDD relative to the case with no selective transformation (blue curves). The bias is more acute for rarer species (A). Even without the selective transformation, the Ricker model (blue curves) provides a poor fit to the average trend (black lines) because of the forced zero intercept; a Ricker model with an intercept term characterizes the data more accurately (green curves; $F_{1,1245} = 5372.5$, $P = 6 \times 10^{-454}$ for *C. argenteum*; $F_{1,1245} = 1800.1$, $P = 5 \times 10^{-244}$ for *D. panamensis*).
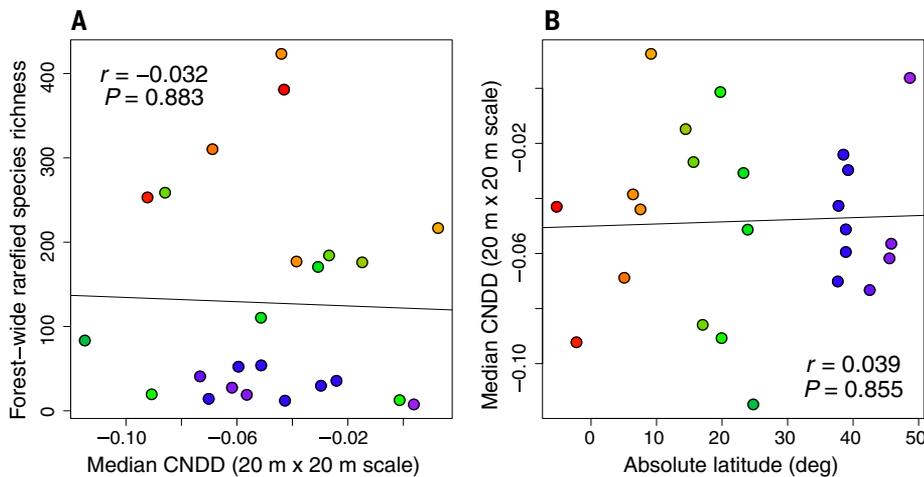
Fig. 2. Species richness exhibits no systematic relationship with the strength of CNDD across tropical and temperate forests. (**A**) Species richness versus estimated CNDD (median over all species in a plot) for the 24 forest plots of LaManna *et al.* (points) with fitted least-squares regression line. (**B**) Estimated CNDD versus latitude. The methods and data here are identical to those used to produce the results of LaManna *et al.*, except that we have not applied a selective data transformation prior to analysis and we have used an intercept in the fitted Ricker model (see text and Fig. 1; the graphs here should be directly compared with figures 1E and 1C, respectively, in LaManna *et al.*). Spearman rank correlation coefficients (*r*) with *P* values are shown.

higher CNDD in tropical species-rich forests? The selective transformation moved data points with nonzero sapling abundance and zero adult abundance off the vertical axis, which caused the fitted Ricker model to estimate an artificially high intrinsic growth rate and consequently artificially strong negative density dependence to compensate (Fig. 1). This effect was more pronounced for rare species, which have a higher proportion of presence quadrats with nonzero sapling abundance and zero adult abundance, and thus a higher proportion of transformed data points (e.g., Fig. 1A; Spearman $r = -0.25$, $P = 2 \times 10^{-52}$ for the relationship between species abundance and fraction of presence quadrats that were transformed). This then led to more strongly biased CNDD estimates for rare species. Because species-rich sites have more rare species than species-poor sites, the fraction of data points affected by the selective transformation of LaManna *et al.* was positively correlated with site richness (Spearman $r = 0.95$, $P = 2 \times 10^{-6}$). For example, at the most species-poor site, Zofin, the average abundance is 212.7 trees/ha and LaManna *et al.* transformed 7% of presence quadrats, whereas at the most species-rich site, Khao Chong, the average abundance is 6.4 trees/ha and they transformed 50% of presence quadrats. The higher fraction of selectively transformed points at species-rich sites led to a stronger bias in CNDD estimates at these sites and ultimately inflated the latitudinal gradient in estimated CNDD. LaManna *et al.* also investigated shifts of +0.01 and +0.001 (their table S19), but these analyses suffer from the same rare-species bias.

The second problem in the analysis of LaManna *et al.* was that the Ricker model was forced to have a zero intercept, when the data do not suggest this (e.g., Fig. 1) and the resulting residual plots are skewed (not shown by LaManna *et al.*). We fitted a Ricker model with a nonzero intercept to the same forest data and obtained better fits than with a zero intercept [as judged by *F* tests: $P < 0.05$ for 99.4% of species; $P < 3 \times 10^{-5}$ (Bonferroni-adjusted threshold) for 98.3% of species]. Statistically, the nonzero intercept is a valid solution (unlike the selective transformation of LaManna *et al.*) to the problem of quadrats with nonzero sapling abundance and zero adult abundance. Biologically, the nonzero intercept for each species can be interpreted as the central tendency of a stochastic immigration process that does not vary systematically with the number of adults in a quadrat. With our improved model, we found that the median estimated CNDD over all species at all plots was lower by about a factor of 30 than in LaManna *et al.*, the relationship between plot richness and estimated CNDD disappeared, and the latitudinal pattern in estimated CNDD also disappeared (Fig. 2).

LaManna *et al.* claimed that their results were robust because qualitatively similar patterns arose when they excluded quadrats with nonzero sapling abundance and zero adult abundance. But doing this remedied only the problem of selective transformation and not the problem of using a zero intercept. LaManna *et al.* also claimed that their results were robust because qualitatively similar patterns arose when they fitted a model with a different functional form: the "offset-power model" presented in their supplementary materials. However, the offset-power model also suffers from fatal statistical flaws. The offset-power model of LaManna *et al.*, as shown by their own simulations, estimated strong CNDD even when there was none (figure S11B in LaManna *et al.* shows that the parameter *r* is estimated at less than 0.4 on average when the true value is 1.0).

Overall, we found that the main results of LaManna *et al.* are artifacts of a selective transformation of the data prior to analysis and a forced zero intercept not suggested by the data. Our corrected analysis yields much weaker CNDD overall and no global CNDD gradient with species richness or latitude. We recommend that future studies test the robustness of our conclusion by using models that are fully spatial, dynamic, and stochastic.

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