Is tree species diversity impacted by trees having more near neighbors of the same species and does this change with elevation?

Tree species diversity increases with conspecific negative density dependence across an elevation gradient

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Topic Summary

How do conspecific density dependence (CDD) and heterospecific density dependence (HDD) affect tree species richness? Does the density of conspecifics have greater effects on survival and growth than the effects of having more neighbors in general, is CDD>HDD? The authors used CDD-HDD, which is a measure of conspecific suppression or facilitation, to determine whether conspecific density effects were more important in lower elevations with greater species diversity and in microclimates with greater humidity.

Is CDD>HDD? Do the effects differ with tree size or elevation?

- Conspecific density effects were greater than heterospecific effects on survival for smaller trees, especially at lower elevations. Density suppression by conspecifics occurred for the two smallest size classes at lower elevations and the smallest size class at higher elevations.
- For intermediate-sized trees (15-25 dm diameter), conspecific density effects were more suppressive in low-elevation valley bottoms than at low-elevation ridges or at high elevation mid-slopes and ridges. Ridges and higher elevations generally have higher minimum spring temperatures and lower humidity.
- Conspecific density effects for diameter growth relative to heterospecifc effects were suppressive for all size classes, especially for trees 15-52 cm diameter. The difference between conspecific and heterospecific effects did not change across elevations for smaller or larger trees.
- Conspecific density effects were more suppressive in low-elevation valley bottoms than at low-elevation ridges or at higher elevation midslopes and ridges for intermediate-sized trees. Ridges and high-elevation midslopes are generally lower humidity sites with warmer summer temperatures.

Did conspecific density impact survival and growth?

- CDD-HDD reduced lifetime cumulative survival probability for intermediate trees at low elevations from 61% when near large heterospecifics to 13% when near large conspecifics, thus decreasing the likelihood that large trees will be replaced by conspecifics when they die.
- Conspecific density effects were strongest in survival for smaller trees and in growth for intermediate trees. Growth suppression by conspecific density impacted all size-classes. The authors suggest that diverse stands may have higher growth, resulting in greater carbon sequestration.

- The relative effects of conspecific and heterospecific densities on growth and survival were not related to species abundance, which is consistent with the expectation that stronger conspecific density effects will contribute to tree species diversity patterns along elevation gradients.

Will climate change impact the strength of these density effects?

- Differences in the relative strength of conspecific density effects were associated with climatic conditions. Current analyses couldn't evaluate possible mechanisms; however, warmer, more humid conditions may increase pathogen load and dispersal, decrease impacts of host-specific mutualists, or increase interspecific competition.

Can managers use these findings to better understand forest responses to environmental or climatic variation?

- Managers and policy makers could use estimates of CDD-HDD to understand forest dynamics and estimate possible responses to environmental fluctuations under current conditions.
- Warming associated with climate change may decrease relative humidity, leading to more positive CDD-HDD. More positive levels of CDD-HDD are associated with lower tree species diversity. Managers may be able to predict forest responses to changing climate conditions by estimating tree species survival and growth with a range of possible CDD-HDD values.

Research Approach/Methods

- The authors analyzed data collected at 23 old-growth forest sites along a 1000-m elevation gradient over 44 years. For each census they rarified the species richness at each plot to 51 individuals and to a 0.25-ha sample area.
- They used a Bayesian approach with linear-mixed models to see if tree species richness was associated with elevation.
- The authors calculated local CDD-HDD to determine the effect of more conspecific neighbors separately from the effects of having a greater number of neighbors.
- They used Bayesian generalized linear mixed models (GLMMs) to calculate CDD-HDD in local space across elevations and microclimates and to account for differences in survival and growth among plots and tree species.
- They also used Bayesian GLMMs to estimate growth as a function of initial tree size class, sampling year, the abundance of nearby large conspecifics and heterospecifics, and interactions of DBH with local CDD and HDD. Elevation was used a proxy for basin-wide relative humidity differences and understory microclimate temperature differences were used as a proxy for cross-valley relative humidity differences.

Keywords biodiversity, conspecifics, density dependence, elevational gradient, environment-diversity relationship, species interactions, conspecific negative density dependence, forest dynamics

Images

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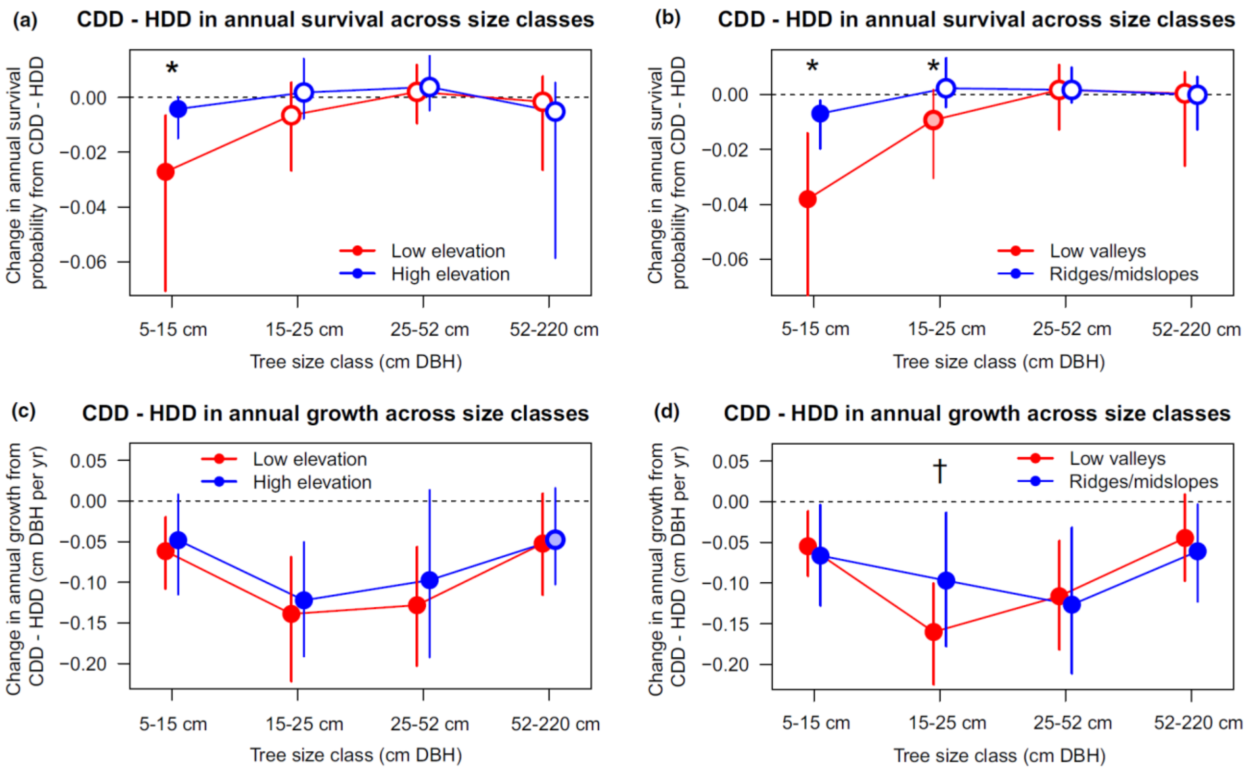

Figure 3 in LaManna et al. 2022. Average-predictive comparisons of CDD–HDD in survival (a and b) and growth (c and d) across tree size classes. (a) Differences in CDD–HDD in survival across size classes at high (1,450 m) and low (450 m) elevations. (b) Differences in CDD–HDD in survival between forest plots with lower values of PC2MinSpring, indicative of lower elevation valley bottoms that experience colder minimum spring temperatures associated with greater relative humidity, and forest plots with higher values of PC2MinSpring, indicative of low-elevation ridges and higher elevation midslopes/ridges that experience warmer minimum spring temperatures associated with lower relative humidity (Figures S1 and S3). (c) Differences in CDD–HDD in growth across size classes at high (1,450 m) and low (450 m) elevations. (b) Differences in CDD–HDD in growth between forest plots with lower values of PC2MeanSummer, indicative of lower elevation valley bottoms that experience colder mean summer temperatures associated with greater relative humidity, and forest plots with higher values of PC2MeanSummer, indicative of low-elevation ridges and higher elevation midslopes/ridges that experience warmer mean summer temperatures associated with lower relative humidity (Figures S1 and S3). Solid-filled values have ≥95% probability of being different from zero, lightly filled points have a 90%–95% probability of being different from zero, and open points have a <90% probability of being different from zero. Error bars reflect 95% credible intervals. Stars indicate highly probable differences (≥95%), and crosses indicate probable differences (90%–95%) across elevations or PC2 (i.e. difference between red and blue values).

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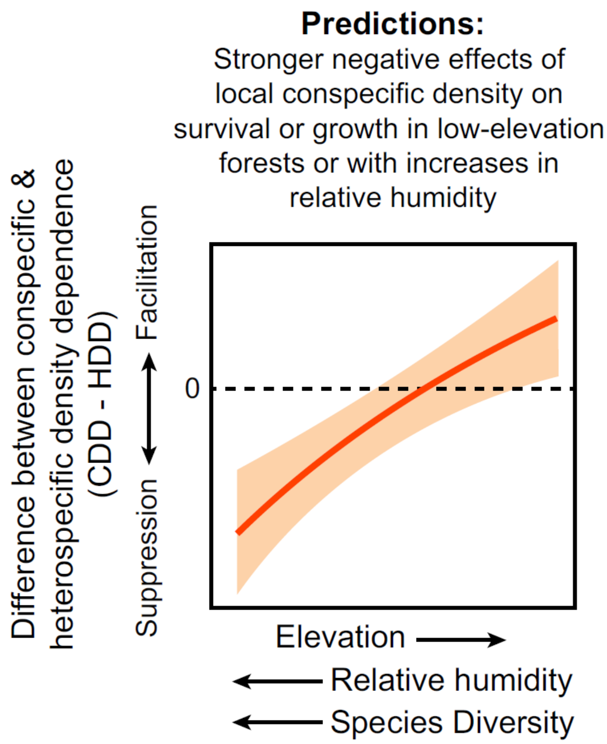

Figure 1 in LaManna et al. 2022. Key predictions evaluated in this study, which are generated from the hypothesis that increases in relative humidity associated with elevation alter interactions among plants and their host-specific enemies/mutualists and generate stronger negative effects of conspecific density on survival and growth. CDD–HDD is measured as the effect of local conspecifics on survival or growth (i.e. CDD) minus the effect of local heterospecifics (i.e. HDD; Comita et al., 2010; Hulsmann et al., 2020; LaManna, Mangan, et al., 2017). Mean CDD–HDD across species (orange line) is predicted to be stronger in lower elevation forests associated with greater relative humidity and greater tree species diversity. Negative CDD–HDD is generated by intraspecific competition or interactions with host-specific natural enemies. Disease risk is greater and growing seasons longer at lower elevations which may generate negative CDD–HDD by favouring host-specific pathogens. At higher elevations, freezing temperatures, lower humidity, greater seasonality, more precipitation falling as snow and lower nutrient availability may generate neutral or positive CDD–HDD by reducing pathogen loads and favouring host-specific mutualists.

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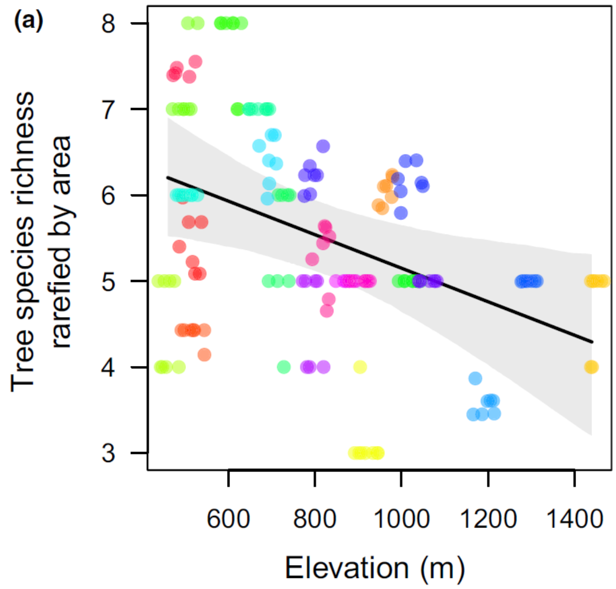

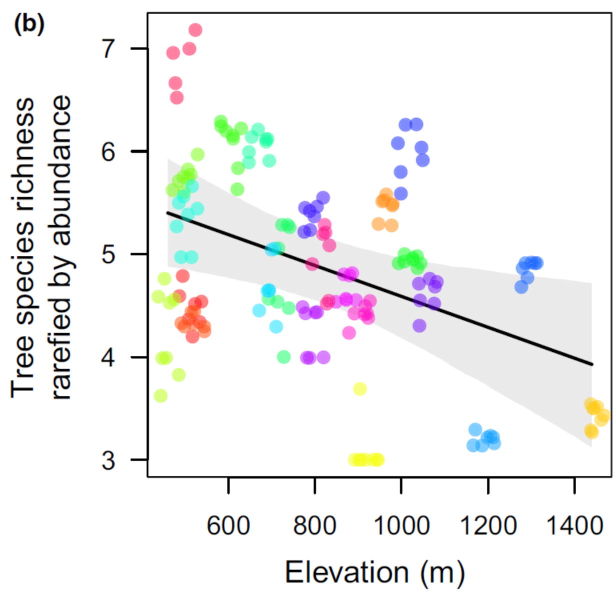

Figure 2 in LaManna et al. 2022. Relationships between rarefied species richness and elevation across forest plots in the H. J. Andrews Experimental Forest between 1971 and 2014. (a) Species richness in each census of
each forest plot rarefied to 0.25 ha area, the minimum area across forest plots. (b) Species richness in each census of each forest plot rarefied to 51 individuals, which was the minimum abundance across forest plots and censuses. Values of rarefied species richness from the same forest plot (i.e. from different censuses of the same forest plot) have the same colour. The 95% credible interval of the posterior distribution for the slope is shown in grey. Bayesian inference from mixed-effects models that contain random effects of forest plot and census to account for temporal and spatial autocorrelation indicated that slope of the fixed-effects relationship had a 98.2% and 98.6% probability of being less than zero in panels (a) and (b) respectively. Values are slightly adjusted (± 5–30 m elevation) on the x-axis and points transparent for ease of visualization.