Neighbour effects on tree growth in a reforestation project in Costa Rica

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Background

Trees in tropical wet climates potentially grow very fast. Individual growth rates depend on species traits and on their environment, which includes direct or indirect interactions with neighbouring trees. Neighbours can either compete (for light, nutrients or water) or provide benefits, for instance by shading species that are not adapted to full sunlight. Such interactions are important to understand ecological processes in the most diverse ecosystem on earth and the high tree diversity in tropical rainforests is ideal to test various ecological theories. Tree interactions are also important for practical reasons such as selecting and managing trees in reforestation projects.

We tested if trees with different ecological strategies along the gradient from light demanding pioneer trees typically found in secondary forests to shade-tolerant species regenerating in the understory and typically found in old-growth forests respond in different ways to competition or facilitation. After canopy closure we expected tree growth to be affected by neighbours and hypothesized that species from old-growth forests profit from shading whereas pioneer trees are light-demanding and will always be negatively affected by competition. We also tested if the strength of the neighbour effect in different species is related to functional traits (wood density - WD, specific leaf area – SLA and leaf nitrogen content - N) that are known to be related to shade tolerance or habitat preference.

Fig. 1.: Aerial photograph of the reforestated area (Anton Weissenhofer).

Methods

The study was conducted in a 14-ha reforestation area (Finca Amable) where >100 native tree species have been planted in 2012-2015 as part of the reforestation project "Corredor Biológico La Gamba" (COBIGA) in Costa Rica (Fig. 1).
Diameter and height were measured for c. 4000 trees in 2016 and 2018. In 2018 distance measurements were carried out using a laser-based electronic mapping equipment and crown diameter was measured for 24 dominant species. We calculated several neighbour indices based on the size (dbh or crown diameter) of neighbours and the distance to the target tree (NI Table 1). Some (NI 2, NI 3, NI 4, NI 6, NI 7, NI8) also included the size of the target tree. Trees within 10 m were considered to potentially affect growth.

Neighbour index	Equation	Source	Mean r^2
NI 1	$NIi = \sum_{j=1}^{n} \left(\frac{dj^2}{Lij^2}\right)$	Lasky et al., 2014	0.068
NI 2	$NIi = \sum_{j=1}^{n} \frac{\left(\frac{dj}{Lij}\right)}{di}$	Hegyi, 1974	**0.259**
NI 3	$NIi = \sum_{j=1}^{n} \frac{\left(\frac{hj}{Lij}\right)}{hi}$	Braathe, 1980	0.142
NI 4	$NIi = \sum_{j=1}^{n} \frac{(di - dj)^{\alpha}}{Lij^{\beta}}$	Canham et al., 2014	0.201
NI 5	$NIi = \sum_{j=1}^{n} \frac{(dj)^{\alpha}}{Lij^{\beta}}$	Canham et al., 2014	0.086
NI 6	$NIi = \sum_{j=1}^{n} \left(\frac{1}{di}\right) * \left(\frac{(dj)^{\alpha}}{Lij^{\beta}}\right)$	Canham et al., 2014	0.230
NI 7	$NIi = \sum_{j=1}^{n} \frac{\left(\frac{dj}{di}\right)}{Lij^2}$	Rouvinen & Kuuluvainen, 1997	0.223
NI 8	$NIi = \sum_{j=1}^{n} \frac{\left(\frac{dj}{di}\right)^2}{Lij}$	Rouvinen & Kuuluvainen, 1997	0.190

Table 1 Distance-dependent neighbour indices calculated to evaluate neighbour effect on growth. NIi : neighbour index for the target tree (i); dj :diameter (d) of the neighbour (j); di: diameter of target tree; Lij :distance to neighbour; α and β are estimated with α = 2, β = 1.
r^2 is the mean r^2 of the regression NI : diameter growth (see Fig. 3) for 24 species with > 30 individuals.

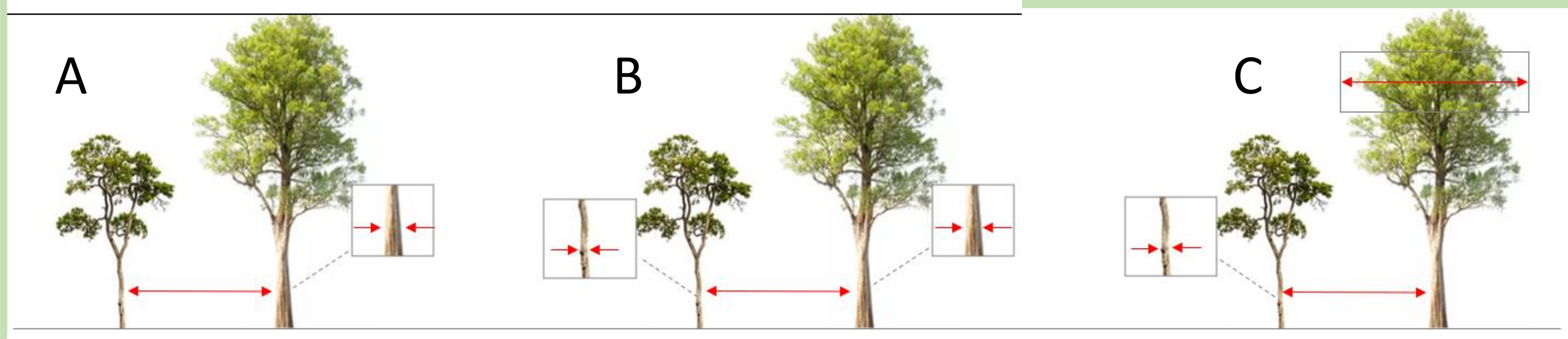

Fig. 2.: The neighbour index can be a function of the distance between the target tree and its neighbour and the neighbour dbh (A, NI1, NI5), includes the dbh of the target tree (B , NI 2, NI 3, NI 4, NI 6, NI 7, NI8) or the crown diameter of the neighbours (C,).

We took diameter increment between 2016 and 2018 as a measure of growth and calculated species-wise linear regressions (Fig. 3, growth ~ a + log(NI)*b) and used the slope of this regression as a measure of the strength of the neighbour effect. Negative slopes would indicate competition and positive slopes facilitation.
The position along a successional gradient (habitat preference) was based on literature (Letcher et al. J Ecol. 103:1276) and local data on the occurrence of trees in either old growth or secondary forest and ranged between 0 (all individuals recorded in second growth forests) to 1 (recorded only in old-growth forests). SLA, N and WD were measured from trees in the reforestation area. WD and N, but not SLA were related to habitat preference.

Results

- From the eight indices tested, NI 2, which uses distance and dbh of the neighbour relative to the dbh of the target tree, best explained growth of individual trees (Fig. 3, r2 in Table 1). Using the species-specific crown diameter of the neighbours instead of the stem diameter did not better quantify the neighbour effects.
- Tree growth was often significantly affected by the size and distance of neighbouring trees. After 3 – 5 years of growth, the stand had clearly reached a density where interaction between trees had become significant.
- The different NIs showed mostly negative (competition) and rarely no, but never positive (facilitation) effect of neighbours on tree growth.

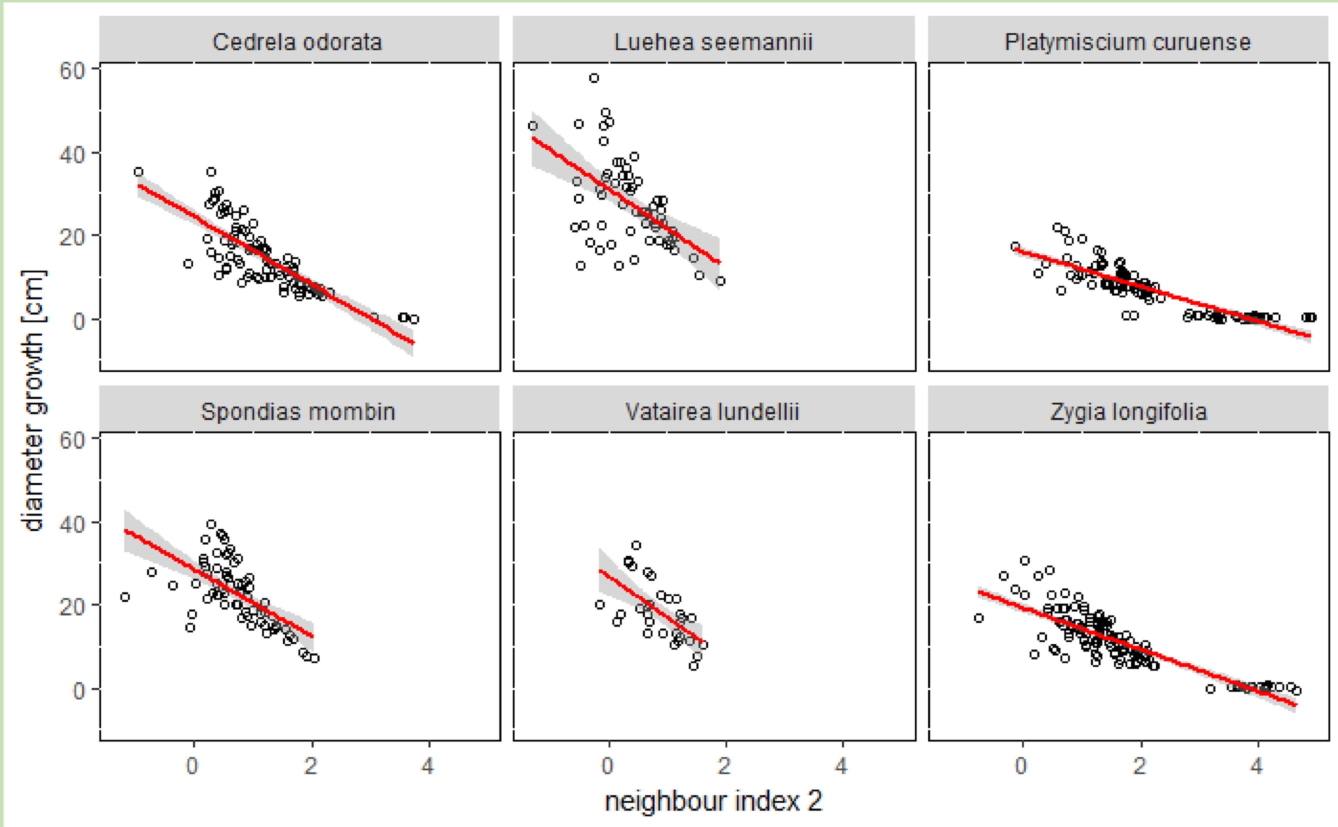

Fig. 3.: Relationship between NI2 (log-scale) and the diameter growth of six species.

- We found no significant correlation between NI2 and habitat preferences (Fig.4.), thus growth is reduced also in species that should be shade tolerant.
- Out of the functional traits observed in our study only the nitrogen content was marginally significantly related to NI 2 (Fig. 4.). SLA or WD were not related to the strength of the neighbour effect.

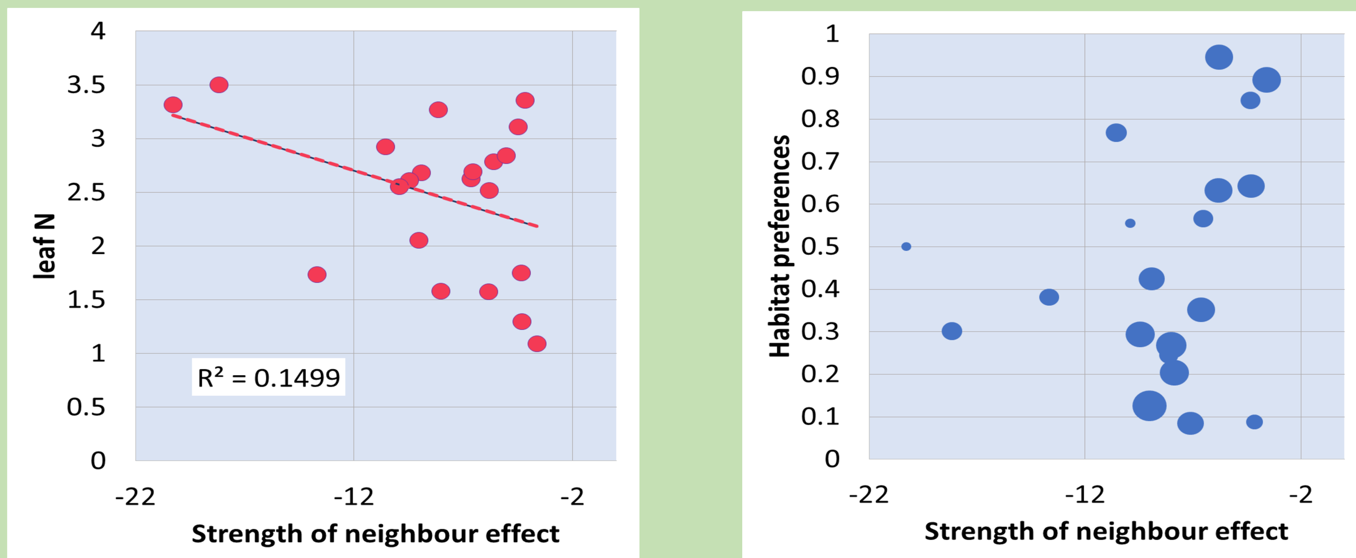

Fig. 4.: Relationship between the strength of the neighbour effect (slope of NI2) and habitat preferences (left/top) or leaf N content (right(bottom).

Discussion

- In the young planted forest, effects of neighbouring trees strongly affected tree growth after only four years. As species responded differently to shading, this information could be used to plant species in different densities or with different neighbours.
- We found no evidence that pioneer trees or old-growth specialists were differently affected and little evidence that traits matter.
- For future decisions on species selection in reforestation projects the possible effect of neighbours on tree mortality should also be included and will be studied in the ongoing project.

Acknowledgements

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