**Density dependence in forests**

**Background**

The Janzen-Connell hypothesis attempts to explain the large diversity of tree species in forests. It states tree species may attract/accumulate species-specific enemies over time, reducing the fitness of their nearby offspring and thereby controlling the species’ abundance. This mechanism of population density regulating population growth is called Conspecific Negative Density Dependence (CNDD, e.g., Hülsmann et al. 2021, Fig 1). Mathematical models suggest that when CNDD is relatively strong compared to density-dependent effects exerted by other species (Heterospecific Negative Density Dependence, HNDD), it can promote the coexistence of many tree species within a community (e.g., Eppinga et al. 2018).

Diagram

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***Figure 1:*** *Mechanism of Conspecific Negative Density Dependence with the Janzen-Connell approach, taken from Hülsmann et al., 2021. This shows individual performance is a function of seedling density (blue) and adult distance (red).*

Given the size and lifespan of trees, measuring CNDD and HNDD experimentally is challenging. Previous studies have inferred the strengths of these effects from observational data of adult trees and seedlings taken from forest inventory surveys (e.g., LaManna et al. 2017a, b). Selecting the appropriate analysis framework for this type of data is challenging, as both variables: adult density and seedling density, are error-prone proxies (Dickie et al. 2012; Detto et al. 2019). This error may lead to a regression dilution effect that interacts with the abundance of tree species investigated (e.g., Hülsmann and Hartig 2018; Hülsmann et al. 2021). We will develop a Bayesian analysis framework to study how error-prone proxies may propagate into the uncertainty of model estimates, and/or to provide a framework that integrates these observations with known information from pot experiments with tree seedlings. Hence, we aim to identify to what extent forest inventory-type (and experimental) data are able to accurately estimate important parameters describing density dependence of tree species. We will start exploring this question with simulated data, and then apply the developed approaches to an an empirical dataset as well, which is described in further detail below.

**Dataset**

We use the US Forest Service’s Forest Inventory and Analysis (FIA) census from 2009 (Fig. 2) extracted by Johnson et al. (2012) and analyzed in Eppinga et al. (2018). All plots east of the 100th meridian were selected (~200,000 plots, with ~7m radius). At ~60,000 locations, 2-4 plots (referred to as subplots) were measured (Fig. 2b). In total, the plots contain ~1,000,000 observations, where an observation could be: i) the number of adults of a tree species in the plot and their cumulative basal area; ii) the number of tree seedlings of a particular tree species in a ~2m radius microplot. Previous studies quantified strengths of conspecific and heterospecific density dependence of all tree species for each grid cell in which they were observed ≥ 30 times.

Chart

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***Figure 2:*** *a) Representation of Forest Inventory and Analysis (FIA) dataset from US Forest Service. b) Schematics of sampling within the whole dataset with subplots and microplots (Johnson et al. 2012).*

**Previous approach**

Previous studies used a standard regression approach (exponential fit with negative binomial error distribution), using adult species density (either number of adults in plot or cumulative basal area in plot) as an independent variable and seedling density (number of individuals in the subplot) as the dependent variable (Fig. 3). Conspecific effects were determined using seedling data and adult data from the same species; only an average heterospecific effect was calculated, i.e., summing the adult data of all competitor tree species to create one aggregate independent variable. The slope parameter was then used as a measure of density dependence, with negative slopes indicating negative density dependence, and positive slopes indicating positive density dependence.

Graphical user interface, application

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***Figure 3:*** *Previous approach to calculate number of seedlings proportional to cumulative basal area from Eppinga et al. 2018.*

**Current approach**

Our first goal is to incorporate the uncertainty in the observed adult densities within the statistical modelling framework. Specifically, we aim to describe adult density as a latent variable, that is estimated from the observational data. We started with an extremely, (over)simplified situation where ‘true adult density’ is known, and the density-dependent effect is deterministic. We would expect that the latent variable approach would work very well in this extremely oversimplified case. Then, we can add complexity in steps to see whether the approach keeps doing well. In the extremely simplified case, three levels of spatial scale are considered:

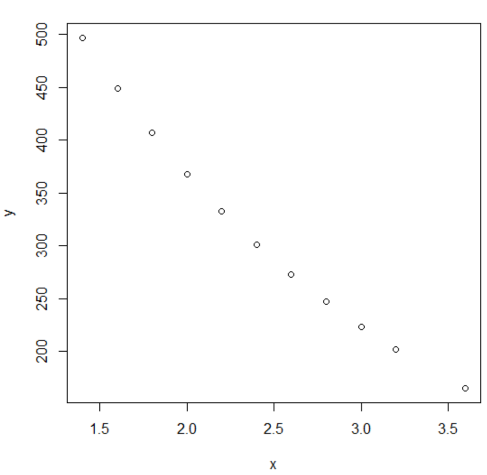
1. **The (continental-scale) species pool: all species that are in the system, their densities supposedly relatively homogeneously distributed (created species abundances using the function of Lisa and Florian)**
2. **The community-scale species pool: this is the actual composition of species that determines the density-dependent effects on seedlings.(For now, we only considered conspecific effects).**
3. **The plot-scale, observed species: these are the observed trees in the plot, but it is assumed that this is only a subset of the trees that are exerting density dependent-effects within the plot.**

*Continental species pool*

*Community pool (exerting the effect)*

*Observed pool (sample of community pool)*

1000 seedlings – conspecific density effects

To get a clean, true signal of density dependence, we started with the major assumption that in the absence of density-dependent effects, there would be 1000 seedlings in the plot. Hence, any reduction of this number is due to conspecific density dependent effects, exerted by adult species that are present in the community pool. Specifically, there is a perfect negative exponential relationship between number of conspecific trees in the community and seedling number:

Where x is the number of adult conspecific trees

(not whole number as a correction is made to convert to

plot density equivalents), and y is the number of surviving

seedlings.

Although each community has the same number of trees, differences in composition emerge because this number is limited, and sampled from the continental species pool. Observed species pools are also sampled, from the community pool. However, we sample a number of replicate plots from the same community, so we can use this variation between replicates to quantify the error in adult densities, and create the latent variable.

**NEXT STEPS**

1. change the distributions in the model, as assumed for the number of seedlings and the number of adults in each plot, from normal to either Poisson or neg-binomial
2. change the function for the number of seedlings, no longer assuming 1000 seedlings everywhere, but:
3. it has to be proportional to adults and CNDD; this can be first done in a deterministic way
4. advanced step: draw the number of seedlings from a distribution of recruits/adults ratio, so that there is a random error in the response variable as well.

1. sampling variation by changing the plot number or size, which would vary the magnitude of uncertainty within the estimate tree densities.
2. accounting for the adults that were also once present in the plot but not observable anymore
3. seedling number can be calculated with both adults that are present + adults that were present once
4. we can account for the unobservable adults with a survival probability
5. also maybe account for time, because longer the time means more deaths will occur

**Further aims of the group assignment**

After the above steps, we could be develop the project in multiple directions, for example:

* Use a hierarchical modelling approach, where climatic variables are directly included as covariates (rather than separate fitting for 2 by 2 degree grid cells).
* Use recent experimental studies of density dependence of tree species to inform priors for the density dependence parameters. Priors could be species-specific is information is available (Bennett et al. 2017), or based more generally on mycorrhizal association (Steidinger et al. 2019).
* Compare the empirical dataset with simulated datasets with known strengths of density dependence to infer the explanatory power of the data.

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