Master Thesis Proposal

Impact of Density Dependency on Community Assembly: A Simulation Approach

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Abstract

This thesis investigates how local stabilizing conspecific density dependence (CDD) and its interplay with destabilizing forces shape species coexistence. While observational studies suggest CDD contributes to maintaining diversity, underlying mechanisms and causality remain unclear. To disentangle stabilizing and destabilizing density-dependent components, I simulate forest community dynamics using an agent-based model (Phylo-Sim), incorporating ecological processes that have a stabilizing and destabilizing effect on community diversity. The simulation outcomes are analyzed using statistical methods adapted from recent empirical work. This approach allows assessment of how local CDD correlates with species abundance across scales and under varying ecological conditions. A secondary aim explores the use of image recognition artificial intelligence to detect statistical artifacts and quantify process contributions in complex simulations, potentially improving theoretical model comparability.

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1 Introduction

How does high species diversity persist despite a limited number of resources? Various ecosystems pose this question (Hutchinson, 1961). For tropical forests Connell, J. H (1971) and Janzen, D. H. (1970) proposed that high diversity can be maintained by (partly) host specific enemies that cause seed and seedling mortality at small scales, increasing the distance and lowering the densities between conspecific adult. Other species can then settle in this gaps, forming a species rich environment even at community level. Expressed in a more mathematical way, diversity can be maintained if (apparent) intra specific competition is higher then the inter specific competition (Chesson, 2000). Factors that increase intraspecific competition, relative to interspecific, are termed "stabilizing". Accordingly, recent literature defines local stabilizing conspecifc density dependence (CDD)[1] as the degree to which conspecifics decrease survival probability more then heterospecifics (Hülsmann et al., 2024). When formulated first, it was suggested that common species suffer more from local stabilizing CDD (Connell, J. H, 1971; Janzen, D. H., 1970). However, observational- and manipulative studies suggest that rare species suffer more (LaManna et al., 2024).

Theories pick up on those findings and try to explain, how this negative correlation between local stabilizing CDD and species abundance leads to diversity maintenance (Schroeder et al., 2020; Yenni et al., 2012). A recent observational study could even show that rare species have higher local stabilizing CDD in the tropics then in higher latitude (Hülsmann et al., 2024). While these findings show that local stabilizing CDD potentially maintains diversity even at community level, the underlying mechanistic understandings as well as the causal direction between local stabilizing CDD and species abundance remain unknown (Hülsmann et al., 2024). One approach to deepen the mechanistic understanding is to explicitly model the stabilizing and destabilizing components that together make up the net local (de-)stabilizing CDD.

Critically, the net stabilizing or destabilizing effect of local CDD emerges from the balance between CDD (i.e., stabilizing component), HDD (i.e., destabilizing component) and their possible interactions. Focusing exclusively on net effects overlooks the underlying mechanistic interplay between CDD and HDD that can shape coexistence (Chesson, 2000). Also, the role of confounder on stabilizing- (e.g., seed dispersal, disturbances, spatial storage effect) and destabilizing components (e.g., invasiveness advantage; see Werner et al. (2010)) remains hidden this way (Chesson, 2000; Hülsmann et al., 2024). Therefore, I try to explicitly account for stabilizing and destabilizing components in my simulation. This approach is inspired by the research of plant-soil feedback (PSF).

PSF questions how plants alter their adjacent soil microbe fauna and how this impacts nearby recruiting (see Fig. 1). Thereby microbes can facilitate or hamper recruiting. Separately looking at both processes disentangles the net density effect into its stabilizing and destabilizing components, as well as their interaction (Schroeder et al., 2020). I will simulate forest growth and include a mutualistic density-dependent effect, inspired by the PSF research, in addition to a detrimental density-dependent effect (e.g., Chisholm and Fung, 2020; May et al., 2020; Miranda et al., 2015; Stump and Comita, 2018). This will generate a finer understanding of how destabilizing and stabilizing components of density dependence as well as their interaction contribute to community assembly. Further, I want to explore these relationships at different spatio-temporal scales (Chesson, 2000; LaManna et al., 2024; Perea et al., 2025).

Broader ecological theories incorporate density dependence at population level (Chesson, 2000) and there are few attempts to scale up local stabilizing CDD to such levels (LaManna et al., 2024). Simulation studies suggest that local stabilizing CDD can maintain diversity at small scales, neutral

[1] I refer to local stabilizing CDD for simplicity but note that a destabilizing effect is possible too (LaManna et al., 2024). Note that quantification of local stabilizing CDD is not consistent in the literature and may consider distance or frequency of neighbors as well (Hülsmann et al., 2021).

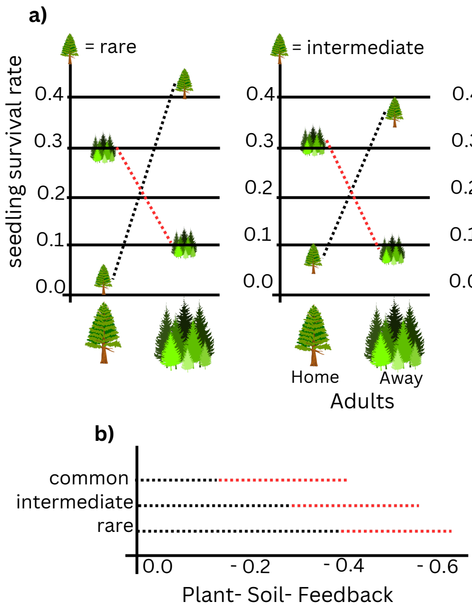

Figure 1: Scheme of how plant-soil feedback is assessed. a): seedling survival rates for home and away scenarios. A home scenario contains a conspecific recruitment at the focal plant (=single tree) and a heterospecific recruitment at the focal plant (=tree group). An away scenario is when the same recruitment happen near a heterospecific. The abundance status of the focal plant species changes in the sub-figures. b): The differences between the specific seedling survival rates in a home and away scenario are added up to the Plant-Soil-Feedback (PSF). Hence, the PSF accounts all possible recruitment scenarios with con- and heterospecific recruit near con- and heterospecific neighbors. By adding up the seedling survival rates, it appears that rare species have the lowest PSF. Redrawn after Schroeder et al. (2020)

setting, or in closed communities (Chisholm and Fung, 2020; May et al., 2020; Miranda et al., 2015; Stump and Comita, 2018). However, sptial and temporal upscaling with more realistic assumptions shows that community level processes, such as mass movements or speciation, can easily override local stabilizing CDD (Chisholm and Fung, 2020; May et al., 2020). Further, the role other stabilizing or destabilizing factors such as drift, seed dispersal, habitat preferences/ spatial storage interact with local stabilizing CDD at community level to fuel or dampen coexistence is not fully understood (Chesson, 2000; Chisholm and Fung, 2020; Levi et al., 2019).

With a theoretical approach that consists of a simulation and a statistical analysis (see section 2), I 1) explore how local stabilizing CDD correlates with species abundance in different scenarios. Linked to this, I 2) analyze how (de-)stabilizing components of CDD drive coexistence and the role of confounder (e.g., habitat preferences) in that process. As 1) and 2) are intertwined, I assess their relationships also. All investigations happen at varying spatio-temporal scales to infer if and how each process and their interaction impact community assembly and maintenance of coexistence.

Another – but lower prioritized – approach applies image recognition artificial inteligence (AI) to understand how mentioned upscaling mechanisms interact with local stabiliting CDD on larger temporal and spatial scales to eventually promote a diverse community. LaManna et al. (2024) cautions that "theoretical frameworks with different underlying mechanisms often predict similar outcomes at the individual, population, and community levels. Therefore, we advise caution when inferring mechanism from a pattern, and additional predictions should be tested where possible to disentangle alternative mechanisms". This probably holds true within a complex model too. Additionally, the interaction of some processes might lead to statistical artifacts that may de- or inflate the effect of local stabilizing CDD on community assembly (Detto et al., 2019; Hülsmann and Hartig, 2018). Therefore, my third facultative research question is 3) Can AI tools quantify the relative influence of distinct processes on model outcomes across scales and, thereby, detect statistical artifacts? In a next step, such a tool could be used for other theoretical models, thus enhancing comparability even between differently parameterized models.

2 Methods

I first simulate multiple scenarios with an agent based simulation model. The resulting time series with dynamic variables will be further analyzed with in empirical statistical pipeline, leaned on Hülsmann et al. (2024). Overall the impact of a set of ecological processes on community assembly and spatial distribution pattern will be analyzed. In this section I first describe the simulation model, followed by the statistical model.

2.1 Simulation model: Phylo-Sim

I use Phylo-Sim, an agent-based raster model, to explore how local stabilizing CDD impacts community assembly (Bauche et al., 2015). Each agent can be fully described by its phylogeny and its position P_{xy}, whereby cells are always occupied. Former dictates four possible traits. Individuals with similar traits have higher mortality, resembling competition for shared resources. Besides, mortality depends on neighbor-density, -distance, and a species environmental preferences. Resulting community assembly can be visualized at small and large spatial scales as well as at several steps in time, which allows investigate temporal and local upscaling of local stabilizing CDD. The model is written and will be modified in C++. It can be run in R (R Core Team, 2022) through an interface (Eddelbuettel and François, 2011).

Modeled ecological processes will be analyzed separately and in interaction to clarify their contribution to a diverse community at different scales. Since every process can be fine-tuned in strength or range, I can examine their respective and interactive impacts on community assembly by changing parameter configurations. Next, I describe which processes will be included and how.

local stabilizing CDD — is implemented via neighborhood density dependent mortality. However, from one generation to the next, it is not obvious if an individual died or if it was mutated by speciation. I will extend Phylo-Sim to quantify local stabilizing CDD based on the calculations in Hülsmann et al. (2024).

Seed dispersal — can be finite or infinite (i.e., global). The scenarios should cover a large range of dispersal. However, very high dispersal – except global – might be computationally heavy. Therefore, I satrt with dispersal = (1, global). These values are commonly used, hence, allow comparison with other simulation studies (Chisholm and Fung, 2020; May et al., 2020).

Habitat preferences — or spatial storage effect can be modeled via an environmental matrix. The heterogeneity will favor some species relative to other and I can investigate how this will impact community assembly.

Meta-community mass movement — the speciation option inserts a number of individuals in the community each generation. Different kinds of speciation are possible. To start with, I use the default – point- speciation –, where a random individuals becomes a new species.

Drift — each individual born will have an averaged phylogeny from both parents, an attraction towards the species mean, and a random fluctuation. The fluctuation can be interpreted as drift. A previous study showed that local stabilizing CDD can offset drift (Levi et al., 2019). However, this result is weak, because drift is negligible at communities of realistic scales (Chisholm and Fung, 2020).

Mutualism — or another process that facilitates individual survival with increasing neighborhood density, thus acts destabilizing. This process is not implemented yet. The kernel and strength of this process will be based on a literature research of pervasive mutualistic processes.

2.2 Regression model

After simulating possible scenarios and quantify local stabilizing CDD, I will feed the results into the analysis-pipeline used in Hülsmann et al., 2024 to estimate the effect size of local stabilizing CDD on mortality. I will largely stick to an unpublished tutorial (Hülsmann Lisa, 2023) that describes the workflow in Hülsmann et al., 2024. Working through the tutorial and modifying to existing analysis-pipeline will be part of this thesis.

3 Defining mandatory- & facultative goals and potential challenges

In what follows, I will list tasks that will definitely be covered (i.e., are mandatory) and tasks that I can choose from, given their feasibility (i.e., facultative) (see Tbl. 1).

Table 1: Tasks during my thesis and possible challenges

task	option	challenges
correlation between local stabilizing CDD and species abundance	mandatory	• direction of causality • implement species abundance in the model – a follow-up difficulty is the evolution of a rare species to a common one and how that interactis with local stabilizing CDD

upscaling to community level	facultative	• assessment of community assembly
		  – I need to develop a metric with wich to describe and compare the resulting community assembly
		  – this metric should work at different scales
		• accounting for community level processes when upscaling and, if needed, implement those in Phylo-Sim (see their Fig. 1 LaManna et al., 2024)
		  – e.g., habitat preferences can be modeled with Phylo-Sim and are known to potentially act stabilizing (Chesson, 2000)
		  – Phylo-Sim offers an option for habitat preferences
		  – quantification of
		• computational time
		  – find a trade off between realistic community size and computation time
		  – time needs to be long enough for equilibrium. Therefore, space must be adjusted with more care

coupling simulation results with regression model	mandatory	• quantify model parameter (e.g., CDD, HDD, species abundance)
		• adapting the the assessment of to changes in survival probability. Hülsmann et al. (2024) added a conspecific individual of 1m distance and 3cm DBH
		  – the distance must be converted in cells
		  – including DBH is not possible, because individuals are not defined by size nor by life stages
		• difficult inference due to high abstraction
		  – produce realistic CDD or HDD values in the simulation
		  – interpret changes in survival probability within that abstract frame work
		  – susceptibility to local stabilizing CDD is static throughout the life-history of an individuals, which in reality likely is not the case (Zhu et al., 2018)

possible statistical artifacts might distort or veil results (compare Detto et al., 2019; Hülsmann and Hartig, 2018)	facultative	• how to detect statistical artifacts is not clear yet
		  – using null models
		  – with AI

implement mutualism	mandatory	• must be realistic in strength and range
		  – this requires a literature review in the field of PSF or related
		  – the implemented kernel will probably vary with the density dependent mortality kerne. It must be analyzed how both processes interact
		  – will the mutualistic effect depend on traits or be idiosyncratic ?
		• how can be a mutualistic effect interpreted in the real world ?

phylogeny and the relation with local stabilizing CDD	facultative	• direction of causality • how does the relationship drive community assembly

multi-level interactions at small and large spatio-temporal scales	mandatory	• choose multiple sets of processes and parameter
		  – as the model is computationally heavy, I must apriori choose a set of parameter that allows valid conclusions
		  – conclusions should consider possible interactions and correlations at varying time- and spatial scales

4 Time line

To ensure systematic progress, I outline my planned workflow below. This schedule will serve as both a organizational tool and broad accountability framework (see Tbl. 2).

Table 2: Thesis Timeline

Month	A	A	A	M	M	M	M	M	J	J	J	J	Jy	Jy	Jy	Jy	A	A	A	A	A	S	S	S	S	S
Week	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
C++ workshop		X	X	X	X	X	X	X	X	X	X	X	X													
ML workshop					X																					
modify Phylo-Sim		X	X	X	X	X	X	X	X	X	X	X	X													
run model	X	X	X	X	X	X	X	X	X	X	X	X	X													
apply ML						X	X	X	X	X	X	X	X													
regression model														X	X	X	X	X								
introduction	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							
methods	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X							
results analysis									X	X	X	X	X	X	X	X	X	X	X							
results section																			X	X	X					
discussion																					X	X	X	X		
abstract																									X	X
proof reading																									X	X

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