

Proposal: CNDD Pattern detection via Machine Learning

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Abstract

1 Introduction

How does high species diversity persist despite a limited number of resources? Many ecosystems pose this question (**Korallen ...**; Hutchinson, 1961). For tropical forests Connell, J. H (1971) and Janzen, D. H. (1970) proposed that (partly) host specific enemies cause seed and seedling mortality locally, increasing the distance and lowering the densities between conspecific adult. Other species can then settle in this gaps, which forms a species rich environment. In the words of modern coexistence theory (Chesson, 2000), diversity can be maintained by the stabilization that emerges from the (apparent) intra specific competition being higher than the inter specific competition. Accordingly, recent literature defines local stabilizing conspecific density dependence (CDD) as the degree to which conspecifics decrease survival probability more than heterospecifics (Hülsmann et al., 2024). Vice versa local destabilizing CDD comes with $HDD > CDD$ and undermines coexistence. Note that quantification of local stabilizing CDD may consider distance to- or frequency of neighbors as well (Song et al., 2021). I refer to local stabilizing CDD for simplicity but note that a destabilizing effect is possible too (LaManna et al., 2024). In fact, the circumstances under which local CDD acts stabilizing or destabilizing are not clear. Related to this, the relationship between the local (de-)stabilizing CDD and species abundance isn't fully explored too.

A long debated idea is that rare species can persist in a community because they experience excessive population growth rates at low abundances, preventing their extinction (Yenni et al., 2012). Empirical studies suggest that, indeed, common species experience weaker local stabilizing CDD than rare species in the tropics but don't show causal relationships (Hülsmann et al., 2024; LaManna et al., 2017). However, simulations showed, that local CDD can act destabilizing for rare species, if they are more susceptible to local CDD than common species, leading to rare species extinction (Miranda et al., 2015; Stump and Comita, 2018). Thus, the interaction and causal

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relationship between local stabilizing CDD and species abundances is not yet solved (LaManna et al., 2024).

I want to explore this interaction and relationship between local stabilizing CDD and species abundance by coupling a simulation approach with the empirical analysis-pipeline applied in Hülsmann et al. (2024). Thereby, the simulation results will be fed into the analysis-pipeline to further explore the impact of con- and hetero specific neighbors on the individual survival probabilities. The logistic generalized linear mixed effect model (GLMM) in Hülsmann et al., 2024 is defined as follows.

$$\log(-\log(1 - \Pr(y_{ij} = 1))) = \beta_0 + f_{conD}(x_{conD}) + f_{totD}(x_{totD}) + f_{DBH}(x_{DBH}) + u_j + \log(\Delta t)$$

The impact is evaluated by altering the independent variables (on the right side of the equation) and measuring the resulting response, namely survival probability (on the left side of the equation). However, the regression model must be updated to fit simulated data. For example, diameter at breast height (DBH) is not simulated. Further, a GLMM to account for variability between time steps is superfluous, as there are no possible confounder in the simulation. Altered components could for example be $\Pr(y_{xyz} = 1)$, which is the mortality probability for the individual at grid position xy at the time z , $conD$ and $totD$ are the local stabilizing CDD and total density dependence, in order. Overall, it is difficult to precisely define the model, as the format of the simulation output is not clear yet. Therefore, the development of an appropriate regression model to further investigate the impact of local stabilizing CDD on survival probability is part of the thesis. This framework can examine, if stabilizing CDD maintains rare species locally. However, a pervasive question remains, if local stabilizing CDD scales up to community level LaManna et al., 2024.

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 setting, or in closed communities (Chisholm and Fung, 2020; May et al., 2020; Miranda et al., 2015; Stump and Comita, 2018). However, when upscaling the model in space and time, while applying more realistic model assumptions, theory shows that large scale processes, such as mass movements or speciation, can easily override local stabilizing CDD (Chisholm and Fung, 2020; May et al., 2020). Further, how other stabilizing or destabilizing factors such as drift, seed dispersal, habitat preferences/ spatial storage, or invasive traits interact with local stabilizing CDD at larger scales to fuel or dampen coexistence is not fully understood (Chesson, 2000; Chisholm and Fung, 2020; Levi et al., 2019; XXXXX, n.d.). I first run a simulation with density dependent survival accounting for habitat preferences with an environmental matrix (Bauche et al., 2015). Then, I apply image recognition artificial intelligence (AI) to understand how mentioned upscaling mechanisms interact with local stabilizing CDD on larger temporal and spatial scales to eventually promote a diverse community. 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). I will apply AI to search for such patterns. Besides understanding the upscaling process, I want to break down local stabilizing CDD into its stabilizing and destabilizing components, deepening the understanding of how the net effect is formed.

Critically, the net stabilizing or destabilizing effect of local CDD emerges from the balance between CDD (i.e., stabilizing component) and 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 e.g., **werner**) remains hidden this way (Chesson, 2000; Hülsmann

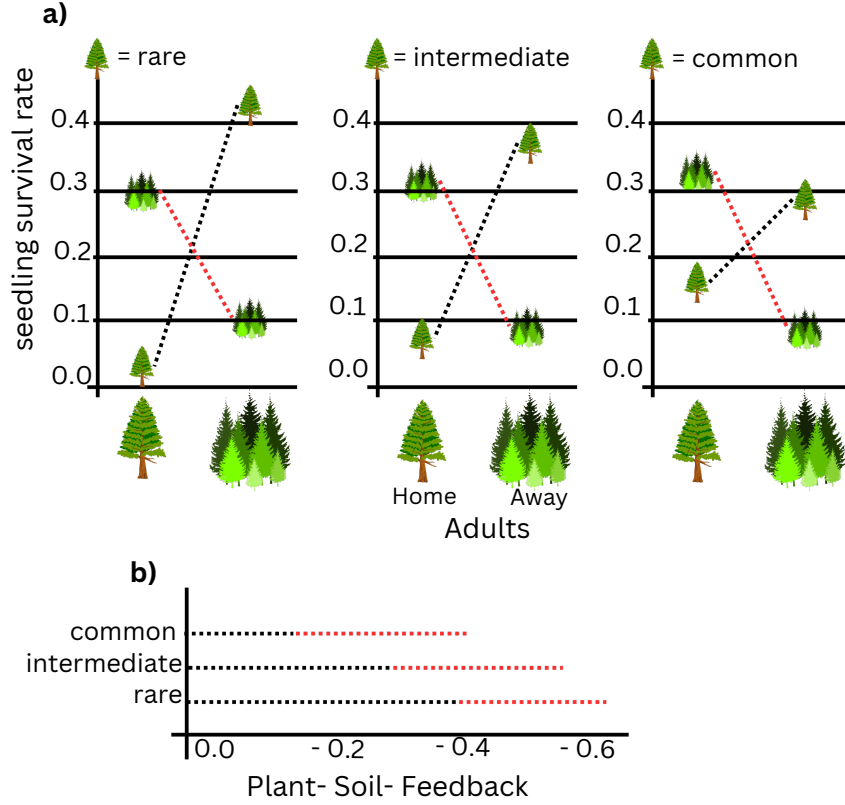


Figure 1: Scheme of how plant-soil feedback is assessed. a) ... b) ... Redrawn after Schroeder et al. (2020)

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 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/distance-dependent effect, inspired by the PSF research, in addition to a detrimental density- and/or distance-dependent effect (e.g., Chisholm and Fung, 2020; May et al., 2020; Miranda et al., 2015; Stump and Comita, 2018). I aim at disentangling destabilizing and stabilizing components of density dependence, assessing their separate and interactive contribution to community assembly across different spatio-temporal scales (Chesson, 2000; LaManna et al., 2024; Perea et al., 2025). Another driver of community assemblage which I analyze is the evolution of species (Mittelbach and Schemske, 2015).

The applied model stands out of other studies, as its definition of a species is not purely binary (May et al., 2020) but based on a phylogeny gradient (Webb et al., 2006; Zhu et al., 2015). This comes with two advantages. First, it relaxes the assumption that all heterospecifics exhibit the same effect on the focal species, which is more realistic (Chisholm and Fung, 2020). Accordingly, neighbors with more similar traits are more detrimental. Second, I can investigate the role of stabilizing CDD (and its interactions with other mentioned mechanisms) on the creation of species and how this in turn drives community assembly (Travis et al., 2013).

To sum up, this thesis investigates (1) how local stabilizing CDD can be upscaled while interacting with large scale processes or other (de-)stabilizing mechanisms; (2) how stabilizing and destabilizing components form net CDD and how those in turn interact with processes described

in (1); (3) how local stabilizing CDD shapes speciation and thereby community assembly. The next section first describes the model and then how it will be used to answer posed questions.

2 Methods

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 position P_{xy} , whereby cells can remain vacant, and by its phylogeny. Latter dictates four possible traits. Individuals with similar traits have higher mortality. 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 makes it suited to 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.

Processes at different scales will be analyzed separately and in interaction to clarify their contribution to a diverse community. For example, at each step, new species can enter the community, resembling meta-community mass movements. Additionally, each individual born will have an averaged phylogeny from both parents, an attraction towards the species mean, and a random fluctuation, i.e., drift. Further, I will integrate a density-dependent synergism intended to act in a destabilizing manner, which could ecologically be interpreted as mutualism. Drift and mass movements are possible stabilizing processes that can interfere with stabilizing or destabilizing density-dependent components during community assembly (Chisholm and Fung, 2020; May et al., 2020). 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. Mentioned example just tackles question (1) and (2).

Other processes that can be analyzed in this framework are habitat preferences, seed dispersal, strength of density dependence or distance dependence to neighbors, stochastic extinctions, whereby latter must still be implemented. Another idea is to examine local stabilizing CDD dynamics in dominant invaders (Werner et al., 2010) by using the already implemented protracted speciation (Rosindell et al., 2010). Working on all these processes is unrealistic for a master's thesis, and furthermore, mixing them may hinder the ability to infer the role of each individually. Therefore, along the way I will check which option is most feasible and decide for a subset of processes to work on.

Community assembly can be assessed visualizing the individuals spatial distribution, species area relationships, rank-abundance curves, and phylogenetic community trees, all from small to large scales. The implementation of a quantification of local stabilization CDD is also part of this thesis.

The model results contain a matrix that maps individuals. A minimum of two matrices of consequent time steps will be analyzed to assess local stabilizing CDD analogous to Hülsmann et al., 2024.

2.2 Feeding simulation results into a regression model

After simulating possible scenarios, I will feed the results into the analysis-pipeline used in Hülsmann et al., 2024 to quantify real world local stabilizing CDD. 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.

2.3 Image recognition AI as analyzing tool for drivers for spatial patterns

The idea is to use an AI algorithm to detect which ecological process drives the spatial pattern resulting from the simulation. Prospectively, I will train the AI in a gradual process. First, I will run the simulations with only one ecological process that drives individual spatial distribution and community assembly, at a time (pure scenario). I will do this for all or for a subset of processes at different spatial and temporal scales. Then, I train the AI in a simulation scenario with two ecological processes acting simultaneously (interacting scenario). I gradually increase the number of simultaneously acting processes. The predictions can be evaluated first in the pure scenarios, then in simple interacting scenarios, and, finally in more complex interacting scenarios. The gradual increase ensures that the AI can recognize patterns in a pure scenario as well as patterns caused by possible interactions of varying degree (e.g., two-way, three-way, ...). The goal is to attribute the resulting spatial distribution of the individuals or the community to one or more ecological processes. So, we can understand which ecological process drives community assembly or individual spatial distribution most. I acknowledge 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" (LaManna et al., 2024). I will follow the advise and, additionally, explicitly define the limitation of my methods in my discussion section.

3 Defining mandatory- & facultative goals and potential challenges

This thesis covers a complex topic, because a number of ecological processes interact and shape the results. Willingly, I vaguely describe the goals of this thesis, because possible challenges are many. The ample pool of ideas allows to fallback and focus on another question in case that I get stuck somewhere. 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 1).

Table 1: Tasks during my thesis and possible challenges

task	option	challenges
correlation between local stabilizing CDD and species abundance	mandatory	<ul style="list-style-type: none"> • direction of causality • implement stochastic extinction (as counterpart to stochastic speciation) ??? • implement species abundance in the model <ul style="list-style-type: none"> – a follow-up difficulty is the evolution of a rare species to a common one and how that interactis with local stabilizing CDD • reach an equilibrium that maintains rare species • if speciation is activated, community might become saturated with species: implement different invasion growth rates (Yenni et al., 2012)

upscaling to community level	facultative	<ul style="list-style-type: none"> • assessment of community assembly <ul style="list-style-type: none"> – I need to develop a metric with which to describe and compare the resulting community assembly – this metric should work at different scales • accounting for large scale processes when upscaling and, if needed, implement those in Phylo-Sim (see their Fig. 1 LaManna et al., 2024) <ul style="list-style-type: none"> – 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 <ul style="list-style-type: none"> – find a trade off between realizable 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	???	<ul style="list-style-type: none"> • 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 <ul style="list-style-type: none"> – 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 <ul style="list-style-type: none"> – 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	<ul style="list-style-type: none"> • how to detect statistical artifacts is not clear yet <ul style="list-style-type: none"> – using null models – with AI

implement mutualism	mandatory	<ul style="list-style-type: none"> • must be realistic in strength and range <ul style="list-style-type: none"> – this requires a literature review in the field of PSF or related – the implemented kernel will probably vary with the density dependent mortality kernel. It must be analyzed how both processes interact – will the mutualistic effect depend on traits or be idiosyncratic ? • How can the effect of each mechanism be extracted from the final result, if both processes are at play and interact with one another ? <ul style="list-style-type: none"> – this may be solved with mentioned AI algorithm • how can be a mutualistic effect interpreted in the real world ?
phylogeny and the relation with local stabilizing CDD	facultative	<ul style="list-style-type: none"> • direction of causality • how does the relationship drive community assembly
multi-level interactions at small and large spatio-temporal scales	mandatory	<ul style="list-style-type: none"> • choose multiple sets of processes and parameter <ul style="list-style-type: none"> – as the model is computationally heavy, I must apriori choose a set of parameter that allows valid conclusions – conclusions should consider possible interactions and relations at varying time- and spatial scales

4 Time line

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	

5 References

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