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sDiv working group meeting report

”INTRACO”

Introduction

The workshop took place at iDiv in Leipzig from Monday 25th to Friday 29th of September 2023. It was the 6th and final INTRACO workshop. The aim of the INTRACO project is to unravel the role of intraspecific variability in tree species coexistence in tropical forest.

Summary of the objectives of the project

Hundreds of tree species can coexist within a single hectare of tropical forest. Several mechanisms have been proposed to explain how so many species can stably coexist while competing for a limited number of resources (mainly light, water, and nutrients). Among these mechanisms, the role of intraspecific variability (IV), which is large in tree communities, has only been recently considered. Studies that have so far explored the effect of IV on species coexistence focused on species-poor systems, used disparate approaches, and reached contrasting results. IV can result from genetic variability and could make species less different, hindering their stable coexistence. A different view is that observed IV is primarily the result of fine-scale environmental variability and could reveal differences among species on unobserved dimensions, promoting species coexistence. INTRACO proposes to provide a clear synthesis of the effect of IV on species coexistence in hyperdiverse communities combining literature review, empirical data-set analyses, and both theoretical and data-based models.

Participants

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Nadja, Claire, Adam, and Ghislain were present in person at iDiv while Isabelle, Camille, Georges, and Benoît participated remotely. Jim was not available at those dates. We planned Zoom meetings at the beginning of the week to define the tasks and the working groups. Then one Zoom meeting was planned on each day to present the progress of each working group on the different tasks.

Tasks of the workshop

We identified three main tasks for the workshop at iDiv:

- The first task aimed at answering the reviews of a paper led by Camille which is untitled «Beyond variance: simple random distributions are not a good proxy for intraspecific variability in systems with environmental structure». The manuscript has been submitted to Peer Community in Ecology and has been reviewed by Matthieu Barbier, Simon Blanchet and Bart Haegeman.

- The second task aimed at discussing the ways to improve the text of a paper led by Jim which is untitled «A universal coexistence hypothesis resolves the biodiversity paradox: Species differences that generate diverse forests». This paper has been rejected after a first submission to *Ecology Letters*. The submitted manuscript is available as a preprint on Authorea.

- The objective of the third task of the workshop was to interpret the results we obtained during the previous workshops regarding the difference between forest types for the strength of intraspecific correlations in comparison with interspecific correlations (for tree growth and fecundity). The first analysis suggested that diagonal dominance (the fact that intraspecific correlation > interspecific correlation) was lower in harsh environments (e.g. dry forests, tundra, boreal forests) than in less constrained environments (e.g. wet tropics). But these initial results needed to be confirmed with more in-depth investigations.

Results of the workshop

First task on Camille's paper

We spent time writing the cover letter to answer the reviewer's comments. Since then, the article has been recommended by Matthieu Barbier for Peer Community in Ecology. The article will soon be published in Peer Community Journal.

In this article, we show that when individual performance are determined by a varying multidimensional environment (15 variables in our case), the fact of representing intraspecific variability with a variance around species means, when several dimensions of the environment are not observed, leads to incorrect simulations of community dynamics in term of number of coexisting species (Fig. 1 below) and community composition. When a variance is used to represent intraspecific variability, conspecific individuals (i.e. individuals from the same species) have different performance in the same environment. On the contrary, when observed intraspecific variability emerges from a variable environment in multiple dimensions, this does not imply that conspecific individuals are intrinsically different. In this case, conspecific individuals have identical performance in the same environment. This difference between random and structured intraspecific variability has large consequences on community dynamics in community models. When individual variability is random, community dynamics is stochastic, leading to an ecological drift and the extinction of many species. On the contrary, when intraspecific variability is the result of the variation of the environment in multiple dimensions, each species is able to outperform the other at some sites with particular environmental conditions, thus allowing the coexistence of a high number of species. This important distinction and the results of

our study have been very well summarised in Matthieu Barbier's recommendation untitled "Two paradigms for intraspecific variability".

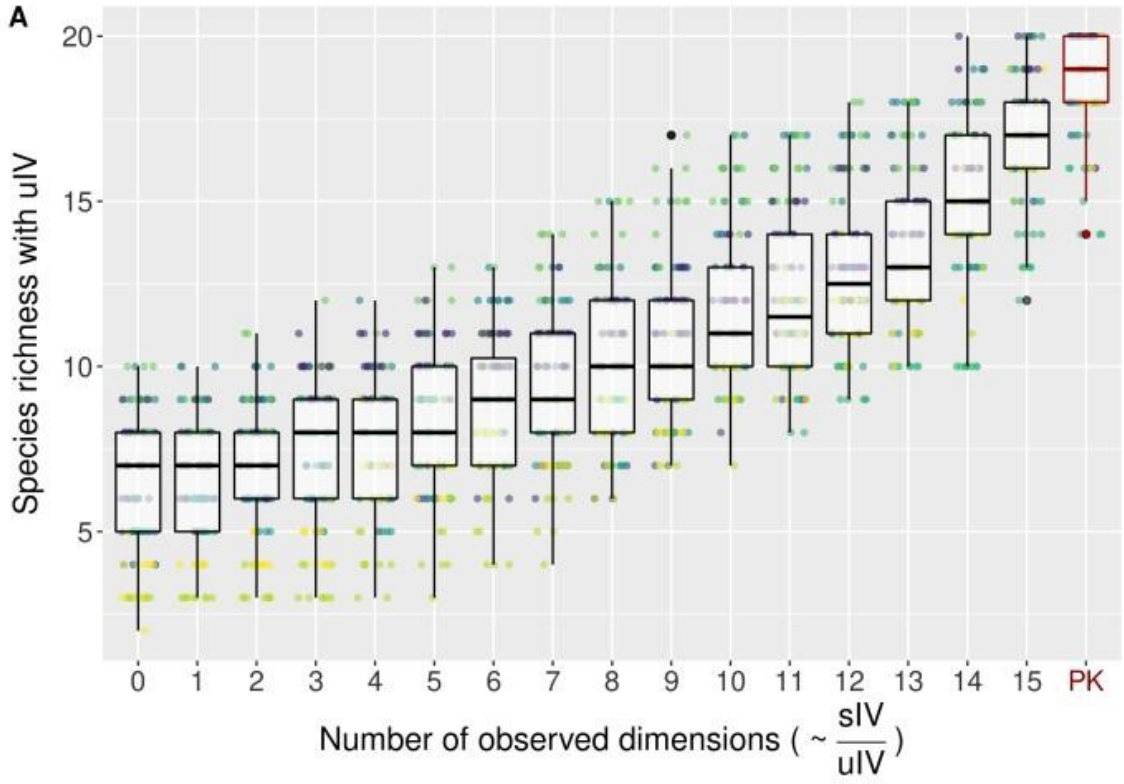

Figure 1: **Effect of using a random variance around species means on the number of coexisting species.** PK is the Perfect Knowledge model with 15 environmental variables. Models using a variance to represent intraspecific variability when some dimensions of the environment are not observed lead to communities with fewer species at the end of the simulations in comparison with the perfect knowledge model.

Second task on Jim's paper

In the preprint led by Jim, we aim at demonstrating that the multidimensionality of species response to the environment, which is responsible for the large observed intraspecific variability (as shown in Camille's first article, a product of the previous INTRACO workshops), allow for the coexistence of a high number of species without considering particular trade-offs. The main points raised by the reviewers was that (i) trade-offs were inevitably present in our model and were responsible for species coexistence, and that (ii) several other mechanisms different from the multidimensionality of species response to the environment can lead to a strong diagonal dominance in the species interaction matrix.

As a consequence, we decided to improve the text of the article to answer these two specific points raised by the reviewers and make our assertions clearer and less questionable. In particular, we tried to provide a clearer definition of what we mean by trade-off as the definitions found in the literature are variable. According to us, it can be defined as the fact that, because living organisms follow the laws of physics and chemistry, one species cannot outperform the others in all the environments. We also rephrased some parts of the text acknowledging that trade-offs are inevitable in nature

and are responsible for species coexistence in our model. We further modified the text to clarify the fact that the multidimensionality of species response to the environment releases the condition for tight (or strict) trade-offs to reach stable species coexistence. Indeed, when the number of environmental dimensions is high, the parameter space allowing a species to outperform the others in at least a fraction of the environment becomes very large. As a demonstration, in our model, there were no a priori conditions on species parameters to make species stably coexist. We finally modified the text to underline the true novelty of the paper which is about demonstrating that multidimensionality of species response to the environment is a simple mechanism to explain the strong diagonal dominance in the species interaction matrix and thus species coexistence. Although we acknowledge that it is not the only mechanism that can drive species coexistence, we underline that it is a very simple one which is in accordance with naturalistic observations of the diversity of species and variability of the environment.

Third task on interpreting new results

For these third task, we tried to interpret further our results showing that intraspecific correlation was greater than interspecific correlation in all the different forest types of our data-set (Fig. 2) but that difference between intra vs interspecific correlation (the strength of the diagonal dominance) was variable from one forest type to another.

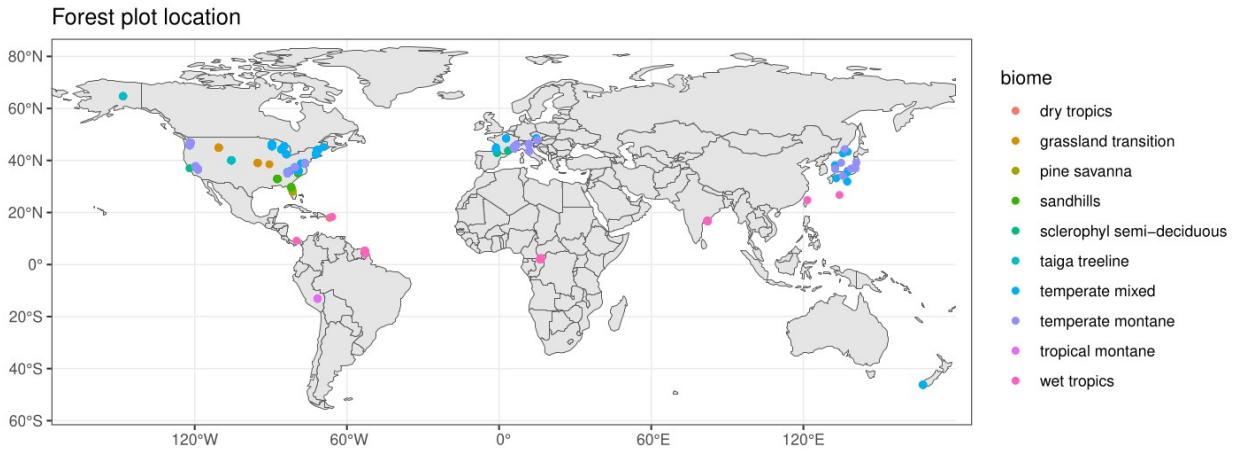

Figure 2: **Location of the forest plot inventories used in our analysis to compare intra vs interspecific correlation for tree growth and fecundity.**

We first tested for a correlation between the strength of the diagonal dominance and the environmental stress associated with each forest type. The hypothesis was that diagonal dominance decreases with environmental stress because of the decrease in the number of dimensions on which species can differ. Differently put, species would tend to be more similar in stressful environments (dry conditions, frost periods), where the environmental filtering of the species is stronger. We found a weak correlation between the strength of the diagonal dominance and either the climatic water deficit or the length of the growing season used to describe the environmental stress. Searching for other potential explanations to the change in diagonal dominance between forest types, we found that diagonal dominance increased with the level of disturbance of the forest plot (Fig. 3). We used forest inventory data from Paracou with different levels of disturbance (thinning intensity) between forest plots to perform this test.

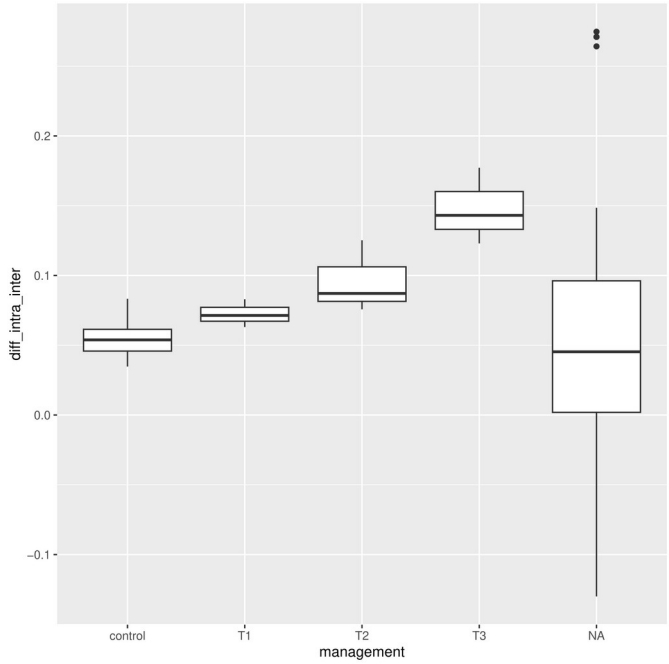

Figure 3: **Increase in diagonal dominance with the level of disturbance in forest.** The strength of the diagonal dominance was estimated by computing the mean difference between intraspecific and interspecific correlations for tree growth for each forest plot. The level of disturbance on each plot was determined by three treatments (T1, T2, T3 with increasing level of thinning) or the absence of treatments (control plots with no thinning).

We spent time discussing these results. They could be explained by the fact that disturbed forest plots include pioneer shade intolerant species (e.g. *Cecropia sp.*) that are absent from control plots. Pioneer shade intolerant species would have very contrasted growth behaviour in comparison with shade tolerant species in disturbed forest plots with a more heterogeneous light environment than in control plots.

We concluded the workshop by planning a more in-depth analysis to fully explain differences in the strength of diagonal dominance between forest types.

General comments

We spent a nice week at sDiv and the workshop was successful as we advanced the different tasks of the project. Our group benefited greatly from the support of the people at sDiv, in particular Luise Dietel who organised our stay in Leipzig, Doreen Brückner who welcomed us to iDiv, and Marten Winter who gave us some useful tips for organising productive workshops. The facilities made available to us at iDiv allowed us to work efficiently, whether in groups on site or by videoconference with people who were not able to attend the meeting in person.

Although the INTRACO project is coming to an end, we will try to value all the results obtained during the workshops. In particular we aim at publishing the two papers which have been initiated, the first one led by Jim on how differences between species in an environment varying in multiple dimensions allow the coexistence of a large number of

species without considering tight trade-offs, the second one on the factors explaining the differences in the strength of the diagonal dominance between different tree communities. We would also like to pursue our investigations and see how our theoretical results could be used to obtain more realistic empirical forest dynamics models. In particular, we would like to fit a hybrid model (with both a part describing species response to the environment and a residual species variance-covariance matrix) to forest inventory data to see if this type of model is able to generate stable species coexistence without the need to incorporate a seed rain in the dynamics.