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sDiv working group meeting report

INTRACO - Unravelling the role of intraspecific variability in tree species coexistence in tropical forest

The <u>INTRACO project</u> aims at better understanding the role of intraspecific variability in species coexistence. While several theoretical models (eg. perfect niche trade-offs in low dimensions, neutral theory) have been proposed to explain the coexistence of a high number of species, underlying model assumptions have not been verified when confronted with empirical data. Because these models have generally disregarded individual differences, while a large intraspecific variability is observed in data, intraspecific variability has been seen as the possible missing explanation for species coexistence. Several studies have thus investigated the role of intraspecific variability in species coexistence leading to contrasting results. The objective of the INTRACO project is to reunify the results of these previous studies and settle the question of the role of individual variability in species coexistence. In particular, we propose to distinguish the sources of the observed intraspecific variability (genetic or environmental) and to study how the nature and structure of the intraspecific variability impacts community dynamics and species coexistence.

The INTRACO project was selected from the <u>2019 SYNERGY call for proposals</u> opened by CESAB, the synthesis center of the French Foundation for Research on Biodiversity (FRB) and sDiv, the synthesis center of iDiv (DFG FZT 118, 202548816). Five workshops at CESAB and sDiv have been funded through the INTRACO project. The third workshop took place at iDiv in Leipzig from 16 to 20 May 2022.

Project participants include theoreticians, modelers, and field ecologists from various research institutes and universities in France, USA, Germany, and Austria: Isabelle Marechaux (INRAE, France, co-PI), Ghislain Vieilledent (CIRAD, France, co-PI), Adam T. Clark (iDiv, Germany), James S. Clark (Duke University, USA / INRAE, France), Benoit Courbaud (INRAE, France), Camille Girard-Tercieux (CNRS, France), Nadja Rüger (iDiv, Germany). Georges Kunstler (INRAE, France) and Claire Fortunel (IRD, France) were also invited to participate in the workshop in Leipzig.

During the workshop at sDiv, we finalized the first article from the INTRACO working group which calls for rethinking the nature of intraspecific variability and its consequences on species coexistence (Girard-Tercieux et al. 2022a). In this article, using a combination of theory, experimental data, and field observations, we show that the large intraspecific variability observed in data can result from the imperfect knowledge of the environment. As a consequence, a large observed intraspecific variability does not imply that conspecific individuals perform differently in the same environment nor that species niche overlap because of individual differences. We conclude saying that intraspecific variability does not necessarily impact species coexistence *per se* but can reveal species response to a high-dimensional environment, which is consistent with niche theory and the observation of the many differences between species in nature. During this same workshop, we also build the outline of the second article of the INTRACO working group which aims at showing that a random variance around a mean is not a good way of representing intraspecific variability and testing its effect on species coexistence in community models (Girard-Tercieux et al. 2022b). We also started discussing a third article in which we aim at demonstrating that the



multidimensionality of species response to the environment, responsible for the large observed intraspecific variability (as shown in Girard-Tercieux et al. 2022a), allow for the coexistence of a high number of species without considering particular trade-offs (Clark et al. 2022).

Our group benefited greatly from the support of the people at sDiv, in particular Luise Dietel who organized our stay in Leipzig and Marten Winter who introduced us to the sDiv research center and gave us some useful tips for organizing 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. During the week, we had an opportunity to present INTRACO's objectives and first results at an iDiv seminar and were able to interact with some people at sDiv. The possibility of inviting researchers external to the project was also very appreciable.

The workshop at sDiv in Leipzig was followed by one at CESAB in Montpellier in September 2022 where we finalized the second and third articles of the INTRACO group (Girard-Tercieux et al. 2022b, Clark et al. 2022). We did so by splitting the group into several smaller groups with regular feedback meetings with everyone. As at sDiv, this was facilitated by the CESAB infrastructure, with multiple rooms, and the efficiency of the staff, in particular Maud Calmet and Nicolas Mouquet. The last workshop of the INTRACO group is planned to be held at CESAB in the first semester of 2023. For this last workshop, we will test our theoretical model of coexistence (Girard-Tercieux et al. 2022b, Clark et al. 2022) on empirical data. We plan to analyze several forest inventories in tropical, temperate, and boreal forests which include time-series data on tree growth and fecundity. We will aim at showing that despite large observed intraspecific variability (i) correlations between individuals of the same species are stronger than between individuals from different species locally (ie. in the same environment) and that (ii) species hierarchy is changing in space and time. This would allow each species to outperform the other locally in space and sporadically in time, thus enabling species coexistence.

References

Girard-Tercieux C., I. Maréchaux, A. T. Clark, J. S. Clark, B. Courbaud, C. Fortunel, J. Guillemot, G. Kunstler, G. le Maire, R. Pélissier, N. Rüger, and <u>G. Vieilledent</u>. 2022a. Rethinking the nature of intraspecific variability and its consequences on species coexistence. *bioRxiv*. [doi:10.1101/2022.03.16.484259].

Girard-Tercieux C., G. Vieilledent, A. T. Clark, J. S. Clark, B. Courbaud, C. Fortunel, G. Kunstler, R. Pélissier, N. Rüger, and I. Maréchaux. 2022b. Beyond variance: simple random distributions are not a good proxy for intraspecific variability in systems with environmental structure. *bioRxiv*. [doi:10.1101/2022.08.06.503032].

Clark J. S., A. T. Clark, B. Courbaud, C. Fortunel, C. Girard-Tercieux, G. Kunstler, I. Maréchaux, N. Rüger, G. Vieilledent. 2022. A universal coexistence hypothesis resolves the biodiversity paradox: Species differences that generate diverse forests. *Authorea*. [doi:10.22541/au.166029509.96486640/v1].