PhD thesis Thomas Galland Evaluation

In the 90s David Tilman and his collaborators published papers demonstrating functional significance of plant species diversity (Tilman & Downing 1994. *Nature* 367, 363–365; Tilman *et al.* 1997. *Science* 277, 1300–1302). Since then, research on how diversity affects ecosystem functioning has been booming, aiming at understanding how human-induced species loss influences ecosystem functioning and services. Early biodiversity ecosystem-functioning research (BEFR) focused on species richness to predict functioning of artificially assembled communities. At present, BEFR attempts to be more realistic by exploring functioning of natural communities distributed along species richness gradients (Fischer et al. 2010. Basic and Applied Ecology 11, 473-485). The field has also shifted towards emphasizing functional diversity as a driver of ecosystem functioning (hereafter EF), as it provides a better mechanistic understanding of the diversity-functioning relationship (Gagic et al. 2015. Proc. R. Soc. B 282:20142620). How community functional structure parameters determine different aspects of EF is also a principal focus of Thomas Galland's thesis.

Thomas explores links between community functional structure and EF using different approaches. First, based on a large biodiversity experiment set up in the field he explores the effect of functional and phylogenetic diversity on colonization resistance, and on above- and belowground EF. In the next research part, he capitalizes on a worldwide database of plant community time series to estimate the role of species diversity and that of species synchrony in driving the community stability. In the final research part, a simulation approach is used to estimate how well different indices (including classical and novel indices, redundancy, as well as indices describing taxonomic and functional structure of the communities) can predict community vulnerability to species loss.

The results of the research are summarized in four chapters presented as four papers, with three papers already published. The unpublished manuscript (Chapter II) is ready for submission. Thomas is the first author of the three studies, and his contribution to all chapters is always clearly stated.

The thesis starts with a comprehensive introduction that nicely summarizes the present state of the art. It introduces different biodiversity facets and how to measure them. Further, an overview of processes driving community assembly is provided. Finally, ecosystem functioning and mechanisms of enhanced EF in more diverse communities are summarized. The introduction concludes with the scope of the thesis research.

The thesis ends with General Discussion & Perspectives. Here, Thomas nicely discusses findings of the research, and outlines possible avenues for future research. Personally, I would have appreciated a better synthesis of the four papers: what do they have in common, how do they complement each other, limitations of the methods used etc.

Overall, I enjoyed reading the thesis of Thomas Galland, and would like to emphasize several strong aspects. As I described above, Thomas combines multiple approaches to address interesting and highly topical research questions. Three of the four research chapters have already been published in highly-ranked scientific journals (which provides, on the other hand, less space for the thesis evaluator to improve the text), and I am sure that the remaining paper will be published soon. It is evident that Thomas profited from being part of a research team including established researchers, and implemented experimental research parts thanks to an existing research infrastructure. While this has doubtlessly provided excellent training, I would have appreciated a stronger involvement of Thomas in the research conceptualization: he was involved in the conceptualization of one out of four research parts (based on information provided on

p. vi-vii). Further, though I judge the quality of the thesis very high, I have several questions concerning the individual research parts.

Questions related to chapters I and II:

1) Assemblage of experimental communities: I wonder why you set up communities in which you independently manipulated phylogenetic and functional diversity (p. 28)? I would expect that the two types of diversity would co-vary in real-world communities. Although you argue that the two are not necessarily correlated based on some studies (p. 26), what is the general pattern in the relationship of the two (see e.g. Jochum et al. 2020. *Nature Ecology & Evolution* 4: 1485–1494)? Why were the communities assembled from 6 species?

2) Please, could you comment on why you chose to use a "natural colonization" design (p. 31) instead of a "seed addition" design (e.g. Kempel et al. 2013, PNAS 110: 12727-12732) to measure colonization success? Where were the unsown species coming from? Could the soil seed bank be an important source of colonizers? Could the high relative success of annual colonizers with therophytic life forms (p. 40) during the first year (in 2016) be due to recruitment from the soil seed bank?

3) Timeline of your experiment: I am a little bit concerned about the timing of the community establishment and the measurements, conducted one and two years, respectively, after the community establishment (p. 29). Could the observed variation of community resistance to colonization (namely the conclusion that FD decreased community resistance to natural colonization; p.22) be transient, accounting for the fact that the sown community was not fully developed yet? In a similar line, could the short time span since the establishment of experimental communities explain the missing effect of fertilization (cf. Foster et al. 2011, Journal of Ecology, 99: 473-481)?

4) I am wondering to what extent the colonization success might be driven by neutral processes relative to the nonneutral ones (that were explored in the study) (e.g. Fargione et al. PNAS 2003: 8916-8920). Do you have any data about the abundance of successful (and failing) colonizers from the surroundings of your experimental plots?

5) To rephrase one of the research questions from Catford et al. (2019. Ecology Letters 22: 593-604): what is more important for colonization success: i) traits of the colonizers, ii) characteristics of the recipient communities, or iii) the interaction between the two?

6) Please, could you comment on one of the main findings of your study: cover of the successful colonizers was not statistically different between communities with high and low levels in both functional and phylogenetic diversity (p. 37). This finding made me wonder whether the two types of diversity are indeed important drivers of community resistance.

7) With respect to the second research part, could the weak effect of fertilization and of community functional structure parameters (FD and PD) on soil EF be a result of the short time period since establishment of experimental communities?

8) You showed that litter decomposability was lower in communities with higher values of functional diversity and those with higher C:N ratio and lower SLA (communities with higher CWN_pca2 scores, p. 81). I would then expect that variation in decomposability would also lead to differences in the

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amount of available soil nutrients (e.g. Aerts & Chapin 1999, Advances in Ecological Research 30: 1-67). This was however not the case (based on non-significant relationship of decomposability with multF_NutPool indicated by the coefficients in Table S1 on p. 102). How do you explain this pattern? Have you considered linking decomposability to individual nutrient levels instead of composite multF_NutPool?

9) If I had to choose a single plant functional structure parameter (from those used in Chapter II) that best captures variation in (above- and below-ground) EF, which one should I go for?

Questions related to Chapter III

10) One of your main conclusions of Chapter III is that richness promotes stability, but this effect is not necessarily caused by a direct, negative effect of richness on synchrony (p. 116-117). So, what are the alternative mechanisms underlying this positive effect of species richness on stability?

11) I wonder whether you examined the effect of species-level stability on community stability (Majekova et al. 2014. Ecology 95: 2369-2374, Leps et al. 2018 Ecology, 99: 360-371)? I would expect that presence of more stable species in the community will also promote its stability (p. 113). If you did analyze this, what was the relative effect of species stability, species synchrony and species richness on community stability?

12) You frame your research by stressing the importance of the stability of ecological communities for the stable provisioning of ecosystem services (p. 110), and also show that anthropogenic activities can significantly alter the stability (via synchrony; p.117). I wonder how important natural gradients (e.g. precipitation) are compared to human activities in altering the stability.

13) Your research shows that association between richness and synchrony, and between synchrony and stability depends on choice of synchrony indices. Could you comment on whether researchers should give preference to/abandon using some indices and why?

Questions related to Chapter IV

14) The text is quite dense and I would appreciate more detailed explanations to the analyses. Specifically, I was a little puzzled by the fact that you used functional richness (FRich) and Functional divergence (RaoQ) as parameters of community vulnerability to species loss, but at the same time you used FRich and RaoQ as predictors of the vulnerability. Please explain.

Conclusion: Thomas has proven his ability to produce independent scientific work, including data collection, analysis and manuscript preparation and publication. I am pleased to recommend the thesis to be defended.

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Review of "Plant community diversity effect on ecosystem functioning: a functional trait story"
PhD thesis by Thomas Galland

Overall assessment
This thesis looks at the role of functional and phylogenetic plant diversity in affecting ecosystem functioning and stability. There are four data chapters together with a general introduction and discussion, Mr Galland is first author on three of the chapters. Three chapters are published already.

Overall, I think this is an excellent thesis. The topics addressed are all timely and interesting. I think that considering multiple diversity dimensions and their role in affecting the functioning and stability of ecosystems is of importance and a key current frontier in biodiversity research. The studies are well thought out, present some very interesting results and discuss the findings well. The interpretation does not go beyond the results and it integrates them well into the context of functional trait and functional biodiversity research. The only area I found less theoretically developed was the consideration of phylogenetic diversity. There is frequent speculation that phylogenetic diversity may capture "unmeasured traits" but not much speculation as to what these might be. There is also less background and citation of community phylogenetic work. However, this is a fairly minor concern. Three of the chapters are already published and all in good to excellent journals, which is a great achievement, in my view.

I also really appreciate that the work covers such a variety of approaches: two chapters deal with a field experiment, one with a large-scale synthesis of a global dataset and one is a simulation study. This shows that Mr Galland has developed a wide range of skills during his PhD and is able to use a variety of approaches to tackle key questions from different angles. I was impressed by the fact that he had tackled such a range of complex analyses. Most of the analyses deal with complex multivariate datasets with multiple functions, traits and diversity dimensions. Dealing with this is a huge challenge and I think the thesis does a very good of navigating the complexity and providing clear results. Overall, I have no hesitation in recommending that Thomas Galland be awarded a PhD.

I have a number of detailed comments and questions and I have outlined these below, for the different chapters. I also highlight some questions for each chapter.

Detailed assessment of each chapter
<u>General introduction</u>
This is an excellent introduction to the thesis. I felt it was a very interesting and engaging review of the literature on functional trait ecology, I especially appreciated the historical overview of how functional trait ecology developed. All of the main topics that are dealt with in the thesis are introduced.

<u>Functional and phylogenetic diversity experiment</u>
The experiment used in chapters 1 and 2 manipulates functional and phylogenetic diversity, factorially. This is very interesting as no other experiments have manipulated both of these diversity dimensions, and in general explicit manipulations of diversity dimensions other than species richness remain rare. It is important to explicitly manipulate these diversity dimensions as they may be

confounded with other factors, or lack variation, in standard biodiversity experiments that manipulate species number. Although I am enthusiastic about the experiment, I have several questions related to it, the most important of which is whether the experiment was weeded. Most biodiversity experiments are weeded to maintain the sown species compositions, as certain plots are generally heavily invaded and diversity gradients cannot be adequately maintained without weeding. It seems that this experiment was not weeded, and I therefore wonder how reliable the effects are, given that some of the plots are likely to be heavily invaded (the average cover of weeds was 30% in 2017, which is very high). This is especially a problem for chapter 2, but also for chapter 1, in order to understand whether the species are really invading different communities or just establishing at the same time as the residents. It would be useful to know what the range in weed biomass was across the different communities and whether realized diversity metrics still cover an adequate range to judge how serious a problem this is.

- ➔ how large was the weed biomass in the different plots in the two years and how well are the diversity gradients maintained without weeding?

Designing such experiments is challenging and this one is very ambitious as it manipulates functional diversity using 7 traits. My concern here is how to disentangle effects of mean traits from functional diversity. In particular, Fig S4 in chapter 1 shows that functional diversity (FD sown) is strongly correlated with mean traits such as nitrogen fixation. The presence of legumes is well known to have a strong effect in biodiversity experiments and some (e.g. Jena Experiment) explicitly cross legume presence with diversity (or avoid legumes altogether as in Wagningen).

- ➔ How do you separate effects of functional trait diversity and functional composition when the two are so correlated?

<u>Chapter 1</u>

This chapter presents first results from the phylogenetic and functional diversity experiment, testing how colonization is affected by both measures of diversity. The results are interesting in showing that functional diversity increases colonization, i.e. diverse communities are more susceptible to invasion, because they have more "gaps" in functional space that can be filled. Phylogenetic diversity interacts with functional diversity and moderates its negative effect on invasion resistance. These results are intriguing and highlight the complex effects that functional diversity can have. There are also some nice analyses looking at which traits make species a good invader. Overall, this is a very interesting study with a large dataset and some novel findings about the role of functional trait diversity in affecting invasion resistance. My one critique is that while the analysis is mostly good, and analysing such large datasets with multiple species and traits is challenging, two aspects were a bit inconsistent. Firstly, mean traits were analysed individually whereas only multivariate trait distances were analysed, and distances and mean trait effects were dealt with in separate models. This means that it is hard to compare the effects of mean traits and trait distances and it is perhaps not surprising that the distances turn out to be less important. However, the results are well discussed, and I think they will inspire other studies and research.

- ➔ Why did you not consider analysing trait means and distances in the same model?

<u>Chapter 2</u>

This chapter looks at the effect of functional and phylogenetic diversity on multifunctionality, using the experiment manipulating functional and phylogenetic diversity. It shows that functional diversity and composition are key drivers of several functions but that phylogenetic diversity seems less important. The aspect I find most novel and interesting is to look at the indirect effects of the diversity treatments on soil functions, through changing other functions like plant biomass and litter decomposability. These indirect effects are often strong, showing the importance of considering cascading effects of diversity through linked functions. This chapter is very ambitious in terms of the number of aspects and is a bit less developed than the others. I have several questions about it. Firstly, I think the lack of weeding is a major issue here and I feel it would be necessary to consider either realized diversity measures or using weed cover as a covariate to correct for the fact that some plots are heavily invaded (using weed biomass as a function makes things even more complicated). The high weed cover may also be a problem for the additive partition as I can imagine some monocultures are heavily invaded, potentially biasing the estimates of complementarity and selection. Some analysis with total biomass (weed + target) might be useful to check that invasion is not driving the effects. Secondly, I am not sure about the direction of causality between functional composition measures and soil abiotic properties. Community weighted means are used, which are partly determined by the sowing treatments and partly determined by shifts in abundance, which could occur in response to soil conditions. It would be good to know how much variation in pH there was across the field at the start of the experiment, to judge how plausible it is that the plant communities have changed pH in two years. Overall, I think there are still some issues to address in this chapter, but it is a nice piece of work that will advance our understanding of diversity-multifunctionality relationships

- ➔ How sure are you that plant functional composition affects soil properties and not the other way around?
- ➔ There are few effects of the plant community measures on soil functions. Is that due to the very short time scale of the experiment?

Chapter 3

This chapter presents an analysis of a large global dataset looking at effects of species richness and synchrony on stability. The study is robust because it tests these relationships across a large number of studies, and it is very valuable to explore diversity-stability relationships in "real-world" systems. The results are highly interesting in showing that synchrony is a key driver of stability, but that species richness actually *increases* synchrony, in contrast to theory and experimental results. Despite increasing synchrony richness still increases stability, directly. These results have the potential to force a rethink of how richness and synchrony are related. However, I wonder if this positive relationship is really driven by covarying factors like functional diversity/composition, this is mentioned in the paper and would be very interesting to test. In addition, it would be interesting to think more about what causes the direct effect of richness on stability, not mediated through synchrony. I also really appreciate the fact that the study included environmental drivers of stability and their direct and indirect effects. Overall, this is an excellent study that is likely to be influential on diversity-stability research.

- ➔ What mechanism explains the direct effect of richness on stability? In light of the results from chapter 4, is this an effect of redundancy?

Chapter 4

This chapter uses simulations to explore the behaviour of various indices of functional redundancy and compares them to classic measures like species richness, functional evenness and functional richness. The analysis shows that the redundancy measures do not add much information compared to classic measures and are strongly correlated with them. It is also shown that the community most resistant to species loss is one with high species richness, low functional richness and high evenness and that none of the redundancy indices captures this. I think this is a valuable paper and pointing out that the redundancy indices do not add much information is useful. The conclusion is somewhat frustrating as it would be good to have an index of redundancy, independent of richness of functional diversity, however, the study does suggest some ways forward.

- ➔ How does the relationship between the redundancy indices and the other metrics depend on the number of traits used? E.g. if you used only one effect trait would this reduce some of the correlations with species richness?

Yours sincerely,

Prof. Dr. Eric Allan