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## Community assembly and plant soil feedback

Tamara Münkemüller

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# Community assembly and plant soil feedback

MÉMOIRE POUR  
L'OBTENTION DE L'HABILITATION  
À DIRIGER DES RECHERCHES

**Université Grenoble Alpes**

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## FOREWORD

(Why) must we protect biodiversity? – At the beginning of my career I had the repeated and deeply disturbing experience that my arguments could not convince people from “out-of-the-ecologist” box of the value of nature and biodiversity. During my further studies, I began to understand that my arguments were a mixture of ideas rooted in anthropocentric vs. biocentric morality, and that this was the core of my failure. It is almost impossible to convince non-believers of an intrinsic value of nature (biocentrism), it can be very difficult to convince people with different perceptions and different (cultural) backgrounds of a non-instrumental value (anthropocentrism), and therefore it is the most logical and scientifically simplest option to argue with instrumental values. The frustration with the contrasting nature of these different lines of argumentation motivated my master's thesis in environmental psychology and - although I did not pursue this career path - still influences my work. Although I usually highlight the instrumental arguments for biodiversity conservation in my professional work, my true motivation is still a combination of non-instrumental and intrinsic value assignment. And while I try to focus on projects that link biodiversity to ecosystem functions useful to humans, I am even more driven by the beauty of hidden complex processes, the understanding of the small screws that can be turned to change trajectories, and the amazing magnificence of the resulting visible.

## Acknowledgements

First of all, I am very grateful to my PhD students Loïc Chalmandrier, Ceres Barros, Camille Martinez-Almoyna, Irene Calderón-Sanou and Billur Bektaş. The supervision of your theses was not only formally important for my habilitation but also very inspiring. I learned and learn a lot from and with you! Most of all that every person is different and that the most important characteristic of a supervisor is to listen, listen, and listen ... (which is not particular helpful for a person who likes to speak). Thank you as well for the great time we spent in the field, during group retreats, scientific beer discussions, climbing and swimming.

My warmest thanks go to Wilfrid Thuiller and Sébastien Lavergne who started as my bosses and became very good friends over the years. I do not know where to start and where to end – so thank you for all of it! It is most valuable and instructive to be supervised by two people so different in approaching science and life.

I am still very grateful to my PhD supervisor Karin Johst who, together with Justin Travis, has profoundly influenced my scientific thinking and the direction of my scientific career until today.

A scientist without a research group is like a fish without water. The list of people who made and are making life at LECA and beyond so great is long and I will not be able to do everyone justice here. Most of all I would like to thank Laure Gallien for sharing all these great moments, humor, genius ideas, and craziness. Thank you for your support during all the ups and downs and for being such a wonderful friend.

I would like to especially highlight all the supporters of the experiment AlpagesVolant. Without all of you this great piece of work would not have been possible. My particular thanks for their continuous support, hard work on the project, and the great time up in the mountains go to Amelie Saillard, Wilfried Thuiller, Maya Guéguen, Julien Renaud, Jean-Gabriel Valay, Franck Delbart, Pascale Salze and Rolland Douzet. I would like to thank Ludovic Gielly, Marie-Pascale Colace, Irene Calderón-Sanou, Billur Bektaş, Louise Boulangeat, Raphaël Della Vedova, Mélodie Bourreau, Matthieu Fleuet, Nakita Rubuliak, Audrey Labonte, the teams from the SAJF and the LECA, and all the other people helping during field- and labwork.

I also would like to thank our current working group for all the enthusiasm, discussions and great ideas as well as for the sportive challenges, beer evenings, and great food. Special thanks go to Amelie Saillard, Maya Guéguen, Julien Renaud, Camille Martinez-Almoyna, Irene Calderón-Sanou, Billur Bektaş, Louise Boulangeat, Giovanni Poggiato, Sarah Weil, Louise O'Connor, Paul Dufour, Marc Ohlmann, and all the others. Thanks to Gabin Piton and Arnaud Foulquier for introducing me to the dark world. And thanks to Florian Boucher and Laure Gallien for showing us the world of the “fesses vertes”. There are also many former members of the group who were and are still important to my work and life as a scientist: Many thanks to Katja Schiffers, Marta Carboni, Laura Pollock, Rafael Wüest, Cécile Albert, Laura Meller, Francesco de Bello, Laure Zupan, Florent Mazel, Isabelle Boulangeat, João Braga, and all other former group members.

So here I am at the end. With the people that matter most and longest in life. I would never be where I am without my family, my mother, sister, grandaunt and grandmother, and without my friends.

Most of all I would like to thank my husband and kids. It is the slightly grumpy but ever so steady support and humor of my husband, Björn Reineking, that helped me to master this habilitation, and even more the earlier stages of my academic career - from writing a PhD, over emigrating to another country, to applying and re-re-applying for a permanent position. And without the chaotic interruptions, furious complaints but also amazing patience, infectious humor and most beautiful smiles of Helena and Anouk, all of this would only have been half of the fun and happiness! Thank you for everything.

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## 1. INTRODUCTION

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My research aims at understanding, describing and predicting biodiversity and resulting ecosystem functions at different spatial scales and in response to different drivers. Biodiversity can be defined as “the variability among living organisms from all sources [...] and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (CBD, 2005, p. 89, Article 2: Use of terms). This definition draws attention to the many dimensions and facets of biodiversity. It explicitly recognizes that every living organism, but also every group of organisms, can be described by different characteristics including their taxonomic, functional, and phylogenetic diversity. The functional facet of biodiversity describes “the variation in the degree of expression of functions at the different levels of organization of the living world” (Garnier, Navas et al., 2015, p. 6). Functional diversity can be measured as the diversity of functionally relevant species’ characteristics, or so-called functional traits (Violle, Navas et al., 2007). It can provide a direct link to both biodiversity responses to environmental conditions as well as biodiversity effects on ecosystem processes (Lavorel & Garnier, 2002) and as such is a key component of biodiversity (Mouillot, Villeger et al., 2011). The phylogenetic facet of biodiversity represents evolutionary history (Faith, 1994) and more precisely how much of this history is shared by the living organisms of interest. Assuming that shared ancestry – through processes of natural selection and genetic drift – leads to shared functions, phylogenetic diversity can be used as a proxy for functional diversity.

Biodiversity in all its facets is important for mankind (Isbell, Gonzalez et al., 2017). It sustains ecosystem processes and resilience of ecosystems to environmental change (Chapin, Zavaleta et al., 2000) as well as healthy ecosystems (Perkins, Bailey et al., 2015). It is an essential part of the solution to climate change (van Vuuren, Stehfest et al., 2018), can be important to economy (e.g. food, pest control, fuel, medicines, eco-tourism) especially for struggling communities in developing countries, and it is an integral part of culture and identity (Chapin et al., 2000). Biodiversity can also be seen as an insurance: We do not know the future and which facets of biodiversity may then become important. Finally, biodiversity is in many of its facets simply stunningly beautiful and enriches the lives of humans.

However, biodiversity is in danger (IPBES, 2019; Thomas, Cameron et al., 2004). Species extinction rates are an estimated 1000 times the “background” rate (De Vos, Joppa et al., 2015) and greater than at any time in the history of the Earth. The tendency is further acceleration (Pimm, Jenkins et al., 2014). The loss of the functional facet of biodiversity can be even faster than species loss (Petchey & Gaston, 2002; Teixidó, Gambi et al., 2018), and the phylogenetic facet is susceptible to points of non-reversible change (Faith, 2015). Biodiversity is mainly threatened by climate change, land-use changes, exotic species invasions, overexploitation of organisms and pollution (IPBES, 2019). The most important of these threats are predominantly caused by humans (Reusswig, 2013). Offsetting these threats will benefit from a better understanding of drivers and dynamics of biodiversity.

My past research contributed to the improved understanding of biodiversity drivers and dynamics with a focus on mountain vegetation. This ecosystem is of particular interest due to its high biodiversity and small-scale heterogeneity. The complex topography of mountain regions determines sharp environmental gradients over short distances leading to a typical sequence of different vegetation stages and local adaptations of plant species. Climate and

land-use changes alter this stratification and require species to either acclimatize and adapt, migrate, or they will force species to local extinction. With the aim to better understand these dynamics my past research (after the PhD) was guided by the following research questions (chapter 2):

**(1) How to disentangle community assembly rules from diversity patterns?**

**(2) How to predict invasion success from diversity patterns?**

Over the last years, I have increasingly realized that a simple focus on vegetation and the rules of plant community assembly is not enough to understand global change impacts. Plants respond directly to global changes, but also indirectly to the shifts that these global changes may exert on soil communities and on the functions of the soil ecosystem, notably nutrient and water supply. Inversely, plant communities influence soil communities, their decomposition activities, and soil fertility through the quantity and quality of their litter and their root exudates. These plant-soil feedbacks are key to understand and predict how global change effects will cascade through plant and soil compartments. To better understand these plant-soil feedbacks in mountain ecosystems my current and future research tries to find answers to the following research questions (chapter 3):

**(3) Do plant-soil feedbacks change over environmental gradients?**

**(4) How do plant-soil feedbacks respond to experimental warming and cooling?**

**(5) Do plant-soil feedbacks improve the performance of process-based vegetation models?**



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## 2. COMMUNITY ASSEMBLY & INVASION

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### 2.1 How to disentangle community assembly rules from diversity patterns?<sup>1</sup>

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#### 2.1.1 Context

The diversity of ecological communities is increasingly compromised by ongoing global changes (Pereira, Navarro et al., 2012). Mitigating these threats requires to understand the distribution of diversity along geographic, abiotic and biotic gradients and the underlying assembly processes (HilleRisLambers, Adler et al., 2012; Lavergne, Mouquet et al., 2010). A focal question is whether abiotic constraints or rather biotic interactions drive the taxonomic and trait structure of communities. In community ecology, this question has historically been addressed by experiments, with the limitation that these methods are typically constrained to small scales and few species. Thus, to study community assembly at large spatial scales, ecologists have assembled increasingly large community datasets spanning broad spatial extents with both trait and phylogenetic information (Diaz, Kattge et al., 2016; Kunstler, Falster et al., 2016, see Fig. 1a, b). Combining data on distribution, traits, and phylogeny in a meaningful way holds promise for a revolution in community ecology by opening the door to large-scale analyses of assembly processes (Mc Gill, Enquist et al., 2006; Webb, Ackerly et al., 2002). The idea is to harness the information on species niches contained in phylogenetic and trait data. Under the assumption that a set of traits represents species' niches well, we could move from a simple species-based description of communities towards a functional characterization, using community weighted mean traits as an estimate of the community niche optimum, and trait diversity as an estimate of species niche overlap (see below for more detail, Kraft, Valencia et al., 2008; Violle et al., 2007).

#### 2.1.2 The filtering framework – theory & research questions

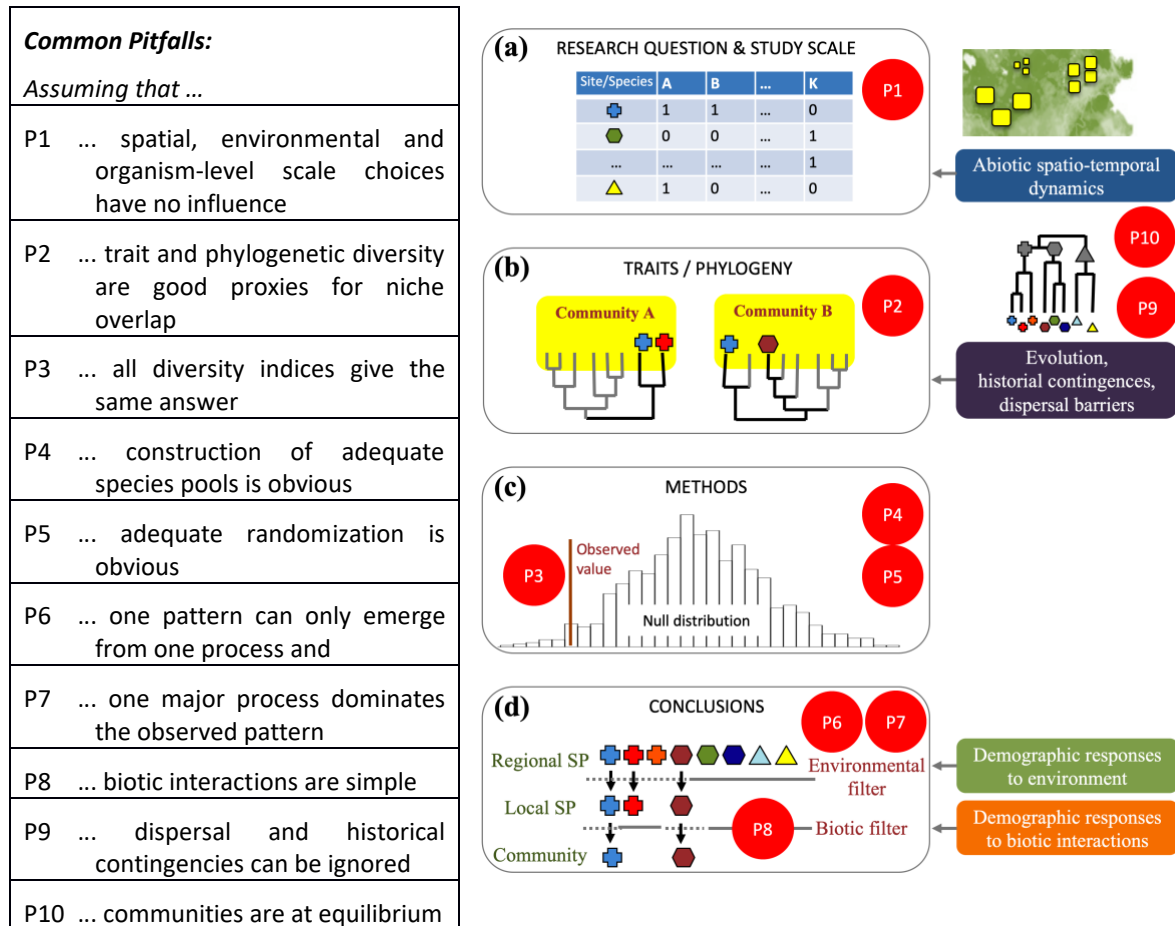
The filtering framework (Diamond, 1975; Keddy, 1992) builds on the idea that a series of filters decides which species from a regional species pool, originally shaped by biogeographical history (Carstensen, Lessard et al., 2013), can enter local communities. It assumes that both abiotic (e.g. climate or land use) and biotic factors (e.g. competition) define species' carrying capacities and/or growth rates and thus influence their occurrences and abundances (Fig. 1d). The abiotic conditions define the environmental filters selecting species from a, into the local species pool containing all species adapted to the local conditions. Then, biotic interactions influence which species from the local pool can eventually coexist in the community (Chesson, 2000; Shmida & Ellner, 1984).

Relatively early on, studies that began to apply this filtering framework used trait diversity patterns (e.g. including behavioural, life-history, morphological and physiological traits, Violle et al., 2007) and phylogenetic relatedness (Webb et al., 2002) to account for species' niche similarities. Doing so assumes that measured traits are relevant for assembly processes (Mayfield, Boni et al., 2009) and that closely related species in the phylogeny are ecologically more similar than distantly related ones (Burns & Strauss, 2011). To infer assembly processes,

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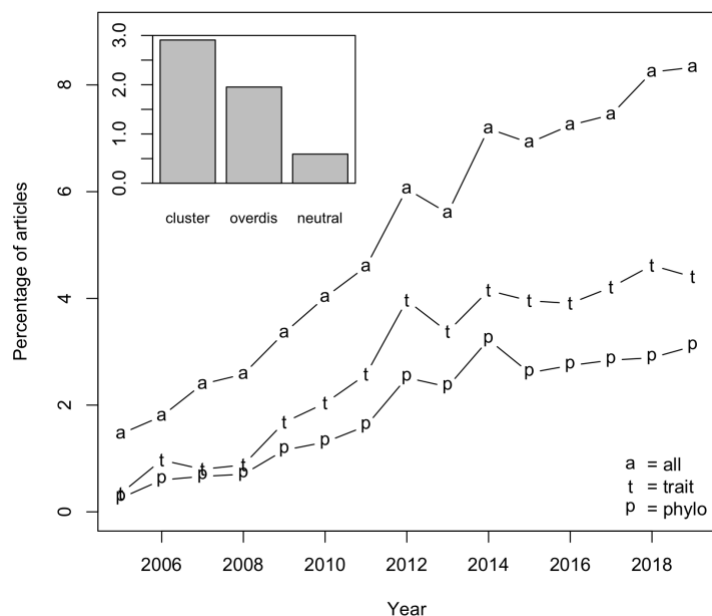
<sup>1</sup> This section is based in large parts on our review paper Münkemüller et al. (in press).

observed patterns of trait and phylogenetic diversity within a community (i.e.  $\alpha$ -diversity) are commonly compared to null expectations (i.e. patterns under random assembly, Fig. 1c). Low trait or phylogenetic  $\alpha$ -diversity is assumed to indicate ecological processes that foster the co-occurrence of species with similar niches, such as environmental filtering (Fig. 1b, community A). Conversely, high trait or phylogenetic  $\alpha$ -diversity can reveal ecological processes that result in limiting similarity, such as competition due to niche overlap (Fig.1b, community B, Mac Arthur & Levins, 1967).



**Figure 1** - Conceptual representation of the steps of the classical ecological filtering framework and related ten common pitfalls (cf. left table and red points in the figure): (a) Identifying research question(s) and study design, including focal organism level, spatial and temporal scales (potential pitfall 1); (b) sampling data, specifically choice of traits and/or phylogeny (P2); (c) choice of methodological approaches, including diversity indices, null models, species pools and statistical tests (P3-5) and, finally, (d) drawing conclusions on the potential underlying processes, an approach with inherent problems (P6-7) but specific limitations in face of complex biotic interactions (P8) and influential background factors (P9-10, Münkemüller et al., in press).

An increasingly large number of studies apply the filtering framework (see Fig. 2). However, first reviews and meta-analyses of empirical (Emerson and Gillespie 2008, Vamosi et al. 2009, Götzenberger et al. 2012, HilleRisLambers et al. 2012) and simulation experiments (Gallien, Carboni et al., 2014; Miller, Farine et al., 2017; Münkemüller, de Bello et al., 2012) have strongly dampened the enthusiasm, as they demonstrate that no simple general conclusion can be drawn from the sole observation of trait and phylogenetic diversity patterns.



**Figure 2** – Literature search demonstrating the increasing percentage of community assembly studies based on traits and/or phylogenies within the domain of community ecology over time; the insert shows the percentage of studies focused on clustering, overdispersion and/or neutral dynamics within community ecology; WoS search words (29.01.2020) for all: “community assembly” AND (“filter” OR “overdispers\*” OR “cluster\*” OR “converg\*” OR “diverg\*”) and in addition to this for trait: AND (“trait” OR “functional”); for phylo: AND “phylo\*”; for cluster: AND (“cluster\*” OR “converg\*”); for overdis: AND (“overdis\*” OR “diverge\*”) and for neutral: AND “neutral”. Numbers of publications for these searches are divided by numbers of publications for the search “community ecology” to account for the overall increasing number of publications over time (Münkemüller et al., in press).

One prominent example of the filtering framework’s limitations is the ongoing debate on the role of competition: While the filtering framework often fails to detect signals of competition, theoretical and empirical research underscores its importance even at broad scales. Seemingly, we are not much further than 20 years ago when Lawton concluded that community ecology is a ‘mess’ (Lawton, 2000). The lingering question is why the filtering framework does not provide general results.

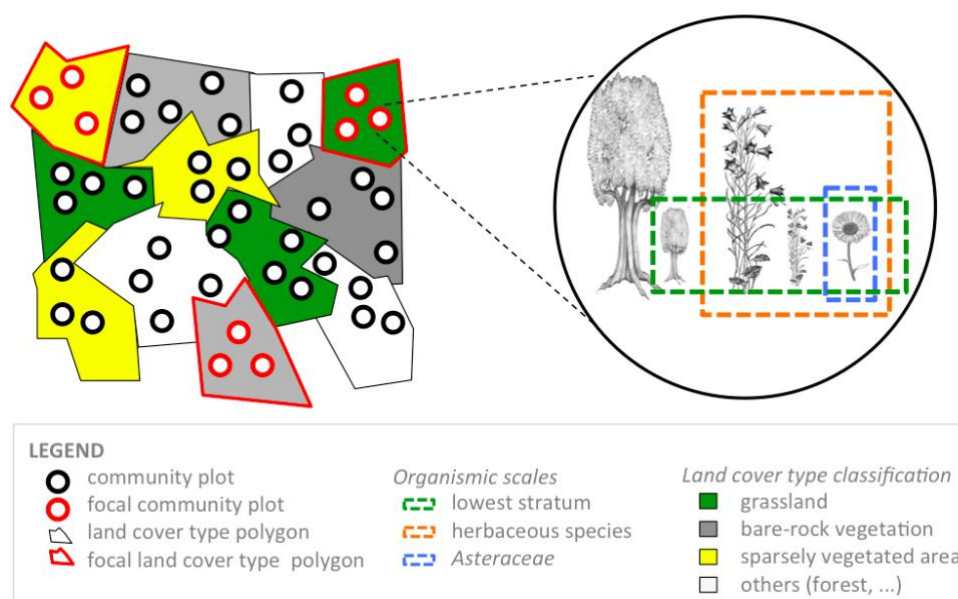
**Research questions are:**

- What are potential pitfalls in the application of the filtering approach? (2.1.3)
- What are solutions and guidelines for best practice? (2.1.4)

### 2.1.3 Pitfalls

Applying the filtering framework requires (1) choosing the study design with focal spatial, environmental, and organism-level scales, (2) collecting information, and (3) choosing methodological approaches relevant to the research question. Finally, (4) conclusions should be drawn from the results while accounting for study limitations. In my past work, I have identified different pitfalls lying in wait along these steps (Fig. 1):

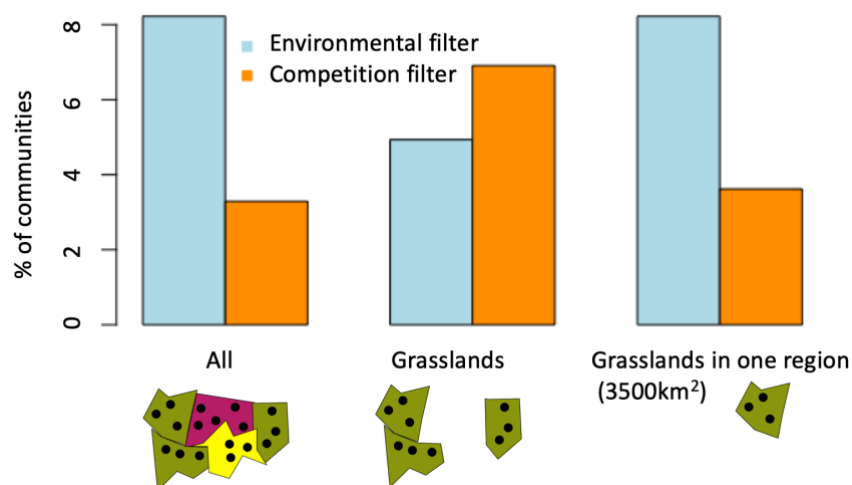
**(1) Study design** – A major challenge of the filtering framework is to define an appropriate database. This requires choosing a spatial scale, an environmental scale, and a specific subset of individuals and species that are appropriate for the research question (Levin, 1992; Meyer, Jopp et al., 2010; Meyer, Schiffrers et al., 2010). The basic underlying question is ‘what defines a community?’ (Magurran, 2004): At which spatial and environmental scales should communities be compared? Which organisms should be studied as entities of one community? Although it has already been shown that the consideration of different spatial and phylogenetic scales can reveal contrasting assembly patterns (Cavender-Bares, Keen et al., 2006; Swenson, Enquist et al., 2006), little attention has been devoted so far to systematically comparing and quantifying how the choice of specific scales may influence the identification of community assembly processes. The first pitfall is thus to assume that spatial, environmental, and organism-level scale choices have no influence on study results (P1, Fig. 1).



**Figure 3** – Schematic overview of the scale choices and their influence on the species pools’ composition and the focal community plots’ diversity. For example, when the scale constraints include reducing the environmental extent to only grasslands and the organismic scale to only herbaceous species in the lowest stratum, then diversity is calculated by considering only herbaceous species from the lowest stratum in the focal grassland polygon (three community plots and three plant individuals in the figure, Münkemüller, Gallien et al., 2014).

To answer the question “**How strong is the influence of scales on the results and conclusions of the filtering framework?**”, I applied the indirect approach to a range of different field data utilizing different community definitions, diversity indices, and null models.

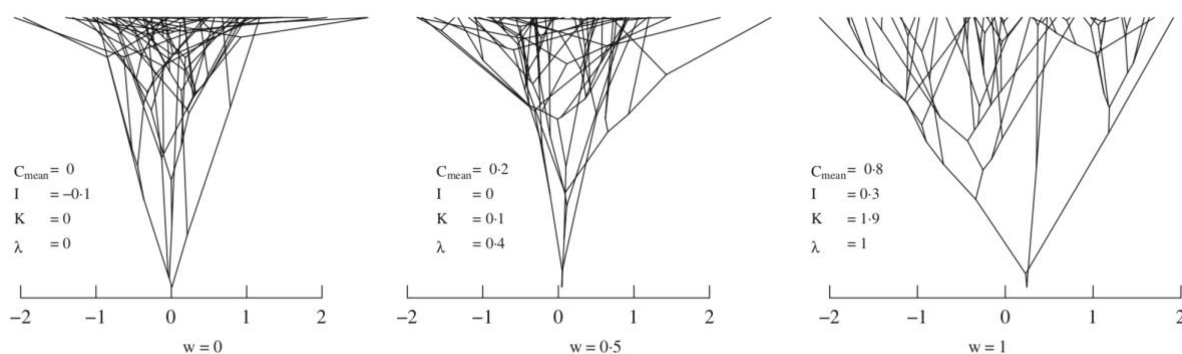
- Spatial, environmental and organism level scales are important. We studied a vegetation survey dataset covering the entire Alps and compared the influence of different scale choices on diversity patterns (Fig. 3, considering different spatial, environmental and phylogenetic scales as well as growth forms and vegetation strata, Münkemüller et al., 2014). Scale choices were decisive for revealing signals in phylogenetic diversity patterns and thus for conclusions on assembly processes (Fig. 4). Notably, changes in scale choices could turn a pattern of limiting similarity (phylogenetic overdispersion) into a pattern of environmental filtering (phylogenetic clustering). We could confirm this result for spatial extent in a study on plant invasion: At fine spatial resolutions, we found a signal of competition (phylogenetic overdispersion). Yet at coarser spatial resolutions, we found a signal of environmental filtering for the same plant metacommunity (phylogenetic clustering, Carboni, Münkemüller et al., 2013).
- Temporal scales are important as well. Together with my PhD student L. Chalmandrier, we investigated bird diversity over spatial and temporal scales. We found that temporal change was more pronounced in Mediterranean regions than in Atlantic regions (Chalmandrier, Münkemüller, Devictor et al., 2015), a result well in concordance with earlier studies showing substantial temporal turnover in bird communities in inland Mediterranean areas due to major changes in land use (Sirami, Brotons et al., 2007).



**Figure 4** – The filtering approach is not robust to scale choices: The same group of grassland communities shows different percentages of significant low diversity (i.e. potential signal of environmental filter) vs. significant high diversity (i.e. potential signal of biotic filter) depending on whether all communities, only grassland communities or only grassland communities in one region are in the considered species pools (the figure is based on analyses from Münkemüller et al., 2014).

**(2) Collecting information** – Trait and phylogenetic diversity are often used as proxies for niche overlap, yet this common practice is being challenged (Cadotte, Albert et al., 2013; Gerhold, Cahill et al., 2015; Li, Ives et al., 2017). A first set of questions with regard to trait diversity is whether we are able to identify and measure the traits of ecological relevance for each ecological filter (Funk, Larson et al., 2017; Mc Gill et al., 2006), whether traits are closely enough linked to species niches (D'Andrea, Ostling et al., 2018), and whether we can avoid

irrelevant traits that might confound the patterns and lead us to spurious conclusions (Kraft, Godoy et al., 2015). Even if we are able to identify the relevant traits, it remains the question whether it is more informative to analyze each trait separately or all traits in combination. The main argument for the former is that different traits may drive different processes, and that analyses should thus be process- and trait-specific (Bernard-Verdier, Navas et al., 2012; Gross, Boerger et al., 2013; Spasojevic, Copeland et al., 2014). On the other hand, ecological niches are multidimensional and, consequently, multi-trait diversity is more likely to capture niche overlap between species across multiple niche dimensions (Kraft et al., 2015). Further, traits are correlated as a result of physiological trade-offs. Ignoring these trade-offs may lead to spurious conclusions (Wüest, Münkemüller et al., 2018). Moreover, the importance of intraspecific trait variability in this approach remains open (Guisan, Mod et al., 2019).



**Figure 5** – Traitgram for different weighting factors ( $w$ ) for the Brownian motion component relative to random trait assignment (i.e. the higher  $w$  the stronger phylogenetic signal should be). Traitgrams arrange species along a continuous trait axis (the x-axis) and connect them with their underlying phylogenetic tree (time on the y-axis). This way, the degree of line crossings in the branches that connect species with their ancestors gives an intuitive picture of phylogenetic signal: The more the lines cross, the more randomly is the trait distributed. As an example, the values of different selected indices of phylogenetic signal (Abouheif's  $C_{\text{mean}}$ , Moran's  $I$ , Blomberg's  $K$  and Pagel's  $\lambda$ ) in relation to  $w$  are displayed at the bottom of each traitgram (Münkemüller, Lavergne et al., 2012).

For phylogeny-based analyses, the assumption is that phylogenetic relatedness is a good proxy for overlap in the multidimensional niche space (Anacker & Strauss, 2016; Burns et al., 2011). However, phylogeny does not always represent relationships of traits that are relevant for species' niches (Blomberg, Garland et al., 2003; Saito, Cianciaruso et al., 2016), and phylogenetic signal of relevant traits should be tested, rather than assumed. It is well acknowledged that conclusions are only valid if the phylogeny captures information about niche, trait or more generally species similarity (Webb et al., 2002). While some authors (Mouquet, Devictor et al., 2012) claim that we need to test for phylogenetic signal, i.e. the tendency of closely related species to resemble each other more than they resemble species drawn randomly from the phylogeny (Blomberg & Garland, 2002), in order to test this assumptions, others (Willis, Halina et al., 2010) call for tests of phylogenetic niche conservatism, i.e. the tendency of species to retain ancestral niches (Harvey & Pagel, 1991; Wiens, Ackerly et al., 2010; Wiens & Graham, 2005). The second pitfall is thus to assume that trait and phylogenetic diversity are always good proxies for species niche overlap (P2, Fig. 1).

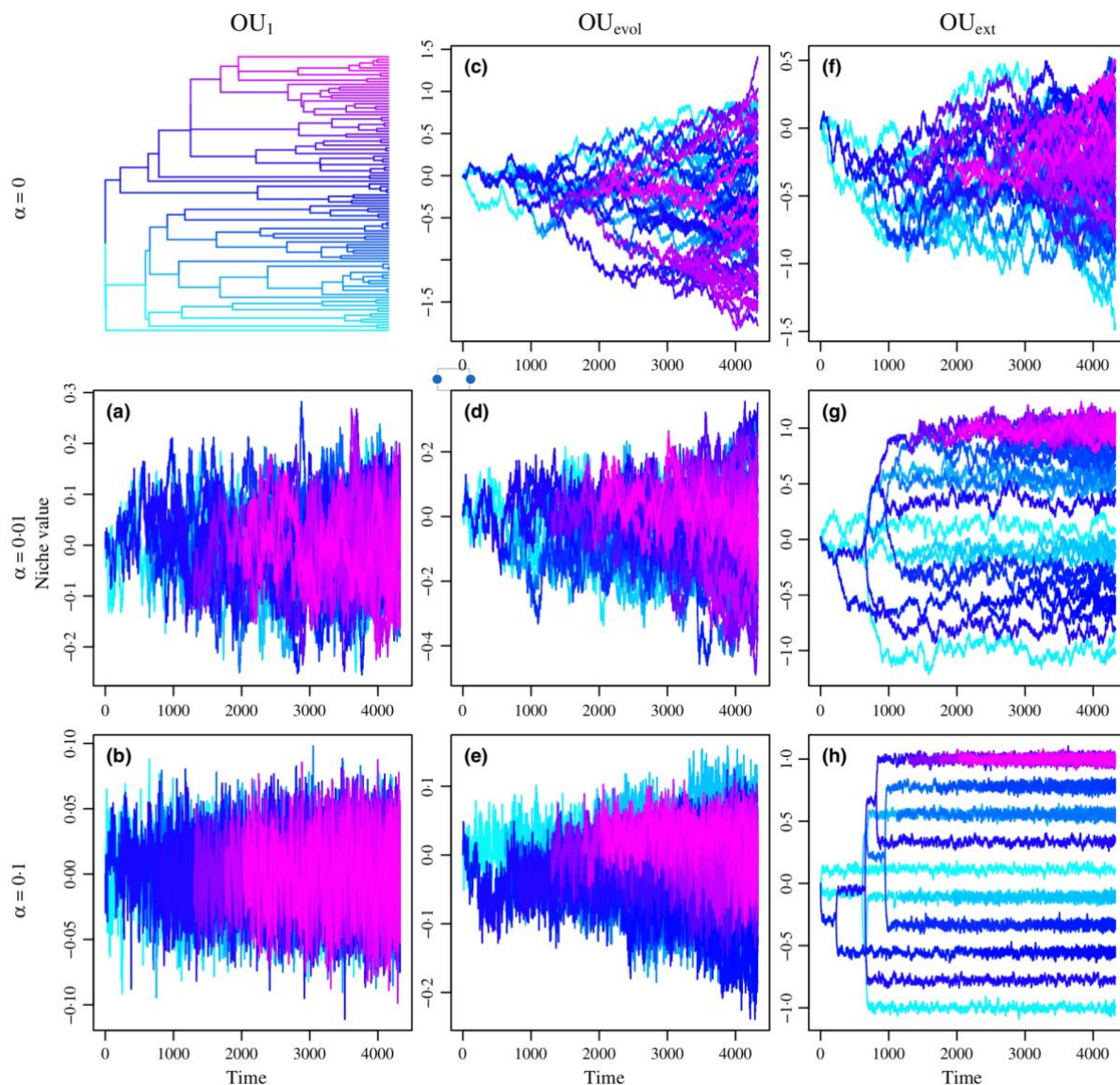
I tested the potential of using phylogenetic diversity in the filtering approach with the so called “virtual ecologist approach” (Zurell, Berger et al., 2010). In this approach, simulated data are

used to mimic real diversity patterns and how they are “virtually” observed. This virtual data is then subjected to statistical analyses, and the results are evaluated against the “true” simulated data. Specifically, I asked “**What is the underlying assumption of using phylogenetic diversity patterns?**” and “**How to best measure phylogenetic signal?**”. I studied phylogenetic signal and phylogenetic niche conservatism using numerical simulations of niche evolution along phylogenetic trees and then applied commonly used indices and tests.

- For the study of phylogenetic signal, we compared the estimated values of indices and the power of the associated tests for different topologies of the phylogenetic trees (number of tips, presence of polytomies, and availability of branch length information) and for evolutionary models with increasingly strong Brownian motion<sup>2</sup> (neutral drift) vs. random trait evolution. Pagel’s  $\lambda$  (Pagel, 1999), an approach based on a Brownian motion process of niche evolution, and Abouheif’s  $C_{mean}$  (Abouheif, 1999), an autocorrelation measure, performed best (Münkemüller, Lavergne, et al., 2012, Fig. 5). However, Blomberg’s  $K$  (Blomberg et al., 2003) was a good choice for simulation studies with simulated data where overall trends were in the focus of interest and measures could be repeated (Münkemüller, Lavergne, et al., 2012).
- For the study of phylogenetic niche conservatism, we assumed that niche conservatism results from constraints on the emergence of niche novelties (Gomulkiewicz & Houle, 2009; Holt, 1996) and simulated niche evolution accordingly with an Ornstein-Uhlenbeck process, which combines a Brownian motion process with selection towards one or several optimal niche values (Butler & King, 2004). Analysing the resulting “virtual” niche data, we found that even under strong niche conservatism species trait overlap can be unrelated to phylogenetic distances and labile niches sometimes lead to a strong relation between niche overlap and phylogenetic distance (Münkemüller, Boucher et al., 2015, Fig. 6). This result highlights that it is not phylogenetic niche conservatism but phylogenetic signal that is the underlying assumption of studies utilizing phylogenetic diversities as proxies for trait similarities.
- Finally, it is also important to note that, if all niche-relevant traits were known and available, phylogenetic proxies would not be needed and the filtering approach could be based on functional diversity. The logic of the demand that phylogenetic signal always needs to be tested before phylogenetic diversity can be used in the filtering approach is thus questionable.

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<sup>2</sup> Brownian motion is a simple continuous stochastic process that is widely used for modeling random behavior that evolves over time.



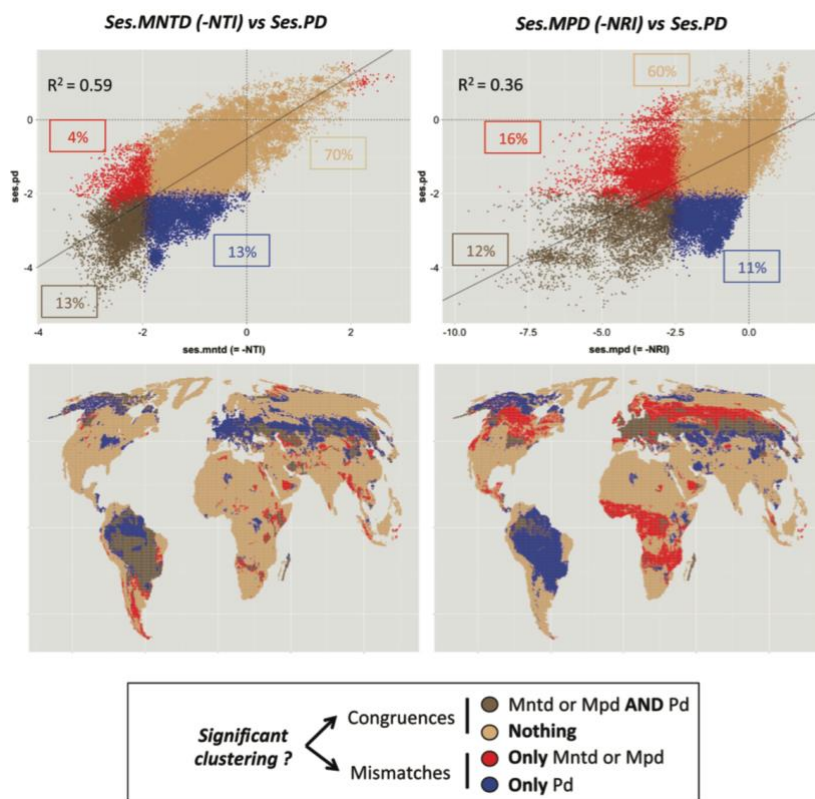
**Figure 6** – Niche evolution over time for an Ornstein-Uhlenbeck (OU) models with a single optimum ( $OU_1$ , left column), OU models with evolving internal optima ( $OU_{evol}$ , middle column) and OU models with multiple external optima ( $OU_{ext}$ , right column). Selection strength towards optima ( $\alpha$ ) increases along rows. The upper left plot shows the phylogeny; the middle and the upper right plot show two realizations of Brownian motion (BM). Colors indicate the position of branches in the phylogeny. When considering only the final distribution of niche values in the tips, then a  $OU_1$  model with strong  $\alpha$  (plot b) can be easily misidentified as a white noise model and an  $OU_{ext}$  model with moderate  $\alpha$  can be easily misidentified as a BM model (plot g, Münkemüller, Boucher, et al., 2015).

**(3) Methodological approach** – It has been demonstrated that different methodological choices can give different answers (Münkemüller et al., 2014; Perronne, Munoz et al., 2017). Thus, pitfalls three, four, and five are to assume that (P3) all supposedly similar diversity indices give the same results, and that the construction of (P4) adequate species pools or (P5) randomization algorithms for testing deviations from expectations is obvious and straightforward (Fig. 1).

I have tested these pitfalls both with the “virtual ecologist approach” and with observed data and asked: “Do different diversity indices give the same answer?”, “Do different species pools and randomizations give the same answer?”.

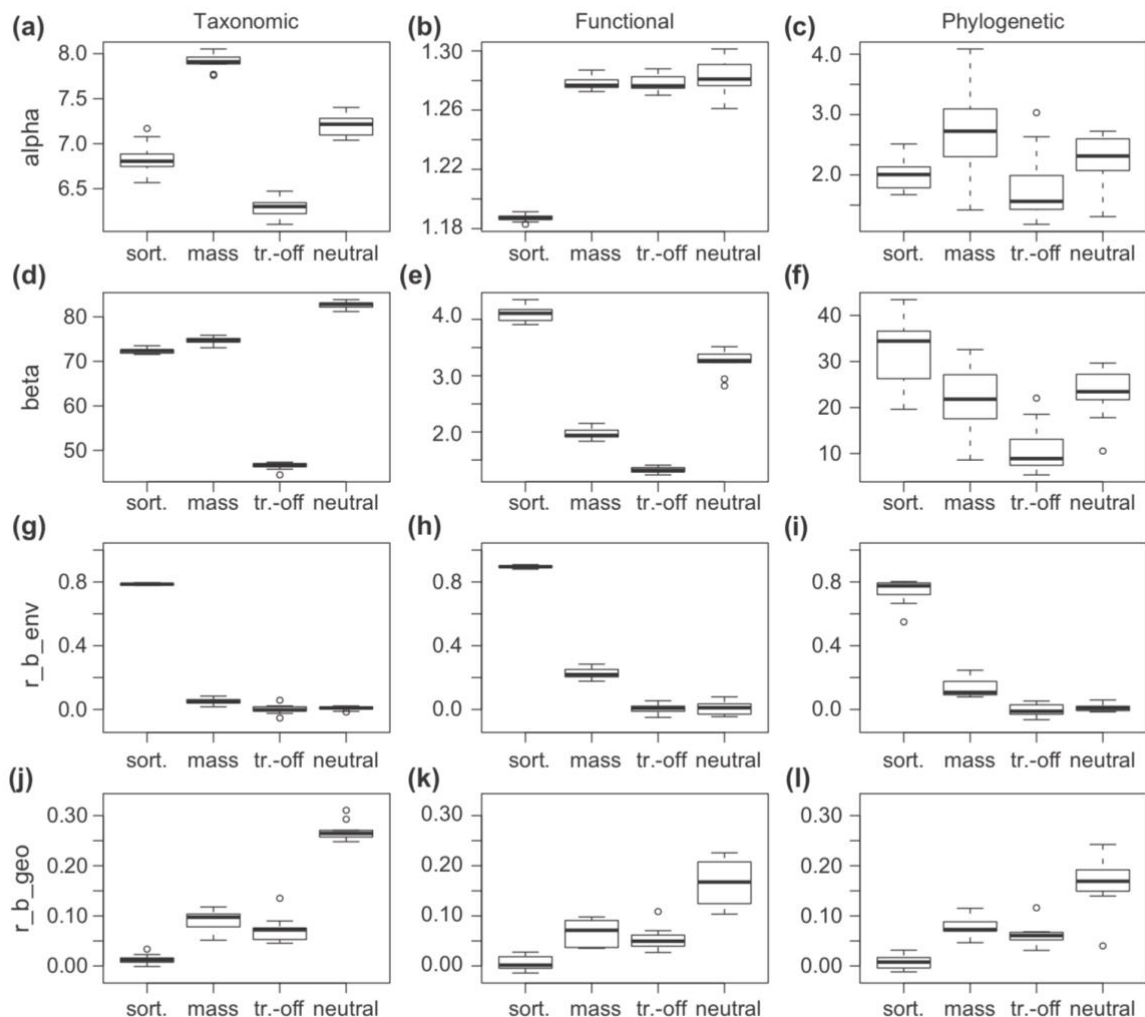


- We investigated the mismatch between different phylogenetic diversity metrics for global carnivoran assemblages. We measured the mismatch between Faith’s phylogenetic diversity ( $PD_{Faith}$ ), which represents the sum of the branch lengths of the phylogenetic tree linking all species of a particular assemblage, the mean pairwise distance between all species in an assemblage (MPD) and the pairwise distance between the closest relatives in an assemblage (MNTD, Fig. 7). The comparisons between studies using one or several of these metrics are difficult because there has been no comprehensive evaluation of the phylogenetic properties each metric captures. In particular it was unknown how  $PD_{Faith}$  relates to MDP and MNTD. Consequently, it is possible that apparently opposing patterns in different studies might simply reflect differences in metric properties. Our results show that MNTD and  $PD_{Faith}$  provide similar information on phylogenetic structure, and respond similarly to variation in species richness and assemblage structure. However, MPD demonstrates a very different behavior, and is highly sensitive to deep branching structure (Mazel, Davies et al., 2016).



**Figure 7** – Phylogenetic structure of carnivoran assemblages. The top graphs represent the relationships between  $ses.PD_{Faith}$  and  $ses.MPD$  or  $ses.MNTD$  together with the  $R^2$  of their linear relationships. The proportion of congruence and divergence are also represented in four groups: whether  $PD_{Faith}$  and MPD (or MNTD) show congruent (significant/non-significant clustering: dark and light brown dots, respectively) or diverging results (only significant  $PD_{Faith}$ /only significant MPD (or MNTD); blue and red dots, respectively). Bottom graphs show the spatial structure of these four types of assemblages (Mazel et al., 2016).

- In order to be able to compare mismatches between indices with a known truth we studied simulated species' assemblages that emerge under various landscape structures in a spatially explicit individual-based model with contrasting, predefined assembly processes ("virtual ecologist approach"). We focused on four assembly processes (species-sorting, mass effect, neutral dynamics, and competition colonization trade-off) and investigated the emerging species' distributions with varied diversity indices measured at different spatial scales (alpha, beta, and gamma) and for different diversity facets (taxonomic, functional and phylogenetic). We found that (i) the four assembly processes result in distinct spatial distributions of species under any landscape structure, (ii) a broad range of diversity indices allows distinguishing between communities driven by different assembly processes, (iii) null models provide congruent results only for a small fraction of diversity indices, and (iv) only a combination of diversity indices allows identifying the correct assembly processes (Fig. 8, Münkemüller, de Bello, et al., 2012).



**Figure 8** – Different facets and spatial scales of diversity patterns measured based on simulated data with different community assembly rules. Taxonomic, functional and phylogenetic facets are combined with indices for alpha (Rao index), beta (proportional), correlations of beta with environmental distance,  $r_{b\_env}$ , and beta with geographic distance,  $r_{b\_geo}$ . Four different assembly types were investigated: neutral, species- sorting (sort.), mass effect (mass) and trade-off (tr.-off) assemblies (Münkemüller, de Bello, et al., 2012).

- We also found that a signal of competition can be disentangled from an overlaying signal of environmental filtering by adequately constraining the statistical null models. One option is to restrict which species can be drawn into a random community, i.e. allowing only species with matching functional composition (e.g. using Ellenberg indicator values, de Bello, Price et al., 2012) or with matching environmental demands (e.g. using suitability estimates from species distribution models, Chalmandrier, Münkemüller et al., 2013). Another option is to utilize the increasing evidence that environmental filtering influences more strongly presence-absence patterns while competition more strongly influences abundance patterns (Boulangeat, Gravel et al., 2012). We found that using diversity indices that switch on and off the effect of abundance can reveal so-far hidden competition patterns (Chalmandrier, Münkemüller, Lavergne et al., 2015).

**(4) Drawing conclusions** – The most basic shortcoming of the filtering approach is inherent to most observational studies in ecology—it is impossible to deduce in the strict sense a process from an observed pattern. However, given the complexity of nature, ecological research often uses pattern observations to formulate hypotheses or to conclude that a pattern is in (dis)agreement with hypothesized processes. The three major related pitfalls are to assume: (P6) that one pattern can only emerge from one single process, (P7) that one major process dominates the observed pattern, and (P8) that biotic interactions are simple (Fig. 1).

Beyond these pitfalls inherent to the investigated processes, there are further pitfalls associated to unrelated processes but influential to the studied patterns and thus to the final conclusions. A common misconception of the filtering framework is that we can test for a selection of ecological assembly processes while ignoring background factors. In reality, biogeography, evolution, and ecological processes jointly influence species' distributions (Thuiller, Münkemüller et al., 2013). Common pitfalls are to assume that (P9) dispersal and historical contingencies can be ignored and that (P10) communities are at equilibrium (Fig. 1).

Together with my PhD student C. Barros we studied the equilibrium assumption in more detail and specifically asked **“How stable are Alpine ecosystems in face of ongoing global changes?”**.

- In order to account for the full complexity of an ecosystem (e.g. different species, functional groups, traits, habitats), we proposed to utilize n-dimensional hypervolumes for studying ecosystem stability (Barros, Thuiller et al., 2016). This approach describes an ecosystem state as a point in n-dimensional space (e.g. each dimension representing the abundance of a species), and thus allows comparing pre-disturbance with post-disturbance states. For statistical evaluation it is required that each state is sampled multiple times. The resulting point clouds are compared based on three metrics: the distance between centroids, the size of the final hypervolume, and the overlap of the final and initial hypervolume; the larger these metrics are, the more unstable the analyzed ecosystem with respect to the analyzed disturbance.
- We then applied this framework to study drought and climate-change effects on the stability of forest-grassland ecotones (Barros, Thuiller et al., 2018). We found that forests were more stable than grasslands, despite a functional shift towards more warm-adapted species. Overall, unmanaged grasslands were the least stable, suffering the loss of characteristic alpine species.

COMMUNITY ASSEMBLY & INVASION

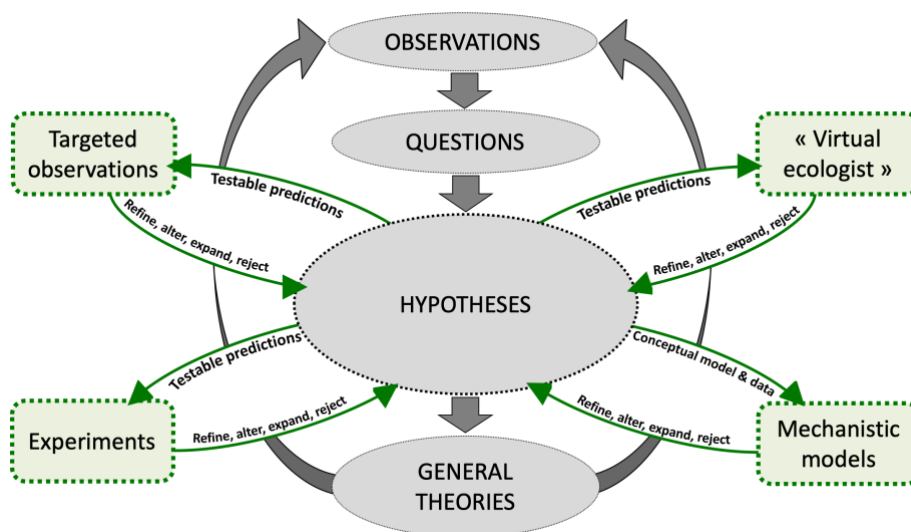
**Table 1** – Six solutions to pitfalls with examples from the literature: In green the pitfall they directly address, in blue the pitfalls that they can indirectly help to solve; Check marks indicate how well-developed solutions are (Münkemüller et al., in press).

<i>Solutions:</i>	<i>Pitfalls:</i>									
	(P1) scale choices not important	(P2) funct./phylo $\approx$ niche overlap	(P3) diversity index is irrelevant	(P4) species pool is obvious	(P5) randomization is obvious	(P6) one pattern = one process	(P7) one process dominates	(P8) one type of interaction	(P9) ignore dispersal & history	(P10) equilibrium assumption
<b>(S1) Consider alternative scales of analysis ✓✓</b>	Green									
• sample at different spatial and taxonomic scales [1]	Green									
• account for temporal (e.g. seasonal) dynamics in sampling design [2]										
• simulate a variation of spatial and taxonomic scales with adapted null models [3]	Green									
• across environmental gradients and variation [4]	Green									
<b>(S2) Measure more dynamic responses ✓</b>	Blue									
• demographic rates as response variable [2]										
• set up experiments [2]	Blue									
• invasive species as “natural experiments” [5]										
• sample time-series [6]	Blue									
<b>(S3) Consider different biodiversity aspects and indices ✓✓</b>		Green	Green							
• traits need to be adequately chosen and grouped [7]		Green								
• integrate trait and phylogenetic diversity [8]		Green								
• weight species by their abundances [9]										
• incorporate intra-specific variability [9]										
• compare richness, regularity and divergence [10]			Green							
• different indices for testing symmetric vs. hierarchical competition [11]										
<b>(S4) Consider alternative species pools and randomizations ✓✓</b>	Blue		Green	Green	Green	Blue	Blue	Blue	Blue	Blue
• use more ecological based species pools [12]	Blue									
• partition diversity across evolutionary periods [13]			Green							
• choose appropriate randomization algorithms [14]	Blue				Green					
<b>(S5) Validate and test the approaches applied ✓</b>	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue
• undertake robustness analyses to identify mismatches between tests [15]										
• apply virtual ecologist approach, with tests of analyses using simulated data [16]	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue	Blue
• account for uncertainty in phylogenies [17]										
<b>(S6) Model multiple processes jointly ✓</b>		Green				Blue	Green	Green	Green	Green
• indirectly with regressions by accounting for non-linear responses [18]										
• estimating relative importance of env. filtering, competition and dispersal [19]							Green			
• explicitly account for allopatric speciation, colonization and local extinction [20]		Green							Green	
• mechanistic models with inverse parameterization based on diversity patterns [21]		Green				Blue	Green	Green	Green	Green

[1] (Cavender-Bares et al., 2006); [2] (Conti, Block et al., 2018); [3] (Münkemüller et al., 2014); [4] (Bryant, Lamanna et al., 2008); [5] (Carboni, Münkemüller et al., 2016); [6] (Campbell & Mandrak, 2017); [7] (Leps et al., 2006); [8] (Cadotte et al., 2013); [9] (Chalmandrier et al., 2015); [10] (Raevel, Violle et al., 2012); [11] (Kunstler, Lavergne et al., 2012); [12] (Lessard et al., 2016); [13] (Pavoine, Love et al., 2009); [14] (Hardy, 2008); [15] (Aiba, Katabuchi et al., 2013); [16] (Münkemüller, de Bello, et al., 2012); [17] (Molina-Venegas & Roquet, 2014); [18] (Gallien et al., 2014); [19] (Van der Plas, Janzen et al., 2015); [20] (Pigot & Etienne, 2015); [21] (Pontarp, Brännström et al., 2019)

### 2.1.4 Solutions and guidelines

In a recent review paper we provide a novel comprehensive and structured overview of the different pitfalls (Münkemüller et al., in press). We outline solutions for each pitfall that we partly developed or advanced ourselves (Tab. 1): This includes methods spanning broad spatial, environmental or phylogenetic scales (Brun, Zimmermann et al., 2019), measuring more dynamic response variables (Conti et al., 2018), considering different biodiversity aspects, indices and null models (Münkemüller, de Bello, et al., 2012), validate the approach applied (Münkemüller & Gallien, 2015), and model multiple processes jointly (Pontarp, Bunnefeld et al., 2019).



**Figure 9** – Conceptual representation of the ongoing scientific process of generating knowledge and general theories with the ecological filtering framework. The process starts by an experience or undirected observation that leads to further reflection about ecologically interesting questions, related hypotheses and testable predictions. To test these hypotheses, we suggest an interplay of studies using observations, experiments, virtual ecologist approaches and/or parameterized mechanistic models to refine, alter, expand and reject the hypotheses on ecological assembly processes. Each of the cycles can repeat many times until a hypothesis becomes well supported (Münkemüller et al., in press, inspired by the figure “The scientific method as an ongoing process” developed by Theodore Garland, University of California, 2015).

Based on the integration of reviewed work we then suggest **step-by-step guidelines** for correctly applying the filtering framework that should result in better interpretable results in community ecology (Münkemüller et al., in press):

(1) Translate research question(s) into specific hypotheses and testable predictions. The expected patterns in support of each hypothesis must be identified *a priori*, and each hypothesis should be tested against each of these predetermined patterns (Fig. 9, solution S4, Tab. 1).

(2) Assemble all data necessary to answer the research question (across scales and diversity facets) but not more (S1, S3). Importantly, use existing naturalist knowledge to decide on ecologically relevant traits. Including extraneous species or irrelevant traits, or conducting the analysis at an inappropriate scale can obscure or distort any signal in the diversity patterns.

- (3) Measure dynamic response variables in a spatially explicit context and consider complementing with targeted experiments if the research question and setting allow for it (S2). This seems especially important when focusing on biotic interactions or studying communities that are far from equilibrium.
- (4) Select the diversity metrics most appropriate to the question of interest based on the conceptual framework and existing naturalist knowledge (S3).
- (5) Choose species pools and randomization techniques such that null models only break the pattern to be tested and not additional patterns (S4). If this is not possible, use a combination of tests that together allow an unbiased answer to the research question. Test the sensitivity of this methodological choice and interpret in consequence (S5).
- (6) If possible, test for the reliability and power of the chosen approach with simulated data (S5).
- (7) Test whether signals identified as significant are congruent across the *a priori* identified relevant patterns for each research hypothesis and always interpret them together (Fig. 9, S6).
- (8) If your research question is complex, it may be necessary to build and parameterize a mechanistic simulation model that embraces the underlying complexity and allows disentangling the different drivers (S6).
- (9) Remember that studying causal processes in the strict sense always requires an experiment and accordingly report results of pattern analyses with the necessary care.

### 2.1.5 Conclusions

If we are to fully exploit the filtering framework for a better understanding of community assembly, we need to:

- ensure we rely on the solutions provided for most of the known pitfalls and follow the guidelines suggested for good scientific practice, and
- improve current solutions that begin to accommodate multiple confounding processes, more complex biotic interaction types, and different spatial scales.

Adapting the filtering approach to circumvent traditional pitfalls, account for uncertainty, and accommodate new data – all while retaining core fundamental ideas – holds promise to significantly improve our understanding of the ever-widening definition of the ecological community.

### 2.1.6 Perspectives

Novel methods, theoretical advances, and newly available data offer opportunities, but also pose challenges to the study of community assembly. Their application for inferring assembly rules from diversity patterns has just started. While broad-scale testing remains to be undertaken, we highlight here general ideas and the potential benefits to community assembly research in each of these areas:

- One strong, and certainly in most cases wrong, assumption of the filtering approach is that all species interact with each other, and based on the same underlying processes. Species distribution modelling techniques that allow estimating the covariation of species while modelling their response to abiotic variables may help to relax this assumption (e.g. joint species distribution models, Clark, Gelfand et al., 2014; Pollock, Tingley et al., 2014). The estimated residual covariance matrices in JSDMs can result from model misspecification, influential but hidden abiotic variables, but could potentially also result from biotic interactions and thus be a signal of assembly rules (Ovaskainen, Tikhonov et al., 2017; Tikhonov, Abrego et al., 2017; Zurell, Pollock Laura et al., 2018). Within the ANR project GAMBAS I am local PI and leader of a work package that aims to better understand the ecological meaning of these residual covariance matrices. Together with the GAMBAS PhD G. Poggiato, we currently prepare a short paper on the interpretation of JSDMs residual covariance matrices through the lens of biotic community assembly processes. The message is clear. In comparison to single species distribution models, JSDMs can improve co-occurrence and conditional predictions. However, JSDMs still ignore the effect of biotic interactions on the mean probability of occurrence (i.e. the  $\beta$ -parameters in the deterministic part of the regression) and thus confound the effect of species interactions with the environmental effects. Consequently, just like SDMs, JSDMs can only retrieve the center of the realized niches. Depending on the context, the estimated distributions of  $\beta$ -parameters around the mean can be influenced by biotic interaction. Thus, in the most optimistic scenario, the residual covariance matrices of JSDMs can contain some trace components of biotic interactions. We conclude that the challenge of disentangling the fundamental from the realized niche is not met by currently applied JSDMs (Poggiato, Münkemüller et al., in prep.).
- New types of data are becoming rapidly available. One example is amplicon-based DNA analysis of environmental samples (i.e. metabarcoding data, eDNA, Creer, Deiner et al., 2016; Taberlet, Prud'homme et al., 2012). These data provide new information on the potential presence of organisms for calculating diversity patterns (Calderón-Sanou, Münkemüller et al., 2020; Martínez-Almoyna, Thuiller et al., 2019). Combined with databases or expert knowledge on functional traits, phylogenies or trophic meta-webs (containing information on all predator-prey interactions in a regional pool of present taxa) these diversity patterns allow to better approximate niche overlap in communities. The great advantage is the coverage of almost all prokaryote and eukaryote species present in a sample (or taxonomic units with lower resolution, depending on the reference libraries). While promising, eDNA data also bring new uncertainty with respect to traditional surveys, such as amplification errors, DNA degradation, and contamination and barcode assignment (Calderón-Sanou et al., 2020). Methodological advances in this area will allow studying entirely new types of ecosystems. For example, by combining soil metabarcoding with information from trait databases one can study the interplay of fungi and bacteria with nematodes and plants.
- Finally, I am interested in developing a conceptual framework integrating plant soil feedbacks (PSF, see next chapter) and community assembly theory in order to better understand

functional plant community composition, diversity, and functioning in local communities. I am especially interested in how the coupled plant-soil system responds to above or belowground changes induced by climate and land-use change. The idea would be to explicitly include PSF in the simulation models I used for the “virtual ecologist” approach in earlier projects (Münkemüller, de Bello, et al., 2012; Münkemüller & Gallien, 2015) and to develop theoretical predictions to PSF driven filters of symmetric competition, hierarchical competition, and facilitation (see Tab. 2 for first ideas).

**Table 2** – Conceptual links of plant soil feedbacks and community assembly theory and its proposed ecological filters in the process-based simulation model. BIF: Biotic interaction filter, Symmetric competition: x has the same competitive effect on y as y on x, Hierarchical competition: The species with the best adapted functional traits win the competition, FD: functional diversity, CWM: Community weighted means.

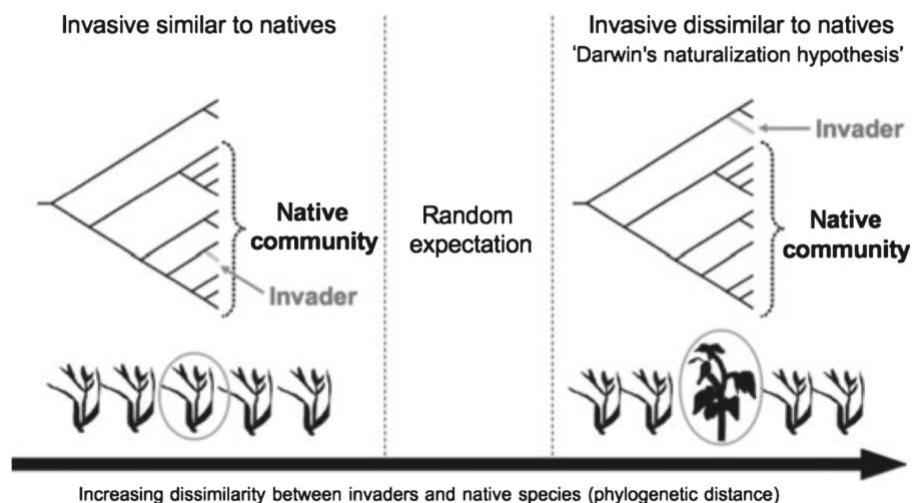
Simulated process	Plant soil feedback	Ecological filters (Expected patterns)
Direct competition	Soil antagonists	BIF: Symmetric competition through niche differentiation (high FD)
Competition for nitrogen	Fungal vs. bacteria based nutrient cycle	BIF: Hierarchical competition (specific CWM, low FD)
	Narrow vs. broad functional diversity	BIF: Symmetric competition through niche differentiation (high FD)
Competition for light	Soil mutualists	BIF: Facilitation (? , first assumption: low FD)
	-	BIF: Hierarchical competition (specific CWM, low FD)
Influence of climate	-	Environmental filter (specific CWM, low FD)



## 2.2 How to predict invasion success from diversity patterns?

### 2.2.1 Context

A major threat to biodiversity is the anthropogenic displacement of species when followed by permanent establishment, rapid colonization, and uncontrolled spread (Pyšek, Richardson et al., 2004). Biological invasions modify native diversity, ecosystem functioning and associated nature's contributions to people, and are thus a major component of global change (Vitousek, Mooney et al., 1997). Predicting and understanding invasion processes and patterns is essential to counteract their impacts (Gallien, Münkemüller et al., 2010). The search for common patterns among different invasion events has focused on three questions including the intrinsic properties of invaders ("species invasiveness"), the propensity of natural communities to be invaded ("community invasibility"), and the relationship between invaders' distributions and environmental factors (Rejmanek, Richardson et al., 2005).



**Figure 10** – Conceptual diagram depicting classic hypotheses about species naturalizations and phylogenetic relatedness. The bold arrow at the bottom represents a gradient of species dissimilarity (phylogenetic distance) between invasive and native species. Left panel illustrates the hypothesis that invaders tend to be more closely related to native species than expected under random expectation. Right panel depicts the actual Darwin's naturalization hypothesis that immigrant species that are phylogenetically unrelated to the native species will be more likely to naturalize because they may harbor different traits and possibly exploit distinct niches than native species. In both panels, the invasive species is represented in grey (grey branch in the phylogenetic tree or grey circle in the drawing of hypothetical community, Thuiller, Gallien et al., 2010).

### 2.2.2 Darwin's naturalization conundrum

Already Darwin posed two hypotheses to explain invasion success that integrate questions of species invasiveness and community invasibility and are seemingly contradictory ("Darwin's naturalization conundrum", Diez, Sullivan et al., 2008). On the one hand, introduced species that are dissimilar to local communities should be more successful because they can exploit unfilled ecological niches in native communities (Fig. 10, "Darwin's naturalization hypothesis"). On the other hand, immigrant species that are similar to local communities

might have a better chance to naturalize because they share similar pre-adaptations to local environmental conditions with allied species (Fig. 10). Both hypotheses make testable predictions: if successful invaders show distant niches to natural communities, then invasion success should be driven by niche differentiation and niche gap-filling. In contrast, if successful invaders are very similar to natural communities, then environmental pre-adaptation should be the dominant process. First tests of these opposing hypotheses relied on patterns of taxonomic relatedness of the invasive species with native species, with the assumption that closer related taxa show more niche overlap (Proches, Wilson et al., 2008). These comparisons of taxonomic relatedness were very rough tests of niche overlap. With the background of the filtering framework from community ecology (as described in detail in section 2.1), we thus asked whether adapted techniques from the filtering framework with more refined indices of phylogenetic and functional diversity would not improve these tests (Thuiller et al., 2010).

**Research questions are:**

- Can we adopt the filtering framework to invasion ecology? (3.1.3)
- Can “solutions” from community ecology improve invasion studies? (3.1.4)

**2.2.3 The filtering framework – an adaptation to invasion ecology**

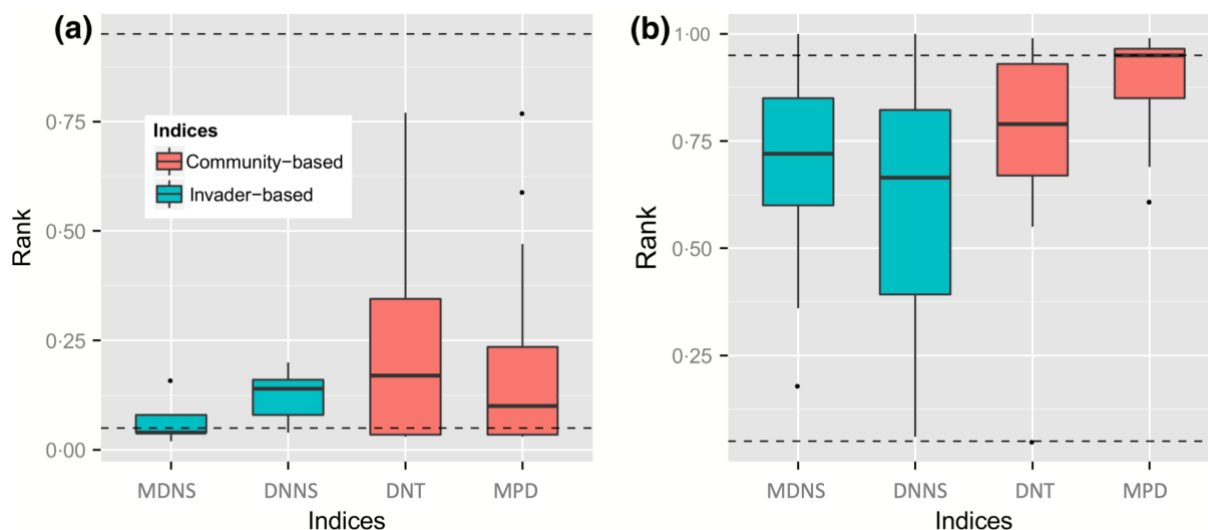
The adaptation of techniques from the filtering framework in community ecology gave rise to a new sub-field: invasion community ecology (Gallien & Carboni, 2017). In one of our own papers we specifically highlighted the value of using not only phylogenetic information but also functional trait information to describe species niche overlaps. In addition, we suggested a set of diversity metrics derived from the  $\alpha$  niche concept to measure invaders relatedness to native communities (Thuiller et al., 2010). The  $\alpha$  niche of a species is a community-scale measurement that quantifies the resources exploited by this species in comparison with the resources exploited by co-existing species (Pickett & Bazzaz, 1978). In other words, the  $\alpha$  niche describes the niche differentiation between a focal species and the other community members. It can be applied to functional and phylogenetic dissimilarities. For example, Ackerly & Cornwell (2007) define the  $\alpha$  trait niche as the deviation of the trait value of a focal species from the community average trait value (i.e. the community weighted mean, CWM). A large  $\alpha$  trait niche means that the considered functional traits of the focal species are very different from the traits of the rest of its community.

In order to confront these new ideas to data with a known truth we used again the “virtual ecologist” approach. For this, we developed a simulation model that integrates processes leading to correlated taxonomic, phylogenetic and functional patterns and processes of both community assembly and invasion. VirtualCom is a mechanistic individual-based simulation model (Münkemüller & Gallien, 2015). It allows simulating diversity patterns of communities with pre-defined assembly and invasion over time. Based on community diversity indices or invader  $\alpha$  niche indices, we can test whether these patterns contain signals of the simulated community assembly and invasion processes.

More specifically, each simulation of VirtualCom starts with the generation of a species pool through a trait evolution process on a simulated phylogeny. In a second step and over a few

to hundreds of years, native communities assemble from the species pool of natives according to the chosen assembly rules. The choice of the number of simulated years should depend on a pre-analysis that determines the time period necessary to obtain stable diversity patterns. In a last step, invasions can be added by allowing invasive species from the species pool to enter communities for some additional years. The model does not account for dispersal between communities. Using simulations from this model we asked **“Does the filtering approach detect invasion processes as easily as community assembly processes?”**

- We assembled native communities either under an environmental filtering or under a competition assembly scenario. Then, the stabilized native communities were invaded following the same assembly processes. Based on species functional traits, we tested two types of indices: on the one hand, indices reflecting the diversity of the community as a whole (community-based); on the other hand, indices measuring the functional distance between the invader and all other species (invader-based  $\alpha$  niche indices). The performance of the indices was then evaluated with null models, where the rank of the observed diversity within the null diversity distribution represents the significance of diversity signals.
- We found that in the environmental filtering scenario, an index based on the invaders (i.e. mean distance to the native species, MDNS, Fig. 11a) outperformed all other indices. However, in the competition scenario a diversity index based on the entire community (i.e. mean pairwise distances across all community members, MPD, Fig. 11b) performed best. These first results suggested a strong need for a comparative evaluation of index performance in order to identify those indices that allow the detection of ecological processes under a variety of scenarios.

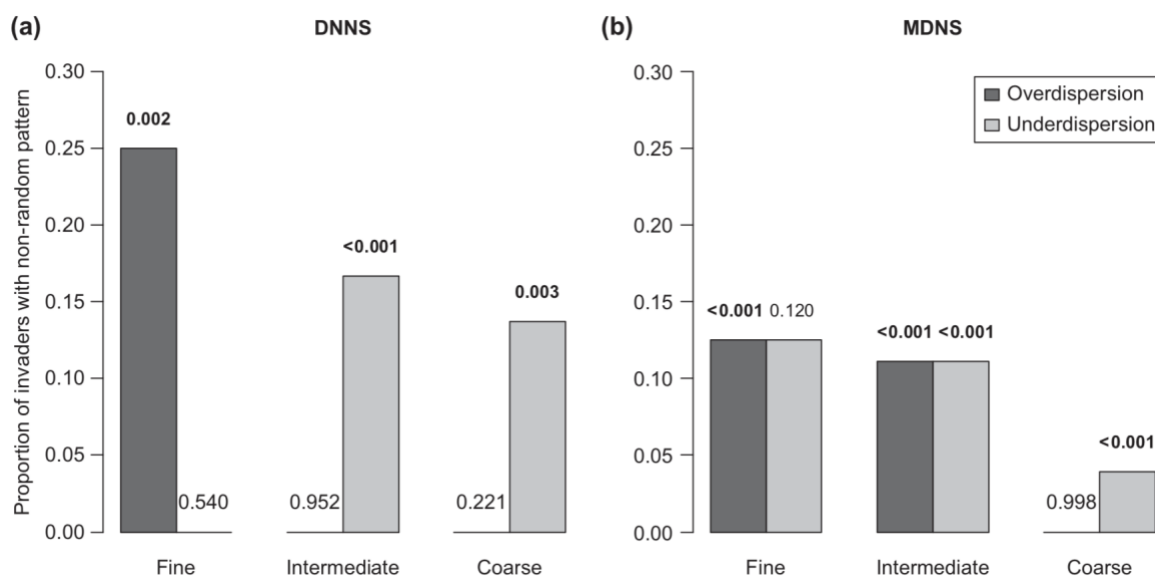


**Figure 11** – Ranks of community-based vs. invader-based diversity indices under environmental filtering (a) and competition (b). The theoretical expectations are clustering (low ranks) under environmental filtering and overdispersion (high ranks) under competition processes; MDNS: mean distance to the native species, DNNS: distance to the nearest native species, DNT: distance to the nearest taxon, MPD: mean pairwise distance between all species (Münkemüller & Gallien, 2015).

### 2.2.4 Applying solutions from community ecology

As in community ecology, the filtering approach is fraught with problems in invasion ecology. This led to the results of the first studies being inconsistent and not generalizable (Thuiller et al., 2010). We argued that most of the inconsistencies arise from discrepancies in the applied scales, metrics and analytical tests, and not from different model organisms and different ecological contexts (Thuiller et al., 2010). Given the similarities of this assessment to the review of pitfalls and solutions for the filtering framework in community ecology (Tab. 1), I will order my past work on invasion success along the identified solutions for community ecology to answer the question **“Can ‘solutions’ from community ecology improve invasion studies?”**

**(1) Consider alternative scales of analysis (Solution 1)** – The apparent contradiction between the two hypotheses of Darwin’s naturalization conundrum could only be a matter of spatial scale. Theoretically, we anticipate more niche dissimilarity among species (overdispersion) at finer resolutions where biotic interactions take place because of the effect of interspecific competition/facilitation or shared natural enemies. At coarser scales with important environmental turnover we rather anticipate greater similarity (clustering) among species because of shared resource requirements. We thus asked: **“Is spatial resolution the key to reconciling apparently contrasting hypotheses and empirical results in the field of invasion ecology?”**

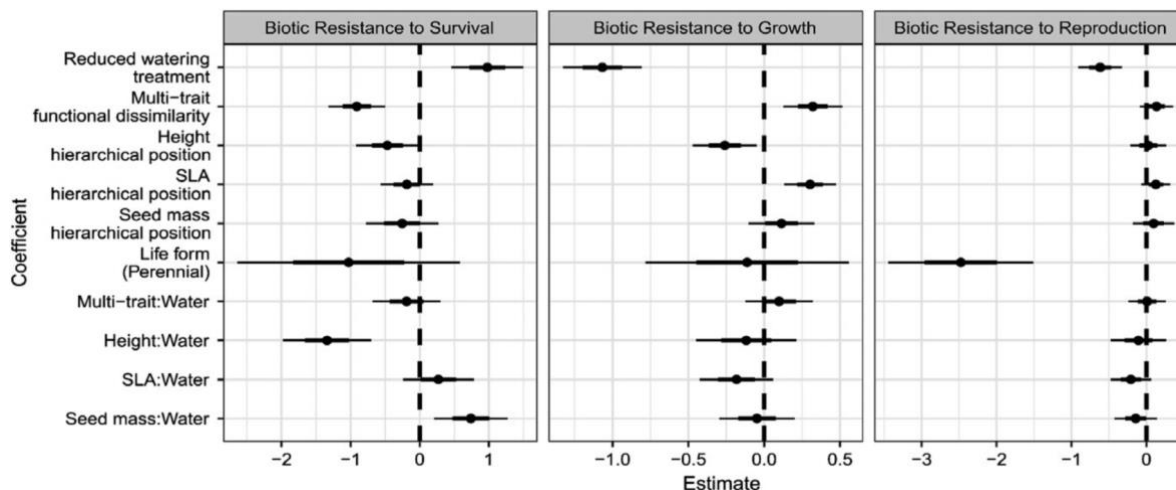


**Figure 12** – Proportion of invaders for which phylogenetic distance of the invader to the native community deviated from random patterns. P-values on top of the bars are obtained by combining the p-values of randomization tests for each single invader through a Fisher’s test. Bold type indicates overall significant deviations from random expectations (i.e. across invaders). In each panel sampling resolutions from left to right are 4 m<sup>2</sup>, 64 m<sup>2</sup>, and ca. 35 km<sup>2</sup>; DNNS: distance to the nearest native species, MDNS: mean distance to the native species (Carboni et al., 2013).

- We used phylogenetic relatedness as a measure of niche overlap and tested the effects of sampling resolution in highly invaded coastal plant communities in Italy (Carboni et al., 2013). At spatial resolutions fine enough to detect signatures of biotic interactions, we find that most invaders are less related to their nearest relative in invaded plant communities than expected by chance (phylogenetic overdispersion, Fig. 12). This result is congruent with a signal of biotic exclusion at fine scales. Yet at coarser spatial resolutions, native assemblages become more invulnerable for closely-related species as a consequence of habitat filtering (phylogenetic clustering).
- In a more comprehensive study over a larger region, with a refined quantification of invasion success and with added measures of functional diversity, we could confirm these results (Carboni et al., 2016). Using permanent grasslands across France (50 000 vegetation plots, 2000 species, 130 aliens) and building on Rabinowitz's classification to quantify invasion success (along the axes of "regional distribution", "local abundance" and "niche breadths"), we showed that phylogenetic and functional similarities of invaders to natives were the most important correlates of overall invasion success compared to intrinsic functional characteristics and introduction history. Results contrasted between spatial scales and axes of invasion success. Widespread and common aliens were similar to co-occurring natives at coarse scales (indicating environmental filtering), but dissimilar at finer scales (indicating local competition). In contrast, regionally widespread but locally rare aliens showed patterns of competitive exclusion already at coarse scale.

**(2) Measure more dynamic responses (S2)** – Abundances, or even more refined invasion spread estimates, are relatively coarse indicators of invasion success. We hypothesized that it would be more informative to study demographic response variables. On the one hand, smaller effects that do not express in significant abundance differences may be revealed at the level of demographic variables, such as growth rate. On the other hand, identifying the demographic stages on which invasion success depends most improves our understanding of underlying mechanisms and may allow developing more refined management strategies. We thus asked **"Which invader traits influence the biotic resistance of native communities most? And at which demographic stages?"**.

- Based on a mesocosm experiment with 25 alien species invading native plant communities, we studied the resistance of native communities to different invaders (Conti et al., 2018). Each invasive species was grown with and without the native community under two watering treatments (regular and reduced). We measured biotic resistance as the difference in performance of invasive individuals grown with and without the community in terms of their survival, growth, and reproduction. We quantified overall functional dissimilarity between invasive individuals and native communities based on the combination of plant height, specific leaf area, and seed mass. Then, assuming each of these traits is also potentially linked to competitive ability, we measured the position of invaders on trait hierarchies. While height is positively correlated with competitive ability for light interception, conservative leaf and seed characteristics provide greater tolerance to competition for other resources. Finally, we quantified plastic trait shifts of invasive individuals induced by competition.

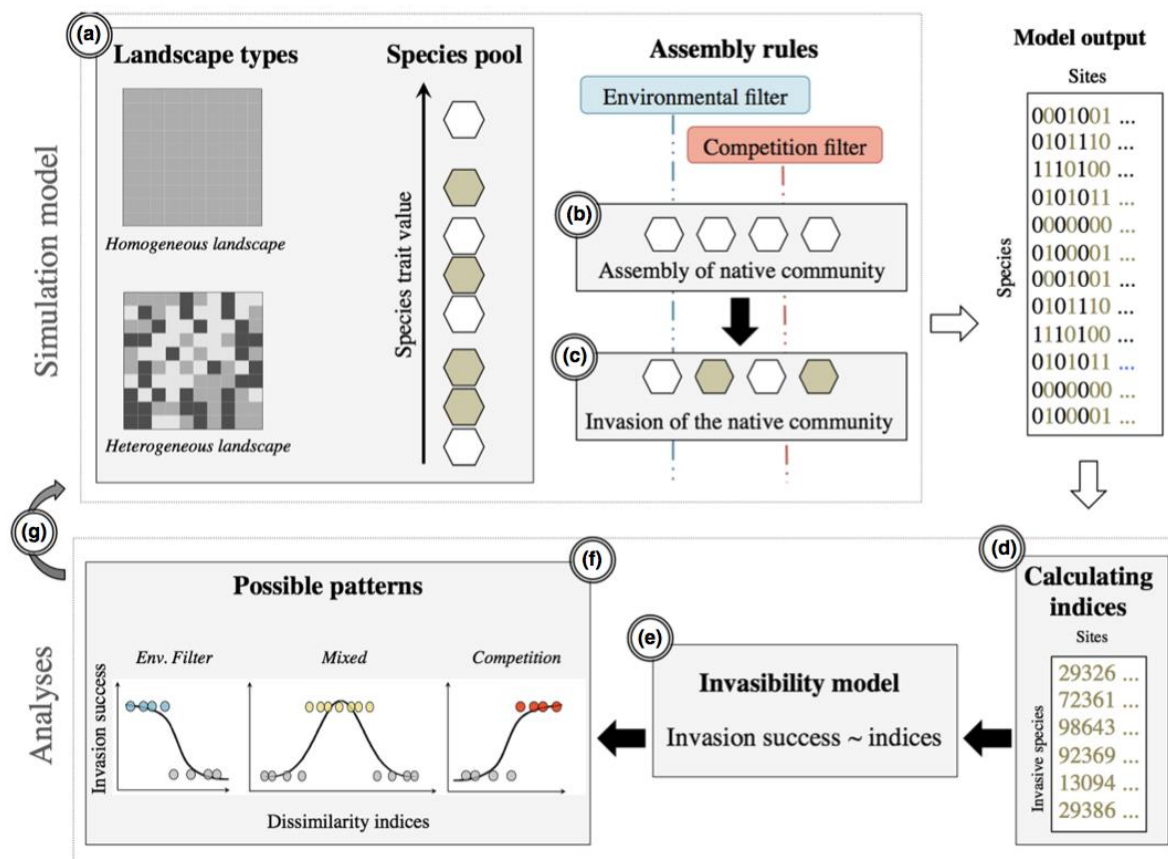


**Figure 13** – Biotic resistance of the native community to invasion: Effect sizes for fixed factors in the linear mixed effect models of survival, growth, and reproduction plotted on the standard deviation scale. Biotic resistance is calculated as the percentage reduction in success in terms of survival, growth, and reproduction of the invasive individual in the native community pots compared to the average success of the invasive individuals growing alone. Models were fitted to the multi-trait functional dissimilarity, plant height hierarchical position, specific leaf area (SLA) hierarchical position, seed mass hierarchical position, and their interaction with the watering treatment. For example, a high multi-trait functional dissimilarity decreases resistance to survival, increases resistance to growth, and has no significant effect on resistance to reproduction (Conti et al., 2018).

- We found that the native community repelled functionally similar invasive individuals better than functionally dissimilar invaders by lowering the invader’s survival rate (Fig. 13). Simultaneously, shorter ornamental individuals with larger specific leaf areas were less tolerant to biotic resistance from the native community during growth, although the effect of trait hierarchies often depended on watering conditions (Fig. 13). Finally, invaders with more competitive traits were able to overcome biotic resistance from native communities also through competition-induced plastic trait shifts (Conti et al., 2018).

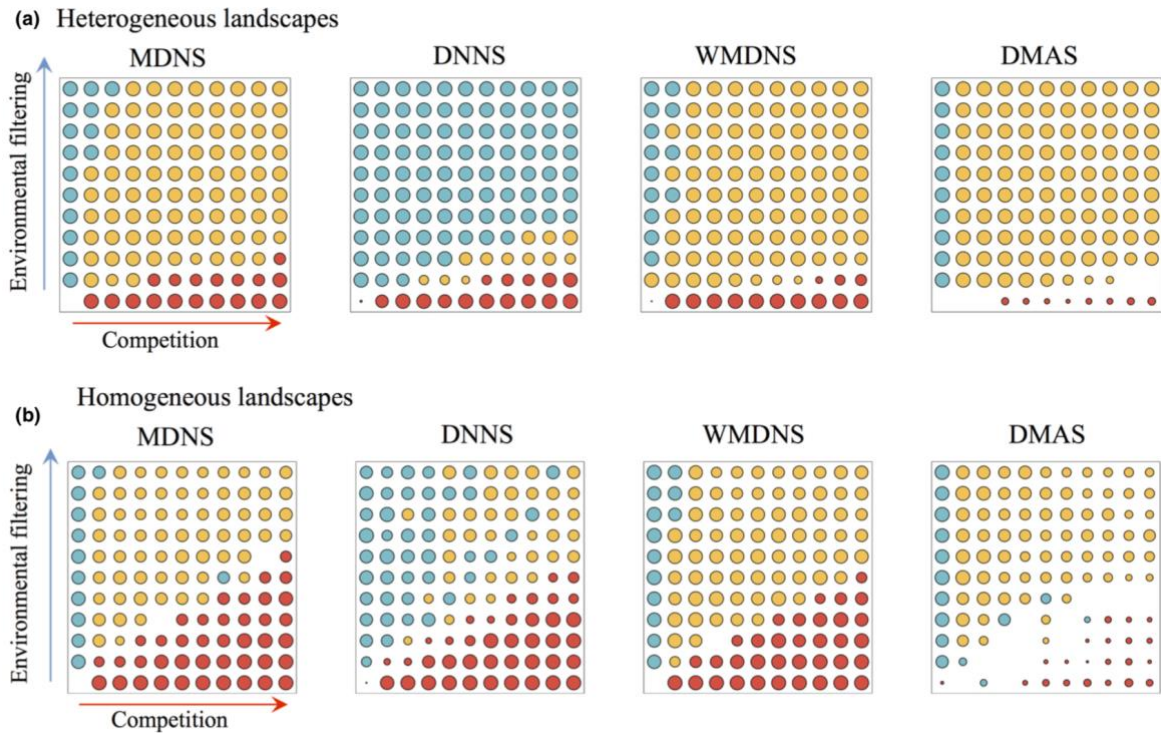
**(3) Consider different biodiversity aspects and indices (S3) & Validate and test the approaches applied (S5)** - The toolbox of indices and statistical approaches developed to test for drivers of invasion success (Thuiller et al., 2010) has for long been widely applied without a thorough evaluation. Using the virtual ecologist approach (Zurell et al., 2010), we asked: **“How do the different diversity indices perform in disentangling environmental from biotic filters?”**, **“How sensitive is the method to common biases in field data?”**.

- We based our study on VirtualCom (Fig. 14, section 3.1.3 for a short model description). To account for environmental heterogeneity, we created two contrasting landscapes. A landscape was defined as a set of 99 communities. The homogeneous landscape contained communities within the same environmental conditions, while the heterogeneous landscape contained an equal representation of three distinct environmental conditions (Gallien et al., 2014).



**Figure 14** – Schematic description of the simulation model VirtualCom and the statistical analysis of the “virtual ecologist” approach applied to test different  $\alpha$  niche indices. The simulation model can be described in three steps: (a) the creation of landscapes and species pools (native species are represented by white hexagons, invaders by grey hexagons), (b) the assembly of the native communities according to the parameterized assembly rules (environmental filtering, competition), and (c) the invasion of these communities. The statistical analyses consist of: (d) calculating dissimilarity indices for both successful and unsuccessful invasions, (e) regressing the invader success on the dissimilarity indices, and (f) interpreting regression results: environmental filtering should result in an inverse s-shaped relation between dissimilarity and invasion success, competition should result in an s-shaped relationship and combining the two processes should result in a hump-shaped relationship. Finally, (g) conclusions can be compared with the simulated assembly rules (Gallien et al., 2014).

- We plotted the strength of the true, simulated process on the x and y axes and the most common conclusions from the regression model as the colors of points (red=competition, blue=environmental filtering, yellow: jointly acting filters). We found that the best performing  $\alpha$  niche index (i.e. the one that best distinguished between simulated processes) was the mean distance to the native species (MDNS, the average functional distance between the invader and all the species of the community), especially in heterogeneous landscapes (Fig. 15, Gallien et al., 2014).

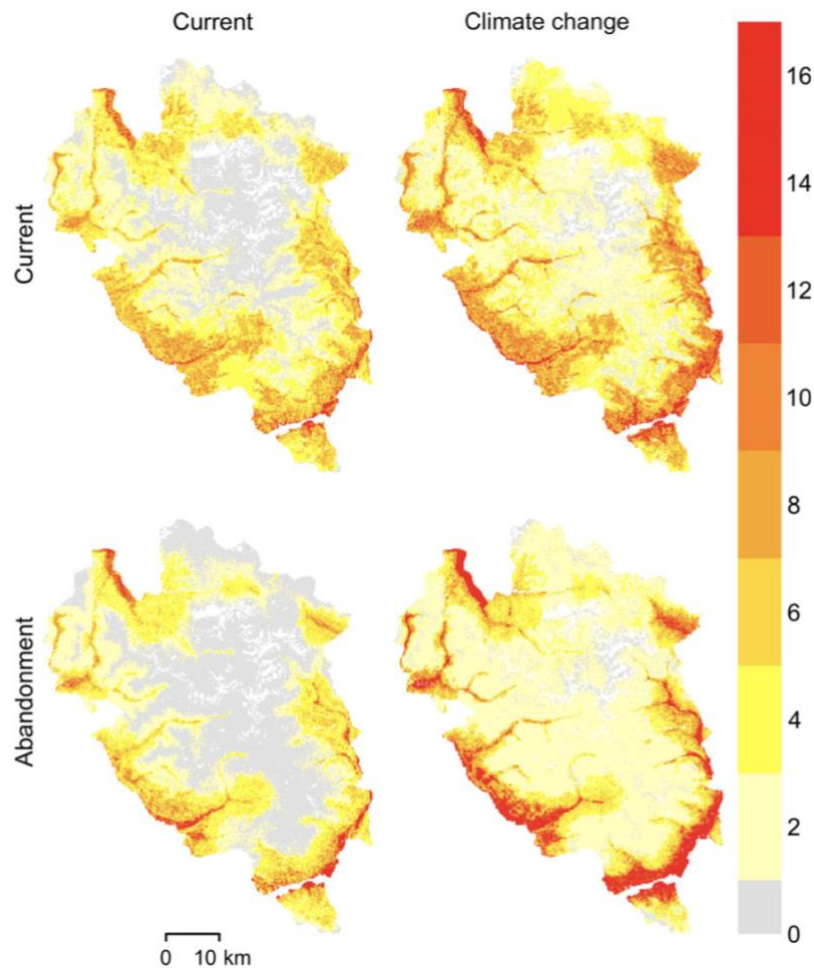


**Figure 15** – Performance of different  $\alpha$  niche indices for different combinations of simulated competition strength vs. environmental filtering strength and heterogeneous vs. homogeneous environments. The x and y axes represent the simulated and thus the true underlying assembly rules. The colors of each circle show the most common conclusions from the regression models, red for competition (i.e. more invasion success when native species are functionally different: positive linear regression coefficient), blue for environmental filtering (i.e. more success when native species are similar: negative linear regression coefficient) and yellow for mixed processes (i.e. more success when the invader is not too similar and not too dissimilar from the natives: bell shaped, negative quadratic regression coefficient). Each circle size represents the proportion of significant relationships from the 30 repetitions of each simulation scenario. MDNS: mean distance to the native species, DNNS: distance to the nearest native species, WMDNS: abundance weighted distance to the nearest taxon, DMAS: Distance to the most abundant species (Gallien et al., 2014).

**(4) Model multiple processes jointly (S6)** – The idea is to build more mechanistic, dynamic models of community assembly that are general enough to include and contrast different ecological theories and processes and can be parameterized inversely with a selection of complementary diversity patterns. The logic of this inverse parameterization, in simple terms, is to run the model across the relevant parameter space, to compare simulated patterns with observed patterns using appropriate summary statistics, and to choose the parameter combinations that lead to the best match between simulated and observed patterns (Grimm, Revilla, Berger, Jeltsch, Mooij et al., 2005; Hartig, Calabrese, Reineking, Wiegand & Huth, 2011). Interpretation of the identified best parameter values allows quantifying the relative influence of the different underlying processes. Very importantly, the parameterized model can also be used to account for transient dynamics and to make predictions for different global change scenarios. Here we asked **“What are the functional characteristics of the invaders that allow for invasion success?”** and **“Which future invasion patterns do we expect under different scenarios?”**.



- We used a spatially and temporally explicit simulation model of vegetation dynamics (FATE-HD) to forecast invasion risks in a protected mountain area in the French Alps under future conditions (Carboni, Guéguen et al., 2018). We combined scenarios of climate change, land-use abandonment, and tourism-linked increases in propagule pressure to test if the spread of invaders in the region will increase in the future. We accounted for interactions among global change components (environmental filters), and competition with the native vegetation (biotic filters).



**Figure 16** – Number of invader plant functional groups predicted to occur across the Ecrins National Park at the end of the FATE-HD simulation (shown for one repetition), after reaching quasi-equilibrium under different combinations of climate (current or climate change) and land-use scenarios (current or abandonment). The baseline scenario (upper left) represents the persistence of the current conditions in the ENP (current climate and current land-use under current propagule pressure, Carboni et al., 2018).

- Our results show that propagule pressure and climate change will interact to increase overall species richness of invaders, as well as their upper elevational limits and regional range-sizes (Fig. 16). Under climate change, woody invaders are predicted to more than double in range-size and herbaceous species to occupy up to 20% of the park area. Land-use abandonment will open new invasion opportunities for woody invaders, but decrease

invasion probability for invasive herbs as a consequence of colonization by native trees. This emphasizes the importance of interactions with the native vegetation either for facilitating or potentially for curbing invasions. Overall, this work highlights an additional and previously underestimated threat for the fragile mountain flora of the Alps already facing climate changes, land-use transformations and overexploitation by tourism (Carboni et al., 2018).

- Using similar approaches with colleagues from our BIODIVERSA project “Who is next?” we focused on new ornamental species that currently only exist in gardens but may invade into the wild in the future. We found that with global change their climatically suitable areas do increase and that an invasion debt is likely accumulating. Restricting cultivation of species can be effective in preventing species spread, irrespective of how the climate develops (Klonner, Wessely et al., 2019). We also identified species with high future naturalization risk. This species list may allow for prioritization of monitoring and regulation of ornamental plants to mitigate the invasion debt (Haeuser, Dawson et al., 2018).

### 2.2.5 Conclusions

Our results demonstrate that the filtering approach can be applied in invasion ecology to disentangle environmental and biotic filters. However, different indices and scale choices strongly influence results. Improvements developed first in community ecology, promise to improve the application of this approach in invasion ecology as well:

- Specifically, biotic resistance of native communities to invasion was important in several field studies, highlighting the need to identify the relevant scale for these interactions.
- It also seemed highly valuable to use invasion success indicators that are more informative than only presence-absences or abundances.
- Finally, we have shown that it is possible to combine invasion community indices with more classical indices such as propagule pressure and that some more advanced statistical approaches allow not only the improvement of understanding but also of building future scenarios.

In sum, the filtering framework is a promising tool of invasion ecology that should ideally be combined with existing tools accounting for additional drivers and allowing to make predictions.

### 2.2.6 Perspectives

I am currently not working anymore with invasive species in the strict sense (but with range limits questions, see section 3.2.1). However, the  $\alpha$  niche concept and metrics could be interesting for other research questions as well.

- Notably, in collaboration with a postdoc in our group we are exploring the utility of this approach for better understanding functional rarity: **Are species that have rare functional traits in some communities, have functionally rare traits in other communities as well?**

**Are species that are functionally rare in the species pool are rare in all local communities as well? Are there communities that select for functional rarity?**

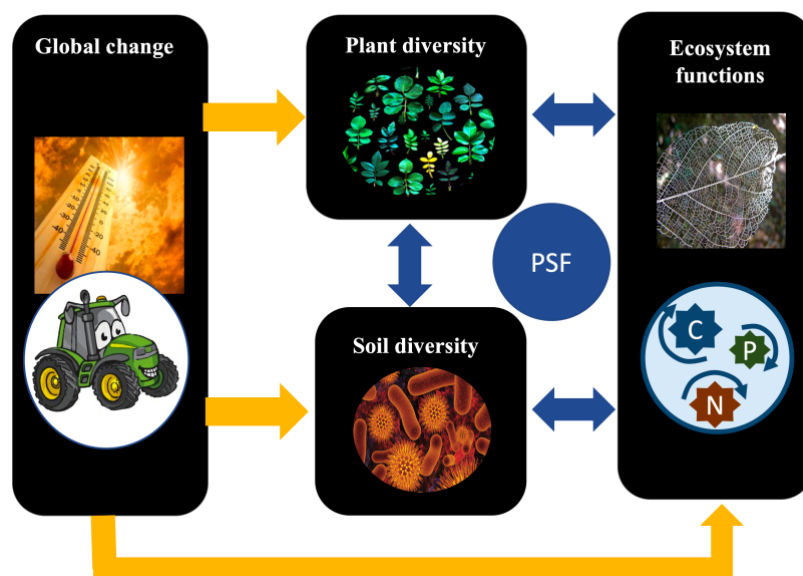
- In an ongoing sDiv group (2 more workshops over the next 2 years), we use a global database of 101 manipulative resource experiments where the fate of the species in response to the manipulation is documented over several years. We are collecting at the moment trait and functional information for all species in the database. Within this group I am leading a project that aims at characterizing winners and losers of global change drivers with respect to the rest of the species: **Do winners or losers stand out from the background community, i.e. do they have characteristic  $\alpha$  niches compared to the rest of the community? Do they have characteristic functional traits and outstanding positions in the trait hierarchies? Do winners replace functionally similar losers in their niche (could indicate replacement) or are niches from losers and winners very different (could indicate new niche filling)?** Similar ideas could be applied to my climate warming experiment (AlpagesVolants, see section 3.2.1).

### 3. PLANT-SOIL FEEDBACKS

#### 3.1 Do plant-soil feedbacks change over environmental gradients?

##### 3.1.1 Context

There is now compelling evidence that the ecosystems of the French Alps are strongly endangered by multiple threats, first and foremost land-use change and ongoing regional climate change (Körner, 2014). Mountains are globally important ecosystems for biodiversity, water supply, regional agriculture and forestry as well as tourism (Körner, 2014). Therefore, a large body of research has been dedicated to better predict the future distributions of biodiversity and associated functions with the overarching aim of developing management actions and solutions to global change. As in other ecosystem types, the majority of this work has focused on vegetation or aboveground animals, but has ignored the invisible diversity in the soil. However, land-use and climate changes can substantially alter soil communities and therewith the ecosystem functions that they perform (Geisen, Wall et al., 2019). These ecosystem functions, such as nutrient cycling and energy fluxes, form the basis of nature's contributions to people. Moreover, ignoring soil communities in models of vegetation and ecosystem functions can lead to erroneous predictions (van den Hoogen, Geisen et al., 2019), because above- and belowground compartments are tightly linked by plant-soil feedbacks (PSF) and trophic interactions (Fig. 17, Hagedorn, Gavazov et al., 2019). Improved understanding, future predictions and scenarios of ecosystem responses to environmental changes thus require to jointly study the distribution of different compartments of biodiversity and associated ecosystem functions.



**Figure 17** – Global change will affect biodiversity and ecosystem functions directly (orange arrows). Feedbacks between plants, soil diversity and soil functions will lead to further, indirect impacts (blue arrows).

### 3.1.2 First results

Jointly modelling the distribution of plant diversity, soil diversity and associated ecosystem functions can become an immense task in highly diverse plant-soil communities. In order to break down this complexity, in our past work we started by focussing on more specific links in plant-soil feedbacks (by cutting out parts of Fig. 17).

**Research questions are:**

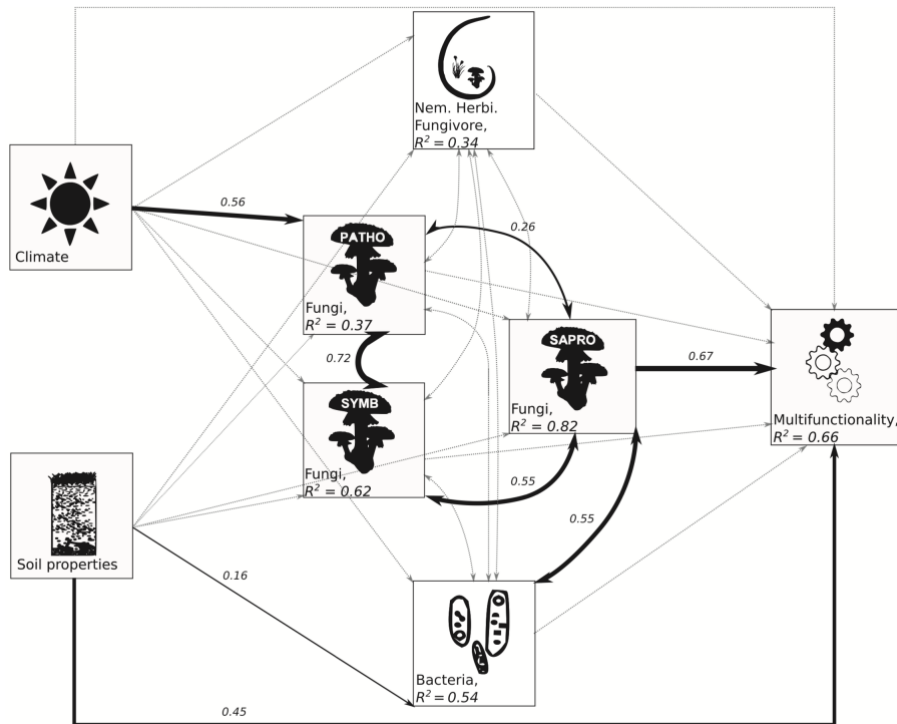
- (1) How does soil diversity impact soil functions?
- (2) How does plant diversity impact soil functions?
- (3) How do soil functions affect plant diversity?
- (4) What are the links between different ecosystem compartments?

**(1) How does soil diversity impact soil functions?** [Abiotic -> Soil diversity -> Soil functions]

While there is a growing recognition that along environmental gradients, the compositional turnover of multiple trophic groups in the soil influences not only productivity but multiple ecosystem functions, we do not yet know which components of diversity influence which ecosystem functions. In order to answer to this question, we studied the biodiversity found in soils using environmental DNA along a 1,000 m elevational gradient in the French Alps. Subalpine grasslands dominate the bottom of the gradient while sparsely vegetated alpine meadows characterize higher elevations.

- Ten sites were sampled in summer 2012 along the same south-facing slope and they were separated by an 100m elevation difference and an average distance of 340m. Each site consisted of two 10mx10m plots with homogeneous vegetation. In each plot, soil samples were collected and analyzed with DNA metabarcoding based on four different DNA markers: eukaryotes (v6-v7 region of the 18S rRNA gene), bacteria (v5-v6 region of the 16S rRNA gene), fungi (Internal Transcribed Spacer 1) and vascular plants (Chloroplast trnL-P6 loop). Molecular analyses and data curation followed the description in Ohlmann et al. (2018). MOTUs were grouped based on their taxonomic affiliation, shared trophic resources and main functions, such as organic matter decomposition, to receive a presence-absence matrix of tropho-functional groups per plot (Martinez-Almoyna et al., 2019).

## PLANT-SOIL FEEDBACKS



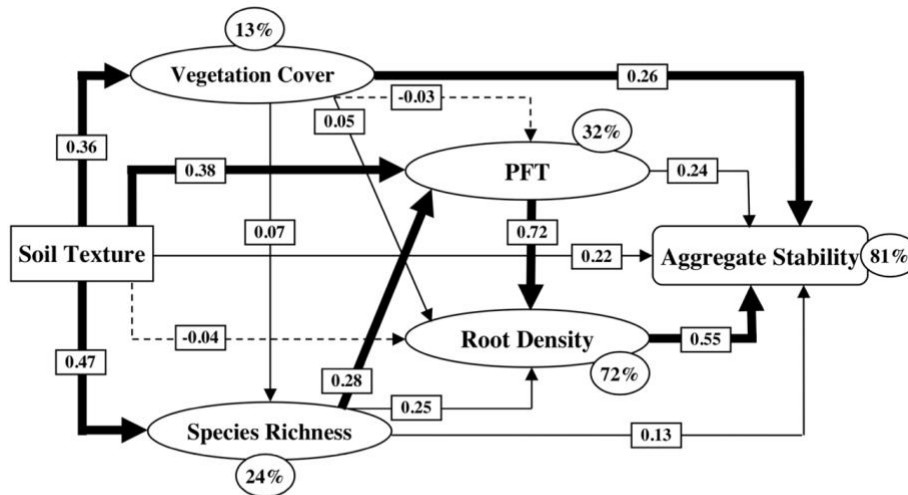
**Figure 18** – Integrated path model highlighting the direct and indirect effects of climate and soil properties on the turnover of ecosystem multifunctionality. The size of the arrows is proportional to the size of the associated standardized path coefficients (only for significant paths). Dotted grey lines represent non-significant paths. Paths with double arrows represent correlations (Martinez-Almoyna et al., 2019).

- Together with my PhD student C. Martinez-Almoyna, we studied the impact of different components of  $\beta$ -diversity of soil communities on different soil functions, including productivity, N-cycling, N-leaching and a measure of overall multi-functionality. We compared the influence of total soil multi-trophic  $\beta$ -diversity (between all taxa regardless of their tropho-functional group), horizontal  $\beta$ -diversities ( $\beta$ -diversities within tropho-functional groups), and vertical  $\beta$ -diversity ( $\beta$ -diversity across tropho-functional groups). Using path analyses, we quantified how these different  $\beta$ -diversity components mediate the effects of environmental turnover on the turnover of ecosystem functions.
- Not only the direct effect of soil properties on the turnover of multiple ecosystem functions was strong, but we also found important indirect effects of climate and soil properties through multi-trophic  $\beta$ -diversity (Fig. 18). More specifically, only total multi-trophic  $\beta$ -diversity and the horizontal  $\beta$ -diversity of saprophytic fungi were strongly related to the turnover of multifunctionality and, to a lower extent, the turnover of productivity and N-cycling. Our results suggest that decomposition processes and resulting nutrient availability are key to understand how ecosystem functions change along soil properties and climatic gradients in alpine ecosystems (Martinez-Almoyna et al., 2019).

### **(2) How does plant diversity impact soil functions?** [Abiotic -> Plant diversity -> Soil functions]

Not only soil diversity influences soil functions but plant diversity can be important as well. In a study together with a student that I mentored during his PhD, H. Elsayed Ali, we studied the impact of plant communities on soil stability as a key ecosystem function in agricultural

landscapes (Ali, Reineking et al., 2017). So far, few studies compared the relative importance of abiotic factors and plant community structure for soil stability in the field. In addition, studies on effects of plant traits on soil stability have ignored intraspecific trait variability (ITV) despite growing evidence of its importance for ecosystem functioning.

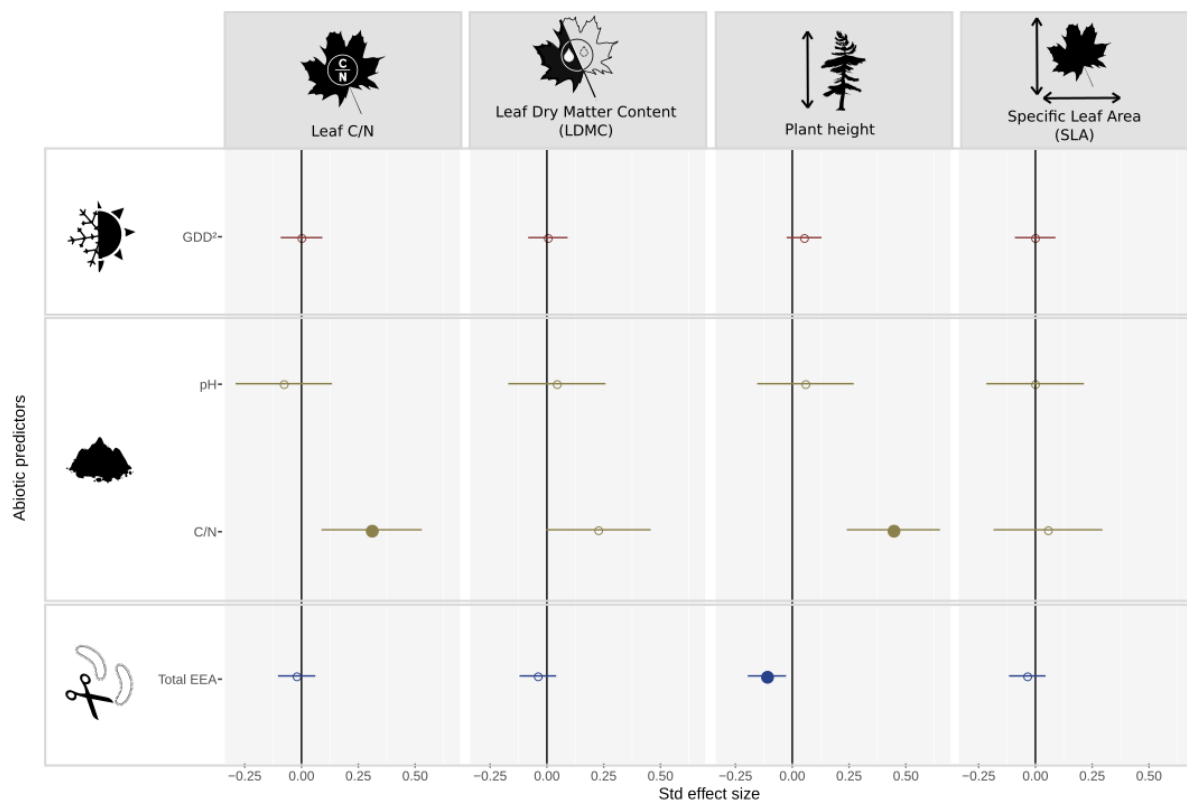


**Figure 19** – Path model on the effects of soil texture (silt % and clay %), vegetation cover, species richness, root density and intraspecifically measured plant functional traits (root/shoot ratio, root length and root horizontal width), on soil aggregate stability. Numbers on arrows are standardized path coefficients. Solid arrows are positive and dashed are negative, bold arrows indicate significant standardized paths ( $P < 0.05$ ); thin arrows indicate non-significant path coefficient ( $P > 0.05$ ). Percentages close to the variable boxes indicate the variance explained by the model ( $R^2$ ). The goodness-of-fit index for the model is 0.58 (Ali et al., 2017).

- The study was conducted in an agriculture landscape in the Haeon-myun catchment in South Korea. The area is subjected to very heavy rains during the monsoon season, which causes severe damages to the soil, and thus soil stability is a very important ecosystem function. Over the whole catchment, 30 plots of 1 m<sup>2</sup> were randomly chosen. In each plot, H. Elsayed Ali estimated (1) vegetation characteristics, (2) plant functional leaf and root traits of in total 10 selected species, (3) soil characteristics and (4) measures of soil stability.
- Using path models, we quantified the effect of plant functional traits (PFTs), abiotic soil characteristics (soil texture) and vegetation characteristics on three soil stability measures, comparing models with and without intraspecific trait variability. We found that variance in soil stability was explained to varying degrees (from 81% for soil aggregate stability to 35% for soil shear vane strength). The three soil stability measures were mainly affected directly by root density, while PFTs and soil texture exerted indirect effects through root density and vegetation parameters, respectively (Fig. 19). Including intraspecific trait variability improved model explained variance and goodness-of-fit in all cases (Ali et al., 2017). Our study shows the role of intraspecific trait variability not only in the response of plant communities to changing conditions, but also in their impact on important ecosystem functions. In addition, the functional trait composition of communities can be much more important for ecosystem function than vegetation cover or species richness. These findings have important implications for the management of field margins to improve soil stability, as communities should not only be enriched by species with favorable root properties, but also consider that species have important plasticity in their root properties.

**(3) How do soil functions affect plants?** [Abiotic + Soil functions -> Plants]

Not only do plants affect soil functions but there exists a feedback as well. However, the vast majority of plant species distribution studies so far only consider climatic predictors and few account in addition for soil abiotic variables and indicators of overall nutrient stocks. But plants cannot use all parts of the overall nutrient stocks. Instead they require soil microbial communities to decompose organic matter into accessible nutrients (e.g. ammonium and nitrate). We thus asked whether accounting for microbial extracellular activities (i.e. exoenzymes) as a proxy for element decomposition in plant-accessible nutrients in addition to climate and general nutrient stocks improves species distribution models (Martinez-Almoyna, Piton et al., in prep.).



**Figure 20** – Standardized effect sizes of the interaction between functional traits (columns) and abiotic predictors (rows) in four hierarchical multispecies distribution models for 44 plants in the French Alps (one model per trait, i.e. column, binary responses). Considered functional traits are: leaf carbon/nitrogen ratio (leaf C/N), leaf dry matter content (LDMC), plant height, and specific leaf area (SLA). Considered abiotic predictors are: growing degree days (GDD), soil carbon/nitrogen ratio (C/N), and total extracellular activity of soil microbes (total EEA). Filled circles represent significant effects, empty circles represent non-significant effects. Red points represent abiotic predictors related to climate, green ones represent abiotic predictors related to soil physico-chemical properties, blue ones represent abiotic predictors related to enzymatic activities (Martinez-Almoyna et al., in prep.).

- We studied this question along 18 elevation gradients that were chosen to represent typical vegetation in the French Alps (long-term observatory ORCHAMP: [www.orchamp.osug.fr](http://www.orchamp.osug.fr)). Gradients range from about 900 m to 3000 m and thus from forests dominated plots at the bottom up to alpine meadow plots. Each gradient consists



of a minimum of five sampling plots (30 m\*30 m) with an average of 200 m elevation difference where plant releves, physico-chemical soil characteristics, extracellular enzymatic activities of soil microbes (hereafter microbial activity) and a number of other environmental variables are measured.

- Based on this data, we build hierarchical multispecies distribution models for 44 well distributed species of the French Alps (Martinez-Almoyna et al., in prep.). In these models we tested whether plant functional traits modulate responses to climatic variables, soil properties and exoenzymes. We found that most species were predicted with high accuracy ( $0,15 < TSS < 0,8$ ) and that both climate and soil variables were important predictors. Not only physico-chemical soil properties but also microbial activity was important, highlighting the necessity to represent not only overall soil stocks but more precisely plant-available resources. Plant traits modulated the responses to soil characteristics, with species with more exploitative traits preferring benign soil conditions and conservative species prevailing in more stressful and limiting conditions. For example, species with high leaf carbon/nitrogen ratio (C/N), a pivotal trait to describe the ability of plants for nutrient retention, increased the occurrence probability on soils with high C/N (Fig. 20).

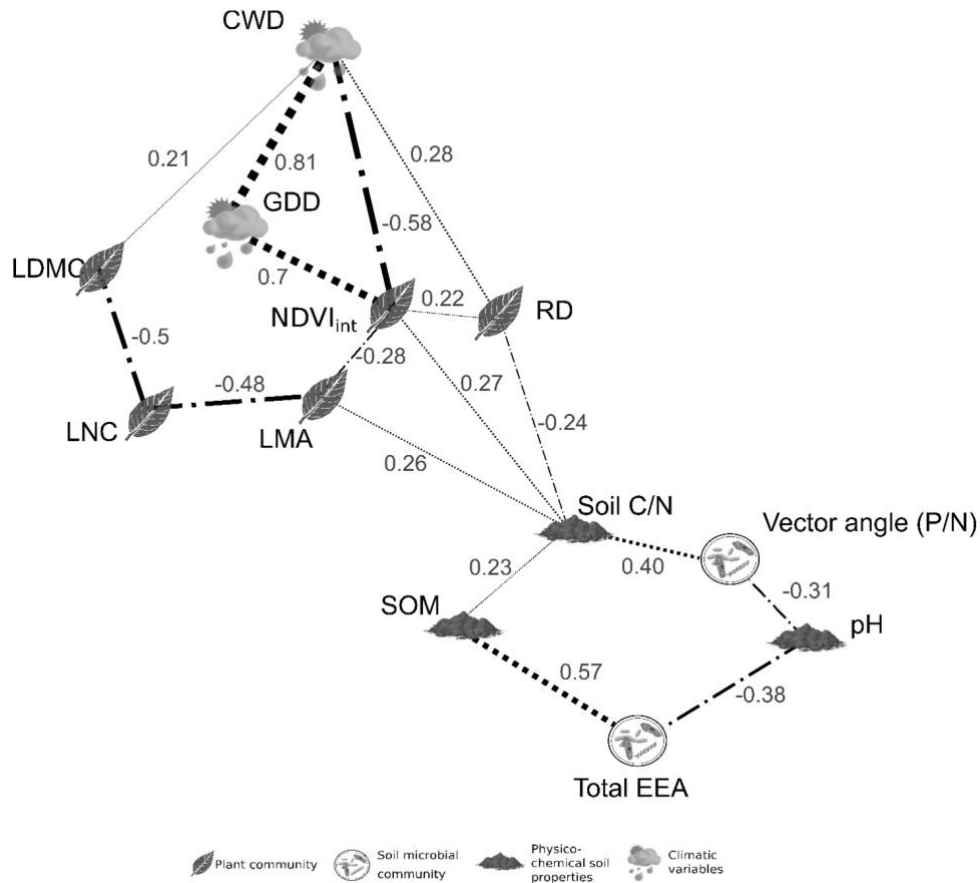
#### **(4) What are the links between different ecosystem compartments?**

[Climate – Plants– Soil diversity – Soil functions]

With a more integrative and explorative study we aimed to shed light on the complexity of PSFs and the responses of the implicated actors to abiotic conditions across the French Alps. We asked: What is the importance of general abiotic and biotic linkages between the four components implicated in PSFs – aboveground community (characterized by plant trait composition), belowground community (characterized through soil enzymatic activities), soil physico-chemical properties, and climate (Weil, Martinez-Almoyna et al., subm.)?

- Based on the data from ORCHAMP ([www.orchamp.osug.fr](http://www.orchamp.osug.fr)), we investigated partial correlations between plant community characteristics, soil microbial activities, and environmental conditions along the 18 elevational gradients in the French Alps, using Graphical Lasso.
- Climate and plant related variables (Fig. 21, upper left part) vs. soil relate variables (Fig. 21, lower right part) were linked via tight associations of plant traits with microbial activities via soil carbon/nitrogen ratio. Specifically, our network shows an increased investment in microbial nutrient acquisition in sites with conservative plant traits and reduced organic matter quality. In these interactions between plants and soil, the dominance of specific plant traits was more important than their diversity, thus highlighting the key role of a mass effect (and not a diversity effect) on ecosystem functioning. The main advancement of this study is that it identifies the – conceptually and from experimental work well-known – feedback between the conservative-exploitative plant continuum and microbial nutrient acquisition strategies on a large scale, the French Alps (Weil et al., subm.).

## PLANT-SOIL FEEDBACKS



**Figure 21** – Graph of a partial correlations network including plant community weighted means, soil microbial enzymatic activities, climatic variables and physico-chemical soil properties. Positive partial correlations are represented by dotted edges, negative ones by dash-dotted ones. The weight of the edges (thickness) corresponds to the absolute strength of their partial correlations. Abbreviations: RD: root depth, LMA: leaf mass per area, LNC: leaf nitrogen content, LDMC: leaf dry matter content, NDVI<sub>int</sub>: integrated normalized vegetation index, GDD: growing degree days, CWD: climate water deficit, soil C/N: soil carbon to nitrogen ratio, SOM: soil organic matter content, total EEA: total enzymatic activity (Weil et al., subm.).

### 3.1.3 Conclusions

Our results so far highlight the pivotal role of nutrient decomposition in alpine plant soil feedbacks. Soil microbial groups, plant functional traits, and ecosystem functions linked to nutrient decomposition were repeatedly identified among the most important variables in our models. So far, these studies were mostly explorative and not driven by strong directional hypotheses.

### 3.1.4 Perspectives

In my future research, I would like to further develop this work. From my point of view two advancements are important for studying plant soil feedbacks with large-scale observational data:

- (1) The development of a **comprehensive theory** that integrates plant functional traits, soil tropho-functional groups, decomposition activities in addition to above and belowground abiotic drivers and **makes testable hypotheses**
- (2) The **large-scale test** of the developed hypotheses and, as a pre-requisite, the improvement of approaches that allow jointly modelling species, functional and tropho-functional groups, abiotic drivers and ecosystem functions

**(1) Conceptual development for large-scale testing** – Instead of modelling distributions blindly, I propose to build on and integrate existing pieces of theory on ecosystem energy spectrums that exist in the literature: (1) The fast-slow plant economic spectrum postulates a gradient from fertile soils with fast growing plant species (e.g. high specific leaf area [SLA], low leaf dry matter content [LDMC], tall, high litter quality) and bacteria-based energy channels to infertile soils with conservative plant species with opposite traits and fungal-based energy channels (de Vries, Thébault et al., 2013). Compared to the ‘slow’ plant economic spectrum, in the ‘fast’ spectrum, many ecosystem functions work at higher rates: more biomass is produced, nutrient quality is higher, litter decomposition, mineralization and nitrification are faster. (2) In parallel, the copiotroph-oligotroph framework postulates a gradient from copiotroph microbes with fast growth rates and competitive advantages in fertile soils vs. oligotroph microbes with slower growth rates but a higher investment in carbon (C), nitrogen (N) and phosphorus (P) acquisition from complex organic molecules and thus advantages in infertile soils. For both the plant economic spectrum and the copiotroph-oligotroph framework, we expect a shift to the fast part of the spectrum under warming (short to long term), elevated CO<sub>2</sub> (mid-term), and extensive management (long-term), and a shift to the slow end of the spectrum under increased drought intensity and frequency (mid-term) and at the end of a succession (long-term). These shifts should also affect higher trophic levels that directly depend on plants and microbes and are well known to be sensitive to environmental changes (e.g. protists and nematodes, Ferris, 2019; Markussen Bjorbækmo, Evenstad et al., 2019; Nguyen, Song et al., 2016).

Integrating the “plant economic spectrum”, the “copiotroph-oligotroph framework”, research on potential cascades in trophic networks and studies on expected responses to abiotic drivers in a joint ‘fast–slow’ spectrum of ecosystems should thus allow for specific hypotheses (Fig. 22): (i) on large-scale co-variations of different tropho-functional groups, decomposition activities, plant diversity and ecosystem functions along environmental gradients in space and time, and (ii) on environmental change impacts on the diversity and functioning of ecosystems. The next challenge will then be to test this conceptually developed spectrum of ecosystems with data.

The French Alps, and especially the data from the observatory ORCHAMP, provide an excellent model system for this test, as they cover multiple steep climate, soil and land-use gradients and ongoing environmental changes are relatively fast. However, we cannot expect that a

simplified ‘fast-slow’ framework will fit across the French Alps. On the one hand, ecosystem responses may differ because of specific responses of different energy channels. There can be, for example, differences between ‘low nutrient’, ‘low temperature’ or ‘low water’ strategies (Reich, 2014). Furthermore, ecosystems are often not at equilibrium. Observed tropho-functional groups and ecosystem functions may thus not be linked to current environmental conditions but may represent the delayed responses to past climatic or land-use changes (Hagedorn et al., 2019). Novel models of biodiversity and ecosystem functions should thus account for transient dynamics and the processes influencing these temporal dynamics, such as feedbacks between tropho-functional groups, between ecosystem functions and between tropho-functional groups and ecosystem functions. One way to meet this challenge are experiments (see chapter 3.2).

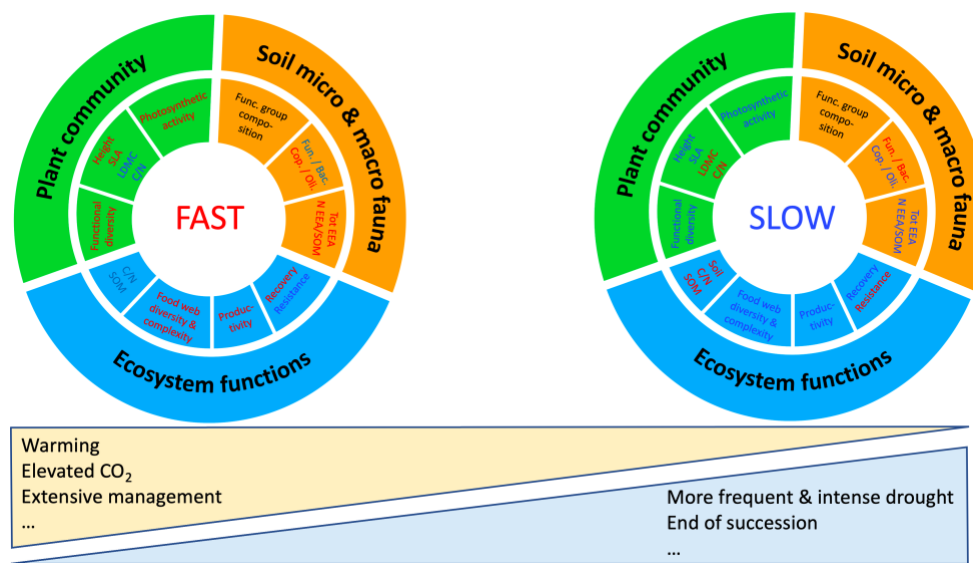


Figure 22 – Conceptual representation of the ‘fast–slow’ spectrum of ecosystems for several limiting factors

**(2) Multi-species distribution models** – Much research has focused on a single (or at best a few) species at a time, its specific functional traits or ecosystem functions, neglecting biotic interactions between species as well as synergies and trade-offs between traits and ecosystem functions. However, biodiversity is not merely the sum of species or their traits, but is the result of multiple interactions and feedbacks at various spatial and temporal scales, thus resulting in constrained species assemblages with characteristic trait distributions as well as bundles of ecosystem functions. Global change studies that ignore these dependencies are prone to provide erroneous projections. Recently, progress has been made in extending regression-based species distribution models (SDMs) to multi species (MSDMs) and joint species distribution models (JSDMs) that have been developed to account for these interdependencies. However, as promising as they are, the large and extensive use of these models is still hampered by a number of limitations. In the ANR project GAMBAS, where I am local PI and WP leader, we work on the ecological interpretability and applicability of these models and test for which ecological questions which model is most adequate.

JSDMs can model multiple species simultaneously, provide estimates of their statistical non-independencies after accounting for influential environmental effects, can integrate trait and phylogenetic information and can be used to model time-series. Our recent work has shown, that “static” JSDMs cannot disentangle environmental effects from biotic interactions (Poggiato et al., in prep.), but could dynamic JSDMs better meet this challenge? Can we test the multi-component hypotheses of the ‘fast–slow’ spectrum of ecosystems with JSDMs? How should we account for the different components in the different model parts (i.e. which components should be predictors, responses or hierarchical factors influencing  $\beta$ -parameter estimates of the regressions)? Would it be better to use network analyses (as we did in Weil et al., *subm.*) to account for feedbacks?

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## 3.2 How do plant-soil feedbacks respond to experimental climate change?

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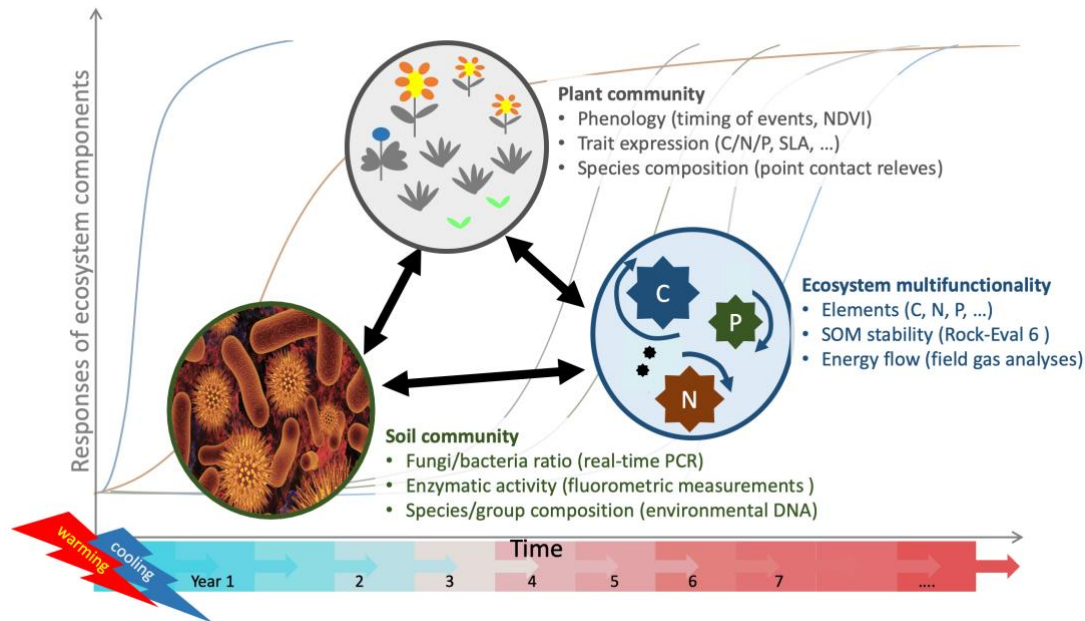
### 3.2.1 Context

In this chapter, I will focus on temperature, as one specific driver of the ‘fast–slow’ spectrum of ecosystems. I propose a local and experimental approach (in contrast to the large-scale, correlational approaches in section 3.1), which allows for more refined hypotheses and analyses of ecosystem responses to warming and cooling (Fig. 23).

Predicting the response of ecological communities to changing climate has emerged as one of the most important goals for ecology (Bardgett & van der Putten, 2014; Urban, Bacedi et al., 2016). Past research has shown that climate can directly affect species’ demographic performance by altering their phenology and functional traits, but can also indirectly affect them by changing interactions with competitors, consumers, and mutualists (Harley, 2011; Van der Putten, Macel et al., 2010). More recent work suggests that among the most important determinants of how plant and soil communities respond to future conditions will be the novel interactions that emerge with the asynchronous responses of species to climate change including their different pace of migration (Alexander, Diez et al., 2016). However, the timeline of the different responses of species, the resulting biotic interactions and feedbacks and, ultimately, the emerging dynamics of community assembly and ecosystem functioning remain largely unknown (Gonzalez-Megias & Menendez, 2012; Svenning & Sandel, 2013).

In Alpine grasslands, warming is expected to advance plant phenology (e.g. bud burst or flowering, Korner & Basler, 2010) and promote plant species with warm-adapted traits, which may lead to local changes in abundance structure and local extinctions of cold-adapted species (Alexander, Diez et al., 2015). Additionally, warming is expected to change soil diversity and trophic interactions (Crowther, Thomas et al., 2015) and the abundances of specific groups (Classen, Sundqvist et al., 2015). Warming also directly influences soil functioning by changing reaction rates (e.g. decomposition, Xue, M. Yuan et al., 2016) that impact input-output balances of chemical elements (e.g. shifting the ratio of inorganic vs. organic soil N pools, Pries, Castanha et al., 2017). Importantly, these components are not independent of each other. Plant communities influence soil communities and their ecosystem functions (e.g. through litter quality/quantity), soil communities influence plant communities (e.g. through the availability of inorganic N) and ecosystem functions also influence plant and soil diversity (e.g. through decomposition and nutrient recycling rates, Bardgett et al., 2014). Studying these effects jointly requires a holistic approach where warming is applied to an entire ecosystem.

## PLANT-SOIL FEEDBACKS



**Figure 23** – Conceptual representation of the dynamic responses of different ecosystem components to climate warming or cooling

While warming experiments are motivated by the global warming crises and thus a question related to temporal change, cooling experiments are interesting as well. On the one hand, they allow testing whether warming and cooling effects are symmetric and thus enhance understanding of underlying processes. On the other hand, they can be used to study why species ranges are limited by a cold border, thus a question related to spatial turn-over.

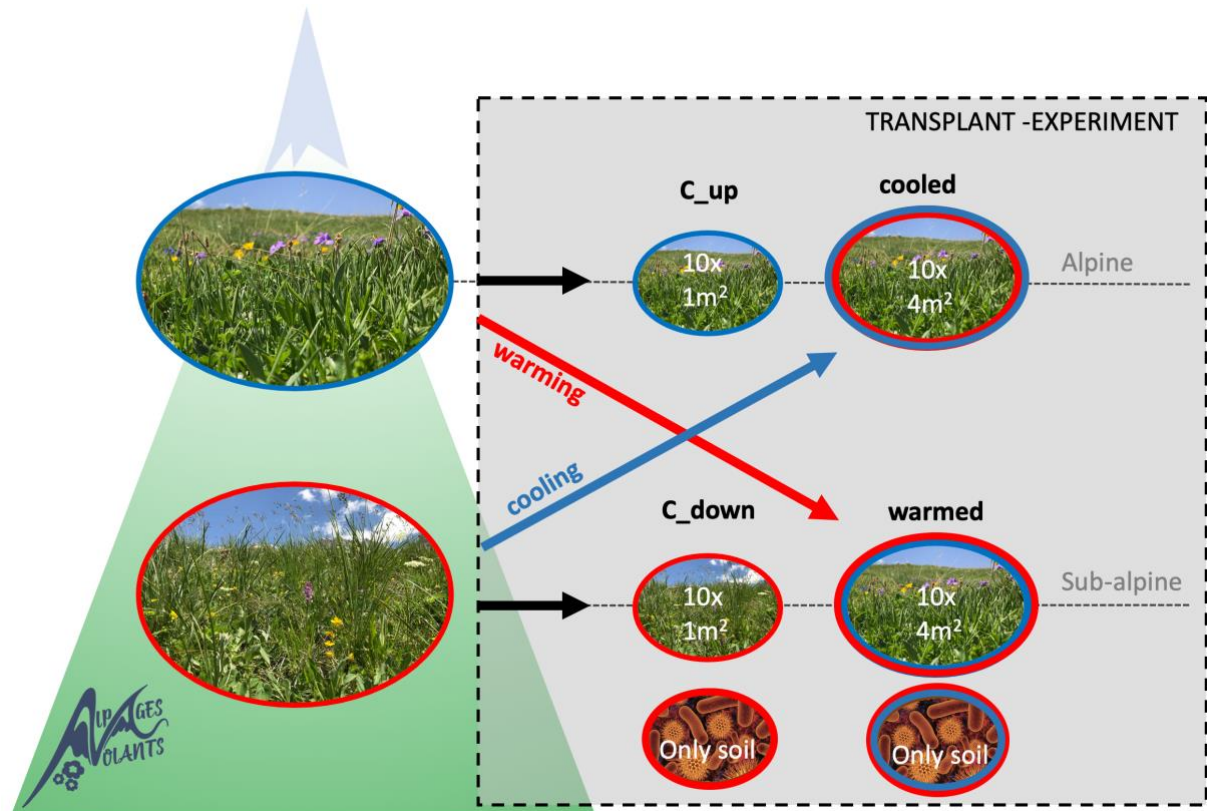
Due to the steep environmental gradients alpine and sub-alpine grasslands harbour distinct species compositions and many sub-alpine species have not been observed at the alpine stage. However, spatial distances between warm-adapted and cold-adapted communities in mountains are relatively short and thus dispersal limitation as a major driver of range limits is unlikely. The question is whether the sub-alpine species are excluded by the harsher climate or whether they are competitively inferior to alpine species under harsh conditions and are thus ultimately excluded by competition. Climate and competition effects are not straightforward to disentangle, because growing sub-alpine species without neighbours at an alpine site means to deprive them of protection against harsh wind and snow that a closed vegetation cover provides.

### Research questions are:

- What are effects of climate warming and cooling on multiple ecosystem components over time?
- What is the relative importance of dispersal, climate and biotic interactions in limiting the upwards shift of sub-alpine species?

### 3.2.2 Experiment: AlpagesVolants

I developed, planned and implemented a transplant experiment with the support of LECA (Laboratoire d'Ecologie Alpine) and SAJF (Jardin Alpine de Lautaret). The experiment simulates a warming and cooling of about 3-degree Celsius. It was installed in 2016, ecosystem components have been observed during the growing season since then and the work is supposed to continue for at least 10 years.



**Figure 24** – Schematic overview of the AlpagesVolant experiment; Alpine plots have been transplanted to a sub-alpine site to simulate warming, sub-alpine plants (and soil-only plots) have been transplanted to alpine sites; outer circles indicate the climate at the current position (red for warm at sub-alpine site and blue for cold at alpine sites), if the colour of the inner circle differs it indicates a different origin (red for sub-alpine and blue for alpine).

In autumn 2016, grassland turfs (10 turfs of 4 m<sup>2</sup>) have been transplanted from alpine conditions at 2450 m a.s.l. downwards to subalpine conditions at 1950 m a.s.l., thus subjecting them to a 3-degree increase in temperature (Fig. 24). Control turfs have been transplanted from subalpine to subalpine conditions (10 turfs of 1 m<sup>2</sup>) and from alpine to alpine conditions (10 turfs of 1 m<sup>2</sup>). Each of the transplanted community turfs consists of the above- and belowground parts of meadow communities and 20-25 cm of their associated soil and soil communities.

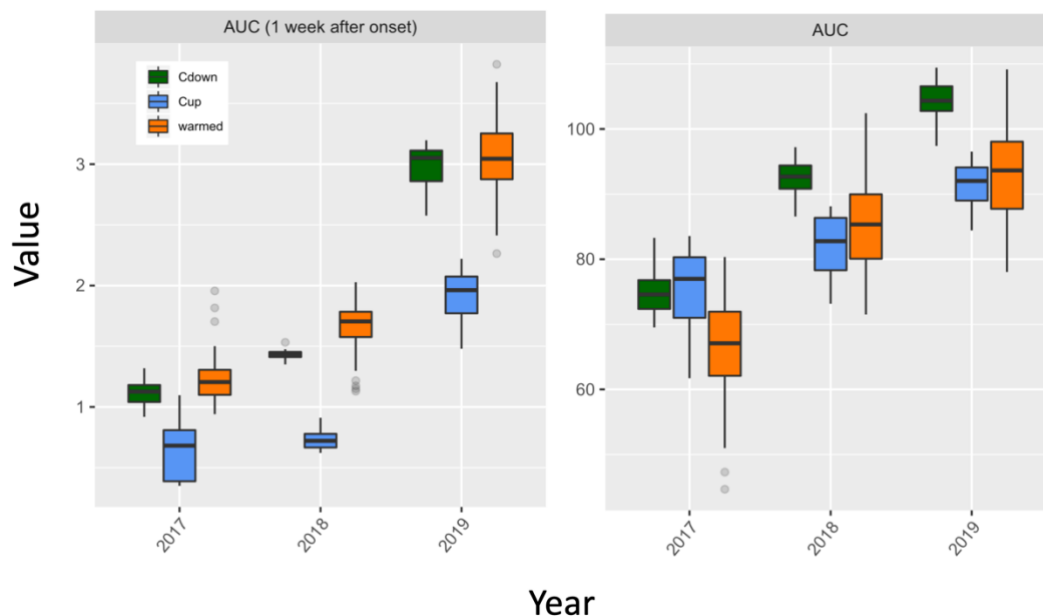
In 2017, we introduced individuals of 4 focal sub-alpine species in a part of all transplanted communities (each with 3 individuals per species and plot; *Festuca paniculata*, *Centaurea uniflora*, *Plantago serpentine*, *Alchillea millefolium*). This way we simulated additional invasion

of climate-adapted sub-alpine species in the warmed plots at the sub-alpine site and range expansion in the alpine controls. Transplanting individuals in cooled plots (and thus in their home communities) at the alpine site allowed inducing a cooler climate without new competitors but also without depriving the individuals from potential protective effects of neighbouring plants.

### 3.2.3 First results and perspectives

AlpagesVolants is a long-term experiment and the idea is to analyze the temporal dynamics of responses to experimentally induced climate change. Therefore, so far only preliminary results are available.

**Phenology & Productivity** – Recent work has shown that phenological responses to warming and cooling do not simply mirror one another, and that low temperature may limit reproductive allocation in the alpine region (Li, Jiang et al., 2016). Also, responses are species specific (Block, Alexander et al., 2020). Together with my PhD student B. Bektaş we investigate effects of warming and cooling on phenology, pollination and productivity (approximated via NDVI, normalized difference vegetation index). First results show that, in the very beginning of the season, warmed alpine plots tend to have equal or even higher productivity than sub-alpine controls and considerably higher productivity than alpine controls (Fig. 25, left), but that sub-alpine controls largely outperform warmed and alpine plots over the entire year (Fig. 25, right).



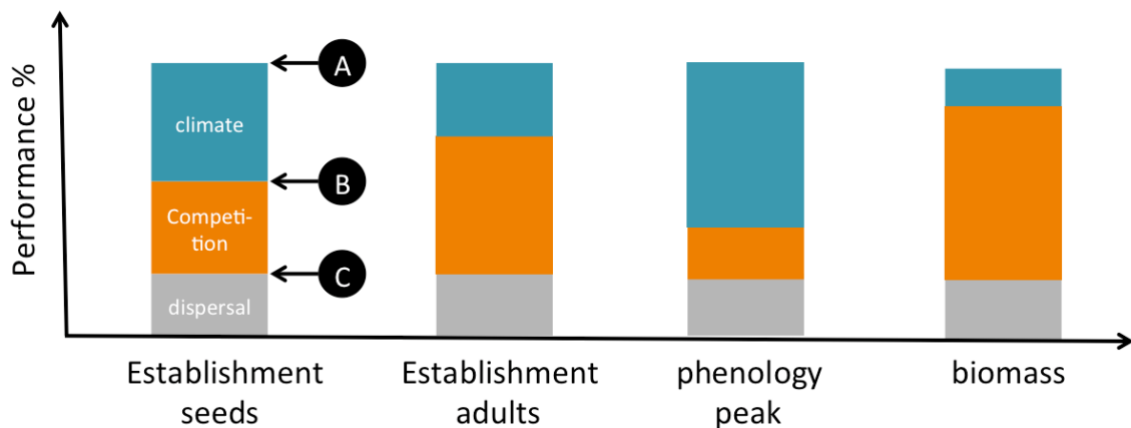
**Figure 25** – Preliminary results: Area under the curve of NDVI time series in alpine controls (Cup), sub-alpine controls (Cdown), and warmed communities (warmed) over the years 2017, 2018, 2019 for the first week of the vegetation period (left) and for the entire vegetation period (right).

**Plant composition and intraspecific traits** – Together with my PhD student B. Bektaş we will ask how plant community composition, diversity, and community weighted traits will respond



to climate warming over time. Does the relative importance of signals of environmental filtering vs. competition changes after warming? We will also investigate the role of intraspecific trait plasticity in these responses.

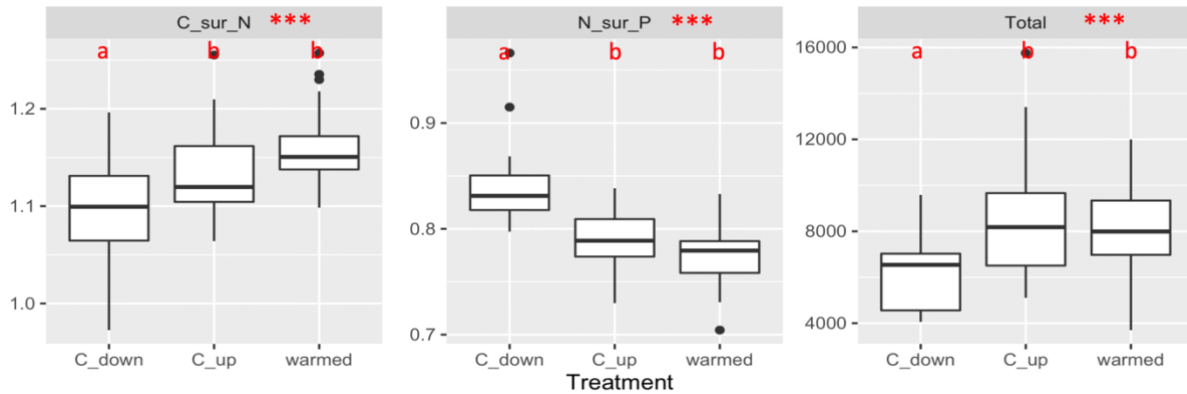
**Range limits** – In my future work, we will disentangle the drivers of range limits of sub-alpine species at different life stages using the transplanted focal individuals from sub-alpine conditions (section 3.2.2). We transplanted the focals in their common climatic conditions with their common neighbors (control) and beyond their range limit once with their common neighbors (only climate impact) and once with new, alpine neighbors (climate and competition impact). We transplanted both seeds and grown individuals. We will ask (Fig. 26): (i) What is the relative importance of dispersal, environmental filtering, and competition for the performance of the four focal species (survival, biomass, size) and thus potentially for their range limit? (ii) Are there differences between different “life stages” (establishment from seeds, establishment of transplanted adult individual, phenology, performance)?



**Figure 26** – Expected results: Comparing the performance of a focal sub-alpine species in (A) the control plot under subalpine conditions, (B) the uphill transplanted subalpine community (i.e. only climate change, no new competitors), and (C) the control plot under alpine conditions (i.e. climate change and new competitors) allows disentangling effects of potential dispersal limitation, competition, and climate filters on range limits. Different performance aspects are considered at different life stages.

**Microbial composition and extracellular enzymatic activity (EEA)** – We will study how microbial community composition (measured via eDNA and quantitative PCR) and functioning (via trait-databases and EEA) are affected by climate warming. First data from 2018 for EEA show that even after two years of warming the origin effect of the plot is much more important than the new climate (i.e. warmed plots are more similar to alpine control than to sub-alpine control, Fig. 27).

## PLANT-SOIL FEEDBACKS



**Figure 27** – Preliminary results: Differences in ratios of extracellular enzymatic activities of soil microbes (EEA) between the alpine control (C\_up), the sub-alpine control (C\_down) and the warmed plots. C\_sur\_N: EEA for enzymes active in carbon decomposition / EEA for nitrogen decomposition; N\_sur\_P: EEA for nitrogen decomposition / EEA for phosphor decomposition; Total: EEA summed over seven different enzymes.

**Test the ability of ultra-high-resolution imagery for monitoring** – We will test the value of ultra-high-resolution imagery (UHR, <1 cm) for monitoring changes in the structure and functioning of vegetation in the transplant experiment. I propose to collect once every 10 days during the growing season a high number of visible and near-infrared images from the alpine and sub-alpine experimental site with hand-held cameras and to analyze them using machine learning techniques that allow generating 3D, geo-localized ortho-mosaics with multi-spectral information (Kolyaie, Treier et al., 2019). I will then compare the 3D, multi-spectral representations of the vegetation to data from the ongoing field-sampling. More specifically I ask, whether our proposed imagery-based approach is able to capture the differences in the dynamic vegetation functioning and structure between the four treatments in the transplant experiment (alpine vs. sub- alpine control, warming vs. cooling) with regard to (1)  $\alpha$ - and  $\beta$ -species and trait diversity, (2) the timing of the phenological sequences of 10 focal species, and (3) individual level species identity, trait values and growth rates (including newly arriving species). The aim is to ensure the cost-efficient and standardized long-term monitoring of AlpagesVolants and its climate change triggered trajectories at high spatio-temporal resolution.

### 3.2.4 Perspectives

My ambition is to use AlpagesVolants as a proof of concept for a larger future project (i.e. ANR, Biodiversa) to establish multiple representative transplant gradients across the French Alps. This will provide us with an unprecedented database on the dynamic responses of vegetation structure and functioning with high spatio-temporal resolution and standardization – thus paving the way for a more comprehensive understanding of why, how and when different facets of vegetation respond to climatic changes.

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### 3.3 Do plant-soil feedbacks improve process-based vegetation models?

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#### 3.3.1 Context

Process-based models are important tools to integrate and formalize existing knowledge on ecosystem processes. These models can on the one hand be directly compared to data in order to judge how useful they are for describing observable patterns and, on the other hand, can be used to run virtual experiments for further advancing theory. FATE-HD is a dynamic landscape vegetation model developed and frequently applied at LECA (Barros, Gueguen et al., 2017; Boulangéat, Damien et al., 2014). The model simulates the spatio-temporal dynamics of plant functional groups (PFGs), defined via their functional characteristics, within landscape pixels and considers explicitly competition for light between plant PFGs, their local demography, dispersal between pixels, and responses to climate change. Up to date, the model is still not very well performing for grassland ecosystems and for herbaceous PFGs. We think that this is due to the fact that the model ignores plant soil feedbacks.

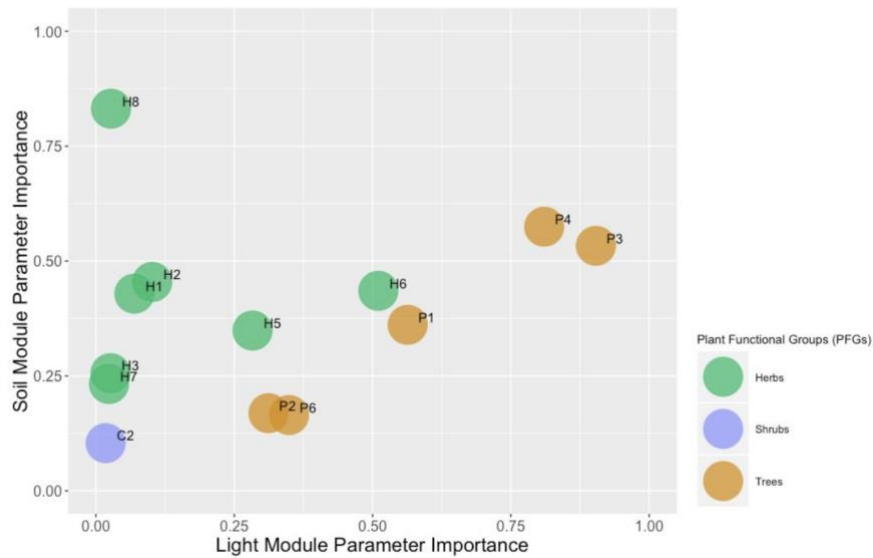
**The research question is:**

Will the integration of plant soil feedbacks in FATE-HD improve model predictions for grasslands and herbaceous PFGs?

#### 3.3.2 First results & perspectives

Together with my PhD student B. Bektaş, we started to work on this task during her master thesis. So far, the novel soil sub-model accounts for the effect of the soil nutrient stock on plant communities and the effect of plant communities back on soil nutrient stock. In short, in each cell of the model, *soil nutrient stock* depends on the value of the former timestep and on the community-weighted mean of *soil nutrient contribution* of present PFGs (i.e. taken from Landolt nutrient indicator). Each PFG has a tolerance range of soil nutrient content around its *soil nutrient contribution*. The match of PFGs tolerance with local *soil nutrient stock* affects PFGs' survival. First tests with the new FATE-HD-SOIL model show that adding plant soil feedbacks is especially important for herbaceous species and for grassland ecosystems (Fig. 28, Bektaş, 2019 master thesis).

## PLANT-SOIL FEEDBACKS



**Figure 28** – FATE-HD-Soil preliminary results, Comparison of combined importance of light module related parameters and soil module related parameters for different PFGs.

In the future, we would like to further refine the new soil sub-model by explicitly incorporating the part of the soil nutrient stock that is made available to plants. As outlined in chapter 3.1, information on nutrient stocks are often not enough to model plant species distribution but we also require information on the directly accessible parts (Martinez-Almoyna et al., in prep.). We thus need to account for the abiotic and biotic drivers of nutrient decomposition in the soil (e.g. microbial activities, soil tropho-functional group abundance and diversity) and how they dynamically depend on vegetation structure.

### 3.3.3 Perspectives

Combining data from the ORCHAMP long-term observatory and transplant experiments along elevational gradients will allow to better describe, analyze and understand transient dynamics of tropho-functional groups and ecosystem functions, and the role of feedbacks between them, in response to environmental changes. This improved understanding can guide the integration of plant soil feedbacks in a process-based vegetation model. This model can then be used to simulate how global change effects will cascade dynamically through plant and soil compartments. The emerging larger scale patterns provide future scenarios of the distribution of multi-trophic biodiversity and ecosystem functions.

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## 4. CURRICULUM VITÆ

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### PERSONAL DATA

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Date of birth: 22.06.1976  
 Place of birth: Mettingen, Germany  
 Nationality: German  
 Family status: Married, 2 children

### RESEARCH POSITIONS

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since 2015 CNRS research scientist (CR, chargé de recherche), LECA, Grenoble, France  
 2009 – 2015<sup>3</sup> Researcher and Postdoc in the EMABIO Team, CNRS Grenoble, France  
 (Wilfried Thuiller, Sébastien Lavergne)  
 2010 Two months research stay at the Department of Environmental Science  
 and Policy, University of California, Davis, USA (Alan Hastings)  
 2008 – 2009 Postdoc at the Institute of Biological and Environmental Science, Aberdeen  
 University, UK (Justin Travis)  
 2004 – 2008 Ph.D. research at the Department of Ecological Modelling, UFZ Leipzig,  
 Germany

### EDUCATION

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2004 – 2008 Ph.D. at the ETH Zurich: ‘Density regulation: Linking theory and applications  
 to understand population- to community-level dynamics and responses to  
 environmental change’, Thesis jury members: Karin Johst (UFZ), Harald  
 Bugmann (ETH), Christian Wissel (UFZ), und Sebastian Bonhoeffer (ETH).  
 Ph.D. thesis awarded with the ETH Zurich medal (distinction)<sup>4</sup>  
 2005 – 2007 Postgraduate Diploma Course in Applied Statistics, ETH Zurich  
 1999 – 2004 Diploma in Biology, University Marburg, Germany (grade: verbal: 1.1,  
 thesis: 1.0)<sup>5</sup>  
 1995 –2003 Diploma in Psychology, University Marburg (grade: verbal: 1.1, thesis: 1.0)  
 1995 Abitur, Kardinal-von-Galen Gymnasium in Mettingen, Germany (grade: 1.4)

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<sup>3</sup> Maternity leave and part-time work (in total 12 months spread over 20 months)

<sup>4</sup> Awarded to the top 7%

<sup>5</sup> Grading system: 1: outstanding, 2: good, 3: satisfactory, 4: sufficient, 5 to 6: not sufficient

## SUPERVISION

**PhD students**

- 2019-2022 Billur Bektaş - Transient dynamics of Alpine grasslands – linking biodiversity and ecosystem functions in a warming world. Co-supervised with Wilfried Thuiller. Funded by the French Ministry of Research.
- 2018-2021 Irene Calderón-Sanou - Towards a better understanding of multi-trophic assemblages through the use of eDNA. Co-supervised with Wilfried Thuiller. Funded by the ANR GlobNets.
- 2017-2020 Camille Martinez-Almoyna - Structure, dynamics and functioning of multi-trophic meta-communities – spatial and environmental effects. Co-supervised with Wilfried Thuiller. Funded by the French Ministry of Research.
- 2014-2017 Ceres Barros - Study of ecosystem stability across spatial and trophic scales. Co-supervised with Wilfried Thuiller. Funded by the ERC TEEMBIO project.
- 2012-2015 Loïc Chalmandrier - From communities to multi-trophic metacommunities: disentangling the features of diversity patterns. Co-supervised with Wilfried Thuiller and Sébastien Lavergne. Funded by the ENS Paris.

**Mentored PhD student**

- 2011-2015 Hamada Alsayed Ali - Plant Communities in Field Margins of Agricultural Landscapes: Species Distributions, functional Traits, and Contributions to Landscape Function. University of Bayreuth, supervisor: Björn Reineking.

**Master students (M2)**

- 2019 Billur Bektaş Master 2 BEE, Univ. Grenoble Alpes. Supervision together with: Wilfried Thuiller.
- 2019 Sarah Weil, Master 2 Sciences de l'environnement, Dijon. Supervision together with: Wilfried Thuiller.
- 2018 Raphaël Della Vedova, M2 GEOIDES, Univ. Grenoble Alpes.
- 2017 Camille Martinez, Univ. of Montpellier. Supervision together with: Wilfried Thuiller.
- 2011 Loïc Chalmandrier, ENS - INAPG, Paris. Supervision together with: Wilfried Thuiller and Sébastien Lavergne.

**M1 & L1-3 students**

- 2019 M. Fleuet, M1 École des Métiers de l'Environnement (EME) à Bruz. 12 weeks.
- 2019 E. Mesquida, Stage d'excellence L1 Sciences de la Vie, Grenoble. 4 weeks.
- 2019 C. Trochard, L2 Bio. des Organismes, Ecol. Ethologie et Evol. à Rennes. 5 weeks.
- 2019 C. Mahieu, L3 de Biologie à L'UGA. 6 weeks.
- 2019 M. Bourreau, L2 DUT L'IUT de la Roche-sur-Yon. 12 weeks.
- 2018 B. Bektaş, BEE-M1, UGA. Supervision together with: Wilfried Thuiller. 12 weeks.
- 2018 L. Mainguy, BEE-M1, Univ. Grenoble Alps. 7 weeks.
- 2018 L. Rocher, L3 de Science de la Vie - Option Ecologie, USMB Chambéry. 8 weeks.
- 2017 R. Della Vedova, M1 GEOIDES, Univ. Grenoble Alpes. 12 weeks.
- 2017 A. Labonte, M1 Bioingénieur, Agro-Bio Tech, ULg, Belgique. 6 weeks.
- 2017 M. Tessereau, BTS C. de Form. aux Métiers de la Montagne, Thônes. 5 weeks.
- 2017 Nakita Rubuliak, University of Alberta, Canada. 6 weeks.

## PROJECT LEAD

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2019-2023	ANR – GAMBAS, local PI, WP leader, (€ 133M)
2019-2020	DIPEE-FREE 2019, PI of the project: The role of dynamic plant community assembly and plant-soil feedbacks in environmental change responses (€ 21M).
2018-2019	DiPEE-FREE-ZAA, PI of the project: Early plant-soil responses of alpine meadow communities to a warming climate (€ 14M)
2018-2019	LECA-internal call, PI of the project: Response of soil microbial composition and functioning to experimental climate warming (€ 7M)
2017-2018	AP2016-DiPEE-ZAA, PI of the project: Abiotic, biotic and demographic range limits of sup-alpine plant species (€ 14M)

## SCIENTIFIC RESPONSABILITIES

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<i>LECA</i>	“Conseil de Labo” (since March 2016) Responsible for the weekly LECA seminars (since 2016) Responsible for the LECA webpage (since 2019)
<i>Associate Editor</i>	Methods in Ecology and Evolution (since beginning of 2013)
Reviewer	Applied Vegetation Science, Diversity and Distribution, Ecological Modelling, Ecology Letters, Journal of Biogeography, Journal of Theoretical Biology, Journal of Vegetation Science, Landscape Ecology, OIKOS, PLOS ONE, American Naturalist, Methods in Ecology and Evolution

## ORGANISATION OF SCIENTIFIC WORKSHOPS AND SYMPOSIA

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11/2011	Organized and carried out a one-week workshop on ecological modelling
11/2009	Symposium at the GfÖ (yearly meeting of the German Association of Ecology): “Coexistence in changing environments – between niche and neutrality”
09/2005 – 09/2009	Founding member of the YoMos (Young Modellers in Ecology) <ul style="list-style-type: none"> <li>• Developed the YoMo internet presence (<a href="http://www.yomos.de">www.yomos.de</a>)</li> <li>• Organised the annual 3-4 days YoMo Workshops</li> <li>• Organised the annual meetings at the GfÖ</li> </ul>
11/2008	Symposium at the GfÖ: “Across scales: From organismic interactions to biodiversity and ecosystem functioning” (Special Issue: Meyer et al. 2010a, Meyer et al. 2010b)
02/2008	Organized a 10-day course: “Applied statistics in Ecology” in Białowieża, Poland

TEACHING

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2016-2019	Taught ½ day modules in the Master BEE UGA in each year
2009	Taught a lecture at the Univ. of Aberdeen on ecological modelling
2008	Taught a ten-day course in Białowieża, Poland, on ecological experiments, statistics and mechanistic modelling
2007	Taught a two-day course at the Univ. of Marburg on statistics with R
2007	Assisted and supervised an obligatory two-week module of the M.Sc. Biodiversity Management & Research at the University of Namibia
2005-2007	Taught statistic lectures at the UFZ
2005-2006	Assisted and supervised two one-week courses at the University of Potsdam on analyses in plant ecology
2005-2006	Assisted and supervised two one-week courses at the UFZ on process-based modelling in Ecology (using C++)
2002	Assisted and supervised a graduate level plant-ecology course

KEYNOTES & INVITED PRESENTATIONS

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**Keynotes**

Keynote at the Biodiversity Exploratories Meeting: Catch me if you can – Chasing assembly processes in diversity patterns, Wernigerode (Germany), 21-24 February 2017.

Keynote at the 10-year-anniversary of the YoMos: Processes of plant community assembly, drivers and resulting ecosystem functioning, Lachen (Switzerland), 5-8 May 2015.

**Invited presentations**

Münkemüller (2018) *AlpagesVolants* – Species range limits & climate warming in alpine communities. Oral presentation, L'inauguration des serres du Jardin du Lautaret (Grenoble), 24 September.

Münkemüller, T., de Bello, F., Meynard, C.N., Gravel, D., Lavergne, S., Mouillot, D., Mouquet, N. and Thuiller, W. (2010). Taxonomic, functional and phylogenetic diversity: Perspectives for disentangling community assembly mechanisms. *PhyloCo: Journée de conférences sur la Phylogénie des Communautés*, Montpellier (France), 5 Mai.



## PUBLICATION LIST

**Summary** (03/2020)

h-index= 25, 57 publications, 4560 citations, 9 papers cited more than 100 times

1<sup>st</sup> author publications: 13

\*publications of supervised PhD students

\*\*publications from my PhD or earlier

**Peer-reviewed**

- (57) **Münkemüller, T.**, Gallien, L., Pollock, L.J., Barros, C., Carboni, M., Chalmandrier, L., Mazel, F., Mokany, K., Roquet, C., Smycka, J., Talluto, M., & Thuiller, W. (in press). Do's and don'ts when inferring assembly rules from diversity patterns. *Global Ecology & Biogeography*.
- (56) Thuiller, W., Gravel, D., Ficetola, G.F., Lavergne, S., **Münkemüller, T.**, Pollock, L.J., Zimmermann, N.E. & Mazel, F. (2020) Productivity begets less phylogenetic diversity but higher uniqueness than expected. *Journal of Biogeography*, 47, 44–58.
- (55) Brun, P., Zimmermann, N.E., Graham, C.H., Lavergne, S., Pellissier, L., **Münkemüller, T.** & Thuiller, W. (2019). The biodiversity-productivity relationship varies across diversity dimensions. *Nature Communications* 10 (5691).
- (54) \*Chalmandrier, L., Pansu, J., Zinger, L., Boyer, F., Coissac, E., Genin, A., Gielly, L., Lavergne, S., Legay, N., Schilling, V., Taberlet, P., **Münkemüller, T.** & Thuiller, W. (2019). Environmental and biotic drivers of soil microbial beta-diversity across spatial and phylogenetic scale. *Ecography*, 42(12) 2144-2156.
- (53) \*Calderon-Sanou, I., **Münkemüller, T.**, Boyer, F., Zinger, L. & Thuiller, W. (2019). From environmental DNA sequences to ecological conclusions: How strong is the influence of methodological choices? *Journal of Biogeography*, 47(1) 193-206.
- (52) \*Martinez-Almoyna, C., Thuiller, W., Chalmandrier, L., Clement, J.C., Foulquier, A., Ohlmann, M., Zinger, L. & **Münkemüller, T.** (2019). Multi-trophic beta-diversity mediates the effect of environmental gradients on the turnover of multiple ecosystem functions. *Functional Ecology*, 23(10) 2053-2064.
- (51) Guisan, A., Mod, H., Scherrer, D. **Münkemüller, T.**, Pottier, J., Alexander, J. & D'Amen, M. (2019) Scaling the linkage between environmental niches and functional traits for improved spatial predictions of biological communities. *Global Ecology & Biogeography*, 28(10) 1384-1392.
- (50) Klöner, G., ..., **Münkemüller, T.**, ... & Dullinger, S. (in press). Effects of climate change and horticultural use on the spread of naturalized alien garden plants in Europe. *Ecography*, 42(9) 1548-1557.
- (49) Pontarp, M., ..., **Münkemüller, T.**, ... & Hurlbert, A. (2019). The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. *TREE*, 34(3) 211-223.
- (48) \*Barros, C., Thuiller, W. & **Münkemüller, T.** (2018). Drought changes the effects of climate warming on forest-grassland ecotone stability. *Plos One*, 13(10): e0206138.
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- (2) **\*\*Münkemüller, T.** and Johst, K. (2006): Compensatory versus over-compensatory density regulation: Implications for metapopulation persistence in dynamic landscapes. *Ecological Modelling*, 197, 171-178.

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### PRESENTATIONS (SELECTED)

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Thuiller, Piffady, **Münkemüller** (2019). Les JSDM, généralités, enjeux et hypothèses écologiques. Oral presentation, ANR Gambas 1st project meeting, Montpellier, 27-29 May.

**Münkemüller, Laroche & Thuiller** (2019). Comment simuler des distributions d'espèces en interaction. Oral presentation, ANR Gambas 1st project meeting, Montpellier, 27-29 May.

**Münkemüller** (2019) AlpinesVolants – Species range limits & climate warming in alpine communities. Oral presentation, AG FREE Alpes (Grenoble), 25 November.

**Münkemüller, T. and Thuiller, W.** (2017). Plant-soil feedbacks in alpine meadow communities under warming climate. Oral presentation, Functional Ecology Conference, JEF ANAEE, Grande Motte (France), 28-31 March.

**Münkemüller, T., Saillard, A., Delbart, F., Valay, J-G and Thuiller, W.** (2017). Transient dynamics of alpine meadow communities under warming climate. Poster presentation, Functional Ecology Conference, JEF ANAEE, Grande Motte (France), 28-31 March.

**Münkemüller, T., Gallien, L., Lavergne, S., Renaud, J., Roquet, C., Dullinger, S., Guisan, A., Lenoir, J., Svenning, J.-C., Vittoz, P., Willner, W., Wohlgemuth, T., Zimmermann, N. and Thuiller, W.** (2013). Scale decisions can reverse conclusions on assembly processes of Alpine plant communities. Oral presentation, « Faster, Higher, More? Past, Present and Future Dynamics of Alpine and Arctic Flora under Climate Change » conference, Bergün (Switzerland), 22-25 September.

**Münkemüller, T., Lavergne, S., Chalmardrier, L. & Thuiller, W.** (2011). Beyond patterns – from phylogenetic diversity to community assembly. Oral presentation, 12th European Ecological Congress (formerly EURECO), Avilla (Spain), 25 - 29 September.

**Münkemüller, T., Lavergne, S. & Thuiller, W.** (2010). Phylogenetic signal in community niche structure. Oral presentation, 40th annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Gießen (Germany), 30 August - 3 September.

**Münkemüller, T., Gravel, D., Lavergne, S., Mouquet, N. and Thuiller, W.** (2009). Can phylogenetic diversity patterns help to better understand community functioning? Oral presentation, 39th annual meeting of the Ecological Society of Germany, Austria and Switzerland (GfÖ) in Bayreuth (Germany), 14-18 September.

**Münkemüller, T., Bugmann, H. & Johst, K.** (2007): Hutchinson revisited: Over-compensation promotes species coexistence. Oral presentation, 6th European Conference on Ecological Modelling, ECEM, in Trieste (Italy), 27-30 November.

**Münkemüller, T., Bugmann, H. & Johst, K.** (2007): Hutchinson revisited: Over-compensation promotes species coexistence. Oral presentation, 37th annual meeting of the Ecological

## CURRICULUM VITÆ

Society of Germany, Austria and Switzerland (GfÖ) in Marburg (Germany), 10-14 September.

Münkemüller, T., Bugmann, H. & Johst, K. (2006): Chaos schafft Artenvielfalt. Oral presentation. UFZ-PhD-Conference, Leipzig (Germany). Award for the best talk.

Münkemüller, T., Bugmann, H. & Johst, K. (2005): Over-compensation maintains species diversity. Poster presentation. First DIVERSITAS Open Science Conference, Oaxaca (Mexico), 9-12 November. Winner of the 'Young Scientist Award for the best poster'.

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