

Ecole de Biologie

Investigating differences in the fungi's taxonomic & functional groups niche and their distribution in the Western Swiss Alps

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et
conservation, spécialisation « Géosciences, Ecologie et Environnement »**
*Master Thesis of Science in Behaviour, Evolution and Conservation,
specialisation «Geosciences, Ecology and Environment»*

par

Axel Aubert

Directeur : Antoine Guisan

Superviseur : Lucie Malard

Expert : Anonymous

Département d'Ecologie et d'Evolution

Janvier 2021

Abstract

Climate change is a real problem that impacts the geographical distribution of ecological niches of different species and their distribution. Some species, such as micro-organisms, are essential for the proper functioning of soils ecosystems. It is therefore important to acquire knowledge about their ecological niche, and their potential response to these changes. In this paper, using soil data from 136 sites in the western Swiss Alps, a study of the ecological niche of three functional groups of Fungi: Pathotrophs, Saprotrophs and Symbiotrophs and five taxonomic groups: *Chytridiomycota*, *Ascomycota*, *Basidiomycota*, *Zygomycota* and *Glomeromycota*, as well as the variation of their abundance along certain edaphic and climatic variables, was performed. Here, I show that the niche breadth of all groups are similar, and that the majority of zOTUs are qualified as specialists, and therefore subject to extinction risk during abrupt changes. Moreover, for all groups, the abundance of zOTUs increases when two edaphic variables, Total Organic Carbon and Soil Water Content, increase. Regarding the variation of zOTU abundance along climatic variables, this project shows that both low and high temperatures are beneficial for zOTUs of all three functional groups and all five taxonomic groups.

Le changement climatique est un réel problème qui impacte la distribution géographique des niches écologiques des différentes espèces ainsi que leur distribution. Certaines espèces, comme les micro-organismes sont essentiels pour le bon fonctionnement des sols. Il est donc important d'acquérir des connaissances concernant leur niche écologique, et leur potentielle réaction face à ces changements. Dans cet article, en utilisant des données de sols de 136 sites dans les Alpes Suisses, une étude de niche écologique de trois groupes fonctionnels de Fungi : les Pathotrophes, les Saprotrophes et les Symbiotrophes, et de cinq groupes taxonomiques : Chytridiomycota, Ascomycota, Basidiomycota, Zygomycota et Glomeromycota, ainsi que la variation de leur abondance le long de certaines variables édaphiques et climatiques, ont été réalisées. Ici, je montre que les niches des trois groupes fonctionnels et des cinq groupes taxonomiques sont similaires, et que la majorité des zOTUs sont qualifiés de spécialistes, donc sujets à un risque d'extinction lors de changements trop brutaux. De plus, pour la totalité des groupes, l'abondance des zOTUs augmente lorsque deux variables édaphiques, Total Organic Carbon and Soil Water Content, augmentent.

Concernant la variation de l'abondance des zOTUs le long de variables climatiques, ce projet montre qu'à la fois des basses, ainsi que des hautes températures sont bénéfiques pour les zOTUs des différents groupes.

Introduction

Mountains have complex structures with steep slopes, various aspects, high relief, and important elevation shift that leads to a large diversity species (Körner, 2004). However, temperatures above 4,000 m have warmed 75% faster than temperatures in areas below 2,000m (Pepin et al., 2015). Therefore, the range shift of mountain species is changing very fast (Colwell et al., 2008; Elsen & Tingley, 2015). For example, plant species already underwent a significant upward shift during the 20th century (Lenoir et al., 2008). Climate change strongly disturbs species distribution by changing their environment, particularly species with narrow tolerance of environmental conditions (Thuiller et al., 2005). Those species are particularly affected because they are more specialised in the exploitation of their environment, and therefore have more difficulty adapting to changes (Slatyer et al., 2013). Thus, in order to develop conservation plan for mountain ecosystems, it's important to know the ecology and species distribution that populate them.

A tool to estimate the specie range limits and to predict how species may react to environmental changes is the niche breadth (Fisher-Reid, Kozak, & Wiens, 2012; Morin & Lechowicz, 2013). The niche breadth is the range of conditions that permit a species to maintain their population alive or to have a positive growth rate (Carscadden et al., 2020). The principle of ecological niche was first defined by Hutchison in 1957 (Hutchinson, 1957). It describes a space where a species can grow, governed by two parameters : biological parameters, corresponding to the interspecific interactions in that "space", and physical and chemical parameters, corresponding to the environmental gradients or environmental barriers. Another important tool to forecast how species might respond to climate changes, is species distribution models (SDMs). Species distribution models quantify the correlation between environmental variable and the distribution of species (Miller, 2010) It is widely used on macroorganisms, in most cases with presence-absence data but can also be used on microorganisms with relative abundance data (Mod et al., 2021).

While the species distribution of macroorganisms are well studied (Rubidge et al., 2011; Williams et al., 2009), microorganisms are lagging behind, mainly due to difficulties characterizing microbial taxa. Indeed, the fact that the species studied are not visible to naked eyes, the poor accessibility to the soil matrix, and the high biodiversity of 100,000 to 1,000,000 different species per gram (T.P. Curtis et W.T. Sloan, 2005), are a challenge to determine their taxonomy. With the improvement of molecular methods, the number of studies investigating patterns of microorganisms distribution are increasing (Case et al., 2007; Yashiro et al., 2016; Malard et al., 2021; Mazel et al., 2021.; Mod et al., 2021). For example, it has been shown that soil protist function vary strongly with elevation with an increase of the ratio consumers/parasites as the elevation increase (Mazel et al., 2021), and spatial patterns of soil bacteria under current and future environmental conditions has been modelled in mountains environments (Mod et al., 2021).

Although global fungal distribution has been studied (Tedersoo et al., 2014), regional fungi distribution models are lacking, despite their essential role in soil ecosystems such as nutrient cycle or organic matter decomposition (Käärik, 1975; Powlson, Hirsch, & Brookes, 2001; Yuan, Ge, Chen, O'Donnell, & Wu, 2012) . Fungal taxonomy is important because different taxa can have different roles in the soil ecosystem. Fungi can be divided in three main functional groups, that cover different trophic modes (Nguyen et al., 2016). Symbiotrophs are important for plant richness and plant growth by a process of partnership called symbioses, allowing the fungi to acquire carbon from their partnership and the plants to acquire nitrogen and phosphor (Harman, 2011; Hiiesalu et al., 2014). Saprotrophs play a major role in organic matter decomposition, carbon and nitrogen cycle, nutrient cycling, and nutrient retention (Käärik, 1975; Powlson, Hirsch, & Brookes, 2001; Yuan et al., 2012). Moreover, Pathotrophs can act as biocontrol agents, that prevent or reduce damage done by harmful organisms, but can also cause diseases for other organisms, like trees, plants or cultures (Sun et al., 2019). Therefore, determining the drivers of taxonomical and functional group distribution, and evaluating changes in their niche breadth may be relevant to understand fungi's tolerance and forecast how they might respond to climatic changes.

The aim of this study was to examine differences in fungal niche breadth, determine the importance of environmental variables on fungal zOTUs (Zero-radius Operational Taxonomic Unit) abundance, and model the zOTUs abundance of taxonomic and functional groups along different gradients.

Here, using data from 136 soil samples collected from the western Swiss Alps, I investigated different hypotheses. First, I expected a difference of niche breadth between the different taxonomic groups and their respective functional groups as each group occupies a different trophic environment and rely on different strategies to maintain their growth (Käärik, 1975; Powlson et al., 2001; Harman, 2011; Yuan et al., 2012; Hiiesalu et al., 2014; Sun et al., 2019). Secondly, I expected that edaphic and climatic variables would change the abundance of the different functional and taxonomic groups as microorganisms distribution partly rely on edaphic and climatic variables.

Materials & Methods

Study area

In this study, 136 sites, in 700km² were sampled at different elevation ranging from 425m to 3120m in a well-studied area in the western Swiss Alps. In general, climate conditions are heterogeneous, with annual mean temperatures between 8°C at 1600 m and -5°C at 3000 m. Precipitations sums varying from 1200 mm at 600 m and 2600 mm at 3000 m (Buchot, 1975).

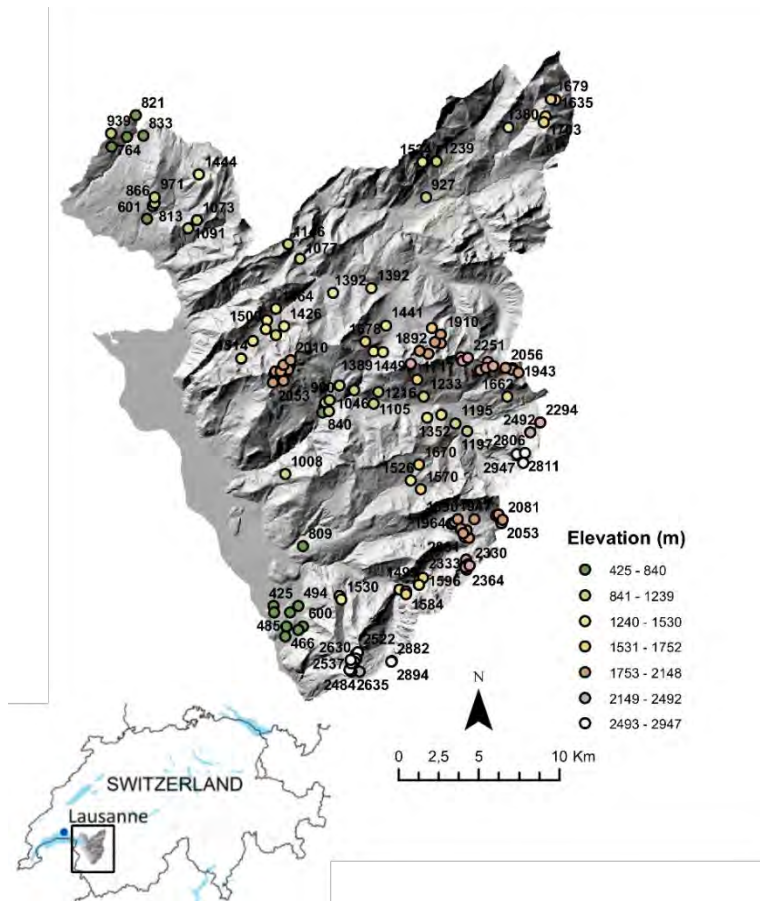


Figure 1 : Location of the 136 study sites in the western Swiss Alps

Environmental predictors

A total of 12 environmental predictors were selected based on a previous study conducted by Malard et al., 2021 in review in the same study area : *Soil temperature*, *Soil Water Content*, *pH*, *Total Organic Carbon*, *Max temperature of warmest month (bio5_tmax)*, *Electroconductivity*, *Sum of growing day degree days above 3°C (gdd3)*, *Freezing Degrees Day*, *phosphate*, *Annual precipitation (bio12)*, *plant richness* and *Snow Cover Duration*. A second selection has been conducted in order to remove collinearity in the analysis by calculating the correlation with the package *corrgram* between predictors. All environmental variables with a correlation higher than 0.7 have been removed. At the end, 9 environmental predictors were conserved : *Soil temperature*, *Soil Water Content*, *pH*, *Total Organic Carbon*, *Max temperature of warmest month (bio5_tmax)*, *Electroconductivity*, *Sum of growing day degree days above 3°C (gdd3)*, *Freezing Degrees Day* and *phosphate*.

Data collection, DNA extraction, amplicon sequencing and bioinformatic processing

All those steps had been conducted before starting my project. They are described in Malard et al. (2021). Soil DNA was extracted using the PowerSoil kit (Qiagen) and then the ITS region was sequenced using the primers ITS1F and ITS2 using Illumina sequencing HiSeq 2500 platform at the Genomic Technologies Facility of the University of Lausanne. A custom bioinformatic pipeline was created to process the sequences and to obtain a zOTUs table. Taxonomy was assigned against the full SILVA v132 database (Yilmaz et al., 2014) using the RDP (ribosomal database project) naive Bayesian classifier v2.12 (Wang et al., 2007) with the UNITE (fungal ITS trainset 07/04/2014).

Niche breadth and niche position calculation

All analyses were performed in the R environment (Team, 2017). Functional groups were assigned based on the taxonomy using the *microeco* package (Liu et al., 2021), with the FUNGUILD database (Nguyen et al., 2016). In total, nine-teen functional groups were assigned to all the zOTUs. However, only the three main fungal functional groups were conserved: Saprotrophs, Pathotrophs and Symbiotrophs. The niche breadth and niche position were calculated for each zOTUs, using the function “*ecospat.nichePOSNB*” in the *ecospat* package (Di Cola et al., 2017; Malard et al., 2021).

The niche breadth was calculated as the standard deviation of each abiotic variable, weighted by the abundance of the zOTUs at each sampling site, and the niche position as the mean of the variable, weighted by the abundance of the zOTUs at each sampling site. This process was repeated for each of the nine variables. This function results in a value for the niche breadth, associated with a niche position values. To characterize the relation of the regression between the niche breadth and the niche position, R-squared value between both was calculated, as well as the p-value. Results were plotted using the *ggplot2* package (Wickham, 2016).

Modelling

In order to predict the zOTUs abundance for all 136 sites, species distribution models (SDMs) were fitted by relating zOTU abundance to the environmental predictors using Generalized Additive Models (GAMs; Guisan et al., 2002) using the *mgcv* package in R (Wood, 2011). First,

all zOTUs with less than 10 occurrences in all sites were removed to reduce the impact of rare species on the model, reducing the total number of zOTUs from 82375 to 43483.

Then, RandomForest model were built to investigate the importance of environmental variables on the abundance of each zOTUs. This model was chosen because it is one of the most used in species distribution studies. The increase of the mean squared error (%IncMSE) has been used for this purpose. This metric indicates the increase in the mean squared error of prediction after permuting this variable. This give us the most important variable for the abundance of zOTUs.

In order to have an understanding of the fungi's abundance variation, the abundance of each zOTU was modelled as a function of the nine environmental predictors (*Total Organic Carbon, Soil Water Content, gdd3, Electronical Conductivity, Total Phosphorus, bio5_tmax, pH, Soil temperature and Freezing degree days*) using generalized additive models with negative binomial distribution (GAMnb) from the R-package mgcv (Wood, 2011). The choice of this model was based on a previous study showing the higher performance of this model compared to others (Mod et al., 2021). The logarithm of the total sequence count for each zOTU has been added as an offset to reduce the effect of the varying abundance of each zOTU (Mod et al., 2021).

The model fit, which is the success with which the model has managed to adjust to the data, was assessed by the correlation between our observed values and the fitted values.

To evaluate the model prediction performance, cross-validation has been used. The model was evaluated 100 times, each time taking randomly 80% of the data to train the training, and 20% for evaluation. This way, each site was used the same number of times as the other sites. As for the fit, the correlation between observed values and predicted values was calculated and used to evaluate the model.

Finally, response curves (Elith et al., 2005) that represent the predicted abundance in function of a specific gradient were obtained for each zOTU and for each environmental variables. Then, all response curves were aggregated into taxonomic and functional groups. To obtain those response curves the predicted abundance has been calculated with only the variable of interest that changed from its minimum to its maximum value while, all others variables were fixed at their median.

Results

Functional group's niche

Table 1: Niche breadth analysis. Adjusted R-squared values and their significance according to three functional groups and unassigned zOTUs, for 9 specific gradients. The red gradient is relative to the correlation values: the higher the correlation value, the redder the cell. Significance levels: ***: p-value < 0.001; **: p-value < 0.01; *: p-value ≤ 0.05; NS: p-value > 0.05.

Environmental gradients	Pathotroph		Saprotroph		Symbiotroph		Unassigned	
	adj.R2	p-val.	adj.R2	p-val.	adj.R2	p-val.	adj.R2	p-val.
Total Organic Carbon content (wt %)	0,47	***	0,35	***	0,34	***	0,5	***
Soil Water Content (%)	0,44	***	0,4	***	0,38	***	0,52	***
Sum of growing degree days above 3°C (°C)	0,26	***	0,22	***	0,21	***	0,33	***
Electrical Conductivity (1:1 µS/cm)	0,24	***	0,21	***	0,16	***	0,28	***
Total Phosphorus (mg/g)	0,19	***	0,24	***	0,21	***	0,3	***
Max temperature of warmest month (°C)	0,09	***	0,03	***	0,03	***	0,1	***
pH	0,08	***	0,15	***	0,05	***	0,14	***
Soil Temperature (C°)	0,03	***	0,03	***	0,04	***	0,01	***
Freezing degree days - Sum of temperatures <0°C (°C)	0,03	***	0,01	***	0,01	***	0,01	***
Total zOTUs	2511		16241		10960		36881	

The results of the niche calculation for the three functional groups (Table 1) indicate that two environmental gradients have an important correlation with the niche breadth of all three functional groups. Indeed, TOC have a adj.R² of 0.47 for Pathotrophs, 0.35 for Saprotrophs and 0.34 for Symbiotrophs. Unassigned zOTU have a adj.R² of 0.5. SWC have also high adj.R², 0.44 for Pathotrophs, 0.4 for Saprotrophs, 0.38 for Symbiotrophs and 0.52 for unassigned zOTUs.

Of all of three functional groups, Pathotrophs have the two highest adj.R² values of TOC and SWC, suggesting that the niche breadth of Pathotrophs is more correlated with TOC and SWC gradient. The seven other gradients generally have an adj.R² lower than 0.20. The trend of this correlation is represented in Figure 2.

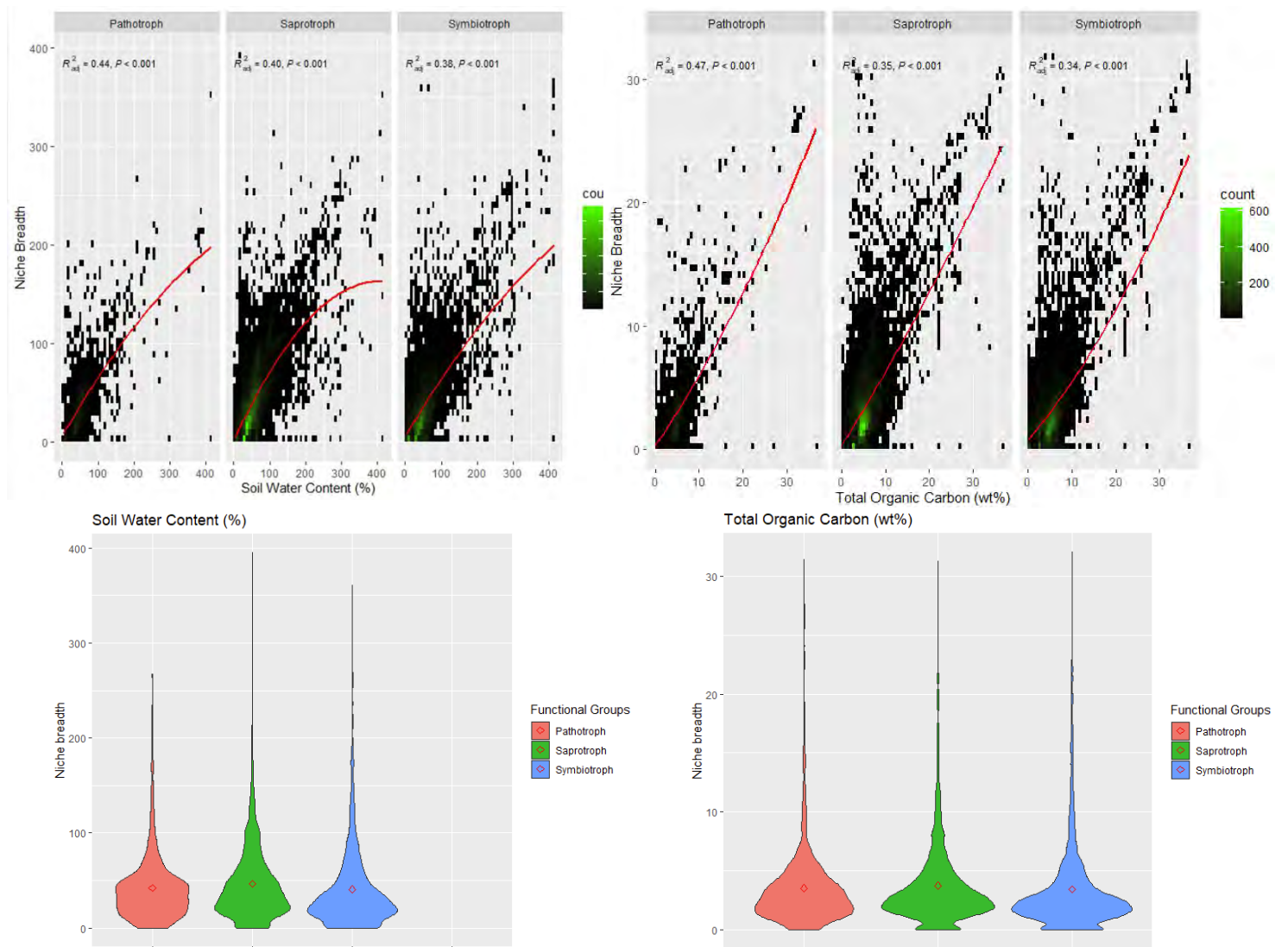


Figure 2: Niche breadth values in function of Soil Water Content and Total Organic Carbon gradients, for 3 functional groups. Each square represents an zOTU, the red line is a regression line based on a second degree polynomial ($y \sim \text{poly}(x, 2)$). The point density is represented in green to black. The violin plots represent the niche breadth distribution, the mean is represented by the square.

For Soil Water Content and Total Organic Carbon, although all functional groups have an important zOTUs density with low niche breadth value, it seems that Saprotrophs and Symbiotrophs have a higher number of zOTUs with a high niche breadth value. However, this observation must be interpreted carefully due to the differences of zOTUs number (Table 1) between Pathotrophs (2511), Saprotrophs (16 241) and Symbiotrophs (10 960).

Taxonomic group's niche

Table 2: Niche breadth analysis. Adjusted R-squared values and their significance according to five taxonomic groups and unassigned zOTUs, for 9 specific gradients. The red gradient is relative to the correlation values: the higher the correlation value, the redder the cell. Significance levels: ***: p-value < 0.001; **: p-value < 0.01; *: p-value ≤ 0.05; NS: p-value > 0.05.

Environmental gradients	Ascomycota		Basidiomycota		Chytridiomycota		Glomeromycota		Zygomycota		Unidentified	
	adj.R2	p-val.	adj.R2	p-val.	adj.R2	p-val.	adj.R2	p-val.	adj.R2	p-val.	adj.R2	p-val.
Total Organic Carbon	0,4	***	0,36	***	0,65	***	0,54	***	0,51	***	0,54	***
Soil Water Content (%)	0,43	***	0,3	***	0,53	***	0,42	***	0,5	***	0,56	***
Growing Degree-Day 3	0,21	***	0,17	***	0,2	***	0,18	***	0,3	***	0,42	***
Electronical Conductivity	0,22	***	0,18	***	0,26	***	0,14	***	0,2	***	0,32	***
Total Phosphorus (mg/g)	0,23	***	0,24	***	0,33	***	0,26	***	0,31	***	0,3	***
bio5_tmaxw	0,03	***	0,03	***	0,04	***	0,04	***	0,08	***	0,16	***
pH	0,12	***	0,07	***	0,11	***	0,12	***	0,17	***	0,18	***
Soil Temperature (C°)	0,05	***	0,02	***	0,02	***	0,03	***	0,04	***	0,02	***
Freezing Degree-Day	0,01	***	0,01	**	0,01	**	0,02	***	0,02	***	0,01	***
Total zOTUs	31240		16425		937		24007		5593		4173	

The niche calculation is similar to the three functional groups for the five taxonomic groups at the phylum level (Table 2). Indeed, TOC and SWC have the highest R^2 value for all of the groups, with a maximum value of TOC (0.65) and SWC (0.53) for *Chytridiomycota*. The trend of this relation is shown on Figure 3. However, as before, this observation must be interpreted with care due to the low number of zOTUs belonging to *Chytridiomycota* (937) compare to the other taxonomic groups.

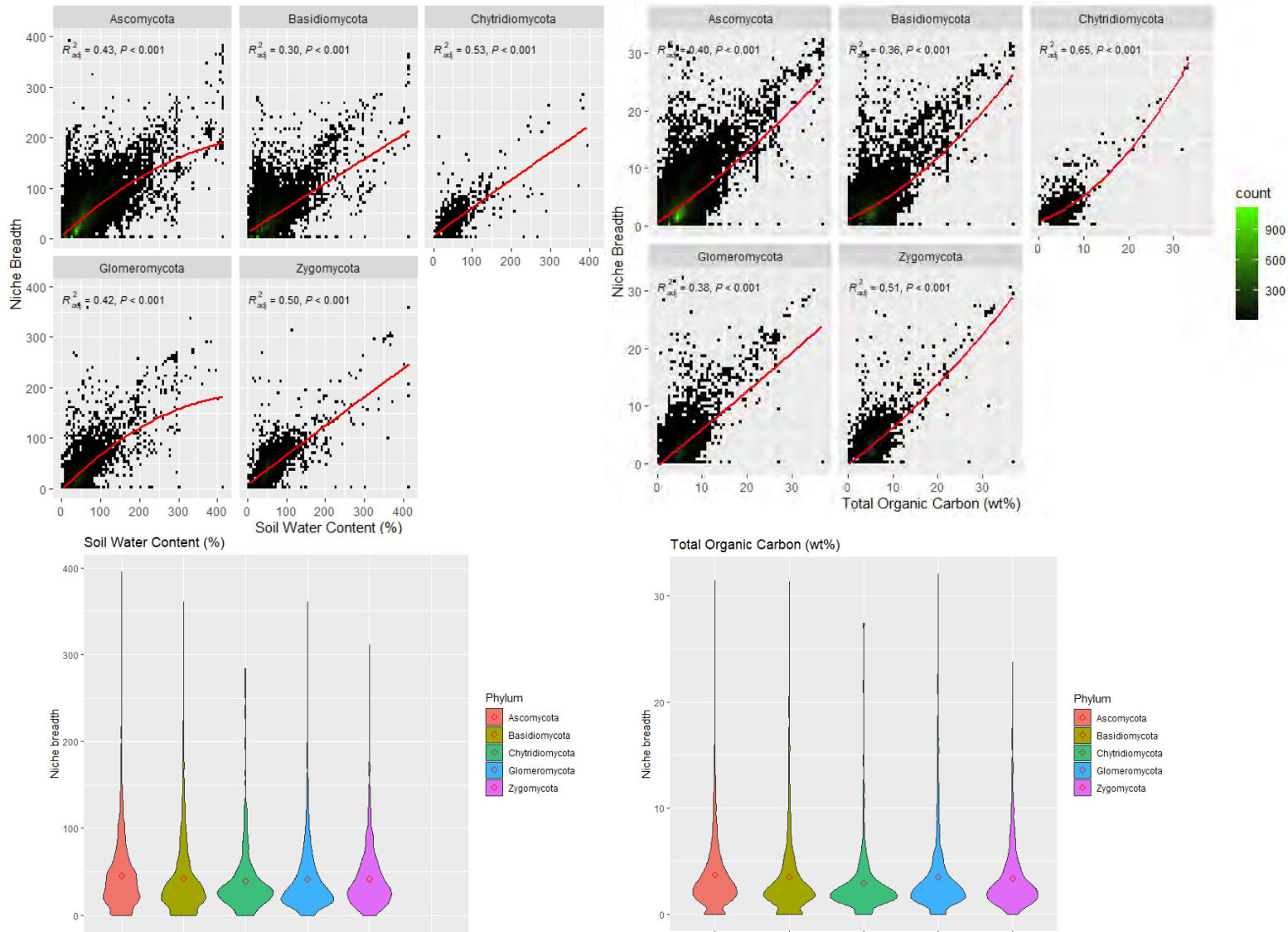


Figure 3: Niche breadth values in function of SWC and TOC gradients, for 5 taxonomical groups. TOC (wt%) : weight pourcent. Each point represents a zOTU, the red line is a regression line based on a second degree polynomial ($y \sim \text{poly}(x, 2)$). The point density is represented in green to black. The violin plots represent the niche breadth distribution, the mean is represented by the square.

Random Forest

The importance of the variables was calculated for each functional group but each functional group has the same results as the ones shown in Figure 4.

The Random Forest results (Figure 4) indicated that two climatic variables, gdd3 and bio5_tmaxw are the predictors that influence the distribution of zOTUs the most with an increase of the mean squared error(%IncMSE) of ~6.5. Three edaphic variables, pH, Freezing Degree Day and Total Organic Carbon are behind with a respective %IncMSE of 4.1, 3.7 and 2.9.

Finally, total phosphorus, Soil Water Content, soil Temperature and Electrical Conductivity have an %IncMSE lower than 1.5. The importance of the variables was also calculated for each functional group but these are not shown here because each functional group has the same results as in Figure 4.

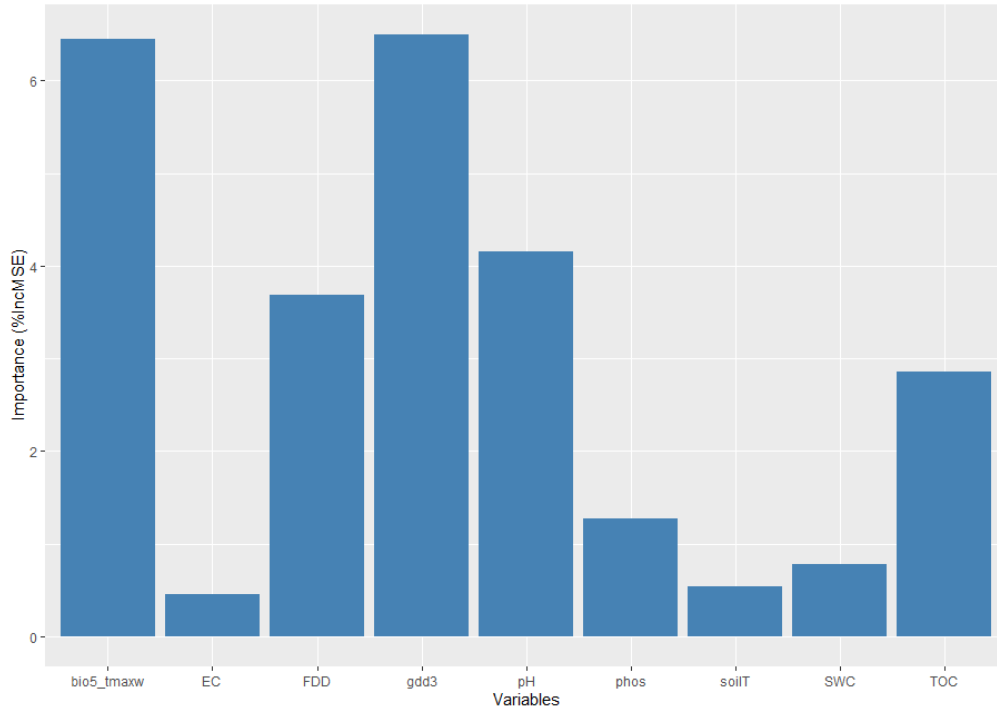


Figure 4: Importance of the nine different variables based on Random Forest for all zOTUs. The importance is expressed in percentage of the mean square error increase, bio5_tmaxw max temperature of warmest month (°C), EC electrical conductivity (1:1 $\mu\text{S}/\text{cm}$), FDD freezing degree days – Sum of temperature $<0^\circ\text{C}$ (°C), gdd3 Sum of growing degree days above 3°C (°C), pH soil pH, phos total phosphorus content (mg/g), soilT soil temperature (°C), SWC bulk soil water content (%), TOC Total organic carbon content (wt %).

GAMnb's performance

According to the measures of model's performance (Figure 5), the average correlation between observed and fitted abundance is 0.5. Moreover, the average correlation between observed and predicted abundance is 0.3.

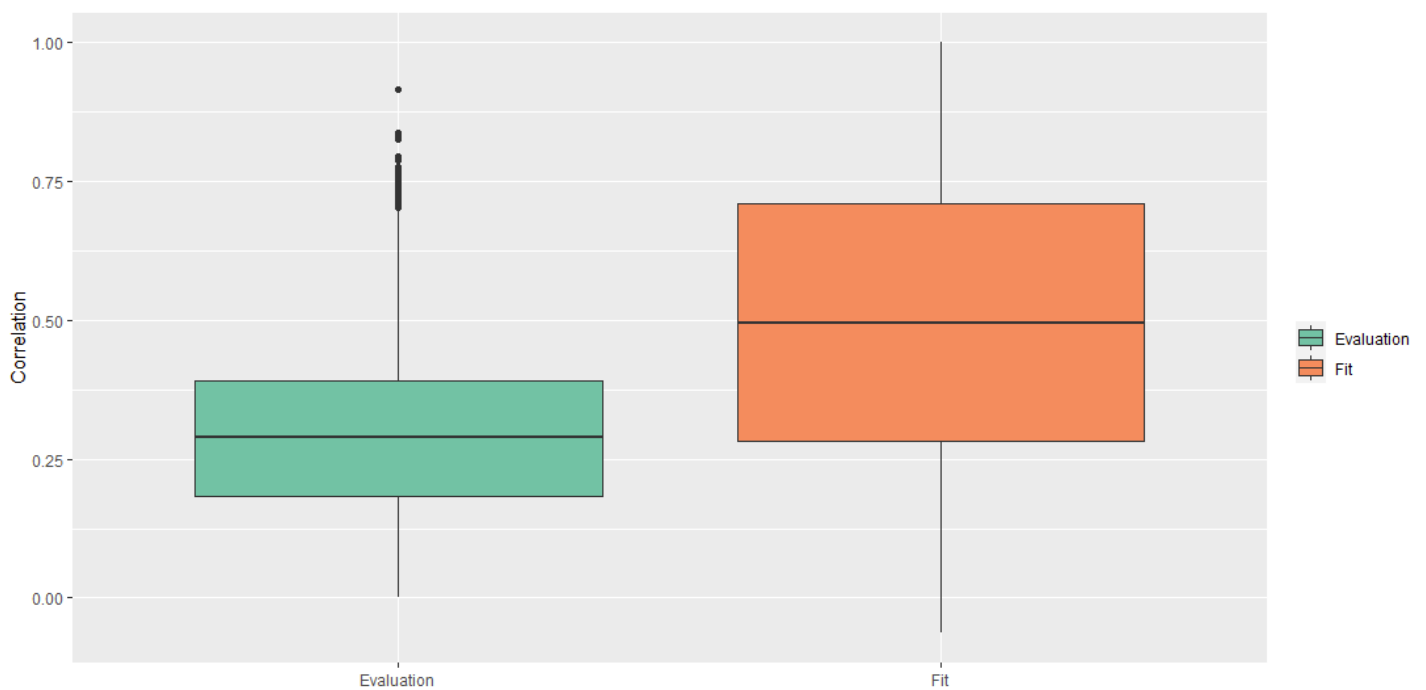


Figure 5: Model performance of GAMnb, measured with correlation between observed and predicted abundance (Evaluation), and correlation between observed and fitted abundance (Fit).

Functional groups GAMnb

The response curves of functional groups are shown on Figure 6 and Figure 7. Six environmental gradient are represented : gdd3, bio5_tmaxw and FDD for climatic variables, and pH, TOC and SWC for the edaphic variables, as the random forest identified them as key variables. For all functional groups, as the soil water content or the total organic carbon increases, the zOTUs abundance also increases (Figure 6).

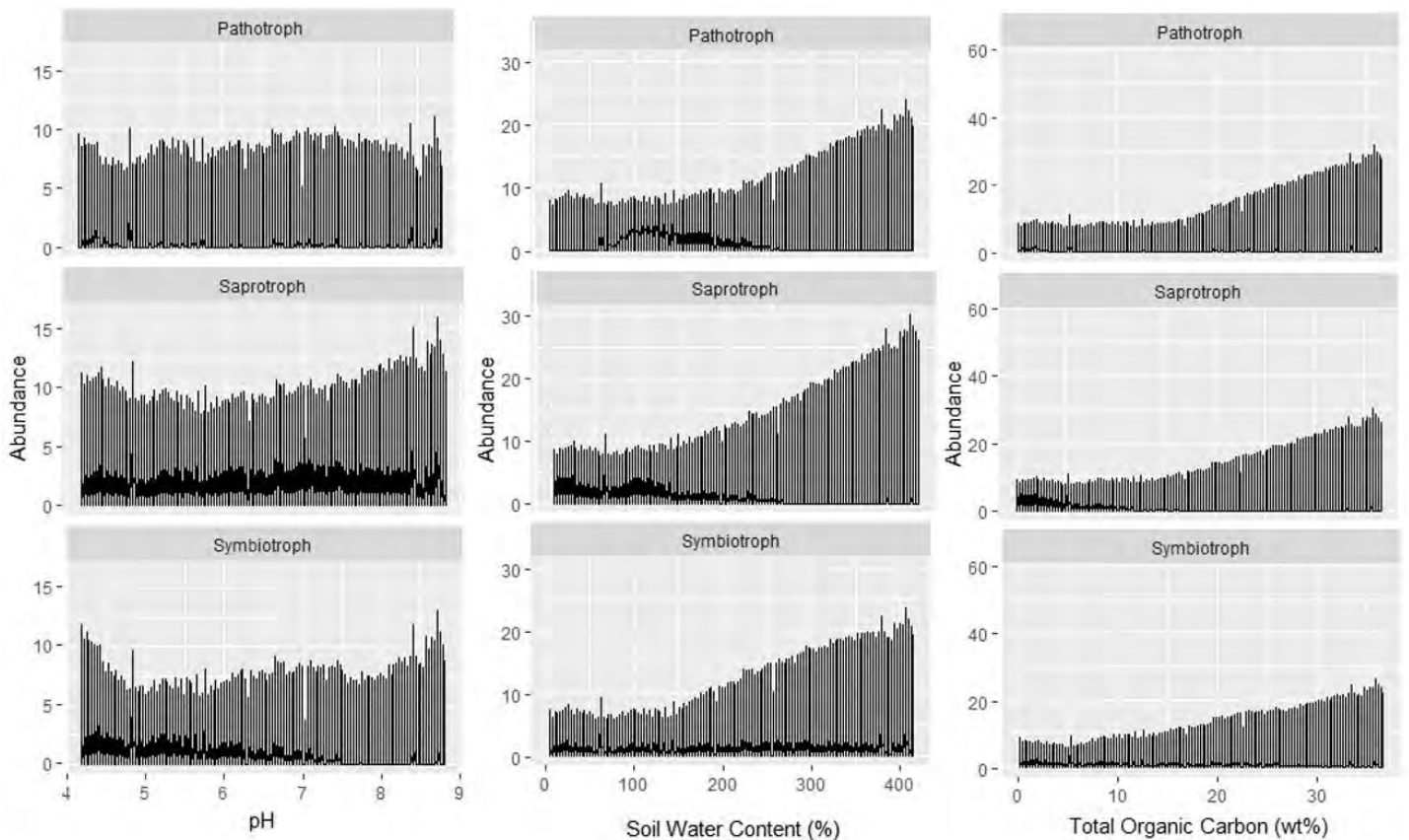


Figure 6: Response curves representing the variation of three functional groups along three edaphic gradients, based on aggregation of GAMnb of all individual zOTUs. . Each line represent the maximum abundance of all zOTUs at a specific value of the gradient. The response curves can be obtain by following the top of each line. Black lines are an artefact.

However, the abundance of all functional group doesn't really change along the pH gradient. Indeed, the abundance stagnate around 8, with a slightly increase of Saprotrophs abundance when the pH is high, and an abundance maximal at both high and low pH for Symbiotrophs.

Concerning the abundance along the climatic gradients (Figure 7), results indicate for all functional groups a similar trend. Between the minimal value and the medium value of the gradient, the abundance is decreasing to attain a minimum , then stagnate until increasing.

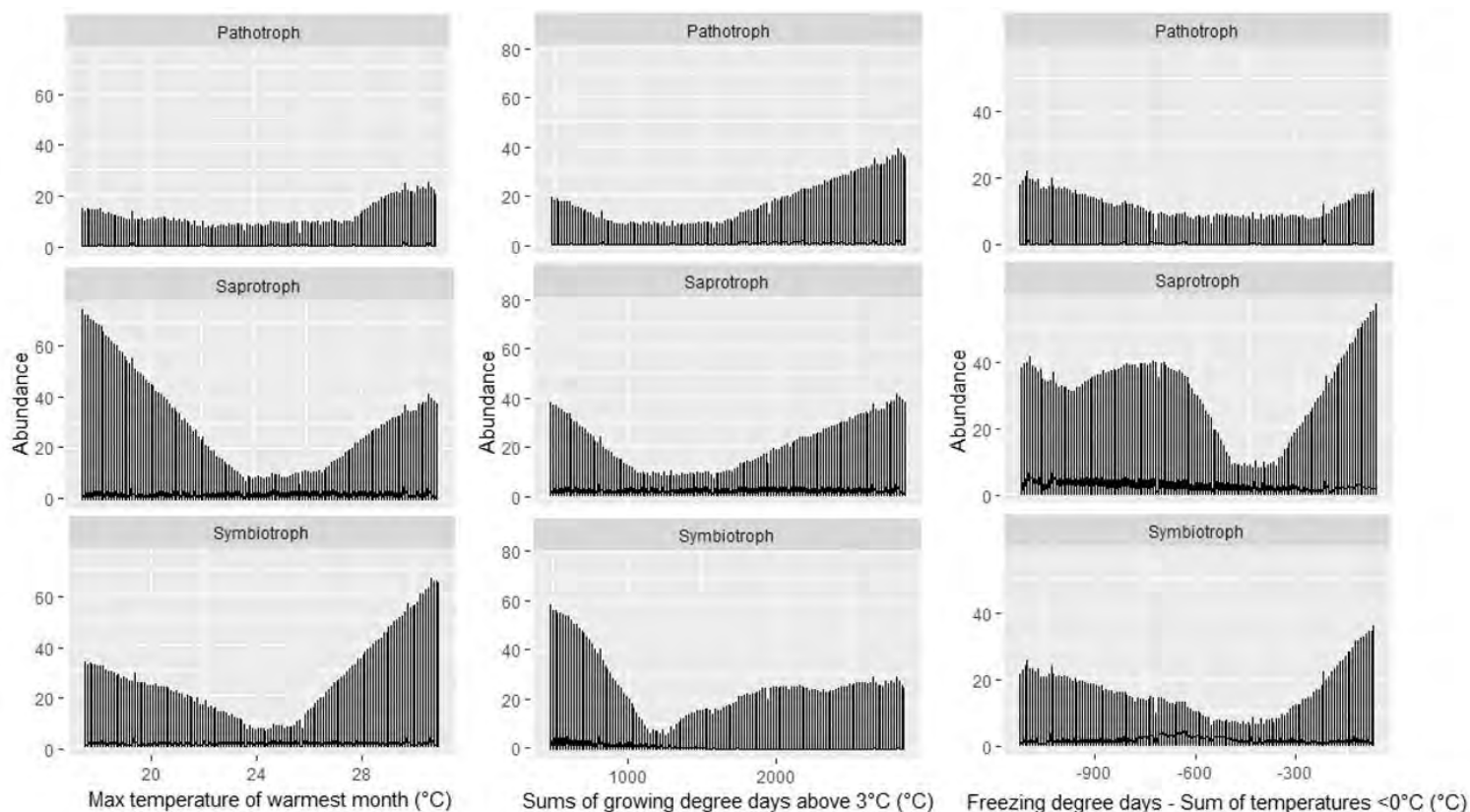


Figure 7: Response curves representing the variation of three functional groups along three climatic gradients, based on aggregation of GAMnb of all individual zOTUs. . Each line represent the maximum abundance of all zOTUs at a specific value of the gradient. The response curves can be obtain by following the top of each line. Black lines are an artefact.

Taxonomic groups GAMnb

The response curves of functional groups are shown on Figure 8 and Figure 9. As before, six environmental gradients are represented : gdd3, bio5_tmaxw and FDD for climatic variables, and pH, TOC and SWC for the edaphic variables. For all taxonomic groups, as the soil water content or the total organic carbon increases, the zOTUs abundance also increases (Figure 8). However, the abundance of all taxonomic group doesn't really change along the pH gradient. Indeed, the abundance stagnate around 8, with a slightly increase of *Ascomycota* abundance when the pH is high, and an abundance maximal at both high and low pH for *Zygomycota* and *Basidiomycota*.

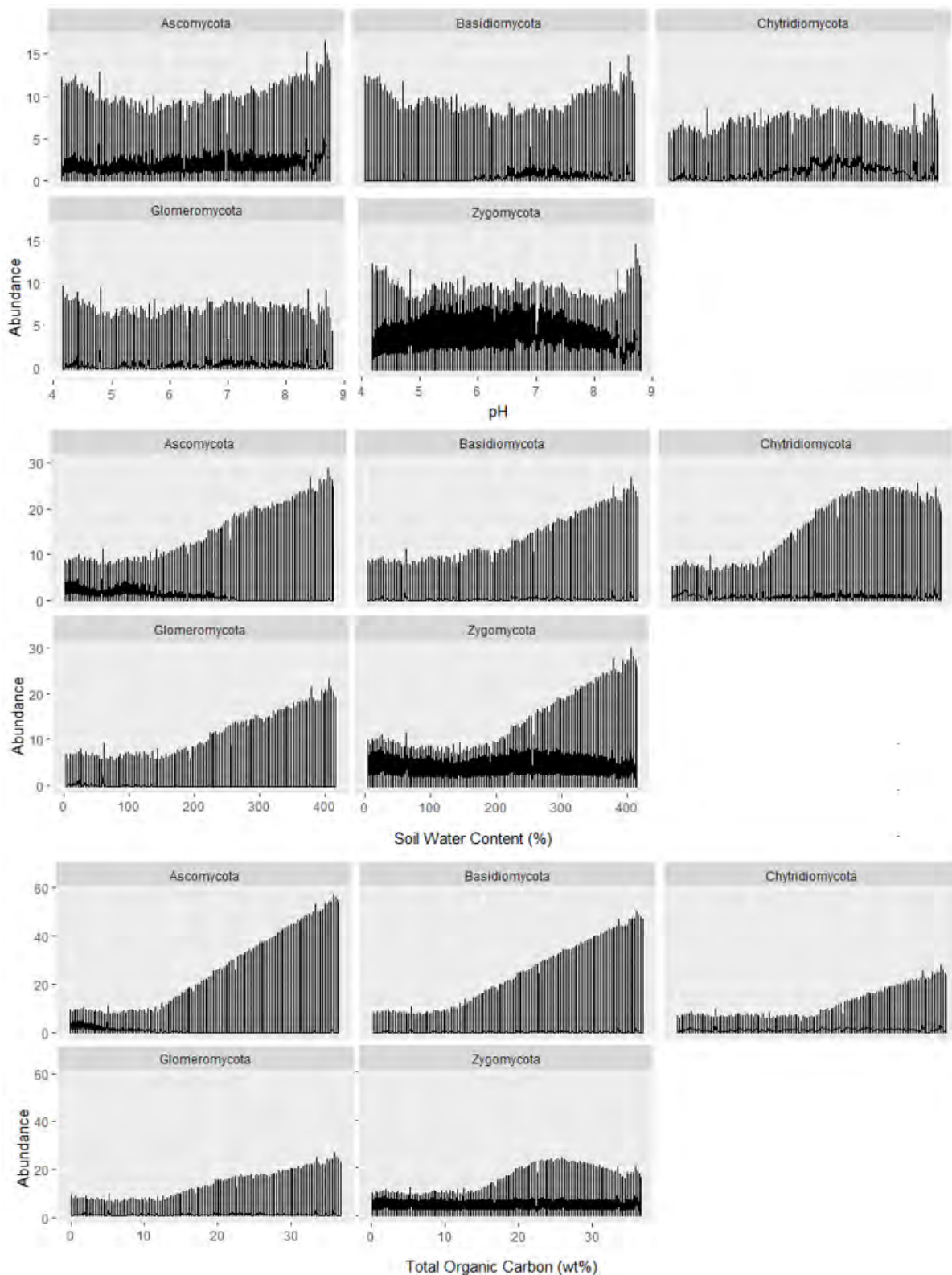


Figure 8: Response curves representing the variation of five taxonomic groups along three edaphic gradients, based on aggregation of GAMnb of all individual zOTUs. Each line represent the maximum abundance of all zOTUs at a specific value of the gradient. The response curves can be obtain by following the top of each line. Black lines are an artefact.

Concerning the abundance along the climatic gradients (Figure 9), results indicate for all taxonomic groups a similar trend. Between the minimal value and the medium value of the gradient, the abundance is decreasing to attain a minimum, then stagnate until increasing. However, *Chytridiomycota*'s abundance seems to increase as bio5_tmaxw and FDD increase, but for gdd3, the abundance is decreasing. Moreover, *Zygomycota*'s abundance decrease as all three gradients increase.

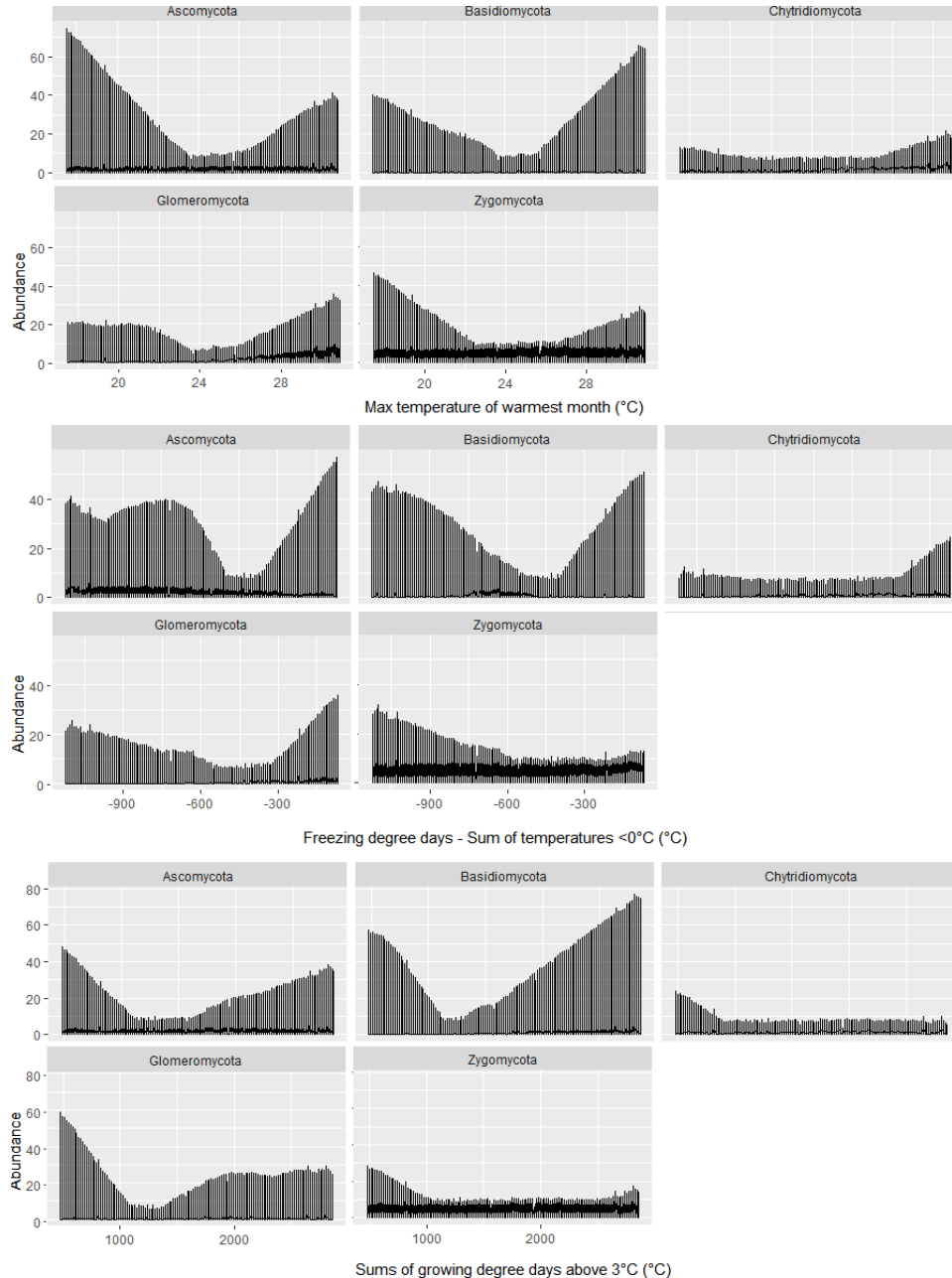


Figure 9: Response curves representing the variation of five taxonomic groups along three climatic gradients based on aggregation of GAMnb of all individual zOTUs. Each line represent the maximum abundance of all zOTUs at a specific value of the gradient. The response curves can be obtain by following the top of each line. Black lines are an artefact

Discussion

In this study, the variation of the niche breadth and the niche position, along different climatic and edaphic variable as well as the variation of fungi's abundance along environmental gradients was tested in order to assess how essential ecological function might change in the face of climatic changes, as well as to forecast how fungi abundance change along different environmental gradients. For this, I posed two hypotheses (i) Niche breadth change between groups, (ii) fungi abundance varies along environmental gradients.

Niche breadth calculation allowed us to observe the value of the niche breadth as a function of the niche position. Overall, the three functional groups, Pathotrophs, Saprotrophs and Symbiotrophs as well as the 5 taxonomic groups have the same niche breadth for the same environmental predictors. For the majority of environmental variables, zOTUs have a low niche breadth value regardless of the niche position value (Table 1, Table 2). Species with a low niche breadth can be considered as low tolerance and therefore qualified as specialists (Binzer et al., 2011). These species are likely to be more sensitive to climate change and have a higher risk of extinction during abrupt changes. (Slatyer et al., 2013).

However, two edaphic variables stand out : Total Organic Carbon (TOC) and Soil Water Content (SWC). Indeed, zOTUs with a high niche position have a high breadth value for these two variables. A high niche breadth value implies that these species can withstand a wider range of environmental conditions and may be more tolerant to climate changes. (Thuiller et al., 2005). Those zOTUs are qualified as generalists.

These initial results show that there are no strong differences between functional and taxonomic groups and indicate that most species are specialists for most environmental variables, and therefore subject to extinction risk in the face of climate change.

In addition to investigating the niche breadth of different fungal groups, the abundance of these groups was tested along different environmental gradients. The random forest analysis indicates that climatic variables are the main driver of the abundance (Figure 4), followed by edaphic variables.

The variation in abundance of the different functional groups as well as that of the different taxonomic groups is similar. There is little or no difference between them. Indeed, along the gradients of edaphic variables, the abundance of species increases when SWC increases or TOC increases. This can be explained by the fact that fungi are heterotrophic organisms and grow efficiently in carbon-rich environments that allow them to increase their growth rate and their protein production (Broach, 2012). Moreover, it has been shown that precipitation, which is correlated with SWC, have an positive impact on fungi's abundance (Zhang et al., 2016).

However, the abundance remains stable for pH, which is quit unexpected. The important role of pH in richness and diversity of the majority of the microbial groups has already been discussed quite often (Delgado-Baquerizo et al., 2018; Malard et al., 2019; Malard et al., 2021; Mod et al., 2021), leading to an important knowledge of it impact on microbial communities. A previous study show that most of the species with a low or high niche position for pH tend to be specialists (Malard et al., 2021). This master project highlight that if the pH is increasing or decreasing, the overall abundance remains stable. A potential explanation to this is that species have a high potential of adaptation against pH changes.

For climatic gradients, the abundance of different functional and taxonomic groups is high when the gradients take their maximum or minimum value, and low when they take an intermediate value . Both high temperature and low temperature seems to be beneficial for zOTUs abundance. However, some results contradict each other. Indeed, the three different predictors (*gdd3*, *bio5_tmaxw* and *FDD*) are directly correlated with temperature, but each predicts a different abundance. For example, Symbiotrophs are more abundant when *bio5_tmaxw* is high than when it is low, while for *gdd3* and *FDD*, it is the opposite (Figure 7). Chytridiomycota's abundance decrease as *gdd3* increase, but increase as *bio5_tmaxw* and *FDD* increase.

These inconsistencies are probably due to poor model performance. Furthermore, even if the correlation value is low (0.3), the value is positive, which means that the model predicts better than random prediction. The higher the correlation value is, the more predictive of reality the model is. However, Mod et al., 2021 compare different model performances and GAMnb is the best performing. Furthermore, their correlation values are similar to those found for this study. Although these seem low, they are not unexpected for this kind of data. An explanation for such low values may be that edaphic and climatic variables are not the only variables that shape the fungi's abundance. Other variable like dispersal rate or dispersal vector can explain zOTUs abundance (Edman et al., 2004). Biotic interactions can also shape fungi's distribution.

For example, Pathotrophs and Symbiotrophs rely on other organisms to survive, and so their distribution depend partly on their hosts distribution. Moreover, as explained in Ferrier & Guisan (2006), different modelling strategies are possible. In this project, the strategy “predict first, assemble later” has been used. Indeed, a model (GAMnb) was run for all zOTUs, and then we classified them by taxonomic groups and functional groups. However, the abundance of each zOTUs in each groups wasn’t added up. An interesting perspective would be to the sum of all abundance in each group, or to use another strategy “assemble first, predict later”. In this case, I would have classified all zOTUs corresponding to the same taxonomic group or functional group together, and then run a model for each group.

Moreover, niche breadth investigation was carried out on a reduced area, with only a restricted range of environmental data and can lead to a niche truncation (Chevalier et al., 2021). Niche truncation refers to niches that are incompletely characterized. Those results are only applicable for the well-studied and well-referenced region of the western Swiss Alps. Indeed, here, we cover a specific range of the different gradient. It is possible that zOTUs appearing as specialist here may have larger niches. A worldwide study is necessary to have deeper knowledge of fungi’s niche breadth and distribution faced to climate change, but data are lacking, especially soil data.

To conclude, this study shows that overall, all taxonomical groups or functional group have similar niche breadth along same environmental variable, and that fungi’s population are mainly specialists, subject to extinction risk in the face of climate change. It also show that fungi’s abundance is more likely to increase as edaphic gradient increase, and that both high and low temperature are favourable for zOTUs abundance.

Acknowledgments

I would like to thank Lucie Malard for her supervision all throughout the entire project, and her feedbacks concerning this manuscript. Special thanks to Valentin Verdon who helped me understand and code the modelisation part, and also gave me feedback on my work. Finally, I would like to thank Antoine Guisan for his advice and commentaries on this Master project.

References

- Binzer, A., Brose, U., Curtsdotter, A., Eklöf, A., Rall, B. C., Riede, J. O., & de Castro, F. (2011). The susceptibility of species to extinctions in model communities. *Basic and Applied Ecology*, 12(7), 590–599. doi: 10.1016/j.baae.2011.09.002
- Broach, J. R. (2012). Nutritional Control of Growth and Development in Yeast. *Genetics*, 192(1), 73–105. doi: 10.1534/genetics.111.135731
- Carscadden, K. A., Emery, N. C., Arnillas, C. A., Cadotte, M. W., Afkhami, M. E., Gravel, D., ... Wiens, J. J. (2020). Niche Breadth: Causes and Consequences for Ecology, Evolution, and Conservation. *The Quarterly Review of Biology*, 95(3), 179–214. doi: 10.1086/710388
- Case, R. J., Boucher, Y., Dahllöf, I., Holmström, C., Doolittle, W. F., & Kjelleberg, S. (2007). Use of 16S rRNA and rpoB Genes as Molecular Markers for Microbial Ecology Studies. *Applied and Environmental Microbiology*, 73(1), 278–288. doi: 10.1128/AEM.01177-06
- Chevalier, M., Broennimann, O., Cornuault, J., & Guisan, A. (2021). Data integration methods to account for spatial niche truncation effects in regional projections of species distribution. *Ecological Applications*, 31(7), e02427. doi: 10.1002/eap.2427
- Colwell, R., Brehm, G., Cardelus, C., Gilman, A., & Longino, J. (2008). Global Warming, Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science (New York, N.Y.)*, 322, 258–261. doi: 10.1126/science.1162547
- Delgado-Baquerizo, M., Oliverio, A. M., Brewer, T. E., Benavent-González, A., Eldridge, D. J., Bardgett, R. D., ... Fierer, N. (2018). A global atlas of the dominant bacteria found in soil. *Science. (world)*. doi: 10.1126/science.aap9516

- Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., ...
 Guisan, A. (2017). ecospat: An R package to support spatial analyses and modeling of
 species niches and distributions. *Ecography*, 40(6), 774–787. doi: 10.1111/ecog.02671
- Edman, M., Kruys, N., & Jonsson, B. G. (2004). Local Dispersal Sources Strongly Affect
 Colonization Patterns of Wood-Decaying Fungi on Spruce Logs. *Ecological
 Applications*, 14(3), 893–901. doi: 10.1890/03-5103
- Elith, J., Ferrier, S., Huettmann, F., & Leathwick, J. (2005). The evaluation strip: A new and
 robust method for plotting predicted responses from species distribution models.
Ecological Modelling, 186(3), 280–289. doi: 10.1016/j.ecolmodel.2004.12.007
- Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane
 species under climate change. *Nature Climate Change*, 5(8), 772–776. doi:
 10.1038/nclimate2656
- Exploring Microbial Diversity—A Vast Below. (n.d.). Retrieved January 8, 2022, from
<https://www.science.org/doi/full/10.1126/science.1118176>
- Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level.
Journal of Applied Ecology, 43(3), 393–404. doi: 10.1111/j.1365-2664.2006.01149.x
- Fisher-Reid, M. C., Kozak, K. H., & Wiens, J. J. (2012). How Is the Rate of Climatic-Niche
 Evolution Related to Climatic-Niche Breadth? *Evolution*, 66(12), 3836–3851. doi:
<https://doi.org/10.1111/j.1558-5646.2012.01729.x>
- Gehrig-Fasel, J., Guisan, A., & Zimmermann, N. E. (2007). Tree line shifts in the Swiss Alps:
 Climate change or land abandonment? *Journal of Vegetation Science*, 18(4), 571–582.
 doi: <https://doi.org/10.1111/j.1654-1103.2007.tb02571.x>
- Guisan, A., Edwards, T. C., & Hastie, T. (2002). Generalized linear and generalized additive
 models in studies of species distributions: Setting the scene. *Ecological Modelling*,
 157(2), 89–100. doi: 10.1016/S0304-3800(02)00204-1

- Harman, G. E. (2011). Multifunctional fungal plant symbionts: New tools to enhance plant growth and productivity. *New Phytologist*, 189(3), 647–649. doi: 10.1111/j.1469-8137.2010.03614.x
- Hiiesalu, I., Pärtel, M., Davison, J., Gerhold, P., Metsis, M., Moora, M., ... Wilson, S. D. (2014). Species richness of arbuscular mycorrhizal fungi: Associations with grassland plant richness and biomass. *New Phytologist*, 203(1), 233–244. doi: 10.1111/nph.12765
- Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415–427. doi: 10.1101/SQB.1957.022.01.039
- Käärik, A. (1975). Succession of Microorganisms during Wood Decay. In W. Liese (Ed.), *Biological Transformation of Wood by Microorganisms* (pp. 39–51). Berlin, Heidelberg: Springer. doi: 10.1007/978-3-642-85778-2_4
- Körner, C. (2004). Mountain Biodiversity, Its Causes and Function. *AMBIO: A Journal of the Human Environment*, 33(sp13), 11–17. doi: 10.1007/0044-7447-33.sp13.11
- Lenoir, J., Gégout, J. C., Marquet, P. A., Ruffray, P. de, & Brisse, H. (2008). A Significant Upward Shift in Plant Species Optimum Elevation During the 20th Century. *Science*. (world). doi: 10.1126/science.1156831
- Liu, C., Cui, Y., Li, X., & Yao, M. (2021). *microeco*: An R package for data mining in microbial community ecology. *FEMS Microbiology Ecology*, 97(2), fiae255. doi: 10.1093/femsec/fiae255
- Malard, L. A., Anwar, M. Z., Jacobsen, C. S., & Pearce, D. A. (2019). Biogeographical patterns in soil bacterial communities across the Arctic region. *FEMS Microbiology Ecology*, 95(9), fiz128. doi: 10.1093/femsec/fiz128

- Malard, L., Mod, H., Guex, N., Broennimann, O., Yashiro, E., Lara, E., ... Guisan, A. (2021a). *Comparative analysis of diversity and environmental niches of soil bacterial, archaeal, fungal and protist communities reveal niche divergences along environmental gradients in the Alps*. doi: 10.21203/rs.3.rs-609984/v2
- Malard, L., Mod, H., Guex, N., Broennimann, O., Yashiro, E., Lara, E., ... Guisan, A. (2021b). *The environmental niche of soil bacterial, archaeal, fungal and protist communities differ along edaphic and topoclimatic gradients in the Alps*. doi: 10.21203/rs.3.rs-609984/v1
- Mazel, F., Malard, L., Niculita-Hirzel, H., Yashiro, E., Mod, H. K., Mitchell, E. A. D., ... Guisan, A. (n.d.). Soil protist function varies with elevation in the Swiss Alps. *Environmental Microbiology*, n/a(n/a). doi: 10.1111/1462-2920.15686
- Mod, H. K., Buri, A., Yashiro, E., Guex, N., Malard, L., Pinto-Figueroa, E., ... Guisan, A. (2021). Predicting spatial patterns of soil bacteria under current and future environmental conditions. *The ISME Journal*. doi: 10.1038/s41396-021-00947-5
- Morin, X., & Lechowicz, M. J. (2013). Niche breadth and range area in North American trees. *Ecography*, 36(3), 300–312. doi: <https://doi.org/10.1111/j.1600-0587.2012.07340.x>
- Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., ... Kennedy, P. G. (2016). FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology*, 20, 241–248. doi: 10.1016/j.funeco.2015.06.006
- Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., ... Mountain Research Initiative EDW Working Group. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5(5), 424–430. doi: 10.1038/nclimate2563

- Powlson, D. S., Hirsch, P. R., & Brookes, P. C. (2001). The role of soil microorganisms in soil organic matter conservation in the tropics. *Nutrient Cycling in Agroecosystems*, 61(1), 41–51. doi: 10.1023/A:1013338028454
- Rubidge, E. M., Monahan, W. B., Parra, J. L., Cameron, S. E., & Brashares, J. S. (2011). The role of climate, habitat, and species co-occurrence as drivers of change in small mammal distributions over the past century. *Global Change Biology*, 17(2), 696–708. doi: 10.1111/j.1365-2486.2010.02297.x
- Sensitivity of predictive species distribution models to change in grain size—Guisan—2007—Diversity and Distributions—Wiley Online Library. (n.d.). Retrieved January 8, 2022, from <https://onlinelibrary.wiley.com/doi/full/10.1111/j.1472-4642.2007.00342.x>
- Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, 16(8), 1104–1114. doi: 10.1111/ele.12140
- Species Distribution Modeling—Miller—2010—Geography Compass—Wiley Online Library. (n.d.). Retrieved January 13, 2022, from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1749-8198.2010.00351.x?casa_token=mcUD0MhC1-gAAAAA:dsFHFks5jONoXQ6A2V3NlnKHf7U_ZjS706YYVotEo-e2hGCdy7e2gSlemIsJHPgKv-S4eB3ECSuUr-Qk
- Sun, J.-Z., Liu, X.-Z., McKenzie, E. H. C., Jeewon, R., Liu, J.-K. (Jack), Zhang, X.-L., ... Hyde, K. D. (2019). Fungicolous fungi: Terminology, diversity, distribution, evolution, and species checklist. *Fungal Diversity*, 95(1), 337–430. doi: 10.1007/s13225-019-00422-9

- Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., ...
Abarenkov, K. (2014). Global diversity and geography of soil fungi. *Science*,
346(6213). doi: 10.1126/science.1256688
- Theurillat, J.-P., & Guisan, A. (2001). Potential Impact of Climate Change on Vegetation in
the European Alps: A Review. *Climatic Change*, 50, 77–109. doi:
10.1023/A:1010632015572
- Thuiller, W., Lavorel, S., & Araújo, M. B. (2005). Niche properties and geographical extent
as predictors of species sensitivity to climate change. *Global Ecology and
Biogeography*, 14(4), 347–357. doi: [https://doi.org/10.1111/j.1466-
822X.2005.00162.x](https://doi.org/10.1111/j.1466-822X.2005.00162.x)
- Wang, Q., Garrity, G. M., Tiedje, J. M., & Cole, J. R. (2007). Naive Bayesian classifier for
rapid assignment of rRNA sequences into the new bacterial taxonomy. *Applied and
Environmental Microbiology*, 73(16), 5261–5267. doi: 10.1128/AEM.00062-07
- Wickham, H. (2016). *Ggplot2: Elegant graphics for data analysis* (2nd ed.) [PDF].
Springer International Publishing.
- Williams, J. N., Seo, C., Thorne, J., Nelson, J. K., Erwin, S., O'Brien, J. M., & Schwartz, M.
W. (2009). Using species distribution models to predict new occurrences for rare
plants. *Diversity and Distributions*, 15(4), 565–576. doi: 10.1111/j.1472-
4642.2009.00567.x
- Wood, S. (2012). *mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness
estimation*. Retrieved from <http://cran.r-project.org/web/packages/mgcv/index.html>
- Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood
estimation of semiparametric generalized linear models. *Journal of the Royal
Statistical Society: Series B (Statistical Methodology)*, 73(1), 3–36. doi:
10.1111/j.1467-9868.2010.00749.x

- Yashiro, E., Pinto-Figueroa, E., Buri, A., Spangenberg, J. E., Adatte, T., Niculita-Hirzel, H., ... Meer, J. R. van der. (2016). Local Environmental Factors Drive Divergent Grassland Soil Bacterial Communities in the Western Swiss Alps. *Applied and Environmental Microbiology*, 82(21), 6303–6316. doi: 10.1128/AEM.01170-16
- Yilmaz, P., Parfrey, L. W., Yarza, P., Gerken, J., Priesse, E., Quast, C., ... Glöckner, F. O. (2014). The SILVA and “All-species Living Tree Project (LTP)” taxonomic frameworks. *Nucleic Acids Research*, 42(D1), D643–D648. doi: 10.1093/nar/gkt1209
- Yuan, H., Ge, T., Chen, C., O'Donnell, A. G., & Wu, J. (2012). Significant Role for Microbial Autotrophy in the Sequestration of Soil Carbon. *Applied and Environmental Microbiology*, 78(7), 2328–2336. doi: 10.1128/AEM.06881-11
- Zhang, J., Wang, F., Che, R., Wang, P., Liu, H., Ji, B., & Cui, X. (2016). Precipitation shapes communities of arbuscular mycorrhizal fungi in Tibetan alpine steppe. *Scientific Reports*, 6(1), 23488. doi: 10.1038/srep23488