

# Measuring and Analysing Fungal Diversity on Temporal and Spatial Scale in Multiple Comprehensive-Taxa Inventories

Dissertation

zur Erlangung des Doktorgrades  
der Naturwissenschaften

vorgelegt beim Fachbereich 15  
der Johann Wolfgang Goethe - Universität  
in Frankfurt am Main

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**Frankfurt am Main**

**2016**

**D30**



vom Fachbereich Biowissenschaften der  
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Datum der Disputation:



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## Abbreviations

AUT	..... Austria
DEU	..... Germany
DNA	.....deoxyribonucleic acid
ESP	..... Spain
FFH	..... flora-fauna-habitat
GAM	..... generalized additive model
GBIF	..... Global Biodiversity Information Facility
GLM	.....generalized linear model
GPS	..... Global Positioning System
ICE	..... incidence coverage estimator
IPF	.....Integrative Pilzforschung
LOESS	.....locally weighted regression
m.a.s.l.	..... meters above sea level
MYP	..... malt yeast peptone agar
NCBI	..... National Center for Biotechnology Information
NMDS	..... non-metric multidimensional scaling
PAN	.....Panama
PERMANOVA	..... permutational analysis of variance
rDNA	..... ribosomale deoxyribonucleic acid
sp.	..... species
spp.	..... multiple species of one genus
WGS	..... World Geodetic System



## Summary

Fungi are an important component of every ecosystem but hardly considered in biodiversity monitoring projects. This thesis aims at characterizing fungal diversity, with an emphasis on epigeous fungi, encompassing different biogeographic zones and points in time. A main sampling area was established in the Taunus mountain range in Germany, which was sampled monthly over three years.

For testing species richness on spatial scale, the Taunus transect was compared with four other areas, which were assessed with lower sampling effort. One of these areas was Bulau in Germany, in which four excursions were made. Furthermore, two sampling events were performed in Somiedo in Spain and one sampling event in Kleinwalsertal in Austria. Already existing data of a two-year monitoring project in Panama next to the river Majagua were additionally used for comparison.

All these areas were investigated with a standardized sampling protocol focusing on macroscopically evident fungi and vascular plants using a time-restricted transect design. The transects consisted of strips, which were 500 m long and about 20 m broad, and were sampled for 2 hours at each single sampling event.

In the first part of this work, fungal richness is analysed and compared between sampling areas. The second part focuses on analysing the temporal changes in fungal diversity in the Taunus study, and on assessing possible ecological factors driving these changes.

In the Taunus area, the established sampling design revealed 855 different fungal species, which were identified at least up to genus level. This high diversity can be explained partly by recording all macroscopically evident fungi because in similar monitoring projects with lower species numbers, small ascomycetes and plant parasites were mostly not considered.

In the Taunus area, 51% of all recorded species belonged to the division Ascomycota (436 species) with a high number of species in the order Helotiales (20% of ascomycetous records). These species are often small and live frequently in hidden habitats. In total, 45% of all recorded species could be

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assigned to Basidiomycota (389 species). This division was most frequently represented by the order Agaricales (45% of basidiomycetous records), which contains many species with easily observable fruit bodies in the field. Furthermore, a few slime moulds (25 species, 3% of all recorded species), Oomycota (three species, 0.4% of all recorded species) and zygomycetes (two species, 0.2% of all recorded species) were documented. This taxonomic distribution of records is different from that found in most other monitoring activities in which Basidiomycota usually dominate.

In the Taunus area, most species lived as saprotrophs (69%, 591 species), which is a lifestyle assumed to be associated with the largest part of fungi. Other frequent ecological groups were parasites (20%, 169 species) and mycorrhizal fungi (5%, 41 species). The host specificity of plant parasitic fungi, which represented the main part of the parasites, varied between species, but most species were recorded on one host species or genus only. In contrast to many fungal inventories, the number of mycorrhizal fungi was relatively low in this study. This was probably due to dry conditions, missing plant hosts, and the monthly sampling frequency, which is not sufficient to detect short-living sporocarps.

The most frequently recorded fungus was *Fomes fomentarius* with records in 33 sampling events, followed by *Hypoxyylon fragiforme* and *Schizophyllum commune* with 32 records each. The species documented during more than two years developed either long-living sporocarps or different spore stages over the year. This work shows that several fungal groups can be detected regularly throughout the year but considerable experience is required for the sampling of all macroscopically evident fruit bodies.

In the Taunus area, the majority of fungi were found only once or twice and new fungi were discovered in each sampling event. Based on the species records per sampling event, an accumulation curve for fungi was calculated, which steadily increased. In contrast, the plant curve was almost in saturation. Accordingly, three years of monitoring were not sufficient to reveal the total fungal diversity in the Taunus area.

For the sampled area in Taunus, the recorded data with 218 plant and 855 fungal species resulted in a plant:fungus ratio of 1:4. The assumed best

estimator for fungal incidence data is Chao 2, which would yield a plant:fungus ratio of 1:6. This coincides with the plant:fungus ratio of 1:6 proposed for worldwide ecosystems by some authors. Based on Chao 2, about 60% of fungal diversity was recorded after three sampling years, which would be reasonable based on the high number of newly recorded fungi in each sampling event. The percentage of already recorded fungal richness regarding total estimated diversity differed between orders. The lowest percentage of recorded species was found for Agaricales (44%) and the highest percentage for Polyporales (94%).

Single sampling events in the Taunus area were compared on spatial scale with the other sampling areas. The fungal species richness of single sampling events in Europe was highest in the mountainous regions with the highest precipitation (Somiedo and Kleinwalsertal). Altitude and precipitation are already published as important factors for fungal fruiting. However, the highest precipitation was recorded for Panama, but the direct comparison between Taunus and Majagua revealed greater species numbers in Taunus, despite the assumed higher richness in the tropics. This can be partly explained with the higher difficulties in identifying tropical fungi because of missing literature, high diversity and many species that are probably new to science.

The plant:fungus ratio was similar between the European areas, but differed strongly between Germany and Panama. This supports the hypothesis that the plant:fungus ratio is comparable on regional but not on global scale.

A comparison of the sampling areas revealed similar patterns on a higher taxonomic scale, notwithstanding their differences in vegetation and geographical location. Except during the mushroom season in autumn, when basidiomycetes dominated fungal diversity in Europe, the number of Ascomycota was usually higher, followed by Basidiomycota and by a small number of slime moulds.

At order level, members of Agaricales were recorded most frequently in almost all sampling areas. At sampling events during dry conditions only, like the first inventory in Somiedo, other orders were more frequent. The hypothesis that the diversity of Pucciniales and Xylariales is higher in tropical areas was not confirmed in this study.

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In contrast to the comparison on higher taxonomic levels, the species composition was different across sampling sites and the Panamanian area was most dissimilar compared to the European areas. No common fungal species was found in all sampling areas, but six species were recorded in the four European sampling sites. Only one species was shared between three European sites and Panama. All these species inhabit wood, which shows the importance of wood for fungal diversity recorded within the performed sampling design. Furthermore, the monitoring of many fungal groups including small and/or inconspicuous fruit bodies is essential for comparing regions because some of the previously mentioned species found in four different areas develop only small fruit bodies.

Comparing all sampling events, the percentage of completely identified species was highest in Taunus or at least equal to the others. This is probably due to the better knowledge of the area and the recorded species after repeated sampling. In Panama, the percentage of fungi, identified up to species level, was lowest, probably due to the earlier explained difficulties in tropical mycology.

Based on this inventory, trees were most frequently used as substrate, and the abundance of trees was more important than the tree species itself. The main substrate in Taunus was the broad-leaved tree *Fagus sylvatica*, and in Kleinwalsertal the coniferous tree *Picea abies*, the most abundant trees in each area.

For the second part of this thesis, the temporal variation in fungal richness and species composition, grouped at different taxonomic levels and ecological lifestyles, was checked for correlation with the recorded climatic variables humidity, temperature, and precipitation. For these analyses, the most frequent divisions and orders in the Taunus, namely Ascomycota including Helotiales, Pleosporales, and Xylariales, and Basidiomycota with Agaricales, Polyporales and Pucciniales, were analysed. Furthermore, three ecological groups, namely saprobionts, parasites, and mycorrhizal fungi, were investigated.

Total fungal richness and species composition showed a clear trend in richness from the first to the two subsequent sampling years and 7% of the variation in species composition could be explained by the variable year. The increasing

richness and the strong differences in species composition might be explained with the improved skills of the investigators, and possibly with changes in precipitation, which was lowest in the first year. At the beginning, more Basidiomycota were recorded potentially due to their higher conspicuousness. After repeated samplings, and thereby better knowledge of the area and its habitats, this trend was reversed to more Ascomycota.

The richness varied strongly during different months and nearly 40% of the total variance in species composition could be explained by monthly variation. The seasonal peak of fungal fruiting in autumn was confirmed in this study. However, more than 20% of all fungi would be lacking by excluding winter and early spring from the inventory in Taunus. The occurrence of Basidiomycota, Agaricales, and mycorrhizal fungi was strongly influenced by monthly seasonality. In contrast, Ascomycota and their investigated orders as well as the basidiomycetous orders Polyporales and Pucciniales were almost stable over the year.

Taxonomic and ecological groups showed diverse patterns in richness and species composition, which were differently associated with weather conditions. The species richness within Basidiomycota displayed a significant positive correlation with humidity and precipitation, whereas the basidiomycetous species composition was influenced by humidity and by temperature. A negative correlation was obtained for ascomycetous richness with temperature, but the ascomycetous species composition was affected by precipitation and by temperature.

At order level, only the species richness of Helotiales and Agaricales was positively affected by humidity and precipitation. Additionally, Helotiales richness was negatively influenced by temperature. In contrast to the species richness, the species composition of almost all orders was influenced by humidity and/or temperature, except the one of Xylariales.

For the ecological groups, the richness of saprobionts was positively influenced by humidity and precipitation. Temperature had a negative impact on the richness of mycorrhizal fungi and saprobionts. The species composition of all tested ecological groups was affected by humidity and the one of saprobionts and parasites was additionally influenced by temperature.

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The second part of this thesis shows that the effect of weather conditions on fungi differed strongly depending on the taxonomic and ecological group. Furthermore, fungal richness and species composition were not influenced by the same climatic variables, even in the same group.

Fungi are important in conservational aspects, because they play essential roles in any ecosystem. This study revealed that habitat and plant diversity are essential for fungal richness and especially wood is an important substrate for many fungi. In total, 30 fungal species in the Taunus are listed in the Red List of Hesse and four fungi are classified as indicator species, which show near-natural habitats.

With the performed sampling design, it is possible to record a high number of fungi with morphological data, including more Ascomycota than Basidiomycota. This distribution is usually evidenced by molecular studies and reflects the higher proportion of known ascomycetous species within the kingdom Fungi. This result was obtained due to the sampling of all macroscopically visible fungi and the participation of experts for different groups, including small Ascomycota and plant parasites.

Single sampling events can reveal a high species number of fungi, like documented in the areas Kleinwalsertal and Somiedo. Nevertheless, the recorded species richness is highly dependent on abiotic and biotic conditions. No statement about the total diversity can be given if no regular monitoring events were performed, which was shown by the differences in species richness and species compositions in the different sampling events, especially in the Taunus area.

This study shows that it is possible to perform an extensive-fungal-taxa inventory with classical methods. Furthermore, this work highlights the importance of repeated and regular sampling by trained mycologists. With this sampling design, the richness and species composition of different sampling areas can be compared and reliable conclusions can be drawn concerning temporal changes in fungal diversity and possible drivers of these changes.

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## Zusammenfassung

Pilze sind ein wichtiger Teil eines jeden Ökosystems, werden aber meist kaum in Biodiversitätsaufnahmen berücksichtigt. Diese Doktorarbeit zielt auf die Charakterisierung der Pilzdiversität von oberirdisch wachsenden Pilzen in verschiedenen geographischen Gebieten und zu unterschiedlichen Zeitpunkten.

Das Hauptsammelgebiet befand sich in dem deutschen Mittelgebirge Taunus, wo monatlich über drei Jahre gesammelt wurde. Für den Vergleich auf räumlicher Ebene wurden vier weitere Areale mit geringerer Sammelintensität untersucht. Diese Gebiete waren Bulau in Deutschland mit vier Sammelexkursionen, Somiedo in Spanien mit zwei und Kleinwalsertal in Österreich mit einem Sammeltermin. Zusätzlich wurden schon vorhandene Daten eines zweijährigen Monitoring-Projekts in Panama in der Nähe des Flusses Majagua für die Auswertung verwendet.

In allen Gebieten wurden makroskopisch sichtbare Pilze und Gefäßpflanzen mit einem standardisierten Protokoll gesammelt. Als Sammelareal wurde jeweils ein Transsekt mit einer Länge von 500 Metern und einer Breite von 20 Metern genutzt.

Im ersten Teil dieser Doktorarbeit wurde die Pilzartenzahl im Taunusareal analysiert und zusätzlich mit den anderen Sammelgebieten verglichen. Im zweiten Teil wurden die zeitlichen Änderungen der Pilzanzahl und Artenzusammensetzung des Taunusareals analysiert.

Das verwendete Sammelprotokoll ermöglichte die Erfassung einer hohen Anzahl von 855 verschiedenen Pilzen im Taunusareal, die mindestens bis zur Gattung bestimmt wurden. Diese hohe Diversität kann zumindest teilweise mit der Erfassung aller sichtbaren Pilz-Fruchtkörper erklärt werden. In den meisten anderen Monitoring-Projekten mit niedrigeren Artenzahl wurden oft kleine Ascomyceten- Fruchtkörper oder Pflanzenparasiten nicht miteinbezogen.

Im Taunus gehörten 51% aller erfassten Arten zur Abteilung der Ascomycota (436 Arten) mit einer großen Artenzahl in der Ordnung Helotiales (20% aller Ascomyceten), die oft kleine und versteckt lebende Fruchtkörper bilden. Zu den Basidiomycota konnten insgesamt 45% aller erfassten Arten (389 Arten) zugeordnet werden, mit dem größten Teil der Arten in der Ordnung Agaricales

(45% aller Basidiomyceten), die meist gut im Feld sichtbare Fruchtkörper ausbilden. Zusätzlich wurden noch einige Schleimpilze (25 Arten, 3% aller erfassten Arten), Oomycota (drei Arten, 0,4% aller erfassten Arten) und „Zygomyceten“ (zwei Arten, 0,2% aller erfassten Arten) dokumentiert. Die Verteilung der taxonomischen Großgruppen unterscheidet sich von der anderer Monitoring-Projekte, in denen gewöhnlich Basidiomycota dominierten.

Die meisten Arten im Taunus lebten saprobiontisch (69%, 591 Arten), was auch die wahrscheinlich am weitesten verbreitete Lebensweise der Pilze ist. Andere häufige ökologische Gruppen waren Parasiten (20%, 169 Arten) und Mykorrhizapilze (5%, 41 Arten). Ein Großteil der Parasiten wurde auf Pflanzen gefunden. Die Wirtsspektren der Pflanzenparasiten variierten zwischen verschiedenen Pilzen, der größte Teil wurde jedoch auf nur einer Wirtsart oder –gattung dokumentiert. Im Gegensatz zu vielen anderen Studien war die Anzahl der Mykorrhizapilze relativ gering, wahrscheinlich beeinflusst von dem Fehlen einiger Pflanzenpartner und der generellen Trockenheit des Sammelareals. Zudem war die monatliche Sammelfrequenz zu niedrig, um alle kurzlebigen Fruchtkörper zu erfassen.

Die häufigste Art war *Fomes fomentarius* mit Funden in 33 Sammelereignissen, gefolgt von *Hypoxylon fragiforme* und *Schizophyllum commune* mit 32 Funden. Die Arten, die über mehr als zwei Jahre dokumentiert werden konnten, produzierten entweder langlebige Fruchtkörper oder verschiedene Sporenstadien im Jahresverlauf. Diese Arbeit zeigt, dass unterschiedliche Pilzgruppen für eine vom Zeitpunkt unabhängige Erfassung genutzt werden können. Allerdings ist für die Aufnahme des gesamten makroskopisch sichtbaren Pilzspektrums sehr große Erfahrung notwendig.

Die Mehrheit der Pilze im Taunusareal wurde nur ein bis zweimal gefunden und in jedem Sammelereignis wurden neue Pilze dokumentiert. Anhand der erfassten Pilzartenzahl je Sammelereignis wurde eine Akkumulationskurve berechnet, welche kontinuierlich anstieg. Dementsprechend waren drei Sammeljahre nicht ausreichend, um die Gesamtdiversität der Pilze im Taunusareal zu erfassen.

Im Taunus wurden insgesamt 218 Pflanzen- und 855 Pilzarten erfasst, was einem Verhältnis von 1 zu 4 von Pflanzen zu Pilzen entspricht. Laut Schätzung



mit Chao 2 wurde etwa 60% der Pilzdiversität nach dreijährigem Sammeln im Taunus erfasst und ein Gesamtverhältnis von Pflanzen- zu Pilzarten von 1:6 geschätzt, was laut Literatur auch der weltweiten Hypothese entspricht. Der Anteil der erfassten zu den geschätzten Pilzarten variierte zwischen den Ordnungen mit dem niedrigsten Anteil von dokumentierten Arten bei den Agaricales (44%) und den höchsten bei den Polyporales (94%).

Auf räumlicher Ebene wurden die anderen Sammelgebiete mit dem zeitlich nächsten Sammelereignis im Taunus verglichen. Die Artenvielfalt war in den europäischen Arealen in den höher gelegenen und niederschlagsreichsten Regionen (Somiedo und Kleinwalsertal) am höchsten. Diese Faktoren beeinflussen bekannter Weise die Pilzdiversität. Obwohl Panama die größte Niederschlagsmenge aufwies und die Diversität in tropischen Gebieten erwartungsgemäß höher sein sollte, war der Artenreichtum im direkten Vergleich niedriger als im Taunus. Dies kann mit der erschwerten Bestimmung tropischer Pilze erklärt werden, verursacht durch fehlender Literatur, hoher Diversität, und vielen neuen Arten für die Wissenschaft.

Das Verhältnis von Pflanzen zu Pilzen war zwischen den europäischen Sammelgebieten relativ ähnlich, zeigte jedoch einen großen Unterschied zwischen Deutschland und Panama. Diese Ergebnisse stützen die Hypothese, dass das Verhältnis von Pflanzen zu Pilzen auf regionaler Ebene vergleichbar ist, jedoch nicht auf globaler Ebene.

Ein Vergleich der verschiedenen Sammelgebiete zeigte ähnliche Trends auf höherer taxonomischer Ebene, trotz der Unterschiede in Vegetation und geographischer Lage. Die Mehrheit der Pilze konnte über alle Sammelereignisse gesehen den Ascomyceten zugeordnet werden. Lediglich während der Hauptpilzsaison im Herbst wurden mehr Basidiomyceten dokumentiert.

Auf Ordnungslevel wurden im Gesamtvergleich aller Areale sehr viele Pilze innerhalb der artenreichen Gruppe der Agaricales erfasst. Nur bei Sammelereignissen mit sehr trockenen Bedingungen war der Anteil anderer Ordnungen höher. Die Hypothese einer höheren Diversität von Pucciniales und Xylariales in tropischen Gebieten, konnte in dieser Studie nicht bestätigt werden.

Entgegen der ähnlichen Verteilung auf höherer taxonomischer Ebene war die Artenzusammensetzung der einzelnen Gebiete sehr unterschiedlich. Besonders das panamaische Gebiet unterschied sich stark von den europäischen Regionen. Keine gemeinsame Pilzart wurde für alle Areale dokumentiert, jedoch wurden sechs Pilzarten in allen vier europäischen Gebieten erfasst. Nur eine Art war sowohl in Panama als auch in drei europäischen Gebieten vorhanden. Alle Pilze, die in vier Arealen gefunden wurden waren Holzbewohner, was die Bedeutung von Holz für die mit dieser Sammelmethode erfassbare Pilzdiversität zeigt. Zudem wurde bestätigt, dass die Erfassung einer hohen taxonomischen Vielfalt unter Einbezug von unauffälligen Arten notwendig ist, da einige der mehrfach gefundenen Arten nur sehr kleine Fruchtkörper bilden.

Der prozentuale Anteil von bis zu Artniveau bestimmten Pilzen war im Taunus stets höher oder zumindest gleich im Vergleich zu den anderen Gebieten. Dies kann mit der besseren Kenntnis des Gebietes und der dortigen Arten nach wiederholtem Sammeln begründet werden. Dagegen war der Anteil der bis zu Artniveau identifizierten Pilze in Panama am niedrigsten, vermutlich aufgrund der schon erklärten Schwierigkeiten in der tropischen Mykologie.

In dieser Studie waren Bäume die häufigsten Substrate. Dabei war die Abundanz einer Baumart wichtiger als die Baumart selbst. Das wichtigste Substrat im Taunus war *Fagus sylvatica* und im Kleinwalsertal *Picea abies*. Beide Arten stellten in den jeweiligen Gebieten die häufigste Baumart dar.

Im zweiten Teil dieser Studie wurde die zeitliche Variation in Artenzahl und Artenzusammensetzung der Pilze im Taunus, basierend auf verschiedenen taxonomischen und ökologischen Gruppen, untersucht und auf ihre Korrelation mit Luftfeuchtigkeit, Temperatur und Niederschlag geprüft. Dafür wurde die häufigste Abteilung Ascomycota mit den zahlreichsten Ordnungen Helotiales, Pleosporales und Xylariales, sowie die zweithäufigste Abteilung Basidiomycota mit den Ordnungen Agaricales, Polyporales und Pucciniales ausgewählt. Zusätzlich wurden noch die häufigsten ökologischen Gruppen, also Saprobionten, Parasiten und Mykorrhiza-Pilze analysiert.

Die Gesamtartenzahl der Pilze und die Artenzusammensetzung zeigten einen deutlichen Trend vom ersten zu den beiden darauffolgenden Jahren und 7%

der Variation in der Artenzusammensetzung konnte mit dem Sammeljahr erklärt werden. Mögliche Erklärungen für die ansteigende Pilzdiversität und den Unterschied in der Artenzusammensetzung sind die verbesserten Kenntnisse der Wissenschaftler und die ansteigenden Niederschläge. Im ersten Jahr wurden mehr Basidiomycota erfasst, wahrscheinlich aufgrund der auffälligeren Fruchtkörper. Nach wiederholtem Sammeln und dadurch besserer Kenntnisse des Gebietes und seiner Habitats wurden mehr Ascomycota dokumentiert.

Die Pilzvielfalt variierte stark zwischen den einzelnen Monaten und fast 40% der Variabilität in der Artenzusammensetzung konnte mit dem Faktor Monat erklärt werden. Das Pilzmaximum im Herbst wurde in dieser Studie bestätigt. Würde man allerdings die Erfassung der Pilzvielfalt nur auf die Vegetationsperiode einschränken und Winter und Frühlingsanfang nicht erfassen, wäre im Taunus 20% der Vielfalt nicht dokumentiert worden. Von den untersuchten Gruppen zeigte lediglich das Auftreten von Basidiomyceten, Agaricales und Mykorrhiza-Pilzen starke monatliche Schwankungen.

Taxonomische und ökologische Gruppen zeigten verschiedene Trends in Artenreichtum und Artenzusammensetzung. Die Artenvielfalt der Basidiomyceten korrelierte signifikant positiv mit Luftfeuchtigkeit und Niederschlag, während die Artenzusammensetzung von Luftfeuchtigkeit und Temperatur beeinflusst wurde. Die Artenzahl der Ascomyceten zeigte eine negative Korrelation mit Temperatur, während die Artenzusammensetzung dieser Abteilung von Niederschlag und Temperatur beeinflusst wurde.

Auf Ordnungslevel wurde die Artenzahl der Agaricales und Helotiales positiv von Luftfeuchtigkeit und Niederschlag beeinflusst und Helotiales zeigten noch zusätzlich eine negative Korrelation mit der Temperatur. Im Gegensatz zur Artenzahl wurde die Artenzusammensetzung fast aller untersuchten Ordnungen von Luftfeuchtigkeit und/oder Temperatur beeinflusst, mit Ausnahme der Xylariales.

Für die ökologischen Gruppen wurde die Artenzahl der Saprobionten positiv von höherer Luftfeuchtigkeit und Niederschlag beeinflusst. Niedrige Temperaturen hatten einen negativen Effekt auf die Artenvielfalt von Mykorrhiza-Pilzen und Saprobionten. Die Artenzusammensetzung aller

getesteten ökologischen Gruppen änderte sich mit der Luftfeuchtigkeit und diejenige von Saprobionten und Parasiten zusätzlich mit der Temperatur.

Der zweite Teil dieser Arbeit zeigt, dass der Effekt von klimatischen Faktoren auf die Pilzdiversität stark von der taxonomischen und ökologischen Gruppe abhängt. Weiterhin werden Artenzahl und Artenzusammensetzung selbst in derselben Gruppe von verschiedenen Faktoren unterschiedlich beeinflusst.

Pilze spielen eine wesentliche Rolle im Ökosystem. Diese Studie zeigt, dass Habitat- und Pflanzendiversität für die Pilzvielfalt wesentlich ist und besonders Totholz ein sehr wichtiges Substrat darstellt. Insgesamt 30 Arten im Taunus haben einen Schutzstatus in der hessischen Roten Liste der Großpilze und vier Pilze zählen als Indikator-Arten, welche naturnahe Habitate kennzeichnen.

Mit Hilfe der hier verwendeten Sammelmethode kann eine hohe Artenvielfalt der Pilze mit morphologischer Charakterisierung erfasst werden, welche im Gegensatz zu vielen anderen Studien einen höheren Anteil an Ascomyceten gegenüber Basidiomyceten ergibt. Dies entspricht auch dem Verhältnis der bekannten Pilzarten. Grundlage für diese Sammelmethode ist die Einbeziehung von Wissenschaftlern, die Erfahrung mit unterschiedlichen taxonomischen Pilzgruppen haben, inklusive kleiner Ascomyceten und Pflanzenparasiten.

Einzelne Sammelereignisse können zwar eine hohe Artenzahl zeigen, wie beispielsweise in Somiedo und im Kleinwalsertal, jedoch sind die Ergebnisse stark von abiotischen und biotischen Faktoren abhängig. Dementsprechend können keine Aussagen zur Gesamtdiversität ohne wiederholte Sammelereignisse getroffen werden, was durch die Unterschiede sowohl in der Artenzahl als auch in der Artenzusammensetzung in den Sammelereignissen im Taunus gezeigt wurde.

Diese Studie zeigt, dass eine umfassende mykologische Untersuchung mit einer hohen Artenvielfalt mit klassischen Methoden möglich ist. Zusätzlich stellt diese Arbeit die Bedeutung von regelmäßigen Sammelereignissen über einen längeren Zeitraum mit erfahrenen Mykologen heraus, um den Artenreichtum und die Artenzusammensetzung in verschiedenen Gebieten zu vergleichen und zuverlässige Schlussfolgerungen bezüglich der zeitlichen Veränderungen und deren Ursachen ziehen zu können.

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## 1 Introduction

### 1.1 The fungi

Fungi form a highly diverse kingdom including unicellular organisms, and species that develop a multicellular mycelium formed by hyphae, which can extend over several hectares (Cannon 1999; Zak and Willig 2004; Aime and Brearley 2012; Heilmann-Clausen et al. 2015). Some typical features are their heterotrophic, absorptive nutrition and the presence of a cell wall, which consists typically of chitin and glucan, sometimes of cellulose and glucan (Webster and Weber 2006; Seifert et al. 2011). The term “fungi” has been historically applied to encompass two different sets of organisms. The traditional use of the term “fungi” has been taken to refer to a polyphyletic group comprising the fungus-like groups of slime moulds in Amoebozoa (kingdom Protozoa) and slime moulds in other kingdoms, Oomycota (kingdom Chromista), as well as “True Fungi” (kingdom Fungi, including the most abundant divisions Ascomycota and Basidiomycota). Recently the term “fungi” is applied to the monophyletic clades conforming the kingdom Fungi, in which most species are characterized by a cell wall with chitin (Rossmann and Palm-Hernández 2008; Seifert 2009). In general, the heterotrophic lifestyle of fungi is similar to that of animals but, regarding their immobility, fungal lifestyle is comparable to plants (Blaschke et al. 2004). However, molecular studies show that true fungi are phylogenetically closer to animals than to plants (Rossmann and Palm-Hernández 2008). In this work, fungi in the traditional sense, including slime moulds and Oomycota, were investigated due to their similar lifestyle and ecological niches.

Fungi can be classified in microfungi or macrofungi, based on the non-systematic character of fruit-body size. The latter ones include all fungi with fruit bodies large enough to be well visible with the naked eye, i.e. larger than 3 mm diameter. Basidiomycota with easily visible fruit bodies are predominantly considered macrofungi, but also large Ascomycota and slime moulds are assigned to this group (Watling 1995). Macrofungi are important for the ecosystem as mutualistic symbionts, decomposers of organic matter, and food source for other organisms (Castellano et al. 1999). According to European

national Red Lists of fungi, about 10-20% of macrofungi in Europe are threatened (Perini et al. 2008). Fruit bodies of microfungi are not or hardly visible with the naked eye. However, by using hand lens, some microfungi such as parasites of plants, are still observable in the field. But the most members of this group are microscopic species without any fruit bodies (Castellano et al. 1999).

Fungi interact with nearly all organisms (Blackwell 2011) and can be found in almost all habitats (Castellano et al. 1999; Blackwell 2011). They play essential roles in terrestrial ecosystems as decomposers of dead organisms, as mutualistic symbionts and/or parasites of plants and animals, as commensals, or as creators of microhabitats for other organisms (Hawksworth 1991; Hawksworth and Wiltshire 2011; Tedersoo et al. 2014; Heilmann-Clausen et al. 2015). In addition to terrestrial areas, fungi inhabit aquatic habitats, even though their diversity is probably lower in water than on land. One reason might be that the diversity of host plants is lower in water, which results in lower diversity of substrates for fungal colonization (Shearer et al. 2007; Blackwell 2011), because many fungi are associated with plants (Grayer and Kokubun 2001).

A high proportion of fungal species is associated with soil at least during one period in their life. Rocks are also used as habitat by some fungi. The total diversity of rock-inhabiting fungi is under-investigated, whereas soil fungi are known to be highly diverse. Fungi are essential for soil ecosystems (Bridge and Spooner 2001; Ruibal et al. 2009; Jones and Richards 2011). Some important tasks of soil fungi are the degradation of dead material, the formation of mutualistic symbioses with plants and the supply of food source for other organisms. Beside the fungi actively growing in soil, dormant stages are also present in this habitat (Bridge and Spooner 2001).

Fungi and plants form complex relationships (Berndt 2012). Based on the minimal estimation of global fungal diversity published by Schmit and Mueller (2007), more than 82% of the estimated fungal richness are probably associated with terrestrial plants. The plant-fungus relationship possibly played an essential role in the origin of land plants due to the establishment of mutualistic symbioses that assisted plants with the uptake of nutrient (Pirozynski and Malloch 1975). Fungi form complex communities in and on

almost every plant organ by forming commensalistic, parasitic, or mutualistic symbioses (Cannon 1999; Hyde et al. 2007; Blackwell 2011). Not only living but also dead plant parts, such as wood, are an important substrate, and usually a high diversity of interacting species can be found in this habitat (Lonsdale et al. 2008; Ovaskainen et al. 2013).

Animals are also frequently associated with fungi. A high number of fungal species is expected to be associated with insects due to the supposed host specificity of fungal invertebrate parasites and the high estimated diversity of insects (Hyde et al. 2007; Mueller et al. 2007a). A well-studied association is the mutualistic symbiosis between fungus-growing ants and their crop fungi, which evolved millions of years ago (Mehdiabadi et al. 2012). Other mutualistic relationships are known between fungi and marine snails (Silliman and Newell 2011) or wood-boring insects (Hawksworth 1991). Some fungi inhabit animals as commensals and mutualistic symbionts, for example in guts of ruminants and insects (Akin and Borneman 1990; Jones and Richards 2011; Lichtwardt 2012). Many organisms, like different mammals and invertebrates, use fungi as food source (Cannon 1999; Heilmann-Clausen et al. 2015). Some species even feed up to 90% on fungi (Castellano et al. 1999) and a specialized ant species has adapted completely on fungal nutrition (Witte and Maschwitz 2008). The fungal food source has also been used by humans for thousands of years (Heilmann-Clausen et al. 2015).

Especially important for humans is the traditional use of fungi in the production of cheese, beer, bread and other products. Furthermore, the commercial use of fungi in biotechnological applications is important, like the production of amino acids, pharmaceuticals, especially antibiotics, and other compounds (Hawksworth 1991; Jones and Richards 2011; Heilmann-Clausen et al. 2015). Another application is the use of fungi in bioremediation of degraded or polluted habitats (Harms et al. 2011). Fungi are able to degrade various substances, like pesticides or oil, and to reduce the bioavailability of toxic substances like metals and radionuclides, for instance, by their absorption. Another use of fungi is the identification of deposition time or death time of corpses in forensics based on fungal species diversity and growth (Hawksworth and Wiltshire 2011).

### 1.1.1 Ecological groups

#### Saprobionts

Fungal species express different ecological preferences that can be used for the classification of their diversity (Blackwell 2011). One of the most abundant ecological groups of fungi is that of saprobionts (Grayer and Kokubun 2001), which are responsible for the degradation of organic matter originating from dead organisms. Lignin decomposition is especially important for the nutrient recycling process of dead plants (Hawksworth 1991; Cannon 1999; Unterseher et al. 2012), and thereby for all organisms that are not able to exploit nutrients fixed in dead plant material (Heilmann-Clausen et al. 2015). By softening wood through degradation, fungi provide habitats for other organisms like birds and insects (Castellano et al. 1999). Even though preferences for different hosts and decay stages are known, saprobionts are probably less host specific than parasites (Zhou and Hyde 2001).

#### Parasites

Many fungi are parasites of other organisms, and different relationships between fungi and their hosts are known. Some parasites need living host cells (biotrophs), whereas others first kill the host cells and continue their life cycle on the dead cells (necrotroph). Furthermore, fungi can affect the whole host organism (systemic) or only parts of it (local) (Piepenbring 2015). Fungal parasites are able to cause numerous harmful diseases on host organisms (Jones and Richards 2011), which can even lead to the extinction of species, as it is assumed to have occurred for several species of amphibians affected by species of the fungal genus *Batrachochytrium* (Pounds et al. 2006; Heilmann-Clausen et al. 2015). However, climate change has probably a high influence in the previous example (Pounds et al. 2006). Usually, systemic plant pathogens show a strong relationship and coevolution with the host, while non-systemic pathogens have often only local effects on the infected plant part (Burdon 1993). Due to the strong host-fungus relationship, plant pathogens are often host specific, so knowledge on their host species is necessary for their identification. This is probably true for some but not for all species of plant parasitic fungi (Zhou and Hyde 2001).



Parasites are important for the ecosystem. A study in temperate areas revealed a higher diversity of phytopathogenic fungi with increasing host plant diversity, but lower infection rates of single parasites and less parasites per plant (Rottstock et al. 2014). Parasites are probably involved in the plant species richness of tropical forests due to the evolutionary pressure to develop a defence against fungal pathogens (Heilmann-Clausen et al. 2015).

Furthermore, parasites and hyperparasites can be used for the environmentally friendly biocontrol of different plant diseases, weeds and invertebrate pests, as an alternative to chemical pesticides (Hawksworth 1991; Butt et al. 2001; Hawksworth 2002; Hyde et al. 2007; Blackwell 2011). If parasites kill their host, new habitats and nutrients are generated for other organisms (Berglund et al. 2005).

### **Mycorrhizal fungi**

A very important lifestyle in all ecosystems worldwide is the mutualistic symbiosis between fungi and plant roots called mycorrhiza, which is formed by the majority of plants (Pringle and Wolfe 2011). Different types of mycorrhizal associations are known. In ectomycorrhizal relationships, hyphae remain outside the plant cells and the fungus does not grow into living cells, whereas endomycorrhizal fungi penetrate the plant cells and establish specialized intracellular interfaces. An example of the latter are the arbuscular mycorrhiza, in which intracellular vesicles and arbuscles are formed (Malloch et al. 1980; Parniske 2008; Blackwell 2011).

In the mycorrhizal relationship, the fungal partner provides water, compounds with nitrogen and phosphorus, as well as other soil minerals for the plant, because the hyphal system of the fungus extends further into the soil than the plant roots and has therefore a larger surface for nutrient absorption. In return, the fungus receives fixed carbon from the plant, produced through photosynthesis (Castellano et al. 1999; Horton and Bruns 2001; Courty et al. 2008; Heilmann-Clausen et al. 2015). Another function of mycorrhizal fungi is protecting their partner against pathogens (Cox et al. 2010).

The diversity of ectomycorrhizal fungi is higher than the one of fungi forming arbuscular mycorrhizae. Some studies reveal almost a hundred ectomycorrhizal fungi on the roots of selected trees like some *Fagus* specimens (Lang et al.

2011). In the soil ecosystem, ectomycorrhizal fungi are one of the most important ecological groups (Ovaskainen et al. 2013) and their fruit bodies are essential as food source or habitat (Berglund et al. 2005). Despite their high abundance and importance, functional studies of ectomycorrhizal fungi are difficult. Their need for a specific living plant partner complicates their cultivation, so that the symbiosis is difficult to establish for experiments (Horton and Bruns 2001; Blackwell 2011).

The ectomycorrhizal lifestyle developed several times in evolution. Fungi forming arbuscular mycorrhizae are monophyletic and all included in one division, the Glomeromycota (Horton and Bruns 2001; Lang et al. 2011; da Silva et al. 2012). Arbuscular mycorrhizae can be found in 80% of all plant species and are essential for establishing vegetation in extreme habitats (Blackwell 2011; da Silva et al. 2012). Experiments showed that an increase of arbuscular mycorrhizal species in grasslands results in higher plant diversity and productivity (Sanders et al. 1998).

### **Lichens**

Lichens are another important mutualistic symbiosis of fungi (mycobiont), in this case associated with green algae and/or cyanobacteria (photobiont). The known diversity of mycobionts is higher than the one of photobionts (Lutzoni and Miadlikowska 2009). About 20% of all fungi are obligatorily lichenized, which means these fungi cannot live without a suitable photobiont (Feuerer and Hawksworth 2007). Only 2% of all lichen-forming fungi are Basidiomycota, whereas the majority (98%) comprises 40% of all ascomycetous species (Lutzoni and Miadlikowska 2009).

Due to the mutualistic symbiosis, lichens are able to perform primary production like plants. They are able to survive in extreme environments, to grow with temperatures under 0°C and inhabit even substrates like mammals and plastic (Lutzoni and Miadlikowska 2009; Wirth et al. 2011; Heilmann-Clausen et al. 2015). Various lichens have very long life-spans, some more than 1 000 years, and produce an ample range of secondary metabolites, which are exploited industrially, for example in the production of perfumes (Lutzoni and Miadlikowska 2009; Wirth et al. 2011). Another important characteristic of some lichens is their sensitivity to air pollution, which have favoured their use as

bioindicators (Lutzoni and Miadlikowska 2009; Wirth et al. 2011). Lichens are easier to monitor than many other macrofungi because their thalli are often easily detectable due to their size (Cannon 1999) and visibility throughout the year (Wirth et al. 2011).

## **Endophytes**

Endophytes are a polyphyletic and hyperdiverse group of fungi which live, at least in a part of their life cycle, inter- and intracellularly in host plant tissues without causing any disease symptoms (Arnold et al. 2000; Arnold 2008). Endophytes seem to live as mutualists, commensals, or parasites with all higher plants (Arnold 2008; Heilmann-Clausen et al. 2015), and are also documented for algae, mosses and ferns (Blackwell 2011; Mishra et al. 2014). Experiments have revealed that some endophytes can protect their plant hosts against pathogens (Arnold et al. 2011). In contrast, other species tend to change their behaviour into a parasitic lifestyle under certain environmental conditions, like drought (Arnold 2008; Heilmann-Clausen et al. 2015).

### **1.1.2 Systematic groups**

Up to now, approximately 100 000 species are known in the kingdom Fungi. In this study, species of the divisions Ascomycota, Basidiomycota, and the polyphyletic “Zygomycota” within the True Fungi were recorded. Other important divisions within the True Fungi, namely Glomeromycota and the basal groups Chytridiomycota and Blastocladiomycota, do not develop fruit bodies and therefore were not included in this survey (James et al. 2007; Kirk et al. 2008).

## **Ascomycota**

The largest group within the True Fungi is the division Ascomycota with about 65 000 known species. Species of Ascomycota are characterized by the formation of sexual spores (ascospores) inside sac-like cells called asci (Castellano et al. 1999; Kirk et al. 2008). Due to the high number of ascomycetous species, the ecology and nutrition of this group is diverse and includes almost every possible fungal lifestyle. Many well-known microfungi, like *Penicillium chrysogenum* with its antibiotic substances, and macrofungi, like truffles from the genus *Tuber*, are assigned to this division (Webster and Weber

2006). In the following paragraphs, an overview of the most abundant orders, as observed in this work, is given.

Helotiales contain about 4 000 known species and belong morphologically to the polyphyletic form group of inoperculate fungi (asci do not have an operculum to release the ascospores), which mostly produce small apothecia (cup-shaped fruit bodies). Many species are saprobionts or plant parasites, but they can also have other lifestyles like mycorrhizal and endophytic (Wang et al. 2006; Kirk et al. 2008; Piepenbring 2015).

The order Pleosporales contains about 5 000 known species (Kirk et al. 2008). The whole group is traditionally characterized morphologically by pseudothecia (bottle-shaped fruit bodies), containing fissitunicate asci (asci with two different cell walls) with diverse ascospore forms (shape, colour, septation) (Zhang et al. 2009; Piepenbring 2015). Species within the Pleosporales have a highly diverse ecology, being parasites, saprobionts, endophytes, and/or coprophilous fungi (Zhang et al. 2009).

Xylariales contain approximately 2 500 known species. Species of this order develop black perithecia (bottle-shaped fruit bodies) containing mostly dark ascospores (Webster and Weber 2006). Most species are saprobionts or parasites on wood or bark (Kirk et al. 2008). The diversity of Xylariales fruit bodies and xylariaceous endophytes seem to be higher in tropical areas than in temperate ones (Ikeda et al. 2014).

### **Basidiomycota**

The second most abundant division of fungi is Basidiomycota with about 30 000 known species. They differ from Ascomycota by their sexual spore formation (basidiospores), which in Basidiomycota takes place on the outside of a mostly club-shaped cell called basidium (Castellano et al. 1999; Kirk et al. 2008). This group is what the public generally recognises as fungus, because many well-known mushrooms like *Agaricus bisporus* and toadstools like *Amanita phalloides* are included. However, this division also includes other less conspicuous forms, like many important phytopathogens. Similarly to Ascomycota, almost all fungal lifestyles can be found in the division Basidiomycota. Basidiomycetous species are represented in practically all habitats, though predominantly in terrestrial areas (Webster and Weber 2006).

In the following paragraphs, the most abundant basidiomycetes according to their frequency in this study are introduced.

About 13 000 species are known for the order Agaricales within the Basidiomycota (Kirk et al. 2008). This order includes the largest number of mushroom-developing fungi (Matheny et al. 2007). The lifestyle and nutrition of Agaricales covers a wide ecological range. Many species live as saprobionts or form mycorrhizal associations within a wide climatic range, others are parasitic on plants or fungi (Kirk et al. 2008; Fernando 2009).

The order Polyporales is a monophyletic group that contains about 2 000 known species (Hibbett 2007; Kirk et al. 2008). They are prominently wood-decomposers, which can be classified into two groups regarding the type of wood decomposition, a classification generally used for wood-decomposers: white-rot fungi, which decay lignin and cellulose and brown-rot fungi, which degrade cellulose but not lignin (Webster and Weber 2006; Binder et al. 2013).

A clear differentiation has to be made between the taxonomic order Polyporales and the morphological group of polypores. Polypores are a polyphyletic group, with usually poroid hymenophores and long-living fruit bodies, often forming easily observable brackets. They comprise important decomposers, but also some obligate and facultative parasites (Berglund et al. 2005; Hattori et al. 2012; Yamashita et al. 2015). Most species of polypores belong to the wood-rotting fungi in the order Polyporales, others to Hymenochaetales, or other orders (Miettinen 2011).

About 8 000 species are known in the plant-parasitic order Pucciniales, which are also called rust fungi due to their partly rust-coloured appearance (Kirk et al. 2008; Kolmer et al. 2009). This group includes economically important species because they cause diseases on crop plants (Hiratsuka and Sato 1982; Kolmer et al. 2009). Characteristic features of rust fungi are their obligate biotrophic lifestyle and their host specificity (Hiratsuka and Sato 1982; Berndt 2012). Their dependence on living host cells of specific plants is the reason why the cultivation of Pucciniales species is usually not successful (Kolmer et al. 2009).

The relationship between Pucciniales species and their host is very specific, what makes the knowledge on host identity essential for the identification of rust fungi (Hiratsuka and Sato 1982). Many species are heteroecious, which means

that the fungus alternates hosts over its life cycle. Other species, especially in the tropics, are autoecious, therefore they only have one host species (Hiratsuka and Sato 1982; Kirk et al. 2008; Piepenbring et al. 2011). The known diversity of Pucciniales seems to be similar in tropical and temperate regions, although it can be expected to be richer in tropics due the higher plant diversity and the host specificity of Pucciniales (Piepenbring et al. 2011).

Many Pucciniales species have complex life cycles with up to five developmental stages, each with its respective type of spore. The first spores (0) are spermatia that correspond to monokaryotic gametes. The aecidiospores (I) and uredospores (II), called summer spores, are vegetative spores. The teleutospores (III), also called winter spores, produce basidia, which develop basidiospores (IV) after meiosis (Hiratsuka and Sato 1982; Kirk et al. 2008). Not all species produce all these types of spores (Hiratsuka and Sato 1982), and especially in the tropics many Pucciniales apparently reproduce only via uredospores (Piepenbring et al. 2011).

Some examples of fungal fruit bodies from the previously described orders are shown in Figure 1.

### **“Zygomycota”**

The basal lineage of zygomycetes was traditionally identified by their thick-walled sexual spores (zygospores) and assigned to the division “Zygomycota”. Later, phylogenetic analyses showed that this group is polyphyletic (White et al. 2007). Many species of zygomycetes live in soil, on dung, or on insects (Webster and Weber 2006).





Figure 1: Examples of ascomycetous and basidiomycetous orders. The species assigned to Basidiomycota are *Mycena cyanorrhiza* in the order Agaricales (a), *Piptoporus betulinus* in the order Polyporales (b), and *Puccinia punctiformis* in the order Pucciniales (c). The species belonging to the Ascomycota are *Bisporella citrina* in the order Helotiales (d), *Rhopoglyphus filicinus* in the order Pleosporales (e), and *Diatrype decorticata* in the order Xylariales (f). The photos (a, d) were taken by S. Rudolph, (b, f) by H. Lotz-Winter, and (c, e) by N. Kühnberger.

### **Oomycota and slime moulds**

Members of the Oomycota and slime moulds in the Amoebozoa, which do not belong to the True Fungi, were also included in this investigation, when symptoms caused by these organisms on plants or their fruit bodies were seen in the field (Kirk et al. 2008).

The monophyletic group of Oomycota contains nearly 1 000 known species and is related to yellow-brown algae in the kingdom Chromista. Oomycota differ from True Fungi by their sexual reproduction by oogamy, their cell wall with cellulose, and the production of zoospores with heterokont flagellae. Most species live saprotrophically or parasitically (Kirk et al. 2008; Rossman and Palm-Hernández 2008). However, investigations on Oomycota mostly focus on their high impact as phytoparasites, with important examples like *Phytophthora infestans* affecting potato (Webster and Weber 2006).

The group of Amoebozoa contains about 1 000 known species of slime moulds (Kirk et al. 2008), which differ from True Fungi, among other things, by their nutrition and physiology. During their usually anterior-flagellated vegetative state, slime moulds live as unicellular amoebae, and they form multinuclear amoebae or plasmodia in later stages. They can move over decaying vegetative substrates and their nutrition is mostly based on phagocytosis of other microorganisms. For their sexual state, slime moulds develop one or several sporangia, often at elevated places, which can be recorded and identified in field trips (Webster and Weber 2006). Species diversity is especially rich on wooden substrates (Mueller et al. 2007b). Although slime moulds do not belong to the True Fungi, they are traditionally investigated by mycologists (Webster and Weber 2006).

#### **1.1.3 Morphologic and molecular identification in monitoring**

The basic methodology in classical fungal diversity studies consists in recording and identifying directly observable fruit bodies in the field, and to preserve these species for taxonomic purposes and molecular analyses (Halme et al. 2012). Furthermore, species which are easy to cultivate and reproduce at high rates in growth media are often included in such studies (Jones and Richards 2011).



One important aim in the classic approach is to obtain species lists, including information concerning lifestyle, association with other organisms, and morphological features (Schmit and Lodge 2005). With these data, information on ecosystem processes like fruiting patterns and changes in these ecosystems can be detected (Tóth and Barta 2010). A huge amount of data is available through the field work of amateur mycologists (Halme et al. 2012). However, high taxonomic expertise and time requirement are necessary to identify many fungal groups (Schmit and Lodge 2005).

Classical methods are limited to species that produce fruit bodies and develop distinctive morphologies, so cryptic species cannot be distinguished with this approach (Schmit and Lodge 2005; Jones and Richards 2011; Hawksworth 2012). If rarely fruiting fungi shall be included, classic sampling is often more cost efficient than molecular methods, because the search is more directed and can be performed for large areas. In contrast, environmental sampling is mostly undirected because only substrate without macroscopically visible fungal structure is processed (Halme et al. 2012).

Direct sequencing of environmental DNA, especially using new technologies for the high-throughput analysis of samples (Orgiazzi et al. 2015), reveals a higher microbial diversity than morphological studies (Bass and Richards 2011). This method is often the only possibility to investigate ecological niches with many non-fruit-body developing species (Bass and Richards 2011), like soil (Tedersoo et al. 2014), water (Jones and Richards 2011), and plant tissues (Bálint et al. 2015). Soil contains many different fungi, some actively growing in this environment, some associated with other organisms, some surviving as dormant spores, and others already dead. All these species will be documented by sequencing (Bridge and Spooner 2001). An example of a group without fruit-body development is the class Archaeorhizomycetes, a taxon recently described solely based on sequences obtained during environmental sequencing studies (Rosling et al. 2011).

Due to the high number of sequences without taxonomic classification in public databases like NCBI (National Center for Biotechnology Information) (Sayers et al. 2009), the description of species based on the internal transcribed spacers (ITS) of the rDNA as a barcode locus has been proposed (Hawksworth 2012;

Hibbett and Taylor 2013). However, this procedure has its own problems, like the variation differences within and between species that are not yet solved (Ovaskainen et al. 2010). Furthermore, many molecular studies are restricted on spatial and temporal scale (Schmit and Lodge 2005; Baptista et al. 2015), whereas inventories based on fruit bodies are often performed for large areas and long periods of time (Straatsma and Krisai-Greilhuber 2003).

Several studies show that the recorded diversity differs strongly between data obtained by molecular methods and data obtained by fruit-body inventories, like the comparison of ectomycorrhizal fungi (Horton and Bruns 2001), wood-inhabiting fungi (Hattori et al. 2012), or epigeous fruit bodies with soil fungi (Baptista et al. 2015). For an all-taxa inventory, different approaches are necessary and the data from classical samplings are needed to connect sequence data to morphological concepts of fungal species (Hyde et al. 2010).

### **1.2 Fungal diversity**

Biological diversity is defined as the variation of all organisms in every habitat, including the intra- and interspecific diversity as well as diversity between habitats (Hawksworth 1991; Secretariat of the Convention on Biological Diversity 2005). The magnitude of global diversity in general, and of fungal diversity in particular, is largely unknown, even though fungi represent a huge proportion of the global microbial biomass and genomic variation (Baillie et al. 2008; Jones and Richards 2011; Baptista et al. 2015).

The general term “diversity” can be divided into different levels of diversity (Whittaker 1960). The local species richness, which is the species number in an investigation, is called  $\alpha$  – diversity. The dissimilarity in species composition along habitat gradients corresponds to  $\beta$  – diversity. The combination of both described levels, encompassing the diversity of species in different environments, corresponds to  $\gamma$  – diversity (Whittaker 1960, 1972; Lande 1996).

Reasons for the lack of knowledge in fungal diversity are diverse. During most of their life cycle, many fungi grow as inconspicuous microorganisms with subterranean mycelium. Therefore, they are not visible during this period without the aid of specialized tools like molecular methods (Watling 2010; Unterseher et al. 2012).

Even if fungi develop fruit bodies, these are often ephemeral and their occurrence cannot be reliably predicted (Cannon 1997, 1999). There are also some species-rich habitats which are poorly studied (Cannon 1999; Shearer et al. 2007). This, in conjunction with a generally low interest in mycology by the general public, which entail low funding and few scientists working in the topic (Unterseher et al. 2012), has contributed to a limited knowledge on the global but also the local number of fungal species (Dai et al. 2015).

### **1.2.1 Fungal diversity worldwide**

Currently, approximately 100 000 species of fungi are described, but this number is far from the total estimated species richness (Kirk et al. 2008; Dai et al. 2015). The number of new fungal taxa increased nearly constantly since many years (Dai et al. 2015), and probably only about 2-6% of existing fungi are currently described (Jones and Richards 2011). The most frequently cited estimate of global fungal diversity is that of 1.5 million species given by Hawksworth (1991). This number is based on the observation that multiple habitats have an average of six fungal species per every plant species (the Hawksworth index), therefore it logically arises from the number of known plant species at that time.

Recent research on the assessment of fungal biodiversity using molecular methods suggests more pronounced ratios of fungal respect to plant richness. These updated estimates assume much higher numbers of fungal species, ranging from 3.5 to 5.1 million species (Blackwell 2011).

Global biodiversity is not equally distributed (Gaston 2000). Generally, the diversity of most groups of organisms, including fungi, is supposed to be higher in the tropics than in temperate zones (Fröhlich and Hyde 1999; Gaston 2000). Probably, a high number of new species can be found in tropical regions by studying particular fungal groups (Hawksworth 2012). This pattern was proven in a study of wood-inhabiting polypores (Yamashita et al. 2015) and lichens with more than 50% of the global lichen diversity inhabiting tropical regions (Lücking 2012). Therefore, different plant:macrofungus ratios for tropics (ratio 1:5) and temperate zones (ratio 1:2) were proposed (Mueller et al. 2007a).

In contrast, the diversity of ectomycorrhizal fungi is assumed to be higher in temperate zones than in the tropics, so that the richness within this group seems to increase with latitude (Tedersoo and Nara 2010). The pattern that different ecological groups of fungi have their maximal richness in different climate zones was also shown by Tedersoo et al. (2014). Hawksworth and Rossman (1997) concluded that a huge number of new fungal species is waiting to be discovered everywhere.

### **1.2.2 Fungal diversity at a local scale**

To obtain a comprehensive species list of all existing fungi, an all-taxa inventory at global scale would be necessary. This is unpractical in terms of resources and time constraints (Rossman et al. 1998), and therefore estimations of fungal diversity must rely on data extrapolations from inventories at landscape or local scales (Green et al. 2004). Based on a comparison of different molecular studies, only few fungal taxa in soil and plants are worldwide distributed. Most fungi occur locally and are replaced across geographic distance (Meiser et al. 2014). However, uncovering completely fungal diversity in an area is difficult because fungi are highly diverse even at local scales (Bass and Richards 2011). Overviews of different checklists are available online (Mycotaxon Ltd. 1996-2015; Mycology.Net 2000–2015) and although lists for some fungal groups or countries are available, these are often incomplete (e.g. Berndt et al. 2004; Piepenbring 2006), and comprehensive lists of extant fungal species are mostly not available (Cannon 1997; Aime and Brearley 2012).

For temperate regions, several inventories of fungi are known but most are based on fruit bodies of specific groups and comprise mostly macrofungi with a high number of Basidiomycota (e.g. Hawksworth 1991; Straatsma et al. 2001; Newton et al. 2003; Karasch 2005; Unterseher et al. 2012; Angelini et al. 2015). However, literature for fungal identification and Red lists are also available for some other groups like lichens, slime moulds and plant parasitic microfungi (Schnittler et al. 2011; Wirth et al. 2011; Klenke and Scholler 2015).

No checklist for all fungi exists currently for Germany, but the species number is probably higher than 14 400 species including all taxonomic groups of fungi and fungal-like organisms (Bundesamt für Naturschutz 2012). For the federal state of Hesse, in which two sampling areas were located, 2 007 species of

macrofungi are known, although smut and rust fungi, mildews and asexual fungi are not listed (Langer 2000).

In a provisional checklist of Panama, in which one sampling area was situated, 2 772 published fungal species are recorded in literature (Piepenbring 2013). In Spain, several lists exist for ecological groups like lichens (Llimona et al. 2001), and taxonomic groups like Albuginales and Peronosporales, but no general list is published (Garcia-Blazquez et al. 2006). For the natural park of Somiedo in Spain, in which two sampling events were performed in this thesis, 1 520 fungal taxa of macromycetes are known (Rubio et al. 2015). For Austria, 7 732 fungal taxa are published (Dämon and Krisai-Greilhuber 2012), and in the region of Kleinwalsertal and Allgäu, visited once for this thesis, 950 species were recorded by short-time sampling events in the middle of September for several years (Kost et al. 2011). The informative value of compared species lists from different areas is limited without evaluating differences in sampling methods and in abiotic and biotic conditions (Cannon 1999).

Within the species lists, fungi are often assigned to a specific conservation category based on Red Lists. However, the classification into these categories is a big challenge and immense effort is still required to get a complete species list (Mueller et al. 2014; Taylor 2014). Only Red Lists for single countries or federal states are currently available (e.g. Benkert et al. 1996; Wirth et al. 2011).

### **1.2.3 Assessment of fungal diversity**

Biodiversity can be assessed by monitoring, which involves the process of the compilation of information about ecosystems, communities or species diversity, and their changes during time (Yoccoz et al. 2001). Monitoring is necessary to understand the mechanisms defining the fungal richness in particular habitats or areas, which can be used to infer the magnitude of diversity at a larger scale (Lodge and Cantrell 1995; Peay 2014).

The reason, the target organisms, and the method for monitoring have to be considered carefully before starting a project (Yoccoz et al. 2001; Bonar et al. 2011). The question of how and for how long a monitoring should be carried out has been repeatedly addressed in several publications (e.g. Cantrell 2004; Tofts

and Orton 1998; Berglund et al. 2005; Bonar et al. 2011; Halme and Kotiaho 2012). Each monitoring method is limited and not a single method is known to detect all species in an area (Cannon 1999), so the results of each investigation depend on the used methodology (Zak and Willig 2004). Fungal monitoring methods can focus for instance on direct observation, cultivation, direct molecular analyses, or assessment of diversity through association methods such as extrapolating from plant diversity and vegetation type (Cannon 1999).

In the direct observation method, already described as a classical method in Section 1.1.3, the target organisms are characterized by taxonomic, ecological, or morphological (e.g. by size) groups, the latter being often used in mycological fieldwork. Due to their size, macrofungi are usually easier to investigate than microfungi (Castellano et al. 1999).

In samplings, presence/absence (incidence) or abundance (e.g. number of specimens or total biomass) of the target organisms can be recorded. In fungal monitoring, incidence data usually correspond to presence data only, because the reason for non-detection might be variable. The non-detection of a species can either be due to its real absence, to its lack of conspicuous structures, or to overlooking (Cunningham and Lindenmayer 2005). Incidence data are easier to record for most ecological studies, because assessing fungal abundance data is difficult and time-consuming (Debinski and Brussard 1994). In this study, only incidence data were used.

Danielsen et al. (2005) discussed the importance of monitoring as well as the problems of long-term inventories, and underlined the possibility to use local data to elucidate global factors affecting richness and its variation over time. An inventory should consist of repeated samplings to increase the chances of detecting new species that have previously remained undetected (Schmit and Lodge 2005), encompassing seasonal variations within the fungal communities (Cannon 1997; Halme and Kotiaho 2012). To perform such time-intensive inventories, the cooperation of several persons is mostly necessary (Watling 1995).

Usually, macrofungal inventories in one plot for several years yield higher fungal diversity than investigating different plots in one year (Cannon 1999), due to the unpredictable and often short-time fruit-body production of many fungi (Halme

et al. 2012). Fungal sampling activities of five to ten years have been proposed (Watling et al. 2005), but monitoring activities on fungi have not reached saturation even after more than 40 years of sampling (Hawksworth 2012). Such long-term studies are generally unpractical, and therefore appropriate tools for the extrapolation of richness data are necessary (Cannon 1999). However, the initial calibration is often time-consuming and expensive (Cannon 1999), and further inventories are necessary to check the consistency of proposed estimation factors and relationships (Schmit and Mueller 2007). In one part of this work, the diversity of macroscopically evident fungi is monitored in an exhaustive inventory to estimate the total species richness in this area.

Most extrapolations of richness are based on assumptions, like the fungus-host ratio or the relationships between anamorph and teleomorph. Sometimes, investigations of understudied habitats and fungal groups are also taken into account. Due to the various approaches, the estimations of total number of fungal species are different, depending on the used assumptions and organisms. Especially for statistical methods, the high number of rare species in fungal surveys increases the difficulties for estimations (Unterseher et al. 2012).

The most widely used estimation of fungal richness is based on the plant:fungus ratio (Hawksworth 2012), because most fungi are directly or indirectly associated with plants (Grayer and Kokubun 2001). The advantage of using plants in estimations is that they are usually easier to detect and better known than fungi (Rudolf et al. 2013). However, the applicability of the plant:fungus ratio is widely discussed because it was established for an incompletely investigated temperate area. Tropical and polar regions were not considered as well as special ecosystems like insects. Furthermore, the data are only based on morphological species concepts without considering cryptic species (Hawksworth 1991; Schmit and Mueller 2007; Jones and Richards 2011; Hawksworth 2012). All these reasons explain why the ratio varies strongly in different studies (Hawksworth 1991, 2012; Taylor 2014) and a correlation between fungal and plant richness has been found in some studies, whereas others have failed to find such relationship (Rudolf et al. 2013).

These criticisms underline the necessity of comparable and repeatable assessments based on standardized survey protocols for fungi in all regions

(Cannon 1999). Most monitoring projects are based on various sampling methods of selected fungal groups that are often relatively easy to observe, like Basidiomycota (Cannon 1997). To the best of the author's knowledge, the approach to record all macroscopically evident fungi on a monthly basis, including small Ascomycetes and groups like phytoparasites, has previously been performed in the tropics only (Piepenbring et al. 2012), from which the data was used for comparison, and in Italy (Angelini et al. 2015). The fact is that more fungal groups are considered with this method and a higher fungal diversity can be compiled for relatively small sampling areas, in comparison to similar studies concentrating on few ecological or taxonomic groups. Due to the same sampling method being applied in different areas, the factor sampling-area size, which seems to have a strong influence on species richness in general (Connor and McCoy 1979), is minimized.

### **1.3 Temporal variation in fungal diversity**

Studies on the phenology of mycorrhizal fungi and diverse groups of Basidiomycetes show a strong seasonal effect (Vogt et al. 1992; Stankeviciene et al. 2008; Halme and Kotiaho 2012). The evaluation of temporal changes and the drivers of these changes can be used for analysing ecological processes and their variation (Tóth and Barta 2010), and are important to forecast future processes (Dornelas et al. 2012).

#### **1.3.1 Seasonal changes**

In general, seasonal patterns in fungal diversity are commonly known. This fact is especially important for macrofungal inventories, because fruit-body production is ephemeral and single sampling events can yield false conclusions about the diversity of a certain area (Watling 1995). Therefore, repeated samplings are important for monitoring activities (Bonar et al. 2011).

Seasonality is strongly dependent on the geographical area. In Europe, a strong peak of fungal occurrence can be found usually in autumn and minor peaks in spring, so the change is often associated with the four different seasons and is slightly shifted in Mediterranean areas (Watling 1995). In tropical regions,



seasonality is mostly associated with rainy and dry season (Piepenbring et al. 2012).

One problem in studying seasonal changes of fungi is that their occurrence depends on the investigated group, defined by ecological or taxonomic aspects. The seasonal variation is usually higher in species developing epigeous sporocarps than in others producing hypogeous sporocarps (O'Dell et al. 2000). Further examples of differences in seasonality are described for the ecological groups of mycorrhizal and saprotrophic fungi (Straatsma et al. 2001), as well as the taxonomic group Agaricales (Halme et al. 2012). Other fungal groups, like perennial polypores including Polyporales (Halme and Kotiaho 2012), and lichens, do not show seasonality (Wirth et al. 2011).

As an example for seasonality, studies of ectomycorrhizal fungi in temperate areas show similar patterns either by using molecular methods of plant roots or classical fruit-body inventories, with minima of species richness in June, and a rapid change to the maximum in September (Vogt et al. 1981; Courty et al. 2008; Stankeviciene et al. 2008; Burke et al. 2009). In contrast, other studies did not reveal any seasonality and changes between years for ectomycorrhizal roots (Smith et al. 2007). This shows that the results of fungal seasonality studies are often contradictory and further investigations of different taxonomic and ecological groups is necessary.

### **1.3.2 Drivers of changes**

Different aspects influence the abundance and composition of fungal species. One of the most important abiotic factors is weather. Several studies show an influence of temperature, humidity and precipitation on fungal occurrence, but the effect of these variables differs strongly depending on the fungal groups considered. Different temperature and humidity optima and ranges are known for certain species (Fogel 1976; Straatsma et al. 2001; Krivtsov et al. 2003; Moore et al. 2008; Li et al. 2012; Karim et al. 2013). Precipitation seems to be very important for fungal development, especially during spring and autumn, but drought stress has also strong influence so that later precipitation does not show any effect (O'Dell et al. 2000; Straatsma et al. 2001; Krivtsov et al. 2003; Ceska 2013).

Other studies showed that, even though weather variables have an effect, specific fungal groups are more dependent on substrate conditions and geographical location (Kennedy et al. 2006; Gómez-Hernández et al. 2012; Heilmann-Clausen et al. 2014). Further factors influencing fungal communities are carbon dioxide and nitrogen concentrations, pH of the substrate, calcium, and nutrient availability (Watling 1995; Avis et al. 2003; Moore et al. 2008; Cox et al. 2010; Tedersoo et al. 2014). For organisms associated with dead material, like wood-inhabiting fungi, factors such as the stage of decay and the age of the substrate influence the fungal community (Kutszegi et al. 2015).

Beside abiotic factors, also biotic factors, like interactions with other organisms, are important drivers of fungal changes in richness and community structure (Fogel 1976; Moore et al. 2008; Karim et al. 2013). For fungi associated with plants, the associated plant itself and the host species composition has probably an influence on fruiting (Tóth and Barta 2010; Kutszegi et al. 2015). The already explained plant:fungus ratio (Section 1.2.3) for estimating fungal richness shows the importance of plants on fungal diversity.

The influence of abiotic and biotic factors is dependent on the investigated fungi, and differs between ecological and taxonomic groups (Kutszegi et al. 2015). To understand the influence of seasonality, each group has to be analysed separately to test their association with selected abiotic or biotic factors. Furthermore, sampling-specific characteristics like investigated group (e.g. macrofungi, soil fungi), type of analyses (e.g. morphological, molecular), and investigators (e.g. specialists vs. amateurs, number of people), have to be taken into account.

### **1.4 Aims of the study**

This thesis aims at analysing the macroscopically evident fungal diversity on temporal and spatial scale, including comparisons of fungal richness and composition on different taxonomic and ecological levels.

The thesis is divided in two parts, the first one focuses on fungal richness including comparisons on spatial scale, and the second one on temporal changes of fungal diversity and its possible drivers.

Several goals concerning fungal richness were defined:

- Finding out the diversity obtainable through the regular sampling of all macroscopically evident fungi, aiming at a comprehensive-taxa inventory in a region with temperate climate
- Estimating the total number of fungal species in the main sampling area, based on different methods and proving the globally proposed plant:fungus ratio of 1:6 for its validity for a smaller sampling area than the one it was established for by Hawksworth (1991)
- Evaluating, if the investigated areas in Germany, Austria, Spain, and Panama differ in the fungal diversity at different taxonomic levels
- Using the spatial data for testing the possibility of richness estimations based on lower sampling effort

Further goals concerning temporal variation in the main sampling area:

- Analysing the changes of richness and species composition over three sampling years
- Checking the assumption of typical fungal diversity peaks in autumn in an extensive-taxa inventory, and verifying if sampling only during the main fruiting period, as performed in many monitoring projects, is sufficient to provide a statement about the diversity in an area
- Evaluating if temporal variation differs between taxonomic or ecological groups for the complete sampling period and for different sampling years, months and seasons, with special focus on the less investigated species in Ascomycota
- Evaluating the importance of the factors humidity, temperature, and precipitation as possible drivers for changes in richness and species composition for different investigated groups

## 2 Material and methods

### 2.1 Study areas

For this thesis, several sampling areas were studied, two in Germany (DEU), one in Spain (ESP), and one in Austria (AUT). In addition, existing data from one area in Panama (PAN) were used (Table 1, Figure 2). In the descriptive parts of this work, the use of the terms Taunus (main sampling area, DEU), Bulau (DEU), Somiedo (ESP), Kleinwalsertal (AUT), and Majagua (PAN) refer to the respective sampling areas.

Vegetation was heterogeneous both among and within the sites. However, in almost all study sites, at least a part of the sampling area contained a forest area and another part a meadow area. This ensured the presence of a high number of niches with a high variability of fungal species. For all sampling areas, a transect of 500 m was established and the samplings covered approximately 10 m at each side of the transect. This approach is based on a strip-transect design without plots and constrained by time (Castellano et al. 1999; Fasham and Mustoe 2005).

Maps of all sites were created with ArcGIS 10 (copyright: OpenStreetMap (and contributors, CC-BY-SA; Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community). Further editing of the maps was made with Adobe Photoshop CS5.1.

Table 1: Characteristics of the sampling areas and number of sample events performed (N). Altitudes (meters above sea level, m.a.s.l.) and coordinates correspond to start and end of the sampling transect. Coordinates were taken with a GPS device (Garmin GPSmap 62s) in the WGS 1984 system.

Area	Altitude start [m.a.s.l.]	Altitude end [m.a.s.l.]	Coordinates start	Coordinates end	N	Sampling period
Taunus (DEU)	399	400	N50°08'28.0", E008°16'05.5"	N50°08'29.6", E008°16'21.1"	36	Monthly 2011-2013
Majagua (PAN)	109	151	N8°29'44.34", W82°25'53.64"	N8°29'15", W82°26'7.02"	24	Monthly 2009-2011
Bulau (DEU)	112	124	N50°07'56.2", E008°57'52.7"	N50°07'55.8", E008°57'46.5"	4	All 3 to 4 months 2013-2014
Somiedo (ESP)	686	719	N43°07'03.8", W006°15'14.0"	N43°06'50.1", W006°15'16.4"	2	Jun 2013 Oct 2014
Kleinwalsertal (AUT)	1149	1183	N47°21'29.6", E10°9'39.4"	N47°21'35.5", E10°9'31.9"	1	Sep 2013

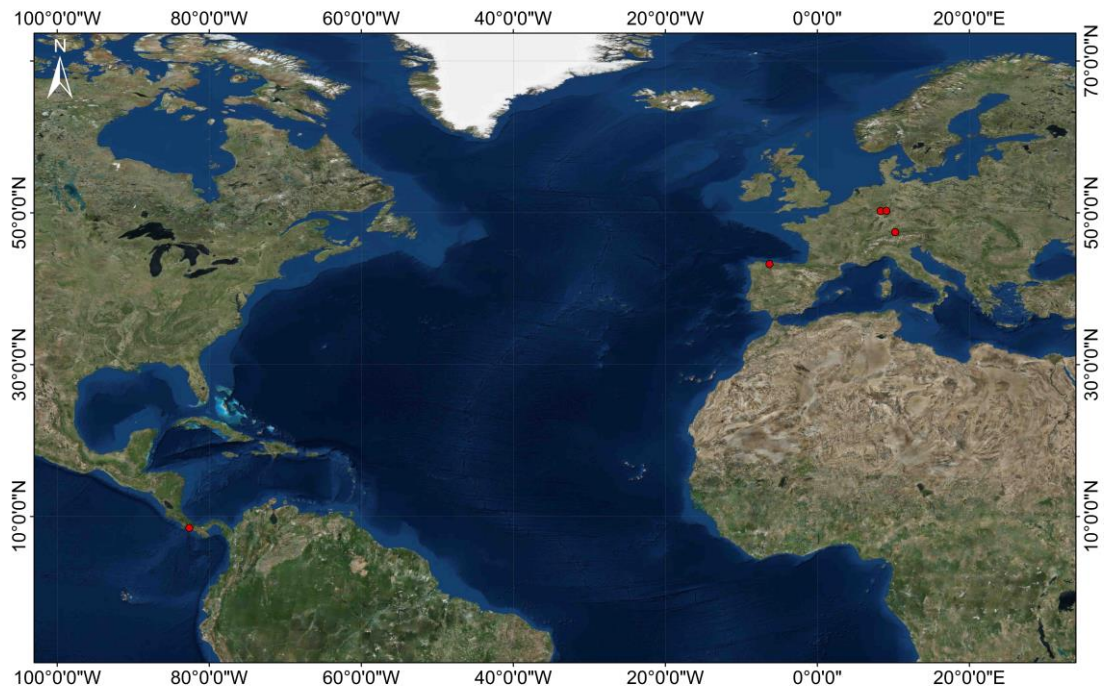


Figure 2: World map with the different sampling areas (in Panama, Spain, Austria, and two sites in Germany) marked in red.

The two sampling areas in Germany and the one in Spain are integrated within habitat directive sites (flora-fauna-habitat area (FFH)). These sites are part of European conservation zones (Natura 2000) intended to maintain biological diversity in Europe (European Union 2012). In Hesse (Germany), 9.9% of the federal state territory is protected by the Natura 2000 directive, including the two German sampling areas Taunus and Bulau (HMUKLV 2008a).

In the following chapters, the investigated areas are described in decreasing order of the sampling intensities applied to them in this investigation. Panama is the only area in which data already existing from a previous work were used. The original data were kindly provided by M. Piepenbring, and parts of them have been already published by Piepenbring et al. (2012) and Piepenbring et al. (2015).

### 2.1.1 Taunus (Germany), main study area

The main study area is located in the Taunus mountain range in the federal state of Hesse, central-western Germany. The mountain range is divided in three areas: the north Back-Taunus (Hintertaunus), the middle High Taunus (Hoher Taunus) and the south Pre-Taunus (Vordertaunus) (Stahr and Bender 2007).

## Study areas

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The investigated area is integrated within the FFH area “Troockenborn /Kellerskopf bei Rambach” with a total surface of about 55 hectares (HMUKLV 2008b). This zone is divided into a small river valley and a higher grassland called Troockenborn surrounded by forest. The lower part belongs to Pre-Taunus and the upper part to High Taunus, in which the collection area is located (Wenzel et al. 2001). The sampling was conducted with the knowledge of the Forestry Department Wiesbaden.

The examined area is situated at about 400 m above sea level, along a 500-meter-long section of a footpath at the border of a forest (Figure 3). The annual precipitation in the area ranged from 630 mm to 760 mm for the sampling period (data based on the weather station Wiesbaden Auringen, provided by Deutscher Wetterdienst 2015). The difference in altitude between the beginning and the end of the path is small, even though the whole area shows a continuous incline.

During the sampling period, the vegetation was affected by forestry work by the Forestry Department and several fallen logs were lying within the sampling area. The investigated zone comprises mainly broadleaved trees and an extensively managed meadow. This grassland was mowed twice a year by personnel of the Forestry Department. Only some spots with small bushes and a wetland in the middle of the meadow were left out. With exception of the wetland, the meadow was mostly dry, even though one part of the grassland was overflowed by a little stream after heavy rain.

The vegetation in the sampling area can be divided into secondary forest, meadow, and wetland vegetation. The mixed beech forest consists mostly of trees like *Fagus sylvatica*, *Picea abies*, *Populus tremula*, *Quercus petraea*, *Quercus robur*, and grasses like *Luzula luzuloides*. On the other side of the path, several grass species in the families Poaceae, Cyperaceae and Juncaceae are growing on the meadow. The small wetland within the meadow contains one willow (*Salix caprea*), one alder (*Alnus glutinosa*), and typical vegetation for this ecosystem, for example *Juncus effusus*. Some photos of the sampling area are shown in Figure 4.

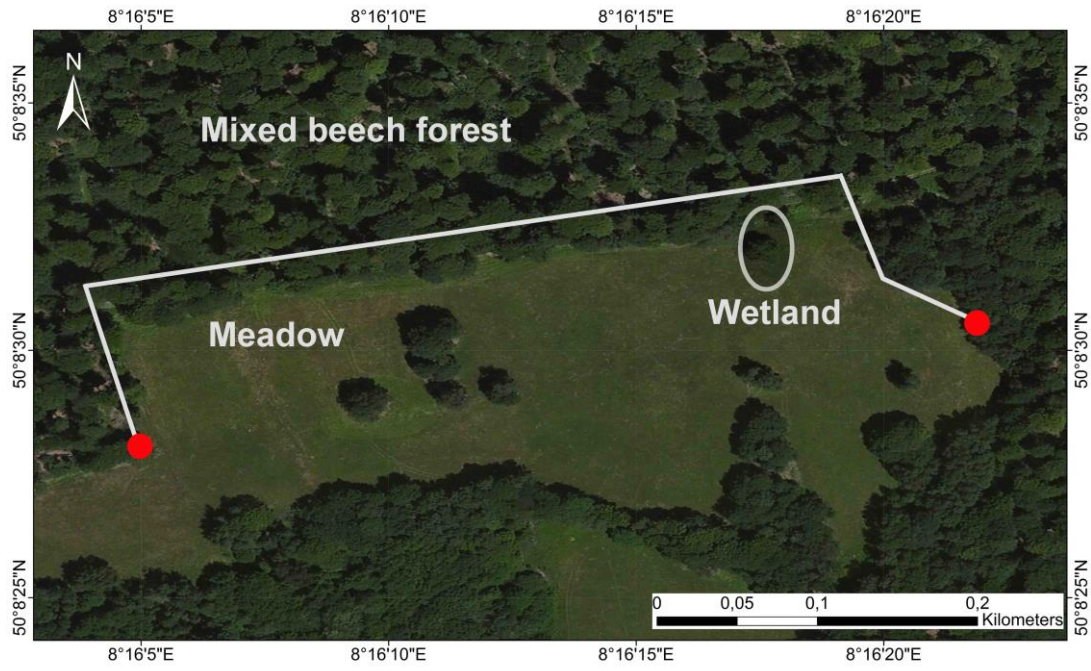


Figure 3: Sampling area in Taunus (DEU). The sampling transect is indicated by a white line. The grey elliptic area delimits a small wetland.



## Study areas

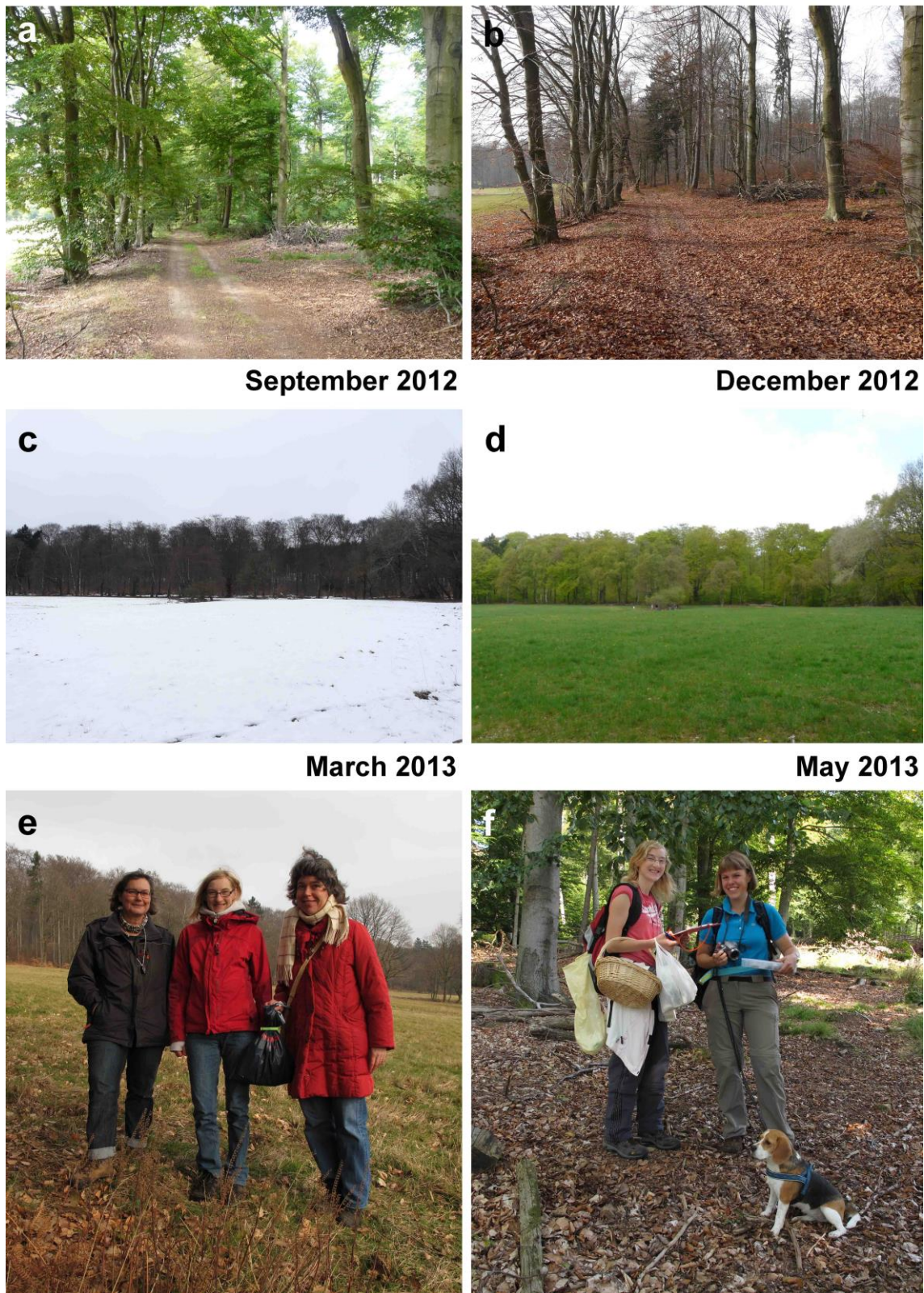


Figure 4: Sampling area of Taurus. The photos were taken during different sampling events. Photos (a-d) were taken by S. Rudolph. The group photos in (e-f) were taken by M. Piepenbring (e) and H. Lotz-Winter (f). The names of the samplers from left to right are H. Lotz-Winter, S. Rudolph, and M. Piepenbring (e) and S. Rudolph and N. N. Völxen (f).



### 2.1.2 Majagua (Panama)

The investigated area is located in Panama in the province of Chiriquí. The climate is tropical, in contrast to all other sampling areas presented in this work. The sampling area is located near the village Los Algarrobos on a path towards the river Majagua. The vegetation is typical for secondary lowland forests in Panama.

The Panamanian sampling area showed the largest differences in altitude from the starting to the end point, with more than 40 m. One side of the path is a meadow area used as cattle pasture, whereas the other side is covered with trees (Figure 5). Further information regarding the sampling area is provided by Piepenbring et al. (2012) and Piepenbring et al. (2015).



Figure 5: Sampling area next to the river Majagua (PAN). The sampling transect is indicated with a white line.

### 2.1.3 Bulau (Germany)

The Bulau region is located in the federal state of Hesse between the town of Hanau and the lake Erlensee. The annual precipitation in the area ranges from 600 to 650 mm and the average temperature is higher than 9°C (Buttler et al. 2003). The river Kinzig is essential for this ecosystem as it is responsible for the riparian forest next to the riverbank (Buttler et al. 2003). High efforts have been made to restore this river and adjacent areas (Hufmann 2013).

## Study areas

Bulau is integrated within the FFH area “Erlensee bei Erlensee und Bulau bei Hanau” with a total size of about 603 hectares (HMUKLV 2008c). The whole area is divided into an eastern and a western part by a motorway. The two parts “Erlensee bei Rückingen” and “Langendiebacher Unterwald” are situated in the eastern zone. The study area is located in the western part of this area called “Bulau bei Hanau und Wolfgang” (Buttler et al. 2003).

There was almost no difference in altitude along the collection transect. The river Kinzig is next to the studied area and has great influence on the vegetation. In contrast to all other areas, the chosen transect in Bulau is a small trail which follows the meandering river only at a few metres distance (Figure 6). Therefore, most of this area is humid and temporarily flooded.

The vegetation in the studied area is characterized by riparian zone trees like White Willow (*Salix alba*) and Black Alder (*Alnus glutinosa*) in areas next to the river. Common Beech (*Fagus sylvatica*) and Pedunculate Oak (*Quercus robur*) are common in parts that are higher or farther away from the river. Especially during fruiting season, *Urtica dioica* was very abundant in some parts of the investigated zone. Some photos of the sampling area are shown in Figure 7.

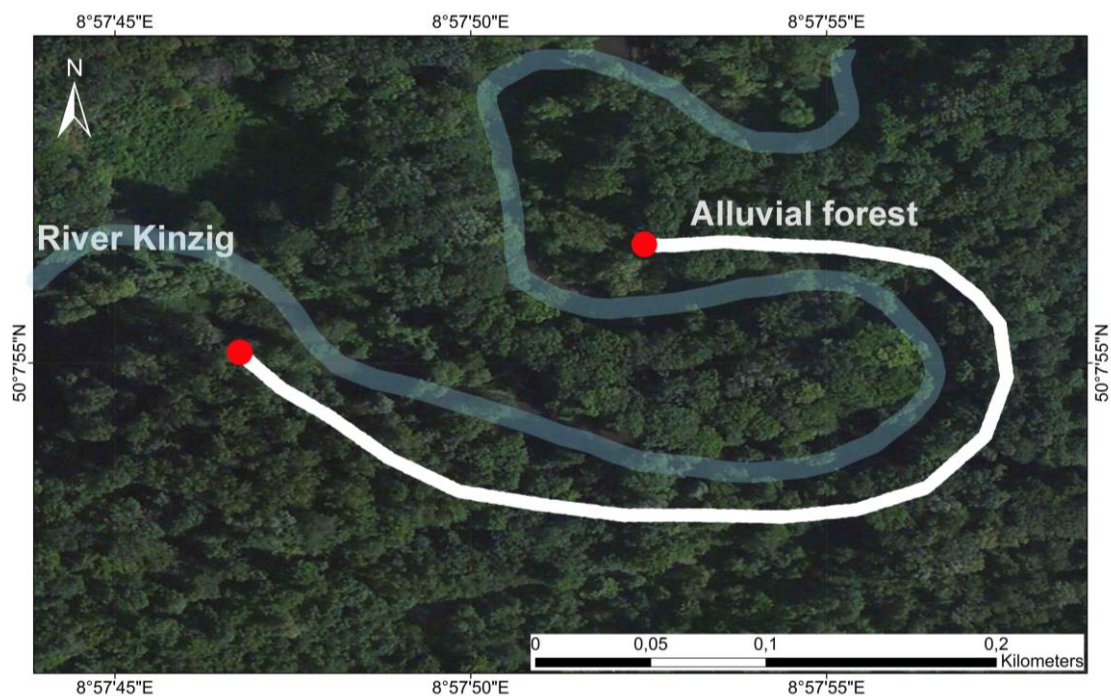


Figure 6: Sampling area in Bulau (DEU). The sampling transect is indicated with a white line and the river with a blue line.





Figure 7: Sampling area of Bulau. The photos were taken during different sampling events. Photos (a-d) were taken by J. Werdecker. The group photos in (e-f) were taken by M. Piepenbring. The names of the samplers from left to right are H. Lotz-Winter, S. Rudolph, J. Werdecker and M. Piepenbring (e) and S. Rudolph and H. Lotz-Winter (f).

### 2.1.4 Somiedo (Spain)

Somiedo is situated in the Cordillera Cantabrica, a mountainous region of nearly 300 km<sup>2</sup> in Asturias, northern Spain, with a temperate and humid climate. The annual precipitation ranges from 1 038 mm to 1 250 mm, with the highest peaks of rainfall in autumn. Depending on the altitude, the average temperature varies between 8.2°C and 11.5°C (Rubio et al. 2010).

The region of Somiedo is part of a large Natura 2000 site with a total size of 29 144 hectares. One characteristic of this site is the occurrence of the brown bear (*Ursus arctos*). Furthermore, the high richness of flora and fauna and the naturalness of the habitats are important reasons to protect this region (NATURA 2000 2004).

The altitude difference between start and end of the studied area is more than 30 m, and some parts are steep and rocky with precipitous slopes on both sites of the trail. The area of Somiedo has the second highest altitude of the sampling sites in this study, after that in Austria. At one part on the wayside, running water along a rock created a small wetland, whereas other parts on rocky ground were exposed to the sun and dry (Figure 8). The weather conditions in Somiedo were very dry during the weeks before the first sampling and humid before the second sampling event.

The sampling area is along a hiking trail which is called “La Malva” (Asturnatura 2015). *Acer pseudoplatanus*, *Salix caprea*, and different Iberian species of *Quercus* are growing in the sampling area. In contrast to all other European sampling areas, *Fagus sylvatica* was not recorded, even though it is documented for this area (Rubio et al. 2010). Some photos of the area are shown in Figure 9.



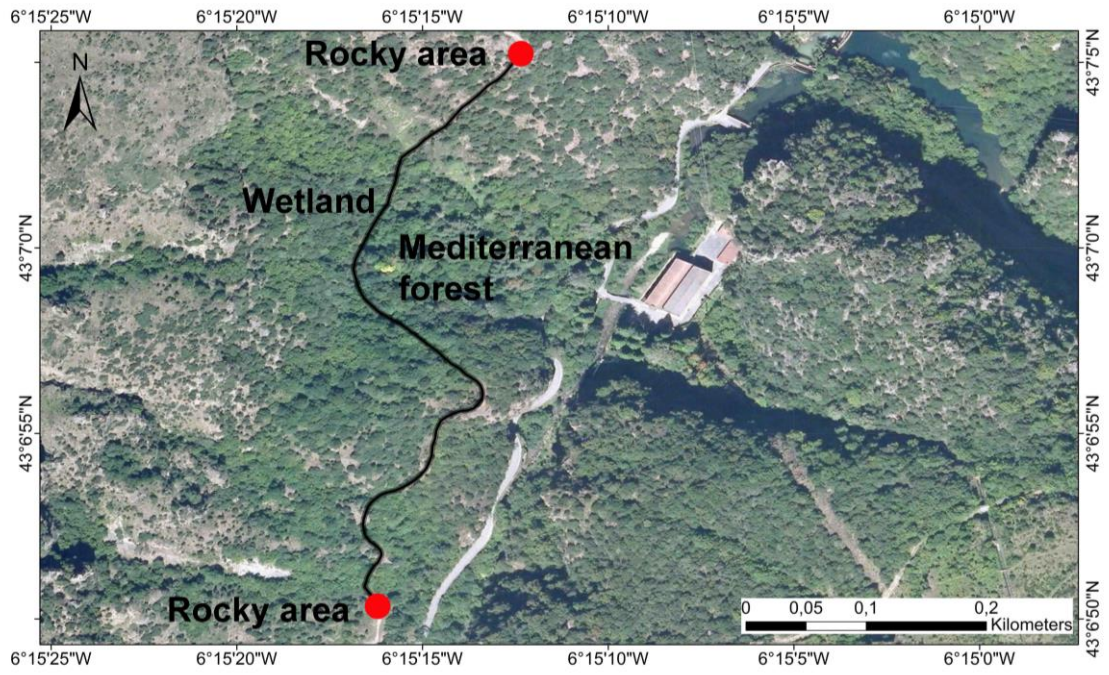


Figure 8: Sampling area in Somiedo (ESP). The sampling transect is indicated with a black line.



## Study areas



Figure 9: Sampling area of Somiedo. Photos (a-c) were taken during the first sampling event on 06.06.2013 by S. Rudolph. The group photos in (d-f) were taken by M. Piepenbring (d-e) and by H. Lotz-Winter (f). The names of the samplers from left to right are H. Lotz-Winter, J. Linde, E. Rubio Dominguez and S. Rudolph (d), M. Piepenbring, S. Rudolph and H. Lotz-Winter (e) and M. Piepenbring and S. Rudolph (f).



### 2.1.5 Kleinwalsertal (Austria)

Kleinwalsertal is located in Austria in the northern Alps adjacent to the German border. The annual precipitation is higher than 1 000 mm (Kost et al. 2011) with the highest monthly precipitation of more than 200 mm during the months June, July and August (Jensen et al. 2007). The vegetation period is relatively short and small habitats contain a high diversity of fungi (Kost et al. 2011). The mean temperature is about 6°C according to measurements during the last century (Jensen et al. 2007). Kleinwalsertal is the only European sampling area in this investigation that is not part of a FFH-area.

The difference in altitude from the highest to the lowest point is about 30 m, nearly the same as in Somiedo. Nevertheless, the absolute altitude is 400 m higher than in Spain. The studied transect starts with a steep path and ends with a plane meadow at the border of a forest (Figure 10). The weather conditions in Kleinwalsertal were rainy the time before sampling. In the forest next to the investigated trail, plant species like *Abies alba*, *Fagus sylvatica*, *Picea abies* and different *Salix* species were found. Some photos of the area are shown in Figure 11.

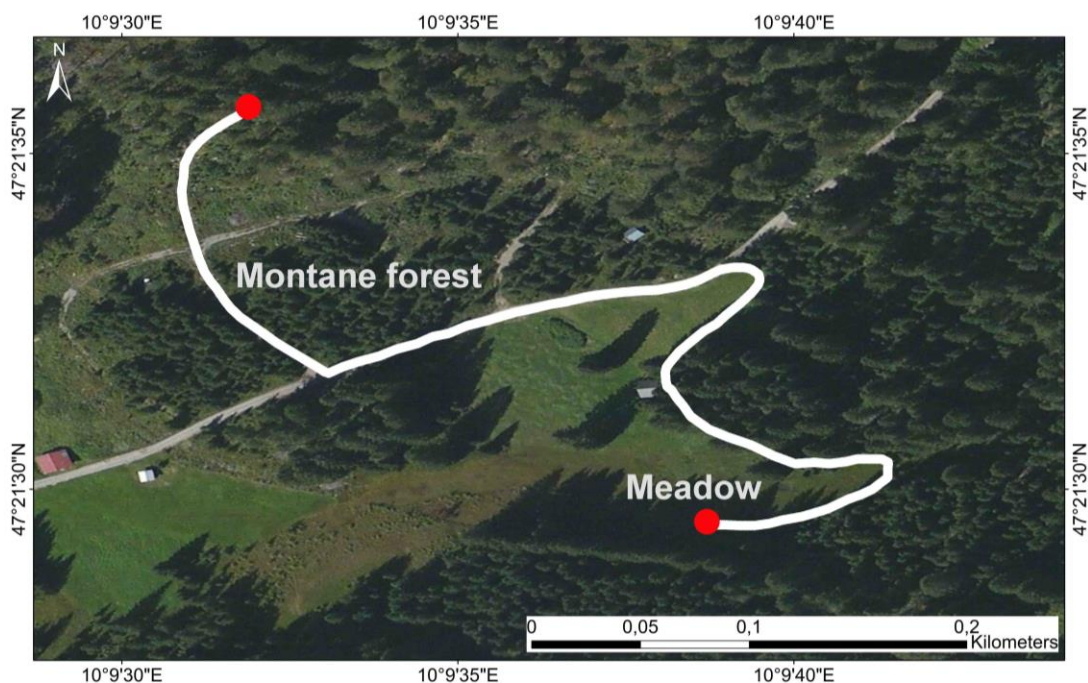


Figure 10: Sampling area in Kleinwalsertal (AUS). The sampling area is indicated with a white line.



## Study areas



Figure 11: Sampling area of Kleinwalsertal. Photos (a-c) were taken in October 2013 by M. Piepenbring. The group photos in (d-f) were taken by S. Rudolph (d), by M. Piepenbring (e) and by H. Lotz-Winter (f). The names of the samplers from left to right are H. Lotz-Winter (d), K.-H. Rexer (e), and S. Rudolph and M. Piepenbring (f).



## 2.2 Sampling and identification

### 2.2.1 General methods of sampling, recording and documentation

For this monitoring project, fungi and vascular plants were sampled. Even though the main focus was to analyse fungal diversity, plants were included in order to calculate the plant:fungus species ratio. This ratio is widely used for estimations of fungal species richness at local and global scales. All discernible plants except mosses and algae were recorded, using a comparable sampling effort in all investigated areas.

The sampling activity for fungi was performed during approximately two hours per sampling event and study area. During this time span, the entire sampling transect was covered. For sites in which several sampling events were carried out, the start and end of the transects were alternated across samplings to ensure a comparable sampling effort in the whole area over time.

General aspects of the sampling areas were documented in the field. In each sampling event, the areas were photographed for documentation of weather conditions and vegetation period. Further annotations of the collection area, like recently mowed grass, etc., were notated.

All fungi discernible with the naked eye or with a hand lens were recorded. This included saprobionts on the ground and on plant material like dead leaves or wood, parasites on plants and insects, as well as mushroom-producing mycorrhizal fungi. Lichens and members of non-fungal groups like slime moulds and Oomycota were included. Fungal groups that cannot be detected without the aid of culturing or molecular techniques (e.g. yeasts, most soil fungi, and endophytes) were not considered.

Plants and fungi were identified in the field as far as possible. The presence of the species observed was recorded for their later analysis as incidence data (presence/absence of species). Undoubtedly identified species were marked in field lists and/or photographed in the field for documentation.

Fungi and plants that could not be identified in the field were collected and taken to the laboratory for identification. For transport, fungi associated with plant organs were placed individually in paper bags in closed plastic bags. Mushrooms were maintained in plastic boxes with individual compartments for

each species in order to prevent mixing of spores, which can lead to difficulties for the later microscopic identification.

In the laboratory, the fungal fruit bodies were identified to the lowest possible taxonomic level by observation of macroscopic and microscopic features, using either a CX41 Olympus or an Eclipse 80i Nikon light microscope. Selected fungal specimens were cultivated on malt-yeast-peptone agar (MYP) and deposited in the IPF (Integrative Pilzforschung) culture collection maintained at Goethe Universität Frankfurt. The living cultures generated are thus available for further analyses and to other researchers.

The identification of fungal specimens was based on common literature, such as Breitenbach and Kränzlin (1986-2005) and Knudsen and Vesterholt (2008) for macrofungi, Ellis and Ellis (1997), Brandenburger (1985) and Vánky (2012) for plant parasitic fungi, or Seifert et al. (2011) for Hyphomycetes. Other specialised literature was used for particular fungal groups, such as Câmara et al. (2001) for *Paraphaeosphaeria* sp. or von Arx et al. (1984) for *Chaetomium* spp. Furthermore, websites like the fungus-host distribution database from the U.S. Department of Agriculture (USDA, <http://nt.ars-grin.gov/fungaldatabases/fungushost/fungushost.cfm>) were used as orientation for the identification of plant parasites based on their host.

The nomenclature of fungi (division, order, genus, and specific epithet) herein used is based on Index Fungorum (Royal Botanic Gardens Kew 2008, <http://www.indexfungorum.org>). Organisms that could only be identified up to genus level were numbered and considered as morphospecies. All other organisms were named using the lowest possible taxonomic level. When found and recognized as such, sexual and asexual fungal forms were treated as a single species.

Fungal records were roughly assigned to ecological categories. These categories consisted of saprobionts, i.e. those fungi growing on dead plants, animals or ground; parasites, present on living plants and penetrating the host tissue or recognized according to their taxonomy; mycorrhizal fungi, recognized according to their taxonomy; lichens, forming symbioses with algae or cyanobacteria and fungi feeding on microorganisms, recognized according to their taxonomy. The classification into the ecological categories was based on

common literature used for identification (see above), field observation and on the knowledge of the researchers performing the samplings and/or identifications.

For documentation, differentiation, and curation of the specimens, index cards of identified species and morphospecies were made. These cards contained information on the specimen's taxonomy, substrate or host, as well as descriptions, measurements and drawings of the most important macroscopic and microscopic features (Figure 12). Furthermore, the literature used for identification of the specimen was annotated. This procedure, together with the photos of specimens, helped to assign a newly collected fungus to a species already recorded or to recognize it as a record of a new species.

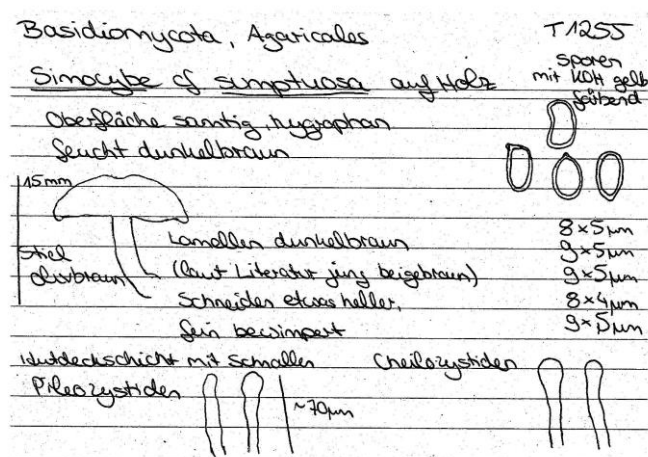


Figure 12: Example of an index card, containing the most important morphological features.

Plant specimens were mainly identified with the books Seybold (2011) and Jäger et al. (2013). The indicated taxonomic levels were family, genus and specific epithet. If the identification until species level was not possible, the earlier procedure described for fungi was used. The nomenclature of plants was based on Floraweb (Bundesamt für Naturschutz 2013, <http://floraweb.de/index.html>).

Two species lists for each sampling area were obtained, one for fungi and one for plants. These lists include taxonomic and ecological data for each species, and data on the sampling, such as the date, geographical coordinates, identifier, collection number, host species, substrate, the availability of index cards, and further notes. The selected date format is day, month, and year. All these data were imported into the database Diversity Workbench (Workbench

contributors 2013), in cooperation with personnel and editors of this program from the Bavarian Natural History Collections (Munich). After conclusion of publications related to this thesis, species lists will be contributed to GBIF and publically available.

For almost all plant and fungal species, dried herbarium specimens, and/or photographs were obtained for documentation. The specimens will be deposited in the Herbarium Senckenbergianum in Frankfurt, and in the herbarium of the Botanische Staatssammlung München.

### **2.2.2 Sampling methodology in different areas**

#### **Taunus**

For the study area in the Taunus in Germany, the collection activities started in May 2011 at the beginning of the vegetation period in spring. From this date on, monthly samplings were performed for a total period of three years, until April 2013. Detailed information concerning dates and further sampling data are provided in the Appendix (Table S1 in appendix). The samplings for fungi were mostly carried out by four to five persons in each sampling event, sometimes with support from specialists on particular fungal groups (Table S2 in appendix). The samplers, and in some cases specialists (e.g. R. Cezanne, M. Eichler and C. Printzen for lichens), identified the specimens collected. In a few sampling events, undergraduate students helped during samplings and identification of specimens, within the framework of their respective studies.

#### **Majagua**

The samplings in a lowland forest in Panama were carried out monthly for two years (from February 2009 to January 2011). The data of the Panamanian inventory were used in order to compare repeated sampling activities in geographically distant sites. The Panamanian monitoring is the only inventory in this work in which the author was neither involved in sampling nor in identification. Nevertheless, the sampling method was similar to that used in the other areas. Detailed information about the methods used are available in Piepenbring et al. (2012) and Piepenbring et al. (2015).

### **Bulau**

In the Bulau area in Germany, four sampling events were conducted once every three to four months (8.5.2013, 5.9.2013, 10.12.2013, 18.3.2014). Like in the Taunus area, four to five persons recorded fungi and plants during two hours (Table S3 in appendix). The samplers, and in some cases specialists, identified the collected specimens in the laboratory. Part of the original data were recorded and used for a master thesis by J. Werdecker (2014), but they were newly analysed for this work.

### **Somiedo**

Sampling in Somiedo (Spain) consisted of two collection events. The first one took place on 6.6.2013 to record plant and fungal diversity in spring, while the second was on 25.10.2014 to document species richness in autumn. Six persons collected fungi in both sampling events (Table S4 in appendix). Identification of the collected specimens was performed as previously described, with specialists working in this area (E. Rubio Dominguez, J. Linde, L. Calvo) being consulted for the identification of local species.

### **Kleinwalsertal**

In Kleinwalsertal (Austria), one sampling event was carried out (29.9.2013). Six persons collected fungal and plant specimens during the sampling event (Table S5 in appendix). The collection and identification was performed with the help of specialists (G. Kost, K.-H. Rexer, F. Popa) from the University of Marburg, who have been working on a fungal inventory in this area for several years.

#### **2.2.3 Recording of weather data in the Taunus area**

For analysing the effect of environmental variables on fungal richness in the Taunus area over time, ambient temperature and relative humidity were continuously monitored with a Hygrochron data logger (iButton, model DS1923-F5, Fuchs Electronic, Weingarten, Germany) from 4.4.2011 to 30.3.2014. The iButtons recorded the temperature and humidity four times a day at 12 am, 6 am, 12 pm and 6 pm.

Recordings of temperature and humidity data during the initial sampling events at Taunus (4.4.2011 to 2.8.2012) were performed in Naurod, about 2.5 km distance. In later events, recordings were performed in the study area. Therefore, the devices were placed on branches of trees a few centimetres above ground level at the start and the end of the transect. To account for potential differences of the data that could have affected the analyses of results, three iButtons were placed in the sampling area, and their measurements were compared to the simultaneous recordings in Naurod. Only small differences were observed between the two locations. Due to technical problems, only one iButton recorded continuously from 2.8.2012 to 29.8.2012 and another one from 30.8.2012 to 30.3.2014. Therefore, only values from these devices were used for statistical analyses.

The original records of temperature and humidity data are provided in the digital appendix (1. climate). Daily recorded precipitation data from Wiesbaden-Auringen (263 m above sea level) published online by Deutscher Wetterdienst (2015) were also used, because the iButtons did not record precipitation data. The study area is at 3.5 km distance from the weather station based on Google Maps (GeoBasis-DE/BKG 2009).

## **2.3 Statistical analyses**

### **2.3.1 General methods**

The statistical analyses were focused on the richness and diversity of fungal data at each sampling site, including species composition. The records were available as incidence data per sampling unit. Consequently, frequencies correspond to counts of fungal records across sampling events.

Calculations were based on identified species and morphospecies identified up to genus level. The species lists were used for analyses at different taxonomic and ecological levels. Specimens identified only at higher taxonomic level were only considered for a comparison of identification levels between different sampling areas.

Statistical analyses were carried out with the program R version 3.1.3 (R Core Team 2013) with the use of several packages especially “vegan” version 2.2-1

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(Oksanen 2011), “Hmisc” version 3.16-0 (Harrell and Dupont 2014), “gplots” version 2.17.0 (Warnes et al. 2015) and “limma” version 3.22.7 (Ritchie et al. 2015). The scripts are provided in the digital appendix (R-Scripts).

For the analyses of species composition, ecological distances based on shared/unshared species among sampling events were calculated with the Sørensen dissimilarity index. For the calculation of the Sørensen index (Sørensen 1948), the species number in the first area (a), the species number in the second area (b) and the number of common species (c) are needed. The formula is:

$$QS = \frac{2c}{a+b} 100 \text{ (Sørensen 1948)}$$

The differences in species composition among samplings were explored graphically with the aid of ordination plots. In these plots, sites or sampling events are represented by points, and the relative distances between points reflect the calculated ecological distances (e.g. Sørensen dissimilarity index) based on species composition (i.e. samples with similar sets of species appear closer than sites sharing less species). In this thesis, the ordination method selected to explore differences between samples was the non-metric multidimensional scaling (NMDS), because this method is rank-based (the distance matrix is transformed into rank-orders) and therefore more robust than other techniques, which preserve the exact value of the distances. Furthermore, this method allows to use any dissimilarity distance and to handle missing values (Kindt and Coe 2005; Legendre and Legendre 2012).

The reliability of the NMDS in representing accurately the ecological distances across samples can be measured with a “stress” index. The higher the stress value, the poorer is the representation of the ecological distances in a two-dimensional plot. Ordinations with stress value above 30% are generally considered non-informative. All species displayed next to one site are probably more frequent there than in sites farther away (Kindt and Coe 2005). The species scores in this work were grouped by different variables like taxonomic group, ecological group, area and sampling year.

The significance of the effects of areas, time (in Taunus) and other ecological factors (e.g. temperature and humidity) on species composition were

investigated using the permutational analysis of variance (PERMANOVA, adonis function in R) (Anderson 2001) with 5 000 permutations.

### **2.3.2 Estimations of richness**

The total number of fungal species in the Taunus area could not be recorded in three years of sampling. However, there are different approaches to estimate the total species richness in an area based on incomplete sampling data. These computational methods can be grouped in parametric estimators, asymptotic functions, and non-parametric methods. The parametric estimators are the most accurate but require that the species data follow particular distributions (e.g. normal or Poisson distributions). The asymptotic functions do not require previous knowledge on the distribution of data, but they usually yield large variances and confidence intervals in the estimates, and therefore are less precise. Probably the best results for richness estimations, and therefore used in this thesis, are obtained with non-parametric methods, for which the distribution does not need to have a certain form and the variance is usually narrower than for asymptotic functions (Gotelli and Colwell 2011).

For the calculation of total fungal and plant richness in the Taunus area, several non-parametric estimators were used, namely Bootstrap, Chao 2, ICE (incidence coverage estimator), Jackknife 1, and Jackknife 2 (Colwell 2013). All these methods are based on the frequency of species, especially uniques (species recorded once) and duplicates (species recorded twice) of incidence data (Unterseher et al. 2008; Gotelli and Colwell 2011; Colwell 2013; Gotelli and Chao 2013). The estimations were calculated with EstimateS version 9.1.0 (Colwell 2013). The exact formulae for all used estimators in EstimateS are available in Table S6 in the appendix.

Randomized sample-based accumulation curves were calculated with 1 000 permutations (Colwell et al. 2012). Because the species accumulation curve for fungi did not reach saturation at the end of the samplings, data were extrapolated until doubling the number of samples. For extrapolation, the classic formula of Chao 2 was used following procedures in the EstimateS manual. Extrapolation beyond this limit is not recommended because the variance increases significantly rendering estimations of richness unreliable (Colwell



2013). The data were extrapolated for plants and fungi to calculate the plant:fungus ratio.

Extrapolations and estimations were performed for the most abundant taxonomic groups. The Chao 2 estimator was used for these calculations. The choice of this method is based on a study by Unterseher et al. (2008) in which this estimator revealed the best results for fungal incidence data.

### **2.3.3 Comparison of several areas**

The results obtained in the Taunus area were compared with those from the other areas investigated with lower sampling efforts. Fungal richness and diversity from different sampling areas were compared at the taxonomic levels of division and order, and the ratio plant:fungus was determined for each area. Furthermore, the levels of identification (until species level, genus level, and unidentified, which contain all fungi identified on a level less than genus) were compared across sites.

Each sampling area was assessed with a different sampling intensity (see Section 2.2.2). To reduce the effect of differential sampling efforts in the comparisons between sites, the same number of sampling events was analysed for each area. The closest dates between the samplings in the Taunus area and the area to be compared were chosen. However, this was not possible for the two-year sampling in Majagua (Panama), which took place two years earlier.

#### **Comparison between Majagua and Taunus**

The extensive inventories of taxa in the main sampling area of Taunus (first two years) and the monitoring project of Majagua, in the tropics, were compared. The sampling took place in Majagua from February 2009 to January 2011 and in Taunus from May 2011 to April 2013. The original fungal species table, kindly provided by M. Piepenbring, was formatted like those generated in this study to facilitate comparisons. The distance between the Taunus and the Majagua area is about 9 000 km, based on Google Maps (GeoBasis-DE/BKG 2009).

#### **Comparison between Bulau and Taunus**

The sampling events performed in the Bulau area were compared to four sampling events in the Taunus (Table 2). Accumulation and estimation of the

Bulau area were calculated as described before for Taunus. The distance between the Taunus and the Bulau area is about 50 km, based on Google Maps (GeoBasis-DE/BKG 2009).

Table 2: Sampling data of the two compared areas Bulau and Taunus with the number of days between the compared sampling dates.

Sampling date Bulau	Sampling date Taunus	Days difference
08.05.2013	02.05.2013	6
05.09.2013	27.08.2013	9
10.12.2013	18.12.2013	8
18.03.2014	31.03.2014	13

### **Comparison between Somiedo and Taunus**

For the comparison of the Somiedo area with the Taunus area, only the first sampling event of Somiedo was used, because the project in the Taunus was already finished for the time of the second sampling event in Somiedo (Table 3). Due to the small number of samples, no accumulation curves and estimates from the Somiedo areas were calculated. The distance between the Taunus and the Somiedo area is about 1 400 km, based on Google Maps (GeoBasis-DE/BKG 2009).

Table 3: Sampling data of the two compared areas Somiedo and Taunus with the number of days between the compared sampling dates.

Sampling date Somiedo	Sampling date Taunus	Days difference
06.06.2013	27.05.2013	10
25.10.2014	Sampling already finished	-

### **Comparison Kleinwalsertal and Taunus**

One sampling event was performed in Kleinwalsertal and compared with the sampling event in the Taunus with ten days difference (Table 4). No estimations and accumulations were calculated from the Kleinwalsertal because only one sampling event was performed. The distance between the Taunus and the Kleinwalsertal area is about 400 km, based on Google Maps (GeoBasis-DE/BKG 2009).

Table 4: Sampling data of the two compared areas Kleinwalsertal and Taunus with the number of days between the compared sampling dates.

Sampling date Kleinwalsertal	Sampling date Taunus	Days difference
29.09.2013	19.09.2013	10

### Comparison of all areas

Finally, the species lists of all areas and for all sampling events were compared. The comparison was performed considering only specimens identified at species level. Taxa identified until genus level were excluded because it could not be assured that morphospecies from the same genus were the same species across different sampling areas. For the graphical representation, a Venn diagram was calculated, which shows all intersecting counts between all possible relations of the five sampling areas (Ritchie et al. 2015).

The species composition between all five areas was compared. The differences in species composition for all sampling areas were analysed by permutational analysis of variance and displayed by NMDS, using the previous procedure, described in Section 2.3.1.

#### 2.3.4 Temporal changes of fungal occurrence in the Taunus

The influence of season and other factors on fungal richness was investigated. This was performed through a seasonal-trend decomposition process (stl function in R) based on locally weighted regression (loess) (Cleveland et al. 1990). Seasonal trend decomposition is useful for visualizing different patterns within the data, but no analysis is available regarding the significance of these changes (Kennedy et al. 2015). After detrending the data, normality of residuals was assessed.

The effect of the categorical variable month (explanatory variable) on species richness (predicted value) was assessed with the non-parametric Kruskal-Wallis test, because in most cases the data were not normally distributed. Measurements of richness at each of the three sampling years were used as independent observations (replicates) for this analysis (McCune et al. 2002).

The results of the Kruskal-Wallis test were described by its chi-squared value ( $\chi^2$ ), degrees of freedom (df) and p-value ( $P$ ). For all significant relationships (p-value less than 0.05) between month and richness, a nonparametric general

additive model was fitted to the scatterplot displaying species richness on different taxonomic and ecological levels (dependent variable richness on y-axis) to the explanatory variable month (on x-axis). Therefore, a local polynomial regression (loess) was performed for different taxonomic and ecological groups.

Temperature, humidity and precipitation were recorded as possible drivers for the seasonal changes of fungal richness. To choose the number of days before sampling, a Spearman's  $\rho$  rank correlation coefficient was calculated from one day before the sampling date to four weeks before the sampling date (Croux and Dehon 2010). The data of temperature and humidity used for the analyses consisted of the averaged values for the eight days prior to each sampling, because these showed the best correlation values. Selection of other measurement combinations for these values always yielded significant results in the same directions. Humidity and temperature were strongly correlated with each other (Spearman correlation:  $\rho=-0.71$ ;  $P<0.001$ ). Therefore, the interaction of these response variables was not tested in the generalized linear models (GLM).

The total amount of precipitation four days before sampling was used because it showed the best correlation with the fungal richness per sampling event. The analyses based on precipitation should be interpreted with caution because the data acquisition took place a few kilometres away from the sampling area. Consequently, the precipitation might be different in the investigated zone. Humidity and precipitation showed a nearly significant correlation ( $\rho=0.33$ ;  $P=0.05$ ).

A generalized linear model (GLM) with quasi-poisson regression was used to explain the changes in species richness by the explanatory variables humidity, temperature, and precipitation. The quasi-poisson regression was chosen because the species count data were not normally distributed and the dispersion parameter was higher than two (Kindt and Coe 2005). The results of richness on different taxonomic and ecological groups with at least one significant value for one variable were shown by their estimate, standard error (SE), t-value, p-value, and explained variance.

$$\text{Explained variance} = \frac{\text{Null deviance} - \text{Residual deviance}}{\text{Null deviance}} \text{ (Kindt and Coe 2005)}$$

Species composition was compared across sites. For the analyses of species composition, uniques (species represented by only one observation) were removed from the Taunus dataset (as in Lang et al. 2011; Ji et al. 2013). Rare species are often excluded from datasets to reduce noise in the analyses (e.g. Unterseher et al. 2008). The ecological distances were visualized using a NMDS like previously explained in Section 2.3.1.

The NMDS species scores were grouped by either their taxonomic affiliation, using the most frequent orders within Ascomycota and Basidiomycota, or their lifestyles, and visualized independently by confidence ellipses, using the standard deviation. The variable month was visualized with contours in the ordination plot by fitting a generalized additive model (GAM) to the data and the weather variables were included with vectors (Kindt and Coe 2005).

### **3 Results**

In the first part of this study, the fungal richness was compared within the sampling areas studied, namely Taunus, Majagua, Bulau, Somiedo, and Kleinwalsertal, and then between Taunus and the other sites. In the second part, the temporal variation of fungal diversity in the Taunus was analysed, and possible environmental causes for these changes were investigated.

#### **3.1 Fungal diversity in the Taunus**

Due to the repeated sampling every four weeks during three years, a high number of fungi was recorded in the Taunus area.

##### **3.1.1 Richness of recorded fungi and plants**

During the entire survey, 2 976 fungal specimens were obtained. Out of these specimens, 855 taxa could be identified and assigned to 741 species (79% of all records) and 114 morphospecies (12% of all records) identified up to genus level. An additional 80 records (9%) were identified at a higher taxonomic level and corresponded to 28 records identified up to division level, and six up to order level. The remaining 46 records could not be assigned to any taxonomic category. A total of 3 264 plant records were obtained, which could be assigned to 218 species. The most abundant fungal families are shown in the appendix in Table S10. A complete list of all recorded fungi and plants across sampling events and their associated metadata is provided in the digital appendix (2. Fungi Taunus; 3. Plants Taunus).

The distribution of fungal occurrence was uneven in contrast to the occurrence of plants. In total, 423 fungal species (49%) were only found once (uniques), and 152 fungi (18%) were recorded twice (duplicates). No fungus was recorded in all sampling events. The occurrence of plants was more balanced across samplings, with only 16 plant species (7%) being found once and 17 species (8%) twice. In total, 12 species of plants were recorded during all sampling events (Figure 13).

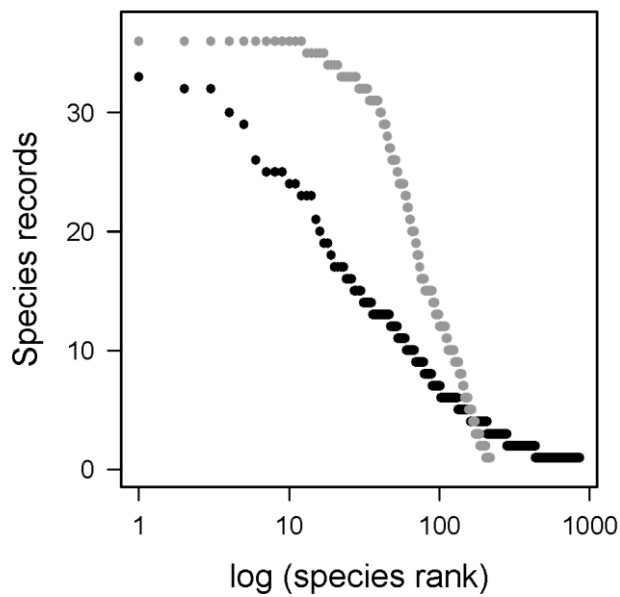


Figure 13: Rank-frequency plot of fungal (black points) and plant (grey points) species in the Taunus area. The species rank is plotted in logarithmic scale against the total number of records during the 36 sample events.

Due to the differences in the frequency distributions, the accumulation curves of plants and fungi followed distinct patterns. At the end of the survey, the saturation of fungal richness was not reached, with the accumulation curve still showing a steady increase in the number of species with sampling effort, and new fungi were discovered in each sampling event (Figure 14a). In contrast to the fungi, the entire plant richness in the sampling area was almost uncovered after 15-20 sampling events, as shown by a plateau in the accumulation curve (Figure 14b).

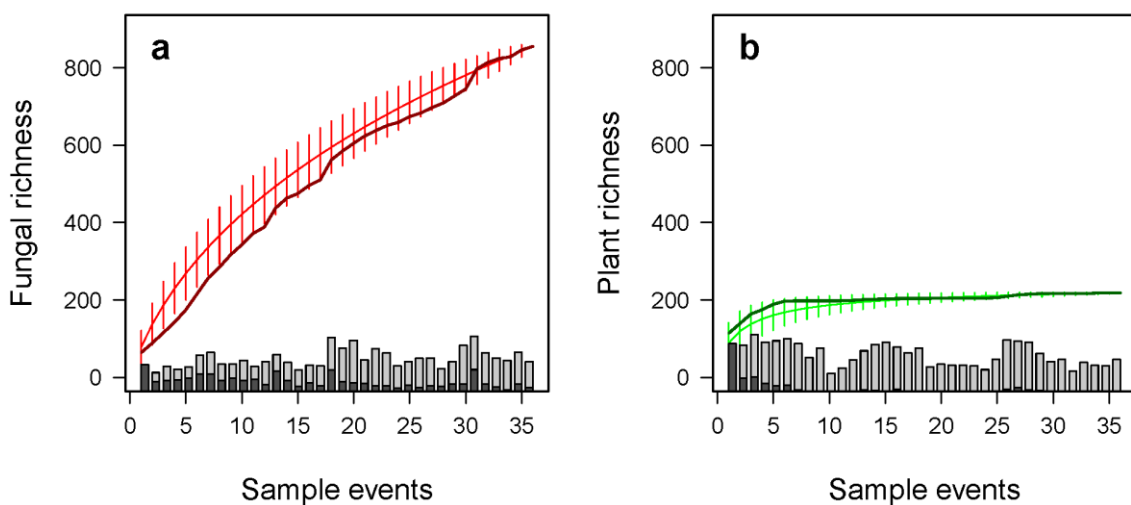


Figure 14: Accumulation curves of fungi and plants with their standard deviation in the Taunus area for 36 sampling events. Light colours display rarefied accumulation curves and dark colours show collectors' curves (in correct sampling order). The dark grey bar parts indicate newly recorded species for each sampling event and the light grey bar parts species recorded repeatedly.

### 3.1.2 Fungal diversity patterns in taxonomic and ecological groups

The fungal records were classified with varying taxonomic precision according to morphological traits. The total number of 855 fungal species, at least identified to genus level, could be assigned to three divisions of true fungi (Ascomycota, Basidiomycota, and zygomycetes), as well as the fungal-like organisms in Oomycota and slime moulds in Amoebozoa.

A total of 454 genera of fungi could be assigned to 66 orders. Ascomycota (436 species, 51% of all species) and Basidiomycota (389 species, 45% of all species) were the most frequently represented divisions, slime moulds in the Amoebozoa (25 species, 3% of all species) represented only a small part. Oomycota were represented by three species (0.2% of all species) and zygomycetes by two species (0.4% of all species).

Within the Ascomycota, the order with most species was Helotiales (20% of all species of Ascomycota), mainly represented by *Mollisia* spp. (eight species). Most species of the Pleosporales (15% of all Ascomycota) belonged to the genus *Ascochyta* (eight species). In Xylariales (10% of all Ascomycota), six species belonged to the genus *Hypoxylon*.

Within the Basidiomycota, the order with the most species detected was Agaricales (45%), represented by many *Mycena* species (29 species).



Polyporales contained 12% of all species within the Basidiomycota, five of which belonged to the genus *Polyporus*. Pucciniales accounted for 11% of species richness within the Basidiomycota, with 21 species that could be assigned to the genus *Puccinia*. More details about the taxonomic distribution of the recorded species are shown in Table 5.

Table 5: Most common taxonomic groups and species recorded in the Taunus area during three years of monthly sampling.

Division	Total <sup>1</sup>	% <sup>2</sup>	Order	Total	%	Genus	Total	%	Species	Records	Lifestyle			
Ascomycota	436	51	Helotiales	87	20	<i>Mollisia</i>	8	9	<i>Mollisia cinerea</i>	9	saprobiont			
						<i>Lachnum</i>	6	7	<i>Lachnum impudicum</i>	10	saprobiont			
									<i>Lachnum virgineum</i>	6	saprobiont			
						<i>Ascocoryne</i>	4	5	<i>Ascocoryne sarcoides</i>	4	saprobiont			
						<i>Bisporella</i>	3	3	<i>Bisporella citrina</i>	12	saprobiont			
						<i>Neodasyscypha</i>	1	1	<i>Neodasyscypha cerina</i>	16	saprobiont			
						<i>Lachnellula</i>	1	1	<i>Lachnellula occidentalis</i>	13	saprobiont			
			Pleosporales	64	15				<i>Ascochyta</i>	8	12	<i>Ascochyta festucae</i>	7	parasite
									<i>Epicoccum</i>	1	2	<i>Epicoccum nigrum</i>	13	saprobiont
									<i>Melanomma</i>	1	2	<i>Melanomma pulvis-pyrius</i>	13	saprobiont
			Xylariales	45	10				<i>Hypoxyton</i>	6	13	<i>Hypoxyton fragiforme</i>	32	saprobiont
												<i>Hypoxyton fuscum</i>	5	saprobiont
												<i>Hypoxyton macrocarpum</i>	5	saprobiont
									<i>Nodulisporium</i>	5	11	<i>Nodulisporium</i> sp.	5	saprobiont
									<i>Diatrype</i>	4	9	<i>Diatrype stigma</i>	21	saprobiont
												<i>Diatrype decorticata</i>	17	saprobiont
												<i>Diatrype disciformis</i>	13	saprobiont
									<i>Eutypa</i>	4	9	<i>Eutypa spinosa</i>	17	saprobiont
												<i>Eutypa flavovirens</i>	10	saprobiont
									<i>Annulohypoxyton</i>	2	4	<i>Annulohypoxyton cohaerens</i>	25	saprobiont
									<i>Anthostoma</i>	2	4	<i>Anthostoma turgidum</i>	13	saprobiont
									<i>Nemania</i>	2	4	<i>Nemania serpens</i>	12	saprobiont
									<i>Diatrypella</i>	2	4	<i>Diatrypella quercina</i>	11	saprobiont
<i>Biscogniauxia</i>	1	2							<i>Biscogniauxia nummularia</i>	23	saprobiont			
<i>Kretzschmaria</i>	1	2							<i>Kretzschmaria deusta</i>	15	parasite			
Hypocreales	41	9										<i>Nectria</i>	4	10
			<i>Dialonectria</i>	1	2	<i>Dialonectria episphaeria</i>	19	saprobiont						
Capnodiales	27	6				<i>Cladosporium</i>	6	22	<i>Cladosporium herbarum</i>	19	saprobiont			
						<i>Mycosphaerella</i>	5	19	<i>Mycosphaerella punctiformis</i>	16	parasite			
						<i>Ramularia</i>	4	15	<i>Ramularia digitalis-ambiguae</i>	17	parasite			
Diaporthales	18	4				<i>Gnomonia</i>	4	22	<i>Gnomonia setacea</i>	14	saprobiont			
Chaetosphaeriales	6	1				<i>Chaetosphaeria</i>	4	67	<i>Chaetosphaeria ovoidea</i>	13	saprobiont			
Rhytismatales	5	1				<i>Colpoma</i>	1	20	<i>Colpoma quercinum</i>	17	saprobiont			
						<i>Propolis</i>	1	20	<i>Propolis farinosa</i>	12	saprobiont			
Basidiomycota	389	45	Agaricales	174	45	<i>Mycena</i>	29	17	<i>Mycena pura</i>	6	saprobiont			
						<i>Hygrocybe</i>	16	9	<i>Hygrocybe pratensis</i>	5	saprobiont			
						<i>Schizo-</i>	1	1	<i>Schizophyllum</i>	32	saprobiont			

<sup>1</sup> Total number of different species in each division / order / genus

<sup>2</sup> Percentage of the total number of the previous category

## Fungal diversity in the Taunus

Division	Total <sup>1</sup>	% <sup>2</sup>	Order	Total	%	Genus	Total	%	Species	Records	Lifestyle
						<i>phyllum</i>			<i>commune</i>		
						<i>Cylindrobasidium</i>	1	1	<i>Cylindrobasidium evolvens</i>	12	saprobiont
			Polyporales	45	12	<i>Polyporus</i>	5	11	<i>Polyporus brumalis</i>	10	saprobiont
									<i>Polyporus varius</i>	6	saprobiont
						<i>Trametes</i>	5	11	<i>Trametes versicolor</i>	29	saprobiont
									<i>Trametes ochracea</i>	8	saprobiont
									<i>Trametes gibbosa</i>	7	saprobiont
						<i>Fomes</i>	1	2	<i>Fomes fomentarius</i>	33	parasite
						<i>Ganoderma</i>	1	2	<i>Ganoderma applanatum</i>	23	parasite
						<i>Bjerkandera</i>	1	2	<i>Bjerkandera adusta</i>	14	saprobiont
						<i>Piptoporus</i>	1	2	<i>Piptoporus betulinus</i>	13	saprobiont
						<i>Daedaleopsis</i>	1	2	<i>Daedaleopsis confragosa</i>	11	saprobiont
			Pucciniales	43	11	<i>Puccinia</i>	21	49	<i>Puccinia coronata</i>	24	parasite
									<i>Puccinia annularis</i>	15	parasite
									<i>Puccinia obscura</i>	14	parasite
									<i>Puccinia hieracii</i>	11	parasite
						<i>Phragmidium</i>	5	12	<i>Phragmidium violaceum</i>	25	parasite
									<i>Phragmidium mucronatum</i>	6	parasite
						<i>Melampsora</i>	3	7	<i>Melampsora populnea</i>	24	parasite
									<i>Melampsora caprearum</i>	23	parasite
			Russulales	39	10	<i>Stereum</i>	10	26	<i>Stereum hirsutum</i>	30	saprobiont
									<i>Stereum rugosum</i>	9	saprobiont
									<i>Stereum gausapatum</i>	6	saprobiont
						<i>Peniophora</i>	6	15	<i>Peniophora quercina</i>	15	saprobiont
									<i>Peniophora incarnata</i>	13	saprobiont
									<i>Peniophora polygonia</i>	10	saprobiont
						<i>Hericium</i>	1	3	<i>Hericium coralloides</i>	12	saprobiont
			Hymenochaetales	12	3	<i>Fuscoporia</i>	2	17	<i>Fuscoporia ferruginosa</i>	13	parasite
						<i>Schizopora</i>	1	8	<i>Schizopora paradoxa</i>	20	saprobiont
			Auriculariales	7	2	<i>Exidia</i>	4	57	<i>Exidia plana</i>	15	saprobiont
									<i>Exidia glandulosa</i>	13	saprobiont
			Dacrymycetales	7	2	<i>Dacrymyces</i>	5	71	<i>Dacrymyces stillatus</i>	26	saprobiont

The most frequently recorded fungus in the Taunus survey was *Fomes fomentarius* with records in 33 sampling events, followed by *Hypoxyylon fragiforme* and *Schizophyllum commune*, which were recorded 32 times each. All species recorded at least 20 times (16 species in total) are shown in Table 6 and photos of some species in Figure 15. Most of these species were assigned to Basidiomycota. The most frequently recorded orders were Pucciniales within the Basidiomycota and Xylariales within the Ascomycota. Polyporales were represented by three frequent species. An overview of species recorded more than five times is provided in the Appendix (Table S7). Furthermore, a complete list of all recorded fungi and plants across sampling events and their associated metadata, including frequencies, is provided in the digital appendix (2 Fungi Taunus).

Table 6: Fungal species recorded for  $\geq 20$  sampling events (total 36) in the Taunus area.

Division	Order	Species	Number of records
Basidiomycota	Polyporales	<i>Fomes fomentarius</i>	33
Ascomycota	Xylariales	<i>Hypoxylon fragiforme</i>	32
Basidiomycota	Agaricales	<i>Schizophyllum commune</i>	32
Basidiomycota	Russulales	<i>Stereum hirsutum</i>	30
Basidiomycota	Polyporales	<i>Trametes versicolor</i>	29
Basidiomycota	Dacrymycetales	<i>Dacrymyces stillatus</i>	26
Ascomycota	Xylariales	<i>Annulohypoxylon cohaerens</i>	25
Ascomycota	Lecanorales	<i>Parmelia sulcata</i>	25
Basidiomycota	Pucciniales	<i>Phragmidium violaceum</i>	25
Basidiomycota	Pucciniales	<i>Melampsora populnea</i>	24
Basidiomycota	Pucciniales	<i>Puccinia coronata</i>	24
Ascomycota	Xylariales	<i>Biscogniauxia nummularia</i>	23
Basidiomycota	Polyporales	<i>Ganoderma applanatum</i>	23
Basidiomycota	Pucciniales	<i>Melampsora caprearum</i>	23
Ascomycota	Xylariales	<i>Diatrype stigma</i>	21
Basidiomycota	Hymenochaetales	<i>Schizopora paradoxa</i>	20



Figure 15: Most frequent species in the Taunus area: *Fomes fomentarius* (a), *Hypoxylon fragiforme* (b), *Schizophyllum commune* (c), *Stereum hirsutum* (d), *Trametes versicolor* (e), and *Dacrymyces stillatus* (f). The photos were taken by N. Kühnberger (d) and by H. Lotz-Winter (a-c, e-f).

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The ecological groups, to which fungal records were most frequently assigned, were saprobionts (591 species, 69%), parasites (169 species, 20%), and mycorrhizal fungi (41 species, 5%). Lichen-forming fungi (29 species, 3%) and fungi feeding on microorganisms (25 species, 3%) represented a smaller part.

The identification of lichens during one sampling event was assisted by the specialists R. Cezanne, M. Eichler and C. Printzen, who identified 77 lichens. Many of these species could not be recognised again by the collection team. Therefore, these data were not included in the analyses because the number of uniques would then increase artificially, because these species were probably in the Taunus area during all sampling events. Nevertheless, including these data, lichens would represent the third most frequent ecological group (86 species). A comparison table with the recorded and identified lichens by the experts and by the investigators of this study is provided in the appendix (Table S9). The original lichen list, kindly provided by C. Printzen, R. Cezanne and M. Eichler, is available in the digital appendix (4. Lichens by C. Printzen).

A high number (about three-quarter) of all recorded specimens was associated with plants (parasites or saprobionts). *Fagus sylvatica* was found as the most frequent substrate for fungal occurrence (17% of all plant hosts). The two species *Quercus petraea* and *Q. robur* represented 13% of all host plants, followed by *Betula pendula* and *B. pubescens* with 6% and *Populus tremula* with 5%.

Within the parasites, most species showed a strong host specificity and were only associated with one plant species or genus. Examples of these were *Melampsora populnea* (Basidiomycota) on *Populus tremula*, and *Ramularia digitalis-ambiguae* (Ascomycota) on *Digitalis purpurea*. Other species had a broad host range, like *Puccinia coronata* (Basidiomycota), and *Puccinia graminis* (Basidiomycota), which were both recorded on several different species of grasses.

### 3.1.3 Fungal richness estimations

The curve for fungal richness did not reach saturation even after the extrapolation of data up to doubling the sampling effort (Figure 16), indicating that the survey time was not sufficient to discover the complete fungal diversity



in the study area. At the end of the survey (36 samplings), a plant:fungus species ratio of 1:4 was obtained, which changed to 1:5 upon a rarefied extrapolation of the data for 36 additional sampling events, totalling 72 (Figure 16).

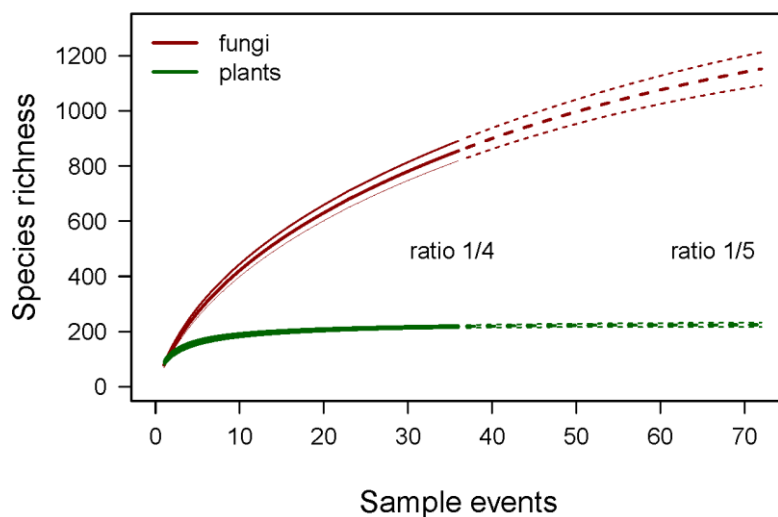


Figure 16: Rarefaction curves of species accumulation with sampling effort. The number of species recorded (36 sampling events, continuous lines) and estimated (for sampling events 37–72, dashed lines) with 95% confidence intervals, was calculated with the Chao 2 estimator. The ratio of plants to fungi was calculated for the recorded species number (36<sup>th</sup> sampling event) and the estimated species number (72<sup>nd</sup> sampling event).

The insufficient sampling of fungi resulted in a wide variation in the estimated total number of fungal species as calculated using different richness estimators. The difference between the lowest estimation (using the Bootstrap estimator) and the highest estimation (with ICE) was almost 500 species, yielding a plant:fungus ratio of 1:7 in the most species-rich scenario (Table 7). The shapes of the species accumulation curves for the different estimation methods were rather similar, except for that calculated with ICE. The latter one showed a strong increase at the beginning (Figure 17), because the upper limit for ICE estimations is 10 sampling events (Colwell 2013). For further analyses, the estimator Chao 2, which has been shown to be the most reliable method for fungal incidence data (Unterseher et al. 2008), was used.

Table 7: Estimated richness of fungal and plant species with the corresponding plant:fungus ratio based on different estimators. The percentages of observed respect to estimated richness are shown.

	Estimated plant richness	Estimated fungal richness	Plant:fungus ratio	Proportion of observed fungal richness based on estimation [%]
Bootstrap	227	1032	1:4.5	83
Chao 2	225	1427	1:6.0	60
ICE	226	1522	1:7.0	56
Jackknife 1	234	1266	1:5.0	68
Jackknife 2	233	1526	1:7.0	56

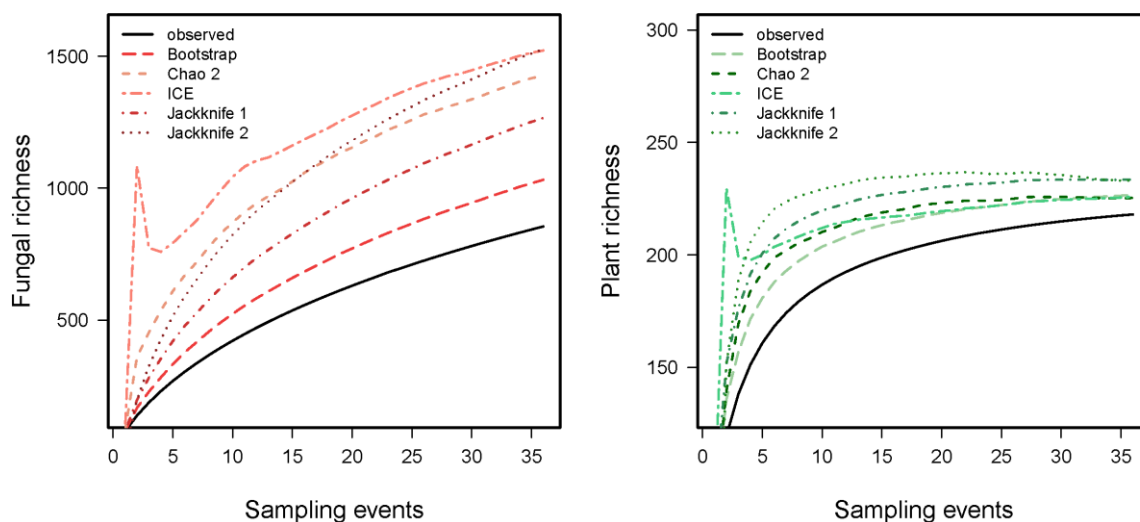


Figure 17: Estimations of (a) fungal and (b) plant richness in the Taunus area. Different estimators are visualized with dashed lines and the rarefied species accumulation curves with solid lines. For better resolution, different y-axis scalings were used.

The estimations of the total species number showed that a high fungal diversity remained to be discovered, but not all taxonomic groups were equally affected by this trend. The proportion of already recorded species in the most frequent ascomycetous orders showed almost the same percentage of already recorded species respective to the estimated richness. In contrast, the proportions of recorded species in the division of Basidiomycota differed strongly. The minimal percentage of recorded species (Agaricales) as well as the maximal percentage (Polyporales) could be found in this division. The recorded species number does not explain all estimated values because for Xylariales, within the Ascomycota, and for Polyporales in the division Basidiomycota, the same number of species was recorded, but the estimations were different (Table 8).

## Fungal diversity in the Taunus

Table 8: Total number of fungal species in the most frequent ascomycetous and basidiomycetous orders. The estimations of total species richness are based on the Chao 2 estimator.

Order	Division	Recorded species	Estimated species	Proportion of observed species based on the estimation [%]
Helotiales	Ascomycota	87	133	65
Pleosporales	Ascomycota	64	99	65
Xylariales	Ascomycota	45	76	59
Agaricales	Basidiomycota	174	394	44
Polyporales	Basidiomycota	45	48	94
Pucciniales	Basidiomycota	43	53	81

The species accumulation curves for the ascomycetous orders showed only small differences in shape, and these differences could be explained by the differences in the observed species richness (Figure 18a). The accumulation curve of Agaricales (Basidiomycota), which showed by far the highest value of recorded and estimated species, increased most strongly. In contrast, Polyporales and Pucciniales showed the lowest richness and the accumulation curves were nearly saturated (Figure 18b).

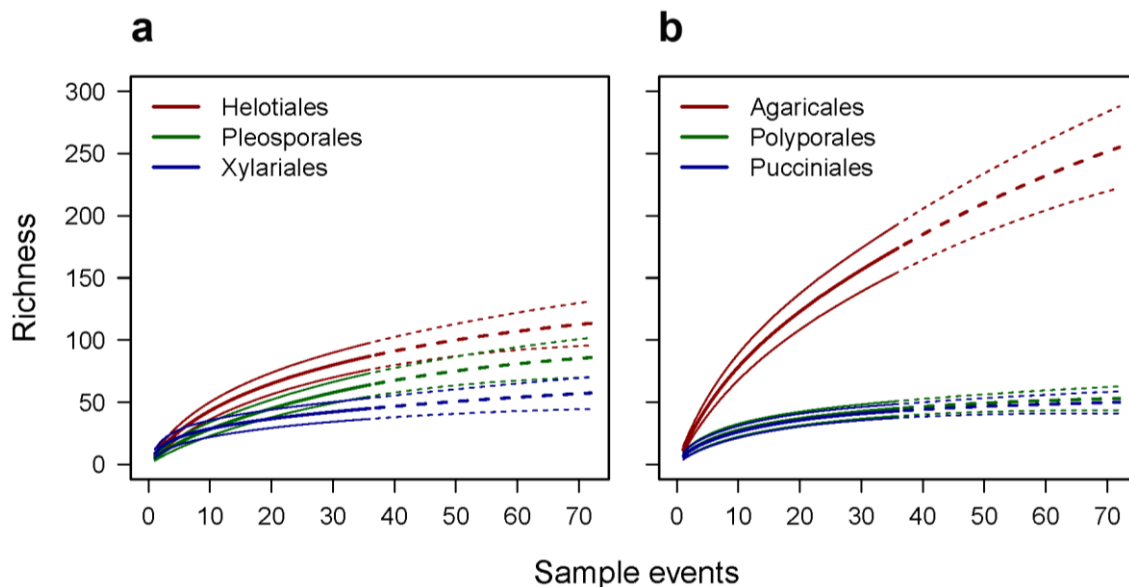


Figure 18: Extrapolation of the most frequent orders within Ascomycota (a) and Basidiomycota (b) for the Taunus area. The number of species recorded (36 sampling events, continuous lines) and estimated (for sampling events 37–72, dashed lines) with 95% confidence intervals, calculated with the Chao 2 estimator. The x and y-axes are the same in both plots.



## 3.2 Spatial variation of fungal richness

Beside the main sampling area, four other areas were investigated at least once. In this section, the species richness of the different sampling areas is described and compared to the Taunus area. The order of descriptions reflects the sampling intensities.

### 3.2.1 Comparison of samplings in Taunus and Majagua

The most frequently sampled areas in this study were Taunus (Germany) and Majagua (Panama), for which 24 sampling events per area were compared. Both locations revealed a large number of fungal species after two years of sampling. The total number of fungi identified up to genus level was higher in Taunus than in Majagua, whereas more plants were recorded in Majagua. The complete species list for the Majagua area is provided in the digital appendix (5. Fungi Panama). Therefore, the plant:fungus ratio was different between both sites (Table 9). In Majagua, the species accumulation curve for fungi strongly increased over samplings (Figure 2 in Piepenbring et al. 2012) similarly to that obtained for the Taunus area.

The percentages of uniques and duplicates were almost the same in both areas (Table 9), and the rank frequency distributions (Figure 3 in Piepenbring et al. 2012) almost overlap. In both sampling zones, no species was found at all compared sampling events (= 24 times in both areas), but in both projects, one species was recorded 23 times. These species were *Fomes fomentarius* (Basidiomycota) in the Taunus area, and *Phyllachora ocoteae* (Ascomycota) in the Majagua area.

Table 9: Comparison of fungal and plant richness identified at least up to genus level and the percentage of rare fungal species in Taunus and Majagua for two years of monthly sampling.

	Taunus	Majagua
Fungal richness	659	439
Plant richness	205	311
Plant:fungus ratio	1:3.2	1:1.4
Fungal uniques [%]	51	48
Fungal duplicates [%]	19	17

A comparison at the division level for two years of sampling revealed the same tendency and sequence of divisions in both areas. Ascomycota represented the

most frequent group followed by Basidiomycota, and by far by the slime moulds in Amoebozoa (Figure 19).

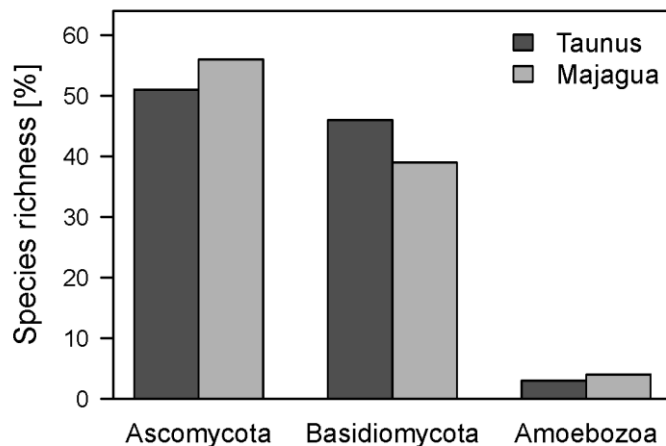


Figure 19: Most frequent divisions in the sampling areas of Taunus (DEU) and Majagua (PAN) after two years of monthly sampling.

Comparing the two areas, the taxonomic composition revealed some differences between the recorded fungi at the order level. However, Agaricales were the most frequent group, and Polyporales the fourth most frequent group in both sampling zones. In the Taunus area, Helotiales and Pleosporales were the second and third most frequently sampled orders, but these orders were not represented in the six most frequently recorded groups in Majagua. In both areas, only six orders represented 53% or 52% of the total diversity (Table 10). The number of genera was higher in Taunus than in Majagua, with 374 and 230 genera, respectively.

Table 10: Comparison of the fungal composition in Taunus and Majagua at the order level after two years of sampling, with their respective divisions, Ascomycota (Asco.) and Basidiomycota (Bas.). The dark grey background shows orders that are represented on the same position in the frequency table for both sampling areas. The light grey background marks orders that are represented within the six most frequent orders of both sampling areas but not on the same position. The orders without background colour were found only in one sampling area within the six most frequent orders.

Most frequent orders (Taunus)	Proportion, respective to the total species richness (Taunus) [%]	Proportion, respective to the total species richness (Majagua) [%]	Most frequent orders (Majagua)
Agaricales (Bas.)	19	20	Agaricales (Bas.)
Helotiales (Asco.)	10	8	Xylariales (Asco.)
Pleosporales (Asco.)	7	8	Hypocreales (Asco.)
Polyporales (Bas.)	6	7	Polyporales (Bas.)
Xylariales (Asco.)	6	5	Pucciniales (Bas.)
Pucciniales (Bas.)	5	4	Capnodiales (Asco.)

A comparison of the fully identified species showed more identified fungal specimens in the Taunus than in the Majagua area (Figure 20). In Taunus, about 80% of fungi could be identified to species level and more than 90% to genus level. In contrast, only about 30% of species could be determined to species level and 75% to genus level in the Majagua area (Figure 20). The comparison of the total number of records from Taunus respect to all Majagua records (including further sampling events), showed the same trend (Piepenbring et al. 2016).

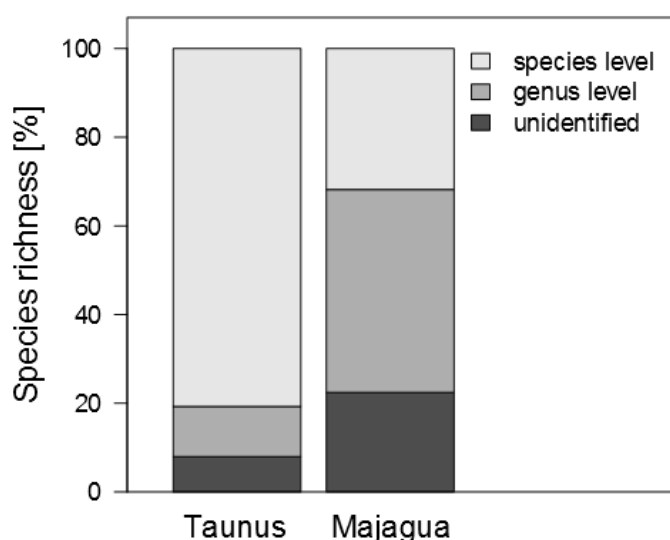


Figure 20: Comparison of the identification level between two years of sampling in the Taunus (DEU) and Majagua (PAN). The levels of identification are provided up to species level and genus level. Species with identification less than genus level are referred as unidentified.

### 3.2.2 Comparison of samplings in Taunus and Bulau

In the Bulau area (Germany), 168 fungi could be identified and assigned to species level, while 28 species were recorded as morphospecies and determined up to genus level. Furthermore, two specimens could only be determined to division level and twelve could not be assigned to any taxonomic category. The complete species list is provided in the digital appendix (6. Fungi Bulau).

The fungal richness of four sampling events in both German sampling areas at Taunus and Bulau was very similar, but the diversity of plant species differed. In total, 86 species of plants were recorded in the Bulau area (digital appendix:

7. Plants Bulau), which were less than in the Taunus area. Therefore, the plant:fungus ratio was slightly different (Table 11).

The number of fungal uniques was higher in the Bulau area than in the Taunus area, whereas the duplicates followed the opposite trend (Table 11). The number of plant uniques, with 30%, and plants found in all four sampling events, with 29% in the Bulau was nearly the same as in the Taunus area, with 29% and 28%, respectively. Therefore, the distribution of plant occurrence was in both areas more similar across the four sampling events than the distribution of fungal species. Due to the higher number of uniques in the Bulau, the estimator Chao 2 yielded a higher fungal richness for the Bulau area.

Table 11: The comparison of fungal and plant richness and the frequencies of fungal uniques and duplicates for four sampling events each in Taunus and in Bulau. Based on the frequency data, the estimated total richness with the Chao 2 estimator was calculated.

	Taunus	Bulau
Fungal richness	199	196
Plant richness	125	86
Plant:fungus ratio	1:1.6	1:2.3
Fungal uniques	138	150
Fungal duplicates	38	28
Chao 2 estimation	387	497

The number of species recorded in all four sampling events was slightly higher in the Taunus than in the Bulau area. Only five fungal species (3%) were found in all four sampling events in Bulau, namely *Kretzschmaria deusta*, *Leptosphaeria acuta*, *Schizopora paradoxa*, *Stereum hirsutum* and *Trametes versicolor*. Fourteen species were found three times. The number of species assigned to the divisions Ascomycota and Basidiomycota was the same for the species recorded at least three times in the Bulau with each 10 species per division (Table 12).

In the Taunus area, 10 species (5%) were recorded in all four sampling events that were compared with Bulau, two of them, *Stereum hirsutum* and *Trametes versicolor* were also recorded in the Bulau area.

Table 12: Most frequently recorded species in Bulau after four sampling events.

Division	Order	Species	Number of records
Ascomycota	Xylariales	<i>Kretzschmaria deusta</i>	4
Ascomycota	Pleosporales	<i>Leptosphaeria acuta</i>	4
Basidiomycota	Hymenochaetales	<i>Schizopora paradoxa</i>	4
Basidiomycota	Russulales	<i>Stereum hirsutum</i>	4
Basidiomycota	Polyporales	<i>Trametes versicolor</i>	4
Basidiomycota	Pucciniales	<i>Uromyces dactylidis</i>	4
Ascomycota	Diaporthales	<i>Aporhytisma urticae</i>	3
Basidiomycota	Corticiales	<i>Dendrothele acerina</i>	3
Basidiomycota	Polyporales	<i>Ganoderma applanatum</i>	3
Basidiomycota	Polyporales	<i>Hyphoderma sambuci</i>	3
Ascomycota	Xylariales	<i>Hypoxylon intermedium</i>	3
Ascomycota	Hysteriales	<i>Hysterium angustatum</i>	3
Basidiomycota	Russulales	<i>Peniophora limitata</i>	3
Ascomycota	Teloschistales	<i>Physcia</i> sp.	3
Basidiomycota	Polyporales	<i>Polyporus badius</i>	3
Basidiomycota	Pucciniales	<i>Puccinia sessilis</i>	3
Ascomycota	Rhytismatales	<i>Rhytisma acerinum</i>	3
Ascomycota	Teloschistales	<i>Xanthoria parietina</i>	3
Ascomycota	Xylariales	<i>Xylaria hypoxylon</i>	3
Ascomycota	Xylariales	<i>Xylaria longipes</i>	3

The species richness recorded in the Bulau area showed the same tendency described for Taunus, with a steadily increasing fungal richness and almost saturated plant richness (Figure 21). The plant:fungus ratio was 1:2 after the performed sampling events in the Bulau and 1:3 after including four further estimated sampling events.

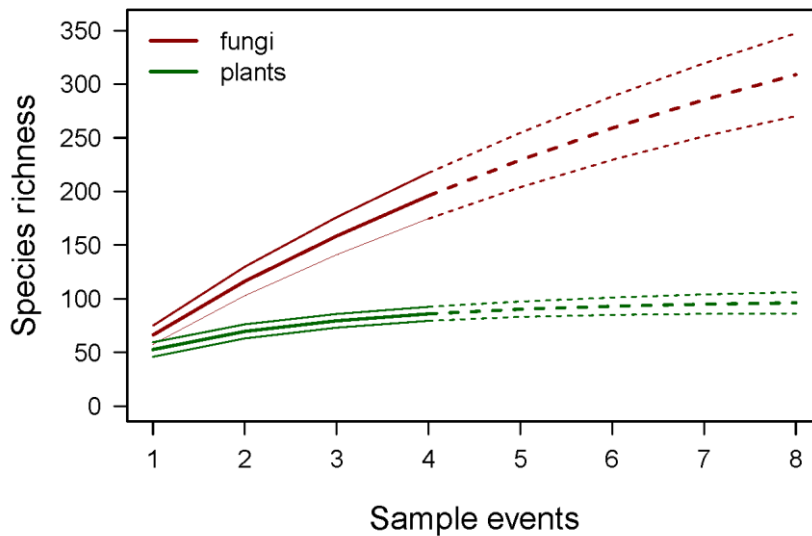


Figure 21: Accumulation curves and extrapolations of plants and fungi recorded in the Bulau area. The extrapolation of species richness for four further sampling events was calculated with the estimator Chao 2. The continuous lines show the rarefied species accumulation curves (thick lines) with its 95% confidence interval (thin lines). The dashed lines display the estimated species richness up to the 8<sup>th</sup> sampling event with its 95% confidence interval.

The comparison of the most frequent divisions Ascomycota and Basidiomycota in Taunus and Bulau showed similar results. More Ascomycota than Basidiomycota were collected and the differences in proportions between the two areas were only small (Figure 22). In total, 104 species of Ascomycota and 80 species of Basidiomycota were recorded in the Bulau region.

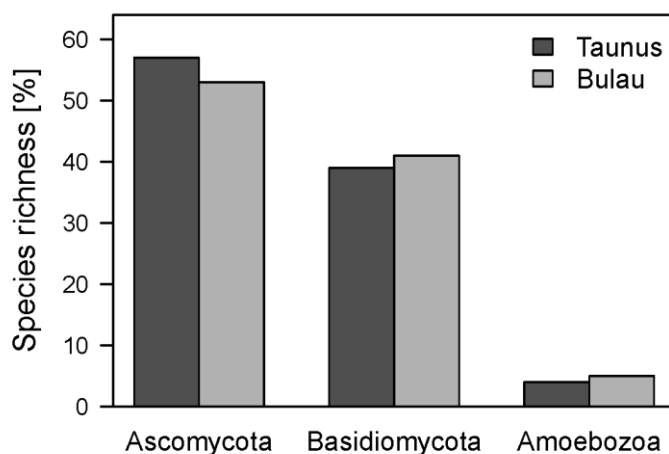


Figure 22: Most frequent divisions in the German sampling areas of Taunus and Bulau after four sampling events.

A taxonomic overview of the Bulau data shows that most species within the Basidiomycota could be assigned to Agaricales (41%), followed by Polyporales

(21%), Russulales (9%), and Pucciniales (8%). Species of the genus *Mycena* were the most frequent within the Basidiomycota (5 species, 15%). Species of the order Xylariales were the most frequent within the Ascomycota (18%), followed by Helotiales (15%), Hypocreales (12%), and Capnodiales (8%). Within Xylariales, most species could be assigned to the genus *Hypoxylon* with six different species (32% of species within the Xylariales).

Comparing the taxonomy of specimens between areas at the order level, the most frequent groups were rather different for the compared sampling events. Three orders could be assigned to Ascomycota and three to Basidiomycota in Taunus. In the Bulau area, four orders belonged to Ascomycota and only two to Basidiomycota. The proportions of the different orders were similar in the Taunus area and varied strongly in the Bulau area. The percentage of species included in the six first orders was similar in both areas (56% and 55% respectively, Table 13). The number of genera was higher in the Bulau area with 161 genera than in the Taunus area with 157 genera.

Table 13: Comparison of the two German sampling areas in Taunus and Bulau (four sampling events each) at the order level, with their respective division Ascomycota (Asco.) and Basidiomycota (Bas.). The dark grey background shows orders that are represented on the same position in the frequency table of both sampling areas. The light grey background marks orders that are represented within the six most frequent orders in both sampling areas. The orders without background colour are groups that could be found only in one sampling area within the six most frequent orders.

Most frequent orders (Taunus)	Proportion, respective to the total species richness (Taunus) [%]	Proportion, respective to the total species richness (Bulau) [%]	Most frequent orders (Bulau)
Agaricales/Helotiales (Bas./Asco.)	11	17	Agaricales (Bas.)
Agaricales/Helotiales (Bas./Asco.)	11	10	Xylariales (Asco.)
Xylariales (Asco.)	10	9	Polyporales (Bas.)
Pleosporales (Asco.)	9	8	Helotiales (Asco.)
Polyporales (Bas.)	8	7	Hypocreales (Asco.)
Pucciniales (Bas.)	7	4	Capnodiales (Asco.)

A large number of recorded species in the Bulau were associated with plants as parasites or saprobionts. The genus *Fraxinus* was the most frequently associated host (15% of records), followed by *Urtica* (8%), *Acer* (5%) and *Quercus* (5%).

## Spatial variation of fungal richness

The percentage of identified fungi to species and genus level was higher in Taunus than in Bulau. Nevertheless, more than half of the species could be identified to species level in both areas, but the number of unidentified fungi in Bulau was nearly the double of the Taunus value (Figure 23).

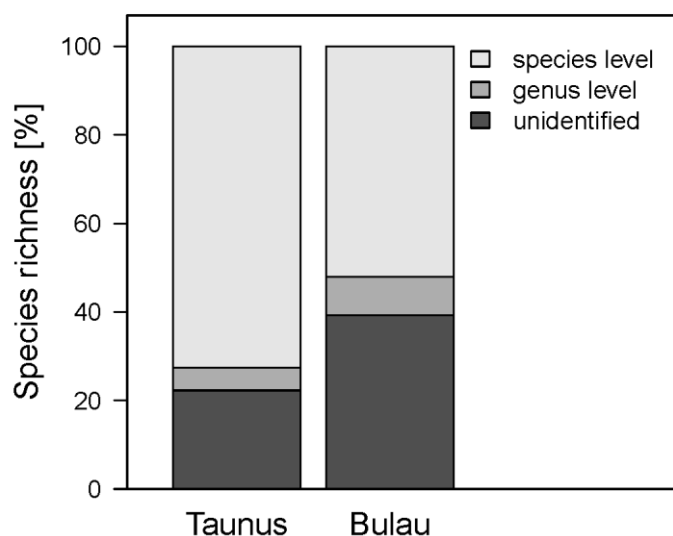


Figure 23: Comparison of the level of identification between the two German sampling areas Taunus and Bulau. The levels of identification are provided up to species level and up to genus level. Species with identification less than genus level are referred as unidentified.

The comparison of species composition displayed strong differences between Taunus and Bulau (Figure 24). Almost one third of the variance in species composition could be explained by the respective area (Table 14) and this difference is also displayed in the ordination graph (Figure 24).

Table 14: Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in species composition between the Taunus and the Bulau sampling area for four sampling events in each area.

	Df	Sums of squares	Mean squares	F. Model	R <sup>2</sup>	Pr (>F)
Area (Residuals)	1 (6)	0.76 (1.59)	0.76 (0.27)	2.88	0.32	0.03



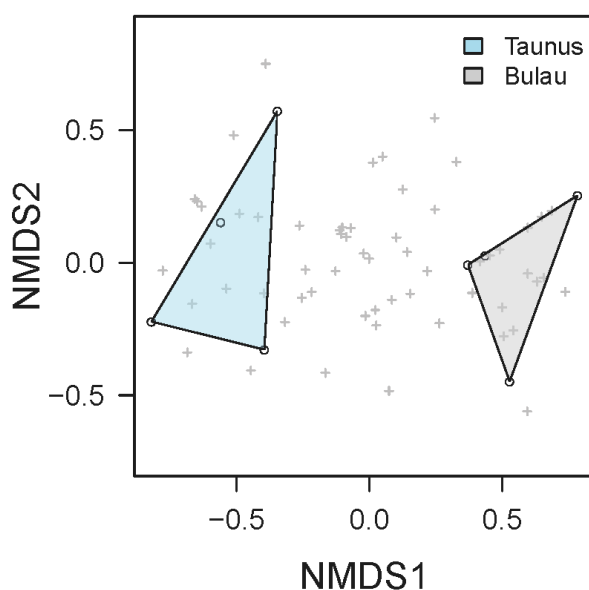


Figure 24: Fungal species composition in the Taunus and the Bulau areas for eight sampling events displayed in a non-metric-multidimensional scaling ordination plot (stress = 0.03) based on Sørensen dissimilarities. Species scores (grey crosses) for the entire survey show the variation of the Taunus area and the Bulau area for four sampling events (circles) in each area (May 2013, September 2013, December 2013, March 2014). Sampling events in the same area are surrounded by a polygon.

### 3.2.3 Comparison of samplings in Taunus and Somiedo

The recorded fungal diversity in Somiedo (Spain) was very high after two sampling events. In total, 269 fungi could be identified up to genus level. 105 and 195 fungal species were recorded in the first and second year of sampling, respectively. In total, 31 fungal species were found in both sample events. The complete table is provided in the digital appendix (8. Fungi Somiedo). Not only the species richness differed strongly between the sampling events in June and October, but also the distribution of divisions showed major differences. In June, the proportion of Ascomycota was high with almost 80%. In contrast, Basidiomycota were more frequent in October, but the difference between the two main divisions was not that strong as in June (Figure 25). In the first sampling year, 13 species could not be identified up to genus level and in the second 8 species. In total, 208 plant species were recorded. In the first year, 168 plant species were found, in the second year 151 species and 111 species in both sampling events. The complete table is provided in the digital appendix (9. Plants Somiedo).

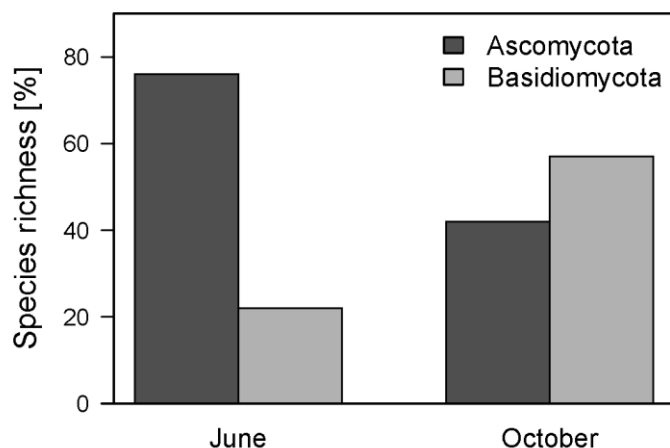


Figure 25: Most frequent divisions in two sampling events in Somiedo, the first one in June 2013 and the second one in October 2014.

The fungal and plant diversity was higher in Somiedo than in Taunus. The richness in Taunus was about 75% of that found in Somiedo for both fungi and plants. Therefore, the plant:fungus ratio was the same in both areas (Table 15).

Table 15: The comparison of fungal and plant richness between one sampling event in Taunus and one sampling event in Somiedo.

	Taunus	Somiedo
Fungal richness	79	105
Plant richness	123	168
Plant:fungus ratio	1:0.6	1:0.6

The taxonomic distribution at the division level was different between the Taunus and the first Somiedo sampling event. For the Taunus area, the percentage of Ascomycota and Basidiomycota was nearly the same, whereas Ascomycota contained more than the double of species than the Basidiomycota in the first sampling in Somiedo (Figure 26).

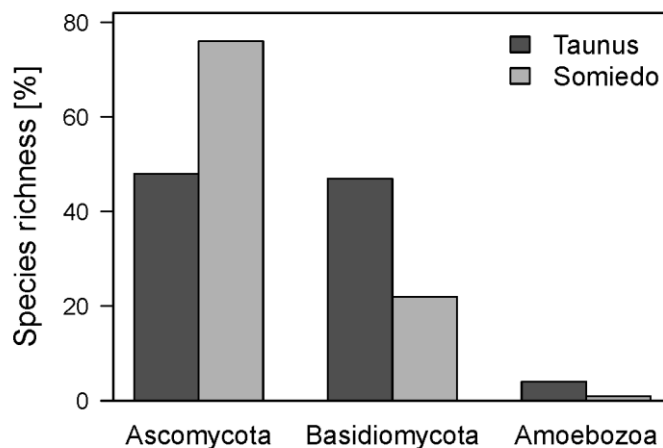


Figure 26: Most frequent divisions after one sampling event in Taunus and one sampling event in Somiedo.

The large number of Ascomycota in Somiedo was also reflected in the distribution of fungal orders. Five orders of the six most frequent groups in Somiedo were assigned to Ascomycota. In Taunus, two orders of the six most frequent groups were Basidiomycota and out of these, Agaricales were on second place. The first and third most frequent orders were equal in both sampling areas. The first six orders contained 65% and 63% of the total richness for each area (Table 16). In Somiedo, 81 genera were recorded. The number of genera in Taunus was lower, with 63 genera.

Table 16: Comparison of the taxonomic composition of one sampling event each in the two sampling areas in Taunus and Somiedo (sampling event in June) at the order level, with their respective divisions Ascomycota (Asco.) and Basidiomycota (Bas.). The dark grey background shows orders that are represented on the same position in the frequency table of both sampling areas. The light grey background marks orders that area represented within the six most frequent orders of both sampling areas. The orders without background colour are orders that could be found within the six most frequent orders only in one sampling area.

Most frequent orders (Taunus)	Proportion, respective to the total species richness (Taunus) [%]	Proportion, respective to the total species richness (Somiedo) [%]	Most frequent orders (Somiedo)
Xylariales (Asco.)	16	16	Xylariales (Asco.)
Agaricales (Bas.)	13	13	Pleosporales (Asco.)
Helotiales (Asco.)	13	10	Helotiales (Asco.)
Pucciniales (Bas.)	11	10	Capnodiales (Asco.)
Polyporales (Bas.)	6	8	Agaricales (Bas.)
Pleosporales (Asco.)	4	8	Diaporthales (Asco.)

The second sampling event in Somiedo revealed a different distribution of orders, with a high number of Agaricales. For the six most frequent orders,

## Spatial variation of fungal richness

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three orders could be assigned to Ascomycota and three to Basidiomycota (Table 17).

Table 17: Fungal taxonomic composition of the second sampling event in Somiedo (sampling event in October) at the order level, with their respective divisions Ascomycota and Basidiomycota.

Most frequent orders (Somiedo, second sampling event)	Proportion, respective to the total species richness (Somiedo, second sampling event) [%]
Agaricales (Basidiomycota)	36
Lecanorales (Ascomycota)	6
Pleosporales (Ascomycota)	6
Helotiales (Ascomycota)	6
Russulales (Basidiomycota)	5
Polyporales (Basidiomycota)	4

A large number of recorded specimens was associated with plants as parasites or saprobionts. The genus *Corylus* was the most frequently associated host or substrate (16%), followed by *Quercus* (12%), *Rosa* (5%) and *Brachypodium* (5%).

The number of fungi that were unidentified or identified to genus level was higher in the first sampling event in Somiedo than in Taunus (Figure 27). The level of completely identified species was the same for the first and the second sampling events in Somiedo (not shown in graph). Nevertheless, the number of unidentified species was smaller in the second sampling event, with only 3%.

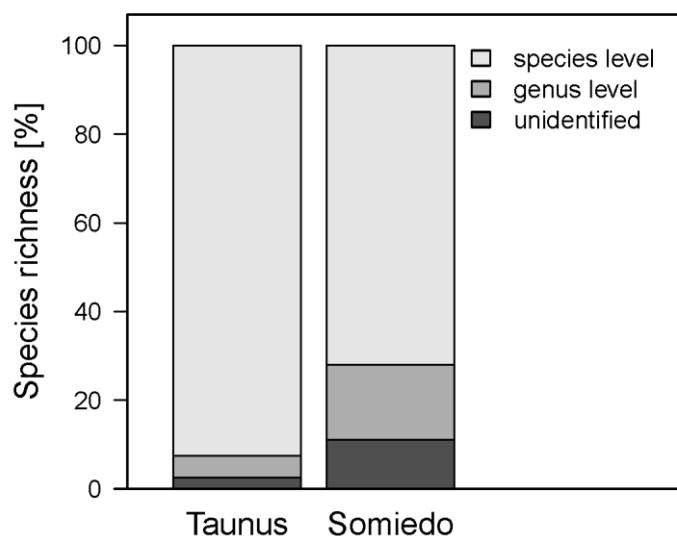


Figure 27: Comparison of the level of identification between the sampling areas Taunus and Somiedo. The levels of identification are provided up to species and genus level. Species with identification less than genus level are referred as unidentified.

### 3.2.4 Comparison of samplings in Taunus and Kleinwalsertal

The sampling in Kleinwalsertal (Austria) revealed the highest species richness of all sampling events performed in this thesis, with 205 fungi identified up to species level, 5 to genus level, and 8 identified at a higher taxonomic level. The complete table is provided in the digital appendix (10. Fungi Kleinwalsertal). However, the species number in Taunus during the same month also was relatively high. In both areas, more fungi than plants were recorded in one sampling event. Comparing the total species numbers, the fungal and plant richness in Taunus were 52% and 47% of those found in Kleinwalsertal, respectively. Therefore, the plant:fungus ratio was rather similar for both sites (Table 18).

Table 18: Comparison of fungal and plant richness between one sampling event in the Taunus and one sampling event in Kleinwalsertal.

	Taunus	Kleinwalsertal
Fungal richness	110	210
Plant richness	71	148
Plant:fungus ratio	1:1.5	1:1.4

## Spatial variation of fungal richness

The taxonomic distribution of records at the division level was similar for Taunus and Kleinwalsertal. The proportions of Basidiomycota were the same and the proportions of Ascomycota were only slightly different (Figure 28). In absolute numbers, 124 basidiomycetous species, 84 ascomycetous species and only 1 species of slime moulds in Amoebozoa were recorded for Kleinwalsertal.

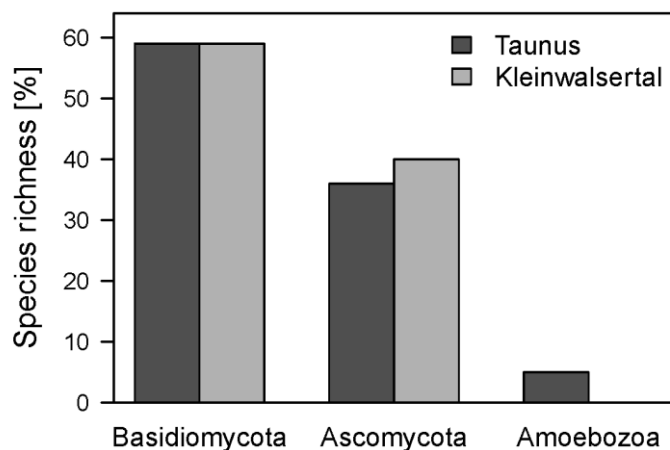


Figure 28: Most frequent divisions in the sampling area of Taunus and the sampling area of Kleinwalsertal for one sampling event.

The distribution and the proportion of orders were similar between the two sampling areas. The first, second and the fourth most frequent orders were equally represented. Nevertheless, three orders within Basidiomycota in Kleinwalsertal, and four basidiomycetous orders in Taunus, were included in the six most frequent groups. The first six orders contained 61% and 66% of the total richness for each area (Table 19). The richness of genera was higher in Kleinwalsertal, with 127 genera, than in Taunus, with 87 genera.

Table 19: Comparison of one sampling event each in the two sampling areas Taunus and Kleinwalsertal at the order level, with their respective divisions Ascomycota (Asco.) and Basidiomycota (Bas.). The dark grey background shows orders that are represented on the same position in the frequency table of both sampling areas. The light grey background marks orders that are represented within the six most frequent orders of both sampling areas. The orders without background colour are orders that could be found within the six most frequent orders only in one sampling area.

Most frequent orders (Taunus)	Proportion, respective to the total species richness (Taunus) [%]	Proportion, respective to the total species richness (Kleinwalsertal) [%]	Most frequent orders (Kleinwalsertal)
Agaricales (Bas.)	30	31	Agaricales (Bas.)
Helotiales (Asco.)	8	9	Helotiales (Asco.)
Polyporales (Bas.)	6	8	Russulales (Bas.)
Pucciniales (Bas.)	6	7	Pucciniales (Bas.)
Xylariales (Asco.)	6	6	Lecanorales (Asco.)
Russulales (Bas.)	5	5	Capnodiales (Asco.)

A high number of recorded specimens was associated with plants as parasites or saprobionts. The genus *Picea* was the most frequently associated host or substrate (23%), followed by *Fagus* (14%), *Trifolium* (5%), and *Dactylis* (4%).

The level of fungal identification was nearly the same in both sampling areas. More than 90% of records were determined up to species level. These two sampling events revealed the highest number of completely identified species (up to species level) for all compared sampling events (Figure 29).

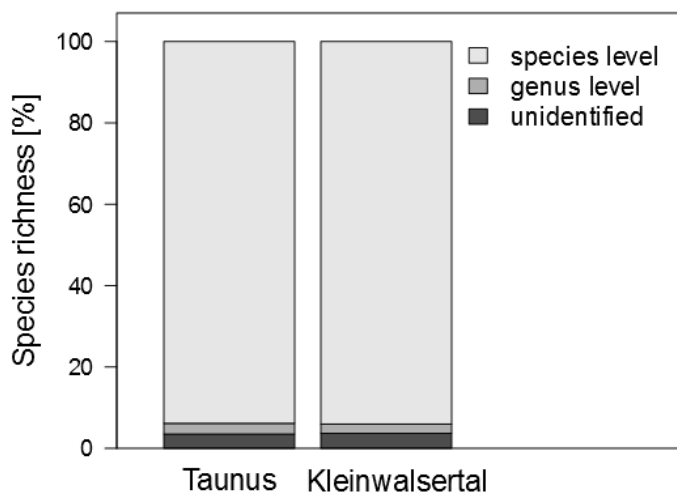


Figure 29: Comparison of the identification levels between the sampling areas Taunus and Somiedo. The levels of identification are provided up to species and genus level. Species with identification less than genus level are referred as unidentified.

### 3.2.5 Joint examination of the fungal richness in all sampling areas

A summary of the diversity measurements obtained for all areas is shown in Table 20. The trends between the compared sampling areas were rather similar. The species richness was highest in the mountainous regions of Somiedo and Kleinwalsertal. Major differences in the plant:fungus ratio between Taunus and Majagua, and a slight difference between Taunus and Bulau, were observed. The compared percentage of completely identified species showed maxima in the Taunus area or was at least equal (Table 20).



## Spatial variation of fungal richness

Table 20: Overview of the comparison between the different sampling areas.

	Taunus / Majagua	Taunus / Bulau	Taunus / Somiedo	Taunus / Kleinwalsertal	Taunus all
Higher species number	Taunus	Taunus	Somiedo	Kleinwalsertal	-
Plant:fungus ratio Taunus / other	1:3.2 / 1:1.4	1:1.6 / 1:2.3	1:0.6 / 1:0.6	1:1.5 / 1:1.4	1:4
Most frequent division Taunus / other	Ascomycota / Ascomycota	Ascomycota / Ascomycota	Ascomycota / Ascomycota	Basidiomycota / Basidiomycota	Ascomycot a
Most frequent order Taunus / other	Agaricales / Agaricales	Helotiales, Agaricales / Agaricales	Xylariales / Xylariales	Agaricales / Agaricales	Agaricales
Ratio of genus richness Taunus:other	1.6	1.0	0.8	0.7	-
Ratio of species richness Taunus:other	1.5	1.0	0.8	0.5	-
Identified to species level [%] Taunus / other	81 / 32	73 / 52	93 / 72	94 / 94	79
Number of compared sample events	24	4	1	1	-

The data on fungal richness were compared across all sampling areas, including all sampling events. The comparison was focused on the species recorded in several areas. The evaluation revealed that no species was found in all five investigated zones. The Majagua area had the lowest number of overlapping species with all other sampling areas (13 species), while the Taunus had the highest value (187 species), probably because of the highest sampling effort (Figure 30). The number of shared fungal species for the other areas was 89 species in Bulau, 86 species in Kleinwalsertal, and 79 species in Somiedo.

The Bulau and the Taunus areas had nearly the same number of shared species as the Taunus and the Kleinwalsertal area, even though only one sampling event was performed in Kleinwalsertal, and four in Bulau. The number of overlapping species in the Somiedo areas in two sampling events was only slightly lower than the number obtained for the other two referred sampling areas (the Bulau and the Kleinwalsertal areas with the Taunus area).

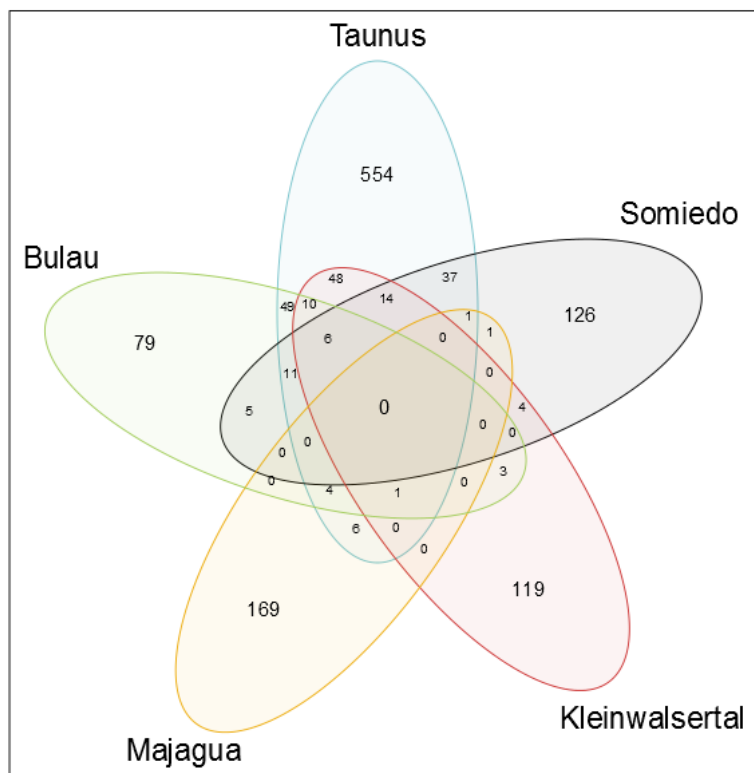


Figure 30: Venn diagram of the overlapping species in the different sampling areas Taunus, Bulau, Majagua, Kleinwalsertal, and Somiedo. The numbers in the intersecting areas correspond to the number of shared species in the specific areas.

In total, seven species were recorded four times and out of these, six were not found in Majagua. These six species were *Bisporella citrina*, *Dialonectria episphaeria*, *Hyalorbilia inflatula*, *Parmelia sulcata*, *Trametes versicolor*, and *Xylaria hypoxylon*. The only species recorded four times and found in the Majagua area was *Schizophyllum commune*, which was not documented for Somiedo. Five species could be assigned to the division Ascomycota and two to Basidiomycota, but each species was classified into different orders. An overview of the overlapping species in at least three areas is provided in Table 21 and photos with some examples in Figure 31. A table with all shared species is shown in the appendix (Table S11).

Table 21: Shared species in the different compared sampling areas. The divisions Ascomycota (Asco.), Basidiomycota (Bas.) and Amoebozoa (Amoeb.) and the areas Bulau (Bul), Taunus (Tau), Somiedo (Som) and Majagua (Maj) are abbreviated.

Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
Asco.	Helotiales	<i>Bisporella citrina</i>	1	1	1	1	0	4
Asco.	Hypocreales	<i>Dialonectria episphaeria</i>	1	1	1	1	0	4
Asco.	Orbiliiales	<i>Hyalorbilia inflatula</i>	1	1	1	1	0	4
Asco.	Lecanorales	<i>Parmelia sulcata</i>	1	1	1	1	0	4
Bas.	Agaricales	<i>Schizophyllum commune</i>	1	1	0	1	1	4

## Spatial variation of fungal richness

Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
Bas.	Polyporales	<i>Trametes versicolor</i>	1	1	1	1	0	4
Asco.	Xylariales	<i>Xylaria hypoxylon</i>	1	1	1	1	0	4
Bas.	Agaricales	<i>Armillaria mellea</i>	0	1	1	1	0	3
Asco.	Coronophorales	<i>Bertia moriformis</i>	0	1	1	1	0	3
Amoeb.	Ceratiomyxales	<i>Ceratiomyxa fruticulosa</i>	1	1	0	0	1	3
Bas.	Agaricales	<i>Collybia cookei</i>	0	1	1	1	0	3
Asco.	Helotiales	<i>Crocicreas cyathoideum</i>	1	1	1	0	0	3
Bas.	Agaricales	<i>Cyphellopsis anomala</i>	1	1	1	0	0	3
Asco.	Xylariales	<i>Diatrype decorticata</i>	0	1	1	1	0	3
Asco.	Xylariales	<i>Diatrypella quercina</i>	1	1	1	0	0	3
Bas.	Agaricales	<i>Entoloma rhodopolium</i>	0	1	1	1	0	3
Asco.	Pleosporales	<i>Epicoccum nigrum</i>	0	1	1	1	0	3
Asco.	Pleosporales	<i>Eudarluca caricis</i>	0	1	1	0	1	3
Asco.	Xylariales	<i>Eutypa lata</i>	1	1	1	0	0	3
Asco.	Lecanorales	<i>Flavoparmelia caperata</i>	1	1	1	0	0	3
Amoeb.	Physarida	<i>Fuligo septica</i>	1	1	0	1	0	3
Bas.	Agaricales	<i>Galerina marginata</i>	1	1	0	1	0	3
Amoeb.	Trichiida	<i>Hemitrichia calyculata</i>	1	1	0	0	1	3
Bas.	Agaricales	<i>Hygrocybe conica</i>	0	1	1	1	0	3
Bas.	Agaricales	<i>Hypholoma fasciculare</i>	0	1	1	1	0	3
Asco.	Xylariales	<i>Hypoxylon fragiforme</i>	1	1	0	1	0	3
Asco.	Xylariales	<i>Hypoxylon fuscum</i>	1	1	1	0	0	3
Asco.	Hysteriales	<i>Hysterium angustatum</i>	1	1	1	0	0	3
Asco.	Pleosporales	<i>Leptosphaeria acuta</i>	1	1	0	1	0	3
Amoeb.	Liceida	<i>Lycogala epidendrum</i>	1	1	0	0	1	3
Bas.	Agaricales	<i>Lycoperdon perlatum</i>	1	1	1	0	0	3
Asco.	Pleosporales	<i>Melanomma pulvis-pyrius</i>	0	1	1	1	0	3
Bas.	Agaricales	<i>Mycena galericulata</i>	1	1	0	1	0	3
Bas.	Agaricales	<i>Mycena pura</i>	0	1	1	1	0	3
Bas.	Polyporales	<i>Mycoacia uda</i>	1	1	1	0	0	3
Asco.	Helotiales	<i>Neodasyscypha cerina</i>	0	1	1	1	0	3
Asco.	Lecanorales	<i>Parmelia saxatilis</i>	1	1	0	1	0	3
Bas.	Russulales	<i>Peniophora lycii</i>	0	1	1	1	0	3
Bas.	Pucciniales	<i>Phragmidium violaceum</i>	1	1	1	0	0	3
Oomy- cota	Peronosporales	<i>Plasmopara nivea</i>	1	1	0	1	0	3
Bas.	Polyporales	<i>Polyporus brumalis</i>	1	1	0	1	0	3
Bas.	Agaricales	<i>Psathyrella candolleana</i>	1	1	0	0	1	3
Asco.	Lecanorales	<i>Pseudevernia furfuracea</i>	0	1	1	1	0	3
Asco.	Helotiales	<i>Psilachnum chrysostigmum</i>	1	1	0	1	0	3
Bas.	Pucciniales	<i>Puccinia graminis</i>	0	1	1	1	0	3
Asco.	Rhytismatales	<i>Rhytisma acerinum</i>	1	1	0	1	0	3
Bas.	Russulales	<i>Stereum hirsutum</i>	1	1	1	0	0	3



Figure 31: Species that were recorded in at least three different sampling areas of this study, *Dialonectria episphaeria* (a), *Parmelia sulcata* (b), *Xylaria hypoxylon* (c), *Armillaria mellea* (d), *Neodasyscypha cerina* (e), and *Rhytisma acerinum* (f). The photos were taken by N. Kühnberger (a) and by H. Lotz-Winter (b-f).



A comparison of the species composition in all sampling events revealed that the areas were significantly different from each other (Table 22). The graphical representation in the ordination plot shows that especially the tropical region is very distant to the European areas, in terms of composition of fungal species. Somiedo had the largest variability between the two sampling events performed, whereas the sampling events in the Majagua area were most similar (Figure 32).

Table 22: Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in species composition based on sampling areas.

	Df	Sums of squares	Mean squares	F Model	R <sup>2</sup>	Pr (>F)
<b>Area (Residuals)</b>	<b>4 (62)</b>	<b>9.14 (16.12)</b>	<b>2.28 (0.26)</b>	<b>8.79</b>	<b>0.36</b>	<b>0.0002***</b>

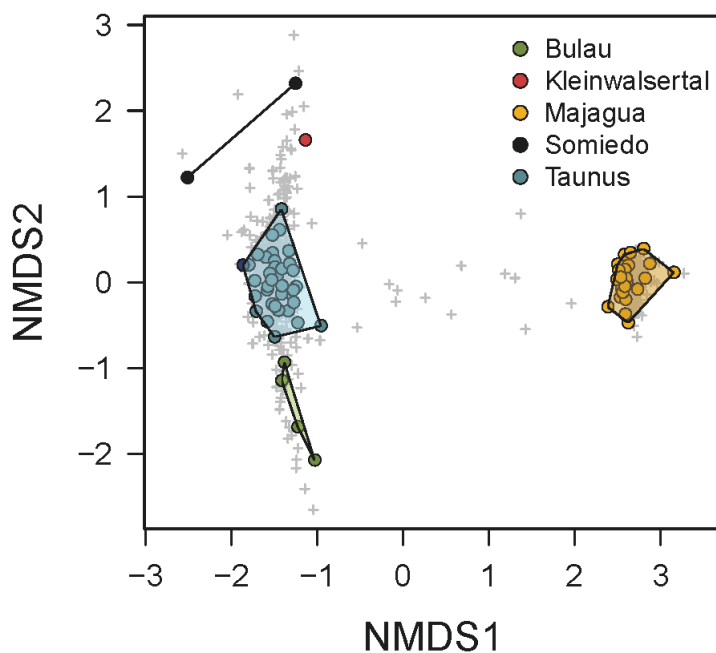


Figure 32: Fungal species composition of all performed sampling events displayed in a non-metric-multidimensional scaling ordination plot (stress = 0.1) based on Sørensen dissimilarities. The dark grey crosses display the species scores and the points display the different sampling events. Sampling events in the same area have the same colour.

### 3.3 Temporal variation of fungal occurrence in the Taunus

Due to the continuous sampling over three years, the temporal changes in richness and species composition could be evaluated for the Taunus area. The fungal richness and species composition fluctuated strongly between the

sampling events. An overview of the species numbers for different taxonomic and ecological groups per sampling event is provided in the appendix (Table S8).

### 3.3.1 Variation in fungal richness

For further investigation of the species richness, the raw data of species richness per sampling event was divided into seasonal components and trend, factors that are already visible in the graph of the raw data. The influence of these factors was confirmed by the graphical analysis through decomposition (Figure 33).

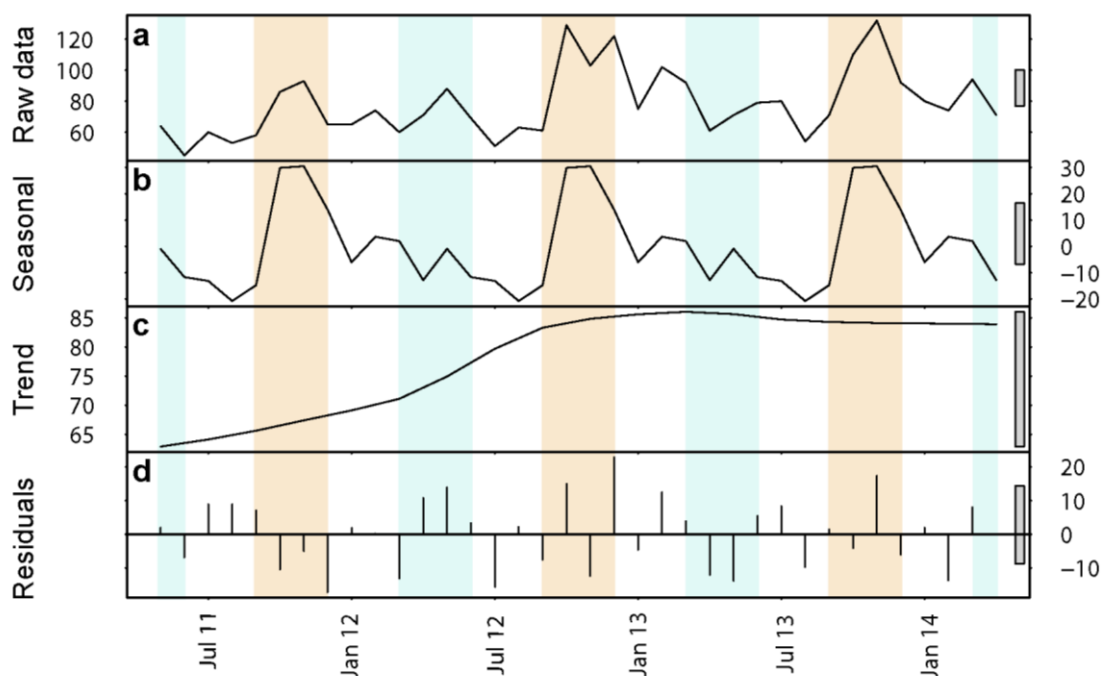


Figure 33: Seasonal trend decomposition based on loess for the fungal richness in the Taunus area. (a) shows the original richness data for each sampling event, including the sum of seasonal variation, trend and residuals. (b) displays the seasonal variation. (c) indicates the trend. (d) shows the remaining variation that could not be explained by season or trend. The scales are different for each panel; therefore, the relative variance of the components is displayed by the grey bar on the right side of each panel. The brown background shows the months of autumn (Sep – Dec) and the blue background shows the spring months (Mar – Jun).

The total number of fungi differed strongly between the first and the two subsequent sampling years. Dividing the records into respective sampling years, 388 species were found in the first year (45% of all records), 482 species in the second year (after second year 77%, 659 species were recorded) and 485 species in the third year. In summary, the number of recorded fungi was

nearly 100 species lower in the first year than in the two subsequent years and led to the increasing trend line.

The same pattern of lower richness in the first year was visible by dividing the total diversity into divisions. The difference between the two divisions was 37 species from first to second year and only 12 species from second to third year (Figure 34). In the first year more Basidiomycota than Ascomycota were found, with a total difference of nine species. In subsequent years, more Ascomycota than Basidiomycota were recorded.

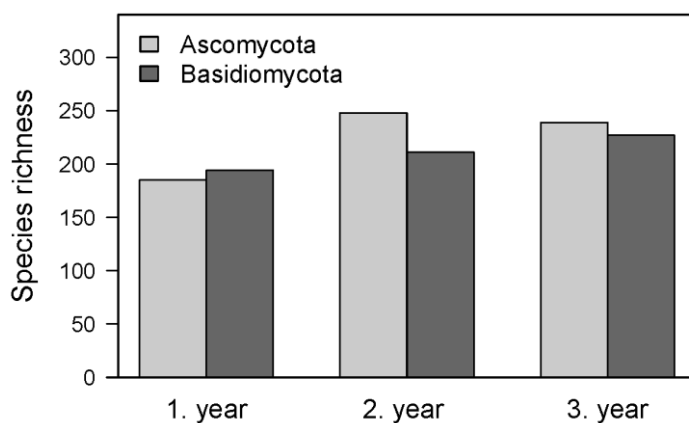


Figure 34: Species richness of Ascomycota and Basidiomycota. The richness is divided into the three sampling years (May 2011-April 2012; May 2012-April 2013; May 2013-April 2014) of the Taunus area.

An assessment of the temporal autocorrelation of fungal richness over a year revealed a clear lag of one year, indicating a clear temporal succession of fungal diversity (Figure S1 in appendix). This yearly pattern was confirmed by decomposing the data. Autumn and the beginning of winter were the periods showing the highest fungal richness, whereas the lowest values could be found in summer. The course of the total fungal richness curve is displayed by the loess model (Figure 35).

The change of fungal richness over the year was significant, but dividing the richness into different taxonomic groups revealed different patterns. Only groups with a high number of basidiomycetous species seemed to change significantly over the year (Table 23).

Table 23: Results of Kruskal-Wallis-test with the explanatory variable months and 11 degrees of freedom. Significant variables with p-values less than 0.05 are marked in bold.

Richness of response variable	$\chi^2$	P-value
<b>Fungi</b>	<b>21.01</b>	<b>0.03*</b>
Ascomycota (division)	16.01	0.14
Helotiales (order)	12.25	0.34
Pleosporales (order)	12.25	0.34
Xylariales (order)	8.76	0.64
<b>Basidiomycota (division)</b>	<b>27.53</b>	<b>0.004**</b>
<b>Agaricales (order)</b>	<b>23.84</b>	<b>0.013*</b>
Polyporales (order)	19.70	0.05
Pucciniales (order)	14.57	0.20
<b>Mycorrhizal fungi (lifestyle)</b>	<b>27.24</b>	<b>0.004**</b>
Saprobionts (lifestyle)	17.86	0.08
Parasites (lifestyle)	14.16	0.22

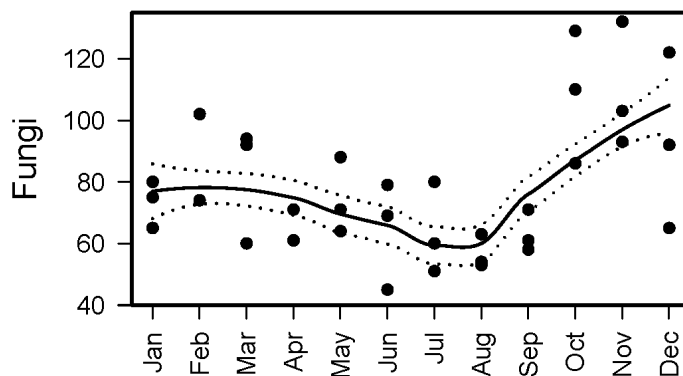


Figure 35: Temporal changes of fungal richness in the Taunus area. The points show the recorded richness per sampling event over the three years. The line represents the model calculated with loess and the dashed lines the corresponding standard errors.

In the next step, the year was divided into fruiting season (May to November, which is often used in monitoring studies) and non-fruiting season (December to April). In total, 394 species (46%) occurred only during fruiting season, 182 species (21%) during non-fruiting season, and 279 species (33%) in both periods.

An example of a species only occurring in winter / beginning of spring was *Ciboria amentacea* in the division Ascomycota, which was recorded only in February and March. Another example is the species *Mycena tintinnabulum* in the division Basidiomycota, which was recorded four times between January and March during the non-fruiting season.

The general trend of seasonality changes was dependent on taxonomic groups. The smallest number of Ascomycota was recorded in August (25 species) and



the highest in March (47 species). Conversely, the smallest number of Basidiomycota occurred in April (23 species), and the highest value (70 species) in October.

The difference between minimal and maximal species number was higher for Basidiomycota (47 species) than for Ascomycota (22 species). The ascomycetous richness did not show a significant change over the year and the loess model only displayed a slight increase at the end of winter and spring but no clear pattern. However, the basidiomycetous richness varied significantly and this change was displayed by the loess fitted model (Figure 36). The results of the statistical analyses for the described changes are shown in Table 23.

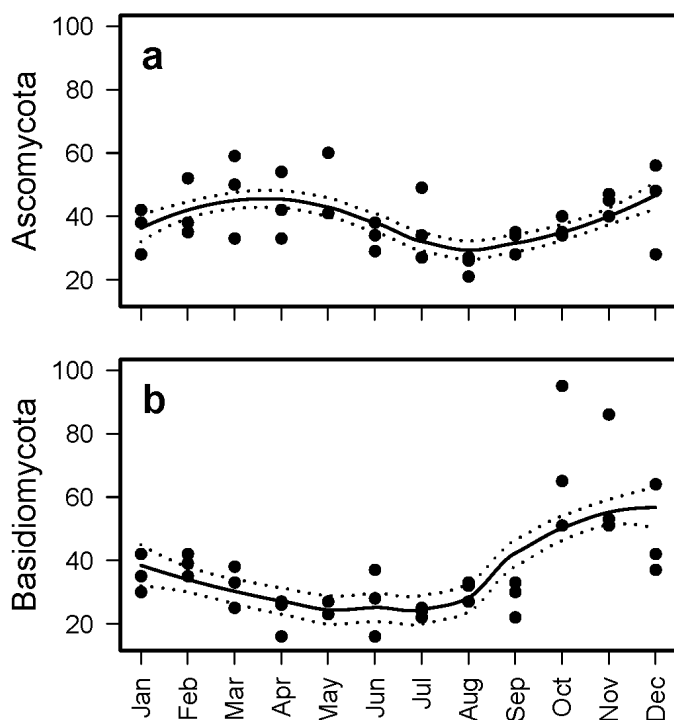


Figure 36: Temporal changes of the richness of Ascomycota and Basidiomycota in the Taunus area. The points display the recorded richness per sampling event over the three years. The line represents the model calculated with loess and the dashed lines the corresponding standard errors. The x-scales are the same for both graphs.

The most frequent ascomycetous orders, Helotiales, Pleosporales, and Xylariales, did not show significant changes of richness over the year (Table 23). Therefore, no graphs are provided for these orders.

The variance of Basidiomycota differed between the orders. Agaricales, which contained most species, showed significantly different patterns over the year (Table 23). This was also obvious by the loess model (Figure 37). Polyporales

differed nearly significantly. For this reason, a fitted line was visualized. The graph shows that the number of Polyporales was generally small and only a slight increase was observable in winter (Figure 37). Pucciniales showed similar richness during the year, therefore no graph is provided for this order. The results of the statistical tests are shown in Table 23.

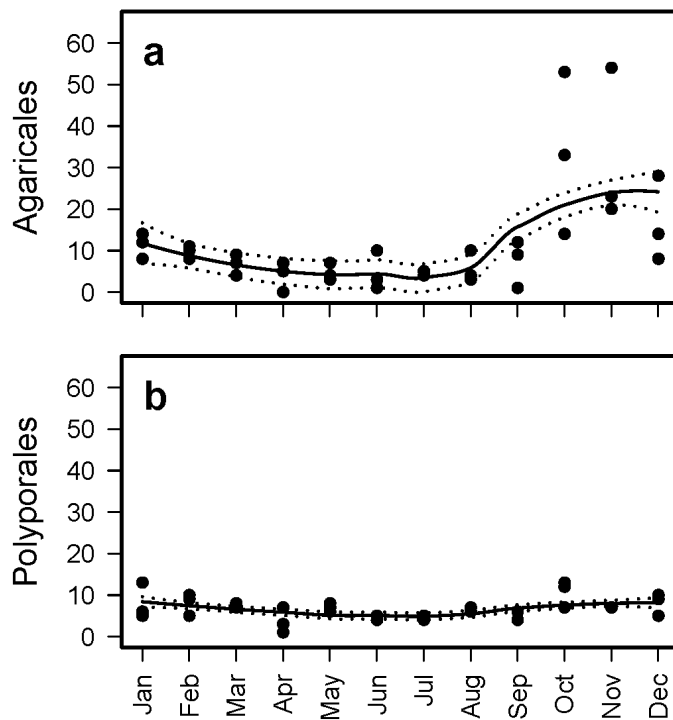


Figure 37: Temporal changes of the richness of Agaricales and Polyporales in the Taunus area. The points display the recorded richness per sampling event over the three years. The line represents the model calculated with loess and the dashed lines the corresponding standard errors. The x-scale is the same for both graphs.

Among the most frequent ecological groups, only mycorrhizal fungi showed a significant change of richness during the year. A number of more than 5% of mycorrhizal fungi was obtained for the months of August to November. In June and July, values of 2% and 3% were found, respectively, whereas 0% was documented in all other months. This strong increase in autumn was indicated by the loess model (Figure 38). The results of the statistical analyses for the most frequent ecological groups are provided in Table 23.

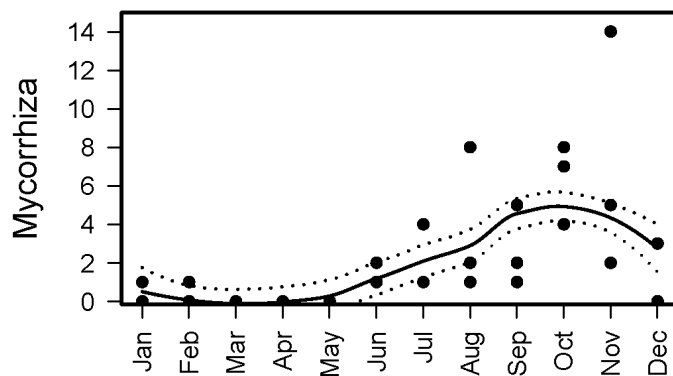


Figure 38: Temporal changes of the richness of mycorrhizal fungi in the Taunus area. The points show the recorded richness per sampling event over the three years. The line represents the model calculated with loess and the dashed lines the corresponding standard errors.

### 3.3.2 Drivers for the temporal changes of fungal richness

Humidity, precipitation and temperature were analysed as possible drivers for the temporal changes of fungal richness. No significant change of humidity and temperature was measured if the three sampling years were compared between each other, whereas precipitation differed during the sampling years. The lowest precipitation was recorded in the first year and increased until the third year. Humidity and temperature varied significantly over different months, but precipitation did not (Table 24).

Table 24: Results of Kruskal-Wallis-test for the possible drivers of changes in richness. Variables with p-values less than 0.05 are written in bold.

Explanatory variable	Response variable	$\chi^2$	Df	P-value
Year	Humidity	0.52	2	0.77
<b>Year</b>	<b>Precipitation</b>	<b>6.99</b>	<b>2</b>	<b>0.03*</b>
Year	Temperature	0.50	2	0.78
<b>Month</b>	<b>Humidity</b>	<b>28.23</b>	<b>11</b>	<b>0.003**</b>
Month	Precipitation	17.41	11	0.10
<b>Month</b>	<b>Temperature</b>	<b>28.65</b>	<b>11</b>	<b>0.003**</b>

Fungal richness, humidity and temperature showed significant differences during the year. Therefore, these factors were displayed in one graph to analyse the patterns shown by the different variables. Temperature and humidity showed rather contradictory patterns. The shapes of the curves of fungal richness and humidity followed a similar trend (Figure 39).

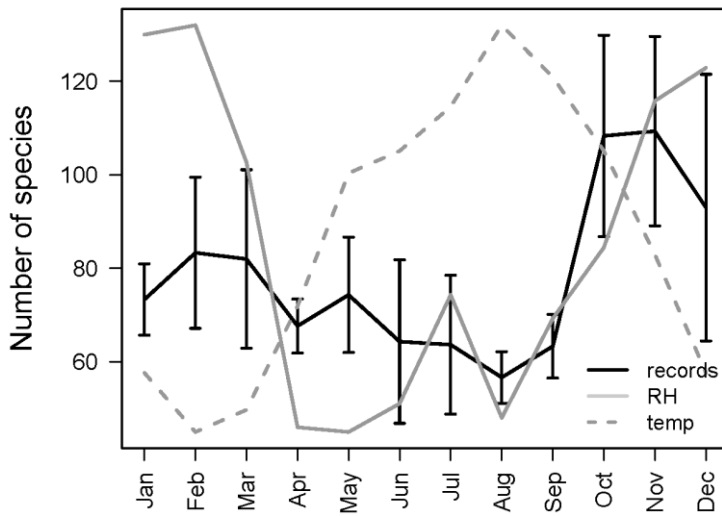


Figure 39: Averaged values of fungal richness (records), relative humidity (RH) and temperature (temp) across months, during the entire sampling. Error bars indicate the standard deviation. The mean relative humidity ranged between 75% and 104% and the mean temperature between 0°C and 20°C.

The visualized patterns were tested for significant relationships of fungal richness and the measured weather variables. Generally, the richness of the tested taxonomic and ecological groups showed a strong positive relationship with humidity and precipitation, whereas temperature mostly displayed a negative one and a significance level above 0.01. Humidity and precipitation showed both, either a significant or a non-significant value for the same taxonomic or ecological group (Table 25). Therefore, only the graphs for significant relationship between fungal richness and humidity or temperature are displayed in graphs.

## Temporal variation of fungal occurrence in the Taunus

Table 25: Summary of the results of the generalized linear models. Variables with p-values less than 0.05 are written in bold.

Explanatory variable	Response variable (richness)	Estimate	Standard error	T-value	P-value	Explained variance
<b>Humidity</b>	<b>Fungi</b>	<b>0.01</b>	<b>0.003</b>	<b>3.2</b>	<b>0.003**</b>	<b>24</b>
Humidity	Ascomycota (division)	0.004	0.003	1.2	0.3	4
<b>Humidity</b>	<b>Basidiomycota (division)</b>	<b>0.02</b>	<b>0.006</b>	<b>3.1</b>	<b>0.004**</b>	<b>26</b>
<b>Humidity</b>	<b>Agaricales (order)</b>	<b>0.04</b>	<b>0.01</b>	<b>2.7</b>	<b>0.01*</b>	<b>24</b>
<b>Humidity</b>	<b>Helotiales (order)</b>	<b>0.02</b>	<b>0.007</b>	<b>2.8</b>	<b>0.009**</b>	<b>16</b>
Humidity	Mycorrhizal (lifestyle)	0.007	0.02	0.4	0.7	0.5
<b>Humidity</b>	<b>Saprobionts (lifestyle)</b>	<b>0.01</b>	<b>0.004</b>	<b>3.1</b>	<b>0.004**</b>	<b>23</b>
<b>Precipitation</b>	<b>Fungi</b>	<b>0.01</b>	<b>0.004</b>	<b>2.7</b>	<b>0.01*</b>	<b>18</b>
Precipitation	Ascomycota (division)	0.002	0.005	0.4	0.6	0.5
<b>Precipitation</b>	<b>Basidiomycota (division)</b>	<b>0.02</b>	<b>0.007</b>	<b>2.8</b>	<b>0.008**</b>	<b>19</b>
<b>Precipitation</b>	<b>Agaricales (order)</b>	<b>0.04</b>	<b>0.01</b>	<b>3.0</b>	<b>0.005**</b>	<b>20</b>
<b>Precipitation</b>	<b>Helotiales (order)</b>	<b>0.02</b>	<b>0.008</b>	<b>2.5</b>	<b>0.02*</b>	<b>13</b>
Precipitation	Mycorrhizal (lifestyle)	0.04	0.02	2.0	0.05	11
<b>Precipitation</b>	<b>Saprobionts (lifestyle)</b>	<b>0.01</b>	<b>0.005</b>	<b>2.7</b>	<b>0.01*</b>	<b>16</b>
Temperature	Fungi	-0.01	0.007	-1.9	0.06	11
<b>Temperature</b>	<b>Ascomycota (division)</b>	<b>-0.02</b>	<b>0.006</b>	<b>-2.7</b>	<b>0.01*</b>	<b>18</b>
Temperature	Basidiomycota (division)	-0.01	0.01	-0.8	0.4	2
Temperature	Agaricales (order)	-0.01	0.03	-0.4	0.7	0.7
<b>Temperature</b>	<b>Helotiales (order)</b>	<b>-0.03</b>	<b>0.01</b>	<b>-2.2</b>	<b>0.03*</b>	<b>11</b>
<b>Temperature</b>	<b>Mycorrhizal (lifestyle)</b>	<b>0.09</b>	<b>0.04</b>	<b>2.2</b>	<b>0.03*</b>	<b>17</b>
<b>Temperature</b>	<b>Saprobionts (lifestyle)</b>	<b>-0.02</b>	<b>0.008</b>	<b>-2.3</b>	<b>0.03*</b>	<b>14</b>

Total fungal richness increased with higher humidity and precipitation. In contrast, the number of recorded fungal species decreased with increasing temperature. The species richness of the most frequent divisions, Ascomycota and Basidiomycota, behaved differently to the weather variables (Figure 40). For the other divisions, only few species were recorded and therefore no relationships were analysed.

The ascomycetous species richness seemed to decline with increasing temperature and did not show a change of species number with increasing or decreasing humidity or precipitation. Consequently, more Ascomycota were recorded in colder months. For Basidiomycota, the number of species showed a stronger relationship with humidity and precipitation than the total number of fungi. These variables seemed to influence the number of Basidiomycota more than the fluctuating values of temperature (Figure 40).

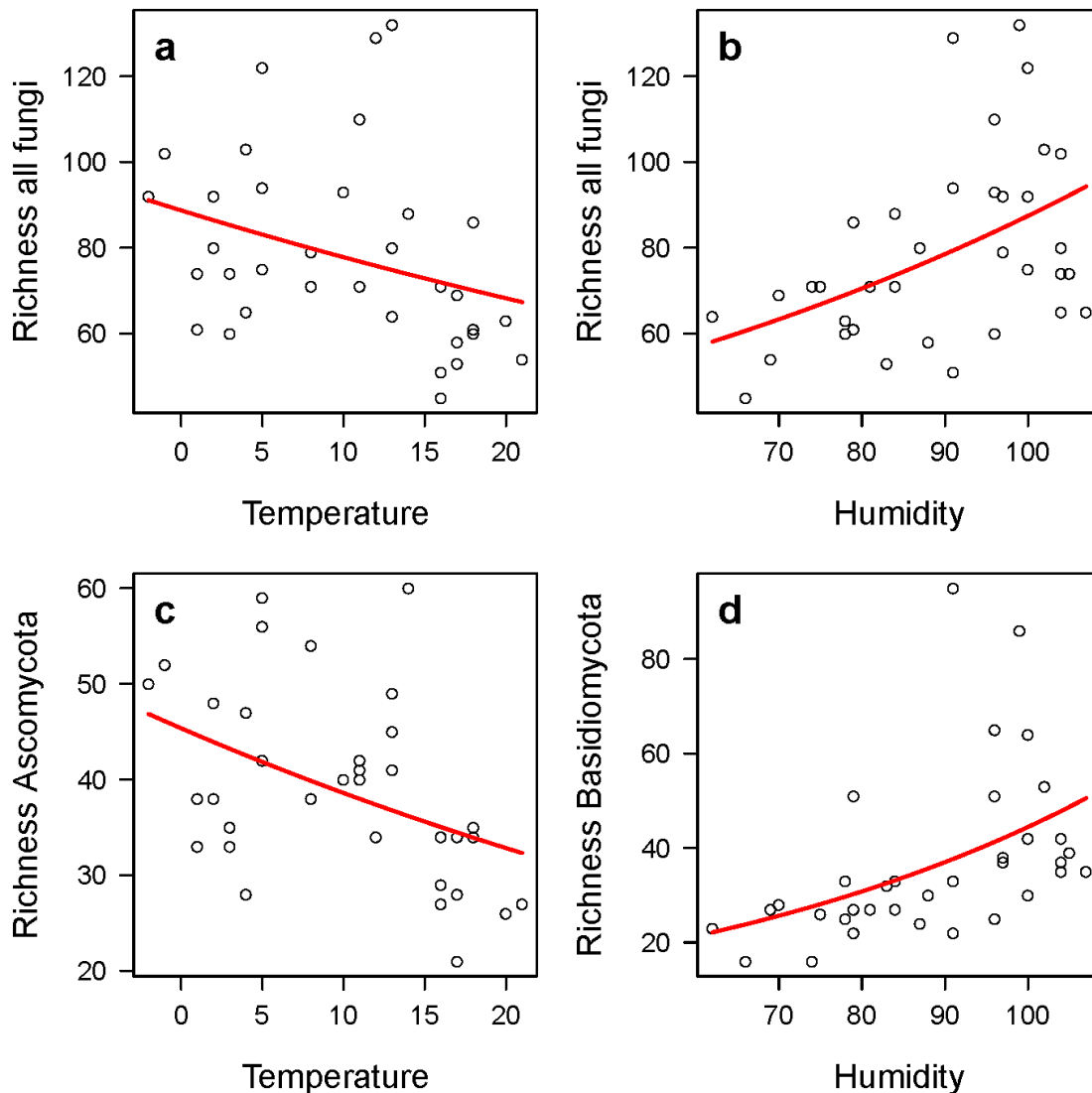


Figure 40: The graphs show the relationship between explanatory weather variables and fungal richness fitted through generalized linear models with quasi-poisson regression (GLM) during 36 sampling events in the Taunus area. Displayed is the effect of temperature (a) and humidity (b) on fungal richness. Furthermore, the effects of temperature on the richness of Ascomycota (c) and humidity on the richness of Basidiomycota (d) are shown.

The analyses at the order level revealed significant relationships with environmental variables for Helotiales (Ascomycota) and Agaricales (Basidiomycota). The species richness of the other most frequent ascomycetous orders, Pleosporales and Xylariales, and of the basidiomycetous orders Polyporales and Pucciniales, did not show any significant relationship with any climatic variable.

Helotiales was the only order that showed significant relationships with humidity, precipitation, and temperature. Consequently, the number of Helotiales increased with higher humidity and precipitation and lower temperatures. The order Agaricales showed an increasing number of species

with higher humidity, with a pattern analogous to that of Basidiomycota. However, the data fit was not as good as in the other models (diagnostic plot in appendix Figure S2), probably due to the high number of recorded Agaricales in October 2012, October 2013 and November 2013 (Figure 41).

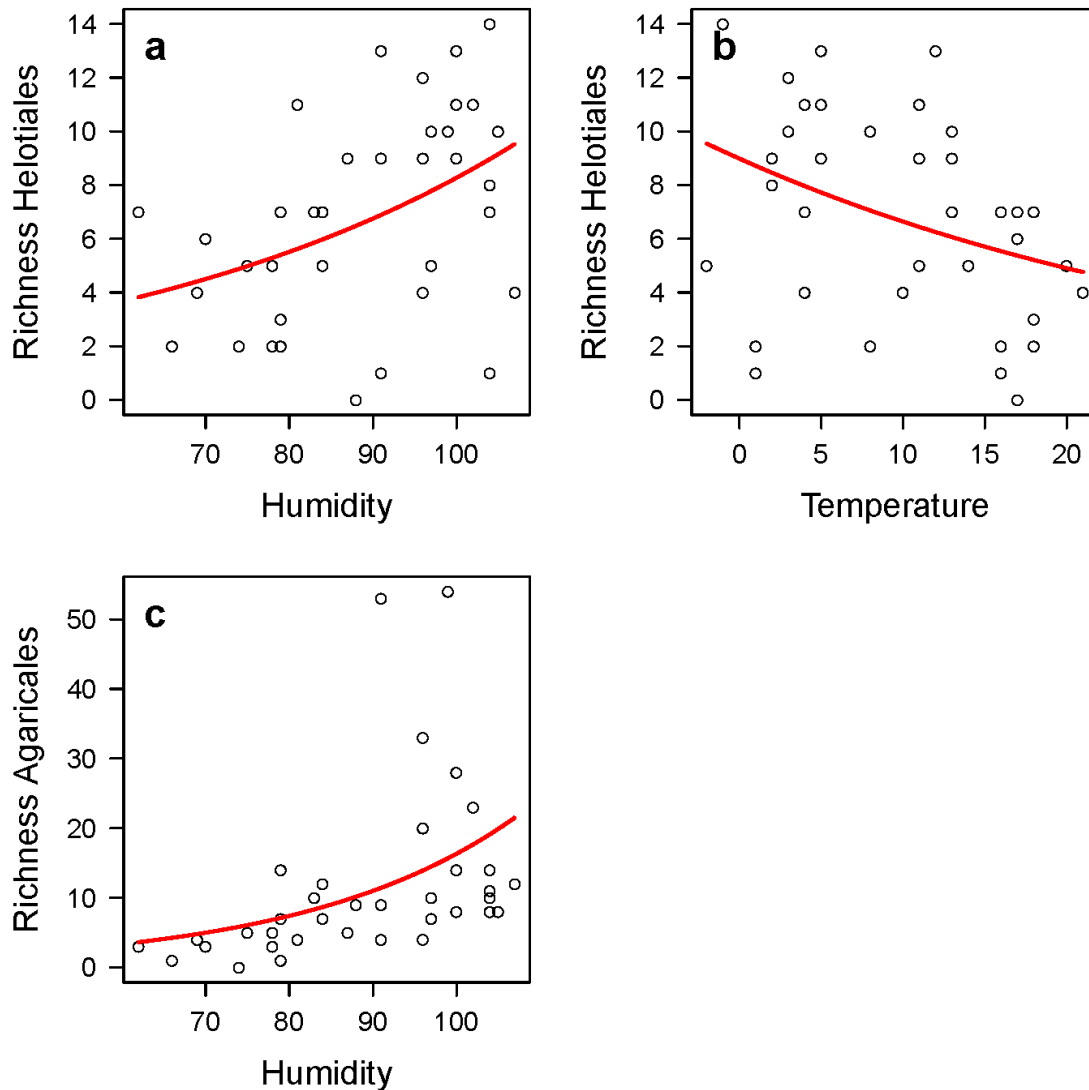


Figure 41: The graphs show the relationship between explanatory weather variables and fungal species richness fitted through generalized linear models with quasi-poisson regression (GLM) during 36 sampling events in the Taunus area. Displayed is the effect of humidity (a) and temperature (b) on the richness of Helotiales and the effect of humidity on the richness of Agaricales (c).

The species richness of ecological groups of fungi was also tested for potential relationships with the climatic variables. Saprobiotics showed significant relationships for all measured variables, similarly to those found within the Helotiales. The number of saprobiontic species increased with higher humidity and precipitation as well as lower temperature. In contrast, the group of mycorrhizal fungi showed the opposite pattern like Basidiomycota and

Agaricales, so the number of mycorrhizal species increased with higher temperatures (Figure 42). However, the diagnostic plot in the appendix (Figure S3) shows that the model does not fit the data accurately, probably due to a high number of mycorrhizal fungi in November 2013.

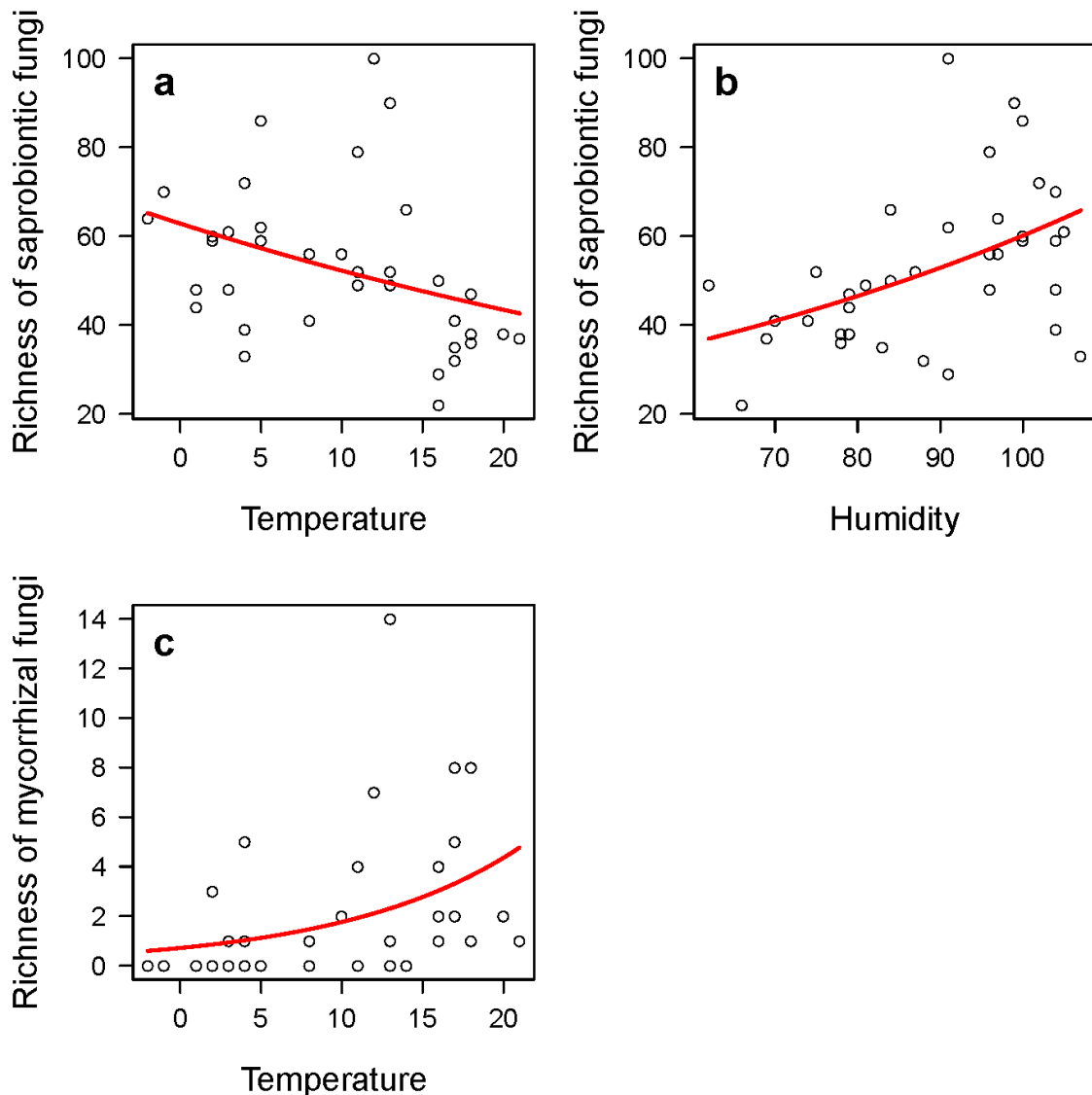


Figure 42: The graphs show the relationship between explanatory weather variables and fungal species richness fitted through generalized linear models with quasi-poisson regression (GLM) during 36 sampling events in the Taunus area. Displayed is the effect of temperature (a) and humidity (b) on the richness of saprotrophic fungi. The effect of temperature on the fungal richness of mycorrhizal fungi is shown (c).

### 3.3.3 Changes in fungal species composition

So far, only the richness values for various groups were considered, but not the identity of their species or rather species composition, which differed during the sampling events. The factor sampling year, similar to the trend line for the richness analyses, was responsible for 7% of the variation in species



composition (Table 26). The assemblage of fungi recorded in the first sampling year differed strongly from those obtained in subsequent years (Figure 43). However, the most important factor driving differences in species composition was month, which explained nearly 40% of the variance (Table 26) and determined a gradual differentiation in fungal composition that reached maximal dissimilarities between the months of autumn-early winter and spring (Figure 43).

Table 26: Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in species composition between the sampling year and month in the Taunus area for 36 sampling events.

	Df	Sums of squares	Mean squares	F Model	R <sup>2</sup>	Pr (>F)
<b>Year</b>	<b>1</b>	<b>0.66</b>	<b>0.66</b>	<b>3.00</b>	<b>0.07</b>	<b>0.0002***</b>
<b>Month</b>	<b>11</b>	<b>3.47</b>	<b>0.32</b>	<b>1.44</b>	<b>0.38</b>	<b>0.0002***</b>
Residuals	23	5.04	0.22		0.55	

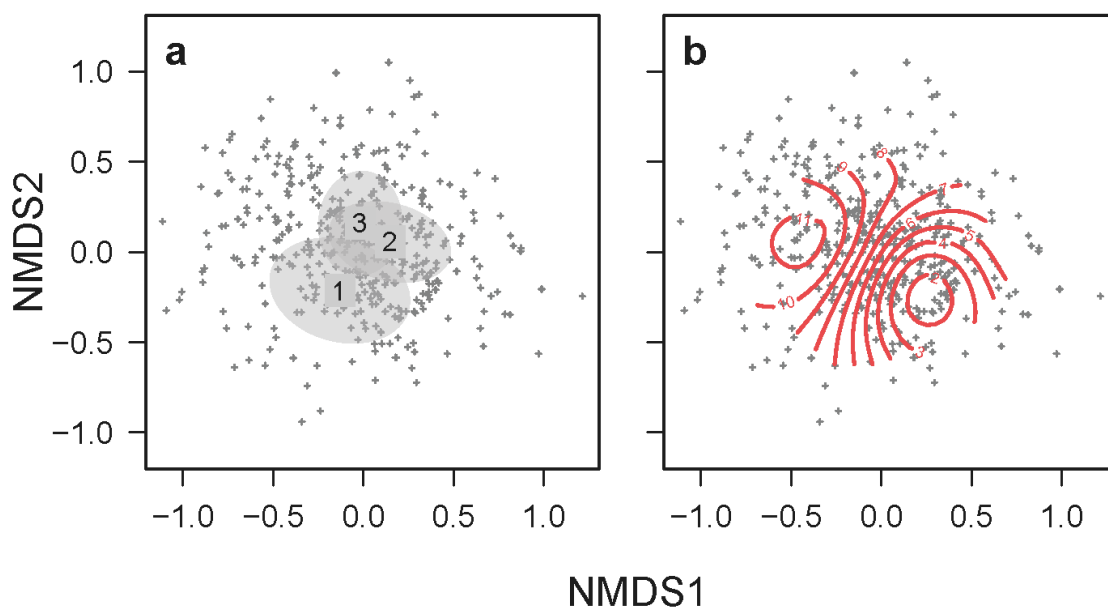


Figure 43: Fungal species composition of the Taunus area for 36 sampling events displayed in a non-metric-multidimensional scaling ordination plot (stress = 0.25) based on Sørensen dissimilarities. The dark grey crosses display the species scores, which are the same in both plots. (a) Dispersion ellipses based on the standard deviations of the three sampling years, numbered with 1, 2, and 3, are shown. (b) The variable month is fitted to a smooth surface using generalized additive model (GAM). The y-scale is the same for both graphs.

The species composition of the three most frequent ascomycetous orders did not change significantly during the sampling events (Table 27) and did not show a temporal effect on their assemblages (Figure 44a). In contrast, the species compositions of the three most frequent basidiomycetous orders and the most frequent lifestyles changed during the year (Table 27). Figure 44 shows that the different groups within the Basidiomycota and the lifestyles displayed different

patterns. Species in the orders Polyporales and Pucciniales (Figure 44b) and fungal groups with a saprotrophic and plant-parasitic lifestyle (Figure 44c) did not show a temporal effect on their assemblages. Records that could be classified as either within the basidiomycetous order Agaricales (Figure 44b) or with a mycorrhizal lifestyle (Figure 44c), on the contrary, had a preferential occurrence in autumn and winter.

Table 27: Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in species composition in the Taunus area for 36 sampling events. The evaluated groups were the ascomycetous orders Xylariales, Pleosporales, and Helotiales, the basidiomycetous orders Agaricales, Polyporales, and Pucciniales and the ecological groups saprobionts, parasites and mycorrhizal fungi. The bold letters mark significant values less than  $p=0.05$ .

	Df	Sums of squares	Mean squares	F Model	R <sup>2</sup>	Pr (>F)
Ascomycetous orders (Residuals)	2 (33)	0.81 (13.61)	0.40 (0.41)	0.98	0.06	0.49
<b>Basidiomycetous orders (Residuals)</b>	<b>2 (42)</b>	<b>1.57 (15.23)</b>	<b>0.78 (0.36)</b>	<b>2.16</b>	<b>0.09</b>	<b>0.002**</b>
<b>Ecological groups (Residuals)</b>	<b>2 (137)</b>	<b>1.40 (54.28)</b>	<b>0.70 (0.40)</b>	<b>1.76</b>	<b>0.03</b>	<b>0.01*</b>

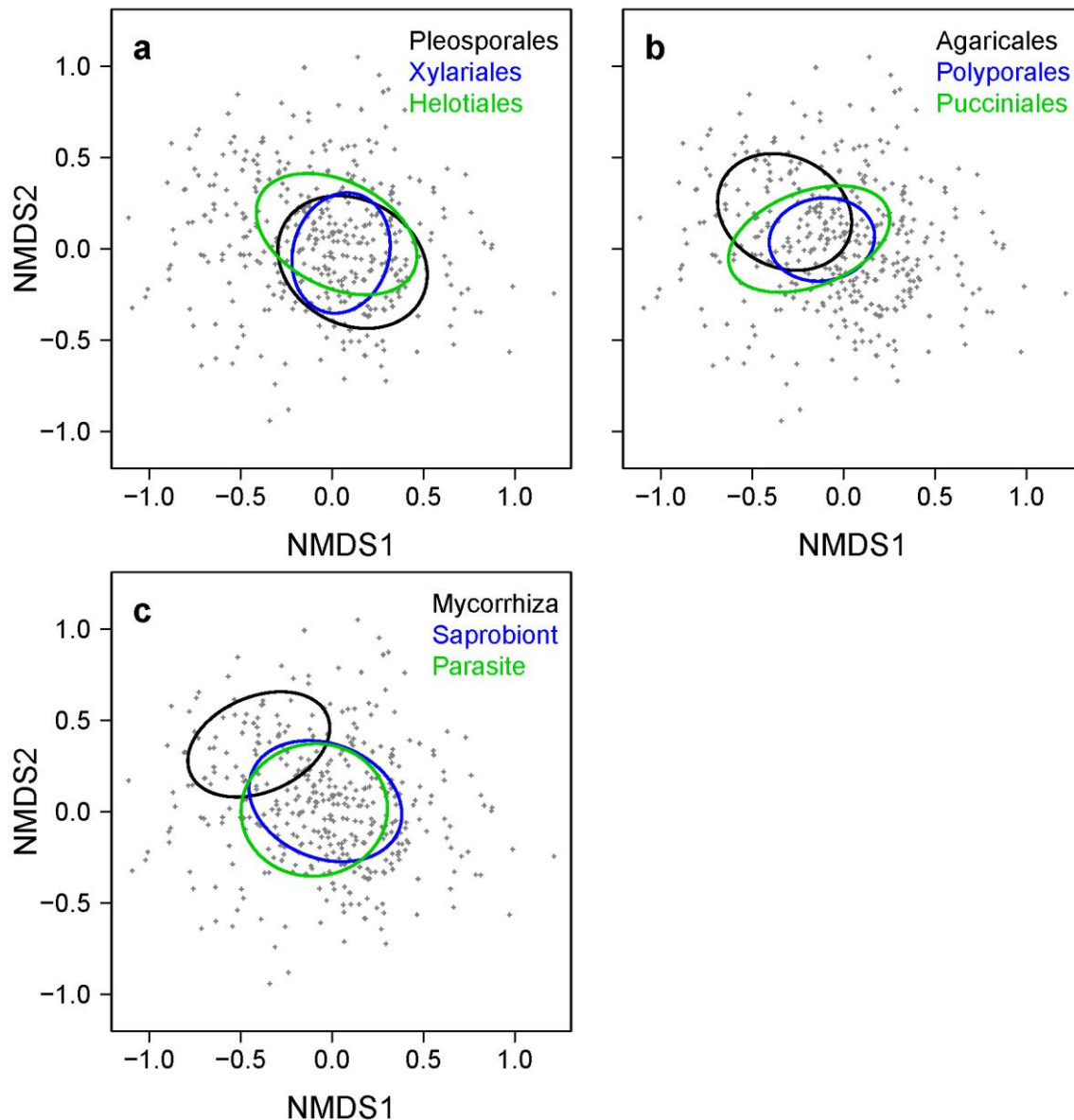


Figure 44: Fungal species composition in the Taunus area for 36 sampling events displayed in a non-metric-multidimensional scaling ordination plot (stress = 0.25) based on Sørensen dissimilarities. The dark grey crosses display the species scores, which are the same in all plots. The ellipses show (a) the species distribution of the three most frequent orders within the Ascomycota, (b) the species distribution of the three most frequent orders of the Basidiomycota and (c) the species distribution of the three most frequent ecological groups. The scales are the same for all graphs.

### 3.3.4 Drivers for the temporal changes of fungal species composition

The species composition was significantly affected by the environmental variables humidity, precipitation, and temperature, with almost the same percentage of explained variance by each variable (Table 28). Figure 45 displays the ordination graph with the climatic variables.

Table 28 Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in species composition based on humidity, precipitation and temperature in the Taunus area for 36 sampling events. P-values less than 0.05 are marked in bold.

	Df	Sums of squares	Mean squares	F Model	R <sup>2</sup>	Pr (>F)
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>0.45 (8.71)</b>	<b>0.45 (0.26)</b>	<b>1.74</b>	<b>0.05</b>	<b>0.005**</b>
<b>Precipitation (Residuals)</b>	<b>1 (34)</b>	<b>0.41 (8.75)</b>	<b>0.41 (0.26)</b>	<b>1.61</b>	<b>0.05</b>	<b>0.01*</b>
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>0.65 (8.51)</b>	<b>0.65 (0.25)</b>	<b>2.61</b>	<b>0.07</b>	<b>0.0002***</b>

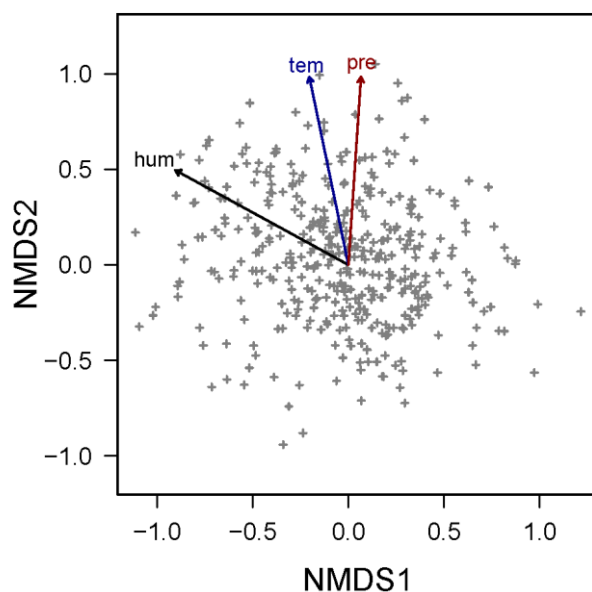


Figure 45: Species composition of the Taunus area for 36 sampling events displayed in a non-metric-multidimensional scaling ordination plot (stress = 0.25) based on Sørensen dissimilarities. The dark grey crosses display the species scores. The arrows display the direction with maximal correlation of the weather variables humidity (hum), temperature (tem), and precipitation (pre) on the ordination plot.

The influence of climatic data on species composition was tested for Ascomycota and Basidiomycota. Precipitation and temperature seemed to have a small influence on the species composition of Ascomycota. In contrast, humidity and temperature probably affected the species composition of Basidiomycota more strongly, with a high p-value of 0.0002. Additionally, the influence of precipitation on basidiomycetous species composition was nearly significant, with 0.06 (Table 29).

## Temporal variation of fungal occurrence in the Taunus

Table 29: Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in the species composition of the divisions Ascomycota and Basidiomycota based on humidity, precipitation and temperature in the Taunus area for 36 sampling events.

	Df	Sums of squares	Mean squares	F Model	R <sup>2</sup>	P-value
<b>Ascomycota</b>						
Humidity (Residuals)	1 (34)	0.31 (9.32)	0.31 (0.27)	1.14	0.03	0.3
<b>Precipitation (Residuals)</b>	<b>1 (34)</b>	<b>0.43 (9.21)</b>	<b>0.43 (0.27)</b>	<b>1.59</b>	<b>0.04</b>	<b>0.03*</b>
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>0.53 (9.11)</b>	<b>0.53 (0.27)</b>	<b>1.96</b>	<b>0.05</b>	<b>0.004**</b>
<b>Basidiomycota</b>						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>0.60 (8.02)</b>	<b>0.60 (0.24)</b>	<b>2.53</b>	<b>0.07</b>	<b>0.0002***</b>
Precipitation (Residuals)	1 (34)	0.36 (8.26)	0.36 (0.24)	1.47	0.04	0.06
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>0.77 (7.85)</b>	<b>0.77 (0.23)</b>	<b>3.32</b>	<b>0.09</b>	<b>0.0002***</b>

The influence of the climatic variables on species compositions within individual orders was tested separately. The order that was most influenced by changes in climatic conditions was Agaricales. For this order, the highest value of explained variance on species composition was found, with 11% by humidity and 14% by temperature ( $R^2 = 0.11$  and  $0.14$ ). Polyporales showed changes in species composition respective to humidity and temperature. However, the explained variance and the p-values were lower.

In general, humidity seemed to influence the species composition of four orders and temperature the species composition of three orders. Precipitation did not seem to affect the species composition of the investigated orders. The only order that did not show any relation to weather variables was Xylariales within the Ascomycota (Table 30).

Table 30: Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in the fungal species composition of different orders based on humidity, precipitation and temperature in the Taunus area for 36 sampling events.

	Df	Sums of squares	Mean squares	F Model	R <sup>2</sup>	P-value
<b>Agaricales</b>						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>1.21 (10.07)</b>	<b>1.21 (0.30)</b>	<b>4.07</b>	<b>0.11</b>	<b>0.0002***</b>
Precipitation (Residuals)	1 (34)	0.39 (10.89)	0.39 (0.32)	1.22	0.03	0.2
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>1.54 (9.74)</b>	<b>1.54 (0.29)</b>	<b>5.36</b>	<b>0.14</b>	<b>0.0002***</b>
<b>Polyporales</b>						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>0.42 (6.29)</b>	<b>0.42 (0.19)</b>	<b>2.28</b>	<b>0.06</b>	<b>0.02*</b>
Precipitation (Residuals)	1 (34)	0.31 (6.41)	0.31 (0.19)	1.62	0.05	0.1
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>0.41 (6.31)</b>	<b>0.41 (0.19)</b>	<b>2.21</b>	<b>0.06</b>	<b>0.03*</b>
<b>Pucciniales</b>						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>0.53 (7.39)</b>	<b>0.53 (0.22)</b>	<b>2.42</b>	<b>0.07</b>	<b>0.02*</b>
Precipitation (Residuals)	1 (34)	0.20 (7.71)	0.20 (0.23)	0.89	0.03	0.5
Temperature (Residuals)	1 (34)	0.36 (7.55)	0.36 (0.22)	1.64	0.05	0.1
<b>Helotiales</b>						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>0.63 (13.01)</b>	<b>0.63 (0.38)</b>	<b>1.66</b>	<b>0.05</b>	<b>0.04*</b>
Precipitation (Residuals)	1 (34)	0.52 (13.12)	0.52 (0.39)	1.36	0.04	0.2
Temperature (Residuals)	1 (34)	0.60 (13.05)	0.60 (0.38)	1.56	0.04	0.07
<b>Pleosporales</b>						
Humidity (Residuals)	1 (34)	0.28 (12.60)	0.28 (0.37)	0.77	0.02	0.6
Precipitation (Residuals)	1 (34)	0.43 (12.46)	0.43 (0.37)	1.17	0.03	0.3
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>0.82 (12.07)</b>	<b>0.82 (0.35)</b>	<b>2.30</b>	<b>0.06</b>	<b>0.02*</b>
<b>Xylariales</b>						
Humidity (Residuals)	1 (34)	0.23 (6.41)	0.23 (0.19)	1.19	0.03	0.3
Precipitation (Residuals)	1 (34)	0.12 (6.52)	0.12 (0.19)	0.65	0.02	0.7
Temperature (Residuals)	1 (34)	0.19 (6.45)	0.19 (0.19)	1.02	0.03	0.4

The ecological groups were tested for their relationship with climatic conditions. All tested groups showed differences in species composition due to changes in humidity. Furthermore, the richness of saprobionts and parasites seemed to change also with temperature (Table 31).

## Temporal variation of fungal occurrence in the Taunus

Table 31: Non-parametric analysis of variance using Sørensen distances for the evaluation of differences in the fungal species composition of different ecological groups based on humidity, precipitation and temperature in the Taunus area for 36 sampling events.

	Df	Sums of squares	Mean squares	F Model	R <sup>2</sup>	P-value
Saprobionts						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>1.21 (10.07)</b>	<b>1.21 (0.30)</b>	<b>4.07</b>	<b>0.11</b>	<b>0.0002***</b>
Precipitation (Residuals)	1 (34)	0.39 (9.07)	0.39 (0.27)	1.47	0.04	0.05
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>0.70 (8.76)</b>	<b>0.70 (0.26)</b>	<b>2.70</b>	<b>0.07</b>	<b>0.0002***</b>
Parasites						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>1.21 (10.07)</b>	<b>1.21 (0.30)</b>	<b>4.07</b>	<b>0.11</b>	<b>0.0002***</b>
Precipitation (Residuals)	1 (34)	0.35 (7.72)	0.35 (0.23)	1.52	0.04	0.08
<b>Temperature (Residuals)</b>	<b>1 (34)</b>	<b>0.58 (7.48)</b>	<b>0.58 (0.22)</b>	<b>2.66</b>	<b>0.07</b>	<b>0.0002***</b>
Mycorrhizal fungi						
<b>Humidity (Residuals)</b>	<b>1 (34)</b>	<b>1.21 (10.07)</b>	<b>1.21 (0.30)</b>	<b>4.07</b>	<b>0.11</b>	<b>0.0002***</b>
Precipitation (Residuals)	1 (34)	NA	NA	NA	NA	NA
Temperature (Residuals)	1 (34)	NA	NA	NA	NA	NA

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## 4 Discussion

### 4.1 Fungal diversity

Each sampling event in this investigation was processed with a standardized protocol and similar sampling effort to perform a comparison between various collection events (Cannon 1997; Dornelas et al. 2014). All investigated areas revealed a high fungal diversity including microscopic and macroscopic species with ecological characterizations for most of them. This information is essential for a comprehensive understanding of fungal communities, because most fungi are poorly known at taxonomic, distributional, and ecological levels (Molina et al. 2011).

#### 4.1.1 Fungal richness in the Taunus

The number of recorded fungal species in the Taunus area was higher (855 species), than that published in many monitoring studies based on regular sampling of fungal fruit bodies. Some examples for such studies are: 621 recorded species in the Botanical Garden in Edinburgh (Scotland) for 7 years (Krivtsov et al. 2003); 408 species in 1 500 m<sup>2</sup> in Switzerland for 21 years (Straatsma et al. 2001); 401 species in 25 ha in Rhineland-Palatinate for almost 30 years (Zehfuß 1999); 305 species in six woodlands in Italy for 2.5 years (Angelini et al. 2015). One probable explanation for the comparably high richness in the Taunus area is the attempt to include all visible fungi and not only macrofungi like in the previously mentioned studies. The high species number in the Taunus area shows the importance of including many different taxonomic groups in monitoring projects in order to obtain a comprehensive species list, as proposed by Rudolf et al. (2013).

Other inventories revealed similar or higher fungal richness than in the Taunus area. In total, 886 species were recorded near Vienna (Straatsma and Krisai-Greilhuber 2003), 982 species in Bavaria (Karasch 2005) and 1 166 species in Canada (Ceska 2013). However, the high macrofungal diversity can be explained by the large monitoring areas, between 3.8 ha and 71 ha, during long study periods, between seven and nine years (Straatsma and Krisai-Greilhuber 2003; Karasch 2005; Ceska 2013). In contrast, a comparable diversity by



recording all evident fungi was documented in a single transect of 500 m in the Taunus area for a study period of three years.

Even after 36 sampling events, many fungi were recorded only once in the Taunus area, whereas the distribution of plant species over frequencies was rather even. Similar distributions of fungal species frequencies have been shown in other studies even after longer sampling for nine and 21 years (Straatsma et al. 2001; Ceska 2013). A high frequency of rare species is a typical feature of ecological data (Tofts and Orton 1998; Magurran and Henderson 2003), particularly of hyperdiverse and/or undersampled communities (Piepenbring et al. 2012). The continuous appearance of new records in each sampling event in the Taunus area suggests that, after a survey of three years, this area is still undersampled.

Species can be rare either because they disappeared from the study area after the first recording, or because they were present but not detected. Non-detection is important for macrofungal inventories because fruit bodies of many fungal species are mostly rare, but their mycelia can be present without the formation of fruit bodies. The development of sporocarps depends on fungus' habitat specificity, weather conditions, or phenology (O'Dell et al. 2000; Straatsma et al. 2001; Cunningham and Lindenmayer 2005; Baptista et al. 2010). Therefore, missing fruit bodies do not necessarily show the absence of a species in an area. For some species, it is difficult to detect fruit bodies because the probability of detecting a sporocarp differs between species, for example due to small fruit bodies like those of *Hyalorbilia inflatula* (Halme and Kotiaho 2012). These facts complicate the approach of an extensive fungal inventory based on fruit bodies.

The proportion of recorded Ascomycota was lower in this study than the total one listed by Kirk et al. (2008). In contrast, the proportion of Basidiomycota was higher in this study compared to Kirk et al. (2008). The relatively high number of Basidiomycota might be caused by their usually larger and easily observable fruit bodies (Piepenbring et al. 2012). This is why many monitoring studies are mainly based on Basidiomycota (e.g. Langer 2000; Krivtsov et al. 2003; Angelini et al. 2015). The proportion of Basidiomycota recorded in the Taunus, representing 41% of all records, was lower than in most macrofungal

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inventories, such as those by Angelini et al. (2015), with 97%; Kutszegi et al. (2015), with 92%; Krivtsov et al. (2003), with 91%; and Karasch (2005), with 78%. This can be partly explained with the increased focus on small Ascomycota during the own sampling, but also with the sampling frequency. Several other studies showed that a sampling of basidiomycetes even on a weekly basis is not sufficient to detect all sporocarps during the main fructification period (Richardson 1970; Vogt et al. 1992) because some fruit bodies last only a few days like many species of the genus *Mycena* (Egli et al. 1997). The monthly sampling frequency in Taunus was even lower. This leads to the assumption that a high diversity of Basidiomycota is still hidden in the Taunus area.

An increased focus on species of Ascomycota is important because their ecology is less known than the one of Basidiomycota (Mueller and Gerhardt 1995b). In this thesis, an attempt was performed to include more ascomycetous species in a classic survey than in previous studies. Fruit bodies of this division often grow in non-directly visible, hidden habitats, which have to be specifically searched for (Mueller and Gerhardt 1994). The proportion and the number of recorded Ascomycota in the Taunus area was, with a 51% of all records, higher than that found in other monitoring activities of macrofungi, which reported only between 3% and 18% of ascomycetes in several studies (Krivtsov et al. 2003; Karasch 2005; Angelini et al. 2015; Kutszegi et al. 2015). The distribution of divisions in the Taunus area was more similar to that found in molecular studies of soil fungi, than in common fruit-body inventories. The molecular studies of Tedersoo et al. (2014) and O'Brien et al. (2005) revealed a proportion in soil of about 49% and 46% Ascomycota, and of about 42% and 41% Basidiomycota, respectively. The high percentage of Ascomycota shows that by intensive sampling, many inconspicuous species can be detected, which results in similar proportions as those found in molecular studies and reflecting the higher proportion of known ascomycetous species (Kirk et al. 2008), but with the advantage of providing morphological data.

At the order level, the most species-rich group was Agaricales within the Basidiomycota, which is also the order, considered in this study, that contains the highest number of known species (Kirk et al. 2008). A comparison of species, contained in orders considered, is shown in Table 32. In most cases,

investigations based on macrofungi and soil fungi revealed highest proportions of Agaricales and Russulales (e.g. O'Brien et al. 2005; Li et al. 2012; Angelini et al. 2015), even though Russulales (8<sup>th</sup> in frequency in the Taunus area) are only on twelfth place in their total number of known species. The high recorded abundance in many investigations is probably due to their mostly conspicuous fruit bodies and their cosmopolitan distribution (Kirk et al. 2008). Many species of Russulales produce their fruit bodies in autumn during the main fruiting period. The lack of some tree partners of mycorrhizal relationships and the monthly sampling frequency, which was too sparse to record short-living fruit bodies as described before, together with the generally dry sampling area, might explain the low number of Russulales in the Taunus area.

Table 32: Comparison of the most frequent orders of known species based on Kirk et al. (2008) with the most recorded orders in the Taunus area. The dark grey background shows orders that are represented on the same position in the compared categories. The light grey background marks orders that are represented within the 10 most frequent orders in both categories. The orders without background colour are groups that could be found only within the 10 most frequent orders of one category.

Frequency order	Orders based on frequency of known species	Known species number	Species number in Taunus	Orders based on frequency of Taunus records	Frequency order respective to known species
1	Agaricales	13233	174	Agaricales	1
2	Pucciniales	7798	87	Helotiales	6
3	Capnodiales	7244	64	Pleosporales	5
4	Lecanorales	5695	45	Xylariales	9
5	Pleosporales	4764	45	Polyporales	11
6	Helotiales	3881	43	Pucciniales	2
7	Ostropales	2753	41	Hypocreales	8
8	Hypocreales	2647	39	Russulales	12
9	Xylariales	2487	27	Capnodiales	3
10	Teloschistales	1954	18	Diaporthales	16

The next most species rich orders in the Taunus inventory were Helotiales, Pleosporales and Xylariales, which are on sixth, fifth, and ninth places, respectively according to their total number of known species (Kirk et al. 2008). Fruit bodies in these orders are usually small and/or inconspicuous and can be found on wood and plants (Wang et al. 2006; Kirk et al. 2008). The Taunus area provided good conditions for these fungal groups due to a high amount of dead wood and many different plants in forest and meadow. Because of their inconspicuousness and their small size, these groups are probably not considered in most surveys (Mueller and Gerhardt 1994).

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The most frequently recorded fungi in the Taunus area developed fruit bodies, which lasted considerable time (sometimes more than two years). Strategies for these long-lasting sporocarps are different: several species, which do not show any seasonal changes during the year, produced durable sporocarps (Xylariales, Polyporales) or long living thalli in the case of lichen-forming fungi (Lecanorales), whereas others develop relatively small fruit bodies that are able to survive dehydration (Dacrymycetales). Other fungi develop different spore stages (Pucciniales) during seasons. This study shows that a monitoring of fungi observable during the whole year might include other fungi than polypores or lichens, which are often proposed for time-independent monitoring (Berglund et al. 2005; Wirth et al. 2011). Nevertheless, polypores and lichens form the most conspicuous fruit bodies, whereas expert knowledge is required to find dry Dacrymycetales, small Xylariales or to assign the different spore stages of Pucciniales to one species.

Most species recorded in this study had a saprotrophic lifestyle, with 69% of the total number of species, which matches the assumption that the majority of fungi are saprobionts (Grayer and Kokubun 2001). This is consistent with some macrofungal studies, which found between 68% and 82% of species being saprobionts (Mueller and Gerhardt 1994; Ceska 2013; Langer et al. 2014). In contrast, the study of Straatsma et al. (2001) revealed a number of mycorrhizal fungi twice as high as that of saprobionts during a 21-year-long sampling of epigeous macromycetes, which was probably due to a strong focus on mycorrhizal fungi.

Mycorrhizal fungi seem to be underrepresented in this study with only 5% of the species. The low number of ectomycorrhizal fungi might be related to the already discussed hidden diversity of Russulales due to monthly sampling (Richardson 1970; Vogt et al. 1992; Egli et al. 1997). Furthermore, the dry conditions of the sampling area are not generally suitable for many basidiomycetous groups, which often are dependent on humidity and precipitation (e.g. Moore et al. 2008; Baptista et al. 2010).

Another important ecological group is the one of parasites, which was frequently detected in this survey. The substrate-host interaction and host specificity differed between species of plant parasites, as has also been shown by other

studies (Hantsch et al. 2014). Biotrophic fungi, like those within the order Pucciniales, are more often host specific than necrotrophic fungi. Studies on host specificity of plant pathogens are rare and mostly investigated in small areas. In this study, most plant parasites were restricted to one host plant species or genus. A study on global datasets showed that about half of the investigated microbial pathogens, including fungi, were restricted to one single plant genus (Gilbert et al. 2012). However, this host specificity seems to change in connection with climate change, because an expansion of host range has already been proven for individual species (Gange et al. 2011). The investigation period in this study was too short to analyse any changes of fungus-host interactions over time.

### **4.1.2 Fungal richness estimations in the Taunus**

In the Taunus area, the accumulation curve did not reach saturation, although more than 20 sampling events (36 in total) were performed, which were suggested to be necessary as the minimal sampling effort to calculate rarefaction curves (Gotelli and Colwell 2011). Recording the total number of fungal species in an area to reach the saturation of accumulation curves is almost impossible (Hawksworth 2012) due to the usually high fungal richness. In a single sampling event, not all species can be recorded because the probability of detecting a fruit body varies between species, due to factors like their size, colour, habitat or seasonal variation (Mueller and Gerhardt 1994; Gotelli and Colwell 2011; Halme and Kotiaho 2012). These facts highlight the importance of repeated sampling over long time to maximize the reporting of the extant fungal diversity.

This study and several others, including studies lasting more than 40 years (e.g. Straatsma et al. 2001; Hawksworth 2012; Ceska 2013), showed that uncovering the entire fungal richness in large or even small areas entirely is not possible. Therefore, the total diversity in these areas has to be predicted by indirect methods (Yoccoz et al. 2001). However, some fungal groups are more difficult to monitor than others, and hence the percentage of fungi to be still expected differs between fungal taxa. In this study, the proportion of recorded richness was lowest for Agaricales and highest for Polyporales. Reasons for this are probably the ephemeral and short-living fruit bodies of Agaricales, and the often

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durable and long-living sporocarps of Polyporales. The results obtained confirm observations from other studies which show that the chance to redetect Polyporales is high, and that the total species number of polypores, containing many Polyporales, is uncovered in few sampling events (Berglund et al. 2005; Yamashita et al. 2015). Due to this fact, Berglund et al. (2005) proposed to monitor only perennial fruit bodies. However, in this survey, only a few species were assigned to Polyporales. Considering only this group, suitable calculation methods have to be established to estimate the total richness of an area. This issue is discussed within the framework of indicator species in Section 4.5 of this thesis.

Several estimation methods were used to assess the total number of fungi, in order to obtain a range of values that hopefully contain the correct richness (Kindt and Coe 2005). Unterseher et al. (2008) concluded that Chao 2 is the most suitable method for mycological incidence data collected through repeated sampling. In this investigation, a value in the middle of the estimated values for all estimations was calculated with the method Chao 2. This estimator proposed that 60% of the fungal species were recorded after three sampling years in the Taunus area, which is similar to the percentage in a study by Egli et al. (1997). These authors revealed an average percentage of 62% after three years of sampling. Angelini et al. (2015) calculated that about 80% of the total richness was uncovered after 2.5 years of inventorying a temperate forest in Italy. This value is similar to the calculation by the Bootstrap method in the Taunus area, which resulted in an 83% of the richness uncovered. However, the Chao 2 estimation seems to be more reasonable, due to the still strongly increasing accumulation curve, than the Bootstrap value. The differences between the study by Angelini et al. (2015) and the Taunus study might be caused by the lower number of species reported in the former.

Because the total fungal richness could not be estimated in the Taunus area, the calculated plant:fungus ratio of 1:4 is not realistic. Chao 2 was the only estimator which calculated a plant:fungus ratio of 1:6, similar to that proposed by Hawksworth (1991) for most situations. The updated factor of 1:8.4, suggested by Hawksworth (2001), was not reached. Nevertheless, this ratio was established for the British Isles, a large area, which includes many different habitats. In contrast, the sampling area in Taunus was very restricted and

generally dry. The sampling area did not contain all possible ecological niches for the Taunus region, because some important host plants and habitats of the surrounding landscape were missing. So, even if the plant:fungus ratio 1:8.4 would be valid for the Central European climate zone, it is not surprising that this ratio was not estimated for the sampling area in Taunus. A larger area and more sampling events would be necessary to reach that value.

### **4.2 Spatial analyses of fungal diversity**

Despite the differences in vegetation and geographic location of the sampling areas, the proportions at division and order level were often similar. This confirms that monitoring results are comparable with a similar sampling design. Other studies already stated that similar sampling effort is necessary to compare data (Dornelas et al. 2012), whereas data obtained by other sampling designs and investigators are more difficult to evaluate. For fungal inventories, most studies concentrate only on macrofungi (e.g. Langer 2000; Krivtsov et al. 2003). A similar sampling design to this thesis in the study of Angelini et al. (2015), comprising monthly samplings of all fungi and including small ones larger than 1 mm in several plots in Italy for 2.5 years, appeared similar, but revealed a lower fungal diversity of 305 species (Angelini et al. 2015).

In the Taunus area, more species were recorded than in the areas of Majagua and Bulau. The mountainous regions of Somiedo and Kleinwalsertal, with higher elevations and more marked altitudinal gradients along the sampled transect, were both sampled once and hosted more species than Taunus during the same months. Comparing the areas in Europe, precipitation was highest in Somiedo and Kleinwalsertal, which is regarded to have a strong effect on fungal richness (Straatsma et al. 2001; Baptista et al. 2010). Gómez-Hernández et al. (2012) revealed highest macrofungal richness on an elevation of 1 000 m.a.s.l., which supports the higher richness detected in the two sampled mountainous regions (around 700 and 1100 m.a.s.l.). In contrast, other studies showed a continued richness decrease with increasing elevation from 100 m.a.s.l. to 2700 m.a.s.l. (Bahram et al. 2012). However, biodiversity depends on many biotic and abiotic factors like geographic location, climate and forest management (Gaston 2000; Purahong et al. 2014). To compare the areas and

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recognize a real trend, more sampling events are necessary in the compared areas.

The number of fungal species after two years of sampling in the Taunus area exceeded the recorded number obtained in the study in Panama (Piepenbring et al. 2012). In general, the identification of tropical fungi is complicated by the limited availability of literature for identification, the presence of many undescribed species, and problems derived of the poor conditions for the conservation of specimens for later determination, mostly due to the high humidity (Piepenbring et al. 2012; Piepenbring et al. 2016). Furthermore, more experts are available for the identification of difficult fungal groups from temperate areas than from the tropics. The previously described problems are probably some reasons for the higher fungal diversity in temperate sampling areas than in the tropics in this study, even though the tropics probably maintain a higher real diversity (Hawksworth 2001).

The differences in the plant:fungus ratio were highest between Taunus and Majagua. Factors contributing to the relatively low value for Majagua are the high number of plant species (more than 300 instead of more than 200 in the Taunus) and less numerous and on average less qualified mycologists. The plant:fungus ratios were rather similar between Taunus and the compared European areas, regardless of the vegetation and geographical distances, which ranged between 50 and 1 400 km. One important reason for this similar ratio is probably the application of the same sampling protocol by the same persons. The use of different plant and fungus species concepts was thereby prevented, which might be a source of variation for the assessment of plant:fungus ratios (Berndt 2012). Furthermore, all investigated areas included various habitats, which ensured a high diversity of host plants and thereby a high diversity of substrates (Rudolf et al. 2013). The results of this study confirm the hypothesis that the plant:fungus ratio is useful for regional estimations of fungal diversity because the European sampling areas were comparable (Taylor et al. 2014). However, the ratio is not stable over time, as observable by the different ratios in different sampling events in Taunus. Single sampling events cannot be compared without considering seasonal factors. Furthermore, the plant:fungus ratio is difficult to apply globally, because the factor changes with other factors like latitude (Hawksworth 2012; Tedersoo et al. 2014). Factors, like



the involved persons and the different sampling year, also probably contributed to the differences between the Panamanian and the European sampling areas in this study.

Beside the plant diversity, which is the basis of the plant:fungus ratio, other factors, for example increasing ectomycorrhizal richness with older host plants, influence the number of fungi (Tóth and Barta 2010). These reasons might be partly responsible for the contradictory results regarding the applicability of the plant:fungus ratio in different studies (Rudolf et al. 2013).

One problem in comparing the investigated areas in this thesis is that no absolute values of species numbers could be used due to the differences in total richness. Therefore, the proportions of taxonomic groups in the different areas were compared to each other. The richest divisions and orders were predominantly the same in all investigated areas. A high number of ascomycetous species shows the importance and necessity to include also smaller ascomycetes and phytoparasites in an exhaustive inventory, which was often not considered in other studies (e.g. Straatsma et al. 2001; Angelini et al. 2015). Only during the mushroom season in autumn, divergent results from the high proportion of Ascomycota were obtained, when the number of Basidiomycota increased strongly and passed the ascomycetous richness. However, the basidiomycetous richness of autumn is generally known (Moore et al. 2008).

The proportions of zygomycetes and Oomycota were underrepresented in all sampling areas, whereas Amoebozoa were overrepresented compared to the total number of known species they include (Kirk et al. 2008). The sampling method and the sampled habitats, as well as their often microscopic size, were probably the reason for the low abundance of these fungal groups. Many species of Oomycota live in aquatic habitats and even though this group is also abundant in terrestrial areas, it still needs humid environments that were not explored in the samplings. The group of zygomycetes is probably rare in this investigation because many species inhabit soil and insects, habitats that were not or sparsely sampled (Webster and Weber 2006). In contrast, slime moulds were recorded more frequently in this investigation probably due to their often

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conspicuous fruit bodies and high abundance of wood, their main substrate, in the surveyed areas (Mueller et al. 2007b).

The order Agaricales was usually in the first place in richness except for the compared samplings in Somiedo and Taunus, which were performed in spring. This is firstly explainable by the season, because, even though some Agaricales like *Schizophyllum commune* can be found throughout the year, many Agaricales fruit during autumn. However, the exceptional low percentage of Agaricales in the first sampling event in Somiedo was probably caused by the weather conditions. The period before the sampling in Somiedo was very dry, a condition commonly reported to impact the presence of macrofungi (Ceska 2013). Therefore, only small ascomycetes, but no larger basidiomycetes, were mostly found. However, the second sampling event in October revealed the typical species distribution of autumn, with more Basidiomycota than Ascomycota, and the Agaricales as the most frequent group.

No difference was recorded between tropical and temperate areas in the percentage of Pucciniales, similar to results from other studies even though higher richness is assumed for the tropics (Piepenbring et al. 2011). The areas of Taunus and Majagua contained both 5% of Pucciniales species. In the other sampling areas, the proportion of Pucciniales ranged between 3% and 11%. One reason for the small abundance of Pucciniales might be the limited diversity of host plants, because even though different habitats and plants were included in all sampling transects, 500 m are not sufficient to include all typical ecosystems of an area. Missing host plants result in lower diversity of Pucciniales, because they are mostly host specific (Berndt 2012). Furthermore, especially for single sample events, the sampling date could have been not suitable for Pucciniales because these small fungi are difficult to be recognized especially with rainy weather and dew, even though species of this order were present all over the year.

The generally assumed higher diversity of Xylariales in the tropics respect to other biogeographic regions (Ikeda et al. 2014) could not be confirmed by the inventories in this study. The percentage of Xylariales in Panama comprised 8% of the species, while it ranged in the other areas from 6% to 16%, and was only lower in Kleinwalsertal. Based on macroscopic fruit bodies, no differences in

species numbers were observed between tropical and temperate areas. However, a higher number of surveys and probably different sampling designs have to be conducted in order to make a general statement about the occurrence of Xylariales.

In the performed samplings, trees were most frequently reported as substrates for fungi. In Taunus, the most abundant substrate was beech. The importance of this tree and broad-leaved trees for wood-inhabiting fungi in general was already noted by Kutzschi et al. (2015). The proportion of broad-leaved trees was higher in most sampling areas investigated in this thesis than the proportion of coniferous trees. The only area, in which a coniferous tree, from the genus *Picea*, was most abundant and most frequently found as substrate, was in Kleinwalsertal. Unterseher et al. (2012) already assumed that the abundance of a tree is probably more important for fungal richness than a specific tree species, which is supported by this investigation.

Continuous learning by repeated sampling increases the knowledge of the scientists and their identification skills. Throughout the entire investigation, the proportion of fungi identified to species level was mostly higher in the Taunus area. The Taunus species data improved strongly during the investigation, for example due to the collection of different development stages. The percentage of identified species in Taunus was only equalled in Kleinwalsertal. In the latter area, the cooperating scientists were experienced in identifying local species because they had been working there for several years, which explains the high percentage of full identifications. For the first sampling event in Somiedo, the sampling was performed with fungal specialists, expert in particular taxa, but only a few persons had experience in the specific sampling area. The situation was similar for the samplings in Bulau, and it explains the lower proportion of identifications there. The second sampling event in Somiedo was done with experts from this area and the percentage of unidentified species was considerably lower than the first sampling.

The number of identified species was much lower in Majagua, with 30% of all specimens, than in other areas studied in this thesis. In another macrofungal study in the tropics, 48% of the fungi were identified up to species level (López-Quintero et al. 2012). The already described difficulties in tropical inventories do

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not only affect the number of recorded species, but also the number of identified species.

Generally, the study in Panama differed from the samplings in temperate areas respect to their species composition, which is not surprising due to the geographical distance across sites. Studies from isolated fungi in soil and in plants revealed no global distribution for most species (Meiser et al. 2014), and this study showed the same result in respect to classic sampling of macroscopically evident fungi.

All seven species recorded in four different areas in this study (Table 33) are known for their wide distribution in Europe. It is surprising that each species recorded in four sampling areas is assigned to a different order, which underlines the importance of extensive taxa inventories. From them, four species were assigned to Ascomycota, for which often more targeted search is necessary (Mueller and Gerhardt 1995b). This is easier with good knowledge of the area and suitable habitats after several sampling events. For all species recorded at least in three areas, mostly Agaricales were documented, the most frequent order in the entire survey, like already discussed.

Six species, which were recorded in four different areas, namely *Bisporella citrina*, *Dialonectria episphaeria*, *Schizophyllum commune*, *Trametes versicolor*, *Xylaria hypoxylon*, and the lichen *Parmelia sulcata*, are distributed throughout Europe (GBIF Secretariat 2013). The presented fungi are categorized into the level Least Concern in the Red List of Hesse (Langer 2000) or the German Red List of lichens (Wirth et al. 2011). The category of Least Concern comprises widely distributed fungi with stable or increasing populations (Ludwig et al. 2006). *Dialonectria episphaeria*, *Schizophyllum commune* and *Trametes versicolor* are also known from Panama (Piepenbring 2006, 2013). These data are summarized in Table 33.

The last species, which was found in four different areas, is *Hyalorbilia inflatula*. Based on the distribution map in the Global Biodiversity Information Facility (GBIF) (GBIF Secretariat 2013), this species was recorded from Germany and Spain and, based on an online Austrian database, in Austria (Austrian Mycological Society 2015). However, the comparable few records in GBIF, with 230 occurrences (most species had a few thousand) of *Hyalorbilia inflatula*, was

probably due to overlooking because of their small fruit bodies with a diameter of about 1 mm (Karsten 1869). This species is not included in the compared Red Lists, which focus mainly on macrofungi (Winterhoff and Krieglsteiner 1984; Langer 2000; Zehfuß et al. 2001; Karasch et al. 2010) or in the checklist from Panama (Piepenbring 2006).

All species recorded in four sampling areas were found on dead wood and had a saprotrophic or lichen-forming lifestyle. This supports the general concept that dead wood contains a high proportion of fungi in an ecosystem (Christensen et al. 2004). The own results show that not only the easy observable fungi but also the small species are widely distributed and can be recognized by trained samplers. Therefore, these species should also be considered in monitoring projects.

Table 33: Species reported for four sampling areas, their known distribution and ecology.

	Included in Red List Hesse <sup>3</sup>	Included in Red List lichens Germany <sup>4</sup>	Included in Checklist Panama <sup>5</sup>	Distribution <sup>6</sup>	Lifestyle	Substrate
<i>Bisporella citrina</i>	yes	-	-	Europe, America	Saprobiont	wood
<i>Dialonectria episphaeria</i>	yes	-	yes	Europe, America with few records	Saprobiont	wood
<i>Hyalorbilia inflatula</i>	-	-	-	Europe	Saprobiont	wood
<i>Parmelia sulcata</i>	-	yes	-	Europe, America	Lichen	wood
<i>Schizophyllum commune</i>	yes	-	yes	Europe, America	Saprobiont	wood
<i>Trametes versicolor</i>	yes	-	yes	Europe, America	Saprobiont	wood
<i>Xylaria hypoxylon</i>	yes	-	-	Europe America	Saprobiont	wood

<sup>3</sup> Based on Langer (2000)

<sup>4</sup> Based on Wirth et al. (2011)

<sup>5</sup> Based on Piepenbring (2006)

<sup>6</sup> Based on GBIF Secretariat (2013)

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### 4.3 Temporal analyses of fungal occurrence

Based on the monthly sampling in Taunus, the change of species richness and composition could be analysed throughout the year and showed a strong fluctuation. This is not surprising because many fungi produce ephemeral fruit bodies and/or develop small and inconspicuous sporocarps, which are difficult to detect (Cannon 1999). Therefore, repeated sampling is recommended for analysing fungal changes in diversity over time (e.g. Newton et al. 2003; Tóth and Barta 2010).

#### 4.3.1 Fungal variations between different years

In the Taunus area, strong differences in species richness as well as in species composition were observed in consecutive years, which resulted in an increasing trend in the discovery of new species and in differences in composition. In general, variations between years are common in long-term investigations of fungi (e.g. Straatsma et al. 2001). Several aspects influence this variation, such as the collectors and specialists performing the survey (Watling 1995; Egli et al. 1997; Guevara and Dirzo 1998; Pinna et al. 2010). The positive trend in species richness from the first to the second year in Panama can be explained by the “learning effect” (Piepenbring et al. 2012). The learning effect is caused by the improved ability of the collectors to find and identify fungi. In a similar way, all investigators in the Taunus experienced increased knowledge and more effective collecting skills during the continued sampling. This effect is also shown by the high number of identified versus unidentified species in Taunus, as compared to the other investigated areas.

Increasing precipitation from the first year to the subsequent years in the Taunus survey might had an additional influence on the number of species detected, which was also shown in other surveys (Straatsma et al. 2001; Baptista et al. 2010). Studies of Straatsma et al. (2001) and Baptista et al. (2010) explained yearly variation by climatic conditions, periodical fruiting patterns of fungi and changes of species composition. In contrast, Hering (1966) could not find any relationship between yearly variation and climatic changes. He assumed that varying reactions of different fungal groups to climatic conditions are responsible for this result. To assess the effect of

precipitation on yearly fungal richness more precisely, longer monitoring activities are necessary in the Taunus area.

At the division level, the proportion of Ascomycota and Basidiomycota changed from the first to the subsequent years, with an initial prevalence of Basidiomycota turning into a higher representation of Ascomycota both in Taunus and in Majagua. Basidiomycetous species are generally easier to observe than Ascomycota, because the latter form small and hidden fruit bodies (Mueller and Gerhardt 1994, 1995b). Better knowledge of the habitats and the higher probability of detecting species after the first record (Halme and Kotiaho 2012) increase the prerequisites of recording also inconspicuous species and thereby more ascomycetes.

### **4.3.2 Seasonal variations in fungal diversity**

Seasonality had a stronger influence on species richness and species composition than other factors. The usual peak of fungal richness during autumn was confirmed in this study. Despite the strong effect of seasonality, concentrating all monitoring activity on the fruiting period from March to November (e.g. in Straatsma et al. 2001; Straatsma and Krisai-Greilhuber 2003) would have led to a richness decrease of more than 20% for the Taunus area. The possibility for fungi to grow during winter under appropriate climate conditions was already recorded in the long-term study of Ceska (2013) in Canada. Therefore, collecting during different periods of the year was already proposed by Watling et al. (2005), and a weekly, or at least a monthly sampling all over the year was strongly recommended by Mueller and Gerhardt (1995b).

Seasonal changes depend on the taxonomic and ecological groups considered. In this study, the temporal changes in fungal richness and species composition over the year were high for Agaricales and for mycorrhizal fungi. Temporal changes of the other most frequent groups, namely the ascomycetous orders Helotiales, Pleosporales, and Xylariales, the basidiomycetous orders Polyporales and Pucciniales, and for the ecological groups of saprobionts and parasites, were less important.

Similar results for the most frequent ecological and taxonomic groups were also found in other studies (Egli et al. 1997; Kolmer et al. 2009; Halme and Kotiaho

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2012). Agaricales often show strong seasonality and short-living fruit bodies. In contrast, mostly low seasonality and many durable fruit bodies (e.g. species in the genus *Fomes*) are documented for Polyporales (Halme and Kotiaho 2012). However, some seasonality of Polyporales in the Taunus area is probably due to more short living species like *Polyporus badius*. Pucciniales are known to be present throughout the year, in winter with the telia on dead leaves and in spring, summer, and autumn, with other spore stages (Kolmer et al. 2009) like also observed in this study.

The reasons for the seasonality in species richness and composition are diverse. In this study, the richness of ascomycetous species seemed to be influenced primarily by temperature and the species composition by temperature and precipitation. In contrast, basidiomycetous richness is probably more affected by humidity and precipitation, whereas the basidiomycetous species composition is likely to be influenced by humidity and temperature. However, these are only tendencies because the precipitation in the sampling area and weather conditions in general might be slightly different in specific microhabitats. Furthermore, the influence of climatic conditions on fungal fruit bodies changes over the year. Mueller and Gerhardt (1995a) showed that for macrofungal sporocarp production, mainly based on basidiomycetes, precipitation in summer, followed by high humidity in autumn and temperatures above 0°C in winter, are important. These factors are not generally valid because heavy rain might also have negative effects on fungal diversity under specific conditions, like for soil fungi in deforested areas (Saikia 2012). However, detailed investigations on effects of climatic conditions on specific taxonomic groups, especially in Ascomycota, are still lacking.

At the order level, only the richness of Helotiales and Agaricales, the two most species rich orders in this study, changed significantly due to the investigated climatic conditions. In contrast, the species composition of all tested taxonomic groups was affected by these variables, except Xylariales. This difference between effects on richness and species composition shows that even if no seasonal variation in richness is detectable, the species community changes strongly. The dependence of Agaricales richness on humidity was already shown in other studies (e.g. Piepenbring et al. 2015).



The richness of mycorrhizal fungi and the species composition of the most frequent ecological groups (saprobionts, parasites, and mycorrhizal fungi) seemed to be influenced by climatic conditions in this study. Similar results with differences between trophic groups was already shown by Sato et al. (2012).

Based on Sato et al. (2012), seasonal fruiting can be predicted easiest for ectomycorrhizal fungi, the only group in this study that showed significant changes in richness over the year. It was proposed in other studies that the fruiting of ectomycorrhizal fungi is probably adjusted to the activity and the end of the biomass production of their host plant. Based on this, climatic conditions, such as temperature and precipitation, would have more influence on the host plant than on ectomycorrhizal fungi (Egli et al. 1997; Baptista et al. 2010; Sato et al. 2012).

The occurrence of plant parasitic fungi throughout the year, like many Pucciniales in this study, was already shown by Rottstock et al. (2014). The importance of temperature and humidity for the plant infection of phytoparasites is strongly investigated in order to use the data for disease forecast models (Magarey et al. 2005). However, this is not possible for all phytoparasites. Piepenbring et al. (2015) showed that some plant-parasitic fungi are more dependent on the presence of host-plant tissues than weather conditions. Probably, weather changes influence phytoparasites differently depending on the fungal species. This fact might explain contradictory reactions of different plant parasites on climatic conditions, resulting in a lack of a general fluctuation in their richness when considering the entire parasite dataset.

In other studies, lowest seasonality was observed for wood-inhabiting fungi (Sato et al. 2012), similar to the Taunus results. Such fungi depend on their substrate dead wood, which was available in the Taunus all over the year.

The results of the seasonal changes show that timing for inventories is important for particular fungal groups (Halme and Kotiaho 2012). Studies, such as the one performed in this thesis, can be used to estimate the optimal time for sampling events in future surveys, as has been proposed by Halme and Kotiaho (2012). For most groups of fungi, the months of October and November revealed the highest diversity. Nevertheless, this study also shows the high

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diversity that would be missed by concentrating sampling activities on a short period.

#### 4.4 Strategies for fungal inventory projects

Fungal diversity is embedded in dynamic processes of complex interactions with many different elements of the ecosystem, which are not fully understood up to now. Monitoring and analyses on spatial and temporal scale are important for fungal assessments to understand ecological interrelations and consequences of changing factors (Zak and Willig 2004; Danielsen et al. 2005; Magnuson 2014). Therefore, taxonomic and ecological data like host ranges have to be considered in monitoring projects (Gange et al. 2011). Different sampling strategies allow to record diverse fungal groups, because the probability of detection differs between methods (Yoccoz et al. 2001).

Differences in above- (data mostly based on fruit-body inventories) and below-ground diversity (data mostly based on molecular analyses of soil or substrate) show that both methods are not able to detect every fungal species (e.g. Horton and Bruns 2001; Hattori et al. 2012; Baptista et al. 2015). A molecular study of ectomycorrhizal fungi in the Taunus region, but not in the same sampling area studied in this thesis, revealed only few species overlapping with the species recorded in this inventory (Schirkonyer 2013). Nevertheless, the most abundant species from the molecular study, namely *Paxillus involutus* and *Russula ochroleuca*, and some frequent and occasionally documented ectomycorrhizal species, namely *Boletus edulis*, *Lactarius subdulcis*, *Scleroderma citrinum*, *Lactarius necator* and *Lactarius quietus* were recorded in both studies, in this study and the one by Schirkonyer (2013). Some examples of species recorded in both studies are shown in Figure 46.



Figure 46: Species, which were recorded in a molecular study by Schirkonyer (2013), and in this study based on fruit bodies in the Taunus: *Boletus edulis* (a), *Lactarius quietus* (b), *Lactarius subdulcis* (c), *Paxillus involutus* (d), *Russula ochroleuca* (e), and *Scleroderma citrinum* (f). All photos were taken by N. Kühnberger.

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The presented sampling design based on macroscopically evident fungi has advantages, like the workability of large areas and the obtainability of morphological data. However, it also has disadvantages, such as only fruiting species are recordable and cryptic species cannot be discovered (Cannon 1999; Schmit and Lodge 2005; Jones and Richards 2011). The fungal monitoring in this investigation was based on incidence data, which is assumed to provide faster and more objective measurements than calculating abundances of fungal species by counting or weighing sporocarps (Debinski and Brussard 1994; Schmit et al. 1999). Furthermore, the concept of individuals among fungi is problematic because not each fruit bodies corresponds to one individual (Yamashita et al. 2015). Based on the experience in this sampling, assessing abundance data would provide strong difficulties in an extensive taxa inventory, for example, for plant parasites, and is not necessary.

In this study, a strip transect with time-constrained sampling was chosen to include a high variety of habitats, as described in Castellano et al. (1999). Previously assumed to be species-rich and assumed to be species-poor habitats were intensely sampled, which often yielded a surprising diversity in both cases. Cantrell (2004) found that transects were more suitable for Discomycetes than plots, but differently to the strategy adopted in this thesis, small plots along the transect were defined. For comparing different areas, it is especially important to establish one sampling protocol. Furthermore, the continuity of involved persons is helpful for the comparability of surveys, as has been already shown by Egli et al. (1997). This approach yielded high species richness and similar taxonomic patterns in all investigated areas. Furthermore, a continuous analysis at a temporal scale in the Taunus area showed the success of the used sampling design.

In macrofungal inventories, the skills of samplers and the number of detection errors due to observer effects play an important role for recording fungi (Cannon 1999; Yoccoz et al. 2001; Halme and Kotiaho 2012). The high number of species with many inconspicuous ascomycetes in this survey shows that an experienced team is able to record a high fungal diversity (Halme and Kotiaho 2012). The sampling of fruit bodies has no adverse effects on fungal diversity (Egli et al. 2006), and can be therefore performed for long time periods without changing the ecosystem (Bonar et al. 2011). Additionally, this approach is



useful to record morphological and ecological data, and to collect herbarium specimens for further studies.

Single sampling events can reveal a high diversity, but these events are strongly influenced by environmental conditions and the knowledge of identifiers. Therefore, single sampling events cannot be used for the estimation of total richness in an area. Changing weather conditions might yield totally different numbers of species richness in the same area during years or months (Egli et al. 1997). These differences in richness and taxonomic groups for the sampling events were visible in the entire survey, but most clearly in the two Somiedo samplings.

Regular sampling of a single area over a longer period, like in the Taunus, results in higher richness than sampling of several areas in one year (Cannon 1999; Schmit et al. 1999; Halme and Kotiaho 2012). Furthermore, repeated sampling provides ample information on the ecology of the recorded groups (O'Dell et al. 2000; Ceska 2013; Peay 2014). However, such samplings are expensive and time consuming (Rossman et al. 1998), because, in this survey, they required several people working for at least two weeks after each sampling event to complete the identification, drying, documentation and preparation of specimens for herbaria. Even after one year of regular sampling in the Taunus, not even 50% of the total diversity obtained after three years had been recorded. This underlines the importance of long-term studies, despite the high time requirement. Furthermore, the Taunus data show that, if the accumulation curve did not even reach the saturation in temperate zone, it should be even more difficult to document total diversity in the proposed species-richer tropics, in which a smaller proportion of fungi can be found in short-time samplings (Hawksworth 2012).

The performed surveys revealed a broad taxonomic range of fungi. Nevertheless, an inclusion of soil fungi and endophytes would yield an even higher number of species. An additional survey on soil fungi in the Taunus sampling transect, performed by M. Rosas, displayed 26 genera of identified cultured fungi from soil. Of these, only the four genera *Cladosporium*, *Clonostachys*, *Hypocrea*, and *Trichoderma* were also found in the inventory performed in this thesis. At the species level, not a single match between both

studies was found (the list of cultured soil fungi has been kindly provided by M. Rosas).

A different approach to that adopted in this thesis was proposed, consisting on assessing the diversity of fungi at higher taxonomic levels. Based on a macrofungal study, identification at the genus level would be sufficient to identify areas worthy of protection (Balmford et al. 2000). This study supports these results by comparing different areas regarding their species and genus richness, because the ratio was nearly the same on both taxonomic levels. Therefore, for determining the most diverse area, identification up to genus level would be sufficient. Nevertheless, a high amount of information would be lost, like species richness and associated ecological species data. Guevara and Dirzo (1998) worked in their study with morphospecies only. This thesis gives an example of various analyses and comparisons based on different taxonomic levels, which would not be possible by using morphospecies.

In addition to the scientific value of this work, the investigation was used for teaching purposes on fungal and plant diversity for several students. Furthermore, interested persons and amateurs with high knowledge on fungal species contributed to the identifications of fungi. Fungal fruit bodies attract attention and are therefore monitored by many amateur mycologists or mushroom pickers (Straatsma et al. 2001). This information is an important possibility to improve scientific data (Cohn 2008).

#### **4.5 Aspects of conservation**

Preserving biodiversity is an important goal for direct human use of species diversity as food source, for product manufacture (e.g. drugs), for biocontrol, and for other purposes. Besides, one missing organism can have strong effects on many other organisms. Diversity is essential for a balanced, sustainable, and productive ecosystem. Understanding these relationships is especially important to predict the current threats of a changing climate (Zehfuß et al. 2001; Gaston and Spicer 2004; Hui 2013).

The high species number and the huge lack of knowledge in fungal richness and ecosystem functions complicates fungal conservation (Molina et al. 2011). Fungi are considered the group of organisms with the lowest investment of

research and funds (IUCN 2012). However, the question of how to conserve biodiversity is widely discussed and different approaches are known (Molina et al. 2011).

Biodiversity is strongly threatened by habitat loss (Nordén et al. 2013) and fragmentation, which affect more profoundly rare than generalist species (Nordén et al. 2013). Therefore, one possibility is to focus on protecting species-rich habitats with many niches (system approach) that are essential for the ecosystem and associated organisms (Christensen et al. 2005; Molina et al. 2011). Some highly specialised wood-inhabiting fungi fruit only sparsely and are therefore difficult to monitor (Ovaskainen et al. 2013). Protecting their specific host plant or dead wood habitats is essential even without fruit bodies of these fungi because these species would probably disappear if their substrate is no longer available (Karasch et al. 2010). Another example is an experiment on plant communities that are dependent on arbuscular mycorrhizae, which means that for a sustainable conservation, the entire habitat has to be protected (Sanders et al. 1998).

The classification of forest conservation status is based on many factors like tree size, coarse woody debris (dead wood) and fungi (Keddy and Drummond 1996). Assessments of biodiversity, like in this study, are important to prioritize possible areas and habitats for conservation, which should represent a high amount of the total regional diversity (Margules et al. 2002). Several investigated areas belong to the European conservation zones Natura 2000 (European Union 2012) and for such areas, an action plan was established to prevent deterioration of the habitats. This study shows that habitat diversity, including forest, meadow, and dead wood are important for fungal richness because each niche was inhabited by different fungi. For maintaining this habitat diversity, sustainable landscape management has to be performed.

In this study, all species recorded in four areas, and the most frequent fungi in the Taunus area, were associated with wood. Studies in different countries show that about 25% of fungi on dead wood are supposed to be threatened (Lonsdale et al. 2008), which demonstrates the importance of protecting niches available by dead wood. The number of wood-inhabiting fungi can be increased with the availability of wood from different plant species, and of different sizes

and ages (Christensen et al. 2005; Lonsdale et al. 2008). In Taunus and all other sampling areas, old and thick wood was mostly missing, and, consequently, also an important niche for fungi.

Beside the previously described system approach, another possibility to define areas of conservation is to protect certain rare species and their associated habitats, the so-called species approach (Newton et al. 2003; Molina et al. 2011). Langer et al. (2015) proposed to evaluate the actual forest stage based on fungal species of natural value, which are species important for the ecosystem, as well as on IUCN lists, which include rare species. Nearly all mentioned species in the context of conservation and in Red Lists are members of the division Basidiomycota. Indicator species, which are often wood-inhabiting fungi, can be used to assign conservation priorities to investigated forests, by determining forest quality due to their habitat requirements (Christensen et al. 2004).

Several species recorded in the main sampling area are categorized in the Hessian Red List, or are important as indicator species for near-natural habitats. The originally used categories in the German classification system for Red Lists were translated into the IUCN system as proposed by Ludwig et al. (2006) (Table 34). The protection status of fungi in the Hessian Red List was compared to the Red List classifications of the federal states next to southern Hesse (Table 35). However, for many species, no data of conservation status are available.

Table 34: Used categories for conservation status of the recorded species in the German classification system and the international IUCN system. The term in brackets is not used anymore in the IUCN system but corresponds to the German category R. The table was modified based on Ludwig et al. (2006).

Germany	IUCN	
0	RE	Regionally extinct
1	CR	Critically Endangered
2	EN	Endangered
3	VU	Vulnerable
R=4	[R]	[Rare]
D	DD	Data Deficient
x	LC	Least concern



## Aspects of conservation

Table 35: Recorded species in the Taunus area that are included in the Hessian Red List, their Red List category in the neighbour provinces and their usability as indicator species.

	Records	Red List Hes <sup>7</sup>	Red List Bav <sup>8</sup>	Red List B-W <sup>9</sup>	Red List R-P <sup>10</sup>	Indicator <sup>11</sup>	Indicator <sup>12</sup>	Lifestyle
<i>Aleurodiscus disciformis</i>	2	2	-	-	R	-	yes	Saprobiont, bark
<i>Auricularia mesenterica</i>	9	3	-	-	-	-	-	Saprobiont, wood
<i>Boletus edulis</i>	6	3	-	-	-	-	-	Mycorrhiza
<i>Ceriporiopsis gilvescens</i>	1	D	-	-	-	yes	-	Saprobiont, bark
<i>Chlorociboria aeruginascens</i>	1	2	R	-	3	-	-	Saprobiont, wood
<i>Clitocybe odora</i>	1	3	-	-	-	-	-	Saprobiont, soil
<i>Coprinus silvaticus</i>	1	R	V	-	-	-	-	Saprobiont, meadow
<i>Daldinia concentrica</i>	1	R	-	-	-	-	-	Saprobiont, wood
<i>Hericium coralloides</i>	12	2	3	3	1	yes	yes	Saprobiont, wood
<i>Hygrocybe coccinea</i>	1	2	-	3	3	-	-	Saprobiont, meadow
<i>Hygrocybe miniata</i>	1	3	3	-	-	-	-	Saprobiont, meadow
<i>Hygrocybe psittacina</i>	1	2	-	-	3	-	-	Saprobiont, meadow
<i>Hymenochaete rubiginosa</i>	4	3	-	-	-	-	-	Saprobiont, wood
<i>Leccinum duriusculum</i>	2	3	2	2	1	-	-	Mycorrhiza
<i>Lentinellus ursinus</i>	1	R	3	2	R	yes	yes	Saprobiont
<i>Macrolepiota mastoidea</i>	5	3	-	-	-	-	-	Saprobiont
<i>Macrolepiota procera</i>	6	3	-	-	-	-	-	Saprobiont
<i>Mycena flavescens</i>	1	3	-	-	-	-	-	Saprobiont
<i>Mycena flavoalba</i>	1	3	-	-	-	-	-	Saprobiont
<i>Panaeolus papilionaceus</i>	1	2	-	-	-	-	-	Saprobiont

<sup>7</sup> Red List of fungi in Hesse based on Langer (2000)

<sup>8</sup> Red List of fungi in Bavaria based on Karasch et al. (2010)

<sup>9</sup> Red List of fungi in Baden-Wuerttemberg based on Winterhoff and Krieglsteiner (1984)

<sup>10</sup> Red List of fungi in Rhineland-Palatinate based on Zehfuß et al. (2001)

<sup>11</sup> Indicator species based on Christensen et al. (2004)

<sup>12</sup> Indicator species based on Blaschke et al. (2009)

	Rec ords	Red List Hes <sup>7</sup>	Red List Bav <sup>8</sup>	Red List B-W <sup>9</sup>	Red List R-P <sup>10</sup>	Indica tor <sup>11</sup>	Indica tor <sup>12</sup>	Lifestyle
<i>Pluteus salicinus</i>	1	3	-	-	-	-	-	Saprobiont, wood
<i>Resupinatus trichotis</i>	1	3	-	-	-	-	-	Saprobiont
<i>Russula graveolens</i>	1	2	-	-	-	-	-	Mycorrhiza
<i>Russula ionochlora</i>	1	3	3	-	-	-	-	Mycorrhiza
<i>Russula queletii</i>	1	3	-	-	-	-	-	Mycorrhiza
<i>Russula rosea</i>	1	3	-	-	-	-	-	Mycorrhiza
<i>Russula virescens</i>	1	3	3	-	-	-	-	Mycorrhiza
<i>Scytinostroma portentosum</i>	2	3	-	-	3	-	-	Saprobiont, wood
<i>Stereum insignitum</i>	4	0	-	4	1	-	-	Saprobiont, wood
<i>Vuilleminia cystidiata</i>	2	3	-	-	-	-	-	Saprobiont, wood

### ***Hericium coralloides***

Regarding the conservational aspect, one of the most important species in the Taunus is *Hericium coralloides* (Basidiomycota, Russulales), because it is the only species classified at least in the category Vulnerable in all compared Red Lists (Winterhoff and Krieglsteiner 1984; Langer 2000; Zehfuß et al. 2001; Karasch et al. 2010). Furthermore, it is considered to show closeness to natural habitats as indicator species for nature value (Christensen et al. 2004; Blaschke et al. 2009). In Rhineland-Palatinate, *Hericium coralloides* is considered as Critically Endangered (Zehfuß et al. 2001), whereas it is categorized as Endangered in Hesse (Langer 2000) and Vulnerable in Bavaria (Karasch et al. 2010) and Baden-Wuerttemberg (Winterhoff and Krieglsteiner 1984). Fruit bodies of probably the same organism on one trunk were found in 12 sampling events in autumn and winter of 2011, 2012 and 2013. This species is distributed in Europe and America, including Central America (GBIF Secretariat 2013), but it is not listed in the Panamanian checklist (Piepenbring 2006, 2013).

### ***Lentinellus ursinus***

Another species mentioned in all investigated lists is *Lentinellus ursinus* (Basidiomycota, Russulales). In Hesse and in Rhineland-Palatinate, this

species is only assigned to the category Rare (Langer 2000; Zehfuß et al. 2001). In contrast, this species is assigned to Vulnerable and Endangered in Bavaria and Baden-Wuerttemberg, respectively (Winterhoff and Krieglsteiner 1984; Karasch et al. 2010). Based on Blaschke et al. (2009) and Christensen et al. (2004), *Lentinellus ursinus* is an indicator species for dead-wood and forest quality. In this study, the only record was obtained in the end of October 2013. Based on GBIF, this species is distributed in Europe and America, including Central America (GBIF Secretariat 2013), but not in Panama (Piepenbring 2006).

### ***Aleurodiscus disciformis***

Based on Blaschke et al. (2009), *Aleurodiscus disciformis* (Basidiomycota, Russulales) is another indicator species. It is assigned to the category Endangered in Hesse, and nearly threatened in Rhineland-Palatinate (Langer 2000; Zehfuß et al. 2001). However, this species is not mentioned in the Red Lists of Bavaria and Baden-Wuerttemberg (Winterhoff and Krieglsteiner 1984; Karasch et al. 2010). This species was recorded twice in Taunus in June and July 2011. The distribution of this species is restricted almost exclusively to Europe (GBIF Secretariat 2013).

### ***Ceriporiopsis gilvescens***

A further indicator species recorded in Taunus, based on Christensen et al. (2004), is *Ceriporiopsis gilvescens* (Basidiomycota, Polyporales). In contrast to the previously described species, *Ceriporiopsis gilvescens* is not assigned to any conservation status in the compared Red Lists. Only in the Red List from Hesse, this species is mentioned as Data Deficient (Winterhoff and Krieglsteiner 1984; Langer 2000; Zehfuß et al. 2001; Karasch et al. 2010). *Ceriporiopsis gilvescens* was only found once in October 2011 in Taunus. This species is mainly distributed in Europe (GBIF Secretariat 2013), but other species of the genus *Ceriporiopsis* are known from Panama (Piepenbring 2006).

### ***Stereum insignitum***

The species with the highest conservation assignment in the Taunus is *Stereum insignitum* (Basidiomycota, Russulales), which is assigned to the category 0 in the Hessian Red List, indicating Regionally Extinct (Langer 2000). However, this classification is probably wrong, because *Stereum insignitum* was recorded in

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Hesse by H. Große-Brauckmann based on GBIF (GBIF Secretariat 2013). In the species list of Rhineland-Palatinate, it is assigned to Endangered (Zehfuß et al. 2001) and in Baden-Wuerttemberg to Rare (Winterhoff and Krieglsteiner 1984). This species is not included in the Red List of Bavaria (Karasch et al. 2010). *Stereum insignitum* was found four times in Taunus, three records at the beginning of the year 2013, and one record at the end of 2013. It is mainly distributed in Europe. However, under the name of *Stereum ostrea*, which is deemed to be the same as *Stereum insignitum* in America published by Mycobank (International Mycological Association 2016), it is widely distributed in America (GBIF Secretariat 2013) and also known from Panama (Piepenbring 2013).

The few examples described in the previous paragraphs (Figure 47) show the large differences in the conservation status classification in different German provinces. A high number of species is assigned to a conservation category in Hesse (Langer 2000), but most are not even mentioned in the Red Lists of the provinces next to the sampling area like Bavaria (Karasch et al. 2010), Baden-Wuerttemberg (Winterhoff and Krieglsteiner 1984) and Rhineland-Palatinate (Zehfuß et al. 2001). This is not surprising, comparing the publication dates of the different Red Lists with more than 20 years of difference between them (Winterhoff and Krieglsteiner 1984; Karasch et al. 2010), and involving different persons and different approaches. The German Red List is older than most regional Red Lists (Benkert et al. 1996) and therefore less suitable to categorize the species than the regional lists. A new Red List for Germany with actual data is urgently needed for evaluating the conservation status of fungi and will be published soon (pers. comm. H. Lotz-Winter). Most of the previously described species important for conservation belong to the order Russulales, and were mostly recorded only a few times in the Taunus area. However, Russulales were generally not very frequent in the Taunus area.

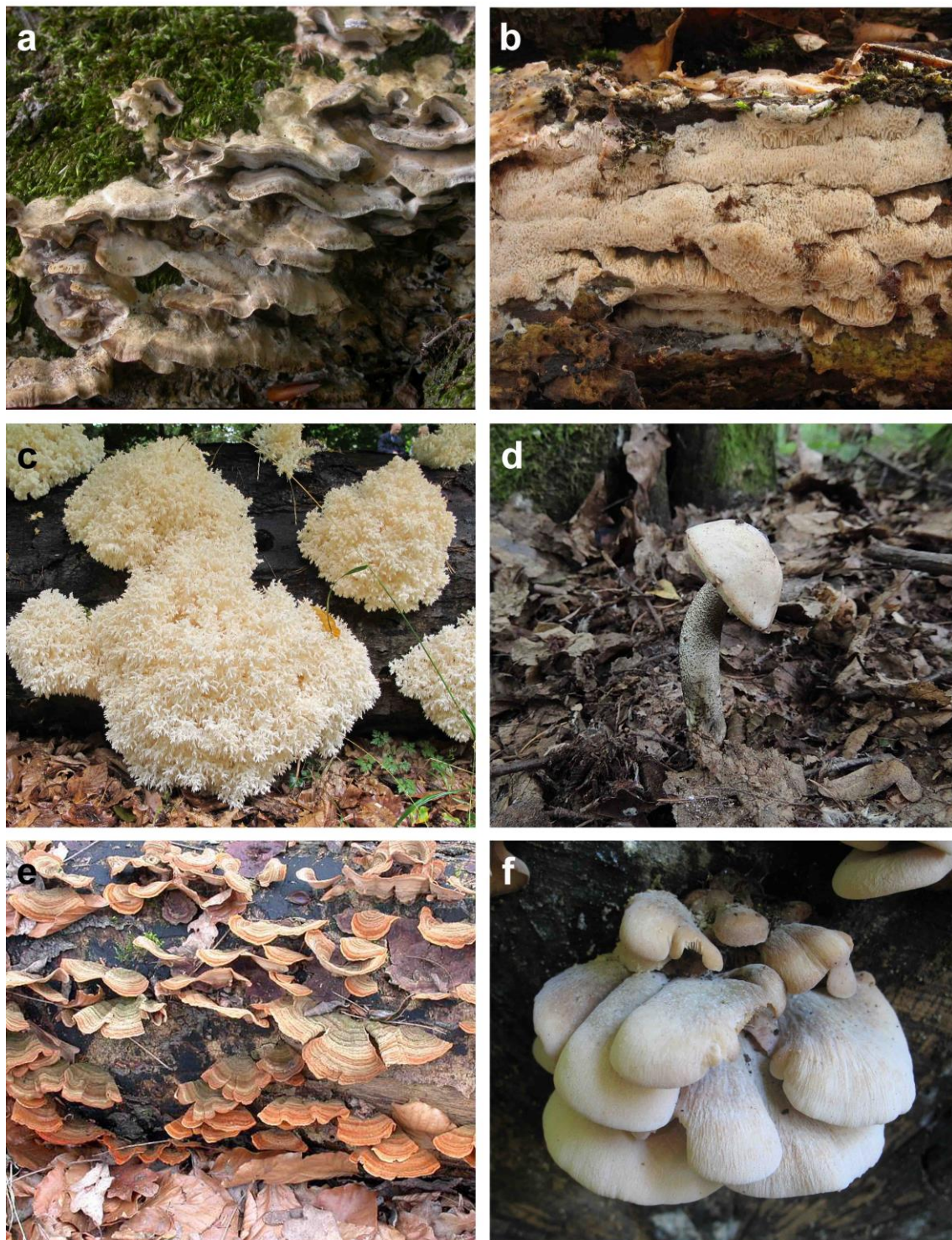


Figure 47: Species, which were assigned to a conservation status in the Red List of Hesse (Langer 2000) or are published as indicator species: *Aleurodiscus disciformis* (a), *Ceriporiopsis gilvescens* (b), *Hericium coralloides* (c), *Leccinum duriusculum* (d), *Stereum insignitum* (e), and *Lentinellus ursinus* (f). The photos were taken by R. Kirschner (a), by W. Pohl (b), by H. Lotz-Winter (c, f), and by N. Kühnberger (d-e).



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In addition to the indicator species, Blaschke et al. (2009) proposed another category of fungi, which show forest quality due to their (high) abundance. Four of these species were found in Taunus, namely *Fomes fomentarius* (33 records), *Botryobasidium aureum* (9 records), *Polyporus badius* (5 records) and *Ceriporiopsis gilvescens* (1 record). The latter species was already discussed as indicator species by Christensen et al. (2004). However, indicator species based on abundance cannot be used in this study because no abundance data were recorded.

Estimations of total diversity based on single species have to be considered carefully. An advantage of using indicator species is the easier monitoring of single species than all species in an ecosystem. Nevertheless, it has to be considered that the richness of one single group or indicator species does not necessarily reflect total diversity in any case (Flather et al. 1997; Berglund and Jonsson 2001).

Data are missing on the importance of Ascomycota as indicator species and their risk of extinction. A study of this division revealed data deficiency for 95% of all evaluated ascomycetous species and an estimated lack of data for 99% of all described and undescribed fungi (Minter 2011). Minter (2011) published an attempt of monitoring fungal groups with randomly selected species. In the Taunus area, four of the recorded species are listed on the website described in Minter (2011). These species are *Hypoxyton fragiforme*, *Melogramma campylosporium*, *Dematioscypha dematiicola*, and *Claviceps purpurea*, which are all widely distributed and have no status of protection.

Due to their non-seasonal fruit bodies that are recordable throughout the year, polypores and lichens are proposed for monitoring processes in the aspect of conservation (Berglund et al. 2005; Wirth et al. 2011). As it has been already discussed, a few other groups can be recorded regularly over the year, such as Pucciniales, but good taxonomic knowledge of the investigators including plants is necessary to identify these species.

Besides the system and species approaches, also fungal richness was investigated for conservation processes. However, the species number itself does not seem to be suitable for the identification of conservations zones, because it is strongly linked to the sampling effort and sampling time (Newton et

al. 2003). Based on absolute values, Taunus would be the most species rich area in this study. However, comparing single sampling events, Kleinwalsertal and Somiedo are probably richer in fungal species if the sampling would have been performed with the same effort as in Taunus.

Another important aspect of conservation is to show the importance of fungi and their habitat to public and politicians, so that fungi will be included into the conservation measurements of plants and animals (Dahlberg et al. 2010). The high number of approximately 1 000 fungal species recorded for the Taunus area, which included results from this work and soil fungi investigated by M. Rosas, was published as Biozahl 2014 and drew the attention of the public to the fungal kingdom (Jung 2014). Biozahl is published yearly and points out interesting facts of biological diversity for the information of the public (BioFrankfurt 2016).

A further current topic is the impact of climate change on fungi. This study is too short to make predictions about effects of climate change. Long-term inventories are necessary for global change studies (Suz et al. 2015). A fungal database with long-term phenological data would be especially useful. Such a database is already available for plants but not yet for fungi (Dierenbach et al. 2013). Nevertheless, some studies, including this investigation, already showed that the effect of environmental variables on fungal fruiting is highly complex and differs between species, ecological groups and geographic location, which complicates the forecast of changes in fungal diversity on climate change (Boddy et al. 2014).

In general, climate change seems to prolong the fruit period, so it starts earlier and lasts longer and some species even fruit twice. Furthermore, some species like *Auricularia auricula-judae* show an expansion of host range (Gange et al. 2011). More research has to be done on this topic and establishing long-term sampling designs, including ecological and morphological information, is recommended to investigate the effect of climate change on fungi. For a sustainable protection of fungi, the cooperation of amateur and professional scientists with politicians is essential (Dahlberg et al. 2010).

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## 5 Conclusions

A high fungal richness can be documented with the sampling of all macroscopically evident fungi including small ascomycetes and plant parasites. However, three years of sampling in fungal inventories are neither sufficient to reveal the total fungal diversity, nor sufficient to estimate the total fungal diversity of this area exactly.

Species richness and composition differ strongly between different areas. However, the proportions on higher taxonomic levels are rather similar, which highlights the importance of inventories with the same sampling protocol. Altitude and precipitation seem to have a positive influence on fungal diversity. However, single sampling events are not sufficient to estimate total richness, therefore only tendencies can be shown from this thesis and further long-term inventories in all areas would be necessary to verify these trends.

Repeated sampling during the whole year is necessary. This is because time strongly affects fungal species number and species composition at different taxonomic and ecological levels. Inventories are necessary to understand temporal changes of fungal diversity during the year, and to analyse possible drivers of these changes.

Species richness and species composition are affected differently by weather conditions. Based on the results of this thesis, Ascomycota are more influenced by temperature and Basidiomycota more by humidity.

This work highlights the importance of comprehensive-taxa inventories because they are essential for uncovering and comparing fungal diversity within and between areas.



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## 7 Appendices

### 7.1 Sampling data

Table S 1: Sampling data of the monitoring project in the Taunus area.

Sample	Sample year	Month	Year	Date	Samplers	Temp	Weather conditions
S01	1	May	2011	06.05.2011	3	18	sunny, dry
S02	1	Jun	2011	02.06.2011	4	18	sunny, dry
S03	1	Jul	2011	02.07.2011	5	16	sunny, dry
S04	1	Aug	2011	03.08.2011	4	21	sunny, dry
S05	1	Sep	2011	01.09.2011	4	18	sunny, dry
S06	1	Oct	2011	03.10.2011	4	22	sunny, dry
S07	1	Nov	2011	07.11.2011	4	10	sunny, rainy
S08	1	Dec	2011	03.12.2011	3	5	rainy
S09	1	Jan	2012	28.12.2011	4	4	rainy
S10	1	Feb	2012	30.01.2012	3	-1	cloudy, dry
S11	1	Mar	2012	27.02.2012	5	6	cloudy, sunny, dry
S12	1	Apr	2012	26.03.2012	3	19	sunny, dry
S13	2	May	2012	02.05.2012	5	20	sunny, rainy
S14	2	Jun	2012	04.06.2012	5	15	sunny, rainy
S15	2	Jul	2012	28.06.2012	3	22	sunny, dry
S16	2	Aug	2012	01.08.2012	4	22	sunny, dry
S17	2	Sep	2012	29.08.2012	5	21	sunny, dry
S18	2	Oct	2012	08.10.2012	5	10	sunny, rainy
S19	2	Nov	2012	01.11.2012	4	6	cloudy, sunny, dry
S20	2	Dec	2012	01.12.2012	3	-1	sunny, dry
S21	2	Jan	2013	07.01.2013	3	7	cloudy, rainy
S22	2	Feb	2013	31.01.2013	4	5	cloudy, rainy
S23	2	Mar	2013	27.02.2013	3	0	cloudy, snow
S24	2	Apr	2013	27.03.2013	3	1	sunny, dry
S25	3	May	2013	02.05.2013	4	15	sunny, dry
S26	3	Jun	2013	27.05.2013	3	11	rainy
S27	3	Jul	2013	02.07.2013	4	20	cloudy, dry
S28	3	Aug	2013	06.08.2013	3	25	sunny, dry
S29	3	Sep	2013	27.08.2013	3	17	cloudy, dry
S30	3	Oct	2013	19.09.2013	3	12	cloudy, dry
S31	3	Nov	2013	29.10.2013	2	11	sunny, cloudy, dry
S32	3	Dec	2013	28.11.2013	3	1	foggy
S33	3	Jan	2014	18.12.2013	3	5	sunny, cloudy, dry
S34	3	Feb	2014	24.01.2014	3	2	cloudy, snow
S35	3	Mar	2014	27.02.2014	3	7	cloudy, dry
S36	3	Apr	2014	31.03.2014	3		cloudy, dry

## Appendices

Table S 2: The persons who collected mainly in the Taunus area. Their participation in particular sampling events is indicated by “x” in the table.

Collectors	S 01	S 02	S 03	S 04	S 05	S 06	S 07	S 08	S 09	S 10	S 11	S 12	S 13	S 14	S 15	S 16	S 17	S 18	S 19	S 20	S 21	S 22	S 23	S 24	S 25	S 26	S 27	S 28	S 29	S 30	S 31	S 32	S 33	S 34	S 35	S 36	
Gießel, A.					x				x	x	x	x	x	x			x	x	x		x	x	x		x	x		x									
Lotz-Winter, H.	x		x	x		x	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	
Mangelsdorff, R.			x	x	x			x		x		x			x	x		x								x	x	x					x		x		
Piepenbring, M.		x	x		x	x		x	x	x			x	x				x		x	x		x		x	x		x		x	x	x		x		x	x
Rudolph, S.	x	x	x	x	x	x	x				x		x	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x	x	x	x	x	x	
Völxen, N.	x	x	x	x	x	x	x	x	x		x		x	x	x	x	x	x																			

Further specialists contributed by sampling and identification: Cezanne, R.; Eichler, M.; Kirschner, R.; Popa, F.; Printzen, C.; Rexer, K. H. Additionally, students participated in several sampling events

Table S 3: The persons who collected mainly in the Bulau area. Their participation in particular sampling events is indicated by “x” in the table. Additionally, students participated in several sampling events.

	S01	S02	S03	S04
H. Lotz-Winter	x	x	x	x
M. Piepenbring	x	x		
S. Rudolph	x	x	x	x
J. Werdecker		x	x	x

Table S 4: The persons who collected mainly in the Somiedo area. Their participation in particular sampling events is indicated by “x” in the table.

	L. Calvo	J. Fournier	M. Fournier	C. Léchat	J. Linde	H. Lotz-Winter	M. Piepenbring	E. Rubio Dominguez	S. Rudolph
S01		x	x	x		x	x		x
S02	x				x	x	x	x	x

Table S 5: All persons who collected during the sampling event in the Kleinwalsertal area. Additionally, students participated in the sampling event

	J. Ballauff	H. Lotz-Winter	M. Mardones	M. Piepenbring	F. Popa	K.-H. Rexer	S. Rudolph
S01	x	x	x	x	x	x	x

## 7.2 Fungal diversity

Table S 6: Estimation methods used in this investigation with their formula based on the EstimateS manual (Colwell 2013).

Method	Formula
Chao 2 (classic)	$S_{Chao\ 2} = S_{obs} + \left(\frac{m-1}{m}\right) \frac{Q_1^2}{2Q_2}$
Incidence coefficient of variation (ICE)	$\gamma_{ICE}^2 = \max\left[\frac{S_{infr}}{C_{ICE}} \frac{m_{infr}}{(m_{infr}-1)} \frac{\sum_{j=1}^{10} j(j-1)Q_j}{(N_{infr})^2}\right]$
First-order Jackknife (Jack 1)	$S_{Jack1} = S_{obs} + Q_1 \left(\frac{m-1}{m}\right)$
Second-order Jackknife (Jack 2)	$S_{Jack2} = S_{obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right]$
Bootstrap	$S_{Boot} = S_{obs} + \sum_{K=1}^{S_{obs}} (1-p_k)^m$

$C_{ICE}$  = Sample incidence coverage estimator

$m$  = Total number of samples

$m_{infr}$  = Number of samples that have at least one infrequent species

$N_{infr}$  = Total number of incidences (occurrences) of infrequent species

$p_k$  = Proportion of samples that contain species k

$Q_1$  = Number of uniques

$Q_2$  = Number of duplicates

$Q_j$  = Number of species that occur in exactly j samples (Q1 is the frequency of uniques, Q2 the frequency of duplicates)

$S_{Chao\ 2}$  = Estimated species richness based on Chao 2

$S_{infr}$  = Number of infrequent species

$S_{Jack1}$  = Estimated species richness based on Jack 1

$S_{obs}$  = Total number of observed species

$\gamma_{ICE}^2$  = Estimated coefficient of variation of the Qi for infrequent species

Table S 7: Most frequently recorded fungi in Taunus after 36 sampling events.

Division	Order	Species	Author	Number of records
Basidiomycota	Polyporales	<i>Fomes fomentarius</i>	(L.) J. Kickx f.	33
Ascomycota	Xylariales	<i>Hypoxylon fragiforme</i>	(Pers.) J. Kickx f.	32
Basidiomycota	Agaricales	<i>Schizophyllum commune</i>	Fr.	32
Basidiomycota	Russulales	<i>Stereum hirsutum</i>	(Willd.) Pers.	30
Basidiomycota	Polyporales	<i>Trametes versicolor</i>	(L.) Lloyd	29
Basidiomycota	Dacrymycetales	<i>Dacrymyces stillatus</i>	Nees	26
Ascomycota	Xylariales	<i>Annulohypoxylon cohaerens</i>	(Pers.) Y.M. Ju, J.D. Rogers & H.M. Hsieh	25
Ascomycota	Lecanorales	<i>Parmelia sulcata</i>	Taylor	25
Basidiomycota	Pucciniales	<i>Phragmidium violaceum</i>	(Schultz) G. Winter	25
Basidiomycota	Pucciniales	<i>Melampsora populnea</i>	(Pers.) P. Karst.	24

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Division	Order	Species	Author	Number of records
Basidiomycota	Pucciniales	<i>Puccinia coronata</i>	Corda	24
Ascomycota	Xylariales	<i>Biscogniauxia nummularia</i>	(Bull.) Kuntze	23
Basidiomycota	Polyporales	<i>Ganoderma applanatum</i>	(Pers.) Pat.	23
Basidiomycota	Pucciniales	<i>Melampsora caprearum</i>	Thüm.	23
Ascomycota	Xylariales	<i>Diatrype stigma</i>	(Hoffm.) Fr.	21
Basidiomycota	Hymenochaetales	<i>Schizopora paradoxa</i>	(Schrad.) Donk	20
Ascomycota	Capnodiales	<i>Cladosporium herbarum</i>	(Pers.) Link	19
Ascomycota	Hypocreales	<i>Dialonectria episphaeria</i>	(Tode) Cooke	19
Ascomycota	Xylariales	<i>Phomatospora dinemasporium</i>	J. Webster	18
Ascomycota	Rhytismatales	<i>Colpoma quercinum</i>	(Pers.) Wallr.	17
Ascomycota	Xylariales	<i>Diatrype decorticata</i>	(Pers.) Rappaz	17
Ascomycota	Xylariales	<i>Eutypa spinosa</i>	(Pers.) Tul. & C. Tul.	17
Ascomycota	Capnodiales	<i>Ramularia digitalis-ambiguae</i>	Arx	17
Ascomycota	Capnodiales	<i>Mycosphaerella punctiformis</i>	(Pers.) Starbäck	16
Ascomycota	Helotiales	<i>Neodasyscypha cerina</i>	(Pers.) Spooner	16
Ascomycota	Teloschistales	<i>Xanthoria parietina</i>	(L.) Beltr.	16
Basidiomycota	Auriculariales	<i>Exidia plana</i>	Donk	15
Ascomycota	Xylariales	<i>Kretzschmaria deusta</i>	(Hoffm.) P.M.D. Martin	15
Basidiomycota	Russulales	<i>Peniophora quercina</i>	(Pers.) Cooke	15
Basidiomycota	Pucciniales	<i>Puccinia annularis</i>	(F. Strauss) G. Winter	15
Basidiomycota	Polyporales	<i>Bjerkandera adusta</i>	(Willd.) P. Karst.	14
Ascomycota	Diaporthales	<i>Gnomonia setacea</i>	(Pers.) Ces. & De Not.	14
Ascomycota	Lecanorales	<i>Hypogymnia physodes</i>	(L.) Nyl.	14
Ascomycota	Hypocreales	<i>Nectria cinnabarina</i>	(Tode) Fr.	14
Basidiomycota	Pucciniales	<i>Puccinia obscura</i>	J. Schröt.	14
Ascomycota	Xylariales	<i>Anthostoma turgidum</i>	(Pers.) Nitschke	13
Ascomycota	Chaetosphaeriales	<i>Chaetosphaeria ovoidea</i>	(Fr.) Constant., K. Holm & L. Holm	13
Ascomycota	Xylariales	<i>Diatrype disciformis</i>	(Hoffm.) Fr.	13
Ascomycota	Pleosporales	<i>Epicoccum nigrum</i>	Link	13
Basidiomycota	Auriculariales	<i>Exidia glandulosa</i>	(Bull.) Fr.	13
Basidiomycota	Hymenochaetales	<i>Fuscoporia ferruginosa</i>	(Schrad.) Murrill	13
Ascomycota	Helotiales	<i>Lachnellula occidentalis</i>	(G.G. Han & Ayers) Dharue	13
Ascomycota	Pleosporales	<i>Melanomma pulvis-pyrius</i>	(Pers.) Fuckel	13
Basidiomycota	Russulales	<i>Peniophora incarnata</i>	(Pers.) P. Karst.	13
Basidiomycota	Polyporales	<i>Piptoporus betulinus</i>	(Bull.) P. Karst.	13
Ascomycota	Pleosporales	<i>Rhopographus filicinus</i>	(Fr.) Nitschke ex Fuckel	13
Ascomycota	Helotiales	<i>Bisporella citrina</i>	(Batsch) Korf & S.E. Carp.	12
Basidiomycota	Agaricales	<i>Cylindrobasidium evolvens</i>	(Fr.) Jülich	12
Basidiomycota	Russulales	<i>Hericium coralloides</i>	(Scop.) Pers.	12
Ascomycota	Xylariales	<i>Nemania serpens</i>	(Pers.) Gray	12
Ascomycota	Teloschistales	<i>Physcia tenella</i>	(Scop.) DC.	12
Ascomycota	Rhytismatales	<i>Propolis farinosa</i>	(Pers.) Fr.	12
Ascomycota	Incertae sedis	<i>Bispora antennata</i>	(Pers.) E.W. Mason	11
Ascomycota	Incertae sedis	<i>Cryptomycina pteridis</i>	(Rebent.) Höhnelt	11
Basidiomycota	Polyporales	<i>Daedaleopsis confragosa</i>	(Bolton) J. Schröt.	11
Ascomycota	Xylariales	<i>Diatrypella quercina</i>	(Pers.) Cooke	11

Division	Order	Species	Author	Number of records
Amoebozoa	Trichiida	<i>Metatrachia vesparium</i>	(Batsch) Nann.-Bremek.	11
Basidiomycota	Pucciniales	<i>Puccinia hieracii</i>	(Röhl.) H. Mart.	11
Ascomycota	Pleosporales	<i>Venturia ditricha</i>	(Fr.) P. Karst.	11
Ascomycota	Coronophorales	<i>Bertia moriformis</i>	(Tode) De Not	10
Ascomycota	Xylariales	<i>Eutypa flavovirens</i>	(Pers.) Tul. & C. Tul.	10
Ascomycota	Helotiales	<i>Lachnum impudicum</i>	Baral	10
Basidiomycota	Russulales	<i>Peniophora polygonia</i>	(Pers.) Bourdot & Galzin	10
Basidiomycota	Agaricales	<i>Plicaturopsis crispa</i>	(Pers.) D.A. Reid	10
Basidiomycota	Polyporales	<i>Polyporus brumalis</i>	(Pers.) Fr.	10
Basidiomycota	Agaricales	<i>Tubaria furfuracea</i>	(Pers.) Gillet	10
Ascomycota	Diaporthales	<i>Valsa nivea</i>	(Hoffm.) Fr.	10
Ascomycota	Xylariales	<i>Xylaria hypoxylon</i>	(L.) Grev.	10
Basidiomycota	Atheliales	<i>Athelia epiphylla</i>	sensu Eriksson/Ryvarden	9
Basidiomycota	Auriculariales	<i>Auricularia mesenterica</i>	(Dicks.) Pers.	9
Basidiomycota	Cantharellales	<i>Botryobasidium aureum</i>	Parmasto	9
Ascomycota	Pleosporales	<i>Eudarlucia caricis</i>	(Fr.) O.E. Erikss.	9
Ascomycota	Lecanorales	<i>Lepraria incana</i>	(L.) Ach.	9
Ascomycota	Helotiales	<i>Mollisia cinerea</i>	(Batsch) P. Karst.	9
Ascomycota	Orbiliales	<i>Orbilina delicatula</i>	(P. Karst.) P. Karst.	9
Ascomycota	Pleosporales	<i>Periconia atra</i>	Corda	9
Basidiomycota	Russulales	<i>Stereum rugosum</i>	Pers.	9
Ascomycota	Pleosporales	<i>Tubeufia cerea</i>	(Berk. & M.A. Curtis) Höhn.	9
Ascomycota	Helotiales	<i>Arachnopeziza aurata</i>	Fuckel	8
Basidiomycota	Agaricales	<i>Armillaria sp.1</i>		8
Basidiomycota	Dacrymycetales	<i>Calocera cornea</i>	(Batsch) Fr.	8
Basidiomycota	Agaricales	<i>Coprinellus micaceus</i>	(Bull.) Vilgalys, Hopple & Jacq. Johnson	8
Ascomycota	Xylariales	<i>Diatrypella favacea</i>	(Fr.) Ces. & De Not.	8
Ascomycota	Erysiphales	<i>Erysiphe alphitoides</i>	(Griffon & Maubl.) U. Braun & S. Takam.	8
Ascomycota	Erysiphales	<i>Erysiphe hyperici</i>	(Wallr.) S. Blumer	8
Ascomycota	Lecanorales	<i>Flavoparmelia caperata</i>	(L.) Hale	8
Basidiomycota	Pucciniales	<i>Puccinia graminis</i>	Pers.	8
Basidiomycota	Polyporales	<i>Trametes ochracea</i>	(Pers.) Gilb. & Ryvarden	8
Ascomycota	Xylariales	<i>Annulohypoxylon multiforme</i>	(Fr.) Y.M. Ju, J.D. Rogers & H.M. Hsieh	7
Ascomycota	Pleosporales	<i>Ascochyta festucae</i>	Punith.	7
Amoebozoa	Ceratiomyxales	<i>Ceratiomyxa fruticulosa</i>	(O.F. Müll.) T. Macbr.	7
Basidiomycota	Agaricales	<i>Chondrostereum purpureum</i>	(Pers.) Pouzar	7
Ascomycota	Hypocreales	<i>Claviceps purpurea</i>	(Fr.) Tul.	7
Ascomycota	Helotiales	<i>Hyaloscypha albohyalina</i>	(P. Karst.) Boud.	7
Ascomycota	Umbilicariales	<i>Hypocenomyce scalaris</i>	(Ach. ex Lilj.) M. Choisy	7
Ascomycota	Microthyriales	<i>Leptopeltis litigiosa</i>	(Desm.) L. Holms & Holm	7
Basidiomycota	Agaricales	<i>Merismodes fasciculata</i>	(Schwein.) Donk	7
Basidiomycota	Agaricales	<i>Pleurotus ostreatus</i>	(Jacq.) P. Kumm.	7
Ascomycota	Helotiales	<i>Tapesia lividofusca</i>	(Fr.) Rehm	7
Basidiomycota	Polyporales	<i>Trametes gibbosa</i>	(Pers.) Fr.	7
Basidiomycota	Polyporales	<i>Trichaptum abietinum</i>	(Dicks.) Ryvarden	7
Basidiomycota	Agaricales	<i>Amanita muscaria</i>	(L.) Lam.	6



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Division	Order	Species	Author	Number of records
Basidiomycota	Boletales	<i>Boletus edulis</i>	Bull.	6
Ascomycota	Leotiales	<i>Bulgaria inquinans</i>	(Pers.) Fr.	6
Ascomycota	Helotiales	<i>Ciboria amentacea</i>	(Balb.) Fuckel	6
Basidiomycota	Agaricales	<i>Clitopilus hobsonii</i>	(Berk.) P.D. Orton	6
Basidiomycota	Agaricales	<i>Cyathus striatus</i>	(Huds.) Willd.	6
Ascomycota	Incertae sedis	<i>Discogloeum veronicae</i>	(Lib.) Petr.	6
Ascomycota	Erysiphales	<i>Erysiphe adunca</i>	(Wallr.) Fr.	6
Ascomycota	Xylariales	<i>Eutypella quaternata</i>	(Pers.) Rappaz	6
Basidiomycota	Agaricales	<i>Flagelloscypha minutissima</i>	(Burt) Donk	6
Basidiomycota	Agaricales	<i>Gymnopus dryophilus</i>	(Bull.) Murrill	6
Ascomycota	Lecanorales	<i>Hypogymnia tubulosa</i>	(Schaeer.) Hav.	6
Ascomycota	Helotiales	<i>Lachnum virgineum</i>	(Batsch) P. Karst.	6
Amoebozoa	Liceida	<i>Lycogala epidendrum</i>	(J.C. Buxb. ex L.) Fr.	6
Basidiomycota	Agaricales	<i>Macrolepiota procera</i>	(Scop.) Singer	6
Basidiomycota	Polyporales	<i>Merulius tremellosus</i>	Schrad.	6
Basidiomycota	Agaricales	<i>Mycena pura</i>	(Pers.) P. Kumm.	6
Basidiomycota	Agaricales	<i>Panellus stipticus</i>	(Bull.) P. Karst.	6
Basidiomycota	Pucciniales	<i>Phragmidium mucronatum</i>	(Pers.) Schltld.	6
Basidiomycota	Agaricales	<i>Pluteus cervinus</i>	(Schaeff.) P. Kumm.	6
Ascomycota	Helotiales	<i>Polydesmia pruinosa</i>	(Gerd. ex Berk. & Broome) Boud.	6
Basidiomycota	Polyporales	<i>Polyporus varius</i>	Grev.	6
Ascomycota	Helotiales	<i>Pseudopeziza trifolii</i>	(Biv.) Fuckel	6
Basidiomycota	Pucciniales	<i>Puccinia punctiformis</i>	(F. Strauss) Röhl.	6
Basidiomycota	Agaricales	<i>Radulomyces molaris</i>	(Chaillat ex Fr.) M.P. Christ.	6
Basidiomycota	Hymenochaetales	<i>Rickenella fibula</i>	(Bull.) Raitthel.	6
Basidiomycota	Russulales	<i>Stereum gausapatum</i>	(Fr.) Fr.	6
Basidiomycota	Russulales	<i>Stereum subtomentosum</i>	Pouzar	6
Basidiomycota	Cantharellales	<i>Tulasnella violea</i>	(Quél.) Bourdot & Galzin	6
Basidiomycota	Corticiales	<i>Vuilleminia comedens</i>	(Nees) Maire	6

Table S 8: Information on sampling events in Taunus with weather data and richness of fungal and plant diversity and different taxonomic groups.

Sample	Month	Year	Sampling year	Relative Humidity	Temperature [°C]	Fungi	Plants	Asco-mycota	Basidio-mycota	Agari-cales	Polypo-rales	Puccini-ales	Heloti-ales	Pleospo-rales	Xylari-ales	Sapro-biont	Para-site	Mycorr-hiza
S01	May	2011	1	62	13	64	114	41	23	3	8	2	7	2	12	49	10	0
S02	Jun	2011	1	66	16	45	111	29	16	1	5	3	2	0	8	22	13	1
S03	Jul	2011	1	78	18	60	136	34	25	5	4	6	2	5	9	36	18	1
S04	Aug	2011	1	83	17	53	118	21	32	10	7	2	7	1	6	35	10	8
S05	Sep	2011	1	88	17	58	121	28	30	9	4	9	0	5	5	32	18	5
S06	Oct	2011	1	79	18	86	126	35	51	14	12	14	7	5	3	47	24	8
S07	Nov	2011	1	96	10	93	114	40	51	20	7	18	4	2	11	56	30	2
S08	Dec	2011	1	104	4	65	81	28	37	14	5	11	7	5	4	39	23	0
S09	Jan	2012	1	107	4	65	104	28	35	12	5	7	4	4	4	33	21	1
S10	Feb	2012	1	104	1	74	43	38	35	10	5	3	1	6	10	48	17	0
S11	Mar	2012	1	96	3	60	56	33	25	4	7	3	12	3	4	48	9	0
S12	Apr	2012	1	75	11	71	75	42	26	5	7	1	5	3	13	52	10	0
S13	May	2012	2	84	14	88	97	60	27	7	7	3	5	8	8	66	14	0
S14	Jun	2012	2	70	17	69	112	34	28	3	4	4	6	7	6	41	18	2
S15	Jul	2012	2	91	16	51	118	27	22	4	4	5	1	7	6	29	13	4
S16	Aug	2012	2	78	20	63	106	26	33	3	6	14	5	1	9	38	19	2
S17	Sep	2012	2	79	18	61	92	35	22	1	6	6	3	2	8	38	14	1
S18	Oct	2012	2	91	12	129	104	34	95	53	13	7	13	4	6	100	21	7
S19	Nov	2012	2	102	4	103	58	47	53	23	7	6	11	6	7	72	20	5
S20	Dec	2012	2	100	5	122	65	56	64	28	10	12	11	9	11	86	30	0
S21	Jan	2013	2	100	5	75	63	42	30	14	6	3	13	4	6	59	11	0
S22	Feb	2013	2	104	-1	102	63	52	42	11	9	7	14	6	9	70	21	0
S23	Mar	2013	2	97	-2	92	61	50	38	7	8	4	5	5	15	64	16	0
S24	Apr	2013	2	79	1	61	52	33	27	7	3	5	2	5	9	44	14	0
S25	May	2013	3	81	11	71	77	41	27	4	6	5	11	7	8	49	16	0
S26	Jun	2013	3	97	8	79	123	38	37	10	5	9	10	3	13	56	18	1

## Appendices

Sample	Month	Year	Sampling year	Relative Humidity	Temperature [°C]	Fungi	Plants	Asco-mycota	Basidio-mycota	Agari-cales	Polypo-rales	Puccini-ales	Heloti-ales	Pleospo-rales	Xylari-ales	Sapro-biont	Para-site	Mycorr-hiza
S27	Jul	2013	3	87	13	80	120	49	24	5	5	6	9	5	15	52	20	1
S28	Aug	2013	3	69	21	54	118	27	27	4	6	7	4	2	8	37	16	1
S29	Sep	2013	3	84	16	71	91	34	33	12	6	5	7	1	11	50	13	2
S30	Oct	2013	3	96	11	110	71	40	65	33	7	7	9	4	7	79	22	4
S31	Nov	2013	3	99	13	132	76	45	86	54	7	6	10	4	4	90	16	14
S32	Dec	2013	3	100	2	92	49	48	42	8	9	10	9	4	16	60	23	3
S33	Jan	2014	3	104	2	80	69	38	42	8	13	4	8	4	10	59	18	0
S34	Feb	2014	3	105	3	74	62	35	39	8	10	4	10	2	10	61	9	1
S35	Mar	2014	3	91	5	94	61	59	33	9	8	7	9	12	10	62	26	0
S36	Apr	2014	3	74	8	71	76	54	16	0	1	8	2	13	11	41	23	0

Table S 9: Recorded and identified lichens during one sampling with experts and recorded lichens during all other sampling events.

Species	Author	Sample event with experts	Usual sampling
<i>Absconditella lignicola</i>	Vězda & Pišút	1	0
<i>Amandinea punctata</i>	(Hoffm.) Coppins & Scheid.	1	1
<i>Bacidina sulphurella</i>	(Samp.) M. Hauck & V. Wirth	1	0
<i>Buellia griseovirens</i>	(Turner & Borrer ex Sm.) Almb.	1	0
<i>Calicium salicinum</i>	Pers.	1	1
<i>Caloplaca cerinella</i>	(Nyl.) Flagey	1	0
<i>Caloplaca pyracea</i>	(Ach.) Th. Fr.	1	0
<i>Candelaria concolor</i>	(Dicks.) Stein	1	0
<i>Candelariella reflexa</i>	(Nyl.) Lettau	1	1
<i>Candelariella xanthostigma</i>	(Pers. ex Ach.) Lettau	1	0
<i>Catillaria nigroclavata</i>	(Nyl.) Schuler	1	0
<i>Chaenotheca ferruginea</i>	(Turner ex Sm.) Mig.	1	0
<i>Cladonia coniocraea</i>	(Flörke) Spreng.	1	1
<i>Cladonia fimbriata</i>	(L.) Fr.	0	1
<i>Cladonia pyxidata</i>	(L.) Hoffm.	1	1
<i>Coenogonium pineti</i>	(Schrad.) Lücking & Lumbsch	1	1
<i>Evernia prunastri</i>	(L.) Ach.	1	1
<i>Flavoparmelia caperata</i>	(L.) Hale	1	1
<i>Halecania viridescens</i>	Coppins & P. James	1	0
<i>Hyperphyscia adglutinata</i>	(Flörke) H. Mayrhofer & Poelt	1	0
<i>Hypocenomyce scalaris</i>	(Ach. ex Lilj.) M. Choisy	1	1
<i>Hypogymnia physodes</i>	(L.) Nyl.	1	1
<i>Hypogymnia tubulosa</i>	(Schaer.) Hav.	1	1
<i>Hypotrachyna afrorevoluta</i>	(Krog & Swinscow) Krog & Swinscow	1	0
<i>Jamesiella anastomosans</i>	(P. James & Vězda) Lücking, Sérus. & Vězda	1	0
<i>Lecania cyrtella</i>	(Ach.) Th. Fr.	1	0
<i>Lecania naegelii</i>	(Hepp) Diederich & Van den Boom	1	0
<i>Lecanora carpinea</i>	(L.) Vain.	1	0
<i>Lecanora conizaeoides</i>	Nyl. ex Cromb.	1	1
<i>Lecanora dispersa</i>	(Pers.) Röhl.	1	0
<i>Lecanora expallens</i>	Ach.	1	0
<i>Lecanora persimilis</i>	Th. Fr.	1	0
<i>Lecanora pulicaris</i>	(Pers.) Ach.	1	0
<i>Lecanora saligna</i>	(Wahlenb. ex Ach.) Hillmann	1	0
<i>Lecanora sambuci</i>	(Pers.) Nyl.	1	0
<i>Lecanora symmicta</i>	(Ach.) Ach.	1	0
<i>Lepraria incana</i>	(L.) Ach.	1	1
<i>Lepraria lobificans</i>	Nyl.	1	0
<i>Lepraria rigidula</i>	(de Lesd.) Tønsberg	1	0
<i>Lepraria sp.1</i>		0	1
<i>Lepraria sp.2</i>		0	1

## Appendices

Species	Author	Sample event with experts	Usual sampling
<i>Lichenocodium lecanorae</i>	(Jaap) D. Hawksw.	1	1
<i>Melanelia subaurifera</i>	(Nyl.) Essl.	0	1
<i>Melanelixia fuliginosa</i>	(Fr. ex Duby) O. Blanco, A. Crespo, Divakar, Essl., D. Hawksw. & Lumbsch	0	1
<i>Melanelixia glabratula</i>	(Lamy) Sandler & Arup	1	1
<i>Melanelixia subaurifera</i>	(Nyl.) O. Blanco et al.	1	0
<i>Melanohalea elegantula</i>	(Zahlbr.) O. Blanco et al.	1	0
<i>Melanohalea exasperatula</i>	(Nyl.) O. Blanco et al.	1	0
<i>Micarea cf. deminuta</i>		1	0
<i>Micarea micrococca</i>	(Körb.) Gams ex Coppins	1	0
<i>Micarea misella</i>	(Nyl.) Hedl.	1	0
<i>Micarea prasina</i>	Fr.	1	0
<i>Parmelia saxatilis</i>	(L.) Ach.	1	1
<i>Parmelia sp. 1</i>		0	0
<i>Parmelia subrudecta</i>	Nyl.	0	0
<i>Parmelia sulcata</i>	Taylor	1	1
<i>Parmeliopsis ambigua</i>	(Wulfen) Nyl.	1	0
<i>Parmotrema perlatum</i>	(Huds.) M. Choisy	1	0
<i>Phaeophyscia nigricans</i>	(Flörke) Moberg	1	0
<i>Phaeophyscia orbicularis</i>	(Neck.) Moberg	1	0
<i>Phlyctis argena</i>	(Spreng.) Flot.	1	0
<i>Physcia adscendens</i>	H. Olivier	1	1
<i>Physcia stellaris</i>	(L.) Nyl.	1	1
<i>Physcia tenella</i>	(Scop.) DC.	1	1
<i>Placynthiella dasaea</i>	(Stirt.) Tønsberg	1	0
<i>Placynthiella icmalea</i>	(Ach.) Coppins & P. James	1	0
<i>Placynthiella uliginosa</i>	(Schrad.) Coppins & P. James	1	0
<i>Polycauliona polycarpa</i>	(Hoffm.) Frödén, Arup & Söchting	1	0
<i>Porina aenea</i>	(Wallr.) Zahlbr.	1	0
<i>Porpidia crustulata</i>	(Ach.) Hertel & Knoph	1	0
<i>Pseudevernia furfuracea</i>	(L.) Zopf	0	1
<i>Pseudosagedia chlorotica</i>	(Ach.) Hafellner & Kalb	1	0
<i>Punctelia jeckeri</i>	(Roum.) Kalb	1	0
<i>Punctelia subrudecta</i>	(Nyl.) Krog	1	0
<i>Rinodina pyrina</i>	(Ach.) Arnold	1	0
<i>Roselliniella microthelia</i>	(Wallr.) Nik. Hoffm. & Hafellner	1	0
<i>Scoliciosporum chlorococcum</i>	(Graewe ex Stenh.) Vězda	1	0
<i>Thelocarpon intermediellum</i>	Nyl.	1	0
<i>Thelocarpon lichenicola</i>	(Fuckel) Poelt & Hafellner	1	0
<i>Trapelia coarctata</i>	(Turner ex Sm.) M. Choisy	1	1
<i>Trapeliopsis flexuosa</i>	(Fr.) Coppins & P. James	1	0
<i>Trapeliopsis</i>	Coppins & P. James	1	0

Species	Author	Sample event with experts	Usual sampling
<i>pseudogranulosa</i>			
<i>Xanthoria parietina</i>	(L.) Th. Fr.	1	1
<i>Xanthoria ucrainica</i>	S. Y. Kondr.	1	0

### 7.3 Plant diversity

Table S 10: Most common taxonomic groups of plants recorded in the Taunus area during three years of monthly sampling.

Family	Total	%	Genus	Total	%	Species	Records
Poaceae	32	15	<i>Agrostis</i>	4	12	<i>Agrostis canina</i>	25
			<i>Bromus</i>	4	12	<i>Bromus erectus</i>	2
			<i>Festuca</i>	4	12	<i>Festuca gigantea</i>	15
			<i>Poa</i>	4	12	<i>Poa annua</i>	30
Asteraceae	26	12	<i>Hieracium</i>	4	15	<i>Hieracium pilosella</i>	31
			<i>Cirsium</i>	3	12	<i>Cirsium palustre</i>	35
			<i>Senecio</i>	3	12	<i>Senecio ovatus</i>	12
Rosaceae	21	10	<i>Rubus</i>	4	19	<i>Rubus fruticosus</i>	35
			<i>Prunus</i>	3	14	<i>Prunus spinosa</i>	32
			<i>Crataegus</i>	2	10	<i>Crataegus laevigata</i>	36
			<i>Potentilla</i>	2	10	<i>Potentilla erecta</i>	31
			<i>Sanguisorba</i>	2	10	<i>Sanguisorba minor</i>	19
			<i>Sorbus</i>	2	10	<i>Sorbus aucuparia</i>	16
Fabaceae	18	8	<i>Trifolium</i>	6	33	<i>Trifolium repens</i>	27
			<i>Vicia</i>	5	28	<i>Vicia angustifolia</i>	5
			<i>Lathyrus</i>	3	17	<i>Lathyrus linifolius</i>	34
			<i>Lotus</i>	2	11	<i>Lotus corniculatus</i>	19
Plantaginaceae	7	3	<i>Digitalis</i>	1	14	<i>Digitalis purpurea</i>	36
Fagaceae	4	2	<i>Quercus</i>	2	50	<i>Quercus petraea</i>	36
			<i>Castanea</i>	1	25	<i>Castanea sativa</i>	36
			<i>Fagus</i>	1	25	<i>Fagus sylvatica</i>	36
Pinaceae	4	2	<i>Larix</i>	1	25	<i>Larix decidua</i>	36
			<i>Picea</i>	1	25	<i>Picea abies</i>	36
Betulaceae	3	1	<i>Betula</i>	1	33	<i>Betula pendula</i>	36
Salicaceae	2	1	<i>Populus</i>	1	50	<i>Populus tremula</i>	36
			<i>Salix</i>	1	50	<i>Salix caprea</i>	36
Dennstaedtiaceae	1	0	<i>Pteridium</i>	1	100	<i>Pteridium aquilinum</i>	36

## 7.4 Joint examination of fungal diversity in all sampling areas

Table S 11: Shared species in the different compared sampling areas Bulau (Bul), Taunus (Tau), Somiedo (Som), Kleinwalsertal (Kle), and Majagua (Maj).

Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
Ascomycota	Helotiales	<i>Bisporella citrina</i>	1	1	1	1	0	4
Ascomycota	Hypocreales	<i>Dialonectria episphaeria</i>	1	1	1	1	0	4
Ascomycota	Orbiliales	<i>Hyalorbilia inflatula</i>	1	1	1	1	0	4
Ascomycota	Lecanorales	<i>Parmelia sulcata</i>	1	1	1	1	0	4
Basidiomycota	Agaricales	<i>Schizophyllum commune</i>	1	1	0	1	1	4
Basidiomycota	Polyporales	<i>Trametes versicolor</i>	1	1	1	1	0	4
Ascomycota	Xylariales	<i>Xylaria hypoxylon</i>	1	1	1	1	0	4
Basidiomycota	Agaricales	<i>Armillaria mellea</i>	0	1	1	1	0	3
Ascomycota	Coronophorales	<i>Bertia moriformis</i>	0	1	1	1	0	3
Amoebozoa	Ceratiomyxales	<i>Ceratiomyxa fruticulosa</i>	1	1	0	0	1	3
Basidiomycota	Agaricales	<i>Collybia cookei</i>	0	1	1	1	0	3
Ascomycota	Helotiales	<i>Crocicreas cyathoideum</i>	1	1	1	0	0	3
Basidiomycota	Agaricales	<i>Cyphellopsis anomala</i>	1	1	1	0	0	3
Ascomycota	Xylariales	<i>Diatrype decorticata</i>	0	1	1	1	0	3
Ascomycota	Xylariales	<i>Diatrypella quercina</i>	1	1	1	0	0	3
Basidiomycota	Agaricales	<i>Entoloma rhodopolium</i>	0	1	1	1	0	3
Ascomycota	Pleosporales	<i>Epicoccum nigrum</i>	0	1	1	1	0	3
Ascomycota	Pleosporales	<i>Eudarluca caricis</i>	0	1	1	0	1	3
Ascomycota	Xylariales	<i>Eutypa lata</i>	1	1	1	0	0	3
Ascomycota	Lecanorales	<i>Flavoparmelia caperata</i>	1	1	1	0	0	3
Amoebozoa	Physarida	<i>Fuligo septica</i>	1	1	0	1	0	3
Basidiomycota	Agaricales	<i>Galerina marginata</i>	1	1	0	1	0	3
Amoebozoa	Trichiida	<i>Hemitrichia calyculata</i>	1	1	0	0	1	3
Basidiomycota	Agaricales	<i>Hygrocybe conica</i>	0	1	1	1	0	3
Basidiomycota	Agaricales	<i>Hypholoma fasciculare</i>	0	1	1	1	0	3
Ascomycota	Xylariales	<i>Hypoxylon fragiforme</i>	1	1	0	1	0	3
Ascomycota	Xylariales	<i>Hypoxylon fuscum</i>	1	1	1	0	0	3
Ascomycota	Hysteriales	<i>Hysterium angustatum</i>	1	1	1	0	0	3
Ascomycota	Pleosporales	<i>Leptosphaeria acuta</i>	1	1	0	1	0	3
Amoebozoa	Liceida	<i>Lycogala epidendrum</i>	1	1	0	0	1	3
Basidiomycota	Agaricales	<i>Lycoperdon perlatum</i>	1	1	1	0	0	3
Ascomycota	Pleosporales	<i>Melanomma pulvis-</i>	0	1	1	1	0	3

Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
		<i>pyrius</i>						
Basidiomycota	Agaricales	<i>Mycena galericulata</i>	1	1	0	1	0	3
Basidiomycota	Agaricales	<i>Mycena pura</i>	0	1	1	1	0	3
Basidiomycota	Polyporales	<i>Mycoacia uda</i>	1	1	1	0	0	3
Ascomycota	Helotiales	<i>Neodasyscypha cerina</i>	0	1	1	1	0	3
Ascomycota	Lecanorales	<i>Parmelia saxatilis</i>	1	1	0	1	0	3
Basidiomycota	Russulales	<i>Peniophora lycii</i>	0	1	1	1	0	3
Basidiomycota	Pucciniales	<i>Phragmidium violaceum</i>	1	1	1	0	0	3
Oomycota	Peronosporales	<i>Plasmopara nivea</i>	1	1	0	1	0	3
Basidiomycota	Polyporales	<i>Polyporus brumalis</i>	1	1	0	1	0	3
Basidiomycota	Agaricales	<i>Psathyrella candolleana</i>	1	1	0	0	1	3
Ascomycota	Lecanorales	<i>Pseudevernia furfuracea</i>	0	1	1	1	0	3
Ascomycota	Helotiales	<i>Psilachnum chrysostigmum</i>	1	1	0	1	0	3
Basidiomycota	Pucciniales	<i>Puccinia graminis</i>	0	1	1	1	0	3
Ascomycota	Rhytismatales	<i>Rhytisma acerinum</i>	1	1	0	1	0	3
Basidiomycota	Russulales	<i>Stereum hirsutum</i>	1	1	1	0	0	3
Ascomycota	Rythismatales	<i>Actinothyrium graminis</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Amanita muscaria</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Amanita rubescens</i>	0	1	0	1	0	2
Ascomycota	Xylariales	<i>Annulohyphoxylon multiforme</i>	1	1	0	0	0	2
Ascomycota	Helotiales	<i>Arachnopeziza aurata</i>	0	1	1	0	0	2
Amoebozoa	Trichiida	<i>Arcyria denudata</i>	0	1	0	0	1	2
Basidiomycota	Auriculariales	<i>Auricularia mesenterica</i>	0	1	0	0	1	2
Ascomycota	Helotiales	<i>Belonidium sulphureum</i>	0	1	0	1	0	2
Ascomycota	Incertae sedis	<i>Bispora antennata</i>	0	1	0	1	0	2
Ascomycota	Erysiphales	<i>Blumeria graminis</i>	0	1	0	1	0	2
Basidiomycota	Cantharellales	<i>Botryobasidium aureum</i>	1	1	0	0	0	2
Basidiomycota	Polyporales	<i>Byssomerulius corium</i>	1	0	1	0	0	2
Basidiomycota	Dacrymycetales	<i>Calocera viscosa</i>	0	1	0	1	0	2
Ascomycota	Helotiales	<i>Cejpia hystrix</i>	0	1	0	1	0	2
Ascomycota	Chaetosphaeriales	<i>Chaetosphaeria vermicularioides</i>	1	1	0	0	0	2
Basidiomycota	Boletales	<i>Chalciporus piperatus</i>	0	1	0	1	0	2
Ascomycota	Helotiales	<i>Chlorociboria</i>	0	1	1	0	0	2



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Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
		<i>aeruginascens</i>						
Basidiomycota	Agaricales	<i>Chondrostereum purpureum</i>	0	1	0	0	1	2
Ascomycota	Lecanorales	<i>Cladonia coniocraea</i>	0	1	0	1	0	2
Ascomycota	Lecanorales	<i>Cladonia fimbriata</i>	1	1	0	0	0	2
Ascomycota	Lecanorales	<i>Cladonia pyxidata</i>	0	1	0	1	0	2
Ascomycota	Capnodiales	<i>Cladosporium herbarum</i>	0	1	0	1	0	2
Ascomycota	Hypocreales	<i>Claviceps purpurea</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Clitocybe nebularis</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Clitopilus hobsonii</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Clitopilus prunulus</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Collybia tuberosa</i>	0	1	0	1	0	2
Amoebozoa	Stemonitida	<i>Comatricha nigra</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Cortinarius infractus</i>	0	0	1	1	0	2
Basidiomycota	Agaricales	<i>Crucibulum laeve</i>	0	1	1	0	0	2
Ascomycota	Xylariales	<i>Cryptosphaeria eunomia</i>	1	0	1	0	0	2
Basidiomycota	Dacrymycetales	<i>Dacrymyces stillatus</i>	0	1	0	1	0	2
Basidiomycota	Polyporales	<i>Daedaleopsis confragosa</i>	1	1	0	0	0	2
Ascomycota	Diaporthales	<i>Diaporthe arctii</i>	0	1	1	0	0	2
Ascomycota	Diaporthales	<i>Diaporthe scobina</i>	1	0	1	0	0	2
Ascomycota	Xylariales	<i>Diatrype bullata</i>	1	1	0	0	0	2
Ascomycota	Xylariales	<i>Diatrype disciformis</i>	0	1	0	1	0	2
Ascomycota	Xylariales	<i>Diatrype stigma</i>	0	1	1	0	0	2
Ascomycota	Xylariales	<i>Diatrypella favacea</i>	0	1	1	0	0	2
Ascomycota	Ostropales	<i>Dimerella pineti</i>	0	1	1	0	0	2
Ascomycota	Xylariales	<i>Discosia artocreas</i>	1	1	0	0	0	2
Ascomycota	Xylariales	<i>Discosia fraxinea</i>	0	1	1	0	0	2
Basidiomycota	Entylomatales	<i>Entyloma ficariae</i>	1	1	0	0	0	2
Ascomycota	Hypocreales	<i>Epichloe typhina</i>	0	1	1	0	0	2
Ascomycota	Erysiphales	<i>Erysiphe hyperici</i>	0	1	0	1	0	2
Ascomycota	Xylariales	<i>Eutypa flavovirens</i>	0	1	0	1	0	2
Basidiomycota	Polyporales	<i>Fomes fomentarius</i>	1	1	0	0	0	2
Basidiomycota	Polyporales	<i>Fomitopsis pinicola</i>	0	1	0	1	0	2
Basidiomycota	Hymenochaetales	<i>Fuscoporia ferruginosa</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Galerina vittiformis</i>	0	1	0	1	0	2
Basidiomycota	Polyporales	<i>Ganoderma applanatum</i>	1	1	0	0	0	2
Basidiomycota	Geastrales	<i>Geastrum triplex</i>	0	0	1	0	1	2
Basidiomycota	Agaricales	<i>Gymnopus dryophilus</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Hebeloma sinapizans</i>	0	0	1	1	0	2

Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
Ascomycota	Helotiales	<i>Hyaloscypha aureliella</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Hygrocybe punicea</i>	0	1	1	0	0	2
Basidiomycota	Hymenochaetales	<i>Hymenochaete rubiginosa</i>	1	1	0	0	0	2
Ascomycota	Helotiales	<i>Hymenoscyphus scutula</i>	0	1	0	1	0	2
Basidiomycota	Polyporales	<i>Hyphoderma setigerum</i>	1	1	0	0	0	2
Ascomycota	Lecanorales	<i>Hypogymnia physodes</i>	0	1	0	1	0	2
Ascomycota	Diaporthales	<i>Hypospilina pustula</i>	0	1	1	0	0	2
Ascomycota	Xylariales	<i>Hypoxylon howeanum</i>	0	1	1	0	0	2
Ascomycota	Xylariales	<i>Hypoxylon macrocarpum</i>	1	1	0	0	0	2
Ascomycota	Xylariales	<i>Hypoxylon rubiginosum</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Inocybe fraudans</i>	0	0	1	1	0	2
Ascomycota	Xylariales	<i>Kretzschmaria deusta</i>	1	1	0	0	0	2
Basidiomycota	Pucciniales	<i>Kuehneola uredinis</i>	1	1	0	0	0	2
Ascomycota	Helotiales	<i>Lachnum fuscescens</i>	1	1	0	0	0	2
Basidiomycota	Polyporales	<i>Lenzites betulina</i>	0	1	0	1	0	2
Ascomycota	Microthyriales	<i>Leptopeltis litigiosa</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Lycoperdon lividum</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Lycoperdon pyriforme</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Marasmiellus ramealis</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Megacollybia platyphylla</i>	1	1	0	0	0	2
Basidiomycota	Pucciniales	<i>Melampsora populnea</i>	1	1	0	0	0	2
Ascomycota	Lecanorales	<i>Melanelixia fuliginosa</i>	1	1	0	0	0	2
Ascomycota	Diaporthales	<i>Melogramma campylosporum</i>	1	1	0	0	0	2
Ascomycota	Helotiales	<i>Mollisia cinerea</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Mycena acicula</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Mycena filopes</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Mycena flavescens</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Mycena flavoalba</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Mycena galopus</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Mycena haematopus</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Mycena pterigena</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Mycena speirea</i>	0	1	0	1	0	2
Ascomycota	Capnodiales	<i>Mycosphaerella punctiformis</i>	0	1	1	0	0	2

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Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
Basidiomycota	Tremellales	<i>Myxarium nucleatum</i>	1	1	0	0	0	2
Ascomycota	Helotiales	<i>Naevula perexigua</i>	0	1	1	0	0	2
Ascomycota	Hypocreales	<i>Nectria cinnabarina</i>	1	1	0	0	0	2
Ascomycota	Hypocreales	<i>Nectria peziza</i>	1	1	0	0	0	2
Ascomycota	Xylariales	<i>Nemania confluens</i>	0	1	1	0	0	2
Ascomycota	Xylariales	<i>Nemania serpens</i>	0	1	1	0	0	2
Ascomycota	Incertae sedis	<i>Oncopodiella trigonella</i>	1	1	0	0	0	2
Ascomycota	Orbiliales	<i>Orbilia delicatula</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Panellus stipticus</i>	1	1	0	0	0	2
Basidiomycota	Boletales	<i>Paxillus involutus</i>	0	1	1	0	0	2
Ascomycota	Peltigerales	<i>Peltigera praetextata</i>	0	0	1	1	0	2
Basidiomycota	Russulales	<i>Peniophora cinerea</i>	1	1	0	0	0	2
Basidiomycota	Russulales	<i>Peniophora incarnata</i>	1	1	0	0	0	2
Ascomycota	Pleosporales	<i>Periconia minutissima</i>	0	1	1	0	0	2
Ascomycota	Xylariales	<i>Peroneutypa scoparia</i>	1	0	1	0	0	2
Ascomycota	Pezizales	<i>Peziza micropus</i>	0	1	0	1	0	2
Ascomycota	Pleosporales	<i>Phaeosphaeria fuckelii</i>	1	1	0	0	0	2
Basidiomycota	Polyporales	<i>Phlebia lilascens</i>	1	1	0	0	0	2
Basidiomycota	Pucciniales	<i>Phragmidium mucronatum</i>	0	1	1	0	0	2
Basidiomycota	Pucciniales	<i>Phragmidium potentillae</i>	0	1	0	1	0	2
Basidiomycota	Pucciniales	<i>Phragmidium rubi- idaei</i>	0	1	0	1	0	2
Ascomycota	Incertae sedis	<i>Phragmotrichum chailletii</i>	0	1	0	1	0	2
Amoebozoa	Physarida	<i>Physarum robustum</i>	1	1	0	0	0	2
Ascomycota	Teloschistales	<i>Physcia adscendens</i>	1	1	0	0	0	2
Ascomycota	Sordariales	<i>Pleurothecium recurvatum</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Plicaturopsis crispa</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Pluteus cervinus</i>	1	1	0	0	0	2
Basidiomycota	Agaricales	<i>Pluteus phlebophorus</i>	0	1	0	0	1	2
Basidiomycota	Agaricales	<i>Pluteus salicinus</i>	1	1	0	0	0	2
Ascomycota	Erysiphales	<i>Podosphaera aphanis</i>	0	1	0	1	0	2
Ascomycota	Erysiphales	<i>Podosphaera fusca</i>	0	1	0	1	0	2
Basidiomycota	Polyporales	<i>Polyporus arcularius</i>	1	0	0	1	0	2
Basidiomycota	Polyporales	<i>Polyporus badius</i>	1	1	0	0	0	2
Basidiomycota	Polyporales	<i>Polyporus ciliatus</i>	0	1	0	0	1	2
Ascomycota	Helotiales	<i>Pseudopeziza trifolii</i>	0	1	0	1	0	2
Basidiomycota	Pucciniales	<i>Puccinia arenariae</i>	0	1	1	0	0	2

Division	Order	Species	Bul	Tau	Som	Kle	Maj	Total
Basidiomycota	Pucciniales	<i>Puccinia brachypodii</i>	0	1	1	0	0	2
Basidiomycota	Pucciniales	<i>Puccinia caricina</i>	0	1	0	1	0	2
Basidiomycota	Pucciniales	<i>Puccinia obscura</i>	0	1	0	1	0	2
Basidiomycota	Polyporales	<i>Pycnoporus cinnabarinus</i>	0	1	0	1	0	2
Basidiomycota	Incertae sedis	<i>Resinicium bicolor</i>	0	1	0	1	0	2
Ascomycota	Patellariales	<i>Rhizodiscina lignyota</i>	0	1	1	0	0	2
Basidiomycota	Agaricales	<i>Rhodocollybia butyracea</i>	0	1	0	1	0	2
Ascomycota	Pleosporales	<i>Rhopoglyphus filicinus</i>	0	1	1	0	0	2
Basidiomycota	Hymenochaetales	<i>Rickenella fibula</i>	0	1	0	1	0	2
Basidiomycota	Russulales	<i>Russula nigricans</i>	0	1	1	0	0	2
Basidiomycota	Russulales	<i>Russula ochroleuca</i>	0	1	0	1	0	2
Basidiomycota	Russulales	<i>Russula queletii</i>	0	1	0	1	0	2
Basidiomycota	Agaricales	<i>Sarcomyxa serotina</i>	1	1	0	0	0	2
Basidiomycota	Hymenochaetales	<i>Schizopora paradoxa</i>	1	1	0	0	0	2
Basidiomycota	Geastrales	<i>Sphaerobolus stellatus</i>	0	1	0	0	1	2
Ascomycota	Pleosporales	<i>Stagonospora agrostidis</i>	0	1	1	0	0	2
Basidiomycota	Polyporales	<i>Steccherinum fimbriatum</i>	1	0	1	0	0	2
Basidiomycota	Russulales	<i>Stereum subtomentosum</i>	1	1	0	0	0	2
Basidiomycota	Trechisporales	<i>Subulicystidium longisporum</i>	1	1	0	0	0	2
Ascomycota	Helotiales	<i>Tapesia fusca</i>	0	1	1	0	0	2
Basidiomycota	Polyporales	<i>Trametes gibbosa</i>	0	1	0	1	0	2
Basidiomycota	Trechisporales	<i>Trechispora farinacea</i>	0	1	0	1	0	2
Amoebozoa	Trichiida	<i>Trichia varia</i>	1	1	0	0	0	2
Basidiomycota	Pucciniales	<i>Uromyces dactylidis</i>	1	0	0	1	0	2
Basidiomycota	Pucciniales	<i>Uromyces junci</i>	0	1	1	0	0	2
Basidiomycota	Pucciniales	<i>Uromyces trifolii- repentis</i>	0	1	0	1	0	2
Ascomycota	Xylariales	<i>Virgaria nigra</i>	0	1	1	0	0	2
Basidiomycota	Corticiales	<i>Vuilleminia comedens</i>	1	1	0	0	0	2
Ascomycota	Teloschistales	<i>Xanthoria parietina</i>	1	1	0	0	0	2
Ascomycota	Xylariales	<i>Xylaria longipes</i>	1	0	0	1	0	2

## 7.5 Temporal variation in richness

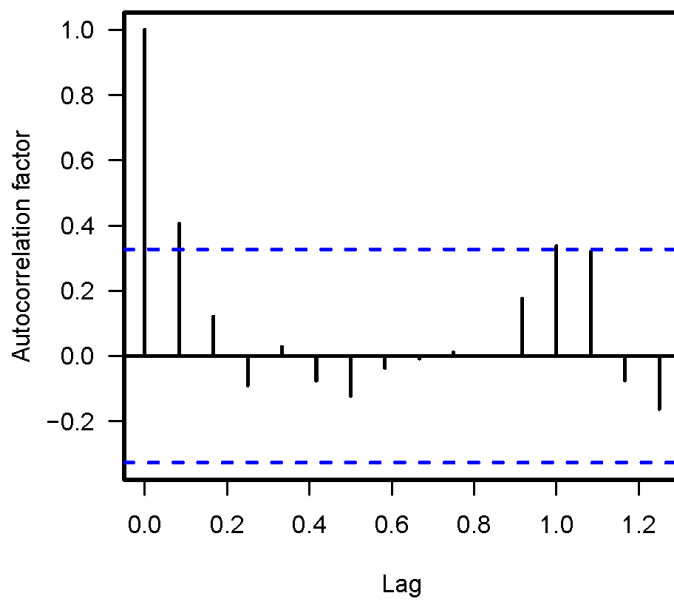


Figure S 1: Correlogram of fungal richness, showing autocorrelation across months (1.0 in the x-axis corresponds to a lag of 12 months). The dashed lines delimit the confidence interval.

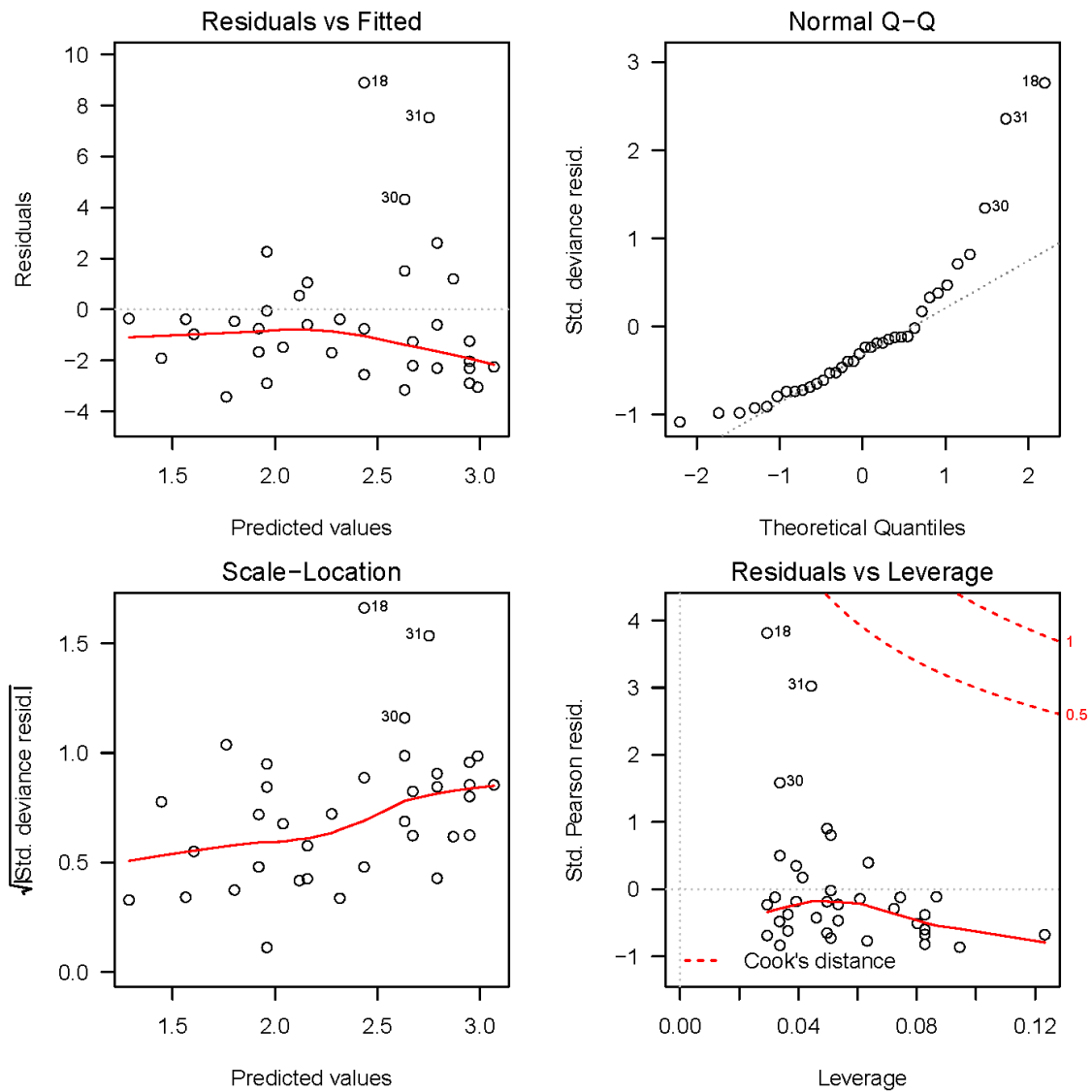


Figure S 2: Diagnostic plot for the generalized linear model (GLM) with the quasi-poisson regression for the explanatory variable temperature and the response variable richness of Agaricales species.

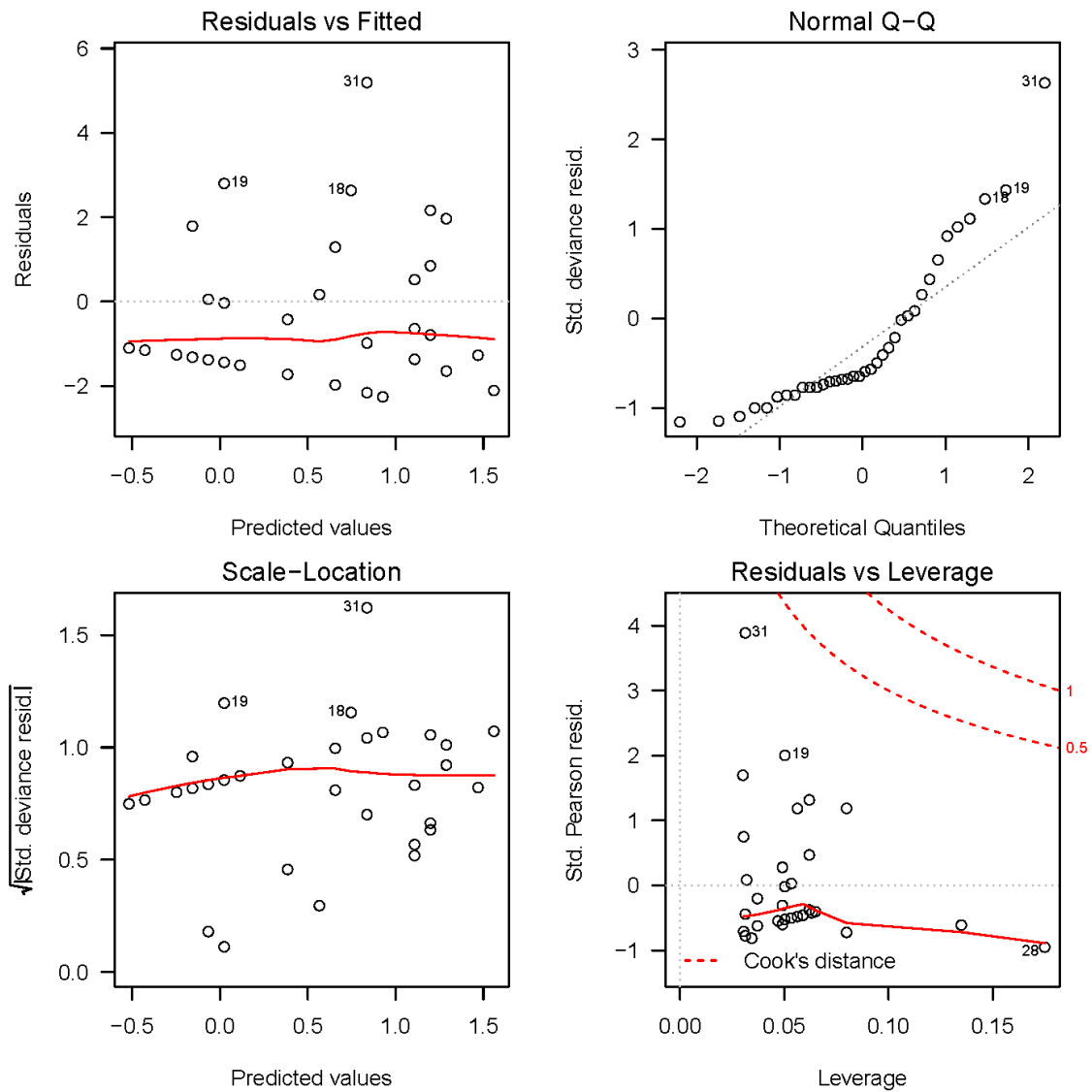


Figure S 3: Diagnostic plot for the generalized linear model (GLM) with the quasi-poisson regression for the explanatory variable temperature and the response variable richness of mycorrhizal species.