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Title

Ectomycorrhizal and saprotrophic soil fungal biomass are driven by different factors and vary among broadleaf and coniferous temperate forests

Authors and addresses

Abdallah Awad[1], Andrzej Majcherczyk[2], Peter Schall[3], Kristina Schröter[1], Ingo Schöning[4] Marion Schrumpf[4], Martin Ehbrecht[3], Steffen Boch[5,7], Tiemo Kahl[6], Jürgen Bauhus[6], Dominik Seidel[3], Christian Ammer[3], Markus Fischer[5], Ursula Kües[2], Rodica Pena[1]

[1] Forest Botany and Tree Physiology, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

[2] Molecular Wood Biotechnology and Technical Mycology, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

[3] Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

[4] Biogeochemical Processes and Biogeochemical Integration, Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745 Jena, Germany

[5] Institute of Plant Sciences and Botanical Garden, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland

[6] Chair of Silviculture, Faculty of Environment and Natural Resources, University of Freiburg, Tennenbacherstraße 4, 79106 Freiburg in Breisgau, Germany

[7] Biodiversity and Conservation Biology, Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

Corresponding author

Rodica Pena, Forest Botany and Tree Physiology, Faculty of Forest Sciences, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany

E-Mail: rpena@gwdg.de; Fax +49-(0)551-39-22705; Phone +49-(0)551-39-33485.

Running title

Ectomycorrhizal and saprotrophic fungal biomass

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Abstract

Functionally, ectomycorrhizal (ECM) and saprotrophic (SAP) fungi belong to different guilds, and they play contrasting roles in forest ecosystem C-cycling. SAP fungi acquire C by degrading the soil organic material, which precipitates massive CO_2 release, whereas, as plant symbionts, ECM fungi receive C from plants representing a channel of recently assimilated C to the soil. In this study, we aim to measure the amounts and identify the drivers of ECM and SAP fungal biomass in temperate forest topsoil. To this end, we measured ECM and SAP fungal biomass in mineral topsoils (0 -12 cm depth) of different forest types (pure European beech, pure conifers, and mixed European beech with other broadleaf trees or conifers) in a range of about 800 km across Germany; moreover, we conducted multi-model inference analyses using variables for forest and vegetation, nutritive resources from soil and roots, and soil conditions as potential drivers of fungal biomass. Total fungal biomass ranged from 2.4 ± 0.3 mg g^{-1} (soil dry weight) in pure European beech to 5.2 ± 0.8 mg g^{-1} in pure conifer forests. Forest type, particularly the conifer presence, had a strong effect on SAP biomass, which ranged from a mean value of 1.5 ± 0.1 mg g^{-1} in broadleaf to 3.3 ± 0.6 mg g^{-1} in conifer forests. The European beech forests had the lowest ECM fungal biomass (1.1 ± 0.3 mg g^{-1}), but in mixtures with other broadleaf species, ECM biomass had the highest value (2.3 ± 0.2 mg g^{-1}) among other forest types. Resources from soil and roots such as N and C concentrations or C: N ratios were the most influential variables for both SAP and ECM biomass. Furthermore, SAP biomass were driven by factors related to forest structure and vegetation, whereas ECM biomass was mainly influenced by factors related to soil conditions, such as soil temperature, moisture, and pH. Our results show that we need to consider a complex of factors differentially affecting biomass of soil fungal functional groups

58 and highlight the potential of forest management to control forest C-storage and the
59 consequences of changes in soil fungal biomass.

1. Introduction

In temperate and boreal forests, soil microbial biomass is dominated by free-living saprotrophic (SAP) and biotrophic fungi (Joergensen and Wichern, 2008), which access large pools of carbon (C) and other nutrients (Baldrian and Valásková, 2008; Ekblad et al., 2016; Heinemeyer et al., 2007; Högberg et al., 2001). The biotrophic fungi are in principal associate with roots, and in the temperate forests, where majority of trees form ectomycorrhizal (ECM) symbiosis, at the soil level, mycelial biomass mainly belong to ECM fungi (Goldmann et al., 2015; Schröter et al., 2018). The two fungal guilds (*sensu* Root, 1967; Nguyen et al., 2016) accomplish contrasting functions, which contribute to how much of C-input to the soil is stored or released into the atmosphere as CO_2 (Averill et al., 2014; Johnson and Gehring, 2007). SAP fungi acquire C by degrading the soil organic material, which precipitates massive CO_2 release (Boddy et al., 2007). As plant symbionts, ECM fungi receive C from plants (20-30% of total net primary production, Hobbie et al., 2012; Söderström and Read, 1987) and represent the main channel of recently assimilated C to the soil (Godbold et al., 2006; Hendricks et al., 2016). Soil fungi contribute to C-storage through their mycelial biomass (Averill et al., 2014; Clemmensen et al., 2013); this has been estimated to be as high as 11.6×10^3 kg ha^{-1} in mixed forests of conifer with broadleaf species (soil depth 0.7 m, Ekblad et al., 2013) with a turnover of about 10x yr^{-1} (reported only for ECM fungi by Ekblad et al., 2016; Hagenbo et al., 2017; Hendricks et al., 2016). As such, quantifying the relative abundance and identifying drivers of SAP and ECM biomass are critical for predicting forest soil C-storage and the consequences of changes in fungal biomass.

ECM and SAP guilds share the same habitat and interact with each other, competing for limited soil resources, which can result in growth inhibition for both (microcosm study; Leake et al., 2002). Inhibition of SAP growth and activity due, in some cases, being outcompeted by ECM

fungi (Koide and Wu, 2003; Lindahl et al., 2001; Rasanayagam and Jeffries, 1992) slows down decomposition rates (Fernandez and Kennedy, 2016; Gadgil and Gadgil, 1971) and leads to a potential increased C-storage in the forest soils. The outcome of inter-guild interactions depends, however, on C-availability. SAP fungi show higher competitive abilities for nutrient uptake than ECM fungi when C- availability is not limited (Bödeker et al., 2016; Lindahl et al., 2001).

It has been suggested that site nutrient availability is the main driver of the amount of C-input into the soil either via leaf litter or ECM fungi, i.e., recently assimilated C (Högberg et al., 2003). Thus, under nutrient limitations, plants deliver high amounts of C to ECM fungi boosting their abilities to acquire and transfer the scarce amounts of nutrients. Under unrestricted nutrient availability, plants generate large quantities of nutrient-rich litter providing a plentiful C-source for SAP fungi (Högberg et al., 2010, 2003). In accordance with this suggestion, nitrogen (N) deposition and fertilization lower ECM fungal biomass (Högberg et al., 2010; Nilsson et al., 2007; Nilsson and Wallander, 2003). Other studies have reported that the most nutrient-rich conditions, in the absence of anthropogenic N deposition (Kalliokoski et al., 2010; Sterkenburg et al., 2015; Lindahl and Clemmensen, 2016), and N-addition to a nutrient-poor site (Clemmensen et al., 2006) or to the microcosms (Bidartondo et al., 2001) resulted in a positive effect on ECM biomass. In addition, Hendricks et al. (2016) reported an increase in ECM biomass through the use of N-fertilizers in conjunction with a diminution of C-availability resulting from leaf scorching. ECM and SAP biomass might be driven by C-availability via site fertility, but the contrasting results suggest that additional factors might be involved. For example, all of the following have been reported to influence SAP or ECM fungal biomass: soil pH (Bååth et al., 2004, 1995; Rousk et al., 2009; Sterkenburg et al., 2015), moisture (Majdi et al., 2008; Mohan et al., 2014), and temperature (Clemmensen et al., 2006), fungal diversity

(Tedersoo et al., 2016), tree basal area (Tedersoo et al., 2016), and forest age (Wallander et al., 2010) (details in Appendix S1). Although each of these factors may contribute to variation of SAP and ECM fungal biomass in a particular environment, a comprehensive analysis across a range of forest types has not yet been performed.

In this study, one of our aims was to identify the relative importance of forest and vegetation attributes, soil and root chemical components, and soil conditions in explaining a unique part of variation in SAP and ECM biomass across 69 stands of typical Central European temperate forests (in a range of 800 Km, Biodiversity Exploratories Project, Fischer et al., 2010). The forests, composed of the most dominant temperate tree species, were classified into four types: (1) pure European beech, (2) pure conifers, (3) mixed European beech with other broadleaf tree species, and (4) mixed European beech with conifers. Because different tree species have profoundly diverging effects on soil pH, nutrient cycling, and site fertility (Augusto et al., 2015), we anticipated contrasting effects of the various forests on SAP and ECM biomass.

Given the strong link between site fertility and plant investment in ECM fungal symbionts, as well as the strong connection between the amount and quality of plant litter and SAP fungal growth, we hypothesized that SAP biomass would increase and ECM biomass would decrease in broadleaf relative to conifer forests. This is because broadleaf forest soils are characterized by higher pH values, lower C/N ratios, a higher content of base cations, and a faster rate of organic matter decomposition, whereby plant dependency on ECM fungi is possibly lower than in conifer forests (Augusto et al., 2015; Dawud et al., 2017). Furthermore, we hypothesized that forest attributes have a stronger influence on SAP than on ECM biomass. In contrast, we expected that resources would have similar effects on both guilds, but soil conditions (pH, temperature, moisture, and structure) have less influence on SAP than on ECM biomass.

Although SAP fungi are trophically independent and ECM fungi are biotrophic depending on plant partners, the association between ECM and the plant is regulated by soil fertility and quality, whereas SAP fungi have, via leaf litter, a direct relationship with the plant.

2 Materials and Methods

2.1 Study sites

We conducted the study using 69 experimental plots (EPs) established in the large-scale and long-term Biodiversity Exploratories Project (Fischer et al., 2010). The plots were located in three regions (Exploratories) of Germany: Schorfheide-Chorin (SCH) in the Northeast; Hainich-Dün (HAI) in the Central part; and Schwäbische Alb (ALB) in the Southwest. Details on the region characteristics, including climatic parameters, are given in Table 1. EPs (100 × 100 m) encompassed forest stands of varied composition (Schall et al., 2018) as follows: 1) pure European beech (*Fagus sylvatica* L ., beech, 28 EPs); 2) European beech mixed with other broadleaf species such as ash (*Fraxinus excelsior* L.), maple (*Acer pseudoplatanus* L.), and hornbeam (*Carpinus betulus* L.) (beech/ broadleaves, 16 EPs); 3) European beech mixed with coniferous species such as Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst) (beech/conifers, 13 EPs); 4) coniferous stands of Scots pine or Norway spruce (conifers, 12 EPs). We selected EPs over a range of silvicultural management from long-term unmanaged forests in nature reserves to managed forests, where repeated thinning or selective tree harvests had been applied (Schall and Ammer, 2013) and across a gradient of 43 explanatory variables, hypothesized to influence soil fungal biomass. The variables related to forest and vegetation (22), soil and root chemical components, nutritional resources for fungi (14), and soil conditions (7 variables) (Table S1). A detailed description of reasons for selection of explanatory

variables is given in the supplementary material (Appendix S1). For details on the measurement of environmental variables, see the supplementary material (Appendix S2). Data are available from the Biodiversity Exploratory Information System (BExIS, www.bexis.uni-jena.de).

2.2 Sample collection

We collected the samples during November 2014 using a soil core: diameter = 5 cm and length = 12 cm. In each EP we plotted two 40 m long transects perpendicular to each other (north-south and east-west). To account for plot heterogeneity, we collected the samples at seven locations: at the 1, 13, 25, and 37 m mark on the north-south and at 7, 19, and 31 m on the east-west transect. We then combined them into a composite sample for each EP. The samples were all extracted from the upper 12 cm of topsoil (A- horizon). We kept them at a constant temperature of 4°C. Within six to eight hours after gathering our samples, we stored soil aliquots at -20°C for the subsequent extraction of ergosterol.

2.3 Extraction and analysis of ergosterol

To distinguish between ECM and SAP fungal biomass, we used the approach described by Bååth et al. (2004) and modified by Hendricks et al. (2016). This method assumes that in the soil samples, ECM fungal ergosterol degrades during incubation of soil in darkness at 25°C and constant moisture for five months, since ECM fungi in contrast to SAP fungi, cannot survive a deprival of their plant carbon supply (Bååth et al., 2004). Thus, by subtracting the ergosterol concentration in the soil, which was measured post-incubation, from that measured before incubation, we obtained the ergosterol concentration attributed to ECM (Bååth et al., 2004). To

this same end, we also measured the ergosterol concentration in soil samples prior to incubation and in samples incubated for five months.

For ergosterol extraction, we used 20 g samples of previously freeze-dried soil material (Dieter Piatkowski, Forschungsgeräte-Vertrieb, Munich, Germany), which we then ground into a powder using a mortar and a pestle. Taken from each sample, we placed 2.0 g of soil in a 15-ml Falcon tube and added, as an internal standard, 10.0 ml of 10% KOH-methanol extraction solvent (100 g KOH, 1000 ml methanol), 200 mg l^{-1} 2.6-di-tetrabutyl-4-methyl-4-methyphenol, and 5.0 mg l^{-1} cholesterol (Sigma-Aldrich, Steinheim, Germany). We incubated the mixture in a water bath at 60°C vigorously shaking it every 30 min for 3 hours. After that, we let it cool to room temperature and then applied centrifugation for 15 min at 2000 rpm (Eppendorf Centrifuge 5810R, Eppendorf GmbH, Hamburg, Germany). We transferred 4 ml of the supernatant mixed with 2.0 ml of n-hexane and 4 ml of dH2O to a 15-ml Falcon tube. After shaking the samples for 15 min on a horizontal shaker (SA-31, Yamato Scientific Co. Ltd., Tokyo, Japan), we centrifuged them for 15 min at 2000 rpm and transferred 1.0 ml of the upper hexane phase to a 1.5-ml Eppendorf tube. Subsequently, we dried the hexane extract using a vacuum centrifuge (Eppendorf concentrator 5301, Eppendorf GmbH, Hamburg, Germany), and stored it at -20 °C.

Prior to analysis, sterol (ergosterol and cholesterol as internal standards) were silylated with 50 µl BSTFA (Serva, Heidelberg, Germany) and 50µl dry pyridine (Thermo Fisher Scientific, Dreieich, Germany). We incubated the samples at 70°C for 30 min, dried them using the vacuum centrifuge, and then dissolved them in 300 µl dry toluene. We analyzed the samples by GC-MS (Gas-Chromatography with programmable temperature vaporization inlet, Agilent6890N, coupled to a mass selective detector Agilent MSD 5973, Agilent, Little Falls, DE, USA). The column used for GC-MS was the DB-5M. Its dimensions were 30 m long x 0.25 mm int. diam x

0.25 µm film (Agilent, Little Falls, DE, USA). We applied the following temperature program: initial temperature 80 °C for 1 min followed by 30°C min^{-1} to 240°C and 7°C min^{-1} to 320°C maintaining the final temperature for 3.5 min. Dilutions of pure ergosterol in concentrations of 25, 12.5, 6.25, 3.125, 1.563, and 0.78 µg ml^{-1} spiked with cholesterol (10.0 µg ml^{-1}) as internal standard were used for calibrations.

To determine ergosterol recovery using the above-described extraction procedure, we applied the sample preparation procedure using 2.0 g of autoclaved soil samples, spiked with 2.0 µg ergosterol. The trials revealed that in our soil samples the ergosterol recovery level was approximately 78%. We calculated the fungal biomass-based both on a conversion factor of 3.0 µg ergosterol to 1.0 mg dry fungal biomass in accordance with previous studies (Salmanowicz and Nylund, 1988; Wallander et al., 2001), and on a correction factor of 1/0.78 to compensate for the recovery of ergosterol (Hendricks et al., 2016). Although ergosterol has been long used as biomarker for fungal biomass in forested soils (Wallander et al., 2013 and references therein), it is important to bear in mind the possible bias in estimation of living biomass or contamination with soil ergosterol of non-fungal origin. Particularly, in the mineral soil, a portion of the total ergosterol appertains to esterified forms (Wallander et al., 2010), which are stable to degradation after fungal death (Yuan et al., 2008). Thus, in contrast to the common view that ergosterol is a good proxy of living fungal biomass (Antibus and Sinsabaugh, 1993; Montgomery et al., 2000; Nylund and Wallander, 1992), estimation of total ergosterol may also include a proportion of dead fungal mycelium. An advantage of using ergosterol to account for fungal biomass in the temperate forest soils is its specificity and abundance in Ascomycota and Basidiomycota fungi (Weete et al., 2010), which dominate this habitat (Schröter et al., 2018). However, ergosterol appears in small amounts in green microalgae (Avivi et al., 1967; Patterson, 1971) and protozoa

220 (Williams et al., 1966), which also may influence to a small extent (Fenchel, 2013) soil fungal
221 biomass estimation.
222 We converted soil fungal biomass concentration from weight (mg g^{-1}) to area (kg ha^{-1}) units
223 using the soil bulk density, which we calculated based on soil dry mass after removing stones
224 and root fragments. We also calculated the amount of C in fungal biomass assuming a C-content
225 of 45% in dry matter (Ekblad et al., 2013).
226
227 **2.4 Data analysis**
228 To analyze the data we utilized R statistical software (R Core Team, 2016, version 3.3.1). To
229 improve normal distribution and homoscedasticity of residuals, we checked the normality of
230 variables using the Jarque-Bera test, based on skewness and kurtosis measures, and, when
231 necessary, we transformed the data using ln-, sqrt-, or Box-Cox transformation. We checked the
232 collinearity between explanatory variables by inspecting the Pearson's pairwise correlation
233 matrix (corr function from hmisc package; Harrell Jr, 2016). Correlation coefficients $-0.7<r<0.7$
234 were regarded as high, and in these cases, we removed the variable in the pair, which we
235 considered the least biologically relevant (Table S2). We further assessed the linear relationships
236 between explanatory and response variables. The explanatory variables with a weak explanatory
237 power, $0.1 \leq r \leq 0.1$ (Fløjgaard et al. 2011) were excluded from the dataset (Table S1, S2). These
238 assessments resulted in slightly different explanatory variables for each response variable, ECM
239 or SAP biomass (Table S1).
240 To investigate the changes in SAP and ECM biomass with respect to forest type, we used linear
241 mixed-effect models (lmer function from lme4 package; Bates et al., 2015). To obtain R^2 from
242 the models, we calculated marginal and conditional R^2 (Nakagawa and Schielzeth, 2013). In the

mixed models, we used forest types as fixed factors and Exploratory (i.e., SCH, HAI, and ALB) as a random factor. We included Exploratory in the model, considering effects that may apply to all samples within a region (block random effects, Bolker et al., 2009). To account for a different number of observations per forest type, the modeling was based on the restricted maximum likelihood (REML) approach (Meyer, 1989). To identify in which forest type fungal biomass was significantly different, we performed Dunnett's Modified Tukey-Kramer pairwise multiple comparison test adjusted for unequal sample size (dtk function from DTK package; Lau, 2013).

We used two independent approaches to assess the importance of explanatory variables in predicting a unique portion of the variation of soil fungal biomass. We separated the variables in three groups, as follows: forest-, resources-, and soil conditions-related variables (Appendix 1, Table S1). We first used variance partitioning, based on partial linear regression of SAP or SAP fungal biomass variable on a matrix containing each group of explanatory variables (Legendre, 2008) as implemented by varpart function from vegan package (Oksanen et al., 2017), to assess the influence of previously defined groups. Second, we employed the multimodel inference approach (Burnham and Anderson, 2002) to partition the relative importance of each variable. This approach compares and ranks a set of priori formulated competing models, and enables inference from more than one model (model averaging; Burnham and Anderson, 2002; Grueber et al., 2011). We constructed a global linear regression model for each explanatory variable group (Forest, Resources, and Soil) of each response variable; using the dredge function from MuMIn package (Barton, 2013) we run the selection of the best-fitted model with subsets of all possible combinations of variables of the global model. For each group, the top model set, containing all models with $\Delta AICc < 2$ relative to the model with the lowest AICc value, were averaged (model.avg function from MuMIn package; Barton, 2013). The explanatory variables

with a significant relative importance in each group in the averaged model were selected for a final global model. This model was dredged, and the best AICc ranked models were averaged in a very last model of the analysis.

In the group Resources, in ECM fungal biomass global model, we included the interaction term between the root fructose and inorganic N soil concentrations. The justification for this inclusion is that the possible effect of root nonstructural carbohydrates on ECM fungal biomass may depend on the values of soil N availability (but see Wallander and Nylund, 1991).

In order to evaluate the predictive accuracy of the selected models, we calculated the area under the receiver operating characteristic (ROC) curve using multiclass.roc function from package pROC (Robin et al., 2011) as an internal validation. To assess the robustness of the final model, containing the most important selected variables, we performed the 10 k-folds cross-validation procedure to estimate the mean square prediction error (cv.lm function from DAAG package; Maindonald and Braun, 2015). The K-fold algorithm split the entire dataset into 10 random subsets of approximately equal size, fitting the model with a k-1 subset and measuring prediction accuracy of the remaining subset (Olson and Delen, 2008). This step was repeated 10 times until each subset was predicted once and used to fit the model 10-1 times. We calculated the mean squared error (MSE) of the model and compared it to the mean square prediction error. The similar values of the two means indicate a validated predictive accuracy of the selected model (Neter et al., 1996).

Further, we accounted for predictor variation with respect to the forest type by utilizing one-way ANOVAs followed by the post-hoc Tukey HSD (aov and TukeyHSD functions from multcomp package; Hothorn et al., 2008).

290 **3 Results**

291 **3.1 Saprotrophic and ectomycorrhizal fungal biomass varies with the forest type**

292 Across all 69 forest plots mean total fungal biomass ranged from 2.4 ± 0.3 in pure beech to 5.2 ±
293 0.8 mg g^{-1} (soil dry weight) in conifer stands. Intermediate values were determined in mixed
294 beech/broadleaf (3.9 ± 0.3 mg g^{-1}) and beech/conifer stands (4.6 ± 0.6 mg g^{-1}). The amount of
295 SAP biomass was approximately twice as high as ECM biomass in conifer (t-test, $P = 0.002$) and
296 beech/conifer (t-test, $P = 0.008$) forests. We found no differences between SAP and ECM
297 biomass in pure beech or mixed beech/broadleaf stands (Fig. 1A, B).
298 SAP biomass was higher in pure conifer and mixed beech/conifer than in pure beech or mixed
299 beech/broadleaf stands (Fig. 1A). ECM biomass was similar in all forest types, except for the
300 significant difference ($P = 0.003$) between beech/broadleaf and pure beech stands (Fig. 1B).
301 Mixed effect models showed that both SAP ($F_{3, 64}$=11.44; $P < 0.001$) and ECM ($F_{3, 64}$=3.98; $P =$
302 0.011) biomasses were significantly influenced by forest type, which explained the 31% and
303 15% variance of SAP and ECM biomass, respectively (Table S3 and S4). The mixed effects
304 models explained together with the study region (Exploratory) as a random factor, 44% of SAP
305 and 21% of ECM biomass (Table S3 and S4). The low level of contribution of the study region
306 on the final model output indicates that the effect of forest type on fungal biomass was apparent
307 throughout all three geographical locations (Table S3 and S4).
308

309 **3.2 Relative importance of explanatory variables in predicting soil fungal biomass**

310 Variance partitioning revealed that 51.6% (SAP biomass, 18 variables), and 23.9% (ECM
311 biomass, 16 variables) of the total variance was explained by selected variable groups (Fig. 2A).
312 Variation of SAP biomass was mainly explained by Resources group (50%), including a large

313 share (20%) of overlapping contribution with the Forest group, the second most influential
314 group, whereas Soil conditions group had the lowest (5%) contribution (Fig. 2A). In contrast to
315 SAP, variance of ECM biomass was mainly explained by Soil (22%), and Resources (24%)
316 variables, whereas Forest group accounted only for a total contribution of 10% (Fig 2B).
317 Relative importance of individual explanatory variables, considered in each group, varied with
318 the fungal guild (Table 2). For SAP biomass, the most important Forest-related variables were
319 tree basal area and proportion of harvested tree biomass, while for ECM biomass, the stand
320 structural complexity (Table 2). In the Resources group, the most important variables were soil
321 organic C concentration for SAP biomass and N concentration and root fructose concentrations
322 for ECM biomass (Table 2), whereas soil C: N ratio had a strong effect, equally important, on
323 both fungal guilds (Table 2). In the Soil conditions group, the soil temperature revealed the
324 largest relative importance for ECM biomass (Table 2).
325 The final averaged models, based on pre-selection of most important variables of each variable
326 groups, revealed that SAP biomass was best predicted by two Resource-related variables, soil C:
327 N ratio and organic C concentration, and two Forest-related variables, tree basal area, and to a
328 lesser extent proportion of harvested tree biomass (Table 3). The linear model comprising the
329 selected best explanatory variables explained 54% of the variation within SAP fungal biomass
330 data (Table 3). Variation of ECM biomass was best explained by similar Resources-related
331 variables as SAP biomass, soil C: N ratio and N concentration. Organic C and N soil
332 concentrations were highly correlated ($r = 0.9$, Table S2). In addition, root fructose
333 concentration, with a negative influence, contributed to partition of ECM biomass variance to
334 Resources (Table 3). In contrast to SAP biomass, which was not influenced by Soil conditions

variables, ECM biomass revealed strong negative effects of soil temperature (Table 3). The model, which best predicted ECM biomass explained 31% of ECM biomass variation (Table 3). We next considered whether the important variables, selected by model-averaging procedure, mediate the differences in fungal biomass among the forest types and if this is, indeed the case, how this occurs. To this end, we analyzed the variation of model-selected variables with regard to the forest type. The pattern of SAP biomass variation of larger amounts in the conifer compared with deciduous forests, or ECM biomass of higher values in beech/broadleaves compared with other forest types were not followed by any variable (Fig. 3).

4 Discussion

4.1 Carbon pools in saprotrophic and ectomycorrhizal fungal biomass in coniferous and deciduous temperate forests

This study shows that fungal biomass is an important C-pool in temperate forest soils. Assuming that fungal mycelium is comprised of approximately 45% C (Ekblad et al., 2013), we calculated C-pool of fungal biomass to be about 1450 kg C ha^{-1}, which represents about 5% of organic C in the soil (Table S5). In other studies, fungal biomass C-pool exceeded the fine root biomass C-pool by a factor of almost two (Majdi et al., 2008; Soudzilovskaia et al., 2015) that may also correspond in our study region (data not shown). However, this fungal contribution to soil C-stock might be regarded as high in comparison to other reports (Bauhus and Khanna, 1999). The mean values of ECM fungal biomass (900-1900 kg ha^{-1}) were similar to those reported in Norway spruce and mixed Norway spruce-oak forests in the boreal zone (700 kg ha^{-1}, Wallander et al. 2001; 1700 kg ha^{-1}, Wallander et al., 2004; Wallander et al., 2001), and three to six times higher than values found in a subtropical longleaf pine forest (300 kg ha^{-1}, Hendricks et al.,

2016). SAP fungal biomass ranged from 1200 (beech forests) to 3300 kg ha^{-1} (conifer forests). These values exceeded, by far, those reported in Norway spruce (500 kg ha^{-1}) or mixed Norway spruce-oak (800 kg ha^{-1}) forests in Sweden at a similar soil depth (Wallander et al., 2004). It is probable that SAP reside and proliferate in the topsoil (Zavišić et al., 2016) of temperate forests more than in boreal forests. The latter are characterized by an abundant organic layer and a clear vertical distribution of the two fungal guilds (Edwards and Zak, 2010; Kyaschenko et al., 2017; Lindahl et al., 2007). In the boreal forests, SAP fungi are restricted to organic layer though they can colonize and even out-compete ECM fungi in different soil substrates (Bödeker et al., 2016). However, the direct comparison of biomass values with those reported in other studies requires caution since the ergosterol to biomass conversion factor may vary among fungal species, structures, and growth conditions (Wallander et al., 2013). Also, variation in sampling procedure or sampling season (Ekblad et al., 2013) could contribute to a different output as compared with other studies.

SAP and ECM fungal biomass varied according to forest type; both followed relatively similar patterns of being less prevalent in the pure beech than all other forests. However, in contrast to SAP fungal biomass, which was clearly influenced by the presence of conifers, ECM fungi displayed similar levels of biomass in mixed beech/broadleaf and conifer forests. These results infirm our hypothesis that ECM biomass decreases and SAP biomass increases in broadleaf in comparison to conifer forests, also contradicting the theory of Högberg et al. (2003, 2010) that ECM are favored under poor, and SAP fungi under rich soil nutrient conditions. The explanatory variables related to resources in soil also failed to explain variation of fungal biomass with forest type that indicates some more complex mechanisms behind regulation of soil fungal biomass. However, the amount of standing biomass depends on concurrent processes of biomass

production and death (Ekblad et al., 2016; Hagenbo et al., 2017, 2018; Hendricks et al., 2016). The drivers of these proceses are different (Hagenbo et al., 2017). In principle, it is possible that fungal (i.e., SAP) production alone is linked to organic C-availability, which, in turn, increases with the availability of soil nutrients (Högberg et al., 2003), but in the same time, fungal turnover varies with other variables (soil moisture, Ekblad et al., 2013). A major critical factor for both fungal production and turnover is fungal community composition (Clemmensen et al., 2015, 2013; Hagenbo et al., 2018), since the abundance and type of hyphae forming external mycelium (e.g., C-demanding hyphal cords, decomposition resistant melanized hyphae) vary with taxa identity (Agerer, 2001). In the studied area, long-distance exploration type ECM taxa (Agerer, 2001), which produce long-lived rhizomorphs (Cairney, 2012; Pritchard et al., 2008), are more common in the conifer than pure beech forests (Pena et al., 2017; Rosinger et al., 2018). The presence of rhizomorphs leads to lower turnover rate (Ekblad et al., 2013) and consequently enhances soil fungal biomass with conifer presence. Forest tree composition largely influences fungal communities (Bahnmann et al., 2018; Urbanová et al., 2015; Uroz et al., 2016). The difference between conifer and deciduous forests are particularly critic for SAP fungal community composition (Schröter et al., 2018) since SAP fungi largely rely on plant litter. The mixed as compared with monospecific forests give rise to enhanced variety of organic material sources, root exudation, soil distribution of fine roots (Genney et al., 2006; Rosling et al., 2003), and abundance of microclimates (Setälä, 2002). All these factors may contribute to a higher ECM fungal diversity and abundance in the mixed than pure forests (Lang et al., 2011). Based on the concept of species complementarity (Cardinale et al., 2007; Koide, 2000), higher ECM fungal diversity result into a higher biomass in mixed than pure beech forests.

4.2 Predictors of saprotrophic and ectomycorrhizal fungal biomass

All three categories of variables related to forest, resources for fungi, and soil conditions were important drivers of SAP and ECM biomass; however, according to our second hypothesis, SAP biomass was predicted by attributes related to forest (tree basal area, and proportion of harvested tree biomass) and resources (soil organic C and C: N ratio) and hardly by soil conditions. Contrastingly, the variation of ECM biomass was mainly explained by soil conditions (temperature) and resources (soil N, soil C: N ratio, and root fructose concentration), and less by forest stand properties. This may also explain the less differences among the forest types revealed by ECM compared with SAP biomass. We speculate that the plant influence through resource availability and niche differentiation was higher for SAP than ECM fungi. We assume that tree basal area, positively related to litterfall (Turnbull and Madden, 1983) and root biomass (Helmisaari et al., 2007), led to enhanced substrate availability and quantity of root exudates that positively influenced SAP fungal biomass (Eisenhauer et al., 2017; Philippot et al., 2013). In addition, the tree roots remain on the felling site after tree harvesting, offering a new enriched substrate for SAP fungal proliferation.

Both SAP and ECM biomass revealed a strong relationship concerning soil resources, organic C and total N. The two variables were highly correlated, therefore, we may expect that their influence is equally important for both fungal guilds as it was confirmed by the effects of soil C: N ratio. Abilities of SAP fungi to decompose organic substrates are stimulated by high substrate C: N ratio (Bossuyt et al., 2001; Six et al., 2006; Thiel et al., 2014), but also a positive relationship between fungal growth and N-concentration (Boberg et al., 2008) or inorganic N-addition in soil has been previously reported (Bardgett et al., 1999; Rousk and Bååth, 2007). There is, however, the possibility that soil mineral N-concentration may have a negative effect

on ECM fungal biomass (Wallander, 1995). This is because when N is readily available, C is more readily used for nitrogen assimilation (Bidartondo et al., 2001; Högberg et al., 2008) than for fungal vegetative growth. In our study, the bulk of the total soil N-pool is in organic form and is thereby less accessible for fungi and only a weak indicator of substrate N availability (Schulten and Schnitzer, 1997). Additionally, fungal community composition may shift from less mycelial biomass producing ascomycetes in poor N-soils to potential mycelial abundant basidiomycetes in rich N-soils (Lindahl and Clemmensen, 2016; Sterkenburg et al., 2015), resulting in a positive relationship between soil N concentration and ECM fungal biomass.

The negative effects of root fructose concentrations on ECM fungal biomass was contrary to what was anticipated. That was surprising given the dependence of ECM fungi on plant nonstructural carbohydrates (Nehls, 2008). As we mentioned above, the standing biomass measured in this study is the result of the contrasting processes of production and decomposition. Biomass production relies on the plant C investment into to fungal structures, but maintaining the external mycelium under a low turnover requires no high C costs (Hagenbo et al. 2017). A major critical factor for the ratio between production and decomposition is the fungal community composition (Clemmensen et al., 2015, 2013), since the abundance and type of hyphae forming external mycelium (e.g., C-demanding hyphal cords, decomposition resistant melanized hyphae) vary with taxa identity. We are aware that further research needs to address the importance of variables referring to biotic component represented by fungal community composition and chemical (Fernandez and Kennedy, 2018), structural and morphological (Hobbie and Agerer, 2009), and functional (Pena and Polle, 2014) diversity, as well as soil bacteria, protozoa, and animal communities.

4.3 Conclusions

Our study shows that forest type, especially when conifers are present, has a profound influence on SAP and less on ECM fungal biomass. Still, this effect does not appear to be connected to an alteration of soil organic C-stocks through differences in C-pools of the fungal biomass of the two fungal guilds. In comparison to the values reported from boreal forests, we recorded higher fungal biomass in the topsoils of temperate forests (representing about 5% of soil organic C-stock) that must be taken into account in C cycling models of forest ecosystems.

SAP and ECM fungal biomass are driven by different factors. In both fungal guilds, root and soil resources, such as N and C, are the most influential factors for fungal biomass. Factors related to forest structure and vegetation are more important for SAP than ECM biomass, whereas factors related to soil environment, such as soil temperature, moisture, and pH are in particular important for ECM biomass. The negative effect of root nonstructural carbohydrates on ECM fungal biomass is a surprising result, emphasizing the need to analyzing fungal biomass on a wider level in relationship with fungal taxonomical and functional community composition.

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818 **Figure captions**

819

820 Figure 1. Biomass of (A) saprotrophic (SAP) and (B) ectomycorrhizal (ECM) fungi in soil of
821 different forest types: pure European beech (Beech), European beech mixed with other broadleaf
822 species (Beech/Broadleaves), European beech mixed with coniferous species (Beech/Conifers),
823 and conifers (Conifers). All values are means ± SE (N = 28 for Beech, 16 for Beech/Broadleaves,
824 13 for Beech/Conifers, and 12 for Conifers). Different letters indicate significant different values
825 ($P \leq 0.05$).

826

827 Figure 2. Variance partitioning of the effects of Forest-, Resources-, and Soil conditions- related
828 explanatory variables on (A) saprotrophic (SAP) and (B) ectomycorrhizal (ECM) fungal
829 biomass. Cumulative values for each variance component are presented in each panel. (N = 69).

830

831 Figure 3. Variation of the most important explanatory variables of saprotrophic (SAP) and
832 ectomycorrhizal (ECM) fungal biomass among different forest types: pure European beech
833 (Beech), European beech mixed with other broadleaf species (Beech/Broadleaves), European
834 beech mixed with coniferous species (Beech/Conifers), and conifers (Conifers). Tree basal area
835 (A); stand structural complexity index (B); proportion of harvested tree biomass (C); soil total
836 nitrogen (D); soil organic carbon (E); soil C:N ratio (F); root fructose (G); root glucose (H); and
837 soil temperature (I). Panels (A), (C) (E), (F), and (H) present variables related to SAP biomass.
838 Panels (B), (D), (F), (G), and (I) present variables related to ECM biomass. All values are means
839 ± SE (N = 28 for Beech, 16 for Beech/Broadleaves, 13 for Beech/Conifers, and 12 for Conifers).
840 Different letters indicate significant different values ($P \leq 0.05$).

Tables

Table 1. Location, climatic conditions and sampling design in three geographic regions (Exploratories) in Germany (Fisher et al. 2010).

Region	Longitude	Latitude	Size (km²)	Elevation a.s.l (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Forest type (no. of plots)			
							Beech	Beech/ broadleaves	Beech/ conifers*	Conifers
SCH	13.39 - 14.14	52.79 - 53.22	1300	3 - 140	8 - 8.5	520 - 600	8	0	8	6
HAI	10.17 - 10.77	50.93 - 51.37	1300	285 - 550	6.5 – 8.0	750 - 800	14	6	2	1
ALB	09.18 - 09.59	48.34 - 48.53	422	460 - 860	6.0 – 7.0	938 - 963	6	10	3	5

*Conifers were spruce (*Picea abies*) in ALB and HAI, and pine (*Pinus sylvestris*) in SCH.

Table 2. Relative importance of explanatory variables for saprotrophic (SAP) and ectomycorrhizal (ECM) fungal biomass following the model-averaging procedure for each variable groups: Forest, Resources, and Soil conditions. (N = 69).

		SAP			ECM		
Group	Explanatory variables	Relative importance	Estimate	P-value	Relative importance	Estimate	P-value
Forest	Age of the main tree species	0.12	0.00 (0.00)	0.43	0.56	0.00 (0.00)	0.03
	Tree basal area	1.00	0.02 (0.01)	<0.00			
	Proportion of harvested tree biomass	1.00	0.68 (0.19)	<0.00	0.55	0.37 (0.23)	0.10
	Canopy openness	0.29	0.15 (0.11)	0.20	0.32	-0.21 (0.15)	0.18
	Number of deciduous tree species		-0.04 (0.07)	0.53			
	Shannon index (herb species)	0.11	0.05 (0.07)	0.48			
	Stand structural complexity				0.72	0.09 (0.04)	0.03
	Stand tree density	0.21	0.1 (0.13)	0.42	0.43	0.21 (0.16)	0.19
Resources	C:N ratio in mineral soil	1.00	0.68 (0.11)	<0.00	1.00	0.34 (0.16)	0.03
	Organic C in mineral soil	1.00	0.17 (0.02)	<0.00			
	Total N in mineral soil				1.00	0.14 (0.04)	0.00
	C:N ratio in organic layer	0.12	-0.43 (0.57)	0.46			
	C in the fine tree roots				0.29	0.00 (0.00)	0.35
	Fructose in the fine tree roots	0.44	0.05 (0.04)	0.14	0.86	-0.1 (0.05)	0.05
	Glucose in the fine tree roots	0.68	0.03 (0.02)	0.08			
	Root resource index				0.50	0.05 (0.03)	0.18
Soil conditions	Soil bulk density	na	-0.35 (0.19)	0.06	0.60	-0.38 (0.23)	0.11
	Soil moisture				0.34	-0.01 (0.01)	0.26
	Soil pH				0.52	1.05 (0.73)	0.16
	Soil temperature	na	-0.01 (0.05)	0.77	1.00	-0.13 (0.06)	0.02

na = no averaged-model possible, only one model available

Table 3. Relative importance of explanatory variables for saprotrophic (SAP) and ectomycorrhizal (ECM) fungal biomass following the model-averaging procedure. The variables were pre-selected by group-based model-averaging. (*N* = 69).

SAP	Relative importance	Estimate (SE)	P-value
Tree basal area	1.00	0.01 (0.00)	0.01
Proportion of harvested tree biomass	0.60	0.28 (0.16)	0.08
C:N ratio in mineral soil	1.00	0.61 (0.11)	0.00
Organic C in mineral soil	1.00	0.16 (0.03)	0.00
Glucose in the fine tree roots	0.35	0.02 (0.02)	0.30

Four component model (52.4>AICc<54.2). Area under ROC curve= 0.99.
[SAP ~ basal_area + Iharv + Mineral_CN + Organic_C + Root_Glucose]
Residual standard error= 0.23, multiple R^2= 0.57, adjusted R^2= 0.54, F= 17.1, on 63 degrees of freedom, P < **0.001**. Overall mean square of prediction error = 0.063.

ECM	Relative importance	Estimate (SE)	P-value
C:N ratio in mineral soil	1.00	0.42 (0.15)	0.01
Total N in mineral soil	1.00	0.09 (0.04)	0.01
Fructose in the fine tree roots	1.00	-0.12 (0.05)	0.01
Soil temperature	1.00	-0.15 (0.05)	0.01
Stand structural complexity	0.29	0.03 (0.04)	0.43

Two component model (6.42>AICc<8.21). Area under ROC curve= 0.96.
[ECM ~ Mineral_CN + Mineral_temperature + Mineral_Total_N + ssc_mean + Root_Glucose]
Residual standard error= 0.33, multiple R^2= 0.36, adjusted R^2= 0.31, F= 7.28, on 63 degrees of freedom, P < **0.001**. Overall mean square of prediction error = 0.123.

Figure 1

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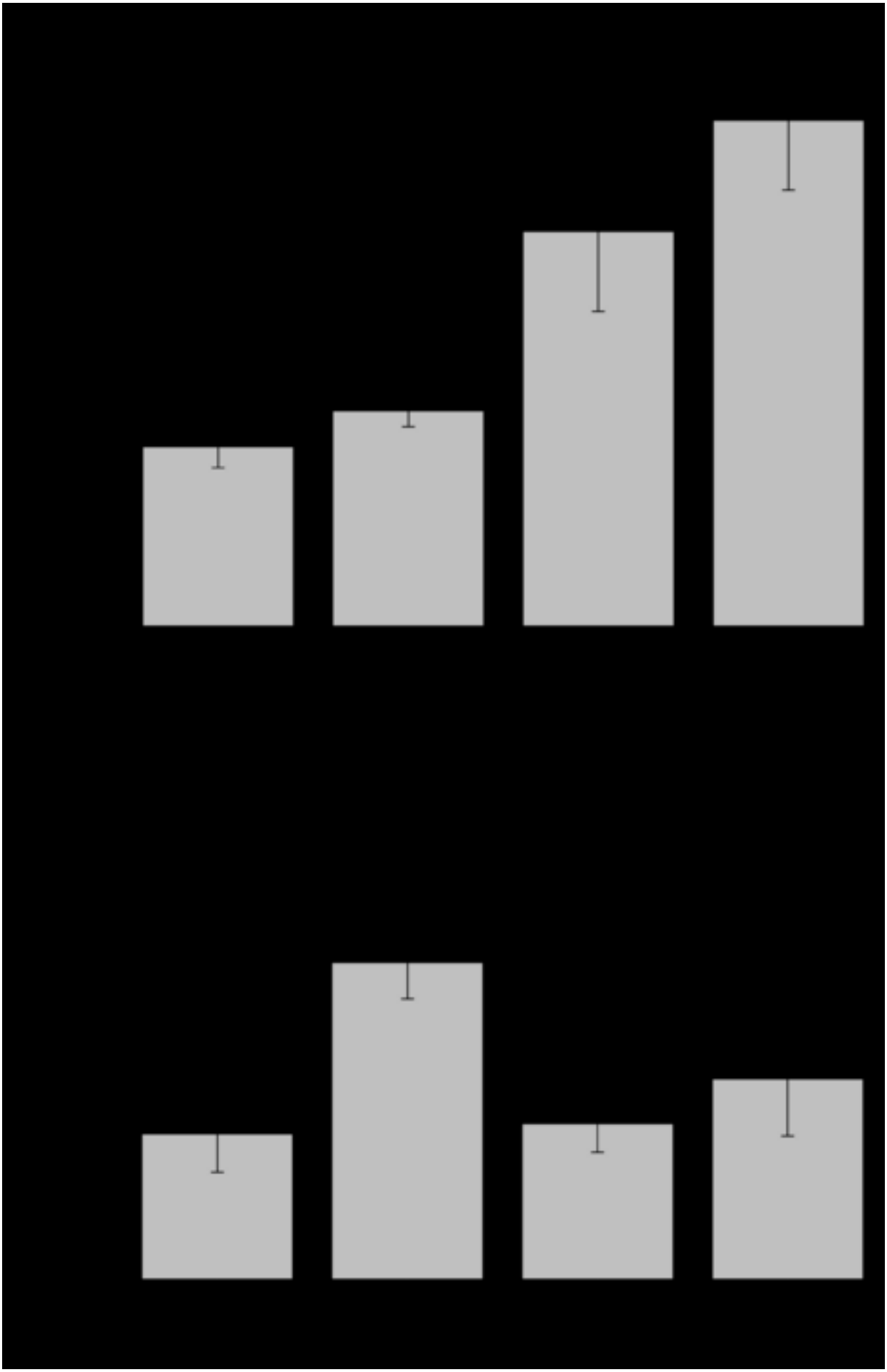

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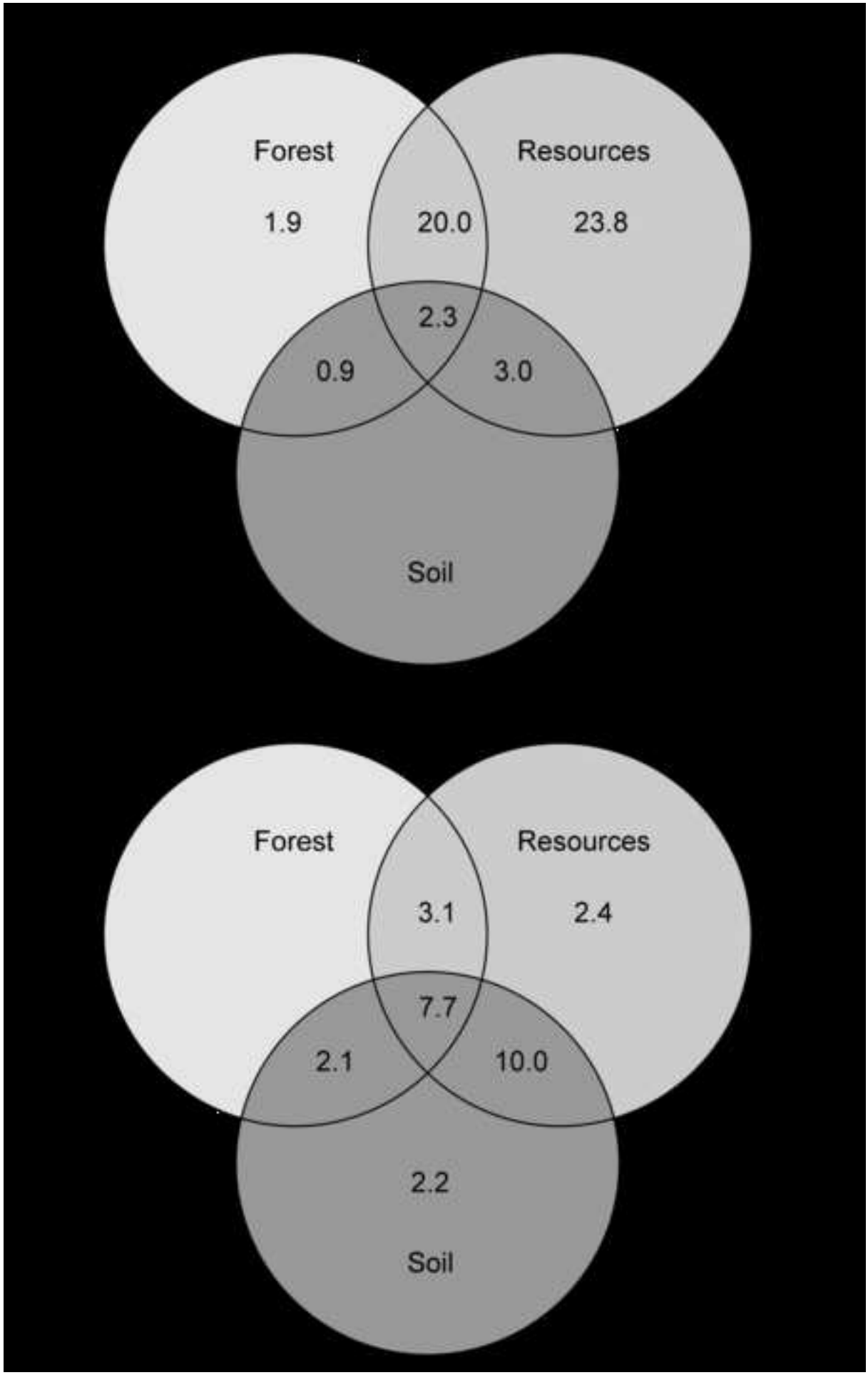

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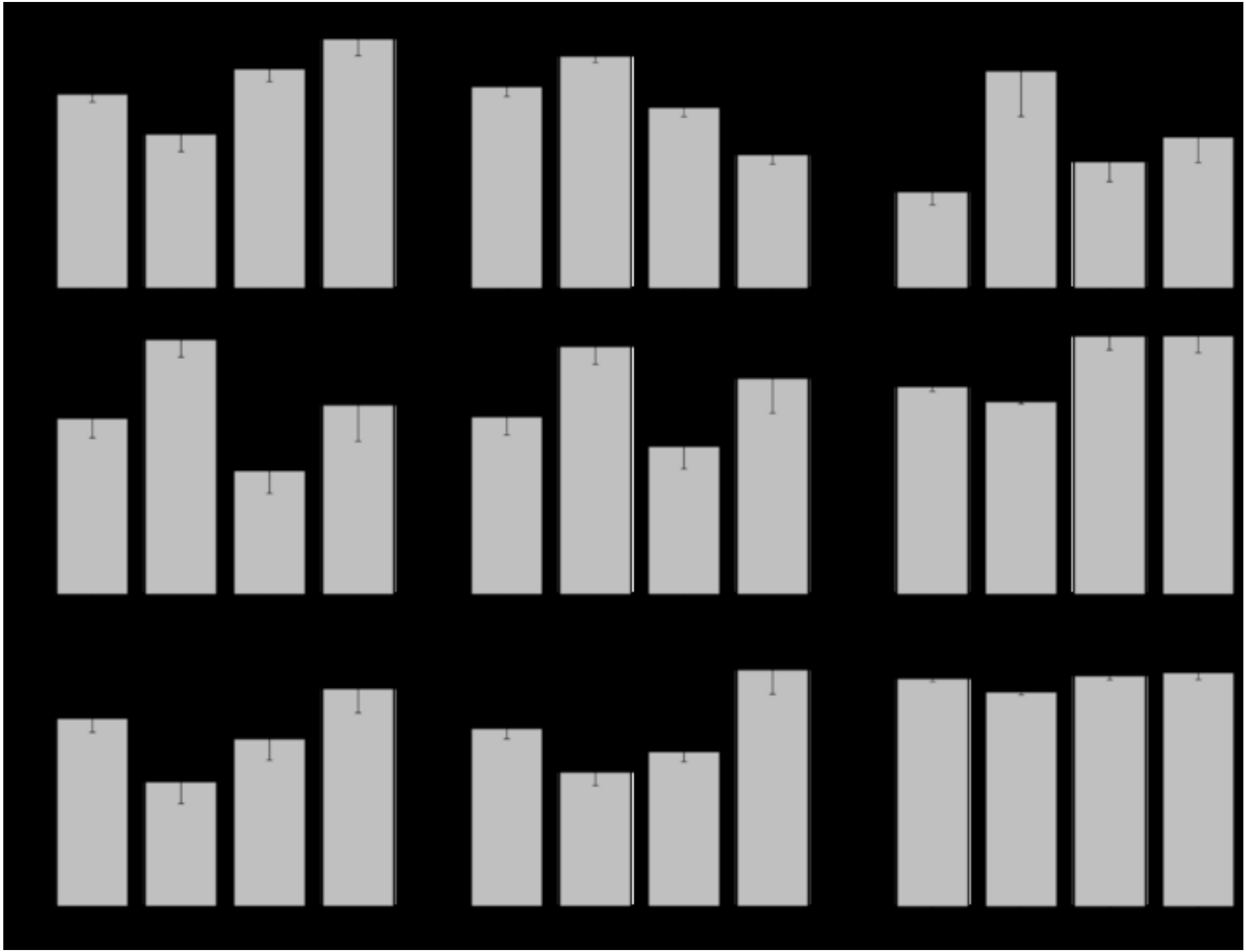

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