



Distribution patterns of arbuscular mycorrhizal and non-mycorrhizal plant species in Germany



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ABSTRACT

We analysed the spatial distribution patterns of plant species' arbuscular mycorrhizal status across an intermediate geographical scale (i.e. the country of Germany) and related these distributions to environmental drivers. Three levels of arbuscular mycorrhizal status of plant species could be defined: (1) obligate arbuscular mycorrhizal species that are always colonised by mycorrhizal fungi, (2) facultative arbuscular mycorrhizal species that are colonised under some conditions but not colonised under others and (3) non-mycorrhizal species that are never found to be colonised by mycorrhizal fungi. We aimed to investigate whether plant species assemblages at the studied grid cell scale are composed of different proportions of species regarding their arbuscular mycorrhizal status, and whether the variation of these proportions can be linked to the geographical variation of ecological and environmental factors. We fitted a vector generalised additive model (VGAM) for log-ratios of proportions of plant species' arbuscular mycorrhizal status per grid cell (2859 grid cells, each c. 130 km²). The spatially explicit plant arbuscular mycorrhizal status distribution model was based on environmental predictors related to climate, geology and land use. The spatial distribution of plant arbuscular mycorrhizal status can be explained as a function of nine environmental predictors ($D^2 = 0.54$). Proportion of obligate arbuscular mycorrhizal plant species per grid cell increased with increasing temperature range, mean annual temperature, urban area and area of lime as geological parent material and decreased with increasing area of mixed forest and coniferous forest. Annual temperature range was by far the most important predictor. These results extend the comparative context of former studies that established relationships between mycorrhizal status and other plant characteristics at species level, including those describing species ecological requirements, to a context at the level of assemblages and species distributions. We encourage integrating plant mycorrhizal status as a functional trait in future macroecological analyses.

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1. Introduction

Mutualistic associations formed by arbuscular mycorrhizal (AM) fungi and terrestrial plants are ancient and probably have existed since vascular plants colonised terrestrial habitats (Brundrett, 2002; Pirozynski and Malloch, 1975). AM fungi are widely dis-

tributed across most terrestrial ecosystems (Davison et al., 2015; Öpik et al., 2006, 2013; Smith and Read, 2008) and potentially establish a symbiosis with approximately 75% of all vascular plant species (Brundrett, 2009; Smith and Read, 2008). Mycorrhizas are known to affect plant nutrition (Koide, 1991), to improve and regulate plant water status (Augé, 2001), to offer protection from pathogens (Veresoglou and Rillig, 2012) and to possibly enhance biomass productivity (Klironomos et al., 2000). Whereas the symbiosis is obligate for AM fungi, some terrestrial plant species and families have partly or entirely lost their ability to form mycor-

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rhizal relationships (Brundrett, 2002; Fitter and Moyersoen, 1996). In principle, there are three levels of plant mycorrhizal status: (1) obligate arbuscular mycorrhizal plant species (OM) that are always colonised by AM fungi, (2) facultative arbuscular mycorrhizal plant species (FM) that are colonised under some conditions but not colonised under others and (3) non-mycorrhizal plant species (NM) that are never found to be colonised by mycorrhizal fungi (Moora, 2014; Smith and Read, 2008). Thereby, OM and NM plant species are specialised regarding their mycorrhizal strategy, whereas FM plant species are generalists and additionally show great differences in life-history trait characteristics compared to OM and NM species (Hempel et al., 2013).

Plant mycorrhizal status and plant mycorrhizal dependency (or responsiveness) are distinct plant traits not to be confused (Moora, 2014). A plant species' mycorrhizal status does not give direct information about functional significance of mycorrhizal colonisation of individuals of this species, but rather on the mere presence/absence of fungal colonisation among individuals of plant species. Thereby it offers a coarse proxy for estimating the importance of the mycorrhizal symbiosis for a plant at species level. Interactions of plants with AM fungi are potentially of great importance in shaping the ecology of the partners and whole communities (Klironomos et al., 2011; van der Heijden et al., 2003). Although there are a few biogeographic studies of AM fungi on a global scale (e.g. Davison et al., 2015; Kivlin et al., 2011; Öpik et al., 2010, 2013; Treseder and Cross, 2006), our understanding of the co-variation of plants and their associated mycorrhizal fungi (and thereby variation of importance of the mycorrhizal symbiosis) at larger scales remains quite limited. At the same time, distributions of plant species are relatively well studied and this provides an opportunity to study environmental drivers of the mycorrhizal symbiosis using plant mycorrhizal traits (e.g. mycorrhizal status) as a response variable in macroecological frameworks.

The recently published MycoFlor data base (Hempel et al., 2013) compiles information on plant mycorrhizal status for about half the species of the German flora (i.e. 1752 species; thus a major part of the Central European flora). It is publicly available and allows investigating whether plant species assemblages are composed of different proportions of plant species regarding their AM status, using available plant species distribution data. Hempel et al. (2013) showed that plant species with different mycorrhizal status are associated with different ecological requirements (i.e. species attributes). For example, using ecological indicator values of Ellenberg et al. (1992), they found that OM species tend to be associated with warmer, drier and more alkaline habitats, whereas NM species are species of wet and disturbed habitats. Following these associations, we predict to find different spatial patterns of plant species assemblages composed of species with different AM statuses, which are based on the geographical variation of these ecological and environmental conditions. While Hempel et al. (2013) analysed species attributes (functional traits and species realised preference, i.e. having species as replicates), the aim of the present study was to test whether actual spatial distributions of proportions of OM, FM and NM plant species exist (i.e. having spatial replicates). We used available literature information, including the findings reported by Hempel et al. (2013), to formulate predictions concerning the relationship between the distribution of the proportions of plant species with different mycorrhizal status and actual environmental predictors (Table 1: environmental drivers; Table 2: ecological predictions) to further extend the knowledge on this relationship in a spatial context. To test these predictions, we based a distribution model across the ordnance survey maps grid at the German country scale (i.e. grid cells with a size of 10' (arc minutes) longitude \times 6' latitude, i.e. circa 130 km² each) on a set of environmental predictors. We aim to unravel whether the rather locally acting plant-fungi interactions have an impact on plant

species distributions across a larger, intermediate geographical scale. Thereby we intend to detect the underlying environmental drivers of different AM plant strategies. This will not only help to understand the macroecology of plant-fungi relationships, but will contribute to establish plants' mycorrhizal status as a functional trait in analyses related to plant assemblages.

2. Materials and methods

2.1. Data sources

Plant species distribution data were compiled from the 2003 version of FLORKART, a database of the German Network for Phytodiversity, provided by the German Federal Agency for Nature Conservation (<http://www.floraweb.de>). For our analysis we used a grid where the total area of Germany is divided into cells of 10' longitude \times 6' latitude (arcminutes, i.e., c. 130 km²) size, resulting in 2995 grid cells. The database was assembled with the help of thousands of volunteer helpers, organised at a regional level. Therefore, mapping quality is heterogeneous across grid cells. To this end we followed a procedure suggested by Kühn et al. (2006), using 50 'control plant species' (which are considered to be ubiquitous) to characterise grid cells according to their mapping quality. Only grid cells containing at least 45 of these 50 species were considered during the analysis, finally resulting in 2859 cells.

We used the MycoFlor database (Hempel et al., 2013) to obtain information on mycorrhizal status per plant species. Although MycoFlor contains information on a range of mycorrhizal associations, we restricted the analysis to symbioses involving AM fungi, as they are the most cosmopolitan and largest group represented in MycoFlor. We then distinguished between OM, FM and NM plant species. We assigned the NM status to strictly non-mycorrhizal plant species, i.e. non-AM species that may form symbiotic relationships with other mycorrhiza types (e.g. ecto- or ericoid mycorrhiza) were excluded to avoid confounding the analysis by incorporating other types of mycorrhizal interaction. Information on plant mycorrhizal status within MycoFlor was verified and quality controlled. Successive citations were traced back and primary studies were counted to obtain information about data reliability. To assure appropriate data quality the authors recorded whether the source of information originated from a journal listed in Web of Science, EBSCO, SCOPUS, CABl, or a book/book chapter from an international publisher as a proxy for data quality. In that case, they assumed the publications passed through a peer review process or similar robust quality assessment (Hempel et al., 2013). They furthermore used a reduced 'core data set', only including plant species with at least two primary literature references reporting their mycorrhizal status and fulfilling their criteria for data quality. Using this core data set, AM status information was available for a total of 1019 plant species (i.e. 39% of the plant species with distributional information in Germany according to FLORKART as a reference); 438 were OM, 485 FM and 96 NM plant species. By amending plant compositional data with AM status information, each grid cell was characterised by compositional data of three proportions – p(OM), p(FM), p(NM) – that sum up to 1.

For each cell we compiled data on climate, land use and geology. Geological and pedological data were obtained from the Geological Survey Map of Germany (Bundesanstalt für Geowissenschaften und Rohstoffe, 1993). We used the covered area of geological substrate classes such as lime, sand, clay and loess per grid cell. Land-use data were taken from CORINE land cover data sets (Statistisches Bundesamt, 1997). We included area of rivers, area of agricultural fields, urban area (continuous and non-continuous urban areas classified by CORINE summed up), as well as the area of deciduous (i.e. broad-leaved trees), mixed and coniferous forest stands as

Table 1
Summary of selected environmental predictors, their abbreviations, units (per grid cell), mean, standard deviation (sd), minimum values (min) and maximum values (max) as well as data sources, i.e. CORINE Land Cover (CLC, Statistisches Bundesamt, 1997), EU project ALARM (ALA, Fronzek et al., 2012), and Geological Survey Map of Germany (GEO, Bundesanstalt für Geowissenschaften und Rohstoffe, 1993).

| Environmental predictor | Abbreviation | Source | Unit | Mean | Sd | Min | Max |
|---|---------------------------------------|--------|-----------------|------|-----|------|------|
| area of stream courses | stream area | CLC | km ² | 0.2 | 0.7 | 0 | 7 |
| area of deciduous forest stands | deciduous forest area | CLC | km ² | 7 | 10 | 0 | 87 |
| area of mixed forest stands | mixed forest area | CLC | km ² | 7 | 10 | 0 | 97 |
| area of coniferous forest stands | coniferous forest area | CLC | km ² | 16 | 19 | 0 | 106 |
| area of agricultural land use | agricultural area | CLC | km ² | 58 | 31 | 0 | 123 |
| area of urban land use | urban area | CLC | km ² | 8 | 10 | 0 | 104 |
| area of lime as geological parental material | lime area | GEO | km ² | 6 | 19 | 0 | 135 |
| area of loess as geological parental material | loess area | GEO | km ² | 6 | 15 | 0 | 114 |
| area of sand as geological parental material | sand area | GEO | km ² | 45 | 41 | 0 | 135 |
| area of clay as geological parental material | clay area | GEO | km ² | 7 | 19 | 0 | 123 |
| mean annual temperature (1961–1990) | mean temperature | ALA | °C | 8.4 | 0.8 | 4.2 | 10.6 |
| mean annual temperature range (1961–1990) | temperature range | ALA | °C | 25.1 | 1.7 | 21.1 | 29.1 |
| mean annual precipitation (1961–1990) | mean precipitation | ALA | mm | 724 | 130 | 480 | 1384 |
| mean annual precipitation range (1961–1990) | precipitation range | ALA | mm | 40 | 13 | 23 | 104 |
| number of CORINE land use classes | number of land use types | CLC | none | 10 | 2.7 | 1 | 23 |
| number of classes of geological parental material | number of geological parent materials | GEO | none | 7 | 2.5 | 1 | 24 |
| number of soil types | number of soil types | GEO | none | 4 | 1.7 | 1 | 12 |

environmental predictors in the distribution model. As climate data we used mean annual temperature and mean annual within-year temperature range (1961–1990) as well as the mean annual precipitation and its range (1961–1990) provided by the European Union ALARM project (Fronzek et al., 2012; cf. Table 1). Each environmental predictor was centred by subtracting its mean and scaled by dividing the centred value by the standard deviation to ensure comparable effect sizes of the final distribution model. We assessed the collinearity of the selected environmental predictors prior to the analysis (Fig. S1). We only used predictors with Kendall's $\tau < 0.7$ (Dormann et al., 2013).

2.2. Modelling compositional data considering residual spatial autocorrelation

Dealing with compositional data poses the problem that by adding up to one, the proportions are not independent of each other. If one proportion decreases, another one has to increase. This so-called 'unit-sum-constraint' can be broken by replacing the observed proportions by logarithms of ratios (log-ratios, Aitchison, 1986; Billheimer et al., 2001; see Kühn et al., 2006 for details). We chose the total number of plant species with FM status as denominator and the other two statuses as numerators for both log-ratios. This resulted in one log-ratio $\log(\text{OM}/\text{FM})$ representing the relative proportion of obligate AM plant species and another log-ratio $\log(\text{NM}/\text{FM})$ representing the relative proportion of non-mycorrhizal plant species. Mathematically, the choice of numerator and denominator is arbitrary and does not affect the results (Aitchison, 1986). Ecologically, however, the choice of numerator and denominator affects the interpretation of the model. We chose OM and NM species as numerators, because we were especially interested in the obligate plant strategies regarding the symbiosis (both, obligate mycorrhizal and obligate non-mycorrhizal). As FM plant species represent the ecologically flexible, intermediate position, we identified this status as the most suiting denominator.

We used a vector generalised additive model (VGAM) – a non-parametric extension of generalised linear models (Yee and Mackenzie, 2002) – for distribution modelling, including a multinomial distribution family (cf. Lososová et al., 2012) that accounts for the described log-ratio procedure. Unlike ordinary GAMs (or GLMs), this technique allows modelling the two selected log-ratios in one model. For each of the 17 initially selected environmental predictors, (vector) smooth terms with a maximum of two degrees of freedom were allowed, i.e. a smoothing function up to a quadratic function per predictor fit. Following the initial predictions, the

predictors were backward-selected based on error probabilities. Predictors with one significant p-value ($p \leq 0.05$) for at least one log-ratio were kept in the model. Our approach hence follows the recommendations of Crawley (2012). Though recent studies recommend the use of multi-model inference (Burnham and Anderson 2002), the approach to be followed depends on the purpose, i.e. whether to test predictions/hypotheses or to improve descriptive models by optimising information context. Our aim is the former and not the latter. Anyhow, multi-model inference approaches are to the best of our knowledge not yet custom fit to use VGAM approaches and would need considerable additional programming efforts. The VGAM was implemented using the respective R package (Yee, 2010).

We used a residuals autocovariate (RAC) approach (Crane et al., 2012) to account for spatial autocorrelation (SAC) within the residuals of the distribution model. This approach derives an autocovariate from the residuals of the environment-only model instead of deriving it from the response variable itself. Therefore, this approach does not suffer from biased parameter estimates reported in Dormann (2007). Due to two log-ratios there are two resulting VGAM residuals per grid cell. Hence, two autocovariates accounting for spatial dependencies were calculated using a mean focal operation including the maximum eight neighbouring cells of each grid cell. Afterwards, both RACs (one for each log-ratio) were added as predictors accounting for residual spatial autocorrelation to the backward-selected environment-only model. A second backward selection process was run to control for changing significance levels of the pre-selected predictors after adding the RACs.

The model's ability to account for SAC is indicated by the reduction of SAC in model residuals. SAC was measured by calculating Moran's Index and plotting these values as correlograms. P-values indicating whether the Moran's I for each distance class was significantly different from zero were sequentially adjusted using Holm's (1979) procedure. For both, Moran's I calculation and correlogram plotting, we used the package 'spdep' (Bivand et al., 2013). The RAC approach successfully reduced the residual SAC of our distribution model. Subsequently, the residuals could not be distinguished from the pattern expected under a white noise process, as the variance appeared homogenous and the autocorrelation was reduced to a sufficient level.

We partitioned the explained variance of our final model into the variance that is explained by the environment-only and by the residual autocovariate-only model. We subtracted the overlap in explained variance of both of these models from the final model's explained variance, including the environmental predic-

Table 2

Summary of predictions relating plant arbuscular mycorrhizal status and the environmental predictors selected for this study.

| Predictor | Background and predictions |
|---------------------------------------|--|
| Stream area | Occurrence of AM fungi in riparian systems is patchy in space (Harner et al., 2009) and time (Harner et al., 2011; Piotrowski et al., 2008) since local conditions can change dramatically. Consequently, we predict that in riparian ecosystems generalist FM plant species occur in greater proportion than specific OM and NM species. |
| Deciduous forest area | The abundance of potential AM host plant species is greater in deciduous forest than in coniferous forest (Lang et al., 2011; Read 1991). Plants grown with coniferous forest soil inoculum exhibit low root colonisation by AM fungi (Moora et al., 2004) as well as a low fungal diversity (Öpik et al., 2003). We expect that being FM is more viable than being OM in such conditions. Given that the presence of coniferous trees is associated with soil acidification (Augusto et al., 2003) we also expect fewer OM plant species in coniferous forests (Hempel et al., 2013). At the same time, there is no specific information about the occurrence of NM plant species in different forest types. We therefore predict that the proportion of OM plant species decreases along the transition from deciduous to coniferous forests, which might be associated with an accompanying increase of FM plant species. |
| Mixed forest area | |
| Coniferous forest area | |
| Agricultural area | Intensive agriculture as practiced in Central Europe shows negative effects on AM fungal diversity (Oehl et al., 2003, 2010). Main reasons are the supply of fertiliser (Johnson, 1993; Santos et al., 2006) and tillage activities, which rupture the hyphal network (Jansa et al., 2002). In addition, agriculture fragments the landscape leaving patchy fragments of the more natural plant communities. We therefore expect a higher proportion of NM plant species and a general decrease of OM species with increased agricultural land use. |
| Urban area | (1) Urban areas are highly disturbed and fragmented environments (McDonnell and Pickett, 1990). The same plant species exhibit lower AM root colonisation in urban than in rural environments (Bainard et al., 2011). This could be due to increased nitrogen deposition in the soil (Egerton-Warburton and Allen, 2000), for instance caused by air pollution (Cairney and Meharg, 1999); various other factors (other types of pollution, mechanical disturbances) may be important. This may be associated with an increase in NM plant species with urbanity. (2) Urban areas are typically species rich (Kühn et al., 2004). Still, they show a larger share of alien plant species, compared with less urbanised or rural areas (Kühn and Klotz, 2006). As alien plant species are more frequently OM species (Hempel et al., 2013), an increase in OM species with increasing urbanisation is possible. |
| Lime area | Different geological parent materials and the resulting soil types differ in soil pH, nutrient and water availability. Soil conditions influence the distribution of both plant and AM fungal species. In particular, soil pH (Dumbrell et al., 2010) or soil type in general (Oehl et al., 2010) may be strong drivers of AM fungal community composition. Hempel et al. (2013) showed that OM plant species are more frequently those adapted to high pH, dry and less fertile habitats. We predict that more fertile parent material like loess will lead to a lower proportion of OM species, whereas typically nutrient poor soils like sand will promote OM species instead. We predict that soils derived from lime rich parent material inhabit more OM species, as they show a high microbial and fungal activity due their high pH and saturation with calcium ions. |
| Loess area | |
| Sand area | |
| Clay area | |
| Mean temperature | AM fungi grow better and show higher plant root colonisation rates in areas of higher temperatures (Tungate et al., 2007) and OM status is positively associated with species' preference of higher temperatures (Hempel et al., 2013). Plant roots show changes in morphology (Haugen and Smith, 1992), growth rate and longevity (Forbes et al., 1997) in relation to increased soil temperatures, which may be compensated by increasing growth of extraradical fungal hyphae. Consequently, we expect an increase in OM plant species under higher temperatures. |
| Temperature range | High temperature variability influences the ecology of plant species and their fungal partners (Heinemeyer and Fitter, 2004). We predict a larger proportion of FM plant species in regions of larger temperature range, as this generalist strategy may allow a greater plant ecological amplitude. |
| Mean precipitation | Plant productivity is often limited by water availability. AM fungi potentially improve individual plant water uptake by different mechanisms, e.g. by accessing small soil pores and increased absorption rates due to high density of fine hyphae (Augé, 2001) and may reduce plant stress in this way. Worchel et al. (2013) showed that the positive growth response of grasses to AM fungi increased under drought conditions and Hempel et al. (2013) found a positive association of OM species with their preference of drier habitats. We therefore predict a higher proportion of OM plant species in regions of less precipitation. |
| Precipitation range | As OM plant species are positively associated with dry and NM species with wet conditions (Hempel et al., 2013), we expect a decrease of both statuses and an increase of FM species with an increased precipitation range. |
| Number of land use types | A more heterogeneous, patchy landscape, either due to diversity of land-use types, geological parent material or soil type classes, should promote a larger number of plant species due to a larger amount of distinctive habitats (Deutschewitz et al., 2003; Stein et al., 2014). Since we see no reason for a disproportioned advantage of any of the three statuses under such a scenario, we predict no correlation between any of the three statuses and grid cell heterogeneity. |
| Number of geological parent materials | |
| Number of soil types | |

Table 3

The relationship between the two chosen log-ratios representing the ratio of obligate to facultative arbuscular mycorrhizal plant species $\log(\text{OM}/\text{FM})$ and the ratio of non-mycorrhizal to facultative arbuscular mycorrhizal plant species $\log(\text{NM}/\text{FM})$ as well as the nine final environmental predictors using a vector generalised additive model (VGAM). Degrees of freedom; rounded, approximate chi-square values as measure of non-parametric effect size and significance levels: $p \leq 0.001$ ***, $0.001 < p \leq 0.01$ **, $0.01 < p \leq 0.05$ *.

| Predictor | Df | Chi-square | P(chi) |
|---|----|------------|--------|
| Mixed forest area: $\log(\text{OM}/\text{FM})$ | 1 | 5 | * |
| Mixed forest area: $\log(\text{NM}/\text{FM})$ | 1 | 1 | – |
| Coniferous forest area: $\log(\text{OM}/\text{FM})$ | 1 | 23 | *** |
| Coniferous forest area: $\log(\text{NM}/\text{FM})$ | 1 | 1 | – |
| Urban area: $\log(\text{OM}/\text{FM})$ | 1 | 7 | ** |
| Urban area: $\log(\text{NM}/\text{FM})$ | 1 | 4 | – |
| Lime area: $\log(\text{OM}/\text{FM})$ | 1 | 10 | ** |
| Lime area: $\log(\text{NM}/\text{FM})$ | 1 | 1 | – |
| Mean temperature: $\log(\text{OM}/\text{FM})$ | 1 | 4 | * |
| Mean temperature: $\log(\text{NM}/\text{FM})$ | 1 | 1 | – |
| Temperature range: $\log(\text{OM}/\text{FM})$ | 1 | 53 | *** |
| Temperature range: $\log(\text{NM}/\text{FM})$ | 1 | 9 | ** |
| Mean precipitation: $\log(\text{OM}/\text{FM})$ | 1 | 1 | – |
| Mean precipitation: $\log(\text{NM}/\text{FM})$ | 1 | 8 | ** |
| Precipitation range: $\log(\text{OM}/\text{FM})$ | 1 | 6 | * |
| Precipitation range: $\log(\text{NM}/\text{FM})$ | 1 | 2 | – |
| Number of soil types: $\log(\text{OM}/\text{FM})$ | 1 | 1 | – |
| Number of soil types: $\log(\text{NM}/\text{FM})$ | 1 | 5 | * |

tors and residual autocovariates, to obtain an adjusted explained variance D^2 (Borcard et al., 1992). We assessed the robustness of the final model with five-fold cross-validation. For this purpose, the data set of 2859 grid cells was split into five equally large, mutually exclusive and non-random subsets. Thereby we assured to use the spatial heterogeneity in the data set for out-of-area predictions during the cross-validation (Wenger and Olden, 2012). We split the data from west to east, as stronger environmental gradients in Germany are acting from north to south.

As the graphical VGAM output illustrates the relationship of both log-ratios only (Fig. S2), it is not distinguishable whether changes in both log-ratios with environmental predictors are due to changes in OM and NM proportions, respectively, or due to a change in FM species proportion. Therefore, we present the model outcome using loess smoother functions to illustrate the relationship of all three plant mycorrhizal statuses at the same time. Nevertheless, the VGAM approach does not allow presenting any kind of significance test for the FM proportions.

All statistical analyses were performed using the statistical software R (version 3.0.2, R Development Core Team, 2012).

3. Results

Nine of the initially 17 environmental predictors remained in our final distribution model of plant species' AM status across Germany (Fig. 1), also including the two residual autocovariates. These predictors were at least significant for one of the two log-ratios (Table 3). The final model explained 54% of the variation within the distribution data, corrected for the overlap in explained variance by environmental ($D^2 = 0.47$) and residual spatial covariates ($D^2 = 0.39$). Predictions showed a root-mean-square error (RMSE) of 0.013 (cross-validated: 0.021) for proportions of OM, 0.013 (cross-validated: 0.021) for proportions of FM and 0.007 (cross-validated: 0.009) for proportions of NM plant species (Table S1). The assemblages of proportions of plant species with different AM status (Fig. 2) followed a non-random spatial distribution, even at the chosen intermediate geographical extent with a relatively coarse grid cell grain of c. 130 km² per cell. OM plant species proportion was highest along the Central and South-Western basins of Germany and lowest in the North German Plain, drawing a clear line along the upland range (Fig. 2). The relative FM plant species

distribution showed an opposing pattern with highest values in the North German Plain and along the low mountain ranges at the Czech-German border (Fig. 2). NM plant species proportion was highest in northern Germany, but showing a relatively scattered distribution within the rest of Germany (Fig. 2).

Annual temperature range was the only predictor significantly explaining the distribution of both statistically modelled log-ratios and it was by far the most powerful environmental predictor in terms of effect size (Table 3). With an increase in temperature range per grid cell we detected a strong relative increase in OM species (Fig. 1). NM plant species proportion was highest at low and high values of temperature range, having a minimum in intermediate annual temperature range (Fig. 1). Area of mixed forest and area of coniferous forest per grid cell were significantly negatively related to the relative occurrence of OM plant species (Fig. 1). An increase in urban area per grid cell resulted in an increase in OM proportions (Fig. 1). Likewise, an increase in area of geological parental material originating from lime and mean annual temperature per grid cell were significantly positively related to the proportion of OM plant species (Fig. 1). Mean precipitation and the number of soil types were the two predictors exclusively explaining the distribution of NM plant species (Table 3). There was a strong decline of NM species proportion with an increase in mean precipitation, showing a peak in grid cell regions of low annual precipitation (Fig. 1). NM species proportion increased with an increasing number of soil types (Fig. 1). In regions of low annual precipitation range, there was a decrease in OM proportions. As the annual precipitation range per grid cell increased, this relationship slightly flipped (Fig. 1).

4. Discussion

We analysed whether plant species assemblages across an intermediate spatial scale are composed of different proportions of species regarding their AM status, and if the variation of these proportions are linked to the geographical variation of ecological and environmental conditions. We detected distinct spatial distribution patterns of the proportion of plant species with different AM status across Germany (i.e. 2859 grid cells; each c. 130 km²) and found relationships of these distributions with a set of environmental predictors. Thus, we extended and substantiated many of our initial predictions on associations of plant AM status and the addressed geographical variation of ecological and environmental conditions (Table 4).

The model's outcome matches our initial expectations concerning area of forest stands per grid cell (Table 4). We assume that the inversely proportional relationship (Fig. 1) results from an increase in soil acidity with a higher proportion of coniferous tree species (Augusto et al., 2003), which inhibits activity of AM fungi (van Aarle et al., 2003) and the association of OM with plant species in general (Hempel et al., 2013). Secondly, Europe's coniferous forests in recent silvicultural practice are mostly even-aged stands (Kuuluvainen, 2009) with structurally altered (Moora et al., 2009) and species poor herbal understories (Koorem and Moora, 2010). Therefore they are predominantly lacking a plant layer that is mostly dominated by potential AM host plants. As a third point, at least some deciduous tree species are AM – in addition to being ectomycorrhizal – whereas coniferous tree species are not commonly AM in Europe.

We presented two initial predictions regarding urban area as a predictor (Table 2). We found an increase of OM plant species proportions with increasing urban area per grid cell (Table 4). We explain this relative gain of OM plant species with an increase of alien plant species in urban areas compared to rural areas (Kühn et al., 2004), which are known to be more frequently OM (Hempel

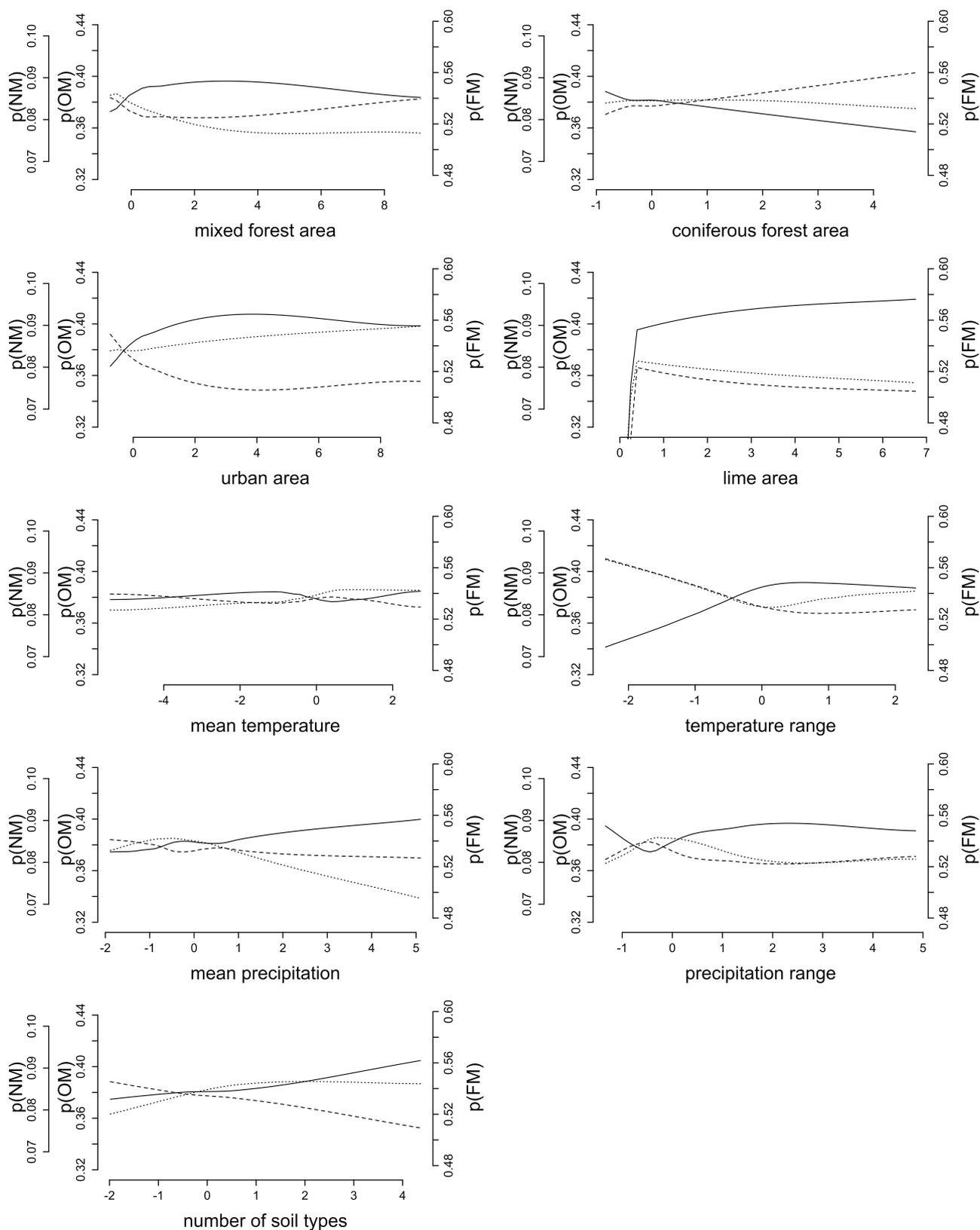


Fig. 1. Loess-smoother functions for all finally selected environmental predictors and the predicted VGAM values for the three mycorrhizal status proportions: p(OM) – solid line (left axis), p(FM) – dashed line (right axis), p(NM) – dotted line (far left axis). Each environmental predictor was centred by subtracting its mean and scaled by dividing the centred value by their respective standard deviation.

et al., 2013). We do not think that the higher proportion of OM plant species in urban areas is caused by higher average temperatures of cities compared to their surrounding areas (urban heat island, Oke,

1982), as the corresponding environmental predictors urban area and average temperature are – at least at our extent and grain size – not strongly correlated (Fig. S1).

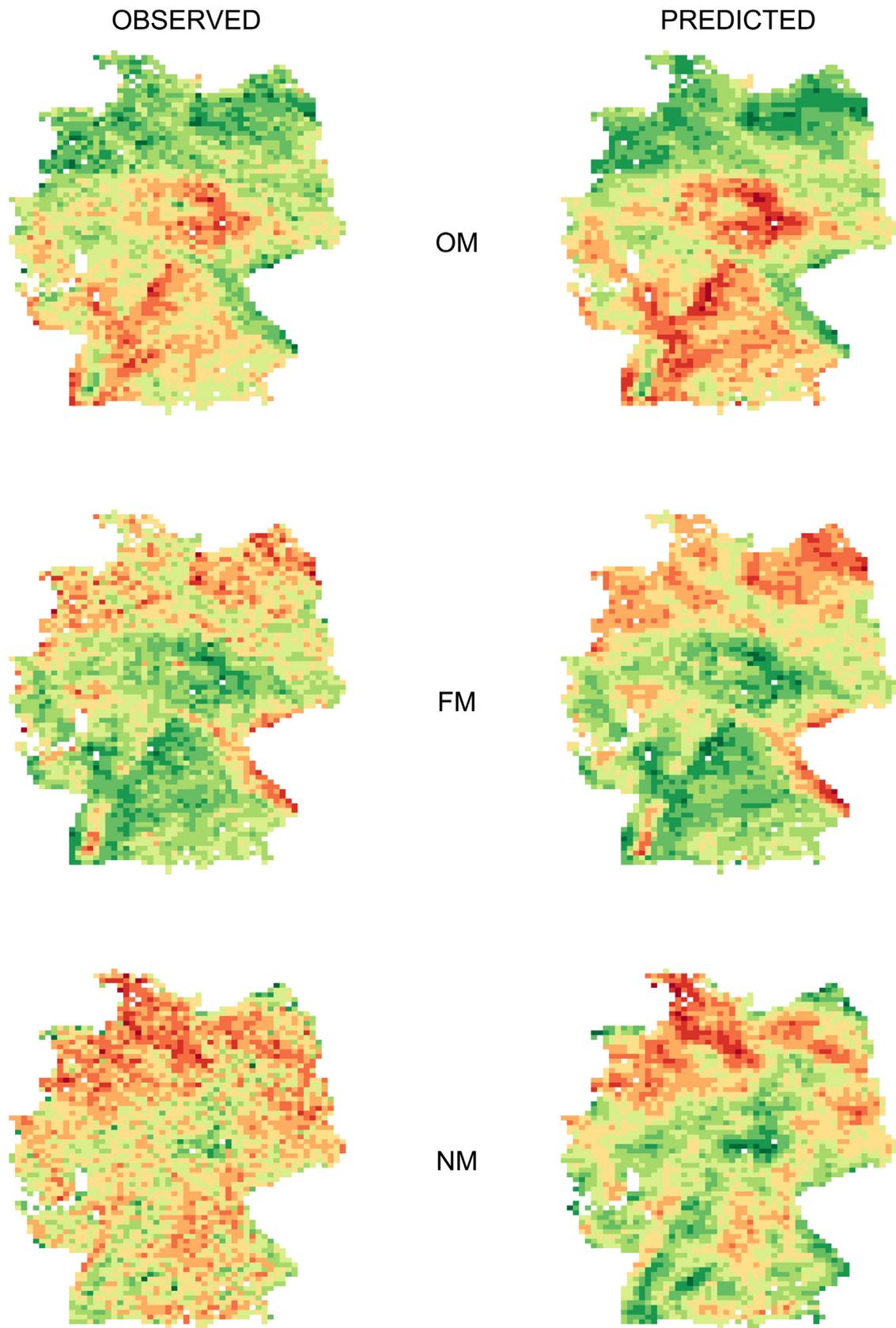


Fig. 2. Observed and predicted distribution of arbuscular mycorrhizal plant status of the 2995 grid cells representing Germany. Compared are the observed values (left column) for the three plant arbuscular mycorrhizal status proportions 1) OM – obligate arbuscular mycorrhizal, 2) FM – facultative arbuscular mycorrhizal 3) NM – non mycorrhizal, and their predicted values of the final VGAM distribution model (right column). To better compare the maps, classes for proportions of plant arbuscular mycorrhizal status are decantiles (i.e. ten classes of equal size with different class limits for each map). High values are indicated by red, low values by green colour. Grid cells classified as insufficiently mapped and excluded from the analysis are illustrated in white. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Concordance of the relationship of initial environmental predictors to one of the three plant arbuscular mycorrhizal statuses (OM: obligate arbuscular mycorrhizal, FM: facultative arbuscular mycorrhizal, NM: non-mycorrhizal) derived from our initial predictions (cf. Table 1) compared to the outcome of the vector generalised additive model.

| Predictor | Predictions | | | Model outcome | | |
|---------------------------------------|-------------|----|----|---------------|----|----|
| | OM | FM | NM | OM | FM | NM |
| Stream area | – | ↑ | – | – | – | – |
| Deciduous forest area | – | – | – | – | – | – |
| Mixed forest area | ↓ | – | – | ↓ | – | – |
| Coniferous forest area | ↓ | – | – | ↓ | – | – |
| Agricultural area | ↓ | – | ↑ | – | – | – |
| Urban area | ↑ | – | ↑ | ↑ | – | – |
| Lime area | ↑ | – | – | ↑ | – | – |
| Loess area | ↓ | – | – | – | – | – |
| Sand area | ↑ | – | – | – | – | – |
| Clay area | – | – | – | – | – | – |
| Mean temperature | ↑ | – | – | ↑ | – | – |
| Temperature range | – | ↑ | – | ↑ | – | ↓ |
| Mean precipitation | ↓ | – | – | – | – | ↓ |
| Precipitation range | ↓ | ↑ | ↓ | ↑ | – | – |
| Number of land-use types | – | – | – | – | – | – |
| Number of geological parent materials | – | – | – | – | – | – |
| Number of soil types | – | – | – | – | – | ↑ |

Other land-use related environmental predictors, especially the amount of agricultural area per grid cell, did not affect plant AM status distribution (Table 4), although most of the crop species are AM (Smith and Smith 2011). Nevertheless, we do not conclude that agricultural transformations and utilisation are of no importance in shaping the trait distribution. As a predictor in our analysis, agricultural area lumps together agricultural practices differing in land-use intensity, nutrient load and management practices such as tillage (Jansa et al., 2002). These parameters may influence the trait distribution on a more local scale (Ngosong et al., 2010), which is not captured at the scale of our analysis. Other predictors such as precipitation or temperature, which lead to different agricultural practices, may overrule the effects of those practices at the scale analysed. The same is true for spatial distributions of nitrogen and phosphorus availability, which influence the composition of plants and their AM status and are influenced by fertilisation regimes (Ceulemans et al., 2011; Landis et al., 2004). Within our grid system of cells with c. 130 km², it is not possible to accurately map differences in nutrient availability, which act on a far finer scale. Considering other environmental predictors as proxy for nutrient availability, e.g. lime area (as discussed in the following paragraph) may mitigate this lack of data availability. Nevertheless, incorporating nutrient level or nutrient availability in our model may substantially improve the model. Unfortunately, such data are not yet available at this scale.

Only lime area significantly explained the distribution of OM plant species proportion, as one of the initial four predictors characterising geological parent material (Table 4). As predicted, we found a relative increase in OM plant species with increasing area of lime per grid cell (Fig. 1). Soils developing on lime-rich parent materials are more alkaline compared to soils on other geological parent materials (Schachtschabel et al., 1998). This promotes AM fungal activity, favours OM plant species in general (Hempel et al., 2013) and increases the share of AM plants at community level (Gerz et al., 2016). High calcium content of lime-rich parent materials leads to reduced availability of phosphorus, which can be alleviated through external hyphae provided by AM fungi (Sanders and Tinker, 1971; Smith et al., 2004). Therefore, plant species associated with AM fungi may have a (local) competitive advantage in such phosphorus limited environments (Olsson and Tyler, 2004).

We did not formulate particular expectations towards proportions of mycorrhizal status and the number of soil types. The detected increase in NM plant species proportion with an increase in number of soil types might be explained by an accompanied higher heterogeneity in soil types (Deutschewitz et al., 2003; Stein et al., 2014). This increases the probability of occurrences of soil types which favour NM species. As NM plant species are by far the minority among plant species, this might explain the exclusive association of this predictor with NM plant species proportion.

With an increase in mean temperature per grid cell we found an increase in OM plant species proportion (Fig. 1). So we corroborated in space what Hempel et al. (2013) found in a cross-species analysis, i.e. that OM plant species are positively associated with higher temperatures. OM plant species may be favoured in warmer habitats driving increased soil temperatures, since AM fungi are able to compensate temperature induced changes in root morphology (Haugen and Smith, 1992), growth rate and longevity (Forbes et al., 1997) of host plants by increasing growth of extraradical fungal hyphae. Additionally, high mean annual temperatures may lead to a higher probability of drought events. OM plant species may better cope with drought stress via a variety of mechanisms (Augé, 2001; Zhu et al., 2011).

Differing from our initial expectation, we found a relative increase in OM plant species with increasing temperature range (Table 4), i.e. highest proportions of OM plant species in Eastern and South-Eastern regions of Germany (Fig. 2), which are climatically the most continental (Fig. S3). Contrary to our expectations, the share of FM plant species continuously decreased with increasing temperature range (Fig. 1). Mycorrhizas help to tolerate low (Zhou et al., 2012) and high temperature stress (Maya and Matsubara, 2013), which may explain the relationship of OM plant species and temperature range. On the other hand, NM plant species are associated with high values of temperature range as well (Fig. 1). At present, we can therefore offer no clear explanation of this correlation at our chosen scale. The mechanism relating plant AM status with continentality remains to be elucidated.

Regarding mean annual precipitation as a predictor, our distribution model revealed a relationship distinctly different from our expectations (Table 4); with NM plant species proportions strongly decreasing with increasing annual precipitation and no significant relationship concerning OM plant species (Fig. 1). As we found a relative increase in OM species share in regions having higher mean temperature and OM plant species have low moisture indicator values (Hempel et al., 2013), this finding may imply that our precipitation related predictors do not fully translate into actual soil moisture conditions. Factors influencing soil moisture such as evapotranspiration and infiltration due to substrate type and texture act on smaller scales, which we cannot address at our scale and grain.

We find a decrease in OM plant species proportion in regions of low annual precipitation range (Fig. 1), which turns into a slight increase with increasing precipitation range per grid cell, slightly contradicting our predictions (Table 4). The same trend appears for NM plant species proportions (Fig. 1), but showing an increase in grid cells of low precipitation range and a slight decrease with increasing precipitation range, a pattern more closely aligned with our prediction. Analogously to temperature stress, mycorrhizas were shown to mitigate plant stress under drought conditions (Li et al., 2014), which may explain this correlation. Again, this result may be related to weak transferability of our precipitation related predictors to actual soil moisture conditions. However, precipitation range shows similar relationships with plant mycorrhizal status as temperature range, emphasising the role of continental climate for the trait's distribution. This correlation as a proxy for continental climate is less strong, which can be explained by the less pronounced gradient within Germany, showing peak values

of precipitation range in the German Alps and pre-alpine foothills only (Fig. S3).

Our results extend the findings of Hempel et al. (2013) from a cross-species analysis to a spatially explicit context, substantiating their findings regarding the association of plant AM status with information of plant species ecological requirements. We thus bridge the gap between former coarse grained global analyses (Davison et al., 2015; Kivlin et al., 2011; Öpik et al., 2010; Treseder and Cross, 2006) and local greenhouse or field experiments (e.g. Hartnett and Wilson, 2002; Klironomos et al., 2011; van der Heijden et al., 1998). We thereby uncovered new patterns regarding the assemblages of plant species differing in their mycorrhizal status at this intermediate scale. Our analysis is not able to disentangle, whether the AM status distributions we found are due to the AM status of plants or other plant traits that correlate with AM status; this needs further testing. The distinct spatial distributions of proportions of different plant AM statuses (Fig. 2) still emphasise the importance of plant mycorrhizal status as a useful functional trait, in particular because root traits are not as commonly and widely used in analyses of plant species distribution and assemblages (Rillig et al., 2015).

Our intermediate study scale may be more suitable for questions about plant mycorrhizal status and its potential capacity to mediate future changes in plant responses due to changes in climatic conditions (Compant et al., 2010; Mohan et al., 2014) or land use. Our results demonstrate that the proportion of plants with different AM status is dependent on climatic predictors, in particular temperature and precipitation, which present the largest effect size (Table 3). If temperatures in Germany will increase (IPCC, 2013), OM plant species may be favoured according to our results (cf. Bunn et al., 2009).

Future studies will certainly benefit from higher resolution of the environmental predictors as well as from improved data on nutrient levels and soil moisture in general. This will help capturing fine-scale processes affecting both symbiotic partners and therefore will deepen our understanding of the mechanisms driving the co-variation of the symbionts. Furthermore, distribution models of plants' AM status accounting for the abundance of species (plant and fungus) instead of their mere presence/absence will increase our knowledge. Finally, such studies may allow further detection of potential driving processes of the mycorrhizal symbiosis that could not have emerged at comparable effort and scale from experimental studies under field conditions and hence help generating new hypotheses that may be tested experimentally.

We encourage including plant mycorrhizal status as a plant trait in future macroecological analyses of plant assemblages and distributions (Moora, 2014). This additional information may help to improve plant species distribution models for instance in interaction with other traits. Pellissier et al. (2013) could already show such advancement by adding the number of soil fungal operational taxonomic units to a plant species distribution model of the Western Swiss Alps. Nevertheless, there is still a need to improve the existing knowledge regarding plant mycorrhizal traits. Hempel et al. (2013) stated that more abundant plant species are better studied regarding their mycorrhizal traits. Furthermore, they were able to compile mycorrhizal status information only for half of the plant species of the German flora in the existing literature. This may be a simple explanation for the performance of our distribution model, which is e.g. biased upwards for NM plant species, i.e. the model predicts higher proportions of NM plant species, especially in the South and Central part of Germany (Fig. 2). Collecting more data even on rare plant species – both in literature review and experimentally – would substantially improve future analyses involving plants' mycorrhizal status as a plant functional trait. Certainly, investigating the biogeography of AM fungi themselves (Davison et al., 2015; Hazard et al., 2013) will stimulate the usage of

plant mycorrhizal status in future analyses of co-variation of plant and AM fungal communities (Zobel and Öpik, 2014).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2016.06.002>.

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