

# Plant diversity in deciduous temperate forests reflects interplay among ancient and recent environmental stress

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## Abstract

**Questions:** Recent studies have suggested that response patterns of species and phylogenetic diversity may differ. Here, we address the following questions: What are the most important drivers and is there a difference in the responses to environmental drivers between species and phylogenetic diversity? If so, which ecological mechanisms determine these patterns and will different habitat types host plants of different evolutionary lineages?

**Location:** Czech Republic.

**Methods:** We used a unique data set of 419 permanent plots in thermophilous temperate deciduous forests. Vegetation of the herbaceous layer was sampled along a wide range of environmental gradients. Soil characteristics were measured in the laboratory from field-collected samples. Topographic variables were derived from a digital elevation model.

**Results:** Communities of shaded habitats on moist fertile soils were characterized by phylogenetically older lineages (pteridophytes and ancient lineages of lilioids and dicots) resulting in a higher phylogenetic diversity. On the other hand, dry oligotrophic habitats were distinguished by short-lived light-demanding species (some asterids) and showed higher species, but relatively lower, phylogenetic diversity. Besides simple effects of soil, light availability and topographic properties, interactions between the factors played an important role.

**Conclusions:** Our results indicate that both types of biodiversity were mainly driven by environmental stress created by the interplay among factors. Patterns of phylogenetic diversity suggest that historical factors, i.e., the shifting of species' habitats at the evolutionary scale, could also provide plausible explanations.

## KEYWORDS

historical processes, old-clade plants, overstorey, plant diversity, stress gradients, topography, understorey, vascular plants

## 1 | INTRODUCTION

Understanding patterns of plant diversity and mechanisms of community assembly has long been one of the major goals of ecology. It is generally assumed that abiotic conditions drive biodiversity patterns

through competitive interactions and environmental filtering. The occurrence of species at a particular site is limited by morphological and physiological similarities among species and by the width of their niche space (Hutchinson, 1959; Whittaker, 1956). In recent decades, neutral processes (e.g., biogeographical historical processes,

stochasticity and dispersal) were also discussed as important drivers of biodiversity (Hubbell, 2001; Tilman, 2004; Zobel, 1997). Many studies conducted in temperate forests tried to determine which biotic and abiotic factors affected forest plant communities (Kreft & Jetz, 2007; Reczyńska & Świerkosz, 2017). These factors include for example canopy openness, soil moisture, soil chemistry and site topography (Ewald, 2003; Gilbert & Lechowicz, 2005; Mittelbach et al., 2001; Moeslund, Arge, Bøcher, Dalgaard, & Svenning, 2013; Zelený, Li, & Chytrý, 2010). Works on plant diversity highlighted topography and edaphic conditions as the strongest selective forces within plant communities (Boerner, 2006; Moeslund et al., 2013; Whittaker, 1956). Authors of the last cited paper argued that among topographical factors thermal energy accumulation exerted the strongest impact on local vegetation. A whole range of studies demonstrated the dominant effect of light availability on plant communities (Moeslund et al., 2013). Researchers also stressed that diversity in mid-latitude forests was positively correlated with soil basicity (Pärtel, Zobel, Liira, & Zobel, 2000). This pattern is probably associated with the high extinction rate of calcifuge species during the Pleistocene in central Europe (Ewald, 2003). Other studies emphasized the importance of interactions among factors in explaining biodiversity patterns (Bobbink et al., 2010; Naaf & Kolk, 2016; Palpurina et al., 2017). Bobbink et al. (2010) revealed that the negative effect of soil nitrogen accumulation on species diversity was influenced by canopy cover. The frequently studied relationship between soil acidity and species diversity is partly influenced by precipitation (Palpurina et al., 2017). Such spectra of results indicate that plant diversity is structured by a variety of environmental factors that are connected by complex interactions.

An exclusive focus on species diversity ignores other components of biodiversity. Species diversity can also be expressed as phylogenetic diversity, which reflects evolutionary history and indirectly expresses the functional diversity of the studied communities (Swenson et al., 2012). Studying communities from the perspective of phylogenetic similarities among species assumes niche conservatism during evolution; that is, closely related species are supposed to have similar niches (Harvey & Pagel, 1991). Examining phylogenetic diversity has recently become a powerful approach in community ecology due to the availability of sophisticated analytical tools and metrics (Chun & Lee, 2017). Phylogenetic diversity is often studied by ecologists to obtain more detailed information about the ecological and evolutionary processes that have shaped current community patterns (Swenson et al., 2012; Webb, Ackerly, McPeck, & Donoghue, 2002). Phylogenetic diversity may be preferred in comparison to the limited information provided by species diversity, which treats each species as evolutionarily independent and ecologically equivalent (Swenson et al., 2012). However, one should not ignore the drawbacks of the phylogenetic approach. In particular, it has to be kept in mind that phylogenetic relatedness and ecological similarity do not always concur (Losos, 2008). Recent studies showed that the phylogenetic diversity of temperate forest communities was mainly driven by topography, soil moisture, or habitat disturbance (e.g.,

seasonal flooding, windthrow or logging) (González-Caro, Umaña, Álvarez, Stevenson, & Swenson, 2014; He et al., 2017; Kitagawa, Mimura, Mori, & Sakai, 2015; Shigyo, Umeki, Ohashi, Kawada, & Hirao, 2017). Several studies suggested that the driving factors may substantially differ if distinguishing for phylogenetic and species diversity (Culmsee & Leuschner, 2013; Grass, Brandl, Botzat, Neuschulz, & Farwig, 2015). Looking for explanations of patterns in phylogenetic diversity, Kitagawa et al. (2015) concluded that relatively stressful sites tended to host phylogenetically similar communities via environmental filtering, and vice versa. Patterns of phylogenetic diversity can be also explained by the geological epoch (moist/dry) of the origin of phylogenetic lineages (Bartish et al., 2015; Lososová et al., 2015). A study by Lososová et al. (2015) suggested that the phylogenetic structure mirrors an expected habitat age at the geological time scale. Consequently, dry or moist habitat types will contain phylogenetic diversities from globally dry or moist epochs, respectively (Bartish et al., 2015).

The main aim of this study is to compare environmental drivers resulting in differences in patterns of species and phylogenetic diversity in temperate-forest understories. In addition, we aim to detect whether the phylogenetic diversity can be linked to specific phylogenetic lineages adapted to specific habitat types.

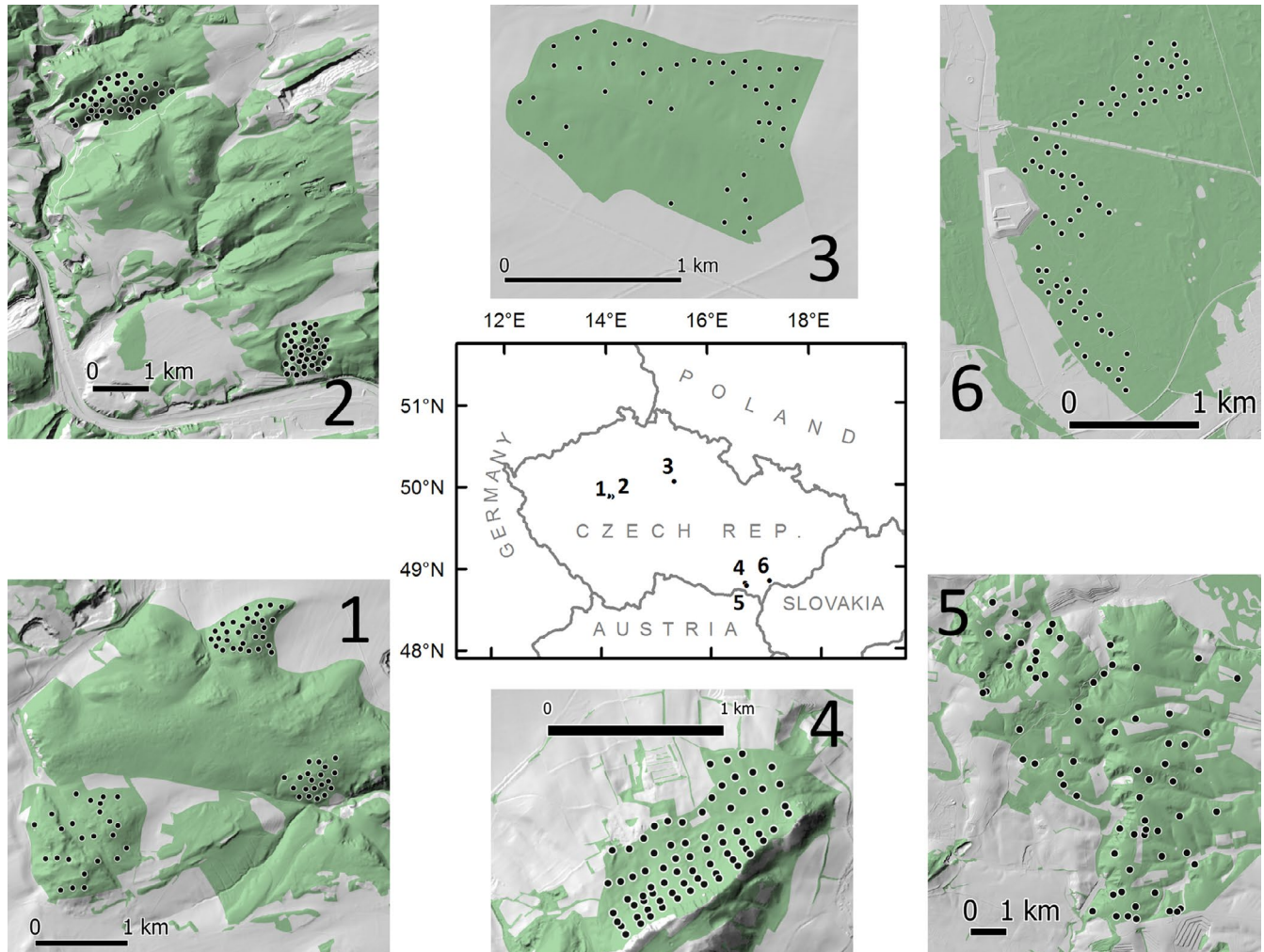
## 2 | MATERIAL AND METHODS

### 2.1 | Study sites

The studied forest communities are distributed over six sites in the lowland deciduous forests of the Czech Republic (Figure 1). The sites are forest patches in mostly agricultural landscapes. Their size is hundreds to thousands of hectares and comprises wide gradients of environmental conditions. Vegetation at each site is composed mainly of natural and semi-natural, mesic and thermophilous temperate deciduous forests dominated by hornbeam (*Carpinus betulus*), lime (*Tilia cordata*, *T. platyphyllos*), oak (mostly *Quercus robur*, *Q. petraea*) or ash (*Fraxinus excelsior*). The forests were historically managed as coppices or sometimes as woodland pastures, while the post-war period was marked by conversions to high forest, with relatively low-intensity management or often no management following an establishment of nature reserves. Large part of the variation in environmental conditions follows from the slope gradient and the character of bedrock. Elevations range from 170 m to 450 m a.s.l., and substrates vary from calcareous carbonates and siliceous metamorphic sediments to eolic sands. Topsoil acidity ranges from around 4 to 8 (pH in water).

### 2.2 | Data acquisition

Between 2008 and 2014, we collected plant community and environmental data in 419 permanent plots sized 225 m<sup>2</sup>. Three types of sampling were performed in the field: (a) vegetation sampling, which consisted of noting down complete lists of species of the herbaceous understory (including juveniles of woody species) along with



**FIGURE 1** Map of the Czech Republic with the locations of six study sites (centre). Permanent plots from where the data were collected is marked as black dots. The study sites are: (1) Koda; (2) Karlštejn; (3) Žiželický les; (4) Děvín; (5) Milovický les; and (6) Důbrava

estimating the relative coverage of each species using a combined Braun-Blanquet scale; (b) soil sampling at five regularly distributed points in each plot, producing a mixed sample of topsoil–organic–mineral soil taken from 0–5 cm; and (c) surveying the tree overstory, i.e., collecting information about tree species and their relative coverage in each plot.

Thirteen environmental parameters were obtained for each plot either from data collected in the field or from external resources (see Appendix S1). Weighted averages of litter quality (LQ) and shade casting ability (SCA) were calculated from tree species composition and relative abundances (Van Calster et al., 2008) (see Appendix S2). Each species was assigned a value ranging from 1 to 5, where the lowest LQ value denotes the worst-decomposing leaf litter (e.g., oak) and the highest value stands for the best-decomposing leaf litter (e.g., lime). In case of SCA, the lowest value indicates relatively sparse canopy (e.g., oak) while the highest value denotes dense canopy casting deep shade (e.g., lime).

Soil properties were measured in air-dried samples sieved to <2 mm. Total nitrogen and exchangeable phosphorus, calcium,

magnesium and potassium contents were analyzed in the Analytic Laboratory of the Institute of Botany of the Czech Academy of Sciences. Soil pH was measured in water suspension. For details of soil analyses, see Appendix S3.

To derive ecologically meaningful terrain attributes, we used a LiDAR-based Digital Terrain Model of the Czech Republic with a horizontal resolution of 5 m (DMR 4G, Czech Office for Surveying, Mapping and Cadastre). Beside elevation, we calculated five topographic variables capturing different terrain characteristics: topographic wetness index, heat load index, convergence index, topographic position index (TPI) and mass balance index (MBI). As a proxy for local soil moisture, we calculated the topographic wetness index (TWI) (Beven & Kirby, 1979) using the FD8Q flow-routing recommended by Kopecký and Čížková (2010). We further calculated plot heat load index (HLI) expressing the relative amount of heat received through solar radiation taking into account local slope and aspect (Böhner & Antonić, 2009). We used 202.5° as the aspect with maximum potential heat load. As a measure of local terrain curvature, we calculated the convergence

	Sum Sq	Mean Sq	NumDF	DenDF	F value	p (>F)
HLI	346.8200	346.8200	1	400.19	3.2887	0.074
Soil pH	914.8145	914.8145	1	405.95	8.6253	<0.01
TPI	678.4541	678.4541	1	403.87	6.3968	0.011
LQ	1,505.9829	1,505.9829	1	405.94	14.1991	<0.001
SCA	368.2451	368.2451	1	405.71	3.4720	0.063
HLI:SCA	480.4924	480.4924	1	403.96	4.5303	0.033
Random effect						<0.001

Note: The table shows the most parsimonious combination of explanatory variables explaining the greatest amount of the variability in species diversity.

Explanatory variables are indicated by acronyms: HLI, Heat load index; LQ, Litter quality; SCA, Shade-casting ability; TPI, Topographic position index.

index (CI) expressing how many surrounding cells point toward the central cell in a radius of 50 m around the plot. To express plot position relative to the surrounding terrain, we calculated the TPI as the difference between plot elevation and the mean elevation of the surrounding terrain (Guisan Weiss, & Weiss, 1999). We calculated TPI up to 100 m from the central cell and we used inverse distance weighted cell values to give higher importance to local topography. To express local erosion/accumulation processes, we calculated the MBI (Möller, Volk, Friedrich, & Lymburner, 2008). For all analyses, elevation was replaced by relative elevation calculated as the ratio of elevation of a particular plot and the maximum elevation of the locality. To calculate terrain attributes, we used SAGA GIS (Conrad et al., 2015).

### 2.3 | Diversity measures

Species diversity was expressed as species richness – the number of vascular plant species per plot. Only species in the herbaceous layer were considered. Juveniles of woody species were excluded because they strongly depend on the overstorey species composition.

To measure phylogenetic diversity, we generated a phylogenetic tree of all recorded plant species based on the recently published database of plant phylogeny, “Daphne” (Durka & Michalski, 2012). The resulting phylogenetic tree has defined branch lengths. We investigated phylogenetic diversity as mean pairwise distance (MPD) by using the *mpd* function which is part of the *picante* package (Kembel et al., 2010).

### 2.4 | Data analysis

To investigate the effects of environmental drivers on species diversity, we used a generalized linear mixed-effect model (GLMM) with Poisson distribution and link function “log”, which is part of the package *lme4* (Bates, Maechler, Bolker, & Walker, 2015). To compensate for the confounding effect of spatial variability, we used locality as a random effect variable in the GLMM. Using a *z* test, we tested the null hypothesis that the regression coefficient for the regression of a dependent variable on species diversity was equal to zero. To test for the effects of environmental drivers on

**TABLE 1** Results of step-wise regression procedure performing automatic backward elimination in the linear mixed-effect model. Species diversity is used as the dependent variable

phylogenetic diversity, we used a linear mixed-effect model (LMM), with locality set as a random effect. The error distribution of the LMM model was set to Gaussian with link function “identity”. The dependent variable was transformed by natural logarithm to ensure that residuals are normally distributed. Using a *t* test, in the LMM model we also tested the null hypothesis that the regression coefficient for the regression of a dependent variable on phylogenetic diversity was equal to zero.

To get the most parsimonious combination of explanatory variables explaining the highest variability in biodiversity, a step-wise regression procedure was applied performing automatic backward elimination of all effects of the mixed-effect model. Step-wise regression using the *step* function was also used to detect linear or quadratic effects of each explanatory variable and significant interactions among environmental variables (R Core Team, R Foundation for Statistical Computing, Vienna, Austria).

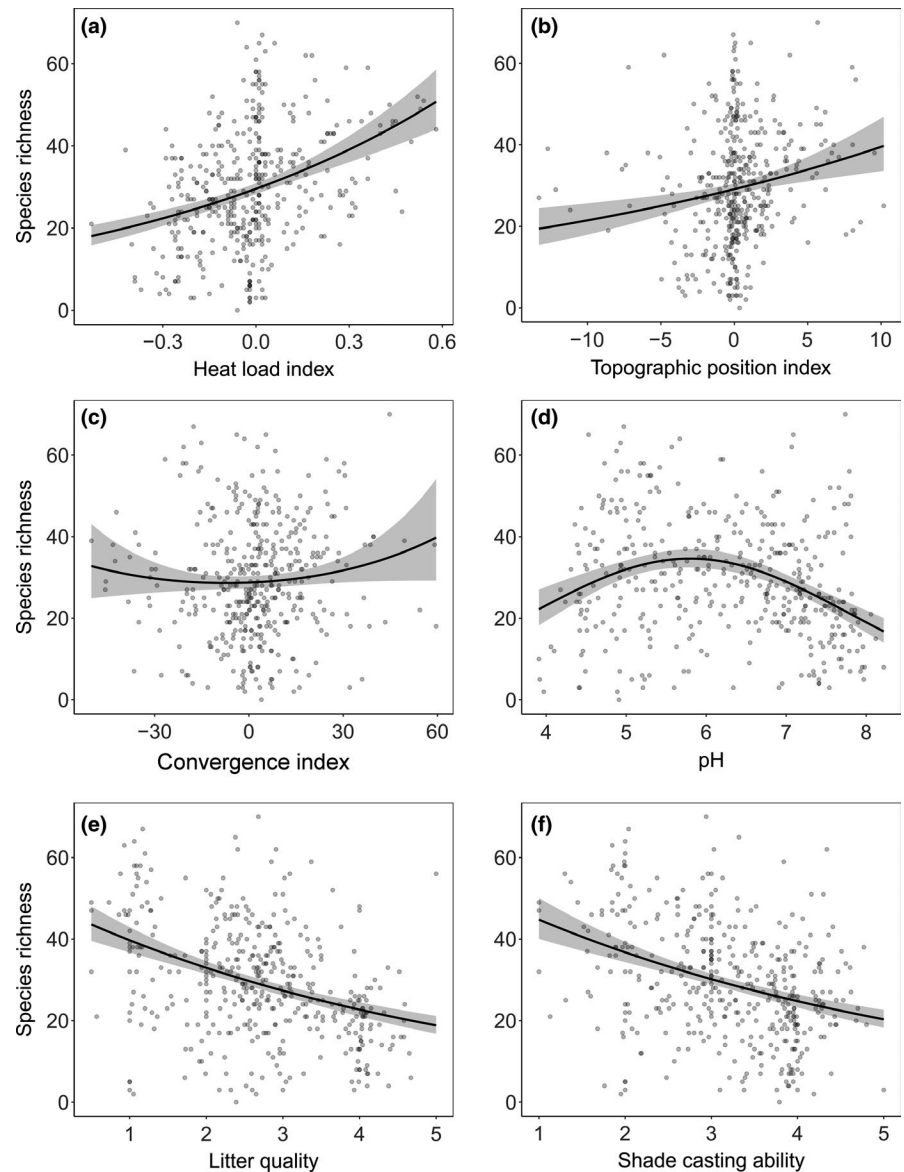
To get the pure effect (partial effect) of each explanatory variable, likelihood ratio analysis (LR analysis) of deviance with  $\chi^2$  was used for both mixed models. LR analysis compares the goodness of fit of two nested models, where a simple model is a special case of the complex model. For both mixed models and each environmental variable, we examined the coefficient of determination ( $R^2$ ) using the *r.squaredGLMM* function (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). This function calculates marginal  $R^2$ , which represents the variance explained only by fixed factors, and conditional  $R^2$ , which represents the variance explained by fixed and random effects together.

## 3 | RESULTS

### 3.1 | Patterns of species diversity

Topographic position index, soil pH, LQ and interactions between HLI and SCA form the combination of environmental variables that best explains the variability in species diversity in the GLMM (marginal  $R^2 = 15.1\%$  and conditional  $R^2 = 48.3\%$ ) (Table 1). The GLMM also revealed that canopy properties (SCA and LQ) explained 4.6% (marginal  $R^2$ ) and topography (TPI, HLI, TWI, MBI and CI) explained 5.1% (marginal  $R^2$ ) of the variability in species diversity. The highest

**FIGURE 2** Relationships between species diversity (number of species per 225 m<sup>2</sup>) and environmental variables. Regression curves with marked 95% confidence intervals were fitted by a generalized linear model with Poisson error distribution and log link function



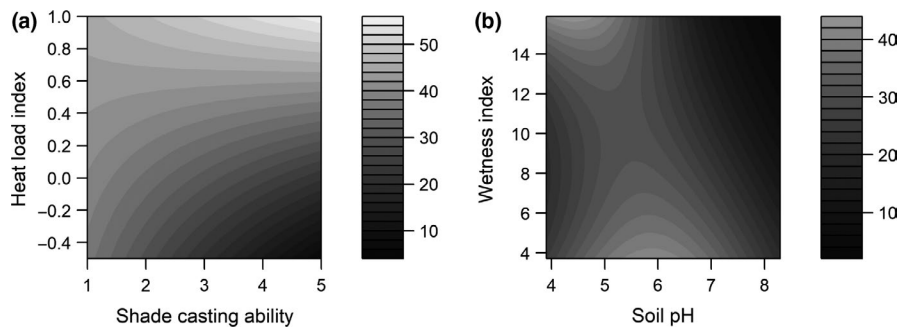
variability in species diversity was explained by site identity (random effect in GLMM) + SCA and LQ, 46.8%; and site identity + topographic variables, 48.2%. The likelihood ratio test of the GLMM revealed significant partial effects for SCA, LQ, TPI, HLI and soil pH (Appendix S4: Table S4.1).

Regarding individual variables, HLI and TPI were significantly positively correlated (Figure 2a, b) while LQ and SCA were significantly negatively correlated with species diversity (Figure 2e, f). We also found polynomial dependence between soil pH and species diversity (Figure 2d). Moreover, we detected a significant effect of interaction between pH and TWI on species diversity (Figure 3b). The peak in species diversity in acidic soils was observed (pH 4–5) in more humid conditions and in slightly acidic soils (pH 6–7) in drier conditions. In addition, the relationship between CI and species diversity showed a U-shaped pattern, which indicates that the lowest diversity was measured in plant communities occurring on flat surfaces (Figure 2c). Significant interaction was found between SCA and HLI (Table 1). Species diversity tended to be higher in plots with

low values of SCA and high values of HLI (i.e., steep south-facing slopes without dense overstorey) (Figure 3a).

### 3.2 | Patterns of phylogenetic diversity

Soil nitrogen, HLI, and interactions among HLI and SCA or LQ explained the greatest part of the variability in MPD (marginal  $R^2 = 8.7\%$  and conditional  $R^2 = 30.9\%$ ) (Table 2). Canopy properties (SCA, LQ) explained as little as 0.5% and topography (TPI, HLI, TWI, MBI and CI) explained just 1.7% of the variability in MPD. The highest variability in MPD (10.3%) was explained by site identity (random effect in LMM) + canopy properties, and by site identity + topographic parameters (10.2%). This is considerably less than the best models for species diversity could explain. Regarding individual variables, a significant partial effect was indicated only for HLI (Appendix S4); this correlation was negative (Appendix S4). In contrast to species diversity, HLI was negatively correlated with MPD (Figure 4a). Moreover, MPD was positively correlated with



**FIGURE 3** Contour plots showing changes in species diversity across: (a) heat load index and shade-casting ability; and (b) soil pH and wetness index. Displayed values were predicted based on the generalized linear model regressing species diversity on the interaction between previously mentioned explanatory variables

the amount of nitrogen in soil (Figure 4b). We detected significant interaction between HLI and SCA, which indicates that plots supporting the highest MPD are associated with low HLI and an open canopy layer (Figure 5a). Significant interaction among TPI and LQ revealed that high MPD was characteristic for plots elevated above the terrain and with high litter quality as well as for plots at the bottom of valleys with low LQ (Figure 5b). We assume that high MPD at shady sites at the bottom of valleys could be explained also by local abiotic conditions (Appendix S5) or by the presence of relatively old phylogenetic lineages, such as *Dryopteridaceae*, *Araceae*, *Aristolochiaceae*, *Liliaceae* and *Orchidaceae* (Appendix S6). We also found that the ecological optima of plant species that decreased MPD were situated in plots with high HLI, and vice versa (Appendix S6).

## 4 | DISCUSSION

### 4.1 | Drivers of species diversity

As expected, the most important driver influencing species diversity was topography. We demonstrated that among the studied topographical variables HLI showed the largest positive effect on species diversity. However, several studies showed that plant species diversity in tropical and subtropical areas was negatively correlated with solar irradiation (Fonty, Sarthou, Larpin, & Ponge, 2009; He et al., 2017). Based on other topographical variables (TPI and CI) we argue that, generally speaking, communities with high diversity occur on locally elevated sites and on sloping ground. Thus, our

results support a global pattern of plant diversity found in topographically complex regions and places with high solar irradiation (Irl et al., 2015; Stein, Gerstner, & Krefl, 2014). We believe that the high species diversity that occurred on steep south-facing slopes could be explained by the simultaneous effects of several factors, such as topographical heterogeneity, irradiation and species pool (Kitagawa et al., 2015; Sádlo, Chytrý, & Pyšek, 2007; Stein et al., 2014; Zelený et al., 2010). Plots situated on sloping terrain with high HLI were covered by sparse forests, often with exposed bedrock. Such xeric and heterogeneous areas can be colonized by highly diverse forest and non-forest vegetation.

Our results correspond to other research on changes in species diversity which recognized soil pH as an important driving force (Baeten et al., 2009; Brunet, Diekmann, & Falkengren-Grerup, 1998). We determined that species diversity was not linearly correlated with soil pH but reached the highest value around pH 6. A worldwide meta-analysis showed that the relationship between soil pH and the diversity of plant communities is influenced by the non-proportional species pool of calcicole and calcifuge species in the surrounding landscape (Pärtel, 2002). Contrary to our results, in central Europe alkaline rather than neutral or slightly acidic soils support greater plant diversity because of the high extinction rate of calcifuge species during the Pleistocene (Ewald, 2003). The low number of species occurring on alkaline soils could be explained as a result of the biotic and microclimatic conditions at the most alkaline locality among our study sites (Děvín). The most alkaline plots at this site are situated on sloping terrain with scree forest communities and are dominated by the competitively superior

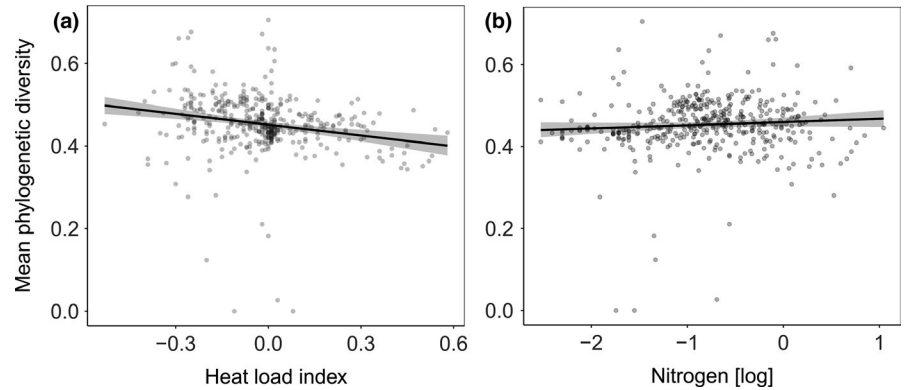
	Sum Sq	Mean Sq	NumDF	DenDF	F value	p (>F)
Soil nitrogen	0.0279	0.0279	1	399.14	8.5519	<0.01
HLI	0.0557	0.0557	1	404.85	17.1064	<0.001
LQ	0.0051	0.0051	1	397.42	1.5634	0.211
SCA	0.0056	0.0056	1	399.92	1.7192	0.191
HLI:LQ	0.0137	0.0137	1	400.55	4.1928	0.041
HLI:SCA	0.0222	0.0222	1	404.47	6.8117	<0.01
Random effect						<0.001

**TABLE 2** Results of step-wise regression procedure performing automatic backward elimination in the linear mixed-effect model. Phylogenetic diversity is used as the dependent variable

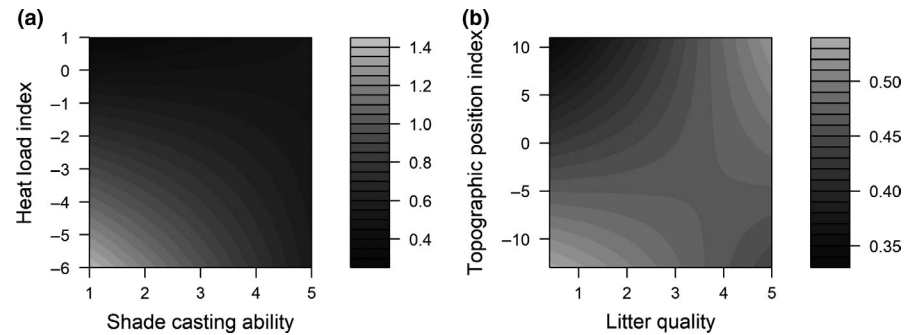
Note: The table shows the most parsimonious combination of explanatory variables explaining the greatest amount of the variability in phylogenetic diversity.

Explanatory variables are indicated by acronyms: HLI, Heat load index; LQ, Litter quality; SCA, Shade-casting ability.

**FIGURE 4** Relationships between phylogenetic diversity and environmental variables. Regression curves with marked 95% confidence interval were fitted by a generalized linear model with Poisson error distribution and log link function



**FIGURE 5** Contour plots showing changes in phylogenetic diversity across: (a) heat load index and shade-casting ability; and (b) litter quality and topographic position index. Displayed values were predicted based on the generalized linear model regressing phylogenetic diversity on the interaction between previously mentioned explanatory variables



species *Aconitum lycoctonum*. Therefore high levels of competition among nitrophilous understory vegetation will lower the species richness of this area (Grime, 1979). By using TWI as a proxy for soil moisture, we also found that the relationship between species diversity and soil acidity was affected by soil moisture. We thus suggest that microclimatic conditions (mainly humidity) can also be responsible for the observed pattern between soil pH and species diversity.

We determined canopy properties (LQ and SCA) as important factors that influence the plant diversity of understory vegetation. Specifically, a negative relationship was found between LQ and species diversity. This contradicts the general assumption that high-quality leaf litter (i.e., highly palatable and easily decomposable leaves) supports diversity via its effect on soil acidity, humidity and productivity (Cornelissen, 1996; Hector, Beale, Minns, Otway, & Lawton, 2000; Tilman, 1999). The negative effect of LQ on species diversity could be explained by the common occurrence of nutrient-rich soils at the studied localities, which means that the positive effect could not be sufficiently demonstrated. Another possible explanation is that the relationship was affected by the presence of *Tilia* spp., which is characterized by high values of SCA and LQ (Vesterdal, Schmidt, Callesen, Nilsson, & Gunderson, 2008). High SCA is connected with high overstory shading, which negatively influences species that are not good competitors for light. Thus, the negative effect of *Tilia* on species diversity can mask the positive effect of its highly palatable litter. Generally speaking, important mechanisms potentially excluding many species from the community appear to be related to high canopy coverage, which limits light availability.

## 4.2 | Drivers of phylogenetic diversity

Contrary to our expectations, the partial effects of environmental variables other than HLI were not significant. We believe this resulted from complex interplays among HLI, SCA and LQ. Such interplays in local-scale micro-habitats can influence the value of MPD. We found evidence that MPD is the highest under a combination of environmental conditions (the negative effect of high HLI is outweighed by the level of SCA and LQ) resulting in a low-stress environment (nutrient- and water-rich soils and enough light in the understory). In concordance with other studies we conclude that harsh conditions on steep south-facing slopes are linked with phylogenetically less diverse communities (Chapman & McEwan, 2018; Kitagawa et al., 2015). These studies suggested that high abiotic stress could cause environmental filtering of phylogenetically conserved traits manifesting in low phylogenetic diversity of species. Interestingly, the significant interaction between HLI and SCA shows that hotspots of MPD are situated in patches with low heat stress (north-facing slopes) which are dominated by tree species with low values of SCA.

The positive relationship between MPD and TPI was linked with high LQ. In contrast, high values of MPD in valleys were connected with low LQ. We believe that litter quality may have a mitigating effect in environmentally extreme habitats (i.e., hills and slopes with high solar irradiation), which is likely due to the influence on the decomposition rates of soil organic matter, the subsequent release of nutrients and soil moisture. The important effect of litter quality on MPD is in concordance with results by Chapman and McEwan (2018), who argued that soil moisture and fertility were key components affecting functional diversity.

### 4.3 | Contrasting patterns of species and phylogenetic diversity

We found that species diversity and MPD showed opposing trends in relation to the explanatory variables HLI, TWI and TPI, which characterize a stress gradient. We believe that this pattern can be explained by two mechanisms. First, by the theory of limiting similarity, where high levels of competition take place between closely related species (Abrams, 1983). Relatively mild conditions (i.e., low sun exposure and water-rich areas) will host phylogenetically diversified communities where competition is less probable. Second, by the species pool hypothesis, which states that local patterns of species diversity in a particular habitat mirror the abundance of this habitat in evolutionary history (Bartish et al., 2015; Zobel et al., 2011). In temperate biomes, forest ecosystems may serve as a refuge for ancient angiosperms of wetland monocots (e.g., *Araceae*) and also for early-diverging lineages of monocots such as lilioids (*Liliaceae* and *Orchidaceae*), which constituted the vegetation of evergreen forests in central Europe until the mid-Miocene (Lososová et al., 2015). These old lineages of plants show limited capacity to adapt to other types of modern drought-stressed habitats (Lososová et al., 2015). After the last glaciation, the phylogenetic lineages of plants that were not able to survive in open habitats colonized only forest types resembling those ancient conditions. Although our data do not allow for strong conclusions about the particular processes underlying the observed pattern, we incline toward the second mechanism because old-clade plants (pteridophytes and ancient lineages of lilioids and dicots) had higher abundance in localities with mild abiotic conditions (i.e., low sun exposure and water-rich areas with closed canopy; Appendix S6). Thus the trend in MPD may be driven by the presence of phylogenetically old and distinct lineages that have low numbers of closely related species. This hypothesis is supported also by the low percentage of variability explained by the model fitting phylogenetic diversity using environmental explanatory variables.

## 5 | CONCLUSIONS

Patterns in the diversity of herbaceous temperate-forest understory were markedly different between species diversity and phylogenetic diversity. Variability explained for species diversity was considerably higher than for phylogenetic diversity, where a few environmental drivers played relatively weak roles. Topographic variables were strongly correlated with species diversity but less so and in the opposite direction with phylogenetic diversity. Tree-derived variables strongly affected species diversity but did not explain any variability in phylogenetic diversity. We interpret the observed patterns as a result of environmental stress. Sites with high solar energy input enable the coexistence of species-rich plant communities, while shady sites with nutrient-rich and moist soils had higher phylogenetic diversity. They may act as refugia for evolutionary old phylogenetic lineages. Thus, both ancient and recent environmental drivers have contributed to plant community diversity in deciduous temperate forests.

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## AUTHOR CONTRIBUTIONS

RH, MC, MK, MM and OV conducted fieldwork and acquired environmental data. MC prepared and JŠ analyzed the data. JŠ, MC, RH, MK, MM, PS and OV wrote the manuscript.

## DATA AVAILABILITY STATEMENT

All raw data used for analysis are stored in a database of forest vegetation plots maintained at the Institute of Botany of the Czech Academy of Sciences (<http://ekolbrno.ibot.cas.cz/en/databaze>).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**APPENDIX S1.** List of all explanatory variables used for data analysis.

**APPENDIX S2.** Values of shade-casting ability and litter quality used in the analyses.

**APPENDIX S3.** Methods of soil analyses.

**APPENDIX S4.** Supplementary tables regarding partial and marginal effects of explanatory variables.

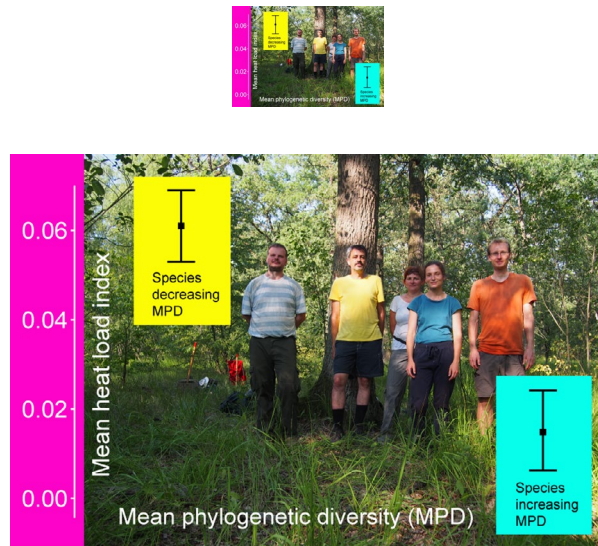
**APPENDIX S5.** Supplementary figure regarding trend in phylogenetic diversity among localities.

**APPENDIX S6.** Supplementary table and figures regarding stress gradient and plant species.

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# Graphical Abstract

The contents of this page will be used as part of the graphical abstract of html only. It will not be published as part of main article.



Our results indicate that old-clade plants (pteridophytes and ancient lineages of lilioids and dicots) were more abundant in localities with mild abiotic conditions (i.e., low sun exposure and water-rich areas with closed canopy); on the other hand, dry oligotrophic habitats were distinguished by short-lived light-demanding species with a phylogenetically younger age structure (some asterids).