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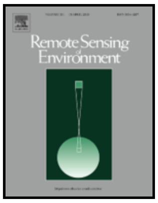

The relationship between spectral and plant diversity: Disentangling the influence of metrics and habitat types at the landscape scale

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ABSTRACT

Biodiversity monitoring is crucial for ecosystem conservation, but ground data collection is limited by cost, time, and scale. Remote sensing is a convenient approach providing frequent, near-real-time information with fine resolution over wide areas. According to the Spectral Variation Hypothesis (SVH), spectral diversity (SD) is an effective proxy of environmental heterogeneity, which ultimately relates to plant diversity. So far, studies testing the relationship between SD and biodiversity have reported contradictory findings, calling for a thorough investigation of the key factors (i.e., metrics applied, habitat type, scale, and temporal effects) and conditions under which such a relationship exists. This study investigates the applicability of the SVH for monitoring plant diversity at the landscape scale by comparing the performance of three types of SD metrics. Species richness and functional diversity were calculated for >2000 grid cells of $5' \times 3'$ covering the Czech Republic. Within each cell, we quantified SD using a Landsat-8 "greenest pixel" composite by applying (i) the standard deviation of NDVI, (ii) Rao's Q entropy index and (iii) the richness of "spectral communities". Habitat type (i.e., land cover) was included in the models of the relationship between SD and ground biodiversity. Both species richness and functional diversity showed positive and significant relationships with each SD metric tested. However, SD alone accounted for a small fraction of the deviance explained by the models. Furthermore, the strength of the relationship depended significantly on habitat type and was highest in natural areas with transitional bushy and herbaceous vegetation. Our results underline that despite the stability of the significance of the relationship between SD and plant diversity at this scale, the applicability of SD for biodiversity monitoring is context-dependent and the factors mediating such a relationship must be carefully considered to avoid misleading conclusions.

1. Introduction

Biodiversity supports multiple ecosystem functions, which ultimately provide the ecosystem services essential to sustain human societies (Cardinale et al., 2012; de Groot et al., 2002). However, human exploitation of Earth's natural resources has led to alterations in plant species' distribution and abundance to the extent that over one-fifth of all vascular plant species are threatened (Díaz and Malhi, 2022; Willis, 2017). There is an urgent need to improve ways to monitor biodiversity effectively across broad spatial scales and assess how plant communities respond to global change. Nonetheless, the ability to measure and monitor biodiversity continues to lag behind (Skidmore et al., 2021).

Remote sensing (hereafter RS) offers remarkable opportunities for biodiversity monitoring from local to global scales (Rocchini et al.,

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2010; Wang and Gamon, 2019). Among the approaches studied, spectral diversity (SD), originally developed in the framework of the Spectral Variation Hypothesis (SVH, Palmer et al., 2000, 2002), has been gaining attention as a basis for relating the remotely sensed spectral signal to ground biodiversity at different spatial scales and resolutions (Fassnacht et al., 2022; Marzialetti et al., 2021; Rocchini et al., 2010, 2021a; Tagliabue et al., 2020; Torresani et al., 2019). At coarser spatial resolution, the underlying assumption is that the spatial variation in reflectance values in a given area (i.e., SD) is likely correlated with the spatial variation in the environment and therefore related to the number of species present. At very fine spatial resolution, the relationship is assumed to be direct, with SD directly related to plant diversity through the diversity of species-specific optical traits associated with plant functional and structural properties (Ustin and Gamon, 2010).

Despite the potential of RS in biodiversity monitoring systems, the hypothesised relationship between spectral diversity and plant ground diversity still needs to be addressed (Fassnacht et al., 2022; Pacheco-Labrador et al., 2022). Although several empirical studies have validated the use of spectral diversity to estimate plant species diversity (Levin et al., 2007; Rocchini, 2007; Rocchini et al., 2014), others have criticised it for being unstable and not reliable in every context (Conti et al., 2021; Schmidtlein and Fassnacht, 2017). Such inconsistent findings may be due to a need for more systematic consideration of the key factors that influence the relationship between plant biodiversity and SD, which complicates the interpretation of spectral variation in many contexts (Fassnacht et al., 2022). Recently, Fassnacht et al. (2022) discussed four of the most important factors that may affect such a relationship: 1) the scale considered, both in terms of spatial extent (i.e., size of the study area) and spatial grain (i.e., pixel size); 2) reflectance changes over time (e.g., seasonality); 3) effects of the metric chosen for quantifying SD; and 4) the identity and number of habitat or vegetation types considered (Czyż et al., 2023; Gamon et al., 2019; Rocchini et al., 2010, 2018; Rossi et al., 2021; Schmidtlein and Fassnacht, 2017; Wang et al., 2022).

The type of habitats considered may strongly influence the relationship between SD and biodiversity, so all other factors should be adjusted accordingly. For instance, small patches of calcareous grassland embedded in intensively managed arable land may be very rich in species. However, when observed with medium-resolution sensors, they have low SD, while surrounding arable land has high SD but very low species richness (Fassnacht et al., 2022). Similarly, the spatial changes in fractional vegetation cover (which encompasses spatial variability in canopy architecture, fraction of bare soil, and plant litter spectra) can be different across habitats and, thus, strongly affect the spectral signal (Hauser et al., 2021). Consequently, not considering the variety and types of habitat can be particularly problematic when multiple habitat types are examined simultaneously, as is the case at large to medium observation scales (Fassnacht et al., 2022; Schmidtlein and Fassnacht, 2017).

Similarly, the SD metrics are thought to be linked to plant diversity through different pathways, which may lead to different results. To date, several SD metrics have been proposed as proxies for biodiversity, with no consensus on which of them best fulfils this role. Wang and Gamon (2019) have described three main classes of SD metrics:

i) metrics based on variation in traditional vegetation reflectance indices based on the correlation between productivity and plant diversity (Tilman et al., 2001; Zhang et al., 2012);
ii) metrics based on spectral information content, which condense the full-spectral information through statistical metrics of variability or spectral entropy;
iii) metrics based on "spectral species" (or "spectral types") that have similar spectral signatures and are derived from partitioning the spectral space (Féret and Asner, 2014).

To date, most empirical studies investigating the relationship between SD and plant diversity have relied on limited datasets (Fassnacht et al., 2022). In addition, efforts to link plant diversity at the landscape scale to SD have focused mainly on taxonomic diversity (e.g., species richness or evenness). However, species influence ecosystem processes and stability through their functional composition, diversity, and abundance (de Bello et al., 2010; Tilman et al., 1997). Functional diversity represents the variability in plant functional traits in a given area. The spatiotemporal mapping of functional diversity at large scales could thus support assessing how environmental changes affect ecosystem functioning. Nonetheless, the potential of SD to infer functional diversity at the landscape scale remains to be demonstrated (Cavender-Bares et al., 2022; Frye et al., 2021; Hauser et al., 2021; Schweiger et al., 2018).

Here we investigate whether plant diversity (species richness and functional diversity) at the landscape scale is related to SD. To assess the context-dependence of such a relationship, we will test the performance of three types of SD metrics, taking into account the effects of habitat types. Specifically, we rely on an extensive, spatially continuous, field-collected dataset covering the Czech Republic and a multitemporal Landsat-8 OLI composite.

2. Materials and methods

2.1. Plant diversity data

Data on plant diversity were obtained from the Pladias Database of the Czech Flora and Vegetation (Chytrý et al., 2021). This nationwide database contains >13 million records of species occurrence (many of them critically reviewed and validated) and traits of almost 5000 taxa (species, subspecies, varieties, and hybrids) of the Czech vascular flora (Chytrý et al., 2021; Wild et al., 2019). We used the latest update of taxonomic concepts and nomenclature (Kaplan et al., 2019). The collection of the species records used for our analysis started in the late 18th century, but >60% of the records were collected in the last 20 years (for a detailed description of the records, see Wild et al., 2019). The data include all native or spontaneously established alien vascular plant taxa, as well as some commonly cultivated crops and woody plants. The study area covers an altitudinal range from 115 to 1603 m a.s.l. with annual precipitation varying from about 400 mm to 1450 mm (Brázdil et al., 2021; Tolasz et al., 2007) and a wide range of environmental conditions, from dry and warm forest-steppe areas to mountainous areas with subalpine vegetation (Chytrý et al., 2017). We counted the number of species, i.e., species richness (SR), and calculated functional diversity (FD) in grid cells of 5′ × 3′ (approx. 6.0 × 5.5 km), forming a grid of >2000 cells covering the entire Czech Republic (Fig. 1) (Wild et al., 2019). The size of the grid cells corresponds to quadrants of the basic fields of the grid template used for Central European floristic mapping (Central European Basic Area; Petřík et al., 2010). All marginal grid cells that were not entirely within the country were excluded from our analysis to avoid potential bias due to undersampling.

To calculate FD, we selected a list of optically and ecologically relevant functional traits. The majority of traits were available in Pladias (see Chytrý et al., 2021 for their description): Mean Height, Growth Form, Life Form, Leaf Shape, Flower Colour, and three traits were taken to Pladias from the BiolFlor database (Klotz et al., 2002): Leaf Life Span, Leaf Anatomy and Reproduction Type. We also added three traits from the LEDA database (Kleyer et al., 2008) that are not included in the Pladias Database: Specific Leaf Area (SLA), Leaf Dry Matter Content (LDMC), and Seed Mass (Appendix A). We relied on database-derived functional trait values as it was not possible to measure them for all species in each grid cell. Since the trait data used in this study come from databases of Central European flora, we assume they accurately represent the trait values present in our study region. For those numerical traits which have measurements from multiple individuals (i.e.,

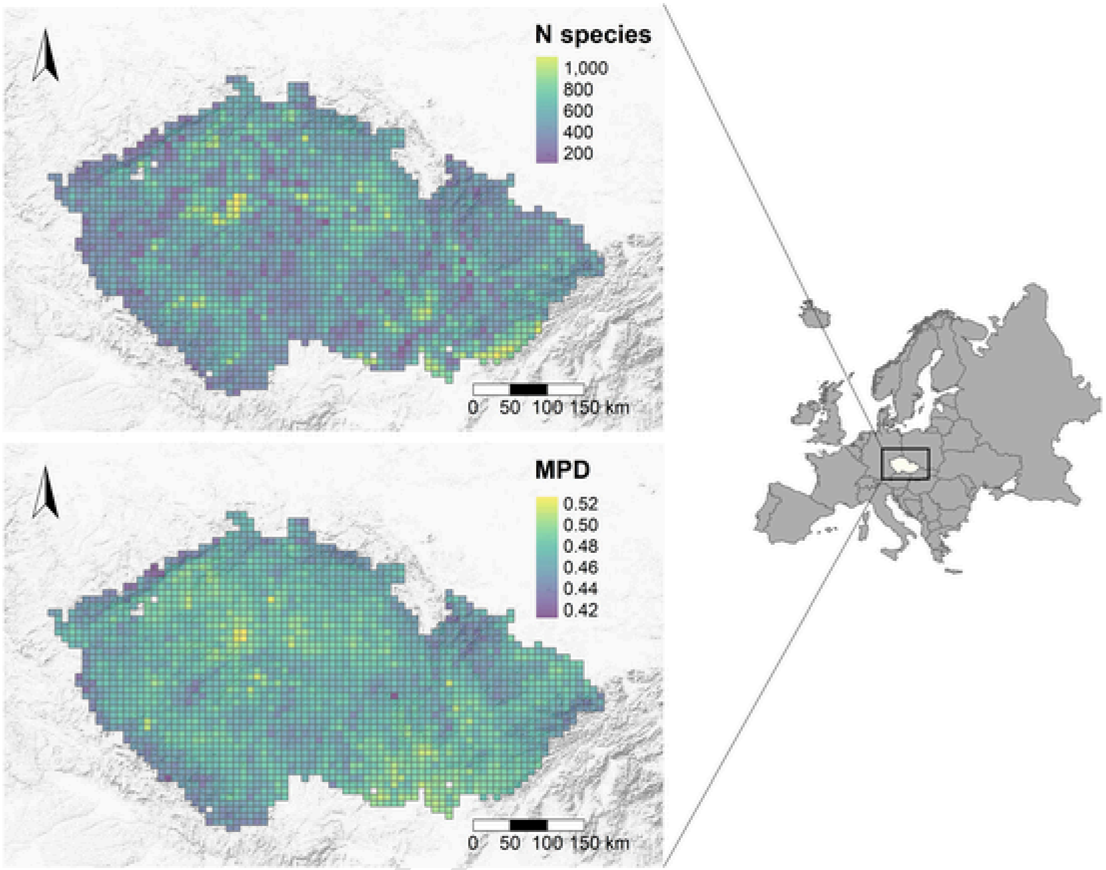

Fig. 1. Plant diversity within each grid cell (n = 2361) covering the Czech Republic. Species richness (SR, number of species, top) was obtained from the Pladias Database of the Czech Flora and Vegetation (Chytrý et al., 2021). Functional diversity (FD), expressed as mean pairwise distance (MPD) in plant traits (bottom), was calculated based on a list of functional traits available in the Pladias and LEDA databases (Chytrý et al., 2021; Kleyer et al., 2008).

traits from LEDA database), we confirmed that, within our dataset, interspecific variation is higher than intraspecific variation. We did it by comparing, for each trait, the standard deviation calculated from the mean values of each species with the mean value of all species' standard deviations (Appendix A). The assumption behind the use of database-derived data is that they are a good approximation of the actual trait diversity of the area. The mean trait values coming from databases result from hundreds of measurements done in different habitats, under different management practices, and variable soil conditions. For this reason, the intraspecific variability that can be estimated from the database approximately corresponds to the in situ intraspecific variability. We compiled trait values for a minimum of 1463 species for LDMC, and for a maximum of 3087 species for Leaf Shape. To account for potential bias due to missing values, only those grid cells that had at least 70% coverage for each of the traits considered were included in the analysis, resulting in a total of 2361 grid cells. For each grid cell, we calculated FD as the mean pairwise distance (MPD) between species in the functional trait space defined by the above-mentioned traits (Fig. 1). Trait distances were measured using Gower distance, where each numerical trait is first standardised by dividing each value by the range of the corresponding trait, after subtracting the minimum value; consequently, the rescaled trait variable has the range [0,1] (Gower, 1971).

2.2. Spectral data

We used the USGS Landsat 8 atmospherically corrected Surface Reflectance catalogue of data acquired with the Operational Land Imager (OLI) sensor and available in Google Earth Engine (GEE) (Gorelick et al., 2017). Specifically, we used Earth's atmospherically corrected surface reflectance in six bands in the visible (B2, B3, B4), near infrared (B5) and short-wave infrared (B6, B7) range of the electromagnetic spectrum, with a spatial resolution of 30 m and a revisit time of 16 days. To select reflectance data for the same phenological period in which the ground biodiversity measurements were made (i.e., the growing season), we processed OLI images acquired over the area of interest during the growing seasons (i.e., between May and August each year) from 2013 to 2017. The annual range was chosen to overlap with the period of field records. Despite the shorter period covered by OLI than Landsat-7 Enhanced Thematic Mapper Plus (ETM+), we chose the OLI dataset due to the Scan Line Corrector (SLC) ETM+ failure in 2003, which has affected data acquisition since then. To further address the temporal mismatch between field data collection and available spectral data, we masked out from the images all pixels where land cover changed between 2000 and 2012 based on the CORINE Land Cover (CLC) classification. This was done to exclude from our analyses those areas that may have experienced changes or severe disturbances during the period when most field data were collected (i.e., after 2000).To minimise weather-related noise, cloud-covered pixels were filtered out based on the Pixel quality attributes (pixel_qa) band (Foga et al., 2017). Then, the Normalized Difference Vegetation Index (NDVI) was calculated, and the NDVI layer was added to each image. Finally, we generated a “greenest-pixel” composite image by selecting the pixels with the highest NDVI value of the overlapping images for the studied time period. This was done to best capture the vegetation cover and smooth out inter-annual variability. By selecting the greenest pixel over the entire period rather than using a median composite, we aimed to get the optimal vegetation cover of the area (which matches the time of the year when field data were collected) and to avoid the effects of extreme events, such as floods or fires. For the sake of completeness, the results of the analyses using the median composite are presented in Appendix

B, showing consistent but weaker results compared to the greenest-pixel composite. Indeed, previous studies have shown that the relationship between reflectance variability in space and plant diversity tends to be higher when vegetation is near its optimum, i.e., when the cover of photosynthetically active vegetation is at its maximum (Feilhauer and Schmidtlein, 2011; Thornley et al., 2022; Torresani et al., 2019).

2.3. Spectral diversity metrics

We quantified the SD values within each 5′ × 3′ grid cell using three different methods, each representing one of the main categories proposed by Wang and Gamon (2019): i) the standard deviation of NDVI (sdNDVI), ii) Rao's Q quadratic entropy index (Rocchini et al., 2017), and iii) richness of "spectral communities" (SpecCom) (Rocchini et al., 2021a).

2.3.1. sdNDVI

The Normalized Difference Vegetation Index (NDVI) is a traditionally used vegetation reflectance index used to quantify vegetation greenness (Tucker, 1979). sdNDVI has often been used as a continuous measure of the dispersion (variation) of NDVI values in a given area since it explains a reasonable portion of the variability in the in-situ diversity data (Gillespie, 2005; Gillespie et al., 2009; Gould, 2000; Hall et al., 2010; Levin et al., 2007).

2.3.2. Rao's Q

Rao's Q index is a continuous metric that quantifies the difference in reflectance values between two pixels drawn randomly with replacement from a defined set of neighbouring pixels, taking into account their abundance and the relative Euclidean distance between them:

$$Q = \Sigma\Sigma\, d\text{ij} \times pi \times pj \qquad (1)$$

where d_{ij} is the spectral distance between pixels *i* and *j*, and p_i and p_j are the relative proportions of pixels *i* and *j*, respectively (Rocchini et al., 2017). The advantage of applying Rao's Q index to spectral data, as opposed to other diversity indices (e.g., Shannon's H′), is its ability to explicitly account for the numerical size of pixels rather than just the relative abundance (evenness) of reflectance values. To calculate Rao's Q index within each grid cell, we used the function `RaoQArea` written in the R language (R Core Team, 2021) and stored in the GitHub repository https://github.com/micheletorresani/RaoQarea. `RaoQArea` calculates Rao's Q heterogeneity index for a limited area based on the Euclidean distance between pixels of a single-band raster. In our case, the `RaoQArea` function was applied to the single-band raster derived by selecting the first component from a principal component analysis (PCA) applied to a large random subset of pixels of the original multi-band image. PCA was performed to simplify spectral information and remove band collinearity.

2.3.3. SpecCom

To differentiate spectral communities as a function of the optical traits underlying the reflectance of each pixel, we used the R package `biodivMapR` (Féret and de Boissieu, 2020; Féret and de Boissieu, 2022), which allows spectral diversity mapping based on the partitioning of the spectral space of RS images into subunits called as "spectral species" (following Féret and Asner, 2014). Due to the resolution of the spectral data used, a direct link between the identified spectral subunits and in-situ plant species is not feasible. Therefore, we refer to such partitions in the spectral space as "spectral communities" (sensu Rocchini et al., 2021a, 2022), assuming that they are linked to a higher level of ecological organisation. After a series of pre-processing steps that are part of the package workflow, e.g., spectral normalisation (i.e., continuum removal) and dimensionality reduction (by PCA), the mapping of spectral communities was based on k-means clustering. Clustering was performed on relevant PCA axes (i.e., three out of four) selected by visual inspection, in which we rejected principal components with no relevant information or including artefacts possibly due to sensor properties (Féret and Asner, 2014). The number of k clusters was set to 200 after a trial-and-error procedure as the trade-off between the number of clusters with stable results and computational effort (Féret and de Boissieu, 2020; Rocchini et al., 2021a). Based on the resulting map of "spectral communities", we calculated the categorical metric "spectral communities" richness (SpecCom) within each grid cell.

2.4. Accounting for habitat type

We hypothesised that habitat type might play a role in the relationship between SD and plant diversity (Schmidtlein and Fassnacht, 2017). In the present study, habitat type was defined by CLC because of the broad coverage and validation of these data. We assigned each 5′ × 3′ grid cell to the most represented CLC type (reference year 2012) within the cell. Although classifying each grid cell with the predominant CLC is an approximation, no other options were possible due to the grain mismatch between the available ground and CLC data. Level I CLC nomenclature was used for artificial land cover types. For forests and semi-natural areas, we assigned land cover codes according to the Level III CLC nomenclature. For agricultural land, we used the Level II nomenclature for arable land and level III for pastures. As a result, the following categories were assigned to the grid cells: CLC 1, CLC 21, CLC 231, CLC 311, CLC 312, CLC 313, and CLC 324 (see Appendix C for a description of the CLC types used). No specific landscape features were masked from our spectral data, as this would be in contrast with the original formulation of SVH (please note that the reason behind the masking described in section 2.2 is only linked to land cover change).

2.5. Statistical analyses

All statistical analyses were performed in R 4.1.2 (R Core Team 2021). We modelled the relationship between in-situ diversity and SD through generalized additive models (GAMs) using the `mgcv` package v. 1.8.39 (Wood, 2017), with SR or FD as *response variables* for a total of six models. For SR, we used a negative binomial (NB) error distribution to account for possible over-dispersed SR count data. For FD, we used the Gaussian error distribution. Each model had the following three sets of *predictors terms*:

1. An interaction between SD and the dominant CLC type. This represents the effect of CLC type on the relationship between SD and plant diversity. In other words, this models the possibility of having different SD-SR or SD-FD relationships in different CLC types.
2. Sampling effort, represented by the logarithm of the number of plant species records within each grid cell. This corrects for the possible effects of uneven sampling effort, when grid cells have higher species diversity because they have been sampled with a higher intensity. Indeed, not considering uneven sampling effort may be a source of bias in models based on species counts (Chao and Chiu, 2016).
3. Smooth two-dimensional splines on a sphere (Wood, 2017) to model the effect of spatial autocorrelation (i.e., spatial pseudo-replication) in the response variable, which can be caused either by the effect of spatially autocorrelated environment, or by contagious biological processes such as species dispersal (Dormann et al., 2007; Legendre, 1993).

To account for possible non-linear patterns, the response of SR and FD to all continuous predictors was modelled as a second-order polynomial (the full six models' formulas are available in Appendix D).

To estimate the relative importance of the effects of the three sets of predictors above (i.e., SD, sampling effort, and spatial autocorrelation), we used partitioning of deviance (Aragón et al., 2010; Carrete et al., 2007), an approach related to variance partitioning (Borcard et al., 1992). Specifically, the deviance from a null model with no predictors was partitioned to (i) a fraction explained by spectral diversity and its interaction with CLC, (ii) an effect of sampling effort, and (iii) a fraction explained by spatial autocorrelation. We estimated both the independent effects of these, as well as their overlapping fractions, where the overlap is caused by collinearity between the predictors (for the formulas used, see Anderson and Cribble, 1998, and Lobo et al., 2002).

The data and code used in the analyses are available at https://github.com/MichelaPerrone/SVH_CZ.git under CC-BY license.

3. Results

3.1. Relationship between plant diversity and SD

We found statistically significant relationships between plant diversity (SR and FD) and SD. The models with SR and FD as responses were similar, all showing positive relationships with SD. The explanatory power of the models, expressed as explained deviance, ranged from 71.7% to 75.3% for models explaining species richness and from 57.6% to 65.4% for models explaining functional diversity (Fig. 2).

For both SR and FD, the models where SD was calculated using SpecCom showed the lowest explained deviance, while the models with continuous metrics (i.e., sdNDVI and Rao's Q) showed the highest explained deviance (Fig. 2).

3.2. Variation partitioning

Variation partitioning showed that the unique contribution of SD accounts for only a small fraction of the total variability, ranging from 2.4% to 6.0% in SR models (Fig. 3a, c, and e), and from 5.4% to 13.2% in FD models (Fig. 3b, d, and f), with the unique contribution of SD showing the highest values when calculated using continuous metrics (i.e., sdNDVI and Rao's Q). Moreover, the partitions of deviance show different results between SR and FD models in terms of relative values of the unique contribution of spectral diversity, spatial autocorrelation, and sampling effort, as well as of their shared fractions. Indeed, in SR models, sampling effort alone explained almost half of the deviance (between 47.2% and 48.0%), while the unique contribution of spatial autocorrelation accounts for a small fraction (Fig. 3a, c, and e). In contrast, in FD models, most of the variability was jointly explained by SD and spatial autocorrelation (between 25.5% and 29.6%) and by spatial autocorrelation alone (between 25.6% and 33.0%), with sampling effort accounting for the smallest independent effect (Fig. 3b, d, and f).

3.3. Effect of habitat type

For simplicity, we focus primarily on how the direction of the relationship between SD and biodiversity varies with CLC types, therefore we describe only the effects of the interaction between the first power of the SD variables and habitat type, since it is the power that determines the direction of the effect (the full list of coefficient estimates can be found in Appendix E). We found that the significance, magnitude, and sign of the effect of SD varied depending on the CLC type dominating the landscape (i.e., grid cell) (Fig. 3). Specifically, in the landscapes dominated by arable land (CLC 21), coniferous forests (CLC 312), and transitional woodland-shrub (CLC 324), the effect of SD was always significant and positive (Fig. 4a, b, c, d, e, and f). In addition, the effects of SD in transitional woodland-shrubs (CLC 324) were remarkably higher than the other interactions (Fig. 4), suggesting that increases in SD were associated with either a higher increase in plant diversity, fractional tree cover and portion of understory visible, or a combination of both in transitional woodland-shrubs than in other habitat types. In the case of artificial surfaces (CLC 1), the effect of SD was significant and positive only when considering sdNDVI and Rao's Q in both SR and FD models (Fig. 4a, b, c, and d). The effect in pastures (CLC 231) was significant and positive only in FD models where SD was calculated using sdNDVI and SpecCom (Fig. 4b and f). The effect in broad-leaved forests (CLC 311) was significantly positive in the FD model where SD was calculated using sdNDVI and in both SR and FD models using SpecCom (Fig. 4b, e, and f). The effect in mixed forests was significant and positive in all models (Fig. 4b, d, e and f) except for SR models where SD was calculated through sdNDVI and Rao's Q. The only case where we observed a significant negative effect of the interaction with the predominant habitat type was when considering artificial surfaces (CLC 1) in the models relating plant diversity to SpecCom (Fig. 4e and f). In all other cases, the effects of predominant habitat type on the relationship between SD and plant diversity were not significant.

4. Discussion

4.1. Spectral diversity and plant diversity

When modelling the ability of different types of SD metrics to explain the variation in plant diversity at the landscape scale, only a small fraction of the variation was explained by SD alone despite the relatively high goodness-of-fit (percentage of explained deviance) observed in our models. However, a relatively large fraction of variation in all models was explained by spatially structured SD, i.e., the joint effect of SD and spatial autocorrelation. Overall, the unique contributions of

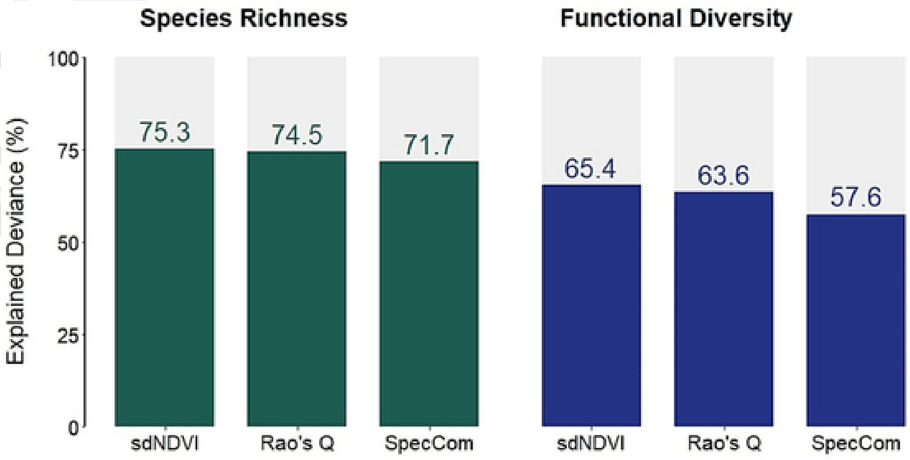

Fig. 2. Total explained percentage deviance of models explaining species richness and functional diversity based on three types of spectral diversity (sdNDVI, Rao's Q, SpecCom), sampling effort, and spatial autocorrelation.

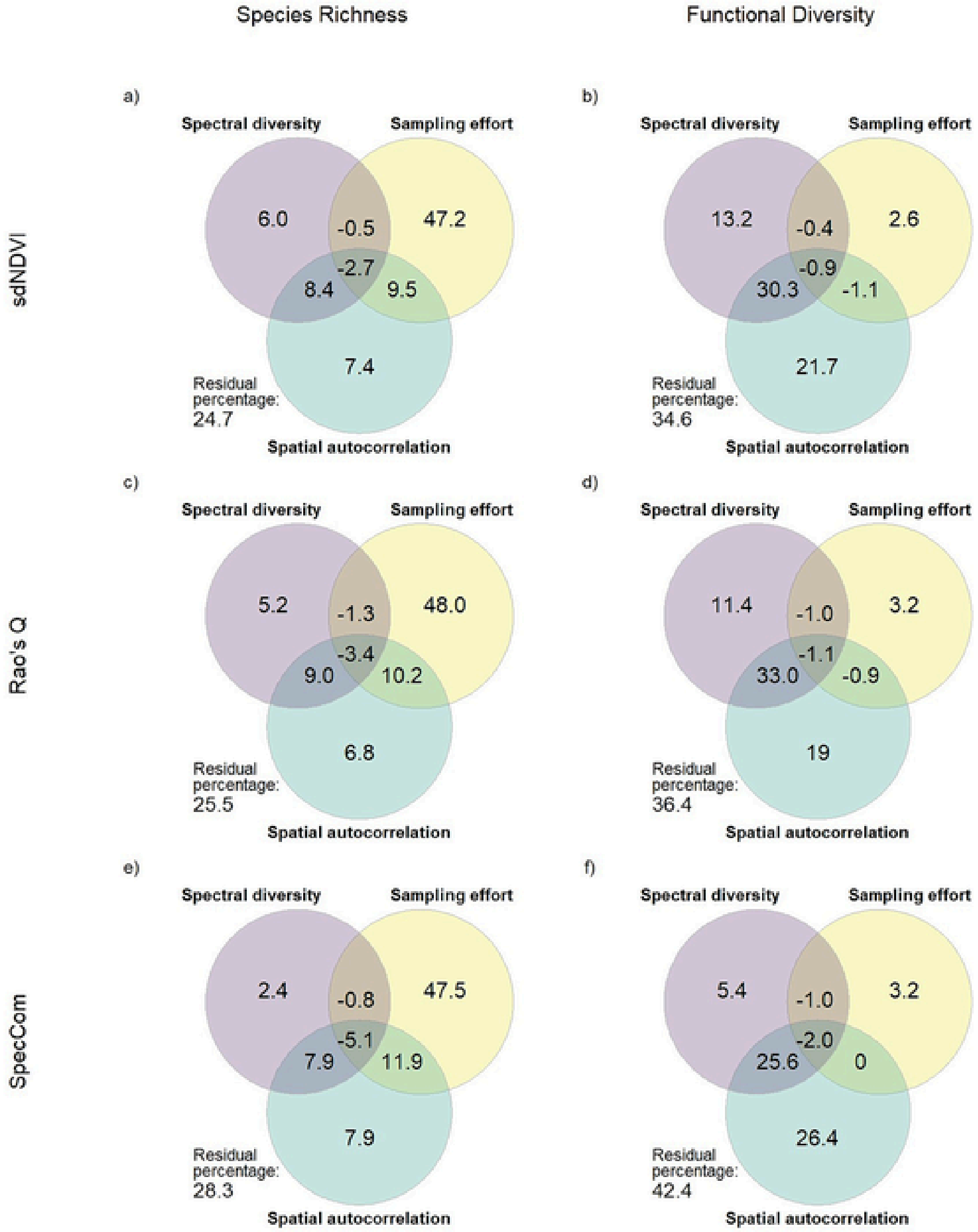

Fig. 3. Venn diagrams showing the percentage of explained deviance in plant diversity explained by the three groups of predictors: spectral diversity, sampling effort, and spatial autocorrelation (splines). Overlaps among circles represent fractions of the variation that cannot be unequivocally attributed to one of the overlapping predictors. For example, when spectral diversity is also spatially autocorrelated, some fraction of the explained deviance will be shared between spatial autocorrelation and spectral diversity. Negative numbers can arise due to the spline optimisation algorithm during model fitting, are usually small, and can be interpreted as zeroes.

sampling effort and spatial autocorrelation explained a large portion of the variation in the diversity values. The variation explained by sampling effort was highest in all SR models, while spatial autocorrelation showed a relatively higher explained variation in FD models. The large contribution of sampling effort in SR-based models is not surprising. It is well known that species richness estimates increase with sampling effort (Walther et al., 1995). In contrast, the importance of spatial autocorrelation (modelled using smooth splines) may reflect both the effect of spatially-autocorrelated environment (e.g., topography, climate) and that of dispersal limitation of species (Dormann et al., 2007). Therefore, routinely inferring plant diversity from SD may lead to inaccurate results if sampling effort and spatial autocorrelation are not accounted for in situations similar to this study.

Although SR models had a better goodness-of-fit, SD accounted for a larger fraction of variation in FD models compared to SR models. These results suggest that SD is linked to FD slightly better than to SR. At small scales of observation, a stronger relationship of SD with FD than with SR is assumed when relying on high spatial resolution spectral data, as a direct relationship between pixels' spectra and plant functional and structural properties is expected (Schweiger et al., 2018; Ustin and Gamon, 2010). At the landscape scale, when relying on coarse spatial resolution data, such a correspondence between spectrum and plant properties decreases due to the mismatching size of pixels and individuals. Thus, the link between spectral and plant diversity can only be of indirect nature and captured through landscape heterogeneity. Our results suggest that SD is more strongly related to FD than

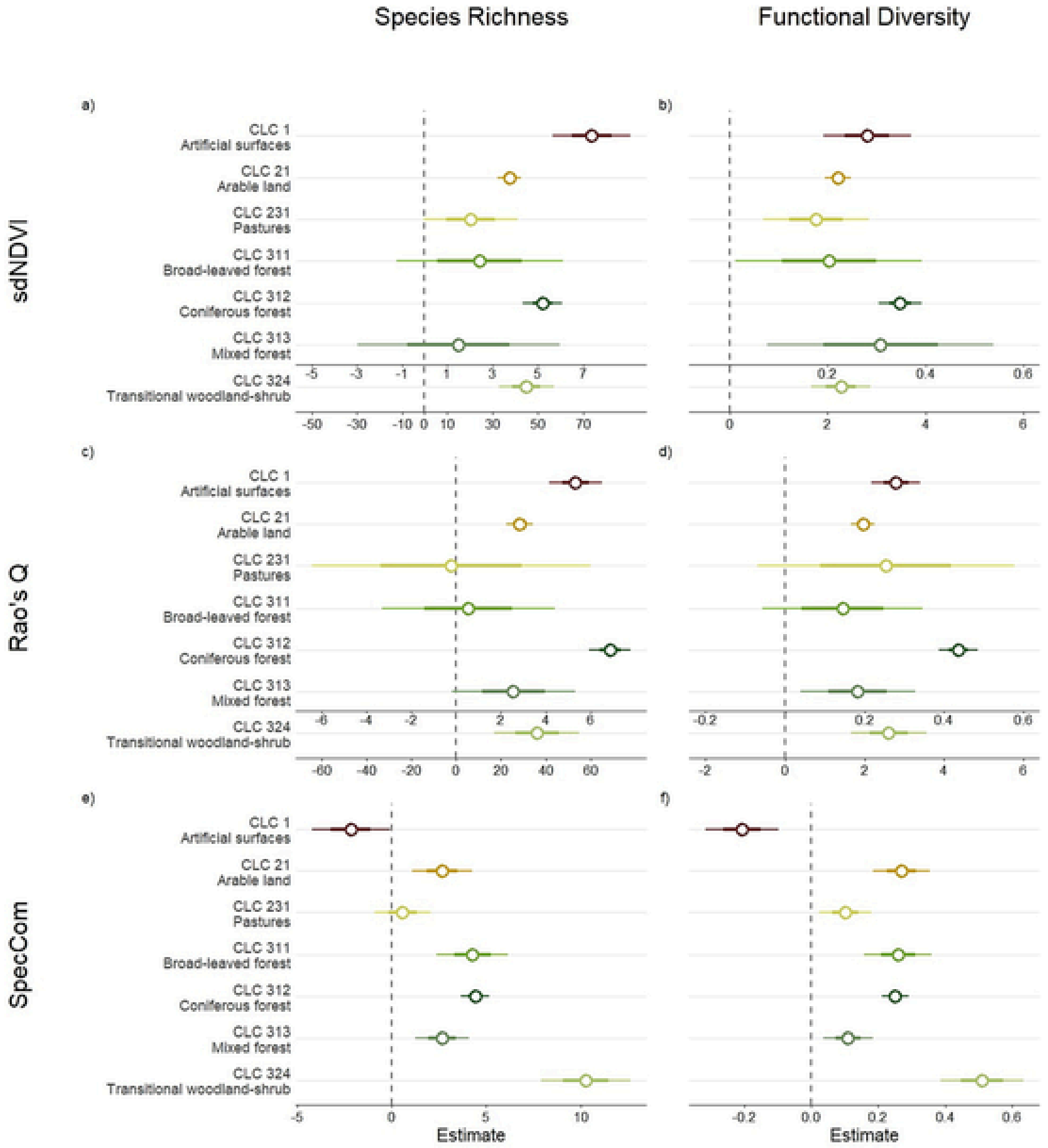

Fig. 4. Effect sizes (standardised coefficients) of interactions between SD and land-cover types in the plant diversity ~ SD models. The dots represent coefficient estimates; the outer error bars are 95% confidence intervals, and the inner error bars indicate one standard error on each side. When the 95% coefficient interval includes a value of zero, the interaction between SD and land-cover type is not significant. Due to the different value ranges of CLC 324 estimates, a second x-axis with appropriate scaling is shown.

SR also when relying on coarser spectral data, differently from what was shown in previous studies (Hauser et al., 2021). This is in agreement with the original formulation of the SVH (Palmer et al., 2002): the heterogeneity of the landscape estimated through SD reflects the diversity of available niches and, thus, both functional and taxonomic diversity. Indeed, SD does not attempt to directly estimate any specific aspect of plant biodiversity (e.g., taxonomic, phylogenetic, functional) (Laliberté et al., 2020; Schweiger et al., 2018; Wang and Gamon, 2019).

4.2. *Spectral diversity and effects of habitat type*

The differences found in the relationship between SD and ground diversity across the habitat types considered were based mainly on the ability of the different metrics (continuous and categorical) used to capture the relationship and on the strength of the relationship.

In landscapes dominated by artificial surfaces, the ability of continuous metrics of SD to predict biodiversity improved. This is unexpected because, unlike categorical spectral metrics, continuous metrics are sensitive to extreme reflectance values of background material (e.g., bare soil, litter, rocks), which can have a considerable influence on the SD estimation (Fassnacht et al., 2022; Wang et al., 2018b). At finer resolutions, this issue can be tackled by masking out soil pixels and unvegetated areas (e.g., Gholizadeh et al., 2018). At coarser spatial resolutions, as in our case, such masking may lead to the erroneous filtering of mixed pixels corresponding to scarcely vegetated - but biologically relevant – areas, resulting in a consequent loss of information (Schmidtlein and Fassnacht, 2017). Landscape mosaics dominated by urban areas are likely to be very species-rich, as cities and suburban areas often harbour more plant species than the surrounding landscape (Araújo, 2003; Kühn et al., 2004). Moreover, masking landscape features based on their reflectance values would contradict the original formulation of the SVH, which states that it is the magnitude of variation in spectral characteristics of an area that relates to habitat (or vegetation type) heterogeneity and, thus, to available niche space. An alternative solution to pixel masking is spectral unmixing (Asner and Heidebrecht, 2002), which would allow estimating the per-pixel percentage of vegetation cover. In contrast, in landscapes dominated by urban habitats, the ability of the categorical approach to make inferences about biodiversity was impaired, which suggests that these metrics do not properly capture the heterogeneity of this landscape type.

The categorical approach of the SpecCom metric can still offer relevant benefits (Fassnacht et al., 2022; Schmidtlein and Fassnacht, 2017). Estimating SD through spectral type classification allows summarising the continuity of spectral space into discrete spatial objects that are likely to correspond to distinct landscape features. With this approach, there is less risk of disproportionate influence of extreme pixel values on the spectral variation metric since they would constitute individual categories among equally meaningful others (Wang and Gamon, 2019). Moreover, spectrally homogeneous spatial units can be identified even when plant optical characteristics change throughout the year according to species phenology, allowing for temporal consistency in spectral type classification. However, this is unlikely to work in larger regions with diverse environmental conditions and, thus, non-synchronous phenological states across similar ecological entities (e.g., communities). In landscapes dominated by transitional woodland-shrub habitats, both categorical and continuous SD metrics exhibited the strongest (albeit still weak) association with plant diversity. Given the inherent spatial vegetation heterogeneity of such areas, which can likely be detected through RS imagery, these results are unsurprising. Indeed, this land-cover type is characterised by patchy, bushy, and herbaceous vegetation with occasional scattered trees (Bossard et al., 2000), and the resulting spectral heterogeneity can be detected even by current, non-commercial spaceborne sensors.

In landscapes dominated by arable land and coniferous forests, we found the same general positive (although weaker) effect of habitat type on the relationship between SD and diversity, indifferently of which metric was used. The agreement among SD metrics indicates that the relationship between SD and ground biodiversity is significant and stable. The landscapes dominated by arable land are widespread in Central Europe including the Czech Republic (see Appendix C) and are characterised by high spectral heterogeneity, mostly given by the mosaic of heterogeneous and species-poor cultivation patterns. However, these landscapes may harbour small “islands” of natural and semi-natural species-rich habitats (e.g., grasslands and shrublands), which are captured by SD. In the case of landscapes dominated by coniferous forests, the low spectral heterogeneity of the canopy is coupled with low plant diversity, which is mirrored by the positive SD-diversity relationship.

In our study, areas classified as pastures (CLC 231) correspond to managed grasslands and meadows. Therefore, the positive and significant interaction between pastures as the predominant habitat type and SD observed in FD models was less expected than for other habitat types. Indeed, the wide mismatch between pixel resolution and size of individuals and populations of plant species has no negative effect on the SD-diversity relationship, as would be expected based on the smoothed reflectance signal (Wang et al., 2018a; Fassnacht et al., 2022).

4.3. *Choice of spectral diversity metrics*

We found that all of our SD metrics can explain a comparable proportion of the variability in the ground diversity at the scale applied. However, there were differences between categorical (i.e., SpecCom) vs continuous metrics (i.e., Rao's Q and sdNDVI), with the continuous metrics performing slightly better. Their performance depended on the habitat type considered. Moreover, some practical aspects could be crucial in choosing the most appropriate metric.

The application of categorical metrics for the routine production of RS biodiversity products with consistency across large scales is complicated by the need for the user's input. Indeed, it is necessary to conduct preliminary experiments to find the perfect compromise between the number of clusters and the computational effort that would allow reliable results (Féret and de Boissieu, 2020; Rocchini et al., 2021a). Regarding continuous metrics, those used in this study differ in the spectral information used to compute SD. Indeed, metrics based on variation in vegetation indices (e.g., sdNDVI) rely on the information provided by specific wavebands related to vegetation condition and biomass and allow discrimination between vegetated and non-vegetated areas, and between different vegetation types. However, the use of this specific (limited) set of spectral bands may exclude some important information about other environmental and biochemical properties (e.g., leaf water content, nitrogen content, pigments, and lignin) (Asner and Martin, 2009). In contrast, spectral entropy metrics (e.g., Rao's Q) use all the available spectral information and describe the spectral “dimensionality” of the data (Wang and Gamon, 2019). Still, they can be computationally costly, possibly needing several days to be computed for large areas at a medium-high spatial resolution. As we showed that a simpler vegetation index-based metric (sdNDVI) performs comparably well to a spectral entropy-based Rao's Q, we recommend using the simpler and computationally low-cost sdNDVI, which already proved performing in other studies (Gholizadeh et al., 2018). However, since previous results (Gholizadeh et al., 2018; Wang et al., 2018b) suggest that the most informative spectral regions for biodiversity assessment can vary with spatial resolution, data properties, and scale of observation, further analyses would be needed to assess whether this metric should be used in other analytical contexts.

4.4. *Limitations and ways forward*

We calculated SD based on the “greenest-pixel” composite image obtained from the overlapping images matching the time of the year when field data were collected. We did this to best capture the vegetation cover and smooth out inter-annual variability. This solution performed best within our study framework (see Appendix B for comparison with the median-composite approach). However, there still is a knowledge gap about the best way to compute SD on multitemporal imagery, and there are two reasons for this. First, for medium-high resolution multitemporal imagery covering wide areas, it is computationally demanding to calculate SD over single images and then aggregating them. Second, it is unclear which is the most appropriate criterion for aggregating SD (e.g., median, mode, maximum value), which is likely to depend on the specific study settings (e.g., SD metric applied). Thus, future work should test and compare SD aggregation practices.

According to the SVH, we expected SD to be a proxy for environmental heterogeneity and, thus, related to plant diversity. Our results indicate that this needs to be reconsidered. Rather than the main predictor, SD can be useful as an additional covariate in multivariate models predicting biodiversity (e.g., Kreft and Jetz, 2007; Večeřa et al., 2019), together with well-known predictors of plant diversity such as climate and topography. As we aimed specifically at testing the SVH, building such multivariate models was beyond the scope of this study. Nevertheless, it is a promising topic for future research, which could be addressed through machine learning (Večeřa et al., 2019) and structural equation modelling (SEM) (Fan et al., 2016; Ullman and Bentler, 2012). Alternatively, the “non-spectral” environmental factors could be included in the estimation of landscape heterogeneity through the area-based multidimensional Rao's Q, which is now possible using the `paRao` function available in the `rasterdiv` R package (v. 0.3.1; Rocchini et al., 2021a, 2021b).

5. Conclusions

We examined the relationship between vascular plant diversity and spectral diversity across >2000 grid cells covering the Czech Republic, taking into account the effects of land cover. We investigated the potential of three SD metrics to infer both species richness and functional diversity. Our results show little to no difference among the metrics tested at this scale, indicating that the association between SD and plant diversity is significant and stable. However, our results confirm that there is no general validity of the SVH. In our setting, only a small percentage of variation could be explained solely by SD and not accounting for sampling effort and spatial autocorrelation in the models could be misleading. We also observed an effect of the habitat type prevalent in the landscape on the relationship between SD and biodiversity, which is strongest in areas with transitional habitats between forests and shrublands. Still, further analyses testing whether spectral diversity is related to plant diversity after accounting for the vegetation type could help further demonstrate the observed pattern, which could not be done given the present study design.

Despite the observed significant relationship between SD and plant diversity, the strong context-dependence of such a relationship suggests that users should always account for the context in which SD is used for mapping biodiversity across space. In addition to spatial variation in biodiversity, it could also be explored whether the information conveyed by SD is useful for monitoring biodiversity changes over time, e.g., by assessing landscape changes based on the remotely-sensed spectral signal.

Although the SD-biodiversity relationship was not strong compared with the other predictors analysed, it was still highly significant. Thus, SD has low potential to serve as the sole proxy for taxonomic or functional diversity, but it can improve diversity models based on other predictors. We suggest that SD should be used for this purpose as one of several predictors alongside other well-known variables that affect diversity, such as productivity, climate, and historical processes (Hawkins et al., 2003; Lomolino et al., 2017; Ricklefs and Schluter, 1994).

Uncited references

Gillespie et al., 2008
Legendre and Legendre, 1998
Rao, 1982
Raunkiaer, 1934
Shannon, 1948
Venables and Ripley, 2002

CRediT authorship contribution statement

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

https://github.com/MichelaPerrone/SVH_CZ.git

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Appendix A. Appendix

Table A1
Functional traits used to calculate functional diversity with their source database (Pladias, Chytrý et al., 2021; LEDA, Kleyer et al., 2008; BiolFlor, Klotz et al., 2002). Information on interspecific variation (expressed as standard deviation calculated from the mean values of each species) is available for all four numeric traits; intraspecific variation (expressed as the mean value of standard deviations of individual species) is available for the three traits obtained from the LEDA database.

Functional trait	Relevance	Source	Number of species	Units	Mean	Interspecific variation	Intraspecific variation
Specific leaf area (SLA)	related to leaf economic spectrum	LEDA	1770	$m^2\ kg^{-1}$	24.6	13.8	6.3

Functional trait	Relevance	Source	Number of species	Units	Mean	Interspecific variation	Intraspecific variation
Leaf dry matter content (LDMC)	related to the average density (fresh mass per fresh volume) of the leaf tissues	LEDA	1463	mg g^{-1}	207.8	80.4	27.0
Seed mass	related to the stored resources in the seed that help young seedlings to survive and establish in the face of environmental hazards	LEDA	1760	mg	17.8	214.8	17.3
Mean height	associated with growth form, position of the species in the vertical light gradient of the vegetation, competitive vigour, whole-plant fecundity, potential lifespan, and whether a species can establish and attain reproductive size between two disturbance events	Pladias	2863	m	1.4	4.0	
Growth form	affects canopy structure; it is associated with ecophysiological adaptations, sheltering from severe climatic conditions, or optimising the height and positioning of the foliage to avoid or resist grazing by herbivores	Pladias	2823	–	–	–	
Life form	position of the buds that survive the unfavourable season	Pladias	2847	–	–	–	
Leaf shape	influences the way how plants interact with the electromagnetic radiation	Pladias	3087	–	–	–	
Leaf life span	related to the nutrient-use strategy of plants	BiolFlor	2020	–	–	–	
Leaf anatomy	related to photosynthetic activity and strategy	BiolFlor	1948	–	–	–	
Flower colour	related to pollination strategy and flower recognition	Pladias	2988	–	–	–	
Reproduction type	related to the stability of the habitat	BiolFlor	2170	–	–	–	

Table B1

Summary of results of models explaining species richness and functional diversity with three types of SD (sdNDVI, Rao's Q, SpecCom) calculated from the Landsat-8 median composite. From left to right column: total explained percentage deviance, unique contribution of SD, unique contribution of spatial autocorrelation, unique contribution of sampling effort, combined variation due to the joint effect of the three predictors, combined variation due to the joint effect of SD and sampling effort, combined variation due to the joint effect of SD and spatial autocorrelation, combined variation due to the joint effect of sampling effort and spatial autocorrelation components.

	SD metric	Total explained deviance	SD	Sampling effort	Spatial autocorrelation	Shared SD + sampling effort + spatial autocorrelation	Shared SD + sampling effort	Shared SD + spatial autocorrelation	Shared sampling effort + spatial autocorrelation
Species richness	sdNDVI	73.8	4.5	45.7	8.0	−4.0	1.0	7.8	10.8
	Rao's Q	72.7	3.4	46.4	8.4	−3.8	0.3	7.4	10.6
	SpecCom	72	2.7	46.4	10.6	−2.3	0.3	5.2	9.1
Functional diversity	sdNDVI	60.1	7.9	2.2	26.2	−1.2	0	25.8	−0.8
	Rao's Q	57.9	5.7	2.6	27.6	−1.2	−0.4	24.4	−0.8
	SpecCom	57.8	5.6	2.7	31.9	−0.8	−0.5	20.1	−1.2

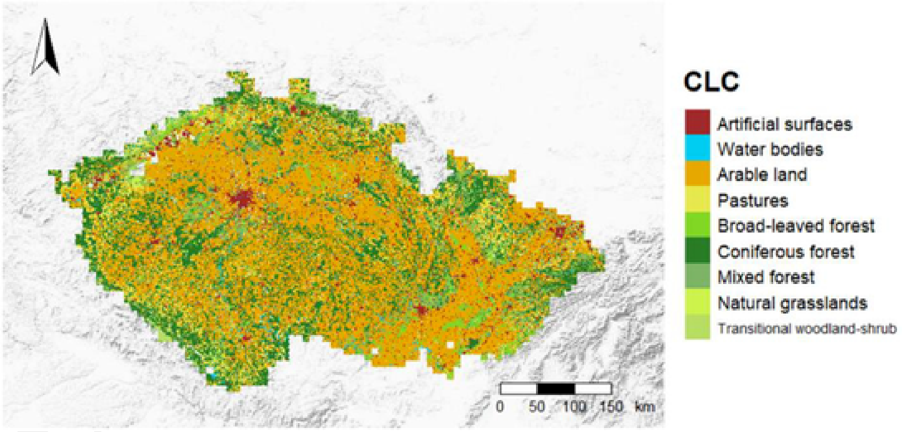

Fig. C1. Corine Land Cover map of the study area (reference year 2012, 100 m resolution)

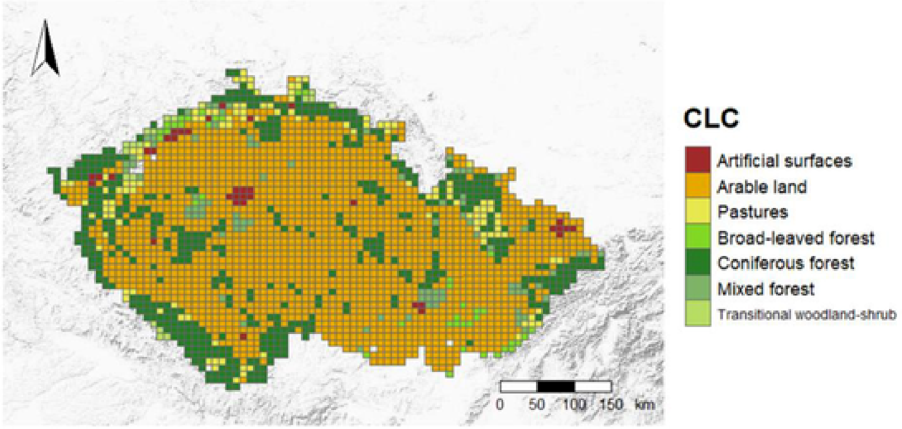

Fig. C2. Map of the most abundant CLC type within each grid cell.

Table C1
Legend of the land cover codes used, with their respective level of detail within the CLC classification and number of grid cells.

Code	CLC Level	Cover type	N
1	I	Artificial surfaces	36
21	II	Arable land	1561
231	III	Pastures	120
311	III	Broad-leaved forest	40
312	III	Coniferous forest	502
313	III	Mixed forest	84
324	III	Transitional woodland-shrub	18

Table D1
Formulas of the six models. SD predictor terms (i.e., sdNDVI, Rao's Q, and SpecCom) are included in the models with their first- and second-order values to account for possible non-linear patterns in the response of SR and FD. The interaction between SD and the dominant CLC type is included to model the possibility of having different SD-SR or SD-FD relationships in different CLC types. The sampling effort term represents the logarithm of the number of records within each grid cell and is included in the models to correct for the possible effects of uneven sampling effort. The spatial autocorrelation term represents smooth two-dimensional splines on a sphere, a parameter of the `gam` function of the `mgcv` R package here used to model the presence of systematic spatial variation in our response variables using generalized additive models (GAMs).

Response variables		Predictor terms						
Species Richness	~	sdNDVI: CLC	+	$(\text{sdNDVI})^2$: CLC	+	sampling effort	+	spatial autocorrelation
Species Richness	~	Rao's Q: CLC	+	(Rao's Q) ^{2}: CLC	+	sampling effort	+	spatial autocorrelation
Species Richness	~	SpecCom: CLC	+	(SpecCom) ^{2}: CLC	+	sampling effort	+	spatial autocorrelation
Functional Diversity	~	sdNDVI: CLC	+	(sdNDVI) ^{2}: CLC	+	sampling effort	+	spatial autocorrelation
Functional Diversity	~	Rao's Q: CLC	+	(Rao's Q) ^{2}: CLC	+	sampling effort	+	spatial autocorrelation
Functional Diversity	~	SpecCom: CLC	+	(SpecCom) ^{2}: CLC	+	sampling effort	+	spatial autocorrelation

Table E1
Coefficient estimate values of the interaction between SD and land-cover type in the plant diversity ~ SD models. Significance codes: *** (p-value <0.001), ** (p-value <0.01), * (p-value <0.05).

	Species Richness						Functional Diversity					
	sdNDVI		Rao's Q		SpecCom		sdNDVI		Rao's Q		SpecCom	
CLC 1 1st power	7.38	***	5.31	***	−2.17	*	0.28	***	0.28	***	−0.21	***
CLC 1 2nd power	−4.12	***	−4.51	*	−0.16		−0.02		−0.08	*	0	
CLC 21 1st power	3.75	***	2.84	***	2.67	**	0.22	***	0.20	***	0.27	***
CLC 21 2nd power	−1.12	***	−2.58	***	1.60		−0.09	***	−0.15	***	0.03	*
CLC 231 1st power	2.04		0.23		0.57		0.17	**	0.25		0.10	*
CLC 231 2nd power	−2.59	*	−6.50		1.72		−0.23	***	−0.27		0.09	
CLC 311 1st power	2.43		0.53		4.27	***	0.20	*	0.15		0.26	***
CLC 311 2nd power	−5.52	*	−8.94	*	2.45		−0.33	***	−0.39	*	0.09	
CLC 312 1st power	5.21	***	6.85	***	4.42	***	0.35	***	0.44	***	0.25	***
CLC 312 2nd power	−2.86	***	−2.59	***	0.90	*	−0.19	***	−0.17	***	0.07	***
CLC 313 1st power	1.50		2.55		2.66	***	0.31	**	0.18	*	0.11	**
CLC 313 2nd power	−3.83		−3.34	*	0.27		0.08		−0.02		0.02	
CLC 324 1st power	45.01	***	35.91	***	10.26	***	2.27	***	2.61	***	0.51	***
CLC 324 2nd power	27.05	***	20.85	*	4.33	***	1.37	***	1.92	***	0.19	***

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