Science of the Total Environment 907 (2024) 167954

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Future changes in key plant traits across Central Europe vary with biogeographical status, woodiness, and habitat type

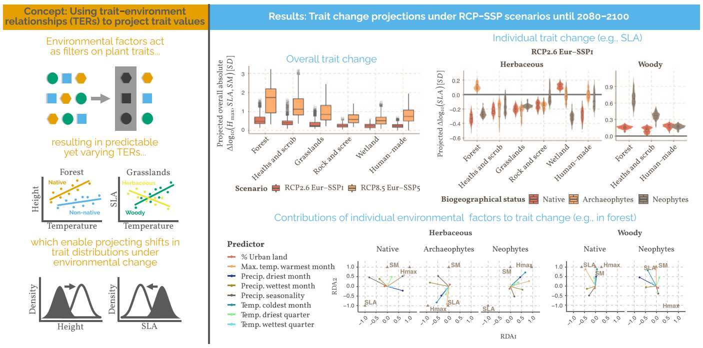
Marina Golivets[a,*], Sonja Knapp[a,b,c], Franz Essl[d], Bernd Lenzner[d], Guillaume Latombe[e], Brian Leung[f,g], Ingolf Kühn[a,c,h]

[a] Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Halle, Germany
[b] Ecosystem Science/Plant Ecology, Department of Ecology, Technische Universität Berlin, Berlin, Germany
[c] German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Leipzig, Germany
[d] Division of Bioinvasions, Global Change & Macroecology, Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria
[e] Institute of Ecology and Evolution, The University of Edinburgh, King's Buildings, Edinburgh, United Kingdom
[f] Department of Biology, McGill University, Montreal, Quebec, Canada
[g] Bieler School of Environment, McGill University, Montreal, Quebec, Canada
[h] Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Halle, Germany

HIGHLIGHTS

- Trait distributions along ecological gradients allow scenario projections for traits.
- Biogeographical status, woodiness, and habitat shape future change in plant traits.
- Future native woody assemblages increase in height, specific leaf area and seed mass.
- Herbaceous height increases and specific leaf area decreases in most habitats.
- Greater overall magnitude of trait change in non-native than native plant assemblages.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Elena Paoletti

Keywords:
Biological invasions
Environmental filtering
Global environmental change
Shared Socio-Economic Pathway (SSP)
Representative Concentration Pathway (RCP)
Trait-based approach
Trait–environment relationship

ABSTRACT

Many plant traits covary with environmental gradients, reflecting shifts in adaptive strategies and thus informing about potential consequences of future environmental change for vegetation and ecosystem functioning. Yet, the evidence of trait–environment relationships (TERs) remains too heterogeneous for reliable predictions, partially due to insufficient consideration of trait syndromes specific to certain growth forms and habitats. Moreover, it is still unclear whether non-native and native plants' traits align similarly along environmental gradients, limiting our ability to assess the impacts of future plant invasions. Using a Bayesian multilevel modelling framework, we assess TERs for native and non-native woody and herbaceous plants across six broad habitat types in Central Europe at a resolution of *c.* 130 km^2 and use them to project trait change under future environmental change scenarios until 2081–2100. We model TERs between three key plant traits (maximum height, H_{max}; specific leaf area, *SLA*; seed mass, *SM*) and individual environmental factors (7 climate variables and % urban land cover) and

---

* Corresponding author at: Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Str. 4, 06120 Halle, Germany.
E-mail address: maryna.golivets@ufz.de (M. Golivets).

https://doi.org/10.1016/j.scitotenv.2023.167954
Received 29 August 2023; Received in revised form 17 October 2023; Accepted 18 October 2023

estimate trait change summed across all environmental effects. We also quantify the change in the average trait difference between native and non-native plants. Our models depict multiple TERs, with important differences attributed to biogeographical status and woodiness within and across habitat types. The overall magnitude of trait change is projected to be greater for non-native than native taxa and to increase under more extreme scenarios. Native woody plant assemblages may generally experience a future increase across all three traits, whereas woody non-natives may decline in $H_{\max}$ and increase in *SLA* and *SM*. Herbaceous $H_{\max}$ is estimated to increase and *SLA* to decrease in most habitats. The obtained trait projections highlight conditions of competitive advantage of non-native plants over natives and vice versa and can serve as starting points for projecting future changes in ecosystem functions and services.

1. Introduction

Economic globalisation and human-induced environmental change over the last centuries have caused vast numbers of species to decline (Díaz et al., 2019) and a smaller yet substantial number of species to expand beyond their historical ranges (i.e., non-native and neonative species; Essl et al., 2019; Seebens et al., 2017). As a result, previously unique species assemblages around the world are increasingly becoming impoverished, more alike, and less stable (Daru et al., 2021; Eichenberg et al., 2021; Finderup Nielsen et al., 2019; Winter et al., 2009; Yang et al., 2021), with severe, often irreversible, consequences for natural ecosystems and humans (Guo et al., 2020; Naeem et al., 2012; Pyšek et al., 2020). In the face of biodiversity's highly threatened and uncertain future (Thuiller et al., 2005, 2019), ensuring that the scientific knowledge used to design biodiversity policies is easily updatable, synthesisable, and transferable across space and time is crucial. This challenge, on the one hand, calls for approaches that generalise scientific outputs beyond individual species and, on the other hand, requires embracing the distinct ecological patterns displayed by different species groups (e.g., native vs non-native; Liu et al., 2017).

Approaches focusing on species traits (i.e., any measurable characteristic of a single organism; Violle et al., 2007) are increasingly put forward as a way towards predictive ecology (McGill et al., 2006; Violle et al., 2014) and have been actively employed to study the effects of global environmental change (e.g., Madani et al., 2018; Myers-Smith et al., 2019). The premise of these approaches is that traits mechanistically link an organism's performance to its environment and can be upscaled to understand and predict how the environment shapes species assemblages and ecosystem functioning (Bjorkman et al., 2018; Dubuis et al., 2013; Küster et al., 2011; Lavorel and Garnier, 2002; Musavi et al., 2016). Moreover, traits yield insights into the mechanisms underlying non-native species' invasiveness (Drenovsky et al., 2012; Küster et al., 2008; Pyšek and Richardson, 2008) and can help reveal differences in the ecological roles and functions of native and non-native species (Hulme and Bernard-Verdier, 2018a, 2018b). However, trait-based studies on native species have asked different questions than those on non-natives. In particular, trait-based research on native species focuses on environmental filtering and adaptation, whereas trait comparisons between natives and non-natives often neglect the importance of the environmental context (e.g., Divíšek et al., 2018; Mathakutha et al., 2019; van Kleunen et al., 2010). Presently, only a few studies have looked at how native and non-native traits shift along environmental gradients, altogether offering insufficient knowledge for identifying the circumstances under which non-natives functionally diverge from or converge with natives (Gross et al., 2013; Hanz et al., 2022; Henn et al., 2019; Knapp and Kühn, 2012; Sandel and Low, 2019; Westerband et al., 2020). Given the steadily increasing extent of biological invasions worldwide (Seebens et al., 2017; Seebens et al., 2021), explicit consideration of trait–environment relationships (TERs) in non-native species is desperately needed for predicting biodiversity and ecosystem functioning.

Despite extensive recent efforts to map TERs globally (mostly focusing on native species, as noted above), these relationships appear heterogeneous and weak (Anderegg, 2023), which questions their usefulness for predictions. This discordance with ecological theory suggesting strong TERs might be partly attributed to insufficient consideration of distinct trait syndromes specific to different growth forms and habitats. Notably, woody and herbaceous plants occupy separate sections in the global spectrum of plant form and function (Díaz et al., 2016), which highlights their unique adaptations to the environment and, hence, divergent TERs (Šímová et al., 2018). Additionally, traits of woody species tend to be more strongly associated with climate than those of herbaceous species (Šímová et al., 2018). This suggests that when all growth forms in a study area are jointly analysed, TERs are likely to appear weak. Nevertheless, it is common for macroecological analyses to pool trait data for woody and herbaceous species together (e.g., Moles et al., 2009, 2014; Wright et al., 2005) or to focus only on woody taxa (e.g., Šímová et al., 2015; Swenson et al., 2012). Moreover, the strength and direction of TERs may vary due to unique environmental conditions in each habitat type. For example, community-weighted specific leaf area shows the opposite relationship with the mean annual temperature in European forest understories (negative relationship; Maes et al., 2020) vs calcareous grasslands (positive relationship; Rosbakh et al., 2015). Yet, TERs have usually been quantified either as pooled across habitats or for a specific habitat type per study (e.g., open montane habitats, Dubuis et al., 2013; forests, Maes et al., 2020; Wieczynski et al., 2019). For non-native species, habitat information has been primarily incorporated to compare the levels of invasion across broadly defined (Chytrý et al., 2008) and selected narrowly defined habitats (e.g., grasslands, Axmanová et al., 2021; coastal dunes, Giulio et al., 2020; forests, Wagner et al., 2017), whereas how traits of non-native species arrange along environmental gradients within or across habitats has not been explored. Altogether, this calls for explicitly considering woodiness, habitat type, and biogeographical status (i.e., native vs non-native) in trait-based analyses.

This study uses comprehensive plant distribution and trait data for Germany and the Czech Republic and a full Bayesian multilevel modelling framework to assess future trait change based on a refined, contextualised set of TERs. We hypothesise that (1) the relationships between traits of plant assemblages and the environment are highly contingent upon the habitat type and whether assemblages are made of non-native (as opposed to native) and woody (as opposed to herbaceous) taxa and, consequently, (2) the effect of future environmental change will be pronounced to a varying extent in different types of plant assemblages and under different scenarios. We follow the ‘assemble first, predict later’ approach (sensu Ferrier and Guisan, 2006), which entails aggregating trait values at the assemblage level, modelling those aggregates as functions of environmental variables, and using the fitted models to project trait values under plausible future conditions. Such an approach efficiently synthesises shared trait patterns across many species while accounting for previously overlooked sources of variation in TERs, namely biogeographical status (native vs non-native, with a further split of non-natives into archaeophytes and neophytes; see 2.1.1. Taxon-level data for definitions), woodiness and habitat type. More precisely, we first quantify relationships of traits central to plant life history (Díaz et al., 2016; Westoby, 1998) – maximum height, specific leaf area, and seed mass – with climate and land use within woody and herbaceous native and non-native plant assemblages. Based on the obtained TERs, we then determine the magnitude and direction of plausible future change in mean trait values, which reflect the turnover of taxa and associated functions. Trait change is projected under seven combined climate and socio-economic scenarios (pairs of Representative Concentration Pathways and four Shared Socio-Economic Pathways) for Europe for 2081–2100.

2. Material and methods

Our study area comprises Germany and the Czech Republic. Both countries have a temperate climate with marked regional differences (DWD, 2017) and relatively homogeneous land cover composition dominated by arable and forested land (EEA, 2021).

2.1. Data

2.1.1. Taxon-level data

We harmonised and collated data on plant taxon occurrences, biogeographical status, habitat affinity, and traits for the entire flora of the study area from multiple open data sources. We omitted aquatic (i.e., taxa with the Ellenberg moisture indicator value >9), holoparasitic, and fully mycotrophic taxa.

2.1.1.1. Occurrence records. For Germany, we obtained gridded plant taxon occurrence data from the FlorKart database (Datenbank FlorKart, NetPhyD, and BfN, 2013) via the information online system FloraWeb (www.floraweb.de; accessed 5 February 2022). For the Czech Republic, we obtained gridded taxon presence data from the Pladias – Database of the Czech Flora and Vegetation (www.pladias.cz; accessed 16 January 2022). From FlorKart, we excluded occurrences marked as cultivated, erroneous, and doubtful and from Pladias, we removed records at the genus level. We also excluded records of presently missing and extinct taxa and taxa known from both countries but with data from only one country. Because both databases are essentially compilations of regional projects with different sampling intensities, we aggregated all data at the resolution of the 10′ longitude × 6′ latitude grid cells (*c.* 130 km^2 on average; $N = 3175$) to achieve a more homogeneous sampling effort. We also cropped the spatial grid to the combined borders of the study area and excluded all grid cells with a land area < 117 km^2, which corresponded to the size of the smallest (northernmost) grid cell not truncated by borders or coastlines. To further control for sampling bias, we removed grid cells containing <83 (95 %) of the 87 benchmark taxa, i.e., taxa occurring in each grid with a probability >0.98 based on the Beals smoothing method (Beals, 1984; Carmona and Pärtel, 2021; listed in Appendix A). The final grid comprised 3031 cells.

2.1.1.2. Biogeographical status. We retrieved information on taxon biogeographical status from the BiolFlor database (Kühn et al., 2004) and FloraWeb (www.floraweb.de) for Germany and from Pyšek et al. (2012) for the Czech Republic. For analyses, we considered only native, established archaeophytes (i.e., non-native taxa introduced before the discovery of the Americas in 1492; Kühn et al., 2004) and established neophytes (i.e., non-native taxa introduced after 1492), excluding casual (i.e., non-established) non-natives. Specifically, for taxa that were native in one country and casual non-native in the other country, we retained only records from where those taxa were native. For non-natives spontaneously occurring in both countries but established in only one country, we kept all known occurrences unless the number of occupied grid cells in each country was 1. Although retaining occurrences of taxa that were considered casual in one of the countries meant overestimating the naturalised secondary range size in some cases, more importantly, it allowed us to ameliorate the differences in expert judgement regarding the degree of taxon establishment within the study area. We retained all records of taxa native to both counties and non-native taxa with established populations in both countries unless they were known from a single grid cell. Finally, for consistency reasons, we assigned a single, highest achieved degree of establishment to each taxon, per the national treatment of taxa having several statuses in the country.

2.1.1.3. Habitat affinity. To enable analyses at the habitat level, we assigned each taxon to at least one of the following six broad habitat types: forest, heaths and scrub, grassland, wetland, rock and scree, and human-made. Information on taxon habitat affinity was collated from multiple reference sources (namely, BiolFlor, Kühn et al., 2004; Bundesamt für Naturschutz, 2017; EUNIS, Chytrý et al., 2020; DAISIE, Roy et al., 2020; Divíšek et al., 2018; KORINA, www.korina.info, accessed 4 August 2021; Sádlo et al., 2007), which used different habitat classification schemes. We grouped the habitat types in each data source into the six habitat types based on the authors' expertise (see Table A.1 for the habitat cross-walk) and merged all the data. To avoid reports of sporadic occurrences, we only retained habitats listed in >1 source for taxa represented in multiple sources.

2.1.1.4. Traits. We selected three traits for our analyses: (1) typical maximum plant height ($H_{\max}$; measured in m), (2) seed mass (*SM*; g), and (3) specific leaf area (*SLA*; mm^2 mg^{-1}). These traits depict major plant life strategies (Díaz et al., 2016; Westoby, 1998), correlate with many other important traits (Moles et al., 2009; Wright et al., 2004), act as both response and effect traits (Hanisch et al., 2020; Kühn et al., 2021; Pollock et al., 2012), and are well represented in open source trait databases (e.g., Kattge et al., 2020). For best possible taxon coverage, we compiled trait data from multiple databases and online resources: LEDA (Kleyer et al., 2008), TRY (Kattge et al., 2011, 2020, accessed 1 October 2019; see Appendix A for references within TRY), EcoFlora (Fitter and Peat, 1994), Info Flora (www.infoflora.ch), iFlora (www.i-flora.com), Kaplan et al. (2019), E-Vojtkó et al. (2020), and World Species (worldspecies.org). We included $H_{\max}$ measurements on vegetative and generative organs, *SM* measurements on dried seeds, and *SLA* measurements on sun and shade leaves and dry biomass. Where possible, we removed trait measurements from biomes outside our study area (e.g., tundra). Climbers were excluded from analyses of $H_{\max}$. When multiple *SLA* and *SM* values were available per taxon, we averaged them using the geometric mean (due to its lower sensitivity to extreme values compared to other measures of central tendency) after accounting for possible outliers; for $H_{\max}$, we calculated as the geometric mean of the $H_{\max}$ values provided in individual data sources. The information on woodiness was obtained directly or inferred from life and growth form. Woody taxa were considered perennials whose stems were either entirely lignified or had a lignified base. Woody plants in grasslands, wetlands, and rock and scree habitats were excluded from all analyses. We also removed woody archaeophytes due to the low sample size (most archaeophytes in our data were herbaceous) and low variation in trait values.

Our final dataset comprised 1812 native, 181 archaeophyte, and 331 neophyte taxa; $H_{\max}$ was available for 96 %, *SLA* for 74 %, and *SM* for 88 % of those taxa. Appendix A provides information on taxonomic name standardisation.

2.1.2. Climate and land use data

2.1.2.1. Baseline data. We retrieved baseline data on 14 macroclimatic variables from the 10′ × 10’ CRU 1961–1990 dataset (New et al., 2002). The variables were total annual precipitation (TAP; mm), precipitation of the driest and wettest quarters, precipitation of the driest month (P_{dry}), precipitation of the wettest month (P_{wet}), precipitation seasonality (coefficient of variation of monthly total precipitation, P_{CV}; %), mean annual temperature (MAT; °C), mean and minimum temperature of the coldest month, mean temperature of the warmest month, maximum temperature of the warmest month (T_{warm}), mean temperature of the driest quarter (T_{dry}), mean temperature of the wettest quarter

(T_{wet}), and temperature seasonality (coefficient of variation of monthly average temperature; %). We rescaled all variables to the $10' \times 6'$ spatial resolution by resampling original values onto a $0.5' \times 0.5'$ grid using bilinear interpolation and then averaging obtained downscaled values within each $10' \times 6'$ grid cell. As a baseline for land use, we used Corine Land Cover (CLC) data for the year 2000 (100 m × 100 m; CLC, 2020), which we aggregated to the $10' \times 6'$ spatial resolution. Additionally, we determined which of the six habitat types were present in each grid cell based on the Ecosystem types of Europe 2012 raster dataset (EEA, 2018). Forests, grasslands, and human-made habitats were present in all 3031 grid cells, whereas heaths and scrub occurred in 2091, wetlands in 966, and rock and scree habitats in 337 grid cells. All spatial data were prepared with the R package *raster* (v.3.4–13; Hijmans, 2021).

2.1.2.2. Scenario projections. We obtained climate and land-use projections at $10' \times 10'$ spatial resolution for 2081–2100 from the IMPRESSIONS project (www.impressions-project.eu). The IMPRESSIONS Integrated Assessment Platform (IAP2) includes three Representative Concentration Pathways (RCP2.6, RCP4.5, and RCP8.5) and four European Shared Socio-economic Pathways (Eur-SSP1, Eur-SSP3, Eur-SSP4, and Eur-SSP5; Kok et al., 2019) and permits modelling individual and joint impacts of climate and socio-economic change until 2081–2100. Because the agreement between land use classes in CLC (chosen baseline) and IAP2 was low for all land-use types except urban, we kept only the percentage of urban land ($U_{\%}$) for further analyses. We used projections for seven RCP–SSP scenario combinations, each based on three dynamically downscaled CMIP5 climate models for each RCP (see Table A.2 for more information on scenarios).

2.2. Data analyses

2.2.1. Data preparation

We first $\log_{10}$-transformed all traits to reduce the skewness of their distributions and the effect of extreme values. Then, separately for woody and herbaceous native, neophyte, and archaeophyte taxa within selected habitats, we averaged each trait at the grid-cell level, omitting taxa with missing trait values. Thus, when all six habitat types were present in a grid cell, we computed up to 24 mean values per trait per grid cell. Trait per-cell means based on fewer than four taxa were heuristically excluded from analyses. Next, we separately scaled trait means of woody and herbaceous native, neophyte, and archaeophyte plant assemblages at the habitat level to zero mean and unit variance. We did so because we aimed to capture how taxon status, woodiness, and habitat moderated the effects of climate and land use rather than to quantify their direct effects on traits. Moreover, such scaling allowed us to impose a single spatial autocorrelation structure across habitats and thus quantify all effects within a single model. Scaled trait per-cell means were used as response variables in statistical models.

To reduce the redundancy among the potential environmental predictor variables, we performed variable selection based on the variance inflation factor (VIF) and Pearson's correlation coefficient (r; shown in Fig. A.2) using the R package *usdm* (v.1.1–18; Naimi et al., 2014). Ultimately, we retained eight predictor variables: P_{dry}, P_{wet}, P_{CV}, T_{cold}, T_{warm}, T_{dry}, T_{wet}, and $U_{\%}$. Before analyses, we scaled these variables to zero mean and unit variance to aid model parametrisation and interpretation. The per-cell number of taxa (N_{taxa}; see 2.2.2. Statistical models) was scaled similarly to traits.

2.2.2. Statistical models

We assessed TERs using linear multilevel models. All models were parameterised within a full Bayesian framework using the R package *brms* (v.2.14.4; Bürkner, 2017). We modelled individual-trait per-cell mean values as the function of climatic variables and $U_{\%}$ (continuous predictors) and taxon biogeographical status, woodiness, and habitat (categorical predictors). More specifically, we developed a suite of slope-only models, in which we included a single continuous predictor and its two- and three-way interactions with biogeographical status and woodiness that were allowed to vary by habitat. Such models allowed us (1) to quantify the extent to which the effects of climate and urbanisation differ between native and non-native taxa, herbaceous and woody taxa, as well as across different habitats, and (2) to incorporate this potential context-dependency into projections of future spatial trait distributions. To account for residual spatial autocorrelation, we included conditional autocorrelation structure (CAR) with grid cell identifier as a grouping factor in all our models. In all our models, we also controlled for N_{taxa} by including this metric as another predictor variable because, in some cases, average trait values correlated with N_{taxa}. In particular, this correlation was negative for $H_{\max}$, suggesting that taxon-richer grid cells had, on average, a higher proportion of shorter taxa. Such a pattern may reflect sampling effort (e.g., smaller plants are more likely to remain undetected; Chen et al., 2013), be a genuine ecological phenomenon (Aarssen et al., 2006), or both. In either case, we chose to control for N_{taxa}, as otherwise, its effect could be incorrectly attributed to environmental predictors. A model for each environmental predictor can be written as follows:

$$\mathrm{y_i} \sim \beta^{\mathrm{ew}}_{\mathrm{j[i]}}\mathrm{e_i w_i} + \beta^{\mathrm{es}}_{\mathrm{j[i]}}\mathrm{e_i s_i} + \beta^{\mathrm{ews}}_{\mathrm{j[i]}}\mathrm{e_i w_i s_i} + \beta^{\mathrm{nws}}_{\mathrm{j[i]}}\mathrm{n_i w_i s_i} + \epsilon_{\mathrm{i}} + \mathrm{z_{k[i]}}$$

$$\beta^{\mathrm{ew}}_{\mathrm{j}} \sim \mathrm{N}\left(\mu_{\mathrm{ew}}, \sigma^2_{\mathrm{ew}}\right)$$

$$\beta^{\mathrm{es}}_{\mathrm{j}} \sim \mathrm{N}\left(\mu_{\mathrm{es}}, \sigma^2_{\mathrm{es}}\right)$$

$$\beta^{\mathrm{ews}}_{\mathrm{j}} \sim \mathrm{N}\left(\mu_{\mathrm{ews}}, \sigma^2_{\mathrm{ews}}\right)$$

$$\beta^{\mathrm{nws}}_{\mathrm{j}} \sim \mathrm{N}\left(\mu_{\mathrm{nws}}, \sigma^2_{\mathrm{nws}}\right)$$

$$\epsilon \sim \mathrm{N}\left(0, \sigma^2_{\mathrm{y}}\right)$$

$$z_k \sim N(0, \Sigma)$$

where y_i is the trait per-cell mean value for the i^{th} observation ($i = 1, \ldots, N_{\mathrm{obs}}$), calculated for each combination of habitat type, woodiness, and biogeographical status; e_i is the environmental predictor; w_i is woodiness; s_i is biogeographical status; n_i is the number of taxa; β_j^{ew}, β_j^{es}, β_j^{ews}, β_j^{nws} are slopes for the interactions between variables indicated in the superscript in the j^{th} habitat type ($j = 1, \ldots, N_{\mathrm{habitats}}$); β_j^{es} is the slope for the interaction between e_i and s_i in the j^{th} habitat type; β_j^{ews} is the slope for the interaction between e_i, w_i and s_i in the j^{th} habitat type; $\epsilon_i$is the residual effect of the i^{th} observation; z_k is the residual spatial random error for the k^{th} grid cell ($k = 1, \ldots, N_{\mathrm{cells}}$); μ_{ew}, μ_{es}, μ_{ews}, μ_{ews} are the overall slopes for the interactions specified in the subscript; σ^2_{ew}, σ^2_{es}, σ^2_{ews}, σ^2_{nws} are the habitat-level variances for the slopes; σ^2_y is the residual variance; and Σ is the covariance matrix, as defined in a conditional autoregressive model. We chose to fit separate models for each environmental predictor because of the high complexity of a full model and possible collinearity due to many interaction terms with the same categorical predictors. To prevent the sampler from considering highly implausible values, we used zero-centred weakly informative priors chosen based on prior predictive checks (Wesner and Pomeranz, 2021).

2.2.3. Model predictive performance

We evaluated the predictive performance using exact k-fold cross-validation. The folds were determined as spatial blocks to avoid potential overestimation of predictive performance (Roberts et al., 2017). For that, we overlaid a 3 × 3 spatial-block grid onto the grid of the study area (see Fig. A.1) using the R package *blockCV* (v2.1.4; Valavi et al., 2019). This resulted in 8 spatial blocks, two of which we merged to achieve a more even distribution of grid cells across folds. We then assigned all data points within a grid cell to a specific fold and performed

7-fold cross-validation with the R package *brms* (Bürkner, 2017). As the measures of predictive model performance, we calculated the k-fold information criterion (*kfoldIC*) and the root mean square error based on cross-validated predictions (*RSME*; both statistics are reported in Table A.3).

2.2.4. Future projections

We obtained projections of per-cell mean values of each trait under baseline and scenario conditions. We set the scaled N_{taxa} to 0 to generate all projections assuming equal taxon numbers across the study area. Projections were computed as the weighted average of posterior predictive distributions from the eight single-environmental-predictor models using Bayesian stacking of predictive distributions (Yao et al., 2018). We then calculated the projected per-cell change in each trait under each scenario as the difference between the medians of the projected future scenario-based and baseline posterior predictive distributions. To enable comparison across biogeographical statuses, we rescaled trait change values of archaeophytes and neophytes to the standard deviations (*SD*) of a baseline trait distribution for native taxa of respective woodiness and habitat (see Table A.4 for $\log_{10}$-transformed native trait values equalling 1 *SD* for each woodiness and habitat combination). We calculated the Euclidean distance between the projected per-cell posterior means of the three traits on the baseline and scenario data to assess the overall magnitude of trait change.

2.2.5. Importance of environmental predictors

To summarise the effects of individual environmental predictors on all three traits and to visualise them in the multivariate space, we performed multiple redundancy analyses (RDA) using the R package *vegan* (v.2.5–7; Oksanen et al., 2020). We chose RDA as a way to report TERs instead of reporting marginal effects from individual models because this allowed us to synthesise the importance of environmental predictors as reflected in projections (i.e., accounting for weighting applied to individual-model posterior predictive distributions; see 2.2.4. Future projections). For each RDA, we used a separate dataset containing the projected trait change (i.e., the difference between scenario and baseline projections) and the change in environmental predictors (i.e., the difference between scenario and baseline values) across all the scenarios corresponding to a unique combination of biogeographical status, woodiness, and habitat. As the measure of individual environmental predictor contribution to trait change, we calculated the length of the vectors with the initial point at (0,0) and the terminal point at the scores of the first two RDA axes. The lengths of the vectors reflected the weighted effect sizes of the predictors used to calculate posterior predictive distributions for all traits. The angles among those vectors and individual traits in the two-dimensional RDA space reflected TERs.

All statistical analyses and visualisations were performed in the R environment v4.1.0 (R Core Team, 2021).

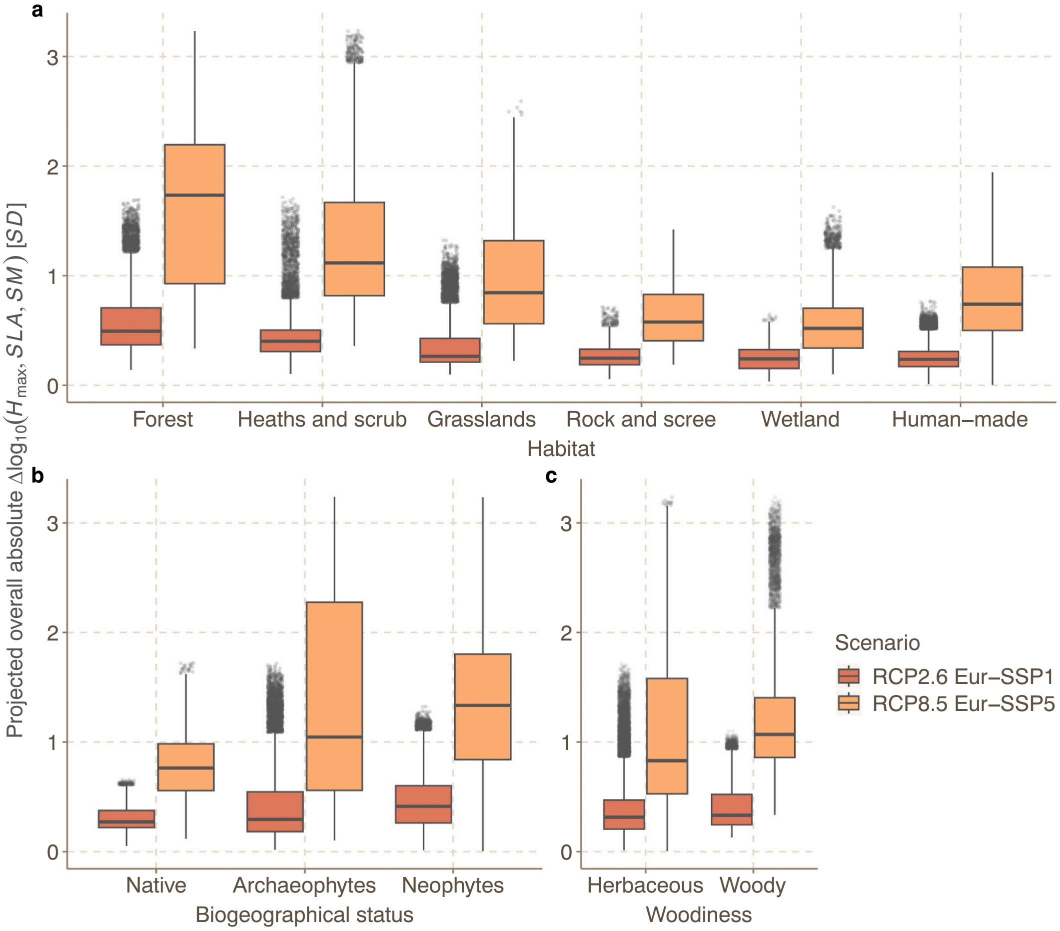


Fig. 1. The projected absolute overall per-cell change across the three traits, plant maximum height ($H_{\max}$), specific leaf area (*SLA*), and seed mass (*SM*), at the habitat (a), biogeographical status (b), and woodiness (c) levels under the least extreme combined climate and socio-economic scenario (RCP2.6 Eur-SSP1, all climate models pooled) and the most extreme one (RCP8.5 Eur-SSP5) for 2081–2100. The overall trait change was calculated as a Euclidean distance between the projected per-cell posterior means of the three traits on the baseline and scenario data. Boxes show 25 %, 50 %, and 75 % quartiles, and whiskers show 95 % credible intervals.

3. Results

3.1. Overview of trait change projections

Overall, we observed high variability (i.e., the spread across posterior distributions) and uncertainty (i.e., the spread within posterior distributions) in the magnitude and direction of the projected per-cell change in $H_{\max}$, *SLA*, and *SM* under environmental change scenarios. The variation in the projected trait change was pronounced at all three grouping levels considered in the analyses, i.e., taxon biogeographical status, woodiness, and habitat type, and increased with the degree of environmental change (the least extreme scenario, RCP2.6 Eur-SSP1 and the most extreme scenario, RCP8.5 Eur-SSP5 are shown Figs. 1–4; other scenarios in B.1–B.6, B.13). Likewise, uncertainty associated with individual per-cell projections varied across the grouping levels and was generally higher under more extreme scenarios, being driven much more by climate change than urbanisation (Figs. B.7–B.12). The likelihood of trait change (measured as the proportion of grid cells with projected posterior credible intervals excluding zero) was lowest under RCP4.5 and RCP8.5 for woody native *SLA* in human-made habitats and archaeophyte *SM* in human-made habitats and heaths and scrub (results not shown).

Below, we focus on the posterior means of the projected per-cell posterior distributions, which reflect the average trends in our projections but do not embrace the uncertainty, for the least and most extreme scenarios to illustrate the maximum future option space for 2081–2100. Results for other scenarios are presented in Appendix B.

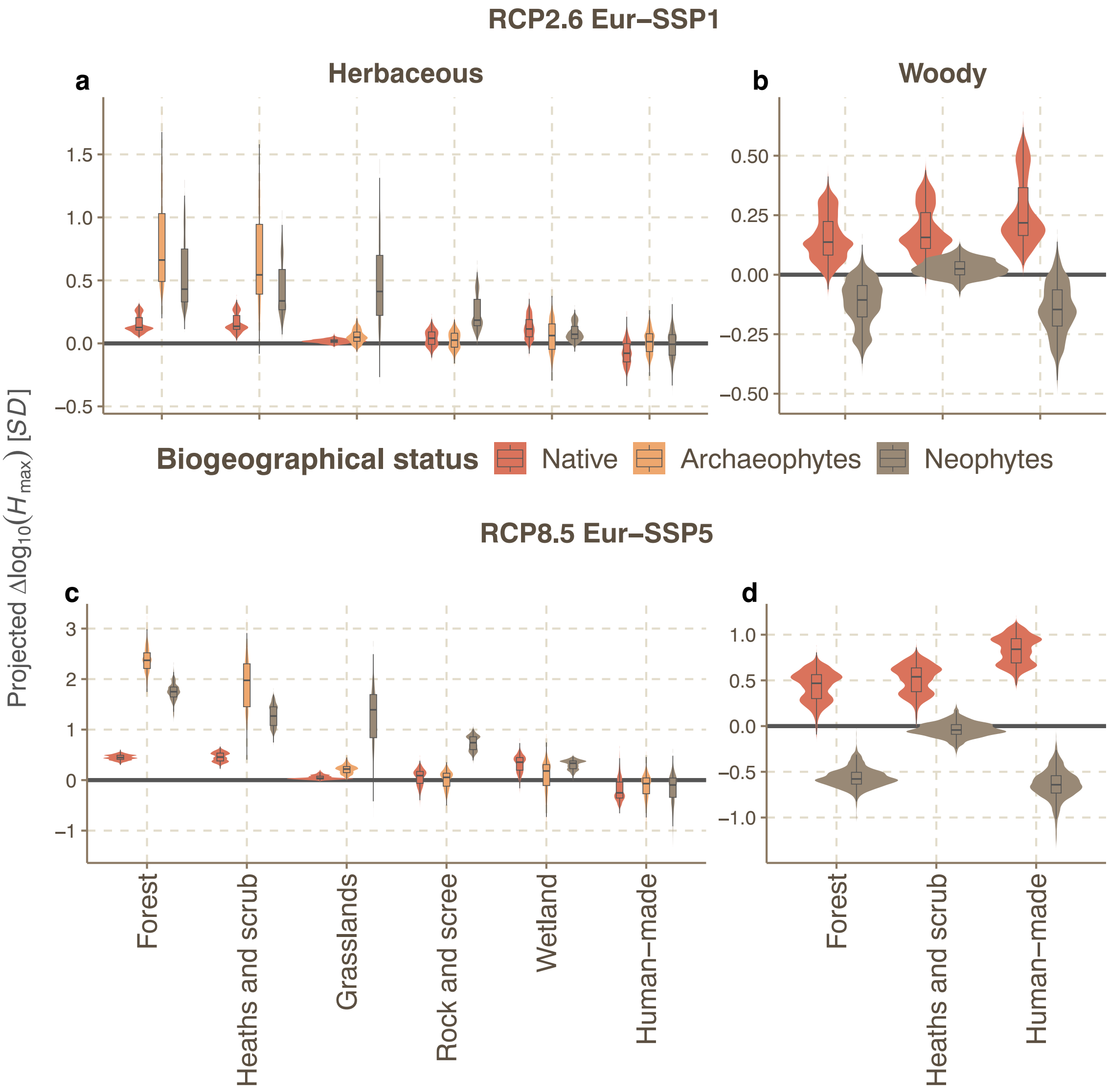


Fig. 2. The projected per-cell (10′ × 10′) change in the $\log_{10}$-transformed maximum plant height ($H_{\max}$) under the least extreme combined climate and socio-economic scenario (RCP2.6 Eur-SSP1, all climate models pooled) and the most extreme one (RCP8.5 Eur-SSP5) for 2081–2100, for herbaceous (a, c) and woody (b, d) taxa in six broad habitat types. The trait change here is the posterior means of per-cell model predictions. The violin plots depict the distributions of predicted values across the study area and climate models (Table S1), and the boxplots provide summary statistics of those distributions (boxes show 25 %, 50 %, and 75 % quartiles, and whiskers give roughly 95 % credible intervals). For each habitat by woodiness combination, the trait change is presented in standard deviations (*SD*) of the baseline trait distribution of native taxa for that combination. For example, the overall change of 0.60 in $H_{\max}$ of forest herbaceous neophytes under the RCP2.6 Eur-SSP1 scenario indicates that the average $H_{\max}$ of this assemblage is projected to increase by 0.60 *SD*, relative to the current $H_{\max}$ distribution of natives. Note the different scaling of Y-axes. Figs. B.1–2 (projected per-cell posterior means) and B.7–8 (projected per-cell posterior standard deviations) illustrate projections under other scenarios.

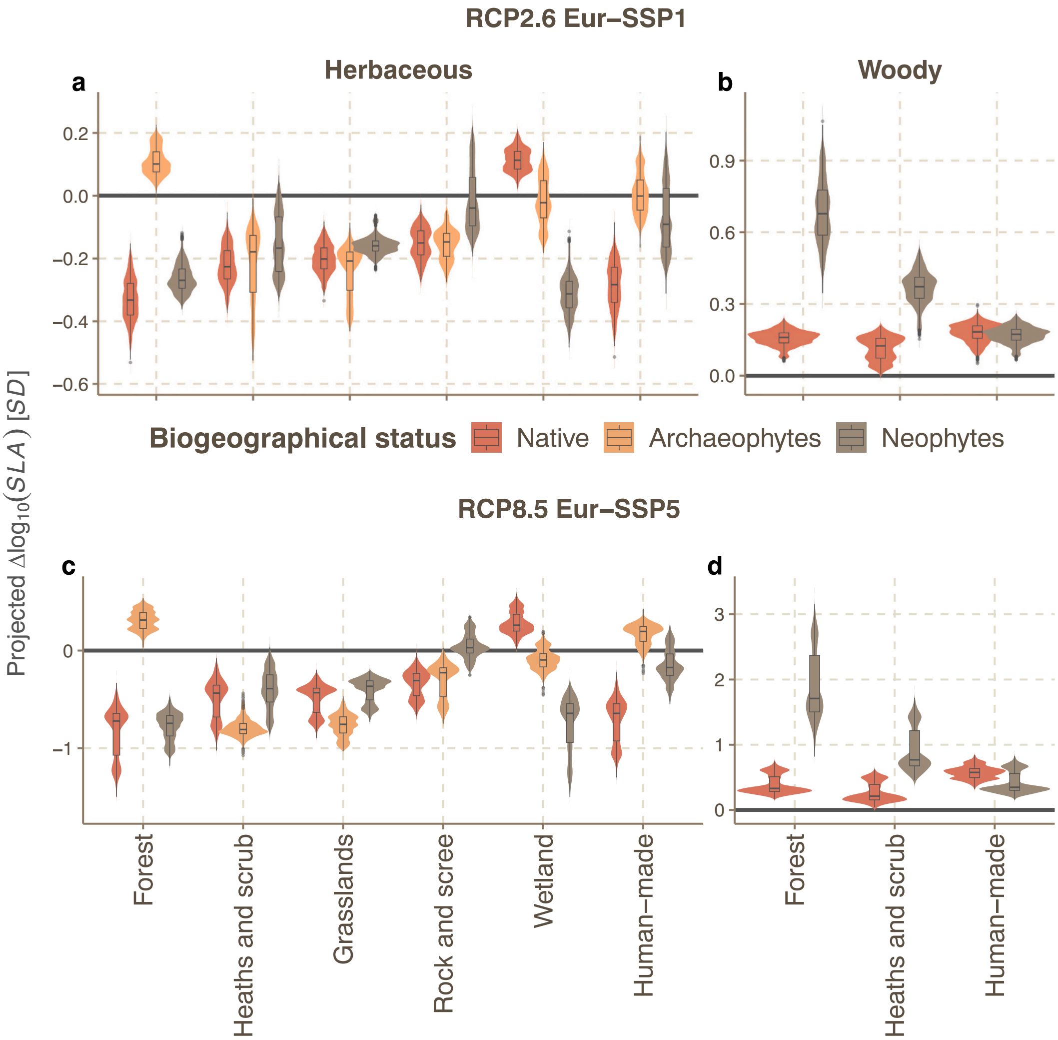


Fig. 3. The projected per-cell ($10' \times 10'$) change in the $\log_{10}$-transformed specific leaf area (*SLA*) under the least extreme combined climate and socio-economic scenario (RCP2.6 Eur-SSP1, all climate models pooled) and the most extreme one (RCP8.5 Eur-SSP5) for herbaceous (a, c) and woody (b, d) taxa in six broad habitat types. Figs. B.3–4 (projected per-cell posterior means) and B.9–10 (projected per-cell posterior standard deviations) illustrate projections under other scenarios. Other details are as in Fig. 2.

3.2. Projected trait change

For all traits considered simultaneously, the magnitude of trait change was projected to be, on average, higher in forests, heaths and scrub, and grasslands than in other habitat types (Fig. 1a), for non-natives rather than natives (Fig. 1b) and for woody rather than herbaceous plants (Fig. 1c). The direction of projected change in individual traits often diverged for herbaceous vs woody plants and natives vs neophytes (Fig. B.13).

Across all scenarios, the mean trend for $H_{\max}$ change in herbaceous plant assemblages within tree- and shrub-dominated habitats was positive throughout the study area, being more pronounced for archaeophytes and neophytes than for natives (Figs. 2a,c, B.1a–f). In other habitats, the projected change of $H_{\max}$ was more heterogeneous spatially and across biogeographical statuses. Notably, in grasslands and rock and scree habitats, herbaceous native $H_{\max}$ showed very little to no change, whereas herbaceous neophytes were projected to increase in $H_{\max}$, especially in grasslands (Figs. 2a,c, B.1g–l, B.14a,c). As for woody plant assemblages, only $H_{\max}$ of natives demonstrated a predominantly positive trend, with the highest increase projected for human-made habitats under RCP8.5 SSP5; meanwhile, $H_{\max}$ of neophytes tended to mainly decrease (Figs. 2b,d, B.2, B.14b,d).

Like $H_{\max}$, the projected change of *SLA* varied with biogeographical status, woodiness, and habitat (Figs. 3, B.3–4). Herbaceous *SLA* was projected to decrease, with some exceptions (e.g., native *SLA* in wetlands; Figs. 3a,c, B.3). The degree of this decrease tended to be greater for natives than neophytes (Fig. B.15a,c). In contrast, woody *SLA* can be expected to increase for both natives and neophytes, with the latter increasing more than natives in forests and heaths and scrub (Figs. 3b,d, B.4, B.15b,d).

The overall magnitude of *SM* change was comparable to that of $H_{\max}$ and *SLA*. In forests and heaths and scrub, woody native and non-native *SM* was projected to only increase, whereas, in human-made habitats, woody neophyte *SM* showed a decline (Figs. 4b,d, B.6a–e, B.16b,d). The direction of projected change in herbaceous *SM* was less uniform and varied spatially as well as with habitat and biogeographical status (Figs. 4a,c, B.5, B.16a,c). Particularly, *SM* of archaeophytes tended to respond opposingly to that of natives and neophytes and was more likely to decrease in most habitats.

3.3. Importance of environmental predictors

Across all three traits, T_{warm} and T_{cold} captured the highest amount of variation in the projected trait change, followed by P_{CV}, P_{dry}, and P_{wet}; the contributions of T_{dry}, T_{wet}, and $U_{\%}$ were considerably smaller (Fig. B.17). The role of individual environmental predictors generally

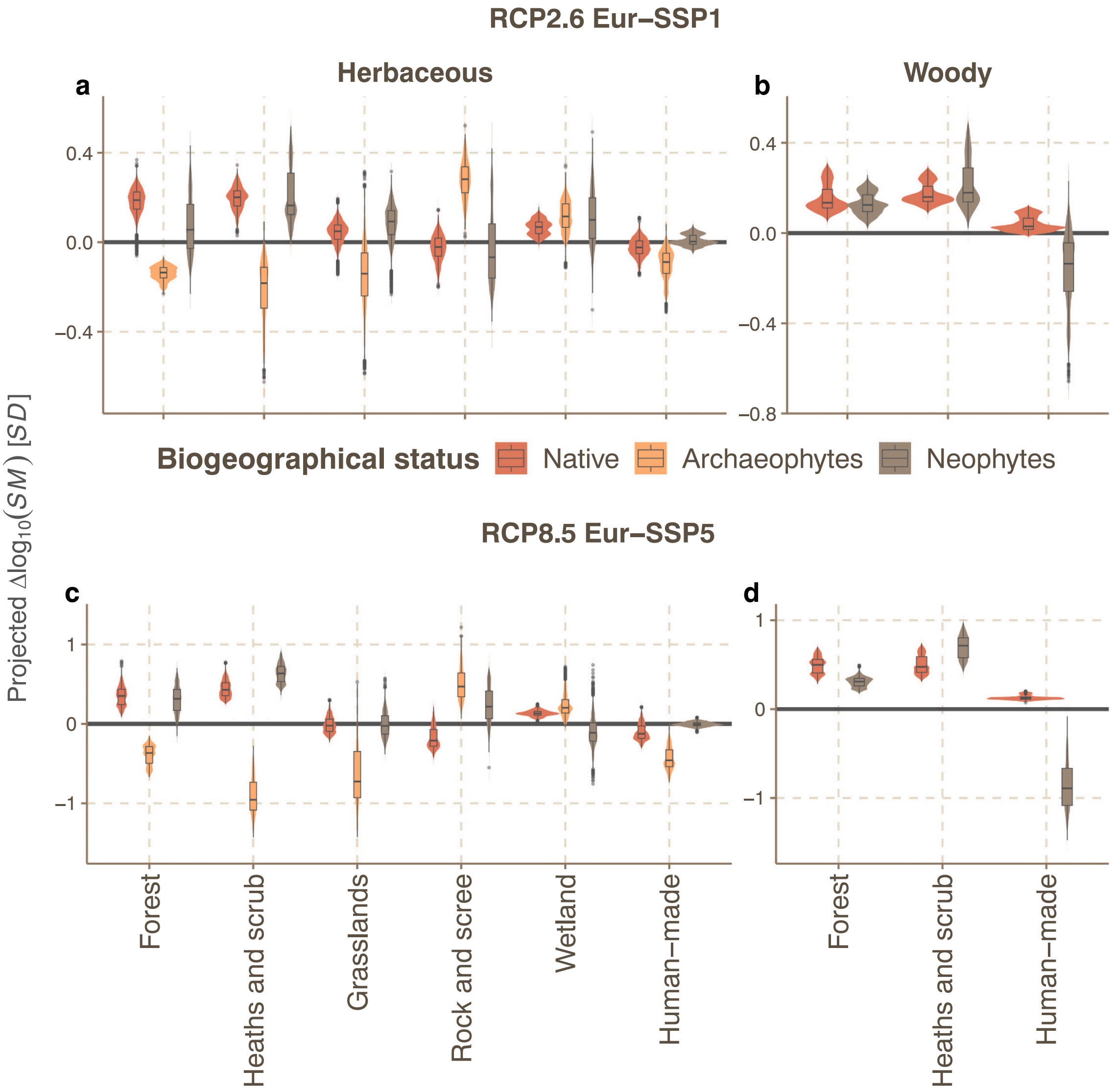
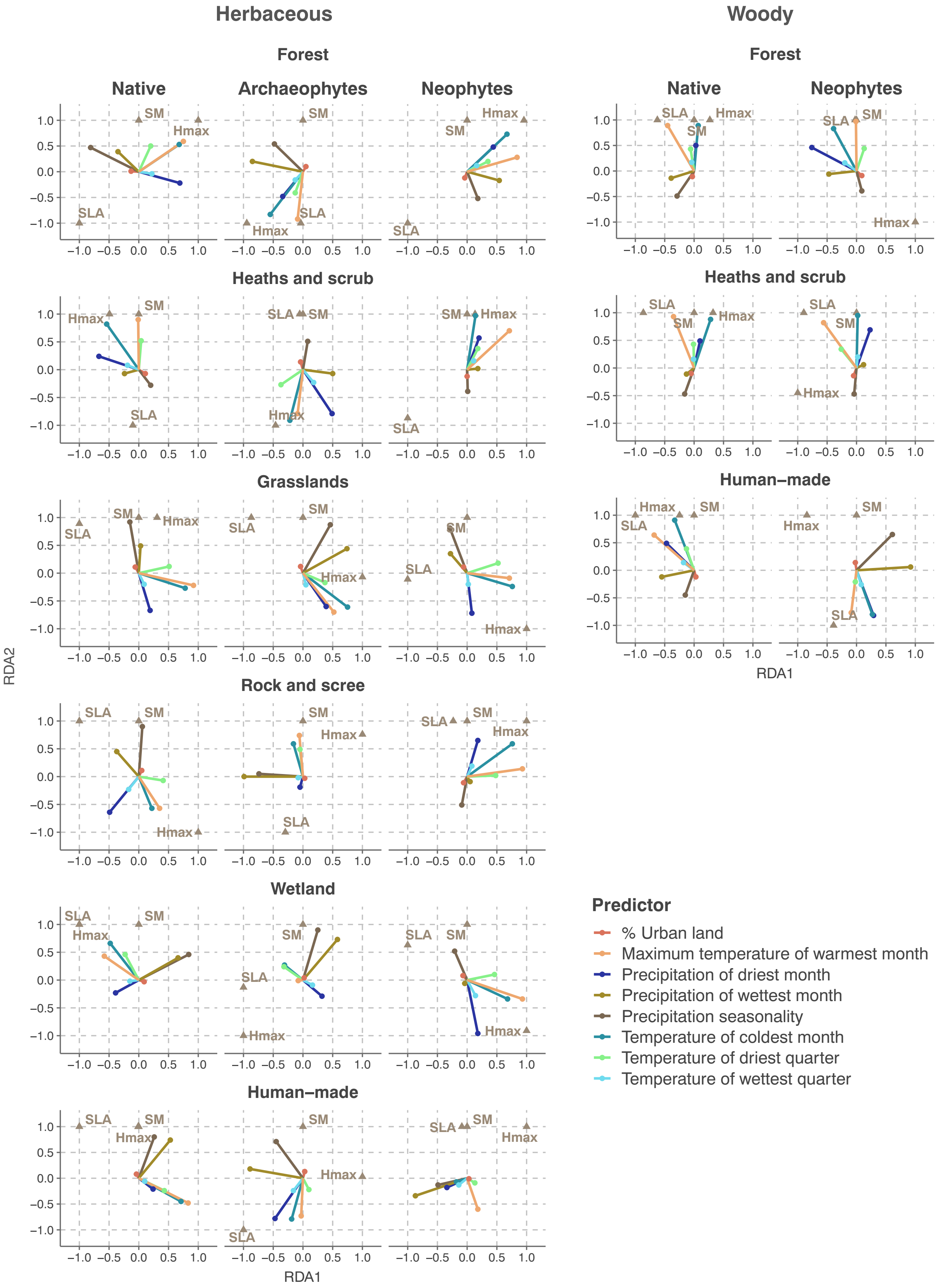


Fig. 4. The projected per-cell (10′ × 10′) change in the $\log_{10}$-transformed plant seed mass (*SM*) under the least extreme combined climate and socio-economic scenario (RCP2.6 Eur-SSP1, all climate models pooled) and the most extreme one (RCP8.5 Eur-SSP5) for 2081–2100, for herbaceous (a, c) and woody (b, d) taxa in six broad habitat types. Figs. B.5–6 (projected per-cell posterior means) and B.12–13 (projected per-cell posterior standard deviations) illustrate projections under other scenarios. Other details are as in Fig. 2.

varied with biogeographical status, habitat, and woodiness (Fig. 5). Nonetheless, some predictors showed highly consistent associations with the projected trait change (as per respective underlying TERs). For example, a projected increase in herbaceous *SM* correlated mostly positively with P_{CV} and negatively with P_{dry}; a negative relationship was, however, observed for herbaceous neophyte *SM* in the forest, heaths and scrub, and rock and scree habitats. Similarly, the increase in T_{cold} contributed positively to the *SM* increase in woody plant assemblages, except for neophytes in human-made habitats. T_{warm} and T_{cold} exhibited a strong positive relationship with herbaceous and woody H_{max}, although the relationship was negative for human-made habitats and woody neophytes. In some cases, the effect of temperature on H_{max} was not as pronounced as that of P_{wet} and P_{CV}. Mainly, native H_{max} in grasslands and human-made habitats was strongly positively affected by P_{wet} and P_{CV}, whereas in rock and scree habitats, native H_{max} was negatively associated with those two predictors. With few exceptions, herbaceous *SLA* correlated negatively with T_{warm}, T_{cold}, and P_{dry}. Furthermore, native herbaceous *SLA* positively correlated with P_{wet} in all habitats besides wetlands, whereas non-native herbaceous *SLA* consistently showed a negative relationship with P_{wet}. Unlike herbaceous *SLA*, native and neophyte woody *SLA* was strongly positively related to T_{warm}, T_{cold}, and P_{dry} (Fig. 5).

4. Discussion

In this study, we quantified broad-scale relationships of three traits central to plant life history – maximum height (H_{max}), specific leaf area (*SLA*), and seed mass (*SM*) – with eight selected environmental variables within Central Europe. We then used the obtained relationships to project trait change under seven plausible scenarios of future environmental change for 2081–2100. We modelled the variation in TERs associated with plant woodiness, biogeographical status, and habitat type to account for unique adaptations of different types of plant assemblages to the environment, hence making particular aspects of mechanistic context-dependence in TERs any resulting trait projections explicit (Catford et al., 2021). We showed that the three traits were projected both to increase and decrease to varying degrees across and – in many cases – within habitats and that the overall magnitude of this change was expected to be, on average, higher for non-native than native taxa (Fig. 1b) and under more extreme scenarios (Figs. B.1–6).



(caption on next page)

Fig. 5. The relative contribution of individual environmental predictors to the projected change in herbaceous and woody plant maximum height (H_{max}), specific leaf area (*SLA*), and seed mass (*SM*), calculated using redundancy analysis (RDA). A separate RDA was performed on each subset ($N = 24$) of per-cell projections across all the scenarios, representing a unique combination of taxon biogeographical status, habitat, and woodiness. Shown are the RDA scores of the predictors (as vectors) and traits (as triangles, centred at seed mass) for the first two RDA axes (RDA1, RDA2). RDA1 and RDA2 captured 91–100 % of the variation in the data. The lengths of vectors are proportional to the magnitude of the effects of respective predictors on the three traits simultaneously. The overall contributions of each predictor, calculated as the combined length of their respective vectors across all the RDA spaces, are shown in Fig. B.17. The angles among the vectors and triangles reflect their correlation, which equals the cosine of the angle. For example, most assemblages' angle between *SM* and precipitation seasonality is acute, indicating their strong positive correlation.

Moreover, we found that in the future, distinct environmental responses of native and non-native plants may lead to even higher trait values than currently observed for non-natives (e.g., herbaceous H_{max} in most habitats) as well as to a reduced average native–non-native trait difference (e.g., woody H_{max}; Figs. B.14–16), which may lead to altered competitive hierarchies among natives and non-natives (Kunstler et al., 2016).

4.1. Projected overall trait change across habitat types

The overall magnitude of trait change was projected to be higher in forests, heaths and scrub, and grassland habitats than in rock and scree, wetland, and human-made habitats (Fig. 1a). This result may reflect the low sensitivity of the latter to environmental change. In particular, rock and scree habitats are highly stable systems defined by environmental stress more than by macroclimate. By contrast, wetlands are strongly shaped by local hydrology and show much less species turnover along macroclimatic gradients than other habitats. Moreover, the spatial resolution of our analyses might have been too coarse to capture finer environmental gradients that traits of wetland and rock and scree plant assemblages respond to. Human-made habitats typically are more environmentally homogeneous and contain plants preadapted to disturbance and warm and dry conditions (Kalusová et al., 2017). Therefore, it is expected for human-made habitats to have plant taxa with relatively large *SLA* and small *SM*, irrespective of macroclimate. Overall, the observed high variation across habitats proved the importance of incorporating habitat information into macroecological analyses, as failing to do so would have blurred TERs.

4.2. Projected change in plant maximum height and its drivers

The hierarchy of environmental drivers shaping the projected change in H_{max} was highly habitat-specific, and the trait change patterns found across non-native plant assemblages often deviated from those in native assemblages. Specifically, temperature variables' positive effects drove the projected change of H_{max} in forests and heaths and scrub, whereas, in other habitats, precipitation variables' positive contributions prevailed (Fig. 5). Previous studies have similarly detected a robust positive association between temperature and plant height both across and within habitat types at the continental scale (e.g., Šímová et al., 2018; forest understories, Padullés Cubino et al., 2021) and the regional scale (e.g., forest understories, Maes et al., 2020; mountain grasslands and rock and scree, Dubuis et al., 2013). Meanwhile, Moles et al. (2009) reported that the best predictor of plant height globally was the precipitation of the wettest month, and our results for grasslands and rock and scree habitats supported this. Notably, while the TERs for native woody assemblages add to the current consensus on the effect of climate on woody plant height (Šímová et al., 2018; Swenson et al., 2012), the results for neophytes suggest that woody non-natives may be preadapted to a different subgradient of the global climatic gradient – in particular, to hotter and drier conditions – where the opposite, negative relationship with temperature can occur (Madani et al., 2018; Moles, 2018). A negative relationship between H_{max} of invasive neophytes and T_{cold} was also shown by Milanović et al. (2020), although the mechanisms behind this phenomenon remain unclear and require further exploration.

4.3. Projected change in specific leaf area and its drivers

Contrary to several previous studies (Dubuis et al., 2013; Rosbakh et al., 2015; Šímová et al., 2018), herbaceous native and neophyte *SLA* correlated primarily negatively with temperature, and only herbaceous archaeophyte *SLA* tended to show the opposite. Speculatively, we can assume that the patterns in the *SLA*–environment relationships were partially confounded with unaccounted environmental drivers, such as continentality and soil fertility. Like temperature, another pronounced driver of herbaceous *SLA* change, P_{dry}, also negatively affected *SLA* across all herbaceous assemblages. In contrast, P_{wet} positively and negatively influenced herbaceous native and neophyte *SLA*, respectively (Fig. 5). A negative shift of native *SLA* along the P_{dry} gradient appears in disagreement with a previously documented negative effect of drought on *SLA* (Wellstein et al., 2017; Wright et al., 2005). This pattern could be attributed to the occurrence of many plant taxa with evergreen, low-*SLA* leaves in the mountains in Central Europe, where precipitation is high (Chytrý et al., 2021). In contrast to herbaceous *SLA,* yet in alignment with previous reports (Šímová et al., 2018; Swenson et al., 2012), *SLA* across all woody assemblages exhibited a strong positive relationship with temperature as well as P_{dry}. Environmental change should, therefore, lead to an increase in woody native *SLA* and even more so in woody neophyte *SLA* (Figs. 3b,d, 5, B.4), which may allow non-natives to gain a further advantage over natives (Pyšek and Richardson, 2008).

Reflecting the combined effect of all the predictors, our projections mainly forecasted a decrease in herbaceous *SLA*; an increase throughout the study area was projected only for native herbaceous *SLA* in wetlands and archaeophyte *SLA* in forests, and a partial increase in *SLA* was projected for archaeophytes in wetlands and human-made habitats and herbaceous neophytes in grasslands and human-made habitats (Figs. 3, B.3). Despite a general projected shift towards more conservative resource-use strategies (i.e., lower *SLA*), our projections suggest that herbaceous neophyte *SLA* may be affected less than *SLA* of herbaceous natives (Figs. B.3, B.15). These changes may lead to a further increase in the *SLA* imbalance between native and non-native taxa towards the latter in the region (Divíšek et al., 2018), possibly resulting in an even higher proportion of invasive non-natives (Pyšek and Richardson, 2008). The alteration of the *SLA* composition will undoubtedly affect ecosystem functioning. For example, an overall decrease of *SLA* in grasslands may lead to higher root biomass (Klimešová et al., 2021) and total soil carbon (Garnier et al., 2004), as well as reduced nutrient cycling (Lavorel et al., 2011) and productivity (Brun et al., 2022).

4.4. Projected change in seed mass and its drivers

Our results showed that overall, drier, less stable climates might, on average, contribute to an increase in herbaceous *SM* but a decrease in woody *SM* (Fig. 5). This finding is congruent with previous studies (Baker, 1972; Dubuis et al., 2013; Šímová et al., 2015; Swenson et al., 2012; Vandelook et al., 2018) and at least partially explains the heterogeneous relationships of *SM* and precipitation in the literature (discussed in Moles, 2018). Notably, while this pattern holds for natives and archaeophytes across all habitats, neophytes often deviate from it. Specifically, we observed the opposite effect of the precipitation amount and seasonality on herbaceous neophyte *SM* in the tree- and shrub-dominated as well as rock and scree habitats and on woody neophyte *SM* in human-made habitats (Figs. 5, B.13). Such divergence from native herbaceous *SM* may be confounded with the turnover in the growth form, i.e., the proportional increase of small-seeded, short-lived neophytes in drier areas (Sandel et al., 2010). Additionally, the contrasting responses of native and non-native plant assemblages to precipitation may be due to the differences in the duration of their environmental exposure and the fact that many non-natives are still actively spreading. For archaeophytes, the positive effect of precipitation is likely to be overwhelmed by the negative impact of higher temperatures, leading to an overall decrease in *SM* (Figs. 4, B.5). Interestingly, for woody *SM*, the overall effect of precipitation was not as pronounced as that of temperature. Notably, our results revealed a strong positive association of woody *SM* with T_{warm} and T_{cold} (Fig. 5), which drove the projected increase in woody *SM* (Figs. 4b,d, B.6). This finding is in line with previous studies which also documented a strong positive effect of temperature on *SM* of woody plants (Moles et al., 2014; Šímová et al., 2015, 2018; Swenson et al., 2012) and highlighted that herbaceous *SM* is less sensitive to temperature than woody *SM* (Šímová et al., 2018).

4.5. Differences between native and non-native taxa

The observed differences in TERs and resulting trait change projections between native and non-native plant assemblages indicate that biogeographical status is pivotal in species performance and community assembly along environmental gradients. The effect of biogeographical status may reflect the eco-evolutionary novelty of non-natives (Heger et al., 2019; Saul et al., 2013) or their pre-adaptation to specific conditions (Maron et al., 2004). For example, non-native species often originate from more nitrogen-rich habitats (Dostál et al., 2013) and, therefore, are typically characterised by high *SLA*. As we have shown, in the long run, the differential response of native and non-native (especially neophyte) species to the change in environmental factors might lead to even more substantial differences in their trait compositions than today (Figs. B.14–16). These differences suggest that ecosystem functions provided by future neophyte assemblages may not be redundant to those currently offered by natives. On the contrary, functions presently provided by natives may be replaced with different functions supplied by neophytes, thus leading to an increase rather than buffering of functional turnover during global change.

4.6. Conclusions

This study assessed how plant trait values might shift at the macroscale under future environmental change until 2081–2100. Our results depicted substantial but frequently neglected contingency of TERs upon plant woodiness, biogeographical status, and habitat type, thereby explaining some of the existing idiosyncrasies within the literature and producing more informative and refined TERs and projections of future trait changes compared to previous studies. The obtained projections provide an insightful perspective on the conditions under which non-native plants may prevail over natives and vice versa and can serve as starting points for exploring changes in ecosystem functions and services in a rapidly changing world. We recommend routinely incorporating information on habitat, growth form, and biogeographical status when making any inference about plant traits' present or future variation along environmental gradients and the impacts of this variation on ecological processes.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.167954.

CRediT authorship contribution statement

Marina Golivets: Conceptualization, Methodology, Data Curation, Formal analysis, Writing – Original draft preparation. **Sonja Knapp:** Conceptualization, Writing – Review & Editing, Funding acquisition. **Franz Essl:** Writing – Review & Editing. **Bernd Lenzner:** Writing – Review & Editing. **Guillaume Latombe:** Writing – Review & Editing. **Brian Leung:** Writing – Review & Editing. **Ingolf Kühn:** Conceptualization, Methodology, Writing – Review & Editing, Funding acquisition.

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

All raw data in this study are freely available and can be acquired from their respective online repositories, cited in the main text. After acceptance, model outputs will be deposited to Zenodo.

Acknowledgements

We thank Milan Chytrý and Hanno Seebens for their valuable comments on the earlier versions of the manuscript. This research was part of the AlienScenarios project, funded through the 2017–2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND program, and with the funding organisations BMBF (project no. 01LC1807C – MG, IK, SK), the Austrian Science Foundation (FWF project no. I 4011-B32 – FE, BeL, GL) and the Canadian Natural Sciences and Engineering Research Council grant (BrL). The scientific results were partially computed at the High-Performance Computing (HPC) Cluster EVE, a joint effort of the Helmholtz Centre for Environmental Research – UFZ (www.ufz.de) and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (www.idiv-biodiversity.de). No permits were required to complete this research.

References

Aarssen, L.W., Schamp, B.S., Pither, J., 2006. Why are there so many small plants? Implications for species coexistence. J. Ecol. 94 (3), 569–580.

Anderegg, L.D., 2023. Why can't we predict traits from the environment? New Phytol. 237 (6), 1998–2004.

Axmanová, I., Kalusová, V., Danihelka, J., Dengler, J., Pergl, J., Pyšek, P., Večeřa, M., Attorre, F., Biurrun, I., Boch, S., 2021. Neophyte invasions in European grasslands. J. Veg. Sci. 32 (2), e12994.

Baker, H.G., 1972. Seed weight in relation to environmental conditions in California. Ecology 53 (6), 997–1010.

Beals, E.W., 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Adv. Ecol. Res. 14, 1–55.

Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Rüger, N., Beck, P.S., Blach-Overgaard, A., Blok, D., Cornelissen, J.H.C., Forbes, B.C., 2018. Plant functional trait change across a warming tundra biome. Nature 562 (7725), 57–62.

Brun, P., Violle, C., Mouillot, D., Mouquet, N., Enquist, B.J., Munoz, F., Thuiller, W., 2022. Plant community impact on productivity: Trait diversity or key (stone) species effects? Ecol. Lett. 25 (4), 913–925.

Bundesamt für Naturschutz, 2017. Bewertungsschemata für die Bewertung des Erhaltungsgrades von Arten und Lebensraumtypen als Grundlage für ein bundesweites FFH-Monitoring. In: Teil II: Lebensraumtypen nach Anhang I der FFH-Richtlinie (mit Ausnahme der marinen und Küstenlebensräume). BfN-Skripten 481. Bonn, Germany.

Bürkner, P.-C., 2017. Brms: an R package for Bayesian multilevel models using Stan. J. Stat. Softw. 80 (1), 1–28.

Carmona, C.P., Pärtel, M., 2021. Estimating probabilistic site-specific species pools and dark diversity from co-occurrence data. Glob. Ecol. Biogeogr. 30 (1), 316–326.

Catford, J.A., Wilson, J.R., Pyšek, P., Hulme, P.E., Duncan, R.P., 2021. Addressing context dependence in ecology. Trends Ecol. Evol. 37 (2), 158–170.

Chen, G., Kéry, M., Plattner, M., Ma, K., Gardner, B., 2013. Imperfect detection is the rule rather than the exception in plant distribution studies. J. Ecol. 101 (1), 183–191.

Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X., Smart, S.M., 2008. Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J. Appl. Ecol. 45 (2), 448–458.

Chytrỳ, M., Tichỳ, L., Hennekens, S.M., Knollová, I., Janssen, J.A., Rodwell, J.S., Peterka, T., Marcenò, C., Landucci, F., Danihelka, J., 2020. EUNIS habitat classification: expert system, characteristic species combinations and distribution maps of European habitats. Appl. Veg. Sci. 23 (4), 648–675.

Chytrý, M., Danihelka, J., Kaplan, Z., Wild, J., Holubova, D., Novotný, P., Pyšek, P., 2021. Pladias database of the Czech flora and vegetation. Preslia 93 (1), 1–87.

CLC, 2020. Corine Land Cover. Version 2020 20u1. Available from: https://land.copernicus.eu/pan-european/corine-land-cover/clc-2000.

Daru, B.H., Davies, T.J., Willis, C.G., Meineke, E.K., Ronk, A., Zobel, M., Davis, C.C., 2021. Widespread homogenization of plant communities in the Anthropocene. Nat. Commun. 12 (1), 1–10.

Datenbank FlorKart, BfN und NetPhyD, 2013. Datenbank FlorKart der Floristischen Kartierung Deutschlands, Stand 2013, Bundesamt für Naturschutz (BfN) und Netzwerk Phytodiversitaet Deutschland (NetPhyD).

Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., 2016. The global spectrum of plant form and function. Nature 529 (7585), 167–171.

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H., Chan, K.M., 2019. Pervasive human-driven decline of life on earth points to the need for transformative change. Science 366 (6471), eaax3100.

Divíšek, J., Chytrỳ, M., Beckage, B., Gotelli, N.J., Lososová, Z., Pyšek, P., Richardson, D. M., Molofsky, J., 2018. Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nat. Commun. 9 (1), 1–10.

Dostál, P., Dawson, W., van Kleunen, M., Keser, L.H., Fischer, M., 2013. Central European plant species from more productive habitats are more invasive at a global scale. Glob. Ecol. Biogeogr. 22, 64–72.

Drenovsky, R.E., Grewell, B.J., D'antonio, C.M., Funk, J.L., James, J.J., Molinari, N., Parker, I.M., Richards, C.L., 2012. A functional trait perspective on plant invasion. Ann. Bot. 110 (1), 141–153.

Dubuis, A., Rossier, L., Pottier, J., Pellissier, L., Vittoz, P., Guisan, A., 2013. Predicting current and future spatial community patterns of plant functional traits. Ecography 36 (11), 1158–1168.

DWD, 2017. Climate Data Center. Available at: ftp://ftp-cdc.dwd.de/pub/CDC.

EEA, 2018. Ecosystem types of Europe 2012 - Terrestrial habitats reliability map, version 3.1.

EEA, 2021. Land cover country fact sheets 2000–2018. https://www.eea.europa.eu/themes/landuse/land-cover-country-fact-sheets.

Eichenberg, D., Bowler, D.E., Bonn, A., Bruelheide, H., Grescho, V., Harter, D., Jandt, U., May, R., Winter, M., Jansen, F., 2021. Widespread decline in Central European plant diversity across six decades. Glob. Chang. Biol. 27 (5), 1097–1110.

Essl, F., Dullinger, S., Genovesi, P., Hulme, P.E., Jeschke, J.M., Katsanevakis, S., Kühn, I., Lenzner, B., Pauchard, A., Pyšek, P., 2019. A conceptual framework for range-expanding species that track human-induced environmental change. BioScience 69 (11), 908–919.

E-Vojtkó, A.E., Balogh, N., Deák, B., Kelemen, A., Kis, S., Kiss, R., Lovas-Kiss, Á., Löki, V., Lukács, K., Molnár, V.A., Nagy, T., 2020. Leaf trait records of vascular plant species in the Pannonian flora with special focus on endemics and rarities. Folia Geobot. 55 (2), 73–79.

Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. J. Appl. Ecol. 43 (3), 393–404.

Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M., Bruun, H.H., 2019. More is less: net gain in species richness, but biotic homogenization over 140 years. Ecol. Lett. 22 (10), 1650–1657.

Fitter, A.H., Peat, H.J., 1994. The ecological flora database. J. Ecol. 415–425.

Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology 85 (9), 2630–2637.

Giulio, S., Acosta, A.T.R., Carboni, M., Campos, J.A., Chytrỳ, M., Loidi, J., Pergl, J., Pyšek, P., Isermann, M., Janssen, J.A., 2020. Alien flora across European coastal dunes. Appl. Veg. Sci. 23 (3), 317–327.

Gross, N., Börger, L., Duncan, R.P., Hulme, P.E., 2013. Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands? Funct. Ecol. 27 (5), 1262–1272.

Guo, J., Jiang, W., Chen, G., 2020. Transient solute dispersion in wetland flows with submerged vegetation: an analytical study in terms of time-dependent properties. Water Resour. Res. 56 (2), e2019WR025586.

Hanisch, M., Schweiger, O., Cord, A.F., Volk, M., Knapp, S., 2020. Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. J. Appl. Ecol. 57 (8), 1535–1550.

Hanz, D.M., Cutts, V., Barajas-Barbosa, M.P., Algar, A.C., Beierkuhnlein, C., Fernández-Palacios, J.M., Field, R., Kreft, H., Steinbauer, M.J., Weigelt, P., Irl, S.D.H., 2022. Climatic and biogeographical drivers of functional diversity in the flora of the Canary Islands. Glob. Ecol. 31 (7), 1313–1331.

Heger, T., Bernard-Verdier, M., Gessler, A., Greenwood, A.D., Grossart, H.P., Hilker, M., Keinath, S., Kowarik, I., Kueffer, C., Marquard, E., Muller, J., Niemeier, S., Onandia, G., Petermann, J.S., Rillig, M.C., Rodel, M.O., Saul, W.C., Schittko, C., Tockner, K., Joshi, J., Jeschke, J.M., 2019. Towards an integrative, eco-evolutionary understanding of ecological novelty: studying and communicating interlinked effects of global change. BioScience 69, 888–899.

Henn, J.J., Yelenik, S., Damschen, E.I., 2019. Environmental gradients influence differences in leaf functional traits between native and non-native plants. Oecologia 191 (2), 397–409.

Hijmans, R.J., 2021. Raster: Geographic Data Analysis and Modeling. R package version 3.4-13. https://CRAN.R-project.org/package=raster.

Hulme, P.E., Bernard-Verdier, M., 2018a. Comparing traits of native and alien plants: can we do better? Funct. Ecol. 32 (1), 117–125.

Hulme, P.E., Bernard-Verdier, M., 2018b. Evaluating differences in the shape of native and alien plant trait distributions will bring new insights into invasions of plant communities. J. Veg. Sci. 29 (2), 348–355.

Kalusová, V., Čeplová, N., Lososová, Z., 2017. Which traits influence the frequency of plant species occurrence in urban habitat types? Urban Ecosyst. 20, 65–75.

Kaplan, Z., Danihelka, J., Chrtek Jr., J., Kirschner, J., Kubát, K., Štěpánek, J., Štech, M. (Eds.), 2019. Klíč ke květeně České republiky [Key to the flora of the Czech Republic]. Ed. 2. – Academia, Praha.

Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Boenisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D. D., Anand, M., Wirth, C., 2011. TRY - a global database of plant traits. Glob. Chang. Biol. 17 (9), 2905–2935.

Kattge, J., Boenisch, G., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcantara, J.M., Alcazar, C.C., Aleixo, I., Ali, H., Wirth, C., 2020. TRY plant trait database—enhanced coverage and open access. Glob. Chang. Biol. 26 (1), 119–188.

van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecol. Lett. 13 (2), 235–245.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., 2008. The LEDA Traitbase: a database of life-history traits of the northwest European flora. J. Ecol. 96 (6), 1266–1274.

Klimešová, J., Mudrák, O., Martínková, J., Lisner, A., Lepš, J., Filartiga, A.L., Ottaviani, G., 2021. Are belowground clonal traits good predictors of ecosystem functioning in temperate grasslands? Funct. Ecol. 35 (3), 787–795.

Knapp, S., Kühn, I., 2012. Origin matters: widely distributed native and non-native species benefit from different functional traits. Ecol. Lett. 15 (7), 696–703.

Kok, K., Pedde, S., Gramberger, M., Harrison, P.A., Holman, I.P., 2019. New European socio-economic scenarios for climate change research: Operationalising concepts to extend the shared socio-economic pathways. Reg. Environ. Chang. 19 (3), 643–654.

Kühn, I., Durka, W., Klotz, S., 2004. BiolFlor: A new plant-trait database as a tool for plant invasion ecology. Divers. Distrib. 10 (5/6), 363–365.

Kühn, N., Tovar, C., Carretero, J., Vandvik, V., Enquist, B.J., Willis, K.J., 2021. Globally important plant functional traits for coping with climate change. Front. Biogeogr. 13 (4), e53774.

Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Westoby, M., 2016. Plant functional traits have globally consistent effects on competition. Nature 529 (7585), 204–207.

Küster, E.C., Kühn, I., Bruelheide, H., Klotz, S., 2008. Trait interactions help explain plant invasion success in the German flora. J. Ecol. 96 (5), 860–868.

Küster, E.C., Bierman, S.M., Klotz, S., Kühn, I., 2011. Modelling the impact of climate and land use change on the geographical distribution of leaf anatomy in a temperate flora. Ecography 34 (3), 507–518.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the holy grail. Funct. Ecol. 16 (5), 545–556.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.P., Garden, D., Girel, J., Douzet, R., 2011. Using plant functional traits to understand the landscape distribution of multiple ecosystem services. J. Ecol. 99 (1), 135–147.

Liu, Y., Oduor, A.M.O., Zhang, Z., Manea, A., Tooth, I.M., Leishman, M.R., Xu, X., van Kleunen, M., 2017. Do invasive alien plants benefit more from global environmental change than native plants? Glob. Chang. Biol. 23 (8), 3363–3370.

Madani, N., Kimball, J.S., Ballantyne, A.P., Affleck, D.L., Van Bodegom, P.M., Reich, P.B., Kattge, J., Sala, A., Nazeri, M., Jones, M.O., 2018. Future global productivity will be affected by plant trait response to climate. Sci. Rep. 8 (1), 1–10.

Maes, S.L., Perring, M.P., Depauw, L., Bernhardt-Römermann, M., Blondeel, H., Brümelis, G., Brunet, J., Decocq, G., den Ouden, J., Govaert, S., 2020. Plant functional trait response to environmental drivers across European temperate forest understorey communities. Plant Biol. 22 (3), 410–424.

Maron, J.L., Vila, M., Bommarco, R., Elmendorf, S., Beardsley, P., 2004. Rapid evolution of an invasive plant. Ecol. Monogr. 74, 261–280.

Mathakutha, R., Steyn, C., le Roux, P.C., Blom, I.J., Chown, S.L., Daru, B.H., Ripley, B.S., Louw, A., Greve, M., 2019. Invasive species differ in key functional traits from native and non-invasive alien plant species. J. Veg. Sci. 30 (5), 994–1006.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21 (4), 178–185.

Milanović, M., Knapp, S., Pyšek, P., Kühn, I., 2020. Trait–environment relationships of plant species at different stages of the introduction process. NeoBiota 58, 55.

Moles, A.T., 2018. Being John Harper: using evolutionary ideas to improve understanding of global patterns in plant traits. J. Ecol. 106 (1), 1–18.

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A., Leishman, M.R., 2009. Global patterns in plant height. J. Ecol. 97 (5), 923–932.

Moles, A.T., Perkins, S.E., Laffan, S.W., Flores-Moreno, H., Awasthy, M., Tindall, M.L., Sack, L., Pitman, A., Kattge, J., Aarssen, L.W., 2014. Which is a better predictor of plant traits: temperature or precipitation? J. Veg. Sci. 25 (5), 1167–1180.

Musavi, T., Migliavacca, M., van de Weg, M.J., Kattge, J., Wohlfahrt, G., van Bodegom, P. M., Mahecha, M.D., 2016. Potential and limitations of inferring ecosystem photosynthetic capacity from leaf functional traits. Ecol. Evol. 6 (20), 7352–7366.

Myers-Smith, I.H., Thomas, H.J.D., Bjorkman, A.D., 2019. Plant traits inform predictions of tundra responses to global change. New Phytol. 221 (4), 1742–1748.

Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. Science 336 (6087), 1401–1406.

Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37 (2), 191–203.

New, M., Lister, D., Hulme, M., Makin, I., 2002. A high-resolution data set of surface climate over global land areas. Climate Res. 21, 1–25.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., 2020. Vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan.

Padullés Cubino, J., Biurrun, I., Bonari, G., Braslavskaya, T., Font, X., Jandt, U., Chytrý, M., 2021. The leaf economic and plant size spectra of European forest understory vegetation. Ecography 44 (9), 1311–1324.

Pollock, L.J., Morris, W.K., Vesk, P.A., 2012. The role of functional traits in species distributions revealed through a hierarchical model. Ecography 35 (8), 716–725.

Pyšek, P., Richardson, D.M., 2008. Traits associated with invasiveness in alien plants: where do we stand?. In: Biological invasions. Springer, pp. 97–125.

Pyšek, P., Danihelka, J., Sádlo, J., Chrtek Jr, J., Chytrý, M., Jarošík, V., Tichý, L., 2012. Catalogue of alien plants of the Czech Republic: checklist update, taxonomic diversity and invasion patterns. Preslia 84 (2), 155–255.

Pyšek, P., Hulme, P.E., Simberloff, D., Bacher, S., Blackburn, T.M., Carlton, J.T., Dawson, W., Essl, F., Foxcroft, L.C., Genovesi, P., 2020. Scientists' warning on invasive alien species. Biol. Rev. 95 (6), 1511–1534.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL. https://www.R-project.org/.

Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. Ecography 40 (8), 913–929.

Rosbakh, S., Römermann, C., Poschlod, P., 2015. Specific leaf area correlates with temperature: New evidence of trait variation at the population, species and community levels. Alp. Bot. 125 (2), 79–86.

Roy, D., Alderman, P., Arianoutsou, M., Augustin, S., 2020. DAISIE - inventory of alien invasive species in Europe. Version 1.7. Research Institute for Nature and Forest (INBO). Checklist dataset. https://doi.org/10.15468/ybwd3x.

Sádlo, J., Chytrý, M., Pyšek, P., 2007. Regional species pools of vascular plants in habitats of the Czech Republic. Preslia 79, 303–321.

Sandel, B., Low, R., 2019. Intraspecific trait variation, functional turnover and trait differences among native and exotic grasses along a precipitation gradient. J. Veg. Sci. 30 (4), 633–643.

Sandel, B., Goldstein, L.J., Kraft, N.J.B., Okie, J.G., Shuldman, M.I., Ackerly, D.D., Cleland, E.E., Suding, K.N., 2010. Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. New Phytol. 188 (2), 565–575.

Saul, W.-C., Jeschke, J., Heger, T., 2013. The role of eco-evolutionary experience in invasion success. NeoBiota 17, 57–74.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., 2017. No saturation in the accumulation of alien species worldwide. Nat. Commun. 8 (1), 1–9.

Seebens, H., Bacher, S., Blackburn, T.M., Capinha, C., Dawson, W., Dullinger, S., Essl, F., 2021. Projecting the continental accumulation of alien species through to 2050. Glob. Chang. Biol. 27 (5), 970–982.

Šímová, I., Violle, C., Kraft, N.J.B., Storch, D., Svenning, J.-C., Boyle, B., Donoghue, J.C., Jørgensen, P., McGill, B.J., Morueta-Holme, N., Piel, W.H., Peet, R.K., Regetz, J., Schildhauer, M., Spencer, N., Thiers, B., Wiser, S., Enquist, B.J., 2015. Shifts in trait means and variances in North American tree assemblages: species richness patterns are loosely related to the functional space. Ecography 38 (7), 649–658.

Šímová, I., Violle, C., Svenning, J.-C., Kattge, J., Engemann, K., Sandel, B., Peet, R.K., Wiser, S.K., Blonder, B., McGill, B.J., 2018. Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. J. Biogeogr. 45 (4), 895–916.

Swenson, N.G., Enquist, B.J., Pither, J., Kerkhoff, A.J., Boyle, B., Weiser, M.D., Elser, J.J., Fagan, W.F., Forero-Montaña, J., Fyllas, N., Kraft, N.J.B., Lake, J.K., Moles, A.T., Patiño, S., Phillips, O.L., Price, C.A., Reich, P.B., Quesada, C.A., Stegen, J.C., Nolting, K.M., 2012. The biogeography and filtering of woody plant functional diversity in north and South America. Glob. Ecol. Biogeogr. 21 (8), 798–808.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. 102 (23), 8245–8250.

Thuiller, W., Guéguen, M., Renaud, J., Karger, D.N., Zimmermann, N.E., 2019. Uncertainty in ensembles of global biodiversity scenarios. Nat. Commun. 10 (1), 1446.

Valavi, R., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G., 2019. blockCV: an r package for generating spatially or environmentally separated folds for k-fold cross-validation of species distribution models. Methods Ecol. Evol. 10 (2), 225–232.

Vandelook, F., Janssens, S.B., Matthies, D., 2018. Ecological niche and phylogeny explain distribution of seed mass in the central European flora. Oikos 127 (10), 1410–1421.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116 (5), 882–892.

Violle, C., Reich, P.B., Pacala, S.W., Enquist, B.J., Kattge, J., 2014. The emergence and promise of functional biogeography. Proc. Natl. Acad. Sci. 111 (38), 13690–13696.

Wagner, V., Chytrỳ, M., Jiménez-Alfaro, B., Pergl, J., Hennekens, S., Biurrun, I., Knollová, I., Berg, C., Vassilev, K., Rodwell, J.S., 2017. Alien plant invasions in European woodlands. Divers. Distrib. 23 (9), 969–981.

Wellstein, C., Poschlod, P., Gohlke, A., Chelli, S., Campetella, G., Rosbakh, S., Canullo, R., Kreyling, J., Jentsch, A., Beierkuhnlein, C., 2017. Effects of extreme drought on specific leaf area of grassland species: a meta-analysis of experimental studies in temperate and sub-Mediterranean systems. Glob. Chang. Biol. 23 (6), 2473–2481.

Wesner, J.S., Pomeranz, J.P., 2021. Choosing priors in Bayesian ecological models by simulating from the prior predictive distribution. Ecosphere 12 (9), e03739.

Westerband, A.C., Knight, T.M., Barton, K.E., 2020. Intraspecific trait variation and reversals of trait strategies across key climate gradients in native Hawaiian plants and non-native invaders. Ann. Bot. 127 (4), 553–564.

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199 (2), 213–227.

Wieczynski, D.J., Boyle, B., Buzzard, V., Duran, S.M., Henderson, A.N., Hulshof, C.M., Kerkhoff, A.J., McCarthy, M.C., Michaletz, S.T., Swenson, N.G., 2019. Climate shapes and shifts functional biodiversity in forests worldwide. Proc. Natl. Acad. Sci. 116 (2), 587–592.

Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C., Delipetrou, P., Didžiulis, V., Hejda, M., 2009. Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. Proc. Natl. Acad. Sci. 106 (51), 21721–21725.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428 (6985), 821–827.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I., Westoby, M., 2005. Modulation of leaf economic traits and trait relationships by climate. Glob. Ecol. Biogeogr. 14 (5), 411–421.

Yang, Q., Weigelt, P., Fristoe, T.S., Zhang, Z., Kreft, H., Stein, A., van Kleunen, M., 2021. The global loss of floristic uniqueness. Nat. Commun. 12 (1), 1–10.

Yao, Y., Vehtari, A., Simpson, D., Gelman, A., 2018. Using stacking to average Bayesian predictive distributions (with discussion). Bayesian Anal. 13 (3), 917–1007.