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RESEARCH ARTICLE

# Climate regulation processes are linked to the functional composition of plant communities in European forests, shrublands, and grasslands

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## Abstract

Terrestrial ecosystems affect climate by reflecting solar irradiation, evaporative cooling, and carbon sequestration. Yet very little is known about how plant traits affect climate regulation processes (CRPs) in different habitat types. Here, we used linear and random forest models to relate the community-weighted mean and variance values of 19 plant traits (summarized into eight trait axes) to the climate-adjusted proportion of reflected solar irradiation, evapotranspiration, and net primary productivity across 36,630 grid cells at the European extent, classified into 10 types of forest, shrubland, and grassland habitats. We found that these trait axes were more tightly linked to log evapotranspiration (with an average of 6.2% explained variation) and the proportion of reflected solar irradiation (6.1%) than to net primary productivity (4.9%). The highest variation in CRPs was explained in forest and temperate shrubland habitats. Yet, the strength and direction of these relationships were strongly habitat-dependent. We conclude that any spatial upscaling of the effects of plant communities on CRPs must consider the relative contribution of different habitat types.

KEYWORDS
albedo, biodiversity change, climate change, climate-surface models, greenhouse gases, land use change, leaf economics spectrum, nature-based solutions, transpiration

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## 1 | INTRODUCTION

Climate change and biodiversity loss pose two of the biggest threats to human well-being in the 21st century (Atwoli et al., 2021; Díaz et al., 2019; Steffen et al., 2015; Stocker et al., 2014; World Resources Institute, 2005). Nature-based solutions to protect, manage and restore natural ecosystems (IUCN, 2020) could provide viable options to mitigate both the climate and biodiversity crisis (Griscom et al., 2017; Seddon et al., 2020). Terrestrial ecosystems affect the local and global balances of energy, water, and carbon via their effects on the proportion of reflected solar irradiation (albedo), evapotranspiration and carbon sequestration (Anderson-Teixeira et al., 2012; Chapin et al. 2008; Pielke et al., 1998), which are all related to important climate regulation processes (CRPs). The mass ratio hypothesis posits that the functioning of ecosystems is driven by the traits of dominant species (Grime, 1998). Accordingly, one could assume that local CRPs should be related to the trait composition of local plant communities (Chapin et al., 2000; Díaz et al., 2016; Garnier et al., 2016; Hinojo-Hinojo & Goulden, 2020; Lavorel & Garnier, 2002), also in interaction with large-scale climatic gradients (Enquist et al., 2015). We further know that trait-ecosystem functioning relationships depend on the type of habitat (Brun, Violle, et al., 2022). Yet, besides the current calls to link the distribution of plant functional traits and vegetation demographics to the distribution and provisioning of CRPs (Fisher et al., 2018; He et al., 2023; Mahecha et al., 2022), such analyses have been hampered by the need for fine-resolution vegetation data of regional to continental extent and trait information across many plant species (cf. Mahecha et al., 2022; Serna-Chavez et al., 2017).

Previous studies on the relationships between plant traits and CRPs have shown that albedo, which quantifies the proportion of reflected irradiation, differs between habitat types (Leonardi et al., 2015; Oehri et al., 2022) and is related to the tree cover, leaf reflectance, and the leaf area index (i.e., the summed area of green leaves per unit of ground area, Alibakhshi et al., 2020; Ridgwell et al., 2009) as well as the amount of plant litter in forest habitats (Serna-Chavez et al., 2017). Evapotranspiration, which is the sum of plant transpiration and evaporation from the land surface, is related to plant hydraulic strategies (Matheny et al., 2017), total plant cover, rooting depth and, potentially, the canopy height of plant communities (Gates & Hanks, 1967). Net primary productivity, which quantifies the amount of carbon captured minus maintenance costs, differs between habitat types (Harper et al., 2016) and is related to the specific leaf area and leaf nitrogen, phosphorus, and chlorophyll content (He et al., 2023) as well as the carbon pool in the different layers of forest habitats (Serna-Chavez et al., 2017). In summary, the impact of plant communities on local CRPs has been estimated to be of comparable magnitude to the impact of local climatic conditions on CRPs (Oehri et al., 2022; Serna-Chavez et al., 2017). Yet, most of the present findings are based on simulation and studies that covered a restricted number of habitat types or geographic extents. Thus, we still lack comprehensive analyses on the generality of traits-CRP relationships, especially under consideration of the potentially confounding effects of local climatic conditions and the habitat type under investigation (Figure 1, He et al., 2023).

Here, we used 49,809 geo-referenced vegetation-plot observations from the European Vegetation Archive (Chytrý et al., 2016), classified into three broad habitats (forests, shrublands, and grasslands) and 10 more narrowly defined habitat subclasses (based on the expert-based EUNIS classification, Chytrý et al., 2020, 2021) and, averaged across 36,620 grid cells of 500 m resolution, assigned them with the community-weighted mean (CWM) and variance values of 19 plant functional traits, as well as six bioclimatic variables and the proportion of reflected solar irradiation, evapotranspiration, and net primary productivity. We hypothesized that the three CRPs jointly depend on climate and on habitat types (Figure 1). Therefore, CRP values should differ between the investigated subclasses of forest, shrubland and grassland habitats. Since the effects of climate on plant trait distributions tend to be habitat-specific (Kambach et al., 2023), we further hypothesized that the predictive power of CRP-trait relationships should also depend on the habitat type under investigation. Yet, if the selected 19 plant traits are (to a certain degree) mechanistically linked to the three CRPs, we hypothesized that the direction of the observed CRP-trait relationships should be

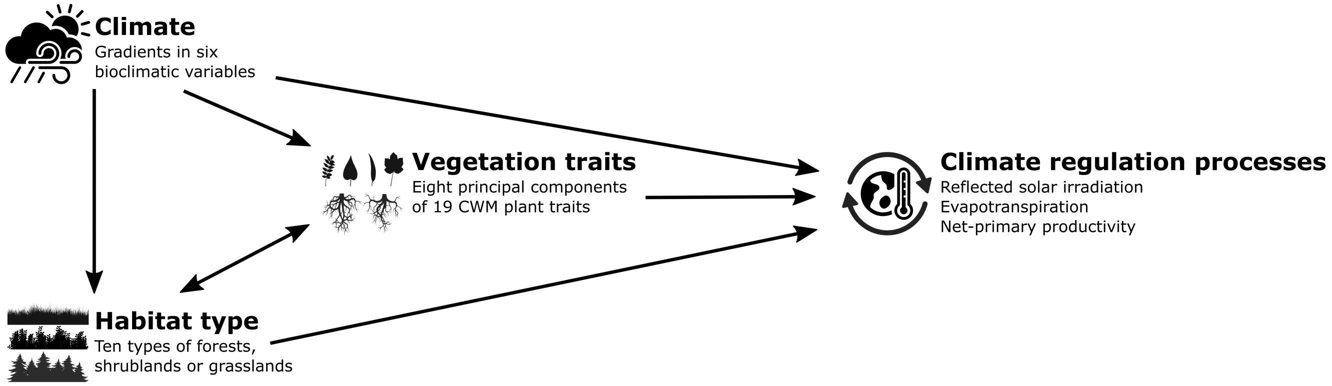


FIGURE 1 Framework depicting the assumed effects of the functional composition of plant communities on climate regulation processes, accounting for the effects of climate and habitat type.

similar among the different subclasses of forest, shrubland, and grassland habitats. In testing these hypotheses, we provide the first comprehensive analysis of the predictability and generality of trait-CRP relationships across large-scale gradients in climatic conditions and habitat types.

## 2 | MATERIALS AND METHODS

### 2.1 | Vegetation data

Raw vegetation survey data consisted of 1,735,298 plots, collated and curated by the European Vegetation Archive (Chytrý et al., 2016) and accessed on May 12th, 2021 (project number 123). Species abundances were converted to percentage cover. Each plot was assigned to a habitat type based on the expert system for the automatic classification of European vegetation plots to EUNIS habitats (European Nature Information System), which was updated on October 25th, 2021 (Chytrý et al., 2020, 2021). For this study, we selected and merged all plots into the following broad habitat types: forest, grassland, or shrubland habitats and, at a finer level, into the following more-narrowly defined habitat subclasses: coniferous, deciduous, or broadleaved evergreen forests, alpine, heathland or temperate shrublands and alpine, dry, mesic, or wet grasslands. The included EUNIS habitat types together with the respective number of vegetation records are listed in Table S1.

To be able to match plot data with satellite data and to reduce unaccounted variability in CRP-trait relationships, we included only those plots that met all of the following criteria: (1) species abundances were recorded, (2) survey date was between January 1, 2000, and December 31, 2017, (3) plot location was between the southernmost point of 34° N and the northernmost point of 82° N and east of the westernmost point of 32° W, (4) location uncertainty was reported and lower than 250 m, (5) water bodies covered less than 10% of the area in a 250 m radius (following the JRC Global Surface Water map, version 1.4, reprojected to 100 m spatial resolution, Pekel et al., 2016), (6) all climatic and satellite variables could be extracted, (7) the cumulative percentage cover of vascular plants was more than 80% of the plot area, and (8) trait information was available for more than 80% of the summed cover of the recorded vascular plants. To reduce the effects of forest management, we excluded all plots that were classified as tree plantations (EUNIS classes T1H, T1K, T29, T2A, T3M, and T3N) or self-sown forests of non-native trees (T1J and T3L).

To match trait data to individual species, we harmonized the species names with the Taxonomic Name Resolution Service 5.0 (tnrs.biendata.org), merged subspecies and varieties at the species level (keeping higher level taxa) and matched the resulting species list with the taxonomic backbone 3.0 of the sPlot Global Vegetation Database (Bruelheide et al., 2019). The resulting species names complied with the taxonomy of the TRY plant trait database (Kattge et al., 2020). We omitted all algae, bryophyte, fungi, and lichen species and, separately for each of the 10 habitat subclasses, we retained only the most recent record for each unique location, which resulted in 49,809 plots with 1,334,114 occurrence observations from 6,214 species, distributed between 10.3° W and 50° E and 35.2° N and 59.5° N, with the highest density in Central Europe (individual databases are listed in Table S2).

### 2.2 | Community-weighted trait means

To assign species-level trait averages, we used the gap-filled TRY plant trait database, version 5 (Kattge et al., 2020), which covered species-level mean values for 33 traits from 50,404 species. In this gap-filled dataset, any missing trait values were predicted at the individual level with Bayesian hierarchical probabilistic matrix factorization based on observed trait records, bivariate Pearson correlations between all pairs of traits (Figure S1), and the taxonomic hierarchy (see Kambach et al., 2023; Schrodt et al., 2015; Shan et al., 2012). The original publications for the trait data are listed in Table S3. From this gap-filled dataset, we extracted species- and genus-level average values of 19 traits that we deemed potentially important for the analyzed CRPs (listed at the bottom of Table 1 and described in Table S4). We matched and extracted species-level trait values for 4,139 species and, when no species-level estimates were available, we assigned the genus-level mean values to an additional number of 385 species. For each trait in each plot, we calculated a community-weighted mean (CWM) and community-weighted variance (CWV) value based on the trait value $t$ and the abundance (i.e., relative cover) $p$ of species $i = 1 \dots n$ (as presented in Bruelheide et al., 2018).

$$\mathrm{CWM} = \sum_{i}^{n} p_i t_i \quad \mathrm{CWV} = \sum_{i}^{n} p_i \left(t_i - \mathrm{CWM}\right)^2{}_i.$$

All CWMs were log-transformed.

To match the spatial resolution between vegetation and satellite data, we calculated an average value for each of the 19 CWMs and CWVs within each trait × habitat combination within the 500 m grid cells of the albedo raster data (which is described below). The resulting dataset contained 36,620 grid cell records (Figure S2) from coniferous (3,452 grid cells), deciduous (10,742), and broadleaved evergreen forests (532), alpine (600), heathland (922), and temperate shrublands (854) and alpine (1,051), dry (6,163), mesic (8,546), and wet grasslands (3,758). For the following analyses, we scaled all grid cell-averaged CWM and CWV values to unit variance (via subtraction of the mean followed by division of the standard deviation).

To remove the covariation among the 19 CWMs, we conducted separate principal component (PC) analyses (within the EUNIS level 1classification, i.e., within forests, shrublands and grasslands) and extracted the first eight PCs, which we varimax-rotated to maximize the correspondence of the PCs to individual plant traits (hereafter main trait axes). The resulting first four trait axes were related to known gradients of plant trait syndromes

**TABLE 1** Varimax-rotated principal components of 19 community-weighted mean traits.

| Main axes structuring the relationships among community-weighted mean trait values | | | | | | |
|---|---|---|---|---|---|---|
| | Forests | | Shrublands | | Grasslands | |
| PCA 1 | 25.4% | Leaf economics spectrum[a] | 27.1% | Leaf economics spectrum[a] | 18.5% | Leaf economics spectrum[a] |
| PCA 2 | 16.8% | Leaf size | 17.8% | Leaf size | 17.8% | Leaf size |
| PCA 3 | 10.8% | Stem diameter/plant height | 11.5% | Stem conduit diameter/leaf delta $^{15}$N | 12.4% | Leaf water content |
| PCA 4 | 9.8% | Stem conduit density | 9.1% | Stem diameter/plant height | 8.4% | Stem diameter/plant height |
| PCA 5 | 8.1% | Leaf thickness | 6.5% | Leaf thickness | 7.7% | Rooting depth |
| PCA 6 | 6.1% | Rooting depth | 6.1% | Specific root length | 6.8% | Stem specific density |
| PCA 7 | 6.1% | Specific root length | 5.8% | Rooting depth | 6.1% | Stem conduit density |
| PCA 8 | 5.9% | Stem conduit diameter | 5.6% | Stem specific density | 6% | Stem conduit diameter |
| | ∑=88.9% | | ∑=89.4% | | ∑=83.7% | |

*Note*: Numbers show the individual and summed variation captured by the first eight varimax-rotated principal component axes within forests, shrublands and grasslands (see Tables S5–S7). Axis naming was based on the most strongly correlated traits. Vegetation traits included in principal component analyses: Leaf dry matter content, leaf nitrogen isotope signature* (leaf delta $^{15}$N), leaf area*, leaf carbon content, leaf carbon to nitrogen ratio, leaf dry mass, leaf fresh mass, leaf nitrogen content, leaf phosphorous content, leaf thickness, leaf water content, plant height*, rooting depth*, specific leaf area*, specific root length*, stem conduit density*, stem conduit diameter*, stem specific density, and stem diameter. "*" Indicates traits included in supplementary analyses on the effects of single CWMs (Figure S8a–d) and CWVs (Figure S9a–d).

Abbreviations: CWM, community-weighted mean; CWV, community-weighted variance.

[a] Refer Díaz et al. (2016).

along the leaf economics spectrum, leaf size/leaf mass and plant height/seed size (Díaz et al., 2016; Weigelt et al., 2021), whereas trait axes five to eight were mostly related to single traits (Table 1; Tables S5–S7).

## 2.3 | Bioclimatic variables

For each plot, we extracted the 19 bioclimatic variables from the CHELSA Climatologies, version 1.2 (Karger et al., 2017, 2018), and the following CHELSA-BIOCLIM+ variables (at a resolution of 30 arc sec [~1 km], Brun, Zimmermann, et al., 2022; Karger et al., 2017): climate moisture index, growing season length, growing season precipitation, growing season temperature, potential net primary productivity, potential evapotranspiration, surface downwelling shortwave radiation, near-surface wind speed and soil water balance (Brun, Zimmermann, et al., 2022). To match the spatial resolution between vegetation and satellite data, we calculated an average value for each of the 19 bioclimatic and the six BIOCLIM+ variables in each trait × habitat combination within the 500 m grid cells of the albedo raster data (which is described below). To reduce the number of bioclimatic variables for the following analyses, we conducted a PC analysis with all bioclimatic and BIOCLIM+ variables and, after visual inspection of the resulting PCs (Figure S3), we decided to keep the following six BIOCLIM+ variables for all further analyses: climate moisture index, growing season length, temperature, precipitation, surface downwelling shortwave radiation and near-surface wind speed. These six BIOCLIM+ variables were reasonably weakly correlated with each other (pairwise Pearson's $r < .6$). Yet, they captured 94.2% of all the variability of the 19 bioclimatic variables, as estimated with a constrained PC analysis. The spatial distributions of the grid-cell averaged values of the six selected BIOCLIM+ variables are shown in Figure S4.

## 2.4 | Climate regulation variables

For each vegetation plot, we calculated (1) the annual proportion of reflected irradiation, (2) the annual evapotranspiration, and (3) the net primary productivity from satellite data.

1. To quantify the proportion of reflected irradiation, we used monthly mean albedo and monthly mean solar surface radiation estimates from 2001 to 2017. Monthly mean albedo was determined as the black-sky albedo for the shortwave broadband from the Moderate Resolution Imaging Spectroradiometer (MODIS) product MCD43A3 version 6 (Schaaf & Wang, 2015), which provides daily albedo estimates (based on 16 days of observation) at a resolution of 500 m and was pre-processed by the Google Earth Engine Catalogue (Gorelick et al., 2017). Monthly mean solar irradiation was quantified using monthly mean surface incoming shortwave radiation from the Satellite Application Facility on Climate Monitoring of the European Organization for the Exploitation of Meteorological Satellites (EUMESAT CM SAF) product SARAH-2.1, which is available at a resolution of 0.05° × 0.05° (~5 km) and was processed to a 500 m resolution (Pfeifroth et al., 2019). Monthly average albedo values were multiplied with the monthly average solar irradiation to determine the absolute amount of monthly reflected irradiation. These monthly reflected irradiation values

were summed across the year to obtain the annual reflected irradiation and divided by the summed monthly mean solar irradiation to obtain the annual proportion of reflected irradiation.

2. Mean annual evapotranspiration from 2001 to 2017 was extracted from the MODIS product MOD16A3GF version 6.1 (Running et al., 2021), which provides the annual total of evapotranspiration (in kg/$m^2$) at a resolution of 500 m. The obtained values of evapotranspiration were log-transformed prior to the following statistical analyses.
3. Mean annual net primary productivity (in kg C $m^{-2}$) from 2001 to 2017 was extracted from the MODIS product MOD17A3HGF version 6 (Running & Zhao, 2019), which provides gap-filled yearly estimates at a resolution of 500 m.

To match the spatial resolution between vegetation and satellite data, we calculated an average value for each of the three climate regulation variables in each trait × habitat combination within the 500 m grid cells of the albedo raster data. The spatial distribution and relationships between the grid cell-averaged values of the three CRPs are shown in Figures S5 and S6.

## 2.5 | Statistical analyses

Variations in mean CRP values among the 10 more narrowly defined habitat types were analyzed with separate analyses of variances, followed by post-hoc pairwise Tukey Honest Significant Difference tests for multiple comparisons at $p < .05$ (two-sided).

All following analyses were separately conducted for each combination of the 10 habitats and the three CRPs. We accounted for the effects of climate on the distribution of CRPs by applying linear regression models with the CRPs as the dependent and the six BIOCLIM+ variables as independent predictor variables and we extracted the model residuals (i.e., the climate-adjusted variation in CRPs) for further analyses.

We analyzed the relationships between the climate-adjusted CRPs and the eight main trait axes as predictor variables with random forest models because they can capture complex non-linear and interaction patterns. For each combination of habitat type and CRP, we constructed a separate random forest model from 2,000 individual trees with two randomly sampled candidate variables at each split, which should minimize the out-of-bag error rates, according to prior tests with different numbers of candidate variables. From each random forest model, we quantified the relative importance and the significance of each predictor variable. Relative importance was determined as the mean increase in mean squared error when the focal variable was randomly permuted. Predictor significance was determined by comparing the value of the variable importance metric against a null distribution obtained from 99 random permutations of the response variable (based on random data subsets of up to 2,000 grid-cell observations to speed up computations). Significant trait-CRP relationships were illustrated by calculating the marginal effects from the respective random forest model. To increase the interpretability of the resulting partial dependence splines, we applied a locally estimated scatterplot smoothing (loess smoothing) with an alpha parameter of 0.2.

To check if the observed variability and multimodality of the obtained trait-CRP relationships could be an artifact from the applied random forest approach, we repeated all analyses with ordinary linear regression instead of random forest models. From each linear-effects model, we determined the set of significant predictors by selecting the best model from the pool of all potential predictor combinations (based on the lowest Akaike information criterion) and we inferred the relative importance of the resulting significant predictors from the absolute of the *t*-statistic of the corresponding coefficient estimates. Individual relationships between significant predictors and individual CRPs were calculated as marginal regression slopes.

To check if our aggregation of 19 CWMs into eight main trait axes could have blurred any individual effects of single traits means or variances, we repeated the outlined linear-effects analyses with the grid cell-averaged CWMs and CWVs of the following eight traits: plant height, leaf area, specific leaf area, leaf nitrogen isotope signature, rooting depth, specific root length, stem conduit density and stem conduit diameter.

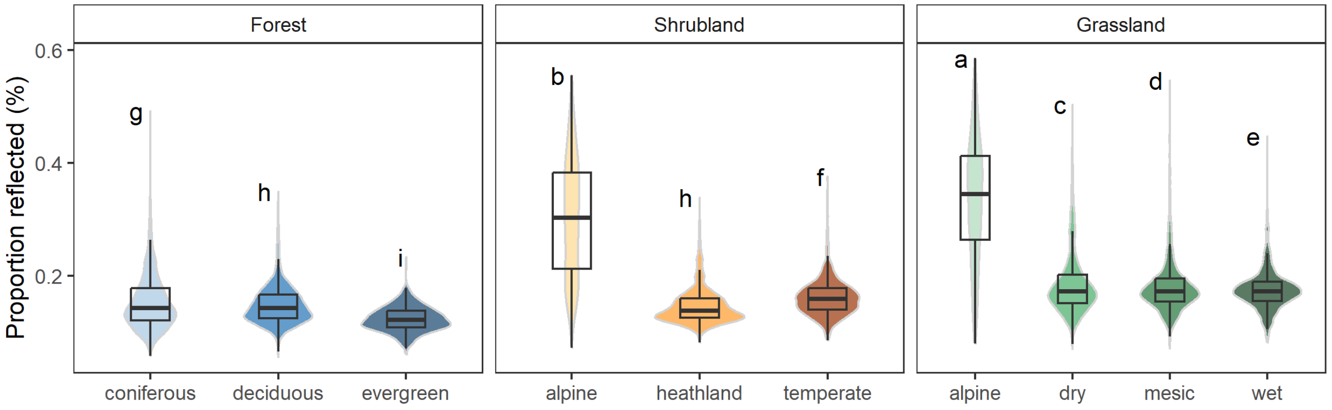
## 2.6 | Software

We extracted plot-level information from satellite-derived CRP and bioclimatic data with the Google Earth Engine platform (Gorelick et al., 2017) and the NASA Application for Extracting and Exploring Analysis Ready Samples (appeears.earthdatacloud.nasa.gov, accessed on November 1st, 2021). An example of the generated earthengine code is stored at github.com/StephanKambach/trait-climate_regulation_relationships. All statistical analyses were conducted in *R* (R Core Team, 2022) using the packages *edarf* for partial dependence plots (Zachary & Linder, 2017), *FactoMineR* for PC analysis (Lê et al., 2008), *ggeffects* for marginal regression slopes (Lüdecke, 2018), *ggplot2* for data visualization and smoothing via generalized additive models (Wickham, 2016), *MuMIn* for AIC-based model selection (Bartoń, 2022), *randomForest* for random forest models (Liaw & Wiener, 2002), and *rfPermute* to determine the significance of random forest predictor variables (Archer, 2023).

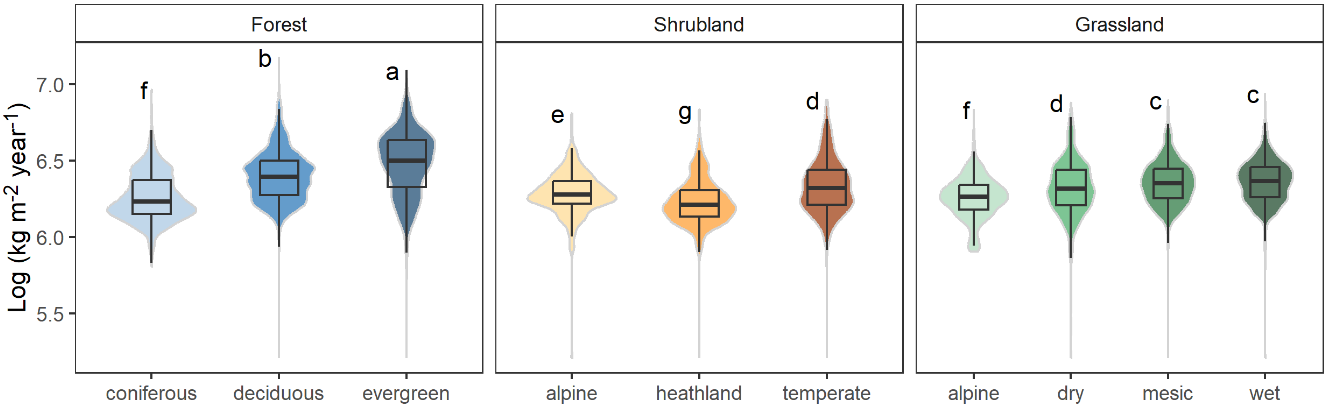
## 3 | RESULTS

Mean values of the grid-cell averaged CRPs differed significantly between the investigated habitat types (see Figure 2, $p < .001$ with $F_{9,\ 36,610} = 2{,}212$, 3,98.7 and 1,277 for the proportion of reflected irradiation, log evapotranspiration, and net primary productivity, respectively). In comparison to all other habitats, we observed that broadleaved evergreen forests had the highest productivity and evapotranspiration and the lowest proportion of reflected irradiation. Alpine shrubland and grassland habitats, on the contrary, had

**(a)** Reflected Irradiation



**(b)** Evapotransiration



Net primary productivity

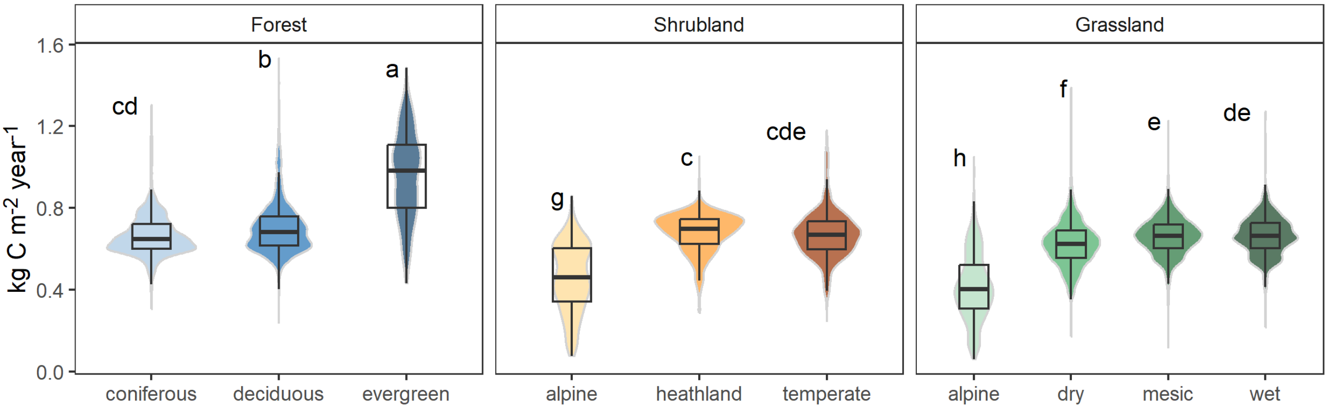


FIGURE 2 Distributions and box-whisker-plots of observed climate regulation processes in forest, shrubland, and grassland habitats. Different letters indicate significant differences between habitats according to Tukey honest significant difference tests for multiple comparisons at $p < .05$.

the highest proportion of reflected irradiation and the lowest net primary productivity.

Across all habitats, climate explained, on average, 37.9% of the observed variation in the proportion of reflected irradiation, 28.0% of the variation in evapotranspiration and 43.8% of variation in net primary productivity (Figure 3). Here, the highest proportion of CRP variability could be explained in alpine grasslands (66% and 66.6% in the proportion of reflected irradiation and net primary productivity, respectively).

After accounting for the effects of climate, the eight main trait axes explained the highest proportion of remaining climate-adjusted variation in log evapotranspiration (6.2%), followed by the proportion of reflected irradiation (6.1%), and net primary productivity (4.9%). Yet, the specific proportion of explained variation in CRPs

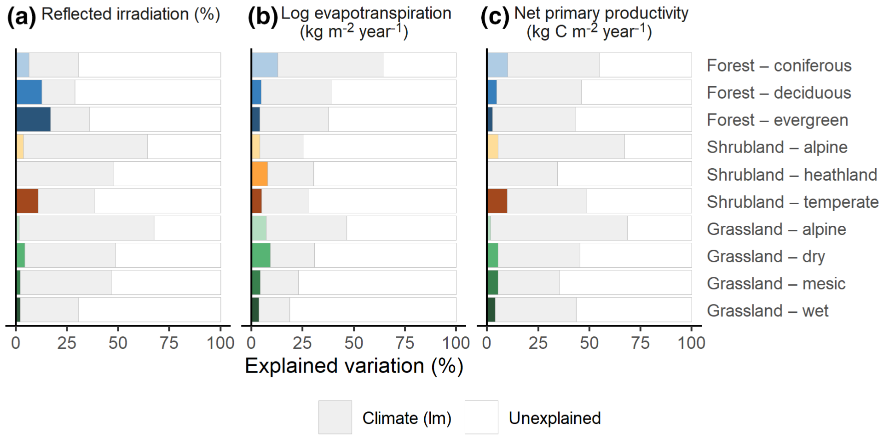


FIGURE 3 Proportion of variation in climate regulation processes (CRPs) explained by climate (with linear models) and the eight main trait axes (with random forest models). The variation explained by climate (in grey) refers to the total explained variation between CRPs and six bioclimatic variables. The variation explained by the trait composition (in color) refers to the explained variation between the climate-adjusted CRPs (i.e., the residuals from the climate models) and the eight varimax-rotated principal components from the community-weighted mean values of 19 plant traits.

depended on the CRP and habitat type investigated and ranged from 0% for the proportion of reflected irradiation and net primary productivity in heathland shrublands to 17% for the proportion of reflected irradiation in evergreen forests (Figure 3).

The relative predictive importance of the first four main trait axes for the three climate-adjusted CRPs was highly habitat-specific, even among habitat types that belonged to the same broad habitat class (Figure 4). The lowest number of significant CRP predictors was found in heathland shrublands and for log evapotranspiration in deciduous and evergreen forests. Individual relationships between climate-adjusted CRPs and the gradients in the leaf economics spectrum, leaf mass and plant height were also habitat- and CRP-specific, indicating mostly monotone (linear and nonlinear), sometimes unimodal, and rarely multimodal relationships (Figure 5).

This observed habitat-specificity of the importance and direction of trait-CRP relationships also emerged when analyzed with linear-effects models (Figure S7a–c). In comparison with random forest models, the linear-effects analyses yielded fewer significant predictors with altered relative importance ranks. Across habitats, we found consistent negative relationships between the plant height axis and the proportion of reflected irradiation, positive relationships between the leaf size axis and log evapotranspiration and positive relationships between the leaf economics spectrum and net primary productivity (Figure S7a–c).

Regarding the effects of the CWMs and CWVs of single traits, we found that the pattern in the explained variation in climate-adjusted CRPs was similar between CWMs and CWVs, albeit CWVs had a generally lower predictive power than CWMs (cf., Figures S8a and S9a). Analogue to the importance of the main trait axes, the relative predictive importance of single CWMs and CWVs depended on the CRP and habitat investigated (cf., Figures S8b and S9b). Only for the proportion of reflected irradiation, the CWV of plant height emerged as the first- or second-best predictor in eight out of the 10 habitats. In search for consistency patterns in trait-CRP relationships (cf., Figures S8c,d and S9c,d), we observed that the proportion of reflected irradiation was negatively correlated with the CWM and CWV of plant height (except for broadleaved evergreen forests). Log evapotranspiration was positively correlated with the CWM and CWV of plant height, leaf area, specific leaf area, and stem conduit diameter (except for broadleaved evergreen forests and alpine shrublands) and negatively correlated with the CWM and CWV of rooting depth. Net primary productivity was positively correlated with the CWM and CWV of plant height and specific leaf area (except for forest habitats).

## 4 | DISCUSSION

In this study, we showed that, after accounting for the effects of local climatic conditions, the functional composition of plant communities within certain habitat types is significantly related to the local provisioning of CRPs. Our results demonstrated that CWMs and CWVs of individual traits are linked to differences in the observed proportion of reflected irradiation, evapotranspiration, and net primary productivity. These relationships are stronger for the means than for the variances of individual traits, suggesting that climate regulation functions are rather determined by the functional composition than by the functional diversity of plant communities. Yet, as often observed in ecology, the strength and direction of the resulting trait-CRP relationship depended on the CRP and the habitat type investigated (e.g., Alibakhshi et al., 2020; Kambach et al., 2023; Oehri et al., 2022).

Overall, the climate-adjusted predictive power of vegetation traits was relatively low and the distribution of all three CRPs was more strongly related to differences in locally prevailing climatic conditions (like in Serna-Chavez et al., 2017). In particular, habitats covered by snow for longer periods (i.e., alpine habitats) showed the highest proportion of reflected solar irradiation and the

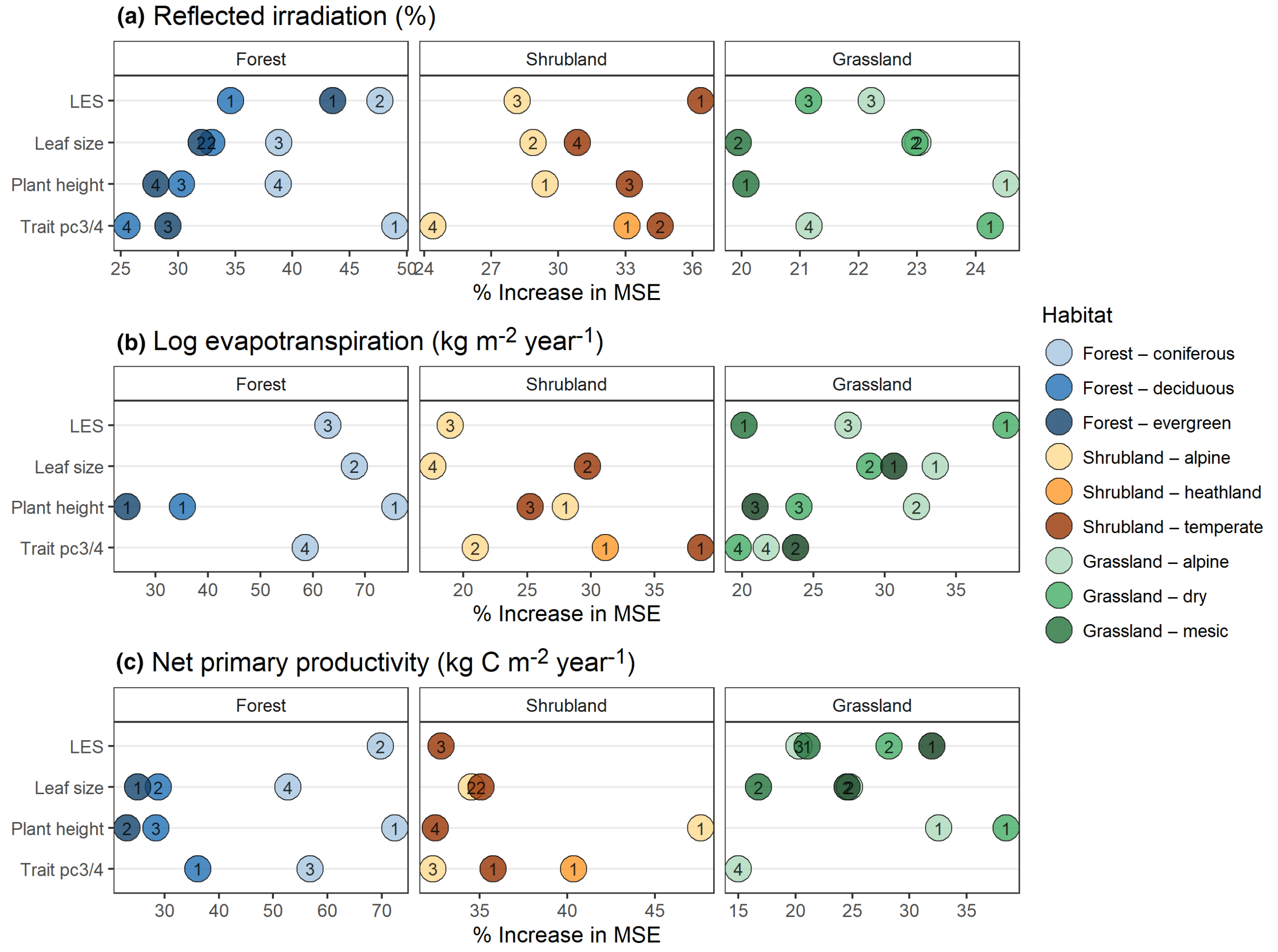


**FIGURE 4** Relative importance of the first four main trait axes for predicting the three climate-adjusted climate regulation processes with random forest models. The numbers in the circles indicate the relative importance rank of significant trait axes (cf., Table 1) within each combination of climate regulation process and habitat (non-significant trait axes are omitted). % Increase in MSE – mean increase in mean squared error when the focal trait axis randomly permuted. Trait pc3/4 refers to trait axes that represent stem conduit density in forests, stem conduit diameter/leaf delta $^{15}$N in shrublands and leaf water content in grasslands.

lowest productivity. Since climatic gradients across the European continent are a significant driver of the distribution of plant traits (Kambach et al., 2023), the remaining predictive power of community mean traits for the climate-adjusted CRPs might be expected to be rather low. Yet, for temperate forests, our approach of using non-linear relationships with the main trait axes yielded a comparable or higher predictive power than previous linear analyses among North American forests (12.6% vs. 12% for albedo, 4.7% vs. 1% for evapotranspiration, and 4.6% vs. 0% for net primary productivity, cf. Serna-Chavez et al., 2017). The relatively high predictability of reflected irradiation in broadleaved evergreen forests might be a result of the less pronounced seasonality and the absence of snow. Tighter trait-CRP relationships for forests and shrublands (as compared to grasslands) might be explained by the co-occurrence of woody and non-woody plant species, resulting in a wider range of plant traits and higher structural complexity, which has been found to be a significant predictor for the reflection of solar irradiation (Alibakhshi et al., 2020; Ridgwell et al., 2009). We hypothesize that higher predictive power for CRPs could be achieved if future studies of trait-CRP relationships include additional mechanistic traits. For instance, the proportion of reflected irradiation is also shaped by leaf angle, glaucousness, and cuticular waxes, mesophyll compartmentation and canopy nitrogen content (Grant et al., 2003; Harding & Pomeroy, 1996; Hollinger et al., 2010; Holmes & Keiller, 2002; Thomas & Rowntree, 1992). Evapotranspiration is influenced by the water-use strategy and its associated traits, such as diffusion resistance, stomata density and type of photosynthesis (Gates & Hanks, 1967; Kannenberg et al., 2022; Matheny et al., 2017). Net primary productivity is additionally affected by the leaf $CO_2$ uptake, chlorophyll content, and the structural density of the plant community as quantified by the leaf area index (He et al., 2023; Hinojo-Hinojo & Goulden, 2020). Yet, most of the required trait data are not (yet) available for a sufficient large number of plots or plant species.

The observed high degree of habitat-specificity in trait effects on ecosystem functioning has also been reported for the productivity of grassland types (Brun, Violle, et al., 2022) and is supported by

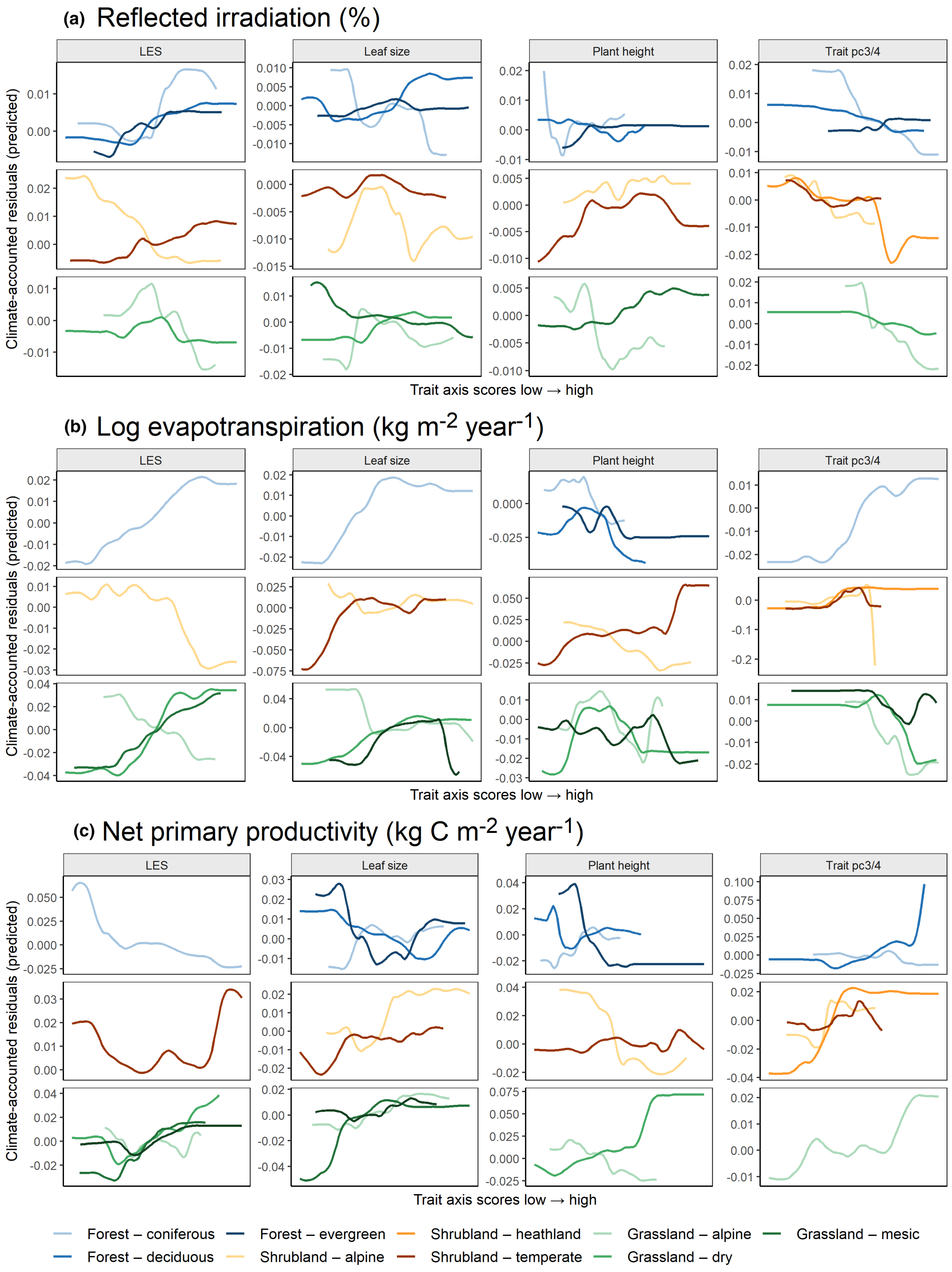


FIGURE 5 Partial dependence plots from random forest models showing the marginal effects of the first four main trait axes on climate-adjusted climate regulation processes. Partial dependence splines were smoothed with generalized additive models to increase interpretability. Trait pc3/4 refers to trait axes that represent stem conduit density in forests, stem conduit diameter/ leaf delta $^{15}$N in shrublands and leaf water content in grasslands (cf., Table 1).

different effects of specific leaf area on light reflectance in tropical versus northern hardwood forests (Doughty et al., 2018; Limberger et al., 2021; Sullivan et al., 2013). Further inconsistencies in the observed strength, direction and non-linearity of trait-CRP relationships might be partly explained by the application of complex random forest models as well as the classification into 10 habitat types of which each one included multiple Level-3 EUNIS habitats (Table S1) that might differ in biophysical properties and trait-climate relationships (Kambach et al., 2023). Accordingly, linear-effect models tended to yield more consistent trait-climate relationships (at least for some traits), such as plant height and leaf area being mostly positively associated with a lower proportion of reflected irradiation and higher evapotranspiration and net primary productivity rates. In temperate and boreal forest, these results are supported by findings of short-statured or broadleaved stands showing a higher proportion of reflected irradiation than comparable stands (Halim et al., 2019; Serna-Chavez et al., 2017).

Since our analyses were based on plot-level plant surveys, we could not account for unreported variables such as soil conditions, topography, ecosystem management, or the effects of the surrounding landscape (Serna-Chavez et al., 2017, 2018). Our analyses did not account for the spatial scale of trait-CRP analyses (Fisher et al., 2018), although previous investigations concluded that trait-CRP relationships might be more pronounced at grid-cell resolution >500 m (Serna-Chavez et al., 2018). Our dataset further only permitted the assignment of plant trait values at the scale of species and not at the site-level, which neglected any specific characteristics of local populations and might have reduced the predictive power of the analyzed trait-CRP relationships. CWM and variance values were only based on species abundances and, thus, did not account for potentially significant effects of individual keystone species (shown for productivity by Brun, Violle, et al., 2022) or the effects of canopy versus understory species in forest and shrubland habitats (as shown by Serna-Chavez et al., 2017). Also, we could not include the effects of leaf area index, as this important measure of vegetation structural density was already used to calculate evapotranspiration and net primary productivity in the MODIS data (Running et al., 2021; Running & Zhao, 2019).

In this study, we demonstrated that changes in the functional composition of local plant communities (especially in forest habitats) can significantly affect the local reflectivity and evapotranspiration, with likely effects on local temperature regimes (Alkama & Cescatti, 2016). Considering the limitations of our approach to link plot-level vegetation data with satellite-based climate regulation data, the actual effects of vegetation traits on the provisioning of CRPs might be expected to be stronger than shown here. Still, the extent to which our correlative results can be translated into nature-based solutions to mitigate the effects of climate warming on the local scale (Alkama et al., 2022) is far from understood. In search for management options to mitigate the climate and biodiversity crisis (Gardner et al., 2020), we still need a better understanding of how the structure, functional composition, and potentially the diversity of different habitats is related to the provisioning, stability, seasonality, or trade-offs among different CRPs. Based on the findings of this study, we emphasize (i) a need for further fine-scaled studies that help us to better predict the local effects vegetation shifts and (ii) the necessity of any upscaling approaches and climate models to consider the proportions of different habitats, as the climate regulation effects of plant communities tend to be site- and habitat-specific.

## AUTHOR CONTRIBUTIONS

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## CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

## CODE AVAILABILITY STATEMENT

The code for the following analysis steps is available at github.com/StephanKambach/trait-climate_regulation_relationships (https://doi.org/10.5281/zenodo.10517769): (i) summarizing the variation in CWM trait values by means of PC analysis, (ii) conducting linear models to account for the effects of climatic gradients on CRP, (iii) conducting random forest models to analyze the relationships between CWM trait values and climate-adjusted CRPs, and (iv) creating figures showing the proportion of explained variation in CRPs, the relative importance of main trait axes and the corresponding partial dependence plots.

## DATA AVAILABILITY STATEMENT

The data generated in this study (plot-level information on plot coordinates, CWMs, and CHELSA BIOCLIM+ variables) were deposited in the data repository of the German Centre for Integrated Biodiversity Research (iDiv) Halle-Jena-Leipzig (idata.idiv.de/ddm/Data/ShowData/3552). Raw vegetation data belong to the owners or contributors of each vegetation database and can be requested at euroveg.org/eva-database-obtaining-data. The bioclimatic and plant trait data used in this study can be downloaded from chelsa-climate.org/bioclim and www.try-db.org/TryWeb/dp.php, respectively.

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## SUPPORTING INFORMATION

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

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