Title: Six decades of losses and gains in alpha diversity of European plant communities

Running title: Interpolation of species richness dynamics

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Data accessibility statement: The data and R code to fully reproduce the analyses are available in the GitHub repository: https://github.com/gmidolo/interpolated_S_change. Output files including model fits are available on Zenodo: https://doi.org/10.5281/zenodo.15836616. An interactive map exploring interpolated spatiotemporal changes in species richness can be accessed at: https://gmidolo.shinyapps.io/interpolated_s_change_app (GitHub repository: https://github.com/gmidolo/interpolated_S_change_app). The use of the data for additional publications, and the access to complete and original vegetation data, are only possible through a request to EVA Coordinating Board (see https://euroveg.org/eva-database/).

Abstract

Biodiversity change forecasts rely on long-term time series, but such data are often scarce in space and time. Here, we interpolated spatiotemporal changes in species richness using a novel machine learning method without requiring temporal replication at sites. Using 698,692 one-time survey vegetation plots, we estimated trends in vascular plant alpha diversity across Europe from 1960 to 2020 and validated our approach against 22,852 independent time series. We found an overall near-zero net change in species richness. However, species richness generally declined from 1960 to 1980 across habitats, followed by an increase from 2000 to 2020. Declines were most pronounced in forests, but trends varied significantly across habitats and regions, with overall increases at higher latitudes and elevations, and declines or stable trends elsewhere. Our findings demonstrate how data without temporal replication can be used to reveal context-dependent biodiversity dynamics, underscoring the importance of such forecasts for conservation and management.

1. Introduction

Humans are driving major biodiversity changes worldwide (Díaz *et al.* 2019; IPBES 2019), but the magnitude of these changes remains poorly understood across most taxa, regions, and scales (Gonzalez *et al.* 2016; Johnson *et al.* 2024). At the finest grain, that of the local biological community, losses and gains often offset each other (Bernhardt-Römermann *et al.* 2015; Blowes *et al.* 2019; Dornelas *et al.* 2014; Jandt *et al.* 2022; Klinkovská *et al.* 2025; Pilotto *et al.* 2020; Vellend *et al.* 2013). In Europe, trends in plant diversity at the community level have been differentially impacted by various causes, such as agricultural intensification, biological invasions, climate change, conservation measures, and eutrophication (Finderup Nielsen *et al.* 2021; Gray *et al.* 2016; Steinbauer *et al.* 2018; Stevens *et al.* 2010; Vellend *et al.* 2017; Vilà *et*

al. 2011). The relative strength of these drivers potentially varies over different historical periods (Klinkovská *et al.* 2024; Wesche *et al.* 2012), and their impacts may lag in time and only unfold after many decades (Dullinger *et al.* 2013). Consequently, the magnitude and direction of plant diversity change can differ across biogeographical regions and habitat types (Blowes *et al.* 2019; Pilotto *et al.* 2020). This wide variety of trends calls for time-series analyses capable of identifying fine-grain temporal changes in plant biodiversity across large spatiotemporal extents.

To quantify plant diversity trends, considerable efforts are underway to resurvey vegetation plots across Europe (Jandt *et al.* 2022; Klinkovská *et al.* 2025), which recently culminated into ReSurveyEurope (Knollová *et al.* 2024), a database collating thousands of vegetation plot observations from numerous resurvey and monitoring projects. Despite the impressive collective effort and the extensive data now available, this database has significant geographical gaps, is biased toward well-preserved habitats and sites, becomes increasingly sparse further back in time, and varies in the length of observation intervals between surveys – with a large fraction of vegetation plots resurveyed only once. Furthermore, trends in plant alpha diversity derived from resurvey studies are potentially sensitive to plot relocation and observer error (Boch *et al.* 2022; Klinkovská *et al.* 2025; Verheyen *et al.* 2018). As a result, we still have limited knowledge of how plant diversity at the community level (i.e., alpha diversity) has changed across various European biogeographical regions and habitats.

To address data gaps in space and time, we employ a novel machine learning approach (Keil & Chase 2022) to interpolate temporal biodiversity change using only *static* data, namely data without temporal replication at any given site. Our approach relies on the well-established fact that biodiversity is spatially (Legendre 1993; Tobler 1970) and temporally (Dornelas *et al.* 2013) *autocorrelated*, which is caused by the continuity of species distributions across space and time

due to dispersal limitation and environmental structure (Dornelas *et al.* 2013). Because of this autocorrelation, we propose that biodiversity can be interpolated jointly in space and time [i.e., in the *space-time cube* (Mahecha *et al.* 2020)] (**Figure 1**). Specifically, we employed Random Forests (Breiman 2001; Wright & Ziegler 2017) to interpolate community-level plant diversity in a multidimensional domain defined by geographical coordinates and time, while also accounting for the effect of varying plot area on species richness estimates (Dengler *et al.* 2020; Storch 2016). Our approach provides predictions of plant diversity within the temporal dimension, ultimately representing *interpolated time series* of biodiversity change.

To this end, we utilized 698,692 static vegetation plots the European Vegetation Archive (EVA) (Chytrý *et al.* 2016) and ReSurveyEurope (Knollová *et al.* 2024), sampled between 1945 and 2023 with plot sizes ranging from 1 m² to 1000 m². Given its extensive temporal and geographic coverage, this dataset is well-suited for interpolating biodiversity change. We modelled plot-level alpha diversity (species richness) of vascular plants as a function of plot size, spatial coordinates (latitude, longitude, and elevation), sampling year, and habitat type (forest, grassland, scrub, or wetland). To validate our interpolation approach, we tested its ability to predict temporal species richness changes using 22,852 independent resurvey time series from ReSurveyEurope within the same period. Specifically, we trained the model on a single randomly selected observation from each time series and evaluated its predictions against observed species richness changes in ReSurveyEurope. Our model successfully predicted the direction of species richness changes and explained 41% of the variability in those changes (see 'Materials and Methods: Model Validation'). Having established the predictive power of our approach, we then applied it to temporally interpolate species richness dynamics across all vegetation plots sampled from 1960 to 2020, covering the last six decades across Europe.

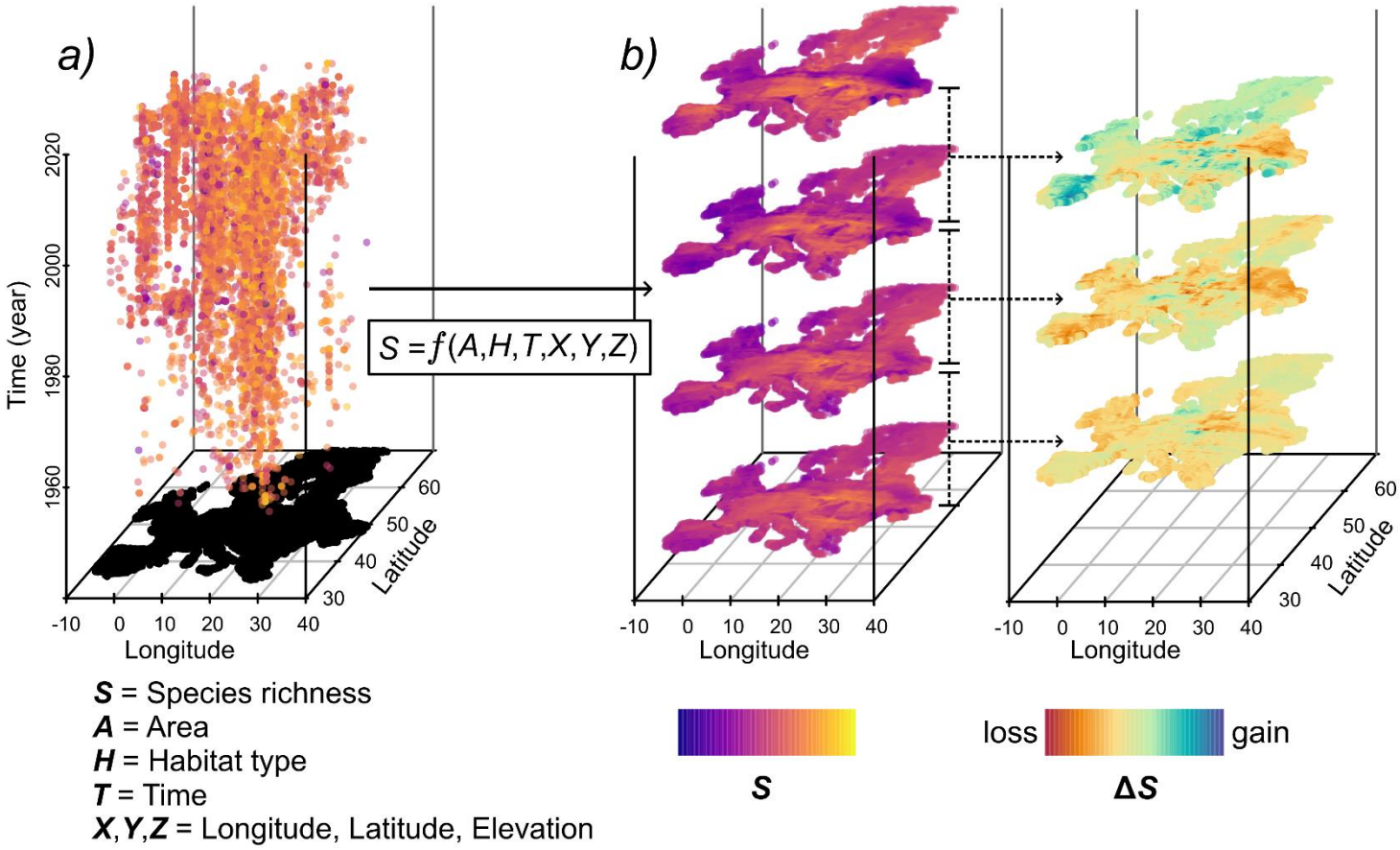

Figure 1: Workflow for spatiotemporal interpolation of plant species richness (*S*) and change in species richness (*ΔS*) in European vegetation plots. Species richness (*S*) from 698,692 static vegetation plots (independent plot observations from different sites that are not paired in time) sampled between 1945 to 2023 from the European Vegetation Archive (EVA) (Chytrý *et al.* 2016) and ReSurveyEurope (Knollová *et al.* 2024) is interpolated using machine learning as a function of area, time, space, habitat type and their interactions aiming to maximize prediction accuracy within the temporal dimension of the space-time cube (panel *a*). Interpolated values are then used to estimate temporal changes in species richness (panel *b*). Colour coding of the dots in panel a*)* represents species richness recorded in 10,000 randomly selected plots from the EVA database for visualization.

2. Materials and Methods

2.1 Vegetation plot data

Our initial data set contained 1,679,403 vegetation plot observations available in the European Vegetation archive (EVA) (Chytrý *et al.* 2016) and ReSurveyEurope (Knollová *et al.* 2024)

(project n. 222; version 2024-02-06: https://doi.org/10.58060/jeht-nr04). We restricted the analysis to plots with complete information on geographical location, habitat type, plot size, and sampling year, applying specific filters based on each of these variables. We included only plots with coordinate uncertainty below 1 km and focused exclusively on habitats classified as forest, grassland, scrub, wetland following the EUNIS habitat classification system (Chytrý *et al.* 2020). Additionally, we only included plots within defined size ranges (1-100 m² for non-forest habitats, 100-1000 m² for forests) and sampled between 1945 and 2023. Further details on data cleaning and preparation are listed in Appendix S1. The application of these filters yielded a subset of 675,840 vegetation plot observations in EVA and 73,886 observations across 22,852 resurvey plots in ReSurveyEurope (Fig. S1), which we used for all subsequent analyses. Both datasets were used for model training and interpolation. The ReSurveyEurope dataset was also used to test whether our approach could predict species richness dynamics observed in time series data (see 'Model Validation').

2.2 Model training

We used Random Forests (Breiman 2001) and Extreme Gradient Boosting (Chen & Guestrin 2016) to model plot-level vascular plant species richness dependence on space (= elevation, latitude, and longitude) and time (= sampling year) while accounting for the effect of plot size and habitat type. We applied these algorithms because they are better suited to modelling complex interactions between predictors and their non-linear effects compared to generalized linear models and related parametric methods, which is a desirable property when the aim is to maximize accuracy of cross-scale predictions of biodiversity metrics (species richness or occupancy) and model grain-dependent interactions between time and spatial scales (Keil & Chase 2022, 2019; Leroy *et al.* 2024).

Our approach is based on *static* biodiversity data (in our case, vegetation plots surveyed only once) for spatiotemporal interpolation (Keil & Chase 2022). We trained the final model used in the interpolation analyses presented in the results of this work on a total of 698,692 vegetation plots, comprising 675,840 plots from EVA and 22,852 plots from ReSurveyEurope. Because plots from ReSurveyEurope have multiple observations, ranging from 2 to 46 (mean = 3.2; SD = 3.5), we randomly selected one observation from each plot. The remaining 51,034 plot observations from ReSurveyEurope were excluded from the final model fit but were later used for model evaluation as test data (see the 'Model Validation' section).

Modelling was fully conducted in R (version 4.4.2) (R Core Team 2024) with the *tidymodels* (Kuhn & Wickham 2020) package collection and included the main steps described below.

- *Training/Test set splitting.* We randomly split the dataset into training (80% of observations) and testing (20% of observations) datasets. We stratified the split by the response variable (= species richness) to balance its distribution in both data sets.

- *Model specification*. We fitted models using vegetation plots as observation units, with the following formula: $S \sim x + y + elevation + plot\ size + year + habitat\ type;$ where S represents vascular plant species richness; x and y are the coordinates (in meters) of easting and northing, respectively; *elevation* corresponds to elevation above the sea level (in meters); *plot size* is the area of the plot (in square meters); *year* is the year of sampling; and *habitat type* is a categorical variable describing the general habitat classification ('forest', 'grassland', 'scrub', or 'wetland'). We used the 'ranger' (Wright & Ziegler 2017) and 'xgboost' (Chen *et al.* 2024) engines available in the *parsnip* R package (Kuhn & Vaughan 2024) for Random Forests and Extreme Gradient Boosting algorithms, respectively.

- *Hyperparameter tuning*. We used a 10-fold random cross validation on the training data to perform hyperparameter tuning without repetition. We selected the best combinations of hyperparameters based on the lowest root mean square error (RMSE). For the Random Forests, we set the number of trees to 1000 and used a regular grid of 25 combinations of other hyperparameters, setting the minimum number of data points in a node for further splitting (= 'node size') to 2, 5, 10, 15, and 20, and the number of randomly sampled predictors (= 'mtry') from 2 to 6. For XGBoost, we tuned all possible hyperparameters (except for the number of trees, which was set to 1000) using default tuning parameters available in the *dials* R package (Kuhn & Frick 2024). We reduced the grid search for XGBoost by fitting 50 combinations of hyperparameters using a space filling design with latin hypercube grids with the 'grid_space_filling' function of the *dials* package. We used hyperparameter settings obtained from the tuning results of these Random Forests (node size = 5 and mtry = 3; see Fig. S4) as default hyperparameters in the final model fit and additional analyses.

- *Model evaluation.* We evaluated the models using a 10-fold cross-validation (repeated 3 times) on the training data and on a separate testing dataset. The Random Forests algorithm (RMSE = 7.0, $R^2 = 0.69$) performed better than the XGBoost algorithm (RMSE = 8.1, $R^2 = 0.58$; Table S1). Therefore, in all subsequent analyses, we exclusively applied Random Forests. Finally, we validated that the distribution of model residuals did not exhibit geographical clusters by plotting the distribution of plot-level residuals calculated from the testing data (observed minus predicted species richness), averaged at a 50 km resolution (Fig. S5).

We also estimated the proportion of prediction variability explained by interactions between each

pair of predictors as well as the proportion of joint effect variability of pairwise interactions by calculating H^2 statistics (Friedman & Popescu 2008) with the 'hstats' function from the *hstats* R package (Mayer 2024) (Fig. S6). We utilized the 'partial_dep' function from the same package to visualize partial dependence plots (Fig. S7).

2.3 Model validation

To assess the reliability of our approach in estimating species richness dynamics, we trained separate Random Forests models on three static datasets: *A*) ReSurveyEurope, *B*) EVA, and *C*) a combination of both. To make the data in ReSurveyEurope 'static' (i.e., select one single plot observation at each vegetation plot site) for datasets *A* and *C*, we randomly selected one observation from each of the 22,852 resurvey plots. We split each of the three datasets, using 80% of the data to train the models. We then evaluated their model performance separately based on the following observations from the three independent testing datasets:

1) *Species richness of the testing data*. Here, formal model evaluation was performed on the 20% of data not used for model training during the data split.

2) *Species richness of data from ReSurveyEurope*. This included all plots from ReSurveyEurope that were not used for model training, i.e. the remaining 51,034 independent plots neither used in training, nor in testing.

3) *Species richness change in ReSurveyEurope*. This was assessed using the log-response ratio (lnRR) of species richness between the initial and final plots within each resurvey time series. A positive correlation indicates that changes in species richness obtained from model predictions can capture observed changes in species richness.

We repeated the model training procedure 100 times for dataset *A)*, each with a new random

selection of training and testing data from each time series. The model evaluation metrics showed that predictions were robust to random selection of plot combinations within the time series when tested using the criteria outlined in points 1, 2, and 3 (see Table S2).

Overall, our test demonstrated the feasibility of predicting species richness dynamics using interpolations from static data: when interpolating over ReSurveyEurope data, predicted and observed changes were positively correlated ($R^2 = 0.41$; Pearson correlation = 0.64) (Fig. S8; Table S2). Predictions overall captured the observed direction of change, but they tended to slightly underestimate the observed magnitude of change, resulting in more conservative estimates (Fig. S9). However, models struggled to accurately predict species richness changes in new, spatially independent data, i.e. when EVA-only trained models were tested in ReSurveyEurope ($R^2 = 0.06$; correlation = 0.23). This was likely due to an uneven spatial distribution of ReSurveyEurope plots relative to EVA plots, an overall higher error of predicting richness over two time periods for lnRR calculation, and different temporal distribution of EVA plots located closely to ReSurveyEurope. Finally, we found no significant differences in model validation results when comparing permanent and quasi-permanent ReSurveyEurope plots (Fig. S10), thus our approach is potentially robust against biases related to plot relocation.

In sum, our approach can explain up to 41% of the variability in species richness change over relatively long temporal spans (from 1945 to 2023). The evaluation of the model trained exclusively on EVA and tested on ReSurveyEurope data suggests that the results should not be geographically extrapolated beyond plot-level predictions. For these reasons, we used the interpolated spatiotemporal model to predict solely along the temporal dimension (i.e., we did not project the models outside the spatial scope of our data) and restricted the predictions of species richness dynamics exclusively to the plots utilized in the main model, combining data

from both EVA and ReSurveyEurope (see 'Model training' section).

2.4 Interpolation of species richness change

We used our model, trained on EVA and ReSurveyEurope data (see the 'Model Training' section), to predict species richness for each year from 1960 to 2020. Predictions were made for the 660,748 plots included in the analysis and sampled during this period, while keeping other predictors fixed. To account for differences in plot size, we used the median plot size for each habitat type (forests: 300 m², grasslands: 20 m², scrub: 64 m², wetlands: 50 m²) in our species richness predictions. To explore changes in species richness across the entire study period (1960-2020), we calculated the percentage change in interpolated species richness between 1960 and 2020 for each plot, as follows: $S_{change} = \frac{100*(S_{2020}-S_{1960})}{S_{1960}}$. Similarly, we also calculated 21-year changes observed in 1980, 2000 and 2020, relative to that in the year 1960, 1980 and 2000, respectively.

We also examined temporal trends in mean species richness across all plots within each habitat type and across plots located in seven European biogeographical regions. For each year, we calculated the estimated mean species richness across all plots per habitat type or biogeographic region, respectively, and used it as the response variable in relation to year in a linear regression, effectively estimating the mean change in number of species per year. Biogeographical regions were sourced from the data of the European Environmental Agency (European Environment Agency 2016). We merged the arctic, boreal, and Scandinavian alpine regions into a single biogeographical unit, to distinguish these regions from the other alpine regions with nemoral-continental (e.g., the Alps, Carpathians, Pyrenees) and nemoral-submediterranean (e.g., Dinaric Alps, Rhodopes) vegetation (Preislerová *et al.* 2024).

To visualize the geographic distribution of species richness change across the European continent, we aggregated plot-level percentages of species richness changes into 50 km × 50 km grids by averaging the predicted values of all plots in each raster cell. We plotted multiple maps for different time periods (1960–1980, 1980–2000, 2000–2020, and 1960–2020) and habitat types. Furthermore, to account for different temporal coverage of some cells (Fig. S2-S3), we calculated and mapped species richness change for each time period, including only plots sampled within each respective period to restrict the interpolations over shorter temporal gaps (Fig. S11). Similarly, we evaluated different metrics of species richness change, namely, log-response ratios (Fig. S12), the raw number of species lost or gained (Fig. S13), and linear slope estimates (Fig. S14) over the three periods (1960–1980, 1980–2000, and 2000–2020) separately, and across the entire focal period (1960–2020). Linear slope estimates were obtained by fitting linear regressions of predicted species richness against year for each plot, estimating the average number of species gained or lost per year over the assessed period. All these metrics quantifying diversity change exhibited overall consistent patterns with one another.

3. Results and Discussion

3.1 Balanced diversity changes, but shifting dynamics: early losses, late gains

We estimated close to zero mean net change in species richness (-2%) between 1960 and 2020 when averaged across all plots and habitat types (**Figure 2a**). This finding is similar to results of previous large-scale analyses of alpha diversity change, which show low net richness change across multiple time series (Bernhardt-Römermann *et al.* 2015; Blowes *et al.* 2019; Dornelas *et al.* 2014; Jandt *et al.* 2022; Vellend *et al.* 2013). Although the overall species loss in our analysis was minor, this average trend hides a substantial proportion of plots exhibiting large changes over the past six decades: 15% of plots showed a steep decline, with losses of more than 20% of

their initial species richness, while 19% of plots showed the opposite trend, with species gains of more than 20%.

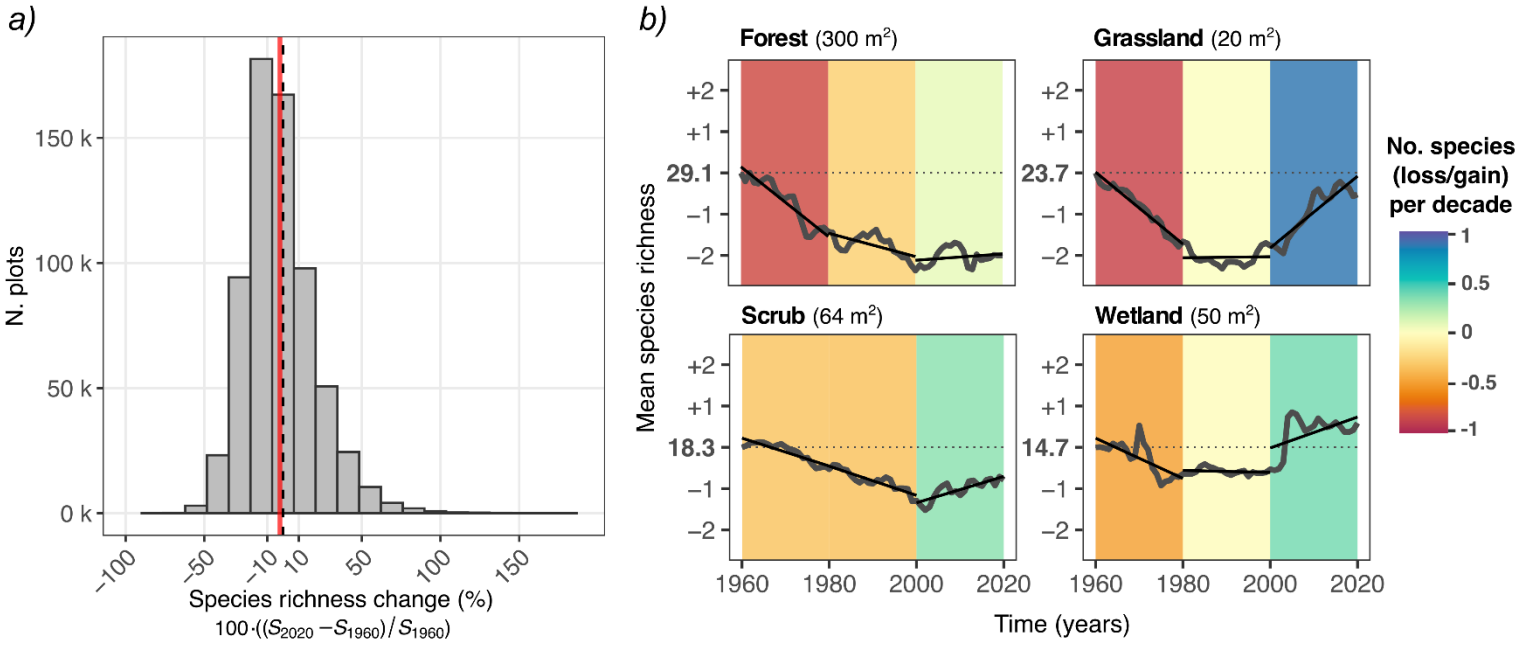

Figure 2: Summary of plant species richness changes over 61 years (1960–2020). Panel ***a)*** shows the distribution of proportional change in interpolated plant species richness for the year 2020 compared to 1960 across 660,748 European vegetation plots sampled over that period. Dashed vertical line corresponds to 0% change; red solid line to the mean (= -1.9%). Panel ***b)*** shows temporal trends in average species richness (mean values across plots per year) for each habitat (dark grey lines). Linear regressions (black lines) and their slopes (coloured backgrounds) are fitted to species richness for three time periods: 1960–1980, 1980–2000, and 2000–2020. The y-axis scale is standardized to the baseline mean species richness estimated for the year 1960. To standardize differences in plot size, species richness was predicted using a fixed plot size equal to the median plot size for each habitat (noted at the top of each panel).

We identified shifting dynamics over time characterized by a prevailing decline in species richness from 1960 to 1980 (continuing up to the 2000s in forests and scrubs), followed by gains in species richness from 2000 to 2020 across all habitat types (**Figure 2b**) and in most biogeographic regions (**Figure 3**). While our approach cannot establish a causal link between species richness changes and potential underlying drivers, the greater losses detected during earlier decades align with well-documented factors contributing to European biodiversity

340 decline. These factors include agricultural intensification and eutrophication driven by nitrogen
341 (N) and phosphorus (P) enrichment, along with acid deposition, all of which began increasing in
342 the early 20th century and peaked in the latter half of the century (Araújo *et al.* 2008; Fuchs *et al.*
343 2015; Schöpp *et al.* 2003; de Vries *et al.* 2024). Each of these drivers has likely impacted
344 different habitats to a different extent, such as acidic deposition in forests (Hédl 2004), and soil
345 drainage and nitrogen deposition favouring encroachment by generalist species in wetlands
346 (Sperle & Bruelheide 2021) and grasslands (Stevens *et al.* 2010). As recently shown for the flora
347 of the Czech Republic (Klinkovská *et al.* 2024), industrialization and land-use intensification
348 during the 1960-1980s has generally advantaged species adapted to anthropogenic disturbances
349 and high nutrient availability. Especially high rates of eutrophication in European countries
350 during this period likely contributed to species richness declines, by promoting the dominance of
351 a few species favoured by high nitrogen availability (Staude *et al.* 2020; Stevens *et al.* 2010).
352 These declines were lessened over time when species numbers gradually reduced as
353 compositions shifted to more nitrophilous vegetation (Bobbink *et al.* 2010), with possible species
354 richness recovery following reduced N input (Storkey *et al.* 2015).

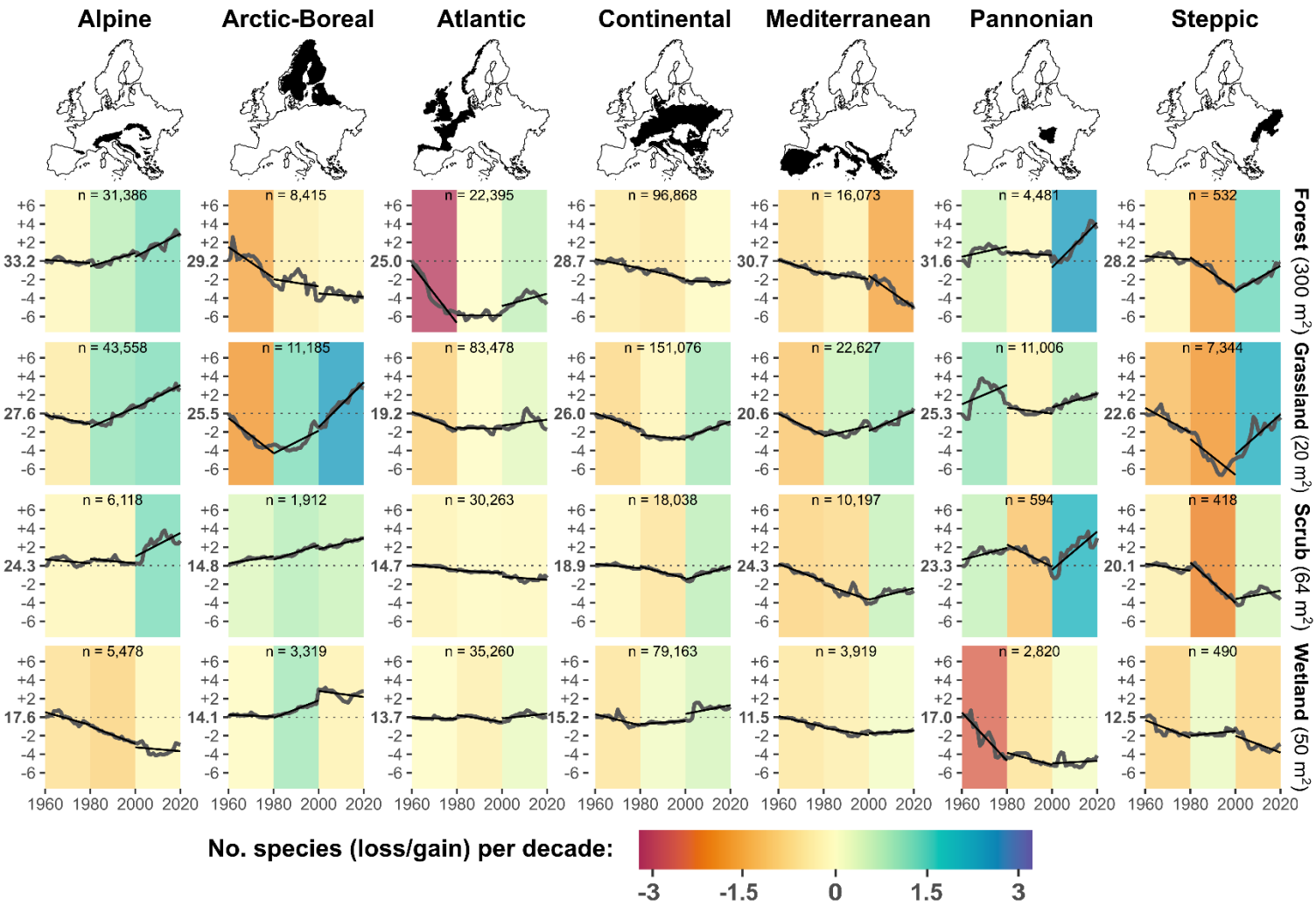

Figure 3: Trends of species richness change over 61 years (1960-2020) in seven European biogeographic regions. Each panel displays the estimated trend (dark grey curves) of the mean interpolated species richness (y-axis) across all plots within a given biogeographic region and habitat type over time (x-axis). The number of plots (n) is indicated at the top of each panel. Linear regressions (black lines) and their slopes (coloured backgrounds) are fitted to species richness for three time periods: 1960–1980, 1980–2000, and 2000–2020. The y-axis scale is standardized to the baseline mean species richness estimated for the year 1960. Species richness was predicted using a fixed plot size equal to the median plot size for each habitat (noted at the right for each habitat).

Subsequently, the increased occupancy of warm-adapted and non-native species (Klinkovská *et al.* 2024), along with overall range shifts of species tracking their thermal niches in response to climate change (Rumpf *et al.* 2018), may have contributed to local species recruitment in recent decades (2000-2020), resulting in a species richness increase. This trend was particularly

368 noticeable at higher latitudes (e.g., in open habitats of the boreal region) and in mountainous
369 areas (**Figure 3** and **Figure 4**), and corroborates previous studies focusing on these ecosystems
370 and regions (Steinbauer *et al.* 2018; Thuiller *et al.* 2005). Furthermore, species richness gains
371 observed since the 2000s could partially reflect the Europe-wide abatement of airborne
372 anthropogenic N and sulphur (S) deposition from the 1990s onwards (Sutton *et al.* 2011; de
373 Vries *et al.* 2024), as well as more recent improvements in nature conservation and restoration
374 policies supported by the European Union [e.g., the 1992 Habitats Directive (European Union
375 1992)]. Preferential sampling could partly explain the observed positive trends in species
376 richness in some regions over the last decades. However, to our knowledge, this bias applies only
377 to those regions where older vegetation surveys, focusing on phytosociological classification
378 (sometimes omitting certain species from the plots, leading to an underestimation of richness),
379 shifted toward sampling of better-preserved vegetation over more recent years (e.g., due to
380 monitoring over protected areas). Yet, older surveys often targeted floristically richer sites, while
381 recent efforts more often include degraded sites too, potentially balancing these trends.

382 3.2 Habitat- and region-specific diversity change

383 We found highly context-dependent trajectories of species richness change (**Figure 3** and **Figure**
384 **4**), consistent with studies challenging the notion of unidirectional biodiversity change (Dornelas
385 *et al.* 2023; Johnson *et al.* 2024; Pilotto *et al.* 2020) and supporting the idea that biodiversity
386 change depends on habitat type (Klinkovská *et al.* 2025), geographic location
387 (Bernhardt-Römermann *et al.* 2015; Blowes *et al.* 2019), and, most crucially, time period
388 considered. Although significant geographic heterogeneity in interpolated species richness trends
389 was observed across Europe, a few distinct geographic patterns emerged. Overall, colder regions,
390 namely the alpine and the arctic-boreal zones, showed increases in species richness, although

391 localized declines were observed in wetlands and forests within these regions; conversely, other
392 regions displayed either stable trends or overall losses.

393 When comparing 2020 to 1960, forest habitats showed the highest proportion of plots with
394 substantial declines of species richness compared to other habitats, with 25% of plots estimated
395 to have lost ≤ 20% of species, and a mean change of -6%. Large declines in forests are
396 interpretable as results of alteration of management practices (i.e., cessation of coppicing and
397 forest grazing coupled with increased canopy density), resulting in a shift towards species-poorer
398 communities representative of denser, moister, and nutrient-richer conditions (i.e., mesification)
399 (Hédl *et al.* 2010; Lelli *et al.* 2021). Our findings partially contrast with the synthesis by
400 Bernhardt-Römermann et al. (2015) on resurvey studies of forest vegetation in Europe, which
401 reported more balanced trends for this habitat type. However, their study covered fewer old sites,
402 potentially reducing their chance to detect losses that occurred in the 1960s or earlier
403 (particularly in the Atlantic region), and focused on temperate forests only. Indeed, we identified
404 constant declines of species richness in boreal and Mediterranean forests (**Figure 3**).
405 Interestingly, forests in the Alpine region displayed an opposite, positive trend. These variations
406 across biogeographic regions reflect the notion that local and regional drivers specific to forest
407 habitats – such as changes in large ungulate densities, management practices, and their
408 interactions with nitrogen deposition and global warming – create context-dependent impacts on
409 plant species richness dynamics of forest vegetation (Bernhardt-Römermann *et al.* 2015; Perring
410 *et al.* 2018; Staude *et al.* 2020).

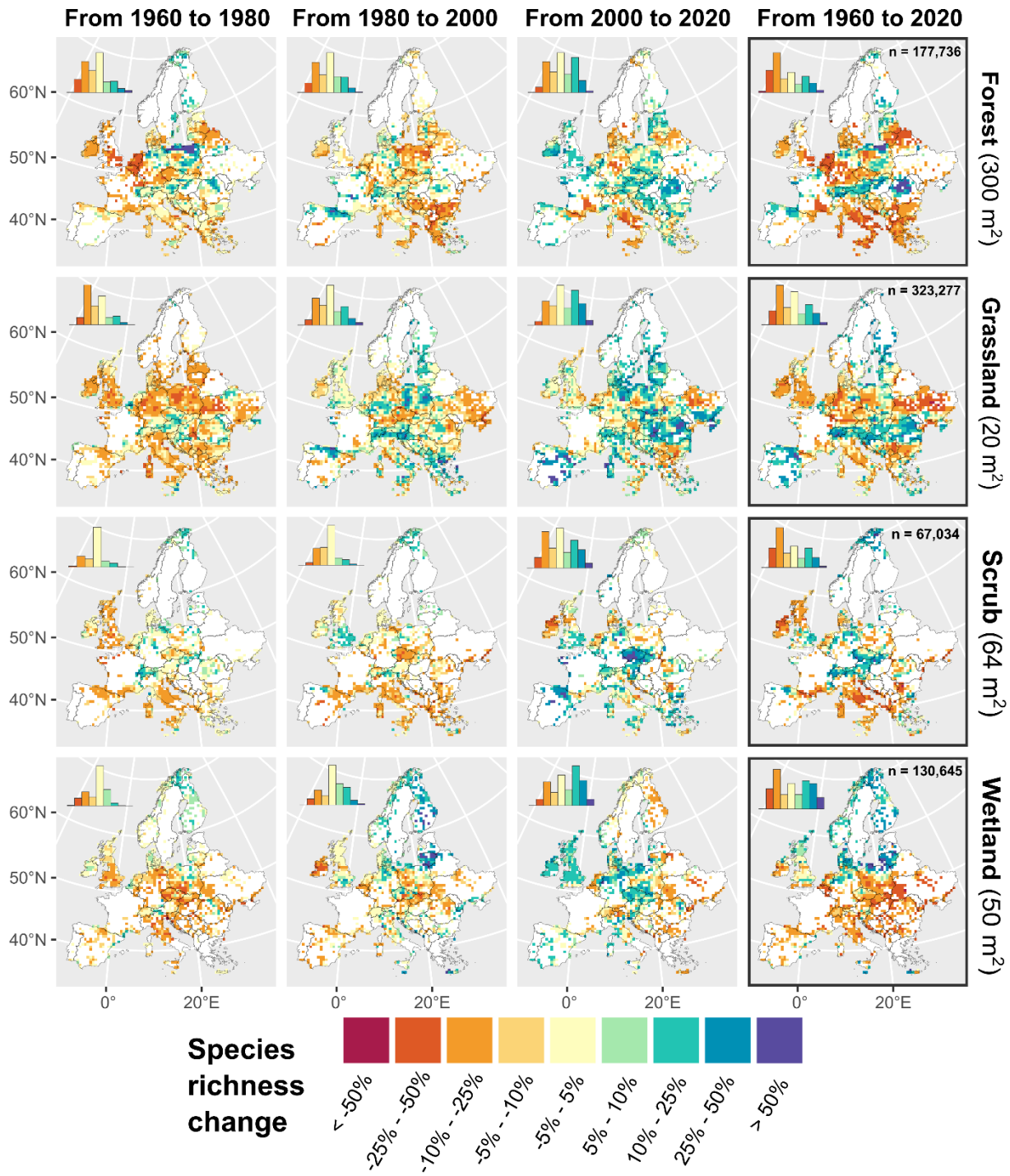

Figure 4: Geographic patterns of plant species richness change in Europe. The maps show the mean percentage change in plot-level species richness between two time points, aggregated within 50 km × 50 km grid cells. Only grid cells containing at least five plots sampled between 1960 and 2020 are shown. Histograms (upper left of each panel) illustrate the distribution of percentage change classes across all plots. The number of plots (n) for each habitat is shown in the panels on the right that estimate richness changes from 1960 to 2020. Species richness was predicted using a fixed plot size equal to the median plot size for each habitat (noted on the right for each habitat).

Grasslands displayed more balanced trends, with a net species richness change close to zero (mean: -1.5%) over the whole study period. The high heterogeneity of grassland diversity trends across Europe (**Figure 4**) could reflect, among many other drivers, highly localized management practices, ranging from strong intensification to complete abandonment, creating a patchy mosaic of biodiversity trends across European grasslands (Shipley *et al.* 2024). Conversely, wetlands had the most polarized results, with large fractions of plots showing high gains and losses (≥20%) in 25% and 18% of the plots, respectively, resulting in a slightly positive average change (mean: +4%) across the whole study period. Compared to other habitats, wetlands also displayed a more distinct geographical gradient: plots with increasing richness or no change were primarily located at higher latitudes (above 55° N). Given the substantial pressures affecting most European wetland ecosystems (Verhoeven 2014), we did not expect large gains in wetlands. This sharp latitudinal pattern may reflect changes in local hydrological regimes (e.g., soil drainage) that promote the encroachment of generalist vascular plant species resulting in higher species richness, at the expense of typical moss species (not included in our analysis) found in northern European mires (Kolari *et al.* 2021; Pedrotti *et al.* 2014). The higher magnitude of change in wetlands also likely reflects their generally lower baseline vascular species richness (see Fig. S7), where the addition of a few species can strongly affect gains in species richness. Nonetheless, most wetlands at lower latitudes, especially in Central Europe (**Figure 4**), experienced large losses in species richness. This find accords with previous studies of wetlands in central and southern European lowlands, which have documented climate change toward warmer conditions, combined with drastic increases in human water extraction from natural systems, as key drivers of wetland specialist losses (Navrátilová *et al.* 2022; Sperle & Bruelheide 2021).

4. Advances, limitations, and implications for addressing biodiversity change

With this study, we provide the first continental-scale analysis of local biodiversity change over continuous time and space, unlocking an unprecedented amount of vegetation-plot data collected over more than six decades. Compared to previous large-scale analyses of time series data (Bernhardt-Römermann *et al.* 2015; Blowes *et al.* 2019; Dornelas *et al.* 2014; Jandt *et al.* 2022; Klinkovská *et al.* 2025; Pilotto *et al.* 2020; Vellend *et al.* 2013), our approach enabled us to i) unravel these trends across a broad geographic extent and different habitat types and ii) compare them to common baselines from the same time period. This was previously difficult to achieve at the continental scale due to data limitations and because past methods rarely leveraged static data to inform analyses of biodiversity dynamics (Jandt *et al.* 2011). Our new method addresses the latter and can potentially be applied to other taxonomic groups and spatial grains (Keil & Chase 2022; Leroy *et al.* 2024) to robustly estimate biodiversity change even in the absence of dedicated time series data. Additionally, our method can be applied to individual species occurrences, offering potential for studies mapping single-species dynamics and composition changes, although this may involve considerable computational costs. Our work is intended to complement, rather than replace, the efforts of field ecologists to resurvey vegetation and collect new data, which are the fundamental source for assessing spatial and temporal patterns of biodiversity. Indeed, geographically and temporally representative long-term monitoring of habitats across Europe is essential for effectively assessing, preserving, and restoring biodiversity (Moersberger *et al.* 2024). Such monitoring data are crucial not only for understanding biodiversity change but also for enhancing the validation of our method from non-systematic data sources like those employed here.

While our approach provides a robust assessment of regional-scale biodiversity trends (i.e., the

465 average local trend in a larger region), as indicated by the results of our model validation (see
466 Fig. S8), it is likely weaker at making precise predictions at individual sites, as indicated by the
467 59% of variance in species richness that was not explained by our predictions. In addition,
468 although habitat changes (e.g., a transition from grassland to scrub) can be integrated into model
469 predictions, our approach does not account for local land-use changes or intensification, such as
470 the destruction of surveyed plant communities due to deforestation, urbanization, or agricultural
471 conversion. In other words, our method is conservative in estimating local species richness
472 change, assuming the preservation of each community type within the time window assessed.
473 Furthermore, we caution that this method may yield unreliable estimates in regions lacking
474 sufficient temporal coverage of geographically close observations in areas that are poorly
475 sampled over time (but see Fig. S5).

476 Species richness dynamics revealed by our study have several key implications for biodiversity
477 assessment and conservation planning in Europe. Our results suggest that vegetation plots
478 experiencing local losses in species richness could also experience gains in the future. Yet, in
479 many cases, a local increase in species richness should not necessarily be interpreted as an
480 improvement in conservation status but could instead indicate habitat quality deterioration
481 (namely, losses in habitat specialists in favour of generalist or non-native species colonizing
482 plant communities and increasing local alpha diversity) (Jandt *et al.* 2022; Klinkovská *et al.*
483 2025). Further investigation of long-term plant diversity trends at broader scales and beyond
484 alpha diversity (e.g., habitat specialist occupancy) is needed to confirm whether the recent rise in
485 local species richness across habitats results from biotic homogenization by generalists and alien
486 species at the expense of specialists. Given the large geographic heterogeneity of diversity trends
487 that we uncovered, we nonetheless emphasize the importance of recognizing regional variations

when implementing conservation and restoration actions. This means tailoring the implementation of joint EU policies, such as the Agri-Environment Schemes (European Commission 2017), the Common Agricultural Policy (CAP) (European Commission 2012), and the Nature Restoration Law(European Commission 2023), to prioritize local and habitat-specific conservation and restoration needs.

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Appendix S1: Additional details on the preparation of vegetation data

We calculated species richness (S) as the number of species in each plot, including subspecies and aggregates as individual species. We focused exclusively on vascular plants and excluded non-vascular plant taxa from the analysis because non-vascular plants were often not recorded. Species nomenclature was based on Euro+Med Plant-Base (Euro+Med PlantBase 2024) and that of aggregates following the EUNIS-ESy system (Chytrý et al. 2020). When counting species richness, we also included taxa identified only at the genus level. Before calculating species richness, we merged species occurrences within the same plot observation if a species was recorded in multiple vegetation layers.

We restricted the analysis to plots with complete information on geographical location, habitat type, plot size, and sampling year, applying specific filters based on each of these variables, as described below.

- ***Geographic location*** We included only plots located in Europe with available geographical coordinates. We excluded plots from Iceland, Svalbard, Russia, and Turkey. Additionally, we excluded plots with a geographic uncertainty greater than 1 km but retained plots without reported uncertainty, assuming that in a large majority of cases, their actual uncertainty is no greater than 1 km (Midolo et al. 2024; Večeřa et al. 2019). We transformed geographic coordinates to latitude and longitude in meters using ETRS89 / UTM zone 32N (EPSG:25832) projection (hereinafter, 'northing' and 'easting', respectively) and used this projection throughout the analysis. To complete the information on spatial location of all plots included in the analyses, we extracted elevation at plot location using a Digital Elevation Model with 90-m horizontal resolution from the European Space Agency (European Space Agency 2024). For the ReSurveyEurope data, we included both permanent plots (83% of the final dataset), which were resurveyed at precisely relocated sites, and quasi-permanent plots (17%), which lacked accurate relocation information. The coordinates of repeated observations for the same plot in ReSurveyEurope are not always consistent, likely due to variations in plot relocation error. Thus, to minimize potential bias in species richness interpolation during model validation, we excluded any plots in ReSurveyEurope where at least one observation was located more than 100 meters from other observations at that same plot site. This procedure resulted in the removal of 3,655 observations from 582 plots.

Additionally, all experimentally manipulated permanent plots were excluded from the ReSurveyEurope dataset.

- ***Habitat types*** We classified the vegetation plots into habitat types based on species composition and cover using the European Nature Information System (EUNIS) Habitat Classification expert system (Chytrý et al. 2020) (version 2021-06-01). We grouped plots into level-1 EUNIS habitat types and restricted the analyses only to plots categorized either as forest (code 'T'), grassland (code 'R'), scrub (code 'S'), or wetland (code 'Q'). We also included coastal dunes and sandy shore habitats (code 'N1') and classified them either as forest, grassland, or scrub depending on the physiognomy of their level-3 EUNIS habitat. We discarded all plots that were not categorized in one of the habitats above, such as man-made vegetation and marine habitats. Data reported in the Danish Nature Database (Nielsen et al. 2012) (which lacks species-cover data needed for classification into EUNIS habitats by the expert system) were classified into level-1 EUNIS category using the Annex I habitat conversion sheet of the same database (European Environment Agency 2023). The final selection of plots included the following number of observations for each of the habitats: 186,719 for forest (171,290 in EVA; 15,429 in ReSurveyEurope); 360,131 for grassland (309,286 in EVA; 50,845 in ReSurveyEurope); 70,334 for scrub (65,644 in EVA; 4,690 in ReSurveyEurope); 132,542 for wetland (129,620 in EVA; 2,922 in ReSurveyEurope).
- ***Plot size*** We included only plots with sizes ranging from 1 to 100 m2 for grasslands, scrub and wetlands, and from 100 to 1000 m2 for forests to exclude outliers as well as potential mistakes of plot size reported in the datasets of EVA and ReSurveyEurope(Midolo et al. 2024). We excluded all plots with no information on plot size.
- ***Sampling year***. We excluded plots sampled before 1945 due to a much lower number of plots compared to later periods. For model training, testing, and evaluation, we focused on plots sampled between 1945 and 2023. However, to further mitigate potential biases associated with older sampling protocols and overall fewer plots before 1960, or due to reporting lags for studies that were conducted within the last few, we restricted interpolations to plots sampled from 1960 to 2020 (see 'Interpolation of diversity change' section). The temporal distribution of ReSurveyEurope data matched that of the EVA

data (Fig. S1), and we had broad temporal coverage of plots sampled in most European regions (Fig. S2-S3). Across the selected time series in the ReSurveyEurope data, the mean time span between the first and last observation was 20 years (ranging from 1 to 73 years; SD = 16 years).

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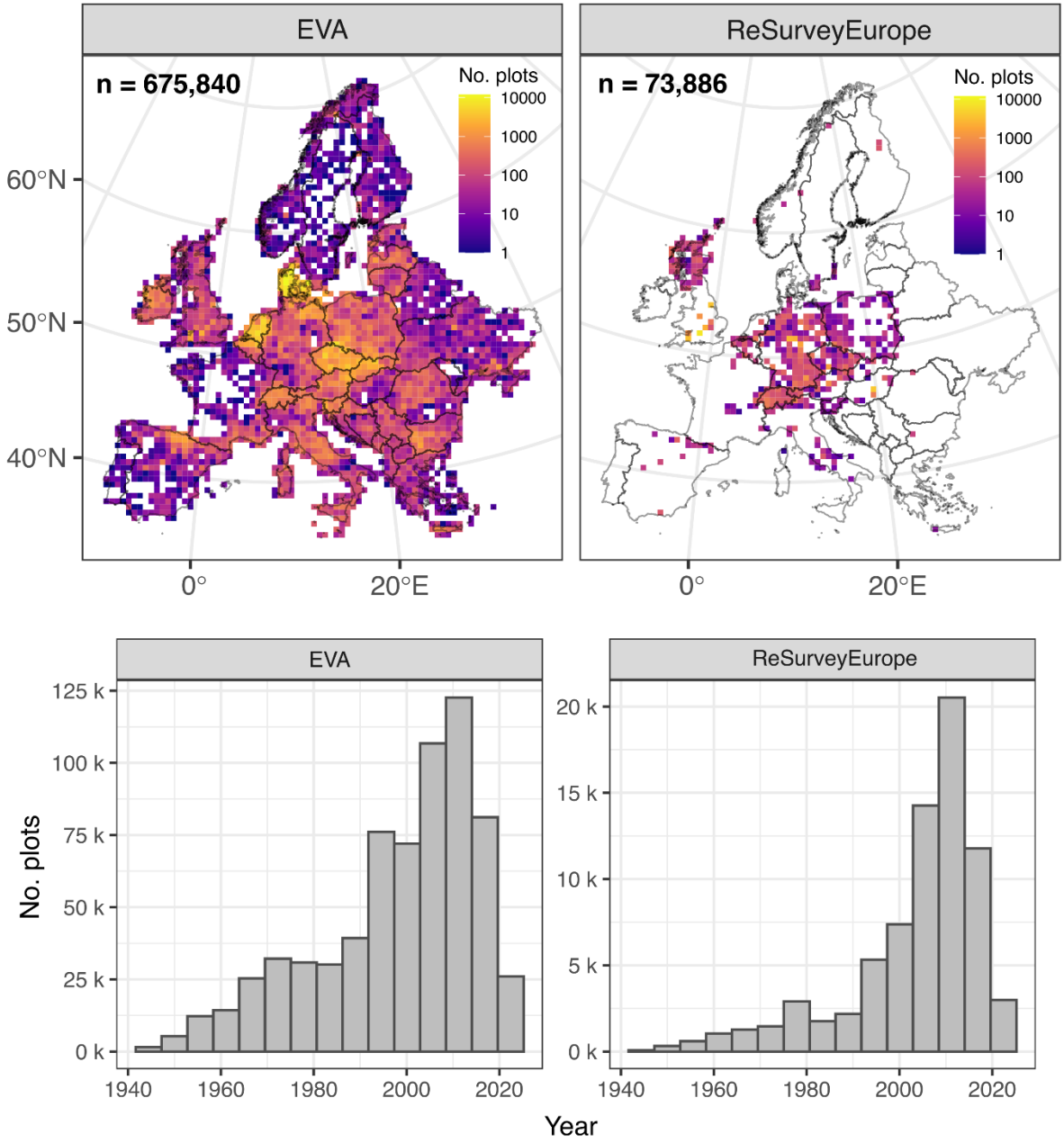

Figure S1: Spatial (top panels; 50 × 50 km resolution) and temporal (bottom panels) distribution across plot observations of the European Vegetation Archive (EVA) and ReSurveyEurope.

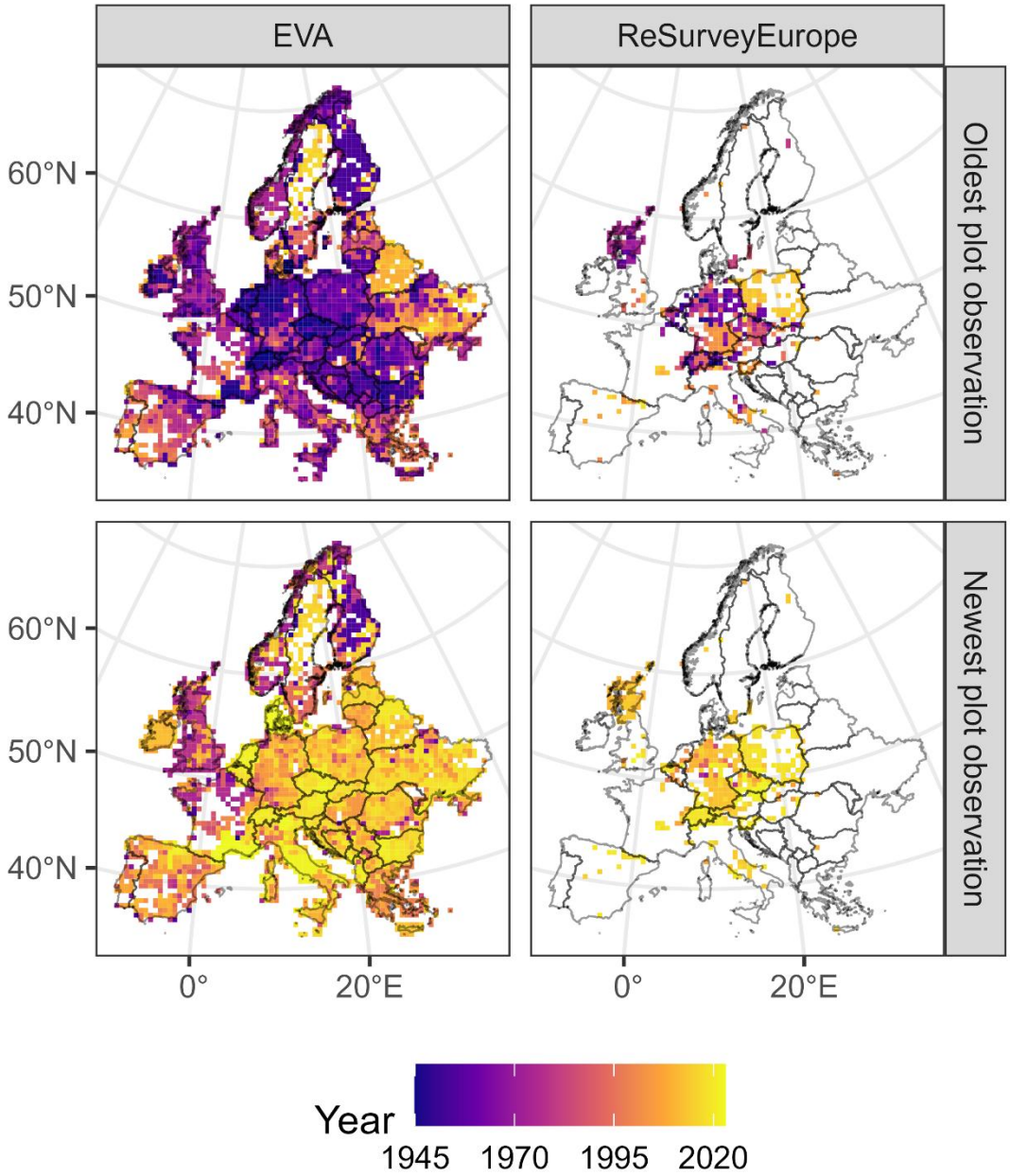

Figure S2: Year of the oldest (top panels) and newest (lowest panels) plot observation located in each grid cell (50 × 50 km resolution) across the vegetation plots of the European Vegetation Archive (EVA) and ReSurveyEurope.

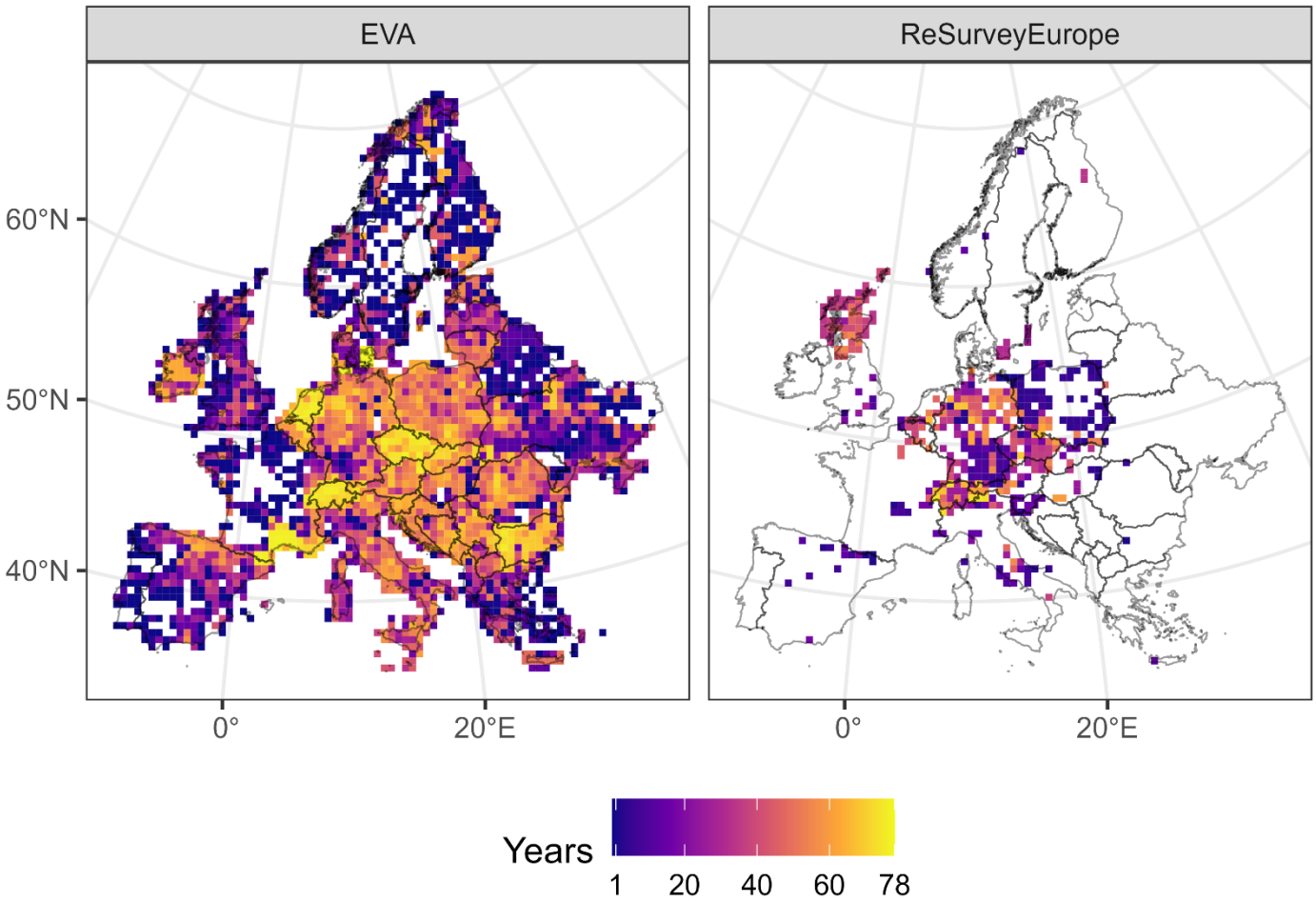

Figure S3: Temporal span (difference in years between the newest and the oldest plot observation) located in each cell on a 50 × 50 km resolution grid across the vegetation plots of the European Vegetation Archive (EVA) and ReSurveyEurope.

Table S1: Evaluation metrics (root mean square error, *RMSE*; coefficient of determination using squared correlation, *rsq*) of the tested algorithms (Random Forests and XGBoost) on the full dataset tested on 10-fold random cross validation (CV) over the training dataset (558,952) and last fit on the testing dataset (139,740).

	Random Forests		**XGBoost**	
	RMSE (species richness)	*rsq*	*RMSE* (species richness)	*rsq*
Random CV on the training set	7.07 (SE: 0.0064)	0.685 (SE: 0.0005)	8.19 (SE: 0.0050)	0.580 (SE: 0.0006)
Last fit on the testing set	7.02	0.688	8.14	0.583

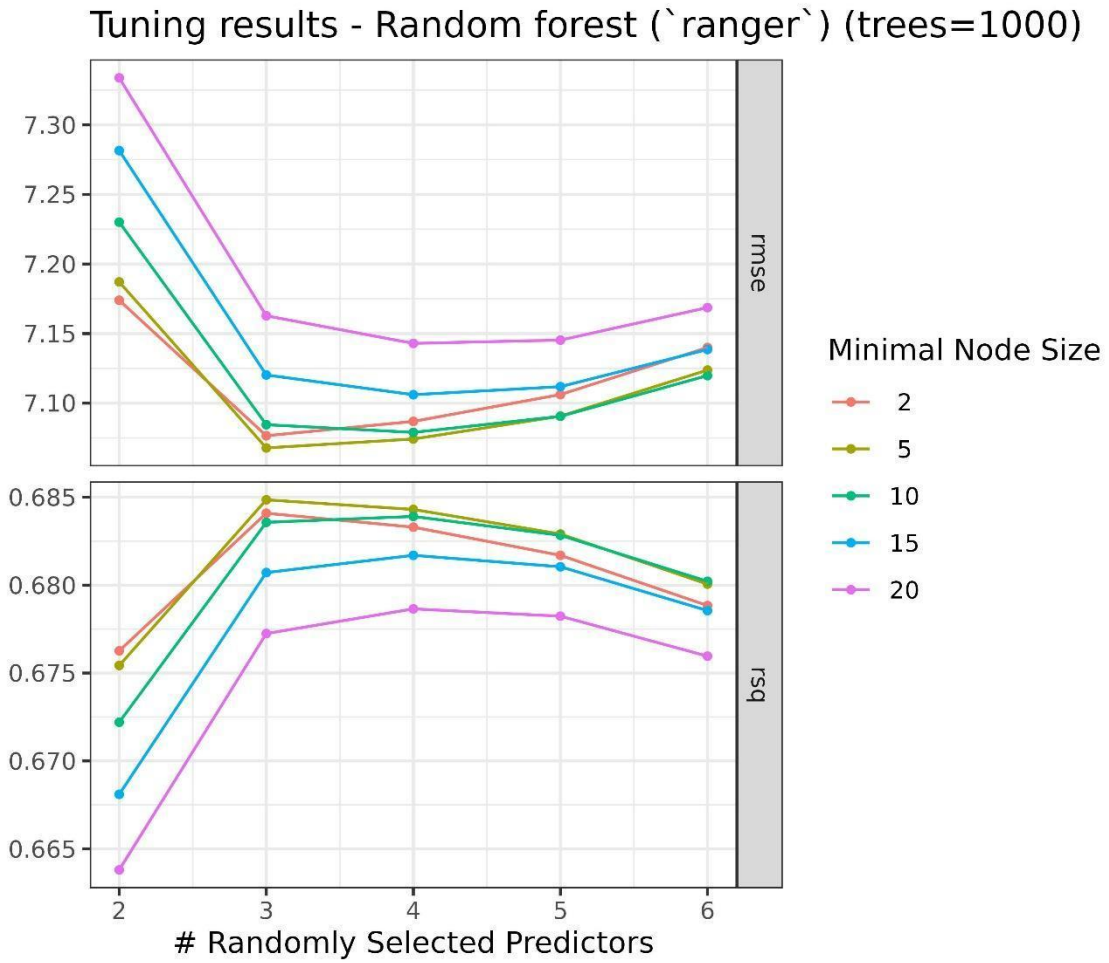

Figure S4: Hyperparameter tuning results of minimal node size and the number of randomly selected predictors in Random Forests.

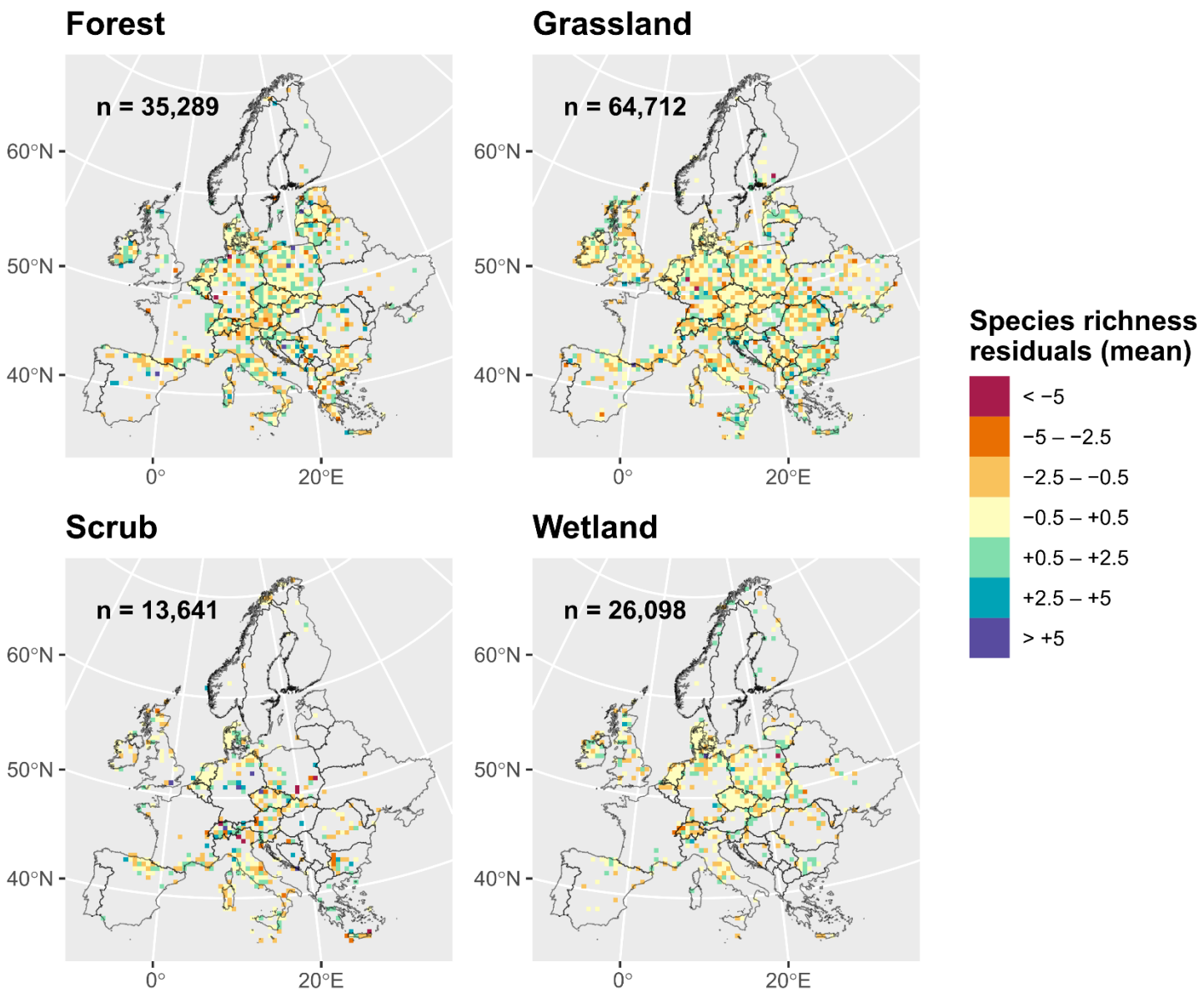

Figure S5: Spatial distribution of model residuals. The map shows the distribution of species richness residuals (observed - predicted) across Europe from the Random Forests model estimated over the testing data. Residuals were averaged within 50 km x 50 km grid cells for each habitat type. Only grid cells with at least five plots are included. The number of plots (n) is indicated within each panel. The lack of distinct geographic patterns in the residuals suggests that the model performed similarly in predicting species richness across different regions.

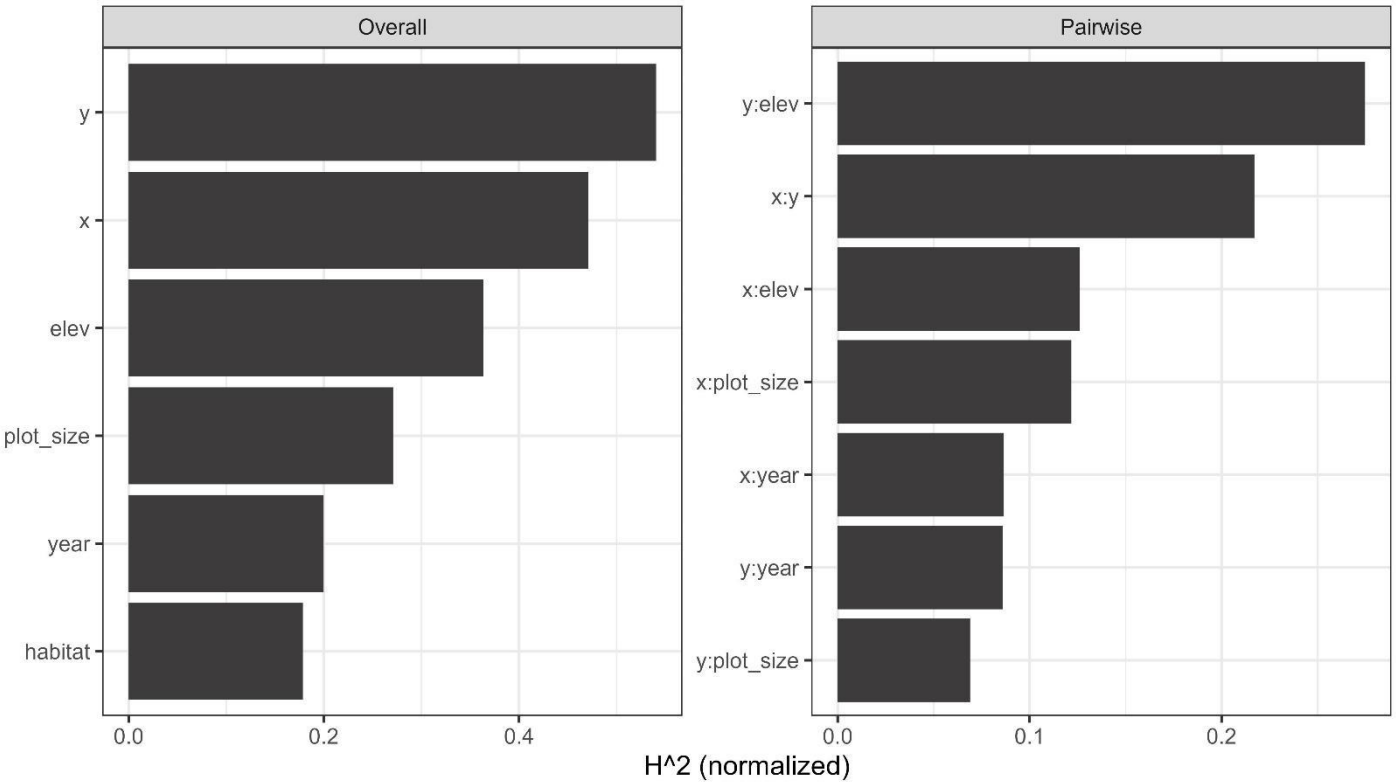

Figure S6: Interaction statistic H^2 describing variation explained by the interactions of terms included in Random Forests. Overall, 71% of the total variation explained by the model was attributable to interactions (H^2 statistic = 0.71, not shown in the figure). Left panel: overall interaction strength per feature H^2_j (= proportion of prediction variability explained by interactions on predictor *j*). Right panel: pairwise interaction strength H^2_{jk} (=proportion of joint effect variability of predictors *j* and *k* coming from their pairwise interaction); only the top seven interactions are shown here.

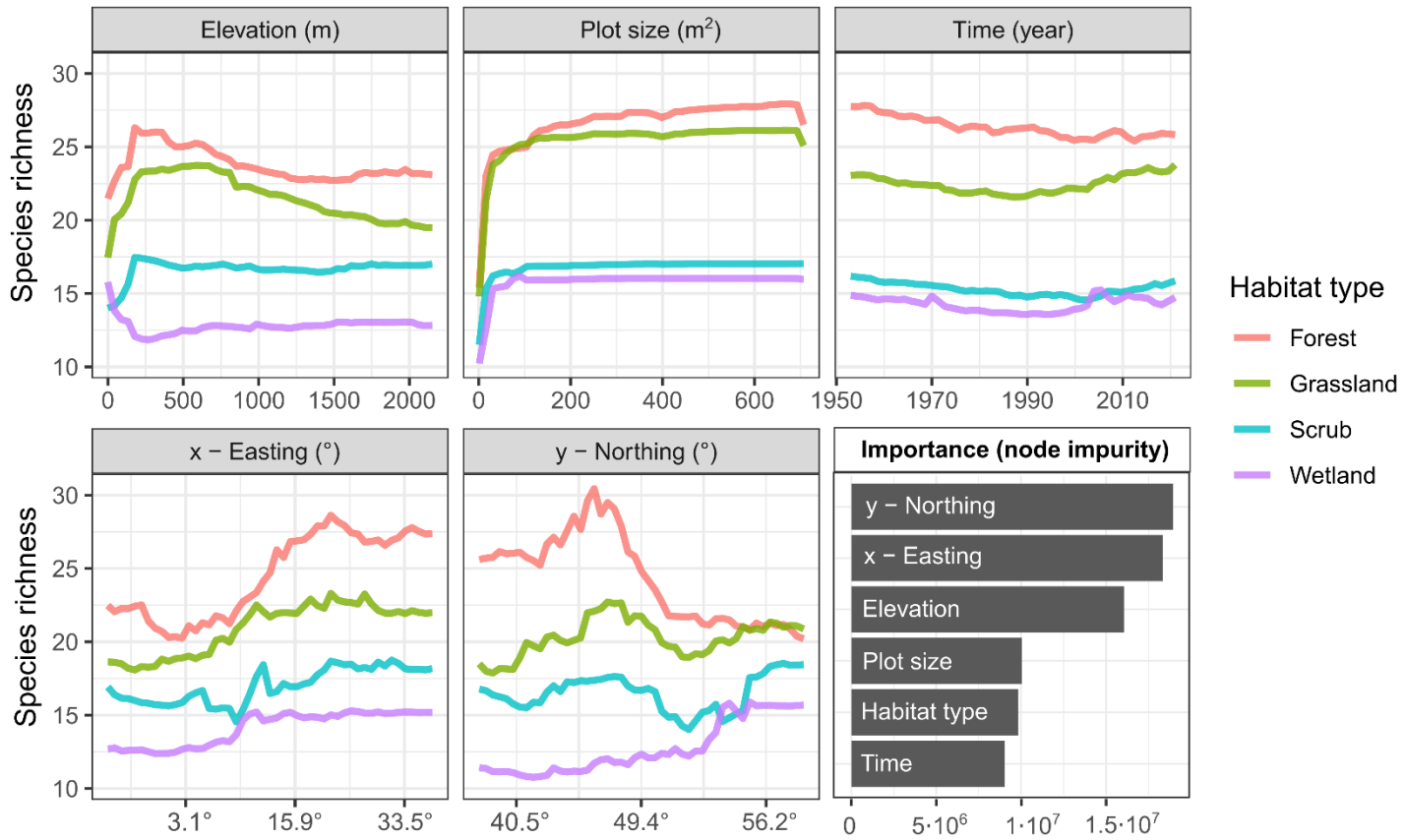

Figure S7: Partial dependence plots and variable importance (bottom-right panel) of predictors in the Random Forests model used for species richness interpolation. Partial dependence plots are grouped by habitat type. Easting (longitude) and northing (latitude) are originally expressed in meters (m) (the x-axis scale is transformed to decimal degrees).

Table S2: Results of model validation trained on a static version of the ReSurveyEurope data only. The model was fitted 100 times, with individual plots randomly selected for each time series from the ReSurveyEurope data in each iteration. The table reports the resulting mean and standard deviation (SD) values of various evaluation metrics (root mean square error, *RMSE*; coefficient of determination using squared correlation, *rsq*; Pearson correlation of observed versus predicted values; *cor*) obtained from three testing datasets. See 'Materials and Methods' and Fig. S8 for additional details.

	RMSE	**rsq**	**cor**
Static *S* (20% testing)	7.40 (SD: 0.1160)	0.639 (SD: 0.0096)	0.799 (SD: 0.0060)
Static *S* (ReSurveyEU)	5.99 (SD: 0.0244)	0.737 (SD: 0.0021)	0.858 (SD: 0.0012)
ΔS (ReSurveyEU)	0.386 (SD: 0.0018)	0.415 (SD: 0.0055)	0.645 (SD: 0.0042)

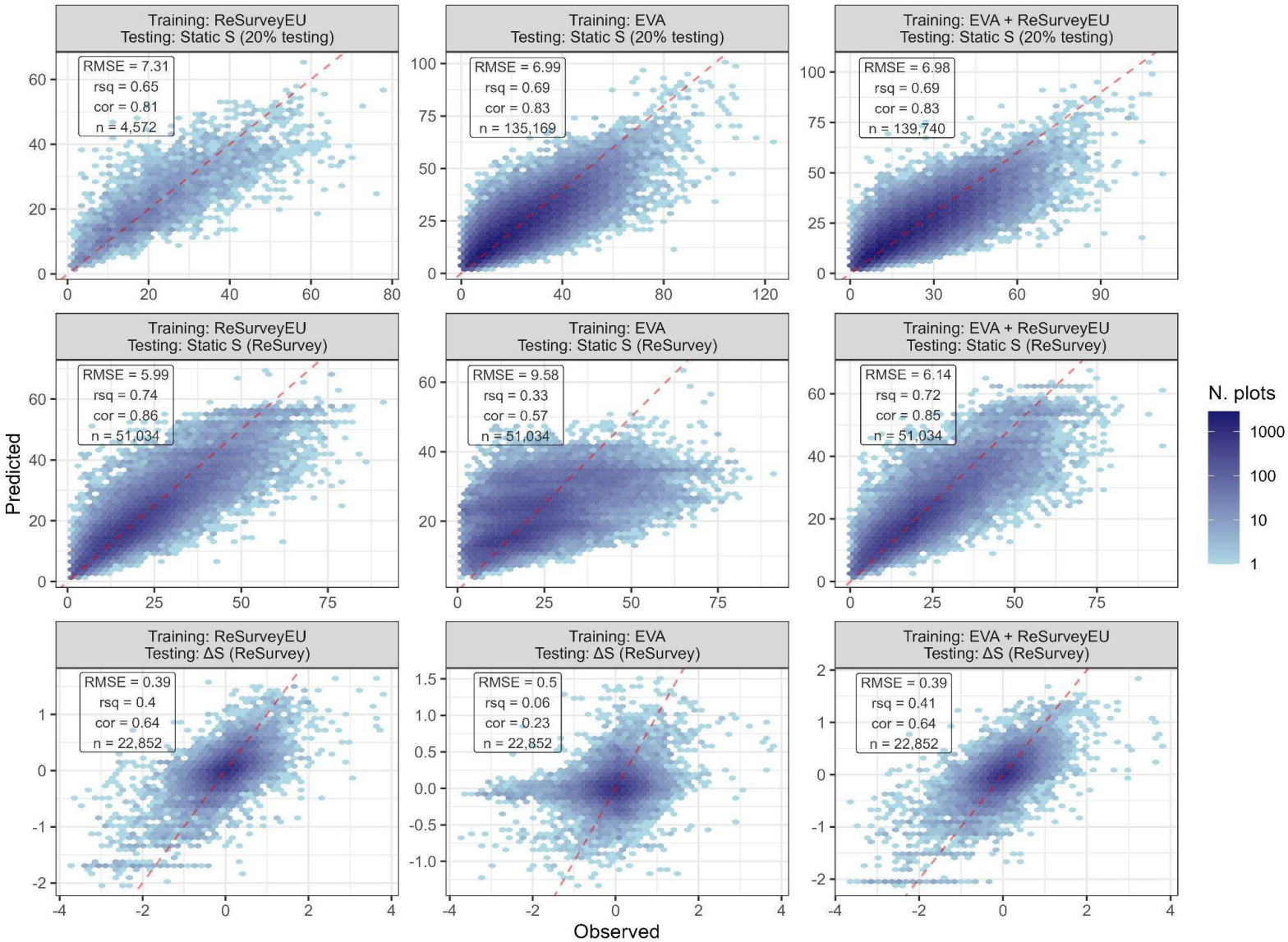

Figure S8: Validation tests for the temporal interpolation of species richness dynamics. The panel matrix reports evaluation results of observed (x-axis) vs. predicted (y-axis) species richness (static S) or its derived change (ΔS). Each panel includes evaluation metrics (root mean square error, *RMSE*; coefficient of determination using squared correlation, *rsq*; Pearson correlation of observed versus predicted values; *cor*) and sample size (*n*). Predictions were obtained from three models trained over different dataset combinations (columns) and tested over three different testing datasets (rows). The training data are obtained from A) ReSurveyEurope only (1st column), B) EVA only (2nd column), and C) a combination of both (3rd column), using no repeated survey. The testing dataset included 1) the 20% data from the initial split (1st row), 2) all remaining plots in ReSurveyEurope not utilized for model training (2nd row), and 3) species richness changes between the initial and final plots within each resurvey time series (3rd row). See 'Model validation' section in 'Materials and Methods' for more details.

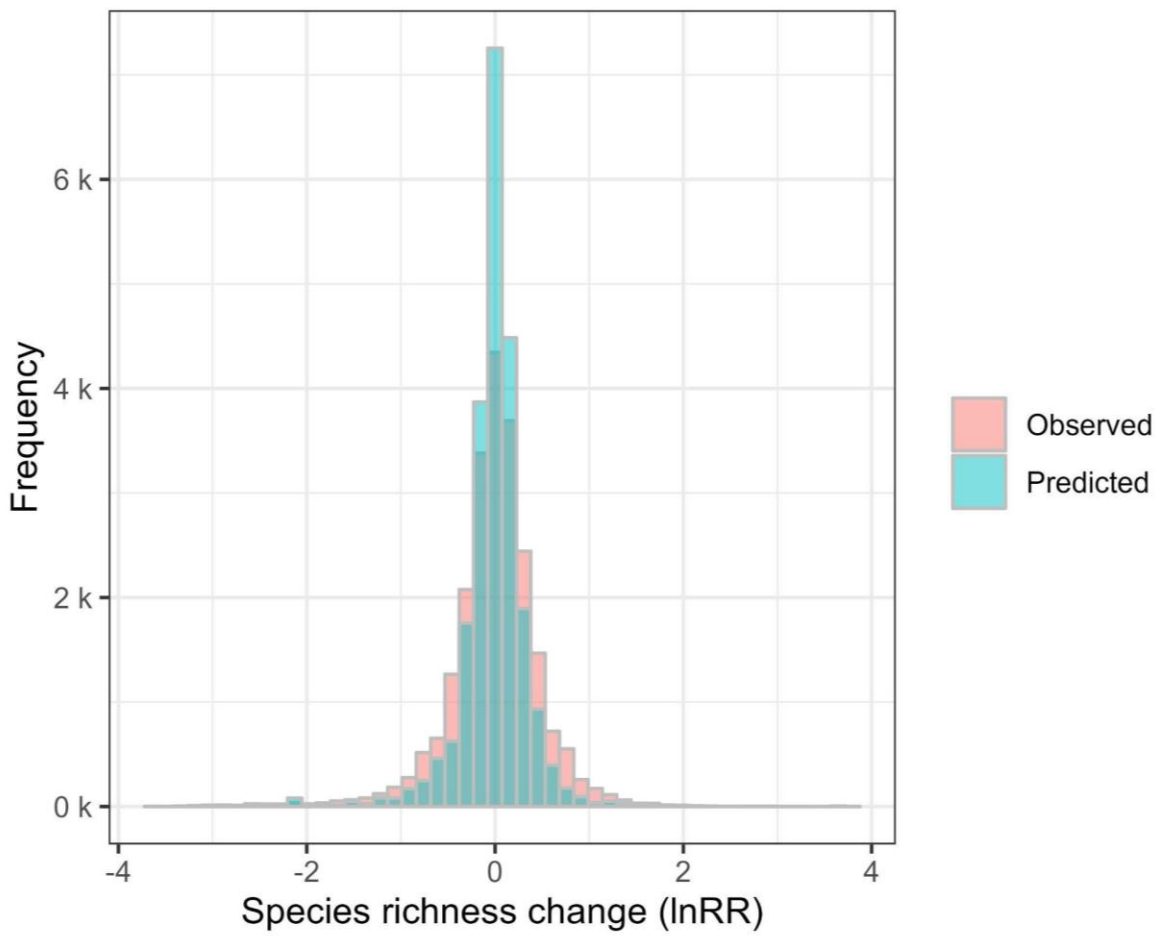

Figure S9: Interpolations tend to predict less strong changes than observed values. The histogram compares the distribution of observed vs. predicted species richness changes across 22,852 resurvey sites. This is calculated as a log response ratio (lnRR) between the species richness in the final plot to the one in the initial plot within each time series of ReSurveyEurope data. Predictions were obtained from a model trained on a static version of ReSurveyEurope data only (= using a single plot randomly selected for each time series). Same values are displayed in the scatter plot on the bottom-left panel of Fig. S8.

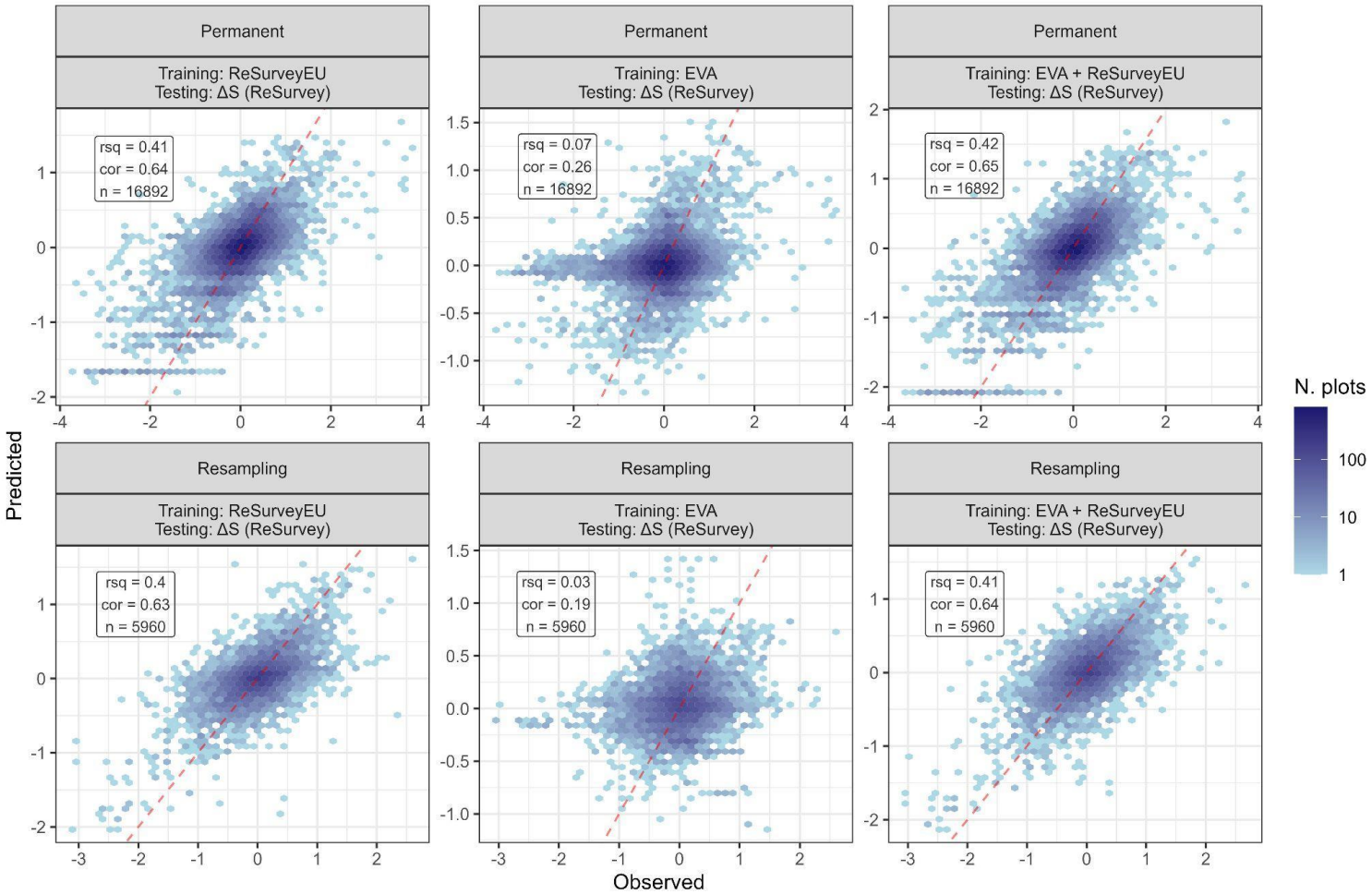

Figure S10: Validation tests for the temporal interpolation of different training datasets (see Fig. S8) comparing observed vs. predicted species richness change (ΔS) over ReSurveyEU data. Here, separate evaluation statistics were computed based upon the type of resurvey: either permanent plots (plots resurveyed at precisely re-located sites; first-row panels) or quasi-permanent ('Resampling') plots lacking accurate re-location (second-row panels). No significant discrepancy in model evaluation results was detected between the two re-survey methods. Species richness change is calculated as a log-response ratio (lnRR) between the species richness in the final plot to the one in the initial plot within each time series of ReSurveyEurope data.

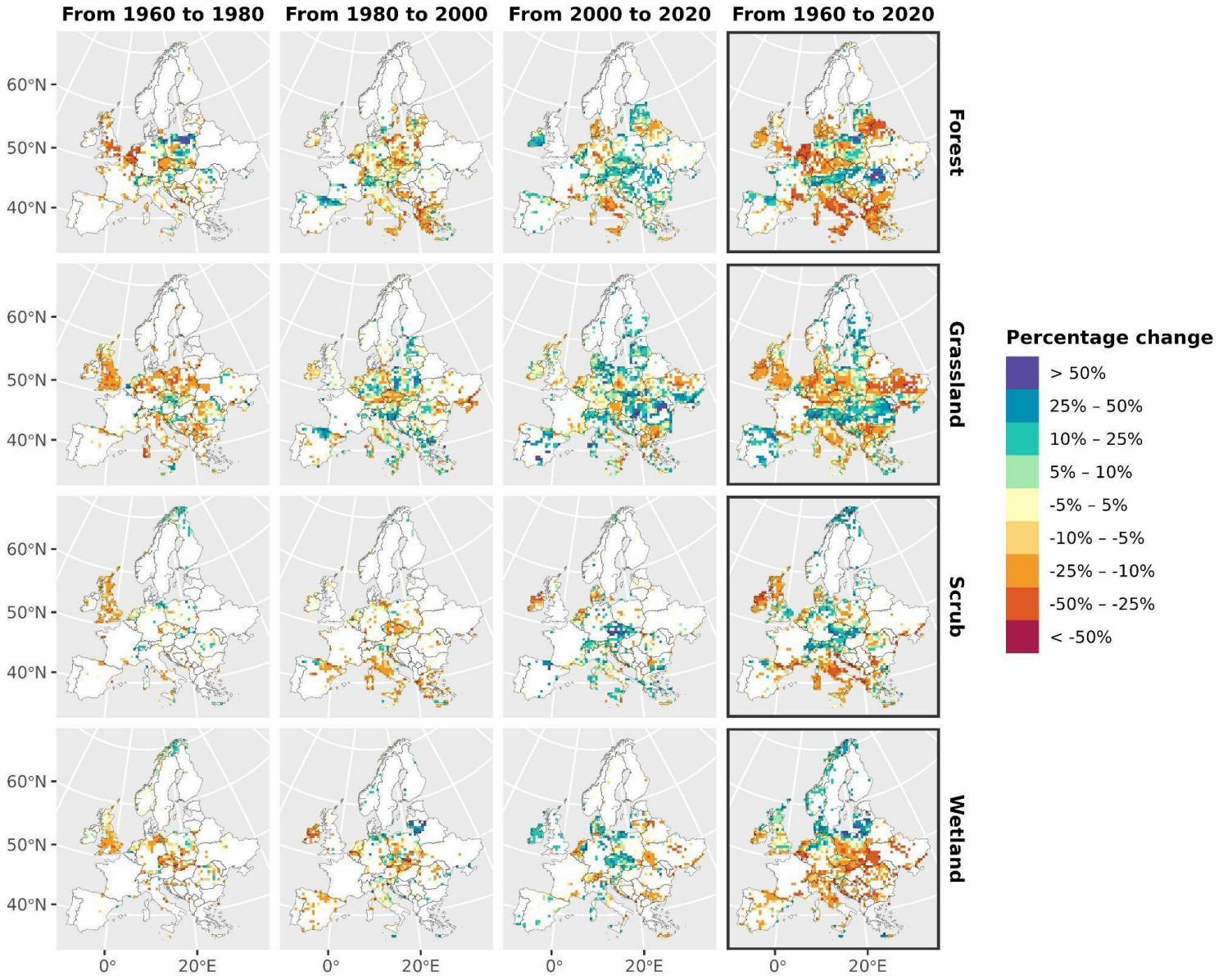

Figure S11: Geographical patterns of interpolated species richness change in Europe across main habitat types based on percentages of change (%). The maps are based on average plot-level percentage of change of species richness between two points in time for each time period, on a 50 km × 50 km grid (as displayed in Fig. 4 in the main text). In comparison to Fig. 4, only grid cells with at least five plots sampled within each time period are displayed (i.e. number of cells varies across panels depending on data availability for a given period). To account for differences in plot sizes, we predicted species richness for each plot and year using the median plot size value for its habitat (i.e., 300 m² for forests, 20 m² for grasslands, 64 m² for scrub, and 50 m² for wetlands).

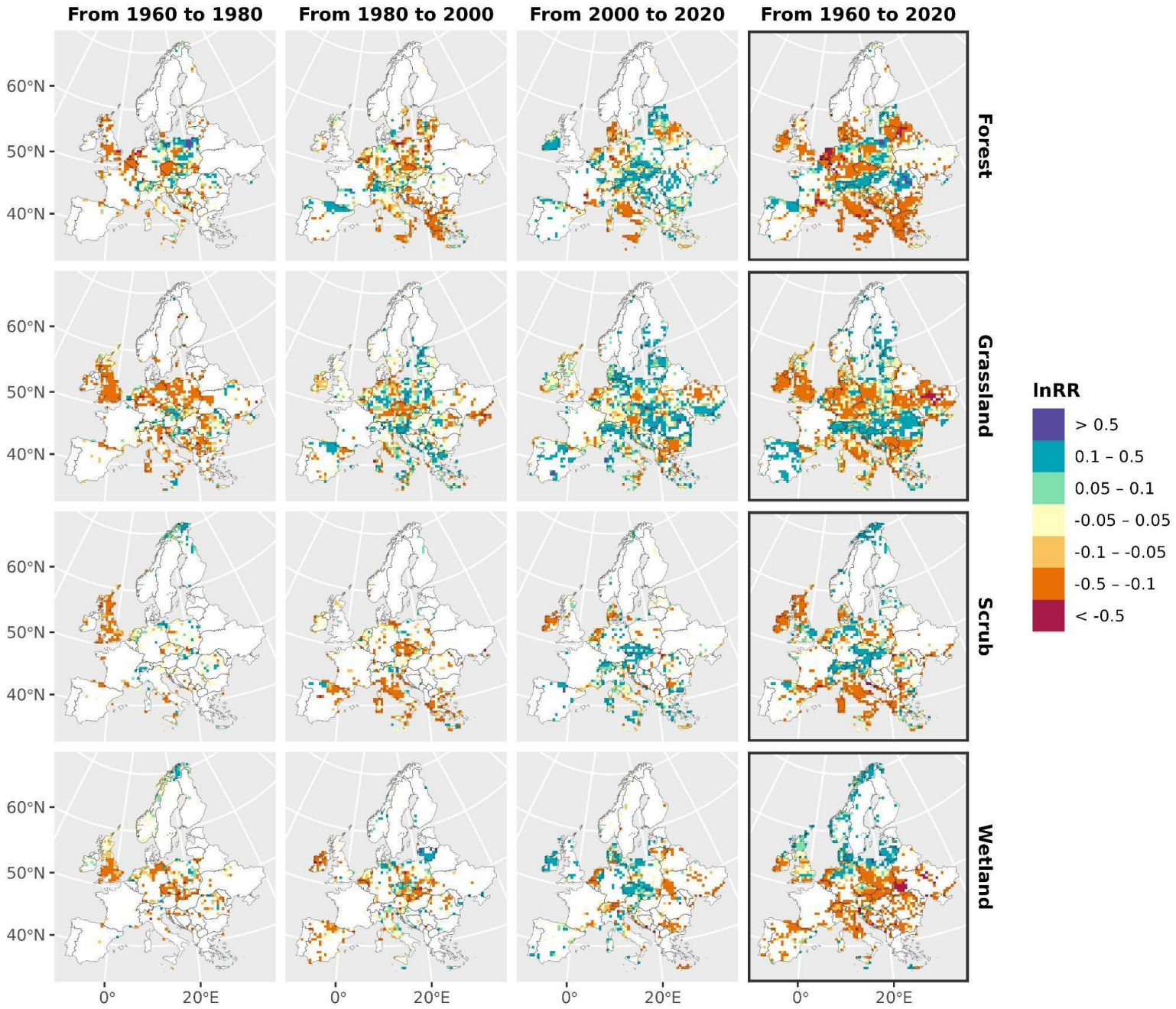

Figure S12: Geographical patterns of interpolated species richness change in Europe across main habitat types based on *log-response ratios* (lnRR) in each plot. The maps are based on average plot-level lnRRs of species richness between two points in time for each time period, on a 50 km × 50 km grid. See Fig. S11 for additional details.

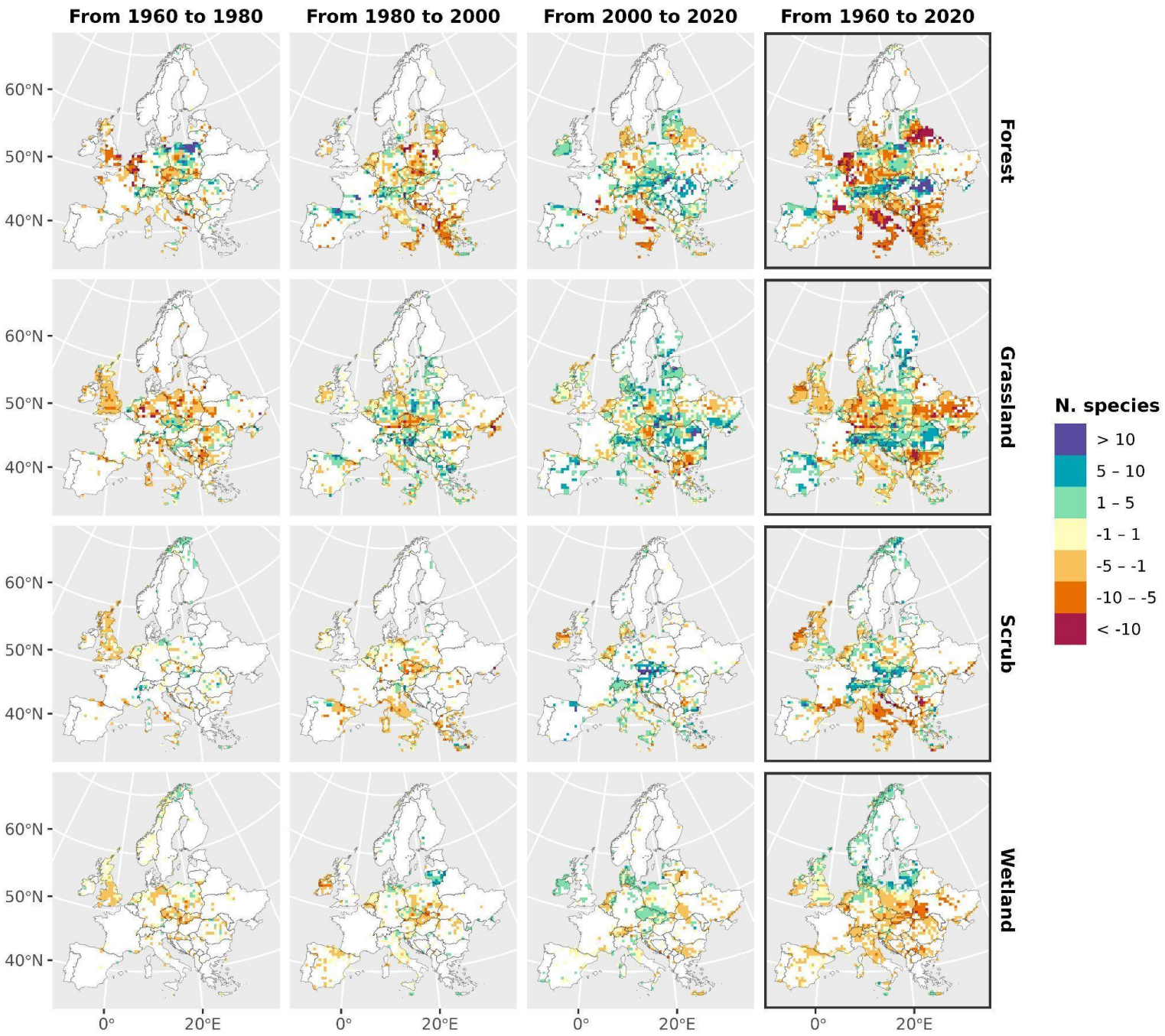

Figure S13: Geographical patterns of interpolated species richness change in Europe across main habitat types based on *absolute number of species change* in each plot. The maps are based on average plot-level number of species change between two points in time for each time period, on a 50 km × 50 km grid. See Fig. S11 for additional details.

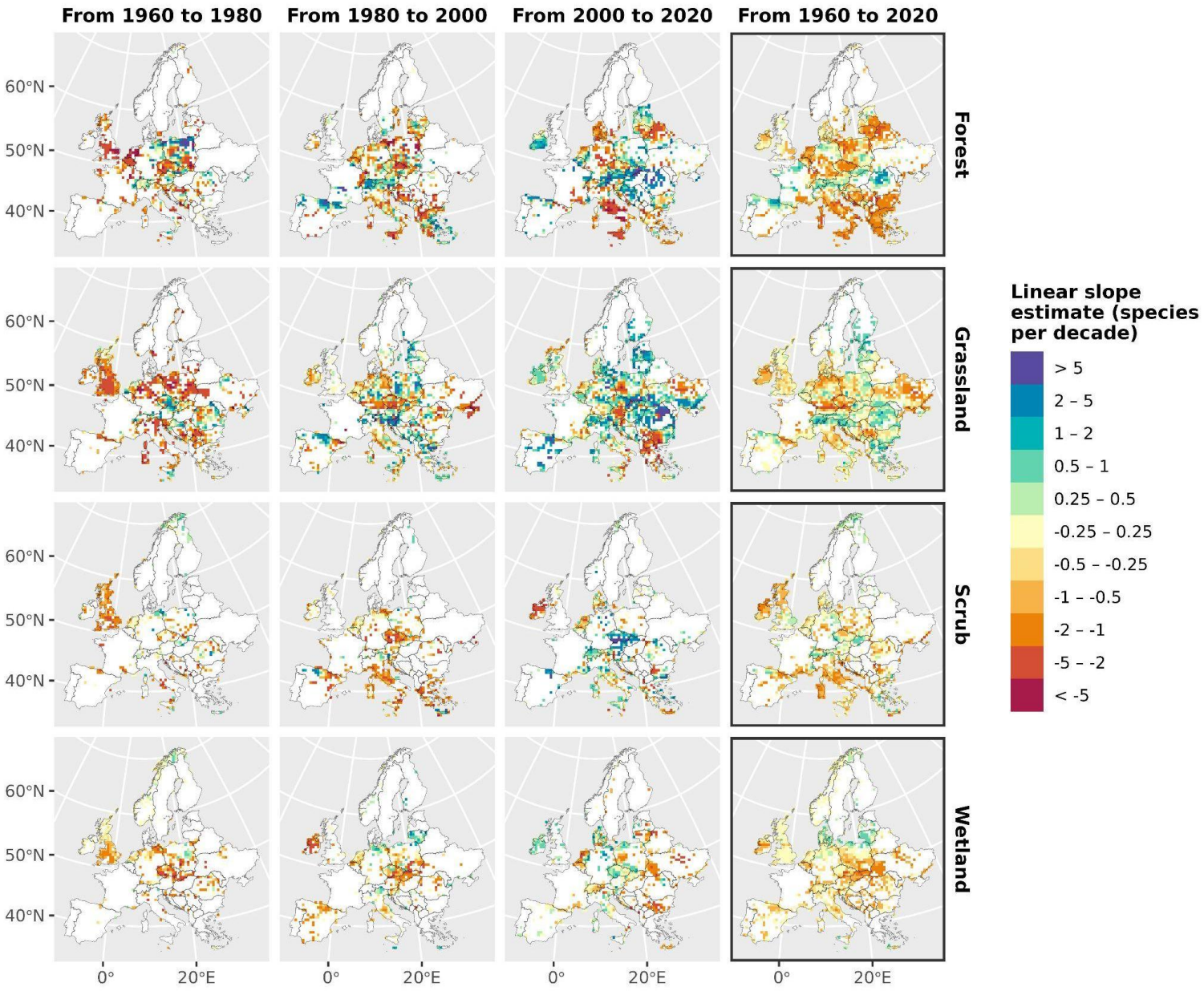

Figure S14: Geographical patterns of interpolated species richness change in Europe across main habitat types based on *linear slope estimates* in each plot. The maps are based on average plot-level slope estimates obtained from linear regressions of species richness against time, on a 50 km × 50 km grid. Species change per year is expressed in decades (multiplied by 10). See Fig. S11 for additional details.