Unveiling the spatial link between geodiversity and biodiversity: a multi-taxon study in the South of France

Moustapha Gakou[1,2*], Tom Souhil[3*], Gladys Barragan-Jason[2], Thierry Feuillet[4#], François Bétard[1#], Maxime Cauchoix[#2]

Affiliations:

1. Sorbonne Université, laboratoire Médiations, Paris, France
2. Station d'Écologie Théorique et Expérimentale, SETE, CNRS, Moulis, France
3. INRAE, Plantes et Systèmes de culture Horticoles, Avignon, France
4. Université de Caen, UMR IDEES CNRS

Corresponding author: gakou9717@gmail.com

* co-lead

co-supervised

ORCID:
MC: 0000-0002-8233-6311
GM: 0009-0009-9168-077X

Abstract

Context: Addressing global environmental challenges requires an integrative conservation approach that spans multiple taxonomic groups and trophic levels. The "Conserving Nature's Stage" (CNS) strategy promotes the protection of geodiversity -abiotic heterogeneity of the Earth's surface and subsurface- as an holistic metric for biodiversity and ecosystems conservation, yet its relationship with biodiversity across multiple taxa and trophic levels remains underexplored.

Objectives: This study investigates the links between geodiversity and biodiversity at the regional scale in Occitanie (southern France) across three taxonomic groups representing distinct trophic levels: vascular plants (producers), butterflies (primary consumers), and birds (ranging from primary consumers to apex predators).

Methods: Species richness for each group, along with geodiversity components, climate, topography, and human footprint metrics, were aggregated within spatial meshes of 5 km, 7.5 km, and 10 km resolution. We applied spatially explicit models to quantify the effects of overall and component-specific geodiversity, alongside classical environmental variables, on species richness across scales.

Results: Geodiversity showed a significant and consistent positive association with species richness for all taxa and spatial resolutions, more robust than climatic, topographic, or naturalness variables. Pedological diversity is the component of geodiversity that shows the most consistent effect across taxa. At local scales, spatial non-stationarity was observed, though biodiversity–geodiversity relationships remained more stable across taxa than those involving other environmental predictors.

Conclusion: Our findings highlight geodiversity—particularly pedodiversity—as a key, underutilized predictor of multi-taxa diversity. We thus advocate its integration into conservation and landscape planning strategies aimed at systemic biodiversity protection and restoration.

Keywords:
geodiversity, biodiversity, bird, plant, butterfly, Occitanie

1. Introduction

Over the past century, human population growth and rising global living standards have increased pressure on ecosystems (Steffen et al., 2015). One of the main visible consequences of increasing human activity is a global decline of biodiversity (Ripple et al., 2015; Wagner, 2020) associated with a general decline of ecosystem functions (Oliver et al 2015) including services that are essential for humanity (IPBES, 2019). Developing effective conservation strategies for terrestrial biodiversity across multiple trophic levels to restore ecosystem functionality remains one major environmental challenge for the years ahead.

Geodiversity -the abiotic variability of the Earth's surface and subsurface- theoretically creates a wide array of ecological niches, offering potential refuges for biodiversity as a whole (e.g. creation of diverse ecological niches for multiple species; Gray, 2013; Maliniemi et al., 2024). The "Conserving Nature's Stage" (CNS) framework builds on this concept by incorporating geodiversity—including geological, geomorphological, soil, and hydrological features—into conservation planning (Beier et al., 2015; Gray, 2013), making it a promising strategy for holistic biodiversity protection and restoration. In addition to providing heterogeneous abiotic conditions that facilitate the coexistence of multiple species, the Conserving Nature's Stage (CNS) framework also suggests that geodiversity can buffer the impacts of global change on biodiversity, as the abiotic "stage" is generally more resilient to above ground global change than the biotic communities it supports (Beier et al., 2015). Empirical studies have demonstrated positive associations between geodiversity and species richness in plants (Tukiainen et al., 2017a) from local (Salminen et al., 2023) to national levels (Bailey et al., 2017; Tukiainen et al., 2017b; Toivanen et al., 2024), but also among stream macroinvertebrates (Kärnä et al., 2018) and birds (Read et al., 2020), highlighting its broader ecological relevance.

While the positive link between geodiversity and biodiversity has been repeatedly confirmed several limitations and four key research gaps need to be explored.

1. Single-taxa studies: While the relationship between geodiversity and biodiversity is generally positive, evidence remains limited regarding its generality (Tukiainen et al., 2023). Most research focuses on vegetation, particularly vascular plants, which often show strong relationships with climatic variables and topographic heterogeneity (Field et al., 2009). However, the effects of geodiversity on other taxonomic groups remains underexplored (Tukiainen et al., 2017a), and studies on geodiversity and animal communities are rare, restricting our understanding of these complex interactions. Including multiple taxonomic groups within the same region is crucial for fully capturing these complexities, assessing the generalizability of biodiversity-geodiversity relationships, and ensuring that conservation programs based on geodiversity do not inadvertently prioritize certain groups over others.
2. Aggregated geodiversity: Hydrology, as an element of geodiversity, plays an essential role through its structures (presence of water) and processes (water flow), contributing

to ecological connectivity, water storage, and habitat diversity (Bailey et al., 2017). Geology, often defined by the diversity of rock types (i.e., lithodiversity), directly influences biodiversity through its substrate properties, which regulate hydrology and mineral resources (Miguez-Macho and Fan, 2012). Soil diversity, a key driver of plant biodiversity patterns, depends on properties such as fertility, chemical composition, and soil types, which shape species distribution (Pellissier et al., 2013). Geomorphology, on the other hand, acts through its landforms and processes (e.g., mass movements, glaciations), providing both diverse habitats and ecological disturbances (Tukiainen et al., 2023). Finally, topographic variations, like elevation and slope, influence biodiversity by interacting with other components of geodiversity, but they remain partial indicators (Gray, 2021).

While these broad patterns are known, it is still unclear which specific components of geodiversity are most beneficial for different taxonomic groups and which promotes biodiversity as a whole across trophic level. Further research is needed to untangle the precise mechanisms involved.

3. Spatial non-stationarity: The effects of geodiversity on biodiversity may vary across regions, reflecting spatial non-stationarity. This means that the strength and direction of relationships between variables can differ depending on spatial context. A positive relationship in one region may be absent or reversed elsewhere. Ignoring this variation can result in oversimplified and potentially misleading conclusions (Ren et al., 2021).
4. Single-scale studies: Many studies had been conducted at only one spatial scale (Tukiainen et al., 2017b; Read et al., 2020), leading to partial conclusions due to the Modifiable Areal Unit Problem (MAUP) (Openshaw & Taylor, 1979). This statistical bias occurred when spatial phenomena were aggregated by areas, with results influenced by the chosen area boundaries. While often overlooked in spatial modeling (Jelinski & Wu, 1996), MAUP could significantly impact statistical results or even lead to contradictory results, as exemplified by the Simpson's paradox, where aggregated data may have obscured or inverted trends observed at finer scales (Simpson, 1951).

Here, we investigate the link between geodiversity and biodiversity at the regional scale of Occitanie (South of France) across three trophic levels (plants, butterflies and birds). By focusing on vascular plants, butterflies, and birds, our objective is to spatially compare this potential relationship across three taxa with different life traits and ecological needs. These three particular taxa have been selected due to the high number of observations available within our study area. These taxonomic groups were among the most well-documented in France (Touroult et al., 2015). The choice of butterflies also reflects the aim of addressing existing knowledge gaps regarding insects within the framework of the CNS. In so doing we will test the following hypotheses: (a) Geodiversity is positively, consistently and significantly correlated with biodiversity across all taxa, with a stronger link for vascular plants, followed by butterflies and, finally, birds due to their respective dependency to belowground resources. (b) The different components of geodiversity do not influence the various taxa uniformly. (c) Geodiversity-biodiversity relationship can show spatial non-stationarity at the local scale. (d) MAUP (scale of spatial data aggregation) has a significant effect on the relationship between geodiversity and biodiversity.

2. Materials and methods

2.1. Study area

Occitanie is a region in the south of France, covering an area of 72,724 km², making it the second-largest region in the country (Fig. 1). Surrounded by the Pyrenees mountains in the south and the Massif Central in the north, Occitanie has a very diverse landscape. In the west, the Aquitaine Basin has flat plains and rolling hills. In the center and east, the region has limestone plateaus like the Causses and dramatic gorges, such as those of the Tarn or Hérault rivers. The Pyrenees rise with peaks over 3,000 meters, such as Aneto or Pic du Midi d'Ossau, while the Massif Central has volcanic plateaus like Aubrac and old eroded mountains like the Cévennes.

From a geological point of view, Occitanie is like a mosaic. The Massif Central has volcanic and granite formations, showing evidence of ancient tectonic activity. The Pyrenees were formed by the collision of the Iberian and Eurasian tectonic plates, creating folded mountain chains. The Languedoc coastline is shaped by lagoons, saltwater ponds, and sandy beaches, which result from coastal erosion and sediment deposition.

Three main types of climate coexist in the region. The Languedoc coastline has a Mediterranean climate, with hot, dry summers and mild, wet winters. The Aquitaine Basin has an oceanic (Atlantic) temperate climate, with mild, wet winters and cooler summers compared to the Mediterranean climate. Finally, the Pyrenees and Massif Central are influenced by mountain climates, with cold winters and cool, wet summers.

This great variety of landscapes and climates creates many transition zones, allowing a rich and diverse range of plants and animals to thrive.

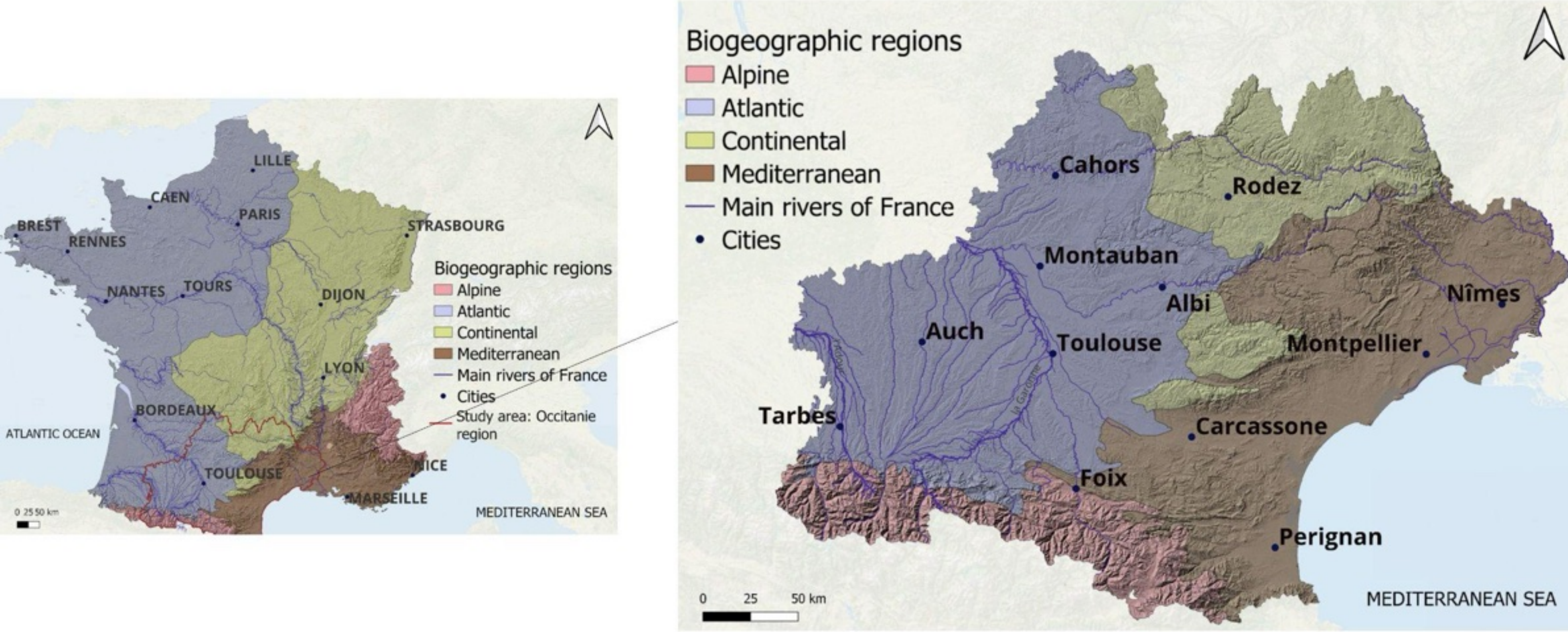


Fig. 1: Location of the Occitanie region, and its different biogeographic regions, in the south of france.

2.2 Biodiversity data

All occurrence data were sourced from the OpenObs database (INPN), the French national biodiversity data portal managed by PatriNat (OFB-CNRS-MNHN-IRD; Norvez et al., 2023). Three datasets were constructed: vascular plants (Tracheophyta, n = 4,279,291), birds (Aves, n = 4,765,000), and butterflies (Papilionidae, Hesperiidae, Pieridae, Riodinidae, Lycaenidae, Nymphalidae, n = 1,106,770). The full list of used datasets is available in Table S1-S3. These data are characterized by significant heterogeneity in terms of sources and protocols. They mainly came from scientific studies, collection records, opportunistic citizen observations, and participatory science initiatives conducted as part of public policies (e.g., the national natural heritage inventory, INPN). Identifying and correcting as many potential biases as possible associated with using such a large and heterogeneous volume of data was essential before any interpretation (Kissling et al., 2018; Jetz et al., 2019; Wüest et al., 2020).

The first filtering operations, such as ensuring compliance with standards and harmonizing scientific names using the TaxRef taxonomic reference was performed by the PatriNat team (Gargominy et al., 2022). For the taxonomic dimension, only observations identified to the species or subspecies level were retained. To limit biases related to the temporal dimension, our research focused on the period from 1990 to the present, excluding older observational data, which were unevenly represented.

The spatial dimension was undoubtedly the one that required the most attention, given our research questions and hypotheses. We retained only observations geolocated at specific geographic points, excluding aggregated occurrences at municipal or national grid scales. The second major issue was the uneven sampling of the territory, with certain areas being under- or over-sampled (e.g., a higher density of observations near urban areas). To address this significant bias, we focused solely on calculating species richness per grid cell, as we deemed diversity indices that account for abundance (e.g., Shannon index) inappropriate for describing diversity at this scale (Kissling et al., 2018).

In addition, to compensate for false absences of species and to identify potentially under-sampled grid cells relative to others, we decided to use non-parametric estimators of species richness (Brose et al., 2003). These estimators are widely recognized as better predictors of true richness compared to observed richness in most cases (Brose et al., 2003; Vallet et al., 2012; Walther et al., 2015).

Given the structure of our data and the method proposed by Brose et al. (2003), which recommends selecting the non-parametric estimator based on the average completeness rate of the grid cells (S_{obs} / S_{est}), we chose to use the first-order Jackknife estimator (1) to simulate species richness.

(1)

$$S_{est} = S_{obs} + n_1 \frac{N-1}{N}$$

Where:

- S_{est}: Estimated richness
- S_{obs}: Observed richness
- N: Number of data points in the grid cell
- n_1: Number of species observed only once in the grid cell (singletons)

Non-parametric estimators can be biased by under-sampled grid cells (Vallet et al., 2012), so we decided to exclude undersampled grid cells from further analysis. To do this, the number of singletons (species observed only once in each grid cell) was calculated for each cell, and any cell with more than 50% singletons was removed from the analysis. In our view, this threshold represents the best compromise given the structure of our data and the recommendations in the literature (Brose et al., 2003; Marcon, 2015).

2.3. Geodiversity data

All the geodiversity data used are listed in Table 1. For the compilation of geological and pedological indices, each type of formation was aggregated within each grid cell, and the Shannon index (2) was then calculated (Manosso et al., 2021; Atkinson et al., 2022):

$$H' = -\sum_{i=1}^{S} p_i \log_2 p_i$$

Where:

(2)

Table 1: Summary of geodiversity, topographic, climatic and anthropic variables used for modeling and the main calculated indices.

Predictors	Variables	Metrics (per grid)	Resolutions	References
Geodiversity	*Geology*	Shannon index of lithological types	1/50,000	BD Charm-50, BRGM, 2019
	Pedology	Shannon index of soil types	1/250,000	Référentiel Régional Pédologique harmonisé de la région Occitanie, 2022
	Hydrology	Shannon index of rivers (Strahler Orders) and water bodies	1/25,000	BD Topage, IGN, 2022
	Geomorphology	Shannon index of Geomorphon types	25 m	BD Alti DTM, IGN
Topography	*Elevation range*	Max elevation - min elevation (m)	25 m	BD Alti DTM, IGN
Climate	*Temperature*	Annual average (°C)	1 km	WorldClim, 1970-2000
	Precipitation	Annual average (mm)	1 km	WorldClim, 1970-2000
Human footprint	*Naturalness*	Average of a composed index of hemerobia, building density and spatial continuity	20 m	Guetté *et al.*, Projet CartNat UICN, 2018

Regarding geomorphology, we used the r.geomorphon algorithm, developed by Jasiewicz and Stepinski (2013) within GRASS GIS 7.1 (GRASS Development Team 2018). The r.geomorphon algorithm enables the automatic classification of landforms (such as ridges, valleys, and slopes) by analyzing the local configuration of terrain within a defined neighborhood. Given the highly rugged terrain of our study area in Occitanie, we set the Threshold Angle parameter to 3° in order to limit the excessive detection of microforms and use the default "radial limit" value of 1000. This threshold angle helps ignore very gentle slopes, thus reducing "noise" in areas with significant elevation changes. It provides a good balance between sensitivity and clarity of geomorphological features. Subsequently, the Shannon index was calculated (2).

The hydrological index was constructed based on the work of Bétard & Peulvast (2019). The first step involves calculating the Strahler index for each watercourse using our digital terrain model (BD Alti 25 m DTM) and the “Strahler order SAGA” tool available in QGIS software. This index captures the complexity of the tributary network of a watercourse (Strahler, 1952). Next, the richness of each watercourse order and the richness of water bodies were quantified per grid cell. A common Shannon index was then calculated based on the length of each type of watercourse and the surface of water bodies.

To ensure our work was comparable to most other studies, we decided to create a global geodiversity index by summing the Shannon scores of our four sub-indices (geology, pedology, hydrology and geomorphology). This method for constructing the geodiversity index appears to be the most commonly used in the literature, according to Crisp et al. (2021).

2.4 Topographic, climatic and human footprint covariates

We used elevation range within each grid cell as a global topographic covariate, selected for its lack of correlation with climatic variables. Climatic covariates included annual mean temperature and annual mean precipitation, both averaged per grid cell from the WorldClim database (1970 - 2000). To account for anthropogenic influence, we used the mean naturalness index per grid cell as a proxy for human footprint.

The naturalness index is a nationally developed metric in France, created as part of the CartNat project (UICN, https://uicn.fr/aires-protegees/wilderness-2/; Guetté et al., 2018). It quantitatively assesses the level of disturbance in natural landscapes, with higher values indicating minimal or no human impact. The index integrates three components: hemeroby (i.e., the degree to which vegetation deviates from its potential natural state), building and road density, and ecological continuity. For detailed methodology, see Guetté et al. (2022).

2.5. Statistical analyses

To address our various research questions, we first aggregated biodiversity, geodiversity and covariates into grid cells and then used two statistical modeling approaches: a regional model to study the average relationship between species richness and geodiversity variables and covariates (to test hypothesis (a) and (b)), and a local model to explore the potential spatial heterogeneity of the relationships between geodiversity variables and species richness (to test hypothesis (c)). All models were repeated for each grid resolution to detect potential spatial aggregation issues (to test hypothesis (d)).

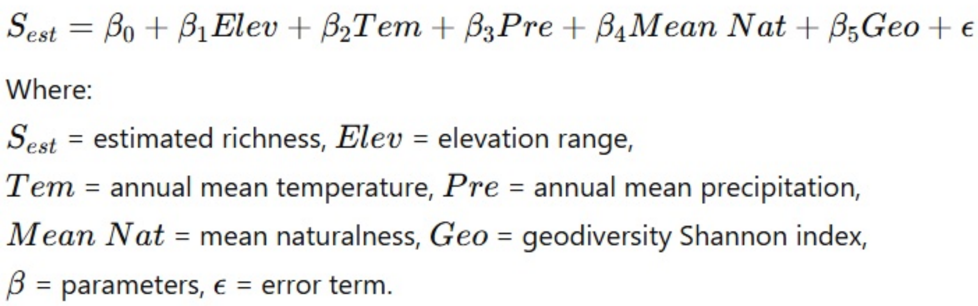
2.5.1. *Data aggregation*

Regular grid cells with sizes of 5 km, 7.5 km, and 10 km were selected as a compromise between analyzing the phenomenon at the finest possible resolution and the resolution of our initial data (the pedology layer being the limiting factor with a resolution of 1/250,000). We used different grid resolutions to consider the modifiable areal unit problem (MAUP) in spatial modeling. For the 5 and 10 km grids, we used spatial referential provided by the French National Inventory of Natural Heritage (INPN) to optimize biodiversity data pooling. Grid cells in contact with the boundaries of our regional study area were excluded from the analysis to account for edge effects, which could also bias our results (Zarnetske et al., 2019). The number of grid cells was n=2,721 for the 5 km resolution, n=1,172 for 7.5 km, and n=641 for 10 km.

2.5.2. *Regional model*

The first step involved creating an initial non-spatial model between the estimated biodiversity richness S_{est} (Jack1) and the predictors (geodiversity Shannon index, and covariates: naturalness, annual mean temperature, annual mean precipitation and elevation range) for each of the three biodiversity categories (vascular plants, birds, butterflies) and for each resolution (5, 7.5 and 10 km). A linear model (3) was selected following a preliminary analysis of the distribution of the dependent variable.

(3)



$$S_{est} = \beta_0 + \beta_1 Elev + \beta_2 Tem + \beta_3 Pre + \beta_4 Mean\ Nat + \beta_5 Geo + \epsilon$$

Where:
S_{est} = estimated richness, $Elev$ = elevation range,
Tem = annual mean temperature, Pre = annual mean precipitation,
$Mean\ Nat$ = mean naturalness, Geo = geodiversity Shannon index,
β = parameters, ϵ = error term.

The explanatory variables were standardized to enable comparison of the coefficient values. The assumptions of the linear model were checked graphically and through the Shapiro-Wilk test (normality of residuals) and the Breusch-Pagan test (homoscedasticity). Variance Inflation Factors (VIF) were also calculated for each explanatory variable to identify potential multicollinearity, with an exclusion threshold set at VIF=4.

To detect potential spatial dependence in the residuals that could bias the coefficient estimation, Moran's Index (Moran, 1950) was calculated using the R package *spdep*, and a spatial analysis of residuals was conducted. A first-order queen contiguity neighborhood matrix was used for this analysis. In the case of positive autocorrelation in the model's residuals, a bottom-up approach was used to select the appropriate spatial model (Le Gallo, 2002; Florax et al., 2003). First, Lagrange Multiplier tests (Anselin et al., 1996) were applied to choose between SAR (Simultaneous AutoRegressive model) and SEM (Spatial Error Model) using AIC values. The optimal choice was based on selecting the spatial model with the smallest AIC for the robust Lagrange Multiplier.

In the SAR model (4), the value of the dependent variable (here, S_{est}) depends on the value of the dependent variable in the neighboring areas. This variable is thus responsible for the spatial effect. To interpret the coefficient values, the total average impact of the independent variables is subsequently calculated.

(4)
$$SAR : y = \rho W y + x\beta + \epsilon$$

Where: y = dependent variable, x = independent variable, β = parameter, ρ = auto-regression coefficient, ϵ = error term, W = spatial weights matrix.

In the SEM model (5), the dependent variable (here S_{est}) is influenced by an unobserved spatial factor that simultaneously affects the observation and its neighborhood.

(5)
$$SEM : \quad y = x\beta + \lambda W \epsilon + u$$

Where: y = dependent variable, x = independent variable, β = parameter, ϵ, u = error terms, λ = auto-regression coefficient, W = spatial weights matrix.

For the SAR and SEM models, the neighborhood matrices (W) were calculated based on a first-order queen contiguity matrix. This type of matrix assigns equal weight to all adjacent cells (maximum neighbors = 8). The two spatial models were computed using the R package Spatialreg. To validate the relevance of our spatial models, we calculated the adjusted R^2 and the AIC (Akaike Information Criterion) for each model to compare them with the linear model without correction.

To evaluate the relative influence of each component of geodiversity, the initial linear model was reconstructed by replacing the global Shannon geodiversity variable by Shannon geology, Shannon hydrology, Shannon geomorphon and Shannon pedology variables. All subsequent steps were then reproduced.

2.5.3. Local Model

The objective of this modeling was to explore the spatial non-stationarity of the relationships between the explanatory variables and the variable of interest. To address this question, we performed a Geographically Weighted Regression (GWR) using the R package GWmodel (Brunsdon et al., 1996). The GWR evaluates local regression model (3) for each grid cell based on the characteristics of its neighborhood only. To account for the neighborhood effect, two parameterization steps were required: the choice of the neighborhood size and the spatial weighting function associated with these neighbors, typically inversely proportional to the distance (Feuillet et al., 2019). The neighborhood radius (in km) was optimally estimated by minimizing the AIC. A Gaussian function was used as the spatial weighting function, assigning weights that approach 0 as the distance from the observation increases. All these parameterization steps were illustrated in the supplemented information (Fig. S1).

3. Results

3.1. Geodiversity Maps

The maps of geological, hydrological, geomorphological, and pedological diversity, along with the overall geodiversity index, are shown in Fig. 2 for the 5 km grid resolution, and in Fig. S2 for all grid resolutions (5, 7.5, and 10 km). A spatial heterogeneity in our geodiversity index is evident, with highly geodiverse areas located in the southwestern part of the territory—particularly in the Haute-Pyrénées and the western part of the Gers (including the Pyrenees and their piedmont)—and much less diverse areas around Toulouse and in the Northern part of Lozère, in the northeastern section of the study area.

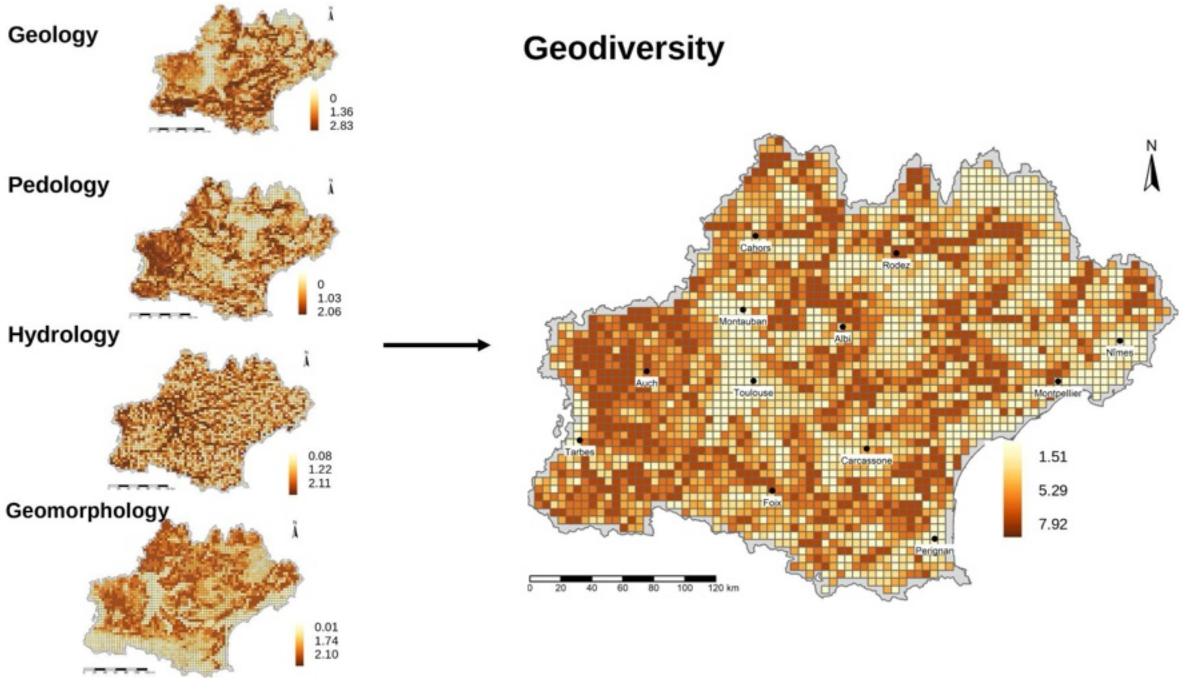


Fig. 2: Compilation of the four geodiversity components (geology, pedology, hydrology, geomorphology) into a global geodiversity index (grid = 5 km)

3.2. Regional Analysis

In our initial modeling approach, which used overall geodiversity, naturalness, annual mean temperature, annual mean precipitation, and altitude range as linear predictors of species richness, no evidence of problematic multicollinearity (all VIFs < 4), heteroscedasticity, or non-normality was detected in any of the models, regardless of the taxonomic group or spatial resolution considered. But in all our models, Moran's I index was positive and significant (p-value < 0.05), indicating positive autocorrelation and therefore spatial dependence in the residuals (Fig. 3, Table S4). This spatial dependence can be observed using the Moran scatterplot (Fig. 3a), which showed the positive linear relationship between the model's residuals and the spatially lagged residuals (mean of neighboring residuals). Another way to check this condition was through a spatial analysis of the residuals on a map (Fig. 3b), allowing us to visualize the structure of the spatial autocorrelation. For example, for birds at a resolution of 5 km, the model seems to underestimate their richness along the Mediterranean coastline. All residual maps and Moran's I values are presented in Fig.S3 and Table S4.

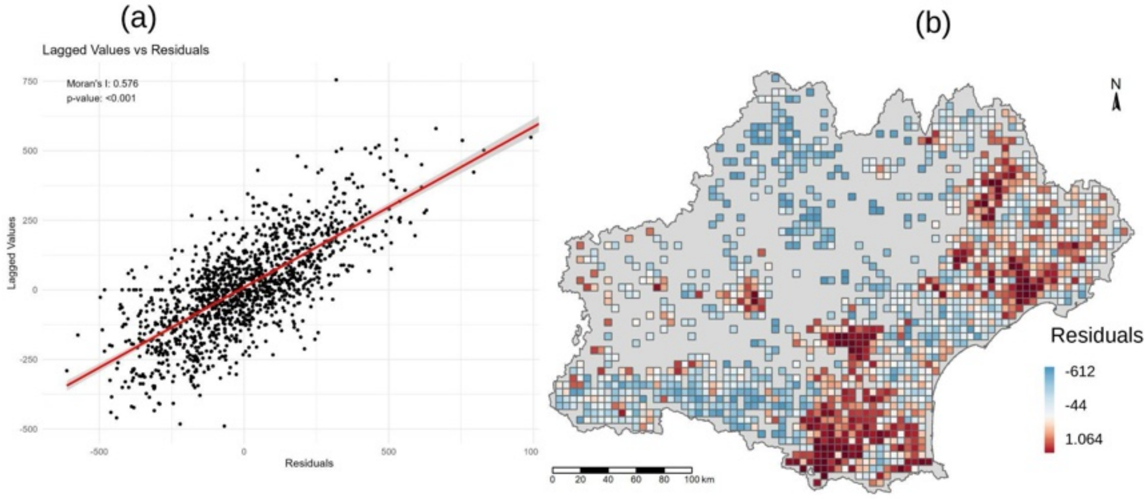


Fig. 3: Analysis of the spatial autocorrelation of the residuals of the linear bird model. (a) Moran diagram. (b) Mapping of linear model residuals (mesh = 5 km)

The violation of spatial independence led us to reject the use of the linear model and to select the appropriate spatial model using Lagrange Multiplier tests. Based on these tests, the SAR model was selected (lowest AIC) for all spatial resolutions in the case of butterflies, whereas the SEM model was preferred for vascular plants and birds (Table S4). This suggests that butterfly species richness in a given cell is directly influenced by species richness in neighboring cells, while for plants and birds, the observed spatial autocorrelation in the residuals is more likely due to spatially structured factors not accounted for in our modeling framework. To ensure that the issue of spatial dependence was resolved by our spatial models, an analysis of the residual distribution from the new models was conducted again (Fig. S3). Following the construction of the SAR and SEM models, no residual autocorrelation was detected (p-value Moran's I > 0.05), and the spatial structures of the residuals previously observed in Fig. 3 also disappeared (e.g., Fig. 4 for birds at 5 km resolution; and Fig. S4 for all taxa and spatial scales).

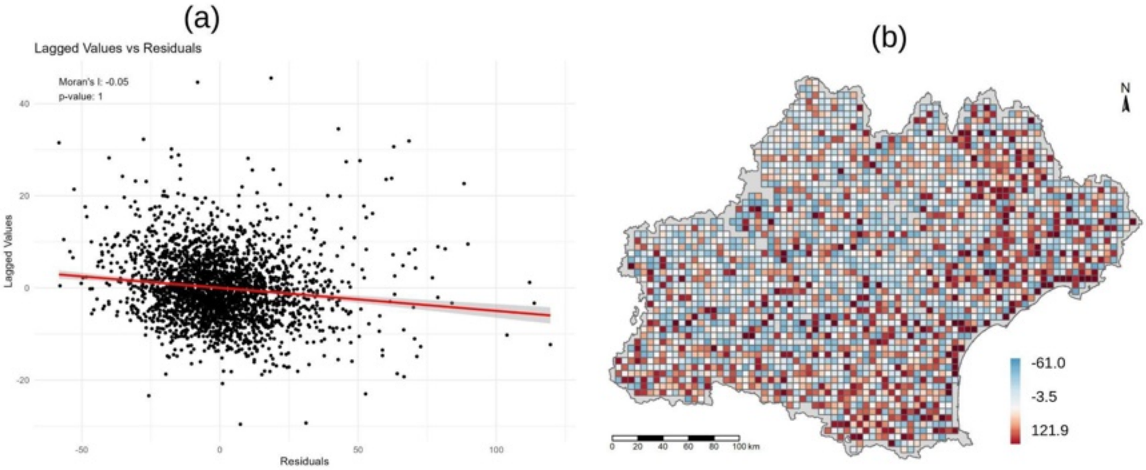


Fig. 4: Analysis of the autocorrelation of the residuals of the bird SEM model. (a) Moran diagram (b) Mapping of residuals from the SEM model (mesh = 5 km)

The coefficients and significance assigned to the different explanatory variables for the best spatial models are then presented in Fig. 5. First, we observed that for all taxa and resolutions, our geodiversity index had a significant positive impact on species richness, consistent across spatial scales considered. Regarding the covariate predictors, their influence and significance were highly taxon-dependent. For vascular plants, species richness was positively correlated with the annual mean temperature and the elevation range of the grid cell. Mean naturalness and annual mean precipitation negatively influenced diversity of plants only at two grid scales (10 km for naturalness and 5 km for precipitation). For butterflies, on the top of geodiversity, naturalness appeared to have an significant positive effect on their diversity as well as elevation range but only at the 7.5km scale.

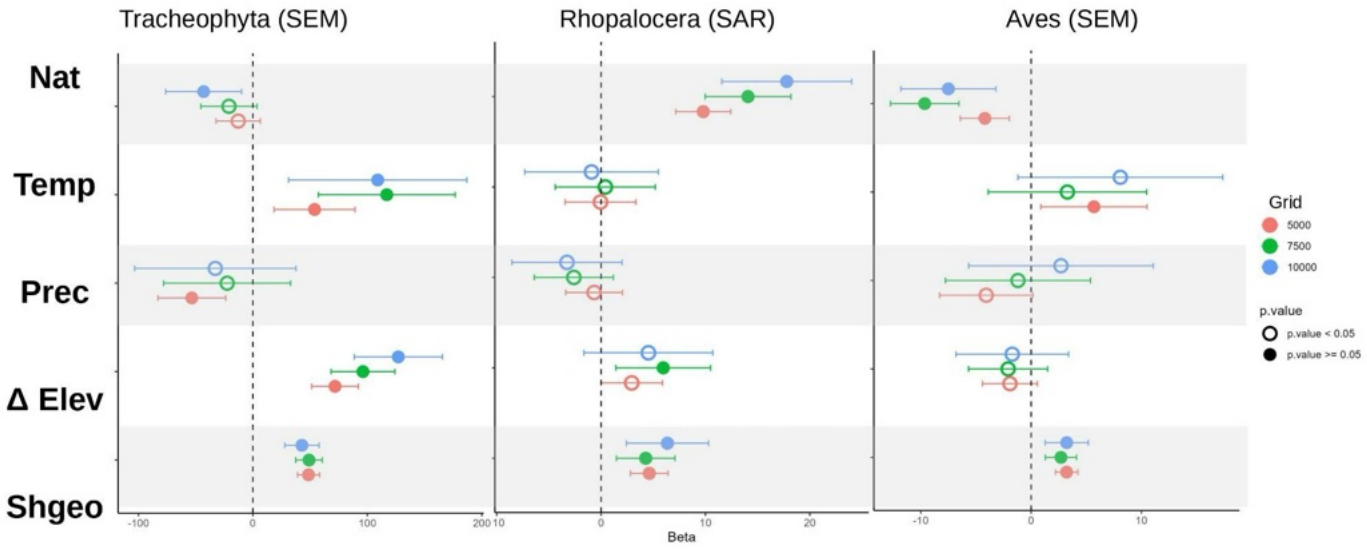


Fig. 5: Standardized coefficients (± 95% CI) from the best-fitting spatial models (SAR and SEM), showing the effects of overall geodiversity and environmental covariates on regional species richness. *Tracheophyta: vascular plants; Rhopalocera: butterflies; Aves: birds; Nat: naturalness; Temp: annual mean temperature; Prec: annual mean precipitation; ΔElev: altitude range; Shgeo: Shannon geodiversity.*

For birds, naturalness has a significant negative effect for all scales. A scale effect is again observed regarding the significance of temperature which is only significant and positive at the 5 km grid level. Regarding the fit quality of our spatial models, all adjusted R² values were higher than those of the classic linear model (Table 3). Similarly, all AIC values of the spatial models were notably lower than those of the classic model.

Table 3: Comparisons of the quality of fit of the best spatial models (SAR, SEM) and the linear model for Tracheophyta (vascular plants), Rhopalocera (butterflies) and Aves (birds)

Taxon	Scale (km)	Test	Autoregression coefficient	p-value	Adjusted R²	Adjusted R² (lm)	AIC	AIC (lm)
Tracheophyta	*5*	SEM	0.765	<0.001	0.663	0.202	18113.31	18993.567
	7.5		0.869	<0.001	0.774	0.342	12168.681	12938.577
	10		0.898	<0.001	0.824	0.414	7703.892	8267.067
Rhopalocera	*5*	SAR	0.527	<0.001	0.478	0.284	14906.629	15322.039
	7.5		0.668	<0.001	0.660	0.442	8323.634	8716.122
	10		0.714	<0.001	0.743	0.522	4943.765	5251.588
Aves	*5*	SEM	0.807	<0.001	0.580	0.119	23196.513	24708.656

7.5	0.851	<0.001	0.626	0.127	10369.967	11136.696
10	0.857	<0.001	0.646	0.150	5714.785	6138.182

For our second modeling approach, which includes the geodiversity components separately (i.e., geology, pedology, geomorphology and hydrology), the same steps were repeated. Once again, problematic spatial autocorrelation of residuals was detected using the Moran's I and residual map analysis. The Lagrange multiplier tests again led us to select the SAR model for butterflies and the SEM model for vascular plants and birds (Table S5).

The analysis of the coefficients from the second model yields broadly similar results for the abiotic variables excluding geodiversity (Fig. 6). Different patterns are observed for each component of geodiversity. As overall geodiversity, pedological diversity is consistently significantly positively correlated with taxonomic richness for each group and spatial scales. On the contrary, the three other components of geodiversity do not have the same effect depending on the taxonomic group studied. Geological diversity appears to have a positive effect only for vascular plants (at all scales) and for birds (only at the 5 km scale). Hydrological diversity does not significantly influence butterflies' richness, but has a significant positive effect on the diversity of vascular plants and birds. Finally, geomorphological diversity does not significantly influence vascular plants or butterflies at the largest scales (7.5km and 10km) but has a positive significant effect on butterflies at 5 km and a significant negative effect on bird diversity whatever the scale.

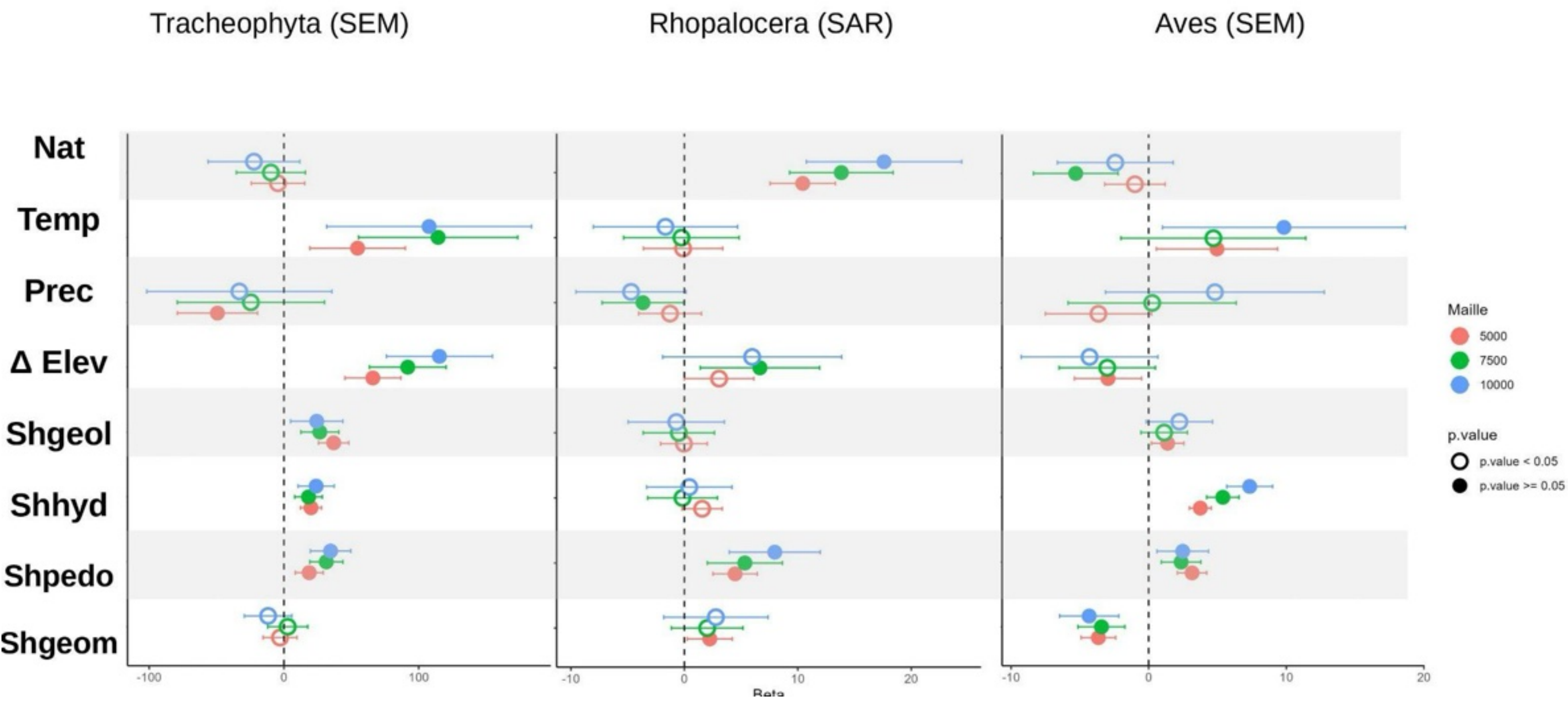


Fig. 6: Standardized coefficients (± 95% CI) from the best-fitting spatial models (SAR and SEM), showing the effects of the four geodiversity components and environmental covariates on regional species richness.

Tracheophyta: terrestrial plants; Rhopalocera: butterflies; Aves: birds; Nat: naturalness; Temp: annual mean temperature; Prec: annual mean precipitation; ΔElev: altitude range; Shgeol: Shannon geology; Shhyd: Shannon hydrology; Shpedo: Shannon pedology, Shgeom: Shannon geomorphology

Finally, all adjusted R^2 values and AIC seem to indicate that the spatial models were better fitted to our data than a classic linear model (Table S6).

3.3. Local analysis

The fit quality of the GWR model, along with the neighborhood radius values selected by AIC minimization, are presented in Table 3.

Table 3: Comparison of the fit quality of Geographically Weighted Regressions (GWR) and neighborhood radius values for Tracheophyta (vascular plants), Rhopalocera (butterflies), and Aves (birds).

Taxon	Scale (km)	Adjusted R^2 (GWR)	Adjusted R^2 (lm)	AIC (GWR)	AIC (lm)	Radius of neighborhood (km)
Tracheophyta	*5*	0.662	1.97	17671.335	19001.875	23
	7.5	0.748	0.338	11926.453	12942.386	20
	10	0.779	0.412	7615.592	8267.187	20
Rhopalocera	*5*	0.529	0.282	14485.713	15324.256	32
	7.5	0.657	0.440	8140.136	8716.358	25
	10	0.741	0.520	4799.290	5251.481	20
Aves	*5*	0.587	0.122	22532.134	24698.681	16
	7.5	0.602	0.133	10120.136	11126.472	21
	10	0.595	0.149	5611.471	6136.907	19

Based on the comparison of adjusted R^2 values and AIC, the GWR model appeared to better capture the structure of our data than the simple linear model. Spatial distribution of the GWR coefficients revealed spatial non-stationarity between overall geodiversity and all predictive environmental variables for all taxa and all scales (Fig .S5). The relationship between species richness and geodiversity (Fig. 7) also shows local spatial variation across the region for all taxa. While some areas, such as the center-west (Gers, Toulouse area), exhibit no significant association or even significant negative correlations, extensive zones of significant positive relationships are consistently observed across taxa, particularly in the northeast (Massif Central) and the south (Pyrenees).

Overall, the local relationship between geodiversity and species richness appears more consistent across taxa (i.e. more significant positive local correlation in common between the three taxa, Fig. S6), with spatial non-stationarity being generally less pronounced than that observed for climatic, global topographic, or human footprint variables (Fig. S5).

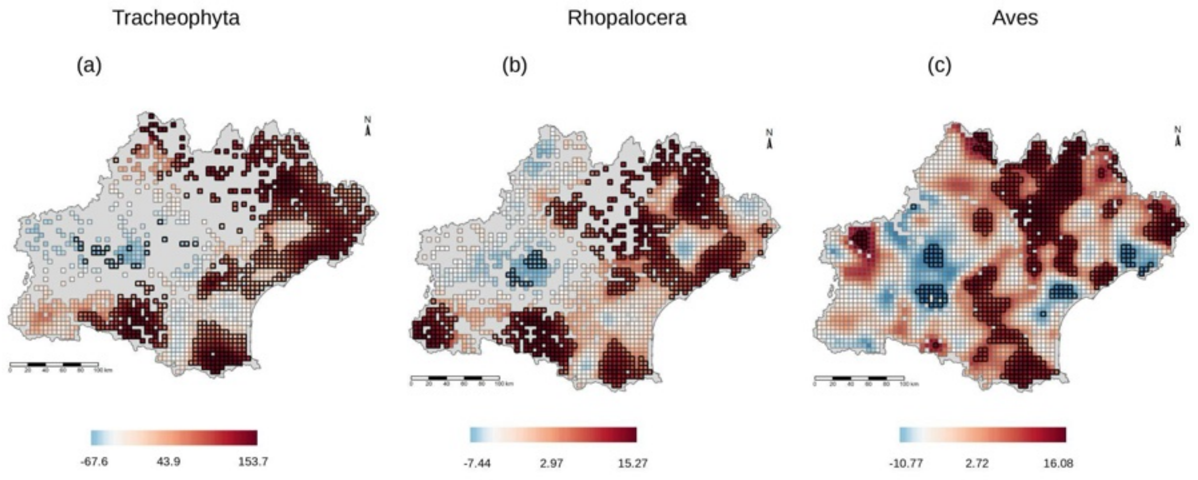


Fig 7: Spatial distribution of geodiversity coefficients following Geographically Weighted Regression (GWR) for a 5 km grid. The meshes whose contours are in bold are those where the local coefficients were significant for Tracheophyta: *vascular plants (a);* Rhopalocera*: butterflies (b);* Aves*: birds (c)*. Red meshes indicate a positive relationship while blue indicates a negative relationship between biodiversity and geodiversity and grey no relationship. Grey area with no mesh occurs because the cell does not meet inclusion criteria for biodiversity exhaustivity (>50% singletons, see methods 2.2).

4. Discussion

This study aimed to evaluate the spatial relationships between geodiversity components (e.g. geology, pedology, geomorphology and hydrology) and biodiversity (i.e. species richness) across vascular plants, butterflies, and birds. In so doing, we provided, for the first time, a detailed assessment of how geodiversity factors influence biodiversity patterns across multiple spatial scales and multiple taxa for one of the biggest and most geodiverse regions of France.

At a regional level, we show that geodiversity was positively, significantly correlated with species richness in a consistent way across the three studied taxa. This result is in line with different previous studies which reported a positive relationship between geodiversity and, (1) the richness of vascular plants (Bailey et al., 2017; Toivanen et al., 2024), (2) butterflies (Tukiainen et al., 2017a), and (3) birds (Read et al., 2020). The positive relationship between our geodiversity index and species richness was consistent across all taxa and spatial resolutions (5, 7.5 and 10 km) and was not higher for taxa at the base of the trophic chain. These results suggest that a CNS program based on geodiversity would be efficient to protect taxonomic groups with very different biological and ecological needs whatever their position in the trophic chain.

Other explanatory variables also had an impact on species richness. For instance, elevation range and annual mean temperature were positively, significantly linked to vascular plant richness, a finding consistent with several studies conducted at various scales on this taxon (Tukiainen et al., 2017b; Zarnetske et al., 2019). This result was expected given the nature of habitats in Occitanie, where the Mediterranean region is considered a hotspot of floral diversity due to its specific climatic conditions, and the mountainous landscapes characterized by a high rate of endemism.

For butterflies and birds, naturalness appeared to play an important role in explaining species richness, but not for plants. The effect of naturalness differed between the two animal taxa. On the one hand, it was positively correlated with butterfly species richness, a result consistent with previous studies highlighting the negative impact of anthropogenic pressures on the taxonomic diversity of this group (Bobo et al., 2006; Gallou et al., 2017). On the other hand, naturalness was negatively correlated with bird species richness. Several explanations might account for this phenomenon, such as the presence of maximum bird diversity in moderately anthropized environments (Blair, 2011; Meynard et al., 2011), an overestimation of species richness near cities, or differences in the influence of the various components of naturalness, making a general interpretation challenging. In addition, naturalness is generally low in the littoral area (high building density) and high in mountain areas. Bird diversity shows the opposite pattern, with higher species richness in coastal areas—likely driven by the coexistence of terrestrial and marine species (Graells et al., 2022)—while high-elevation zones typically support fewer species (Quintero & Jetz, 2018).

We therefore considered that interpreting the effects of naturalness in our study was premature for the time being. Nevertheless, given that it had been one of our most explanatory variables, this phenomenon should be further explored by studying the effect of its three components (i.e., hemeroby, building density, and ecological continuity) on taxonomic diversity at both regional and local scales.

We also found that components of geodiversity do not have the same impact on the diversity of our three taxa. Pedology significantly supports the diversity of all taxa and therefore is of great importance in combating biodiversity collapse, a finding already noted in previous studies (Ibáñez & Feoli 2013; Stein et al., 2014; Molina-Venegas et al., 2016). Hydrological diversity has a positive influence on the diversity of vascular plants and birds, but not on butterflies. One possible explanation is that many bird or plant species are closely tied to aquatic environments. An increase in the diversity of wetlands or water bodies within a grid cell would thus have allowed new specialist species of this habitat to establish themselves, increasing overall species richness. On the contrary, few butterfly species are directly dependent on this type of habitat explaining why this variable did not significantly influence the diversity of this taxon. Compared to the other two components, the effect of geological diversity appears to be weaker, with a positive correlation only for vascular plants. These observations aligned with the results of a previous multi-taxa study (Tukiainen et al., 2017a), which found similar dominance patterns for vascular plants and butterflies. However, that study showed that geological diversity had a strong impact on the richness of bryophytes, lichens, or beetles. Finally, geomorphological diversity - as calculated from the Geomorphon algorithm - was considered by Bailey et al. (2017) as a powerful explanatory variable of biodiversity patterns. However in our study, this variable had no significant impact on vascular plants or butterflies, and was negatively correlated with bird diversity at all spatial resolutions. The spatial scale used in our analysis (≥5 km grid cells) may have hidden the previously observed relationship between vascular plant richness and landform diversity, which has been shown to be stronger at finer spatial grains (e.g., 1 × 1 km cells; Bailey et al., 2017). The negative relationship observed between geomorphological diversity and bird richness may be explained by similar mechanisms to those described above for the negative relationship with naturalness. In particular, an overestimation of species richness near urban areas—typically located on flat terrain—and the high bird diversity in coastal regions, which often exhibit limited landform variety, are likely contributing factors.

Our local analysis (GWR) showed that the relationship between biodiversity and geodiversity is not spatially stationary: the geodiversity of some localities seemed more likely to promote biological diversity than others (Fig. 7). This finding aligns with the work of Ren et al. (2021), who also observed spatial non-stationarity in the effect of geodiversity on biodiversity using GWR. Interestingly, the areas where biodiversity and geodiversity are positively correlated tend to overlap more consistently across the three taxa than do areas of positive correlation between biodiversity and our other environmental variables (Figs. S5 and S6). This further supports the use of geodiversity as a holistic indicator for informing multi-taxa conservation planning at a fine scale (Tukiainen et al., 2017a).

One factor that could best explain this non-stationarity is anthropization, a factor often overlooked in this type of study (Tukiainen et al., 2017b) with currently contradictory results (Rasanen et al., 2016; Ren et al., 2021). For all taxa, the areas where geodiversity has the greatest positive influence on species richness are primarily found in less anthropized spaces (e.g., the Pyrenees, Lozère, Aveyron). Conversely, areas near major urban centers negatively affect the influence of geodiversity on species diversity (e.g., Toulouse and Montpellier metropolitan areas). However, one unexpected result was a locality in the west, near the border between Gers and Tarn-et-Garonne *départements*, which is associated with a negative link between geodiversity and biodiversity (Fig. 7). This environment is highly rural, reinforcing the complex relationship between geodiversity and biodiversity given the interference of various agricultural practices (e.g., intensive vs. extensive) and related landscape mosaics (e.g., openfields, bocage landscape) with possibly very different effects on biodiversity patterns. Future studies in Occitanie should seek to better understand what drives the result in this zone dominated by agricultural lands, despite its high geodiversity (Fig. 2). Overall, these findings highlight the need to better integrate anthropogenic drivers into geodiversity–biodiversity analyses. Despite the scarcity of focused studies, available results remain inconclusive, with some reporting positive (Ren et al., 2021) and others negative (Rasanen et al., 2016; Tukiainen et al., 2017b) effects of anthropization. We therefore encourage further investigation into how human activity interacts with geodiversity to shape biodiversity patterns, especially in the context of conservation planning.

In our regional analysis, we found that overall geodiversity (Fig. 5) and pedological diversity (Fig. 6) significance is not affected by the modifiable areal unit problem (MAUP). On the contrary, the MAUP plays a role on the significance of other components of geodiversity and on most of our other explanatory variables (Fig. 5 and 6). For instance, mean annual precipitation significantly affects vascular plants at a 5 km grid resolution but has no effect at 7.5 km or 10 km resolutions. MAUP also significantly affects the effects of naturalness on vascular plants and the effects of mean annual temperature and elevation range on bird diversity. We therefore consider it essential to systematically include multiple spatial resolutions in biodiversity-geodiversity studies: either to evaluate the robustness of the relationship across spatial scales, or to identify the most appropriate scale for implementing effective conservation actions.

The impact of MAUP could not be fully addressed in our local modeling through GWR. While the neighborhood radii had been optimally selected for each taxon and resolution (Table 4), this approach might have overlooked the spatial heterogeneity of the underlying processes driving non-stationarity. Recent advancements, such as multiscale geographically weighted regression (MGWR), proposed varying the radii by variable or even by observation to better capture these spatially heterogeneous processes. We recommend that future studies explore the use of MGWR or similar approaches to provide a more nuanced understanding of the effects of MAUP and to account for the complex spatial dependencies in biodiversity-geodiversity relationships.

We also believe that more attention should be paid to the landscape scale when analyzing the geodiversity-biodiversity link. Such studies could particularly benefit from the significant advancements in remote sensing made in recent years (Rhodes et al., 2022), enabling increasingly fine-resolution environmental descriptions. For example, LiDAR (Light Detection and Ranging) allowed detailed topographic analysis and modeling of microclimatic indices derived from topography, such as daily solar radiation (Bergen et al., 2009; Anderson & Gaston, 2013). Exploring geodiversity–biodiversity relationships at even finer spatial scales (e.g., plot level) also represents a promising avenue, particularly for studies focusing on how geodiversity influences community composition of plants, fungi, and arthropods (Hjort et al., 2022).

To compute our biodiversity metric, we used data characterized by heterogeneity in terms of sources, validation processes, and spatial-temporal coverage (see 2.2. Biodiversity data, Tables S1-S3). However, we believed that our approach was relevant for detecting general trends. Using species richness allowed us to bypass species abundance data, which are heavily influenced by the number of observations. Moreover, species richness is the most commonly used metric in the literature on this subject (Field et al., 2009; Tukiainen et al., 2023), enabling us to build on previous studies and compare the relevance of our results.

In our statistical models we used a non-parametric species richness estimator which has been shown to be less biased by sampling intensity than species accumulation curves or observed species richness (Brose et al. 2003). To exclude under-sampled grid cells from our modeling, we decided, based on a review of the literature, to remove any grid cell with more than 50% singletons (Brose et al., 2003; Marcon, 2015). Yet, other innovative approaches could be tested in the future. For instance, one could develop a new completeness index that incorporated additional variables, such as the number of observations, the singleton rate, the difference between estimated and observed richness, and more.

Given the rapid increase in freely accessible species occurrence data (e.g., GBIF, OpenObs), it is crucial that more studies adopt standardized protocols for utilizing such data in macroecological research (Wüest et al., 2020). Advancing analytical methods to account for heterogeneous sampling effort will significantly enhance our understanding of biodiversity–geodiversity relationships (Soroye et al., 2018; Botella et al., 2021). More research should also focus on identifying and correcting major knowledge gaps within our territory, particularly in terms of taxonomy and spatial coverage.

The creation of our geodiversity index was largely inspired by previous work related on the CNS strategy as well as studies which focused on geodiversity (e.g., Tukiainen et al., 2017a; Bétard & Peulvast, 2019; Alberico et al., 2023). The high spatial variation in the overall Shannon geodiversity index, and its alignment with known patterns of lower (e.g., seashores, lowlands) and higher (e.g., mountainous regions) geodiversity, suggests that our index effectively captures the spatial heterogeneity of the study area. However, we observed lower geomorphological diversity in the Pyrenees compared to some hilly landscapes. This reduced diversity, as detected by the Geomorphon method, may be due to the dominance of a few broad landform classes in mountainous areas, as well as limitations of the algorithm in capturing fine-scale topographic complexity. Since this method is widely used in global geodiversity assessments, and given that including or excluding geomorphology in our composite index did not significantly alter our results, we chose to retain it. Nevertheless, further research is needed to identify morphological indicators better suited to capturing landform diversity in mountainous regions at the spatial scales considered in our study.
It would also be interesting to optimize our hydrological diversity index by, for example, adding a component on water dynamics in soils (e.g., edaphic humidity). The low resolution of the pedological layer remains a limitation, which restricts our ability to extend our study to a more localized scale. These gaps in the availability of high-resolution data could, however, be addressed in the coming years. The national CarHab project, currently under development, could, for example, provide information on soil parameters such as moisture and pH at a 1:25,000 scale (IGN, PatriNat). The development of new GIS tools and data thus offers promising prospects for conservation strategies based on geodiversity characterization.

5. Conclusion

Our study highlights a consistent positive correlation between overall geodiversity and species richness across all taxa, supporting the relevance of geodiversity as a key factor in biodiversity conservation. However, the influence of different components of geodiversity (except pedological diversity) varied depending on taxonomic group, spatial scale, and environmental context, underscoring the complexity of this relationship.

Our analysis revealed the spatial non-stationarity of geodiversity's effects on biodiversity and highlighted the importance of localized and context-specific studies. Indeed, various spatial modeling tools (SAR, SEM, GWR) allowed us to better understand the complex relationship between geodiversity and biodiversity. Using tools like GWR within the framework of the Conserving Nature's Stage (CNS) strategy and not focusing solely on large-scale global models is warranted if we wanted to consider the fact that the effect of geodiversity on biodiversity is spatially dependent (Bailey et al., 2017; Ren et al., 2021). Conservation measures based on geodiversity might have proven ineffective if not nuanced locally, according to the characteristics of the local context.

Future studies should also focus on this link at multiple levels of diversity (e.g., beta, gamma) and on functional and genetic diversity. Indeed, we believed the success of the CNS strategy relied primarily on a solid local understanding of the structures that truly supported biodiversity in all its forms. Such a strategy could be highly effective in a geodiverse territory for identifying priority areas for establishing new conservation spaces.

Finally, we believed that the CNS strategy should not be used as a substitute for traditional conservation methods but rather as a complement. The systematic use of coarse filters might lead to the neglect of many rare or endemic species that could play crucial roles in specific ecosystems. It is also important to recognize that every species should have benefited from protection, regardless of its utility to humans, highlighting the importance of biodiversity beyond utilitarian perspectives. Therefore, we believed that the most effective strategy to address the urgency of biodiversity collapse would be to multiply conservation strategies to ensure comprehensive protection of all aspects of biodiversity.

Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

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Author Contributions

MC, FB, TF and TS contributed to the study conception and design. Data analysis was performed by TS and MG. The first draft of the manuscript was written by MG. All authors participated in the interpretation of the results, commented, edited and gave substantial feedback on previous versions of the manuscript. All authors approved the final manuscript.

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