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

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31 **Abstract**

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

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

41 **Methods:** Species richness for each taxonomic group, along with geodiversity, climate,
42 topography, and naturalness metrics, were aggregated within spatial meshes of 5 km, 7.5 km,
43 and 10 km resolution. We applied spatially explicit models to quantify the effects of overall
44 and component-specific geodiversity (i.e., geological, pedological, hydrological,
45 geomorphological diversity), alongside elevation range, temperature, precipitation and
46 naturalness on species richness across scales. We used two complementary modeling
47 approaches. **Regional models** were applied to evaluate the overall relationship between
48 geodiversity and species richness across the whole study area. **Local models** were then used to
49 detect whether this relationship varied from one place to another within the region.

50 **Results:** At the regional scale, geodiversity showed a significant and consistent positive
51 association with species richness for all taxa and spatial resolutions, stronger than climatic,
52 topographic, or naturalness variables. Pedological diversity was the component of geodiversity
53 with the most consistent effect across taxa. At the local scale, we found strong variation in the
54 strength of the biodiversity–geodiversity relationship. Still, these relationships were more
55 consistent across taxa than those involving other environmental predictors.

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

60

61 **Keywords:**

62 geodiversity, biodiversity, bird, plant, butterfly, Occitanie

63

1. Introduction

Over the past century, human population growth and rising global living standards have increased pressure on ecosystems (Steffen et al., 2015). One main consequence 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.

Geodiversity, the abiotic variability of the Earth's surface and subsurface including geological, geomorphological, soil, and hydrological features, provides a diversity of physical environments that can serve as refuges and habitats for many species (Gray, 2013; Maliniemi et al., 2024). The concept of the ecological niche is central to understanding the mechanisms linking geodiversity and biodiversity. Following Hutchinson's definition, the niche represents an n-dimensional hypervolume defined by the abiotic and biotic conditions under which a species can persist (Colwell & Rangel, 2009). By broadening the range of environmental conditions available within a landscape, geodiversity can expand the diversity of habitat types, thereby reducing niche overlap and facilitating the co-occurrence of ecologically distinct species (Stein et al., 2014). This mechanism provides a theoretical basis for the frequently observed positive association between geodiversity and species richness. In the literature, geodiversity has repeatedly been shown as a potential driver of terrestrial plant diversity, particularly in terms of species richness, with evidence ranging from local scale (Salminen et al., 2023) to national scale (Bailey et al., 2017; Tukiainen et al., 2017b; Toivanen et al., 2024). Although the link between terrestrial plants and geodiversity seems rather well established, a smaller number of publications concern other taxa: one study found a positive correlation between geodiversity and the diversity of macro-invertebrates in rivers (Kärnä et al., 2018), another one with bird diversity (Read et al., 2020) and third one with the diversity of invertebrates, lichens, and mammals (Tukiainen et al., 2017a).

However, such relationships are not universally positive or similar between taxa, biogeographic areas and studies (Wallis et al., 2021). Several mechanisms can also weaken or reverse this relationship. First, the heterogeneity–area trade-off implies that when habitats are too diverse within a limited area, each habitat becomes smaller, potentially excluding species that require larger continuous patches (Allouche et al., 2012). Second, isolation effects may occur when highly heterogeneous landscapes fragment habitats into disconnected units, limiting species dispersal and reducing population viability (Ricklefs, 1987, Kadmon et al., 2007). Finally, niche mismatches can arise when the abiotic diversity provided by geodiversity does not align with the ecological requirements of local species, resulting in negligible or even negative biodiversity responses (Pagel, et al. 2020).

Yet, the Conserving Nature's Stage framework which incorporates geodiversity into conservation planning (Beier et al., 2015; Gray, 2013), makes it a promising strategy for

107 holistic biodiversity protection and restoration. In addition to providing heterogeneous abiotic
108 conditions that facilitate the co-occurrence of multiple species, the Conserving Nature's Stage
109 framework also suggests that geodiversity can buffer the impacts of global change on
110 biodiversity, as the abiotic "stage" is generally more resilient to above ground global change
111 than the biotic communities it supports (Beier et al., 2015).

112

113 While the positive link between geodiversity and species richness has been repeatedly
114 confirmed, several limitations and four key research gaps need to be explored.

115

116 (1) Single-taxa studies: While the relationship between geodiversity and biodiversity is
117 generally positive, evidence remains limited regarding its generality (Tukiainen et al., 2023).
118 Most research has focused on vegetation, particularly vascular plants, leaving other taxonomic
119 groups much less studied (Field et al., 2009; Tukiainen et al., 2017a). Indeed, studies on linking
120 geodiversity and animal communities are rare, restricting our understanding of these complex
121 interactions. Including multiple taxonomic groups within the same region is crucial for fully
122 capturing these complexities, assessing the generalizability of biodiversity–geodiversity
123 relationships, and ensuring that biodiversity conservation or restoration programs based on
124 geodiversity do not inadvertently prioritize certain groups over others.

125

126 (2) Geodiversity sub-indices: While these broad patterns are known, it is still unclear which
127 specific components of geodiversity are most beneficial for different taxonomic groups and
128 which promotes biodiversity as a whole across trophic level. Indeed, most studies use overall
129 geodiversity indices, which makes it difficult to know how individual components contribute
130 to biodiversity patterns. Yet, each component or geodiversity sub-indices can influence
131 ecosystems in distinct ways. Hydrology, for example, plays an essential role through its
132 structures (presence of water) and processes (water flow), contributing to ecological
133 connectivity, water storage, and habitat diversity (Bailey et al., 2017). Geological diversity,
134 often defined by the diversity of rock types (i.e., lithodiversity), directly influences biodiversity
135 through its substrate properties, which regulate hydrology and mineral resources (Miguez-
136 Macho and Fan, 2012). Soil diversity is a major determinant of plant biodiversity patterns, as
137 variation in fertility, chemical composition, and soil types strongly influences species
138 distributions (Pellissier et al., 2013). Geomorphology, on the other hand, acts through its
139 landforms and processes (e.g., mass movements, glaciations), providing both diverse habitats
140 and ecological disturbances (Tukiainen et al., 2023). Whereas traditional ecological research
141 has extensively used topographic variables such as elevation, elevational range, slope or aspect
142 as proxies for environmental heterogeneity (e.g. Stein & Kreft 2015) geomorphological
143 diversity represents a broader characterization of abiotic heterogeneity than topography alone
144 (Bailey et al. 2017; Stein et al. 2014). Here, we follow recent work that defines geodiversity as
145 distinct from these “crude” measures (Bailey et al. 2017; Tukiainen et al., 2017a). We thus
146 focus on explicit components of geodiversity, including lithology, soils, geomorphological
147 landforms and hydrological features, which can complement topographic descriptors by
148 providing a more detailed appraisal of the abiotic environment (Bailey et al. 2017).

149

150 (3) Local variations of geodiversity-biodiversity relationships: The effects of geodiversity on
151 biodiversity may vary within regions, reflecting spatial non-stationarity (i.e. the idea that
152 relationships between variables can change across space). This means that the strength and
153 direction of relationships between variables can differ depending on spatial context. Here,
154 spatial context refers not just to regions or ecosystems but to the local neighborhood defined
155 by spatial weighting. Such spatial contexts may concern various spatial scales, depending on
156 the spatial patterns of the omitted processes affecting the relationships. Ignoring this variation
157 can result in oversimplified and potentially misleading conclusions (Ren et al., 2021, Tukiainen
158 et al., 2017b). Geographically Weighted Regression (GWR) is a spatial model that lets
159 relationships vary across space rather than assuming one global effect. Instead of fixed
160 coefficients, it estimates local ones, showing how relationships change with spatial context.
161 Such spatial models have only rarely been used to study links between geodiversity and species
162 richness (but see Ren et al., 2021).

163

164 (4) Single-scale studies: Many studies have been conducted at only one spatial scale (Tukiainen
165 et al., 2017b; Read et al., 2020), leading to partial conclusions due to the Modifiable Areal Unit
166 Problem (MAUP) (Openshaw & Taylor, 1979). The MAUP arises because statistical
167 relationships depend on how spatial data are aggregated, being sensitive both to the scale (size
168 of spatial units) and to their zoning (the configuration of boundaries) (Jelinski & Wu, 1996).
169 This means that correlations between biodiversity and geodiversity may appear stronger,
170 weaker, or even contradictory depending on the resolution or partitioning of the study area. A
171 well-known illustration is Simpson's paradox, where aggregated data obscure or invert trends
172 observed at finer scales (Simpson, 1951). Consequently, neglecting the MAUP can undermine
173 the reliability and comparability of biodiversity-geodiversity studies, emphasizing the need for
174 multi-scale approaches.

175

176 Here, we investigate the link between geodiversity and biodiversity at the regional scale of
177 Occitanie (South of France) across three trophic levels (plants, butterflies and birds). By
178 focusing on vascular plants, butterflies, and birds, our objective is to spatially compare this
179 potential relationship across three taxa with different life traits and ecological needs. These
180 three taxa have been selected due to the high number of observations available within our study
181 area. These taxonomic groups were among the most well-documented in France (Touroult et
182 al., 2015). The choice of butterflies and birds also reflects the aim of addressing existing
183 knowledge gaps regarding animals (in particular insects) within the framework of the
184 Conserving Nature's Stage.

185

186 In so doing we will test the following hypotheses:

187

- 188 (a) Overall geodiversity is positively, consistently and significantly correlated with
189 biodiversity across all taxa, with a stronger link for vascular plants, followed by
190 butterflies and, finally, birds due to their respective dependency to belowground
191 resources.
- 192 (b) The different components of geodiversity (i.e. geology, hydrology, pedology and
193 geomorphology) do not influence the various taxa uniformly.

194 (c) Geodiversity–species richness relationship can show local variations.

195 (d) MAUP (scale of spatial data aggregation) has a significant effect on the relationship
196 between geodiversity and biodiversity.

197
198 Our analyses at the regional (hypotheses a, b and d) and local scales (hypotheses c) pursued
199 complementary objectives. The regional approach aimed to test general trends (hypotheses a
200 and b), by assessing whether overall geodiversity (hypothesis a) and its sub-components
201 (hypothesis b) constitutes robust predictors of species richness on average across the entire
202 territory. In hypothesis d, we evaluated how data aggregation at three spatial scales (5, 7.5 and
203 10 km grid size) modulates these results (addressing the MAUP issue). This overall vision is
204 necessary to evaluate the relevance of the Conserving Nature’s Stage strategy at a broad
205 operational scale. In contrast, the study of local variations (hypothesis c) using local models
206 (Geographically Weighted Regression, GWR), allows us to identify areas where associations
207 are stronger, weaker, or even negative. This dual approach thus makes it possible to identify,
208 on the one hand, a robust trend that can be generalized at the regional scale, and, on the other
209 hand, the local nuances crucial for guiding the implementation of conservation measures
210 adapted to landscape and socio-ecological specificities.

212 2. Materials and methods

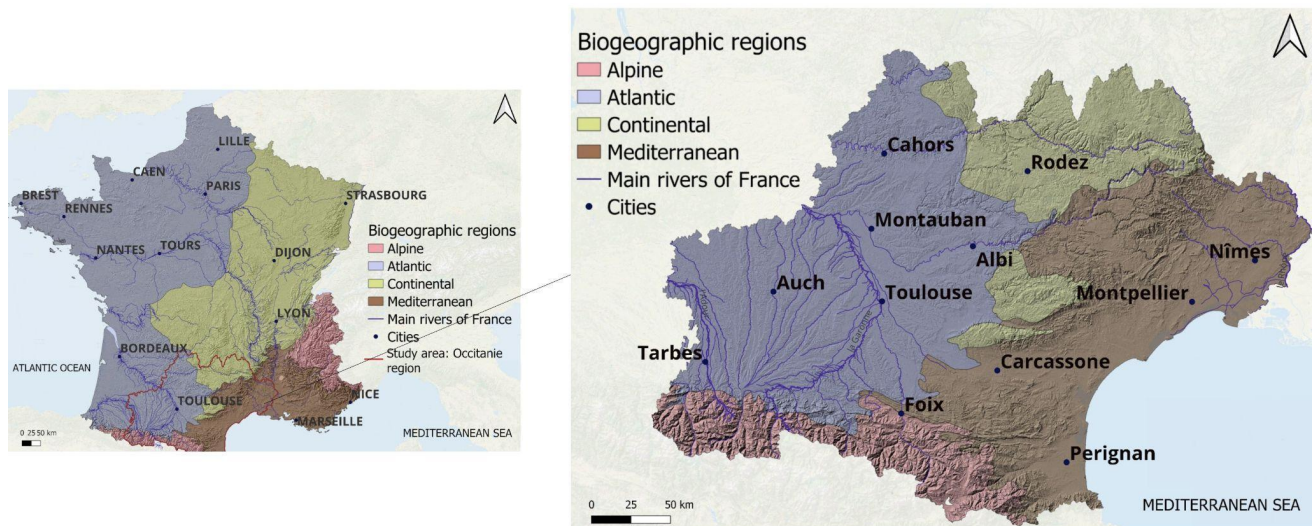
213 2.1. Study area

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

221 From a geological point of view, Occitanie is like a mosaic (Fig. S1A). The Massif Central has
222 volcanic and granite formations, showing evidence of ancient tectonic activity. The Pyrenees
223 were formed by the collision of the Iberian and Eurasian tectonic plates, creating folded
224 mountain chains. The Languedoc coastline is shaped by lagoons, saltwater ponds, and sandy
225 beaches, which result from coastal erosion and sediment deposition.

226 Three main types of climate coexist in the region (Fig. 1). The Languedoc coastline has a
227 Mediterranean climate, with hot, dry summers and mild, wet winters. The Aquitaine Basin has
228 an oceanic (Atlantic) temperate climate, with mild, wet winters and cooler summers compared
229 to the Mediterranean climate. Finally, the Pyrenees and Massif Central are influenced by
230 mountain climates, with cold winters and cool, wet summers.

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



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

234 2.2 Biodiversity data

235 All occurrence data were sourced from the OpenObs database (Ainsa et al., 2023), the French
 236 national biodiversity data portal managed by PatriNat (OFB-CNRS-MNHN-IRD; Norvez et
 237 al., 2023). Three datasets were constructed: vascular plants (Tracheophyta, $n = 4,279,291$),
 238 birds (Aves, $n = 4,765,000$), and butterflies (Papilionidae, Hesperidae, Pieridae, Riodinidae,
 239 Lycaenidae, Nymphalidae, $n = 1,106,770$). The full list of used datasets is available in Table
 240 S1-S3. While these data are characterized by significant heterogeneity in terms of sources and
 241 protocols, the three taxons are those with the highest number of observations and the best
 242 spatial coverage in the Occitanie Region. They mainly came from scientific studies, collection
 243 records, opportunistic citizen observations, and participatory science initiatives conducted as
 244 part of public policies (e.g., the national natural heritage inventory, INPN; Robert et al., 2022).

245 Identifying and correcting as many potential biases as possible associated with using such a
 246 large and heterogeneous volume of data was essential before any interpretation (Kissling et al.,
 247 2018; Jetz et al., 2019; Wüest et al., 2020). Here, we identified and addressed several potential
 248 biases, including taxonomic misidentifications, uneven temporal coverage, spatial aggregation
 249 and uneven sampling effort, abundance-based distortions, and false absences in under-sampled
 250 grid cells.

251 For the taxonomic dimension, PatriNat performs an initial quality check, including compliance
 252 with international standards and taxonomic harmonization using the TaxRef reference system
 253 (Gargominy et al., 2022), to reduce misidentification errors. Only observations identified to the
 254 species or subspecies level were retained.

255 To limit biases related to the temporal dimension, our research focused on the period from 1990
 256 to the present, excluding older observational data, which were unevenly represented.

257 The spatial dimension required the most attention, given our research questions and
 258 hypotheses. We retained only observations geolocated at specific geographic points, excluding
 259 aggregated occurrences at municipal or national grid scales. Another issue was the uneven
 260 sampling of the territory, with certain areas being under- or over-sampled (e.g., a higher density
 261 of observations near urban areas). To address this significant bias, we focused solely on
 262 calculating species richness per grid cell. Our choice not to use abundance-based indices was
 263 intended to limit the influence of sampling biases related to effort heterogeneity in
 264 opportunistic databases. Indeed, in this type of data, abundance values do not reflect ecological
 265 reality, but rather survey intensity (some areas and species being observed much more than
 266 others). Conversely, species richness (presence/absence per grid cell) is less sensitive to these
 267 effort biases, because it does not directly depend on the number of times a species was observed
 268 (Kissling et al., 2018).

269 In addition, to compensate for false absences of species and to identify potentially under-
 270 sampled grid cells relative to others, we decided to use non-parametric estimators of species
 271 richness (Brose et al., 2003). These estimators are widely recognized as better predictors of
 272 true richness compared to observed richness in most cases (Brose et al., 2003; Vallet et al.,
 273 2012; Walther et al., 2015).

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

278

279

280

$$281 \quad (1) \quad S_{est} = S_{obs} + n_1 \frac{N - 1}{N}$$

282

283 Where:

284

- S_{est} : Estimated richness

285

- S_{obs} : Observed richness

286

- N : Number of data points in the grid cell

287

- n_1 : Number of species observed only once in the grid cell (singletons)

288

289

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

296

297 2.3. Geodiversity data

298 All the geodiversity data used are listed in Table 1 and regional maps of original geofeatures
 299 used are shown in Fig.S1. For the compilation of geological and pedological indices, each type
 300 of formation was aggregated within each grid cell, and the Shannon index (2) was then
 301 calculated (Manosso et al., 2021; Atkinson et al., 2022):

302 (2)

$$303 H' = - \sum_{i=1}^S p_i \log_2 p_i$$

304 Where:

- 305 • S : Richness
- 306 • p_i : Area of the formation / Area of the grid cell

307 **Table 1:** Summary of geodiversity, topographic, climatic and land use variables used for modeling and the main
 308 calculated indices.

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

309

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

321

322 The hydrological index was constructed based on the work of Bétard & Peulvast (2019). The
323 first step involves calculating the Strahler index for each watercourse using our digital terrain
324 model (BD Alti 25 m DTM) and the "Strahler order SAGA" tool (Passy & Théry, 2018)
325 available in QGIS software (QGIS.org, 2025). This index captures the complexity of the
326 tributary network of a watercourse (Strahler, 1952). Next, the richness of each watercourse
327 order and the richness of water bodies (i.e. canal, marshes, ponds and gravel pit lakes) were
328 quantified per grid cell. A common Shannon index was then calculated based on the length of
329 each type of watercourse and the surface of water bodies.

330

331 To ensure our work was comparable to most other studies, we decided to create an overall
332 geodiversity index by summing the Shannon scores of our four sub-indices (geology, pedology,
333 hydrology and geomorphology). This method for constructing the geodiversity index preserves
334 the multidimensional character of geodiversity and avoids biases from components with more
335 categories (Bétard & Peulvast, 2019, Ferrando et al. 2021, Polman et al. 2024). Geodiversity
336 maps are presented for each scale in Fig. S3.

337

2.4 Topographic, climatic and naturalness covariates

338 Using the BD Alti 25 m DTM (IGN, <https://geoservices.ign.fr/bdalti>), we calculated elevation
339 range within each grid cell as a global topographic covariate, selected for its lack of correlation
340 with climatic variables. Climatic covariates included annual mean temperature and annual
341 mean precipitation, both averaged per grid cell from the WorldClim database (1970– 2000).

342 To account for anthropogenic influence, we used the mean naturalness index per grid cell. The
343 naturalness index is a nationally developed metric in France, created as part of the CartNat
344 project (UICN, <https://uicn.fr/aires-protegees/wilderness-2/>; Guetté et al., 2018). It
345 quantitatively assesses the level of disturbance in natural landscapes, with higher values
346 indicating minimal or no human impact. The index integrates three components: hemeroby
347 (i.e., the degree to which vegetation deviates from its potential natural state), building and road
348 density, and ecological continuity. For detailed methodology, see Guetté et al. (2022).

349

2.5. Data aggregation

350 All data were aggregated at three spatial scales. Regular grid cells with sizes of 5 km, 7.5 km,
 351 and 10 km were selected as a compromise between analyzing the phenomenon at the finest
 352 possible resolution and the resolution of our initial data (the pedology layer being the limiting
 353 factor with a resolution of 1/250,000). We used different grid resolutions to consider the
 354 modifiable areal unit problem (MAUP) in spatial modeling. For the 5 and 10 km grids, we used
 355 spatial referential provided by the French National Inventory of Natural Heritage (INPN;
 356 Robert et al., 2022) to optimize biodiversity data pooling. We computed the 7,5km with the
 357 Lambert93 referential (EPSG 2154). Grid cells in contact with the boundaries of our regional
 358 study area were excluded from the analysis to account for edge effects, which could also bias
 359 our results (Zarnetske et al., 2019). The number of grid cells was $n=2,721$ for the 5 km
 360 resolution, $n=1,172$ for 7.5 km, and $n=641$ for 10 km.

361 2.6. Statistical analyses

362 All analyses were performed with R software version R Core Team (2024). To address our
 363 research questions, we first aggregated biodiversity, geodiversity and covariates into grid cells
 364 and then used two statistical modeling approaches: a regional model to study the average
 365 relationship between species richness and geodiversity variables and covariates (to test
 366 hypothesis (a) on positive link and (b) on component-specific links), and a local model to
 367 explore the potential spatial heterogeneity of the relationships between geodiversity variables
 368 and species richness (to test hypothesis (c) on local variations). All models were repeated for
 369 each grid resolution to detect potential spatial aggregation issues (to test hypothesis (d) on
 370 MAUP).

371 2.6.1. Regional model

372 The aim of this regional modeling was to explore the average relationship between estimated
 373 species richness (vascular plants, birds, butterflies) and geodiversity variables, while also
 374 considering environmental factors (naturalness, temperature, precipitation, elevation range). A
 375 linear model was first built, then refined with spatial models (SAR, SEM) to correct for spatial
 376 autocorrelation in the residuals and ensure more robust results (see Fig. S4, S5 and Appendix
 377 A in SI).

378 The first step involved creating an initial non-spatial model between the estimated species
 379 richness S_{est} (Jack1) and the predictors (geodiversity Shannon index, and covariates:
 380 naturalness, annual mean temperature, annual mean precipitation and elevation range) for each
 381 of the three biodiversity categories (vascular plants, birds, butterflies) and for each resolution
 382 (5, 7.5 and 10 km). A linear model (3) was selected following a preliminary analysis of the
 383 distribution of the dependent variable.

384

$$385 \quad S_{est} = \beta_0 + \beta_1 Elev + \beta_2 Tem + \beta_3 Pre + \beta_4 Mean Nat + \beta_5 Geo + \epsilon$$

386 (3) 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.

387

388 The explanatory variables were standardized to enable comparison of the coefficient values.
 389 The assumptions of the linear model were checked graphically and through the Shapiro-Wilk
 390 test (normality of residuals) and the Breusch-Pagan test (homoscedasticity). Variance Inflation
 391 Factors (VIF) were also calculated for each explanatory variable to identify potential
 392 multicollinearity. We set the exclusion threshold at $VIF = 4$, following recommendations in the
 393 statistical literature that suggest using stricter cutoffs (between 4 and 5) rather than the more
 394 permissive threshold of 10 (O'Brien, 2007). This conservative choice was made to minimize
 395 the risk of multicollinearity affecting coefficient estimates.

396 To detect potential spatial dependence in the residuals that could bias the coefficient estimation,
 397 Moran's Index (Moran, 1950) was calculated using the R package *spdep* (Bivand et al., 2005),
 398 and a spatial analysis of residuals was conducted. A first-order queen contiguity neighborhood
 399 matrix was used for this analysis. In the case of positive autocorrelation in the model's
 400 residuals, a bottom-up approach was used to select the appropriate spatial model (Le Gallo,
 401 2002; Florax et al., 2003). Lagrange Multiplier tests (Anselin et al., 1996) were applied to
 402 choose between SAR (Simultaneous AutoRegressive model) and SEM (Spatial Error Model)
 403 using AIC values. The optimal choice was based on selecting the spatial model with the
 404 smallest AIC for the robust Lagrange Multiplier.

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

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

409

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

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

$$SEM : y = x\beta + \lambda W \epsilon + u$$

414 (5)

415 Where: y = dependent variable, x = independent variable, β = parameter, ϵ , u = error terms, λ =
 416 auto-regression coefficient, W = spatial weights matrix.
 417

418 For the SAR and SEM models, the neighborhood matrices (W) were calculated based on a first-
 419 order queen contiguity matrix. This type of matrix assigns equal weight to all adjacent cells
 420 (maximum neighbors = 8). The two spatial models were computed using the R package
 421 *Spatialreg* (Bivand et al., 2021). To validate the relevance of our spatial models, we calculated
 422 the adjusted R^2 and the AIC (Akaike Information Criterion) for each model to compare them
 423 with the linear model without correction (see Appendix A in SI).

424 To evaluate the relative influence of each component (sub-indeces) of geodiversity, the initial
425 linear model was reconstructed by replacing the overall Shannon geodiversity variable by
426 Shannon geology, Shannon hydrology, Shannon geomorphon and Shannon pedology variables.
427 All subsequent steps were then reproduced.

428 *2.6.2. Local Model*

429 The objective of this modeling was to explore local variations of the relationships between the
430 explanatory variables and the variable of interest. To address this question, we performed a
431 Geographically Weighted Regression (GWR) using the R package *GWmodel* (Brunsdon et al.,
432 1996). The GWR evaluates local regression model (3) for each grid cell based on the
433 characteristics of its neighborhood only. To account for the neighborhood effect, two
434 parameterization steps were required: the choice of the neighborhood size and the spatial
435 weighting function associated with these neighbors, typically inversely proportional to the
436 distance (Feuillet et al., 2019). The neighborhood radius (in km) was optimally estimated by
437 minimizing the AIC. A Gaussian function was used as the spatial weighting function, assigning
438 weights that approach 0 as the distance from the observation increases. All these
439 parameterization steps were illustrated in the supplemented information (Fig. S2).

440

441 **3. Results**

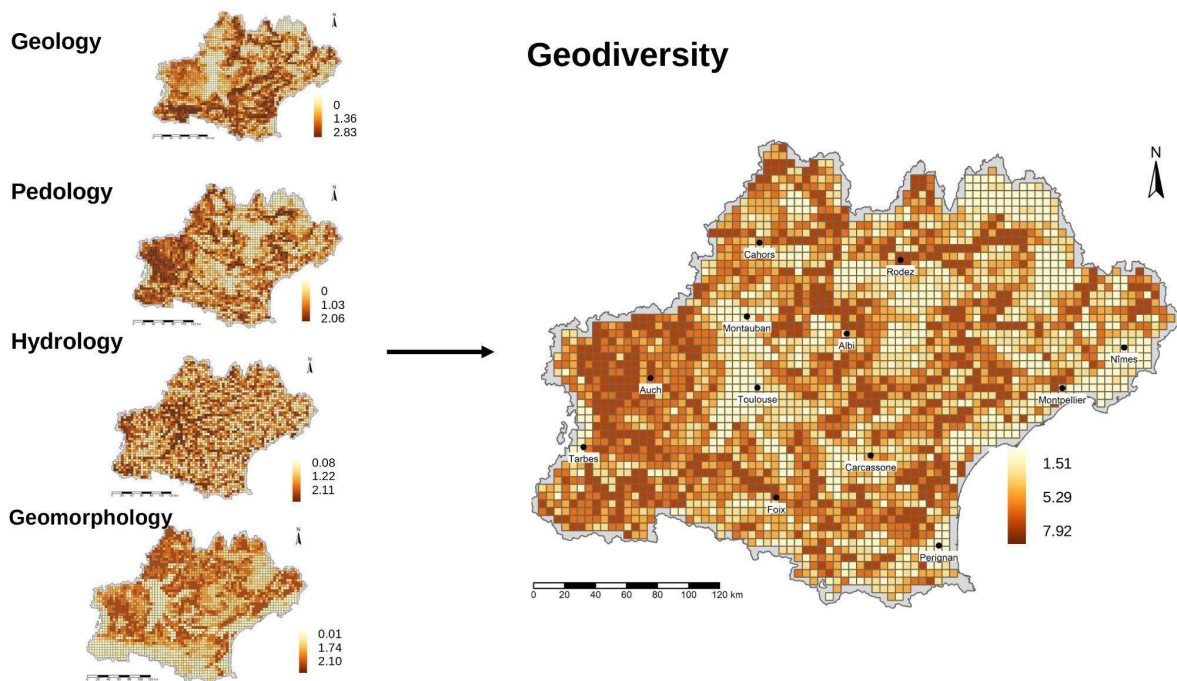
442

443 *3.1. Geodiversity Maps*

444

445 The maps of geological, hydrological, geomorphological, and pedological diversity, along with
446 the overall geodiversity index, are shown in Fig. 2 for the 5 km grid resolution, and in Fig. S3
447 for all grid resolutions (5, 7.5, and 10 km). A spatial heterogeneity in our geodiversity index is
448 evident, with highly geodiverse areas located in the southwestern part of the territory—
449 particularly in the Haute-Pyrénées and the western part of the Gers (including the Pyrenees and
450 their piedmont)—and much less diverse areas around Toulouse, coastal area below Nimes and
451 in the Northern part of Lozère, in the northeastern section of the study area.

452



453

454

455 **Fig. 2: Geodiversity maps.** Compilation of the four geodiversity components (geology, pedology, hydrology,
 456 geomorphology) into an overall geodiversity index (grid = 5 km). The color gradient represents Shannon diversity
 457 index values for each component (left) and their summed index for overall geodiversity (right), from low (light
 458 yellow) to high (dark orange) diversity.

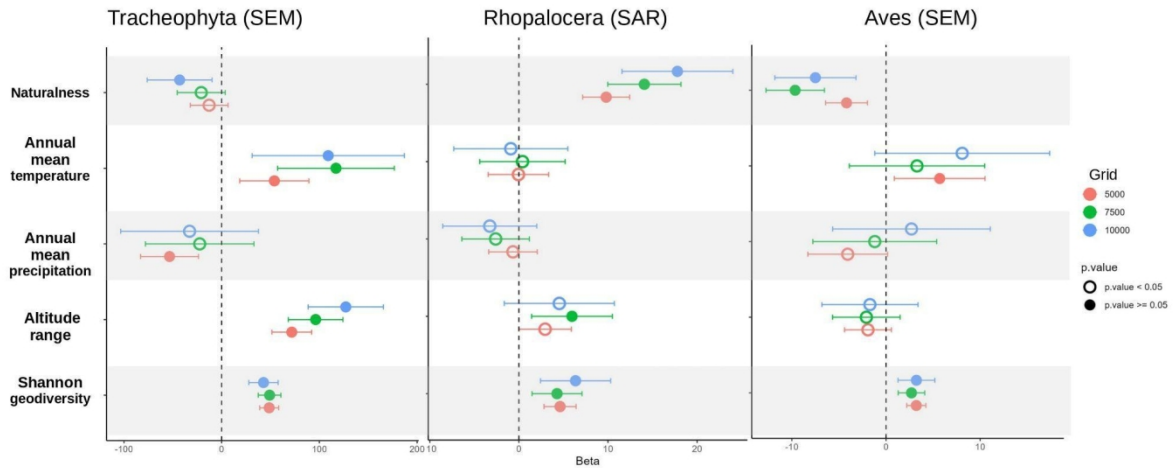
459

460 3.2. *The relationship between geodiversity and species richness: regional analysis*

461

462 The coefficients and significance assigned to the different explanatory variables for the best
 463 spatial models are then presented in Fig. 3. First, we observed that for all taxa and resolutions,
 464 our geodiversity index had a significant positive impact on species richness, consistent across
 465 spatial scales considered. Regarding the covariate predictors, their influence and significance
 466 were highly taxon-dependent. For vascular plants, species richness was positively correlated
 467 with the annual mean temperature and the elevation range of the grid cell. Mean naturalness
 468 and annual mean precipitation negatively influenced diversity of plants only at two grid scales
 469 (10 km for naturalness and 5 km for precipitation). For butterflies, on the top of geodiversity,
 470 naturalness appeared to have a significant positive effect on their diversity as well as elevation
 471 range but only at the 7.5km scale.

472



473
474 **Fig. 3: Overall biodiversity and environmental covariates effects on species richness.** Dots represent
475 standardized coefficients (\pm 95% CI) from the best-fitting spatial models (SAR and SEM) for Tracheophyta
476 (vascular plants); Rhopalocera (butterflies) and Aves (birds). The vertical dashed line indicates the null effect
477 ($\beta = 0$): coefficients to the right indicate a positive relationship, and those to the left a negative one. When
478 the CI overlaps $\beta = 0$, the effect is compatible with zero (no significant effect). Open circles indicate non-
479 significant coefficients ($p \geq 0.05$), while filled circles indicate significant coefficients ($p < 0.05$). Colors
480 correspond to spatial grid sizes (red = 5 km, green = 7.5 km, blue = 10 km).

481 For birds, naturalness has a significant negative effect for all scales. A scale effect is observed
482 regarding the significance of temperature which is only significant and positive at the 5 km
483 grid level. Regarding the fit quality of our spatial models, all adjusted R^2 values were higher
484 than those of the linear model (Table 3). Similarly, all AIC values of the spatial models were
485 notably lower than those of the non-spatial linear 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 R^2	Adjusted R^2 (lm)	AIC	AIC (lm)
<i>Tracheophyta</i>	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
<i>Rhopalocera</i>	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
<i>Aves</i>	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

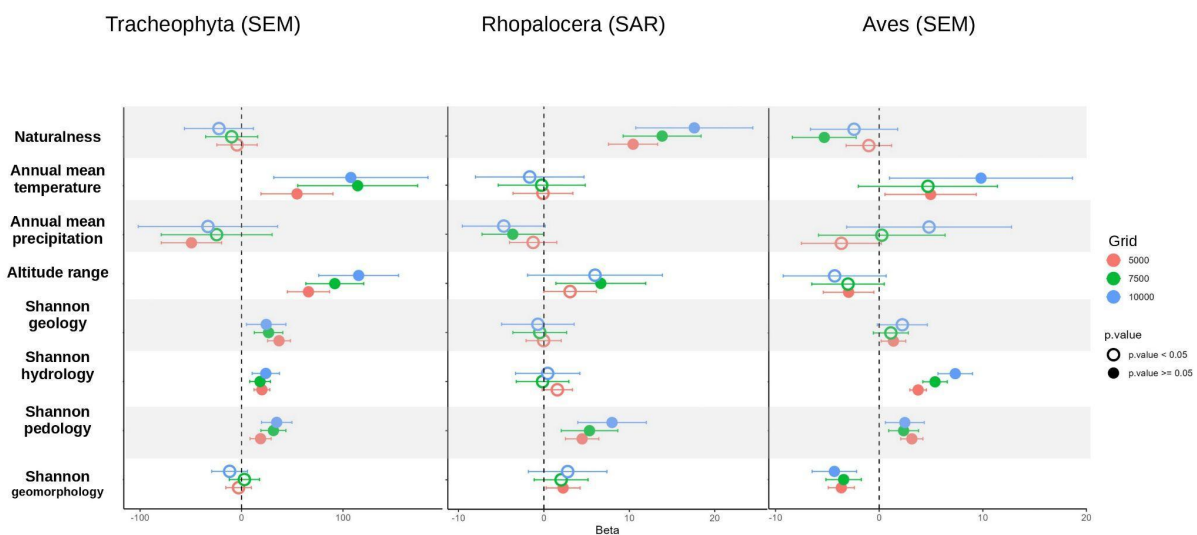
5714.785

6138.182

486

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

492 The analysis of the coefficients from the second model yields broadly similar results for the
 493 abiotic variables excluding geodiversity (Fig. 4). Different patterns are observed for each
 494 component of geodiversity. As overall geodiversity, pedological diversity is consistently
 495 significantly positively correlated with taxonomic richness for each group and spatial scales.
 496 On the contrary, the three other components of geodiversity do not have the same effect
 497 depending on the taxonomic group studied. Geological diversity appears to have a positive
 498 effect only for vascular plants (at all scales) and for birds (only at the 5 km scale). Hydrological
 499 diversity does not significantly influence butterflies' richness, but has a significant positive
 500 effect on the diversity of vascular plants and birds. Finally, geomorphological diversity does
 501 not significantly influence vascular plants or butterflies at the largest scales (7.5km and 10km)
 502 but has a positive significant effect on butterflies at 5 km and a significant negative effect on
 503 bird diversity whatever the scale.



504

505 **Fig. 4: Geodiversity sub-indices and environmental covariates effects on species richness.** Dots represent
 506 standardized coefficients (\pm 95% CI) from the best-fitting spatial models (SAR and SEM) for Tracheophyta
 507 (vascular plants); Rhopalocera (butterflies) and Aves (birds). The vertical dashed line indicates the null effect
 508 ($\beta = 0$): coefficients to the right indicate a positive relationship, and those to the left a negative one. When
 509 the CI overlaps $\beta = 0$, the effect is compatible with zero (no significant effect). Open circles indicate non-
 510 significant coefficients ($p \geq 0.05$), while filled circles indicate significant coefficients ($p < 0.05$). Colors
 511 correspond to spatial grid sizes (red = 5 km, green = 7.5 km, blue = 10 km).

512

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

515

516 3.3. The relationship between geodiversity and species richness: local analysis

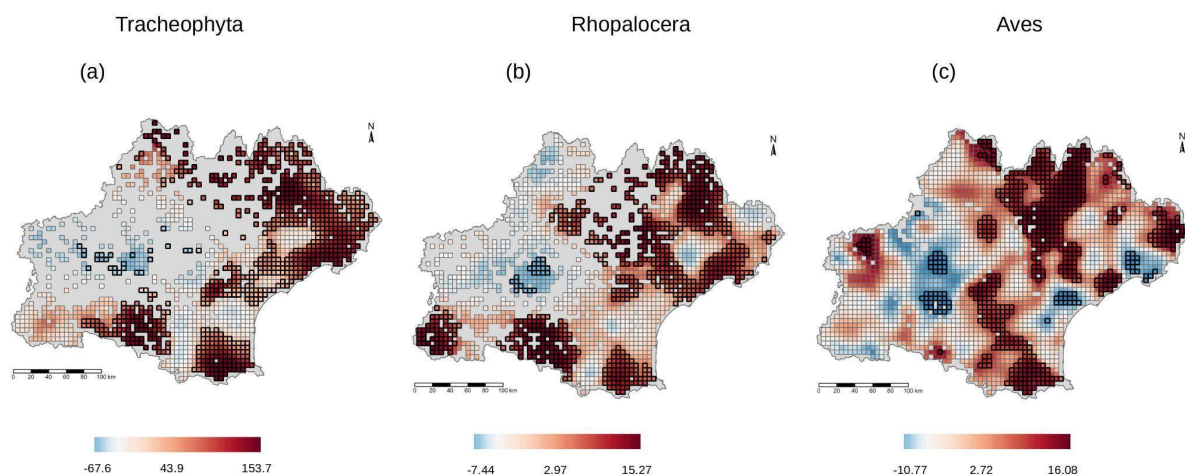
517 Spatial distribution of the GWR coefficients revealed local variations between species richness
 518 and all predictive environmental variables for all taxa and all scales (Fig. S6). The relationship
 519 between species richness and geodiversity (Fig. 5) also shows local spatial variation across the
 520 region for all taxa. While some areas, such as the center-west (Gers, Toulouse area), exhibit no
 521 significant association or even significant negative correlations, extensive zones of significant
 522 positive relationships are consistently observed across taxa, particularly in the northeast
 523 (Massif Central) and the south (Pyrenees).

524

525 Overall, the local relationship between geodiversity and species richness appears more
 526 consistent across taxa (i.e. more significant positive local correlation in common between the
 527 three taxa, Fig. S7), with local variations being generally less pronounced than that observed
 528 for climatic, topographic, or naturalness variables (Fig. S6).

529

530



531

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

538

539 The fit quality of the GWR model, along with the neighborhood radius values selected by AIC
 540 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)
<i>Tracheophyta</i>	5	0.662	0.197	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
<i>Rhopalocera</i>	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
<i>Aves</i>	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

541

542 Based on the comparison of adjusted R² values and AIC, the GWR model appeared to better
543 capture the structure of our data than the simple linear models.

544

545

4. Discussion

546

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

553

554

4.1. Multi-taxon geodiversity–biodiversity relationships at the regional scale

555

556 At a regional level, we show that the overall geodiversity index was positively, significantly
557 correlated with species richness in a consistent way across the three studied taxa. This result is
558 in line with previous studies which reported a positive relationship between geodiversity and,
559 (1) the richness of vascular plants in Great Britain (Bailey et al., 2017), (2) threatened
560 butterflies in Finland's national parks (Tukiainen et al., 2017a), and (3) birds in the USA (Read
561 et al., 2020). The positive relationship between our geodiversity index and species richness was
562 consistent across all taxa and spatial resolutions (5, 7.5 and 10 km) and was not higher for taxa
563 at the base of the trophic chain.

564

565 To our knowledge, our study is the first that shows a positive relationship between geodiversity
566 and species richness across three trophic levels. Our results suggest that a Conserving Nature's
567 Stage program based on geodiversity would be efficient to protect taxonomic groups with very
568 different biological and ecological needs whatever their position in the trophic chain. By
569 prioritizing geodiversity, conservation efforts could help maintain the full spectrum of niches
570 required by primary producers, herbivores, and predators (and other trophic levels) alike. In
571 doing so, this not only conserves species richness at each taxonomic group level but also
572 supports the integrity of interaction networks, facilitating long-term ecosystem function and
573 resilience (Olivier et al. 2015). In addition, conserving geodiversity for itself is equally
574 important and Conserving Nature's Stage approach thus offers a win-win solution to conserve
575 both biotic and abiotic diversity.

576

577 4.2. Differential effects of geodiversity sub-indices

578

579 We also found that components of geodiversity do not have the same impact on the diversity
580 of our three taxa.

581 Pedology significantly supports the diversity of all taxa and therefore is of great importance in
582 combating biodiversity collapse, a finding already noted in previous studies (Ibáñez & Feoli
583 2013; Stein et al., 2014; Molina-Venegas et al., 2016).

584 Hydrological diversity has a positive influence on the diversity of vascular plants and birds,
585 but not on butterflies. One possible explanation is that many bird or plant species are closely
586 tied to aquatic environments. An increase in the diversity of rivers and water bodies within a
587 grid cell -as captured by our hydrological index based on Strahler orders and surface water
588 richness- would thus have provided opportunities for new specialist aquatic or riparian species
589 to establish themselves, thereby increasing overall species richness. It is important to note,
590 however, that this index reflects the structural diversity of the hydrographic network (streams
591 and water bodies) and does not directly account for all fine level of vegetated wetland habitats
592 (e.g., rich fens vs raised bogs), which may therefore only be represented indirectly. On the
593 contrary, few butterfly species are directly dependent on wetlands explaining why this variable
594 did not significantly influence the diversity of this taxon (Van Swaay et al. 2006). Yet wetlands
595 are associated with a high number of endangered lepidoptera species and thus remain an
596 important geodiversity feature to conserve for butterflies (Van Swaay et al. 2006).

597 Compared to the other two components, the effect of geological diversity appears to be weaker,
598 with a positive correlation only for vascular plants. These observations aligned with the results
599 of a previous multi-taxa study (Tukiainen et al., 2017a), which found similar dominance
600 patterns for vascular plants and butterflies. However, that study showed that geological
601 diversity had a strong impact on the richness of bryophytes, lichens, or beetles. The weaker
602 influence of geological diversity on biodiversity may be explained by the more indirect
603 interaction between living organisms and lithology, which is largely confined to the subsurface.
604 Finally, geomorphological diversity - diversity of landform classes identified from topography-
605 was considered by Bailey et al. (2017) as a powerful explanatory variable of plant richness
606 patterns. However in our study, this variable had no significant impact on vascular plants or
607 butterflies, and was negatively correlated with bird diversity at all spatial resolutions. The
608 spatial scale used in our analysis ($\geq 5 \square \text{km}$ grid cells) may have hidden the previously observed

609 relationship between vascular plant richness and landform diversity, which has been shown to
610 be stronger at finer spatial grains (e.g., 1×1 km cells; Bailey et al., 2017). The Threshold
611 Angle, a parameter of the geomorphon algorithm, controls sensitivity to slope gradients: low
612 values ($1-3^\circ$) detect minor variations but can introduce noise in rugged areas. After testing
613 different thresholds, we set it at 3° , acknowledging that some geomorphological changes may
614 remain masked (Bailey et al., 2017).

615 The negative relationship observed between geomorphological diversity and bird richness may
616 be explained by higher species richness in flat coastal areas -likely driven by the co-occurrence
617 of terrestrial and marine species (Graells et al., 2022)- and low species richness in high-
618 elevation mountainous areas (Quintero & Jetz, 2018). In addition, due to chosen databases
619 partly based on opportunistic citizen science data, an overestimation of species richness near
620 urban areas -typically located on flat terrain- is also potentially contributing. While integrating
621 all opportunistic citizen-science data is valuable for building the most comprehensive dataset
622 possible, future studies using spatially balanced sampling designs are needed to assess how
623 sampling bias may influence the observed relationship between geomorphology diversity and
624 bird species richness.

625 626 4.3. Local variations in the geodiversity-biodiversity relationships 627

628 Our local analysis (GWR) showed that the relationship between biodiversity and geodiversity
629 is not spatially stationary: the geodiversity of some localities seemed more likely to promote
630 biological diversity than others (Fig. 5). This finding aligns with the work of Ren et al. (2021),
631 who also observed local variations in the effect of geodiversity on biodiversity using GWR.
632 Interestingly, the areas where biodiversity and geodiversity are positively correlated tend to
633 overlap more consistently across the three taxa than do areas of positive correlation between
634 biodiversity and our other environmental variables (Figs. S5 and S6). This further supports the
635 use of geodiversity as a holistic indicator for informing multi-taxa conservation planning at a
636 fine scale (Tukiainen et al., 2017a).

637
638 One factor that could best explain local variations is anthropization, a factor often overlooked
639 in this type of study (Tukiainen et al., 2017b) with currently contradictory results (Rasanen et
640 al., 2016; Ren et al., 2021). For all taxa, the areas where geodiversity has the greatest positive
641 influence on species richness are primarily found in less anthropized spaces (e.g., the Pyrenees,
642 Lozère, Aveyron). Conversely, a negative relationship between geodiversity and species
643 richness is observed in areas near major urban centers (e.g., Toulouse and Montpellier
644 metropolitan areas). However, one unexpected result was a locality in the west, near the border
645 between Gers and Tarn-et-Garonne *départements*, which is associated with a negative link
646 between geodiversity and biodiversity (Fig. 5). This environment is highly rural, reinforcing
647 the complex relationship between geodiversity and biodiversity given the interference of
648 various agricultural practices (e.g., intensive vs. extensive) and related landscape mosaics (e.g.,
649 openfields, bocage landscape) with possibly very different effects on biodiversity patterns.
650 Future studies in Occitanie should seek to better understand what drives the result in this zone
651 dominated by agricultural lands, despite its high geodiversity (Fig. 2). Overall, these findings
652 highlight the need to better integrate anthropogenic drivers into geodiversity-biodiversity

653 analyses. Despite the scarcity of focused studies, available results remain inconclusive, with
654 some reporting positive (Ren et al., 2021) and others negative (Rasanen et al., 2016; Tukiainen
655 et al., 2017b) effects of anthropization. We therefore encourage further investigation into how
656 human activity interacts with geodiversity to shape biodiversity patterns, especially in the
657 context of conservation planning.

658

659 4.4. Scale dependency and the Modifiable Areal Unit Problem (MAUP)

660

661

662 In our regional analysis, we found that overall geodiversity (Fig. 3) and pedological diversity
663 (Fig. 4) significance is not affected by the modifiable areal unit problem (MAUP). On the
664 contrary, the MAUP plays a role on the significance of other components of geodiversity and
665 on most of our other explanatory variables (Fig. 3, 4 and Fig. S6). For instance, mean annual
666 precipitation significantly affects vascular plants at a 5 km grid resolution but has no effect at
667 7.5 km or 10 km resolutions. MAUP also significantly affects the effects of naturalness on
668 vascular plants and the effects of mean annual temperature and elevation range on bird
669 diversity. We therefore consider it essential to systematically include multiple spatial
670 resolutions in biodiversity-geodiversity studies: either to evaluate the robustness of the
671 relationship across spatial scales, or to identify the most appropriate scale for implementing
672 effective conservation actions.

672

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

682

683 4.5. Effects of environmental covariates

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

691

692 For butterflies and birds, naturalness appeared to play an important role in explaining species
693 richness, but not for plants. The effect of naturalness differed between the two animal taxa. On
694 the one hand, it was positively correlated with butterfly species richness, a result consistent
695 with previous studies highlighting the negative impact of anthropogenic pressures on the
696 taxonomic diversity of this group (Bobo et al., 2006; Gallou et al., 2017). On the other hand,

697 naturalness was negatively correlated with bird species richness. Several explanations might
698 account for this phenomenon, such as the presence of maximum bird diversity in moderately
699 anthropized environments (Blair, 2011; Meynard et al., 2011), an overestimation of species
700 richness near cities, or differences in the influence of the various components of naturalness,
701 making a general interpretation challenging. In addition, naturalness is generally low in the
702 littoral area (high building density) and high in mountain areas (Guetté et al., 2018). Bird
703 diversity shows the opposite pattern, with higher species richness in coastal areas—likely
704 driven by the co-occurrence of terrestrial and marine species (Graells et al., 2022)—while high-
705 elevation zones typically support fewer species (Quintero & Jetz, 2018).
706 Nevertheless, given that it had been one of our most explanatory variables, this phenomenon
707 should be further explored by studying the effect of its three components (i.e., hemeroby,
708 building density, and ecological continuity) on taxonomic diversity.

709

710 4.6. Limitations and future perspectives

711 To compute our biodiversity metrics, we used data characterized by heterogeneity in terms of
712 sources, validation processes, and spatial-temporal coverage (see 2.2. Biodiversity data, Tables
713 S1-S3). However, we believed that our approach was relevant for detecting general trends. We
714 applied strict taxonomic, temporal, and spatial filters to improve data quality, retaining only
715 recent, species-level, georeferenced records (excluding pre-1990 and spatially aggregated
716 records). Using species richness allowed us to bypass species abundance data, which are
717 heavily influenced by the number of observations. Moreover, species richness is the most
718 commonly used metric in the literature on this subject (Field et al., 2009; Tukiainen et al.,
719 2023), enabling us to build on previous studies and compare the relevance of our results.

720

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

729

730 Given the rapid increase in freely accessible species occurrence data (e.g., GBIF, OpenObs), it
731 is crucial that more studies adopt standardized protocols for utilizing such data in
732 macroecological research (Wüest et al., 2020). Advancing analytical methods to account for
733 heterogeneous sampling effort will significantly enhance our understanding of biodiversity–
734 geodiversity relationships (Soroye et al., 2018; Botella et al., 2021).

735

736 Two main approaches have been used to quantify overall geodiversity: (i) pooling all categories
737 into a single dataset to compute georichness (Toivanen et al. 2024), and (ii) calculating indices
738 for each sub-component of geodiversity and then combining them (Bétard & Peulvast, 2019,
739 Ferrando et al. 2021, Polman et al. 2024). Here, we chose the latter, as it preserves the
740 multidimensional character of geodiversity and avoids biases from components with more

741 categories. Summing component-level indices ensures balanced contributions and clearer
742 interpretation, whereas pooling may overemphasize certain components. Comparing the effect
743 of summing Shannon indices of geodiversity components vs pooling all geodiversity
744 component data to produce an index for overall geodiversity should be tested in further studies
745 investigating the link between overall geodiversity and species richness.

746

747 More research is also needed for identifying and correcting major knowledge gaps and data
748 pitfalls within our territory. Firstly, we believe that more attention should be paid to the
749 landscape scale when analyzing the geodiversity–biodiversity link. Such studies could
750 particularly benefit from the significant advancements in remote sensing made in recent years
751 (Rhodes et al., 2022), enabling increasingly fine-resolution environmental descriptions. For
752 example, LiDAR (Light Detection and Ranging) allowed detailed topographic analysis and
753 modeling of microclimatic indices derived from topography, such as daily solar radiation
754 (Bergen et al., 2009; Anderson & Gaston, 2013). Daily solar radiation, similar to other climatic
755 variables such as microclimate mean and variations, could be tested alongside geodiversity to
756 assess whether it provides additional explanatory power in shaping patterns of species richness.
757 Exploring geodiversity–biodiversity relationships at even finer spatial scales (e.g., plot level)
758 also represents a promising avenue, particularly for studies focusing on how geodiversity
759 influences community composition of plant, bacteria, fungi, and arthropods (Hjort et al., 2022).

760

761 The influence of geomorphology on biodiversity patterns has been highlighted in many studies
762 (e.g., Burnett et al., 1998; Nichols et al., 1998; Guitet et al., 2015; Bailey et al., 2017). However,
763 we currently lack geomorphological data or maps at the spatial extent of our study area. An
764 alternative means was to produce a map of landform types using the Geomorphons algorithm
765 (Jasiewicz and Stepinski, 2013). However in the study area, we observed lower
766 geomorphological diversity in the Pyrenees compared to some hilly landscapes, that is
767 counterintuitive. This reduced diversity, as detected by the Geomorphon method, may be due
768 to the dominance of a few broad landform classes in mountainous areas, as well as limitations
769 of the algorithm in capturing fine-scale topographic complexity. Since this method is widely
770 used in overall geodiversity assessments, and given that including or excluding geomorphology
771 in our composite index of overall geodiversity did not significantly alter our results (Fig. S8),
772 we chose to retain it. Nevertheless, further research is needed to identify morphological
773 indicators better suited to capturing landform diversity in mountainous regions at the spatial
774 scales considered in our study.

775

776 It would also be interesting to optimize our hydrological diversity index by, for example,
777 adding a component on water dynamics in soils (e.g., edaphic humidity). The low resolution of
778 the pedological layer remains a limitation, which restricts our ability to extend our study to a
779 more localized scale. These gaps in the availability of high-resolution data could, however, be
780 addressed in the coming years. The national CarHab project, currently under development,
781 could, for example, provide information on soil parameters such as moisture and pH at a
782 1:25,000 scale (IGN, PatriNat). The development of new GIS tools and data thus offers
783 promising prospects for conservation strategies based on geodiversity characterization.

784

4.7. Applied potential for conservation targets

The creation of our geodiversity index was largely inspired by previous work related on the Conserving Nature's Stage 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 believe that the Conserving Nature's Stage strategy should not be used as a substitute for traditional conservation methods but rather as a complement (Beier et al. 2015; Stein et al. 2014). Indeed, if our results confirm geodiversity as a potential driver of species richness, this relationship is not universally positive. Mechanisms such as heterogeneity–area trade-offs, isolation effects, or niche mismatches can weaken or even reverse it (Allouche et al. 2012; Ben-Hur & Kadmon, 2020). Our local analyses illustrate these nuances, with certain areas showing negligible or negative associations. This highlights the need for context-specific approaches: geodiversity can be a powerful conservation tool, but its effectiveness depends on ecological and anthropogenic conditions (Ren et al., 2021).

The systematic use of coarse filters might also 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.

Finally, in the context of climate change and uncertain future environmental conditions, high geodiversity can provide numerous potential refuges and habitats for different species (Gray, 2013; Maliniemi et al., 2024). With global redistribution of biodiversity, the current negative or absence of local relationships between geodiversity and species richness in our study could be positive in the future, with species spatial range shift (Rubenstein et al. 2023). Moreover, conserving geodiversity aligns well with *rewilding* strategies aimed at restoring ecosystems that are functional, self-sustaining, and as little-human-managed as possible (Perino et al., 2019). In such contexts, high geodiversity would promote the return or retention of species across trophic levels and thus foster ecosystem processes highly dependent on trophic networks (Harvey et al. 2017).

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.

828 Our analysis revealed the local variations in geodiversity's effects on species richness and
829 highlighted the importance of localized and context-specific studies. Indeed, various spatial
830 modeling tools (SAR, SEM, GWR) allowed us to better understand the complex relationship
831 between geodiversity and biodiversity. Using powerful tools and fine-scale models like GWR
832 within the framework of the Conserving Nature's Stage strategy is warranted if we wanted to
833 consider the fact that the effect of geodiversity on biodiversity is spatially dependent (Bailey
834 et al., 2017; Ren et al., 2021). Given the local variations we have highlighted in the
835 biodiversity-geodiversity relationships, conservation strategies based on geodiversity should
836 be tailored to local conditions. In areas where biodiversity strongly tracks geodiversity,
837 protecting key geodiversity features may be particularly effective, whereas in regions where
838 other factors dominate, complementary or alternative measures may be required.

839 Future studies should also focus on this link at multiple levels of both geodiversity and
840 biodiversity (e.g., alpha, beta, gamma) and on functional and genetic diversity (Tukiainen et
841 al., 2019; Tukiainen et al. 2023b). Indeed, we believed the success of the Conserving Nature's
842 Stage strategy relied primarily on a solid local understanding of the structures that truly
843 supported biodiversity in all its forms. Such a strategy could be highly effective in a geodiverse
844 territory for identifying priority areas for establishing new conservation spaces.

845

846 **Competing Interests**

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

848

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859

860 **Author Contributions**

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

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