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Uncertain role of conservation areas to protect soil biodiversity and functioning

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ABSTRACT

Soil biodiversity and functioning are the foundation of ecosystem sustainability, but we do not know whether current nature conservation areas are efficiently protecting soils. Here, we investigated the contribution of terrestrial nature conservation areas to protect soil biodiversity and functioning across scales. We found no general positive effect on diversity of bacteria, fungi, protists, invertebrates, and nematodes, captured as richness, Shannon diversity and dissimilarity, and 5 soil functions (pathogen control, nutrient provision, soil carbon, soil organic matter decomposition, and soil aggregate stability). Our findings suggest that nature conservation areas show an inconsistent role in protecting soil biodiversity and functioning, as we found mostly non-significant and otherwise mixed effects across scales. Despite few positive and negative effects of protection status, our work highlights the urgent need to directly target soils in nature conservation.

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1. Introduction

Soils are home of more than half of global biodiversity on the planet (Anthony et al., 2023) and play critical roles in supporting multiple ecosystem services from carbon sequestration to soil fertility (Bardgett and van der Putten, 2014; Delgado-Baquerizo et al., 2020). Moreover, most plants are highly dependent on key soil organisms such as mycorrhizal fungi (Smith and Read, 2010). Strikingly, a recent study suggested that $< 10\,\%$ of global hotspots for soil biodiversity can be found under protected conservation areas (Guerra et al., 2022). Nature conservation areas have played a paramount role in conserving the biodiversity of threatened plants and animals (Geldmann et al., 2013; Hoffmann et al., 2010; Langhammer et al., 2024; Stolton and Dudley, 2010; Watson et al., 2014). However, the capacity of nature conservation areas to protect soils remains unclear (Duarte et al., 2024; Köninger et al., 2022).

We, in fact, do not know whether current nature conservation areas are successful in protecting soil biodiversity and functioning, as these areas were not explicitly designed for that purpose. Soils could co-benefit from conservation measures targeted at aboveground organisms, due to the known links between above- and belowground systems (e.g., microbes and plants; Bardgett and van der Putten, 2014; Eisenhauer et al., 2017; or vertebrates; Tomita et al., 2025), and how soil communities are particularly sensitive to vegetation and land management (i.e., land use; Orgiazzi et al., 2016; Delgado-Baquerizo et al., 2018; Smith et al., 2021). Awareness for sustainable soil management has been raising, for example when farming systems have been evolving towards environmental and economic sustainability based on Voluntary Guidelines for Sustainable Soil Management (FAO,2017; FAO, ITPS, GSBI, SCBD, & EC, 2020). However, the transition of soil-beneficial practices into nature conservation seems to lag behind. Local and regional studies focusing on single functions or groups of soil organisms did not find any positive effect of conservation measures such as protected areas on soil biodiversity and functioning (Ciobanu et al., 2019; Duarte et al., 2024; Zeiss et al., 2022), even though one study did report benefits to food web structure in forests (Duarte et al., 2024). Potential positive effects of protected areas on ecosystem functioning (Allan et al.,

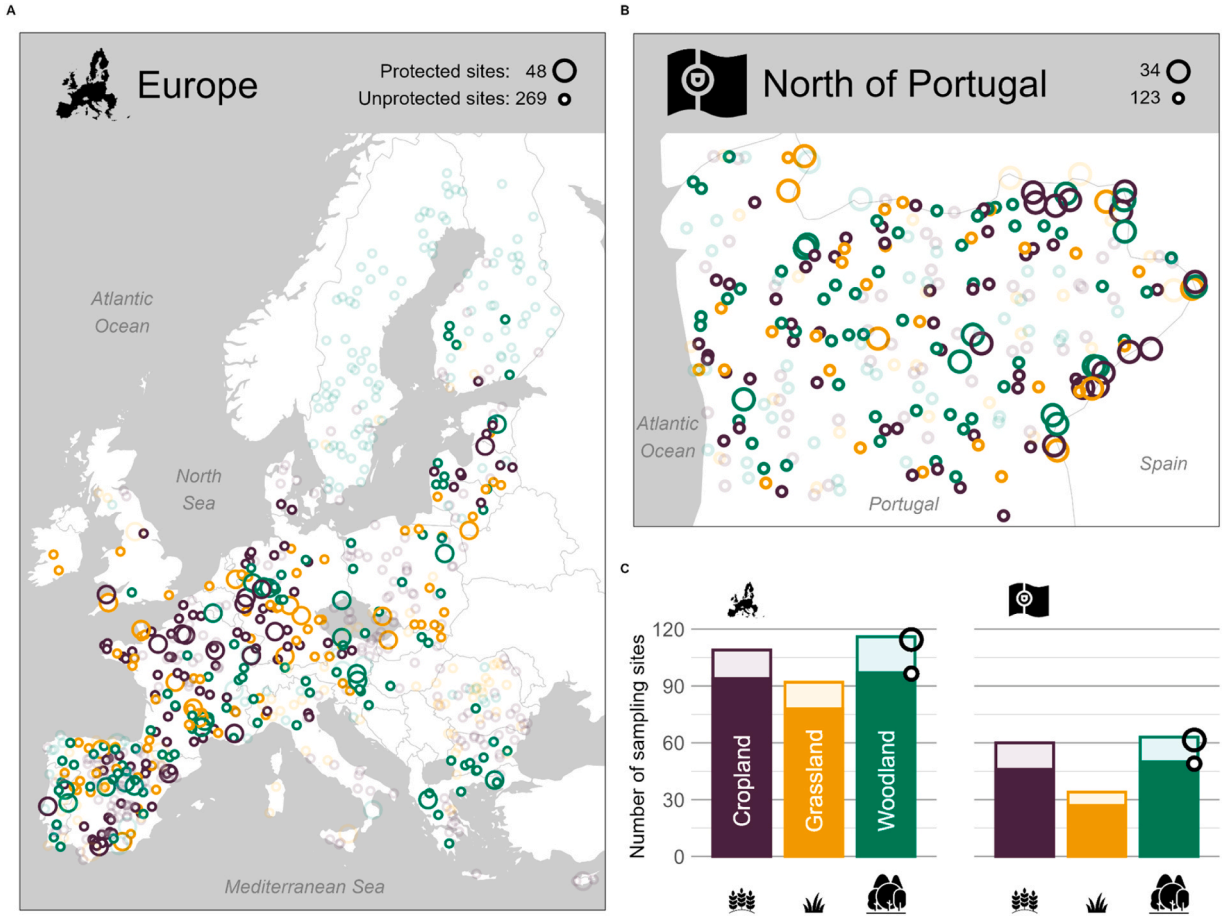

Fig. 1. Location of sampling sites. Sampling site locations at the two spatial scales: continental (Europe, A), and regional (North of Portugal, B). Circles represent sampling sites used in effect size estimation (non-transparent) and in random-intercept and random-slope models (transparent), respectively. Numbers on the maps represent the number of sites per spatial scale and protection status. Lower right panel (C) shows the number of sites per spatial scale (columns), protection status (transparency) and habitat type (bars and colors). Icons: "Grass" and "Flag" created by Freepik, "Europe" modified after icon by amoghdesign, "Forest" by Vitaly Gorbachev, and "Agriculture" by Vectors Tank - Flaticon. The whole figure was created in R.

2015; Eastwood et al., 2016) seem not to transfer into the belowground world. However, the contribution of contrasting nature conservation areas to protect multiple aspects of soil biodiversity and functioning from local to global scales remains virtually unknown. This knowledge is urgently needed to better understand whether we are successful in protecting the soil system, and to further develop environmental soil-focused policies accordingly.

Here, we aimed to investigate the effect of terrestrial conservation areas on multiple aspects of soil biodiversity and functioning across spatial scales, thereby expanding the framework presented in Zeiss et al. (2022). Previous investigations of the effects of conservation on soil biodiversity and functioning focused on single functions or organism groups as well as either regional or continental scale. We use two independent datasets, one each at continental (i.e., Europe) and regional scale (i.e., North of Portugal, Fig. 1), to test whether potential effects of conservation areas are detectable across spatial scales, as well as across functions and organism groups. Based on previous findings and the intended protection of aboveground organisms and habitats, we expect neglectable effects of conservation measures on soil biodiversity and functioning at both regional and continental scale.

2. Methods

Note, where appropriate, we provide author initials as per MeRIT (Nakagawa et al., 2023).

To test effects of conservation areas on soil biodiversity and functioning, RZ and CAG investigated biodiversity and dissimilarity measures (hereafter soil biodiversity attributes) for bacteria, fungi, protists, and invertebrates, richness of nematodes, decomposers, ectomycorrhizal and arbuscular mycorrhizal fungi (Table 1, data S1). Biodiversity attributes included two diversity measures, namely richness (number of taxa) and Shannon diversity (considering richness and relative abundances), and a measure of dissimilarity (variation in taxa composition between sites, with higher values indicating greater divergence). Additionally, we investigated five soil functions (pathogen control, nutrient provision, soil carbon, soil organic matter decomposition, and soil aggregate stability; Table 1, data S1), which are linked to ecosystem services and soil health (Delgado-Baquerizo et al., 2020; Guerra, Bardgett, et al., 2021). Although different measures of soil functions were used across spatial scales, they were chosen based on ecological relevance and data availability. While this introduces some uncertainty when comparing the soil functions, we are confident that our main messages and interpretations remain robust within these constraints. We also did not compare across datasets but analyzed at each spatial scale individually. To evaluate the soil biodiversity and functioning attributes in conservation areas, RZ and CAG compared protected sites with environmentally similar unprotected sites as described elsewhere (Zeiss et al., 2022); an approach known as nearest-neighbor matching in the literature (Andam et al., 2008; Beresford et al., 2013; Carranza et al., 2014; Joppa and Pfaff, 2010b; Nelson and Chomitz, 2009; Nolte et al., 2013). Environmental similarity was here based on geographical location, elevation, annual average temperature and precipitation, content of soil organic carbon, soil pH, soil salinity, soil texture, and soil stability (Table 1, data S1).

We used two independent datasets to address our research question across two different spatial scales. Because sampling design and

Table 1
Soil biodiversity and functioning attributes measured at the two spatial scales. The same attributes were used at continental and regional scale if not indicated differently. Sampling protocols are given in data S1.

Type of variable	Variable	Continental scale	Regional scale
Diversity	Bacterial richness	Number of bacterial zOTUs	
Diversity	Fungal richness	Number of fungal zOTUs	
Diversity	Arbuscular mycorrhizal fungi richness	Number of arbuscular mycorrhizal fungi zOTUs	
Diversity	Ectomycorrhizal fungi richness	Number of ectomycorrhizal fungi zOTUs	
Diversity	Protist richness	Number of protist zOTUs	
Diversity	Nematode richness	Number of nematode zOTUs	
Diversity	Invertebrate richness	Number of invertebrate zOTUs	
Diversity	Decomposer richness	Number of fungal zOTUs	
Diversity	Bacterial Shannon index	Shannon index	
Diversity	Fungal Shannon index	Shannon index	
Diversity	Protist Shannon index	Shannon index	
Diversity	Invertebrate Shannon index	Shannon index	
Diversity	Bacterial dissimilarity	Jaccard distance based on presence-absence matrix	
Diversity	Fungal dissimilarity	Jaccard distance based on presence-absence matrix	
Diversity	Protist dissimilarity	Jaccard distance based on presence-absence matrix	
Diversity	Invertebrate dissimilarity	Jaccard distance based on presence-absence matrix	
Function	Soil carbon	Soil organic carbon content	Soil organic matter content
Function	Organic matter decomposition	Average of standardized activity of N-Acetylglucosaminidase and soil microbial basal respiration	Standardized soil microbial basal respiration
Function	Nutrient cycling	Average of standardized content of nitrogen, phosphorus and potassium in soil	Average of standardized content of phosphorus, potassium, calcium and magnesium in soil
Function	Pathogen control	Inverse proportion of soil-borne potential fungal plant pathogens	
Function	Soil stability	Average of standardized mean weight diameter and water-stable aggregates	Standardized water-stable aggregates

soil function measures differed in Europe and Portugal, datasets were analyzed separately and only allow for qualitative comparisons. Additional data on temperature, precipitation and elevation was collected by RZ from CHELSA v 2.1 (mean annual temperature and annual precipitation; Karger et al., 2017) and WorldClim v 2.1 (elevation; Fick and Hijmans, 2017) using the terra package (Hijmans et al., 2022).

2.1. Continental scale

At continental scale, soil biodiversity and functioning data were retrieved by RZ and ICS from the LUCAS soil survey (sampling campaign in 2018) at 881 sites (European Commission. Joint Research Centre., 2022; Orgiazzi et al., 2018; Zeiss et al., 2022). Raw sequencing data were retrieved from the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) with BioProject IDs PRJNA952168 and PRJNA985135 for bacteria (16S) and eukaryotes (18S), respectively. Soil biodiversity and physicochemical data are described elsewhere (European Commission. Joint Research Centre., 2022; Hiederer, 2018). Biodiversity was estimated using DNA analysis (Orgiazzi et al., 2022) by DNA extraction, amplification and sequencing using Illumina and PacBio platforms. Additionally, soil functioning data were collected by different laboratories (Zeiss et al., 2022).

2.2. Regional scale

At the regional scale, RZ used data collected in a regional monitoring project by CAG, SM, PF, ACD, SRC, CCD, RPC and others; the monitoring project aims to provide a comprehensive, holistic overview of soil ecological features and include variables related to soil chemistry, physical properties, biodiversity, and ecosystem functions in the North of Portugal (Carvalho et al., 2025; Duarte et al., 2024). A description of the study region can be found in Duarte et al. (2024). A hierarchical stratified random sampling scheme was implemented to the whole NUTS II region "Norte Region" (Northern Portugal) allowing for representative coverage of the entire region's environmental gradient. Within each grid cell of 20 × 20 km, six locations were randomly selected each in one of the 6 focal land-use types resulting in 406 sampling sites. For comparability with the dataset at other spatial scales, land-use types were grouped into habitat types as follows: croplands (annual crops, permanent crops), grassland (pasture), woodland (native forest, non-native forest); samples from land-use type urban parks were excluded here. All three habitat types were present inside and outside conservation areas allowing for habitat-specific comparisons, even though differences in type of conservation management existed (Table 2; e.g., protected croplands only belonging to IUCN management category V protected landscapes). Nine soil cores of 5 cm diameter and 5 cm depth were collected in an area of 30 × 30 m; samples were pooled and homogenized in the field. Four subsamples were taken from this: one 15 ml polypropylene tube for DNA analysis (kept at 4 °C during field sampling, stored at −80 °C), two 100 ml flasks for soil functional analysis (stored at −20 °C), two 100 ml flasks for nematode extraction (stored at 5 °C), and about 1 kg of dry soil for subsequent physical and chemical analysis (stored at room temperature, ~23 °C). Soil physico-chemical analysis, and nematode extraction and identification were previously described (Carvalho et al., 2025; Duarte et al., 2024). Additional soil functioning data was collected following known protocols (Guerra et al., 2021; Guerra et al., 2021). For DNA extraction, the subsample was further separated into three 2 ml polypropylene tubes and 3 bead-beating tubes (0.2 g of soil). Total DNA was extracted from the three independent samples using DNeasy® PowerSoil® Pro-Kit (QIAGEN, Hilden, Germany) and a bead beater (Benchmark Scientific, Sayreville, USA) at 4000 rpm for two cycles of 30 s, cooling down for at least 30 s after the first cycle. A mock microbial community with a known composition was used as a control to validate the DNA extraction process (ZymoResearch, Irvine, CA, USA). Purified DNA of the three independent sample extractions was pooled together and UV spectroscopy (Nanodrop, Thermo Fisher Scientific,

Table 2
Number of sampling sites in protected and unprotected areas across spatial scales. Sampling sites for random-intercept and random-slope models are given in parenthesis if different from effect size analysis.

Habitat type	IUCN protected area management category	Regional	Continental
Cropland	IV	0	1
Cropland	V	14	13
Cropland	VI	0	1 (2)
Cropland	Not Assigned	0	1 (4)
Cropland	Not Reported	3 (8)	2 (16)
Cropland	**Unprotected**	**43 (86)**	**91 (295)**
Grassland	II	2	1
Grassland	IV	0	2 (4)
Grassland	V	5 (8)	11 (13)
Grassland	Not Assigned	0	2 (5)
Grassland	Not Reported	1 (6)	9 (22)
Grassland	**Unprotected**	**26 (42)**	**67 (124)**
Woodland	II	2 (4)	0 (2)
Woodland	IV	1	1 (2)
Woodland	V	10 (11)	14 (19)
Woodland	VI	0	4
Woodland	Not Assigned	0	5
Woodland	Not Reported	11 (17)	11 (15)
Woodland	**Unprotected**	**39 (71)**	**81 (198)**

Massachusetts, EUA) and fluorimetry (QUBIT 3.0, Thermo Fisher Scientific, Massachusetts, EUA) was performed to quantify the DNA concentration and 260/280 ratio, respectively. DNA degradation was evaluated using gel electrophoresis using a E-Gel High-Throughput DNA Electrophoresis System (Thermo Fisher Scientific, Massachusetts, EUA) and PCR amplifiability of the pooled DNA samples was tested using 16S rDNA primers, V3F (5′-CCTACGGGAGGCAGCAG-3′) (Muyzer et al., 1993) and 1492 R (Heuer et al., 1997); these PCR amplifications were performed with a total volume of 12 µl containing 6 µl of iTaq Universal SYBR Green Supermix (BioRad, Hercules, California, United States), 0.4 µl of each 10 µM primer (STAB VIDA, Portugal) using a RT-PCR equipment (Bio-Rad CFX96TM Real-time System) under the following conditions: initial denaturation at 95°C for 3 min, denaturation over 40 cycles of 10 s at 95°C, 30 s at 58°C (annealing), and 30 s at 72°C (extension). To estimate soil biodiversity attributes, prokaryotic and eukaryotic small subunit ribosomal RNA (SSU rRNA) genes were amplified using primer pairs 799 F (5′-AACMGGATTAGATACCCKG-3′)/ 1193 R (ACGTCATCCCCACCTTCC-3′) (Bodenhausen et al., 2013) and Euk_1391f (5′-GTACACACCGCCCGTC-3′)/ EukBr (5′-TGATCCTTCTGCAGGTTCACCTAC-3′) (Stoeck et al., 2010) reverse, respectively, and sequenced at the Western Sydney University Next Generation Sequencing facility using the Miseq platform. Raw sequencing data of 16S and 18S can be retrieved from FigShare repository from March 2028 (3-year embargo after completion of the project).

2.3. Bioinformatics

Both the 16S and 18S sequencing data from the two spatial scales were processed by BS with support of KK in a similar manner to ensure comparability, primarily using the same read quality filtering parameters and a denoising (error correction for the sequencing reads) process to infer Zero-radius Operational Taxonomic Units (zOTUs). Briefly, primers were trimmed from the demultiplexed paired-end raw sequences. End-trimming of sequences was performed with a minimum quality score of 10 to enhance the success rate of paired-end read merging, using either USEARCH (Edgar, 2010) or VSEARCH (Rognes et al., 2016). Read merging was conducted with USEARCH, VSEARCH, or FLASH (Magoč and Salzberg, 2011) for continental, and regional datasets, respectively. A maximum expected error of 1.0 was set for the quality filtering of the merged reads. zOTUs were inferred by denoising the dereplicated merged reads using the UNOISE3 algorithm (Edgar, 2016). Representative sequences of zOTUs from the 16S and 18S datasets were annotated to assign taxonomy with the SILVA database v138.1 (Quast et al., 2013) and the PR2 database v5.0 (Guillou et al., 2013), respectively. All the 16S and 18S sequencing datasets from different spatial scales were normalized for sequencing depth by rarifying to 10,000 and 5000 reads, respectively.

Eukaryotic sequences were taxonomically classified into fungi, invertebrates, protists, and nematodes. Additionally, the fungal sequences were functionally annotated based on their trophic modes and ecological guilds, using the FUNGuild database (Nguyen et al., 2016), and categorized into ectomycorrhizal fungi, arbuscular mycorrhizal fungi, plant pathogens, and saprotrophic decomposers. Richness and Shannon diversity indices of the microbial taxonomic and functional groups were calculated using the vegan package (Oksanen et al., 2019). Community dissimilarity between samples was calculated based on the presence-absence matrix with Jaccard distance using vegan package.

2.4. Conservation influence on soil biodiversity and functioning

To evaluate the soil biodiversity and functioning attributes in conservation areas, represented here by protected area networks, RZ and CAG paired protected sites with environmentally similar unprotected sites using Mahalanobis distance (i.e., nearest-neighbor matching; Andam et al., 2008; Beresford et al., 2013; Carranza et al., 2014; Joppa and Pfaff, 2010b; Nelson and Chomitz, 2009; Nolte et al., 2013) as described elsewhere (Zeiss et al., 2022) and estimated the effect of protection status between paired protected and unprotected sites expressed as Cohen's D effect size measure (Cohen, 1988) using psych package (Revelle, 2021; figure S1). The impact of protected areas has to be inferred from other locations or times, as it is not possible to estimate what would have happened without the establishment of the protected area. The nonrandom distribution of protected areas in space makes comparison of protected areas to everywhere and to nearby land less reliable if differences are not accounted for in the analysis (Joppa and Pfaff 2010a; 2010b; Beresford et al., 2013). The purpose of the matching approach is to compare protected areas to sites that are as similar as possible, namely as similar as possible in confounding factors that may otherwise cover or misestimate the impact of protection (Joppa and Pfaff, 2010b). Matching indeed resulted in lower impacts than estimated using other approaches, thereby confirming the influence of covariates on the evaluation of protection impact (Joppa and Pfaff, 2010b; Andam et al., 2008). In addition, matching can account for so-called spillovers, such as pressures shifting towards surrounding areas (Andam et al., 2008), if the matching criteria are defined accordingly, that is if a buffer zone around protected areas is excluded for matching (Joppa and Pfaff, 2010b).

Sampling sites were regarded as "protected" if they fall exactly into one of the protected areas (i.e. IUCN category I-VI) present in the world database on protected areas (UNEP–WCMC, and IUCN,2021). In the nearest-neighbor matching approach, environmental similarity was represented by Mahalanobis distances below a data-specific threshold (here: 17.53), and tries to eliminate the potential influence of covariates on soil biodiversity and functioning (Andam et al., 2008; Beresford et al., 2013; Carranza et al., 2014; Joppa and Pfaff, 2010b; Nelson and Chomitz, 2009; Nolte et al., 2013). Unprotected sites do not represent true control sites with perfectly environmentally similar conditions; thus, RZ and CAG extended the nearest-neighbor matching approach (Andam et al., 2008; Beresford et al., 2013; Carranza et al., 2014; Joppa and Pfaff, 2010b; Nelson and Chomitz, 2009; Nolte et al., 2013) and RZ used 1000 randomized pairings without replacement to allow different pairing scenarios. Variables used to identify environmentally similar sites for building protected-unprotected pairs (also known as covariates) were geographical location (i.e., latitude and longitude), elevation, annual average temperature and precipitation, content of soil organic carbon, soil pH, soil salinity (i.e., electrical conductivity), soil texture (i.e., content of clay and silt) and soil stability (i.e., soil aggregate measurements or plant cover indicating less erosion; Table 1,

data S1). RZ provided mean and 95 % confidence intervals (CI) of the effect sizes across the 1000 runs for each habitat type separately at the two spatial scales.

We tried to maximize sample size, defined here as the number of protected-unprotected pairs, by balancing the following trade-off. If a site's environmental conditions differed greatly from others, few or no pairings were possible. More pairing options per protected site, in turn, allowed more flexibility in pairing after excluding already paired unprotected sites. Increasing the number of pairs (i.e., sample size) reduced the ability to use environmentally unique sites due to their limited pairing options. This decreased the diversity of the set of pairs, leading to repeated use of the same unprotected sites across 1000 randomized pairings, defeating the purpose of randomization. To balance possible pair numbers per habitat type (i.e., sample size) and keep as many sites as possible for broad geographical representation, RZ and CAG excluded sites with fewer than 10 pairing possibilities. In addition, RZ limited the number of sites that should be paired per habitat type to make results for habitat types within each dataset comparable. Number of sites to be paired was set to the minimum number of protected sites across habitat types per dataset, namely 14 and 7 protected sites per habitat type at continental and regional scale, respectively. Furthermore, spatial distance between two samples was limited to 500 km maximum at continental scale by RZ, CAG, and MDB to ensure meaningful pairs and avoid comparing completely different ecosystems and climate zones (e.g., forests in Finland with forests in Central Europe). Final sampling sites considered in the effect size analysis were 316 at continental scale (Cropland protected=15 | unprotected=94, Grassland 14 | 78, Woodland 19 | 97) and 157 at regional scale (Cropland 14 | 46, Grassland 7 | 27, Woodland 13 | 50). Number of sites per protection type differed across spatial scales with few IUCN categories missing, namely IUCN categories IV in croplands and grasslands at regional scale, VI in woodlands at regional scale, and II in woodlands at continental scale (Table 2).

We defined effect sizes and slopes as statistically not significant if 95 % CI of medians cross 0. All analyses were performed by RZ supervised by CAG in R v4.3.0 (R Core Team, 2020) using RStudio v.2023.06.0 + 421 (RStudio Team, 2020). A full list of R packages used can be found in the Data and Code repository.

2.5. Sensitivity analyses

We performed several sensitivity analyses to estimate the impact of methodological choices, namely attribute composition, environmental covariates, sample size, matching criteria like the distance of paired samples, and level of protection. RZ estimated the effect of protection status on attributes that are most similar across scales, but we did not test the exactly same response variables. To align attributes even further, RZ removed three variables in the continental scale, namely N-Actylglucosaminidase that was additionally used as proxy for organic matter decomposition, total nitrogen content for nutrient cycling, and mean width diameter for soil stability. In the regional dataset, RZ removed calcium and magnesium content for nutrient cycling. With this, both datasets had the exactly same response variables for soil biodiversity and functioning attributes (but see Table 1 and table S1 for different soil carbon measures). Note that we did not used this more similar set of attributes in the main analysis because we wanted to include as many information as possible for the proxies of soil functioning. To test the impact of attribute composition on the results, we calculated effect sizes with these, similarly composed attributes. We found all effects to be robust against differences in attribute composition and detected an additional negative effect on decomposition in continental croplands (median [95 % CI]: −0.75 [-1.28; −0.18]) that was not found in the main analysis (-0.45 [-0.892; 0.089]); however, this effect was consistent with the negative effect found in continental woodlands in both main and sensitivity analysis.

Although the pairing of environmentally similar sites is minimizing differences between protected and unprotected sites, we still expect an effect of the environment on soil biodiversity and functioning, but less strong than without pairing (Andam et al., 2008; Beresford et al., 2013). RZ tested for this effect by calculating Spearman's rank correlation coefficient of the Mahalanobis distance of pairs and the difference in soil biodiversity and functioning attributes between unprotected and protected sites (figure S2-S3 and data S2). In addition, RZ calculated and plotted Spearman's rank correlation coefficient of the spatial distance between paired samples and the difference in their soil biodiversity and functioning attributes (data S3).

RZ performed power analysis using the pwr package (Champely et al., 2020) to estimate how likely the chosen test is to detect the true effect under the small sample sizes. When setting the acceptable power value to 0.8 and a significance level of 0.05, minimum detectable effect size was d= 1.1 and 1.6 for tests at continental (n = 14) and regional scale (n = 7), respectively. D-values below 1.1 (continental) and 1.6 (regional) have therefore to be taken with care. We decided against a correction of effect size estimates for multiple comparisons, for example using Bonferroni correction (Cabin and Mitchell, 2000; Rice, 1989), because we are interested in a low Type II error rate (i.e., increase statistical power). However, we did investigate the individual Cohen's D estimate distributions to get a more informed picture on the biological importance of the effects found. We looked at the 95 % CIs from Cohen's D estimates and calculated the number of CIs of the 1000 that did not cross 0 (figure S4).

Matching criteria like distance between samples can bias estimates of the protection effect (Andam et al., 2008; Joppa and Pfaff, 2010b). RZ tested for the impact of the distance threshold when pairing continental sites by repeating the effect size estimation using distance thresholds of 200, 300, 400, 600, 700 and 1000 km. Furthermore, RZ allowed for comparison of protected areas to any unprotected areas across scales and thereby also more distant samples to be paired, namely by building pairs without spatial (<500 km) and environmental threshold (i.e., Mahalanobis distance <17.53). RZ tested 4 scenarios at continental scale (with/without Mahalanobis distance threshold, w/o spatial distance threshold), and 2 scenarios at regional scale (with/without Mahalanobis distance threshold; Supplementary text, table S1-S2).

To account for the effect of different protection types, RZ performed random-intercept and random-slope models for each habitat type and soil biodiversity and functioning attribute. Protection status was considered as a factor (random intercept) and continuous variable (random slope) respectively. Protected areas are classified into one of seven IUCN management categories (Dudley, 2008;

UNEP–WCMC, and IUCN,2021). The Protected Area dataset contains three additional categories (not reported, not assigned and not applicable) that were included, too. Sampling sites outside of any protected area were classified as "unprotected". Habitat type was included in regional and continental models as a fixed effect. Soil biodiversity and functioning attributes (response variable) were not scales. Model formulas were attribute ~ protection status + habitat type for the random-intercept model and attribute ~ protection status * habitat type for the random-slope model. It is important to note that sample size for some protection types is rather low and results for the random-intercept and random-slope model are thus less meaningful than effect size estimates for protected-unprotected pairs. For both random-intercept and random-slope models, RZ run 10,000 iterations, including 2000 warm-up iterations, and 4 chains with the R package brms (Bürkner, 2017, 2018, 2021). Priors of soil biodiversity and functioning attributes were chosen based on data and by default to be non or very weakly informative, keeping their influence on the results negligible (data S4). To extract the effect of protection type gradient, RZ used the emtrends and emmeans function of the emmeans package (Lenth et al., 2022), which calculates the estimated marginal means of the linear trends and provides credible intervals (i.e., highest posterior density (HPD) interval; probability: 95 %) of the posterior distributions. All points within the HPD interval have a higher probability density than the points outside the interval. We defined slopes as statistically not significant if HPD intervals cross 0. In addition, RZ extracted 10,000 posterior samples of the intercept and slope estimates with the modelr (Wickham, 2024) and tidybayes (Kay and Mastny, 2024) package for visualization; plotting of the posterior samples was done using the ggdist (Kay and Wiernik, 2024) and tidybayes package (Kay and Mastny, 2024). Random-intercept and -slope models were compared based on LOO (Leave-One-Out cross-validation) and WAIC (Widely Applicable Information Criterion) using the R package loo (Vehtari et al., 2017). Differences in expected log predictive density (ELPD) for LOO greater than twice their standard error ($\Delta ELPD/SE > 2$) were considered substantial. Random-slope models performed consistently better than random-intercept models, except for two soil biodiversity and functioning attributes at continental scale, namely protist Shannon index and decomposer richness (difference in expected log predictive density for leave-one-out cross--validation −5.024 (SE 1.943) and −4.545 (1.894), respectively). In comparison to the effect size estimation, we did not build pairs of protected and unprotected sites but rather included all data available. Final datasets included 807 sites at continental scale (protected=64 | unprotected=743), and 324 sites at regional scale (49 | 275). It is important to note that the inclusion of more sampling sites in the random-intercept and random-slope models compared to the effect size calculations lead to a broader spatial distribution of points, especially at continental scale (figure S5). Results of the random-intercept and random-slope model can be found in the Supplementary text.

The effect of protection status and types on soil biodiversity and functioning was also tested at global scale but datasets available were not suitable for full comparison. Dataset used for global comparison was retrieved by MDB and BKS (see Supplementary text).

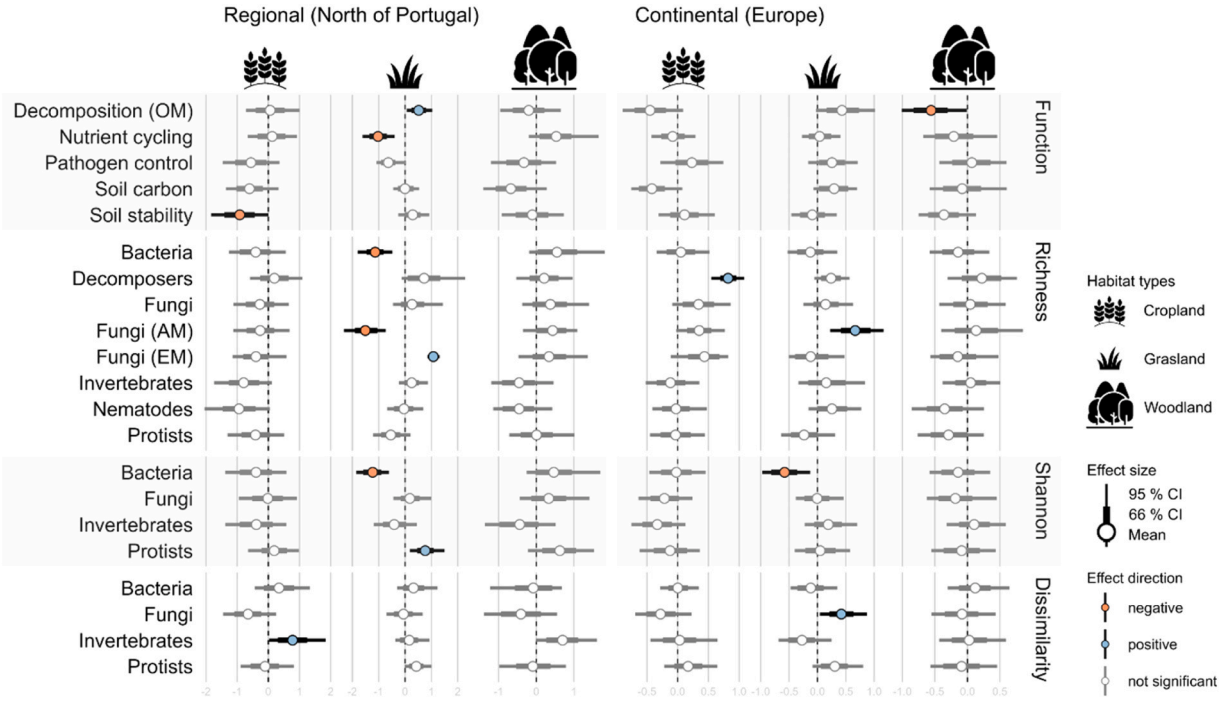

Fig. 2. Effect of nature conservation on soil biodiversity and functioning attributes. Effect size estimates were calculated across three habitat types (cropland, grassland, woodland) and spatial scales (regional, continental) as Cohen's D and averaged across the 1000 randomized pairings. Statistically non-significant effect sizes (unfilled, grey circles) are defined as 95 % confidence intervals (CI) crossing 0. Number of samples was 14 for each habitat type and attribute at the continental scale, and 7 for the regional scale (i.e., 14*1000 and 7*1000, respectively). Underlying data can be found in data S5. Icons: "Grass" created by Freepik, "Forest" by Vitaly Gorbachev, and "Agriculture" by Vectors Tank - Flaticon. Legends to this R plot were added in Inkscape v1.0.1.

Results at global scale are shown in supplementary figures and tables but should be taken with caution.

3. Results

Across the two spatial scales and three habitat types, we found that terrestrial conservation areas contribute minimally and inconsistently to the protection of soil biodiversity and functioning (Fig. 2, data S5). If even significant, effects were not consistently positive or negative across scales, nor across organism groups or biodiversity attributes. We only found significant differences between protected and unprotected areas for 4 out of the 30 tested comparisons on soil functioning attributes (13.3 %) and 10 of the 58 tested soil biodiversity attributes (17.2 %). However, some of these effects were only observable when looking at the distribution of medians of Cohen's D estimates and their confidence intervals (CI) but not necessarily when looking at the 1000 individual confidence intervals of the Cohen's D estimation (figure S4). For instance, protection status was negatively associated with the richness and Shannon index for bacteria in regional grasslands (richness: median effect size [95 % CI]: −1.134 [-1.802; −0.486], Shannon index: −1.23 [-1.848; −0.613]), and continental grasslands (Shannon index: −0.579 [-0.973; −0.127], but not richness: −0.124 [-0.525; 0.349]), but less than 25 % of the 1000 confidence intervals from Cohen's D estimation excluded 0 at continental scale (i.e., n(CI)= 213 for continental scale, but n(CI)= 438 and 519 for bacterial richness and Shannon diversity in regional grasslands). In contrast to bacteria, we found a consistent positive influence of protection status on the dissimilarity of invertebrates in regional croplands (0.778 [0.021; 1.843], n (CI)= 212) and fungi in continental grasslands (0.421 [0.044; 0.873], n(CI)= 52). For the biodiversity of both arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi, we found mixed patterns across scales (Fig. 2, data S5). Soil functioning attributes were mostly negatively influenced by protection status (3 out of 4 significant effects with mean effect size < 0; Fig. 2, data S5). Effects on soil functioning attributes were detected mainly at regional scale, namely on nutrient cycling in regional grasslands (-1.026 [-1.612; −0.395], n(CI)= 328) and soil stability in regional croplands (-0.918 [-1.832; −0.001], n(CI)= 300). Decomposition showed mixed effects across scales: the effect of protection status on decomposition was positive in regional grasslands (0.519 [0.058; 1.035], but note the low number of CI crossing 0: n(CI)= 6) but negative in continental woodlands (-0.559 [-1.011; −0.01], n(CI)= 220). Effects slightly differed across spatial scales and habitat types, which is most obvious when comparing grouped effects on functions, richness, Shannon index and dissimilarity (table S3 and figure S6); however, because of mixed patterns in organisms, averaged effect sizes were nonsignificant (95 % CI cross 0). Different matching scenarios resulted in changed sampling sizes, but revealed also pattern of mixed results (Supplementary text, table S4). Results of the random-intercept and random-slope models, in which we accounted for the different protection types, were similar to the mostly non-significant effect sizes (Supplementary text, figure S5 and S7-S9, data S6-S7, table S5).

3.1. *Effect of environment on soil biodiversity and functioning*

Although the pairing of environmentally similar sites is minimizing differences between protected and unprotected sites (figure S2), we still expected an effect of the environment on soil biodiversity and functioning. We found contradicting results regarding the effect of the environment when testing for the correlation between Mahalanobis distance and environmental variables (figure S2-S3 and data S2), as well as the correlation between spatial distance and pairwise difference in attribute values (data S3). We found significant effects of protection status on soil biodiversity and functioning attributes despite nonsignificant correlations between Mahalanobis distance and environmental variables (figure S2-S3 and data S2), indicating that the effects found cannot fully be explained by Mahalanobis distance (i.e., environmental distinctness). We did find significant correlations between spatial distance and the absolute difference in soil biodiversity and functioning attributes of protected-unprotected pairs (61 out of 63), however, 24 of these correlations were even negative, meaning that the difference between attributes in protected and unprotected soils got smaller with increasing distance (data S3). This indicates that the significant effects cannot be fully explained by differences in environmental conditions and spatial distance of paired samples alone but may in fact be related to the protection status.

4. Discussion

Protected area effectiveness was estimated multiple times but looks more promising for aboveground than soil biodiversity. Previous studies found protected areas to be 2–50 % effective (Watson et al., 2014) and having mainly positive effects such as on preventing habitat loss (Geldmann et al., 2013). However, conservation impact may depend on the taxon, function, and ecosystem considered; and conservation measures seem to not protect the entire ecosystem (Barnes et al., 2016; Eastwood et al., 2016; Geldmann et al., 2013; Gray et al., 2016; Langhammer et al., 2024). Our results show a notable disconnect between current nature conservation efforts and the protection of soil biodiversity and functionality. Specifically, only 14 out of 88 evaluated effects of conservation areas on soil biodiversity or functioning attributes were statistically significant, with a notable 7 of these effects displaying a negative mean effect size (< 0). This suggests that in these cases, soil biodiversity and functioning may actually be lower in nature conservation areas than in comparable unprotected sites. Notably, we found some biodiversity and functioning attributes, which are linked to ecosystem services and soil health (Delgado-Baquerizo et al., 2020; Guerra, Bardgett, et al., 2021), to be affected by protection status, but could not detect effects on all attributes, for example on soil carbon (Fig. 2, data S5). Conservation influence may therefore depend on the soil biodiversity and functioning attribute considered. It is important to state that finding statistically non-significant results when comparing protected and unprotected sites is, on itself, a very important result. We also did not test for multiple comparison problem and are therefore probably even overestimating the effect of protection of soil biodiversity and functioning attributes (i.e., there is likely a lower number of true positive or negative effects than detected here; Cabin and Mitchell, 2000; Rice, 1989). To account for

potential overestimation, we did not rely on practical significance and summary statistics only (i.e., Cohen's D median) but rather considered the whole distribution of effect sizes resulting from the 1000 randomized pairings, thereby keeping and presenting all information provided by the analysis. In general, we found that the conservation of soils by protected areas is highly debatable and remains uncertain with current available information, which has been in line with our expectation. Our results meanwhile contradict the assumption that nature conservation areas, often designed to protect plants and (aboveground) animals, are able to protect the entire ecosystem (Barnes et al., 2016; Eastwood et al., 2016; Geldmann et al., 2013; Gray et al., 2016; Langhammer et al., 2024), from which soils are a big part of it. The mechanisms behind the effects of protection are still unclear (Geldmann et al., 2013), and land use has been only – but at least – explaining a small part (Gray et al., 2016).

We found mixed results across habitat types, which shows that habitat type itself, and the environmental conditions considered here, do not define soil biodiversity and functioning outcomes when comparing the protection status. Furthermore, our findings suggest that the contribution of nature conservation to soil biodiversity and functioning slightly differed across spatial scales, as reflected in the grouped effect sizes for functions, richness, Shannon index, and dissimilarity (table S3 and figure S6). While other factors may be considered to further detail these findings (e.g., pollution (Beaumelle et al., 2021; FAO, and UNEP,2021), land degradation (Eswaran et al., 2001)) and we used different measures of soil functions across scales, our results show either an absence of effect or some negative effects from current nature conservation areas (but also a few positive effects). Given that these results are consistent across scales, current nature conservation areas seem to fail to capture critical soil conservation values, or that even when they do capture them, their conservation management and regulations seem to be inadequate to protect these values.

5. Limitations and knowledge gaps

We are aware of the limitation of the IUCN protected area management categories, and that the categories I-VI do not necessarily represent a gradient in strictness of protection measures (Boitani et al., 2008; Dudley, 2008; Leroux et al., 2010). In addition, results for the protection type analysis (i.e., random-intercept and -slope models; Supplementary text, figure S5 and S7-S9, data S6-S7, table S5) have to be interpreted with caution due to small sample size (number of samples per protection type and habitat type). The datasets used here did not allow testing for the effect of protected area management or protection duration (e.g. Joppa and Pfaff, 2010a) in detail and the large confidence intervals surrounding our estimates highlight the pressing need for more accurate data on protected area management. Protection outcome strength was previously shown to differ with year of establishment (Nelson and Chomitz, 2009) but also with governance type (i.e., indigenous lands; (Nolte et al., 2013) and remoteness (Joppa and Pfaff, 2010a; Nelson and Chomitz, 2009; Nolte et al., 2013). Even though we could not test for these covariates, we found that effects can't be explained by environmental and spatial distance of protected and unprotected sites alone, and were robust against methodological and modelling choices (Supplementary text, figure S2-S3, table S4, data S2-S3). Our attempt to investigate the effect of protection on soils with one of the most comprehensive existing datasets at global scale (Maestre, Eldridge, et al., 2022; Maestre et al., 2015; Maestre, Le Bagousse-Pinguet, et al., 2022) actually failed (see Supplementary text, figure S10-S14, table S6-S7), because its resolution was not good enough for full comparison. At such large scale, more data is required to counteract differences in environmental conditions and habitat types, for example to avoid comparing tropical with temperate forests, which has not been of concern for the two analyzed datasets at regional and continental scale. Our sensitivity analyses indicated that the absence of consistent protection effects is not driven by dataset choice. While the datasets used here currently represent the best available data to study the effect of conservation areas on soil biodiversity and functioning, we acknowledge that more comprehensive soil biodiversity datasets such as the one being developed by Soil BON (Guerra, Bardgett, et al., 2021) will further advance this field. We need global standardized approaches like Soil BON being specifically designed to check for the global effect of protection status in more detail. Although future data may improve robustness, our study provides an important and timely assessment of the limited protection of soil biodiversity and functions, and highlights the need for investigating the contribution of protection areas in conserving soil biodiversity and functioning. In fact, larger datasets will enable analysis of mechanisms of effective nature conservation, such as by identifying management practices that cause positive effects of selected conservation areas on soil biodiversity and functioning.

Our analysis of individual types of nature conservation areas did not show consistent differences in soil biodiversity and functioning across protection types, confirming previous findings about the effects of (higher) levels of protection on biodiversity. We found some significant trends of lower soil biodiversity and functioning in protected sites, namely for soil stability, nutrient cycling, and for richness of bacteria and AM fungi among others. However, strictly protected sites (i.e., IUCN category I-II) showed similar values for several soil biodiversity and functioning attributes as less strictly protected and unprotected sites (figure S7-S9). While there are examples of the positive effects of protection status or type on aboveground organisms (e.g., mammals (Magoulick et al., 2024), mammals and birds (Barnes et al., 2016; Bolam et al., 2021; Brodie et al., 2023), and birds and reptiles (Justin Nowakowski et al., 2023)), previous studies found certain taxa (e.g. nematodes; Ciobanu et al., 2019) and smaller-bodied groups (Barnes et al., 2016) to be unaffected by protection categories. Our analysis shows that the same might be true for soil biodiversity. Especially for soil organisms, local management and other factors (e.g., pollution (Beaumelle et al., 2021; FAO, and UNEP,2021), land degradation (Eswaran et al., 2001)) likely play a more important role in protecting soil biodiversity than conservation status (reflected by IUCN categories) alone. As such, sites may have experienced very diverse land uses over time, leading to long-lasting soil legacy effects (Osburn et al., 2021). In turn, a site protected for multiple years might be more promising to also have soil biodiversity benefits as compared to a few years of protection (e.g. as shown for land-use intensity; Sünnemann et al., 2021). Soils need time to respond, highlighting the need for long-term studies to fully understand these dynamics and long-term protection to maintain their biodiversity and functioning. Multiple stressors, such as atmospheric nitrogen deposition and climate extremes, may co-occur and have non-additive effects on soil biodiversity and ecosystem functioning at small (Rillig et al., 2019) to large scales (Zhou et al., 2024), being relevant across systems and

protection status and requiring targeted measures. Because nature conservation areas were shown before to not align with soil biodiversity hotspots (Guerra et al., 2022), soil biodiversity can only be effectively protected if nature conservation and its management directly target and are tailored to the soils. Effective soil biodiversity conservation could involve liming to reduce acidification, and maintaining vegetation cover, organic soil layers, and deadwood to buffer climate extremes (Guerra et al., 2022), and promoting diverse plant communities that support soil microbial diversity (Wagg et al., 2014). Additionally, reducing soil disturbances, preserving deadwood, and implementing long-term soil monitoring (Bardgett and van der Putten, 2014), as well as extensive pasture management (Sünnemann et al., 2021) could help tailor conservation efforts to different ecosystems and protection statuses. Integrating these measures into nature conservation strategies would ensure that soils receive the attention needed for effective biodiversity protection (Guerra et al., 2022; Teng et al., 2024).

6. Conclusion

Soils provide 95 % of all the food we consume (FAO, 2022, 2023), and capture the largest portion of organic carbon in our ecosystems (Lal, 2004). Our study reveals major uncertainties in the ability of current nature conservation areas to safeguard soil biodiversity and function, underscoring an urgent need for more targeted action. We found that current terrestrial nature conservation areas show inconsistent effects in protecting soil biodiversity and functioning across spatial scales and habitat types. Our results also show that, in parallel to identifying and establishing new areas that specifically target soil biodiversity (Guerra et al., 2022), we require immediate action to adapt current nature conservation management practices to better address soils and their requirements in terms of biodiversity protection. The message for policy makers and natural areas managers is clear. We need to urgently designate new nature conservation areas that specifically target soil systems to protect the biodiversity and functionality of soils. This approach is essential to preserve soil health and resilience for future generations, particularly in the face of accelerating climate change.

CRediT authorship contribution statement

Romy Zeiss: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data Curation, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Kirsten Küsel:** Writing – review & editing. **Susana Mendes:** Writing – review & editing, Investigation, Funding acquisition. **Manuel Delgado-Baquerizo:** Writing – review & editing, Writing – original draft, Funding acquisition, Data curation, Conceptualization. **Alberto Orgiazzi:** Writing – review & editing, Data curation. **Bala Singavarapu:** Writing – review & editing, Writing – original draft, Software, Investigation, Formal analysis. **Brajesh K. Singh:** Writing – review & editing, Investigation. **Nico Eisenhauer:** Writing – review & editing, Resources, Investigation, Funding acquisition. **A. Carolina Duarte:** Writing – review & editing, Investigation. **Paulo Fernandes:** Writing – review & editing, Investigation. **Arwyn Jones:** Writing – review & editing, Funding acquisition. **Carlos A. Guerra:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Concha Cano-Díaz:** Writing – review & editing, Investigation, Data curation. **Irene Calderón-Sanou:** Writing – review & editing, Investigation. **Rui P. Carvalho:** Writing – review & editing. **Sofia R. Costa:** Writing – review & editing, Investigation, Funding acquisition.

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Code availability

All code for data cleaning, analysis and visualization associated with the current submission is available at the iDiv data repository (https://idata.idiv.de/ddm/Data/ShowData/3584). Any updates will also be published on GitHub (https://github.com/JeMaNd-r/Conservation_across_scales).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2026.e04052.

Data Availability

I have shared the link to the data and code repositories in the Data and Code availability statements. The datasets analyzed during the current study are available at the iDiv data repository (https://idata.idiv.de/ddm/Data/ShowData/3584). Raw data were collected from literature or databases (see main text) and are available at the data repository if not under sharing embargo; data under embargo can be requested from Fernando T. Maestre Gil (global dataset of supplementary analysis), through data request to European Soil Data Centre (ESDAC; continental dataset, but coordinates need to be requested separately manually from ESDAC or from Alberto Orgiazzi), and from Concha Cano-Diaz (Portuguese dataset), or from the corresponding author that will forward the request accordingly. R code can be accessed according to the Code Availability statement.

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