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A multitaxonomic assessment of Natura 2000 effectiveness across European biogeographic regions

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Article impact statement: N2K protected areas host more priority species than outside, but they have a different impact across biogeographic regions and taxa.

Abstract

The Natura 2000 (N2K) protected area (PA) network is a crucial tool to limit biodiversity loss in Europe. Despite covering 18% of the European Union's (EU) land area, its effectiveness at conserving biodiversity across taxa and biogeographic regions remains uncertain. Testing this effectiveness is, however, difficult because it requires considering the nonrandom location of PAs, and many possible confounding factors. We used propensity score matching and accounted for the confounding effects of biogeographic regions, terrain ruggedness, and land cover to assess the effectiveness of N2K PAs on the distribution of 1769 species of conservation priority in the EU's Birds and Habitats Directives, including mammals, birds, amphibians, reptiles, arthropods, fishes, mollusks, and vascular and nonvascular plants. We compared alpha, beta, and gamma diversity between matched selections of protected and unprotected areas across EU's biogeographic regions with generalized linear models, generalized mixed models, and nonparametric tests for paired samples, respectively, for each taxonomic group and for the entire set of species. PAs in N2K hosted significantly more priority species than unprotected land, but this difference was not consistent across biogeographic regions or taxa. Total alpha diversity and alpha diversity of amphibians, arthropods, birds, mammals, and vascular plants were significantly higher inside PAs than outside, except in the Boreal biogeographical region. Beta diversity was in general significantly higher inside N2K PAs than outside. Similarly, gamma diversity had the highest values inside PAs, with some exceptions in Boreal and Atlantic regions. The planned expansion of the N2K network, as dictated by the European Biodiversity Strategy for 2030, should therefore target areas in the southern part of the Boreal region where species diversity of amphibians, arthropods, birds, mammals, and vascular plants is high and species are currently underrepresented in N2K.

Análisis multitaxonómico de la efectividad de Natura 2000 en las regiones biogeográficas de Europa

Resumen: La red de áreas protegidas (AP) de Natura 2000 (N2K) es una herramienta importante para reducir la pérdida de biodiversidad en Europa. A pesar de que cubre el 18% del área terrestre de la UE, todavía es incierta la efectividad que tiene para conservar la biodiversidad en los taxones y las regiones biogeográficas. Sin embargo, es complicado analizar esta efectividad porque requiere considerar la ubicación no azarosa de las AP y la posibilidad de muchos factores confusos. Usamos el pareamiento por puntaje de propensión y consideramos los efectos confusos de las regiones biogeográficas, lo accidentado del terreno y la cobertura del suelo para analizar la efectividad de las AP de N2K en la distribución de 1,769 especies (mamíferos, aves, anfibios, reptiles, artrópodos, peces, moluscos y plantas vasculares y no vasculares) con prioridad de conservación en las Directivas de Aves y Hábitats de la UE. Comparamos la diversidad alfa, beta y gamma entre las selecciones pareadas de las áreas protegidas y no protegidas en las regiones biogeográficas de la UE con los modelos generalizados lineales, mixtos y pruebas no paramétricas de las muestras pareadas, respectivamente, para cada grupo taxonómico y para el conjunto completo de especies. Las áreas protegidas en N2K tuvieron una mayoría significativa de especies prioritarias en comparación con el suelo no protegido, pero esta diferencia no fue coherente entre los taxones y las regiones biogeográficas. La diversidad alfa total y la diversidad alfa de anfibios, artrópodos, aves, mamíferos y plantas vasculares fue significativamente mayor dentro de las AP que fuera de ellas, excepto en la región biogeográfica boreal. La diversidad beta fue significativamente más alta dentro de las AP de N2K que fuera de ellas. De forma similar, la diversidad gamma tuvo los valores más altos dentro de las AP, salvo algunas excepciones en las regiones boreal y atlántica. Por lo tanto, la expansión planeada de la red N2K, como dicta la Estrategia de la UE sobre Biodiversidad para 2030, debería enfocarse en las áreas del sur de la región boreal, donde es alta la diversidad de especies de anfibios, artrópodos, aves, mamíferos y plantas vasculares y cuyas especies están poco representadas dentro de N2K.

PALABRAS CLAVE
Directiva de Aves, Directiva de Hábitats, especies anexas, Estrategia de la UE sobre Biodiversidad para 2030, Natura 2000, pareamiento por puntaje de propensión

【摘要】
Natura 2000 (N2K) 保护地网络是阻止欧洲生物多样性丧失的重要工具。该网络已覆盖欧盟 18% 的陆地面积，但其在保护不同类群和生物地理区的生物多样性方面的有效性仍不明确。然而，由于需要考虑保护地的非随机分布以及许多可能的混杂因素，检验这些保护地网络的有效性仍面临困难。本研究利用倾向得分匹配法，同时考虑了生物地理区、地形崎岖性和土地覆盖类型的混杂因素，评估了 N2K 保护地对于保护欧盟《鸟类指令》和《栖息地指令》中 1769 种优先保护物种分布区的有效性，涉及的物种包括哺乳动物、鸟类、两栖类、爬行类、节肢动物、鱼类、软体动物以及维管植物和非维管植物。我们用广义线性模型、广义混合模型和配对样本非参数检验，分别比较了每个类群和所有物种在欧盟生物地理区内保护地和非保护地配对位点之间的 α、β 和 γ 多样性。结果显示，与未受保护的土地相比，N2K 保护地中明显存在更多的优先保护物种，但这一差异在不同生物地理区或类群之间并不一致。总 α 多样性和两栖动物、节肢动物、鸟类、哺乳动物及维管植物的 α 多样性都在保护地内显著高于保护地外，但在北欧生物地理区除外。N2K 保护地内的 β 多样性总体上显著高于保护地外。同样地，保护地内的 γ 多样性最高，但在北欧和大西洋地区存在例外。因此，《欧盟2030年生物多样性战略》中提到的 N2K 网络的扩展计划应针对北欧南部的区域，那里两栖

动物、节肢动物、鸟类、哺乳动物和维管植物的物种多样性较高, 而在当前的 N2K 中的物种代表性不足。【翻译: 胡怡思; 审校: 聂永刚 】

INTRODUCTION

Protected areas (PAs) are key conservation tools to reach global biodiversity and sustainability targets (Hoffmann, 2021). When well managed, these areas can reduce anthropogenic pressures on ecosystems, including land-cover change (Figueroa & Sánchez-Cordero, 2008), forest degradation (Leberger et al., 2019), human-induced forest fires (Nelson & Chomitz, 2011), and carbon release into the atmosphere (Graham et al., 2021). Furthermore, PAs contribute to climate change mitigation and adaptation (MacKinnon et al., 2011), natural disaster control (Xu et al., 2017), poverty reduction (Andam et al., 2010), and tourism and recreational opportunities (Balmford et al., 2009).

Currently, about 16.8% of terrestrial land is protected (IUCN & UNEP-WCMC, 2022). The effectiveness of the global PA system in preserving biodiversity is, however, questionable because PA coverage is increasing, whereas biodiversity is decreasing inside and outside PAs (Geldmann et al., 2019; Visconti et al., 2019). In general, PAs in biodiversity hotspots and those actively managed and well funded effectively conserve biodiversity (Coad et al., 2019; Joppa et al., 2013). Yet, only a fraction of PAs is managed effectively, adequately funded, and supported by governments (Coad et al., 2019; Geldmann et al., 2019; Laurance et al., 2012; Leverington et al., 2010).

The protection status of PAs differs immensely. The International Union for the Conservation of Nature has created a system in which all global PAs are assigned to 1 of 7 management categories (Dudley, 2008), but these categories are not necessarily an indicator of management effectiveness; PAs that allow less human intervention do not consistently show less nature degradation (Boitani et al., 2008; Coetzee et al., 2014; Ferraro et al., 2013; Locke & Dearden, 2005; Loiseau et al., 2021; Pfaff et al., 2015). In addition, climate change is increasingly affecting biodiversity inside PAs, especially in Asia, Africa, and Latin America (Geldmann et al., 2019; Hoffmann & Beierkuhnlein, 2020; Schulze et al., 2018).

The long-term preservation of endangered species is a major goal of PA management (Jetz et al., 2022), and most species and populations are better protected inside than outside PAs (Brown et al., 2019; Chiarucci et al., 2008; Dähler et al., 2019; Pellissier et al., 2020; Pinto et al., 2014). Nevertheless, the contribution of PAs to global species preservation is not fully understood (Geldmann et al., 2013; Rodrigues & Cazalis, 2020; Schulze et al., 2018). Although animal and plant abundances have remained the same or have decline inside selected PAs (Baran et al., 2018; Craigie et al., 2010; Hallmann et al., 2017; Laurance et al., 2012; Oberosler et al., 2020; Rada et al., 2019), a global study shows local species diversity is higher inside than outside PAs (Gray et al., 2016). Species' richness and abundances benefit

particularly from PAs, as revealed in a worldwide meta-analysis (Coetzee et al., 2014). Thus, the mere designation of PAs does not ensure biodiversity conservation because the complexity and differences in protection status and policy could provide inconsistent results (Velazco et al., 2019; Wauchope et al., 2022). A better understanding of the effectiveness of PAs and the mechanisms related to their success is therefore crucial. Measuring the state of biodiversity and its change, however, requires consistent indicators that account for local contexts and highlight conservation gaps. This is a necessary step to inform and justify the establishment of new PAs (Geldmann et al., 2021, 2023).

A statistically sound comparison of the effectiveness of PAs, as opposed to unprotected areas, for the conservation of species diversity is complex. PAs are not located at random in the landscapes and are often overrepresented in particular biogeographic regions, topographical situations, or land-cover categories (Guerra et al., 2019; Joppa & Pfaff, 2009; Lawrence, Hoffmann, et al., 2021). Therefore, these factors need to be accounted for when comparing the species composition or richness of land in- and outside PAs as an indication of their effectiveness. A possible approach is to match protected and unprotected areas in terms of the main confounding factors that affect species composition and species richness, such as biogeographic region, topographical position, and primary land cover (Meng et al., 2023; Rodrigues & Cazalis, 2020), and then perform a comparison. Land cover is of critical importance. It affects the heterogeneity of the landscape, increasing or decreasing habitat differentiation and niche availability and ultimately determining the presence or absence of a species (Haines-Young, 2009; Peters et al., 2019; Simmonds et al., 2019).

Using matching techniques allows one to account for confounding factors when evaluating the effectiveness of different PAs and making inference about PA management that can affect biodiversity outcomes (Geldmann et al., 2018). However, robust attempts to evaluate PA effectiveness are still lacking (Rodrigues & Cazalis, 2020; Wauchope et al., 2022), especially in Europe, where most studies compare species diversity in PAs and unprotected areas without accounting for confounding factors. In Europe, large-scale conservation is particularly challenging because the continent consists of many different countries with diverse political, social, economic, and ecological systems (Henle et al., 2008; Kati et al., 2015). The key biodiversity conservation tool in the European Union (EU) is the Natura 2000 (N2K) network (Campagnaro et al., 2019; Hermoso et al., 2019; Wurzel, 2008). At present, the network includes over 788,000 km^2 of PAs, corresponding to 18% of Europe's terrestrial land and 3% of inland waters (EAA, 2015). The N2K network consists of a large variety of PAs under varying man-

agement regimes, from strict nature reserves to privately owned nature reserves that do not exclude human activities.

N2K represents the implementation of the Birds Directive 2009/147/EC (1979) and Habitats Directive 92/43/EEC (1992), which are legally binding policies for the conservation of species and rare land-cover types. The 2 directives oblige EU member states to report the occurrence of and protect hundreds of land-cover types and thousands of endangered, vulnerable, rare, and endemic species and subspecies in 10 major taxonomic groups. These species (hereafter priority species) are listed in the annexes of the directives and are focal species for biodiversity conservation at the political level but do not represent the full range of species native to EU territory (Gruber et al., 2012; Maiorano et al., 2015; Trochet & Schmeller, 2013). Of these, 77% of species and 84% of land-cover types listed in the Habitats Directive and 48% of species listed in the Birds Directive are facing some risk of extinction (EAA, 2015). Given these threats, it is crucial to evaluate and monitor the performance of N2K PAs.

Despite the N2K network being established to protect priority species, many areas where these species occur lack protection (Kukkala, Arponen, et al., 2016; Maiorano et al., 2007, 2015). Several conservation gaps have been identified for many groups of taxa. For instance, 35% of amphibians and reptiles are not well represented in N2K PAs, and there are fewer conservation gaps for birds listed in the EU directives (Maiorano et al., 2015). Moreover, N2K areas have not protected some target species, such as insects, and this ineffectiveness is primarily related to the inadequate management of habitats of these species (Habel et al., 2019; Rada et al., 2019). Management strongly affects the effectiveness of N2K PAs at preserving priority species, which means that after several years, PAs may no longer host some priority species (Elsen et al., 2020; Geldmann et al., 2015). Thus, investigating whether N2K PAs still support priority species 30 years after their establishment is crucial to providing a fundamental benchmark of their effectiveness and to informing further expansion of this network as planned by the European Biodiversity Strategy for 2030.

We used occurrence data of priority species from the Birds and Habitats Directives to quantify the effectiveness of N2K PAs at conserving biodiversity across the EU. Rather than analyzing overall species richness, which could be a poor indicator of PAs effectiveness (Hillebrand et al., 2018; Rodrigues & Cazalis, 2020), we focused on priority species because they are highly responsive to anthropogenic land-use transformation and most in need of conservation (Hillebrand et al., 2018; Rodrigues & Cazalis, 2020). We examined differences in alpha, beta, and gamma diversity in N2K PAs and unprotected areas after accounting for confounding factors of PA locations.

We hypothesized that N2K PAs contain a more priority species than terrestrial areas outside the network across biogeographic regions and taxonomic groups and N2K PAs host more diverse assemblages (i.e., higher beta diversity) of priority species than unprotected areas with similar site conditions.

METHODS

Data preparation

To obtain species occurrence information, we downloaded the data set (EEA, 2021a, 2021b) used to prepare the fourth (2013–2018) report on the conservation status of habitat types and species, under Article 17 of the Habitats Directive and Article 12 of Birds Directive (EEA, 2020). The data set contains 571,200 records on the presence and absence of 1769 priority species (490 bird species, 71 amphibians, 128 arthropods, 188 fish, 129 mammals, 34 mollusks, 37 nonvascular plants, 105 reptiles, and 587 vascular plant species) at a 10×10-km resolution (EEA, 2020, 2021a, 2021b). Each record was assigned to its respective biogeographic regions (EEA, 2019a) based on the 10×10-km resolution raster in Cervellini et al. (2020).

Geospatial polygon data of N2K sites were downloaded from the European Environment Agency (EEA) (EEA, 2018). We used N2K sites version 2018 to conform to Article 17 reporting period. We converted the N2K polygon data to raster data on a 10×10-km grid (41,789 cells) by calculating the areal proportion of each grid cell covered by N2K sites. Land-cover data were retrieved from Corine Land Cover 2018 (EEA, 2019b) with an original spatial resolution of 100×100 m. We aggregated the 100×100 m land-cover raster to 10×10 km and calculated for each cell the proportion coverage of each of the main land-cover classes (i.e., the official level 1 Corine land-cover nomenclature: artificial surfaces, agricultural areas, and forests and seminatural areas). We considered these land-cover variables, particularly the artificial surfaces and agricultural areas, as proxies for human impact. Purely marine cells were excluded from the analyses. The median terrain ruggedness index was extracted from the EarthEnv database (Amatulli et al., 2018) with a 10×10-km resolution. Terrain ruggedness is the mean of the absolute differences in elevation between a focal cell and its 8 surrounding cells. Plain areas have a value of zero, and mountainous areas have positive values. Geographic processing was conducted in the Lambert Azimuthal Equal Area Coordinate System with the European Terrestrial Reference System 1989. A summary of the data used is in Appendix S1.

Data preparation and all statistical analyses were conducted with R 4.2.1 (R Core Team, 2022) with the packages terra (Hijmans, 2022), rgdal (Bivand et al., 2015), sf (Pebesma, 2018), and rgeos (Bivand et al., 2017).

Classifying grid cells as protected and unprotected

To categorize each 10×10-km cell as protected or unprotected, we applied 2 different thresholds (Appendix S1) to evaluate how sensitive the results were to different levels of PA coverage. In the first scenario, we chose a 100% threshold. In this situation, a cell must be completely (100%) protected or completely unprotected (0%) to be considered for further analysis. Cells with N2K PA coverage ranging for 0% to 100% were excluded. In

the second scenario, we established a threshold of 75%, with cells classified as unprotected if their PA coverage was <25% and protected if it was >75%. All cells with PA coverage from 25% to 75% were excluded from further analysis. Using the 100% and 75% thresholds resulted in 15,410 and 35,007 valid grid cells, corresponding to 37% and 80% of EU's grid cells, respectively.

We limited our focus to the Alpine, Atlantic, Boreal, Continental, and Mediterranean regions because they had large PAs (biogeographic region with >100 protected grid cells with both thresholds). In contrast, we found no or very few protected grid cells when we used both thresholds after accounting for confounding factors for the Pannonian, Steppic, Black Sea, and Macaronesia biogeographic regions, supporting our decision to exclude these regions from the study.

Matching

To account for confounding factors, we used propensity score matching, which is the most used matching technique (Geldmann et al., 2019). Matching is designed to evaluate the effects of a treatment with purely observational data that reduces the bias associated with unequal covariate distribution between treatment and nontreatment groups (Joppa & Pfaff, 2011). Here, PAs were the treatment group. For each protected cell (treatment group), propensity score matching selected the most similar unprotected cell (control group) to provide an unbiased comparison of protection level impact on species diversity (Andam et al., 2008). Based on previous studies (Andam et al., 2008; Geldmann et al., 2019; Joppa & Pfaff, 2009; Meng et al., 2023) and due to differences in abiotic conditions that characterize PAs and unprotected areas, to compare species diversity inside and outside PAs we chose the following matching covariates: biogeographic region; terrain ruggedness; and proportion of a cell covered by artificial surfaces, forest and seminatural areas, and agricultural areas. For biogeographic regions, we used exact matching (i.e., we compared only PAs and unprotected areas in the same region). We did not consider countries as covariates because of their marginal role in explaining species richness patterns at a continental scale, where ecological limits play a much greater role (Rabosky & Hurlbert, 2015). Furthermore, increasing the number of covariates would have drastically decreased the number of matched cells. Given recent criticism of propensity score matching, we also tested coarsened exact matching (Appendix S2). We did not test Mahalanobis distance because this type of matching operates poorly in situations where matching variables are collinear, and this would have led to the exclusion of several covariates.

Matching analyses were performed using the MatchIt package (Ho et al., 2011) with the nearest neighbor method without replacement. The caliper was set to 0.25 and the "ratio" parameter to 1 (Cuenca et al., 2016).

Comparison and validation of matching methods

We used the standardized mean difference test to check the balance between the treated and control groups and verify the validity of the 2 matching methods for both thresholds (Appendix S2). This test is increasingly used to compare the distribution of baseline covariates between treatment groups in observational studies and as a balance measure of individual covariates before and after matching (Rahman & Islam, 2021). We used the cobalt 4.4.0 package to perform the standardized mean difference tests (Greifer & Greifer, 2020). We set a cutoff at a standardized difference of 10%, which often denotes a meaningful imbalance in the baseline covariate (Austin, 2009; Rahman & Islam, 2021). Assessing the balance of the 2 matching methods showed that propensity score matching outperformed the coarsened exact matching (Appendix S2); it returned more similar distributions of covariates between the treated and control groups.

Diversity indices in protected and unprotected grid cells

We calculated alpha diversity as the total number of species and as the number of species of each distinct taxonomic group (i.e., amphibians, arthropods, birds, fishes, reptiles, mammals, mollusks, nonvascular plants, and vascular plants) in every 10×10-km cell. To graphically explore conservation gaps, we built a bivariate map with the percentage of PA coverage and the average value of the standardized species richness for each taxonomic group (alpha diversity).

For each 10×10-km cell, we calculated the relative percentage of PA coverage as the ratio of the cell areas. Due to the great heterogeneity in the number of species represented in each taxonomic group, we calculated for each cell the scaled richness of each taxonomic group, that is, the ratio between the richness observed in the cell (alpha diversity) and the maximum number of species in a cell of that taxonomic group. We standardized values for each taxonomic group with values ranging from 0 to 1 (1, maximum number of priority species for each taxonomic group). We then summed the standardized species richness for each taxonomic group and then standardized it again with values from 0 to 1. Following this, we calculated the average scaled richness across taxonomic groups to obtain a single measure of the diversity of all taxa we sampled. Differences in alpha diversity between protected and unprotected cells for each taxon were assessed by fitting generalized linear models, allowing for the interaction between protection status and biogeographic region, and all the variables included in the propensity score matching as additional covariates. In the same way, when considering total alpha diversity (all taxonomic groups pooled), we fitted generalized linear mixed models (GLMMs) with the same

fixed effect as above, but we added a random intercept and slope for each taxon (Poisson family) (Breslow & Clayton, 1993). The lme4 package (Bates, 2010) was used to perform the GLMMs. Moreover, because there were very few occurrences of reptiles and mollusks (number of occurrences <3) in the Boreal region, this area was removed from the analyses of these taxa.

We tested the presence of spatial autocorrelation in the model residuals with the function correlog of the ncf package (Bjornstad & Bjornstad, 2016). The significance of correlograms was assessed with Moran's *I*. We found significant spatial autocorrelation (Appendix S1). To overcome this issue, we added the residual autocovariate to the initial models and refit them (Crase et al., 2012). The neighborhood distance was set to 100 km, and each point in the neighborhood was weighted by the inverse distance to the observation point. We then checked the correlogram again. For the calculation of residual autocorrelation, we used the spdep package and the function autocov_dist (Bivand & Piras, 2015).

Considering the whole set of species, we calculated total pairwise beta diversity for all possible protected cell pairs and for all unprotected cell pairs in each biogeographic region and for all of Europe. The calculations were based on the Sørensen dissimilarity, a measure of beta diversity, which is widely used on binary data. Total pairwise beta diversity was obtained using the function beta.pair in the betapart package (Baselga & Orme, 2012). We tested significant differences in total pairwise beta diversity between protected and unprotected cells across biogeographic regions with the Wilcoxon rank sum test.

Gamma diversity was calculated as the total number of species occurring in each biogeographic region and all of Europe for each taxonomic group. We calculated gamma diversity for all cells and for cells we split into protected and unprotected. We then calculated the percentage of gamma diversity inside and outside PAs by dividing the number of species found inside or outside PAs by the total number of species occurring in each biogeographic region.

RESULTS

Before matching, the means, differences in standard deviations, and standardized mean differences for most of the confounding factors presented large significant differences between protected and unprotected cells. After matching, the differences between confounding factors were reduced substantially, suggesting a good balance was achieved (Appendix S2). Results were mostly consistent when using the 100% or 75% thresholds. Thus, hereafter, we show only results obtained with the 100% thresholds. The slight difference observed when using the 75% threshold, shown in Appendix S2, was for mammals in the Boreal and for mollusks in the Alpine regions. Mean alpha diversity was consistently higher inside than outside PAs, except for the Boreal and Continental regions (Table 1; Appendix S2). Despite this, when considering the maximum alpha diversity per grid cell, a different pattern was found for the Continental region, which showed a maximum value (189 species) second

only to the Mediterranean region (198 species). The lowest value was recorded outside PAs in the Atlantic region.

We observed low values of species richness but high PA coverage in the northern part of the Boreal region, southern Iberian Peninsula, and northern Britain. Contrastingly, in the southern part of the Boreal region and in some parts of Central and Eastern Europe, we found higher species richness but lower percent PA coverage (Figure 1). Areas of high biodiversity that were well protected were relatively underrepresented and scattered over Europe.

The model results showed higher alpha diversity inside than outside PAs (Figure 2; Appendix S2). Total alpha diversity and alpha diversity of amphibians, arthropods, birds, mammals, and vascular plants were significantly higher inside PAs than outside, across all biogeographic regions, except the Boreal region (Figure 3; Appendix S2). Alpha diversity of birds was significantly lower inside PAs in the Continental region. Alpha diversity was higher in PAs, but not significantly so, for arthropods in the Atlantic region and for fishes, mollusks, and nonvascular plants in the Mediterranean region. Alpha diversity of fishes was not significantly higher in PAs in the Alpine region.

Beta diversity was higher inside PAs; median values ranged from 0.3 to 0.8 (Figure 3; Appendix S2). The minimum median value was obtained in unprotected areas, specifically in the Boreal region, whereas the highest was in PAs of the Continental region (Figure 3; Appendix S2). The Wilcoxon rank sum test showed a similar pattern, with significantly higher beta diversity values inside PAs than unprotected areas across the biogeographic regions, except for the Atlantic region, where the values were higher inside but not significantly different from unprotected areas (Figure 3; Appendix S2).

The pattern for gamma diversity was similar to that of beta diversity; the highest values were in PAs (Figure 4; Appendix S2). This pattern was not observed in the Boreal region, however, where gamma diversity of arthropods, amphibians, mammals, and vascular and nonvascular plants was higher outside PAs. For amphibians, fishes, mammals, and mollusks in the Atlantic region and for amphibians in the Mediterranean region, gamma diversity was higher in unprotected areas (Figure 4; Appendix S2).

DISCUSSION

Evaluating and monitoring the performance of N2K PAs is crucial to ensure the EU is effectively protecting its priority species. Although previous studies mostly report higher biodiversity levels inside PAs than outside PAs, these studies focused on single taxonomic groups (Kukkala, Santangeli, et al., 2016; Musilová et al., 2018; Pellissier et al., 2020; Rada et al., 2019) or on specific European regions (Dähler et al., 2019; Gruber et al., 2012; Knapp et al., 2008; Maiorano et al., 2015; Morelli et al., 2021) and the comparison of protected versus unprotected areas seldom accounted for confounding covariates via matching. Until now, a multitaxa, European-wide evaluation of N2K effectiveness has been lacking. Our results showed that, at a continental

TABLE 1   Minimum, mean, and maximum values of species richness in 10×10-km grid cells after matching inside and outside Natura 2000 protected areas in Europe and across biogeographic regions.

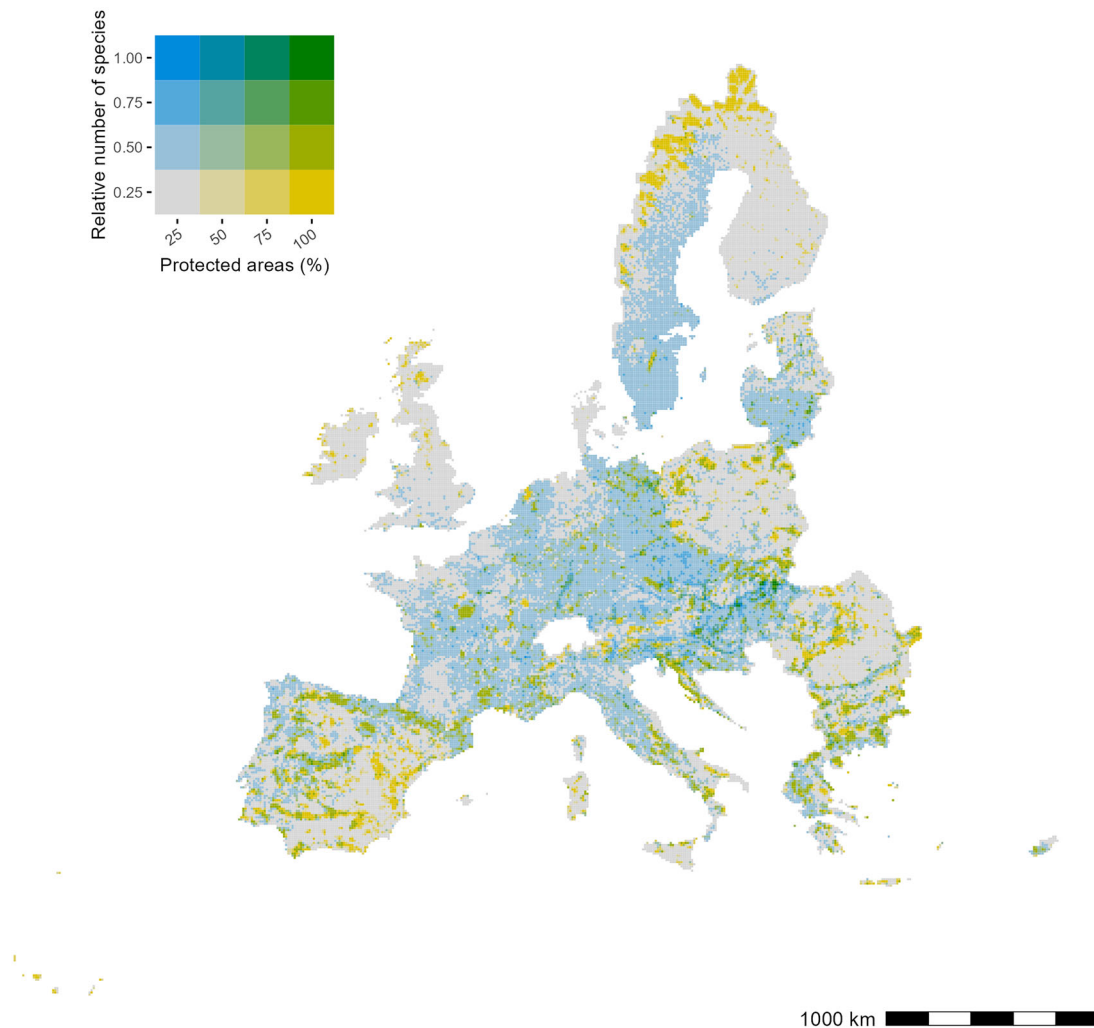| Geographic range	Minimum		Mean		Maximum	
	Protected	**Unprotected**	**Protected**	**Unprotected**	**Protected**	**Unprotected**
Europe	6	1	74.8	70.9	198	170
Alpine	8	1	78.3	66.4	157	145
Atlantic	17	20	87.6	79.7	168	117
Boreal	6	1	47.7	92.1	140	150
Continental	6	1	57.4	68.3	189	170
Mediterranean	14	1	83.6	71.3	198	148

FIGURE 1   Standardized species richness of each taxonomic group and the percentage of protected areas' coverage in a 10×10-km grid across Europe (dark blue, areas with high species richness and low percent protection; dark yellow, areas with low species richness and high percent protection; dark green, high species richness and high percent protection).

scale, N2K PAs are in general an effective conservation tool for most taxonomic groups. Yet, for certain taxonomic groups and biogeographic regions, N2K effectiveness was low; diversity levels of target species in PAs were indistinguishable from those in unprotected areas.

The main exceptions we found were in the Boreal region, where alpha diversity was similar inside and outside N2K PAs (Figure 1). This pattern is probably due to a bias in PA establishment in the Boreal region, where the PA system is mostly represented by large, contiguous areas of land of limited
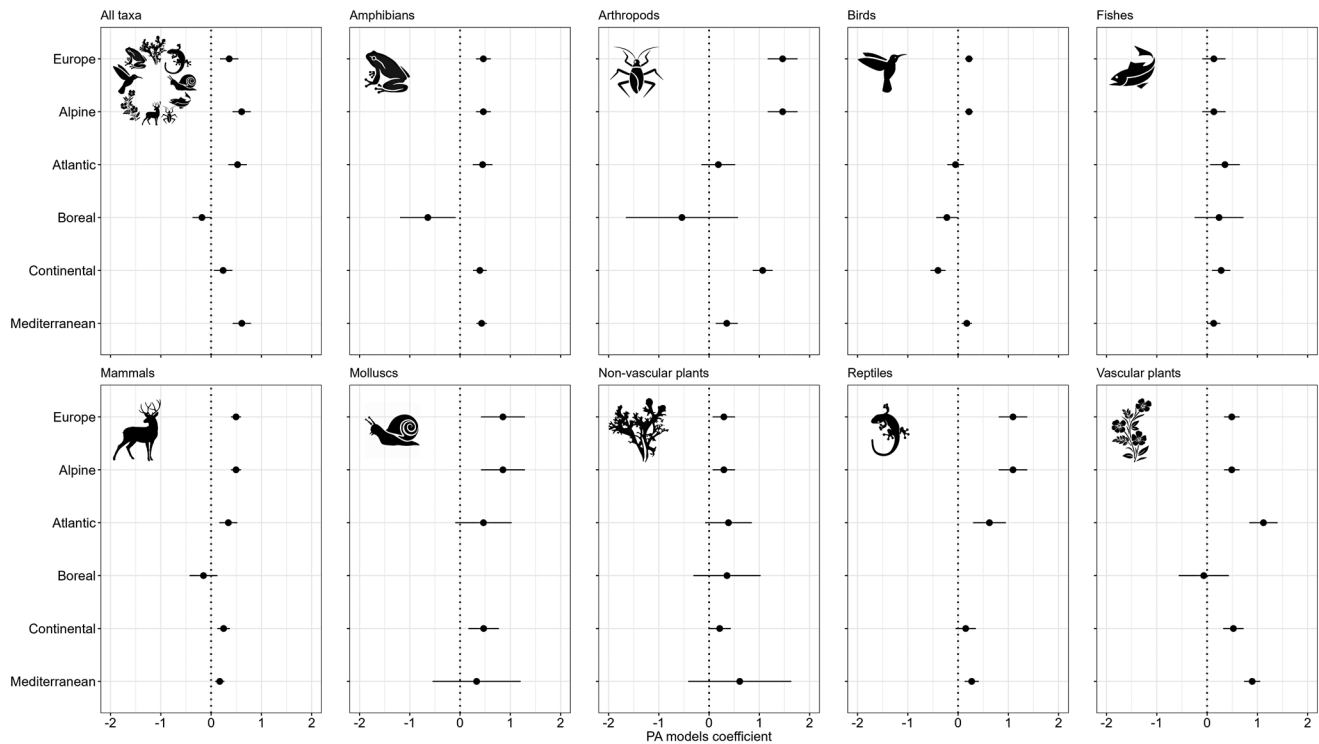
FIGURE 2 Regression coefficients of the effect of protected areas (PAs) on alpha diversity in Europe and across biogeographic regions for amphibians, arthropods, birds, fishes, mammals, mollusks, nonvascular plants, reptiles, vascular plants, and all taxa (black lines, standard error; dots, estimated regression coefficients as obtained by generalized mixed model for all taxa and by generalized models for the different groups). Only 100% protected and unprotected grid cells are represented.

economic value (Gaston et al., 2008). The extent of PAs in the boreal forest biome increased from approximately 0.0015 million ha in 1909 to 23 million ha by 2010 (Elbakidze et al., 2013). Most of these PA additions, however, are in the northern boreal forest subregion. Although this region contains valuable, endangered habitats, these are mostly low-productivity, species-poor forest ecosystems. The species-rich areas of the middle and southern subregions, where agricultural potential is high, are either unprotected or characterized by small and isolated PAs (Elbakidze et al., 2013). According to many studies (Jansson & Andrén, 2003; Linnell et al., 2005; Roberge & Angelstam, 2004), it is evident that this spatial bias in PA distribution and size in the Boreal region makes them often insufficient for the protection of focal and umbrella species, such as specialized birds and area-demanding mammals (Angelstam et al., 2020). We found a similar situation in the Continental region, where bird alpha diversity was higher in unprotected areas. This pattern is most probably due to their living requirements and ecological needs that are not fully satisfied by the current protected network in many biogeographic regions (Kukkala, Arponen, et al., 2016; Kukkala, Santangeli, et al., 2016; Trochet & Schmeller, 2013). Addressing this conservation gap is a crucial step toward building more robust networks of PAs (Lawrence, Friedrich, et al., 2021).

Considering beta diversity, we found higher values inside N2K PAs than outside for all biogeographic regions and all taxa. High beta diversity values suggest that European PAs host very diverse assemblages of priority species, although the mag-

nitude of the difference with non-PA is relatively small. This phenomenon could indicate that the contribution of unprotected land to the maintenance of priority species should not be neglected and that in some regions PAs do not offer a substantial positive benefit to biodiversity compared with unprotected areas. Identifying the location of beta-diversity hotspots for priority species in currently unprotected areas could help conservation practitioners and policy makers prioritize additional areas of high ecological quality for protection (Gering et al., 2003; Wiersma & Urban, 2005).

In general, the pattern for gamma diversity was similar to the pattern for alpha and beta diversity; values were higher inside N2K PAs than outside. Nevertheless, by differentiating among taxonomic groups, we found that in the Boreal region total gamma diversity and gamma diversity of amphibians, arthropods, mammals, and vascular and nonvascular plants were higher outside N2K PAs. The same pattern was also found for gamma diversity of different taxonomic groups in the Mediterranean and Atlantic regions. This could indicate a low effectiveness of N2K PAs in protecting these groups. For example, in the Mediterranean region, gamma diversity of amphibians and reptiles was consistently lower in N2K PAs compared with sites outside the N2K network. These results agree with previous findings from assessments at national scale for some European geographical regions. For instance, Maiorano et al. (2006) found that amphibians are the least protected taxonomic group in Italian reserves. Similarly, Abellán and Sánchez-Fernández (2015) showed that N2K sites are not play-
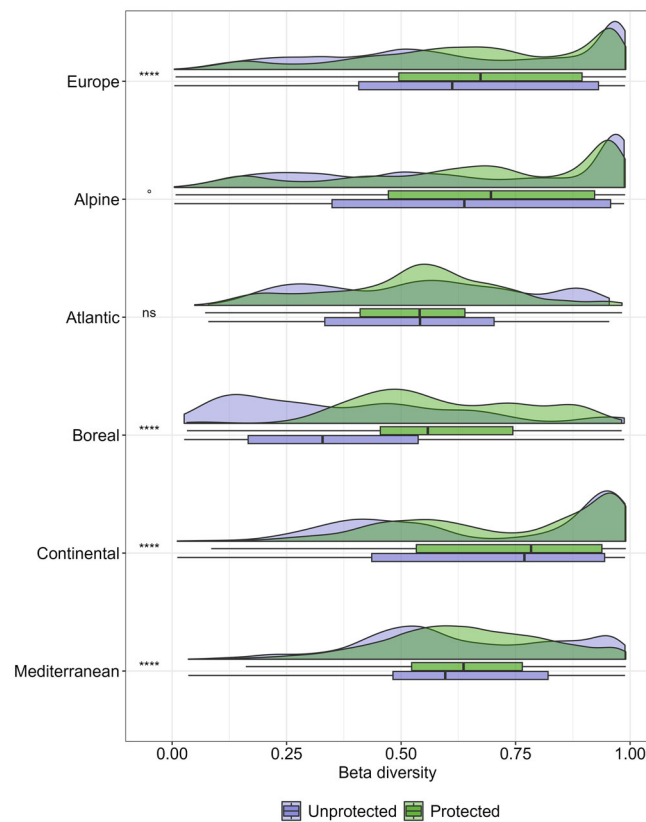
FIGURE 3 Total pairwise beta diversity for all possible protected cell pairs (green) and for all unprotected cell pairs (purple) in Europe and in the different biogeographic regions (asterisks, significant differences in the pairwise comparison [Wilcoxon rank sum test] between protected and unprotected areas: ns, not significant; $°p < 0.1$; $*p < 0.05$; $**p < 0.01$; $***p < 0.001$; $****p < 0.0001$). Only 100% protected and unprotected grid cells are represented.

ing a key role in the conservation of amphibians and reptiles across Europe. This information is crucial because conservation is often subject to a taxonomic bias toward large and charismatic species (dos Santos et al., 2020; Hortal et al., 2015), and previous studies raised important concerns with regards to the extent to which the existing N2K network covers the diversity of some underrepresented taxonomic groups (Abellán & Sánchez-Fernández, 2015; Dimitrakopoulos et al., 2004; Jantke et al., 2011; Maiorano et al., 2006).

Our results can provide an urgently needed outline for targeted conservation action toward filling the gaps in the N2K network coverage for these underrepresented groups. Nonetheless, land use and human population density may play a key role in the disparities between biogeographic regions with large amounts of PAs and those with little PA. The effectiveness of N2K sites may present challenges in densely populated areas, but it becomes even more pronounced in those regions, where urbanization and tourism development have generated fragmentation and habitat loss (Luck, 2007; Trochet & Schmeller, 2013). Many PAs are experiencing an increase in these pressures, which has significant implications for the overall effectiveness of the PAs (DeFries et al., 2005; Watson et al., 2014).

Policy implications

The recent agreements made during the Convention on Biological Diversity post-2020 and the EU Biodiversity Strategy for 2030 heavily focus on biodiversity protection and emphasize the importance of PAs as tools for biodiversity conservation. However, even with additional financial support and the political will to expand the current PA network, the question remains as to where such expansion can achieve the greatest outcome for biodiversity in the EU. Moreover, although PA expansion should be guided by conservation benefits, a myriad of other factors should also be considered. Thus, our results could be used to guide policy makers and conservationists in achieving these goals because they suggest the need to deploy the limited financial resources toward creating new PAs specifically targeting areas hosting priority species of underrepresented taxonomic groups, such as amphibians, fishes, or mollusks. Our results showed that several N2K PAs protect few priority species, especially those in the northern part of the Boreal region, which have lower species richness compared with other unprotected areas. We found large conservation gaps in the southern part of the Boreal region and in some parts of Central and Eastern Europe (Figure 1). Based on these results, we argue that the expansion of N2K PAs should take into consideration these areas to improve biodiversity conservation in the near future.

Study limitations, future directions, and conclusions

Although our study represents the first work to systematically revise the contribution of the EU's N2K PAs to the conservation of priority species, it has limitations. First, the choice of the right diversity metrics, for the purpose of informing conservation science, strongly depends on the set of species analyzed (Whittaker et al., 2005). We used several conservation metrics (alpha, beta, and gamma diversity), but the use of these different metrics could help identify more specific conservation needs. For example, beta diversity metrics can be especially useful in planning PAs in landscapes with a high species' turnover along species gradients (Socolar et al., 2016). Second, we did not assess overall biodiversity; rather, we focused on species listed in the annexes of the Birds and Habitats Directives because these are in the focus of EU-wide conservation efforts and are consistently reported among member states. Also, we did not consider species threat levels (Hochkirch et al., 2013). We recommend considering the conservation status of priority species before making conservation decisions, especially because the financial resources for conservation are limited (Di Marco et al., 2015; Hochkirch et al., 2013; Tittensor et al., 2014).

Finally, our results are limited by the 10×10-km resolution of the reporting data provided by the EEA. Although this is the highest resolution for which EU-wide data are available, we agree with Geldmann et al. (2018) that calculating diversity metrics at too coarse a resolution can weaken the reliability of any assessment of the role of PAs in maintaining species populations
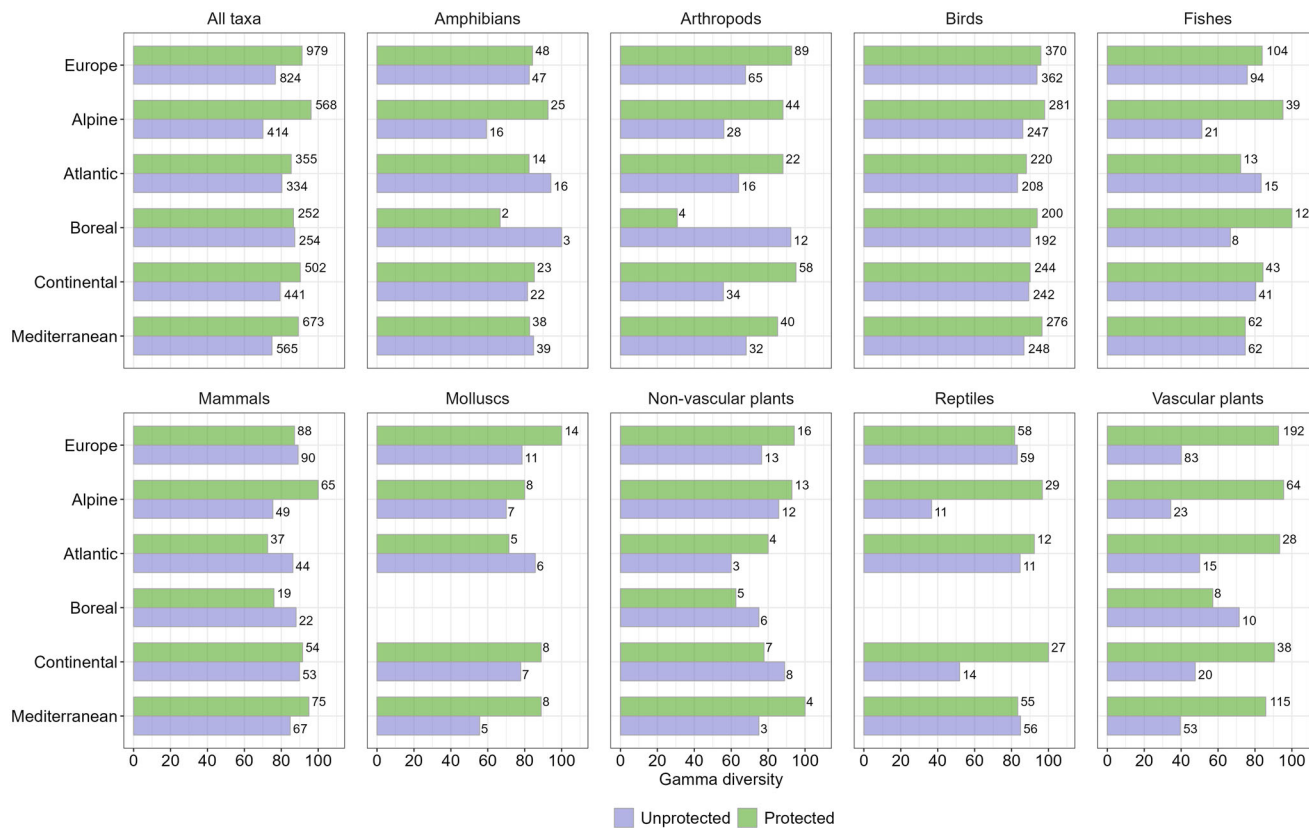
FIGURE 4 Percentage of gamma diversity of 9 taxa and all taxa together inside (green) and outside (purple) Natura 2000 protected areas in Europe across biogeographic regions (numbers at bar ends, number of species reported inside and outside protected areas). Only 100% protected and unprotected grid cells are represented.

across multiple sites. However, we also agree with Di Marco et al. (2017) that using distribution maps at coarse resolutions is the best way to reduce the impact of commission errors while maintaining accuracy in conservation analyses. On the methodological side, our results demonstrate the urgent need for proper accounting of relevant covariates when comparing N2K PA diversity levels with those of unprotected areas and, thus, the importance of expert knowledge when selecting confounding variables.

Monitoring biodiversity in PAs to assess their effectiveness always requires a comparison with unprotected areas (Geldmann et al., 2019). Yet, this type of comparison can only be useful if the areas inside and outside of PAs have comparable environmental conditions (Nelson & Chomitz, 2011; Schulze et al., 2018). Our work showcases how propensity score matching can be used to cope with this issue. By preselecting areas inside and outside N2K PAs with similar topographic and land-use conditions, we avoided masking of the actual effect of protection level on species distribution by confounders. We recommend matching when comparing protected to unprotected areas because this ensures less bias and a more reliable assessment of the effectiveness of PAs. However, fine-scale analyses including PA connectivity, fragmentation, and management will be crucial to address the conservation policy at local scale (Lawrence & Beierkuhnlein, 2023). Finally, improving biodiversity monitoring at the EU scale in the near future should be a

must for all the member states. Better data would lead to better effect estimates.

N2K PAs are more heterogeneous and host a higher diversity of priority species than unprotected areas in similar topographical positions and with similar land covers. Alpha diversity and gamma diversity were typically higher inside than outside N2K PAs across different biogeographic regions and distinct taxonomic groups. The main exception was the Boreal region, where priority species diversity was not significantly higher inside N2K PAs and, in some cases, was lower than outside. Beta diversity was significantly higher inside N2K PAs than outside, even though unprotected areas also displayed high levels of beta diversity. Our results can inform EU-wide conservation planning in the context of the EU Biodiversity Strategy for 2030 because they demonstrate which taxonomic groups are well covered by current PAs and show some glaring conservation gaps.

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