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Linking wildlife conservation with Nature's Contributions to People: The case of the European wildcat in German protected forests

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ABSTRACT

Forests provide essential benefits to human well-being, referred to as Nature's Contributions to People (NCP), including carbon storage, water filtration, biodiversity, and recreation. However, increasing human activities and land use changes have degraded wildlife habitats, threatening biodiversity and reducing NCP. This study presents a novel approach to assessing NCP by integrating keystone species-specific habitat assessment. It explores the synergies and trade-offs between the conservation of the European wildcat (*Felis silvestris silvestris*), an umbrella species promoting large and connected forest habitats, and the supply of forest-related NCP in German protected forests. Key factors influencing wildcat habitats are identified and their overlap with four selected NCP—carbon sequestration, water retention, timber potential, and recreation— are analyzed using remote sensing methodologies, including species distribution modelling and the InVEST water yield model, and statistical analysis, including correlations, spatial congruence, and k-means clustering, to assess synergies and trade-offs. The wildcat habitat model (AUC = 0.814) indicates that suitable habitats are structurally complex, densely forested landscapes that are distant from urban areas and roads but near agricultural land. Wildcat habitat provision shows a synergy with timber potential (ρ = 0.505) but low-to-moderate effects with other NCP (ρ range from −0.050 to 0.138). ANOVA results ($p < 2.2\text{e-}16$) indicate that national parks provide higher NCP levels than biosphere reserves and nature parks in the study areas. The results demonstrate that wildcat habitat provision does not conflict with other NCP, paving the way for further wildlife conservation measures and the establishment of more protection zones.

1. Introduction

Forests are extremely valuable ecosystems that improve human well-being by providing various societal benefits such as clean air and water, biodiversity, timber, and enriching nature experiences (Isaac et al., 2024; Díaz et al., 2018; Felipe-Lucia et al., 2018; Teben'kova et al., 2020). Yet, human impacts on the environment are increasing drastically. Rockström et al. (2009) defined planetary boundaries, a safe operating space for humanity within the Earth system. By 2023, six of nine boundaries have been crossed, causing irreversible changes to land systems, biosphere integrity, and climate (Richardson et al., 2023). Recently, there has been a paradigm shift in conservation biology, moving away from an overly utilitarian perspective to a more mutually respecting relationship between humans and nature (Mace, 2014). The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) developed the concept of Nature's Contributions to People (NCP) to better consider different worldviews and emphasize cultural values of nature, as an evolution of the Ecosystem services (ES) approach (Díaz et al., 2015; Pascual et al., 2017). Among nature's vital contributions, habitat provision is essential, as it directly influences biodiversity and the distribution of organisms that provide or support other NCP (Luck et al., 2009; Costanza et al., 1998; Kass et al., 2023). On the other hand, the loss of biodiversity can considerably reduce NCP by altering ecosystem functioning and stability (Isbell et al., 2017; Cardinale et al., 2012; Loreau et al., 2001; Díaz et al., 2006). This cascading effect has led to a noticeable decline in NCP over the past 50 years (Brauman et al.,

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2020; Díaz et al., 2015).

The European wildcat (*Felis silvestris silvestris*, Schreber 1777), hereinafter wildcat, exemplifies the dependence of species on high-quality habitats. Wildcats require large, undisturbed forest landscapes (Anile et al., 2018). Protecting and restoring such habitats benefits not only wildcats but also a wide range of forest-dependent species that collectively contribute to NCP. Together with its strict protection under Annex IV of the Flora Fauna Habitat Directive (92/43/EWG), wildcats have become an umbrella species for promoting large, connected, and near-natural broad-leaf forests (Birlenbach et al., 2009; Vogel and Mölich, 2008). Despite growing interest, small felid species remain understudied (Brodie, 2009; Zanin et al., 2015). Research on wildcat habitat modelling is particularly limited, and knowledge of the species' large-scale distribution and status is still poor, mainly due to their inconspicuous behavior (Otgontamir et al., 2024). Nevertheless, several studies have attempted to model wildcat habitats across Europe using spatial data and various modelling techniques. Klar et al. (2007) used telemetry data from 12 individuals in the German Eifel Mountains along with ATKIS land-use data. Their model has been applied in other regions in Germany and Switzerland (Klar et al., 2012; Streif et al., 2016; Graf et al., 2013). Weber (2018) applied Boosted Regression Trees in the Swiss Jura based on 429 occurrence points and 11 predictor variables of the wildcat. In Saxony-Anhalt, Germany, Jerosch et al. (2018) used a Generalized Linear Model (GLM) to explore the effects of sex and season on habitat selection. Other studies have employed algorithms such as MaxEnt (Gil-Sánchez et al., 2020), Random Forest, (Cushman et al., 2024) and occupancy models (Silva et al., 2013; Dyck et al., 2022). Despite methodological advances, most studies are constrained by small sample sizes (i.e. less than 100 individuals). In addition, the genetic verification of occurrence data is often lacking, leading to potential biases with domestic cats (Hertwig et al., 2009).

Understanding the interrelations between NCP and wildlife habitats is crucial for managing ecosystems sustainably. Protected areas are particularly critical in this context, serving as conservation strongholds for biodiversity and providing a benchmark for assessing NCP in relatively intact ecosystems. In recent years, remote sensing has become an indispensable tool for monitoring ecosystem functions and NCP, providing spatially continuous, regular and repeatable observations over large areas (Cord et al., 2017). However, few studies employ biodiversity measures, such as species distribution modelling for umbrella species, to enhance NCP prediction (Kass et al., 2023; Brockerhoff et al., 2017).

Here, we explore how conserving wildlife and sustaining NCP are connected by:

1. Modelling potential wildcat (*F. silvestris*) habitats within protected areas and identifying key biophysical and anthropogenic factors influencing their potential distribution in German forests using species distribution modelling (SDM).
2. Analyzing synergies and trade-offs between wildcat habitat provision and other forest-related NCP.
3. Comparing potential NCP supply across areas with different levels of protection status.

We hypothesize that suitable wildcat habitats will show significant synergies with forest-related NCP. However, trade-offs may exist with certain human activity-related NCP, such as recreation. Furthermore, areas with higher protection status are expected to show higher NCP supply.

2. Materials and methods

2.1. Study area

Areas of interest (AOIs) were selected based on the following criteria: i) AOIs should be within the range of wildcat distribution according to the 2019 Flora-Fauna-Habitat monitoring report (Ellwanger et al., 2020). ii) Reliable data of evidence on wildcat occurrence must be available. iii) The areas should be protected under the German Federal Nature Conservation Act (BNatschG) as either national parks (§24), biosphere reserves (§25) or nature parks (§27). National parks are strictly protected areas covering approx. 0.6 % of Germany that aim at preserving natural processes without human interference. Economic uses like farming or hunting are mostly prohibited, though limited public education and research are allowed. Most German national parks do not meet the International Union for Conservation of Nature (IUCN) category II criteria for national parks (Stolton et al., 2013) and are categorized as developmental national parks, involving the subdivision into different zones allowing for maintenance activities. Biosphere reserves aim to balance nature conservation with sustainable human use through zoned areas (core, buffer, development). The core zone falls under the category I-IV of the IUCN guideline (Stolton et al., 2013). About 4 % of Germany are covered by biosphere reserves. Nature parks cover 28 % of Germany and also aim to preserve and protect cultural landscapes, but have a further focus on serving a recreational function and feature sustainable tourism. Nature parks have not an own category in IUCN but they can be considered as IUCN-Category VI (Managed Resource Protected Area).

The study area contained four forested low mountain ranges in Germany: Harz (3254.7 km^2), Solling-Vogler (555.3 km^2), Rhön-Spessart (5254.4 km^2), and Saar-Hunsrück (2059.8 km^2; Fig. 1). The Harz is a highland area spanning Lower Saxony, Saxony-Anhalt, and Thuringia, featuring the Brocken (1141 m), the highest peak among the study sites. It includes four nature parks, one biosphere reserve, and Germany's largest national park (247 km^2). The area is a key tourist destination and spans humid continental (Dfb) to subarctic (Cfc) climates (Beck et al., 2023), with annual precipitation ranging from 500 mm in the east to 2000 mm in the higher western areas.

The Solling-Vogler is a forested region in southern Lower Saxony, defined by the boundaries of the Solling-Vogler Nature Park. Elevations reach up to 528 m above sea level. The area has a humid continental climate (Dfb) (Beck et al., 2023), with 835.7 mm of precipitation in 2020. The Rhön-Spessart is the largest study region, spanning Hesse, Bavaria, and Thuringia. It includes two nature parks in both the Spessart and Rhön regions, as well as the Rhön Biosphere Reserve, which overlaps with the two parks. Elevations reach up to 950 m a.s.l. The area has a humid continental climate (Dfb) (Beck et al., 2023), with 755.8 mm of precipitation in 2020 and higher values in the elevated central north and south areas. The Saar-Hunsrück region spans Rhineland-Palatinate and Saarland, including the Saar-Hunsrück Nature Park and Hunsrück-Hochwald National Park. Elevations reach up to 818 m a.s.l. It is the only study area classified as temperate oceanic (Cfb) (Beck et al., 2023), with 933.5 mm of precipitation recorded in 2020.

2.2. Wildcat occurrence data

Species occurrences were provided by the federal environmental agencies of Germany (see Acknowledgements). Only verified evidence of record falling into Category C1 (= Skin, Dense Connective Tissue, Epicranial Aponeurosis, Loose Areolar Connective Tissue and Periosteum) of the SCALP criteria (Molinari-Jobin et al., 2019) from 2013 to 2023 was used. Locations with less than 1000 m spatial accuracy were removed. Furthermore, dead wildcats near roads were eliminated from the dataset after an initial test run, as these locations are not expected to represent suitable habitats and potentially bias the modelling process (Soley-Guardia et al., 2024). The total number of valid records (n) was 626, including sightings, photo traps, captures, and genetic samples from hair. Occurrences were not equally distributed with 69 occurrences in the Solling-Vogler study site, 268 in the Harz, 282 in the Rhön-Spessart region, and only 7 in the Saar-Hunsrück region.

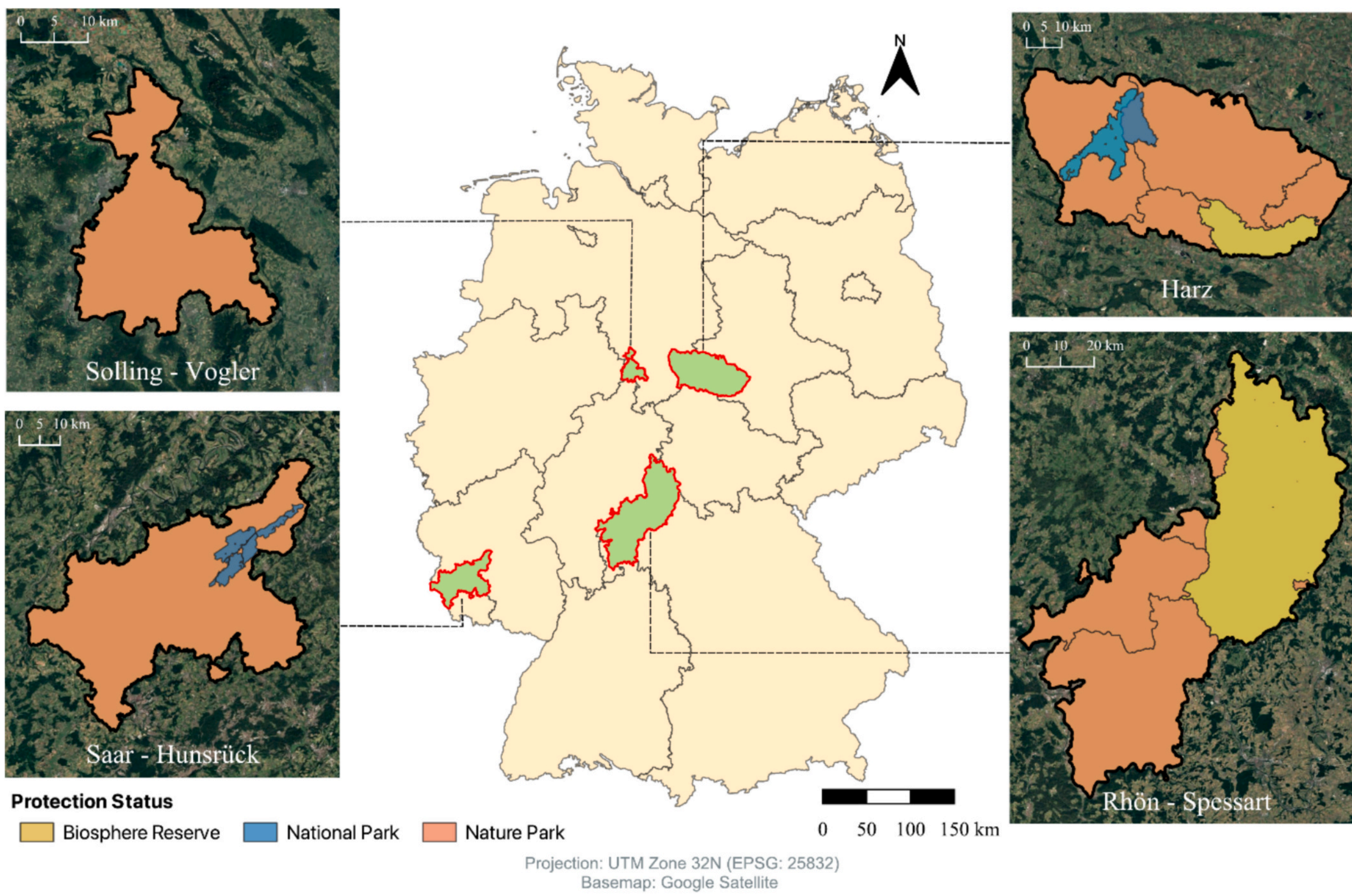

Fig. 1. Areas of interest (AOIs) for the wildcat habitat model as well as for the assessment of forest-related Nature's Contributions to People. The AOIs cover three types of protected areas: National parks, nature parks and biosphere reserves.

2.3. Predictor variables

Predictor variables were grouped into five categories: (1) forest and vegetation (e.g., dominant leaf type, leaf area index); (2) terrain (e.g., elevation, roughness); (3) distance to infrastructure (distance to roads and railways); (4) distance to key land cover classes (forest, water, urban areas); and (5) landscape configuration, derived from landscape metrics. These variables were selected based on a literature review of previous wildcat research and habitat modelling (Klar et al., 2007; Streif et al., 2016; Graf et al., 2013; Weber, 2018; Jerosch et al., 2018; Silva et al., 2013; Gil-Sánchez et al., 2020). The reference year for the dataset was set to 2018, aligning with the midpoint of wildcat occurrence records. Exceptions were the Shuttle Radar Topography Mission (SRTM) digital elevation model, acquired in 2000, and the Open Street Map (OSM) road data, which are constantly updated. All variables were reprojected to ETRS89/UTM zone 32 N and resampled to 100 m resolution. After testing for collinearity, 16 predictor variables remained and were used for further model fitting (Table 1).

2.4. Species distribution modelling

We applied a multi-algorithm ensemble model using the biomod2 package (Thuiller et al., 2024) in R-Studio (Version 2024.04.2). Of the 626 occurrence points, duplicates within the same grid cell were removed, leaving 516 samples. 600 pseudoabsence (PA) points, were randomly generated, resulting in a dataset of 1116 points (516 presences, 600 PA) and 16 predictor variables. Data was split 75 % for calibration and 25 % for evaluation. Two sets of $n = 400$ PA points were randomly sampled for calibration. K-fold cross-validation ($k = 4$) was included plus one run using the full dataset. Five algorithms were tested: Generalized Linear Models (GLM), Random Forest (RF), Gradient Boosting Machine (GBM), Maxent, and Extreme Gradient Boosting (XGBoost), using biomod2's bigboss tuning settings under a normality assumption. Each setup was run twice (Rep1 & Rep2), totaling 95 model runs. Four metrics were used to evaluate model performance: Accuracy, Cohen's Kappa (Cohen, 1960) Area under the Curve (AUC) (Hanley and McNeil, 1982) and True Skill statistic (TSS) (Hanssen and Kuipers, 1965). Performance metrics were calculated for each candidate model for calibration, validation, and evaluation data. The evaluation metrics were used for final model selection, with thresholds set to 0.7 for Accuracy and AUC and 0.5 for Cohen's Kappa and TSS (McHugh, 2012; Swets, 1988; Coetzee et al., 2009).

2.5. Analyzing the capacity of NCP

In addition to habitat provision, we modelled four NCP that are particularly relevant to forest ecosystems: carbon sequestration, water retention, timber potential, and recreational value of the landscape (see Table 2).

Carbon sequestration is defined as Net Ecosystem Production (NEP) of all vegetated areas for one year (Braun et al., 2018). NEP [g/m^2*y] was calculated as the difference between annual Net Primary Production (NPP) and annual soil respiration (Rs). We used MODIS (= Moderate Resolution Imaging Spectroradiometer) annual NPP data (MOD17-A3HGF) with a spatial resolution of 500 m for the year 2020 (Running and Zhao, 2021), in combination with 2020 data from German mereological service (DWD) for air temperature (German Meteorological Service DWD, 2020) and annual precipitation (DWD Climate Data Center CDC, 2020) to account for soil respiration, following the approach of Raich et al. (2002). To calculate water retention for the year

Table 1
Habitat model predictor variables. Predictors in italics were eliminated from the analysis due to high correlations with other variables. Data Source abbreviations: CLMS = Copernicus Land Monitoring Service, 2020, 2018; European Environment Agency, 2020, SRTM = Shuttle Radar Topography Mission (OpenTopography, 2013), OSM = Open Street Map (OpenStreetMap contributors, 2024), CLC = Corine Land Cover (Copernicus Land Monitoring Service, 2019).

Abbreviation	Variable Description	Data Source	Spatial Resolution	Year
DLT	Dominant leaf type (broadleaf or coniferous)	CLMS	10 m	2018
TCD	Level of tree cover density [0 % to 100 %]		100 m	2018
LAI	Green leaf area per unit ground surface area		300 m	2018
Elev	Elevation above sea level	SRTM	1 arcsec	2000
Slope	*Steepness of land surface*		*1 arcsec*	*2000*
Aspect	Aspect - direction of slope		1 arcsec	2000
TRI	Terrain Roughness Index		1 arcsec	2000
dist_motprim	Distance to nearest highway or federal road	OSM	/	2024
dist_sectert	Distance to nearest country- or district-lane		/	2024
dist_rail	Distance to nearest railway		/	2024
dist_nat	Distance to nearest forests and semi-nat. Area	CLM	100 m	2018
dist_agri	Distance to nearest agricultural areas		100 m	2018
dist_art	Distance to nearest built-up area		100 m	2018
dist_wat	Distance to nearest wetland and water body		100 m	2018
LC	*Land cover*		*100 m*	*2018*
lsm_contig	Patch Contiguity		100 m	2018
lsm_enn	Distance to nearest patch of the same class		100 m	2018
lsm_frac	Patch Complexity		100 m	2018

Table 2
Remote sensing proxies for Nature's Contributions to People (NCP) estimation. The data sources for habitat provision are explained in detail in Section 2.4. NPP = Net Primary Production.

NCP analyzed	Proxy	Data Source/ Reference
Carbon sequestration	Net Ecosystem Production	MODIS NPP
Water retention	Annual Water Yield	InVEST Model
Timber potential	Potential Woody Biomass Supply	Verkerk et al. (2019)
Recreational Value	Outdoor Recreation Potential	Komossa et al. (2018)

2020, the InVEST ® (=Integrated Valuation of Ecosystem Services and Trade-offs) annual water yield model was used (Natural Capital Project, 2024). Water retention is therefore defined as the annual water yield within the given area. The model requires five biophysical input parameters as georeferenced raster datasets. These are root restricting layer depth [mm], plant Available Water Content (AWC) [as a proportion], average annual precipitation [mm], average annual potential evapotranspiration (PET) [mm], Land use/Land cover (LULC) plus a vector layer with watersheds (see Annex figures and Annex Table A.1). The configuration parameter for root depth and crop evaporation coefficient (k_c) per land cover class were set according to relevant literature (see Annex Table A.2).

The potential supply of timber in the form of woody biomass was assessed using data from (Verkerk et al., 2019) who apply the European Forest Information Scenario Model (EFISCEN) to estimate the maximum annual forest biomass harvestable within biophysical limits for 2020. This projection is based on age structure, growing stock, resource increment, and management data from national forest inventories. The study then adjusts these estimates by applying environmental (water protection and biodiversity protection) and technical constraints (recovery rate, soil bearing capacity), reducing the available biomass. The provided map was upsampled to 1 km resolution using cubic interpolation. The landscape's recreational value was assessed using data by Komossa et al. (2018), who mapped outdoor recreation potential in the EU. The study identifies five user groups (i.e. the convenience recreationist, the day tripper, the educational recreationist, the nature trekker, the spiritual recreationist) with distinct landscape preferences, determined through a literature review and an expert workshop. Spatial proxies represent these preferences, classified on a scale of 1 to 5. A weighted overlay method was then applied to combine the spatial data for each group, with the weights reflecting the relative importance of each feature as determined by the expert input. The resulting map shows the outdoor recreation potential for each user group across the EU in 1 km resolution. For simplicity, values across groups were summed up, ranging from 0 to 25.

2.6. Synergy and trade-off analysis

To reduce auto-correlation, 500 random points were sampled from the NCP data stack for the synergies and trade-offs analysis. Before subsampling, all layers were resampled to 1 km resolution using cubic interpolation. The analysis of synergies and trade-offs between wildcat habitat provision and other NCP included three steps: Pairwise Spearman rank correlations ($p < 0.05$) (Spearman, 1904), Congruency Analysis (see Khamila et al., 2023; Dittrich et al., 2017), and K-means clustering (Lloyd, 1982). For the congruency analysis, NCP maps were classified into hot-spots (upper 30 % quantile), cold-spots (lower 30 % quantile), and medium areas. These categories were overlaid to create nine congruence classes. K-means cluster analysis was performed to analyze existing patterns and potential NCP bundles (i.e., co-occurrence of multiple NCP in the same area). Here, subsampling was done on a 5 km grid, so that the spatial distribution of clusters could be analyzed. This resulted in 417 data points. The number of clusters was set to three following the elbow method (Hastie et al., 2009). The resulting clusters are visualized using Principal Component Analysis (PCA) (Jolliffe, 2002). ANOVA was used to test for significant differences in NCP supply among clusters (Girden, 1992).

2.7. Comparing NCP supply across varying protection status

Finally, the effect of the nature protection status on NCP supply was tested using an ANOVA (Girden, 1992). A stratified random subsample of 500 data points was selected for each protection class (i.e. national park, biosphere reserve, nature park). The sample dataset was normalized through scale-normalization. First, a multivariate ANOVA test was conducted for overall differences across groups for all five NCP. If the test was significant, the null hypothesis was rejected. Then, Univariate ANOVA was used to identify which NCP differ between groups. The independent pairwise *t*-test was applied to determine which groups differ significantly. Finally, Cohen's d effect size indicated how meaningful differences were, by quantifying the magnitude of effects. Higher values indicate stronger effects, with 0.5 as medium and 0.8 as large effect thresholds (Cohen, 1988).

3. Results

3.1. Species distribution model performance

The performance metrics show that RF and GBM models performed best. GLM, Maxent and XGBoost showed poorer performance, failing to reach the thresholds for Kappa and TSS (Table 3). Of the 95 initial models, 21 met the given thresholds for all four performance metrics using the evaluation dataset and were included in the ensemble model. Spearman correlation between observed and predicted values was $r^2 = 0.842$. Additional performance metrics for the ensemble model were TSS = 0.564, AUC = 0.814, Accuracy = 0.774 and Kappa = 0.553 (see

Table 3
Mean model performance values for the wildcat Species Distribution Model (SDM) per algorithm. AUC = Area under the Curve (Hanley and McNeil, 1982); TSS = True Skill statistic (Hanssen and Kuipers, 1965).

Algorithm	TSS	AUC	Accuracy	Kappa
Gradient Boosting Machine (GBM)	0.513	0.794	0.749	0.502
Generalized Linear Model (GLM)	0.446	0.767	0.717	0.437
Maxent	0.351	0.695	0.672	0.345
Random Forest (RF)	0.528	0.809	0.758	0.518
Extreme Gradient Boosting (XGBOOST)	0.424	0.748	0.705	0.415

Table 4).

Fig. 2 shows the final model projection across the study area. Low suitability values in Solling-Vogler, Harz, and Rhön-Spessart correspond to AOI edges and non-forested agricultural or urban areas. Saar-Hunsrück exhibits low wildcat habitat suitability throughout the region.

3.1.1. Variable importance

Distance to artificial features is the strongest predictor in the ensemble model (0.0571 ± 0.0039), followed by patch complexity (0.054 ± 0.0015) and leaf area index (0.046 ± 0.0008). The weakest predictors are distance to the nearest same land cover-class patch (0.0031 ± 0.0004) and dominant leaf type (0.0033 ± 0.0002). The influence of each predictor variable on the ensemble model is shown in

Table 4
Performance metrics for the final wildcat ensemble model. The cutoff represents the value used to classify the suitability into presence/absence and is automatically set to optimize the corresponding metric. Sensitivity is the true positive rate [%], specificity is the true negative rate [%]. The calibration and evaluation columns display the metrics, indicated in the eval. Metric column, calculated on the calibration and evaluation dataset.

Algorithm	Eval. Metric	Cutoff	Sensitivity	Specificity	Calibration	Evaluation
EMmean	TSS	503	94.629	89.703	0.843	0.564
EMmean	AUC	506.5	94.373	90.389	0.981	0.814
EMmean	Accuracy	539	90.537	93.593	0.921	0.774
EMmean	Kappa	539	90.537	93.593	0.842	0.553

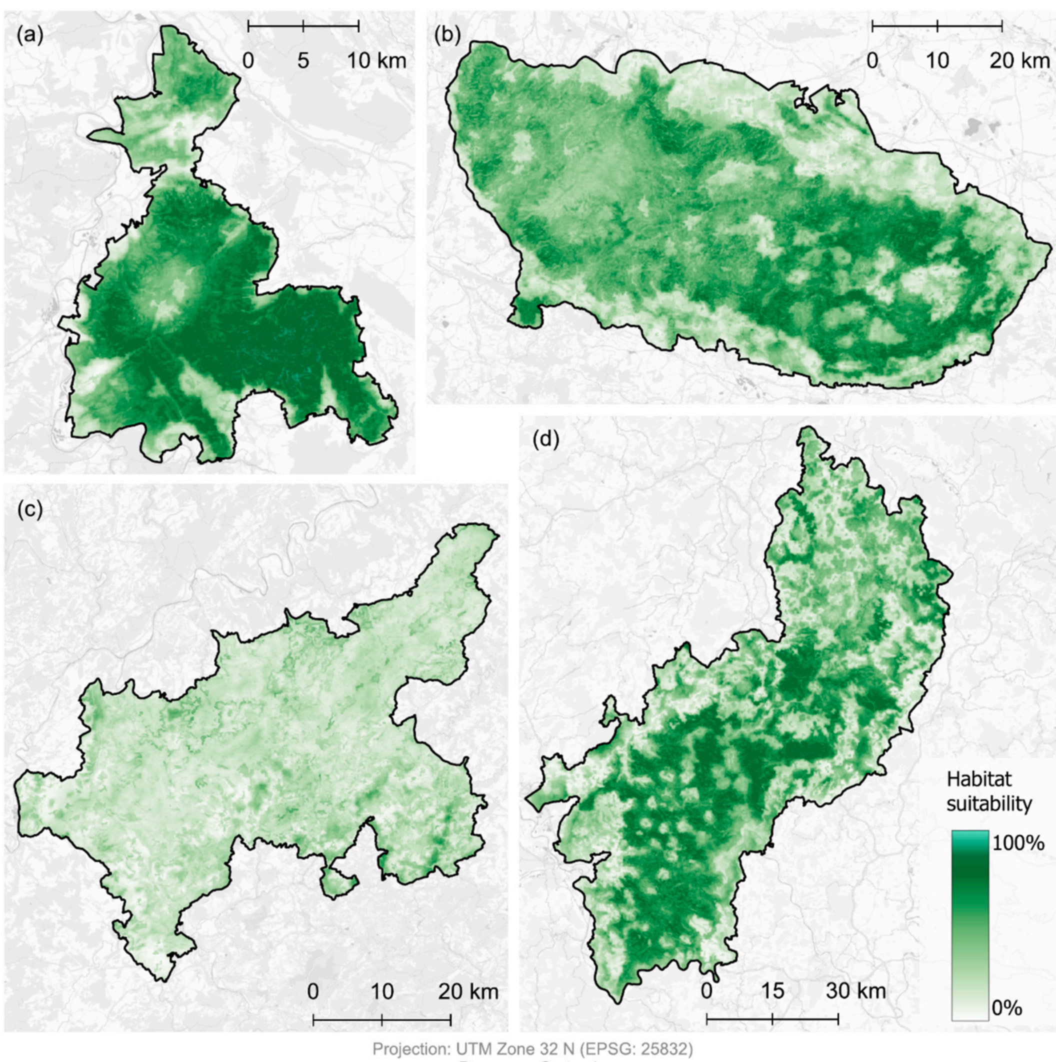

Fig. 2. Ensemble model projection of wildcat habitat suitability for the four study regions: (a) Solling-Vogler, (b) Harz, (c) Saar-Hunsrück and (d) Rhön-Spessart.

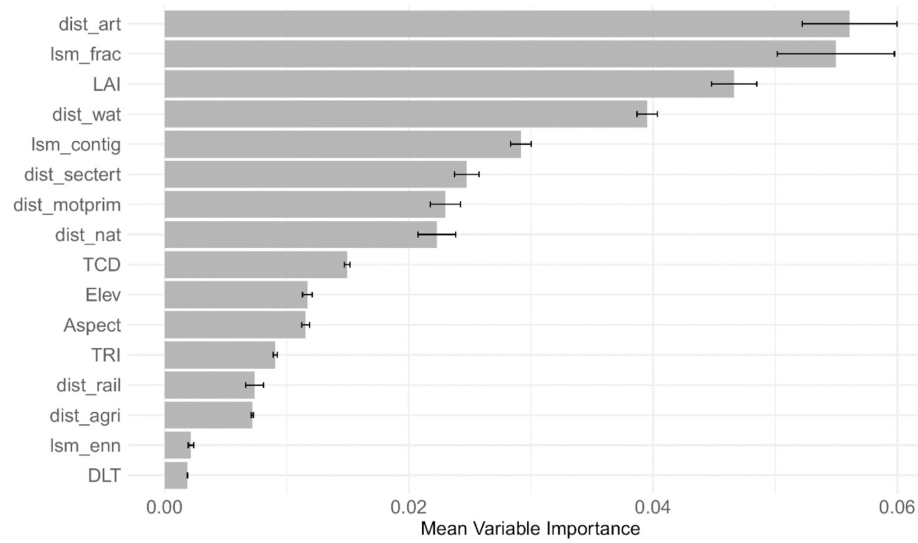

Fig. 3. Mean variable importance with standard deviation across three runs. dist_art = distance artificial, lsm_frac = patch complexity, LAI = Leaf Area Index, dist_wat = distance water, lsm_contig = patch contiguity, dist_sectert = distance country−/district-lane, dist_motprim = distance highway/federal road, dist_nat = distance forest, TCD = Tree Cover Density, Elev = elevation, Aspect = aspect, TRI = Terrain Roughness Index, dist_rail = distance railway, dist_agri = distance agriculture, lsm_enn = distance nearest neighbor patch, DLT = Dominant Leaf Type.

Fig. 3.

3.1.2. Response curves

The response curves illustrate the relationship between the probability of wildcat occurrence and the observed ranges of the environmental variables (Fig. 4). The categorical variable dominant leaf type shows no strong response across its three classes 0 (non-tree), 1 (broadleaved), and 2 (coniferous). For elevation, aspect, terrain roughness index, leaf area index, tree cover density, distance railway and distance country−/district lane, the probabilities initially increase with

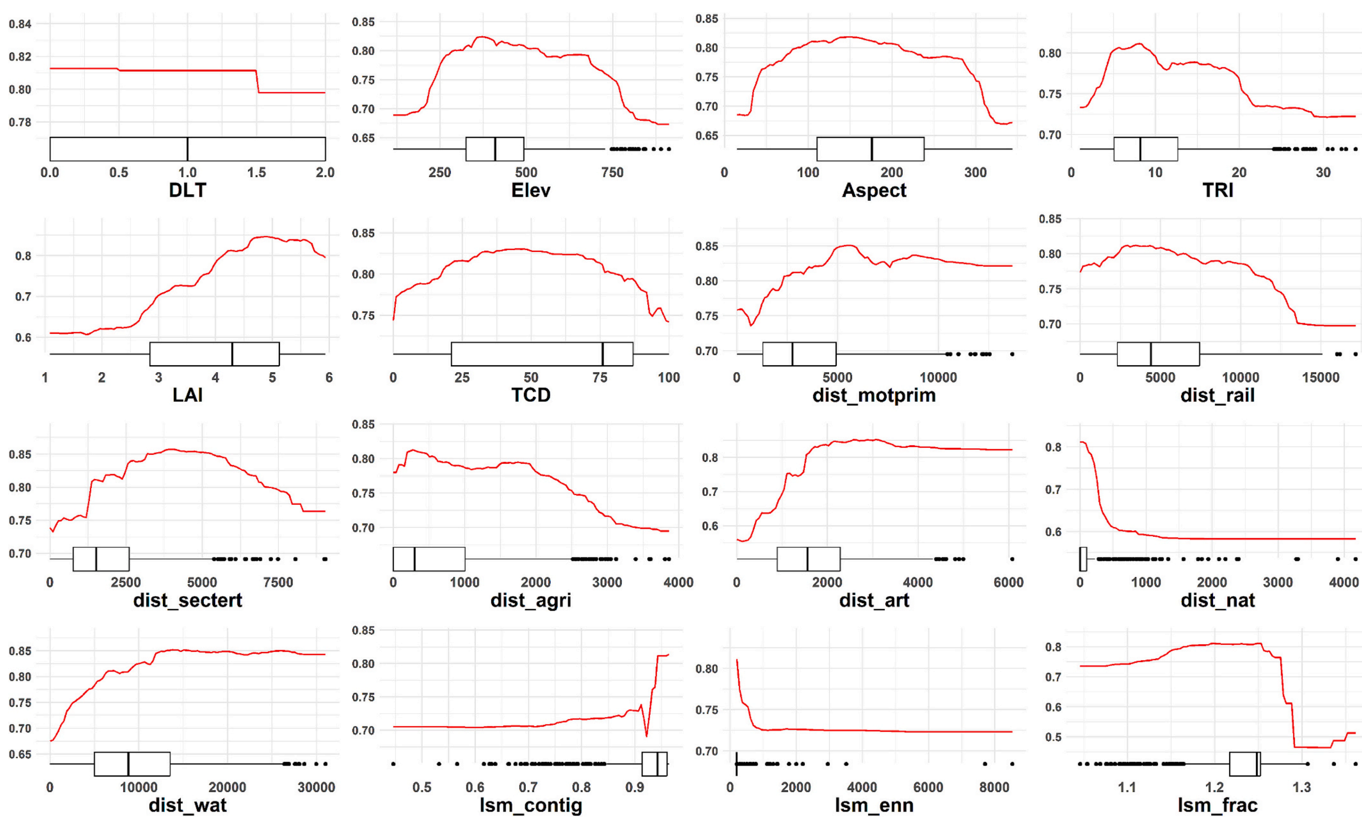

Fig. 4. Response Curves for the final ensemble model showing the relationship between the probability of occurrence and the predictor variables: DLT = Dominant Leaf Type, Elev = elevation, TRI = Terrain Roughness Index, LAI = Leaf Area Index, TCD = Tree Cover Density, dist_motprim = distance highway/federal road, dist_rail = distance railway, dist_sectert = distance country−/district-lane, dist_agri = distance to agriculture, dist_art = distance artificial LC, dist_nat = distance forest, dist_wat = distance water, lsm_contig = patch contiguity, lsm_enn = distance to nearest neighbor patch, lsm_frac = patch complexity. The distribution of the corresponding variable is displayed in box plots underneath each plot.

increasing values until they reach a maximum value, after which probabilities decrease. Distance highway/motorway, distance artificial, and distance water also increase with increasing values but finally stagnate. Distance forest and distance to the nearest neighboring patch of the same land cover class show a strong logarithmic decrease of probability with increasing variable values, while contiguity shows a logarithmic increase with a drop at approx. 0.93. Finally, patch complexity remains relatively stagnant until a sharp decline at ~1.25.

3.2. Synergies and trade-offs with NCP

All NCP pairs showed significant correlations, except habitat/carbon (Table 5). Most correlations were positive, indicating synergies, with habitat/timber showing the strongest synergy (ρ = 0.505). Other pairs ranged from 0.1 to 0.4, indicating moderate correlations. The only exception was carbon/timber (ρ = −0.0091), suggesting only a marginal effect.

The congruency analysis provides a detailed examination of the spatial overlap among NCP. Fig. 5 illustrates the overlap of habitat provision (classified into low, medium, and high) with four other NCP, along with the overlap for the timber/recreation pair. No clear pattern is observed for habitat/carbon and habitat/water, with congruence levels ranging between 24.5 and 39.5 % and 29.5 % – 37.1 %, respectively. In contrast, habitat/timber shows a strong synergy: areas with high habitat values have a 60.4 % probability of high timber potential and only an 11.9 % probability of low timber potential. Conversely, areas with low habitat values have a 46.2 % probability of low timber potential and only 11.9 % of high timber potential. For habitat/recreation, high habitat areas show a 26.2 % likelihood of high recreational value and a 41.8 % likelihood of low recreational value. Low habitat areas are associated with a 51.8 % chance of low recreation and just 12.1 % of high recreation potential, indicating an overlap of cold spots rather than hot spots. A similar pattern is observed for the timber/recreation pair, with 52.6 % of cold spots and only 23 % of hot spots overlapping.

The k-means algorithm identified three clusters with 125, 142, and 150 data points. Their within-cluster sum of squares (WCSS) was 356.59, 404.26, and 631.66, respectively. The ratio of between-cluster sum of squares to total sum of squares accounted for 33.1 % of the total variance. The three clusters are visualized in Fig. 7 using Principal Component Analysis (PCA). The three clusters show a small overlap, indicating no clear distinction between clusters. The distribution of NCP supply for the three clusters is displayed in Fig. 6. Cluster 1 is characterized by lower supply across all five NCP on average. Cluster 2 is characterized by higher supply in carbon sequestration, recreational value and water retention, while cluster 3 is characterized by very high supply in habitat provision and timber potential. ANOVA confirms significant differences across clusters for all NCP, except for timber potential (clusters 1 & 2) and recreational value (clusters 2 & 3). The spatial distribution of clusters reveals distinct geographic patterns: Cluster 1 is predominantly located along the borders of the AOIs. Cluster 2 appears in patchy distributions, often towards the central or northern sections of the AOIs. Cluster 3 is largely concentrated in the central areas of the AOIs (Fig. 7).

Table 5
Spearman correlation coefficients ρ for Nature's Contributions to People pairs. *indicates statistical significance ($p < 0.05$).

Nature's Contributions to People	Habitat provision	Carbon sequestration	Water retention	Timber potential
Carbon sequestration	−0.050			
Water retention	0.093*	0.398*		
Timber potential	0.505*	−0.091*	0.202*	
Recreational value	0.138*	0.105*	0.159*	0.134*

3.3. Effect of nature protection status

The multivariate ANOVA ($p < 2.2e\text{-}16$) reveals significant differences in NCP supply across groups. Univariate ANOVA indicates significant differences for all five NCP, with pairwise *t*-tests confirming differences for all group pairs, except for habitat provision between nature parks and biosphere reserves and for carbon sequestration between national parks and biosphere reserves. Effect sizes (Cohen's d) are shown in Table 6. Nature parks and biosphere reserves showed no significant difference in habitat provision, but when compared to national parks, nature parks had a negative effect while biosphere reserves had a positive effect on habitat provision, though both with small effect sizes. For carbon sequestration, effect sizes were also small, with nature parks having lower values than biosphere reserves but higher than national parks. National parks had a strong positive effect on water retention. Biosphere reserves had significantly lower timber potential than national parks. For recreational value, national parks had higher values than both nature parks and biosphere reserves. Overall, no meaningful differences were observed between nature parks and biosphere reserves.

4. Discussion

4.1. Modelling wildcat habitats

The ensemble model performed well in predicting wildcat habitats, reaching a r_s of 0.842 and an AUC of 0.814, comparable to previous studies (Klar et al. (2007): $r_s = 0.91–1.0$; Weber (2018): AUC = 0.863; Jerosch et al. (2018): AUC = 0.85; Silva et al. (2013): AUC = 0.70). The habitat suitability map supports previous research, highlighting high suitability in densely forested, unfragmented, and undisturbed areas. However, the Saar-Hunsrück region showed lower suitability despite having similar characteristics. This is likely due to the limited occurrence points ($n = 7$) used for training, which suggests model overfitting. A comparative model run with randomly generated occurrences in Saar-Hunsrück increased suitability and reinforced this assumption. Wildlife habitat modelling relies heavily on input data quality. Many occurrence points in this study come from lure stick monitoring, which ensures genetic verification and prevents confusion with domestic cats. However, this method only detects wildcats at preselected, accessible sites, similar to camera traps, potentially introducing bias (Soley-Guardia et al., 2024). Despite this limitation, the methodology produced reasonable habitat predictions. The use of open-source predictor variables allows for broader applicability beyond the study area, but improving model accuracy requires additional training with more evenly distributed occurrence points across AOIs. The variable importance scores and response curves provide insights into identifying factors influencing wildcat habitats. All variables had low importance scores, suggesting that habitat suitability depends on their combined effects rather than individual influence. Thus, individual variable importance should be interpreted cautiously. Response curves indicate that wildcats prefer natural, structurally complex, and densely forested areas with multiple canopy layers, staying away from urban areas and roads while remaining close to crops. These findings confirm results from previous studies (Klar et al., 2007; Weber, 2018; Dyck et al., 2022). Interestingly, this study found that greater distances from water favored wildcat habitats, contrasting with Silva et al. (2013) and Klar et al. (2007), though Weber (2018) reported overall minimal water proximity effects.

4.2. Synergies and trade-offs with NCP

The Spearman correlations show a moderate link between habitat provision and timber potential (ρ = 0.505), aligning with Heinze et al. (2020) who found a stronger correlation (ρ = 0.88) using forest cover as a proxy for wildlife habitat. The weak correlation between carbon sequestration and water retention (ρ = 0.348) matches with Móstiga

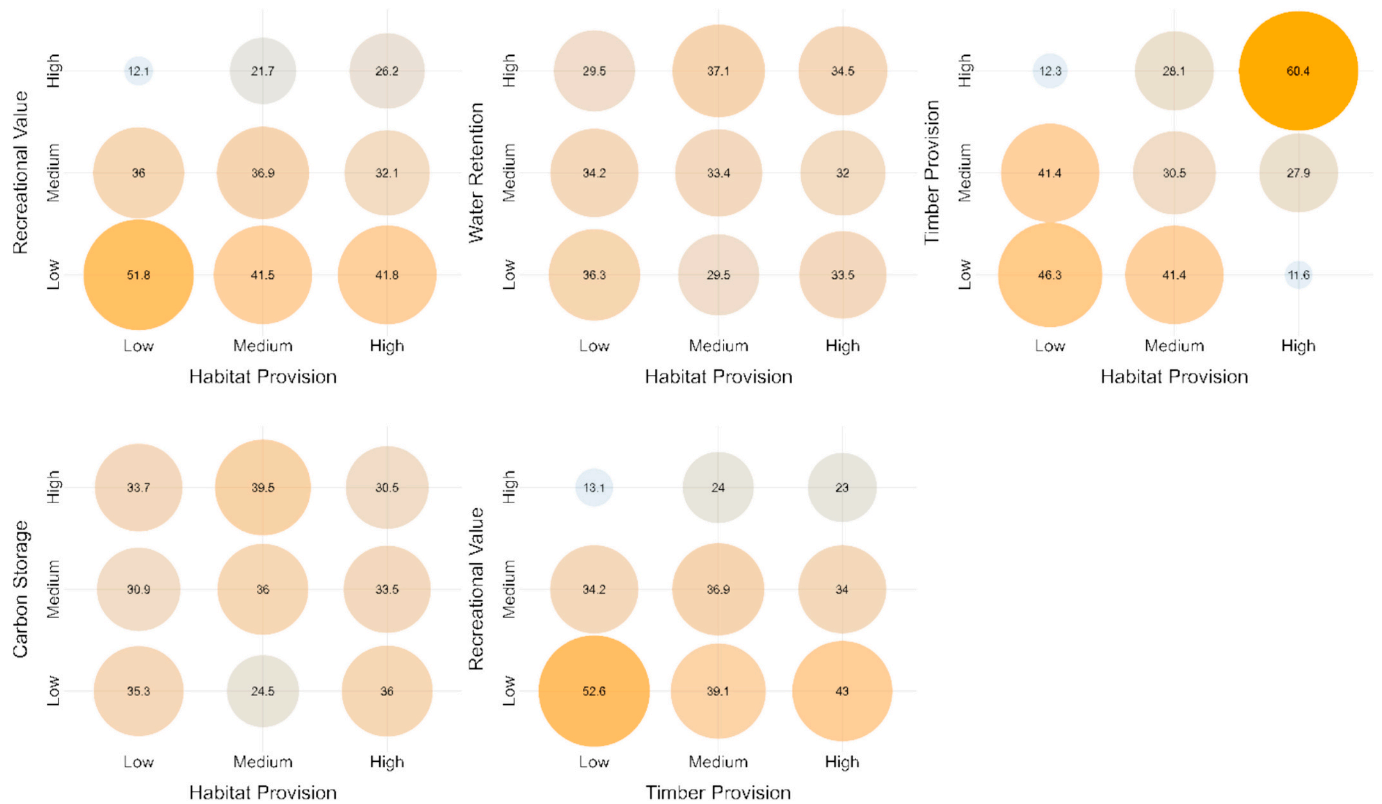

Fig. 5. Spatial overlap [%] of NCP pairs. The x-axis shows the reference NCP; the y-axis shows overlapping pairs. Column values sum to 100. Timber provision refers to the potential woody biomass supply.

et al. (2023) (ρ = 0.37 in tropical rainforests) but contrasts with Naidoo et al. (2008) (ρ = −0.07). Other NCP pairs showed weak correlations, supporting previous studies. Benra (2022) reported low correlations for timber and water regulation (ρ = 0.120), timber and recreation (ρ = −0.076), and water supply and recreation (ρ = −0.154) in southern Chile. For temperate forests, Felipe-Lucia et al. (2018) found weak correlations between tree carbon storage and cultural plant value (ρ = 0.14), between harvestable timber and tree carbon (ρ = −0.08) and between harvestable timber and plant cultural value (ρ = −0.23). In Alpine grasslands, Schmitt et al. (2024) observed weak negative correlations between recreation (photo-user days) and both yield and habitat services (proxied by agri-environmental payments). Zeng et al. (2022) found a negligible correlation (ρ = 0.007) between water yield and habitat quality in urban China. No significant correlation emerged between habitat provision and carbon sequestration, though Móstiga et al. (2023) reported a weak negative correlation (ρ = −0.18) between biodiversity and aboveground carbon density in tropical rainforests. The spatial congruency analysis reinforced a synergy between habitat provision and timber potential, suggesting wildcats favor densely vegetated forests with higher biomass. Surprisingly, no link was found between habitat provision and carbon sequestration or between timber potential and carbon sequestration. Khamila et al. (2023) identified a synergy between forest productivity (via NPP) and biodiversity in temperate forests, which was not reflected here. One possible explanation is the limited reliability of the SDM, due to the quality of occurrence data discussed earlier. Additionally, a mismatch in spatial scales between the variables may have obscured potential relationships. Gutsch et al. (2018) found that mixed-species forests support both habitat provision and carbon storage, though they yield less timber than faster-growing forest monocultures in Germany. Additionally, younger forests sequester carbon more rapidly, while older stands store more total above-ground carbon (AGB) (Murty et al., 1996). In this study, carbon sequestration was measured by AGB production rate, while timber potential was based on total AGB. Another possible explanation is therefore, that wildcats prefer older, complex forest stands, which have lower carbon sequestration rates but higher potential for timber. Habitat provision and recreational value showed little overlap in NCP hotspots but 50 % in cold spots. Wildcats avoid human settlements and roads, suggesting they would also avoid areas with high tourist activity. Likewise, croplands and non-natural areas are unsuitable for both wildcats and recreation. A similar trend was observed between timber potential and recreation, with overlapping cold spots, likely due to non-vegetated land being unsuitable for both. Another synergy emerged between carbon sequestration and water retention, with overlapping hot and cold spots. Both are vegetation-driven: healthy vegetation enhances carbon storage via photosynthesis while improving soil water retention by reducing runoff and increasing infiltration, which is supported by Lin et al. (2018) and Wu et al. (2024).

4.3. *Implications of nature protection status*

Although statistical differences were found for all five NCP, Cohen's d effect sizes indicated that differences were not always meaningful. Habitat provision and carbon sequestration did not meet the threshold criteria, suggesting that varying protection levels had little impact on these NCP. However, timber potential showed a significant effect, likely due to harvesting restrictions in national parks. However, the underlying methodology used for estimating timber potential by Verkerk et al. (2019) relies on Natura2000 sites to account for harvest restrictions. Approximately 80 % of national parks, 23 % of biosphere reserves and 13 % of nature parks in the AOIs are also allocated as Natura2000 sites and are thus considered for harvest restrictions, while in reality all national parks do not allow harvest. Recreational value varied significantly, with national parks scoring higher than nature parks and biosphere reserves. Landscape topography plays a key role in recreation, as geologically significant features, often under strict protection,

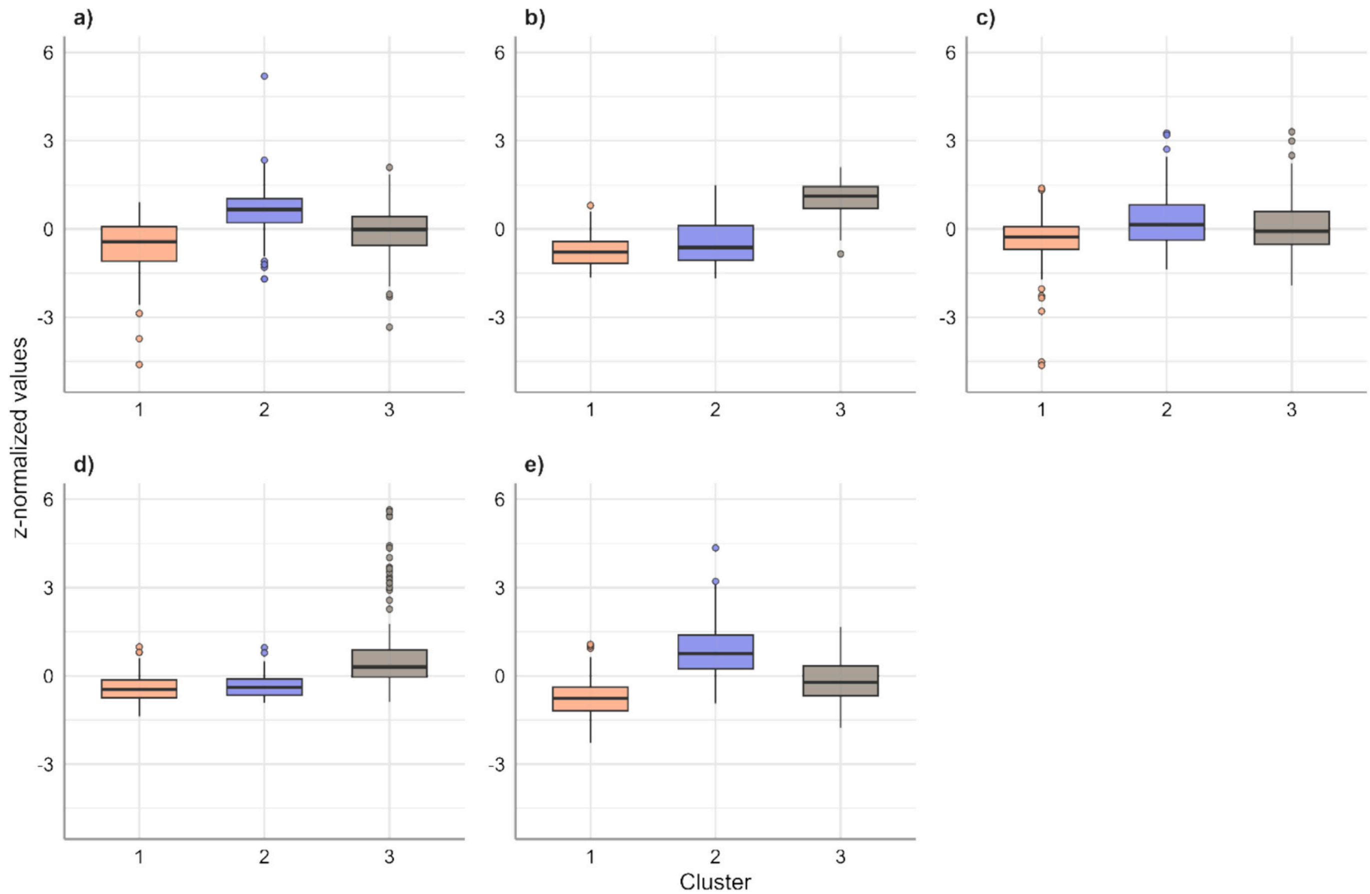

Fig. 6. Boxplot - k-means clustering, showing normalized NCP values across the three clusters. a) Carbon Sequestration; b) Habitat Provision; c) Recreational Value; d) Timber Potential; and e) Water Retention.

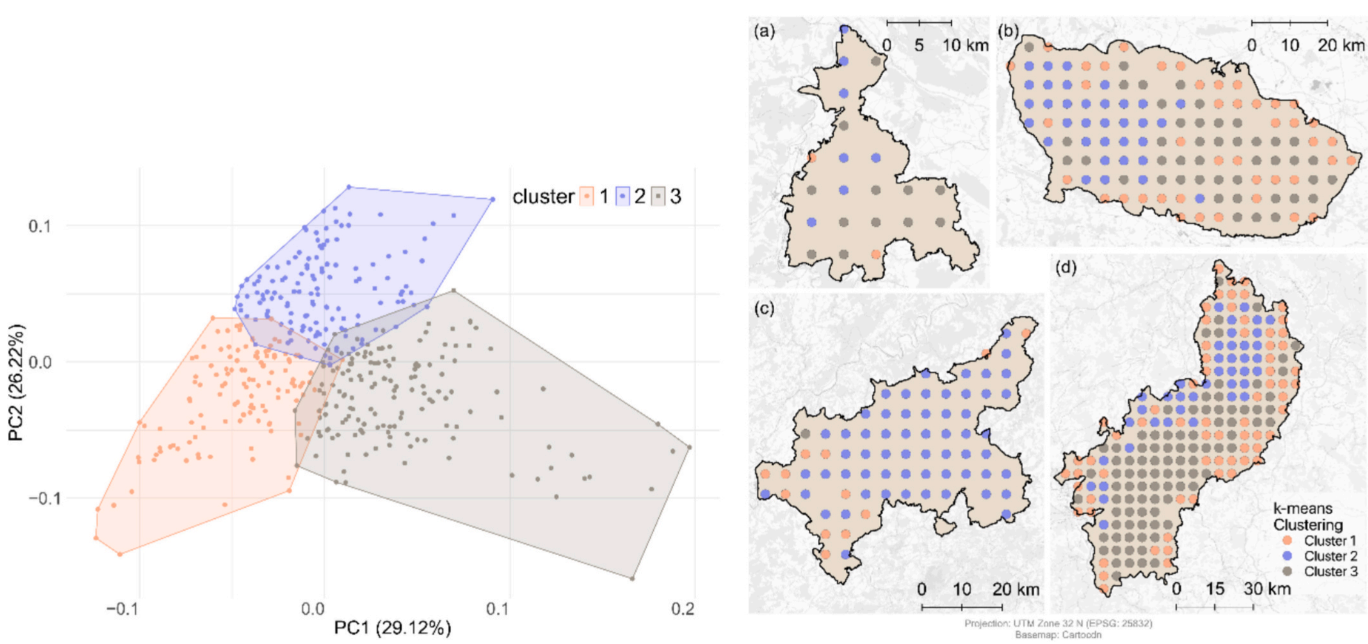

Fig. 7. Left: Autoplot showing the three clusters of the k-means clustering algorithm. Right: Map of the k-means clustering results. (a) Solling-Vogler, (b) Harz, (c) Saar-Hunsrück and (d) Rhön-Spessart.

provide panoramic views and outdoor opportunities. He et al. (2018) and Janeczko et al. (2023) showed that protection status also shapes public perception of cultural services. Water retention showed the strongest effect, with national parks having significantly higher values than nature parks and biosphere reserves, highlighting the role of intact ecosystems for water retention. Like recreation, water retention is

Table 6
Effect size (Cohen's d) for the pairwise t-test. The three protection status pairs are A: Nature Park – Biosphere Reserve; B: Nature Park – National Park; C: Biosphere Reserve – National Park. *indicates statistical significance ($p < 0.05$).

Nature's Contributions to People	A	B	C
Habitat Provision	−0.184	−0.035*	0.173*
Carbon Sequestration	−0.020*	0.117*	0.102
Water Retention	0.499*	−1.564*	−2.157*
Timber Potential	0.493*	0.242*	−0.641*
Recreational Value	0.000	−0.785*	−0.819*

influenced by topography, which also affects protected area allocation.

Previous studies using international protected area classifications (e.g., Natura 2000, IUCN protected area categories) found similar patterns. Bastian (2013) found that provisioning ES are more dependent on vegetation structure and land cover, while cultural and regulating ES depend on specific Natura 2000 habitats and species. Castro et al. (2015) found higher regulating ES supply in Natura 2000 sites and national parks than in nature parks in Spain. Maes et al. (2012) reported that well-conserved habitats provide greater biodiversity and cultural ES supply across Europe. Burkhard et al. (2012) showed that protected areas generally enhance ES provision and mitigate human impacts. Overall, strict protection effectively supports higher NCP supply, particularly for water retention and recreation.

Future research should also address NCP demand by analyzing the distribution of beneficiaries (Schirpke et al., 2016). Incorporating IUCN's protected area categories and management zones would further enhance comparability (Stolton et al., 2013).

Integrating a protected umbrella species into NCP assessment is an innovative approach in conservation science. Other taxa that could be addressed by this approach should likewise be related to high-quality habitats and legally protected, with public interest in their conservation. Examples include the gray wolf (*Canis lupus*), the Eurasian lynx (*Lynx lynx*) and the European mink (*Mustela lutreola*). Our results provide useful insights for spatial adjustments or the establishment of new protection zones for the European wildcat that benefit many other forest-related species. The observed synergies with NCP can help policymakers to argue for the establishment of such areas. Despite these insights, the lack of a standardized NCP assessment framework limits result comparability and integration into decision-making. Additionally, the absence of robust validation data challenges the accuracy and reliability of findings. This highlights the need for standardized, consistent methods to assess NCP (Pascual et al., 2017).

5. Conclusion

This study presents a novel approach to assessing Nature's Contributions to People by integrating habitat analysis for a keystone species — the European wildcat. It bridges the gap between biodiversity conservation and NCP provision, offering insights into synergies and trade-offs in multifunctional landscapes. The key findings are that suitable wildcat habitats are characterized by natural, structurally complex, and densely forested areas with multiple canopy layers, in distance from urban areas and roads but near agricultural land. Synergies between habitat provision and timber potential, as well as between carbon sequestration and water retention were identified. Spatial clustering of NCP supply was observed, with lower supply near the borders of the AOIs and two distinct clusters of higher NCP values: one associated with habitat provision and timber potential, and the other with carbon sequestration, water retention and recreational value. Significant differences in the provision of NCP were found between different levels of protection, particularly for water retention and recreational value. National parks had higher levels of supply than biosphere reserves and nature parks.

Our results demonstrate that suitable wildcat habitats indeed exhibit synergies with forest-related NCPs. In contrast to our expectations, no trade-offs with human activity-related NCP were identified. Furthermore, areas with higher protection status generally supported a higher NCP supply. Ultimately, this study underscores the link between biodiversity and human well-being, demonstrating that wildcat habitat protection aligns with broader NCP goals. These findings support enhanced conservation measures and adaptive strategies for suitable landscape alignment.

CRediT authorship contribution statement

Svenja Dobelmann: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michael Thiel:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Conceptualization. **Janina Kleemann:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization.

Declaration of competing interest

We have nothing to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111506.

Data availability

The authors are unable or have chosen not to specify which data has been used.

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