

Original Articles

Contributions of Landscape Structure and Environmental Gradients to Habitat Quality in Forest-Dominated Heterogeneous Landscapes

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Abstract

Habitat quality reflects the combined influence of landscape structure and environmental conditions, yet their relative contributions remain insufficiently understood in heterogeneous forest landscapes. We evaluated the relative contributions of landscape composition, configuration, and environmental gradients across 519 landscape units by integrating InVEST habitat-quality estimates, landscape metrics, and environmental variables within a hierarchical spatial beta generalized additive modelling framework. Landscape composition accounted for most of the variation in habitat quality, while landscape configuration, nonlinear environmental responses, and spatial structure provided additional explanatory information. Spatially blocked cross-validation indicated high predictive performance ($R^2 = 0.962$, RMSE = 0.040, MAE = 0.023). Forest cover had the strongest positive composition effect, whereas artificial surfaces were negatively associated with habitat quality. Landscape configuration provided additional explanatory information after accounting for landscape composition, although its multivariate relationship cautions against interpreting individual fragmentation metrics in isolation. Among environmental predictors, NDVI showed the strongest response and a distinctly nonlinear relationship with habitat quality. Habitat-quality patterns were highly stable under alternative InVEST half-saturation constants and $\pm 25\%$ changes in threat-impact distances. These results showed that, even where landscape composition accounted for most habitat-quality variation, landscape configuration and nonlinear environmental gradients provided additional information after accounting for spatial dependence and parameter uncertainty. These findings clarified the relative contributions of landscape composition, spatial configuration, and environmental heterogeneity to modelled habitat-quality patterns in forest-dominated heterogeneous landscapes.

Keywords: generalized additive model, fragmentation metrics, InVEST model, spatial modelling, Türkiye.

Introduction

Habitat quality represents the capacity of an ecosystem to provide the environmental conditions required for species to survive, reproduce, and maintain viable populations over time. In forest landscapes, where habitat continuity strongly influences ecological processes, habitat quality has become a key indicator for assessing biodiversity conservation, ecosystem integrity, and the consequences of land-use change (Huang et al., 2023; Liu et al., 2023). It also provides a practical framework for identifying areas where environmental pressures may compromise ecosystem functioning and long-term biodiversity persistence, making it an important component of landscape-scale environmental assessment (Yang et al., 2023; Yuan et al., 2023).

Land-use change affects biodiversity not only through habitat loss but also by altering landscape structure. Changes in patch size, isolation, edge density, and habitat connectivity reduce the capacity of landscapes to sustain ecological processes and species movement. However, the ecological consequences of fragmentation are often context dependent and influenced by interactions among multiple landscape characteristics. Consequently, nonlinear responses are common and cannot be adequately explained using simple linear relationships or individual landscape metrics alone (Zheng et al., 2023; Lin et al., 2024; Xu et al., 2024).

The increasing availability of satellite-derived environmental data and ecosystem-service models has expanded opportunities for habitat-quality research. Among these approaches, the InVEST Habitat Quality model has become one of the most widely used tools because it provides spatially explicit estimates while accounting for anthropogenic threats. Recent studies have increasingly combined InVEST with landscape metrics, geographically weighted regression, and other spatial modelling techniques to investigate landscape effects on habitat quality. Nevertheless, most studies still focus primarily on land-use composition or land-cover dynamics, whereas landscape configuration, environmental gradients, and spatial dependence are commonly evaluated separately. This fragmented perspective limits understanding of how landscape structure and environmental heterogeneity jointly influence habitat quality. (Broquet et al., 2024; Lin et al., 2024; Ma et al., 2025). InVEST habitat-quality estimates are inherently linked to LULC because habitat suitability and sensitivity to anthropogenic threats are assigned according to land-cover classes (Zhao et al., 2022). This model structure creates a close relationship between habitat-quality estimates and landscape composition, highlighting the importance of distinguishing compositional patterns from the additional information provided by landscape configuration, environmental gradients, and spatial structure (Wu et al., 2024).

Despite increasing applications, several methodological limitations remain. Landscape configuration often receives less attention than land-cover composition despite its direct influence on habitat fragmentation and connectivity (Lin et al., 2024; Xu et al., 2024). Likewise, landscape metrics are frequently analysed individually despite their strong intercorrelations, while environmental variables such as topography and vegetation condition are commonly examined separately from landscape structure (Zhang et al., 2024a; Wu et al., 2024; Hu et al., 2026). As a result, the relative contributions of landscape composition, configuration, and environmental gradients remain difficult to distinguish. Integrating these components within a single modelling framework may therefore provide a more realistic explanation of spatial variation in habitat quality.

The aim of this study was to evaluate the relative contributions of landscape composition, landscape configuration, and environmental gradients to spatial variation in InVEST-derived habitat quality within a forest-dominated heterogeneous landscape. We hypothesized that, although landscape composition would account for a substantial proportion of habitat-quality variation, landscape configuration and nonlinear environmental gradients would provide additional explanatory information beyond composition alone. We further evaluated whether these relationships remained consistent after accounting for spatial dependence and uncertainty in key InVEST model parameters.

Methods

Study Area. This study was conducted in Düzce Province, northwestern Türkiye (Figure 1), a heterogeneous landscape dominated by forests and agricultural lands (Doğan et al., 2025). The study area covers approximately 2,416 km² and extends from sea level to 1,800 m a.s.l. Mean annual temperature is 13.6 °C, and annual precipitation ranges from 581 to 1,026 mm (Başaran, 2024). Land cover comprises 48.09% forest and semi-natural areas, 47.65% agricultural areas, 3.79% artificial surfaces, 0.31% water bodies, and 0.17% wetlands. Urbanization, transportation infrastructure, and agricultural expansion contribute to habitat fragmentation (Kaya et al., 2025).

Data Sources. Land-use and land-cover (LULC) data were obtained from the CORINE Land Cover 2018 dataset, using first-level classes to ensure consistent thematic resolution. Spatial data representing anthropogenic threats were obtained from 2024 national geospatial datasets provided by the Republic of Türkiye Ministry of Environment, Urbanization and Climate Change and were processed to generate the threat layers required by the InVEST Habitat Quality model. The road-network threat layers were rasterized at a spatial resolution of 12.5 m.

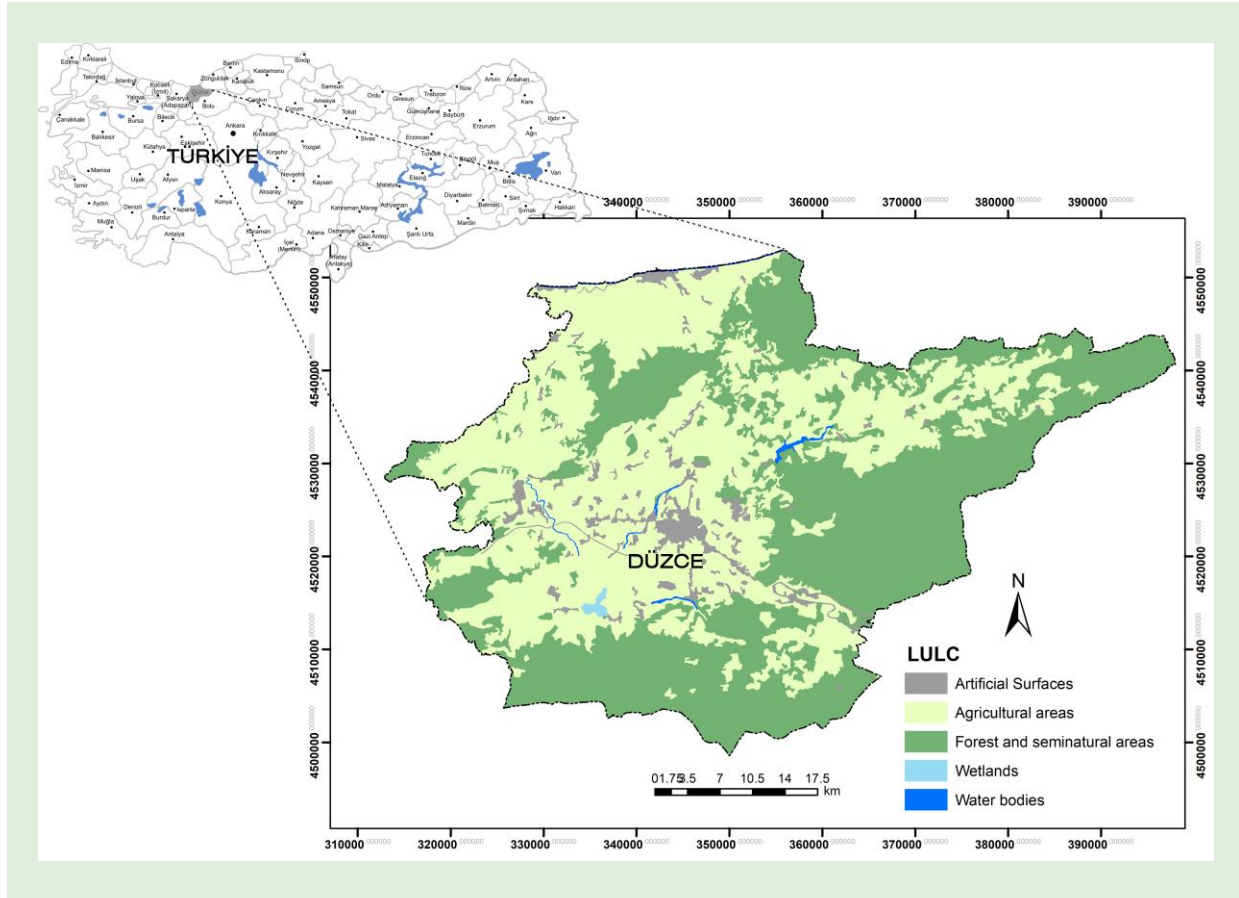


Figure 1. Study Area

Habitat Quality and Degradation Assessment. Habitat quality and degradation were quantified using the InVEST Habitat Quality model (version 3.14.2), which integrates LULC, habitat suitability, anthropogenic threats, and habitat sensitivity to generate spatially explicit habitat quality estimates (Dong et al., 2022; Zhao et al., 2022). Urban areas, industrial areas, roads, agricultural lands, mining sites, and hydroelectric power plants were defined as the principal threats based on previous studies and the InVEST User Guide (Haddad et al., 2015; Huang et al., 2023; Qin et al., 2024; Natural Capital Project, 2025). Threat weights, maximum impact distances, and distance-decay functions are summarized in Table 1. The complete habitat suitability and threat-sensitivity matrix is provided in Supplementary Table S1. Habitat degradation and habitat quality were calculated using the standard InVEST equations 1-2.

Each pixel-level habitat degradation value was calculated using the following equation:

$$D_{xj} = \sum_{r=1}^R \sum_{y=1}^Y \left(\frac{w_r}{\sum_{r=1}^R w_r} \cdot r_y \cdot i_{rxy} \cdot \beta_x \cdot S_{jr} \right) \quad (1)$$

Where r represents the threat type, y the threat source pixel, w_r the threat weight, r_y the presence of the threat (0–1), i_{rxy} the distance-decay impact function, β_x the protection/accessibility coefficient, S_{jr} the habitat sensitivity to the threat, and D_{xj} the total degradation of habitat type j in pixel x .

Habitat quality values were calculated by jointly considering habitat suitability and the corresponding degradation level, using the following formulation:

$$Q_{xj} = H_j \cdot \left(1 - \frac{D_{xj}^z}{D_{xj}^z + k^z} \right) \quad (2)$$

Where Q_{xj} denotes the habitat quality of habitat type j in pixel x , H_j the habitat suitability value, D_{xj} the habitat degradation value, k the half-saturation constant, and z the scaling constant fixed at 2.5 in the InVEST Habitat Quality model (Natural Capital Project, 2025).

Threat effects followed linear or exponential distance-decay functions as specified in Table 1. Agricultural land was included as a threat because agricultural expansion has contributed to natural

land-cover change and forest loss in Düzce Province (Siyavuş, 2021), representing pressure on adjacent habitats rather than uniformly low habitat value. The baseline model used $k = 0.5$; robustness was evaluated using $k = 0.375$ and 0.625 and $\pm 25\%$ changes in individual threat-impact distances while holding other parameters constant (Supplementary Table S2).

Landscape Composition and Configuration Assessment. The study area was divided into 2×2 km grid cells to represent local landscape units. Only grids completely contained within the study boundary were retained; 175 partial boundary cells were excluded, resulting in 519 sampling units. Landscape metrics were calculated using FRAGSTATS 4.2 (McGarigal et al., 2012). Metric selection was based on their ecological relevance for describing landscape composition, configuration, and fragmentation, and the selected metrics are presented in Table 2 (Mirghaed & Souri, 2022; Zheng et al., 2023; Abolmaali et al., 2024).

Environmental Variables. Topographic variables were derived from the SRTM digital elevation model at 30 m spatial resolution. Elevation and slope were calculated for the study area, while vegetation conditions were represented by the Normalized Difference Vegetation Index (NDVI), derived from a mean composite Sentinel-2 Level-2A imagery acquired during July–August 2018 in Google Earth Engine.

Elevation, slope, and NDVI were subsequently summarized for each 2×2 km grid cell and used as environmental predictors in the statistical analyses.

Statistical Analysis. Mean habitat quality and degradation were extracted for the 519 grid cells and linked with landscape metrics and environmental variables. Relationships among variables were examined using Spearman’s rank correlation. Standardized PD, ED, LPI, and CONTAG were subjected to principal component analysis (PCA), with LAND_PC1 retained based on the eigenvalue >1 criterion

Table 1. Threat factors and parameters for habitat quality and degradation

Threat factor	Maximum threat distance (km)	Weight	Type of spatial decay
Urban / Developed land	10	1.00	Exponential
Industrial areas	7	0.90	Linear
Primary roads	3	0.80	Linear
Secondary roads	2	0.60	Linear
Urban roads	0.7	0.40	Linear
Planted agriculture	8	0.70	Linear
Mining sites	2	0.70	Exponential
Hydroelectric power plants	3	0.60	Exponential

Table 2. Landscape metrics used to characterize landscape composition and configuration (Leitão et al., 2012).

Metric	Level	Description
Patch Density (PD)	Landscape	Number of patches per unit area; indicator of landscape fragmentation.
Edge Density (ED)	Landscape	Total edge length per unit area; indicator of edge effects.
Largest Patch Index (LPI)	Landscape	Percentage of the landscape occupied by the largest patch.
Percentage of Landscape (PLAND)	Class	Percentage of the landscape occupied by a class.
Contagion Index (CONTAG)	Landscape	Degree of patch aggregation and landscape integrity.

as the integrated configuration gradient (Jolliffe & Cadima, 2016). Descriptive statistics are provided in Table S3.

Habitat quality was modelled using a beta generalized additive model (GAM) with a logit link; observed values ranged from 0.01 to 0.95, and no observations occurred at the distributional boundaries. Hierarchical models sequentially incorporated land-cover composition, configuration, linear and nonlinear environmental effects, and spatial structure. PLAND coefficients represent substitution effects relative to agriculture. LAND_PC1 was fitted linearly, elevation, slope, and NDVI as smooth terms, and residual spatial dependence as a two-dimensional smooth of grid-centroid coordinates using restricted maximum likelihood (REML) (Wood, 2025). Concurvity and coefficient stability were assessed (Table S4), while predictor distributions and sensitivity to NDVI extremes identified using the $1.5 \times \text{IQR}$ criterion are reported in Table S5.

Model performance was evaluated using AIC, adjusted R^2 , explained deviance, RMSE, MAE, and spatial cross-validation. Based on an estimated residual autocorrelation range of approximately 4.87 km in the non-spatial nonlinear model, five-fold spatial cross-validation was conducted using 6-km spatial blocks, with models refitted within each training fold (Valavi et al., 2019). Residual spatial autocorrelation was evaluated using Moran's I with a 6-km distance-based neighbourhood. Effect magnitudes were quantified using percentile contrasts for continuous predictors and presence-based contrasts for sparse land-cover classes. All analyses were performed in R (R Core Team, 2025).

Results

Spatial patterns of habitat quality and degradation. The InVEST Habitat Quality model revealed considerable spatial variation in habitat quality and degradation across the study area (Figure 2).

High habitat quality values were mainly associated with the extensive forest areas located in the northern and eastern parts of the landscape, whereas lower habitat quality coincided with higher degradation levels in the central-western corridor, where agricultural land, settlements, and road networks are more prevalent.

Exploratory analysis. Spearman's rank correlation analysis showed that habitat quality was positively associated with forest cover and LPI and negatively associated with PD, ED, artificial surfaces, and agricultural land (Figure 3). PD and ED were positively correlated with each other and negatively correlated with LPI.

The PCA biplot further summarized the correlated landscape configuration metrics. LAND_PC1 explained 70.43% of the total variance and was positively associated with PD (loading = 0.551), ED (0.569), and CONTAG (0.315), and negatively associated with LPI (-0.522). LAND_PC2 explained an additional 21.12% of the variance and was primarily associated with CONTAG (loading = 0.912) (Table 3; Figure 4). LAND_PC1 was therefore retained as the integrated landscape configuration gradient for subsequent modelling.

Habitat quality modelling and spatial validation. Model performance improved progressively with the incorporation of landscape configuration, environmental effects, nonlinearity, and spatial structure (Table 4). Explained deviance increased from 95.35% for landscape composition alone to 97.38% after nonlinear environmental effects were incorporated and to 99.11% in the final spatial model (adjusted $R^2 = 0.988$).

Relative to agriculture, forest cover, wetlands, and water bodies showed positive substitution effects, whereas artificial surfaces showed a negative effect; LAND_PC1 was negatively associated with

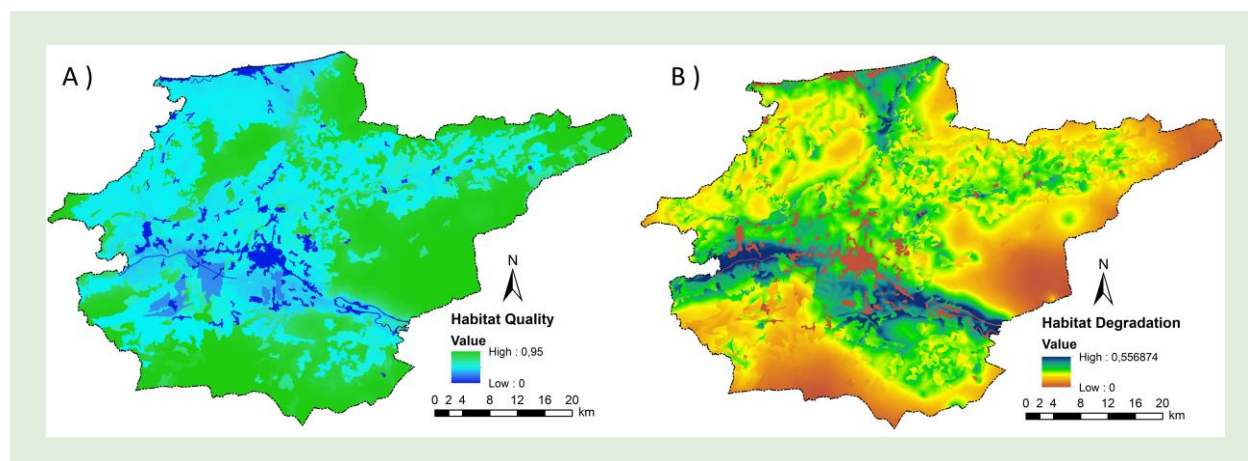


Figure 2. Spatial distribution of (A) habitat quality and (B) habitat degradation across the study area estimated using the InVEST Habitat Quality model.

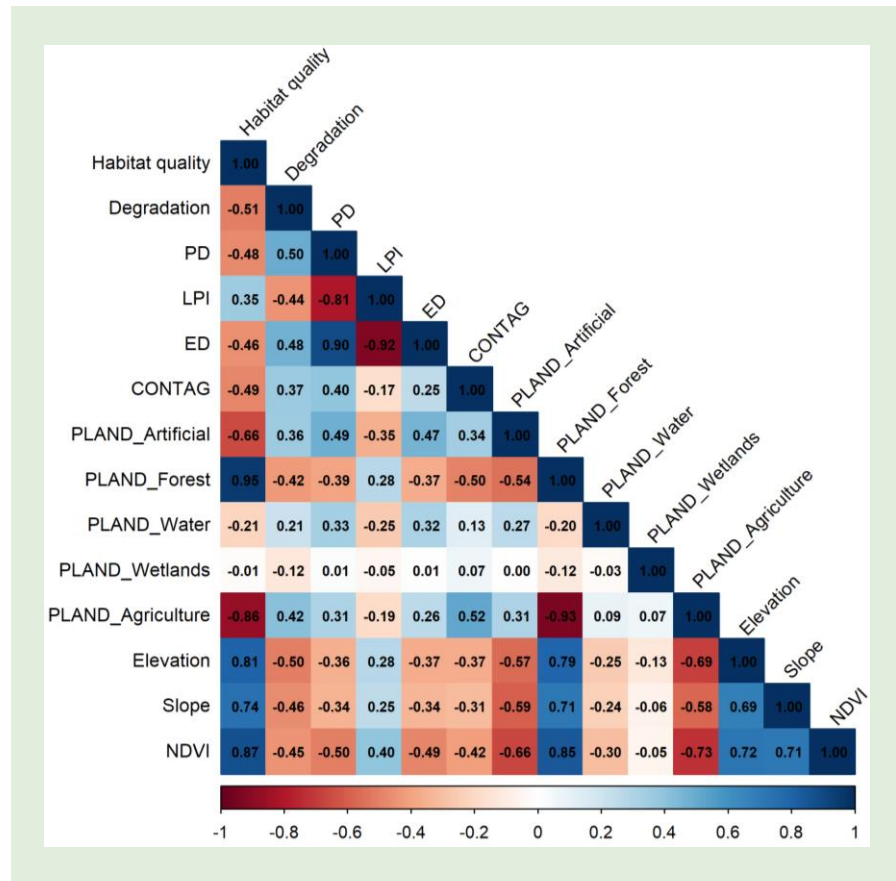


Figure 3. Spearman correlation matrix of habitat quality, landscape, and environmental variables.

Table 3. Principal component loadings of landscape configuration metrics.

Landscape metric	LAND_PC1	LAND_PC2
PD	0.551	0.020
ED	0.569	-0.194
LPI	-0.522	0.360
CONTAG	0.315	0.912
Eigenvalue	2.817	0.845
Variance explained (%)	70.43	21.12

habitat quality (Table 5). Forest cover showed the largest response-scale contrast among the evaluated predictors ($\Delta\text{HQ} = 0.322$), while artificial surfaces and LAND_PC1 produced contrasts of -0.043 and -0.058 , respectively (Table S6). All nonlinear environmental effects

were significant, with the largest Q10–Q90 response-scale contrasts observed for NDVI ($\Delta\text{HQ} = 0.076$) and elevation ($\Delta\text{HQ} = 0.052$); slope showed a small endpoint contrast despite its significant nonlinear response (Figure 5; Table S6). Concurvity was moderate among the retained environmental smooths but higher between these terms and the spatial smooth (Table S4). Nevertheless, all landscape coefficients retained their direction after spatial adjustment, with changes in magnitude ranging from 12.3% to 23.1%. Excluding the 14 low-NDVI extremes did not alter the direction of landscape effects or the significance of environmental smooths (Table S5). Effects of wetlands and water bodies should be interpreted cautiously because of their limited occurrence.

The spatial effect varied across the study area, with positive residual effects concentrated in the eastern and southeastern sectors and negative effects predominantly in the central-western sector (Figure 6). On the response scale, the spatial contrast ($\Delta\text{HQ} = 0.124$) was smaller than the forest-cover effect (0.322) but larger than the NDVI effect (0.076). Spatial cross-validation confirmed high predictive performance ($R^2 = 0.962$, $\text{RMSE} = 0.040$, $\text{MAE} =$

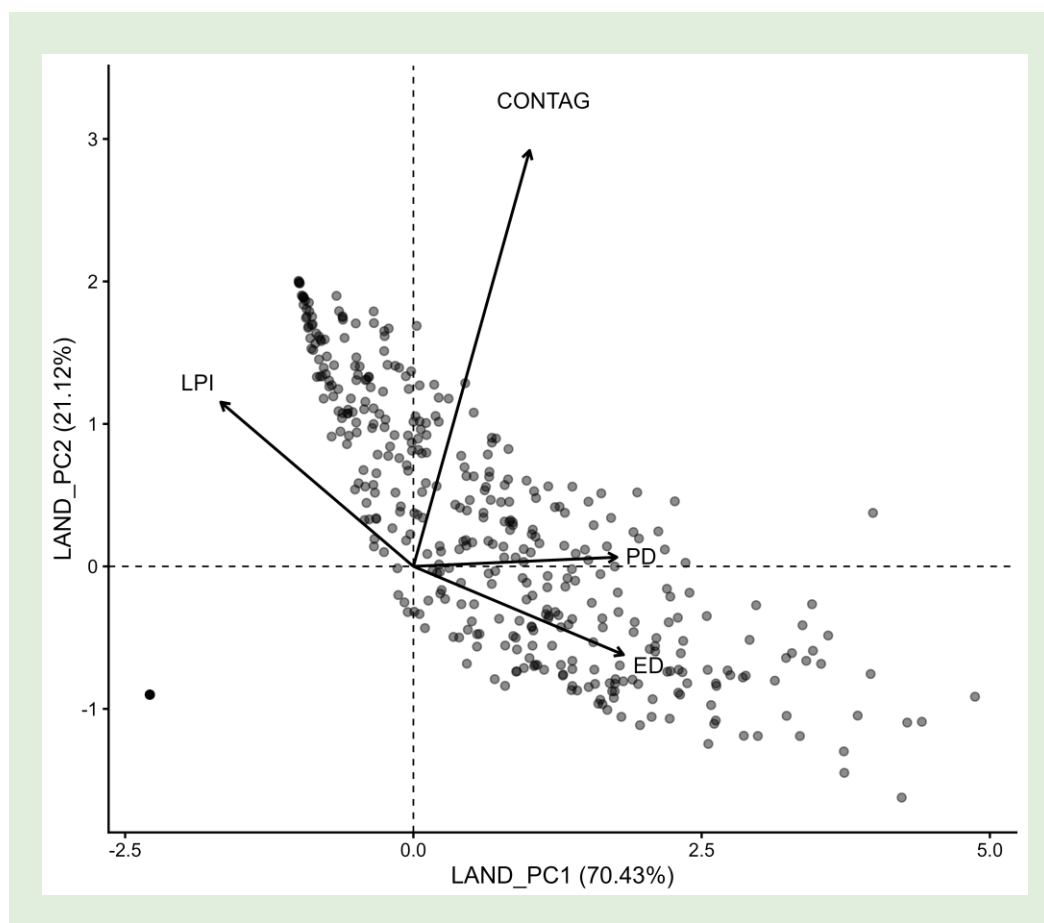


Figure 4. PCA ordination of landscape configuration metrics.

Table 4. Performance of hierarchical beta-GAMs for habitat quality.

Model structure	AIC	Adjusted R ²	Deviance explained (%)	Spatial cross-validation R ²	RMSE	MAE
Landscape composition	-1,754.36	0.954	95.35	0.937	0.051	0.037
Composition and configuration	-1,890.08	0.963	96.45	0.946	0.048	0.032
Composition, configuration, and linear environmental effects	-1,935.64	0.967	96.79	0.949	0.046	0.030
Composition, configuration, and nonlinear environmental effects	-2,024.52	0.970	97.38	0.951	0.045	0.029
Full spatial model	-2,374.51	0.988	99.11	0.962	0.040	0.023

0.023), with CV R² increasing from 0.937 for the composition-only model to 0.962 for the final spatial model (Table 4; Figure 7). The spatial smooth reduced residual Moran’s I from 0.245 in the non-spatial nonlinear model to –0.070 in the final spatial model (both P < 0.001), substantially reducing the strong positive residual spatial dependence, although weak negative autocorrelation remained.

Table 5. Effects of predictors in the final spatial beta-GAM for habitat quality

Predictor	Effect / test statistic	P
Artificial surfaces	β = –0.0142 (SE = 0.0017)	<0.001
Forest cover	β = 0.0163 (SE = 0.0005)	<0.001
Wetlands	β = 0.0238 (SE = 0.0025)	<0.001
Water bodies	β = 0.0248 (SE = 0.0041)	<0.001
Landscape configuration (LAND_PC1)	β = –0.0579 (SE = 0.0066)	<0.001
Elevation	edf = 2.166; χ² = 9.040	0.015
Slope	edf = 3.677; χ² = 35.021	<0.001
NDVI	edf = 3.859; χ² = 87.159	<0.001
Spatial effect	edf = 94.269; χ² = 664.043	<0.001

β: regression coefficient; SE: standard error; edf: effective degrees of freedom; χ²: Chi-square statistic.

Habitat-quality estimates were robust to alternative InVEST parameterizations. Changing the half-saturation constant from k = 0.375 to k = 0.625 preserved the direction of landscape effects, while ±25% changes in individual threat-impact distances produced only minor deviations from baseline estimates (MAE ≤ 0.0033) and virtually unchanged spatial rankings (Spearman’s ρ ≥ 0.9996; Table S2).

Discussion

Habitat-quality variation was primarily associated with landscape composition, while configuration, nonlinear environmental responses, and spatial structure provided additional explanatory information. Similar conclusions have been reported by studies integrating InVEST, landscape metrics, and environmental variables (Wu et al., 2024; Abolmaali et al., 2024; Ma et al., 2025).

Forest cover showed the strongest positive land-cover substitution effect relative to agriculture. Similar positive relationships between forest-dominated landscapes and habitat quality have been documented across different environmental settings (Broquet et al., 2024; Qin et al., 2024). The magnitude of this relationship was ecologically pronounced: increasing forest cover across its observed 10th–90th percentile contrast increased predicted habitat quality by 0.322. However, because land cover is an input to the InVEST Habitat Quality model, this association should not be interpreted as fully independent of model structure. Rather, its magnitude demonstrates how strongly forest-dominated landscape composition contributes to spatial differentiation in modelled habitat quality.

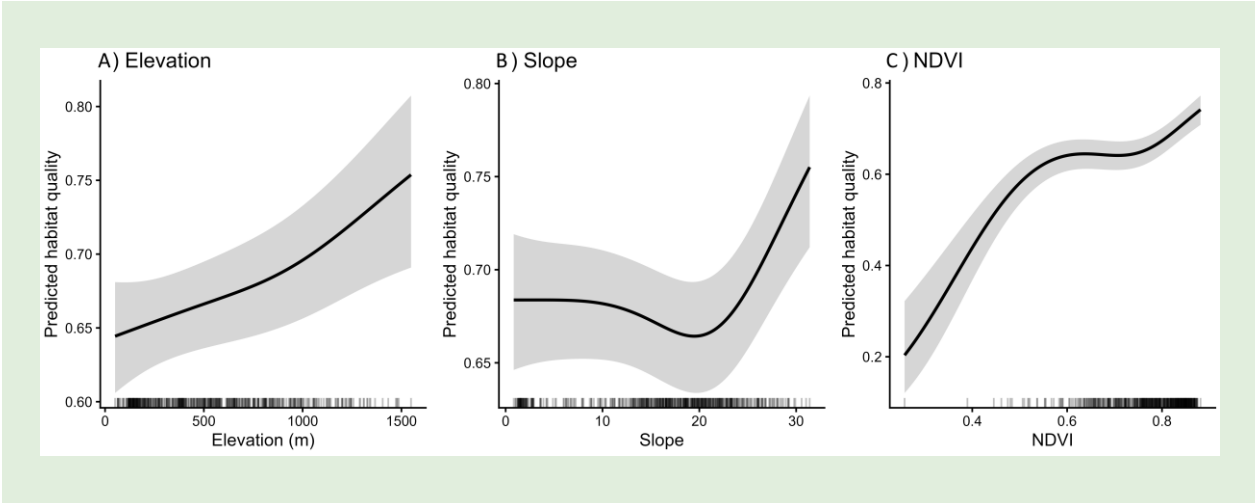


Figure 5. Modelled nonlinear responses of habitat quality to environmental predictors (spatial beta-GAM).

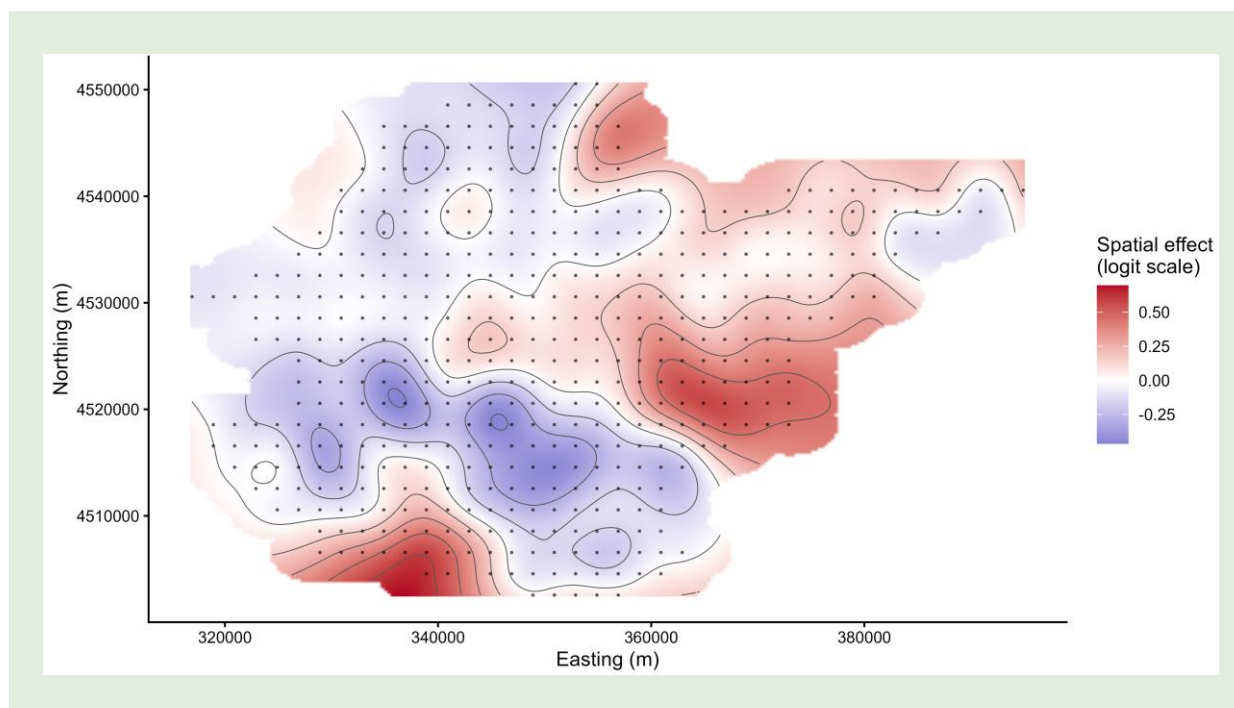


Figure 6. Estimated spatial effect on habitat quality in the final spatial beta-GAM (range: -0.454 to 0.631 on the logit scale).

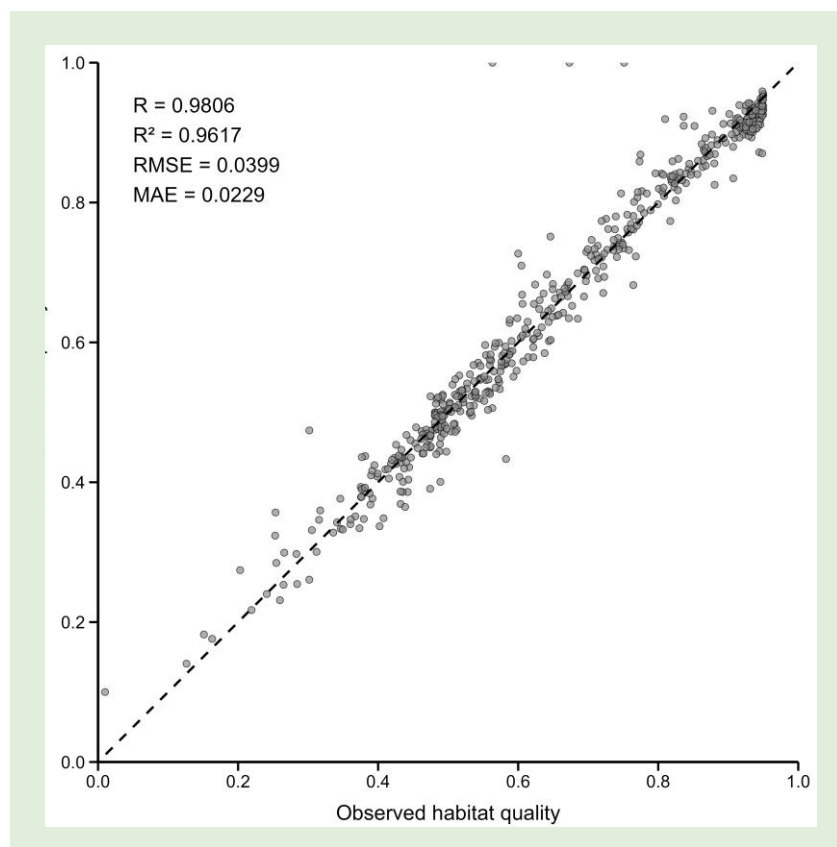


Figure 7. Observed versus predicted habitat quality under five-fold spatial cross-validation.

Artificial surfaces showed a negative substitution effect relative to agriculture with predicted habitat quality decreasing by 0.043 across the evaluated percentile contrast. Comparable negative associations between built-up land and habitat quality have been reported in rapidly urbanizing landscapes (Dong et al., 2022; Zhao et al., 2022). Positive effects were also detected for wetlands and water bodies, but these estimates should be interpreted cautiously because these classes occurred in only 1.2% and 5.4% of grid cells, respectively.

Landscape configuration provided additional explanatory information after accounting for landscape composition, with explained deviance increasing from 95.35% in the composition-only model to 96.45% after LAND_PC1 was added. LAND_PC1 represented a multivariate configuration gradient characterized primarily by increasing patch and edge densities and decreasing largest-patch dominance, with a weaker positive contribution from CONTAG. Its negative association with habitat quality therefore reflects a multivariate configuration gradient rather than the independent effect of any single fragmentation metric, consistent with evidence that habitat-quality patterns are associated with multiple dimensions of landscape configuration and fragmentation (Gu et al., 2023; Zheng et al., 2023; Lin et al., 2024; Xu et al., 2024).

Among the environmental predictors, NDVI showed the largest Q10–Q90 response-scale contrast ($\Delta\text{HQ} = 0.076$), followed by elevation ($\Delta\text{HQ} = 0.052$), whereas the corresponding endpoint contrast for slope was small ($\Delta\text{HQ} = 0.005$) despite its significant nonlinear response. Habitat quality increased toward the upper end of the NDVI gradient. However, this relationship should be interpreted as an association with InVEST-derived habitat quality rather than as evidence of a direct ecological mechanism, potentially reflecting within-class vegetation variation not represented by the CORINE land-cover categories. Remotely sensed vegetation indices have similarly been identified as useful indicators of vegetation structure and ecosystem condition (Liu et al., 2022; Zhang et al., 2024b). Elevation and slope also showed significant nonlinear associations with habitat quality. These relationships are better interpreted as spatial associations with land-cover and vegetation patterns represented in the InVEST-derived response rather than as direct topographic effects on habitat quality.

The significant spatial smooth indicated that geographic structure remained after accounting for the measured landscape and environmental predictors. Given the structure of the InVEST response, this residual pattern may reflect spatial variation in threat exposure and land-cover configuration not fully represented by the grid-level predictors (Gu et al., 2023; Wu et al., 2024). Importantly, high model performance was maintained under spatially blocked cross-validation ($R^2 = 0.962$; RMSE = 0.040; MAE = 0.023), indicating

that the strong model fit was not restricted to spatially neighbouring calibration observations.

Habitat quality patterns remained stable under alternative half-saturation constants and $\pm 25\%$ changes in threat-impact distances, indicating that the main relationships were not dependent on a single parameterization. Similar stability of broad landscape patterns under moderate changes in InVEST threat and sensitivity parameters has been reported in previous habitat-quality modelling (Louis et al., 2024). These analyses distinguish the contributions of landscape composition, configuration, environmental gradients, and residual spatial structure while accounting for uncertainty in the InVEST parameterization.

This study has several limitations. Habitat quality represents an InVEST-derived estimate of potential ecological condition and was not independently validated with field-based biodiversity observations. Moreover, because LULC contributes directly to InVEST habitat-quality estimation, relationships between habitat quality and land-cover composition partly reflect model structure and should not be interpreted as independent causal effects. The use of CORINE Level 1 classes may also obscure within-class heterogeneity, particularly within forest and semi-natural areas. Analyses were conducted at a single 2×2 km grain; therefore, the magnitude and relative importance of landscape relationships may vary at other spatial resolutions because of scale dependence and the modifiable areal unit problem. Exclusion of partial boundary cells may underrepresent edge landscapes and associated fragmentation patterns. Despite strong spatially blocked cross-validation performance, the high flexibility of the final spatial smooth (approximately 94 edf) and the slightly negative residual Moran's I (-0.070) suggest that fine-scale spatial patterns should be interpreted cautiously.

Conclusions

Habitat quality in forest-dominated heterogeneous landscapes was associated with landscape composition, configuration, and environmental gradients. Forest cover had the strongest positive composition effect, whereas artificial surfaces were negatively associated with habitat quality. Landscape configuration explained additional variation after accounting for landscape composition, although its multivariate relationship with habitat quality indicates that individual fragmentation metrics should not be interpreted in isolation. Among the environmental predictors, NDVI showed the strongest response and a distinctly nonlinear relationship with habitat quality.

The consistency of these relationships under spatially blocked cross-validation and alternative InVEST parameterizations indicates

that the main patterns were robust to spatial dependence and the parameter ranges examined. Combining landscape composition and configuration with nonlinear environmental responses, spatial dependence, and parameter sensitivity provides a more rigorous basis for evaluating modelled habitat-quality patterns than mapping model outputs alone. This analytical framework can be applied to other forest-dominated landscapes to examine whether the relative contributions of composition, configuration, and environmental gradients vary under different patterns of land-use pressure.

Author contributions

S.K. and F.C.Y. contributed equally to the conceptualization, methodology, data analysis, and interpretation of the results. S.K. prepared the original draft, and F.C.Y. contributed to revision and editing. Both authors approved the final manuscript.

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AI use declaration

OpenAI ChatGPT (GPT-5.5) was used solely for language editing and improving grammar and readability. All scientific content, analyses, interpretations, and final editorial decisions were reviewed, verified, and approved by the authors, who assume full responsibility for the manuscript.

Data availability statement

The data, InVEST parameter files, and R code are publicly available in Zenodo at <https://doi.org/10.5281/zenodo.22051642>

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Supporting information

Table S1. Habitat suitability and sensitivity of land-use/land-cover classes to anthropogenic threats used in the InVEST Habitat Quality model.

LULC	Habitat	Urban	Industry	Primary road	Secondary road	Urban road	Agriculture	Mining	Hydroelectric power plants
NoData	0	0	0	0	0	0	0	0	0
Continuous urban fabric	0	0	0	0	0	0	0	0	0
Discontinuous urban fabric	0	0	0	0	0	0	0	0	0
Industrial or commercial units	0	0	0	0	0	0	0	0	0
Road and rail networks and associated land	0	0	0	0	0	0	0	0	0
Mineral extraction sites	0	0	0	0	0	0	0	0	0
Construction sites	0	0	0	0	0	0	0	0	0
Sport and leisure facilities	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0	0.1
Non-irrigated arable land	0.5	0.4	0.5	0.5	0.45	0.3	0	0.5	0.3
Permanently irrigated land	0.3	0.4	0.5	0.5	0.45	0.3	0	0.5	0.3
Fruit trees and berry plantations	0.50	0.5	0.5	0.5	0.5	0.35	0.3	0.5	0.3
Pastures	0.65	0.5	0.55	0.55	0.5	0.35	0.3	0.6	0.3
Complex cultivation patterns	0.55	0.55	0.55	0.55	0.5	0.35	0.3	0.5	0.3
Agriculture with significant natural vegetation	0.6	0.55	0.55	0.55	0.5	0.35	0.3	0.5	0.3
Broad-leaved forest	0.95	0.8	0.9	0.9	0.8	0.35	0.4	0.9	0.5
Coniferous forest	0.9	0.75	0.85	0.85	0.75	0.35	0.35	0.8	0.45
Mixed forest	0.95	0.8	0.85	0.85	0.8	0.35	0.35	0.8	0.5
Natural grasslands	0.8	0.6	0.65	0.6	0.55	0.3	0.3	0.7	0.4
Transitional woodland-shrub	0.7	0.65	0.7	0.65	0.55	0.3	0.35	0.7	0.4
Sparsely vegetated areas	0.6	0.65	0.7	0.6	0.55	0.3	0.35	0.7	0.4
Inland marshes	0.95	0.6	0.7	0.4	0.4	0.25	0.4	0.6	0.9
Water courses	0.95	0.6	0.7	0.4	0.4	0.25	0.4	0.6	0.95
Water bodies	0.8	0.5	0.6	0.3	0.3	0.2	0.4	0.5	0.85
Coastal waters	0	0	0	0	0	0	0	0	0

Habitat suitability and sensitivity scores range from 0 to 1. Higher sensitivity scores indicate greater susceptibility of a given LULC class to the corresponding threat.

Table S2. Sensitivity of habitat-quality estimates and landscape relationships to alternative InVEST parameterizations

Panel A. Sensitivity to the half-saturation constant

(k)	Adjusted R ²	Deviance explained	PLAND_111	PLAND_311	PLAND_411	PLAND_511	LAND_PC1
0.375	0.9871	0.9910	-0.0131	0.0130	0.0222	0.0220	-0.0521
0.500 (baseline)	0.9879	0.9911	-0.0142	0.0163	0.0238	0.0248	-0.0579
0.625	0.9877	0.9906	-0.0150	0.0183	0.0250	0.0262	-0.0606

Alternative values correspond to $\pm 25\%$ variation around the baseline half-saturation constant. Coefficients are from the final spatial beta-GAM fitted to the habitat-quality surface generated under each parameterization.

Panel B. Maximum threat-distance sensitivity

Threat	Low distance (km)	Baseline (km)	High distance (km)	MAE from baseline, low	MAE from baseline, high	Spearman ρ , low	Spearman ρ , high
Urban	7.5	10	12.5	0.003232	0.002500	0.999902	0.999941
Industry	5.25	7	8.75	0.002399	0.002680	0.999584	0.999597
Primary roads	2.25	3	3.75	0.000953	0.000990	0.999828	0.999856
Secondary roads	1.5	2	2.5	0.000623	0.000655	0.999948	0.999925
Urban roads	0.525	0.7	0.875	0.000614	0.000555	0.999987	0.999992
Agricultural lands	6	8	10	0.000367	0.000236	0.999975	0.999994
Mining	1.5	2	2.5	0.001317	0.001389	0.999904	0.999908
HPP	2.25	3	3.75	0.000261	0.000301	0.999982	0.999985

Low and high scenarios represent -25% and $+25\%$ changes, respectively, in the maximum impact distance of one threat at a time. All other maximum distances, threat weights, decay functions, habitat suitability scores, and habitat sensitivity coefficients were held constant. MAE represents the mean absolute difference from the baseline habitat-quality output; Spearman's ρ measures stability in the spatial ranking of habitat quality.

Table S3. Descriptive statistics of habitat quality, degradation, landscape composition, landscape configuration, and environmental variables across the 519 analysis units.

Variable	N	Mean	SD	Median	Min	Max
Habitat quality	519	0.655	0.203	0.630	0.010	0.950
Habitat degradation	519	0.137	0.052	0.136	0.005	0.288
Artificial surfaces (PLAND, %)	519	3.862	10.085	0.000	0.000	97.758
Agricultural areas (PLAND, %)	519	50.296	36.942	56.473	0.000	100.000
Forest and semi-natural areas (PLAND, %)	519	45.312	39.696	34.875	0.000	100.000
Wetlands (PLAND, %)	519	0.195	2.740	0.000	0.000	50.410
Water bodies (PLAND, %)	519	0.336	1.969	0.000	0.000	26.105
LAND_PC1	519	0.000	1.678	0.007	-2.286	4.871
Elevation (m)	519	544.025	347.095	497.056	50.647	1,548.648
Slope (°)	519	16.347	7.503	17.759	0.835	31.397
TWI	519	6.457	0.980	6.076	5.440	9.852
NDVI	519	0.769	0.089	0.790	0.257	0.881

Table S4. Concurvity diagnostics for the final spatial beta-GAM and stability of landscape coefficients following inclusion of the spatial smooth.

Panel A. Worst concurvity

	Parametric	Elevation	Slope	NDVI	Spatial
Parametric	1.000	0.000	0.000	0.000	0.000
Elevation	0.000	1.000	0.665	0.542	0.980
Slope	0.000	0.665	1.000	0.655	0.950
NDVI	0.000	0.542	0.655	1.000	0.923
Spatial	0.000	0.980	0.950	0.923	1.000

Panel B. Observed concurvity

	Parametric	Elevation	Slope	NDVI	Spatial
Parametric	1.000	0.000	0.000	0.000	0.000
Elevation	0.000	1.000	0.125	0.380	0.250
Slope	0.000	0.295	1.000	0.373	0.243
NDVI	0.000	0.397	0.069	1.000	0.186
Spatial	0.000	0.971	0.730	0.814	1.000

Panel C. Estimated concurvity

	Parametric	Elevation	Slope	NDVI	Spatial
Parametric	1.000	0.000	0.000	0.000	0.000
Elevation	0.000	1.000	0.569	0.343	0.182
Slope	0.000	0.330	1.000	0.470	0.063
NDVI	0.000	0.401	0.559	1.000	0.042
Spatial	0.000	0.958	0.906	0.827	1.000

Panel D. Stability of landscape coefficients

Predictor	Without spatial smooth	With spatial smooth	Absolute change (%)
Artificial surfaces	−0.0178	−0.0142	20.3
Forest cover	0.0186	0.0163	12.3
Wetlands	0.0310	0.0238	23.1
Water bodies	0.0218	0.0248	13.7
LAND_PC1	−0.0735	−0.0579	21.2

Concurvity values were obtained using `mgcv::concurvity(..., full = FALSE)`. Percentage change represents the absolute proportional difference between coefficients estimated from models fitted without and with the two-dimensional spatial smooth.

Table S5. Descriptive statistics of predictors and sensitivity of model coefficients to NDVI extremes.

Panel A. Descriptive statistics of predictors across the 519 landscape units

Predictor	N	Mean	SD	Min	Q10	Median	Q90	Max
Artificial surfaces (%)	519	3.862	10.085	0.000	0.000	0.000	13.056	97.758
Forest cover (%)	519	45.312	39.696	0.000	0.000	34.875	100.000	100.000
Wetlands (%)	519	0.195	2.740	0.000	0.000	0.000	0.000	50.410
Water bodies (%)	519	0.336	1.969	0.000	0.000	0.000	0.000	26.105
LAND_PC1	519	0.000	1.678	-2.286	-2.286	0.007	2.200	4.871
Elevation (m)	519	544.025	347.095	50.647	141.983	497.056	1,055.543	1,548.648
Slope (°)	519	16.347	7.503	0.835	2.651	17.759	24.900	31.397
NDVI	519	0.769	0.089	0.257	0.652	0.790	0.857	0.881

Panel B. Stability of landscape coefficients after exclusion of NDVI extremes

Predictor	Full model (n = 519)	NDVI-screened model (n = 505)	Absolute change (%)
Artificial surfaces	-0.0142	-0.0148	4.4
Forest cover	0.0163	0.0160	2.0
Wetlands	0.0238	0.0226	5.2
Water bodies	0.0248	0.0222	10.4
LAND_PC1	-0.0579	-0.0488	15.8

Q10 and Q90 denote the 10th and 90th percentiles, respectively. Potential NDVI extremes were identified using the $1.5 \times IQR$ criterion. Fourteen observations with $NDVI < 0.551$ were identified and excluded only for the sensitivity refit; all observations were retained in the primary analysis. Absolute change represents the proportional difference in coefficient magnitude between the full and NDVI-screened models.

Table S6. Response-scale effect contrasts and 95% confidence intervals for predictors in the final spatial beta-GAM.

Predictor	Contrast	Low	High	Δ HQ	95% CI
Artificial surfaces (%)	Q10–Q90	0.000	13.056	–0.043	–0.053, –0.032
Forest cover (%)	Q10–Q90	0.000	100.000	0.322	0.297, 0.347
Wetlands (%)	Absence–positive median	0.000	8.383	0.043	0.034, 0.051
Water bodies (%)	Absence–positive median	0.000	4.607	0.025	0.017, 0.033
LAND_PC1	Q10–Q90	–2.286	2.200	–0.058	–0.071, –0.045
Elevation (m)	Q10–Q90	141.983	1,055.543	0.052	0.015, 0.089
Slope (°)	Q10–Q90	2.651	24.900	0.005	–0.024, 0.034
NDVI	Q10–Q90	0.652	0.857	0.076	0.049, 0.104

Δ HQ represents the change in predicted habitat quality on the response scale between the specified predictor values, with all other predictors held at their median values. Continuous predictors were evaluated over their observed 10th–90th percentile (Q10–Q90) range. Because wetlands and water bodies were absent from most landscape units, their effects were evaluated from absence to the median among positive observations. Confidence intervals are 95% model-based intervals for the response-scale contrast. PLAND contrasts represent substitution of the agricultural reference class by the focal land-cover class.