Finding the Sweet Spot: Habitat Selection and Impervious Surface Thresholds in Urbanized Landscapes

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Abstract

Background: Urbanization affects species differently, with urban exploiters and urban adapters being better able to cope with urban environmental conditions. Yet, even urban exploiters and adapters require certain landscape features and may be subject to thresholds of urbanization beyond which they are no longer able to persist. Hedgehogs (*Erinaceus europaeus*) are considered urban adapters that can benefit from human-made structures and supplementary feeding, yet they remain sensitive to habitat fragmentation.

Aim: This study aimed to identify which landscape features are associated with hedgehog presence and whether a threshold of impervious surface exists beyond which habitat suitability declines.

Organisms: Hedgehogs (*Erinaceus europaeus*)

Place of research: The Netherlands

Methods: Analyses were conducted at two analytical levels; (1) across individual gardens in The Netherlands, and (2) across The Netherlands as a whole. At the garden level, hedgehog presence/absence data were obtained from camera traps. At the nationwide level, hedgehog presence data were obtained from camera traps and pseudo-absences were generated randomly across space. For both analytical levels, habitat characteristics were assessed at three spatial scales representing local, intermediate and landscape extents (100, 500, 1000 m). Land-use data were obtained from Landelijk Grondgebruiksbestand Nederland. Random forest and logistic regression analyses were used to identify key predictors of hedgehog occurrence.

Principal findings: Results from individual gardens indicated weak model fit and should therefore be interpreted carefully, while models based on the nationwide dataset showed strong fit, suggesting these results are more reliable. Hedgehog presence was consistently positively associated with grass in built-up areas across all spatial extents and at both analytical levels, suggesting a preference for moderately urbanized, suburban landscapes.

At the intermediate extent (500 m) agriculture was also positively associated with hedgehog presence, while forested areas were negatively associated. At the broader landscape extent (1000 m), urban built-up and construction in rural and agricultural areas were significant positive predictors. No impervious surface threshold was detected at the garden level; however, clear thresholds across all spatial scales were detected across all scales at the nationwide level (100 m: 26%; 500 m: 22%; 1000 m: 16%).

Conclusion: The results suggested that hedgehogs preferentially select heterogeneous landscapes characterized by an intermediate level of urbanization.

1. Introduction

Urbanization impacts biodiversity by favoring generalist species over specialists, resulting in ecological homogenization and a decline in species richness (Jokimäki et al., 2011). As the urban population continues to rise, with two thirds of the global population expected to live in urban areas by 2050, the pressure on natural habitats and associated wildlife will only intensify in the future (Collins et al., 2021; Lowry et al., 2013). While urban areas may offer different microclimates within short distances, with higher temperatures, increased food availability and shelter in comparison to rural areas (Newsome & Van Eeden, 2017; Rebele, 1994), they also pose threats such as habitat loss and fragmentation (Gomes et al, 2011). Depending on the species, urban areas can represent either relatively safe sites in which they can thrive, or ecological traps, environments where crucial resources are present but occupation leads to a fitness reduction (Zuñiga-Palacios et al., 2021). Urban exploiters, such as the brown rat (*Rattus norvegicus*), and feral pigeon (*Columba livia*) are strongly associated with high levels of urbanization and are dependent on human derived resources (Kark et al., 2007; Shochat et al., 2006; Blair, 1996). In contrast, urban adapters, such as red fox (*Vulpes vulpes*), and squirrels (*Sciurus* spp.), can tolerate moderate levels of urbanization and benefit from suburban landscapes with green spaces (Zuñiga-Palacios et al., 2021; Lowry et al., 2013; Kark et al., 2007; Ditchkoff et al., 2006).

As responses to habitat loss are mainly not linear, there may be thresholds of urbanization beyond which urban exploiters or adapters cannot persist, resulting in an abrupt decline of species occurrence (Graham et al., 2017; Betts et al., 2007). Additionally, the way that species react to urbanization is scale dependent, influenced by both local habitat features, such as gardens, lawns and parks, and broader landscape characteristics, such as locations of water bodies and railways (Sidemo-Holm et al., 2022; Moll et al., 2020; Jokimäki et al., 2011). However, few studies incorporate multi-scale approaches to ecological studies of habitat selection (McGarigal, Wan, et al., 2016), potentially overlooking scale-specific drivers of species occurrence.

An example of an urban adapter is the West European hedgehog (*Erinaceus europaeus*). Previous studies have underlined how this species is more frequently associated with urban settings rather than rural settings (Turner et al., 2022; Hubert et al., 2011; Driezen et al., 2007). Consistent with this, in the Netherlands they are mostly observed in parks and private gardens of urban areas. This preference is thought to be the result from a higher predation pressure in rural areas, caused by the presence of the Eurasian badger (*Meles meles*), making urban environments safer and more attractive (van de Poel et al., 2015). Nevertheless, highly urbanized areas have a higher level of fragmentation, disturbance, and traffic levels, which are barriers to hedgehog movements and potential life threats (Hof & Bright, 2010; Huijser, 2000; Rondinini & Doncaster, 2002). Because hedgehogs tend to avoid rural areas, but they are also sensitive to threats of urban settings, it may be that they preferentially select suburban areas, as they generally offer a higher abundance of green spaces and more corridors (Di Pietro et al., 2021; EBSCO, n.d.).

Based on these considerations, this study aimed to address the following research questions:

(1) How do different degrees of urbanization and land-use characteristics influence hedgehog habitat selection?
(2) How does impervious surface cover influence hedgehog presence across spatial scales, and are there thresholds?

Analyses were conducted at two analytical levels: (1) across individual gardens in The Netherlands, and (2) across The Netherlands as a whole and habitat characteristics were analyzed at three spatial scales representing local, intermediate, and landscape scales.

2. Research methods

2.1 Study area

The Netherlands has experienced a significant increase in urbanization since 1890, and by 2020, it ranked 13th globally, in terms of urban population percentage (Kooman, B., 2022). This rapid urban growth led to a high diversity of landscapes, from historical city centers to newly developed urban areas designed to accommodate a growing population (Pisarevskaya et al., 2022), resulting in habitat fragmentation and in an alteration of wildlife distribution (Van De Poel et al., 2015). With different degrees of urbanization, diverse urban layouts with urban and rural areas existing in close proximity, the Netherlands is an ideal setting for studying impacts of urbanization on hedgehog presence (CBS, n.d.; Statista, n.d.).

1.2 Study Species

Hedgehogs are small mammals which are widely distributed in Europe and are present from Italy to Scandinavia (Rasmussen et al., 2020). As an omnivorous generalists, they feed on a large variety of invertebrates (Rasmussen et al., 2019), and their presence is often associated with ecosystems health, making them important biotic indicators (Gomes et al., 2011). In urban environments they benefit from shelter, natural food availability and additional feeding, intentionally or unintentionally provided by humans (Rautio et al., 2016; Hubert et al., 2011; Hof & Bright, 2010). Nevertheless, habitat configuration is important for their presence, as individuals tend to establish in areas where vegetation is available. Proximity to parks, private gardens, green recreational spaces is an essential habitat feature(Van De Poel et al., 2015).

2.3 Data

2.3.1 Presence/absence data

I obtained hedgehog presence (n = 685) and absence (n = 366) data from 1051 unique locations across the Netherlands. These data were primarily obtained from Project Wildcamera, an ongoing wildlife monitoring initiative focused on gardens coordinated by Wageningen University that started in 2021 and is available at Agouti.eu. The dataset contains wildlife observation data from private and public gardens, across thirty-six different municipalities of the Netherlands. These municipalities vary in size and population, ranging from large cities such as Amsterdam (area:188.1 km^2 inhabitants: 931,298) and Den Haag (area: 82.44 km^2 inhabitants: 566,221) to smaller towns like Meppel (area: 55.50 km^2 inhabitants: 35,810) and Wageningen (area: 30.42 km^2 inhabitants: 42,579) (Brinkhoff, T., NA), offering different degrees of urbanization and structural layouts. Additionally, I placed another 50 camera traps in private gardens of nine additional municipalities across the Netherlands where hedgehogs have been previously observed by the owners. The cameras were installed pre-hibernation between September and October 2024 and collected between the end of January and the beginning of February 2025. The batteries were replaced with new charged ones every 6 to 8 weeks to ensure continuous data collection. The collected data were subsequently uploaded to the dataset of the Project Wildlifecamera.

Project Wildcamera specifically targets gardens suitable for wildlife. In this study, gardens were selected because hedgehog presence was confirmed in the past. While this approach facilitates data collection, it also introduces potential bias. Such gardens likely already represent suitable habitats for hedgehogs, thereby reducing the likelihood of detecting true absences in less optimal sites (Kolowski & Forrester, 2017). Moreover, absences recorded in these gardens cannot be considered true absences with absolute certainty as hedgehogs might have been present but undetected by the camera traps, increasing the risk of false absences. As the aim of my study was to assess how different degrees of urbanization influence hedgehog presence and distribution across urban areas in general, focusing solely on gardens could bias the results. Analyses were therefore conducted at two analytical levels: (1) across individual gardens in The Netherlands, and (2) across The Netherlands as a whole. In addition to analysing the collected presence-absence dataset to identify drivers of hedgehog presence across individual gardens, a random set of pseudo-absences (N=685) was generated across all terrestrial land-use types within The Netherlands, independent of the absence data from Project Wildcamera. Although nationwide hedgehog occurrence data are available from public repositories such as the Global Biodiversity Information Facility (GBIF, n.d.), these records are largely presence-only, spatially biased, and often include roadkill observations, complicating inference about habitat suitability (Beck et al., 2014). We therefore opted for a controlled presence–pseudo-absence approach based on camera-trap data, which allowed explicit assessment of absences and urbanization thresholds. I randomly sampled areas, using the spatSample function from the *terra* package (Barbet-Massin et al., 2012; Hijmans et al., 2025). Since a balanced dataset improves reliability and consistency in statistical models (Barbet-Massin, 2012), a 1:1 ratio was used (Hazel let al, 2021). This approach mitigates potential imbalances between presences and absences and reduces the impact of potentially false absences (Wisz & Guisan, 2009). By separately comparing presence with pseudo-absence data, the probability that observed patterns are due to random change is reduced (Wang et al., 2023). The final dataset used at the individual garden level (the garden dataset) contained true presences and recorded absences (N=685 vs. 366), acknowledging that some absences may be false due to imperfect detection. The final dataset used at the Netherlands level (the Netherlands dataset) contained true presences and pseudo-absences (N=685 vs. 685) (Fig.1). All data processing was conducted in R version 4.3.1 (R Core Team, 2023).

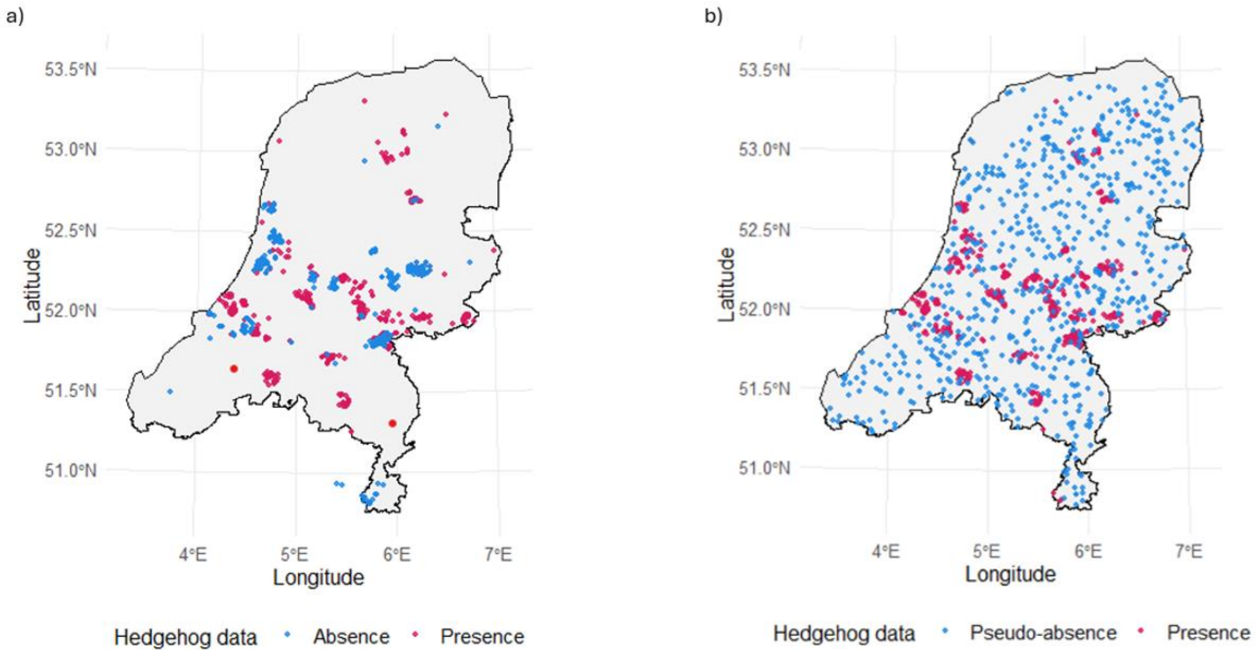

Figure 1: Spatial distribution of hedgehogs observed across the Netherlands. Panel (a) shows true presence and absences in gardens from camera trap data. Panel (b) shows true presences and randomly generated pseudo-absences across The Netherlands

2.3.2 Environmental data

Land-use data were obtained from Landelijk Grondgebruiksbestand Nederland (LGN [LGN, 2023]) to obtain information on land-use surrounding hedgehog presences and (pseudo-)absences. The LGN dataset has a spatial resolution of 5mx5m and contains 51 land-use variables (LNG, 2023, appendix A). To reduce the number of predictors and to avoid multicollinearity, variables having similar characteristics and presumed ecological relevance for hedgehogs were merged by summing the percentage cover of the original land-use classes within each buffer, preserving total proportional area of each aggregated habitat type. Once merged, the original variables were removed. Furthermore, to avoid zero-inflation and spurious relationships driven by land-use classes, only variables with a perceived ecological relevance were kept. Variables with more than 70% zeros were removed using the select() and where() functions from the *dplyr* package (Wickham et al., 2023). This threshold was applied to remove habitat types that were only sparsely represented in the study area to improve model stability. All the land-use variables of the Netherlands can be found in Appendix A while the final dataset with final variables for each buffer can be found in Appendix B.

2.3.3 Habitat selection at different analytical levels and spatial scales

Species tend to respond differently to environmental features based on the spatial scale. Habitat selection is driven by the presence of foraging locations at a fine scale and by dispersal and relocation at a landscape scale (D. W. Morris, 1992), therefore assessing habitat features across multiple scales helps detect habitat selection patterns (McGarigal, et al., 2016; Mayor et al., 2009). To do so, buffer zones of 100 m, 500 m, and 1000 m radii around each presence/ (pseudo-) absence location were created using the *terra* package (Hijmans et al., 2025) in R. These sizes were selected based on known hedgehog movement patterns: females typically have a home range of 1 km while males of 2 km (Reeve, 1994), making the selected scales ecologically meaningful despite the unknown sex of the individuals. Percentage values of each land-use category present within each buffer were then extracted and used for the data analyses.

2.3.4 Data analyses

I used logistic regression, using the glm() function from the *stats* package (R Core Team, 2023), to assess how land-use variables relate to hedgehog presence. Binary hedgehog presence /(pseudo-) absence was used as a response variable. To reduce the large number of predictors (Full list visible in Appendix B), I first applied a Random Forest model, (*randomForest* package; Liaw, A. & Wiener, M., 2002), to rank them by importance, reduce dimensionality and potentially remaining multicollinearity, and to detect potential non-linear relationships (Simon et al., 2023). Random forest model fit was evaluated using the AUC (Area Under Curve). To avoid overfitting, arbitrary selection, maintain methodological consistency across all buffer sizes and to avoid possible mistakes while selecting the variables, the ones scoring higher than the median in the mean decrease accuracy plot of the Random Forest were subsequently defined as key predictors in the logistic regression analysis. Before fitting the regression, multicollinearity was reduced by discarding variables with Variance Inflator Factor (VIF) > 5, calculated using the *car* package (Fox, J. & Weisberg, S., 2019). For ecologically important variables with VIF > 5, I ran different models retaining only one of them at a time, and the best model was selected using the lowest AIC. For each logistic regression, an optimized model was run to obtain an improved fit by minimizing AIC, and model performance was assessed using McFadden's R^2.

To identify a potential threshold of impervious surfaces influencing habitat selection of hedgehogs, I calculated the percentage of impervious surfaces for each location by merging different land-use variables (urban built-up, construction in rural areas, construction in agricultural areas, main infrastructure and railway, semi-paved roads). Hedgehog presence/(pseudo-)absence was used as the binary response variable, and impervious surface percentage was used as the predictor. A logistic regression model was then fitted to assess whether impervious surface significantly explained hedgehog presence, serving as the reference model for threshold comparison. Model fit was determined using McFadden's R^2. To test for potential non-linear responses, which may violate the linearity assumption of the logistic regression, a Generalized Additive Model (GAM) was fitted using the *mgcv* package (Wood, 2017), and the deviance explained was used to assess explanatory power.

To identify a potential threshold effect of impervious surface on hedgehog presence, a segmented regression model was fitted using the logistic regression model as the base model. This model estimated the breaking point (threshold) at which the relationship between impervious surfaces and hedgehog presence changes. Evidence for a statistically supported threshold was evaluate using the difference in Akaike Information Criterion (ΔAIC = AIC logistic – AIC segmented). Values higher than 2 were considered evidence in favor of the segmented model, while values below 2 indicated no meaningful improvement (Burnham & Anderson, 2004). The segmented regression was performed using the *segmented* package (Muggeo, 2008). To visualize the relationship between impervious surface percentage and hedgehog presence, the fitted regression model was plotted with 95% confidence intervals. Predicted probabilities and confidence intervals, extracted using the *stats* and *graphics* packages (R Core Team, 2023), were plotted against impervious surface percentage to visualize the response curve and the position of the estimated threshold. To further visualize the distribution of impervious surface percentages in relation to hedgehog presence and absence and density plots were produced using the *ggplot2* package (Wickham, 2016). The estimated threshold obtained from the segmented regression was shown as a vertical dashed line to visually assess how presence and absence were distributed relative to the threshold.

3.Results

3.1 Drivers of hedgehog presence in gardens

The random forest model to assess drivers of hedgehog presence in gardens had low predictive performance at each scale (table 1). Across all scales (100 m, 500 m, 1000 m) infrastructure, urban built-up areas, and grass in built-up or rural areas consistently ranked among the most important predictors. At the 100 m scale, the most influential predictors were those mentioned and the presence of fresh water. At the 500 m and 1000 m scale, deciduous forests and coniferous forests also became relevant, (table 1).

Logistic regression also had a weak-to-moderate model fit (table 1). Nevertheless, several predictors were statistically significant. The analysis revealed that grass in built-up areas had a strong statistically significant and positive effect on hedgehog presence across all buffer sizes (100 m: $z = 2.93$, $p = 0.034$; 500 m: $z = 2.95$, $p= 0.003$; 1000 m: $z = 3.75$, p =< 0.001). At the 500 m scale agriculture had a strong positive effect ($z = 3.20$, $p = 0.001$) while deciduous forest showed a mild negative effect ($z = -2.13$, $p = 0.033$) on hedgehog presence. At the 1000 m scale, deciduous forest had a strong negative effect ($z = -2.91$, $p = 0.004$) while grass in rural built-up areas in rural areas and grass in built-up areas had a strong positive effect ($z = 3.75$, p =< 0.001; $z = 3.08$, $p = 0.002$) on hedgehog presence.

3.2 Nationwide drivers of hedgehog presence

The random forest model to assess drivers of hedgehog presence throughout the Netherlands had an excellent predictive accuracy (table 1). Infrastructure, urban built-up and grass built-up constantly ranked among the most important predictors across all scales. At the 100 m scale, the most influential predictors were urban built-up, grass built-up, infrastructure and agriculture. At the 500 m and 1000 m scale, more predictors were relevant, including deciduous forests and fresh water.

Logistic regression also showed a strong model performance across all spatial scales (table 1). The analysis revealed that grass in built-up areas had a strong statistically significant and positive effect on hedgehog presence (100 m: z = 15.70, p = <0.001; 500 m: z = 10.95, p: <0.001; 1000 m: z = 6.75, p <0.001). At the 100 m scale, infrastructure showed strong positive effect (z = 7.12, p <0.001). At the 500 m scale, agriculture again showed a strong positive effect (z = 2.98, p = 0.002) while deciduous forest had a negative effect (z = -2.04, p = 0.041) on hedgehog presence. At the 1000 m scale, urban built-up and construction in rural and agricultural sites had positive effect (z = 6.48, p <0.001; z = 2.46, p = 0.014;).

Table 1: Results of the analysis of the relationship between hedgehog presence and land-use variables.

Dataset	**Scale**	**Top predictors (Random Forests)**	**RF model fit**	**Top predictors (Logistic regression)**	**LR model fit**
In gardens					
	100	Infrastructure Grass built-up Urban built-up Fresh Water	AUC=0.70	Grass built-up (z: 2.93, p: 0.0344)	AIC:1355.6 R^2: 0.007
	500	Infrastructure Grass dunes forests Fresh water Grass built-up Urban built-up Agriculture Coniferous forests Grass rural built-up Decidious forests	AUC=0.67	Grass built-up (z: 2.95, p: 0.00314) Agriculture (z:3.20, p: 0.00136) Decidious forests (z: -2.13, p: 0.03309)	AIC:1341.7 R^2:0.018

	1000	Shrub Coniferous forests Infrastructure Grass rural built-up Urban built-up Decidious forests Grass built-up Agriculture	AUC=0.59	Coniferous forests (z: -2.91, p: 0.00360) Grass rural built-up (z:3.75, p: <0.001) Grass built-up (z: 3.08, p: 0.00204)	AIC:1342.9 R^2:0.022
In the Netherlands	100	Agriculture Grass built-up Infrastructure Urban built-up	AUC=0.91	Grass built-up (z: 15.70, p: <0.001) Infrastructure (z: 7.12, p: <0.001)	AIC:1056.8 R^2:0.45
	500	Fresh water Decidious forest built-up Infrastructure Grass built-up Urban built-up	AUC=0.92	Grass built-up (z:10.95, p: <0.001) Agriculture (z: 2.98, p: 0.00292) Decidious forests (z: -2.04, p: 0.04127)	AIC:1073.4 R^2:0.44
	1000	Rural-agricultural construction Fresh water Infrastructure Decidious forest built-up Grass built-up Agriculture Urban built-up	AUC=0.93	Rural-agricultural construction (z: 6.48, p: <0.001) Urban built-up (z: 2.46, p: 0.014) Grass built-up (z: 6,75, p: <0.001)	AIC:1107 R^2:0.42

3.3 Impervious surface thresholds

Impervious surface was not a significant predictor determining hedgehog presence in gardens at any spatial scale in the logistic regression models. Model fit was weak (Table 2). The GAM models were also non-significant across all scales, with deviance explained consistently below 1%, providing no evidence for non-linear responses. Segmented regression analyses produced estimated breakpoints; however, there were no statistically supported ecological thresholds. Nevertheless, there generally was a consistent increase in the probability of hedgehog presence up till a point after which it declined (Fig. 2). There was a strong overlap between hedgehog presence and absence across the impervious surface gradient, indicating high uncertainty in predicting hedgehog occurrence (Fig. 3).

In contrast, impervious surface was a significant predictor of hedgehog presence in The Netherlands as a whole, at all spatial scales in the logistic regression models. Model fit was strong (Table 2). The GAM models provided evidence for the presence of non-linear responses and thresholds were detected. The segmented regressions were also significant across all scales, with a threshold of 26% at the 100 m scale, 22% at the 500 m scale and 16% at the 1000 m scale (Table 2 and Fig. 2). All ΔAIC values were higher than 2, indicating that models were supported. The probability of hedgehog presence consistently increased up till the estimated threshold and slightly decreased after it at the 100 m and 1000 m scale, and plateaued at the 500 m scale (Fig. 2). Hedgehogs were most often present at intermediate levels of impervious surface, peaking shortly after the estimated threshold, while pseudo-absences were concentrated at very low values, reflecting rural areas (Fig. 3).

It is important to note that, for both datasets, neither presence nor absence observations occurred at very high levels of impervious surface (Fig.3).

Table 2: Results of the statistical analysis on the relationship between hedgehog presence and a threshold of impervious surface.

Dataset	**Scale (m)**	**Logistic z**	**Logistic p**	**Logistic AIC**	**Model Fit (McFadden R^2)**	**GAM X^2**	**GAM p**	**Deviance explained (%)**	**Segmented AIC**	**Threshold (%)**
In gardens	100	-0.400	0.690	1362.5	<0.001	3.45	0.336	0.4	1362	24.7±7.8
	500	0.890	0.370	1361.8	0.001	4.05	0.159	0.45	1359.6	32.3±5.3
	1000	1.400	0.160	1360.7	0.001	4.74	0.147	0.4	1359.3	24.9±5.4
In the Netherlands	100	20.480	<0.001	1183.7	0.380	456.8	<2e-16	45.8	1069.8	26.0±0.015
	500	20.340	<2e-16	1124.7	0.410	442	<2e-16	45.7	1064.7	21.9±0.017
	1000	19.670	<2e-16	1163.9	0.390	459.6	<2e-16	41	1127.3	15.9±0.017

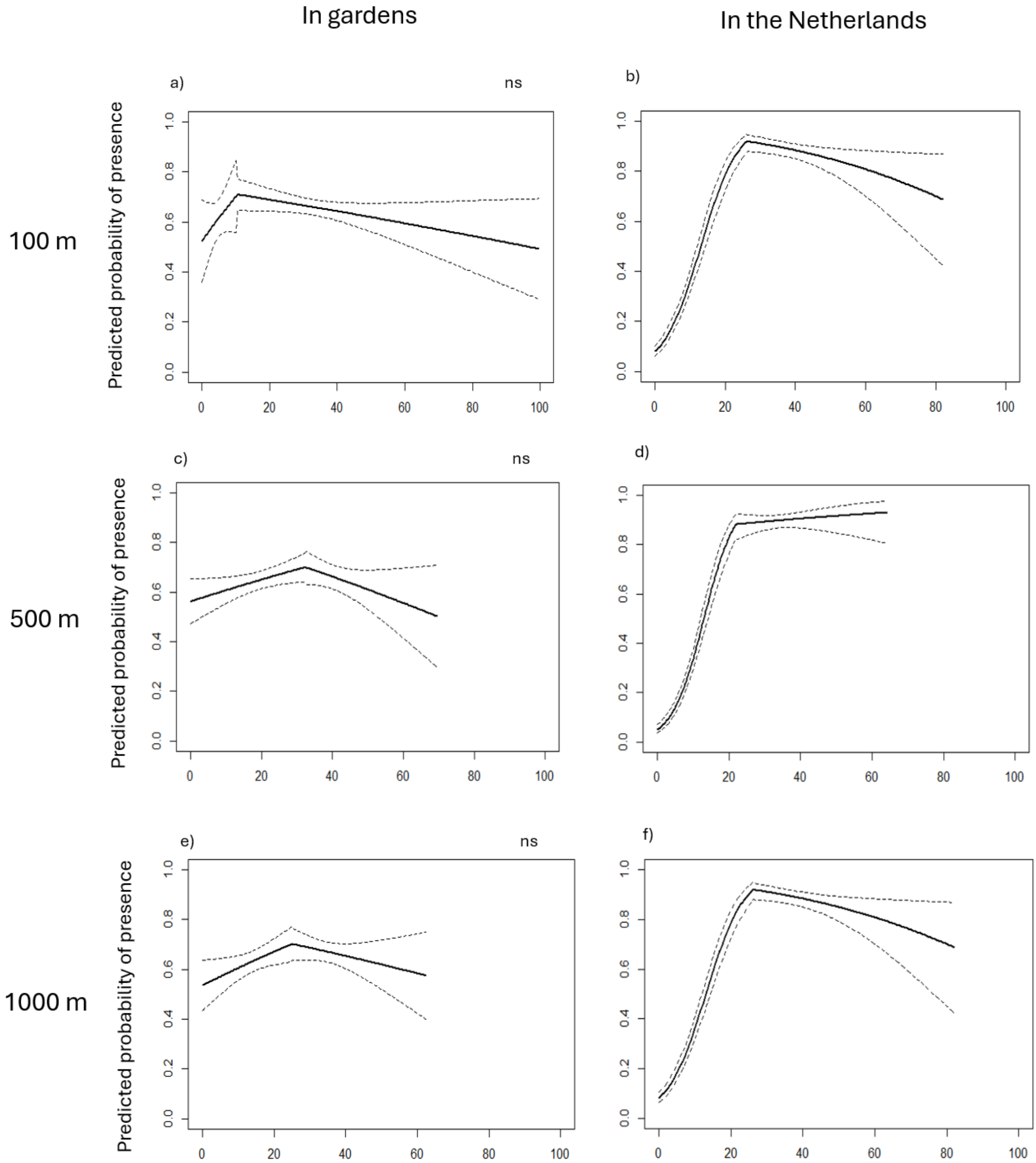

Figure 2: Visualization of the relationship between impervious surface and hedgehog presence through a response curve and the position of the estimated threshold. and Panels show results for the presence in gardens at the three spatial scales a)100m, c) 500m, e)1000 m and for the presence in the Netherlands at the three spatial scales b)100m, d) 500m, f)1000m

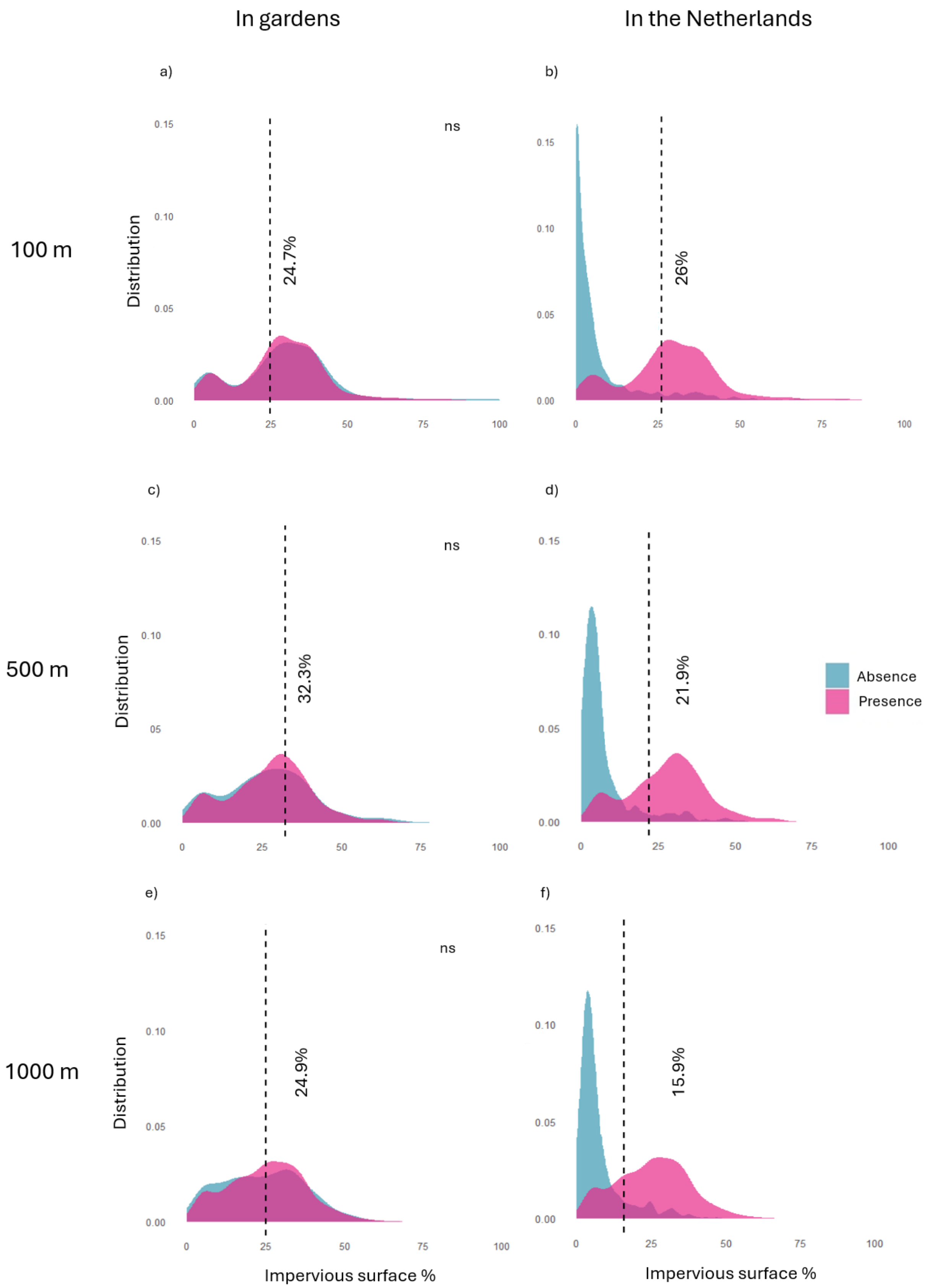

Figure 3: Density plots showing the distribution of hedgehog presence, expressed as probability density per unit of impervious surface percentage, and the corresponding threshold of impervious surface associated with hedgehog presence. Panels show results for the presence in gardens at the three spatial scales a)100m, c) 500m, e)1000 m and for the presence in the Netherlands at the three spatial scales b)100m, d) 500m, f)1000 m.

4. Discussion

Urbanization creates a heterogeneous landscape composed of a mosaic of infrastructure and green areas (Seress et al., 2014; Gomes et al., 2011; Rebele, 1994), to which species respond differently depending on their degree of urban tolerance (Callaghan et al., 2020). This study assessed how land-use variables and impervious surface influence hedgehog presence in The Netherlands. Presence data were derived from garden-based camera trap locations, representing hedgehog occurrences in gardens, while pseudo-absences were generated to characterize available environmental conditions in the Netherlands. Land-use variables and impervious surfaces were investigated at three different spatial scales (100 m, 500 m, 1000 m), to examine how landscape features and characteristics play a role in hedgehog habitat selection.

Models based on the garden dataset had weak explanatory power (McFadden R^2 <0.10), reflecting that these variables alone cannot reliably predict hedgehog presence. Nevertheless, they describe the immediate context of hedgehog locations, such as degree of urbanization and land use surrounding gardens. In contrast, models based on the Netherland dataset had strong explanatory power (McFadden R^2 >0.40), suggesting higher reliability in determining patterns of habitat selection. Therefore, the following discussion focuses primarily on the Netherlands dataset, while using the garden dataset to illustrate local context.

In the garden dataset, hedgehogs were consistently associated with grass in built-up areas across all scales, suggesting that they do not thrive in solely natural environments, but prefer urbanized landscape, possibly due to a lower probability of encountering badgers (Van De Poel et al., 2015), therefore establishing in gardens and lawns. The presence of agriculture at the 500 m scale, as well as forests and grass in rural areas at the 1000 m scale supports, and the absence of variables associated with highly urbanized areas, such as urban built-up, suggest that gardens were most often found in suburban areas, in proximity to rural landscapes. Suburban areas are generally human-dominated and characterized by a mosaic of low-density housing with a great presence of green areas, such as gardens, parks and tree-lined streets (EBSCO, n.d.). Such environments are common in smaller towns, excluding the main streets and in the periphery of large cities (Di Pietro et al., 2021). Previous studies have demonstrated how suburban areas often host the highest level of species richness (Di Pietro et al., 2021), and can provide suitable habitats for small wildlife (Mccleery et al., 2007; Kalinowski & Johnson, 2010; Parsons et al., 2018; Grade et al., 2022).

The Netherlands dataset provides insights into the broad scale habitat characteristics that influence hedgehog occurrence across the nation. Grass built-up remained the strongest predictor across all scales, highlighting the importance of lawns and small grassy patches that can be used as foraging areas and corridors. Hedgehogs have a generalist diet and in gardens they can forage both their natural preys (earthworms and beetles), as well as anthropogenic resources (pet food and human waste) while structures like sheds or specifically designed hedgehog houses and nesting boxes can provide shelter (Pettett et al., 2017b; Hof & Bright, 2010; Morris, 1985). People increasingly provide food to hedgehogs (Gimmel et al., 2021), resulting in a higher occupancy of hedgehogs in sites with supplementary feedings (Benjamin et al., 2025). For instance, a study by Hitchcock et al. (2025) reported that 77.5% of gardens with supplementary food were used by hedgehogs compared to 49.9% of gardens without supplementary food provision. At the 100 m scale, infrastructure was positively associated with hedgehog presence, reinforcing the theory that hedgehogs benefit suburban environments. At the 500m scale, agriculture had a positive effect on hedgehog presence, likely because nearby farmland enhances habitat heterogeneity, connectivity, and provides food resources. Arable soils are in fact rich in organic material content and contain high density of earthworms, an important food source for hedgehogs (Van De Poel et al., 2015). Nevertheless, hedgehogs tend to utilize filed margins and unfarmed grassy strips surrounding fields for both foraging and movement rather than venturing in the middle of fields (Hof et al., 2012;). This edge refuging behavior can be explained by the landscape of fear theory, which states that the way prey species use the landscape, in space and time, is driven by fear of their predators (Laundré et al., 2001). Badger avoidance has been proven to shape hedgehog movement patterns, (Huijser, 2000), therefore, avoiding such exposure in open areas means lowering predation pressure from badgers, who are often found in rural areas (Fung et al., 2024; Hof et al., 2012; Rosalino et al., 2008; Elmeros et al., 2005). Forests had a negative effect at the intermediate scale, potentially due to reduced garden density and increased predation risk. Since badgers prefer woodland and avoid human-dominated landscapes, suburban gardens may provide a safer environment for hedgehogs (Piza-Roca et al., 2018; Van De Poel et al., 2015; Hof & Bright, 2010). At the 1000 m scale, both urban built-up and construction in rural and agricultural areas had a positive effect, indicating that hedgehogs might benefit from a mixed urban-rural transition and not from homogeneous land cover. Such construction include farms, greenhouses, sheds and attached yards (LNG, 2023), which could provide access to shelter and anthropogenic food resources, as well as being perceived as safer due to badgers avoiding human presence (Lovell et al., 2022).

Overall, the results from both datasets consistently indicate that hedgehogs select moderately urbanized areas, or suburban areas, rather than forested areas or urbanized cores. Research underlined how hedgehogs are typically absent from highly urbanized environments, such as city centers, where green spaces are limited or fragmented, while they are often found living in low density suburban areas characterized by gardens and green areas (Reeve et al., 2024). At the local scale (100 m), habitat selection was driven by the presence of grass and infrastructure, while the presence of agricultural areas was important at the intermediate scale (500 m), and construction in rural areas at the landscape scale (1000 m), highlighting the importance of heterogeneous landscapes.

4.3 Impervious surface threshold

No thresholds of impervious surface were detected in gardens. In contrast, there were thresholds of impervious surface across the Dutch landscape. When about 16 to 26 % of the surface was impervious (depending on the scale of the study), hedgehog presence was the highest. Specifically, the threshold of impervious surface decreased with increasing spatial scale (26% at 100 m, 22% at 500 m and 16% at 1000 m). This pattern suggests that hedgehogs are sensitive to landscape features and may tolerate higher levels of impervious surface in their immediate surroundings but preferentially occur in areas surrounded by a lower level of impervious surface, and, potentially, a higher proportion of green spaces. This threshold is in agreement with a threshold of 31% found by Turner et al (2022b). It must be noted that the peak of hedgehog presence based on density plots does not exactly coincide with the threshold of impervious surface detected because the density plots reflect where the observations are more frequent, which is influenced by sampling locations and availability of landscape types, while the threshold is the rate of change of the habitat suitability along the gradient. However, the observed pattern supports the hypothesis that hedgehogs prefer an intermediate level of urbanization, often present in suburban areas. On the other hand, they tend to avoid highly urbanized and highly rural environments. Hedgehogs were especially less often present at lower levels of impervious surfaces, representing rural landscapes. This is in agreement with findings from others who report that rural areas tend to offer less suitable habitat due to e.g. the presence of badgers (Hof et al., 2012; Williams et al., 2018; Yarnell & Pettett, 2020). However, when the amount of impervious surface is higher than the estimated thresholds, hedgehog presence reduced gradually; a trend also observed for other small mammals (Broussin et al., 2024; Gomes et al., 2011). This suggests that there is an optimal ratio of the amount of green areas and buildings, which offers shelter and prey availability together with a lower predation pressure, (Hof & Bright, 2010; Hubert et al., 2011).

There likely also exists a threshold beyond which hedgehogs are not able to occur any longer. It was, however, not possible to detect such thresholds due to constraints regarding the placement of camera traps. It was for instance not possible to place camera traps in highly urbanized areas due to e.g. risk of theft. In fact, at very high levels of impervious surfaces there are neither presence nor absence of hedgehogs. This pattern might partially reflect Duch cities being designed to integrate numerous green spaces within urban and suburban environments. Research indicates that most suburban neighborhoods in Dutch cities contain approximately between 20% and 40% vegetation cover, while urban cores have less than 20% vegetation (Liu et al., 2025).

4.4 Management implications

Understanding how species adapt to urban ecosystems is essential for effective conservation strategies (Rebele, 1994). The results of this study suggest that hedgehogs can tolerate relatively high levels of impervious surface at a local scale, provided that surrounding landscapes at the intermediate and broader scales retain sufficient green space. Specifically, hedgehog occurrences remained possible at local impervious surface levels up to 26%, followed by a decline at the 500m (22%) and 1000m (16%) scales.

These findings indicate that hedgehogs may already benefit from more strategic spatial planning. Increasing green space across the entire city will no doubt benefit wildlife in general, but where such measures are not feasible, strategic spatial planning is likely to offer benefits as well. Small green areas, embedded with built-up environments, may function as steppingstones and corridors (Barthel et al., 2020). As a result, even in highly built-up neighborhoods, individual gardens or small green patches can still be considered suitable habitats and can support hedgehog presence if they are well connected to nearby green areas. Therefore, urban planners should prioritize landscape connectivity. Importantly, these findings indicate that individual gardens located in suburban areas, or even relatively urban settings, can still be suitable. Homeowners interested in supporting hedgehogs can enhance local habitat quality by managing garden features, such as shrub and hedges, overgrown grass, leaf litter, compost heaps and by enhancing garden connectivity through small openings in fences to facilitate movements (Cambridge Hedgehogs, 2025; Mccleery et al., 2007).

4.5 Limitations

During this study I encountered certain limitations. Using camera traps already posed its own limitations, as the university possesses a limited number of cameras, we could only place one or a maximum of two cameras per location. Using a limited number of cameras per location could also lead to false absences, where hedgehogs were indeed present but simply did not get close enough to the cameras to be recorded. Additionally, some malfunctioning was experienced, such as failure to set up correctly or batteries run off before expected. Furthermore, as previously mentioned, we could only place cameras in private gardens and in some public parks, but not in highly urbanized areas to avoid possible theft, resulting in highly urbanized areas being less represented in the dataset, possibly unbalancing the results. Due to time constraints, important data on vegetation type, garden connectivity, presence of pets, food availability, proximity to agricultural land, traffic and human population density were not collected, which could have made the study stronger.

5. Conclusion

The results suggest that species do not respond to urbanization as a simple rural-urban gradient. Instead, their responses are more complex, non-linear, and influenced by spatial scale and likely also by how species use their surrounding habitat. In urban environments, habitat suitability is therefore closely linked to landscape configuration rather than to larger scale urbanization intensity alone.

Moderate degrees of urbanization, typically represented by suburban areas, are often heterogeneous, consisting of a matrix of built-up and green areas that can still support wildlife. These findings suggest that it is not simply the amount of green present that makes an area “suitable”, but rather the degree of fragmentation and connectivity between green elements. This pattern is reflected in the scale-dependent sensitivity to impervious surface: tolerance is higher at the local scale but decreases at the intermediate and landscape scales.

Together, these results suggest that urban-adapted species like the hedgehog can persist in human-dominated landscapes when green areas are strategically arranged and well connected. Enhancing connectivity might therefore be more useful than increasing green cover alone. Overall, urban biodiversity conservation requires the integration of ecological knowledge into spatial planning and consideration of the landscape context.

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Appendix A: LGN categories

Table1. Overview of the LGN land-use variables present in the analysis

Variables	Code	Land-use
	1	Agricultural grass
Agriculture	2	Corn
	3	Potatoes
	4	Beets
	5	Cereals
	6	Other crop
	7	None
	8	Greenhouse/horticulture
	9	Orchard
	10	Flower bulbs
Nature/Forests	11	Decidious forests
	12	Coniferous forests
	13	Dry heat
	14	Open vegetated nature reserve
	15	Bare ground nature reserve
	16	Fresh water
	17	Salt water
	20	Deciduous forests in built-up area
	21	Coniferous forests in built-up area

	22	Forests in secondary built-up
Grass	23	Grass in primary built-up area
	28	Grass in secondary built-up area
	117	Grass in dunes and forests
Rural-agricultural construction	19	Construction in rural areas
	26	Construction in agricultural areas
Infrastructure	251	Main infrastructure and railway bodies
	252	Semi paved roads and slow traffic
Shrubs	253	Shrub vegetation in raised bog area
	323	Other shrub vegetation (low)
	333	Other shrub vegetation (high)
Impervious surfaces	18	Development in primary Built-up area
	251	Main infrastructure and railway
	258	Semi-paved roads

Table2. Overview of the LGN land-use variables merged due to similar characteristics

Merged variables	Code	Land-use

	1	Agricultural grass
Agriculture	2	Corn
	3	Potatoes
	4	Beets
	5	Cereals
	6	Other crop
	7	None
	8	Greenhouse/horticulture
	9	Orchard
	10	Flower bulbs
Forests	11	Decidious forests
	12	Coniferous forests
	20	Decidious forests in built-up area
	21	Coniferous forests in built-up area
	22	Forests in secondary built-up
Grass	23	Grass in primary built-up area
	28	Grass in secondary built-up area
	117	Grass in dunes and forests
Rural-agricultural construction	19	Construction in rural areas
	26	Construction in agricultural areas
Infrastructure	251	Main infrastructure and railway bodies
	252	Semi paved roads and slow traffic
Shrubs	253	Shrub vegetation in raised

		bog area
	323	Other shrub vegetation (low)
	333	Other shrub vegetation (high)
Impervious surfaces	18	Development in primary
		Built-up area
	251	Main infrastructure and railway
	258	Semi-paved roads

Appendix B: land-use variables for each buffer

Scale	In gardens	In the Netherlands
100	Urban built-up Fresh water Decidious forest built-up	Urban built-up Grass built-up Fresh water Agriculture
500	Agriculture Deciduous forests Coniferous forests Fresh water Urban built-up Deciduous forest built-up Rural-grass built -up Grass dunes forests Forests in secondary built-up	Fresh water Urban built-up Deciduous forests built-up Forests secondary built-up Other rural land-use Deciduous forests Coniferous forests Grass dunes forest
1000	Deciduous forests Coniferous forests Fresh water Deciduous forest built-up Forests secondary built-up Grass rural built-up Grass dunes forests	Deciduous forests Coniferous forests Fresh water Urban built-up Deciduous forests built-up Forest secondary built-up Grass rural built-up Grass dunes forests

Appendix C: use of AI

During my thesis I used AI, mostly copilot, ChatGPT and occasionally Perplexity, to help me during the data analysis process, to provide guidance, clarity on why I was doing specific passages, and to give me adequate codes. During the data analysis I used it to prep the dataset, brainstorming on the information I had and how to create the dataset fit for my study. I used it also for statistical tests and plots. Additionally, once I obtained my results, I used it to get additional clarity on the meaning of such outcomes. When writing, I also made use of AI. Sometimes, when some articles were difficult to understand I would ask if my interpretation was correct, but only when I was really confused, not as a default method. Furthermore, I sometimes asked to provide bullet points on how to structure passages of my report in a clear way and asked for feedback and grammar check on passages I wrote. A few times I asked to provide articles supporting my results, when I had difficulties finding some using google scholar. I find it important to clarify that I have never asked AI to read and summarize such articles for me, anytime it would provide an article I would read it myself to check if it was pertinent or not. Basically, during the writing part of my thesis, I used it as a "very smart friend", asking things I would have asked my friends, as a second opinion and perspective can always help. Additionally, I used Grammarly for plagiarism check.

I also would like to add that I started my thesis before the new policy on the chats 'link, therefore not all of them are present here. Initially, I mostly used copilot, which unfortunately does not provide links. After the policy, I relied more on chat GTP as it provides them.

https://chatgpt.com/c/690db729-4bd8-8333-8ba9-ae9bf488130a

https://chatgpt.com/c/6937e7ca-3dc0-832b-a4ce-4eda0dc91924

https://chatgpt.com/c/6926b757-af5c-8332-b069-b8604b127cbc

https://chatgpt.com/c/69230f9e-2a84-832b-a2e9-e485fbb34d1f

https://chatgpt.com/c/67bca568-79c8-8009-9278-8dc6d0d2b803

https://chatgpt.com/c/67c350f3-90e0-8009-8030-d3cd74cd97d2

https://chatgpt.com/c/67c1d2ef-b10c-8009-8bab-813769444dcc

https://chatgpt.com/c/67ecf596-3c40-8009-a6dd-08d546fd6c5c

https://chatgpt.com/c/67bc3fd4-3734-8009-a739-520d86b7a483

https://chatgpt.com/c/67cab3a4-ac9c-8009-ae12-d219941d4b46

https://chatgpt.com/c/67d2ecfb-8014-8009-ae04-6c0d79777a11 https://chatgpt.com/c/67c0444d-b160-8009-9006-73464d76aac6

https://chatgpt.com/c/67bc3e0c-fec8-8009-9157-d177b006fb19

https://chatgpt.com/c/67ee4a1f-7fbc-8009-b4d8-bc22e10d4ca3

https://chatgpt.com/c/67caad30-e1dc-8009-866b-602f553c9e12

https://chatgpt.com/c/67d2d5b2-b71c-8009-8dce-a4aa478cad9c