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Evaluating connectivity metrics for biodiversity conservation

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Abstract

Habitat fragmentation threatens biodiversity by disrupting ecological connectivity. To support conservation planning, we evaluate which spatial connectivity metrics best predict species occurrence. We do so by comparing six common connectivity metrics as predictors of occurrence patterns of three red-listed species in the Dutch River Area. Our results show that simple metrics, and particularly total habitat area, outperform more complex metrics like graph-based indices. Notably, woody linear elements such as hedgerows, which are central to current Dutch policies aiming for 10% 'green-blue connectivity', show no consistent effect. These findings suggest that conservation efforts should likely prioritize increasing habitat area, while reconsidering connectivity metrics that show limited ecological effect.

Keywords: Biodiversity conservation, habitat connectivity, cost-effectiveness

JEL Codes: C21, Q24, Q57, R14

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1 Introduction

Habitat loss due to land use change is a major driver of biodiversity decline (Jaureguiberry et al., 2022), especially in densely populated and highly modified landscapes such as the Netherlands. The independent effect of fragmentation remains contested, with theory offering contrasting predictions (Fahrig, 2017; Fletcher Jr et al., 2018; Fahrig et al., 2019). Some studies suggest strong negative effects, while others suggest minimal or even positive impacts. Despite this uncertainty, conservation practice often prioritizes connectivity to counteract presumed negative effects of fragmentation (Haddad et al., 2015; Grashof-Bokdam and van Langevelde, 2005). This focus has led to widespread use of spatial connectivity metrics in ecological planning and monitoring. Still, there is little evidence that these metrics reliably support conservation outcomes.

Some connectivity metrics are proposed based on models, theoretical arguments, or desirable mathematical properties, aiming to capture key aspects of landscape structure and species movement (e.g. Saura and Pascual-Hortal, 2007; Visconti and Elkin, 2009). Empirical studies, however, often use only one or a few metrics in a case study, sometimes without clear justification or consideration of alternatives (Awade et al., 2012; Pereira et al., 2011). As a result, the choice of metric is frequently driven by convention or data availability rather than empirical validation. What is lacking is a systematic comparison of these metrics in real-world settings, where their practical usefulness can be assessed. Such comparisons are essential for conservation planning, as connectivity metrics increasingly inform spatial prioritization and policy decisions under tight resource constraints.

While this is a land-use and conservation planning topic with deep roots in landscape ecology, it has important economic dimensions. Connectivity interventions compete for scarce resources, and their design involves trade-offs between ecological effectiveness, spatial constraints, and implementation costs. Economic methods can help evaluate which interventions deliver the greatest biodiversity benefits per unit of investment. This perspective is increasingly relevant as conservation budgets tighten and spatial policies in countries like the Netherlands aim to integrate ecological goals with land use planning. By combining ecological indicators with regression-based analysis of effectiveness and cost, this study contributes to a growing body of interdisciplinary work at the interface of ecology and economics (Polasky et al., 2001; Lewis and Plantinga, 2007). It also speaks directly to the economics literature on conservation incentives, such as payment-for-ecosystem-services schemes, auction-based conservation contract design, and agri-environmental measures with spatial targeting such as ‘agglomeration bonuses’ (Cason and Gangadharan, 2004; Wätzold and Drechsler, 2005;

Lundberg et al., 2018; Duke et al., 2023). Integrating the most effective connectivity metric (as we aim to identify in this paper) into these economic instruments can improve both ecological outcomes and reduce costs.

In this paper, we assess the empirical usefulness of six common connectivity metrics by comparing their ability to predict species occurrence for three red-listed species in the Dutch River Area. The metrics include both simple measures such as total habitat area, and more complex indicators such as graph-based indices and least-cost distances. Special attention is paid to woody linear elements, such as hedgerows and tree lines, that feature prominently in Dutch conservation policy as part of the national target for 10% green-blue connectivity. The selected species have different mobility and habitat requirements: *Anguis fragilis* (slow worm), *Aricia agestis* (brown argus butterfly), and *Triturus cristatus* (great crested newt). We use a cross-section of 1×1 km grid cells to combine spatial species occurrence data with GIS-based connectivity metrics. To estimate the predictive value of each metric, we regress both negative binomial and linear regression models on our data. In these models we vary the specification by including or excluding control variables, using full or reduced sets of connectivity metrics, and applying transformations to the dependent variable (species occurrence counts).

Unlike most studies that test one connectivity metric at a time (e.g. Magle et al., 2009), or focus on spatial correlations across species (e.g. Prima et al., 2024), we run a single model where six metrics compete head-to-head. We repeat the exercise for three red-listed species with contrasting dispersal ranges. We then translate the surviving coefficients into cost-effectiveness ratios to compare connectivity metrics, providing direct input for Dutch conservation policy.

Our results show that adding habitat area wins on both statistical power and cost-effectiveness. More generally, simpler metrics appear to outperform more complex alternatives in explaining species occurrence. Surprisingly, this result holds for all three species, despite their differing habitat requirements. The density of woody linear elements showed no clear effect, calling into question its policy prominence. To address possible endogeneity, we also estimated instrumental variables specifications, using historical fragmentation patterns as an instrument for current woody elements. This analysis, together with several robustness checks, yields results consistent with our main findings. Overall, our results indicate that current connectivity targets may need refinement, with greater emphasis on measures that demonstrably benefit biodiversity.

The remainder of this paper is structured as follows. Section 2 gives background information on habitat fragmentation, resulting biodiversity loss, and different perspectives on connectivity. Section 3 outlines the study area, species data, the construction of connectivity metrics, and the empirical strategy. Section 4 presents the results, while Section 5 concludes.

2 Background

Habitat fragmentation—the breaking apart of once-continuous habitat into smaller, isolated patches—has long been recognized as a key driver of species decline and local extinction (Wilcox and Murphy, 1985). Fragmentation can reduce patch size, increase edge effects, and impede dispersal, thereby lowering population viability and genetic diversity (Fischer and Lindenmayer, 2007). Empirical work shows that at least 70% of the world's remaining forests now lie within 1 km of a human-modified edge (Haddad et al., 2015), underscoring the global scope of the problem.

The ecological consequences of fragmentation have sparked debate (Hadley and Betts, 2016; Wilson et al., 2016). Early theory predicted monotonic species loss proportional to area reduction (the "random-sample" hypothesis). More recent models emphasize non-linear responses, proposing critical thresholds below which dispersal is insufficient to rescue local populations (Mönkkönen and Reunanen, 1999). Part of the uncertainty in the literature stems from a failure to distinguish habitat loss from fragmentation (Hadley and Betts, 2016; Fahrig, 2017; Fletcher Jr et al., 2018; Fahrig et al., 2019). This uncertainty motivates robust, data-driven tests of fragmentation effects in real landscapes.

Recent studies on fragmentation in the Netherlands remain limited, but available data illustrate its scale. About 54% of the country (2.2 M ha) is agricultural, 13% (0.5 M ha) built-up, and 34% natural or open water, including 360 kha of forest, 37 kha of heath, and 19 kha of wetlands (CBS, 2025). Major natural areas, such as the Veluwe, Oostvaardersplassen, IJsselmeer, and Waddenzee, form 21 national parks (>1000 ha each) that serve as core patches of the Dutch Nature Network. Yet, only 6% of forest lies within parks, and over 28% occurs in fragments <10 ha, which are unlikely to sustain biodiversity when isolated. Fragmentation impacts vary by taxon: 100% of reptiles and 75% of amphibians face threats, versus 35% of butterflies and 30% of birds (Bergers and Kalkhoven, 1996).

Fragmentation involves not just how much habitat is lost, but also how well the remaining patches are linked. This highlights the importance of connectivity, which the literature recognizes as a key strategy for counteracting fragmentation effects (Luque et al., 2012; Rösch et al., 2013; Belote et al., 2022). Connectivity describes the degree to which a landscape facilitates the movement of species and the flow of ecological processes (Tischendorf and Fahrig, 2000). Two complementary notions are widely used. *Structural connectivity* refers to the physical arrangement of habitat in space, e.g. patch size, distance, and the presence of corridors. *Functional connectivity* additionally incorporates species-specific behavior and matrix permeability, linking landscape structure to actual movement probabilities (Keeley et al., 2021). Because functional data are often scarce, conservation planning typically relies on structural metrics computed from land-cover maps (Saura and Pascual-Hortal, 2007).

Structural connectivity depends on several interrelated factors. The distance between habitat patches is fundamental: shorter gaps ease movement, reduce barrier encounters, and promote gene flow. Physical obstacles such as roads, urban areas, and rivers, further impede dispersal by lowering permeability and increasing mortality (e.g., vehicle collisions), while dense urban centres isolate patches and restrict movement. Continuous habitat strips or "corridors," such as hedgerows, provide safe passages through otherwise inhospitable landscapes, making their identification and protection essential for maintaining connectivity. By quantifying these aspects with structural connectivity metrics, planners can assess how well habitat patches and corridors form an interconnected network; information critical for designing reserves that deliver effective conservation (Tischendorf and Fahrig, 2000).[1]

More recently, concepts from the literature on graph theory have been incorporated into the connectivity debate. This network-based approach treats habitat patches as nodes and potential dispersal pathways as edges to capture both patch attributes and spatial configuration (Kindlmann and Burel, 2008; Rayfield et al., 2011). The difference of this approach is that it moves beyond local or pairwise measures, such as nearest-neighbor distance or corridor width, to quantify how each patch contributes to overall network integrity and species movement potential. By accounting for the entire web of connections, graph-based metrics can identify critical hubs and bottlenecks whose protection or restoration yields disproportionate gains in landscape connectivity. Relevant network measures include node degree, betweenness centrality, and the clustering coefficient (e.g. Keeley et al., 2021).

No single metric captures all facets of connectivity (Kindlmann and Burel, 2008). Distance measures are intuitive but ignore patch area; graph indices integrate multiple components but require arbitrary threshold choices. Simulation studies show that metric performance is highly

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[1] The SLOSS debate (one large reserve or several small ones) directly engages fragmentation and connectivity. Multiple small reserves only succeed if well connected, otherwise isolated patches become fragmentation-driven sinks. The SLOSS literature (e.g. Ovaskainen, 2002; Groeneveld, 2005) highlights contrasting trade-offs between maximizing species richness and ensuring metapopulation persistence via recolonization and risk spreading.

landscape- and species-specific (Driscoll et al., 2013). Empirical head-to-head comparisons remain rare, and published results are mixed (Fischer and Lindenmayer, 2007; Belote et al., 2022). A systematic evaluation across taxa and metric types is therefore essential to guide metric selection in applied planning.

3 Method

In this section we describe how we operationalize six connectivity metrics for the Dutch River Area and link them to species occurrence data in a regression analysis.

3.1 Metrics selection

Building on the discussion of connectivity in the previous section, we selected six complementary metrics representing different aspects of connectivity. A given landscape configuration can be well-connected for one species but poorly connected for another, so using a variety of metrics ensures a robust assessment across different scales and assumptions (Fagan and Calabrese, 2006). Table 1 provides an overview of the six selected connectivity metrics.

We include two metrics that quantify structural connectivity using only the physical layout of habitat. *Distance_EUC* measures the Euclidean distance to the nearest patch, offering a simple measure of spatial proximity (Moilanen and Hanski, 2001). Related, *Distance_LC* measures the least-cost distance to the nearest patch. In a human-dominated landscape like the Netherlands, where roads, urban areas, and agricultural fields create uneven barriers, *Distance_LC* is essential to capture resistance to species movement (Moilanen and Nieminen, 2002; Adriaensen et al., 2003). Jointly, these metrics address whether species can physically reach nearby habitats, a key concern in fragmented systems where isolation drives local extinction (Hanski, 1999).

The next two metrics focus on habitat availability, addressing the habitat amount hypothesis (Fahrig, 2003). *Area_HABITAT* measures the area of suitable habitat within a grid cell (Cormont et al., 2016), quantifying the total resource base for populations. Related, *Area_ELEMENTS* measures the area of woody linear elements (Verboom and Van Apeldoorn, 1990), quantifying the role of fine-scale features like hedgerows. This last metric is particularly relevant given the Netherlands' policy targets for 10% green-blue connectivity, which explicitly prioritizes linear landscape elements.

The final two metrics are derived from graph theory, moving beyond patch-level analysis to evaluate system-wide connectivity. *Graph_IIC* integrates patch size and spatial configura-

Table 1: Connectivity metrics with description.

Metric	Classification	Description
Distance_EUC	Structural connectivity	Euclidean distance to nearest patch
Distance_LC	idem	Least-cost distance to nearest patch
Area_HABITAT	Habitat availability	Total habitat area
Area_ELEMENTS	idem	Total habitat in woody elements
Graph_IIC	System-wide connectivity	Integral index of connectivity
Graph_PC	idem	Probability of connectivity

tion, identifying hubs critical for maintaining metapopulations (Pascual-Hortal and Saura, 2006). Conversely, *Graph_PC* adds a chance component by weighting connections based on dispersal probability (Saura and Pascual-Hortal, 2007). These metrics are more advanced than distance- or habitat-based metrics and the literature suggests that these graph metrics provide stronger explanatory power in many settings.

3.2 Species selection

We focus our analysis on three species occurring in the Dutch River Area. The slow worm (*A. fragilis*) is a small, secretive lizard with relatively limited dispersal range, often confined to structurally connected ground cover and hedgerows; typical movements are under 100 meters. The brown argus butterfly (*A. agestis*) is a short-range butterfly specialized on calcareous grasslands, capable of dispersing among habitat patches over hundreds of meters. The great crested newt (*T. cristatus*) is a pond-breeding amphibian that migrates between aquatic and terrestrial habitats with moderate dispersal ability, typically moving 100-500 meters between ponds. These differences mean that the importance and scale of connectivity may vary by species, allowing us to evaluate metric robustness across mobility gradients.

These species were selected based on four criteria. The first criterion is conservation status. All three are listed as threatened or protected species (Red List or equivalent), indicating conservation concern and policy relevance for the Netherlands. The second criterion is taxonomic and ecological breadth, which allows us to examine whether connectivity metrics perform consistently across varied life histories. The chosen species represent three distinct taxonomic groups (a reptile, an invertebrate, and an amphibian) covering different ecological niches. The third criterion is differing mobility and habitat requirements. Each species has unique dispersal capabilities and habitat preferences, which provides a rigorous test of the metrics under contrasting ecological conditions. The fourth criterion is data availability in the study area. All three species have sufficiently rich occurrence data in the Dutch River Area to support analysis.

In summary, selecting these three species enables a cross-species comparison of connectivity metrics. If a given metric consistently correlates with occurrence for a reptile, an invertebrate, and an amphibian alike, it would suggest that the metric captures a generally useful aspect of landscape connectivity. On the other hand, species-specific differences in metric performance could reveal how species-specific characteristics mediate the relationship between landscape connectivity and species occurrence (Crooks and Sanjayan, 2006).

3.3 Data

We assembled spatial datasets for the Dutch River Area, the core river delta of the Netherlands where the Rhine, Waal and Meuse form floodplains, wetlands and semi-natural landscapes. The region is ecologically valuable but faces serious connectivity challenges caused by dense urbanization and intensive agriculture. Focusing on this small, coherent landscape reduces confounding geographic and policy variability.

We obtained geo-referenced raw occurrence data for *A. fragilis*, *T. cristatus*, and *A. agestis* from the Dutch National Database of Flora and Fauna (NDFF).[2] This includes all verified observations of the three species within the study area over the period 2019-2024, see Figure 1. NDFF compiles spatial data on species from a variety of sources including citizen scientists, research institutions, and environmental consultancy reports. The data is aggregated in square kilometer grid data.[3] This scale, combined with the relatively small dispersal distances of our three selected species, means that spatial spillovers are only a minor concern in our analysis. To minimize bias from annual variability (e.g., climate fluctuations, changes in sampling effort), data from all five years have been aggregated into a single occurrence value per 1×1 km grid cell, ensuring a stable representation of habitat use. Over this relatively short period, we assume that habitat connectivity has remained largely unchanged.

We computed connectivity metrics using the Basisregistratie Grootschalige Topografie (BGT),[4] a high-resolution topographic database maintained by the Dutch government. The database provides detailed vector data on a wide range of physical and constructed features in the Netherlands, including roads, buildings, waterways, green spaces, and other geographic entities. The database is structured with standardized, geo-referenced objects, enabling pre-

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[2] This database can be accessed via https://ndff.nl/.

[3] The selected species are all listed on the Red List. Exact locations within each grid are not disclosed to avoid potential disturbance.

[4] This database, as well as the BRO database introduced below, can be accessed via https://www.pdok.nl/.

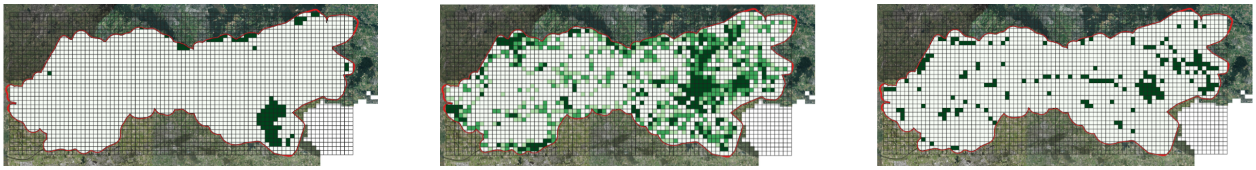
(a) *A. fragilis* (b) *A. agestis* (c) *T. cristatus*

Figure 1: Occurrence of the three species.

cise and consistent spatial analysis across regions. For this study, the BGT allows detailed analysis of landscape elements that influence habitat quality, land use, and fragmentation.

To control for confounding factors affecting species occurrence, four variables are included: soil type, nitrogen deposition, and two land-cover controls: water share and urban share. These improve internal validity by accounting for environmental and human influences. Soil data comes from the Basisregistratie Ondergrond (BRO), which provides detailed information on texture, lime content, and depth profiles. This variable includes four categories: clay, sand, peat, and other. Nitrogen deposition data (in mol N/ha per year) are obtained from RIVM (2021). Water and urban shares, based on BGT data, measure the share of water bodies and built-up area per cell.

To construct the instrument for our instrumental variable (IV) analysis, we use a digitized topographic map from 1950 that provides information on historical landscape fragmentation prior to large-scale land consolidation, combined with spatial data on the timing of land-consolidation projects.[5] Together, these datasets allow us to capture variation in historical parcel structure and subsequent consolidation timing at a fine spatial scale, forming the basis for our interaction-based (Bartik-style) instrument.

3.4 Variable construction

The NDFF 1×1 km grid cells with occurrence data for the target species are used as the basis for the analysis. The BRO and BGT data as well as the nitrogen map have been converted to align with this grid. Spatial analysis was done using a combination of QGIS, R, and Conefor Sensinode (Saura and Torné, 2009).

A habitat suitability layer was created by merging all BGT land-use polygons classified as forest, heathland, natural grassland, and designated natural areas. These land-cover types are broadly suitable for at least one of the three target species and are commonly associated

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[5] These maps are available from the Netherlands' Cadastre via https://www.topotijdreis.nl/ and https://nationaalgeoregister.nl/.

with semi-natural habitat structures in the Netherlands. While each species has specific ecological requirements, the merged layer provides an estimate of potentially suitable and connected habitat across the landscape.

The combined habitat layer was rasterized at 10-meter resolution, resulting in a binary raster where all suitable features—both area-based and buffered linear elements—were coded as 1 (habitat), and all other areas as 0 (non-habitat). To delineate discrete habitat units, the raster was clumped using an 8-cell neighborhood rule, grouping contiguous habitat cells into unique patches. This approach ensures that ecologically connected areas are treated as single patches, regardless of their shape or complexity.

Distance_EUC was computed by sampling 50 random points from each grid cell and subsequently calculating Euclidean distance to the nearest habitat patch edge, which is often located in an adjacent grid cell. The computation of *Distance_LC* followed a similar procedure (replacing Euclidean distance by least-cost distance). For computational reasons, the distance was based on each grid cell's centroid only. To determine the 'least cost' in *Distance_LC*, BGT land use data were reclassified into a resistance surface. Resistance values were assigned to each land use type based on its relative permeability to species movement: lower values indicate high permeability (e.g., forest), and higher values reflect greater resistance (e.g., urban areas). Following Adriaensen et al. (2003), we adopt a relative resistance scale of forest/nature (1), grassland (5), water bodies (10), agricultural land (20), and urban area (100), which (like most least-cost studies) spans two orders of magnitude to ensure clear separation among cover types. After reclassification, the BGT vector data were converted to a raster format with a spatial resolution of 10×10 meters and used as input to calculate least-cost paths.

Area_HABITAT was computed by aggregating all intersected areas of habitat patches based on the land-use raster. For *Area_ELEMENTS* the aggregation was over linear landscape elements, buffered by 6 meters to account for their ecological influence. *Graph_IIC* was computed in Conefor Sensinode using a binary habitat patch network. Patches were considered connected if they lay within 500 m Euclidean distance of each other. This threshold reflects both species-specific dispersal limits and values commonly used in the literature. Finally, *Graph_PC* was computed by incorporating least-cost distances and a negative exponential decay function, which reflects the declining probability of dispersal with increasing resistance.

The instrumental variable is constructed in two steps. First, we measure historical land fragmentation in 1950 as the total perimeter of land parcels within each 1×1 km grid cell.

Meaningful parcel structures were isolated and counted using a sequence of steps: raster sieving, vectorization, polygon creation, filtering on size, and geometric cleaning. Second, we combine this pre-consolidation fragmentation measure with spatial data on the timing of land consolidation projects. The interaction between these two (standardized) variables forms a Bartik-style instrument that captures spatial heterogeneity in exposure to consolidation: highly fragmented areas that were consolidated earlier experienced the strongest loss of woody elements, whereas later-consolidated areas retained more of their historical landscape structure. The resulting measure is expected to be correlated with the current extent of woody linear elements, since historically fragmented landscapes were enclosed by hedgerows, ditches, or tree lines marking parcel boundaries, many of which were removed during early consolidation.

All connectivity metrics were standardized to have zero mean and unit SD to allow comparability. This ensures that estimated effects reflect relative importance rather than raw unit differences and improves numerical stability during model fitting.

Our cross-sectional dataset has 1,933 observations with data on three counts of species occurrence, six connectivity metrics, the instrument, and four control variables. There are few missing observations for two control variables (nitrogen deposition and water share), and since consolidation has not occurred in all areas, the instrument also has missing observations. Summary statistics are shown in Table 2. For occurrence, the data is heavily skewed with many zeroes, as illustrated by Figure 1. All (non-standardized) connectivity metrics are strongly right-skewed. This means most observations cluster at low values, with a long tail of higher values. The skew is especially pronounced for *Graph_IIC* and *Area_ELEMENTS*, suggesting extreme sparsity of high values for these (non-standardized) connectivity metrics in most of the landscape.

Pairwise correlations among the six standardized connectivity metrics are all below $|r| = 0.50$, indicating no severe multicollinearity. The strongest association is the negative relationship between *Distance_EUC* and *Area_HABITAT* ($r = -0.47$), reflecting that cells with more habitat nearby tend to lie closer to other patches. Both distance metrics correlate moderately ($r = 0.40$), as expected since they measure different aspects of isolation. Similarly, the two graph-based indices correlate at $r = 0.40$. All other pairwise r-values fall between -0.30 and $+0.10$. Variance inflation factors for all six metrics are below 2, further confirming low collinearity. Together, these results suggest each metric captures a distinct facet of connectivity and may safely be entered together in multi-variable models without undue multicollinearity.

Table 2: Summary statistics

Variable	Mean	SD	Min	Max	N
A. fragilis (count)	0.38	3.87	0	111	1933
A. agestis (count)	3.37	12.73	0	223	1933
T. cristatus (count)	0.81	6.11	0	122	1933
Distance_EUC (standardized)	0	1	−1.02	4.76	1933
Distance_LC (standardized)	0	1	−0.90	10.16	1933
Area_HABITAT (standardized)	0	1	−0.58	4.29	1933
Area_ELEMENTS (standardized)	0	1	−0.54	10.32	1933
Graph_IIC (standardized)	0	1	−0.21	8.92	1933
Graph_PC (standardized)	0	1	−0.39	3.37	1933
Bartik-style instrument	−0.06	0.98	−4.70	4.21	1554
Nitrogen (mol N/ha per year)	1554.72	245.93	1067.37	2752.25	1920
Water share (proportion)	0.11	0.14	0.00	0.95	1883
Urban share (proportion)	0.12	0.17	0.00	0.89	1933
Soil type (categorical)	4 categories: clay, sand, peat, other				

3.5 Empirical strategy

Our empirical strategy is to quantitatively assess how the different connectivity metrics relate to species occurrence, while addressing potential biases in inference. We model the occurrence of each species as a function of connectivity, controlling for other relevant factors. In practice, for each species we conduct a grid-level analysis: each grid cell is a data point with an occurrence count and with predictor variables including the connectivity metrics. We fit a series of regression models on our cross-sectional data, where the main independent variables are the connectivity metrics for each grid cell.

The regression equation takes the following form:

$$F(Y_i) = \beta_0 + \sum_{k=1}^{6} \beta_k \cdot \text{Metric}_{ki} + \sum_{j=1}^{3} \gamma_j \cdot \text{Control}_{ji} + \varepsilon_i$$

where Y_i denotes species occurrence in grid cell i, Metric_{ki} is a vector of $k = 6$ connectivity metrics, Control_{ji} is a vector of $j = 4$ control variables, and ϵ_i is the error term.

In three models we use the identity function $F(Y_i) = Y_i$, modeling the untransformed occurrence data. These model versions differ in which connectivity metrics and control variables are included: all, no controls, or LASSO-based selection of connectivity metrics. LASSO regression helps to select non-redundant predictors with a penalty parameter that shrinks less informative connectivity metrics to zero, effectively addressing multicollinearity while improving model interpretability. The penalty parameter was chosen via 10-fold cross-validation and further optimized to retain the two strongest predictors for each species.[6] In estimating the regression equation for these models, we use a negative binomial (NB) model to account for over-dispersion in the count data, where the variance exceeds the mean. Poisson models assume equal mean and variance, which is violated in our case. NB relaxes this assumption by introducing a dispersion parameter, making it better suited for ecological count data with high variability across grid cells.

In one model we use $F(Y_i) = \text{arcsinh}(Y_i)$. The inverse hyperbolic sine (arcsinh) transformation of the dependent variable is used to handle zeros while preserving interpretability. Species occurrence is count-based and, depending on the species, includes many grid cells with zero values, as Figure 1 illustrates. Unlike the logarithm, arcsinh is defined at zero and behaves similarly to the log for large values. This makes it suitable for skewed data that include zeros, without requiring arbitrary shifts or data exclusion. Since we use $\text{arcsinh}(Y_i)$ as the response variable, we are not modeling counts directly. Instead, this results in a transformed linear model, which we estimate using linear regression (OLS).

In a final model, we use $F(Y_i) = \mathbf{1}(Y_i > 0)$. That is, we transform the occurrence data to a binary variable where '1' indicates any level of species occurrence. This approach serves to correct for a possible bias in our count data. When a species is observed multiple times at a location, nature enthusiasts may concentrate their efforts there, inflating local counts. A presence/absence model can therefore be a useful simplification. We estimate this model using OLS, which allows for straightforward interpretation of the coefficients.

In all models, we used robust standard errors, which correct for heteroskedasticity and remain valid when error variance is not constant.

Comparing across models, our aim is to identify which connectivity metrics best explain species occurrence. Rather than selecting a single model based solely on goodness of fit, we compare models across the six metrics to evaluate which ones show the strongest and most consistent associations with species occurrence. This approach helps reveal generalizable patterns rather than species- or model-specific outcomes.

To interpret the association between connectivity and species occurrence causally, we

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[6] We depart from standard LASSO selection rules to improve interpretability. In our dataset, using the one-standard-error rule selects no connectivity metrics for two of the three species, whereas the minimum-error solution retains either five or all six metrics. Neither extreme is very informative for our purposes. To strike a compromise, we fit the full LASSO path on the six connectivity metrics and then choose the smallest penalty parameter at which exactly two coefficients remain non-zero. Those two selected connectivity metrics are then included alongside our control variables in a negative binomial regression.

assume that, conditional on other covariates, the connectivity metrics are exogenous. That is, unobserved factors affecting occurrence are uncorrelated with the connectivity metrics once we control for habitat characteristics such as soil type and urbanization. This identifying assumption is strong, since habitat configuration is not randomly assigned and omitted environmental factors could still influence both connectivity and species occurrence.

To probe this concern, we complement our baseline regressions with IV regressions. We treat the current extent of woody linear elements (hedgerows, boundaries, riparian strips) as endogenous and use historical landscape fragmentation in 1950 as an instrument. Specifically, we instrument *Area_ELEMENTS* using an interaction-based (Bartik-style) variable that combines (i) pre-consolidation landscape fragmentation in 1950, measured as total parcel perimeter, with (ii) the timing of postwar land consolidation projects. After World War II (especially between the 1950s and early 1970s) the Netherlands undertook massive land consolidation programs that reshaped the rural landscape. The instrument exploits the fact that fragmented landscapes were targeted first and restructured most intensively during consolidation, leading to large-scale hedgerow removal and field enlargement. Consequently, areas with high historical fragmentation that were consolidated early experienced the strongest loss of woody elements, while later-consolidated areas retained more of their historical structure.

Identification relies on two conditions. First, relevance: historical fragmentation interacted with consolidation timing strongly predicts current woody element density (first-stage $F = 12.43$). Second, exclusion: conditional on soil, nitrogen deposition, and land-cover controls, the timing of consolidation affects current species occurrence only through its effect on woody elements. This assumption is plausible because consolidation timing was primarily determined by administrative, logistical, and economic factors (e.g., farm parcel size, drainage modernization) rather than local ecological conditions. Moreover, the long temporal gap and limited creation of new hedgerows reduce risks of reverse causality. While no historical instrument can fully rule out omitted spatial or land-management effects, the mechanism linking consolidation to present woody elements is well-documented, and the exclusion restriction is supported by the institutional history of Dutch land consolidation. To our knowledge, this application of consolidation history in an instrumental variable analysis is novel in the context of species occurrence and landscape connectivity research.

In addition, we apply three robustness checks that do not rely on instrumental variables. First, we estimate interaction models including the product of woody linear elements and urban share to test whether effects differ across more anthropogenic landscapes. Second, we perform a jack-knife analysis by omitting one connectivity metric at a time to assess whether results depend on the inclusion of any specific metric. Third, we re-estimate the model on a restricted subsample excluding grid cells without habitat, ensuring that results are not driven by zero observations. Together, these checks show that the main findings are not sensitive to sample composition or model specification.

We do not model spatial spillovers explicitly, as the dispersal distances of all three focal species are well below the 1 km size of our grid cells. This makes ecological dependence across cells unlikely and supports the assumption of independent observations. Finally, we interpret consistency of results across species and models as an additional form of robustness: if a connectivity metric shows strong associations with occurrence in multiple species with different ecological traits across different models, it is more likely to reflect a genuine underlying effect.

4 Results

4.1 Regression results

For each of the three species, we estimate five models. As explained in Section 3.5, three of these are NB models using $F(Y_i) = Y_i$, featuring different combinations of connectivity metrics and control variables. The fourth and fifth model are OLS models using transformations of the dependent variable: respectively $F(Y_i) = \text{arcsinh}(Y_i)$ and $F(Y_i) = \mathbf{1}(Y_i > 0)$.

Regression results are shown in Tables 3–5. Across all three species and five model specifications, *Area_HABITAT* consistently shows a strong and statistically significant positive association with species occurrence. The size and significance of the coefficients are remarkably stable, whether the dependent variable is treated as a count, arcsinh-transformed, or binary. While some variation exists in the performance of other metrics, such as *Graph_PC* which is important for *A. fragilis* but less so for the other species, no other metric matches the consistency or magnitude of the habitat area effect. This repeated pattern across species with differing habitat requirements suggests a general ecological relationship rather than a species-specific artifact.

Since every metric is standardized, the coefficients are directly comparable in magnitude. Across all three species and every specification, *Area_HABITAT* is one of the strongest predictors and remains statistically significant in every model. It ranks consistently among the first three in the count models (except model 2 for *A. fragilis*) and exceeds all other metrics in the arcsinh-transformed and binary specifications. That stability and relative size confirm that habitat area is consistently at least as important as (and often more important than) any other metric.

Table 3: Regression results for *A. fragilis* occurrence

	A. fragilis occurrence				
	Count			Arcsinh	Binary
	negative binomial			*OLS*	*OLS*
	(1)	(2)	(3)	(4)	(5)
Distance_EUC	-3.80^{***}	-2.90^{***}		-0.01	-0.01^{*}
	(1.01)	(0.59)		(0.01)	(0.004)
Distance_LC	-1.85^{***}	-0.83^{***}		0.0002	-0.001
	(0.40)	(0.29)		(0.01)	(0.004)
Area_HABITAT	0.31^{*}	0.15	0.73^{***}	0.12^{***}	0.04^{***}
	(0.17)	(0.16)	(0.15)	(0.02)	(0.01)
Area_ELEMENTS	-0.28^{*}	-0.16		-0.02^{**}	-0.01^{*}
	(0.17)	(0.15)		(0.01)	(0.004)
Graph_IIC	-0.01	-0.01		0.01	0.0000
	(0.11)	(0.08)		(0.01)	(0.01)
Graph_PC	0.52^{***}	0.48^{***}	0.73^{***}	0.04^{**}	0.03^{***}
	(0.13)	(0.17)	(0.19)	(0.02)	(0.01)
Controls	–	✓	✓	✓	✓
Observations	1,933	1,883	1,883	1,883	1,883
R^2				0.25	0.23
Adjusted R^2				0.25	0.22
Log Likelihood	-489.22	-380.44	-400.36		
Akaike Inf. Crit.	992.43	786.87	818.71		
Note:	*p<0.1; **p<0.05; ***p<0.01				

This result is especially clear in the LASSO regressions, where *Area_HABITAT* is the only metric selected across all three species. The remaining metrics show less consistent predictive value and are often dropped as the penalty increases. In every case, *Graph_IIC* is the first metric to be excluded, suggesting it contributes the least to explaining species occurrence despite its theoretical advantages. Figure 2 illustrates these coefficient paths.

To assess the size of the relationship between *Area_HABITAT* and species occurrence, we interpret its estimated coefficients for Model 4. We do not use Models 1–3 for this interpretation given their count-based specifications which may be inflated due to over-dispersion. To illustrate, in Model 3 (negative binomial with LASSO-selected metrics), the coefficients on *Area_HABITAT* imply that a one SD increase in habitat area corresponds to expected

Table 4: Regression results for *A. agestis* occurrence

	A. agestis occurrence				
	Count			Arcsinh	Binary
		negative binomial		*OLS*	*OLS*
	(1)	(2)	(3)	(4)	(5)
Distance_EUC	-0.52^{***}	-0.44^{***}		-0.08^{***}	-0.04^{**}
	(0.09)	(0.12)		(0.03)	(0.01)
Distance_LC	0.52^{***}	0.14	-0.06	0.02	-0.001
	(0.07)	(0.09)	(0.08)	(0.04)	(0.02)
Area_HABITAT	0.41^{***}	0.48^{***}	0.54^{***}	0.34^{***}	0.12^{***}
	(0.06)	(0.06)	(0.06)	(0.04)	(0.01)
Area_ELEMENTS	-0.06	-0.09		-0.01	-0.01
	(0.07)	(0.08)		(0.02)	(0.01)
Graph_IIC	0.10	0.12		0.04	0.02
	(0.07)	(0.08)		(0.03)	(0.01)
Graph_PC	-0.06	0.003		0.06^{*}	0.04^{***}
	(0.06)	(0.07)		(0.03)	(0.01)
Controls	–	✓	✓	✓	✓
Observations	1,933	1,883	1,883	1,883	1,883
R^2				0.16	0.14
Adjusted R^2				0.15	0.14
Log Likelihood	-3,364.03	-3,284.23	-3,300.99		
Akaike Inf. Crit.	6,742.05	6,594.46	6,619.98		
Note:	*p<0.1; **p<0.05; ***p<0.01				

count increases of 108%, 72%, and 175%. Model 4 reduces the influence of skewness and zeros in the dependent variable by applying an arcsinh transformation, yielding more conservative estimates. The coefficients can be approximately back-transformed to the original count scale. Using mean counts in grid cells where the species is present (around 8–9 individuals per species), a one SD increase in habitat area corresponds to an increase of approximately 1.1 individuals for *A. fragilis*, 3.4 for *A. agestis*, and 1.3 for *T. cristatus*, or relative increases of roughly 13%, 41%, and 15%, respectively.[7] Taken together, these estimates show that the effect of habitat area is not only statistically robust but also large in magnitude.

A surprising finding is that *Area_ELEMENTS*, representing the area of woody linear

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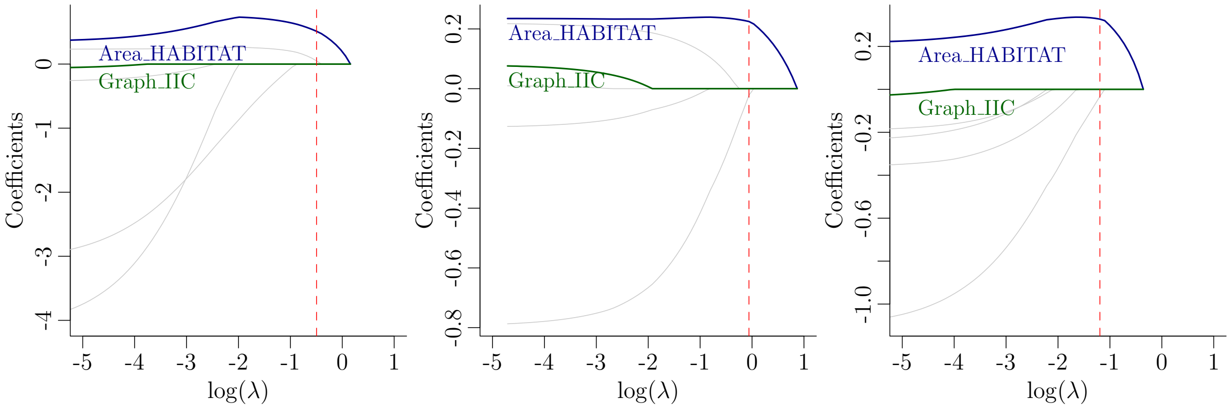
[7] The estimated coefficients on *Area_HABITAT* in Model 5 yield even lower percentages (4%, 12%, and 6%), but note that this model (with binary transformation of the dependent variable) estimates effects on the extensive margin (presence/absence), while the other models capture effects on species occurrence.

Table 5: Regression results for *T. cristatus* occurrence

	T. cristatus occurrence				
		Count		Arcsinh	Binary
		negative binomial		*OLS*	*OLS*
	(1)	(2)	(3)	(4)	(5)
Distance_EUC	−0.96***	−1.14***	−0.91***	−0.05***	−0.02**
	(0.22)	(0.28)	(0.20)	(0.01)	(0.01)
Distance_LC	0.27	−0.08		−0.05***	−0.03***
	(0.17)	(0.24)		(0.02)	(0.01)
Area_HABITAT	0.47***	0.90***	1.01***	0.14***	0.06***
	(0.12)	(0.14)	(0.12)	(0.03)	(0.01)
Area_ELEMENTS	−0.33*	−0.56***		−0.02	−0.004
	(0.17)	(0.15)		(0.01)	(0.01)
Graph_IIC	−0.08	0.01		0.005	0.002
	(0.09)	(0.10)		(0.01)	(0.01)
Graph_PC	−0.25	−0.26		−0.03*	−0.01*
	(0.19)	(0.18)		(0.02)	(0.01)
Controls	–	✓	✓	✓	✓
Observations	1,933	1,883	1,883	1,883	1,883
R^2				0.07	0.07
Adjusted R^2				0.06	0.07
Log Likelihood	-1,045.53	-1,029.99	-1,035.58		
Akaike Inf. Crit.	2,105.06	2,085.98	2,089.17		
Note:	*p<0.1; **p<0.05; ***p<0.01				

elements such as hedgerows, shows a consistently negative and often significant association with species occurrence across all models and species. This is counter to the expectation that such elements support dispersal or provide habitat structure. The negative sign may reflect correlation with other landscape features that are less suitable for the focal species, such as intensive agricultural edges or fragmented land use. It may also suggest that not all structural connectivity contributes positively to species occurrence, underscoring the importance of distinguishing between connectivity quantity and ecological function. These possibilities motivate a closer examination of the robustness and potential endogeneity of this variable, which we address next using an interaction model and IV regressions.



(a) *A. fragilis* (b) *A. agestis* (c) *T. cristatus*

Figure 2: LASSO coefficient paths for the three species. Solid blue line is *Area_HABITAT*, dashed green line is *Graph_IIC*. Other connectivity metrics are gray. Dashed red line is the selected λ.

4.2 Robustness of the *Area_ELEMENTS* effect

The possibly negative association between woody linear elements and species occurrence may depend on surrounding land use. To explore this mechanism, we add an interaction between *Area_ELEMENTS* and *Urban share* to Model 4. Since Model 4 (OLS with arcsinh-transformed outcome) is linear, it serves as the reference model for all robustness checks, including the IV estimation reported below.

Table A1 in the appendix shows that the interaction term is negative for all species and statistically significant for *A. fragilis*, suggesting that the negative effect of woody linear elements is strongest in more urbanized areas. For *A. agestis* and *T. cristatus*, the interaction is also negative but not significant. Across all three species, we find no indication that woody linear elements provide stronger habitat value in anthropogenic landscapes.

To test whether this pattern reflects causality or unobserved spatial factors, we further explore potential endogeneity in the relationship between woody linear elements and species occurrence using IV estimation. In this analysis, we treat the extent of woody linear elements today as endogenous and instrument it using a Bartik-style variable that combines historical landscape fragmentation in 1950 (measured as total parcel perimeter) with the timing of land consolidation. The IV results, reported in Tables A2–A3, qualify the earlier finding of a negative relationship between woody linear elements and species occurrence. In the baseline OLS models, only *A. fragilis* showed a significant negative association, while the effects for the other two species were small and insignificant. The IV analysis provides little evidence that any negative association between woody linear elements and species occurrence is causal.

The instrument is relevant, with a robust first-stage F-statistic of 12.43. The negative first-stage coefficient can be explained by the combined effect of consolidation timing and fragmentation. In an interaction model, we find positive main effects and a negative interaction term, suggesting that early consolidation erased much of the historical hedgerow structure in fragmented landscapes, while later consolidation allowed more of it to persist. In the second stage, coefficients are imprecisely estimated and not statistically different from zero for any of the three species. The Wu–Hausman tests fail to reject the null hypothesis of exogeneity of the hedgerow variable ($p \approx 0.7$), indicating that OLS and IV estimates do not differ significantly. The relatively large standard errors in the IV models reflect the limited identifying variation once historical and spatial controls are included.

Overall, the results suggest that the apparent negative effect of woody linear elements in OLS is weak and not robust to correction for potential endogeneity. We find no consistent evidence that woody elements either promote or hinder species occurrence in this landscape, indicating that their ecological role in this landscape may be more context-dependent than previously assumed. As with any historical instrument, however, the exclusion restriction cannot be verified directly, so these results should be interpreted with caution.

4.3 Robustness of the *Area_HABITAT* effect

To assess the robustness of our results, in particular the effect of the most consistently important predictor, *Area_HABITAT*, we conduct a jack-knife analysis on Model 4 by iteratively omitting each of the six connectivity metrics and re-estimating the model. This procedure tests whether the estimated effect of *Area_HABITAT* depends on the inclusion of specific connectivity measures. The results show stable coefficients: across all species, the *Area_HABITAT* estimates vary only slightly when individual metrics are excluded, and the model fit remains virtually unchanged. This confirms that the relationship between habitat area and species occurrence is robust to model specification and not driven by any single connectivity metric.

Like the other connectivity metrics, *Area_HABITAT* is highly skewed, with many grid cells containing little or no habitat. To test whether our results are driven primarily by the contrast between zero and non-zero habitat area, we re-estimate all models on a restricted sample containing only grid cells with strictly positive (non-zero) raw habitat area. This ensures that the estimated effects reflect variation in habitat quantity rather than mere presence or absence. Regression results on this subset (1,046 observations compared to 1,883 for model 4 in the full sample, see Table A4 in the appendix) are largely consistent with the main analysis. Coefficient estimates for *Area_ELEMENTS* keep the same sign and significance, although slightly smaller in size. This suggests that the main findings are not driven by zero-habitat grid cells and hold across areas with at least some habitat present. Jack-knife estimates remain stable under this restricted sample, further supporting the robustness of the habitat effect across non-zero conditions.

4.4 Cost-effectiveness

To better interpret the policy relevance of our results, we compare the cost-effectiveness of the most consistently predictive metric, *Area_HABITAT*, to its next-best alternative based on the regression results, *Distance_EUC*. This comparison focuses on estimated biological gains relative to the hectares of additional habitat required for a one-SD change in connectivity metric. Note that this comparison treats both connectivity metrics in isolation. In reality, there is of course a combined effect where investments in habitat area will also reduce distances and vice versa. This interdependence does not affect the relative cost-effectiveness.

Recall from Section 4.1 that in Model 4 (OLS with an arcsinh-transformed outcome), a one-SD increase in *Area_HABITAT* corresponds to an increase of 1.1 individuals for *A. fragilis*, 3.4 for *A. agestis*, and 1.3 for *T. cristatus*. For *Distance_EUC*, the corresponding gains are substantially smaller: roughly -0.1, -0.7, and -0.5 individuals, respectively. The negative signs are expected, as greater distance reduces species occurrence. In what follows we will compare increases in *Area_HABITAT* with decreases in *Distance_EUC*.

The smaller ecological changes from decreases in *Distance_EUC* come at a higher cost compared to increases in *Area_HABITAT*. To determine these costs, we compute how many hectares of additional habitat patch correspond to a one-SD change in the connectivity metric for both *Area_HABITAT* and *Distance_EUC*. Since these metrics were standardized, we first translate a one-SD increase back to its real-world equivalent. Based on the unstandardized summary statistics, the SD of *Area_HABITAT* is approximately 20 hectares and the SD of *Distance_EUC* is approximately 400 meters.

Reducing *Distance_EUC* by one SD (roughly 400 meters) likely requires the addition of strategically placed habitat patches that bridge gaps between existing ones. We use a simple linear regression to estimate how much habitat area is typically associated with a 400-meter reduction in *Distance_EUC*. Specifically, we regress the raw Euclidean distance to the nearest patch ($Distance\_EUC\_raw_i$) on the raw habitat area in the same grid cell

($\mathit{Area\_HABITAT\_raw}_i$):

$$\mathit{Distance\_EUC\_raw}_i = \alpha + \beta \cdot \mathit{Area\_HABITAT\_raw}_i + \varepsilon_i.$$

The estimated coefficient $\hat{\beta} = -0.00094$ indicates the change in distance per square meter of added habitat. Inverting this relationship, we compute the habitat area required to achieve a one-SD reduction in *Distance_EUC*. The result suggests that an average increase of approximately 43 hectares is needed to lower *Distance_EUC* by 400 meters.

This result illustrates the spatial inefficiency of targeting isolation directly: it requires far more habitat expansion than a one-SD increase in *Area_HABITAT* (20 hectares) and offers smaller gains in species occurrence. To make this comparison of costs and benefits specific, we combine both factors in a relative ratio for each species. This ratio compares benefits relative to costs of investing in *Area_HABITAT* compared to *Distance_EUC*. Using the numbers derived above, this ratio equals $\left(\frac{1.1}{20}\right) / \left(\frac{0.1}{43}\right) \approx 24$ for *A. fragilis* $\left(\frac{3.4}{20}\right) / \left(\frac{0.7}{43}\right) \approx 10$ for *A. agestis* and $\left(\frac{1.3}{20}\right) / \left(\frac{0.5}{43}\right) \approx 6$ for *T. cristatus*.[8] Investing in connectivity by reducing distances to habitat patches yields much lower ecological returns per euro spent compared to habitat area expansion. Our analysis does not imply that habitat expansion is cheap. It does imply, however, that among available options, it appears to offer the highest biological return on investment among the metrics we evaluate.

5 Conclusion

Habitat fragmentation is a key driver of biodiversity loss. Connectivity is often proposed as a solution, but the effectiveness of different metrics remains uncertain. This paper compares six connectivity metrics across three threatened species in the Dutch River Area. One metric, *Area_HABITAT*, consistently performs best. It is the most robust predictor of species occurrence across models and species. Other metrics—based on distances, woody linear elements, or graph-theoretic measures—show limited or inconsistent explanatory power. This suggests that, within our study area, increasing habitat area is a more reliable strategy for improving species presence.

Our study is intentionally narrow in scope: three species, six connectivity metrics, and

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[8] Since we compute relative benefit/cost ratios, there is no need to make assumptions on actual restoration/conservation costs as in e.g. Groeneveld (2005), Naidoo et al. (2006), or Armsworth et al. (2018). The implicit assumption is that these costs are equal for the two measures. This is a generous assumption for *Distance_EUC*, which is more demanding in terms of location and hence is likely to be more expensive.

one landscape. This design allows for a clear, controlled comparison and avoids the noise of adding poorly documented species or heterogeneous settings. While this necessarily limits generalizability, the consistent dominance of habitat area across such different species and metrics suggests that the main conclusion is not driven by case selection. Methodologically, the paper introduces an instrumental variable approach to mitigate endogeneity concerns in connectivity measures, a technique rarely used in this field.

We also assess cost-effectiveness by estimating the habitat area needed to shift each metric by one standard deviation and evaluating the associated biological gains. $Area\_HABITAT$ offers the highest return on investment, requiring less area to achieve greater effects. These findings have direct implications for Dutch nature policy, which currently emphasizes ecological networks and structural corridors. Our results suggest that, at least in this landscape, expanding habitat area may be a more cost-effective focus. When conservation resources are limited, directing them toward measures with the clearest ecological benefits is likely to yield better outcomes.

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Appendix: Additional tables

Table A1: Robustness check (interaction effect) for species occurrence

	Arcsinh-transformed occurrence (model 4)		
	A. fragilis OLS	*A. agestis* OLS	*T. cristatus* OLS
Distance_EUC	-0.01	-0.09^{***}	-0.05^{***}
	(0.01)	(0.03)	(0.01)
Distance_LC	-0.002	0.02	-0.05^{***}
	(0.01)	(0.04)	(0.02)
Area_HABITAT	0.12^{***}	0.33^{***}	0.14^{***}
	(0.02)	(0.04)	(0.03)
Area_ELEMENTS	-0.01	0.01	-0.01
	(0.01)	(0.03)	(0.02)
Graph_IIC	0.01	0.04	0.005
	(0.01)	(0.03)	(0.01)
Graph_PC	0.04^{**}	0.06^{*}	-0.03^{*}
	(0.02)	(0.03)	(0.02)
Area_ELEMENTS × *Urban share*	-0.15^{**}	-0.23	-0.02
	(0.07)	(0.21)	(0.07)
Controls	✓	✓	✓
Observations	1,883	1,883	1,883
R^2	0.25	0.16	0.07
Adjusted R^2	0.25	0.15	0.06
Note:	*p<0.1; **p<0.05; ***p<0.01		

Table A2: Instrumental variables results: first stage

	DV: *Area_ELEMENTS*
Bartik-style instrument	-0.07^{***}
	(0.02)
First-stage F (robust, IV only)	12.43
Observations	1,548
R^2	0.13
Note:	*p<0.1; **p<0.05; ***p<0.01

Table A3: Instrumental variables results: second stage

	Arcsinh-transformed occurrence (model 4)		
	A. fragilis OLS	*A. agestis* OLS	*T. cristatus* OLS
Distance_EUC	-0.04	-0.13	-0.01
	(0.04)	(0.15)	(0.08)
Distance_LC	-0.004	0.01	-0.04^{*}
	(0.01)	(0.05)	(0.02)
Area_HABITAT	0.01	0.47^{***}	0.22^{***}
	(0.02)	(0.06)	(0.05)
Area_ELEMENTS	-0.10	-0.22	0.06
	(0.12)	(0.39)	(0.22)
Graph_IIC	-0.01	0.04	0.02
	(0.01)	(0.06)	(0.03)
Graph_PC	0.02	0.21^{***}	0.02
	(0.01)	(0.05)	(0.03)
Controls	✓	✓	✓
Observations	1,548	1,548	1,548
R^2	-0.14	0.18	0.07
Note:	*p<0.1; **p<0.05; ***p<0.01		

Table A4: Robustness check (non-zero habitat) for species occurrence

	Arcsinh-transformed occurrence (model 4)		
	A. fragilis OLS	*A. agestis* OLS	*T. cristatus* OLS
Distance_EUC	0.004	-0.34^{**}	-0.18^{*}
	(0.05)	(0.15)	(0.10)
Distance_LC	-0.003	-0.01	-0.11^{**}
	(0.02)	(0.08)	(0.04)
Area_HABITAT	0.11^{***}	0.26^{***}	0.10^{***}
	(0.03)	(0.05)	(0.04)
Area_ELEMENTS	-0.01	0.002	-0.03
	(0.01)	(0.04)	(0.02)
Graph_IIC	0.01	0.11	-0.003
	(0.02)	(0.07)	(0.02)
Graph_PC	0.04	0.03	-0.04
	(0.03)	(0.04)	(0.02)
Controls	✓	✓	✓
Observations	1,046	1,046	1,046
R^2	0.30	0.13	0.06
Adjusted R^2	0.30	0.12	0.05
Note:	$^{*}p<0.1$; $^{**}p<0.05$; $^{***}p<0.01$		