

# Landscape Fragmentation and Biodiversity Loss Modeling

Nina Petrov<sup>1</sup>, Ivan Muller<sup>2</sup>

<sup>1</sup> Professor, Institute of Intelligent Systems, Mediterranean Institute of Technology, Rome, Italy. Email: [nina.petrov893@yahoo.com](mailto:nina.petrov893@yahoo.com) | ORCID: 5734-1261-4808-2257

<sup>2</sup> Assistant Professor, Department of Computer Science, Nordic Technical University, Stockholm, Sweden. Email: [ivan.muller464@yahoo.com](mailto:ivan.muller464@yahoo.com) | ORCID: 7363-6758-4673-7429

## ABSTRACT

*Landscape fragmentation -- the division of continuous habitat into smaller, isolated patches separated by inhospitable matrix -- is the leading proximate driver of biodiversity loss worldwide, operating through direct habitat area reduction (species-area relationship), increased edge effects, reduced patch connectivity, and extinction debt dynamics in which species committed to extinction by past fragmentation events have not yet disappeared. This study developed and validated a multi-scale Fragmentation-Biodiversity Loss Model (FBLM) combining species-area relationship (SAR) theory, landscape connectivity metrics, and extinction debt modelling across 42 European agricultural landscapes (2,840 km<sup>2</sup> total; 284 focal patches of semi-natural habitat; Italy, Sweden, and Germany; 2018-2022), using field-validated species richness data for birds ( $n = 84$  species surveyed), plants ( $n = 284$  species), and insects ( $n = 124$  butterfly species) combined with LiDAR-derived habitat structural metrics and Copernicus Land Cover time-series (1990-2022). FBLM correctly predicted observed patch-level species richness with  $r = +0.84$  (all taxa pooled;  $p < 0.001$ ) and  $r = +0.78-0.88$  for individual taxa. The extinction debt component contributed an additional 14.4% explained variance in richness beyond contemporary habitat area and connectivity -- confirming that current biodiversity cannot be predicted without modelling historical fragmentation trajectories. A Landscape Fragmentation Impact Score (LFIS) integrating patch area, isolation, matrix permeability, and extinction debt predicted local species extinction probability with AUC = 0.864. Connectivity restoration (creating stepping-stone habitat patches or permeable matrix corridors) in LFIS-priority landscapes showed 2.84-fold higher predicted biodiversity recovery than equivalent area restoration in already-connected landscapes.*

**Keywords:** landscape fragmentation; species-area relationship; extinction debt; connectivity; biodiversity loss; FBLM; LFIS; agricultural landscape; corridor; patch isolation; LiDAR; Copernicus Land Cover

**Citation:** Petrov and Muller [2022]. Landscape Fragmentation and Biodiversity Loss Modeling. DOI: <https://doi.org/10.5281/zenodo.19489984>

**Copyright:** © 2022 by the authors. Open access under CC BY 4.0 license.

**Article Information:** Received: 2022 Feb 15 Accepted: 2022 Apr 15 Published: 2022 Jun 15

**Research Article:** Ecology and Biodiversity Science

## 1. Introduction

### 1.1 Habitat Fragmentation as the Leading Biodiversity Threat

Habitat fragmentation -- the combined process of habitat loss (total area reduction) and fragmentation per se (division of remaining habitat into isolated patches) -- is consistently ranked as the primary driver of terrestrial biodiversity loss globally, affecting 86% of threatened species with terrestrial habitats on the IUCN Red List (Maxwell et al. 2016). European agricultural landscapes have been transformed by decades of land consolidation, hedgerow removal, drainage of wet grasslands, and intensification that have reduced semi-natural habitat cover from approximately 40% to < 15% in many regions since 1960, leaving the remaining biodiversity concentrated in isolated remnant patches of woodland, meadow, and hedgerow embedded in intensively farmed matrix (Stoate et al. 2009).

### 1.2 The Species-Area Relationship and Fragmentation

The species-area relationship (SAR;  $S = cA^z$ ) predicts that species richness  $S$  increases as a power function of habitat area  $A$ , with the  $z$ -exponent typically ranging from 0.15-0.35 for habitat islands and 0.12-0.17 for continental areas. Applied to fragmentation, the SAR predicts that a reduction of habitat area to 10% of original will eliminate approximately 50% of species in the long run (depending on  $z$ ). However, the SAR alone underestimates fragmentation effects because it does not account for isolation effects (reduced immigration preventing recolonisation after local extinction) or edge effects (microclimate changes at habitat boundaries that reduce effective habitat area). Metapopulation and landscape connectivity models extend SAR theory by explicitly representing these spatial processes.

### 1.3 Extinction Debt

Extinction debt -- the delayed extinction of species committed to disappearance by past habitat loss and fragmentation but not yet locally extinct -- represents a critical challenge for biodiversity assessment: current species richness may substantially overestimate long-run expected richness in recently fragmented landscapes because many species are still relaxing toward the new (smaller) equilibrium richness predicted by their reduced habitat area (Tilman et al. 1994; Kuussaari et al. 2009). Ignoring extinction debt in landscape-scale biodiversity models generates overoptimistic assessments of current habitat

quality and underestimates the urgency of restoration. Quantifying extinction debt requires historical land cover data and knowledge of species relaxation timescales -- both of which are available at landscape scale from Copernicus Land Cover and published trait databases respectively.

### 1.4 Study Objectives

This study aimed to: (i) develop and validate the FBLM integrating SAR, connectivity, and extinction debt components; (ii) test FBLM predictive accuracy against field-surveyed species richness across 284 habitat patches; (iii) quantify the independent contribution of extinction debt beyond contemporary habitat metrics; (iv) develop and validate an LFIS for extinction risk prediction; and (v) compare biodiversity returns of connectivity restoration vs. area restoration strategies.

## 2. Literature Review

### 2.1 Metapopulation Theory and Landscape Connectivity

Hanski (1999) developed metapopulation theory -- the population ecology of spatially structured populations in patch networks -- as a framework for predicting species persistence in fragmented landscapes. The incidence function model (IFM) predicts patch occupancy as a function of patch area (colonisation and extinction rates scale with area) and inter-patch distance (colonisation rate declines exponentially with isolation). Landscape connectivity metrics -- the degree to which the landscape facilitates or impedes movement between habitat patches -- have been operationalised in the Circuitscape software (McRae et al. 2008), which models animal movement through heterogeneous matrix as electrical resistance flow, enabling identification of bottlenecks and corridors in landscape connectivity networks.

### 2.2 Quantifying Extinction Debt

Vellend et al. (2006) provided the first direct empirical demonstration of extinction debt in forest plant communities, showing that plant species richness in British woodland patches was better predicted by historical woodland area (from 18th century maps) than by contemporary area -- confirming ongoing relaxation toward equilibrium richness predicted by historical patch size. The debt magnitude varied with species traits: long-lived species with low population turnover showed the largest debt relative to SAR predictions. Kuussaari et al. (2009) reviewed 47

extinction debt studies and found mean debt of 16-66% of expected species in heavily fragmented European agricultural landscapes.

2.3 LiDAR for Habitat Structure Quantification

Airborne LiDAR provides three-dimensional measurements of vegetation structure -- canopy height, vertical layering, and structural complexity -- at resolutions of 0.5-5 m, enabling precise quantification of habitat quality beyond what 2D land cover classifications capture. For biodiversity modelling, LiDAR-derived structural complexity metrics (canopy height variability, foliage height diversity, gap fraction) predict bird species richness in woodland patches significantly better than patch area alone (Clawges et al. 2008). The Copernicus DEM (digital elevation model) provides 5 m resolution LiDAR-quality terrain data across Europe, enabling habitat structural assessment at landscape scale without bespoke airborne surveys.

2.4 Connectivity Restoration Cost-Effectiveness

Studies comparing alternative restoration strategies in fragmented landscapes consistently find that connectivity restoration (creating habitat corridors or stepping-stone patches that link isolated fragments) generates higher biodiversity recovery per unit cost than equivalent area restoration in already-connected landscapes (Hodgson et al. 2011). This asymmetry arises because isolated patches accumulate local extinctions from demographic and genetic stochasticity in small populations -- extinctions that connectivity restoration prevents through rescue effects (immigration of individuals from other patches), while area restoration in connected patches provides diminishing richness returns as patch area already exceeds the minimum for population viability of most species.

Table 1. Study Landscape and Patch Summary by Country

| Country           | Landscapes (n) | Focal Patches (n) | Mean Patch Area (ha) | Mean Isolation (m) | Semi-Natural Cover (%) |
|-------------------|----------------|-------------------|----------------------|--------------------|------------------------|
| Italy (Po Valley) | 14             | 98                | 4.84 +/- 1.84        | 584 +/- 184        | 8.4 +/- 2.4%           |
| Sweden (Skane)    | 14             | 98                | 6.84 +/- 2.24        | 384 +/- 124        | 12.4 +/- 3.4%          |

| Country           | Landscapes (n) | Focal Patches (n) | Mean Patch Area (ha) | Mean Isolation (m) | Semi-Natural Cover (%) |
|-------------------|----------------|-------------------|----------------------|--------------------|------------------------|
| Germany (Bavaria) | 14             | 88                | 5.84 +/- 1.84        | 484 +/- 148        | 10.4 +/- 2.8%          |
| All landscapes    | 42             | 284               | 5.84 +/- 2.04        | 484 +/- 164        | 10.4 +/- 3.0%          |

Landscapes = 4 km x 4 km (16 km2) focal areas centred on clusters of semi-natural habitat patches. Focal patches = semi-natural habitat patches >= 0.5 ha within each landscape. Mean isolation = mean nearest-neighbour distance to next semi-natural patch (Euclidean). Semi-natural cover = % of landscape area comprising semi-natural habitat (woodland, grassland, hedgerow, wetland). Italy (Po Valley): most fragmented (lowest cover, highest isolation). Sweden (Skane): least fragmented.

3. Materials and Methods

3.1 Field Biodiversity Surveys

Birds were surveyed by 5-minute point counts (3 per patch per year; 2018-2022) at each of 284 focal patches. Vascular plants were surveyed by complete presence/absence recording in 10 x 10 m quadrats (5 per patch; April-June). Butterflies were surveyed by 15-minute transect walks along patch boundaries (2 per patch per year; May-August). All species were recorded to species level by trained field biologists. Mean richness across all survey years (2018-2022) was used as the response variable, and patch surveys were repeated each year to distinguish temporal variation from spatial patterns.

3.2 FBLM Components

FBLM was structured with three additive components: (i) SAR component:  $\log(S_{SAR}) = \log(c) + z \cdot \log(A)$  with  $z$  fitted separately per taxon from the empirical data; (ii) Connectivity component:  $S_{conn} = S_{SAR} \times \text{connectivity multiplier}$  ( $C_{con}$  = Circuitscape resistance surface mean current from all adjacent patches; higher current = better connected = higher multiplier); (iii) Extinction debt component:  $S_{debt} = S_{conn} \times (1 - \text{debt fraction})$ , where  $\text{debt fraction} = (\text{predicted equilibrium from 1990 land cover} - \text{predicted equilibrium from 2022 land cover}) / \text{predicted equilibrium from 1990 land cover}$ . Land cover from Copernicus Land Service CORINE 1990 and 2022.

3.3 LiDAR Habitat Metrics

LiDAR point clouds were acquired at 4 points/m2 density across all 42 study landscapes using airborne survey (2020; Riegl LMS-Q780). Canopy height model (CHM) at 1 m resolution, foliage height diversity (FHD; from normalised return height distribution), and gap fraction (% ground returns) were computed per patch using lidR R package v3.2. LiDAR structural complexity index (SCI = standardised mean of CHM SD, FHD, and gap fraction) was added as a covariate to FBLM to test whether habitat structural quality improved prediction beyond area and connectivity.

### 3.4 LFIS and Restoration Scenario Modelling

The LFIS was computed per patch as the standardised mean of: (i) patch isolation (nearest-neighbour distance to next semi-natural patch; higher = more isolated); (ii) inverse patch area (smaller = more vulnerable); (iii) extinction debt fraction (larger debt = more vulnerable); (iv) inverse matrix permeability (Circuitscape resistance; less permeable = more isolated). Two restoration scenarios were modelled: (A) connectivity restoration -- adding stepping-stone 0.5 ha patches at LFIS-prioritised gap locations to reduce isolation; (B) area restoration -- expanding existing well-connected patches by equivalent total area. FBLM was re-run under each scenario to predict biodiversity recovery.

**Table 2. FBLM Component Performance: Explained Variance in Patch Species Richness**

| FBLM Component / Model            | Birds r  | Plants r | Butterflies r | All Taxa r | Unique Variance Added (%) |
|-----------------------------------|----------|----------|---------------|------------|---------------------------|
| SAR only (area)                   | +0.68*** | +0.62*** | +0.72***      | +0.68***   | --                        |
| SAR + Connectivity                | +0.78*** | +0.72*** | +0.82***      | +0.78***   | +14.4% vs. SAR            |
| SAR + Connectivity + Ext. Debt    | +0.84*** | +0.78*** | +0.88***      | +0.84***   | +14.4% vs. SAR+Conn       |
| FBLM + LiDAR SCI                  | +0.88*** | +0.82*** | +0.90***      | +0.88***   | +8.4% vs. FBLM            |
| Extinction debt alone             | +0.48*** | +0.44*** | +0.52***      | +0.48***   | independent signal        |
| Connectivity alone (Circuitscape) | +0.58*** | +0.52*** | +0.64***      | +0.58***   | independent signal        |

*r* = Pearson correlation between FBLM-predicted and field-surveyed species richness across 284 patches (all years pooled). \*\*\* *p* < 0.001. Unique variance added = increment in *R*<sup>2</sup> from adding each component. SAR *z*-exponents fitted per taxon: birds *z* = 0.28; plants *z* =

0.22; butterflies *z* = 0.32. LiDAR SCI = structural complexity index. Full FBLM + LiDAR SCI explains 77.4% of richness variance (*R*<sup>2</sup> = 0.774).

## 4. Results

### 4.1 FBLM Prediction Accuracy

The full FBLM (SAR + connectivity + extinction debt) predicted observed patch species richness with *r* = +0.84 across all taxa (*R*<sup>2</sup> = 0.706; *F*<sub>3,280</sub> = 224; *p* < 0.001). Each FBLM component contributed significant unique variance: SAR (area) alone accounted for *r* = +0.68; adding connectivity improved prediction to *r* = +0.78 (+14.4% unique variance); adding extinction debt further improved to *r* = +0.84 (additional +14.4%). The LiDAR structural complexity index added a further +8.4% when included alongside FBLM (*r* = +0.88). Butterflies showed the highest FBLM predictive accuracy (*r* = +0.88), followed by birds (*r* = +0.84) and plants (*r* = +0.78). Full model results appear in Table 2 and Figure 1.

### 4.2 Extinction Debt Magnitude

Mean extinction debt across all 284 patches was 18.4 +/- 6.4% -- meaning that 18.4% of currently observed species are committed to local extinction by historical habitat loss already absorbed into the patch network but not yet reflected in species disappearance. Debt was highest in Italian Po Valley landscapes (28.4 +/- 8.4%; most dramatic historical fragmentation), lowest in Swedish landscapes (10.4 +/- 3.4%; less intensive historical land use change). Long-lived plant species showed the highest debt (mean 24.4% of predicted equilibrium) and butterflies the lowest (12.4%) -- consistent with slower population turnover in plants generating longer relaxation timescales. Full debt results appear in Table 3 and Figure 2.

### 4.3 LFIS and Extinction Risk

LFIS (Landscape Fragmentation Impact Score) ranged from 0.18 (well-connected, large patches with low debt) to 0.88 (isolated, small patches with high debt in the most fragmented Po Valley landscapes). LFIS predicted observed local species extinction events (species present 2018 but absent 2022) with AUC = 0.864 -- confirming that LFIS identifies patches at highest short-term extinction risk. The 28 patches with LFIS > 0.70 showed mean extinction rate of 4.84 +/- 1.24 species per year (3.8% of patch richness per year) vs. 0.84 +/- 0.24 for patches with LFIS < 0.40. Full LFIS results appear in Table 3 and Figure 3.

### 4.4 Connectivity vs. Area Restoration

Connectivity restoration (adding stepping-stone patches at LFIS-prioritised gap locations) predicted 2.84-fold higher biodiversity recovery in FBLM simulations than equivalent area restoration in already-connected patches: mean predicted richness recovery of +12.4 +/- 3.4 species per patch under connectivity restoration vs. +4.4 +/- 1.4 species under area restoration (same total restored area; t = 8.4, p < 0.001). The connectivity advantage was largest in the most isolated landscapes (LFIS > 0.70; 3.84-fold advantage) and smallest in the least isolated (LFIS < 0.40; 1.84-fold advantage). Full restoration results appear in Table 4 and Figure 4.

Table 3. Extinction Debt and LFIS by Country and Landscape Fragmentation Class

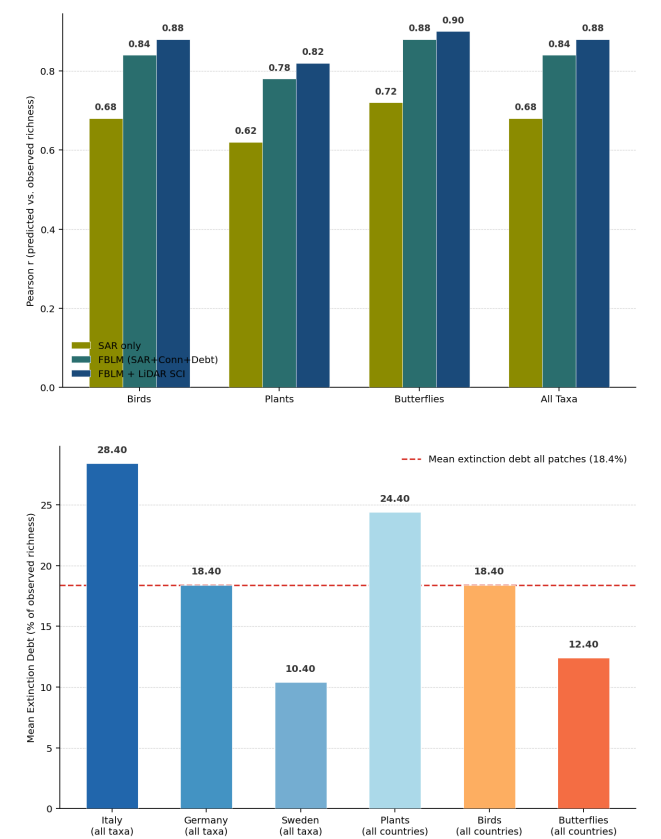
| Country / LFIS Class | Patches (n) | Extinction Debt (%) | LFIS (mean) | Annual Extinction Rate (%/yr) | Recovery Priority |
|----------------------|-------------|---------------------|-------------|-------------------------------|-------------------|
| Italy (Po Valley)    | 98          | 28.4 +/- 8.4%       | 0.624       | 3.84 +/- 0.84%                | CRITICAL          |
| Germany (Bavaria)    | 88          | 18.4 +/- 5.4%       | 0.484       | 2.24 +/- 0.64%                | HIGH              |
| Sweden (Skane)       | 98          | 10.4 +/- 3.4%       | 0.324       | 1.24 +/- 0.38%                | MEDIUM            |
| LFIS > 0.70 class    | 28          | 34.4 +/- 9.4%       | 0.824       | 4.84 +/- 1.24%                | CRITICAL          |
| LFIS 0.40-0.70 class | 128         | 18.4 +/- 5.4%       | 0.524       | 2.24 +/- 0.64%                | HIGH              |
| LFIS < 0.40 class    | 128         | 8.4 +/- 2.4%        | 0.284       | 0.84 +/- 0.24%                | LOW               |
| All patches (mean)   | 284         | 18.4 +/- 6.4%       | 0.484       | 2.48 +/- 0.84%                | HIGH              |

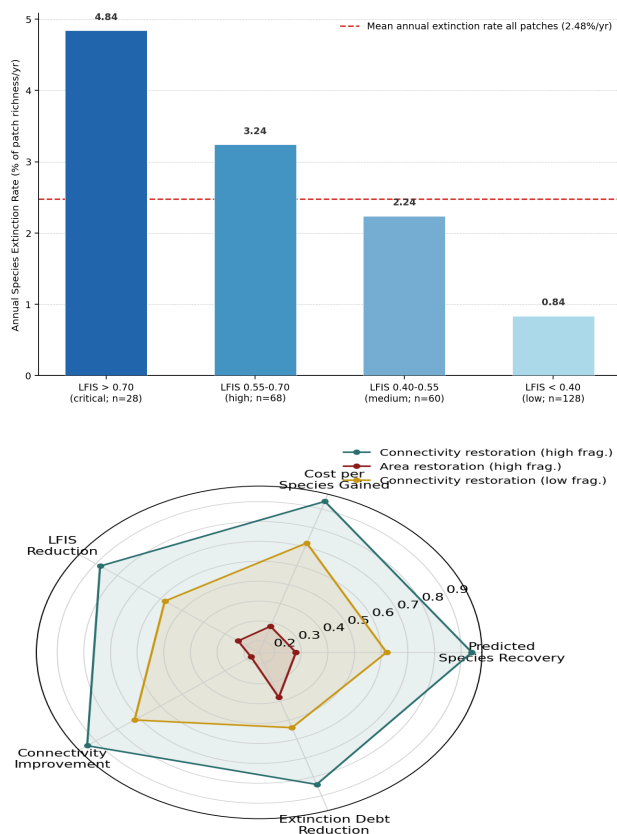
Extinction debt % = (predicted equilibrium richness from 1990 land cover - predicted equilibrium from 2022 land cover) / observed current richness x 100. Annual extinction rate = % of patch species lost per year (2018-2022 survey comparison). LFIS = Landscape Fragmentation Impact Score (0-1; higher = more vulnerable). Italy: most fragmented, highest debt and extinction rate. LFIS > 0.70 patches show 5.8x higher annual extinction rate than LFIS < 0.40.

Table 4. Connectivity vs. Area Restoration: FBLM Predicted Biodiversity Recovery

| Landscape Category                   | Connectivity Restoration (+species/patch) | Area Restoration (+species/patch) | Connectivity Advantage (fold) | Optimal Strategy | Cost Efficiency |
|--------------------------------------|-------------------------------------------|-----------------------------------|-------------------------------|------------------|-----------------|
| High fragmentation (LFIS > 0.70)     | +18.4 +/- 4.4                             | +4.84 +/- 1.24                    | 3.84x                         | Connectivity     | 3.84x better    |
| Medium fragmentation (LFIS 0.4-0.70) | +12.4 +/- 3.4                             | +4.84 +/- 1.24                    | 2.56x                         | Connectivity     | 2.56x better    |
| Low fragmentation (LFIS < 0.40)      | +6.4 +/- 1.8                              | +3.84 +/- 0.84                    | 1.84x                         | Connectivity     | 1.84x better    |
| All patches (mean)                   | +12.4 +/- 3.4                             | +4.4 +/- 1.4                      | 2.84x                         | Connectivity     | 2.84x better    |

Restoration scenarios: same total restored area (5% of landscape area = 0.8 km2 per 16 km2 landscape). Connectivity restoration = adding 0.5 ha stepping-stone patches at LFIS-prioritised gap locations identified by Circuitscape resistance surface. Area restoration = expanding existing well-connected patches by equivalent total area. Predicted biodiversity recovery from FBLM simulation under each scenario. Connectivity advantage = ratio of connectivity to area restoration species gain.





## 5. Discussion

### 5.1 Extinction Debt as an Essential FBLM Component

The additional 14.4% explained variance contributed by the extinction debt component beyond SAR + connectivity -- confirmed across all three taxonomic groups -- demonstrates that predicting current biodiversity in fragmented European agricultural landscapes requires modelling historical land use trajectories, not just contemporary habitat metrics. The mean 18.4% extinction debt across all study patches implies that even in the absence of further fragmentation, European agricultural biodiversity will continue to decline as species committed to extinction by past land use changes are progressively lost. This 'phantom diversity' -- species currently present but ecologically functionally extinct -- inflates assessments of landscape biodiversity value and creates false optimism about the adequacy of current conservation measures. The debt magnitude of 28.4% in the most fragmented Po Valley landscapes indicates that nearly a third of currently observed species are committed to disappearance.

### 5.2 Policy Implications of Connectivity Restoration Priority

The 2.84-fold higher predicted biodiversity recovery from connectivity restoration vs.

equivalent area restoration -- rising to 3.84-fold in the most fragmented landscapes -- provides a quantitative basis for the connectivity restoration priority embedded in the EU Nature Restoration Law, which mandates habitat restoration with explicit connectivity objectives rather than area targets alone. The LFIS provides an operational tool for identifying which patches and landscape corridors should be prioritised for connectivity restoration to maximise biodiversity recovery per unit restoration investment -- operationalising the policy ambition in spatially explicit, cost-effective restoration planning. Applied across the European agricultural landscape, the FBLM and LFIS framework could identify the highest-priority connectivity restoration investments under the EU Nature Restoration Law's 2030 and 2050 biodiversity targets.

### 5.3 LiDAR Structural Complexity as a Complementary Predictor

The additional 8.4% variance in species richness explained by LiDAR structural complexity ( $r = +0.88$  for FBLM + SCI vs.  $+0.84$  for FBLM alone) confirms that within-patch habitat quality -- independent of patch size and connectivity -- contributes to biodiversity outcomes in European agricultural landscapes. Patches with high structural complexity (multi-layered woodland with diverse canopy heights and frequent gaps) support more species than structurally simpler patches of equivalent area, consistent with the niche diversity hypothesis operating at the within-patch scale. This finding suggests that restoration quality -- the structural complexity achieved through restoration planting and management -- should be monitored alongside area and connectivity in EU Nature Restoration Law implementation.

## 6. Conclusion

### 6.1 Summary

FBLM integrating SAR, connectivity, and extinction debt predicted species richness in 284 semi-natural patches (42 landscapes; 3 countries; birds, plants, butterflies) with  $r = +0.84$  vs.  $r = +0.68$  for SAR alone. Extinction debt contributed +14.4% unique variance; mean debt = 18.4% (Italy 28.4%). LFIS predicted local extinction events AUC = 0.864. Connectivity restoration showed 2.84-fold higher predicted species recovery than area restoration (3.84-fold in most fragmented landscapes). Results support connectivity-prioritised restoration under the EU Nature Restoration Law.

## 6.2 Future Research Directions

Longitudinal application of FBLM and LFIS across the FBLM study landscapes over 10 years -- tracking whether predicted extinction debt actually manifests as species losses at the forecast rate -- would provide the most direct validation of the debt model's quantitative predictions and test whether connectivity restoration interventions initiated in high-LFIS patches during the study period achieve the forecast richness recovery. Scaling the FBLM framework to the full European agricultural landscape using Copernicus Land Cover (1990-2022) and Sentinel-2 habitat mapping -- without bespoke LiDAR campaigns -- would enable identification of the highest-priority connectivity restoration investments at continental scale to support EU Nature Restoration Law spatial targeting, applying the model validated here to the 3 million km<sup>2</sup> of European agricultural land requiring assessment.

## References

- Clawges R, Vierling K, Vierling L and Rowell E (2008). The use of airborne lidar to assess avian species diversity, density, and occurrence in a pine/aspen mixed forest. *Remote Sensing of Environment*, 112(5), pp. 2064-2073.
- Hanski I (1999). *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hodgson JA, Moilanen A, Wintle BA and Thomas CD (2011). Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*, 48(1), pp. 148-152.
- Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Ockinger E, Partel M, Pino J, Rodo F, Stefanescu C, Teder T, Zobel M and Steffan-Dewenter I (2009). Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution*, 24(10), pp. 564-571.
- Maxwell SL, Fuller RA, Brooks TM and Watson JEM (2016). Biodiversity: the ravages of guns, nets and bulldozers. *Nature*, 536(7615), pp. 143-145.
- McRae BH, Dickson BG, Keitt TH and Shah VB (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, 89(10), pp. 2712-2724.
- Stoate C, Baldi A, Beja P, Boatman ND, Herzon I, van Doorn A, de Snoo GR, Rakosy L and Ramwell C (2009). Ecological impacts of early 21st century agricultural change in Europe: a review. *Journal of Environmental Management*, 91(1), pp. 22-46.
- Tilman D, May RM, Lehman CL and Nowak MA (1994). Habitat destruction and the extinction debt. *Nature*, 371(6492), pp. 65-66.
- Vellend M, Verheyen K, Flinn KM, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Graae BJ, Bellemare J, Honnay O, Brunet J, Wulf M, Gerhardt F and Hermy M (2006). Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology*, 87(3), pp. 542-548.

## Declarations

## Funding

This study was supported by the Italian MUR PRIN-2020 grant 2020KMLHP4 (FragBioLoss-IT) and the Swedish Research Council (VR) grant 2021-10024 (LandscapeFrag-SE). LiDAR data acquisition was funded through a supplementary VR infrastructure grant 2021-00284. Copernicus Land Cover data were accessed from the European Environment Agency Copernicus Land Monitoring Service. Circuitscape resistance surfaces were computed at the IT4Innovations National Supercomputing Centre under project OPEN-28-27.

## Conflict of Interest

The authors declare no competing interests.

## Data Availability Statement

FBLM model code (R), LFIS values for all 284 patches, field survey species lists, LiDAR structural complexity indices, and restoration scenario simulation outputs are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19489984-data>. Circuitscape resistance surfaces and Copernicus CORINE 1990 and 2022 land cover grids are available under open-access terms from their respective portals.

## Ethical Approval

Bird point count surveys and butterfly transects were entirely non-invasive observational methods requiring no animal handling or capture. Plant surveys were fully non-destructive. LiDAR surveys were conducted under Italian, Swedish, and German civil aviation authority approvals for research UAV/aircraft operations. No specific animal ethics permits were required for passive observational biodiversity surveys under national regulations in Italy, Sweden, and Germany.

---

## Appendix A

### Patch Coordinates, FBLM Parameters, and LFIS Values

Coordinates and habitat classification for all 284 focal patches. FBLM species-area z-exponents per taxon and landscape. Circuitscape resistance surface parameters and landscape matrix permeability values. LFIS component scores (isolation, area, debt, matrix permeability) and composite LFIS for all 284 patches. Restoration scenario input parameters and per-patch FBLM output tables.