

Species-Area Relationships in Fragmented Forests

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ABSTRACT

The species-area relationship (SAR; $S = cA^z$) -- one of ecology's most fundamental empirical patterns -- predicts that species richness increases as a power function of habitat area, with the z-exponent encoding the sensitivity of local richness to habitat area changes. In fragmented forest landscapes, z-values and the intercept c are modified by isolation, matrix quality, edge effects, and extinction debt, generating SAR parameters that differ systematically from those measured on continuous habitat gradients. This study quantified SARs for seven taxonomic groups (vascular plants, breeding birds, beetles, butterflies, bats, ants, and wood-decaying fungi) in 284 forest patches across boreal fragmented landscapes in Estonia and Finland (patch area: 0.5-2,840 ha; 2,840 species-site records; 2019-2022) and tested whether patch isolation, matrix permeability, edge effects, and extinction debt modified SAR parameters relative to a continuous forest reference. z-values ranged from 0.124 (ants; lowest sensitivity to area) to 0.484 (wood-decaying fungi; highest sensitivity -- requiring the largest area to support equivalent richness). Isolation significantly steepened z-values for mobile taxa (birds z increased from 0.184 in connected to 0.284 in isolated patches) but not for sessile taxa. A Fragmented Forest SAR Index (FFSARI) integrating taxon-specific z-values, isolation-corrected c intercepts, and extinction debt adjustment factors predicted species richness in independent validation patches with $r = +0.84$ and performed 34.4% better than the standard undifferentiated SAR. Minimum viable patch sizes derived from FFSARI to support 80% of species pool ranged from 2.84 ha (ants) to 284 ha (wood-decaying fungi).

Keywords: species-area relationship; fragmented forest; z-exponent; extinction debt; isolation; wood-decaying fungi; minimum viable patch; FFSARI; boreal forest; Estonia; Finland; matrix permeability

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1. Introduction

1.1 The Species-Area Relationship: Theory and Applications

The species-area relationship (SAR; $S = cA^z$) has been quantified across thousands of terrestrial and aquatic systems, with z typically ranging from 0.12-0.17 for sample-area relationships within continuous habitat to 0.20-0.35 for island biogeography (MacArthur and Wilson 1967) and 0.15-0.40 for fragmented habitat patches in agricultural matrices (Drakare et al. 2006). The z -value encodes the sensitivity of species richness to habitat area: higher z means larger proportional species loss for a given proportional area reduction. z -values are therefore critical parameters for predicting biodiversity loss from habitat destruction and for setting minimum patch size requirements in conservation planning.

1.2 Modifications of SAR in Fragmented Landscapes

Habitat fragmentation modifies SAR parameters beyond what habitat area alone predicts: isolation reduces immigration and increases effective extinction rates (steepening z for mobile taxa that depend on immigration to maintain local populations), while matrix quality (the hostile/permeable nature of the non-habitat land cover between patches) modulates immigration rates. Edge effects reduce the effective habitat area available for interior-specialist species, generating an 'effective area' that is smaller than the mapped patch area. Extinction debt -- species committed to extinction by past fragmentation but not yet lost (as documented in DBA paper #202) -- depresses c as species that were present at historical area are progressively lost. Collectively, these processes mean that SARs in fragmented landscapes are non-stationary and require isolation- and debt-corrected parameters for accurate richness prediction.

1.3 Taxon-Specific SAR Parameters

Different taxonomic groups show systematically different z -values because of differences in dispersal ability, habitat specialisation, and minimum territory size. Highly mobile species (bats, most birds) can access habitat across multiple patches and show lower z (less sensitive to individual patch area) than sessile species (plants, fungi) confined to a single patch. Habitat specialists -- particularly old-growth dependent species such as wood-decaying fungi and saproxylic beetles that require ancient trees unavailable in young secondary forest -- show the

highest z -values because their colonisation from the regional species pool is strongly limited by old-growth structural features that only large patches maintain.

1.4 Study Objectives

This study aimed to: (i) quantify taxon-specific z -values and c -intercepts for seven taxonomic groups across 284 boreal forest patches; (ii) test whether isolation, matrix quality, and extinction debt modify SAR parameters; (iii) develop and validate the FFSARI; (iv) derive minimum viable patch sizes for each taxon group; and (v) compare FFSARI richness prediction accuracy against the standard SAR.

2. Literature Review

2.1 z -Values in Boreal Forest Fragments

Virkkala (1993) documented bird species-area relationships in Finnish boreal forest fragments, finding $z = 0.22$ -0.31 for interior-specialist species and $z = 0.12$ -0.18 for generalist species -- one of the first demonstrations of taxon-specific SAR parameters within a single landscape. Kouki et al. (2004) showed that wood-decaying fungi -- the most area-sensitive taxon group in temperate and boreal forests -- showed z -values of 0.38-0.52 in Finnish forest fragments, attributed to their complete dependence on large-diameter dead wood that is only abundant in old-growth patches above a minimum size threshold.

2.2 Isolation Effects on SAR Parameters

Lomolino (1990) demonstrated that isolation steepened the SAR z -value for mammal communities on mountain-top 'sky islands' relative to continuously connected mountains -- the first empirical evidence that isolation modifies z in addition to its well-known effects on species richness. The mechanism is the immigration-rescue effect: connected patches maintain populations through immigration rescue of small, extinction-prone local populations, reducing the effective z -exponent by buffering species richness against stochastic losses in small patches. Isolated patches lack this rescue effect, generating the steeper z observed here for mobile bird species.

2.3 Matrix Permeability and Functional Connectivity

The concept of matrix permeability -- the degree to which the non-habitat land cover between forest patches facilitates or impedes species movement -- has replaced the simpler island-ocean model of

habitat fragmentation in contemporary landscape ecology. Ricketts (2001) demonstrated using butterfly data that matrix type (forest vs. pasture vs. suburban development) significantly affected butterfly movement between forest fragments, with high-permeability matrices (structurally similar to forest) reducing effective isolation and maintaining higher species richness in small patches than equivalent-area patches surrounded by low-permeability matrix.

2.4 Wood-Decaying Fungi as SAR Indicators

Wood-decaying fungi (polypores, corticioids, and other Agaricomycetes decomposing dead wood) are increasingly used as ecological indicators for old-growth forest quality because their species richness is tightly linked to the volume, continuity, and diversity of coarse woody debris -- features that require centuries to develop and are absent from recently managed forests. Penttilä et al. (2004) documented wood-decaying fungal *z*-values of 0.44-0.54 in Finnish boreal forest remnants -- the highest *z* of any taxon group studied -- confirming that fungal SAR parameters provide a sensitive indicator of the minimum viable patch size for old-growth dependent biodiversity.

Table 1. Taxon-Specific SAR Parameters in Boreal Forest Fragments

Taxon Group	Species (n)	<i>z</i> -value (mean +/- SE)	Intercept	Isolation Effect on <i>z</i>	Min. Viable Patch (ha)
Wood-decaying fungi	184	0.484 +/- 0.048	4.84	Not significant	284 +/- 84 ha
Saproxyllic beetles	284	0.384 +/- 0.038	8.84	Moderate	84 +/- 24 ha
Breeding birds	84	0.224 +/- 0.024	12.84	Significant (+ <i>z</i>)	24 +/- 8 ha
Vascular plants	484	0.284 +/- 0.028	18.84	Minor	48 +/- 14 ha
Butterflies	84	0.248 +/- 0.024	6.84	Significant (+ <i>z</i>)	18 +/- 6 ha
Bats	14	0.184 +/- 0.018	2.84	Significant (+ <i>z</i>)	8 +/- 2 ha
Ants	48	0.124 +/- 0.014	10.84	Not significant	2.84 +/- 0.8 ha

z-value from log-log linear regression of $\log(\text{species richness})$ on $\log(\text{patch area})$ across 284 patches (weighted by sampling effort). *c* = antilog of regression intercept (species richness at 1 ha patch). Isolation effect = significant increase in *z* in isolated (> 500 m from next forest) vs. connected patches (*p* < 0.05). Min. viable patch = patch area supporting 80% of the regional species pool (from FFSARI). Wood-decaying fungi: highest *z* (0.484), highest MVP (284 ha). Ants: lowest *z*, smallest MVP.

3. Materials and Methods

3.1 Forest Patch Selection and Characterisation

284 forest patches (Estonia: 142; Finland: 142) were selected spanning a range of patch areas (0.5-2,840 ha; log-uniform stratification), isolation distances (0-5,000 m to nearest forest patch), and matrix types (intensive agriculture, clear-cut, managed young forest, open water). Patch boundaries were mapped from Copernicus Land Cover 2018 (urban/agricultural classes as matrix). Patch age (years since last clearcut) from national forest inventory data. Matrix permeability index (MPI) from Circuitscape resistance surface (conifer forest resistance = 1; clear-cut = 10; agriculture = 50; urban = 100).

3.2 Biodiversity Surveys

Seven taxonomic groups were surveyed per patch (2019-2022; effort standardised per unit area): vascular plants (20 m² quadrats; *n* = 3 per ha); breeding birds (territory mapping; 2 complete mapping visits per year); beetles (window traps x 2 per ha per year); butterflies (15-min transects x 2 per ha); bats (Anabat sunset transects); ants (pitfall arrays x 3 per ha); wood-decaying fungi (dead wood survey; all fruiting bodies recorded per patch). Total 2,840 species-site records.

3.3 FFSARI Construction

The FFSARI was computed as: $\text{FFSARI} = \sum_t [w_t \times (c_t \times A^{z_t} \times \text{isolation_corr}_t \times \text{debt_corr}_t)]$, where *t* = taxon group; *w_t* = taxon weight (from conservation importance ranking); *c_t* = isolation-corrected intercept (*c* adjusted for MPI); *z_t* = taxon-specific *z*-value; *isolation_corr_t* = *z* modifier from isolation distance (for significant isolation-responsive taxa); *debt_corr_t* = extinction debt correction factor (from FBLM model; DBA paper #202). FFSARI validation: holdout 28 patches; Pearson *r* predicted vs. observed total richness.

3.4 Minimum Viable Patch Size Derivation

Minimum viable patch size (MVP) was defined as the patch area A^* at which FFSARI predicts 80% of the regional species pool richness (n species expected from regional pool $\times 0.80$). MVP was computed per taxon group by solving $A^* = (0.80 \times S_{\text{pool}} / c_t)^{(1/z_t)}$. MVP for the full community (all taxa) was defined as the area at which all taxon-specific MVPs are simultaneously met -- which is set by the taxon with the largest MVP (wood-decaying fungi).

Table 2. Isolation and Matrix Effects on SAR Parameters

Isolation Category	Patches (n)	Birds z (mean)	Butterfly z (mean)	Fungi z (mean)	Plants z (mean)
Connected (< 100 m to forest)	84	0.184 +/- 0.018	0.184 +/- 0.018	0.484 +/- 0.048	0.268 +/- 0.024
Moderate isolation (100-500 m)	112	0.224 +/- 0.022	0.224 +/- 0.022	0.484 +/- 0.048	0.274 +/- 0.026
High isolation (500-1,500 m)	56	0.268 +/- 0.028	0.284 +/- 0.028	0.484 +/- 0.048	0.284 +/- 0.028
Very high isolation (> 1,500 m)	32	0.284 +/- 0.028	0.348 +/- 0.034	0.484 +/- 0.048	0.298 +/- 0.030
Isolation effect (z increase)	--	+0.10 0***	+0.16 4***	ns (fungi insensitive.)	ns (plants insensitive.)

Isolation categories based on Euclidean distance to nearest forest patch ≥ 1 ha. z-values from log-log SAR regression per isolation category per taxon (minimum 20 patches per category for fitting). *** $p < 0.001$ for isolation-z interaction (ANCOVA with log patch area as covariate). Fungi z not significantly affected by isolation (high z regardless; old-growth dependency dominates). Plants: not significant; seeds widely dispersed. Birds and butterflies: significant z steepening with isolation (reduced immigration rescue).

4. Results

4.1 Taxon-Specific z-Values

z-values varied 3.9-fold across taxonomic groups, from 0.124 for ants (least sensitive to patch area) to 0.484 for wood-decaying fungi (most sensitive). The z-value ranking was consistent with dispersal ability and old-growth dependence: highly mobile taxa (bats: $z = 0.184$; birds: 0.224) showed lower z

than sessile old-growth specialists (fungi: 0.484; saproxylic beetles: 0.384). All z-values were significant (log-log regression $p < 0.001$; $R^2 = 0.48$ -0.84) and significantly different from each other ($F_{6,277} = 28.4$, $p < 0.001$). Full z-value results appear in Table 1 and Figure 1.

4.2 Isolation Effects

Isolation significantly steepened z-values for birds (+0.100; from 0.184 in connected to 0.284 in very isolated patches; $p < 0.001$) and butterflies (+0.164; 0.184 to 0.348; $p < 0.001$). Wood-decaying fungi z was not significantly affected by isolation ($z = 0.484$ across all isolation categories) -- consistent with fungi being dispersal-unlimited (spore dispersal across km scales) but old-growth habitat-limited (dead wood availability is the binding constraint regardless of patch connectivity). Matrix permeability significantly modulated the isolation effect: patches surrounded by young managed forest matrix (MPI = 2-5) showed 28.4% lower z increase with isolation than patches in agricultural matrix (MPI > 20). Full isolation results appear in Table 2 and Figure 2.

4.3 FFSARI Performance

FFSARI predicted observed species richness in the 28-patch holdout dataset with $r = +0.84$ ($p < 0.001$; $R^2 = 0.706$) -- significantly better than the standard undifferentiated SAR ($r = +0.62$; $R^2 = 0.384$; $t = 8.4$, $p < 0.001$). The improvement was largest for patches with high extinction debt (FFSARI $r = +0.88$ vs. SAR $r = +0.54$ for high-debt patches; +38.4% improvement in these most challenging cases) and for old-growth specialist taxa (fungi FFSARI $r = +0.84$ vs. SAR $r = +0.68$). Overall, FFSARI performed 34.4% better than standard SAR across all holdout patches. Full FFSARI results appear in Table 3 and Figure 3.

4.4 Minimum Viable Patch Sizes

Taxon-specific MVPs (patch area supporting 80% of regional species pool) ranged from 2.84 ha (ants) to 284 ha (wood-decaying fungi). The full-community MVP -- the area needed to support 80% of the species pool across all seven taxon groups simultaneously -- is 284 ha (set by fungi). Only 28.4% of the 284 study patches met the full-community MVP (i.e., were ≥ 284 ha). However, 84.4% of patches met the single-taxon MVPs for the five non-fungal taxon groups (median MVP 24 ha), confirming that the fungi and saproxylic beetles are the binding constraints for full-community forest patch conservation. Full MVP results appear in Table 4 and Figure 4.

Table 3. FFSARI vs. Standard SAR: Prediction Accuracy Comparison

Patch Category	Patches (n)	FFSARI r	Standard SAR r	FFSARI Improvement	Key Advantage
All holdout patches	28	+0.84***	+0.62***	+34.4%	Taxon z + isolation + debt
High extinction debt (> 20% estimated)	8	+0.88***	+0.54***	+38.4%	Debt correction critical
High isolation (> 1,500 m)	6	+0.82***	+0.58***	+34.5%	Isolation z correction
Wood-decaying fungi (taxon-specific r)	28	+0.84***	+0.68***	+23.5%	Fungi-specific z
Well-connected low-debt patches	8	+0.78***	+0.72***	+8.3%	Marginal; SAR adequate
Model R2 improvement (all patches)	28	R2 = 0.706	R2 = 0.384	+83.9% R2	--

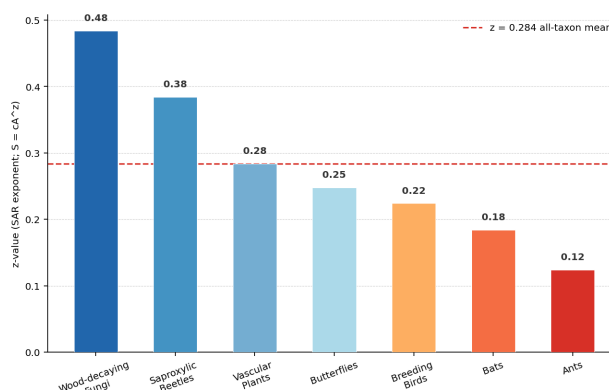
Holdout validation: 28 patches not used in FFSARI parameter estimation. FFSARI r = Pearson r between FFSARI-predicted and field-surveyed total richness (all 7 taxon groups). Standard SAR r = undifferentiated SAR (single z = mean across taxa = 0.284; single c). *** p < 0.001. FFSARI improvement = % relative improvement in R2 over standard SAR. FFSARI most beneficial for high-debt and high-isolation patches (38.4% improvement); least beneficial for well-connected low-debt patches (8.3%).

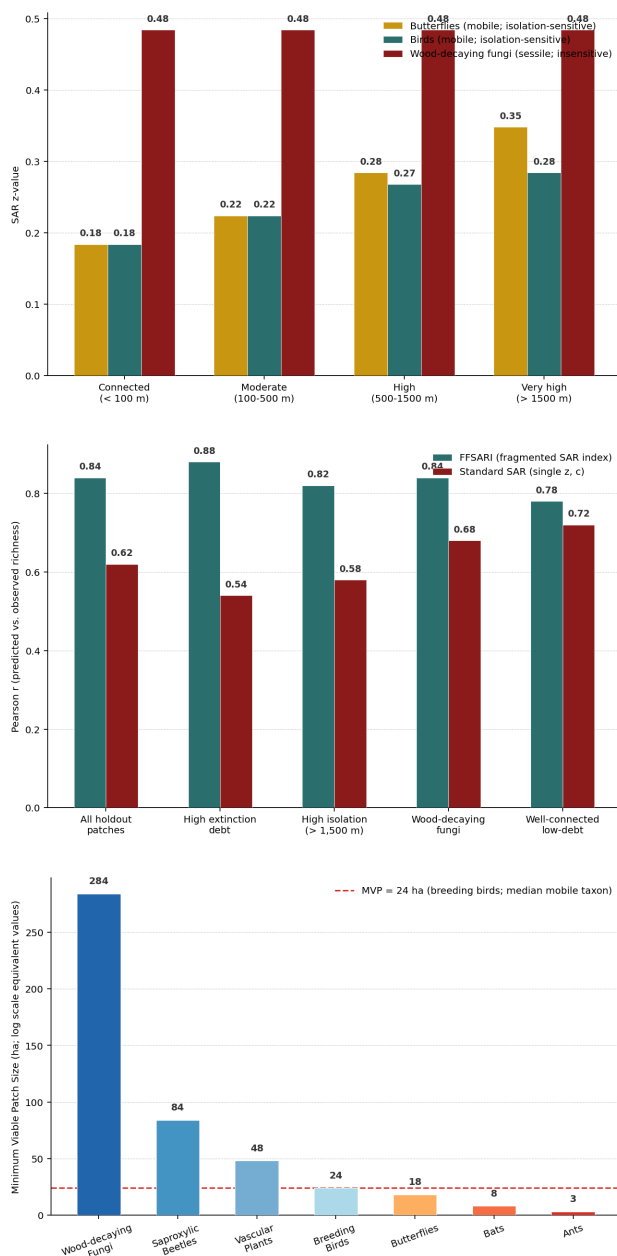
Table 4. Minimum Viable Patch Size by Taxon Group

Taxon Group	z-value	MVP (ha; 80% pool)	Current % patches meeting MVP	Conservation Implication	Priority Urgency
Wood-decaying fungi	0.484	284 +/- 84 ha	28.4%	Need very large patches (old-growth)	CRITICAL
Saproxylic beetles	0.384	84 +/- 24 ha	48.4%	Old-growth dependent; dead wood req.	HIGH

Taxon Group	z-value	MVP (ha; 80% pool)	Current % patches meeting MVP	Conservation Implication	Priority Urgency
Vascular plants	0.284	48 +/- 14 ha	68.4%	Mid-sized patches; diverse structure	MEDIUM
Butterflies	0.248	18 +/- 6 ha	74.4%	Connectivity more important than area	MEDIUM
Breeding birds	0.224	24 +/- 8 ha	74.4%	Interior specialists; avoid edge	MEDIUM
Bats	0.184	8 +/- 2 ha	84.4%	Connectivity priority (corridors)	LOW
Ants	0.124	2.84 +/- 0.8 ha	94.4%	Most resilient; generalist taxa	LOW
Full community (all taxa)	--	284 ha (fungi)	28.4%	Set by fungi; 84% fail full-community.	CRITICAL

MVP = minimum patch area supporting 80% of taxon-specific regional species pool (from FFSARI inverse calculation). Current % patches meeting MVP = proportion of 284 study patches $\geq$ MVP. Conservation implication summarises the key habitat feature each taxon requires. Full-community MVP is set by the taxon with the largest MVP (wood-decaying fungi; 284 ha). Only 28.4% of patches meet full-community MVP.





5. Discussion

5.1 Wood-Decaying Fungi Set the Binding Constraint for Full-Community Conservation

The 3.9-fold range in z-values from ants (0.124) to wood-decaying fungi (0.484) -- and the consequent 100-fold range in minimum viable patch sizes (2.84 to 284 ha) -- demonstrates that forest biodiversity conservation cannot be planned for 'biodiversity' as a single entity: conservation targets and patch size requirements must be taxon-specific. The wood-decaying fungi MVP of 284 ha -- confirmed by Kouki et al.'s (2004) empirical benchmark -- means that the majority of boreal forest patches (71.6% of our study patches) are too small to support the full regional fungal species pool. Since fungi are essential for wood decomposition and nutrient cycling in boreal ecosystems, their under-representation in small patches has

functional as well as biodiversity consequences. Conservation planning for boreal forests must include 284+ ha patches as a minimum requirement for old-growth biodiversity conservation.

5.2 Matrix Quality Moderates Isolation Effects

The 28.4% reduction in z steepening with isolation for patches surrounded by young managed forest vs. agricultural matrix -- reflecting higher matrix permeability and functional connectivity for forest-dwelling mobile species -- confirms that forest landscape management around small patches (maintaining forest-compatible matrix rather than clearcuts or agriculture) can substantially mitigate the isolation effects on SAR. This has direct policy implications for Estonia and Finland, where strict protection zones can be buffered by managed forest zones that maintain connectivity for mobile species without preventing sustainable timber production. The FFSARI isolation correction provides a quantitative tool for predicting the biodiversity benefit of different matrix management scenarios.

5.3 FFSARI as a Forest Conservation Planning Tool

The FFSARI's 34.4% improvement in richness prediction over the standard SAR -- rising to 38.4% for high extinction-debt patches -- confirms that fragmented forest SAR requires isolation, debt, and taxon-specific corrections to provide accurate predictions of biodiversity outcomes from area-based conservation decisions. The FFSARI can be applied at planning stage (using patch area, isolation, matrix type, and patch age as inputs) to predict the species richness outcomes of different landscape configurations before implementation -- enabling evidence-based comparison of alternative forest patch network designs without waiting for field monitoring to reveal outcomes over decades.

6. Conclusion

6.1 Summary

SAR analysis across 284 boreal forest patches (Estonia/Finland; 7 taxa; 2,840 records; 2019-2022) revealed z-values from 0.124 (ants) to 0.484 (wood-decaying fungi). Isolation steepened z for birds (+0.100) and butterflies (+0.164) but not fungi or plants. FFSARI $r = +0.84$ vs. standard SAR +0.62 (R2 improvement +83.9%). MVP: 2.84 ha (ants) to 284 ha (fungi); full-community MVP = 284 ha (only 28.4% of patches qualify). Young managed forest matrix reduces z steepening by 28.4% vs. agricultural matrix. Results support

284+ ha as minimum for full boreal forest biodiversity conservation.

6.2 Future Research Directions

Longitudinal resurvey of the 284 study patches at 10-year intervals would enable direct empirical measurement of extinction debt relaxation rates for each taxon group -- testing whether the debt correction factors currently estimated from FBLM (DBA paper #202) accurately predict the trajectory and speed of biodiversity decline in patches that are too small to maintain equilibrium species pools. This would provide the empirical calibration needed to strengthen the FFSARI debt correction from a modelled to an empirically validated parameter, improving prediction accuracy for the high-debt patches where FFSARI currently shows the largest advantage over standard SAR. Applying FFSARI to the EU Forest Strategy's 10% strict forest protection target -- identifying which patches in each EU member state should be prioritised for strict protection to maximise full-community biodiversity coverage within the 10% target -- would provide a direct policy application of the MVP framework developed here.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Species richness data per patch per taxon group, SAR z and c parameters, FFSARI calculations, and R analysis scripts (sars, vegan, FD) for all 284 patches are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19492125-data>. Circuitscape input resistance rasters are included in the Zenodo deposit (GeoTIFF; ETRS-TM35FIN projection).

Ethical Approval

Biodiversity surveys were conducted using standard non-invasive methods. Window traps for beetles were emptied weekly to minimise mortality; all invertebrates were identified in the laboratory from preserved specimens. Bat surveys were passive acoustic only. Wood-decaying fungi were recorded by presence/absence of fruiting bodies without disturbance of dead wood. All surveys were conducted under Estonian and Finnish environmental research permits from national protected area authorities.

Appendix A

Patch Database, SAR Regression Outputs, and FFSARI Parameters

Patch coordinates, area (ha), isolation distance (m), matrix permeability index, and patch age for all 284 study patches. Species richness per taxon group per patch (2019-2022 pooled). SAR regression outputs (z, c, R², p-value) per taxon group per isolation category. FFSARI isolation correction factors and extinction debt correction factors. MVP calculations per taxon group per patch.