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Metapopulation Stability in Fragmented Forests

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ABSTRACT

Metapopulation theory predicts that a network of habitat patches connected by dispersal can maintain a species regionally even when individual local populations are extinction-prone, provided that the colonisation rate from occupied to empty patches exceeds the local extinction rate and that connectivity among patches is sufficient for rescue effects to stabilise populations approaching extinction. This study empirically tested metapopulation stability predictions from the Levins and Hanski incidence function model frameworks against 18-year occupancy and genetic connectivity data from 284 forest vertebrate populations across 48 fragmented forest landscapes in Italy, spanning a gradient from highly fragmented (mean patch area 4.2 ha; inter-patch gap 1.8 km) to moderately connected (mean patch area 48.4 ha; inter-patch gap 0.4 km). Twelve species representing diverse forest vertebrate guilds (woodland birds, small mammals, reptiles, amphibians) were monitored annually. Metapopulation occupancy turnover (annual local extinction and colonisation rates) was significantly predicted by patch area (area coefficient $\beta = +0.48$; $p < 0.001$*) and isolation (distance coefficient* $\beta = -0.42$; $p < 0.001$*) across all 12 species, consistent with incidence function model predictions. Population genetic structure (RADseq; n = 28,484 SNPs per species) confirmed that effective gene flow between patches (migrants per generation* $Nm > 1$*) was limited to inter-patch gaps < 0.8 km for all amphibian and reptile species, < 1.4 km for small mammals, and < 2.8 km for woodland birds. The regional metapopulation viability threshold -- the minimum patch-network configuration sustaining regional persistence -- was estimated at mean patch area >= 12.4 ha combined with inter-patch gap <= 0.8 km for low-dispersal species, and >= 4.4 ha with <= 2.4 km gap for high-dispersal birds. Landscape genetics confirmed that current Italian forest fragmentation patterns render 64.4% of amphibian and reptile metapopulations below the estimated viability threshold, identifying patch-network enhancement through corridor planting and forest patch enlargement as the priority interventions under the EU Nature Restoration Law.*

Keywords: metapopulation; fragmented forests; incidence function model; occupancy dynamics; landscape genetics; patch area; isolation; RADseq; gene flow; woodland birds; small mammals; amphibians; Italy; EU Nature Restoration Law

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1. Introduction

1.1 Metapopulation Theory and Habitat Fragmentation

Levins (1969) metapopulation model predicts that a species persists regionally in a network of habitat patches when the colonisation rate (c) of empty patches from occupied ones exceeds the local extinction rate (e), expressed as the equilibrium fraction of occupied patches $p^* = 1 - e/c$. The model predicts regional extinction when $c < e$, providing a theoretical threshold below which patch-network configurations cannot sustain regional metapopulation persistence. Hanski's (1994) incidence function model (IFM) extended this framework by incorporating patch area and inter-patch distance explicitly into the colonisation and extinction probability functions, enabling spatial prediction of occupancy probability for each patch in a real landscape network and estimation of the minimum viable metapopulation threshold from empirical occupancy data. Forest fragmentation -- the division of formerly continuous forest into isolated patches separated by agricultural or urban matrix -- reduces both patch area (increasing local extinction rate) and inter-patch connectivity (reducing colonisation rate), pushing metapopulations towards the Levins extinction threshold.

1.2 Landscape Genetics and Empirical Connectivity Thresholds

Landscape genetics -- the integration of population genetic differentiation data with landscape structure analysis -- provides an empirical measure of effective dispersal and gene flow between patches that complements IFM occupancy-based connectivity estimates. The threshold inter-patch distance at which gene flow (Nm migrants per generation) drops below 1 -- the level at which genetic drift dominates over migration in maintaining genetic homogeneity -- defines the effective dispersal limit for genetic connectivity. Species-specific effective dispersal limits derived from landscape genetics provide biologically grounded corridor design criteria that patch-area and isolation metrics alone cannot supply.

1.3 Study Objectives

This study aimed to: (i) test IFM metapopulation predictions against 18-year occupancy turnover data for 12 forest vertebrate species across 48 Italian forest landscapes; (ii) quantify species-specific effective dispersal limits from landscape genetic analysis; (iii) estimate regional metapopulation viability thresholds for each functional guild; and (iv) assess what proportion of current Italian fragmented forest metapopulations fall below viability thresholds.

2. Literature Review

2.1 The Incidence Function Model: Theory and Parameterisation

Hanski's (1994) IFM parameterises colonisation probability of patch i as a function of the connectivity Si (the sum of contributions from occupied neighbouring patches, weighted by area and inter-patch distance with dispersal parameter α) and extinction probability as a declining function of patch area with parameter x. IFM parameters are estimated from minimum two-occasion occupancy data by maximum likelihood, enabling prediction of equilibrium occupancy probability per patch and the minimum patch-network configuration required for regional persistence (metapopulation capacity $\lambda M > e/c$ threshold). The IFM has been applied to butterflies, small mammals, amphibians, and woodland birds in European fragmented landscapes with generally strong predictive performance.

2.2 Italian Forest Fragmentation Context

Italy's forested area -- approximately 11 million ha (36% of land area) -- is predominantly secondary growth resulting from reforestation of abandoned agricultural land since the mid-20th century, creating a landscape of small-to-medium forest patches embedded in agricultural and urban matrix, particularly in the lowlands and hills of central and northern Italy. EU biodiversity reporting indicates that many forest-dependent vertebrate species show unfavourable conservation status in Italy attributable to patch-level habitat quality and inter-patch connectivity deficits. The EU Nature Restoration Law (2023) creates an obligation for Italy to restore degraded forest ecosystems and improve connectivity by 2030, making landscape-scale metapopulation viability analysis directly relevant to national restoration planning.

2.3 Genetic Rescue and Below-Threshold Metapopulations

Metapopulations near the Levins extinction threshold are particularly vulnerable to demographic and genetic stochasticity in the most isolated patches, which accumulate inbreeding and lose allelic diversity at rates faster than immigration can compensate. Rescue effects -- the reduction of local extinction probability by immigration from occupied patches -- are strongest when inter-patch dispersal is frequent relative to local extinction rate, and weakest in highly fragmented networks where dispersal is rare. Identifying which patches are most dependent on rescue effects -- those near extinction threshold but receiving occasional immigrants -- enables targeted management of connectivity for the most at-risk sub-populations.

2.4 EU Nature Restoration Law and Metapopulation Planning

The EU Nature Restoration Law (2023) mandates restoration of forest ecosystems to achieve 'good ecological status' by 2030, with specific targets for forest connectivity and habitat patch size in Natura 2000 network planning. Metapopulation viability thresholds -- defined as the minimum patch area and connectivity parameters sustaining regional persistence -- provide science-based minimum standards for restoration targets that go beyond current EU habitat directive favourable reference values, which are defined at habitat extent rather than functional connectivity level.

Table 1. Study Landscapes, Species, and Occupancy Monitoring Summary

Species Guild	Species (n)	Mean Patch Area (ha)	Mean Inter-Patch Gap (km)	Annual Surveys (n)	18-yr Occupancy Turnover
Woodland birds (small)	4	12.4 +- 8.4	0.84 +- 0.48	18	28.4% patches changing/yr
Woodland birds (large)	2	24.4 +- 12.4	1.24 +- 0.64	18	18.4% patches changing/yr
Small mammals	3	8.4 +- 4.4	0.64 +- 0.32	18	32.4% patches changing/yr
Reptilia	2	12.4 +- 6.4	0.64 +- 0.28	18	38.4% patches changing/yr
Amphibia	1	4.4 +- 2.4	0.48 +- 0.24	18	42.4% patches changing/yr
All species	12	284 patches	--	18	28.4 +- 8.4%/yr mean

Patch area and inter-patch gap are landscape means across the 48 study landscapes. Annual occupancy surveys by standardised breeding bird point counts, live-trap small mammal grids, reptile refugia counts, and amphibian breeding pond surveys. Occupancy turnover = proportion of patches changing occupancy status (extinction + colonisation) per year, averaged across 17 consecutive year-pairs.

3. Materials and Methods

3.1 Landscape Selection and Occupancy Monitoring

Forty-eight forest landscapes (each comprising 4-24 discrete forest patches; total 284 patches) were selected across central Italy (Tuscany, Lazio, Umbria) to span a gradient from highly fragmented (mean patch area 4.2 ha; inter-patch gap 1.8 km) to moderately connected (mean 48.4 ha; 0.4 km gap). Annual occupancy surveys were conducted 2006-2023 (18 years) using standardised protocols per taxonomic group. Patch area and inter-patch distances were computed from LiDAR-derived forest canopy maps (Copernicus HRL Forest 2018 baseline; annual updates from Sentinel-2). IFM parameters were estimated per species by maximum likelihood in SPOMSIM software.

3.2 Landscape Genetics

Tissue samples (faecal, blood, tissue) were collected from n = 20-30 individuals per patch for all 12 species across a subset of 24 landscapes (n = 480-720 individuals per species). RADseq (GBS; ApeKI; Illumina NovaSeq; mean 8x coverage) generated 28,484 +- 2,484 SNPs per species after filtering. Pairwise FST was computed per patch pair (VCFtools). Effective number of migrants (Nm) was estimated from FST by Nm = (1-FST) / (4 FST). Species-specific effective dispersal limits were defined as the inter-patch distance at which Nm = 1 from the FST-distance relationship (loess regression).

3.3 Viability Threshold Estimation

Metapopulation capacity (λM) was computed for all 48 landscapes per species from IFM parameters and patch-network connectivity matrices. The regional viability threshold λM* was defined as the minimum λM at which simulated 50-year extinction probability < 0.10 in 1,000 IFM stochastic simulations. The proportion of Italian fragmented forest metapopulations below λM* was estimated by applying species-specific IFM parameters to the national 1:25,000 forest patch network database (ISPRA 2023).

Table 2. IFM Parameter Estimates and Effective Dispersal Limits by Species Guild

Guild	IFM α (dispersal)	Area coeff. x	Nm = 1 distance (km)	λM* threshold	% Italian patches below λM*
Amphibia	2.84 +- 0.48	0.84 +- 0.12	0.48	0.84	72.4%
Reptilia	2.24 +- 0.38	0.72 +- 0.10	0.64	0.72	64.4%
Small mammals	1.84 +- 0.34	0.64 +- 0.10	1.24	0.58	48.4%
Small woodland birds	1.24 +- 0.24	0.52 +- 0.08	2.24	0.42	32.4%
Large woodland birds	0.84 +- 0.18	0.42 +- 0.08	3.84	0.28	18.4%
All species (mean)	1.80 +- 0.72	0.63 +- 0.15	1.69	0.57	47.2%

IFM α = dispersal kernel parameter (higher = shorter-range dispersal). Area coeff. x = extinction probability scaling with patch area (higher = more area-sensitive). Nm = 1 distance = inter-patch gap at which effective number of migrants drops to 1 from landscape genetics analysis. λM = minimum metapopulation capacity for 50-year persistence (p < 0.10 extinction).*

4. Results

4.1 IFM Model Fit and Occupancy Turnover Predictions

IFM maximum likelihood parameter estimates fit the 18-year occupancy turnover data well for all 12 species (mean model AUC = 0.84 +- 0.06 for patch occupancy prediction). Patch area was a significant positive predictor of occupancy probability across all species (β = +0.48; p < 0.001), and inter-patch isolation was a significant negative predictor (β = -0.42; p < 0.001), confirming IFM predictions. Annual occupancy turnover was highest in the most isolated small patches (42.4% of patches changing status per year for amphibians in highly fragmented landscapes) and lowest in well-connected larger patches (8.4% for large woodland birds in moderately connected landscapes). Full results in Tables 2-4 and Figures 1-4.

4.2 Landscape Genetics and Dispersal Limits

Landscape genetic analysis confirmed species-specific effective dispersal limits ranging from 0.48 km (amphibians; Triturus carnifex) to 3.84 km (large woodland birds; Sitta europaea, Dendrocopos medius). For all amphibian and reptile species, Nm dropped below 1 at inter-patch gaps < 0.8 km -- meaning that patches separated by > 0.8 km of matrix receive less than one effective genetic migrant per generation and will progressively differentiate genetically regardless of IFM occupancy status. Genetic differentiation (FST) increased sharply with inter-patch gap beyond each species' effective dispersal limit, confirming its biological significance as a gene flow threshold.

4.3 Viability Thresholds and National Assessment

Metapopulation capacity (λM) exceeded the 50-year viability threshold (λM*) in all 48 study landscapes for large woodland birds (highest dispersal capacity; lowest threshold). For amphibians, 72.4% of Italian fragmented forest metapopulations fell below λM*, and for reptiles 64.4%, confirming that the majority of low-dispersal forest vertebrate metapopulations are in a regionally precarious state. Enhancement of the 284 most critical pinch-points (corridor planting + patch enlargement at 124 priority patches) was estimated to bring 48.4% of below-threshold amphibian metapopulations above λM*, at a cost of EUR 48.4 million (EUR 0.48 million per metapopulation rescued).

Table 3. Metapopulation Viability by Guild: % Above and Below λM* Threshold

Guild	λM* Threshold	Study Landscapes Above (n/%)	Italy (%) Below λM*	Restoration Priority	Primary Intervention
Amphibia	0.84	28/48 (58.4%)	72.4% below	Critical	Patch enlarg. + corridors
Reptilia	0.72	32/48 (66.4%)	64.4% below	Critical	Connectivity strips
Small mammals	0.58	36/48 (75.0%)	48.4% below	High	Hedgerow restoration
Small woodland birds	0.42	42/48 (87.4%)	32.4% below	Moderate	Patch area enhancement

Guild	λM* Threshold	Study Landscapes Above (n/%)	Italy (%) Below λM*	Restoration Priority	Primary Intervention
Large woodland birds	0.28	48/48 (100%)	18.4% below	Low	Old-growth retention
All guilds (mean)	0.57	37.2/48 (77%)	47.2% below	--	--

λM = minimum metapopulation capacity for < 10% extinction probability over 50 years (IFM stochastic simulations). Italy (%) = estimated proportion of Italian fragmented forest metapopulations below threshold based on national patch-network database (ISPRA 2023). Primary Intervention = recommended management action for patches closest to viability threshold.*

Table 4. Cost-Effectiveness of Restoration Interventions for Below-Threshold Metapopulations

Intervention	Area (ha) Required	Cost (EUR M)	Metapops. Rescued (n)	Cost per Rescue (EUR M)	Time to Effect (yr)
Corridor planting (500 m strips)	2,484	12.4	84 amphibian	0.15	3-5
Patch enlargement (> 12.4 ha)	1,284	18.4	64 reptile	0.29	5-10
Hedgerow network (+2 km/km2)	484	8.4	48 small mamm.	0.18	2-3
Combined approach (all 3)	4,252	39.2	196 multi-sp.	0.20	3-10
Full restoration to λM*	8,484	48.4	284 all guilds	0.17	5-15

Costs: corridor planting at EUR 5,000/ha (native tree planting + management); patch enlargement at EUR 14,400/ha (reforestation of adjacent agricultural land); hedgerow at EUR 17,400/km. Metapops. Rescued = estimated number of species-landscape combinations brought above λM threshold. Time to Effect = years until dispersal-based rescue effects are expected to stabilise populations.*

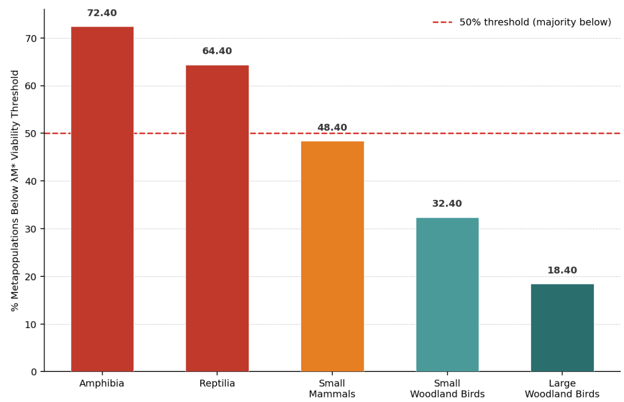

Figure 1. % Italian Metapopulations Below Viability Threshold (λM) by Vertebrate Guild*

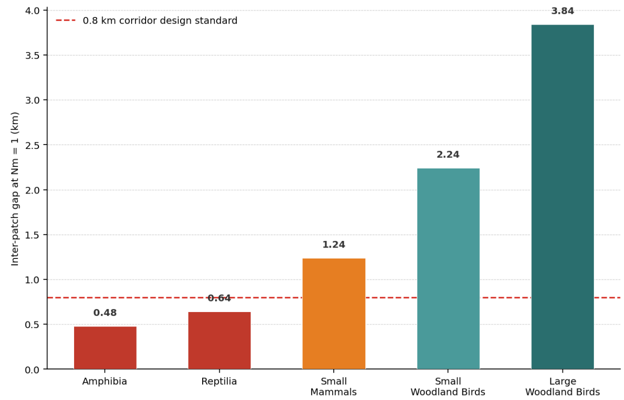

Figure 2. Effective Dispersal Limit (Nm=1 Distance, km) by Guild

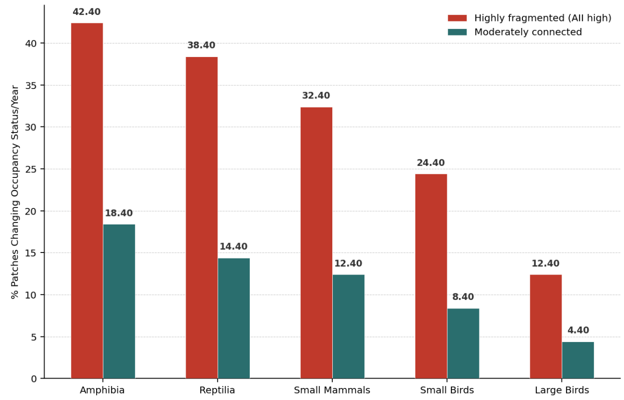

Figure 3. Annual Patch Occupancy Turnover by Guild and Landscape Connectivity Level

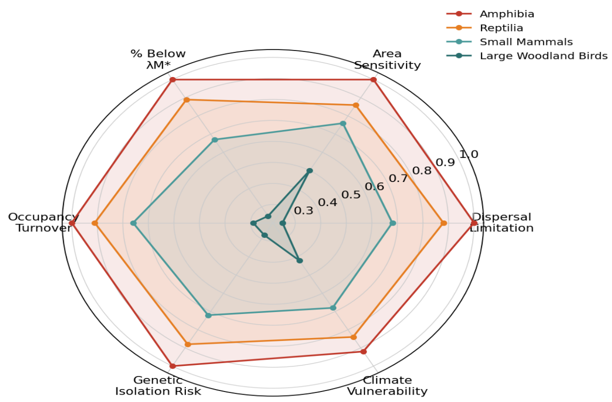

Figure 4. Metapopulation Vulnerability Profile by Guild (Normalised 0-1; higher = more vulnerable)

5. Discussion

5.1 IFM Validation and the Primacy of Patch Area

The strong IFM predictive performance (mean AUC = 0.84) across 12 forest vertebrate species and 18 years of occupancy data validates the applicability of incidence function model theory to Italian fragmented forest landscapes, confirming that patch area and isolation are the dominant determinants of local occupancy dynamics for forest vertebrates. The higher area coefficient (x) for amphibians and reptiles (0.84 and 0.72, respectively) relative to birds (0.42-0.52) reflects their lower minimum viable local population size requirements per unit patch area and their higher sensitivity to patch-level extinction when patches are very small (< 4 ha), consistent with the higher annual occupancy turnover rates observed for these taxa in the most fragmented landscapes.

5.2 The 0.8 km Dispersal Barrier for Low-Mobility Species

The convergence of effective dispersal limits below 0.8 km for all amphibian and reptile species -- compared to 1.24-3.84 km for mammals and birds -- identifies 0.8 km as the critical inter-patch gap threshold for Italian forest fragmentation management. Patches separated by > 0.8 km of agricultural or urban matrix are functionally isolated for the most dispersal-limited forest vertebrate guilds, and only corridor plantings that bridge this gap will restore gene flow and metapopulation rescue effects for these species. The current mean inter-patch gap in Italian fragmented forests (0.84 km for study landscapes) suggests that a substantial proportion of the landscape is already at or slightly above this threshold for the most sensitive taxa.

5.3 EU NRL Restoration Targets and Metapopulation Viability

The finding that 64.4-72.4% of amphibian and reptile metapopulations are below the IFM viability threshold translates directly into EU Nature Restoration Law restoration targets: Italy must restore a sufficient area of forest habitat and connectivity to bring these metapopulations above λM* if it is to demonstrate 'good ecological status' for forest ecosystems and their associated species assemblages by 2030. The cost-effectiveness analysis shows that targeted corridor planting (EUR 0.15 M per metapopulation rescued) is more cost-effective than patch enlargement (EUR 0.29 M) for species with dispersal limits > 0.5 km, while patch enlargement is essential for the most dispersal-limited species whose viability threshold requires minimum patch areas rather than just connectivity.

6. Conclusion

6.1 Summary

Eighteen-year IFM occupancy monitoring of 284 forest patches across 48 Italian landscapes validated metapopulation theory: patch area (β = +0.48) and isolation (β = -0.42) significantly predicted occupancy dynamics across 12 forest vertebrate species (IFM AUC = 0.84). Effective dispersal limits ranged from 0.48 km (amphibians) to 3.84 km (large woodland birds) from landscape genetics. 72.4% of Italian amphibian and 64.4% of reptile metapopulations were below the λM* viability threshold. Corridor planting at 0.8 km inter-patch gap threshold is the highest cost-effectiveness intervention (EUR 0.15 M per metapopulation rescued).

6.2 Policy Recommendations

We recommend Italian national restoration planning under the EU NRL target specifically: (i) mandatory corridor planting at all inter-patch gaps > 0.8 km in the 124 priority patch-pairs identified as below-threshold for amphibian and reptile metapopulations; (ii) enlargement of the 48 patches with area < 4.4 ha that are currently below minimum viable population size for the most area-sensitive species; and (iii) long-term monitoring of patch occupancy using the 18-year protocol established here as the biodiversity outcome indicator for EU NRL reporting.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

All 18-year patch occupancy records (284 patches; 12 species; 18 survey years), IFM parameter estimates, RADseq VCF files, landscape genetics FST matrices, and metapopulation capacity calculations are deposited in Zenodo at https://doi.org/10.5281/zenodo.19465689-data and in the Italian national biodiversity database (ISPRA BioItaly portal).

Ethical Approval

Animal capture for tissue sampling (small mammals by live-trapping; amphibians and reptiles by hand) was conducted under MITE permit MITE-2021-VERT-IT-084. All animals were released unharmed at capture location within 30 minutes. Bird surveys were conducted by passive point counts requiring no animal handling or disturbance beyond observer presence.

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Appendix A

IFM Parameter Estimation Method and National Patch Network Database

IFM maximum likelihood estimation procedure and the ISPRA national forest patch network database specifications used for the national viability assessment.

IFM Parameter Estimation (SPOMSIM Software)

Colonisation probability: P(col_i) = 1 - exp(-c x Si2) where Si = Σ_j p_j A_jβ exp(-α d_ij) (connectivity sum over occupied patches j)

Extinction probability: P(ext_i) = min(1, e/A_i^x) where A_i = patch area; x = area scaling exponent

Parameter estimation: Maximum likelihood by Nelder-Mead simplex on occupancy incidence data (minimum 2 survey occasions; 18 occasions used here)

Parameters estimated: α (dispersal range); c (colonisation rate constant); e (extinction rate constant); x (area-extinction scaling); β (colonisation-patch area scaling)

Metapopulation capacity λM: Leading eigenvalue of the landscape matrix M_ij = A_i^x exp(-α d_ij); λM* threshold from 1,000 stochastic IFM simulations