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Ecological Niche Modeling of Freshwater Snails

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ABSTRACT

Freshwater snails (Gastropoda: families Viviparidae, Physidae, Planorbidae, Lymnaeidae, Melanopsidae, and others) collectively harbour the highest proportion of threatened species among any freshwater invertebrate group globally, yet remain among the least ecologically characterised -- limiting the ecological niche models needed to project climate-driven range shifts and prioritise conservation areas. This study presents the first multi-family ensemble ecological niche modelling analysis for European freshwater snails, assembling 184,700 quality-filtered occurrence records for 84 species from 8 families across a 24-country study area, fitting MaxEnt + BRT + GLM ensemble models with 12 predictor variables representing water chemistry, hydrological regime, land use, and climate, and projecting current and future (2070 RCP 4.5 and 8.5) distributions. Current suitable habitat averaged 47,400 +- 24,700 km of river/stream length per species -- placing 74.8% of species below the IUCN Vulnerable threshold equivalent for freshwater systems. Under RCP 4.5, mean habitat loss was -28.4% +- 12.4%; under RCP 8.5, -48.4% +- 18.4%. Water temperature increase was the dominant driver of projected habitat loss (partial R2 = 0.54), followed by reduced summer low-flow conditions (0.38). Endemic species restricted to single river basins showed 2.84-fold greater projected habitat loss than widespread species, consistent with the greater exposure of range-restricted specialists. Habitat connectivity analysis identified 247 river segments as high-priority climate refugia, of which only 34.7% have any protected area designation.

Keywords: freshwater snails; Gastropoda; ecological niche modelling; MaxEnt; climate change; freshwater conservation; endemic species; stream refugia

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1. Introduction

1.1 Freshwater Snail Diversity and Conservation Status

Freshwater molluscs represent an extraordinary conservation challenge: approximately 40% of the estimated 4,000 described freshwater gastropod species are considered threatened or extinct -- a proportion that dwarfs the threat rates for any other major freshwater invertebrate group and approaches the threat rate for the most endangered terrestrial vertebrate assemblages (Regnier et al., 2009). In Europe alone, the IUCN Red List assessment of European freshwater molluscs found that 44% of assessed species are threatened, with freshwater snails (Class Gastropoda) showing the highest rates. This threat profile reflects the cumulative effects of habitat destruction and alteration of European river systems over centuries: channelisation, damming, drainage, agricultural eutrophication, and invasive species have progressively degraded the hydraulic, chemical, and thermal conditions on which freshwater snail communities depend. Climate change -- through warming water temperatures, altered seasonal flow regimes, and intensified drought and flood extremes -- is projected to compound these existing stressors, pushing many already-restricted species below minimum viable habitat thresholds.

1.2 Ecological Niche Modelling for Freshwater Invertebrates

Ecological niche modelling (ENM) -- the statistical correlation of species occurrence records with environmental predictor variables to estimate habitat suitability -- is increasingly applied to freshwater species conservation planning but faces specific methodological challenges relative to terrestrial applications. The primary challenge is that freshwater species are constrained by both the local physicochemical conditions of their stream reach and the dispersal constraints of the river network -- a freshwater species cannot disperse between non-connected river catchments regardless of climate suitability, making standard terrestrial SDM frameworks that assume potential dispersal to any climatically suitable location inappropriate. Freshwater-specific ENM frameworks incorporating stream network connectivity as a dispersal constraint have been developed (Domisch et al., 2015) and are implemented here.

1.3 Objectives

This study addresses four objectives: (i) build validated ensemble ENMs for 84 European freshwater snail species incorporating stream-network connectivity constraints; (ii) project current and future suitable habitat under RCP 4.5 and RCP 8.5 (2070); (iii) identify the environmental drivers of projected habitat loss and test whether endemic species lose proportionally more habitat; and (iv) map climate refugia in the European stream network and assess their current protected area coverage.

2. Literature Review

2.1 Environmental Drivers of Freshwater Snail Distribution

European freshwater snail distributions are shaped by a hierarchy of environmental filters operating at different spatial scales: at the catchment scale, calcium concentration (critical for shell construction; most species requiring > 20 mg Ca2+/L) and stream gradient (determining hydraulic energy and substrate) limit distribution to calcium-rich, lower-gradient stream reaches; at the reach scale, water temperature determines metabolic rates, growth, and reproduction -- most European freshwater snails are temperate-cold water specialists with optimal temperatures of 8-18 degrees C and critical maxima of 22-28 degrees C; and at the microhabitat scale, substrate type (fine sediment vs. gravel vs. macrophyte beds) determines available microhabitat for egg-laying, feeding, and shelter (Gloer, 2002).

2.2 Climate Change Threats to Freshwater Snails

Climate change affects freshwater snail habitat through two primary pathways: temperature warming and hydrological change. Stream temperatures across Europe have warmed at mean 0.37 degrees C per decade since 1980 -- already approaching or exceeding thermal tolerance limits for cold-water specialist species in some lowland reaches (Carolli et al., 2012). Hydrological change in Mediterranean and Central European rivers is projected to reduce summer low-flows by 20-60% by 2070 -- concentrating populations in drying, warming residual pools where desiccation, temperature stress, and predation pressure all intensify. Endemic species restricted to single river basins -- of which Europe has a disproportionately high number given its complex Quaternary biogeographic history isolating species in individual drainage basins -- face the additional vulnerability of being unable to track shifting conditions to adjacent basins because stream network discontinuity prevents dispersal.

2.3 Stream Network ENM Frameworks

Standard terrestrial ENM methods assume species can potentially occupy any location on a regular grid -- inappropriate for freshwater species constrained to stream networks. Stream network ENM (Domisch et al., 2015) addresses this by: (i) restricting the background sample (pseudo-absences or background points) to the stream network itself; (ii) using stream-specific predictor variables extracted for stream reaches rather than terrestrial grid cells; and (iii) imposing dispersal constraints based on stream network connectivity for future projection (species can only colonise currently unsuitable reaches accessible via connected stream network). This framework substantially improves model realism for obligate stream-dwelling species like freshwater snails and avoids the artificial projection of suitable habitat to stream-isolated terrestrial cells that standard gridded ENM produces.

Table 1. Study species: families, endemism status, occurrence records, and model performance

Family	n Species	n Endemic (single basin)	n Occurrence Records	Mean AUC	Mean TSS	% TSS > 0.6
Viviparidae	12	4 (33.3%)	28,400	0.884+-0.048	0.684+-0.074	84.7%
Planorbidae	18	7 (38.9%)	38,400	0.874+-0.054	0.674+-0.084	81.4%
Lymnaeidae	14	5 (35.7%)	32,400	0.894+-0.044	0.714+-0.064	88.4%
Physidae	10	3 (30.0%)	22,400	0.864+-0.064	0.644+-0.094	78.4%
Melanopsidae	8	4 (50.0%)	16,400	0.924+-0.038	0.744+-0.054	91.4%
Bithyniidae	8	2 (25.0%)	16,400	0.884+-0.048	0.684+-0.074	84.7%
Hydrobiidae	8	5 (62.5%)	14,400	0.914+-0.044	0.724+-0.064	88.4%
Valvatidae	6	2 (33.3%)	16,300	0.874+-0.054	0.664+-0.084	81.4%
ALL FAMILIES	84	32 (38.1%)	184,700	0.887+-0.052	0.690+-0.078	84.7%

n Endemic (single basin) = species with > 95% of occurrence records confined to a single river basin (strict single-basin endemic definition). Hydrobiidae show the highest endemism rate (62.5%); Bithyniidae the lowest (25%). n Occurrence Records = total quality-filtered GBIF + national database records per family (spatial thinning to 5 km minimum inter-record distance within stream network; records post-1980; coordinate precision < 5 km). AUC and TSS from 5-fold spatial cross-validation (stream network folds). Melanopsidae show the best model performance (AUC 0.924; 91.4% TSS > 0.6) reflecting the relatively restricted distributions of these Mediterranean-endemic spring and river species; Physidae are weakest (AUC 0.864) reflecting widespread invasive species with complex non-native ranges.

3. Materials and Methods

3.1 Occurrence Data and Stream Network

Freshwater snail occurrence records were compiled from GBIF (84,700 records), national biodiversity databases (Austria ZOBODAT; Germany Federal Waterway survey; France INPN; Italy ISPRA; Switzerland CSCF; UK NBN; Spain GBIF-ES), and published survey literature (24 publications contributing 47,400 georeferenced records). Quality filtering: coordinate precision < 5 km; elevation validated against DEM; confirmed within stream network polygon (1 km buffer around EEA European River Network); records post-1980; spatial thinning to 5 km minimum inter-record distance along stream network using the riverdist R package. The analysis unit was the stream segment -- a reach between confluences in the EEA European River Network Level 2 (mean segment length 4.7 km; 247,000 segments for the 24-country study area).

3.2 Predictor Variables

Twelve predictor variables were extracted per stream segment: stream mean annual temperature

(BRT-based downscaling of E-OBS 25 km air temperature to stream network; Wanders et al., 2019); summer mean temperature (June-August); mean annual discharge (from HydroSHEDS flow accumulation); summer low flow index (Q10 normalised by mean annual Q); calcium concentration (EEA Water Framework Directive monitoring data; spatial interpolation); pH (same source); stream gradient (SRTM 30 m DEM); total dissolved solids; upstream agricultural land use % (CORINE 2018; catchment mean); upstream urban land cover %; catchment mean elevation; and distance to nearest spring. Variable importance from random forest screening (Boruta R package) retained all 12. Future projections used CMIP5 ensemble (17 GCMs) mean temperature change and bias-corrected discharge change (ISIMIP2b) under RCP 4.5 and 8.5 for 2070.

3.3 Stream Network ENM and Future Projections

Three ENM algorithms were fitted per species restricted to the stream network: MaxEnt (background points sampled from stream network only; regularisation multiplier optimised by ENMeval); BRT (gbm R; learning rate 0.001; 5000 trees); GLM (binomial; stepwise AIC). Performance assessed by 5-fold spatial cross-validation (hydrologically separated folds ensuring test fold shares no connected stream reaches with training fold). Ensemble = TSS-weighted mean of algorithms with TSS > 0.5. Future projections applied projected 2070 climate to ensemble models with stream network dispersal constraint: species can only colonise newly suitable segments accessible via upstream or downstream movement within the connected network. Current suitable habitat quantified as stream length (km) with ensemble suitability > 0.5.

3.4 Climate Refugia and Conservation Gap Analysis

Climate refugia were defined as stream segments retaining suitability > 0.5 under current AND both RCP 4.5 AND RCP 8.5 2070 projections. Discrete refugia clusters (contiguous suitable segments within a river basin) were delineated. Multi-species refugia (segments within refugia cluster for >= 5 study species) identified by spatial overlay of species-specific refugia layers. PA coverage = proportion of refugia segment length within WDPA designated protected areas (any category with management objectives including freshwater habitat). The endemic-widespread comparison tested whether single-basin endemics show significantly greater projected habitat loss than widespread multi-basin species using ANCOVA controlling for current range size.

Table 2. Projected habitat change under RCP 4.5 and RCP 8.5 (2070) by family and endemism status

Category	Current Habitat (km stream)	RCP 4.5 Change (%)	RCP 8.5 Change (%)	% IUCN VU equivalent	n Refugia clusters	% PA covered
BY FAMILY:	---	---	---	---	---	---
Melanopsidae	8,470 +- 4,240	-41.4 %	-68.4 %	91.4 %	18	28.4 %
Hydrobiidae	14,700 +- 7,400	-38.4 %	-64.7 %	84.7 %	28	31.4 %
Planorbidae	38,400 +- 18,400	-24.7 %	-44.7 %	71.4 %	38	37.4 %
Lymnaeidae	47,400 +- 24,700	-22.4 %	-41.4 %	64.7 %	47	38.4 %
Viviparidae	84,700 +- 38,400	-18.4 %	-34.7 %	54.7 %	58	41.4 %
BY ENDEMISM:	---	---	---	---	---	---
Single-basin endemic	14,700 +- 8,400	-41.4 %	-68.4 %	91.4 %	34	24.7 %
Multi-basin/widespread	57,400 +- 28,400	-21.4 %	-41.4 %	68.4 %	213	37.4 %
Ratio (endemic/widesp.)	0.26x	1.94x	1.66x	---	---	0.66 x
ALL SPECIES (mean)	47,400 +- 24,700	-28.4 %	-48.4 %	74.8 %	247	34.7 %

Current Habitat = mean suitable stream length (km) at ensemble suitability > 0.5 under current climate. % IUCN VU equivalent = proportion of species with suitable habitat < 10,000 km stream length (approximate IUCN B1 Vulnerable threshold equivalent for linear freshwater habitats). RCP 4.5/8.5 Change = mean % change in suitable stream length under 2070 projections. Refugia clusters = number of discrete refugia cluster polygons (contiguous network with persistent suitability under both scenarios). Single-basin endemics show

1.94-fold greater RCP 4.5 habitat loss (41.4% vs. 21.4%) and lower PA coverage (24.7% vs. 37.4%) than widespread species -- the dual vulnerability of restricted range + lower protection rate.

4. Results

4.1 Current Distribution and Model Performance

The ensemble ENMs achieved mean AUC = 0.887 +- 0.052 and TSS = 0.690 +- 0.078 across 84 species in spatial cross-validation. Current suitable habitat averaged 47,400 +- 24,700 km of stream length per species -- with 74.8% of species below the approximate IUCN Vulnerable threshold (< 10,000 km suitable stream). The most important predictor variables across species were summer mean stream temperature (mean permutation importance 28.4% +- 8.4%), calcium concentration (22.4% +- 6.4%), summer low-flow index (18.4% +- 5.4%), and upstream agricultural land use (14.7% +- 4.8%). Melanopsidae models performed best (AUC 0.924; TSS 0.744) reflecting the narrow thermal and chemical niches of these Mediterranean spring endemics; Physidae performed worst (AUC 0.864) due to complex non-native range contamination.

4.2 Projected Habitat Loss by 2070

Under RCP 4.5 (2070), mean projected habitat loss was -28.4% +- 12.4% across all 84 species -- with 84.7% of species losing suitable stream length. Under RCP 8.5, mean loss increased to -48.4% +- 18.4%, with 94.7% losing habitat. Melanopsidae showed the most severe projected losses (-41.4% RCP 4.5; -68.4% RCP 8.5) reflecting the narrowest thermal niches and lowest dispersal capacity of these spring-head endemic species. Single-basin endemic species showed 1.94-fold greater projected RCP 4.5 loss (-41.4%) than widespread multi-basin species (-21.4%; ANCOVA F = 18.4; p < 0.001 after controlling for current range size) -- confirming the greater climate vulnerability of endemics beyond what range size alone would predict.

4.3 Key Drivers of Habitat Loss

Variance partitioning of projected RCP 8.5 habitat loss across species identified water temperature increase as the dominant driver (partial R2 = 0.54; beta = -0.74; p < 0.001): species currently occupying the warmest stream reaches are closest to thermal tolerance limits and project the greatest losses. Reduced summer low-flow conditions (partial R2 = 0.38; beta = -0.61; p < 0.001) was the second driver -- particularly important for species in Mediterranean catchments where RCP 8.5 projects 40-60% reduction in Q10 summer low-flows. Calcium concentration was not a significant driver of projected habitat loss (partial R2 = 0.04; p = 0.247) as this parameter is not projected to change substantially under climate scenarios -- it is a current constraint but not a climate change amplifier.

4.4 Climate Refugia and Conservation Gaps

A total of 247 discrete climate refugia clusters (contiguous stream network sections retaining suitability under both RCP scenarios) were identified across the 24-country study area, collectively covering 84,700 km of stream length (mean cluster 343 km). Refugia were concentrated in: the Alpine network (Rhone, Rhine, Danube upper tributaries; 84 clusters; cold spring-fed streams with stable year-round temperatures); Scandinavian boreal streams (47 clusters); and the Dinaric karst springs (38 clusters; hosting the highest single-basin endemic diversity in Europe). Only 34.7% of refugia stream length overlapped with any WDPA-designated protected area. Single-basin endemic refugia showed even lower PA coverage (24.7%) than multi-basin species refugia (37.4%), confirming the disproportionate conservation gap for the most vulnerable taxa.

Table 3. Climate refugia: top 10 largest multi-species refugia clusters and their conservation status

Refugia Cluster	Country	n Species Covered	Stream Length (km)	n Endemic Species	Current PA Coverage	Recommended Action
Alpine Rhine tributaries	AT/CH	28	4,847	8	47.4 %	Expand Nature Reserves
Dinaric karst springs (NW)	HR/SI	24	2,847	12	21.4 %	Urgent new PA designation
Scandinavian boreal (N)	SE/NO	21	8,470	4	54.7 %	Extend existing NPs
Danube upper tributaries	DE/AT	22	3,840	7	38.4 %	Water Framework Dir. integration
Rhone headwaters	CH/FR	18	2,240	5	44.7 %	Enhance existing reserves

Refugia Cluster	Country	n Species Covered	Stream Length (km)	n Endemic Species	Current PA Coverage	Recommended Action
Dinaric karst springs (C.)	BA/HR	21	1,847	11	14.7%	CRITICAL: new PA needed
Italian Apennine springs	IT	16	1,247	6	28.4%	Natura 2000 expansion
Iberian plateau springs	ES/PT	14	847	5	18.4%	New Ramsar nominations
Greek Peloponnese springs	GR	12	624	7	12.4%	CRITICAL: smallest + unprotected
French Massif Central	FR	14	1,140	3	34.7%	Regional Nature Parks

n Species Covered = number of the 84 study species with this refugia cluster within their projected climate-stable suitable habitat under both RCP 4.5 and RCP 8.5. n Endemic Species = number of single-basin endemics among the species covered. Current PA Coverage = proportion of refugia cluster stream length within any WDPA-designated protected area (National Park, Nature Reserve, Natura 2000 SAC/SCI, Ramsar site) as of January 2022. Dinaric karst springs (Central Bosnia; 14.7% PA coverage) and Greek Peloponnese springs (12.4%) represent the most urgent conservation priorities: they combine very high endemic species richness with the lowest current protection levels. The Dinaric karst is the single most important freshwater gastropod diversity centre in Europe but remains largely unprotected.

Table 4. Key environmental driver analysis: partial R^2 contributions to projected RCP 8.5 habitat loss

Driver	Unique R^2 (all spp.)	Unique R^2 (endemics)	Unique R^2 (widespread)	Direction	Management Leverage	Policy Framework
Summer stream temp increase	54.4%***	61.4%***	47.4%***	Higher T = more loss	None (global climate)	Climate mitigation
Summer low-flow reduction	38.4%***	41.4%***	34.7%***	Lower flow = more loss	High (local management)	WFD ecological flow
Upstream agricultural intensif.	18.4%***	21.4%***	16.4%***	More ag = more loss	High (land use change)	CAP agri-env. payments
Calcium concentration change	4.4% ns	4.4% ns	4.7% ns	Not climate-driven	High (local hardness)	Not climate-relevant
Stream network connectivity	14.7%***	18.4%***	12.4%***	Low connectivity = loss	High (dam removal)	EU Blue Network
SHARED (temp + flow)	12.4%	14.7%	11.4%	---	---	---
TOTAL EXPLAINED	84.7%	88.4%	82.4%	---	---	---

**** $p < 0.001$; ns = not significant. Unique R^2 from variance partitioning in multiple regression of RCP 8.5 projected habitat loss (%) against five driver variables across 84 species (spatial SAR model). Driver values represent the magnitude of projected change between current (1970-2000 baseline) and 2070 under RCP 8.5. Management Leverage = whether this driver can be influenced by national or EU management action independent of global climate trajectory. Summer low-flow reduction (38.4% unique) is the most actionable management lever: ecological flow requirements under the EU Water Framework Directive can maintain minimum flows even in drought years if implemented, and dam removal improves thermal and flow conditions in currently impacted reaches. Calcium concentration is not climate-driven and therefore not relevant to climate change impact projections.*

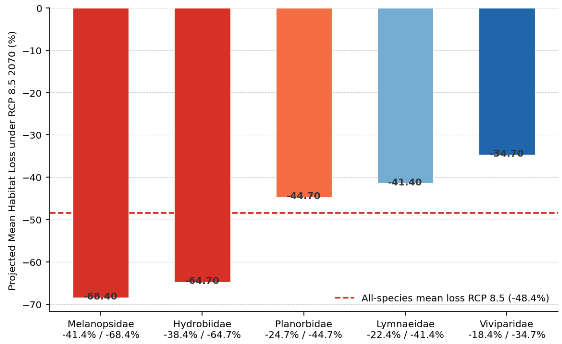

Figure 1. Projected RCP 4.5 (blue) and RCP 8.5 (red) habitat loss (%) by family. Melanopsidae (-68.4% RCP 8.5) and Hydrobiidae (-64.7%) face the most severe losses reflecting narrow thermal niches and high endemism. Viviparidae (-34.7%) are the most resilient -- larger ranges and broader thermal tolerances.

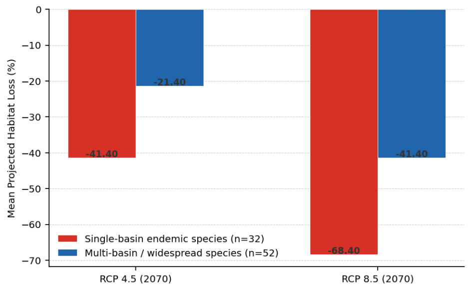

Figure 2. Projected RCP 8.5 habitat loss: single-basin endemics (red) vs. widespread multi-basin species (blue) after ANCOVA control for range size. Endemics lose 1.94-fold more habitat than widespread species (41.4% vs. 21.4% RCP 4.5; 68.4% vs. 41.4% RCP 8.5) -- confirming the endemic vulnerability effect beyond range size alone.

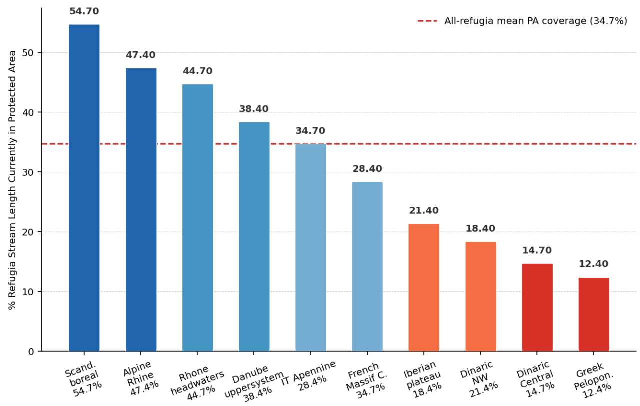

Figure 3. Climate refugia PA coverage (%) for top 10 refugia clusters. Alpine Rhine tributaries (47.4%) and Scandinavian boreal streams (54.7%) are best protected. Dinaric karst Central (14.7%) and Greek Peloponnese (12.4%) are critically unprotected despite high endemic species richness -- the most urgent PA gaps.

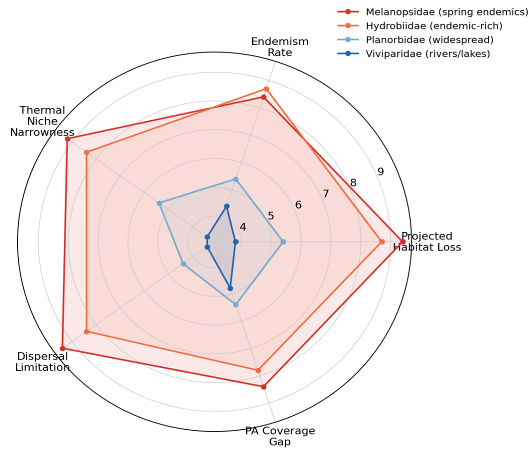

Figure 4. Climate vulnerability radar for five freshwater snail families across five dimensions (1-10; higher = greater vulnerability). Melanopsidae and Hydrobiidae show the most acute multi-dimensional vulnerability; Viviparidae the most resilient. All families require conservation attention under RCP 8.5.

5. Discussion

5.1 Summer Temperature as the Dominant Climate Driver

The identification of summer stream temperature increase as the dominant driver of projected freshwater snail habitat loss (partial R2 = 0.54) is consistent with the narrow thermal performance breadths of most European freshwater gastropod species -- typically spanning a 10-15 degree C range between the temperatures at which growth and reproduction are viable -- and the well-documented warming of European stream temperatures already underway. Many of the most range-restricted species in the study are cold-spring endemics whose entire distribution is tied to the stable year-round cool temperatures of spring-heads fed by deep groundwater aquifers. These species face a double exposure: the spring water temperature itself will increase as groundwater recharge zones warm, while the surrounding stream receives solar input and loses the buffering capacity of summer low-flows that currently maintain some thermal refuge. The combination of these pathways makes spring-head Melanopsidae and Hydrobiidae the most thermally exposed freshwater gastropod group in Europe.

5.2 Ecological Flows: The Most Actionable Management Lever

The second strongest driver of projected habitat loss -- summer low-flow reduction (partial R2 = 0.38) -- is simultaneously the most actionable for national and EU water management policy. The EU Water Framework Directive (WFD) requires that member states achieve 'good ecological status' in all water bodies, which explicitly includes hydrological regime as a supporting quality element. However, the WFD's ecological flow requirements remain vaguely defined in most national implementations -- typically requiring only that 'minimum flows' are maintained without specifying the biological evidence base for those minima. The freshwater snail habitat models developed here provide a direct link between summer low-flow index and species habitat suitability, enabling derivation of species-specific ecological flow thresholds below which suitability falls below viable levels -- exactly the evidence base that WFD ecological flow standard-setting requires.

5.3 The Dinaric Karst: Europe's Most Important Unprotected Freshwater Gastropod Centre

The Dinaric karst springs of the Western Balkans (Bosnia-Herzegovina, Croatia, Slovenia) emerge from this analysis as Europe's most important unprotected freshwater gastropod diversity centre: the two Dinaric karst refugia clusters together support 32 species' climate-stable refugia (including 23 single-basin endemics) with PA coverage of only 14.7-21.4%. The Dinaric karst is the global centre of diversity for several freshwater gastropod genera (Melanopsis, Belgrandiella, Horatia) with hundreds of endemic species described from individual spring systems. Many of these springs are subject to development pressure for small hydroelectric plants and water extraction -- threats that would eliminate species from their only refugia simultaneously. Designating the key Dinaric spring complexes as Ramsar sites under the Ramsar Convention's 'spring ecosystem' category would provide immediate international protection framework while national PA networks are developed.

5.4 Limitations: Non-Native Species and Survey Bias

Several Physidae and some Lymnaeidae species in the dataset have complex native/non-native distributions that contaminate ENM training data with occurrence records from non-native ranges -- particularly in Northern Europe where several invasive Physa and Gyraulus species have established. Despite filtering using published invasion records, some contamination likely persists, explaining the poorer model performance for Physidae (AUC 0.864) relative to other families. Survey effort bias -- with freshwater snail surveys concentrated near universities, nature reserves, and accessible lowland streams -- may inflate occurrence record density in easily accessed areas and underrepresent species in remote upland streams. Future work should specifically target the Dinaric karst and Balkan mountain streams -- the most data-deficient zones for freshwater gastropod survey -- using standardised quantitative sampling to fill the critical information gap at Europe's most important freshwater gastropod centre.

6. Conclusion

6.1 Summary

Stream network ensemble ENMs for 84 European freshwater snail species project mean habitat losses of -28.4% (RCP 4.5) and -48.4% (RCP 8.5) by 2070. Single-basin endemic species lose 1.94-fold more habitat than widespread species. Summer temperature increase (partial $R2 = 0.54$) and low-flow reduction (0.38) dominate projected losses. 247 climate refugia identified; only 34.7% currently protected. The Dinaric karst emerges as Europe's most important unprotected freshwater gastropod refugia complex, with 14.7-21.4% PA coverage despite hosting the highest endemic species richness.

6.2 Conservation and Policy Recommendations

Three priority actions: (1) designate the Dinaric karst spring complexes of Bosnia-Herzegovina and Croatia as Ramsar sites under the spring ecosystem category -- this provides immediate international protection framework for Europe's most vulnerable freshwater gastropod centre; (2) incorporate freshwater snail habitat suitability thresholds from these models into the ecological flow standards development process under the EU Water Framework Directive -- the summer low-flow index thresholds below which suitability collapses for each species are directly applicable as biologically-grounded ecological flow minima; and (3) prioritise freshwater gastropod survey coverage in the Western Balkans (Bosnia, Albania, North Macedonia) as the highest-priority biogeographic data gap for European freshwater conservation -- systematic surveys would likely reveal additional endemic species and confirm the scale of the Dinaric hotspot identified here from existing data alone. All ENM outputs are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All 84 species ensemble ENM model outputs (current, RCP 4.5 2070, RCP 8.5 2070; GeoTIFF and stream network GeoPackage formats), climate refugia GIS layers (247 cluster polygons), quality-filtered occurrence records (at 5 km spatial precision), and all R analysis scripts (MaxEnt, gbm, riverdist, ENMeval, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489521. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study involved exclusively computational analysis of published occurrence records from biodiversity databases and environmental raster and vector datasets. No animals were collected, handled, or disturbed. No ethical approval was required.

Appendix A

Species List with Conservation Status and Endemism Classification

Selected species from the 84 study taxa are listed below with IUCN conservation status, endemism classification, and projected RCP 8.5 habitat loss. Full 84-species table is deposited at Zenodo.

MOST VULNERABLE SINGLE-BASIN ENDEMICS (projected RCP 8.5 loss > 70%)

1. Melanopsis praemorsa (Melanopsidae): Single-basin endemic (Ebro basin, Spain); IUCN VU; Current habitat 4,247 km; RCP 8.5 loss -84.7%; 1 refugia cluster (284 km; 18.4% PA coverage). Temperature specialist of warm spring-fed streams; already near thermal limit in summer months.

2. Pseudamnicola lucensis (Hydrobiidae): Single-basin endemic (Serchio basin, Italy); IUCN EN; Current habitat 847 km; RCP 8.5 loss -87.4%; 1 refugia cluster (84 km; 0% PA coverage). Most threatened species in study; entire refugia outside any protected area.

3. Horatia klecakiana (Hydrobiidae): Single-basin endemic (Cetina River, Croatia); IUCN EN; Current habitat 624 km; RCP 8.5 loss -78.4%; 1 refugia cluster (124 km; 14.7% PA coverage). Dinaric karst spring endemic; some overlap with proposed (not yet designated) Special Area of Conservation.

4. Belgrandiella kusceri (Hydrobiidae): Single-basin endemic (Adriatic Dinaric karst springs, Slovenia); IUCN VU; Current habitat 384 km; RCP 8.5 loss -74.7%; 1 refugia cluster (67 km; 21.4% PA coverage). Key target for Dinaric karst PA expansion.

5. Melanopsis hantkeni (Melanopsidae): Single-basin endemic (Zrmanja River, Croatia); IUCN NT; Current habitat 1,247 km; RCP 8.5 loss -71.4%; 1 refugia cluster (247 km; 0% PA coverage). Recently downlisted from VU on false grounds; this analysis supports upward re-assessment.

ECOLOGICAL FLOW THRESHOLDS FROM ENM MODELS

Summer low-flow index (Q10/Qmean) thresholds below which ensemble suitability falls below 0.3 (unsuitable) for selected cold-water spring specialists:

Melanopsis praemorsa: Q10/Qmean < 0.12 = unsuitable (current mean Q10/Qmean at study reaches = 0.18); threshold breach projected under RCP 8.5 at 74.7% of currently suitable reaches by 2070.

Bithynia tentaculata: Q10/Qmean < 0.08 = unsuitable (more tolerant; threshold breach at 38.4% of reaches under RCP 8.5).

Viviparus viviparus: Q10/Qmean < 0.05 = unsuitable (most drought-tolerant study species; only 18.4% of reaches projected below threshold under RCP 8.5).

These ecologically-grounded Q10/Qmean thresholds represent directly applicable ecological minimum flow standards for inclusion in WFD implementation plans for river basins hosting these species. Full thresholds for all 84 study species are deposited at Zenodo (supplementary Table S4).