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Original Article

Assessing the intrinsic correlates of extinction risk in European freshwater gastropods

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ABSTRACT

Invertebrate biodiversity, especially in the freshwater realm, is severely underrepresented in conservation research and action, leading to an underestimation of current global extinction rates. Species differ in the biological traits that make them susceptible to extinction, and estimating extinction risk for freshwater species can aid conservation measures under limited available knowledge. Identifying traits as predictors of extinction risk may serve as a profile for each group of organisms and contribute to predicting which species will be at higher risk of extinction in the foreseeable future. Here we focus on European freshwater gastropods, a severely understudied taxon of high conservation priority due to many threatened species and high rates of species extinction. Our analyses showed that multiple factors such as body size, shell shape, breadth of habitat types, and even the type of habitat contribute to vulnerability to extinction. Species with smaller body size and narrower habitat breadths are facing greater extinction risk. Shell shape and habitat type may also play a role in extinction risk. Our analysis provides insight into why some gastropod species are more susceptible to extinction than others. This information can guide conservation assessment and action and help identify potentially threatened species lacking sufficient data for evaluation.

Keywords: biodiversity crisis; biological traits; conservation biology; IUCN; threat status

INTRODUCTION

Invertebrates constitute the vast majority (about 95–97%) of known animal species, but are severely underrepresented in conservation research and action (Clark and May 2002, Di Marco *et al.* 2017, Donaldson *et al.* 2017). Indicative of this knowledge gap is the fact that of the ~1.5 million described species accepted by the International Union for the Conservation of Nature (IUCN 2025), only ~1.6% have been evaluated and ~27% of these are Data Deficient (Cardoso *et al.* 2011, Cowie *et al.* 2022). As a comparison, the IUCN Red List covers nearly all tetrapod species. This knowledge gap affects the estimates of global extinction rates, and our efforts to mitigate the outcome of the biodiversity crisis. Most importantly, it may affect the development of appropriate research methodologies aimed at understanding the conservation requirements of invertebrate species and, consequently, the development of effective conservation strategies (Di Marco *et al.* 2017).

To surmount the invertebrate knowledge gap, research has turned its focus on molluscs (Cowie *et al.* 2017, 2022, Régnier *et al.* 2009). Molluscs are the second-largest phylum on Earth with ca. 90 000 species, and can be found from the deep sea to the top of mountains, showing astonishing diversity (Sousa 2024), and providing important ecosystem services such as food, materials, and clean water (Zieritz *et al.* 2022). Molluscs are good candidates for assessing background rates of species extinction (De Vos *et al.* 2015), as their shells have high potential for fossilization. Yet, of the currently known mollusc species, only about 10.5% have been evaluated for their extinction risk, and about 4.6% of these (mostly gastropods) are extinct (Cowie *et al.* 2022).

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Estimates of the existing biodiversity crisis become more complicated when considering freshwater biodiversity. Freshwater ecosystems constitute less than 1% of the total volume of the hydrosphere, but they support over 10% of all known species and they are an essential resource for human life, providing clean water, food, and other ecosystem services. Freshwater habitats are under extensive pressure from anthropogenic threats (Darwall *et al.* 2018), resulting in a global freshwater biodiversity crisis that requires immediate action (Collen *et al.* 2014): one-quarter of freshwater species are at risk of extinction (Sayer *et al.* 2025). Freshwater biodiversity is, as well, underrepresented in conservation research since most of the research focusing on terrestrial biodiversity does not consider freshwater ecosystems (Di Marco *et al.* 2017). However, conservation plans for terrestrial species and systems might have only a limited benefit for freshwater systems (Darwall *et al.* 2011). Freshwater molluscs are amongst the taxa of highest conservation concern; for example, in Europe 44% freshwater molluscs are threatened with extinction and 9.5% of them are considered extinct (Böhm *et al.* 2021).

Freshwater molluscs (close to 7000 species; MolluscaBase 2025) are a mega-diversified group that play key roles in ecosystems such as contributing to water quality, nutrient cycling, providing food for other species, and many more (Böhm *et al.* 2021). The vast majority of freshwater mollusc species belong to Gastropoda (Böhm *et al.* 2021), which in Europe represent 94% of the total freshwater molluscan diversity (Cuttelod *et al.* 2011). The two most diverse groups of freshwater gastropods are Caenogastropoda (formerly grouped within Prosobranchia) and Hygrophila (Cuttelod *et al.* 2011, Neubauer and Georgopoulou 2021). These groups differ in several aspects concerning their ecology, evolutionary history, and life-history traits. For example, *Caenogastropoda* are dioecious species with gills that live and reproduce for 4–5 years (Pyron and Brown 2015) while Hygrophila are hermaphrodites (self-fertilization can occur), mostly annual species with a 1-year life cycle, which breathe through a pocket in their mantle that is used as a lung. Hygrophila have the potential for long-distance dispersal and are considered as ecologically more flexible species, successful colonizers, with on average wider distributions than Caenogastropoda (Dillon 2000, Pyron and Brown 2015), and they have been found to be less prone to extinction than Caenogastropoda (Neubauer and Georgopoulou 2021).

Over the last two decades, comparative extinction risk modelling has aimed to predict patterns and drivers of extinction risk in species, with the ultimate goal of informing monitoring and conservation action (Purvis *et al.* 2000, Cardillo and Meijaard 2012, Cazalis *et al.* 2023). Models build on the role of anthropogenic pressures driving species decline and extinction (Murray *et al.* 2014) as well as the extent of protected areas and other extrinsic factors while accounting for species biological and life-history traits (intrinsic factors) making species more (or less) sensitive to external extinction drivers (Di Marco *et al.* 2015). Several traits have been tested as predictors of extinction risk, since knowing what makes certain species more prone to extinction can aid prediction of future risk (Chichorro *et al.* 2019). Not surprisingly, the majority of the literature on extinction risk concerns well-known taxa, such as mammals and other vertebrates (Purvis and Hector 2000, González-Suárez and Revilla 2013, Tingley *et al.* 2013, Atwood *et al.* 2020, Cardillo 2021) and only a few exercises have been attempted on invertebrates, mainly insects (Koh *et al.* 2004, Terzopoulou *et al.* 2015, Arbetman *et al.* 2017, Palash *et al.* 2022).

Here we model extinction risk of European freshwater gastropods from selected intrinsic traits that have been repeatedly tested for their relationship with extinction risk in several taxa. We hypothesize that a higher risk of extinction is associated with: (i) species of larger body size, since these require more resources and have slower life cycles (Purvis and Hector, 2000), and (ii) species occurring in a limited range of habitats, since these are more exposed to habitat reduction or deterioration from natural or anthropogenic causes (Purvis *et al.* 2000, García-R and Di Marco, 2020). Life-history traits such as generation length, offspring size, and fecundity have also been proposed as important correlates of extinction risk (Purvis *et al.* 2000). However, data on these traits are currently unavailable for most of the European freshwater gastropod species, and their analysis was not possible in the present study (see also Material and Methods section). To test our hypothesis, we analysed a comprehensive dataset of gastropod traits to provide insight into why some species are more susceptible to extinction and identify groups of species of conservation concern. Our results can inform conservation planning since they can be used to identify potentially threatened species that have yet to be formally evaluated.

MATERIALS AND METHODS

Compiling the dataset

We analysed the European freshwater gastropod species assessed by the IUCN (840 species; about one-third of the assessed freshwater gastropod species worldwide) since Europe is one of the best studied regions regarding gastropods and the number of assessments is relatively high compared to other geographical regions (Chichorro *et al.* 2022, Sousa 2024). Species absent from the IUCN Red List assessment were excluded from the analyses, while those assessed as Data Deficient were retained for some of the sensitivity tests (see Imputation of missing data). We obtained threat categories from the IUCN Red List archive (IUCN 2025), the most comprehensive compilation of global species conservation status that is widely used as a tool for conservation planning, monitoring, and decision-making (Cowie *et al.* 2022). Following that, we updated species taxonomy and systematics according to MolluscaBase (MolluscaBase 2025) to be in line with synonyms and taxonomic revisions. The final dataset comprised 814 species (97% of European assessed freshwater gastropod species).

To investigate the relationship between traits and extinction risk (see also Supporting Information), we initially searched for several parameters that have been repeatedly studied, in several taxa, for their relationship with extinction risk, such as body size, breadth of habitats, trophic level, generation length, egg size as a proxy of the offspring size, and altitudinal range (Purvis *et al.* 2000, Keane *et al.* 2005, Chichorro *et al.* 2019, 2022). Furthermore, based on the findings of Chiba and Roy (2011) regarding the relationship between shell shape (measured via spire index) and extinction risk in land snails, we included this variable in analyses as well. Last, we also included the type of habitat in our data list, since there is evidence that most of the freshwater species that went extinct originated from lakes and springs (Sayer *et al.* 2025). After a preliminary search, we discarded variables (i.e. generation length, egg size, clutch size) with a high percentage of missing data (i.e. >70%), to avoid having unpredictable effects over the parameter estimates. Thus, we focused on body size (estimated from shell measurements), shell shape (measured via spire index; high-spired species have more conical shells, while low-spired species have more flattened shells), habitat type (lake, river, springs/slow running waters, brackish waters, and caves/subterranean habitats; see also Supporting Information), and habitat breadth (number of different habitat types a species occupies). Shell measurements (shell length and shell width) were retrieved from AnimalBase (AnimalBase Project Group, 2005-2024) and from the species' original descriptions. We avoided extracting shell measurement values from other published records as this could lead to bias due to species misidentifications by the publishing authors. Note that the original descriptions of species sometimes were the only source of size data since some species are endemic to single locations and have not been described in any other published material in detail. Shell measurements correspond to the maximum recorded values for each species (i.e. measurements of the largest known specimen as reported in the literature), ensuring comparability across species assessed from potentially varying sample sizes in the original descriptions.

Information regarding habitat types was taken from public databases (i.e. AnimalBase, IUCN Red List) and from literature searches (Haase *et al.* 2000, Glöer *et al.* 2010, Glöer and Georgiev 2012). Using the shell measurements, we estimated spire index, a commonly used measure of gastropod shell shape, which is defined as the ratio of shell length to shell width (Chiba and Roy 2011). We also estimated the geometric mean of length and width (Chiba and Roy 2011) as a proxy for body size, following also the work of Chichorro *et al.* (2022) in trait-based prediction of extinction risk.

When shell measurements were not available, we used an imputation procedure to overcome the problem of excluding certain species, since this may create bias in analysis (Nakagawa and Freckleton 2008). Shell measurements and species-specific traits are usually missing from the literature for the least studied species. Thus, such an exclusion of species would insert bias in our analyses since the exclusion would be nonrandom; we would practically have excluded the least studied species or the less abundant ones. Data imputation creates less bias than excluding cases with missing values, especially when more than 30% of the data (as in our case; see Results) are missing (Penone *et al.* 2014). To fill in the missing values (see Supporting Information for details) we used the *missForest* function of the missForest v.1.4 R package (Penone *et al.* 2014) since it allows for missing value imputation on different types of variables and it does not need tuning parameters or assumptions about distributional aspects of the data (Stekhoven and Bühlmann 2012). To obtain more accurate imputation values regarding the shell measurements, in the first compiled dataset (Dataset1; 814 species), Data Deficient taxa were included since for many of them shell measurements were available. We followed the adapted version of an imputation procedure described by van Zuijlen *et al.* (2024). Similarly, we used taxonomy as a proxy for phylogenetic relatedness (see Supporting Information) since no complete phylogeny of all European freshwater gastropods is available. We ran the imputation 10 times resulting in 10 imputed datasets and we randomly selected five of them to identify the significant extinction risk predictors. We log-transformed continuous data (geometric mean, spire index) to avoid significant skewness in their distribution of values and observations spread far away from the main density of trait values.

Phylogeny reconstruction

Extinction risk may depend on species phylogenetic position, and thus to estimate extinction risk taking phylogenetic relationships into account, we also performed phylogenetic generalized least squares (PGLS; Symonds and Blomberg 2014) analyses using the same traits as in the classic approach and the phylogenetic tree presented in Figure 1. The PGLS analyses did not include the full dataset of

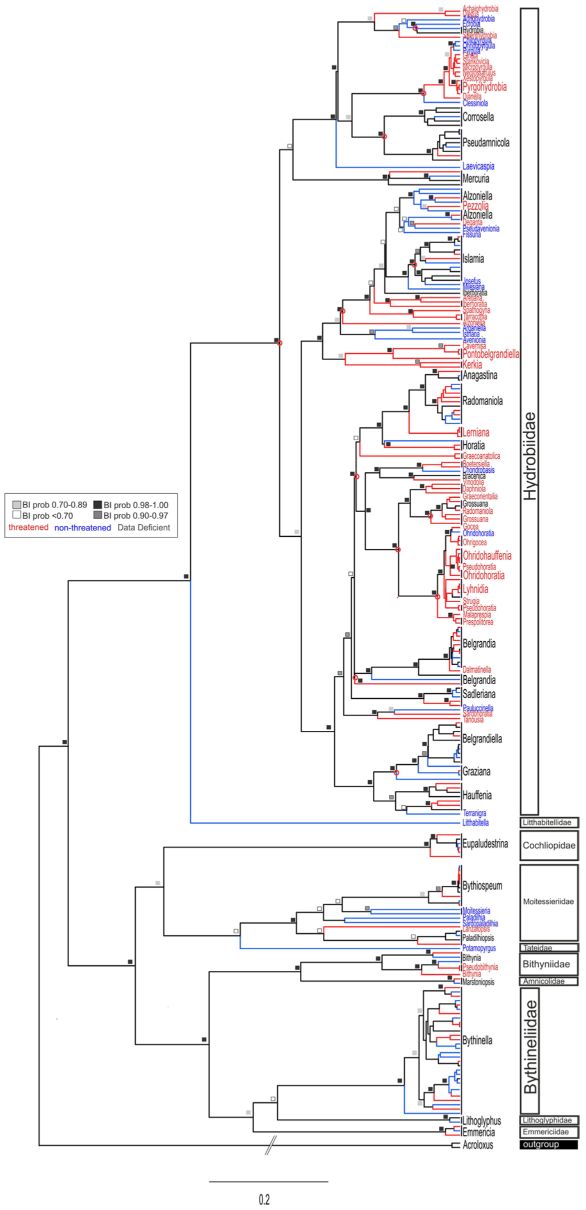

Figure 1. Bayesian inference (BI) phylogenetic tree resulting from BEAST software analysis. *Acroloxus* sequences were used as the outgroup. BI posterior probabilities are shown on the nodes of the tree. The constraints defined based on the Hydrobiidae phylogeny of Delicado *et al.* (2024) are shown using red circles on the respective nodes. Scale bar corresponds to substitutions per site.

gastropod species but were restricted to Littorinimorpha for two principal reasons. First, this order accounts for 85% of species in our dataset and, second, and more fundamentally, no published molecular phylogeny encompasses all orders of European freshwater gastropods. The deep divergence times and the limited genetic data for other orders precluded reliable phylogenetic reconstruction across the full dataset. Therefore, the PGLS results should be treated as a case study illustrating the role of shared evolutionary history within the dominant order, rather than a comprehensive phylogenetic test across the full dataset. For the PGLS approach we used the PhylotaR v.1.3.0 R package (Bennett *et al.* 2018) to download DNA sequences longer than 350 bp from GenBank. Sequence clusters were filtered to keep one sequence per species and considering a requirement for >50 species from our taxon list in each sequence cluster (see Supporting Information), we ended up with four clusters corresponding to two mitochondrial (16S and *COI*) and two nuclear genes (18S and 28S/5.8S).

We aligned each sequence cluster using CodonCode Aligner v.9.02, and obvious misalignments were edited manually. Sequences in each aligned cluster were trimmed such that only sites with coverage of at least 50 species were retained. Last, we concatenated the four sequence clusters resulting in an alignment 3755 bp in length.

We performed preliminary unconstrained maximum-likelihood (ML) tree searches per gene in IQtree (Nguyen *et al.* 2015) to identify rogue taxa. Next, we performed (i) ML and Iii) Bayesian inference (BI) analyses on the concatenated sequence matrix (see Supporting Information) using RaxML-NG v.1.2.2 (Kozlov *et al.* 2019) and BEAST2 v.2.7.4 (Suchard *et al.* 2018) respectively, under the model suggested by IQtree model selection while implementing topological constraints based on the phylogeny of Delicado *et al.* (2024) as presented in Figure 1.

Statistical analysis

We classified species as either threatened (EN, VU, CR or EX; 1) or non-threatened (LC, NT; 0), following previous studies and we excluded Data Deficient taxa as these could not be classified in a category of risk (Dataset2; 611 species). We predicted the binary (threatened/non-threatened) status of species by fitting a generalized linear-mixed model (GLMM) using the trait values as the independent predictors. Following the approach used in similar studies (Chichorro *et al.* 2022, Palash *et al.* 2022) we used family as a random effect to account for missing phylogenetic relationships among all the studied taxa. The response variable was binary and each species could be threatened (EN, VU, CR or EX; 1) or non-threatened (LC, NT; 0), as in other studies (Payne *et al.* 2016, Atwood *et al.* 2020), although in our study we included the Extinct species in the threatened list. Thus, we used a Bernoulli distribution and logit link function to construct the models.

We initially tested for multicollinearity among all predictor variables (Supporting Information Table S3), and we fitted full models (i.e. the most complex ones) using body size, shell shape, habitat breadth, and habitat type as predictor variables. We then used the *drop1* function in R to compare all possible models (including the null model) that can be constructed by dropping a single predictor variable of the existing model and compared the models based on their Akaike Information Criterion (AIC; for all models compared, we used the same dataset and the same random effect). We also tested for interactions between predictor variables that had a significant effect (see also Supporting Information) as shown in Table 1. All models were fit using the R package glmmTBM v.1.1.11 (Brooks *et al.* 2017). To assess the quality of the overall fit of the models, we used the Hosmer–Lemeshow global goodness-of-fit (GOF) test as implemented in the R package ResourceSelection v.0.3-6 (Lele and Keim 2006). Performance metrics of each model such as sensitivity, precision, and F1 were estimated using the *predict* function while values regarding the area under curve (AUC) were estimated using the R packages ISLR v.1.4 (James *et al.* 2021) and ROCR v.11 (Sing *et al.* 2005). Details on the validation procedure are provided in the Supporting Information.

Last, as a case study, we tested the influence of the real phylogenetic relationships among Littorinimorpha species. We built a phylogenetic generalized linear model (PGLS) with habitat breadth, habitat type, body size, and shell shape as predictor variables and binary extinction risk as a response variable. We used the pgls function of the caper v.1.0.3 R package (Orme *et al.* 2013) to fit models (see Supporting Information File S1) to the data under study while accounting for the expected covariance due to shared evolutionary history as presented in the 50% majority rule consensus tree of the phylogenetic analysis. Then, we performed model selection for the variables under study (and their combinations) based on the AIC values.

RESULTS

Data description

Considering that for some species (especially for the Data Deficient ones) habitat was recorded as 'unknown' (so practically it is missing), data for habitat type and breadth were missing for 5.8% in Dataset1 and 1.3% in Dataset2 (not including Data Deficient species and used for the extinction risk modelling). The percentage of missing data was higher for body size and shell shape (Shell Height: 31% missing, Shell Width: 35% missing).

In Dataset1, 46% of the species were threatened, 0.6% were extinct, and 20% were Data Deficient (most of them in the family Hydrobiidae, which belong to Caenogastropoda). The percentage of threatened species rose to 61% considering species of Dataset2, with the majority (176 species) of them being 'Vulnerable' (Supporting Information Fig. S2). In Dataset2, 83.3% of the species were Littorinimorpha, which held the largest percentage of threatened species (Fig. 2; Fig. S3) with their two largest families, Hydrobiidae (379 species; 210 threatened) and Moitessieriidae (179; 42 threatened species), having already three extinct species. Most species living in lakes or caves/subterranean were threatened (62% and 64.3% respectively) while the majority of those living in brackish waters were non-threatened (70.2%) (Fig. 2). However, we must note the lower number of species found in lakes (116 species) compared to other habitats (e.g. springs/slow running waters: 360 species; caves/subterranean habitats: 215 species) and the low number of species found in brackish waters (24 species) in our dataset.

Phylogenetic relationships

In our dataset, consisting of one sequence per species, 43% of species were represented by three or four genes in the concatenated dataset while 20% of species were represented by one gene sequence. Genetic information was missing for most of the species, which was more profound for Data Deficient taxa (79% missing). Comparing

Table 1. Comparison among extinction risk models tested with general linear mixed model (GLMM) analyses on Dataset2 (excluding Data Deficient taxa, 611 species); the best model based on the Akaike Information Criterion (AIC) is shown in bold.

Model: traits	AIC	Estimates [95% CI]	Local performance metrics[#]	GOF test
Model1: *Body size + Shell shape + Habitat breadth + Presence in lake*	730.1	−0.82 [−1.22, −0.42] 1.11 [0.29, 1.94] −0.86 [−1.15, −0.57] 0.96 [0.41, 1.51]	Sens. = 0.78 Spec. = 0.51 Prec.=0.72 F1 = 0.74 AUC = 0.705	$\chi^2 = 9.72$
Model2: ***Body size + Shell shape + Habitat breadth × Presence in lake (interaction)***	715.3	−0.84 [−1.28, −0.40] 1.07 [0.19, 1.95] −0.49 [−0.83, −0.15] 3.47 [1.93, 5.00] −1.74 [−2.74, −0.74]	Sens. = 0.80 Spec. = 0.50 Prec. = 0.72 F1 = 0.76 AUC = 0.722	$\chi^2 = 14.30$
Model3: *Body size + Habitat breadth × Shell shape + Presence in lake (interaction)*	721.6	−0.81 [−1.23, −0.40] −1.24 [−1.67, −0.81] −1.84 [−3.96, 0.28] 1.00 [0.44, 1.58] 2.18 [0.71, 3.66]	Sens. = 0.79 Spec. = 0.51 Prec.=0.72 F1 = 0.75 AUC = 0.713	$\chi^2 = 14.12$
Model4: *Shell shape + Body size × Habitat breadth + Presence in lake (interaction)*	728.2	1.06 [0.22, 1.90] −0.06 [−0.95, 0.82] −0.40 [−0.95, 0.14] 0.95 [0.39, 1.51] −0.53 [−1.10, 0.05]	Sens. = 0.82 Spec. = 0.47 Prec.=0.72 F1 = 0.76 AUC = 0.708	$\chi^2 = 16.36$
Model5: *Shell shape + Habitat breadth + Body size × Presence in lake (interaction)*	730.8	1.18 [0.35, 2.00] −0.86 [−1.15, −0.57] −0.72 [−1.15, −0.29] 1.58 [0.36, 2.79] −0.52 [−1.43, 0.38]	Sens. = 0.78 Spec. = 0.52 Prec.=0.72 F1 = 0.75 AUC = 0.704	$\chi^2 = 11.52$

Sens: the proportion of actual positive cases correctly identified by the model, Spec.: the proportion of actual negative cases correctly identified by the model, Prec.: the ratio of true positive predictions to the total predicted positive cases by the model, F1 score: reflects the balance between the model's ability to predict both positive and negative cases.

threatened and non-threatened taxa, missing data was higher for the threatened ones (genetic information was missing for 62% of threatened species). Note that missing data here was considered in terms of the filters set in data collection (i.e. sequences longer than 350 bp, sequences present in at least 50 species in each cluster). However, a severe taxonomic bias at the genus or family level did not exist, since there was 81% representation of the taxa at the genus level. The 50% majority-rule consensus trees resulting from the BI analysis is presented in Figure 1 and Supporting Information Figure S2. ML and BI analyses resulted in similar phylogenies. More specifically, ML and BI trees were congruent regarding the grouping of species within family and genus levels. However, differences existed regarding the relationships among families (deep phylogenetic events) where low statistical support was observed on the nodes for both analyses.

Extinction risk prediction

Considering the whole dataset of freshwater species (Dataset1), the best-fit model (Table 1) included body size, shell shape (expressed as spire index), habitat breadth, and presence in lakes, and specifically the one including the interaction between habitat breadth and presence in lakes (Table 1). Smaller sized species (Fig. 3A), with high-spired shells (Fig. 3B) and narrower habitat breadth (Fig. 3C) seemed to be at greater risk of extinction, especially if one (or the only) of these habitats happened to be a lake (Fig. 3D). Comparison of body size between species found in lakes and those of other habitat types (Supporting Information Fig. S4) revealed that species in lakes (for our dataset) were bigger (Wilcoxon; $W = 13636$, $P < .001$). Comparison of body size between species found in one habitat type and those found in multiple habitat types (Fig. S5) revealed that the latter were bigger (Wilcoxon; $W = 45\,351$, $P = .005$) while the difference in body size was marginally significant for Caenogastropoda (Wilcoxon; $W = 34685$, $P = .042$). All five imputed datasets indicated the same 'best' model with only slight differences in their estimates (Table S5). The model performed well considering the correct prediction of actual threatened species (sensitivity = 0.80) but the correct prediction of actual non-threatened species was lower (specificity = 0.50) and in general it performed well considering the balance between its ability to predict both positive and negative cases (F1 score = 0.76, AUC = 0.72). The 80/20 validation procedure (see Supporting Information) on the same dataset indicated the same model as the 'best model' and the model's performance metrics (Tables S6 and S7) were similar to those of Table 1.

Extinction risk analyses focused on Caenogastropoda (Supporting Information Table S4) indicated as the best-fit model included body size, habitat breadth, and presence in lakes. Body size and habitat breadth showed a significantly negative effect while presence in lakes had a significantly positive effect (Fig. S6; Table S8). The model performed similarly well to that of Dataset2 (sensitivity = 0.79, specificity = 0.41, F1 = 0.75, AUC = 0.65).

The best model supported by the PGLS analysis on Littorinimorpha present in the tree of Figure 1 included the interaction between habitat breadth and presence in lakes, as shown in Supporting Information Table S9. The relationship between extinction risk and body size was non-significant since the fraction of species (217 species, excluding Data Deficient taxa) that were included in this analysis had on average

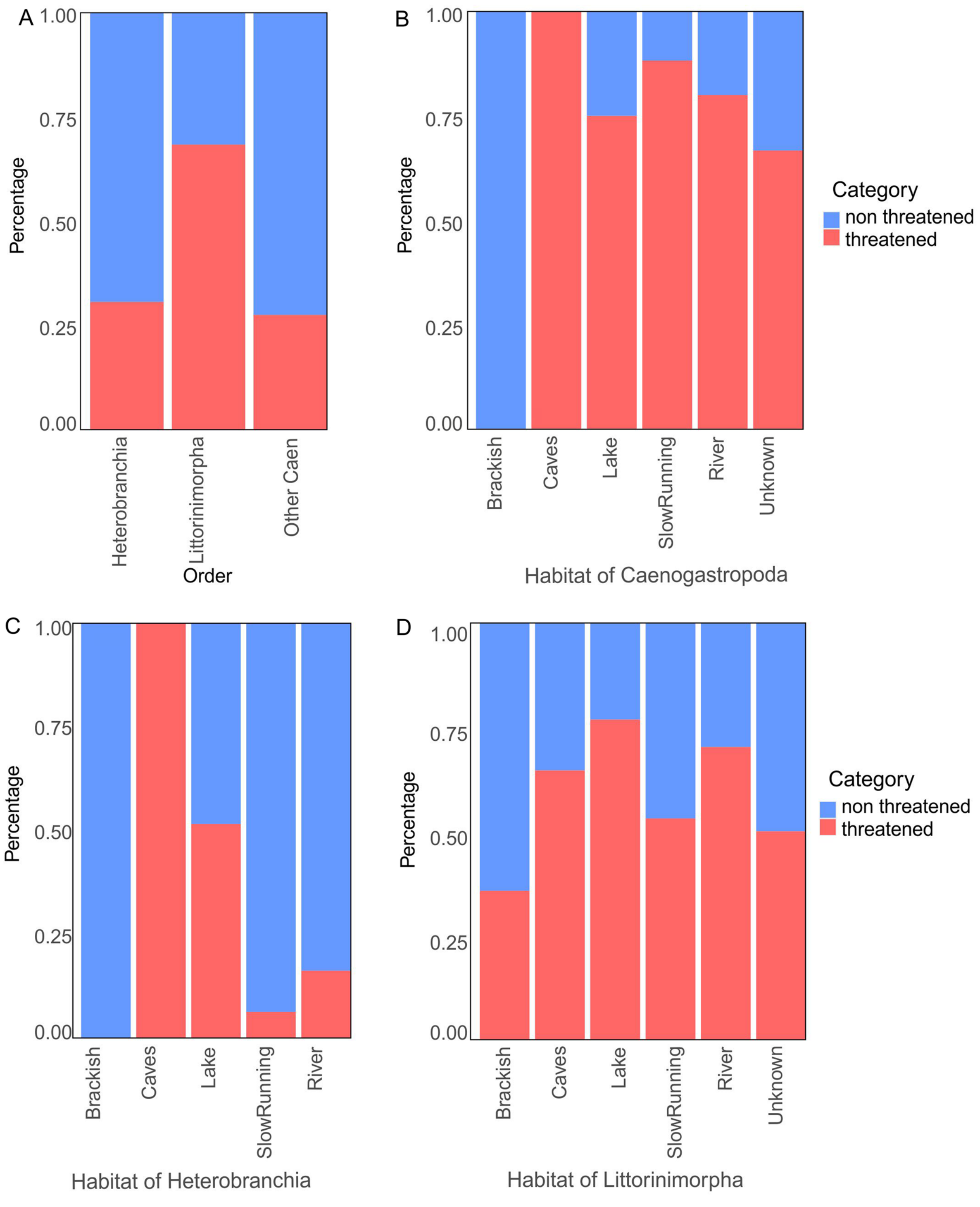

Figure 2. Proportion of threatened (red) and non-threatened (blue) species for all European freshwater species in the study per order (A) and habitat type (B, C, D). Orders with a few representative species (1–58 species) have been pooled under their respective subclass. Caenogastropoda (B) include the families Cycloneritida, Sorbeoconcha, Allogastropoda, Architaenioglossa, and Hypsogastropoda; Heterobranchia (C) include Hygrophila and Ellobiida; while Littorinimoprha (D) are presented separately since they consist of most species.

smaller sized species than those absent from the tree (ANOVA, $F = 17.6$, $P < .001$). Classic GLMM (Table S10) analysis on the same species resulted in the same results as the PGLS analysis.

DISCUSSION

By compiling a comprehensive dataset of biological traits for the European freshwater gastropods assessed by the IUCN, we concluded that multiple factors such as body size, breadth of habitat, and even the type of habitat may contribute to determining extinction risk. Our results indicated that larger freshwater gastropods that occupy a broad range of habitat types are less prone to extinction. Body size and habitat breadth have been extensively studied for their relationship with extinction risk in several taxa (Ripple *et al.* 2017, Chichorro *et al.* 2019, 2022, Cardillo 2021). Habitat breadth is a universal predictor of extinction risk across plant, vertebrate, and invertebrate terrestrial taxa

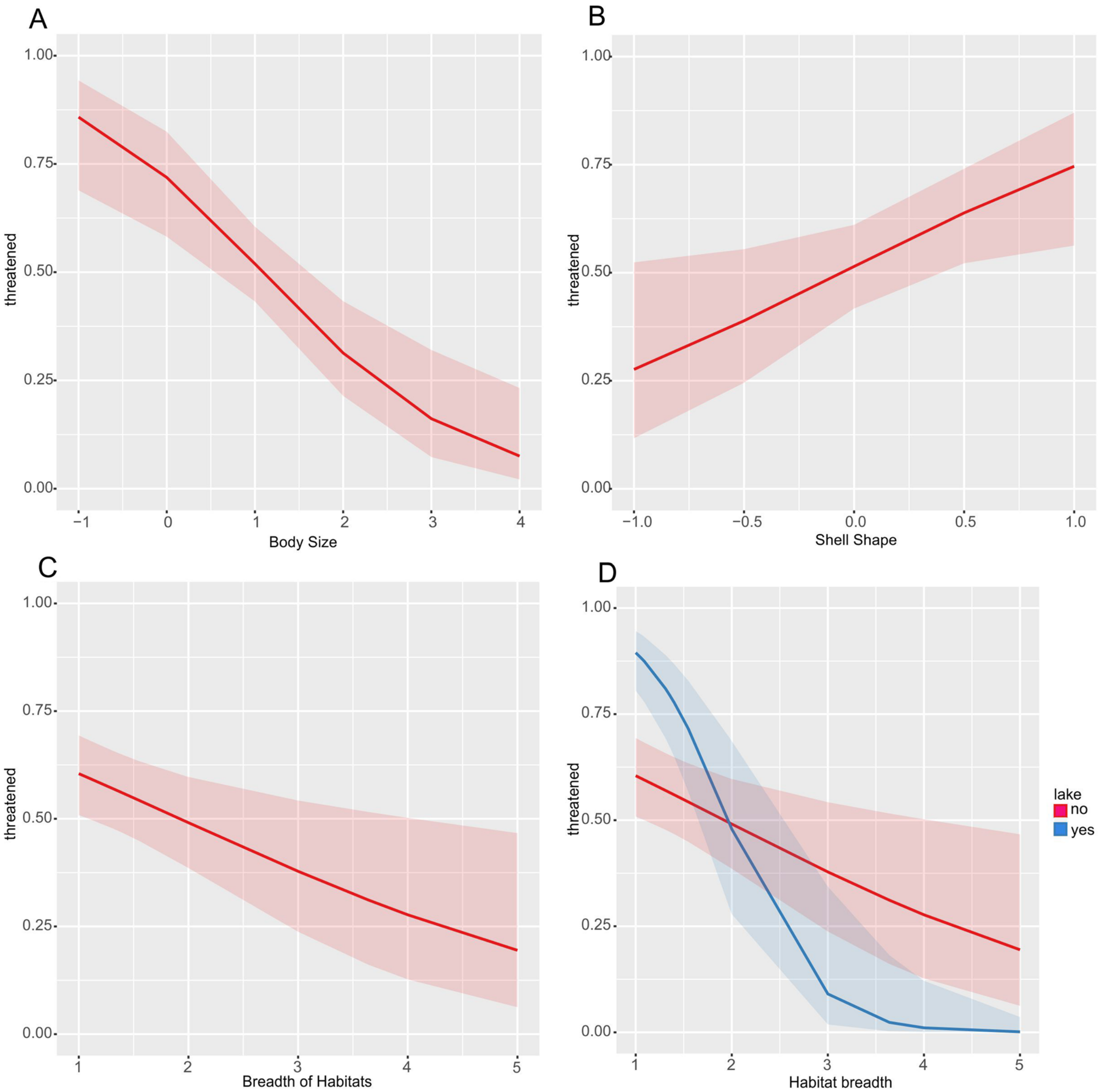

Figure 3. Predicted probabilities of threat in relation to body size (A), shell shape (B), habitat breadth (C), and the interaction between habitat breadth and presence in lakes (D) for all European freshwater species assessed by the IUCN.

including terrestrial gastropods (Chichorro *et al.* 2019, 2022). In line with these findings, we found that habitat breadth was a strong predictor of extinction for freshwater gastropods in all three datasets analysed (all freshwater gastropods, Caenogastropoda, a subset of Littorinimorpha).

The relationship between body size and vulnerability to extinction varies considerably among taxa (Chichorro *et al.* 2019, 2022). Historically, larger body size has been linked to higher extinction risk in endotherms such as mammals and birds, as well as in reptiles and certain invertebrates (Owens and Bennett 2000, Cardillo *et al.* 2005, Tingley *et al.* 2013, Terzopoulou *et al.* 2015, Nolte *et al.* 2017, Palash *et al.* 2022). This vulnerability is typically driven by higher energetic demands, lower population densities, and slower reproductive rates (Purvis *et al.* 2000). However, our results indicate the opposite pattern for freshwater gastropods: smaller species face greater extinction risk. This divergence probably reflects fundamental biological and ecological contrasts between terrestrial endotherms and freshwater ectotherms. In freshwater systems, small body size does not imply higher metabolic costs; instead, it is strongly associated with habitat specialization, restricted geographical ranges, limited dispersal ability, and narrow endemism (Böhm *et al.* 2021). Consequently, these smaller taxa are disproportionately sensitive to localized environmental changes and habitat degradation, whereas larger animals are more frequently threatened by overexploitation (Ripple *et al.* 2017). This specific vulnerability of small-bodied species appears to be a broader characteristic of freshwater ecosystems, with similar trends documented in amphibians, crayfish, and freshwater fishes (Olden *et al.* 2007, Bland 2017, Kopf *et al.* 2017, Cardillo 2021, Chichorro *et al.* 2022). Ultimately, these findings highlight that the link between body size and extinction risk is fundamentally context-dependent, demonstrating the risk of extrapolating terrestrial conservation paradigms to freshwater ectotherms.

We found that shell shape (quantified via spire index) was also an important predictor of extinction risk when we analysed the whole dataset including different orders. However, shell shape was not a significant predictor when more homogeneous (in terms of shell shape) datasets such as the Caenogastropoda or Littorinimorpha were analysed. Shell shape underlies biological and mechanical constraints that vary across gastropod clades. Shell geometry has been found to be driven by material efficiency for land snails (Páll-Gergely *et al.* 2024). Furthermore, shell shape seems to play a functional role leading to microhabitat preferences at least in terrestrial gastropods (Cameron and Cook 1989) with high-spired species being active on steep or vertical surfaces and low-spired species on low-angle or horizontal substrates (Cook and Jaffar 1984, Solem and Climo 1985, Cowie 1995, Wong and Lim 2017, Albarran-Melzer *et al.* 2020). Based on the functional importance of shell shape for terrestrial gastropods, Chiba and Roy (2011) concluded that shell shape is an important correlate of extinction vulnerability.

Lastly, our results indicated that habitat type also plays a role in the risk of extinction since our analysis indicated that species of similar body size living in a limited number of freshwater body types and present in lakes are at a higher risk of extinction. In our data, a high proportion of threatened species are found in lakes in both Caenogastropoda and Heterobranchia. However, for Caenogastropoda, which represent most of the species in this study, a similarly high percentage of threatened species exists also in rivers and caves/subterranean habitats. Most of the extinct freshwater species worldwide inhabited lakes and rivers (Sayer *et al.* 2025). In our analysis, however, only lakes were found to have a significant effect. This may be because we estimated extinction risk based on the threat category (not the number of extinct species) or because our study is not global but focused on a specific region (i.e. Europe) where—according to the IUCN Red List in Europe—five species have gone extinct and they were distributed in different habitat types (one from each habitat type; lake, river/creek, marshes, springs, subterranean systems). We investigated the possibility of the lake species being included in our dataset being smaller (and as such at higher risk of extinction because of their size) but the results indicated that they were in fact larger.

Our finding that occurrence in lakes is associated with elevated extinction risk calls for an ecological explanation. Freshwater molluscs in Europe are highly threatened, with 44% facing extinction (Cuttelod *et al.* 2011). Sayer *et al.* (2025) also found that freshwater species endemic to permanent lakes suffer a disproportionately high rate of extinction because their isolated habitat prevents them from escaping threats such as invasive species, water extraction, and harvesting. The combination of strong and persistent pressures with extremely limited natural recovery potential probably makes lake environments particularly vulnerable for endemic freshwater gastropods. We note, however, that our analysis includes a relatively small number of lake species ($N = 116$), and that more than half (56%) are recorded from a single location according to IUCN assessments. This raises the possibility that the observed pattern partly reflects range restriction rather than habitat type alone. Further studies that explicitly account for geographical range size will be needed to separate these effects more clearly.

An important caveat of our work relates to the possible influence of IUCN assessment practices on our results. Under Criterion B, a 'location' is defined as a geographically or ecologically distinct area in which a single threatening event could rapidly affect all individuals of a taxon (IUCN, 2025). For lake-dwelling gastropods, it is often reasonable to treat an entire lake as a single location, given that threats such as invasive predators, eutrophication, or water abstraction can affect the whole system at once. However, if this approach is applied more consistently to lake species than to taxa in other comparably restricted habitats—such as isolated springs or cave systems—it could lead to a higher proportion of lake species being assigned to elevated threat categories, regardless of their intrinsic vulnerability. We attempted to minimize this issue by excluding geographical range as a predictor from our models, thereby avoiding circularity with Criterion B, which underpins the listing of roughly 60% of the threatened species in our dataset. Even so, we cannot rule out the possibility that part of the 'lake effect' we detect reflects this aspect of the assessment process. Addressing this thoroughly would require analyses that explicitly consider the criteria used in individual assessments, or the use of alternative, criteria-independent measures of distributional restriction.

As Earth's biodiversity crisis accelerates, sometimes considered as an incipient sixth mass extinction (Barnosky *et al.* 2011), knowledge of invertebrate taxa remains largely insufficient. The Linnean shortfall (only a fraction of all species having been described) leads to obstacles in effective conservation actions for these taxa. Despite increasing availability of molecular data and powerful computational methods, we still have a limited understanding of the phylogenetic relationships among living invertebrate species, many species are missing from phylogenies (Hortal *et al.* 2015; Cerretti *et al.* 2026), and our phylogenetic reconstruction for Littorinimorpha was not an exception. Littorinimorpha is the largest order of freshwater gastropods and the one with the highest percentage of threatened species. Our search for genetic markers underlined the lack of data for many species, which was not random, since data were mainly missing for Data Deficient and threatened species. We were able to robustly reconstruct the phylogenetic relationships at the genus or family levels but the relationships among families remained largely unresolved. Considering the phylogenetic tree at the family level, our tree agrees with the phylogeny of Hydrobiidae (Delicado *et al.* 2024) since many constraints were set based on this phylogenetic tree. It is also in agreement with published phylogenies regarding the relationships among the families Bithyniidae and Bythineliidae/Emmericiidae (Gladstone and Whelan 2022) and the close relationship among Bythineliidae/Emmericiidae/Lithoglyphidae (Wilke *et al.* 2013). However, the relationships among these families and Amnicolidae remains unclear. This underlines the need to turn to genomic markers such as ultraconserved elements (UCEs; Goulding *et al.* 2023, González-Delgado *et al.* 2024), or restriction site-associated DNA sequencing (RAD-seq; Herrera and Shank 2016) to resolve the deep phylogenetic events which were poorly supported in our phylogenetic tree.

The partial agreement between the full GLMM and the PGLS model is an indication of the role of phylogenetic structure in driving extinction risk patterns. The convergence of both approaches on habitat breadth and lake presence as significant predictors suggests that these traits are robust correlates of extinction risk that are not simply artefacts of phylogenetic non-independence among species. In contrast, the loss of statistical significance for body size and shell shape in the PGLS model is probably attributable to two compounding factors. First, the PGLS was focused to Littorinimorpha and more specifically on a subset of them for which genetic data were available. This subset comprises on average smaller-bodied species than the full dataset (ANOVA, $F = 17.6$, $P < .001$), substantially reducing variance in body size and thus statistical power to detect its effect. Second, shell shape shows strong phylogenetic conservatism within Littorinimorpha—species within families tend to be morphologically similar—which means that after controlling for shared evolutionary history, little independent variation in shell shape remains for the model to detect. Together, these patterns suggest that the body size and shell shape effects detected in the GLMM may partly reflect phylogenetically structured variation, while habitat-related traits appear to have a more direct and phylogenetically independent relationship with extinction risk. Future studies incorporating a complete molecular phylogeny for all European freshwater gastropods would be needed to fully resolve these questions.

Understanding extinction risk and identifying its potential drivers are essential to conservation research and planning. In this study, we show that freshwater gastropods that are habitat specialists (especially if their only habitat is a lake) and have smaller body sizes are at greater risk of extinction. Identifying possible drivers of extinction is particularly important for shaping the profile of highly threatened species, especially in taxa such as invertebrates, with high levels of Data Deficiency (Cazalis *et al.* 2023). Data Deficiency in freshwater molluscs (36%) is the result of many interacting factors such as the deficiency of experts in the field of invertebrate systematics (Agnarsson and Kuntner 2007, Kotov and Gololobova 2016), the discrepancies among systematists, the lack of monitoring mollusc populations, or the fact that many species have not been studied since their taxonomic description (Böhm *et al.* 2021). Predictive techniques may be useful to assess the threat status of the many Data Deficient species or at least prioritize the research towards species that seem to potentially be at greater risk of extinction, allowing more effective conservation actions (Böhm *et al.* 2021).

CONCLUSION

Although in recent years conservation research has been moving towards a less biased representation of biodiversity, it is likely that biases in the conservation literature will take many years to be overcome (Di Marco *et al.* 2017). Our study identifies predictors of extinction risk in freshwater gastropods and highlights that besides the universal driver of habitat breadth, species with smaller body size are at greater risk of extinction. Considering that this agrees with similar studies in other freshwater taxa, our findings can provide information for conservation biologists to develop effective strategies for freshwater ecosystems.

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P.K.: Conceptualization, Investigation, Formal analysis, Visualization, Writing—Original Draft, Administration, Funding acquisition; A.P.: Resources, Formal analysis, Writing—Review and Editing; M.D.M.: Conceptualization, Writing—Review and Editing; C.R.: Resources, Investigation, Writing—Review and Editing, M.K.: Review and Editing; M.S.: Resources, Writing—Review and Editing; E.S.: Resources, Writing—Review and Editing.

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online

CONFLICT OF INTEREST

The authors declare that no conflict of interest exists.

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DATA AVAILABILITY

The data underlying this article are available in the article and in its online supplementary material.

REFERENCES

Agnarsson I, Kuntner M. Taxonomy in a changing world: seeking solutions for a science in crisis. *Systematic Biology* 2007;**56**:531–9.

Albarran-Melzer N, Ruiz L, Benítez H *et al.* Can temperature shift morphological changes of invasive species? A morphometric approach on the shells of two tropical freshwater snail species. *Hydrobiologia* 2020;**847**:151–60.

AnimalBase Project Group. AnimalBase. Early zoological literature online. 2005-2024. www.animalbase.uni-goettingen.de.

Arbetman MP, Gleiser G, Morales CL *et al.* Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. *Proceedings of the Royal Society B: Biological Sciences* 2017;**284**:20170204.

Atwood TB, Valentine SA, Hammill E *et al.* Herbivores at the highest risk of extinction among mammals, birds, and reptiles. *Science Advances* 2020;**6**:eabb8458.

Barnosky AD, Matzke N, Tomiya S *et al.* Has the Earth's sixth mass extinction already arrived? *Nature* 2011;**471**:51–7.

Bennett DJ, Hettling H, Silvestro D *et al.* phylotaR: An automated pipeline for retrieving orthologous DNA sequences from GenBank in R. *Life (Basel)* 2018;**8**:

Bland LM. Global correlates of extinction risk in freshwater crayfish. *Animal Conservation* 2017;**20**:532–42.

Böhm M, Dewhurst-Richman NI, Seddon M *et al.* The conservation status of the world's freshwater molluscs. *Hydrobiologia* 2021;**848**:3231–54.

Brooks M, Kristensen K, van Benthem K *et al.* glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 2017;**9**:378–400.

Cameron RAD, Cook LM. Shell size and shape in Madeiran land snails: do niches remain unfilled? *Biological Journal of the Linnean Society* 1989;**36**:79–96.

Cardillo M. Clarifying the relationship between body size and extinction risk in amphibians by complete mapping of model space. *Proceedings. Biological Sciences* 2021;**288**:20203011.

Cardillo M, Mace GM, Jones KE *et al.* Multiple causes of high extinction risk in large mammal species. *Science (New York, N.Y.)* 2005;**309**:1239–41.

Cardillo M, Meijaard E. Are comparative studies of extinction risk useful for conservation? *Trends in Ecology & Evolution* 2012;**27**:167–71.

Cardoso P, Erwin TL, Borges PAV *et al.* The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation* 2011;**144**:2647–55.

Cazalis V, Santini L, Lucas PM *et al.* Prioritizing the reassessment of data-deficient species on the IUCN Red List. *Conservation Biology* 2023;**37**:e14139.

Cerretti P, Nania D, Di Marco M *et al.* Declining rates of species description call for improved taxonomic strategies: Insights from a megadiverse insect order. *Systematic Entomology* 2026;**51**:e70019.

Chiba S, Roy K. Selectivity of terrestrial gastropod extinctions on an oceanic archipelago and insights into the anthropogenic extinction process. *Proceedings of the National Academy of Sciences of the United States of America* 2011;**108**:9496–501.

Chichorro F, Juslén A, Cardoso P. A review of the relation between species traits and extinction risk. *Biological Conservation* 2019;**237**:220–9.

Chichorro F, Urbano F, Teixeira D *et al.* Trait-based prediction of extinction risk across terrestrial taxa. *Biological Conservation* 2022;**274**:109738.

Clark JA, May RM. Taxonomic bias in conservation research. *Science (New York, N.Y.)* 2002;**297**:191–2.

Collen B, Whitton F, Dyer EE *et al.* Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography* 2014;**23**:40–51.

Cook L, Jaffar W. Spire index and preferred surface orientation in some land snails. *Biological Journal of the Linnean Society* 1984;**21**:307–13.

Cowie RH. Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution* 1995;**49**:1191–202.

Cowie RH, Bouchet P, Fontaine B. The Sixth Mass Extinction: fact, fiction or speculation? *Biological Reviews of the Cambridge Philosophical Society* 2022;**97**:640–63.

Cowie RH, Régnier C, Fontaine B *et al.* Measuring the Sixth Extinction: what do mollusks tell us? *Nautilus* 2017;**131**:3–41.

Cuttelod A, Seddon M, Neubert E. European Red List of Non-marine Molluscs.*European Red List of Non-Marine Molluscs*. Luxembourg: Publications Office of the European Union. 2011.

Darwall W, Bremerich V, De Wever A *et al.* The Alliance for Freshwater Life: A global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 2018;**28**:1015–22.

Darwall WRT, Holland RA, Smith KG *et al.* Implications of bias in conservation research and investment for freshwater species. *Conservation Letters* 2011;**4**:474–82.

De Vos JM, Joppa LN, Gittleman JL *et al.* Estimating the normal background rate of species extinction. *Conservation Biology* 2015;**29**:452–62.

Delicado D, Hauffe T, Wilke T. Fifth mass extinction event triggered the diversification of the largest family of freshwater gastropods (Caenogastropoda: Truncatelloidea: Hydrobiidae). *Cladistics* 2024;**40**:82–96.

Di Marco M, Chapman S, Althor G *et al.* Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation* 2017;**10**:32–42.

Di Marco M, Collen B, Rondinini C *et al.* Historical drivers of extinction risk: using past evidence to direct future monitoring. *Proceedings. Biological Sciences* 2015;**282**:20150928.

Dillon RT, 2000. *The Ecology of Freshwater Molluscs*. Cambridge: Cambridge University Press.

Donaldson MR, Burnett NJ, Braun DC *et al.* Taxonomic bias and international biodiversity conservation research. *Facets* 2017;**1**:105–13.

García RJ, Di Marco M. Drivers and trends in the extinction risk of New Zealand's endemic birds. *Biological Conservation* 2020;**249**:108730.

Gladstone NS, Whelan NV. Pushing barcodes to their limits: phylogenetic placement of Fontigens Pilsbry, 1933 (Caenogastropoda: Littorinimorpha: Truncatelloidea) and elevation of Fontigentidae Taylor, 1966. *Journal of Molluscan Studies* 2022;**88**:

Glöer P, Falniowski A, Pešić V. The Bithyniidae of Greece (Gastropoda: Bithyniidae). *Journal of Conchology* 2010;**40**:179–87.

Glöer P, Georgiev D. Three new gastropod species from Greece and Turkey (Mollusca: Gastropoda: Rissooidea) with notes on the anatomy of *Bythinella charpentieri cabirius* Reischütz. *North-Western Journal of Zoology* 2012; 1988;**8**:278–82.

González-Delgado S, Rodríguez-Flores PC, Giribet G. Testing ultraconserved elements (UCEs) for phylogenetic inference across bivalves (Mollusca: Bivalvia). *Molecular Phylogenetics and Evolution* 2024;**198**:108129.

González-Suárez M, Revilla E. Variability in life-history and ecological traits is a buffer against extinction in mammals. *Ecology Letters* 2013;**16**:242–51.

Goulding TC, Strong EE, Quattrini AM. Target-capture probes for phylogenomics of the Caenogastropoda. *Molecular Ecology Resources* 2023;**23**:1372–88.

Haase M, Weigand E, Haseke H. Two new species of the family Hydrobiidae (Mollusca: Caenogastropoda) from Austria. *Veliger* 2000;**43**:179–89.

Herrera S, Shank T. RAD sequencing enables unprecedented phylogenetic resolution and objective species delimitation in recalcitrant divergent taxa. *Molecular Phylogenetics and Evolution* 2016;**100**:70–9.

Hortal J, de Bello F, Diniz-Filho JAF *et al.* Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 2015;**46**:523–49.

IUCN. 2025. *The IUCN Red List of Threatened Species. Version 2024-2*. Gland: IUCN.

James G, Witten D, Hastie T, Tibshirani R, 2021. *ISLR: Data for an Introduction to Statistical Learning with Applications in R*. R package version 1.4. Available at: https://CRAN.R-project.org/package=ISLR.

Keane A, Brooke MDL, McGowan PJK. Correlates of extinction risk and hunting pressure in gamebirds (Galliformes). *Biological Conservation* 2005;**126**:216–33.

Koh LP, Dunn RR, Sodhi NS *et al.* Species coextinctions and the biodiversity crisis. *Science (New York, N.Y.)* 2004;**305**:1632–4.

Kopf RK, Shaw C, Humphries P. Trait-based prediction of extinction risk of small-bodied freshwater fishes. *Conservation Biology* 2017;**31**:581–91.

Kotov AA, Gololobova MA. Traditional taxonomy: Quo vadis? *Integrative Zoology* 2016;**11**:500–5.

Kozlov AM, Darriba D, Flouri T *et al.* RAxML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. *Bioinformatics (Oxford, England)* 2019;**35**:4453–5.

Lele SR, Keim JL. Weighted distributions and estimation of resource selection probability functions. *Ecology* 2006;**87**:3021–8.

MolluscaBase eds. 2025. MolluscaBase. https://www.molluscabase.org

Murray KA, Verde Arregoitia LD, Davidson A *et al.* Threat to the point: improving the value of comparative extinction risk analysis for conservation action. *Global Change Biology* 2014;**20**:483–94.

Nakagawa S, Freckleton RP. Missing inaction: the dangers of ignoring missing data. *Trends in Ecology and Evolution* 2008;**23**:592–6.

Neubauer TA, Georgopoulou E. Extinction risk is linked to lifestyle in freshwater gastropods. *Diversity and Distributions* 2021;**27**:2357–68.

Nguyen L-T, Schmidt HA, von Haeseler A *et al.* IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 2015;**32**:268–74.

Nolte D, Schuldt A, Gossner MM *et al.* Functional traits drive ground beetle community structures in Central European forests: Implications for conservation. *Biological Conservation* 2017;**213**:5–12.

Olden JD, Hogan ZS, Vander Zanden MJ. Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography* 2007;**16**:694–701.

Orme D, Freckleton RP, Thomas GH *et al.* CAPER: comparative analyses of phylogenetics and evolution in R. *Methods in Ecology and Evolution* 2013;**3**:145–51.

Owens IP, Bennett PM. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences of the United States of America* 2000;**97**:12144–8.

Palash A, Paul S, Resha SK *et al.* Body size and diet breadth drive local extinction risk in butterflies. *Heliyon* 2022;**8**:e10290.

Páll-Gergely B, Sipos AÁ, Harzhauser M *et al.* Many roads to success: alternative routes to building an economic shell in land snails. *Evolution* 2024;**78**:778–86.

Payne JL, Bush AM, Heim NA *et al.* Ecological selectivity of the emerging mass extinction in the oceans. *Science (New York, N.Y.)* 2016;**353**:1284–6.

Penone C, Davidson AD, Shoemaker KT *et al.* Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods in Ecology and Evolution* 2014;**5**:961–70.

Purvis A, Gittleman JL, Cowlishaw G, Mace GM. Predicting extinction risk in declining species. *Proceedings: Biological Sciences* 2000;**267**: 1947–52.

Purvis A, Hector A. Getting the measure of biodiversity. *Nature* 2000;**405**:212–9.

Pyron M, Brown KM, 2015. Introduction to Mollusca and the Class Gastropoda. In: Thorp JH and Rogers DC, eds. *Thorp and Covich's Freshwater Invertebrates* (Fourth Edition). Boston: Academic Press. 383-421.

Régnier C, Fontaine B, Bouchet P. Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. *Conservation Biology* 2009;**23**:1214–21.

Ripple WJ, Wolf C, Newsome TM *et al.* Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences* 2017;**114**:10678–83.

Sayer CA, Fernando E, Jimenez RR *et al.* One-quarter of freshwater fauna threatened with extinction. *Nature* 2025;**638**:138–45.

Sing T, Sander O, Beerenwinkel N *et al.* ROCR: visualizing classifier performance in R. *Bioinformatics* 2005;**21**:3940–1.

Solem A, Climo FM. Structure and habitat correlations of sympatric New Zealand land snails species. *Malacologia* 1985;**26**:1–30.

Sousa R. A brief global agenda for advancing the study of molluscs. *Frontiers in Ecology and Evolution* 2024;**12**:1176380.

Stekhoven DJ, Bühlmann P. MissForest—non-parametric missing value imputation for mixed-type data. *Bioinformatics (Oxford, England)* 2012;**28**:112–8.

Suchard MA, Lemey P, Baele G *et al.* Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution* 2018;**4**:vey016.

Symonds MRE, Blomberg SP, 2014. A primer on phylogenetic generalised least squares. In: Garamszegi LZ, ed. *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology: Concepts and Practice*. Berlin: Springer, 105-130.

Terzopoulou S, Rigal F, Whittaker R *et al.* Drivers of extinction: The case of Azorean Beetles. *Biology Letters* 2015;**11**:20150273.

Tingley R, Hitchmough RA, Chapple DG. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. *Biological Conservation* 2013;**165**:62–8.

van Zuijlen K, Bisang I, Nobis MP *et al.* Extinction risk of European bryophytes predicted by bioclimate and traits. *Biological Conservation* 2024;**293**:110584.

Wilke T, Haase M, Hershler R *et al.* Pushing short DNA fragments to the limit: Phylogenetic relationships of 'hydrobioid' gastropods (Caenogastropoda: Rissooidea). *Molecular Phylogenetics and Evolution* 2013;**66**:715–36.

Wong YM, Lim SSL. Influence of shell morphometry, microstructure, and thermal conductivity on thermoregulation in two tropical intertidal snails. *Invertebrate Biology* 2017;**136**:228–38.

Zieritz A, Sousa R, Aldridge DC *et al.* A global synthesis of ecosystem services provided and disrupted by freshwater bivalve molluscs. *Biological Reviews of the Cambridge Philosophical Society* 2022;**97**:1967–98.

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