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Extinction risk is linked to lifestyle in freshwater gastropods

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Abstract

Aim: Freshwater ecosystems and their biota are severely endangered by global change today, and predicted extinction levels are skyrocketing for many taxa. Most studies have focused on entire clades, while approaches testing for selective extinction risk with respect to ecological traits are rare. As studies are typically based on modern faunas, the generality of the detected patterns in the context of the current biodiversity crisis remains uncertain. We use a dataset of fossil and modern freshwater gastropods to investigate extinction probability in dependence of lifestyle and geographic distribution.

Location: Europe, Miocene to present-day.

Methods: We performed generalized linear mixed modelling to test for a relationship between extinction probability and taxonomic group (Caenogastropoda vs. Hygrophila, reflecting different lifestyles) and range size, while using time as random effect. Extinction and survival of modern representatives was predicted based on IUCN conservation status. To identify the types of faunas with elevated extinction risk with respect to lifestyle, we tested for a relationship between the proportion of Caenogastropoda and lake surface area and geological duration using generalized linear models.

Results: We found a clear relationship between extinction likelihood and lifestyle, which is linked to differences in range sizes and is independent of geological time. Caenogastropoda are more prone to go extinct. A strong positive relationship between the proportion of Caenogastropoda and geological duration was found, showing that Caenogastropoda are more dominant in long-lived lakes.

Main conclusions: The elevated extinction risk of caenogastropods is linked to their smaller geographic ranges, which reflects their comparably poor colonization ability, and urges enhanced conservation efforts. Their high diversity and high degree of endemism in long-lived lakes render, especially these archives of evolution important conservators of biodiversity. As most of these lakes are under severe anthropogenic pressure, concerted conservation measures are needed to ensure the survival of their unique biota.

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KEYWORDS

conservation, ecological selectivity, fossil record, long-lived lakes, range sizes, species distribution

1 | INTRODUCTION

Freshwater environments and their biota experience critical threats at present (Böhm et al., 2020; Darwall et al., 2020; De Grave et al., 2015; Dudgeon, 2020; Garcia-Moreno et al., 2014; Neubauer et al., 2021; Pimm et al., 2014; Poff et al., 2012; Vörösmarty et al., 2010). Climate change, water pollution, habitat degradation and invasion by exotic species are but a few of the many threats straining modern freshwater biodiversity (Albert et al., 2021; Bowler et al., 2017; Dudgeon et al., 2006; Heino et al., 2009). According to the Living Planet Index, vertebrate populations in fresh water have declined by approximately 84% in the past 50 years (WWF, 2020). As concern invertebrates, about one third of the species of freshwater crabs (Cumberlidge et al., 2009), crayfish (Richman et al., 2015) and molluscs (Böhm et al., 2020) are globally threatened with extinction. Several studies have predicted future freshwater biodiversity loss as a direct or indirect consequence of human impact (e.g., Cordellier et al., 2012; Janse et al., 2015; Markovic et al., 2014; Neubauer et al., 2021; Pereira et al., 2010). Unless serious effort is directed towards freshwater biota and the ecosystems they live in, we are likely to steer into a sixth mass extinction event within the millennium (Neubauer et al., 2021).

Freshwater biota are more isolated compared to marine or terrestrial ones and therefore considered more vulnerable to ecological alteration (Dudgeon, 2020). Profound understanding of the drivers of extinction in freshwater animals is vital not only from a general perspective, but it also forms the basis for a proper coordination of conservation efforts. However, our knowledge of what drives the rise and demise of freshwater faunas is still very limited. In order to disentangle natural and anthropogenic impact, a main task is to identify parameters influencing extinction in the absence of major crises like the current one.

One aspect often neglected concerns the unevenness of extinction among different lifestyles within an animal group. For example, Payne et al. (2016) showed the extinction selectivity of marine taxa with respect to differences in body size, habitat, feeding mode and motility and how it has changed through geological time. Few such assessments are available for freshwater animals and most deal with vertebrates (e.g., Liu et al., 2017; Olden et al., 2007; Reynolds et al., 2005; but see also Bland, 2017). We are not aware of any study taking into account fossil data to make general predictions about selective extinction probability in freshwater biota.

Gastropods are ideal candidates for studying deep-time processes in freshwater ecosystems because of their high diversity, high individual abundance, high rates of endemism and good preservation potential (Strong et al., 2008). Moreover, all of the major groups of freshwater gastropods and lifestyles present today have existed

since the Mesozoic or early Cenozoic, respectively (Gray, 1988; Strong et al., 2008; Taylor, 1988).

The two most diverse groups of freshwater gastropods today are found among the Caenogastropoda (formerly grouped within Prosobranchia) and the Hygrophila (formerly as Pulmonata or Basommatophora) (Pyrón & Brown, 2015). These two groups differ considerably in a number of traits concerning their Bauplan, ecology and evolutionary history. Caenogastropoda comprise dioecious, mainly perennial species that live and reproduce for 4–5 years (Pyrón & Brown, 2015). Hygrophila, in contrast, are hermaphrodites and mostly annual freshwater species with a 1-year life cycle (Pyrón & Brown, 2015). Their higher reproductive rates and shorter life cycles help them survive in ephemeral environments (e.g., Brown et al., 1998). On average, they tolerate wider temperature ranges and can cope with greater variation in the dissolved oxygen (Pyrón & Brown, 2015). Because of their terrestrial evolutionary background, they do not have gills (like caenogastropods) but breathe through a vascularized pocket in the mantle they use as a lung. Also, Hygrophila are considered to be more effective competitors when food is scarce (Pyrón & Brown, 2015).

Because of self-fertilizing Hygrophila theoretically require only a single specimen to effectively colonize new habitats (Baker, 1945; Dillon, 2000). In caenogastropods, this can occur in rare cases of parthenogenetic species (Strong et al., 2008). Additionally, Hygrophila can survive outside the water for an extended period of time because of their capability to supply oxygen directly from the air (e.g., Dillon, 2000; Kendall, 1949; Poznańska et al., 2015), which increases their potential for long-distance dispersal (Yu et al., 2021). On the other hand, caenogastropod species can seal the aperture of the shell with an operculum, which facilitates dispersal via exo- or even endozoochory (Kappes & Haase, 2012).

The abovementioned features seem to make Hygrophila ecologically more flexible, rendering them faster and more successful colonizers. As a result, they have today on average wider distributions than caenogastropods, many of which are endemic and have restricted geographic ranges (e.g., Johnson et al., 2013; Pyron & Brown, 2015; Welter-Schultes, 2012). Nonetheless, exceptions of restricted-range endemic Hygrophila (e.g., Albrecht et al., 2006; Stelbrink et al., 2015) and widely dispersed Caenogastropoda exist as well (e.g., Ponder, 1988), especially among euryhaline or amphidromous groups (Strong et al., 2008).

We hypothesize that the higher colonization ability makes Hygrophila more effective in surviving and increasing their geographic ranges and, by this, lowering the extinction risk compared to Caenogastropoda. However, whether the observed differences in the distributions of the two groups are a general pattern or only true for recent times is unknown.

To test our hypothesis and infer the generality of the pattern, we use a comprehensive dataset of freshwater gastropod faunas spanning entire Europe over the last 23 million years (Myr; Miocene to present). We evaluate extinction probability as a function of taxonomic group (Caenogastropoda vs. Hygrophila, as indicator for differences in lifestyle) and species distributions using generalized linear mixed models. In order to identify the types of lakes in which Caenogastropoda/Hygrophila are particularly common—to pinpoint the types of faunas that are particularly rare today and/or contain a high abundance of species with elevated extinction risk—we assess correlation between the proportion of Caenogastropoda in a fauna and a lake's geological duration and surface area.

2 | METHODS

2.1 | Dataset

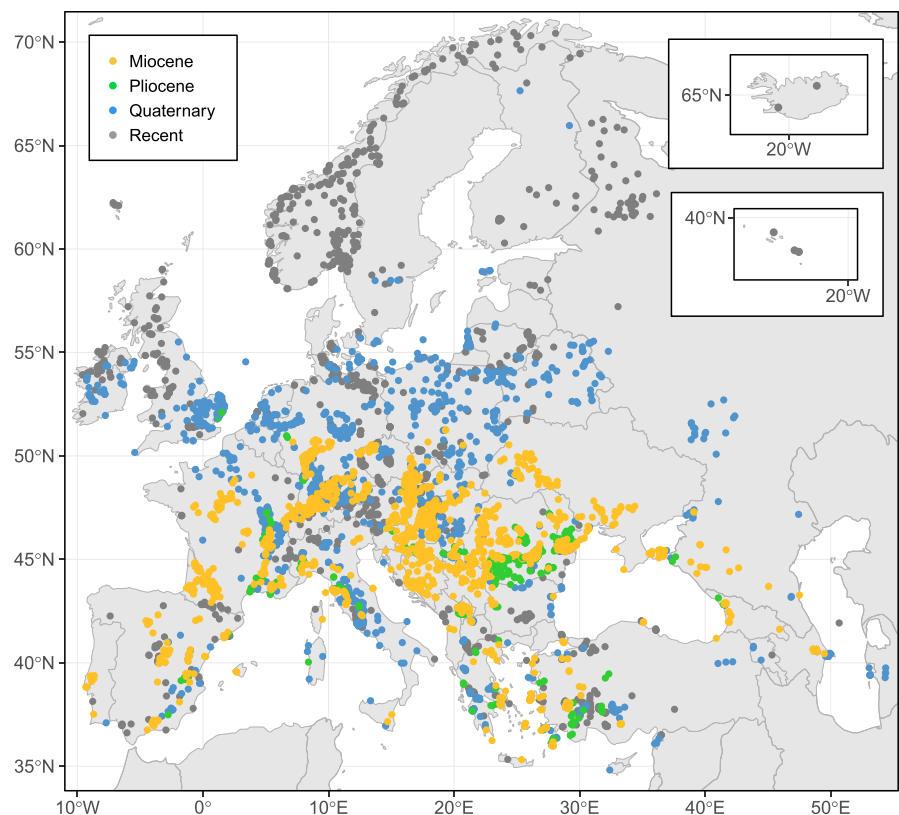
The dataset is an updated version of the data analysed by Neubauer, Harzhauser, Georgopoulou et al. (2015) for reconstructing species richness of European non-marine aquatic gastropods since the Miocene. We accounted for latest faunal assessments and taxonomic/systematic revisions published since then. The dataset includes faunas from Scandinavia in the North to Cyprus in the South, the Azores and Iceland in the West to the Caspian Sea realm in the East (Figure 1). Turkey, the Caucasus countries and Turkmenistan (as part of the Caspian Sea Basin) were included because of their European biogeographic affinities (compare

Neubauer, Harzhauser, Georgopoulou, et al., 2015; Neubauer et al., 2021). The final dataset includes 27,790 occurrences of 2,109 species from 5,374 localities (Figure 1). See Appendix S1 for details on the data selection.

2.2 | Species range sizes

Many different measures of species distributions are available in the literature. A recent comparison of several commonly used methods yielded minimum spanning tree as the best performing method (Boyle, 2017a). This measure gives the minimum distance that connects all species occurrences; hence, the shortest distance a species must have travelled to achieve the observed distribution. As such, it is a conservative estimate of species distribution (Boyle, 2017a). Considering that a species' geographic range may shift over time, we calculated minimum spanning tree distance for each species separately per one-million-year bin using the package GeoRange v. 0.1.0 (Boyle, 2017b) for R v. 4.0.3 (R Core Team, 2020). For localities with stratigraphic age ranges overlapping time bin boundaries, the mean age was used and rounded up to the next integer. In total, we used 24 time bins, whereas extant species (i.e., all occurrences recorded in the last 200 years) were treated separately from the Quaternary records. Given the obvious non-normal distribution of the data, differences between the distributions of Caenogastropoda and Hygrophila were assessed with a Wilcoxon rank-sum test. The test was performed for the overall data as well as for each time bin.

FIGURE 1 Localities/lakes yielding fossil and extant freshwater gastropods used in this study. The insets on the upper right correspond to Iceland and the Azores. Note that no pre-Quaternary fossils are preserved in northern Europe due to glacial erosion



2.3 | Extinction probability

To test for extinction probability in response to lifestyle and range size, species survival status was coded per one-million-year bin. Species were marked as survivors (1) if they occurred in the following time bin and as extinct (0) if they did not. Extant species were assigned to these categories based on their IUCN Red List conservation statuses (IUCN, 2020), whereas taxa labelled as “least concern” and “near threatened” were considered survivors and those marked “vulnerable,” “endangered,” “critically endangered” or “extinct” were considered to become extinct eventually (or are already). Taxa with statuses “data deficient” or “not evaluated” or those not listed in IUCN Red List were variably excluded or included and treated as extinct or survivors (pessimistic/optimistic scenarios sensu Payne et al., 2016) to test for a possible effect of unknown statuses. To account for differences in lifestyles, the taxonomic group (Caenogastropoda vs. Hygrophila) was included as a categorical variable in the models described below.

Extinction probability was assessed via generalized linear mixed models (GLMMs) using the R package lme4 v. 1.1-26 (Bates et al., 2020). GLMMs are superior to standard linear models for they allow incorporating uncertainty factors that potentially obscure a general pattern, such as variation through time. Four logistic models with different combinations of parameters were computed to test for an effect of lifestyle and range size on survival status (see Appendix S2). To specifically disregard variation through geological time—in order to test for the generality of the pattern—we added the time bin as random effect, whereas the effect (i.e., the slope) of lifestyle is allowed to vary within each time bin. Range size was centred and scaled prior to the analyses. Model fit was compared via Akaike information criterion (AIC). Models with $\Delta\text{AIC} > 2$ were considered significantly different (Burnham & Anderson, 2004). Model diagnostics were assessed with the package DHARMa v. 0.3.3.0 (Hartig & Lohse, 2020). The marginal R^2 and the intraclass correlation coefficient (ICC) were computed with the package performance v. 0.6.1 (Lüdtke, Makowski, et al., 2020). Plots were generated using the package ggeffects v. 1.0.1 (Lüdtke, Aust, et al., 2020).

We are aware that the association between extinction probability and distribution for the modern fauna must not be overestimated, as IUCN conservation status is partly based on distribution data (IUCN, 2020). To test for a potential bias, we ran an additional GLMM excluding modern faunas entirely.

2.4 | Effect of lake characteristics on the prevalence of lifestyles

We tested for a relationship between the proportion of Caenogastropoda and the geological duration (but not age per se) and surface area of lakes that contain at least ten species. These data were available for 130 lakes, including 17 palaeo-lakes. See Appendix S1 for more details on the data availability and data sources for the fossil lakes. Following Gorthner (1994), we define a long-lived

lake as one that has existed for at least 100,000 years. Because we also include fossil data, we refrain from using the term “ancient lake”, which is commonly used for modern long-lived lakes only.

We ran several generalized linear models (GLMs) to assess which parameters or combinations thereof best explain the proportion of Caenogastropoda in lacustrine faunas through time. We tested 32 possible combinations of parameters (single vs. both parameters vs. intercept-only model, with and without factor interaction), transformed versus untransformed variables (arcsine-square root transformation for the proportion of Caenogastropoda and decadic logarithm for lake duration and surface area) and error distribution (binomial vs. Gaussian, whereas binomial distribution only allows for untransformed variables) (Table S1 in Appendix S4). Model fit was assessed using AIC with the R package AICcmodavg v. 2.3-1 (Mazerolle, 2020). Normality of model residuals was checked with a Kolmogorov–Smirnov test and by visual examination.

3 | RESULTS

Caenogastropod species are more likely to go extinct than Hygrophila through most of the past 23 Myr (Figure 2a). Only few exceptions are found in selected time bins in the middle and late Miocene. A similar trend is reflected in the species range sizes. On average, Hygrophila have a wider distribution (Wilcoxon rank-sum test, $W = 1,981,901$, $p < .001$; Figure 2b). For individual time bins, the differences between Caenogastropoda and Hygrophila are significant in 12 out of 24 cases; only in a single one (bin 12), caenogastropods have significantly larger geographic ranges (Appendix S3, Table S1 in Appendix S3). This bin coincides with the transition from middle Miocene peri-Paratethyan faunas (sensu Neubauer, Harzhauser, Kroh, et al., 2015), containing several widespread caenogastropod species, to the late Miocene Lake Pannon, including on average more Hygrophila species that are only known from small areas or single localities.

The GLMM testing for extinction probability as a function of taxonomic group (which correlates with differences in lifestyle) and range size, including interaction of both terms as well as adopting a random slope of lifestyle across time bins, received the highest support (see Appendix S2). The model diagnostics indicate that the residuals are not normally distributed and that there is some minor quantile deviation, but the QQ-plots show that the observed distribution closely matches the expected one. Furthermore, there is no sign of overdispersion ($p = .328$), and the model is unaffected by temporal autocorrelation (see Appendix S2, Figure S1 in Appendix S2). The marginal R^2 of 0.822 indicates that the major part of the total variation is due to the fixed effects, while the random effects (i.e., time bins) account only for a small portion of the variation (adjusted ICC = 0.057).

The results demonstrate a strong link between extinction probability and taxonomic group and range size, respectively (Figure 3). More precisely, the model shows that Caenogastropoda and Hygrophila have a different extinction probability with respect to

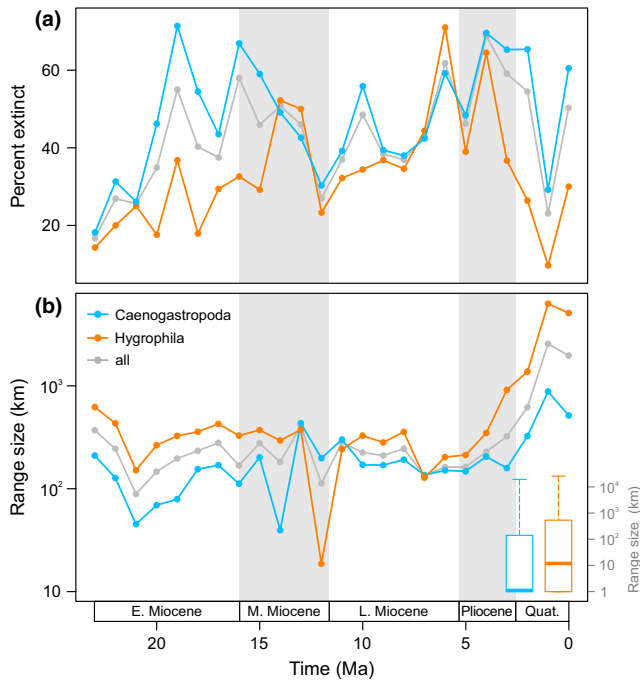


FIGURE 2 Per cent extinct (a) and mean species range sizes (b) of freshwater gastropod species per one-million year bin. The boxplots on the lower right show the statistical distribution of geographic ranges for Caenogastropoda and Hygrophila across all time bins (based on the largest maximum spanning tree of a species across all bins). The medians are significantly different (Wilcoxon rank-sum test, $p < .001$)

range size, whereas there is still some overlap of the two groups. Extinction probability relates with taxonomic group, whereas caenogastropods are more likely to go extinct (Table 1; Figure 3, insert). Conversely, species with larger distributions are—unsurprisingly—less prone to extinction. In particular, the model indicates a general minimum range size, above which species do not become extinct. This threshold is 3,825 km for Caenogastropoda, distinctly higher compared to 2,320 km for Hygrophila (Figure 3).

The relationship between survival status and range size in dependence of taxonomic group varies through time (i.e., the random effects of the GLMM; Table 1; see Appendix S2, Figures S2 and S3 in Appendix S2). Across all time bins, the individual trajectories resemble the overall picture, but the predicted survival probabilities for small distributions vary considerably. For example, the modern fauna (bin 0) is much more prone to extinction compared to the latest Pleistocene–Holocene one (bin 1) at the same range size (Figure S3 in Appendix S2). In most time bins, Hygrophila have higher survival probabilities at the same range size. Only in three out of the 24 bins, caenogastropods have a higher survival status, although the differences between the trajectories are minor and only concern small geographic ranges.

The results of the GLMM hardly differ when adopting a survival status of 1 (optimistic scenario) or 0 (pessimistic scenario) for species with unknown conservation status (Table 1; see Appendix S2, Figures S8–S15 in Appendix S2). Only, in the pessimistic scenario,

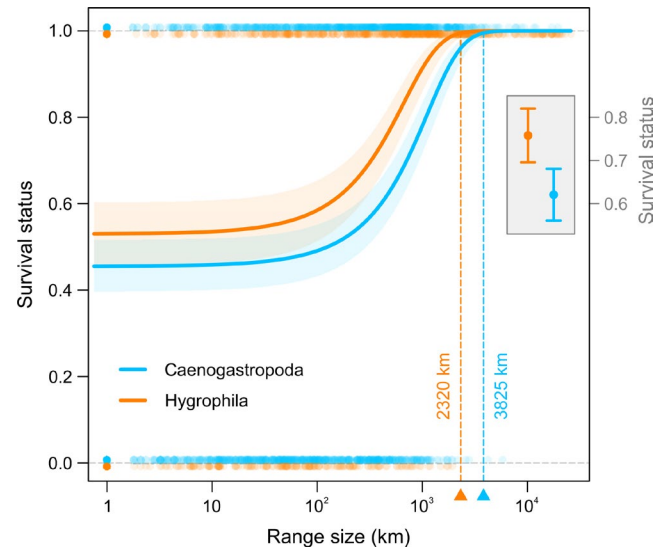


FIGURE 3 Fixed effects of the generalized linear mixed model with taxonomic group (i.e., lifestyle) and geographic range. On average, caenogastropod species are more prone to extinction, both in general (insert) and at the same range size, compared to Hygrophila. The vertical lines and corresponding values indicate the minimum range size, above which species are unlikely to go extinct. See Figure S3 in Appendix S2 for random effects of individual time bins

caenogastropods have a smaller minimum range size at survival status = 1 than Hygrophila (Figure S13 in Appendix S2). This result is probably due to the unevenly distributed number of species with unknown conservation status and their range sizes. About 70% of those species are caenogastropods with a small range size, while some of the Hygrophila have quite large range sizes. Finally, the GLMM excluding modern data—to test for a potential bias from inferring survival status based on distribution data—shows similar results as the main GLMM (see Appendix S2, Figures S4–S7 in Appendix S2). The same model as above received highest AIC support, and the slopes, marginal R^2 and adjusted ICC are in a similar range as the overall model (Table 1).

Of the 32 GLMs testing for an association between the proportion of Caenogastropoda and lake surface area and geological duration, the model with the highest AIC support among all possible combinations of parameters is the Gaussian model combining lake surface area and log10-transformed lake duration (including factor-crossing) and untransformed proportion of Caenogastropoda (see Appendix S4). The residuals are normally distributed (Kolmogorov–Smirnov test, $D = 0.081$, $p = .367$) but show outliers far beyond Cook's distance, suggesting a strong influence of single data points on the model (Figure S1 in Appendix S4). The second best model according to AIC includes only log10-transformed lake duration and untransformed proportion ($\Delta AIC_c = 0.57$). The residuals are normally distributed too ($D = 0.086$, $p = .293$), and there are no major outliers biasing the results (Figure S2 in Appendix S4). Therefore, we consider this more parsimonious model (adjusted $R^2 = .689$, $p < .001$) as best fitting our data while not violating the assumptions of linear regression (Figure 4).

TABLE 1 Main results of the GLMMs discussed in the text

Model	Fixed effects		Random effects		
	Marginal R ²	Slope lifestyle	Slope range size	Slope interaction	SD
Main model (unknown IUCN status excluded)	.822	−0.671	4.138	−1.459	0.533
Optimistic scenario (unknown IUCN status = surviving)	.818	−0.671	4.091	−1.500	0.520
Pessimistic scenario (unknown IUCN status = extinct)	.552	−0.280	1.942	0.650	0.589
Without modern data	.706	−0.571	2.998	−0.942	0.529

Note: For more details and results of other GLMMs see Appendix S2. Note the negative slopes of lifestyle and the interaction term result from the coding of the taxonomic group (0 = Hygrophila, 1 = Caenogastropoda).

Abbreviations: ICC, intraclass correlation coefficient; SD, standard deviation.

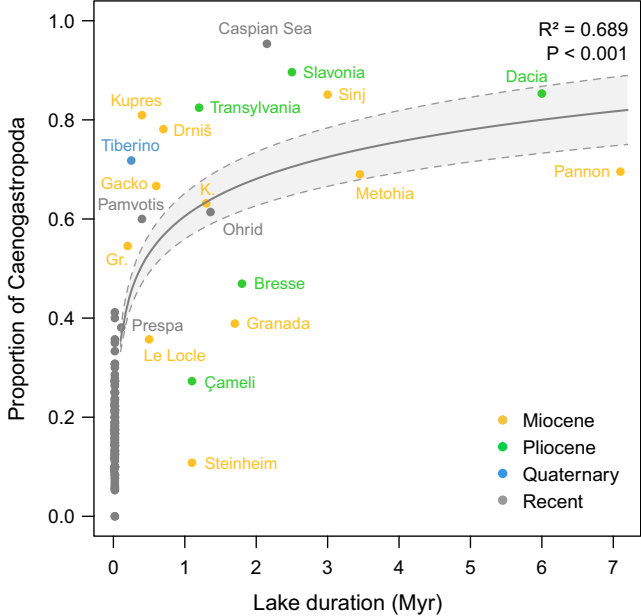


FIGURE 4 Linear regression model showing the logarithmic association between the proportion of Caenogastropoda per fauna and a lake's geological duration. In case of lakes overlapping stratigraphic intervals, age assignment (and colour) was based on the mean stratigraphic age of all fossil-bearing localities included in this study. The grey area shows the 95% confidence interval. Gr., Lake Groisenbach; K., Lake Kosovo

4 | DISCUSSION

4.1 | Caenogastropoda are more prone to extinction

The results of the GLMM show that the extinction probability of freshwater gastropod species correlates with taxonomic group and geographic range (Figure 3). The model supports our hypothesis that caenogastropod species are on average more prone to go extinct. More precisely, their survival probability is lower than that of Hygrophila at the same range size and they have a higher “safety threshold range” (minimum range size above which the predicted survival status = 1). The GLMMs based on different data subsets all show the same tendency (Table 1), proving that our model is independent of time (and particularly modern data) and reflects a general pattern.

The two taxonomic groups coincide with major differences in lifestyle. Because of their gonochoristic mode of reproduction, slower reproduction rates and longer life cycles (Pyron & Brown, 2015), Caenogastropoda are largely out-competed by the air-breathing Hygrophila when it comes to colonizing new habitats quickly. Hygrophila include many species with high ecological tolerances and thus higher dispersal potential and chances of survival in newly colonized environments (Johnson et al., 2013; van Leeuwen et al., 2013). The effect is enhanced by physiological differences: their capability to take up oxygen from the air facilitates survival outside the water and therefore increases the chance for successful

long-term dispersal (e.g., Dillon, 2000; Kendall, 1949; Poznańska et al., 2015). Good dispersers with wide distribution also exist among caenogastropods (e.g., van Leeuwen et al., 2012), but they are exceptions rather than the rule. Examples are parthenogenetic species, such as *Potamopyrgus antipodarum* or *Melanoides tuberculata*, or taxa with high ecological tolerances, like *Bithynia tentaculata* (Mills et al., 1993; Städler et al., 2005; Strong et al., 2008).

4.2 | Long-lived lakes as refuges for caenogastropods

Our analyses show that the relative species richness of Caenogastropoda and Hygrophila in a lake relates to its geological duration (Figure 4). The longer a lake exists, the more caenogastropods can be expected on average. All extant faunas with more than 42% caenogastropods in European lakes are from long-lived lakes (Figure 4). In contrast, the majority of lakes today are geologically young and of glacial origin and typically dominated by Hygrophila (Georgopoulou et al., 2016).

Long-lived lakes harbour unique faunas that have evolved over hundreds of thousands to millions of years and constitute exceptional evolutionary archives (e.g., Cohen, 1994; Hampton et al., 2018; Martens, 1997; Wilke et al., 2016; Wilson et al., 2004). The high species diversity in these ecosystems is typically the result of intralacustrine speciation, resulting in endemic evolutionary lineages (e.g., Hirano et al., 2019; Michel, 1994; Neubauer et al., 2013; Schreiber et al., 2012; Wilson et al., 2004). While many long-lived lakes—both recent and fossil—have experienced major environmental changes, they have still continuously existed as lakes for an extended geological time (e.g., Harzhauser & Mandic, 2008; Jipa & Olariu, 2009; Krijgsman et al., 2019; Mandic et al., 2011; Neubauer, Georgopoulou, et al., 2016; Neubauer, Harzhauser, et al., 2016; Wilke et al., 2020) and as such expectedly lower the extinction risk of the species they harbour.

In a comprehensive review, Michel (1994) demonstrated that, among other factors, gastropod radiations in long-lived lakes are associated with strategies of reproduction and dispersal (see also Boss, 1978; Brooks, 1950; Martens, 1997). Matching our results, she showed that long-lived lakes are typically dominated by caenogastropod species (there as “Prosobranchia”) with dioecious reproduction with a large percentage of them being endemic (Michel, 1994). However, our study is the first to provide quantitative evidence that species composition of gastropods as regards the proportion of Caenogastropoda is (at least to some extent) a function of the lake's geological duration.

The higher relative species richness of caenogastropods in long-lived lakes may have different causes, including but not limited to reproduction strategy, dispersal capability, genetic structure, habitat parameters and physiological constraints (Michel, 1994; Schön & Martens, 2004). A main factor contributing to the differences between Caenogastropoda and Hygrophila species richness involves depth range. Long-lived lakes typically form in geologically stable,

deep tectonic basins (Cohen, 2003). In many of these ecosystems, there is a clear bathymetric zonation of gastropod species (e.g., Hauffe et al., 2011, 2016; Lattuada et al., 2020; Michel, 2000; Neubauer, Harzhauser, et al., 2016; Sitnikova, 2006; Stelbrink et al., 2016). As they are not bound to air oxygen, the dioecious caenogastropods have naturally higher depth tolerances and, on average, can diversity across a wider bathymetric range (Michel, 1994; but see, e.g., Stelbrink et al., 2015 for an exception of abyssal Hygrophila). Some intralacustrine radiations were probably triggered by ecological opportunity arising from lake deepening (e.g., Stelbrink et al., 2020).

The presence of long-lived lakes might also explain a part of the variation in the relationship between extinction probability and taxonomic group across geological time (Figure 2, Figure S3 in Appendix S2). For example, the low extinction risk in the latest Miocene to Pliocene (bins 5, 7, 8 and 9) compared to today or most of the Quaternary may be due to the presence of long-lived lakes such as lakes Pannon or Dacia in central to south-eastern Europe, where many species found stable conditions and existed for several million years (Magyar et al., 2013; Neubauer, Harzhauser, et al., 2016; Wenz, 1942). A potential fossil bias towards long-lived lakes, which have long sedimentary records and might thus be overrepresented in the fossil record, is unlikely in our case. While the number of records and species is particularly high for these lakes, the number of long-lived lake faunas is still comparably low in our dataset.

4.3 | Limitations

The relationship between the proportion of Caenogastropoda and lake duration is not linear, and there are deviations from the general pattern. Probably the most famous among them is the middle Miocene Lake Steinheim (Figure 4), which gave rise to a species-flock of the planorbid genus *Gyraulus* associated with a complex pattern of morphological diversification (Rasser, 2013). Also within late Miocene Lake Pannon, Hygrophila formed evolutionary lineages such as the lymnaeid Valencienniinae (Figure 3a; Neubauer, Georgopoulou, et al., 2016), but these are overshadowed by the more abundant hydrobiids and melanopsids. The Caspian Sea fauna is an outlier in the other direction: It is almost exclusively composed of caenogastropods and dominated by the minute Hydrobiidae (Wesselingh et al., 2019).

Extending the geographic scope shows that the pattern we found is not restricted to Europe. Many long-lived lakes outside the study range are also dominated by caenogastropod species, such as lakes Tanganyika, Malawi and Titicaca (Dejoux, 1992; Van Damme & Gautier, 2013; West et al., 2003). A comparable fossil example is the Miocene Pebas lake system, dominated by Cochliopidae (Wesselingh, 2006). However, some long-lived lakes exist today (e.g., Baikal and Victoria) that have a near equal share or even more Hygrophila species (Lange et al., 2013; Michel, 1994; Vinarski & Kantor, 2016). We are not aware of long-lived lake faunas dominated by Hygrophila, but examples like Lake Baikal or Lake Victoria show that the pattern we find is not as strict as suggested by European

lakes alone. To allow a more general conclusion, more data on the gastropod faunas and geological ages of fossil and recent lakes all around the planet need to be gathered, as far as possible considering lakes of different geological origin, bathymetric range, trophic state and climatic setting.

The relationship between extinction probability and taxonomic group is here interpreted to reflect differences in lifestyles, particularly concerning reproductive mode, life cycle and respiration type, all of which influence the species' dispersal ability. We are aware that extinction probability is not only a function of these traits, particularly as different families, genera and species within the two clades show some degree of variation with respect to these (and other) traits (e.g., Dillon, 2000; Pyron & Brown, 2015; Strong et al., 2008). Also, environmental and climatic factors and, in the Anthropocene, human impact certainly play a role in driving extinction of freshwater gastropods (Cordellier et al., 2012; Georgopoulou et al., 2016; Neubauer, Harzhauser, Georgopoulou, et al., 2015; Neubauer et al., 2021), whereas the two systematic groups may suffer from and react differently to selected pressures. Nonetheless, the differences among Caenogastropoda and Hygrophila concerning the abovementioned lifestyle traits, which are consistent through geological time, support our hypothesis that the discrepancy we found in their extinction likelihood is at least to some degree a result of lifestyle.

4.4 | Implications for conservation

Their gonochoristic mode of reproduction, slower reproduction rates and longer generation times, paired with a lower tolerance to variation in oxygen or temperature (Pyron & Brown, 2015), lower the chances of successful colonization of new habitats for caenogastropod species compared to Hygrophila. As a result, they have smaller geographic ranges and are more vulnerable to extinction (Figure 2b). A query of IUCN conservation statuses of all European freshwater gastropods (not only those used in our study) shows that 64.1% of Caenogastropoda are threatened (status VU, EN or CR), compared to 31.5% for the Hygrophila (IUCN, 2020; data-deficient species were not considered for the calculation of the percentages). In turn, 64.4% of Hygrophila and only 23.9% of Caenogastropoda are marked as "least concern".

Conservation efforts need to focus not only on rare taxa—such as many Caenogastropoda—but on the ecosystems they inhabit as a whole. For caenogastropods, aside of springs, caves and groundwaters (Strong et al., 2008), this concerns particularly long-lived lakes, where they typically form evolutionary lineages often resulting in a high diversity of endemic species. Few of these lakes exist today and all of them are affected directly or indirectly by human activities and face warming of surface waters, eutrophication, pollution, overfishing and/or hydrological alteration (Hampton et al., 2018). Although these or similar factors—unfortunately—also pose threats for many other freshwater ecosystems (Albert et al., 2021; Böhm et al., 2020; Dudgeon, 2020; EEA, 2019; Green et al., 2015; Janse et al., 2015;

Vörösmarty et al., 2010; WWF, 2020), the comparatively small number of long-lived lakes and their status as natural laboratories of evolution make the situation even more critical. In order to safeguard these exceptional evolutionary archives and their biota multilateral basin management strategies, more and extensive aquatic reserves and coordinated conservation efforts across country borders are needed (Hampton et al., 2018; ILEC, 2005). As many long-lived lakes are situated in developing countries, this effort requires financial and scientific support from the international side (Coulter et al., 2006).

5 | CONCLUSION

Our study shows that Caenogastropoda are more likely to go extinct than Hygrophila. The increased extinction risk is reflected in smaller geographic ranges. The relationship between extinction probability and taxonomic group coincides with differences in lifestyle, that is the type of reproduction, life cycle, respiration mode and dispersal ability. While there are minor outliers in certain time bins in the fossil record, our analyses confirm a general pattern that is not driven by fossil or extant faunas alone. Moreover, our findings clearly show the importance of long-lived lakes to the survival of caenogastropods. While such environments were more frequent in Europe's geological past, only few long-lived lakes are present today, also on a global scale. These ecosystems are cradles of evolution and hold levels of species diversity and endemism far above average, and as such, they are in particular need of strict conservation measures to maintain their unique diversity.

The presence of outliers in some time bins as well as the large variance in the relationship between lake duration and proportion of Caenogastropoda indicates that the pattern is not as clear cut. There are certainly other factors impacting species extinction risk as well, like environmental conditions or individual species/family traits, but we believe that our contribution adds relevant data to understanding faunal evolution on large geographic and temporal scales. The outcomes of this study may also be a stimulation to investigate differential extinction risks in other species groups. Future investigations may particularly focus on a more detailed ecological differentiation of the species, with regard to lifestyle (e.g., (ovo)viviparity vs. oviparity), trophic or habitat specialization or depth ranges. Where detailed information on the palaeoecology of extinct representatives is known, the fossil record provides the opportunity to reconstruct general patterns and processes irrespective of short-term influence, such as posed by humankind.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

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REFERENCES

- Albert, J. S., Destouni, G., Duke-Sylvester, S. M., Magurran, A. E., Oberdorff, T., Reis, R. E., Winemiller, K. O., & Ripple, W. J. (2021). Scientists' warning to humanity on the freshwater biodiversity crisis. *Ambio*, 50, 85–94. <https://doi.org/10.1007/s13280-020-01318-8>
- Albrecht, C., Trajanovski, S., Kuhn, K., Streit, B., & Wilke, T. (2006). Rapid evolution of an ancient lake species flock: Freshwater limpets (Gastropoda: Ancyliidae) in the Balkan Lake Ohrid. *Organisms, Diversity & Evolution*, 6, 294–307. <https://doi.org/10.1016/j.ode.2005.12.003>
- Baker, F. C. (1945). *The molluscan family Planorbidae*. The University of Illinois Press.
- Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J., Bauer, A., & Krivitsky, P. N. (2020). *lme4: Linear Mixed-Effects Models using 'Eigen' and S4*. R package version 1.1-26. Retrieved from <http://CRAN.R-project.org/package=lme4>
- Bland, L. M. (2017). Global correlates of extinction risk in freshwater crayfish. *Animal Conservation*, 20, 532–542. <https://doi.org/10.1111/acv.12350>
- Böhm, M., Dewhurst-Richman, N. I., Seddon, M., Ledger, S. E. H., Albrecht, C., Allen, D., Bogan, A. E., Cordeiro, J., Cummings, K. S., Cuttelod, A., Darrigran, G., Darwall, W., Fehér, Z., Gibson, C., Graf, D. L., Köhler, F., Lopes-Lima, M., Pastorino, G., Perez, K. E., ... Collen, B. (2020). The conservation status of the world's freshwater molluscs. *Hydrobiologia*, 848, 3231–3254. <https://doi.org/10.1007/s10750-020-04385-w>
- Boss, K. J. (1978). On the evolution of gastropods in ancient lakes. In V. Fretter, & J. Peake (Eds.), *Pulmonates Vol. 2A. Systematics, evolution and ecology* (pp. 385–428). Academic Press.
- Bowler, D. E., Hof, C., Haase, P., Kröncke, I., Schweiger, O., Adrian, R., Baert, L., Bauer, H.-G., Blick, T., Brooker, R. W., Dekoninck, W., Domisch, S., Eckmann, R., Hendrickx, F., Hickler, T., Klotz, S., Kraberg, A., Kühn, I., Matesanz, S., ... Böhning-Gaese, K. (2017). Cross-realm assessment of climate change impacts on species' abundance trends. *Nature Ecology & Evolution*, 1, 67. <https://doi.org/10.1038/s41559-016-0067>
- Boyle, J. (2017a). Quantifying geographic range measures and their utility as extinction risk proxies. *PeerJ Preprints*, 5, e3379v1. <https://doi.org/10.7287/peerj.preprints.3379v1>
- Boyle, J. (2017b). *GeoRange: Calculating geographic range from occurrence data*. R package version 0.1.0. Retrieved from <http://CRAN.R-project.org/package=GeoRange>
- Brooks, J. L. (1950). Speciation in ancient lakes. *Quarterly Review of Biology*, 25(30–60), 131–176. <https://doi.org/10.1086/397539>
- Brown, K. M., Alexander, J. E., & Thorp, J. H. (1998). Differences in the ecology and distribution of lotic pulmonate and prosobranch gastropods. *American Malacological Bulletin*, 14, 91–101.
- Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods & Research*, 33, 261–304. <https://doi.org/10.1177/0049124104268644>
- Cohen, A. S. (1994). Extinction in ancient lakes: Biodiversity crises and conservation 40 years after J. L. Brooks. In K. Martens, B. Goddeeris, & G. Coulter (Eds.), *Speciation in ancient lakes*. *Archiv für Hydrobiologie – Beiheft: Ergebnisse der Limnologie* (Vol. 44, pp. 451–479). Springer.
- Cohen, A. S. (2003). *Paleolimnology: The history and evolution of lake systems*. Oxford University Press.
- Cordellier, M., Pfenninger, A., Streit, B., & Pfenninger, M. (2012). Assessing the effects of climate change on the distribution of pulmonate freshwater snail biodiversity. *Marine Biology*, 159, 2519–2531. <https://doi.org/10.1007/s00227-012-1894-9>
- Coulter, G., Langenberg, V., Lowe-McConnell, R., Riedel, F., Roest, F., Sarvala, J., & Timoshkin, O. (2006). The problems confronting survival of biodiversity in ancient lakes. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen*, 29, 1178–1181. <https://doi.org/10.1080/03680770.2005.11902870>
- Cumberlidge, N., Ng, P. K. L., Yeo, D. C. J., Magalhães, C., Campos, M. R., Alvarez, F., Naruse, T., Daniels, S. R., Esser, L. J., Attipoe, F. Y. K., Clotilde-Ba, F.-L., Darwall, W., McIvor, A., Baillie, J. E. M., Collen, B., & Ram, M. (2009). Freshwater crabs and the biodiversity crisis: Importance, threats, status, and conservation challenges. *Biological Conservation*, 142, 1665–1673. <https://doi.org/10.1016/j.biocon.2009.02.038>
- Darwall, W., Bremerich, V., De Wever, A., Dell, A. I., Freyhof, J., Gessner, M. O., & Weyl, O. (2020). The alliance for freshwater life: A global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28, 1015–1022. <https://doi.org/10.1002/aqc.2958>
- De Grave, S., Smith, K. G., Adeler, N. A., Allen, D. J., Alvarez, F., Anker, A., Cai, Y., Carrizo, S. F., Klotz, W., Mantelatto, F. L., Page, T. J., Shy, J.-Y., Villalobos, J. L., & Wowor, D. (2015). Dead shrimp blues: A global assessment of extinction risk in freshwater shrimps (Crustacea: Decapoda: Caridea). *PLoS One*, 10, e0120198. <https://doi.org/10.1371/journal.pone.0120198>
- Dejoux, C. (1992). The mollusca. In C. Dejoux, & A. Itis (Eds.), *Lake Titicaca. A synthesis of limnological knowledge* (pp. 311–336). Kluwer Academic.
- Dillon, R. T. (2000). *The ecology of freshwater molluscs*. Cambridge University Press.
- Dudgeon, D. (2020). *Freshwater biodiversity: Status, threats and conservation*. Cambridge University Press.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182. <https://doi.org/10.1017/S1464793105006950>
- EEA (European Environment Agency). (2019). *The European environment – State and outlook 2020. Knowledge for transition to a sustainable Europe*. Publications Office of the European Union.
- García-Moreno, J., Harrison, I. J., Dudgeon, D., Clausnitzer, V., Darwall, W., Farrell, T., & Tubbs, N. (2014). Sustaining freshwater biodiversity in the Anthropocene. In A. Bhaduri, J. Bogardi, J. Leentvaar, & S. Marx (Eds.), *The global water system in the Anthropocene. Challenges for science and governance* (pp. 247–270). Springer.
- Georgopoulou, E., Neubauer, T. A., Harzhauser, M., Kroh, A., & Mandic, O. (2016). Distribution patterns of European lacustrine

- gastropods: A result of environmental factors and deglaciation history. *Hydrobiologia*, 775, 69–82. <https://doi.org/10.1007/s10750-016-2713-y>
- Gorthner, A. (1994). What is an ancient lake? In K. Martens, B. Goddeeris, & G. Coulter (Eds.), *Speciation in ancient lakes*. *Archiv für Hydrobiologie – Beiheft: Ergebnisse der Limnologie* (Vol. 44, pp. 97–100). Springer.
- Gray, J. (1988). Evolution of the freshwater ecosystem: The fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62, 1–214. [https://doi.org/10.1016/0031-0182\(88\)90054-5](https://doi.org/10.1016/0031-0182(88)90054-5)
- Green, P. A., Vörösmarty, C. J., Harrison, I., Farrell, T., Sáenz, L., & Fekete, B. M. (2015). Freshwater ecosystem services supporting humans: Pivoting from water crisis to water solutions. *Global Environmental Change*, 34, 108–118. <https://doi.org/10.1016/j.gloenvcha.2015.06.007>
- Hampton, S. E., McGowan, S., Ozersky, T., Virdis, S. G. P., Vu, T. T., Spanbauer, T. L., Kraemer, B. M., Swann, G., Mackay, A. W., Powers, S. M., Meyer, M. F., Labou, S. G., O'Reilly, C. M., DiCarlo, M., Galloway, A. W. E., & Fritz, S. C. (2018). Recent ecological change in ancient lakes. *Limnology and Oceanography*, 63, 2277–2304. <https://doi.org/10.1002/lno.10938>
- Hartig, F., & Lohse, L. (2020). *DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models*. R package version 0.3.3.0. Retrieved from <http://CRAN.R-project.org/package=DHARMA>
- Harzhauser, M., & Mandic, O. (2008). Neogene lake systems of Central and South-Eastern Europe: Faunal diversity, gradients and interrelations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 260, 417–434. <https://doi.org/10.1016/j.palaeo.2007.12.013>
- Hauffe, T., Albrecht, C., Schreiber, K., Birkhofer, K., Trajanovski, S., & Wilke, T. (2011). Spatially explicit analyses of gastropod biodiversity in ancient Lake Ohrid. *Biogeosciences*, 8, 175–188. <https://doi.org/10.5194/bg-8-175-2011>
- Hauffe, T., Albrecht, C., & Wilke, T. (2016). Assembly processes of gastropod community change with horizontal and vertical zonation in ancient Lake Ohrid: A metacommunity speciation perspective. *Biogeosciences*, 13, 2901–2911. <https://doi.org/10.5194/bg-13-2901-2016>
- Heino, J., Virkkala, R., & Toivonen, H. (2009). Climate change and freshwater biodiversity: Detected patterns, future trends and adaptations in northern regions. *Biological Reviews*, 84, 39–54. <https://doi.org/10.1111/j.1469-185X.2008.00060.x>
- Hirano, T., Saito, T., Tsunamoto, Y., Koseki, J., Prozorova, L., Do, V. T., Matsuoka, K., Nakai, K., Suyama, Y., & Chiba, S. (2019). Role of ancient lakes in genetic and phenotypic diversification of freshwater snails. *Molecular Ecology*, 28, 5032–5051. <https://doi.org/10.1111/mec.15272>
- ILEC (International Lake Environment Committee). (2005). *Managing lakes and their basins for sustainable use: A report for Lake Basin managers and stakeholders*. International Lake Environment Committee Foundation.
- IUCN (International Union for Conservation of Nature). (2020). *The IUCN red list of threatened species. Version 2020-3*. Retrieved from <https://www.iucnredlist.org>
- Janse, J. H., Kuiper, J. J., Weijters, M. J., Westerbeek, E. P., Jeuken, M., Bakkenes, M., Alkemade, R., Mooij, W. M., & Verhoeven, J. (2015). GLOBIO-Aquatic, a global model of human impact on the biodiversity of inland aquatic ecosystems. *Environmental Science & Policy*, 48, 99–114. <https://doi.org/10.1016/j.envsci.2014.12.007>
- Jipa, D. C., & Olariu, C. (2009). *Dacian Basin – Depositional architecture and sedimentary history of a Paratethys Sea*. *GeoEcoMar*.
- Johnson, P. D., Bogan, A. E., Brown, K. M., Burkhead, N. M., Cordeiro, J. R., Garner, J. T., Hartfield, P. D., Lepitzki, D. A. W., Mackie, G. L., Pip, E., Tarpley, T. A., Tiemann, J. S., Whelan, N. V., & Strong, E. E. (2013). Conservation status of freshwater gastropods of Canada and the United States. *Fisheries*, 38, 247–282. <https://doi.org/10.1080/03632415.2013.785396>
- Kappes, H., & Haase, P. (2012). Slow, but steady: Dispersal of freshwater molluscs. *Aquatic Sciences*, 74, 1–14. <https://doi.org/10.1007/s00027-011-0187-6>
- Kendall, S. B. (1949). Bionomics of *Limnaea truncatula* and the parthenitae of *Fasciola hepatica* under drought conditions. *Journal of Helminthology*, 23, 57–68. <https://doi.org/10.1017/S0022149X00032375>
- Krijgsman, W., Tesakov, A., Yanina, T., Lazarev, S., Danukalova, G., Van Baak, C., Agustí, J., Alçiçek, M. C., Aliyeva, E., Bista, D., Bruch, A., Büyükeriç, Y., Bukhsianidze, M., Flecker, R., Frolov, P., Hoyle, T. M., Jorissen, E. L., Kirscher, U., Koriche, S. A., ... Wesselingh, F. P. (2019). Quaternary time scales for the Pontocaspian domain: Interbasinal connectivity and faunal evolution. *Earth-Science Reviews*, 188, 1–40. <https://doi.org/10.1016/j.earscirev.2018.10.013>
- Lange, C. N., Kristensen, T. K., & Madsen, H. (2013). Gastropod diversity, distribution and abundance in habitats with and without anthropogenic disturbances in Lake Victoria, Kenya. *African Journal of Aquatic Science*, 38, 295–304. <https://doi.org/10.2989/16085914.2013.797380>
- Lattuada, M., Albrecht, C., Wesselingh, F. P., Klinkenbuß, D., Vinarski, M. V., Kijashko, P., Raes, N., & Wilke, T. (2020). Endemic Caspian Sea mollusks in hotspot and non-hotspot areas differentially affected by anthropogenic pressures. *Journal of Great Lakes Research*, 46, 1221–1226. <https://doi.org/10.1016/j.jglr.2019.12.007>
- Liu, C., Comte, L., & Olden, J. D. (2017). Heads you win, tails you lose: Life-history traits predict invasion and extinction risk of the world's freshwater fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27, 773–779. <https://doi.org/10.1002/aqc.2740>
- Lüdecke, D., Aust, F., Crawley, S., & Ben-Shachar, M. S. (2020). *ggeffects: Create tidy data frames of marginal effects for 'ggplot' from model outputs*. R package version 1.0.1. Retrieved from <http://CRAN.R-project.org/package=ggeffects>
- Lüdecke, D., Makowski, D., Waggoner, P., Patil, I., & Ben-Shachar, M. S. (2020). *performance: Assessment of regression models performance*. R package version 0.6.1. Retrieved from <http://CRAN.R-project.org/package=performance>
- Magyar, I., Radivojević, D., Sztanó, O., Synak, R., Ujszászi, K., & Pócsik, M. (2013). Progradation of the paleo-Danube shelf margin across the Pannonian Basin during the Late Miocene and Early Pliocene. *Global and Planetary Change*, 103, 168–173. <https://doi.org/10.1016/j.gloplacha.2012.06.007>
- Mandic, O., De Leeuw, A., Vuković, B., Krijgsman, W., Harzhauser, M., & Kuiper, K. F. (2011). Palaeoenvironmental evolution of Lake Gacko (Southern Bosnia and Herzegovina): Impact of the middle Miocene climatic optimum on the Dinaride Lake System. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 299, 475–492. <https://doi.org/10.1016/j.palaeo.2010.11.024>
- Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., Kasperdus, H., & Darwall, W. (2014). Europe's freshwater biodiversity under climate change: Distribution shifts and conservation needs. *Diversity and Distributions*, 20, 1097–1107. <https://doi.org/10.1111/ddi.12232>
- Martens, K. (1997). Speciation in ancient lakes. *Trends in Ecology & Evolution*, 12, 177–182. [https://doi.org/10.1016/S0169-5347\(97\)01039-2](https://doi.org/10.1016/S0169-5347(97)01039-2)
- Mazerolle, M. J. (2020). *AICcmodavg: model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.3-1. Retrieved from <http://CRAN.R-project.org/package=AICcmodavg>
- Michel, E. (1994). Why snails radiate: A review of gastropod evolution in long-lived lakes, both recent and fossil. In K. Martens, B. Goddeeris, & G. Coulter (Eds.), *Speciation in ancient lakes*. *Archiv für Hydrobiologie – Beiheft: Ergebnisse der Limnologie* (Vol. 44, pp. 285–317). Springer.
- Michel, E. (2000). Phylogeny of a gastropod species flock: Exploring speciation in Lake Tanganyika in a molecular framework. *Advances*

- in *Ecological Research*, 31, 275–302. [https://doi.org/10.1016/S0065-2504\(00\)31016-9](https://doi.org/10.1016/S0065-2504(00)31016-9)
- Mills, E. L., Leach, J. H., Carlton, J. T., & Secor, C. L. (1993). Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research*, 19, 1–54. [https://doi.org/10.1016/S0380-1330\(93\)71197-1](https://doi.org/10.1016/S0380-1330(93)71197-1)
- Neubauer, T. A., Georgopoulou, E., Harzhauser, M., Mandic, O., & Kroh, A. (2016). Predictors of shell size in long-lived lake gastropods. *Journal of Biogeography*, 43, 2062–2074. <https://doi.org/10.1111/jbi.12777>
- Neubauer, T. A., Harzhauser, M., Georgopoulou, E., Kroh, A., & Mandic, O. (2015). Tectonics, climate, and the rise and demise of continental aquatic species richness hotspots. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 11478–11483. <https://doi.org/10.1073/pnas.1503992112>
- Neubauer, T. A., Harzhauser, M., & Kroh, A. (2013). Phenotypic evolution in a fossil gastropod species lineage: Evidence for adaptive radiation? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 370, 117–126. <https://doi.org/10.1016/j.palaeo.2012.11.025>
- Neubauer, T. A., Harzhauser, M., Kroh, A., Georgopoulou, E., & Mandic, O. (2015). A gastropod-based biogeographic scheme for the European Neogene freshwater systems. *Earth-Science Reviews*, 143, 98–116. <https://doi.org/10.1016/j.earscirev.2015.01.010>
- Neubauer, T. A., Harzhauser, M., Mandic, O., Kroh, A., & Georgopoulou, E. (2016). Evolution, turnovers and spatial variation of the gastropod fauna of the late Miocene biodiversity hotspot Lake Pannon. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 442, 84–95. <https://doi.org/10.1016/j.palaeo.2015.11.016>
- Neubauer, T. A., Hauffe, T., Silvestro, D., Schauer, J., Kadolsky, D., Wesselingh, F. P., Harzhauser, M., & Wilke, T. (2021). Current extinction rate in European freshwater gastropods greatly exceeds that of the late Cretaceous mass extinction. *Communications Earth & Environment*, 2, 97. <https://doi.org/10.1038/s43247-021-00167-x>
- Olden, J. D., Hogan, Z. S., & Vander Zanden, M. J. (2007). Small fish, big fish, red fish, blue fish: Size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecology and Biogeography*, 16, 694–701. <https://doi.org/10.1111/j.1466-8238.2007.00337.x>
- Payne, J. L., Bush, A. M., Heim, N. A., Knope, M. L., & McCauley, D. J. (2016). Ecological selectivity of the emerging mass extinction in the oceans. *Science*, 353, 1284–1286. <https://doi.org/10.1126/science.aaf2416>
- Pereira, H. M., Leadley, P. W., Proença, V., Alkemade, R., Scharlemann, J. P. W., Fernandez-Manjarrés, J. F., Araújo, M. B., Balvanera, P., Biggs, R., Cheung, W. W. L., Chini, L., Cooper, H. D., Gilman, E. L., Guénette, S., Hurr, G. C., Huntington, H. P., Mace, G. M., Oberdorff, T., Revenga, C., ... Walpole, M. (2010). Scenarios for global biodiversity in the 21st century. *Science*, 330, 1496–1501. <https://doi.org/10.1126/science.1196624>
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., Raven, P. H., Roberts, C. M., & Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 1246752. <https://doi.org/10.1126/science.1246752>
- Poff, N. L., Olden, J. D., & Strayer, D. L. (2012). Climate change and freshwater fauna extinction risk. In L. Hannah (Ed.), *Saving a million species* (pp. 309–336). Island Press/Center for Resource Economics.
- Ponder, W. F. (1988). *Potamopyrgus antipodarum* – A molluscan coloniser of Europe and Australia. *Journal of Molluscan Studies*, 54, 271–285. <https://doi.org/10.1093/mollus/54.3.271>
- Poznańska, M., Goleniewska, D., Gulanicz, T., Kakareko, T., Jermacz, Ł., & Kobak, J. (2015). Effect of substratum drying on the survival and migrations of a freshwater pulmonate snail *Planorbis cornutus* (Linnaeus, 1758). *Hydrobiologia*, 747, 177–188. <https://doi.org/10.1007/s10750-014-2130-z>
- Pyron, M., & Brown, K. M. (2015). Introduction to Mollusca and the class Gastropoda. In J. H. Thorp, & D. C. Rogers (Eds.), *Thorp and Covich's freshwater invertebrates: Ecology and general biology* (Vol. 1, pp. 383–421). Elsevier.
- R Core Team (2020). *R: A language and environment for statistical computing. Version 4.0.3*. R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org>
- Rasser, M. W. (2013). Evolution in isolation: The *Gyraulus* species flock from Miocene Lake Steinheim revisited. In T. von Rintelen, R. M. Marwoto, G. D. Haffner, & F. Herder (Eds.), *Speciation in ancient lakes – Classic concepts and new approaches*. *Hydrobiologia* (Vol. 739, pp. 7–24). Springer. <https://doi.org/10.1007/s10750-013-1677-4>
- Reynolds, J. D., Webb, T. J., & Hawkins, L. A. (2005). Life history and ecological correlates of extinction risk in European freshwater fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 854–862. <https://doi.org/10.1139/f05-066>
- Richman, N. I., Böhm, M., Adams, S. B., Alvarez, F., Bergey, E. A., Bunn, J. J. S., & Collen, B. (2015). Multiple drivers of decline in the global status of freshwater crayfish (Decapoda: Astacidea). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 370, 20140060. <https://doi.org/10.1098/rstb.2014.0060>
- Schön, I., & Martens, K. (2004). Adaptive, pre-adaptive and non-adaptive components of radiations in ancient lakes: A review. *Organisms, Diversity & Evolution*, 4, 137–156. <https://doi.org/10.1016/j.ode.2004.03.001>
- Schreiber, K., Hauffe, T., Albrecht, C., & Wilke, T. (2012). The role of barriers and gradients in differentiation processes of pyrgulinid microgastropods of Lake Ohrid. *Hydrobiologia*, 682, 61–73. <https://doi.org/10.1007/s10750-011-0864-4>
- Sitnikova, T. Y. (2006). Endemic gastropod distribution in Baikal. In G. Coulter, O. Timoshkin, L. Timoshkina, & K. Martens (Eds.), *Species and speciation in ancient lakes*. *Hydrobiologia* (Vol. 568, pp. 207–211). Springer. <https://doi.org/10.1007/s10750-006-0313-y>
- Städler, T., Frye, M., Neiman, M., & Lively, C. M. (2005). Mitochondrial haplotypes and the New Zealand origin of clonal European *Potamopyrgus*, an invasive aquatic snail. *Molecular Ecology*, 14, 2465–2473. <https://doi.org/10.1111/j.1365-294X.2005.02603.x>
- Stelbrink, B., Shirohaya, A. A., Clewing, C., Sitnikova, T. Y., Prozorova, L. A., & Albrecht, C. (2015). Conquest of the deep, old and cold: An exceptional limpet radiation in Lake Baikal. *Biology Letters*, 11, 20150321. <https://doi.org/10.1098/rsbl.2015.0321>
- Stelbrink, B., Shirohaya, A. A., Föller, K., Wilke, T., & Albrecht, C. (2016). Origin and diversification of Lake Ohrid's endemic acroloxid limpets: The role of geography and ecology. *BMC Evolutionary Biology*, 16, 273. <https://doi.org/10.1186/s12862-016-0826-6>
- Stelbrink, B., Wilke, T., & Albrecht, C. (2020). Ecological opportunity enabled invertebrate radiations in ancient Lake Ohrid. *Journal of Great Lakes Research*, 46, 1156–1161. <https://doi.org/10.1016/j.jglr.2020.06.012>
- Strong, E. E., Gargominy, O., Ponder, W. F., & Bouchet, P. (2008). Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia*, 595, 149–166. <https://doi.org/10.1007/s10750-007-9012-6>
- Taylor, D. W. (1988). Aspects of freshwater mollusc ecological biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 62, 511–576. [https://doi.org/10.1016/0031-0182\(88\)90071-5](https://doi.org/10.1016/0031-0182(88)90071-5)
- Van Damme, D., & Gautier, A. (2013). Lacustrine mollusc radiations in the Lake Malawi Basin: Experiments in a natural laboratory for evolution. *Biogeosciences*, 10, 5767–5778. <https://doi.org/10.5194/bg-10-5767-2013>
- Van Leeuwen, C. H. A., Huig, N., Van der Velde, G., Van alen, T. A., Wagemaker, C. A. M., Sherman, C. D. H., Klaassen, M., & Figuerola, J. (2013). How did this snail get here? Several dispersal vectors inferred for an aquatic invasive species. *Freshwater Biology*, 58, 88–99. <https://doi.org/10.1111/fwb.12041>
- van Leeuwen, C. H. A., van der Velde, G., van Lith, B., & Klaassen, M. (2012). Experimental quantification of long distance dispersal

- potential of aquatic snails in the gut of migratory birds. *PLoS One*, 7, e32292. <https://doi.org/10.1371/journal.pone.0032292>
- Vinarski, M. V., & Kantor, Y. I. (2016). *Analytical catalogue of fresh and brackish water molluscs of Russia and adjacent countries*. A.N. Severtsov Institute of Ecology and Evolution of RAS.
- Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R., & Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, 467, 555–561. <https://doi.org/10.1038/nature09440>
- Welter-Schultes, F. W. (2012). *European non-marine molluscs, a guide for species identification*. Planet Poster Editions.
- Wenz, W. (1942). Die Mollusken des Pliozäns der rumänischen Erdöl-Gebiete als Leitversteinerungen für die Aufschluß-Arbeiten. *Senckenbergiana*, 24, 1–293.
- Wesselingh, F. P., Neubauer, T. A., Anistratenko, V. V., Vinarski, M. V., Yanina, T., ter Poorten, J. J., Kijashko, P., Albrecht, C., Anistratenko, O. Y., D'Hont, A., Frolov, P., Gándara, A. M., Gittenberger, A., Gogaladze, A., Karpinsky, M., Lattuada, M., Popa, L., Sands, A. F., van de Velde, S., ... Wilke, T. (2019). Mollusc species from the Pontocaspian region – An expert opinion list. *ZooKeys*, 827, 31–124. <https://doi.org/10.3897/zookeys.827.31365>
- Wesselingh, F. P. (2006). Miocene long-lived lake Pebas as a stage of mollusc radiations, with implications for landscape evolution in western Amazonia. *Scripta Geologica*, 133, 1–17.
- West, K., Michel, E., Todd, J., Brown, D., & Clabaugh, J. (2003). *The gastropods of Lake Tanganyika: diagnostic key, classification, and notes on the fauna*. Centre for African Wetlands Ghana, on behalf of International Association of Theoretical and Applied Limnology.
- Wilke, T., Hauße, T., Jovanovska, E., Cvetkoska, A., Donders, T., Ekschmitt, K., Francke, A., Lacey, J. H., Levkov, Z., Marshall, C. R., Neubauer, T. A., Silvestro, D., Stelbrink, B., Vogel, H., Albrecht, C., Holtvoeth, J., Krastel, S., Leicher, N., Leng, M. J., ... Wagner, B. (2020). Deep drilling reveals massive shifts in evolutionary dynamics after formation of ancient ecosystem. *Science Advances*, 6, eabb2943. <https://doi.org/10.1126/sciadv.abb2943>
- Wilke, T., Wagner, B., Van Bocxlaer, B., Albrecht, C., Ariztegui, D., Delicado, D., Francke, A., Harzhauser, M., Hauße, T., Holtvoeth, J., Just, J., Leng, M. J., Levkov, Z., Penkman, K., Sadori, L., Skinner, A., Stelbrink, B., Vogel, H., Wesselingh, F., & Wonik, T. (2016). Scientific drilling projects in ancient lakes: Integrating geological and biological histories. *Global and Planetary Change*, 143, 118–151. <https://doi.org/10.1016/j.gloplacha.2016.05.005>
- Wilson, A. B., Glaubrecht, M., & Meyer, A. (2004). Ancient lakes as evolutionary reservoirs: Evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society B: Biological Sciences*, 271, 529–536. <https://doi.org/10.1098/rspb.2003.2624>
- WWF. (2020). *Living planet report 2020: Bending the curve of biodiversity loss*. WWF.
- Yu, T., Neubauer, T. A., & Jochum, A. (2021). First freshwater gastropod preserved in amber suggests long-distance dispersal during the Cretaceous Period. *Geological Magazine*, 158(7), 1327–1334. <https://doi.org/10.1017/S0016756821000285>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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