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1 **Title:**

2 **Biotic and abiotic drivers of species loss rate in isolated lakes**

3

4 **Short title:** Age effects on extinction rates

5 Extinction rates in lakes

6

7

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18

19 **Keywords:** aquatic ecosystems, isolation, piscivores, age, fragmentation,

20

21

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23 **Summary**

24 1. Today, anthropogenic impacts are causing a serious crisis for global biodiversity, with rates
25 of extinction increasing at an unprecedented rate. Extinctions typically occur after a certain
26 delay and understanding the mechanisms causing delays is a key challenge for both
27 fundamental and applied perspectives.

28 2. Here, we make use of natural experiments, the isolation of lakes by land up-lift in Northern
29 Scandinavia, to examine how yearly extinction rates are affected by time since isolation and a
30 range of abiotic and biotic factors.

31 3. In this aim, we adapted a model of delayed species loss within isolated communities to test
32 the effects of time since isolation, area, pH, depth and presence/absence of piscivores on
33 extinction rates.

34 4. As expected, we found that small and/or young lakes experience a higher annual rate of
35 extinctions per species than larger and/or older ones. Compared to previous studies that were
36 conducted for either young (few thousand years ago) or very old (>10 000 years ago) isolates,
37 we demonstrated over a large and continuous temporal scales (50-5000 yr), similar
38 relationship between extinction rates and age. We also show that extinction rates are modified
39 by local environmental factors such as a strong negative effect of increasing pH.

40 5. Our results urge for the need to consider the time since critical environmental changes
41 occurred when studying extinction rates. In a wider perspective our study demonstrates the
42 need to consider extinction debts when modeling future effects of climate change, land-use
43 changes, or biological invasions on biodiversity.

44 **Introduction**

45 Today, we are facing the sixth wave of extinctions of our planet (Ceballos et al., 2017; De
46 Vos et al., 2014). In most of deep time, extinctions occurred at a fairly constant rate, called
47 background extinction rate. Today, human activities have raised extinction rates several
48 orders of magnitude above this level. For example, the current rate of extinctions for
49 vertebrates is more than 100 times the background rate, with literally ca. 4 vertebrates going
50 extinct every year since 1900 (Ceballos et al., 2015). Land use changes are responsible for
51 most of the modern extinctions (Collen et al., 2014; Leclerc et al., 2018; Pereira et al., 2010;
52 Sala et al., 2000). Habitat destruction and altered land use have reduced previous continuous
53 habitats to isolated fragments. Local and regional species extinctions may follow but not
54 immediately, leading to decreasing species richness over time at several spatial scales. This
55 means that the ecological cost of current habitat fragmentations could be delayed, a
56 phenomenon termed extinction debt. Studies of extinction debts in a wide range of taxa and
57 ecosystems (Harding et al., 1998; Piessens and Hermy, 2006; Piha et al., 2007) has shown that
58 the time until extinctions take place may vary from weeks and months to hundreds or
59 thousands years (Shaw et al., 2013; Uezu and Metzger, 2016). This gradual loss of species
60 (also known as faunal relaxation to refer, in physics, to the return of perturbed system into
61 equilibrium has first studied by Diamond (1972) and have since been studied in many different
62 systems (Cousins and Vanhoenacker, 2011; Hugueny et al., 2011; Hylander and Ehrlén, 2013;
63 Kuussaari et al., 2009). This observation is particularly important for conservation, as the time
64 from impact to extinction provides a time window within which remedial actions can be
65 taken. Moreover, understanding mechanisms of delayed extinction is essential for predicting
66 the impact of global changes on biodiversity. A range of intrinsic and extrinsic mechanisms
67 may influence the timing and sequence of species losses, including the increased risk of
68 stochastic extinction faced by small populations size and species have narrow habitat

69 requirement (e.g., Almeida et al. 2017). At the regional scale, habitat modifications may result
70 in disequilibrium meta-population dynamics (i.e., extinction and colonization rates are no
71 more balanced), which also can lead to delayed extinctions (Helm et al., 2005). Species loss
72 rates may be accelerated by inter-specific competition, predation, and anthropogenic impacts
73 such as overexploitation and species invasions. Life history traits could also influence species'
74 responses to extinctions (Krauss et al., 2010), e.g., long lived species are expected to persist
75 longer than short lived species (Cronk, 2016; Lindborg and Eriksson, 2004).

76 Recent studies emphasize that species loss rates in isolated habitat fragments can be
77 accurately modelled with a few predictors, like age and area of the isolate, for a large array of
78 terrestrial taxa and for different types of fragments (e.g. true islands, forest remnants,
79 mountaintops) (Halley et al., 2016; Hugueny, 2017). The negative relationship between
80 species loss rate and area is well documented in the literature (Ferraz et al., 2003; Halley and
81 Iwasa, 2011; He and Hubbell, 2011; Hugueny, 2017). Some of these studies also demonstrate
82 that species decay curves often differ from the exponential decay expected for equivalent and
83 non-interacting species. Instead of the constant species loss rate per unit time expected under
84 an exponential decay, empirical data show that species loss rates decrease with increasing age
85 of the isolate. This age effect could arise because the loss of species leads to reduced risk of
86 extinctions due to species interactions, i.e., diversity-dependent dynamics (e.g., Halley et al.
87 2016). Alternatively, it can be the result of interspecific variability in extinction proneness. As
88 species with high probability of extinctions disappear soon after isolation, the remaining
89 community will consist of species with comparably low extinction risk (Ferraz et al., 2003;
90 Hugueny, 2017).

91 Most studies of delayed extinctions have focused on terrestrial assemblages, and little
92 is known about natural extinction rates of aquatic organisms in the absence of catastrophic
93 events. Fortunately, freshwater fish populations frequently occur in isolated habitats such as

94 lakes (Englund et al., 2009) and coastal rivers (Hugueny et al., 2011) that receive no or few
95 colonists. Recently, Hugueny (2017) built a new theoretical model to test the effect of age and
96 area on species loss rates in isolated terrestrial vertebrate communities. We believe the
97 modeling framework built by Hugueny (2017) should prove useful in explaining species
98 extinctions in aquatic systems and allow us to test for the contribution of aquatic variables to
99 explain species loss rates. For instance, small and/or young (recently isolated) lakes and rivers
100 should experience a higher annual rate of extinctions per species than larger and/or older ones.
101 A former study of fish communities in coastal rivers isolated since the beginning of the
102 Holocene confirmed the important contribution of the area of the isolate to extinction rates,
103 but as the rivers became isolated at approximatively the same time the effect of age could not
104 be studied (Hugueny et al., 2011). In fact, few fragmented systems in both terrestrial and
105 aquatic environments allow studying species losses over long and continuous temporal scales.
106 For instance, the fragments analyzed in recent meta-analyses are either young (a few hundred
107 years for the older) and the result of human driven fragmentation, or very old (about 10,000
108 years) resulting from environmental changes that occurred at the end of the Pleistocene, with
109 no values in between (Dias et al., 2017; Halley et al., 2016; Hugueny et al., 2011).

110 Here, we will study extinction rates of freshwater fishes in a natural experiment - bays
111 transformed into lakes by land uplift caused by post-glacial isostatic rebound in Northern
112 Sweden. Because the uplift rate was approximately constant over the last 4000 years, we can
113 estimate the age of isolated lakes. This process has created lakes of various ages covering 0 to
114 5,000 years that provides an opportunity to study the time from isolation to extinction.
115 Besides factors acting across taxon and types of fragment, we expect that specific
116 mechanisms of lacustrine ecosystems are also important in shaping species decay through
117 time. For instance, acidification is known to cause extinctions of fish species (Holmgren,
118 2014), and depth is known to mediate the effects of piscivorous fishes on their prey in this

119 system (Englund et al., 2009). Indeed, shallow lakes are known to serve as a refuge for prey
120 species, while deep lakes are particularly favorable to the presence of two dominant
121 piscivores, Eurasian perch and northern pike. Yet, the relative importance of area, age, depth,
122 pH, and piscivory for extinction patterns have not been unexplored in aquatic ecosystems
123 (justification of used variables are provided in the material and method section). In this study,
124 we adapt the modelling approach introduced by Hugueny (2017) to examine the effects of
125 these factors on extinction rates.

126

127 **Material and Methods**

128 **Study sites:**

129 Lakes are classified as either (i) connected if they are linked to the Baltic Sea by a permanent
130 stream with a gentle gradient or (ii) isolated if they lack permanent stream connections or if
131 their outlet streams have steep sections that act as a dispersal barrier (see Englund et al.,
132 2009). The isolated lakes are not connected to upstream lakes with fish. Thus, all the isolated
133 lakes are fully disconnected from other sources and no event of colonization has been
134 recorded. The study sites also included closed bays that were in the process of forming a lake,
135 but were still well connected to the Baltic Sea with the water surface being in level with the
136 surface of the Baltic Sea. The land uplift caused by the post-ice-age isostatic recovery is thus
137 transforming bays in the Baltic sea to lake environments. Because of the low salinity of the
138 Baltic Sea, it is inhabited by numerous freshwater fish species that could successfully invade
139 bays and maintain self-sustaining populations in newly isolated lakes.

140 The dataset includes 71 isolated lakes, 41 connected lakes, and 12 closed bays located along
141 the coast of the northern Baltic Sea, between latitudes and longitudes of 61.78°-64.48° and
142 17.30°- 21.42°.

143 **Environmental variables:**

144 Detailed physical and chemical properties for a subset of the analyzed lakes are provided in
145 Öhman et al. (2006). In summary, these lakes are small, shallow, and oligotrophic. Primary
146 productivity in the area is limited by light rather than nutrients (Seekell et al., 2015). The
147 abiotic factors identified by previous studies as being important for fish species composition
148 include lake age, lake area, isolation from the Baltic Sea, pH and oxygen (Öhman et al., 2006,
149 Englund et al 2009). We do not have data on oxygen levels for most of the lakes, but previous
150 studies have shown that shallow depth is a good predictor of low oxygen levels (Englund et
151 al., 2009; Öhman et al., 2006). Anthropogenic activities that may also affect species
152 composition include treatment with the piscicide rotenone, liming, and species introductions.
153 Thus, when selecting lakes, we interviewed fishery rights owners and excluded lakes where
154 the interviewees claimed that such activities had occurred. Human activities in the catchments
155 are minor and mostly concerns forestry and ditching for forestry production. The effects on
156 fish extinction rates of these activities are largely unknown.

157 Consequently, we focus our analysis on the following environmental variables for bays,
158 isolated lakes, and connected lakes were extracted from Englund et al. (2009). Digital maps
159 were used to estimate each lake's area, catchment area, and distance to the sea while other
160 variables were measured directly in the field. Elevations were estimated using either a high-
161 resolution GPS instrument or an automatic level. The maximum depth was measured from a
162 boat with an echo-sounder and pH was measured with a portable pH-meter.

163 For isolated lakes at low elevations (0-30 m) the time since isolation could be approximated
164 by a linear equation, $age = 100 * elevation$ (Renberg & Segerstrom 1981) as the uplift rate was
165 approximately constant the last 4,000 years (Berglund et al., 2004). The age of isolated lakes
166 at higher elevations (>30m) was predicted with a log-log model based on data in Pässe et al.,

167 (1996) ($\log(\text{Age}) = 0.57 * \log(\text{elevation}) + 6.048$; see Appendix S1 for further details, with
168 \log as natural logarithms).

169 **Species richness**

170 Data on fish species richness (Sr) were extracted from Englund et al. (2009). Each lake was
171 sampled summer time (June-Aug) on two different occasions during the period 1999–2007,
172 with the aim to detect all fish species present. The methods used in each lake included
173 minnow traps (5–10), spinning rods (90 min), and 2–4 multi-mesh gill nets. The sampling
174 effort for gill nets and minnow traps was adapted to lake size following (Appelberg et al.,
175 1995). The nets each had twelve 2.5 m sections, with knot-to-knot mesh sizes of 5, 6.25, 8,
176 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm. To ensure detection of stickleback species,
177 which were sometimes missed by the other methods, we also surveyed the littoral zone of
178 each lake using either electricity (45 min) or small detonations ($n = 10$ per lake; (Öhman et
179 al., 2006). The salinity of the northern Baltic sea is low (0.1-0.4%) so most (>90%) of the fish
180 species living in lakes are also present in the sea. Among isolated lakes, 18 lakes were fishless
181 and for the other lakes species richness ranges from 1 to 4. Species occurring in these lakes
182 are nine-spined stickleback (*Pungitius pungitius* L.), three-spined stickleback (*Gasterosteus*
183 *aculeatus* L.), roach (*Rutilus rutilus* L.), crucian carp (*Carassius carassius* L.), and two
184 piscivores: perch (*Perca fluviatilis* L.) and pike (*Esox Lucius* L.). In bays and connected lakes
185 we infrequently encountered eight additional freshwater species: bleak (*Alburnus alburnus*
186 L.), bream (*Abramis brama* L.), ide (*Leuciscus idus* L.), ruffe (*Gymnocephalus cernuus* L.),
187 rudd (*Scardinius erythrophthalmus* L.), dace (*Leuciscus leuciscus* L.), white bream (*Blicca*
188 *bjoerkna* L.) and European minnow (*Phoxinus phoxinus* L.), and two marine species (herring:
189 *Clupea harengus* and sprat: *Sprattus sprattus*). The dataset of the isolated lakes used for this
190 study is available from the Dryad Digital Repository (Bellard et al., 2019).

191

192 **Theoretical models to explore drivers of extinction rates**

193 Because no colonization events have been recorded in our isolated lakes and speciation are
194 unlikely to occur in such short time scales, we assumed that the isolation has caused species
195 richness to decrease over time. Under these conditions, the observed species loss rate equals
196 species extinction rate. To model species loss rate, we adapted the modelling approach
197 described in Hugueny (2017, Appendix S2, eq. S9) to deal with more explanatory variables.
198 Using this approach, we modeled the effects of time since isolation (t), lake area (A), pH (P),
199 depth (D), and presence/absence of piscivores ($pisc$) on the proportion of extant species at t
200 years after isolation:

$$201 \quad Sr_t/Sr_0 = 1/[1 + (c + vb * pisc) * m * (A^b) * (P^x) * (D^y) * t]^{1/m} \quad (1)$$

202 It is expected that, all else being equal, Sr_t/Sr_0 decreases with age (as extinction events
203 accumulate). The parameter m , in conjunction with the variable t , sets the shape of this
204 species decay curve. Eqn (1) is undefined when $m=0$, but as $m \rightarrow 0$, the dynamics approaches
205 an exponential decay (constant species loss rate per species per year through time) with
206 $\ln(Sr_t/Sr_0)$ being a linear function of t . Setting $m \gg 0$ results in a convex decreasing
207 relationship between $\ln(Sr_t/Sr_0)$ and t , meaning that species loss rate per species per year is no
208 more constant but slows down as time since isolation elapses (hereafter “Age effect”).

209 The other parameters set the contribution of the selected variables to species loss, and can be
210 interpreted as coefficients in a multiple regression. For instance, if x is negative it means that,
211 all else being equal, there is a negative relationship between pH and species loss rate. Because
212 pH varies with age, we did not model the direct effect of pH. Instead, we included as predictor
213 the residuals of the model ($\log(\text{pH}) \sim \log(\text{Age})$) to account for the pH variation that is not
214 related to age.

215 Note that the parameter vb , which describes the effect of piscivory, enters the equation
216 differently to account for the binary nature of this variable (0: piscivores absent; 1: piscivores
217 present). Note also that the parameter b has been constrained to be null or negative to be
218 consistent with theoretical expectations. From eqn (1) different models could be fitted to the
219 data by setting some parameters to zero (Table 1).

220

221 **Estimating species richness at the time of isolation**

222 Because of the constant rise of the land, the coastal bays are becoming isolated lakes with
223 time. Moreover, as salinity in the bays are low ($<0.3\%$), all the species occurring in coastal
224 lakes are also present in bays. Thus, we can expect that before isolation, species richness
225 within isolated lakes were similar to either bays or connected lakes near the coastline. A
226 common method to estimate species richness before isolation is to use the information about
227 species richness from reference regions within a continuous piece of habitat but otherwise
228 similar to the isolate of interest. Hence, we made the assumption that initial species richness
229 for isolated lakes was similar to the species richness observed in connected lakes and bays and
230 estimated Sr_0 for isolated lakes based on stepwise regression models obtained. Based on
231 connected lakes and bays dataset, we found that only area and elevation significantly
232 influenced species richness when piscivores are included, while elevation and pH were the
233 only significant predictors when piscivores were excluded (see Appendix 2 for details). Based
234 on these minimum adequate models (Appendix S2 for details), we predicted Sr_0 of isolated
235 lakes, by setting elevation and distance to the sea equal to 0 and using modelled pH-values
236 and area. Thus, Sr_0 was also calculated (i) when including all species that occurred in the
237 connected lakes and bays, and (ii) when excluding the two piscivores, pike and perch. This
238 resulted in two different estimates of Sr_0 for each lake. Piscivores were excluded from Sr_0 to
239 allow assessment of their impact on the extinction rate of potential prey species. In all cases,

240 if $Sr_t > Sr_0$ we assumed that $Sr_t = Sr_0$ and no extinction occurred. Table 2 presents the best
241 models and their AICc values, and Appendix S4 and S5 show the parameters values.

242

243 **Estimations of parameter values and comparison between models**

244 For the sake of graphical comparison of observed and predicted values, we computed an
245 average annual extinction rate per species per year over the period 0-t as follows:

$$246 \quad k = -\ln(Sr_t/Sr_0)/t \quad (3)$$

247 Observed and predicted k are computed using the observed and predicted Sr_t , respectively,
248 with the constraint $0 < Sr_t/Sr_0 < 1$ in the case of observed values.

249 Parameter values of eqn (1) were estimated by maximizing the likelihood of observing Sr_t
250 using the function ‘nlminb’ in the R environment (version 3.4.3, R Core Team, 2017). A
251 binomial distribution for Sr_t was assumed, using the integer part of Sr_0 to set the number of
252 trials and the right side of eqn (1) to compute the probability of success. In this way, and in
253 contrast with Hugueny (2017), communities with 0 and 100% of extinct species can be
254 considered. Then, we compared all the models using the Akaike information criterion (AICc)
255 with $AIC = 2k - 2\log(L)$ with k the number of estimated parameters and L the log likelihood
256 and AICc criteria as follows $AICc = AIC + (2k^2 + 2k) / (n-k-1)$ with n the sample number,
257 defined for small samples ($n/k < 40$) (Burnham, K. P. & Anderson, 2002). The sensitivity of
258 parameter estimates to initial species richness estimations (*i.e.*, Sr_0) were examined. In this
259 aim, we modified Sr_0 values by 10% (in other words, we first increase and then decrease Sr_0
260 by 10%) and assess how parameter values from equation (1) vary, compared to results from
261 Table 2 and Appendix 4 and 5.

262 **Results**

263 *Extinction rates at community level*

264 The average of the initial species richness (Sr_0) was 4.05 when including piscivore species,
265 and 2.57 when excluding the piscivores. The observed extinction rate (k in eq. 3) ranged from
266 0.0001 to 0.008 (mean 0.0015) when including piscivores, and from 0 to 0.006 (mean 0.0013)
267 when the piscivores were excluded (Appendix S6). From Figure 1, it is clear that observed
268 extinction rates decrease with the time elapsed since isolation. If extinction rates are constant
269 among species and through time, a flat relationship with age would have been expected. The
270 relationship with area is negative, as expected, but relatively weak. We also observed a clear
271 negative relationship between species loss rates and pH residuals (from a regression of pH on
272 age).

273 Eq. 1 was used to examine the relationships between extinction rate in isolated lakes and the
274 following variables: area, age, piscivores, pH, and depth. In all models the parameter m ,
275 related with age, is positive and high, indicating that species loss rate departs strongly from an
276 exponential decay, as shown by figure 1. For both Sr_0 estimates (with and without piscivores),
277 the best model is the ApH model, which includes negative effects of area and pH on
278 extinction rates (see Table 2 and Appendix S4 and S5 for parameter values). This model
279 slightly outperforms the full model ($\Delta AICc$ 1-3.3) and is much better than all other models.
280 The full model shows that extinction rate decreases with increasing area, pH and depth when
281 piscivores are included. We also found a positive effect of piscivores on extinction rates
282 (when they are excluded of the calculation of Sr_0), meaning that extinction rate increases with
283 the presence of piscivores (i.e., perch and pike), as well as depth. Overall, the ApH model
284 provides a good fit to observed data (Figure 2). Note that models have been fitted with all the
285 lakes, while only lakes having $0 < Sr_t < Sr_0$ are plotted in figure 2. The apparent overestimation
286 of observed extinction rates occurs because fishless lakes (with high extinction rates) are not

287 shown. Sensitivity analyses show parameter estimates are robust to variation in initial species
288 richness, Sr_0 (Appendix S6).

289

290 **Discussion**

291 Extinctions are rarely observable, particularly when they occur over centuries and millennia.
292 Habitats that became isolated many years ago, such as land-bridge islands created by sea level
293 rise at the end of the Pleistocene, are valuable natural experiments to study extinction at work
294 in natural communities. Such natural experiments, also known as relaxation, have greatly
295 contributed to the estimation of extinction rates in terrestrial communities and to the
296 identification of underlying ecological mechanisms. In contrast, freshwater ecosystems have
297 been largely ignored in this regard and to our knowledge our study is the first to estimate and
298 study species loss rate in isolated lakes following a relaxation approach.

299 *Area effect*

300 If area is a surrogate for population size then, on theoretical grounds (Hanski, 1994; Lande,
301 1993), an inverse relationship is predicted between extinction rate and area. Our finding
302 confirms this expectation and is consistent with earlier empirical studies (Diamond, 1972;
303 Halley and Iwasa, 2011; Hugueny, 2017). The estimated strength of the extinction-area
304 relationship varies depending on the method used to estimate initial species richness. In the
305 absence of co-variables and for models accounting for an age effect (A models with and
306 without piscivores), the mean estimate is -0.67, which is similar to the values estimated with
307 the same modelling framework for terrestrial vertebrates, -0.53 (Hugueny, 2017), and river
308 fishes, -0.56 (Hugueny et al., 2011). However, the range of our estimates is rather wide (-1.25
309 to -0.08), and when co-variables are added to the model, the estimated parameter value is
310 even more variable, and sometimes null (the highest value that we considered realistic are
311 returned). We suspect that the narrow range of lake sizes in this data set results in a rather

312 weak area signal (see also Öhman et al., 2006) that can be swamped by the stochasticity
313 inherent to species poor communities or erased when the effects of co-varying variables are
314 accounted for. On this basis, it is not surprising that the area effect was weaker in the analyses
315 conducted by excluding the piscivores as the initial species richness is particularly low in this
316 case. Indeed, for the analyses that exclude the piscivores the average estimated value was low,
317 -0.05, suggesting that area had a weak effect at best. In light of our results, it is therefore
318 difficult to assess whether or not the relationship between extinction rate and area is
319 lacustrine-specific or if a general pattern exists for freshwater fish or all vertebrates.

320 *pH effect*

321 Natural and anthropogenic acidity is a chemical factor known to structure lacustrine fish
322 communities in many regions (Bergquist BC, 1991; Haines, 1981; Rahel, 1984). In our study
323 system acidity is due primarily to natural processes (Öhman et al., 2006). The negative effects
324 of acidity on fish populations are both direct, through impaired gill function and
325 ionoregulation for instance (Fromm, 1980), and indirect such as increasing aluminium toxicity
326 (Wigington Jr. et al., 1996). The inclusion of *pH* in our models largely increased AICc values
327 compared to models without it. Overall, we observed that acid-stressed lakes experienced
328 higher rates of extinctions than more neutral ones, as observed for anthropogenic acidification
329 in other parts of Sweden (Bergquist BC, 1991). This result is coherent with a previous study
330 showing that, in the same region, the occurrence of most fish species was negatively
331 correlated to lake acidity (Öhman et al., 2006), pike and perch being the more tolerant (see
332 also Bergquist BC, 1991). For instance, survey of many lakes showed small probability of
333 finding roach at pH lower than six (Holmgren and Buffam, 2005). Studies of anthropogenic
334 acidification suggest that extinction of populations is due to recruitment failure (Bergquist
335 1991) because the young stages (eggs, fry and alevins) are more vulnerable to acidity.

336 *Age effect*

337 We observed that the average extinction rate per species per year was negatively related to the
338 time elapsed since isolation of the lake, as already noted for terrestrial communities isolated in
339 habitat fragments or islands (Hugueny, 2017). When extinction rates are estimated
340 considering all the species and when area is the only explanatory variable, estimated values
341 for parameter m setting the strength of the age effect is estimated at 5.55. It is likely that those
342 estimates are inflated because of the action of environmental variables that are correlated to
343 altitude, and hence to age of the lakes. When depth and/or pH are added as co-variables, the
344 estimates for the age effect are lower, about 4.4 on average, and comparable to the value of
345 3.9 estimated for terrestrial vertebrates (Hugueny, 2017).

346 A plausible explanation for an age effect is interspecific variability in extinction proneness
347 (Ferraz et al., 2003). Indeed, species that are more sensitive to go extinct (e.g., due to small
348 population size or long generation time) are more likely to disappear rapidly after the isolation
349 events, while species more resistant to extinctions are more likely to persist. This mechanism
350 is analogous to the term “extinction filter” which was used by (Balmford, 1996) to explain
351 why communities may appear more resilient to particular threats if they have faced similar
352 challenges in the past. Restricting the analyses to non-piscivorous species led to a
353 considerably lower age effect (ca. 1) then when all the species are included, giving strong
354 support to the extinction filter hypothesis. Predator species generally have lower population
355 sizes than other species because of the higher energetic demand imposed by their large body
356 size and top position in the food web and, as a result, are extinction-prone species. The fact
357 that the two focal piscivorous species (pike and perch) are particularly vulnerable to winter
358 kill arising from low oxygen levels under the ice, is also worth considering in this regard. In
359 this line of reasoning, excluding pike and perch from analyses is likely to result in lake
360 assemblages with lower interspecific variability in extinction proneness and to weaken the
361 strength of the age effect on species loss rate.

362 Another hypothesis for explaining that extinction rate per species is lower in older lakes is
363 ecological release resulting from the absence of competitors or predators. If some pairs of co-
364 existing species are involved in biotic interactions sufficiently strong to induce population
365 declines or to reduce population densities, then extinction rate per species should be higher in
366 species rich, young, assemblages than in old and species-poor ones. Some diversity dependent
367 models (e. g. Halley et al., 2016) allow integrating the number of coexisting species (more
368 specifically the number of species present at the time of isolation) as a factor controlling
369 extinction rate per species. Unfortunately, they are of limited use in our case because there is
370 not enough variability in the estimated species richness at the time of isolation to assess its
371 contribution to species loss rate. In addition, because our initial species richness is estimated
372 from lake features and not directly extracted from empirical data, it is not possible to separate
373 the effect of the variable entered into the equation used to predict the initial species richness
374 from the direct effect of species richness itself.

375 *Piscivores effect*

376 In contrast with competition, the effects of predators on the loss rates of prey species can be
377 assessed in our study system. The best model including the presence of piscivores as a co-
378 variable is outperformed by the best model without a predation effect, however the difference
379 in AICc values is small ($\Delta AICc = 3.3$). The presence of northern pike and perch positively
380 influenced extinction rates showing that predation by northern pike and perch can cause
381 extinctions at community levels in isolated lakes. We also found that the best models with a
382 predation effect were those with pH and depth as additional co-variables. Interestingly in
383 those models we observed that extinction rates and depth are positively correlated while in
384 models fitted with all species depth always contributed negatively to extinction rates. The
385 contribution of pike and perch to species loss rate is concordant with results from a previous
386 study of the same system of isolated lakes in which negative co-occurrence between predators

387 and prey were observed and interpreted as the result of prey extinction in the presence of
388 predators (Englund et al., 2009). There are other strong evidences in the literature that
389 northern pike influence the abundance and size distributions of crucian carp (Brönmark et al.,
390 2018). The presence of large piscivorous perch is also known to hinder the re-establishment of
391 roach, unless coexistence of perch and roach is mediated by the presence of pike (Persson et
392 al., 2006). Monitoring small lakes after the introduction of perch or pike revealed rapid
393 extinction (within less than 50 years) of nine-spined and three-spined sticklebacks (Englund et
394 al., 2009) and small cyprinidae (Nicholson ME, Rennie MD, 2015). The fact that piscivores
395 enter the best models only in combination with depth clearly suggest that their impact on prey
396 species is sufficiently strong to induce extinction in deep lakes but this outcome is less likely
397 in shallow lakes confirming the complex relationships between piscivores, preys and depth
398 already emphasized in a previous study of the very same system (Englund et al., 2009). Perch
399 and northern pike are more likely to occur in deep lakes (Englund et al., 2009; MacDougall et
400 al., 2018; Magnuson et al., 1998) which are buffered against winter kill (i.e., arising from low
401 oxygen levels under the ice) which induce fish to suffocate (Petrosky and Magnuson, 1973).
402 Therefore, when these two species are taken into account to estimate extinction rates, depth
403 and species loss rate are negatively related as they are more likely to persist in deep lakes. In
404 contrast, when those two piscivores are excluded of the estimation of extinction rates, there is
405 a positive relationship between depth of lakes and extinction rates as in deep lakes piscivores
406 are more likely to occur and are responsible for extinctions of prey species. When predators
407 occur in shallow lakes they are probably present at low density and coexistence with the more
408 vulnerable preys could be facilitated. Shallow lakes are also known to offer refuge from
409 piscivores, such as abundant macrophytes (Sand Jensen & Borum 1991, Snickars 2009).
410 Finally, pike and perch are generalist predators that can potentially drive one or several prey
411 species to extinction without undermining their own persistence. For instance, in our database

412 there are lakes where pike is the only recorded fish species, which is plausible as pike may
413 feed on insects, ducklings and small pike (Dessborn et al., 2010; Venturelli and Tonn, 2006),
414 even rather large pike can have insects as a major part of the diet. However, it is likely that
415 extinction is not the outcome of all prey-predator interactions taking place in the studied
416 lakes. First, as discussed before, predator impact is dependent upon lake environmental
417 features such as depth or pH that may influence trophic dynamics but also population sizes.
418 Second adults of the largest prey species such as carp and roach may be difficult to handle for
419 a perch and even a pike. Third both preys and predators feed on zooplankton in their youngest
420 stages and a prey may therefore have a negative impact on predator population dynamics
421 through competition (Byström et al., 1998). For these reasons it is likely that the contribution
422 of predation to species loss rate in isolated lakes is limited in our system mostly to the two
423 stickleback species as suggested by the fact that these two species are rapidly extirpated after
424 piscivore introductions and possibly to carp which rarely coexist with predatory fishes.

425 *Limitations*

426 Some limitations inherent to our study suggest that some of our findings should be treated
427 with caution. For instance, species richness at time of isolation was modelled, rather than
428 observed, which likely introduces some errors in our calculations (though such data are rarely
429 available, especially at such time scale). The sensitivity analyses of initial species richness
430 had little effect on the estimation of species loss rate per lake on average (Appendix 6). This
431 robustness suggests that, as a whole, our estimates are trustworthy and could be compared to
432 those from other systems. The comparison of species loss rate among lakes with the aim to
433 identify underlying biotic or abiotic factors is much more dependent on the way initial species
434 richness was estimated. However, even in this case, robust results emerged such as a strong
435 and consistent effect of age and pH and the synergetic action of piscivory and depth. Based on
436 geomorphological arguments we assumed that no natural colonization events have taken place

437 in those lakes but we cannot discard with certainty that some (but few) populations have been
438 introduced by humans. Indeed, high quality historical data is a key limiting factor for studying
439 extinction at the scale of centuries and millenia. Based on interviews of fishery rights owners,
440 only lakes where the interviewees claimed that species introductions had not occurred were
441 included. This does not preclude very old introductions or introductions made without
442 informing the fishery rights owner. Such introductions would lead to underestimates of the
443 extinction rate. Lack of data for population abundances also prevented us from exploring
444 extinction rates at species level and more generally to rank species according to their
445 extinction proneness. Moreover, because of the low prevalence of some species (Nine-spined
446 stickleback, 90% of absences; three-spined stickleback: 97% of absences), it was not possible
447 to conduct statistical analyses to investigate factors that may influence their extinction rate,
448 and in particular the role of predators. We also investigate extinction rates considering each
449 lake as an independent unit, but it is most likely that nearby lakes share environmental
450 features not considered in our analyses. Finally, other drivers (not taking into account in our
451 analyses due to data availability) might influence species loss rates in this system. For
452 instance, the effects of anthropogenic activities (e.g., forestry and ditching for forestry
453 production) on fish extinction rates in this area are largely unknown. Moreover, productivity
454 in those lakes is mostly limited by light rather than nutrients. Light limitation is related to
455 water color, which in turn is well correlated with the size of the catchment. Thus, had there
456 been strong effects of productivity on extinction rates, we would expect catchment area to
457 represent this effect.

458

459 *Implications*

460 Our study revealed that to some extent isolated lakes are not so different from terrestrial
461 isolates (islands, habitat patches, ...) with regard to the dynamics of species loss. In both

462 cases species loss rate decreases as time since isolation elapses and extinction rates are higher
463 in small isolates. While based on different processes, age is also a strong component of the
464 unified theory of island biogeography (Borregaard et al., 2016; Whittaker et al., 2008)
465 stressing that this factor should not be overlooked in future works conducted on both true
466 islands and island-like habitats. We also observed peculiarities specific to lacustrine habitat
467 regarding extinction patterns. In particular, we observed that prey extinction rates seem to be
468 regulated by the interplay between depth and predation, which is in line with a conceptual
469 framework for lacustrine community dynamics elaborated by Tonn W. M. and Magnuson
470 (1982). Those observations suggest that our study has a good level of representativeness in
471 light of the available knowledge about vertebrate extinction patterns and lacustrine
472 community dynamics.

473

474 *Conclusion*

475 Our results add to recent studies (Halley et al., 2016; Hugueny, 2017) that emphasize the
476 implications of unpaid extinction debts in isolated habitats for conservation and
477 environmental impact assessments. Many studies modeling future effects of climate change,
478 land use changes, or biological invasions on biodiversity have neglected extinction debts and
479 the implied community and population processes. Knowing at which rate those anticipated
480 extinctions will occur is paramount when prioritizing conservation actions. This is particularly
481 true for freshwaters which cover less than 1% of the earth's surface while supplying 12% of
482 the fish consumed by humans and are increasingly fragmented by human activities. Recently
483 it has been shown that delayed extinctions in terrestrial vertebrates could be analyzed within a
484 common framework. Unfortunately, such a synthesis is not at hand for freshwater fishes
485 because too few relevant studies have been conducted. A more promising avenue is to test
486 whether generalities observed for terrestrial vertebrate hold true for freshwater ones.

487

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492 0002-02).

493 **Data Accessibility**

494 Data of isolated lakes used in this manuscript are available in a dryad deposit
495 ([https://doi:10.5061/dryad.5sv75bd/1](https://doi.org/10.5061/dryad.5sv75bd/1)).

496

497 **Author's contributions**

498 GE provided the data, CB and BH designed the study and conducted the analyses. All the
499 authors interpret the results and CB wrote the first draft of the manuscript.

500

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658 **Tables**

659 **Table 1: Description of the models predicting average annual species loss rate**

Model	Contributing variables	Parameters considered
A	Area	<i>b, m,</i>
ApH	Area pH	<i>b, m, x</i>
Apisc	Area Piscivory	<i>b, m, vb</i>
Adepth	Area Depth	<i>b, m, y</i>
Full	Area Piscivory pH Depth	<i>b, m, x, vb, y</i>

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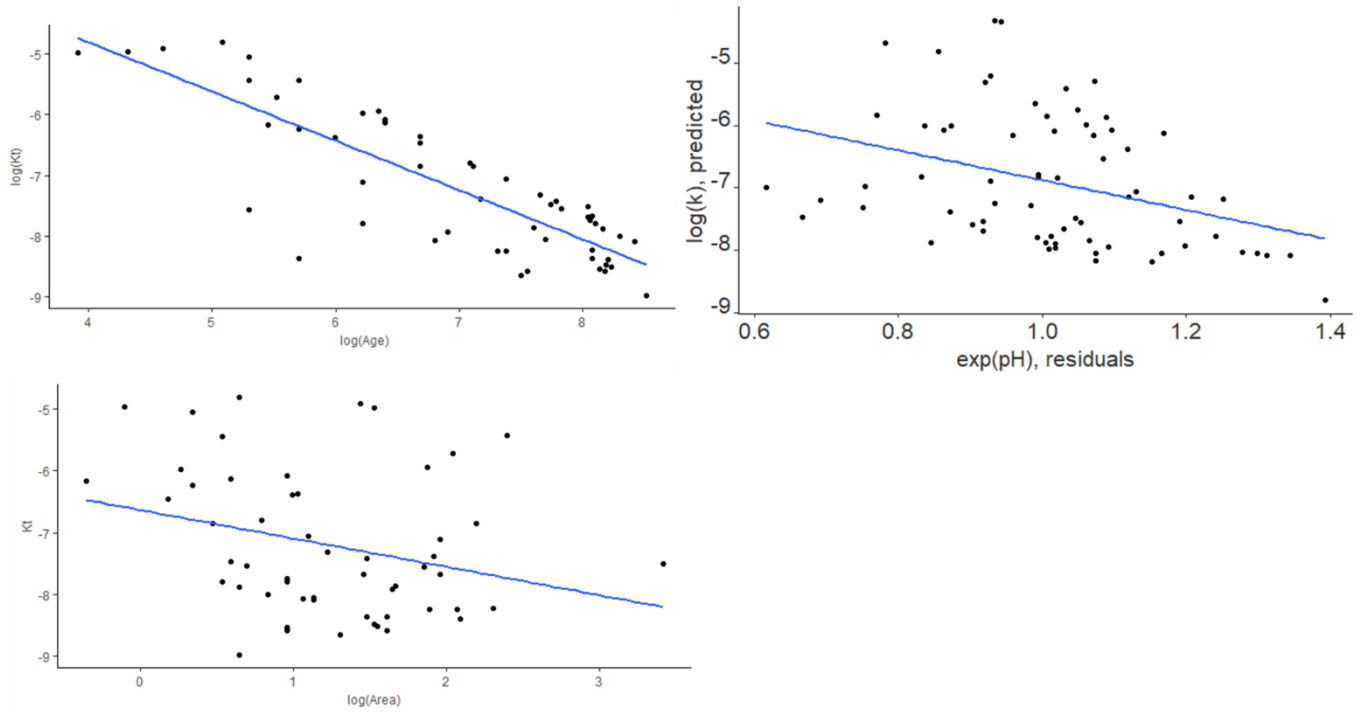
675 **Table 2:** Comparison of models using eq 1 to predict average annual species loss rates on two
 676 datasets (including or excluding piscivores when calculating initial richness). For each
 677 dataset, the best model is highlighted in bold. AICc is the Akaike information criterion with a
 678 correction for small sample sizes, k is the number of free parameters and the sign of the
 679 parameters are shown (see eq. 1 for parameter descriptions). Parameters values are given in
 680 Appendix S2.

681

Including piscivores								
Models	Intercept (c)	Area (b)	Age (m)	pH (x)	Pisc (vb)	Depth (y)	AICc	k
ApH	+	-	+	-			178.1	4
Full	+	-	+	-		-	179.1	5
Adepth	+	-	+			-	187.9	4
A	+	-	+				193.2	3
Excluding piscivores								
ApH	+	0	+	-			147.5	4
Full	+	0	+	-	+	+	150.8	6
A	+	-	+				153.2	3
Apisc	+	-	+		+		155.3	4
Adepth	+	-	+			-	155.4	4

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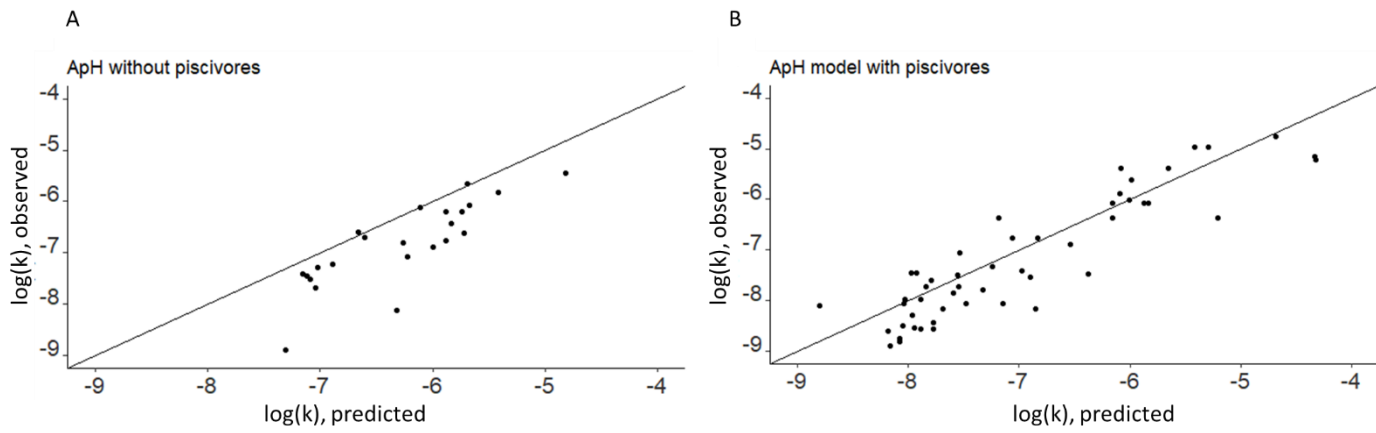
683 **Figure captions**



684

685 **Figure 1:** Observed average annual species loss rate (k) as a function of the area and age of
 686 isolated lakes and predicted annual species loss rates (k) as a function of pH residuals. Area
 687 and age were natural log transformed. The loss rates were calculated with eq 3.

688



690

691 **Figure 2:** Observed average annual species loss rates (k) plotted against the values predicted
692 by the ApH model. The line of perfect agreement between model prediction and observation
693 is shown.

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695