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# Importance of metapopulation dynamics to explain fish persistence in a river system

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1 **Title:**

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

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4 river system. *Freshwater Biology*. 2020; 65: 1858– 1869. <https://doi.org/10.1111/fwb.13571>

5

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

7 Extinction rates in lakes

8

9

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20

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

22

23

24 **Words: 6,128**

25 **Summary**

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

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

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

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

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

## 46 **Introduction**

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

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

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

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

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

112         Here, we will study extinction rates of freshwater fishes in a natural experiment - bays  
113 transformed into lakes by land uplift caused by post-glacial isostatic rebound in Northern  
114 Sweden. Because the uplift rate was approximately constant over the last 4000 years, we can  
115 estimate the age of isolated lakes. This process has created lakes of various ages covering 0 to  
116 5,000 years that provides an opportunity to study the time from isolation to extinction.  
117 Besides factors acting across taxon and types of fragment, we expect that specific  
118 mechanisms of lacustrine ecosystems are also important in shaping species decay through  
119 time. For instance, acidification is known to cause extinctions of fish species (Holmgren,  
120 2014), and depth is known to mediate the effects of piscivorous fishes on their prey in this

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

128

## 129 **Material and Methods**

### 130 **Study sites:**

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

142 The dataset includes 71 isolated lakes, 41 connected lakes, and 12 closed bays located along  
143 the coast of the northern Baltic Sea, between latitudes and longitudes of 61.78°-64.48° and  
144 17.30°- 21.42°.

145 **Environmental variables:**

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

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

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



169 (1996) ( $\log(\text{Age}) = 0.57 * \log(\text{elevation}) + 6.048$ ; see Appendix S1 for further details, with  
170  $\log$  as natural logarithms).

## 171 **Species richness**

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

193

## 194 **Theoretical models to explore drivers of extinction rates**

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

$$203 \quad Sr_t/Sr_0 = 1/[1 + (c + vb * pisc) * m * (A^b) * (P^x) * (D^y) * t]^{1/m} \quad (1)$$

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

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

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

222

### 223 **Estimating species richness at the time of isolation**

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

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

244

### 245 **Estimations of parameter values and comparison between models**

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

$$248 \quad k = -\ln(Sr_t/Sr_0)/t \quad (3)$$

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

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

264 **Results**

265 *Extinction rates at community level*

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

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

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

291

## 292 **Discussion**

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

### 301 *Area effect*

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

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

### 322 *pH effect*

323 Natural and anthropogenic acidity is a chemical factor known to structure lacustrine fish  
324 communities in many regions (Bergquist BC, 1991; Haines, 1981; Rahel, 1984). In our study  
325 system acidity is due primarily to natural processes (Öhman et al., 2006). The negative effects  
326 of acidity on fish populations are both direct, through impaired gill function and  
327 ionoregulation for instance (Fromm, 1980), and indirect such as increasing aluminium toxicity  
328 (Wigington Jr. et al., 1996). The inclusion of *pH* in our models largely increased AICc values  
329 compared to models without it. Overall, we observed that acid-stressed lakes experienced  
330 higher rates of extinctions than more neutral ones, as observed for anthropogenic acidification  
331 in other parts of Sweden (Bergquist BC, 1991). This result is coherent with a previous study  
332 showing that, in the same region, the occurrence of most fish species was negatively  
333 correlated to lake acidity (Öhman et al., 2006), pike and perch being the more tolerant (see  
334 also Bergquist BC, 1991). For instance, survey of many lakes showed small probability of  
335 finding roach at pH lower than six (Holmgren and Buffam, 2005). Studies of anthropogenic  
336 acidification suggest that extinction of populations is due to recruitment failure (Bergquist  
337 1991) because the young stages (eggs, fry and alevins) are more vulnerable to acidity.

### 338 *Age effect*

339 We observed that the average extinction rate per species per year was negatively related to the  
340 time elapsed since isolation of the lake, as already noted for terrestrial communities isolated in  
341 habitat fragments or islands (Hugueny, 2017). When extinction rates are estimated  
342 considering all the species and when area is the only explanatory variable, estimated values  
343 for parameter  $m$  setting the strength of the age effect is estimated at 5.55. It is likely that those  
344 estimates are inflated because of the action of environmental variables that are correlated to  
345 altitude, and hence to age of the lakes. When depth and/or pH are added as co-variables, the  
346 estimates for the age effect are lower, about 4.4 on average, and comparable to the value of  
347 3.9 estimated for terrestrial vertebrates (Hugueny, 2017).

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



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

### 377 *Piscivores effect*

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

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

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

#### 427 *Limitations*

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

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

460

#### 461 *Implications*

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

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

475

#### 476 *Conclusion*

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

489

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## 495 **Data Accessibility**

496 Data of isolated lakes used in this manuscript are available in a dryad deposit  
497 (<https://doi:10.5061/dryad.5sv75bd/1>).

498

## 499 **Author's contributions**

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

502

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## 660 **Tables**

661 **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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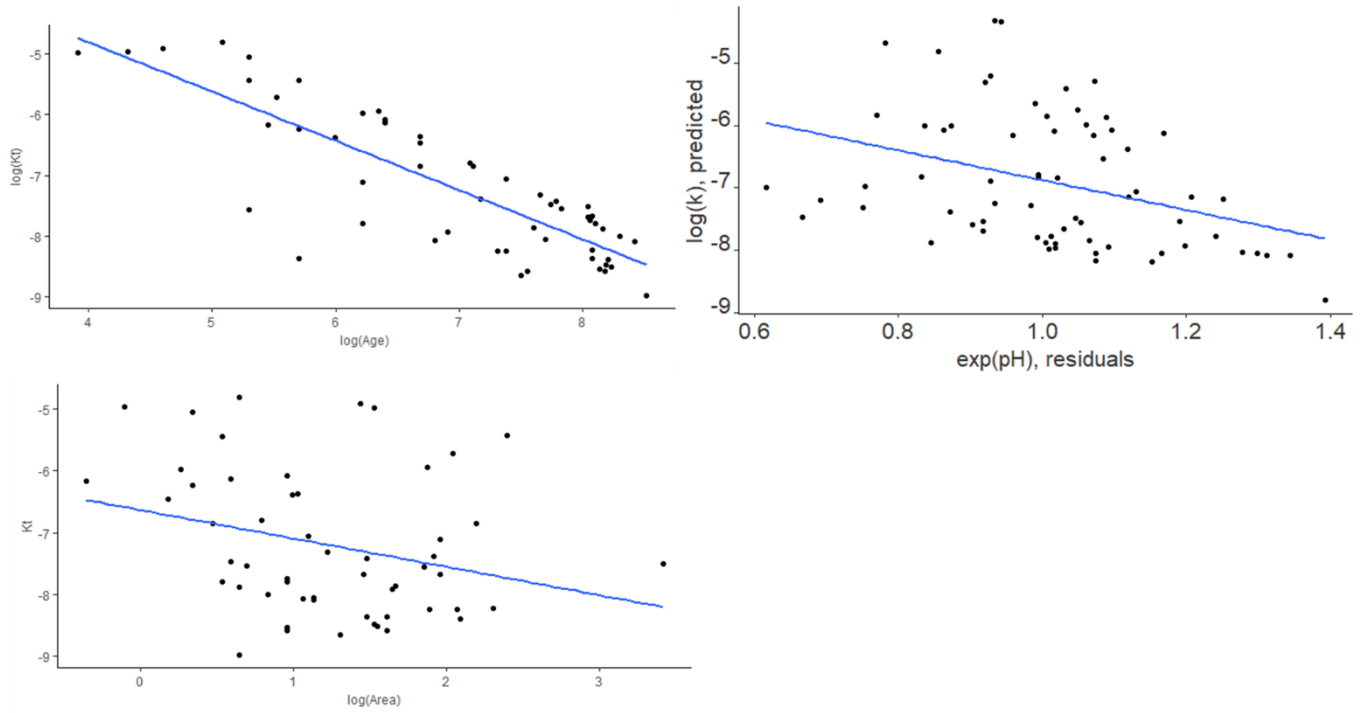
677 **Table 2:** Comparison of models using eq 1 to predict average annual species loss rates on two  
 678 datasets (including or excluding piscivores when calculating initial richness). For each  
 679 dataset, the best model is highlighted in bold. AICc is the Akaike information criterion with a  
 680 correction for small sample sizes,  $k$  is the number of free parameters and the sign of the  
 681 parameters are shown (see eq. 1 for parameter descriptions). Parameters values are given in  
 682 Appendix S2.

683

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

684

685 **Figure captions**

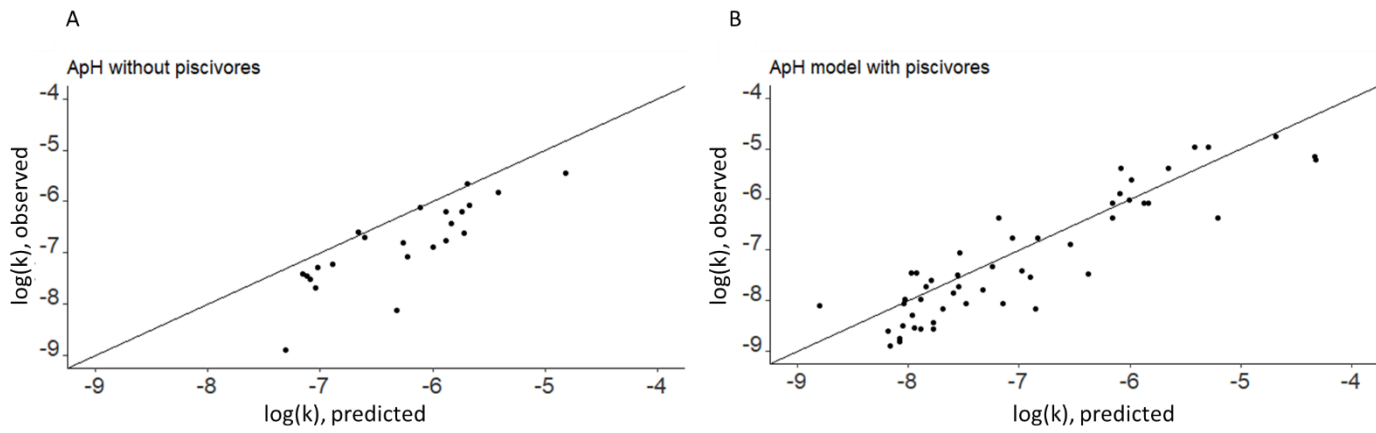


686

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

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

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