

1 Ms. published in *Hydrobiologia* (2017) DOI: 10.1007/s10750-017-3087-5

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3 **Recovery of submersed vegetation in a high mountain oligotrophic soft-water lake over two decades**  
4 **after impoundment**

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20 **Acknowledgements:** EG and EC are members of the Environmental Changes Ecology Group (GECA),  
21 an Excellence Research Group (SGR-DGR) of the Generalitat de Catalunya (Ref. 2014 SGR 1249. 2014–  
22 2017). This study was funded by the Red de Parques Nacionales of the Spanish Ministry of the  
23 Environment (PN I+D+I ref. 118/2003 and AQUAREST ref. OAPN 212/2010) and Intramural CSIC  
24 (Consejo Superior de Investigaciones Científicas) ref. 0065. We are thankful to Lluís Camarero to help

25 processing lake nutrient analysis and to Ana Lumbreras for field and lab assistance during the summer of  
26 2005.

27 **Abstract**

28 Recovery of the submersed vegetation is a target for the management of soft-water shallow lakes if they  
29 are to meet water quality and biodiversity standards. Knowledge of patterns of macrophyte space  
30 occupation and time to recovery is poor and mostly restricted to free floating species or riparian  
31 vegetation. Here we use pre and post-impact monitoring data over 20 years showing the evolution of  
32 submersed aquatic vegetation of lake Baciver (Pyrenees), and develop models to infer space occupation  
33 and time to recovery. We use pre-impact macrophyte distribution in relation to bathymetry-derived data  
34 to fit logistic models to further simulate lake equilibrium scenarios. Depth and slope were found to be the  
35 best predictors, and models suggested that an assemblage dominated by *Sparganium angustifolium* was,  
36 at time of this study, over 95% of its potential distribution area. A dense, newly grown monospecific  
37 *Isoetes lacustris* population occupied <10 % of its potential area and model projections suggest it will  
38 take decades to recover. An *I. lacustris* residual population remains below the estimated depth threshold  
39 for survival and is bound to disappear. The lake appears to evolve towards a new steady-state where the  
40 current lake hypsography promotes the expansion of algae (*Nitella* sp.) over angiosperms.

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46 **Keywords:** *Isoetes lacustris*, *Sparganium angustifolium*, depth, logistic models, niche, recovery

47 **Introduction**

48 Colonization of new or restored water bodies by aquatic plants depends on propagule dispersion,  
49 connectivity between potential sources and new habitats, and the existence of favorable abiotic conditions  
50 for the settlement (Brederveld et al. 2011). Once established, population growth and expansion may vary  
51 substantially depending on the species life strategy and pattern of space occupation, and in response to  
52 interactions with both its abiotic and biotic environment (e.g. competition, facilitation, epiphytism, etc.).

53 Although sexual reproduction and seed dispersal are efficient mechanisms of long-distance dispersal for  
54 submersed aquatic plants, clonal growth has evolved as the most common and efficient strategy in terms  
55 of space occupation (Grace 1993). For clonal aquatic plants, space occupation and progress can be  
56 predicted given architecture rules, seasonality, plastochrone intervals and environmental conditions  
57 (Sintes et al. 2006; Brun et al. 2007). However, difficulties arise when trying to project population growth  
58 for species that rely on non-vegetative reproduction in aquatic environments because spatial patterns of  
59 propagule settlement and patch initiation need to be taken into account in addition to patch growth (Riis  
60 2008).

61 Studies on submersed vegetation recovery or colonization and expansion in freshwater bodies are rare and  
62 mostly restricted to free floating, often invasive species (i.e. Khanna et al. 2012), or to riparian vegetation  
63 (i.e. Sand Jensen and Madsen 1992), regardless of the reproductive strategy of the species involved.

64 Studies on the patterns and time scales of growth and expansion, or of regression, of submersed  
65 macrophytes must resort to time-consuming and often difficult field assessments supplemented with niche  
66 modeling techniques and numerical projections (e.g. Røslett 1989).

67 Shallow soft-water oligotrophic lakes often show extensive meadows of isoetids, a functional typology of  
68 aquatic plants characterized by rosette-forming leaves. Some of these lakes have been severely impacted  
69 by regional eutrophication and other human-driven disturbances in Central and Northern Europe  
70 (Portielje and Van der Molen 1998; Arts 2002; Sand-Jensen et al. 2000), with deleterious consequences  
71 for submersed aquatic vegetation. Management strategies within the last decades have succeeded in  
72 reducing nutrient loads and restoring water quality but recovery of a clear state may require further  
73 management actions such as elimination of organic matter in the upper sediment layer and further seeding  
74 or sowing (Bellemakers et al. 1996; Brower et al. 2002). Moreover, the presence of aquatic plants may

75 also help maintaining a stable clear state in lakes because they improve water quality and turbidity, and  
76 bind lake sediments (Madsen et al. 2001).

77 Management and restoration of soft-water oligotrophic lakes would thus benefit from promoting  
78 reestablishment and growth of isoetid species. Recent studies on lakes dominated by *Lobelia dortmanna*  
79 L. and *Littorella uniflora* Asch. focused on determining thresholds of ecological factors for the growth  
80 and survival of these species. In particular, sediment humidity (Baastrup-Spohr et al., 2015) and organic  
81 matter content (Pulido et al., 2011a, 2011b) were the key factors for species survival and persistence.  
82 There is, however, a big gap in our knowledge of macrophyte population growth patterns in oligotrophic  
83 lakes and of the temporal scales for recovery after impacts on slow-growing species and communities.

84 In this study, we use pre-impact data and 20 years of post-impact monitoring data on the evolution of  
85 submersed aquatic vegetation in lake Baciver, a small, softwater oligotrophic lake in the Pyrenees that  
86 suffered massive plant mortality following the construction of a dam in 1991. Our main goal is to  
87 reconstruct patterns of space occupation since the impact and to infer future scenarios for aquatic plant  
88 colonization of the lake littoral. We take advantage of pre-impact conditions to model the local niche of  
89 the different plant species and communities and use these models to assess the recovery process of the  
90 lake, project space occupation in the future, and provide rough estimates of colonization rates for soft-  
91 water oligotrophic species that are common in the Pyrenean lake flora but are also encountered in Central  
92 and Northern Europe. In addition, we also analyze the regression rates for patches of *Isoetes lacustris* L.  
93 that have remained alive growing below its natural depth limit for more than 20 years.

94 Thus, the specific objectives of this study are (1) to describe the patterns of regression or expansion of  
95 submersed aquatic vegetation (SAV) patches since lake impoundment, (2) to develop pre-impoundment  
96 niche models to project potential space occupation by SAV assemblages under current conditions, (3) to  
97 estimate the time scales of recovery for *Isoetes lacustris* and *Sparganium angustifolium* Michx. -  
98 dominated assemblages, and (4) to describe the regression of a residual *Isoetes lacustris* population 20  
99 years after flooding.

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102 **Methods**

103 Area of study

104 Lake Baciver is a softwater oligotrophic mountain lake located at 2120 m a.s.l. in the Central Pyrenees  
105 (42° 41' 50''N, 0° 58' 57'' E) that was dammed in the fall of 1991 to provide water for snowmaking at a  
106 nearby ski resort. Damming resulted in a water level rise of  $5.5 \pm 0.5$  m and a massive mortality of both  
107 leaf-floating and isoetid species (Gacia and Ballesteros 1998). A residual population ( $<3000$  m<sup>2</sup>) of  
108 perennial *I. lacustris* survived between 5 and 6 m depth (formerly  $0.5 \pm 0.5$  m; Gacia and Ballesteros  
109 1996). The fast recovery of water quality to pre-impact conditions (Gacia and Ballesteros 1996) and the  
110 maintenance of high water levels, with low fluctuations, from spring to autumn (during the growing  
111 period), have allowed the partial recolonization of the lake bottom by macrophyte species. Meanwhile,  
112 the residual population has progressively diminished.

113

114 Data sampling

115 Detailed information on water chemical composition before and just after damming can be found in  
116 Ballesteros et al. (1989) and Gacia and Ballesteros (1996; 1998). Data on plant distribution and depth  
117 ranges before damming has been obtained from Ballesteros et al. (1989). The physical and chemical  
118 characteristics of the water column and the coverage of the different species were further assessed during  
119 subsequent surveys carried out in July of 1996, 2000, 2006 and 2012. Sampling and analysis of the water  
120 column were conducted following Gacia and Ballesteros (1998). Temperature, conductivity and pH were  
121 measured *in situ* while water samples were analyzed in the laboratory for oxygen concentration, alkalinity  
122 and dissolved nutrient concentrations (total reactive phosphorous, nitrate, nitrite and ammonium). All the  
123 protocols, including those for nutrient concentrations, can be found in Catalán et al. (1993).

124 Submersed vegetation maps were produced by an expert scientific diver who surveyed the bottom of the  
125 lake and recorded aquatic macrophyte beds (monospecific stands or multispecies assemblages) along  
126 transects perpendicular to the shore and placed every 20 m. For each vegetation patch encountered along  
127 the transects, the diver noted the minimum and maximum depths, and those field data were subsequently  
128 transferred to a GIS and interpolated to produce the vegetation maps. In the pre-impoundment case, only  
129 a published map is available, but it was produced using the same field protocol (Ballesteros et al. 1989).

130

131 Species distribution models

132 In order to predict the potential steady-state spatial distributions of aquatic vegetation after full recovery,  
133 logistic regression models based on pre-damming vegetation and conditions were developed. Logistic  
134 regressions were used because true presence-absence data were available, the main factors that influence  
135 species distributions were known from previous studies (Gacia et al. 1994; Pulido et al. 2015), and the  
136 aim was to develop models that were both simple and interpretable.

137 Models were based on a set of training data randomly sampled from a pre-damming submerged  
138 vegetation map (Ballesteros et al. 1989). First, we digitized and georeferenced the published vegetation  
139 map. This layer and all geospatial data were projected to the European Datum 1950 UTM 31N coordinate  
140 reference system. We then processed a series of five geospatial predictors. Lake bathymetry was digitized  
141 as contour lines from a published paper map (Ballesteros 1989) and converted to raster format using  
142 function `r.surf.contour` in the GRASS GIS system toolbox (GRASS Development Team 2015). Raster  
143 resolution was set to 2 by 2 meters. The remaining raster predictors were processed with the “raster” R  
144 package (Hijmans, 2014) to the same extent and resolution. Slope and aspect (orientation) were obtained  
145 from bathymetry using the terrain function. We expected depth to be the principal predictor of species  
146 distribution because it restricts leaf-floating species and is a surrogate of light availability. Slope and  
147 orientation were expected to improve the models because slope affects substrate stability (Gacia and  
148 Ballesteros 1993) and orientation affects hours of direct sunlight

149 An inspection of the pre-impoundment vegetation showed a clear effect of the inlet stream (Riu Malo) as  
150 it enters the lake, probably due to the erosive force of the stream water during snowmelt. To take this into  
151 account in a simple manner, we included two new predictors: distance to the inlet point (i.e., the point  
152 along the shore where the stream enters the lake), and distance perpendicular to the channel of lowest  
153 descent from this point towards the central basin of lake Baciver. This channel was digitized on-screen on  
154 top of the aspect and flow direction maps (obtained also with the “terrain” function). Short of a  
155 hydrodynamic model, which was not feasible, we expected that these two predictors, together with depth,  
156 would be sufficient for our modeling goals.

157 In order to fit logistic models, we generated a random sample of 2000 points, for which we extracted  
158 values for both vegetation and the five predictors. We used 1000 points as a training set and the remaining  
159 1000 as a test set. The most parsimonious model for each species was built through an iterative process  
160 with careful inspection of model diagnostics, reduction in deviance and likelihood ratio test for model  
161 comparison, together with visual inspection of the match between simulated 1989 maps and the published  
162 map. Accordingly, we deliberately refrained from using automatic variable selection methods. We used a  
163 large number of points to ensure good coverage of even small patches and stable parameter estimates.  
164 Online Resource (1) shows two examples of the effect of sample size on parameter estimates and  
165 parameter significance. Given the nature of the data (as homogeneous patches), spatial autocorrelation  
166 was to be expected. Accounting for spatial autocorrelation is crucial when developing models for  
167 inferential purposes, but these models are not suited for prediction (i.e., extrapolation), which was our  
168 main goal (e.g., Dormann et al. 2007). Nonetheless, we explored the effect of accounting for spatial  
169 autocorrelation on the significance of explanatory variables by fitting three different types of spatial  
170 models to our data: spatial GAM (Generalized Additive Models), spatial autoregressive models and  
171 autologistic models (Online Resource 2).

172 Correlations among predictive variables were generally low (below 0.35 in absolute value), with the  
173 exception of distance to inlet and distance to channel, which were highly correlated at the lake scale, but  
174 uncorrelated at the scale of the westernmost section of the lake, where they have any effect of macrophyte  
175 distribution. Since models with these two variables were estimable, converged quickly, and improved  
176 models in terms of AIC (Akaike Information Criterion) and visual inspections of spatial fit, we decided to  
177 retain them.

178 Models were built separately for *I. lacustris*, for *Sparganium angustifolium* growing alone, for the mixed  
179 assemblage that included *S. angustifolium*, *Subularia aquatica* L. and *I. lacustris* or *I. echinospora*  
180 Durieu, and for *Nitella* sp. Models were validated on the test dataset using sensitivity (true positive rate)  
181 and specificity (true negative rate), derived from the confusion matrix for the best classification threshold,  
182 defined as the threshold with the highest product of sensitivity and specificity. We acknowledge that this  
183 is only a partial validation, since the two sets of data are not strictly independent, but it is still more  
184 conservative than validating on the training set alone. We also report the area under the receiver operating  
185 characteristic curve (ROC). The ROC plots sensitivity against 1 – specificity for classification thresholds  
186 from 0 to 1, and is often used to display the compromise between error rates in choosing a classification



187 threshold (Fawcett 2006). A perfect classifier would have an area under the curve equal to 1. All  
188 classification performance measures were evaluated with the R package pROC (Robin 2011).

189 Prediction maps were built using a set of predictors derived from current bathymetry and lake  
190 morphology. Post-impoundment bathymetry was obtained as a shapefile of contour lines from a series of  
191 bathymetric transects made with an echo-sounder in 2006. Transects were spaced at 20 m intervals and  
192 processed as described above for the pre-impoundment bathymetry. Raster prediction maps with  
193 probability of occurrence were generated from each of the species alone. A combined map was then  
194 produced by assigning to each raster cell the submersed vegetation type with the highest probability of  
195 occurrence.

196 GIS preprocessing was done using Quantum GIS (QGIS Development Team 2014) with GRASS support.  
197 Raster operations, statistical analyses, and validation and prediction maps were performed in the R  
198 environment for statistics (version 3.1.0, R Core Team 2014).

199

## 200 **Results**

201 Water chemical composition and chlorophyll content did not show substantial changes over time  
202 except for the immediate post-impact conditions (summer 1993). A year after impoundment the  
203 composition of the water column had already recovered and chemical parameters were approaching  
204 pristine conditions (Table 1); therefore, the progression of the aquatic plant coverage after this date  
205 should not be attributed to changes in water quality.

206

### 207 **Macrophyte patch progress**

208 The mixed community of leaf floating *Sparganium angustifolium*, which suffered massive mortality after  
209 flooding in 1993 (Fig. 1a and b), was first detected in the impounded lake seven years later, in 2000. It  
210 was then found at eight different spots along the littoral shore, accompanied by the small isoetid  
211 *Subularia aquatica* (Fig. 1c). In later surveys (2006, Fig. 1d), new colonization spots had appeared and  
212 the community had increased the number of accompanying species, with the presence of *Isoetes*  
213 *echinospora* at depths above 0.8 m and sparse shoots of *I. lacustris* between 0.8 and 1.5 m. The

214 community advanced rapidly in the shallow littoral following a progression that suggest saturation  
215 towards the year 2012 (Fig. 1e). It extends over most of the shallow littoral and is mostly mixed except  
216 for a few small spots where *S. angustifolium* grows alone in the presence of stones.

217 During the survey of the year 2000 we also detected a patch of 1 m<sup>2</sup> of the perennial *Isoetes lacustris* in  
218 the northern area of the lake (Fig. 1c), right at the spot where abundant leaves with sporangia containing  
219 megaspores and microspores were unintentionally left behind before flooding as a result of sample  
220 processing (Gacia and Ballesteros 1993; 1994). Twelve years later, this population occupied 160 m<sup>2</sup> (Fig  
221 1e) and a few single shoots had appeared here and there.

222 Finally, *Nitella* sp. never disappeared completely from the lake after flooding; on the contrary, the area of  
223 distribution substantially expanded. Because of the high seasonal and inter-annual variability of the area  
224 covered by this species, we have not followed in detail its surface area progress but noted that the alga  
225 forms patches below 6 meters depth.

226

227 Logistic models

228 Niche models predicting probability of occurrence as a function of depth, slope, orientation, distance to  
229 inlet, and distance to inlet channel (Online Resource 3) were fitted for each of the SAV types present  
230 before impoundment, i.e. *Isoetes lacustris*, *Sparganium angustifolium* growing alone, mixed assemblage of  
231 *S. angustifolium*, and *Nitella* sp.

232 Logistic models performed very well for all four submersed vegetation types (Table 2). The poorest  
233 classifier was for *Sparganium angustifolium* alone, which in pre-impoundment lake Baciver used to occur  
234 mostly near the stream inlet and flanking the inlet channel. Still, areas under the curve, sensitivities and  
235 specificities were in all cases above 0.80.

236 As expected, depth was the most common and important predictor, appearing in all four models, with  
237 quadratic terms for *I. lacustris* and the mixed assemblage, which occurred in bands at mid-depths. Slope  
238 improved predictions for all vegetation types with the exception of *Nitella* sp., whereas distance to inlet  
239 point and to inlet channel were particularly useful for modeling *S. angustifolium* alone, as mentioned  
240 above.

241

242 Forecasted vegetation

243 After impoundment, lake Baciver evidently became larger and deeper, but its hypsography also changed,  
244 providing less shallow habitat both in relative and in absolute terms (Fig. 2). For example, the volumetric  
245 surface area of the lake between 0 and 2 meters depth was 1.9 hectares (72% of surface area) before  
246 impoundment but was reduced to 0.92 hectares (18% of surface area) after impoundment.

247 To better describe the expansion of both *I. lacustris* and *S. angustifolium* (monospecific or as a mixed  
248 assemblage), and to obtain rough estimates of their time to recovery, we fitted the progress of the  
249 occupied area during the last 20 years using a logistic curve (i.e. a sigmoidal, saturation model), as  
250 suggested by the decrease in the space available to each community within the lake as colonization  
251 progresses. We fitted the logistic curve according to the following parametrization:

$$252 \quad y = \text{Asym} / (1 + e^{(x_{\text{mid}} - t) / \text{scal}})$$

253 with parameters *Asym* (asymptote), *xmid* (time to reach half the maximum cover), *scal* (a shape  
254 parameter).

255 When comparing the area occupied by each community in 2012 (Fig. 1e) with their potential habitats at  
256 equilibrium (Online Resource 4), we found that *S. angustifolium* was already around the potential area  
257 predicted by the binomial logistic model (Fig. 3) for the stand-alone and mixed assemblages together.  
258 This area has increased substantially (by 220%) relative to pre-impoundment conditions.

259 In contrast, the monospecific *I. lacustris* had only occupied 2.8% of its potential area by 2012 (Fig. 1e),  
260 and our simple model of time to recovery suggest that more than 60 years will pass before this species  
261 covers its potential habitat (Online Resource 4). Note, however, that this estimate has considerable  
262 uncertainty, as it is based on the growth of a single patch and assumes that the eventual cover will be that  
263 predicted by our niche model.

264 While the potential habitat for *I. lacustris* is only 40% of the area that it covered before the impact, *Nitella*  
265 sp. has substantially enlarged its potential distribution by 500% (Fig. 4) and has never really discontinued  
266 its presence in the lake, even right after the impact.

267 The model forecasts probably overestimate the areas potentially colonized since we have not taken into  
268 account the presence of areas of exposed, steep rock where submersed vegetation may never establish,  
269 just like in the lake before impoundment. However, according to our estimates, these areas do not occupy  
270 more than 5% of the present littoral area.

271

272 Residual patch of *I. lacustris*

273 The residual population of *I. lacustris* (Fig. 1) that now stands between 4.7 and 5.2 m depth, just around  
274 the lower depth limit of distribution for this species in the Pyrenees (personal observation), has been  
275 progressively regressing by reducing shoot densities per square meter (from a mean of  $2850 \pm 798$  SD  
276 before impoundment (Gacia and Ballesteros 1993), to only  $25 \pm 20$  SD in 2012), by losing individuals at  
277 the deepest areas, and by increasing leaf size (Fig. 5 a). Through those years, we have not seen new  
278 recruitment, most likely due to unfavorable settling conditions (Fig 5 b). Therefore, individuals of this  
279 residual patch are probably from before the impact, which should make the shoots more than 20 years old.  
280 At the moment, the population stands much diminished, with decreased plant densities, and has lost  
281 surface area at a lineal rate of  $130 \text{ m}^2$  per year:

282 
$$y = -132 t + 4110; r^2 = 0.999, p < 0.001$$

283 where  $y$  is the area occupied by residual *I. lacustris* patches (in  $\text{m}^2$ ), and  $t$  is the number of years after  
284 impoundment. The residual patches now cover less than 10% of its original, pre-impoundment area.

285

## 286 **Discussion**

287 Submersed aquatic vegetation (SAV) has been able to recolonize and expand in lake Baciver over two  
288 decades despite the fact that this water body is suffering from water exploitation in winter. The species  
289 and communities that grow in the newly flooded area are the same that used to cover the lake before the  
290 impact. However, time to settlement and particularly expansion rates, differed among species. In addition,  
291 changes in lake hypsography have resulted in a greatly expanded area below the limit of distribution of  
292 rooted macrophytes, favouring the alga *Nitella* sp., which has rapidly occupied its entire potential habitat.

293 We are uncertain about the underlying mechanism of propagule dispersal and recolonization in the lake,  
294 except for the spores of the *I. lacustris* population that had previously been inoculated in the soil. Within  
295 the lake, propagules of the different species may have been mobilized by currents and water level  
296 fluctuations. All the species appearing in the lake (and only those) are abundant upstream within the same  
297 catchment which suggests that hydrochoria may have played a major role. *Sparganium* species are fast  
298 colonizers via dispersal of both seeds and vegetative propagules (Pollux et al. 2006), thus becoming a  
299 widespread pioneer species, as seen in this study. In contrast, *Isoetes* species require high densities of  
300 mature leaves to produce fertile sporangia and expand slowly, as expected for a stress tolerant species  
301 (Farmer and Spence 1986). At any rate, our observations strongly suggest dispersal limitation across  
302 valleys and for long distances in the high mountain range of the Pyrenees, since no other species sharing  
303 the environmental niche of *Isoetes* (Pulido et al. 2015) settled in the space available in the lake during 20  
304 years.

305 Growth and survival of *I. lacustris* in Scandinavian exploited lakes is compatible with survival of the  
306 populations given that the amplitude of the water level fluctuation remains below 6 m and light levels stay  
307 above saturation (Rørslett 1984; 1996). In lake Baciver, the slow regression of the remnant population of  
308 *Isoetes lacustris* below its former lower depth limit of distribution indicates that this species may be  
309 suffering from light- limitation, which it compensates by mechanisms at the population level (i.e. by  
310 reducing shoot densities to avoid self-thinning), and at the individual level (i.e. by increasing leaf surface  
311 area, forming a greatly enlarged leaf rosette, so as to maximize the capture of photons) as seen just after  
312 flooding (Gacia and Ballesteros 1996). Increasing the above to belowground biomass ratio is a common  
313 mechanism utilized by aquatic plants to adapt to light reduction and *I. lacustris* has been shown to present  
314 high plasticity of the photosynthetic tissues (Hickey 1986; Chappuis et al. 2015). The apparent lack of  
315 recruitment of young sprouts in the old remnant population (depths between 4.7 and 5.2 m) may be  
316 explained by unstable sediment conditions (low compactness), which may cause suffocation and prevent  
317 settlement, together with light limitation. These same mechanisms explained the lack of recruitment at the  
318 much shallower lower limit of distribution of this species in the same lake under pristine conditions in a  
319 transplant and shading experiment (Gacia and Ballesteros 1993). Nowadays the light environment has  
320 deteriorated for this residual population due the increase in depth, thus negatively interacting with  
321 unfavorable sediment conditions. Finally, we cannot rule out winter stress associated to ice scour when  
322 water level is very low (Rørslett & Johansen 1996; Helsten 2002).

323

324 Predicting in-lake distribution of submersed vegetation

325 As expected, depth was the single most important variable predicting the distribution of SAV in the lake  
326 because of depth zonation of the different functional typologies of macrophytes (Azzella et al. 2014;  
327 Pulido et al. 2015), but also because depth is a proxy for light availability, which explains the transition  
328 from *Isoetes lacustris* to *Nitella* sp. The leaf floating *S. angustifolium* can only grow at depths above 1.5  
329 m accompanied by shallow littoral species, such as *S. aquatica* and *I. echinospora*, which can withstand  
330 emersion. Monospecific *I. lacustris* meadows follow the mixed assemblage down to about 2 to 2.5 m, and  
331 *Nitella* sp. takes over below the lower limit of distribution of *I. lacustris*. However, as previously  
332 indicated by other authors, other morphological parameters are also relevant as secondary factors  
333 explaining the distribution of macrophytes in lakes (Duarte and Kalff 1986; Kolada 2014; Azzella et al.  
334 2014). In our case slope, most likely as a proxy for sediment stability, played a secondary role.

335 The distribution of *Sparganium angustifolium* growing alone appeared to be determined in part by the  
336 stream inlet (i.e. high energy area), which created a channel with open sediment flanked by *S.*  
337 *angustifolium* alone, without the accompanying species. We were able to reproduce this pattern  
338 approximately using depth, distance to the channel and distance to the inlet entry point, but we recognize  
339 that this is an empirical approximation with uncertain predictions for the post-impoundment lake, which  
340 has different basin morphology and, therefore, different hydrodynamics.

341 Models accounting for spatial autocorrelation tended to drop some of the predictors, but not in a  
342 consistent way across methods, and they never resulted in dropping depth, which is by large the main  
343 predictor for all vegetation types (Online resource 2). We also note that models including spatial  
344 autocorrelation and autologistic models in particular, may underestimate the importance of non-spatial  
345 covariables (Dormann 2007).

346 Our predictions for SAV in lake Baciver may overestimate the cover for all species. We have not taken  
347 into account areas of exposed rock that may never accumulate enough sediment to allow for the  
348 development of submersed vegetation. Even with these overestimates, the changes in the hypsography of  
349 the lake, with a larger area and perimeter but a steeper shore, promote reductions in the area occupied by  
350 *Isoetes* and the mixed community, with implications on their potential role in ecosystem processes at the

351 lake level (see below). Thus, the forecasted area that will likely be occupied by dense mats of *I. lacustris*  
352 may stay essentially the same (0.57 ha in 1989 vs. 0.55 potential area), eventually forming a narrow  
353 ribbon along a longer lake perimeter. *S. angustifolium*, alone or as a mixed assemblage, will likely occupy  
354 a much smaller area along the littoral (from 1.2 ha in 1989 to an expected 0.3 ha). Only *Nitella* sp. is  
355 predicted to grow, although seasonally and patchily, in the central basin of the lake down to its maximum  
356 depth, because this alga has lower light requirements than aquatic angiosperms (Howard et al. 1995,  
357 among others).

358 Our modeling strategy was highly effective but has some caveats. We did not model SAV from a set of  
359 random independent samples collected in the field (what we could have reasonably considered “raw  
360 data”), but from a published map of the distribution of SAV in the lake before impoundment, which had  
361 been drafted from direct observations underwater by diving (Ballesteros et al. 1989). It is important to  
362 recognize that a map already implies a model of the distribution of SAV, and our logistic classifiers are in  
363 part successful because they recover that implicit model.

364 Also, in a small lake such as Baciver, there are simple and strong environmental factors that influence the  
365 distribution of vegetation patches. In a more complex environment, logistic models might have failed and  
366 other types of classifiers might have been needed that were capable of capturing non-linear and  
367 conditional behaviors, such as classification trees (Pasles 2007). In our case, this is exemplified by *S.*  
368 *angustifolium* alone, which used to grow in two patches, one associated with the inlet and conditioned by  
369 hydrodynamics, and a separate patch near the northern shore, which was likely influenced by a different  
370 set of factors. Our logistic models could correctly classify the first patch but not the second. Use of  
371 random forests, a very robust and versatile classifier (Bosch et al. 2007), or other machine learning tools,  
372 might have improved classification accuracy, but possibly at the expense of overfitting and poorer  
373 mechanistic understanding. Despite their simplicity and rigidity, logistic models were still deemed to be  
374 an adequate choice for our case study because species responses to environmental factors, in particular to  
375 depth, were strong and simple, either monotonous or unimodal.

376 Our predictions are predicated on the assumption that environmental factors in the future will have similar  
377 ranges and will interact in similar ways as in the past. In particular, we assume similar water transparency  
378 and incoming irradiance. Under climate change, these assumptions are dubious, since over the next  
379 decades, the lake may change in several ways that can affect submersed vegetation. In particular, there

380 may be a longer ice-free period (Catalán et al. 2009), and this would result in higher water temperatures  
381 and higher incoming irradiance, both crucial factors regulating primary production in Pyrenean  
382 macrophytes (Gacia and Ballesteros 1994).

383

384 Forecasted vegetation

385 As indicated, changes in the hypsography of the lake have resulted in a substantial shift in the proportion  
386 of the different macrophyte species and communities, which will have consequences for lake benthic  
387 production and nutrient cycles. The perennial *I. lacustris* may eventually recover a total area similar to its  
388 pre-impoundment cover, yet much reduced compared to lake area (22% to 11%) , thus reducing its  
389 average relative primary production rates (Gacia and Ballesteros 1994) and denitrification in the lake  
390 sediments (Vila-Costa et al. 2016). By contrast, the leaf floating *S. angustifolium* has substantially  
391 reduced its initial surface area due to the changes in the hypsography of the lake, from 45% of the lake  
392 area to only around 6.5%. Finally the alga *Nitella* sp. is the species that has increased the most its former  
393 extent (from 30 to 78 %), but its annual production per unit area is only 20% that of the other  
394 communities (Gacia 1993). Thus, we expect the average macrophyte production of the system at steady  
395 state to be reduced by 30%, with a major contribution of *Nitella* sp. (500% increase in area) compared to  
396 that of angiosperms and quillworts (165% increase in area).

397 Recovery of the flora in the lake littoral seems to be proceeding very slowly, particularly for species with  
398 limited spread because of a lack of runners and horizontal rhizomes, such as *I. lacustris*, which in here  
399 forms dense patches and rare and isolated shoots. The fact that angiosperms (i.e. *S. angustifolium* and *S.*  
400 *aquatica*) produce fruits that can be transported by water currents instead of spores that remain buried in  
401 the sediment (*Isoetes*) should account for the large differences observed in their rate of the spread.

402 Although efforts have been done during the last decades to improve our understanding of how to recover  
403 isoetids in previously impacted softwater oligotrophic lakes (Pulido et al. 2011a, b), this study is to our  
404 knowledge the first attempt to infer the time scales of recovery for mixed *S. angustifolium* community  
405 (about 20 years, observed) and monospecific perennial *I. lacustris* (of the order of 60 years according to  
406 our models), as well as to predict landscape evolution and steady state conditions for a subalpine shallow  
407 lake. Compared to pre-impact conditions, the dammed lake will suffer from a significant shift in the



408 functional structure of the SAV, with drastic reductions in the area occupied by perennial engineering  
409 species to the benefit of annuals and macroalgae *Nitella* sp.

410 Our results suggest that impoundments in subalpine lakes should be strongly discouraged due to the  
411 severity of their impacts on the aquatic flora, risk of introductions and, most importantly, the long  
412 recovery time for some long-living engineering species, as shown here for *Isoetes lacustris*.

413

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532

533 Table 1. Time progress of water nutrient and chlorophyll content, and light extinction coefficient (k) in Baciver lake. PRS stands for Reactive Dissolved Phosphorous,  $\text{NH}_4^+$   
 534 for ammonia,  $\text{NO}_3^-$  for nitrate and Chl for chlorophyll a. Nutrient data are in  $\mu\text{M}$ , chlorophyll in  $\text{mg L}^{-1}$  and K in  $\text{m}^{-1}$ . Asterisk (\*) corresponds to data before impoundment  
 535 conditions from <sup>1</sup>Ballesteros *et al.* (1989) and <sup>2,3</sup>Gacia and Ballesteros (1996, 1998).

536

	PRS		$\text{NH}_4$		$\text{NO}_3$		Chl		K	
	mean	range	mean	range	mean	range	mean	range	mean	SD
<b>1989</b> <sup>*1</sup>	0.08	0.00-0.97	1.11	0.02-4.63	6.01	0.27-18.2	0.37	0.20-0.60	0.280	0.033
<b>1992</b> <sup>*2,3</sup>	0.56	0.33-1.16	1.83	1.1.1-75.6	3.38	0.79-12.67	1.53	0.41-2.25	0.418*	0.004
<b>1993</b> <sup>*2,3</sup>	0.40	0.04-1.08	10.40	1.64-38.9	2.04	0.15-6.43	0.38	0.04-1.24	0.328	0.051
<b>2000</b>	0.10		1.60		5.10		0.41			
<b>2006</b>	0.25	0.20-0.35	1.85	0.48-8.28	2.40	2.07-2.69	0.29	0.19-0.74		
<b>2012</b>	0.09	0.08-0.12	0.709	0.68-0.76	0.696	0.08-0.12	-		-	

537

538 Table 2: Logistic models for the submerged aquatic vegetation found in lake Baciver. “Linear model”  
 539 gives the formula for the linear predictors of the logistic regressions. “z” is depth, “distChannel” is the  
 540 distance to the inlet channel, and “distInlet” is the distance to the inlet point. “AUC ROC for test data”  
 541 gives the area under the curve for the receiver operating characteristic curve, a measure of the  
 542 performance of a classifier. The “best” threshold is that with the highest value for the product of  
 543 sensitivity (or true positive rate) and specificity (true negative rate). Sensitivity and specificity are for that  
 544 threshold.

545

<b>Species / assemblage</b>	<b>Model terms</b>	<b>AUC ROC</b>	<b>Best threshold</b>	<b>Sensitivity</b>	<b>Specificity</b>
<i>I. lacustris</i>	$z + z^2 + \text{slope}$	0.957	0.10	0.964	0.941
Mixed assemblage	$z + z^2 + \text{slope} + \text{distInlet} + \text{distChannel}$	0.931	0.53	0.822	0.877
<i>S. angustifolium</i>	$z + z^2 + \text{slope} + \text{distInlet} + \text{distChannel}$	0.896	0.16	0.835	0.885
<i>Nitella</i> sp.	$z$	0.996	0.24	0.835	0.885

546

547

548 **Figure captions:**

549 Fig. 1 Time progress of the area occupied by each of the aquatic macrophyte assemblages in lake Baciver  
550 (a) under natural conditions in 1989, (b) just after the impact in 1993, and (c), (d) and (e) during the  
551 recolonization stage in 2000, 2006 and 2012, respectively. Arrows point at the new patch of *Isoetes*  
552 *lacustris*. Inset bar plots show changes in cover as area (in hectares, left axis) and percent of lake surface  
553 area (right axis).

554 Fig. 2 Changes in the hypsography of Lake Baciver from natural conditions (pre-impoundment) to the  
555 current situation (post-impoundment).

556 Fig. 3 Time progress of the *Sparganium angustifolium* mixed community (a) and *Isoetes lacustris*  
557 community (b). Superimposed onto the observed data are logistic curve fits. In (a), the dotted line is the  
558 asymptote estimated from the logistic curve and the dashed line is the maximum expected area based on  
559 the binomial logistic model for *Sparganium*. In (b), the logistic curve was fitted to the maximum expected  
560 area predicted by the binomial logistic model for *Isoetes*, i.e., the asymptote was not estimated but fixed  
561 when fitting the logistic curve. The projected path for the recolonization of *Isoetes* (discontinuous line, 20  
562 years onwards) is thus distinguished from the interpolated period (solid line, first 20 years).

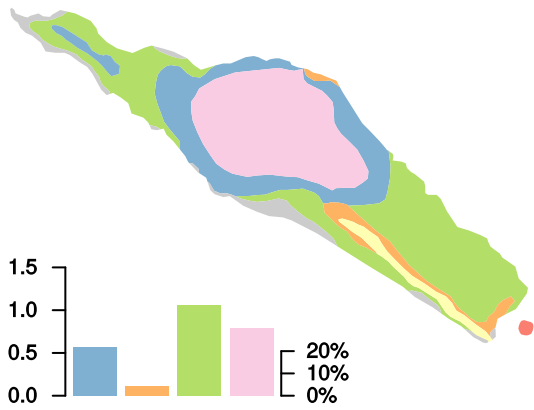
563 Fig. 4 Predicted eventual distribution of macrophytes in post-impoundment lake Baciver. Pixel  
564 assignment was based on the maximum predicted probability of occurrence. The inset bar plot shows  
565 expected area coverage in hectares (left axis) and percent of lake surface area (right axis). The expected  
566 area for *Nitella* sp. (omitted from bar plot) is 4.0 hectares.

567 Fig. 5 a and b. *Isoetes lacustris* from the residual population at the actual upper (4.7 m) and lower (5.2 m)  
568 depth limits of distribution.

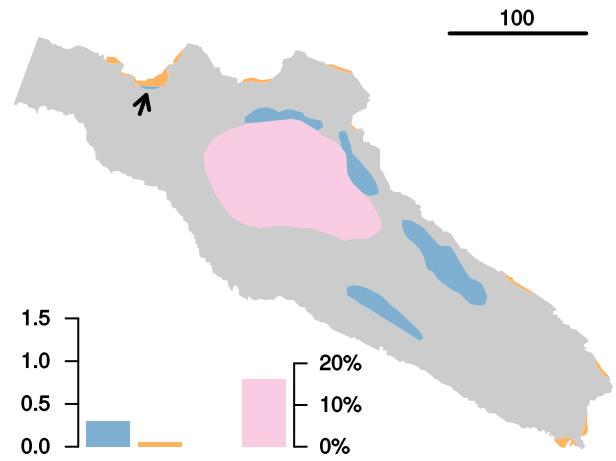
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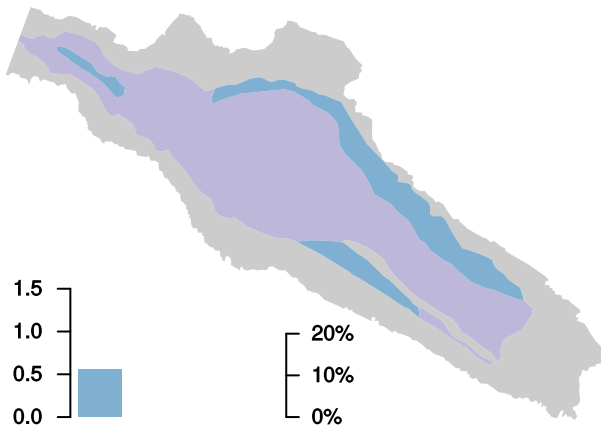
1989



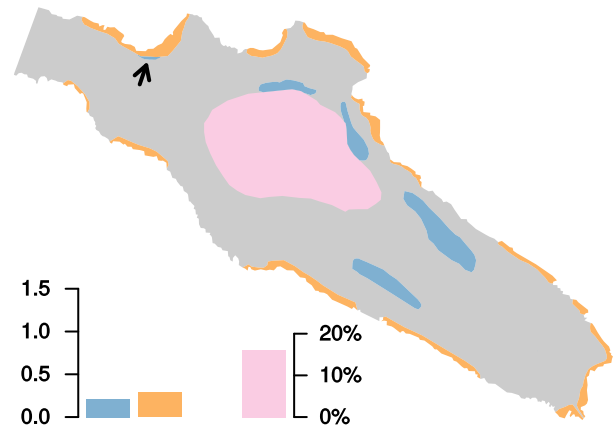
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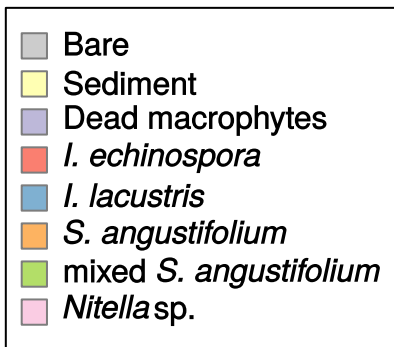
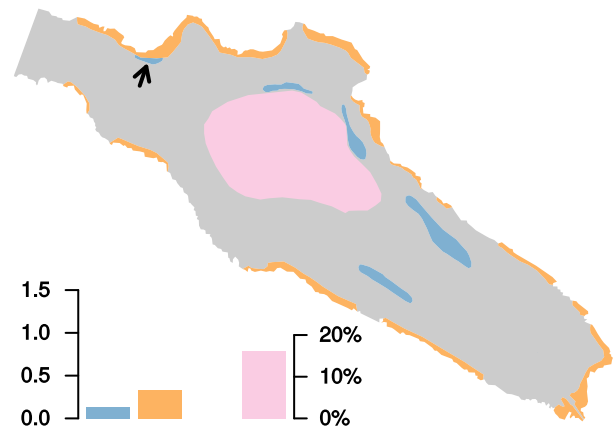
1993

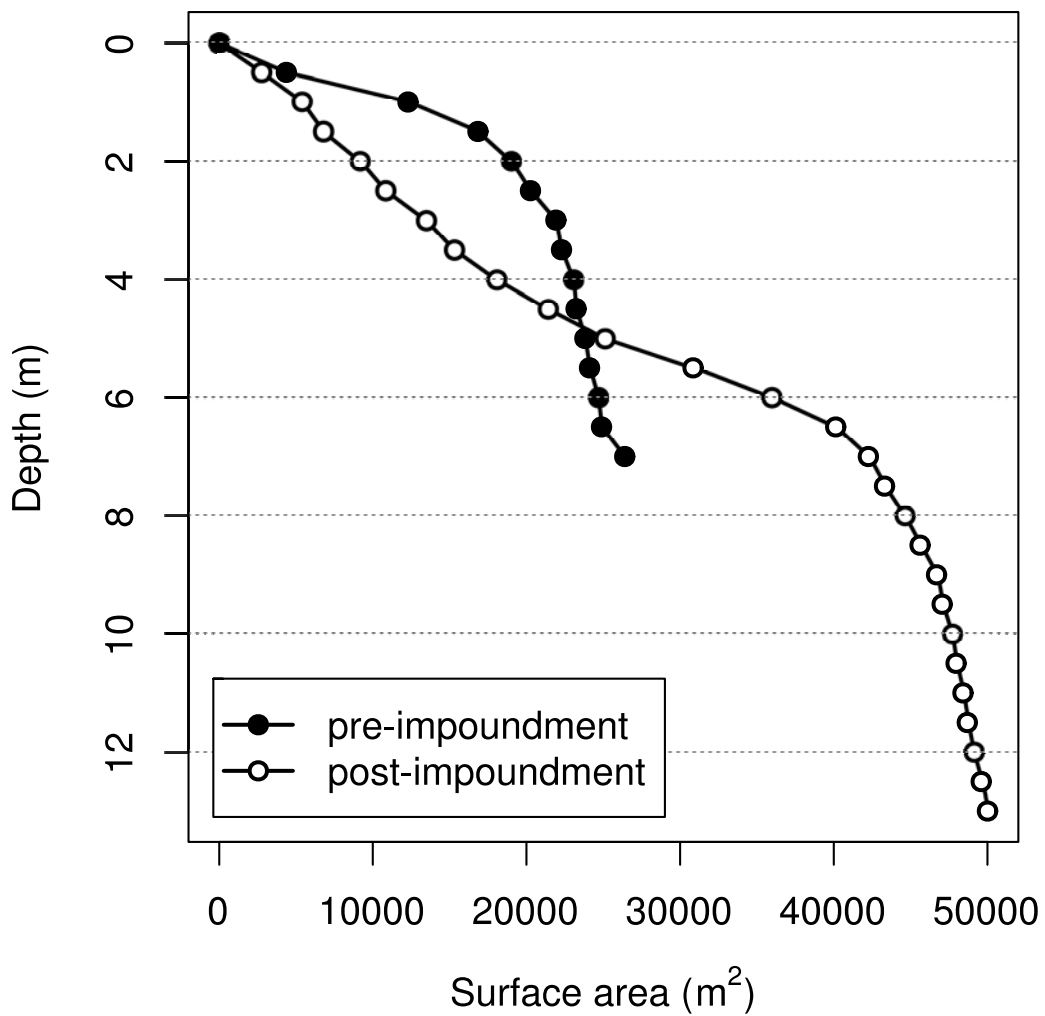


2006

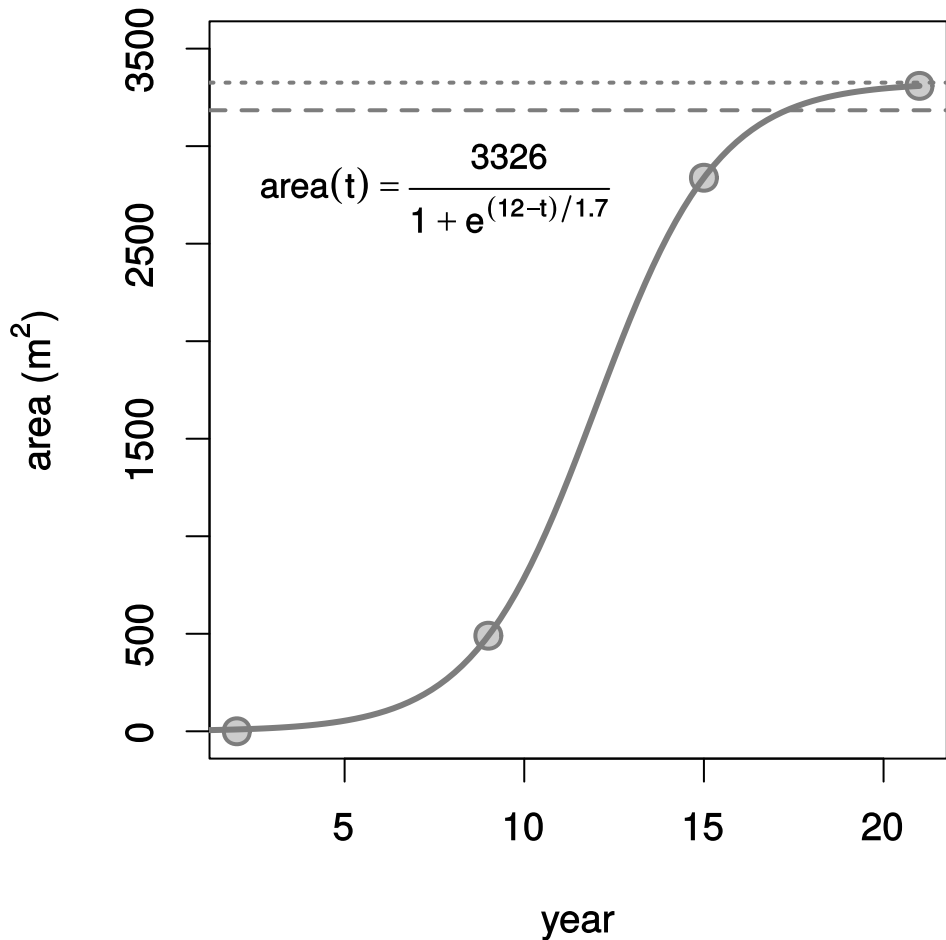


2012

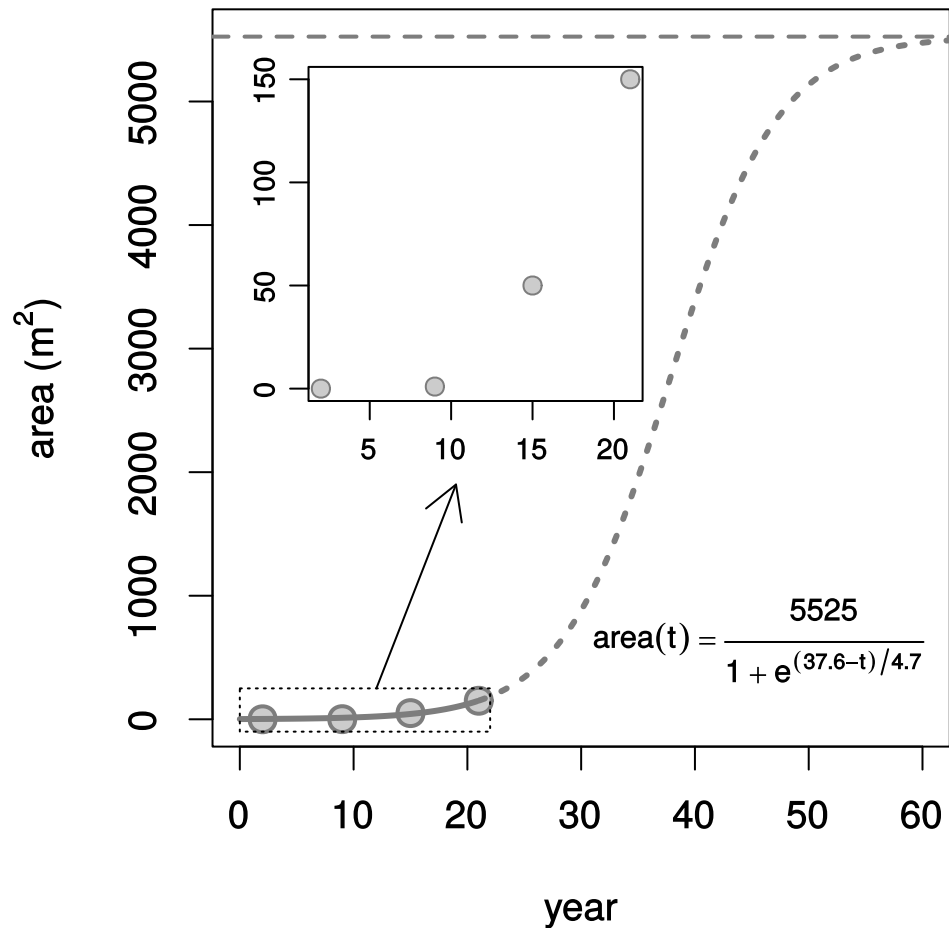








(a) *Sparganium angustifolium*

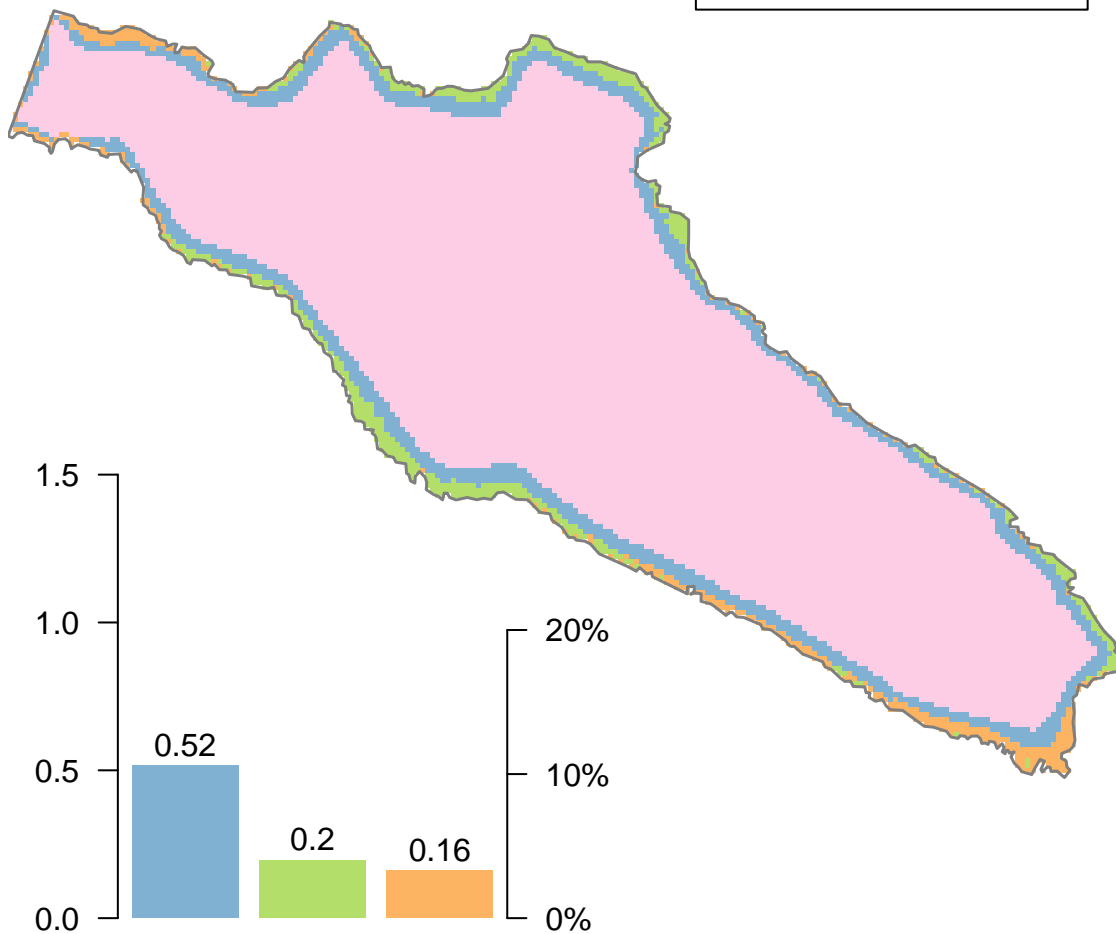


(b) *Isoetes lacustris*



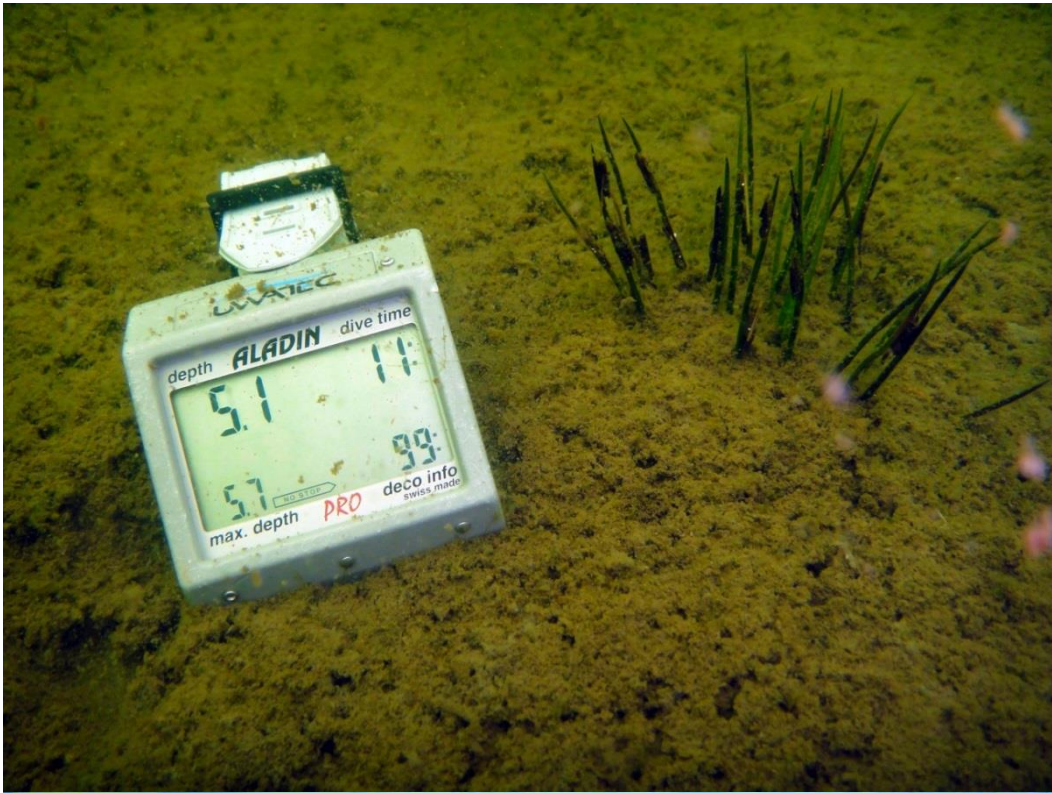
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-  *I. lacustris*
-  mixed assemblage
-  *S. angustifolium*
-  *Nitella* sp.



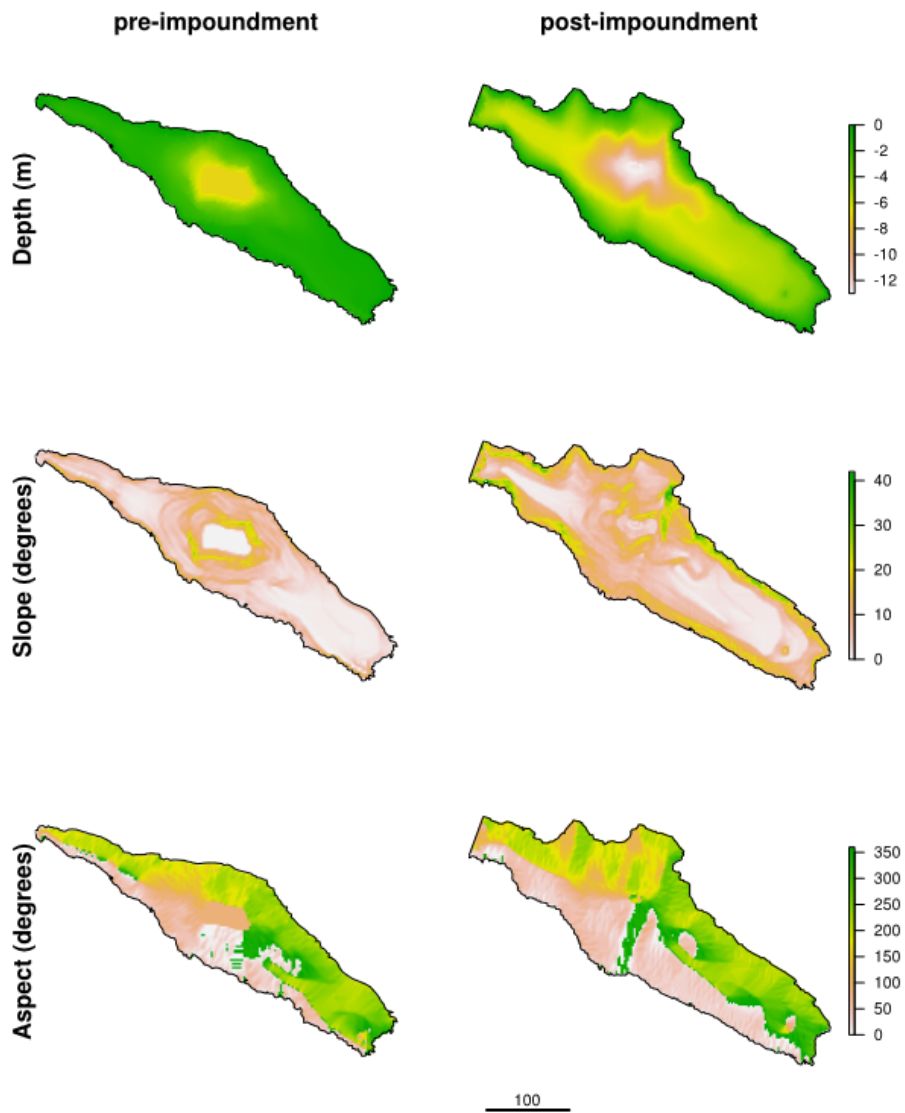
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10%  
0%



1 Annex 1 Models of space occupation in relation to depth (m), slope (degrees) and aspect (orientation) in  
2 lake Baciver before and after impoundment (see Fig. 1). Lake bathymetry was digitized as contour lines  
3 from a published paper map (Ballesteros 1989) and converted to raster format. Slope and aspect were  
4 obtained from bathymetry using the terrain function. Raster resolution was set to 2 by 2 meters.

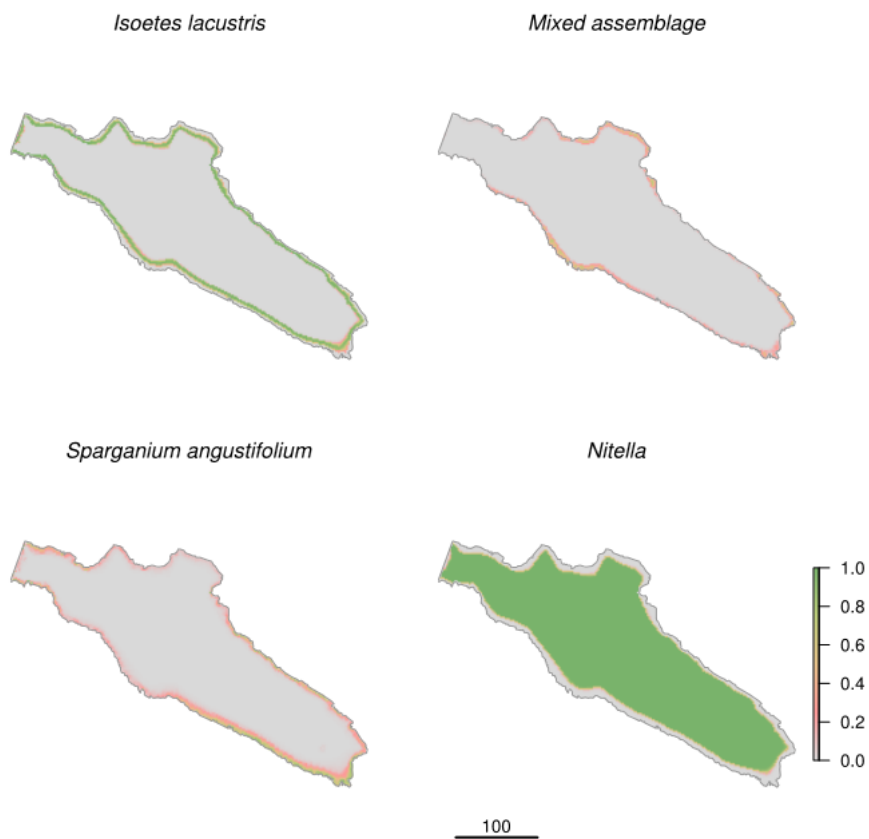
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6

1 Annex 2 Simulations of the distribution of the different macrophyte communities at steady state  
2 based on the logit models (see Table 2) and the variables from annex 1.

3



4

**Annex 3.** Combined prediction map for lake Baciver. Each pixel was assigned the community with the highest prediction probability according to logistic models. Less than 3% of pixels would be below a cutoff probability of  $p = 0.4$ , mostly around the margins.

