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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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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

Introduction

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

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

Studies on submersed vegetation recovery or colonization and expansion in freshwater bodies are rare and mostly restricted to free floating, often invasive species (i.e. Khanna et al. 2012), or to riparian vegetation (i.e. Sand Jensen and Madsen 1992), regardless of the reproductive strategy of the species involved. Studies on the patterns and time scales of growth and expansion, or of regression, of submersed macrophytes must resort to time-consuming and often difficult field assessments supplemented with niche modeling techniques and numerical projections (e.g. Røslett 1989).

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

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

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

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

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

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Methods

Area of study

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

Data sampling

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

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

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Species distribution models

In order to predict the potential steady-state spatial distributions of aquatic vegetation after full recovery,

logistic regression models based on pre-damming vegetation and conditions were developed. Logistic

regressions were used because true presence-absence data were available, the main factors that influence

species distributions were known from previous studies (Gacia et al. 1994; Pulido et al. 2015), and the

aim was to develop models that were both simple and interpretable.

Models were based on a set of training data randomly sampled from a pre-damming submerged

vegetation map (Ballesteros et al. 1989). First, we digitized and georeferenced the published vegetation

map. This layer and all geospatial data were projected to the European Datum 1950 UTM 31N coordinate

reference system. We then processed a series of five geospatial predictors. Lake bathymetry was digitized

as contour lines from a published paper map (Ballesteros 1989) and converted to raster format using

function r.surf.contour in the GRASS GIS system toolbox (GRASS Development Team 2015). Raster

resolution was set to 2 by 2 meters. The remaining raster predictors were processed with the "raster" R

package (Hijmans, 2014) to the same extent and resolution. Slope and aspect (orientation) were obtained

from bathymetry using the terrain function. We expected depth to be the principal predictor of species

distribution because it restricts leaf-floating species and is a surrogate of light availability. Slope and

orientation were expected to improve the models because slope affects substrate stability (Gacia and

Ballesteros 1993) and orientation affects hours of direct sunlight

An inspection of the pre-impoundment vegetation showed a clear effect of the inlet stream (Riu Malo) as

it enters the lake, probably due to the erosive force of the stream water during snowmelt. To take this into

account in a simple manner, we included two new predictors: distance to the inlet point (i.e., the point

along the shore where the stream enters the lake), and distance perpendicular to the channel of lowest

descent from this point towards the central basin of lake Baciver. This channel was digitized on-screen on

top of the aspect and flow direction maps (obtained also with the "terrain" function). Short of a

hydrodynamic model, which was not feasible, we expected that these two predictors, together with depth,

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 that 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 where 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 where 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 were *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^2 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^2 (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) where fitted for each of the SAV types present

230   before impoundment, i.e. *Isoetes lacutris*, *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 $$y = \text{Asym}/(1 + e^{(xmid - t)/scal})$$

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 ± 798 SD

276   before impoundment (Gacia and Ballesteros 1993), to only 25 ± 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 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 m^2), and t is the number of years after

284   impound. 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 detph, were strong and simple, either monotonous o 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 descouraged 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

Table 1. Time progress of water nutrient and chlorophyll content, and light extinction coefficient (k) in Baciver lake. PRS stands for Reactive Dissolved Phosphorous, NH_4^+ for ammonia, NO_3^- for nitrate and Chl for chlorophyll a. Nutrient data are in µM, chlorophyll in mg L^{-1} and K in m^{-1}. Asterisk (*) corresponds to data before impoundment conditions from [1]Ballesteros *et al.* (1989) and [2,3]Gacia and Ballesteros (1996, 1998).

536

	PRS		NH₄		NO₃		Chl		K	
	mean	range	mean	range	mean	range	mean	range	mean	SD
1989*[1]	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
1992*[2,3]	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
1993*[2,3]	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
2000	0.10		1.60		5.10		0.41			
2006	0.25	0.20-0.35	1.85	0.48-8.28	2.40	2.07-2.69	0.29	0.19-0.74		
2012	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

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

546

547

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)
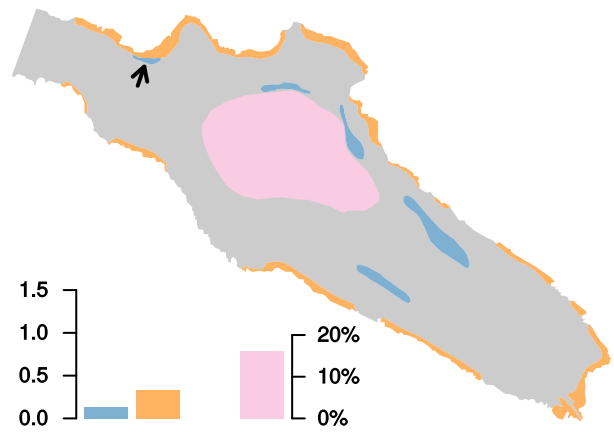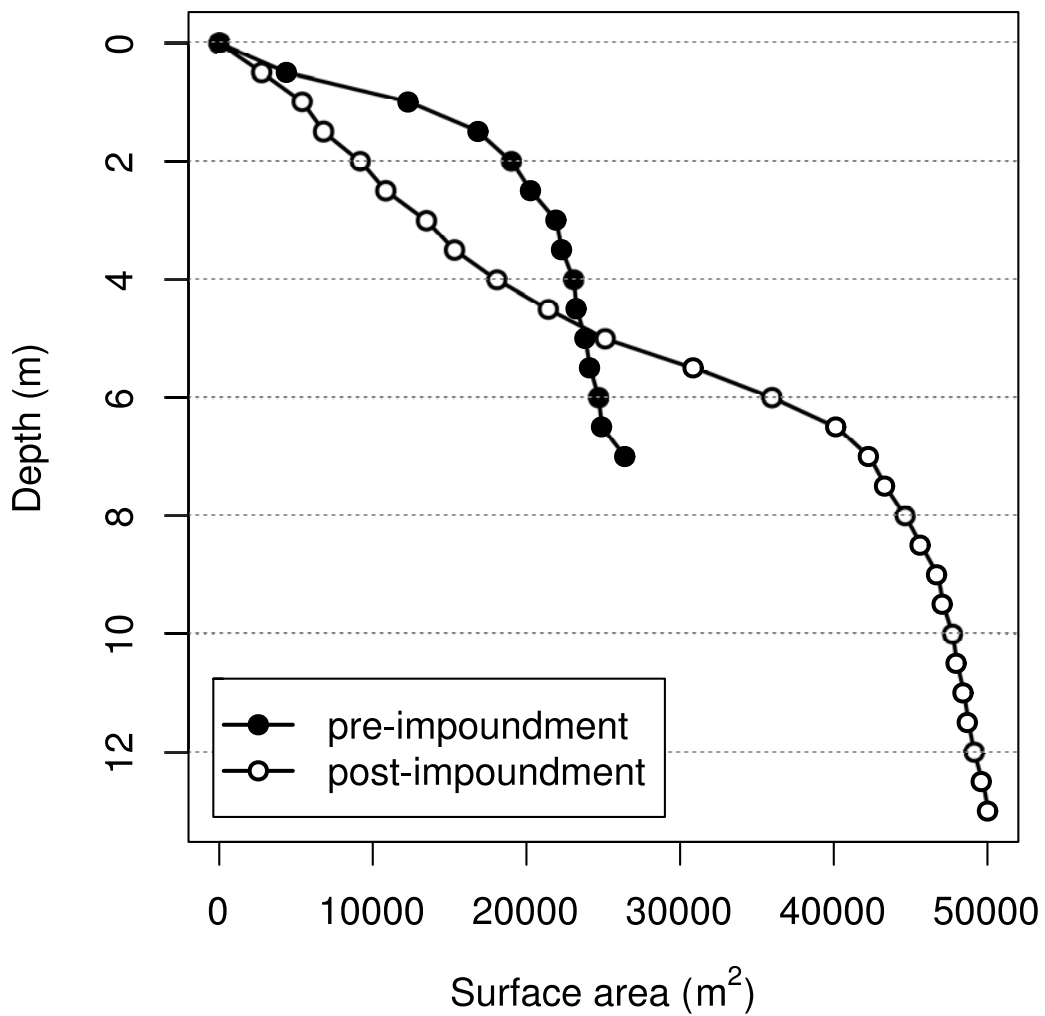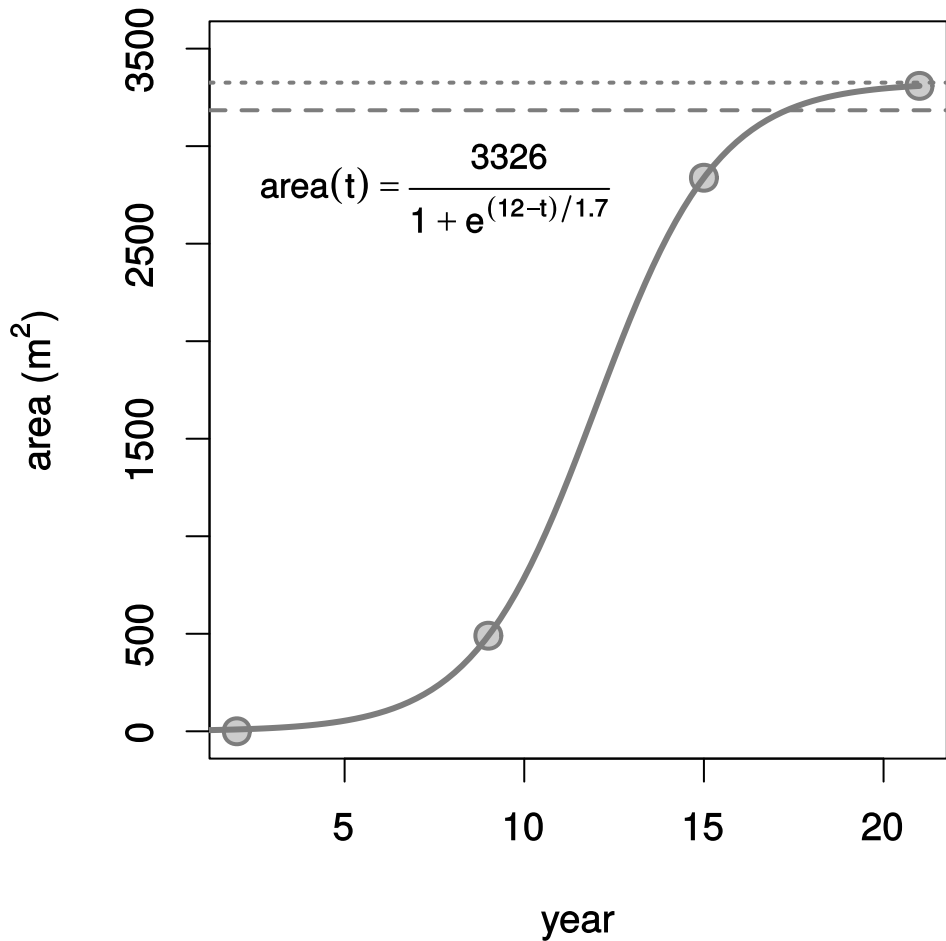
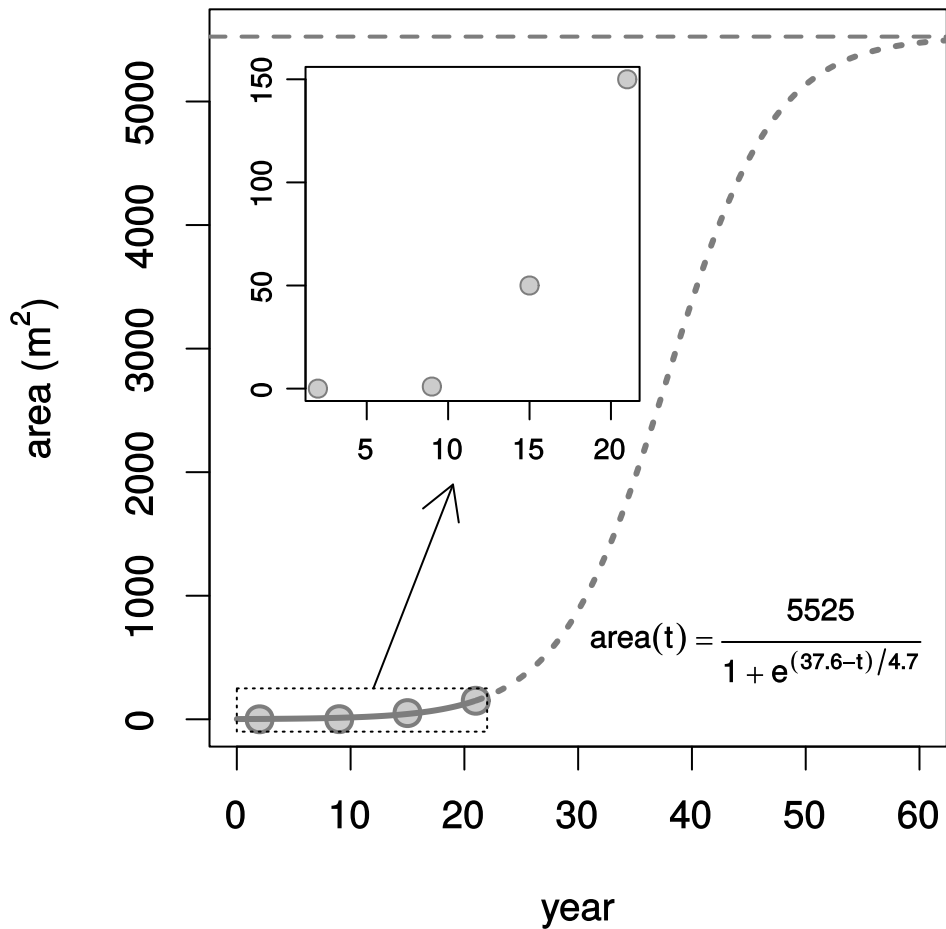568 depth limits of distribution.

569

1989
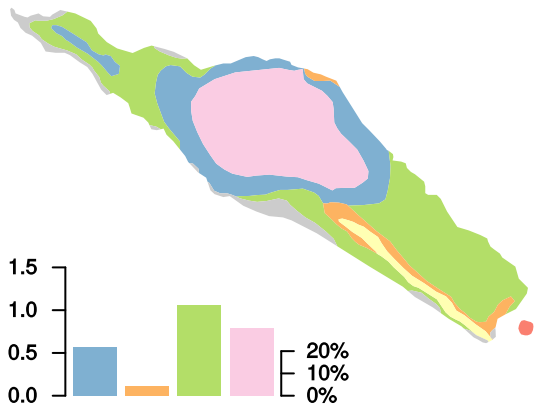
2000

100
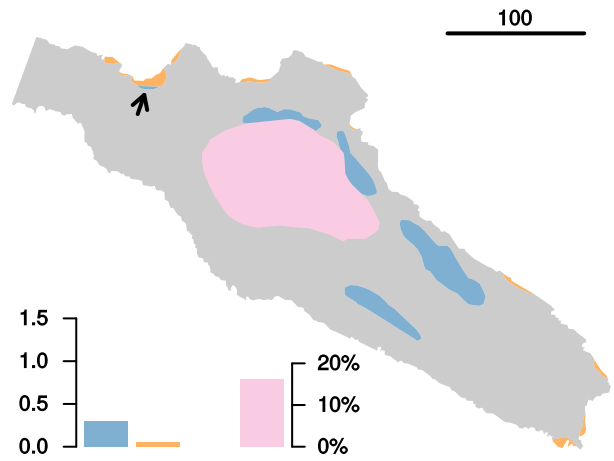
1993
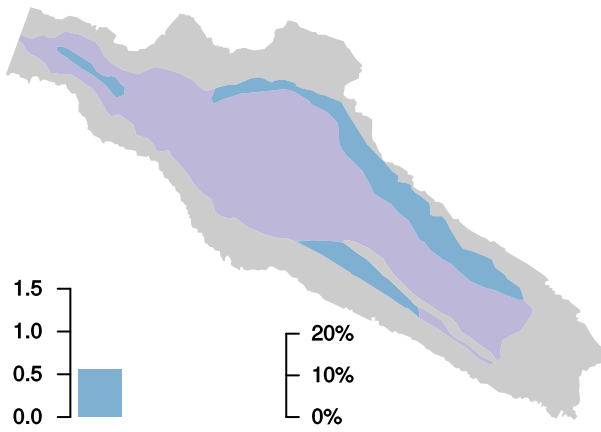
2006
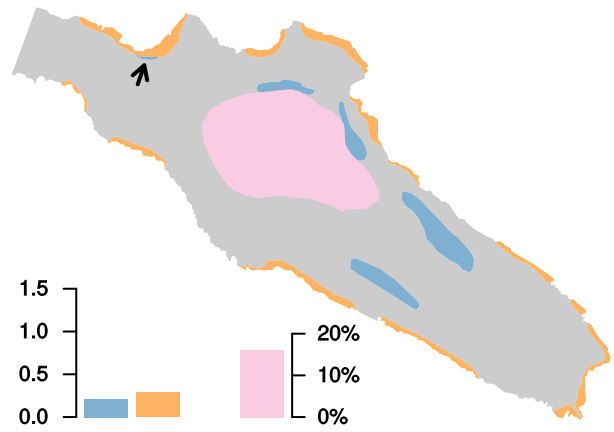
2012

Bare
Sediment
Dead macrophytes
I. echinospora
I. lacustris
S. angustifolium
mixed *S. angustifolium*
Nitella sp.

(a) *Sparganium angustifolium*

$$\text{area}(t) = \frac{3326}{1 + e^{(12-t)/1.7}}$$

area (m^2)

year

(b) *Isoetes lacustris*

$$\text{area}(t) = \frac{5525}{1 + e^{(37.6-t)/4.7}}$$

area (m^2)

year
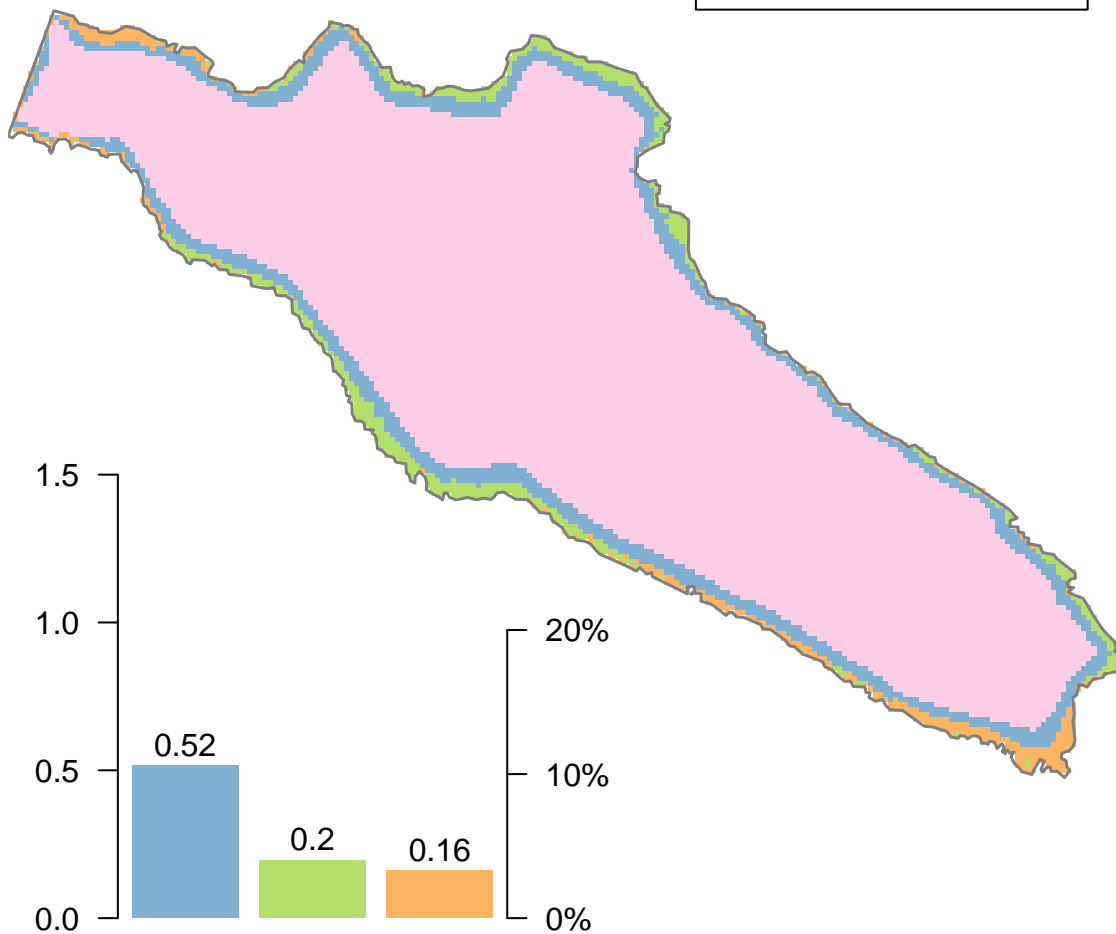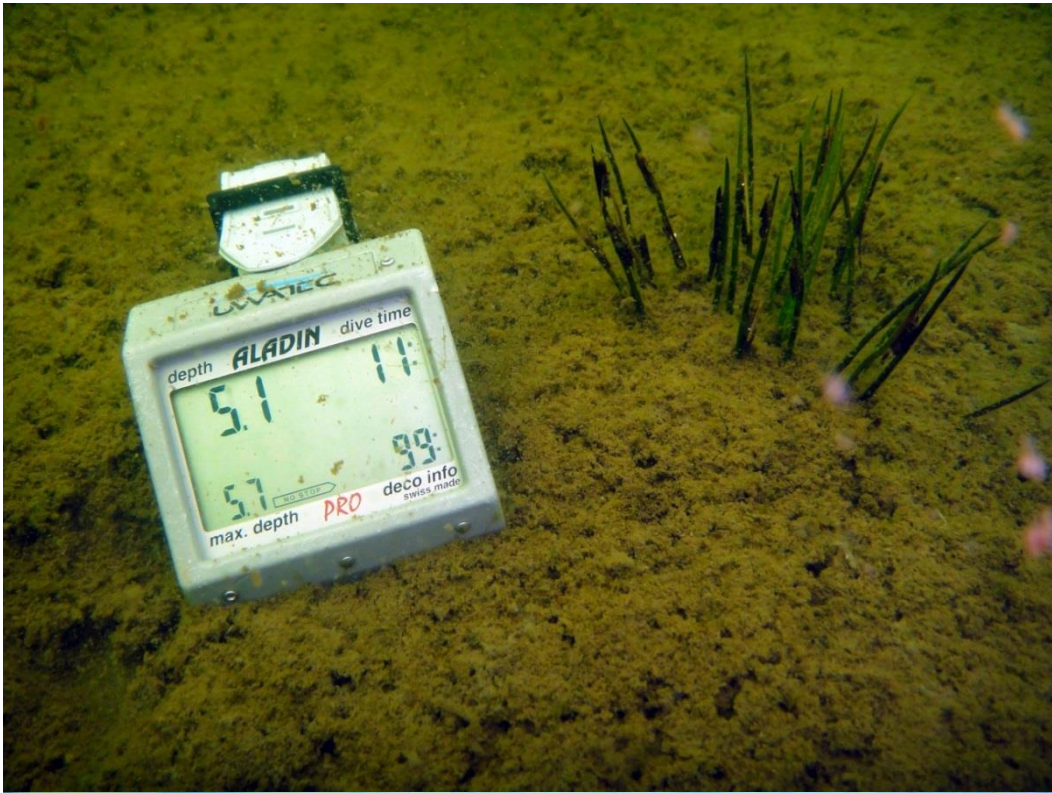
1   Annex 1 Models of space occupation in relation to depth (m), slope (degrees) and aspect (orientation) in

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.
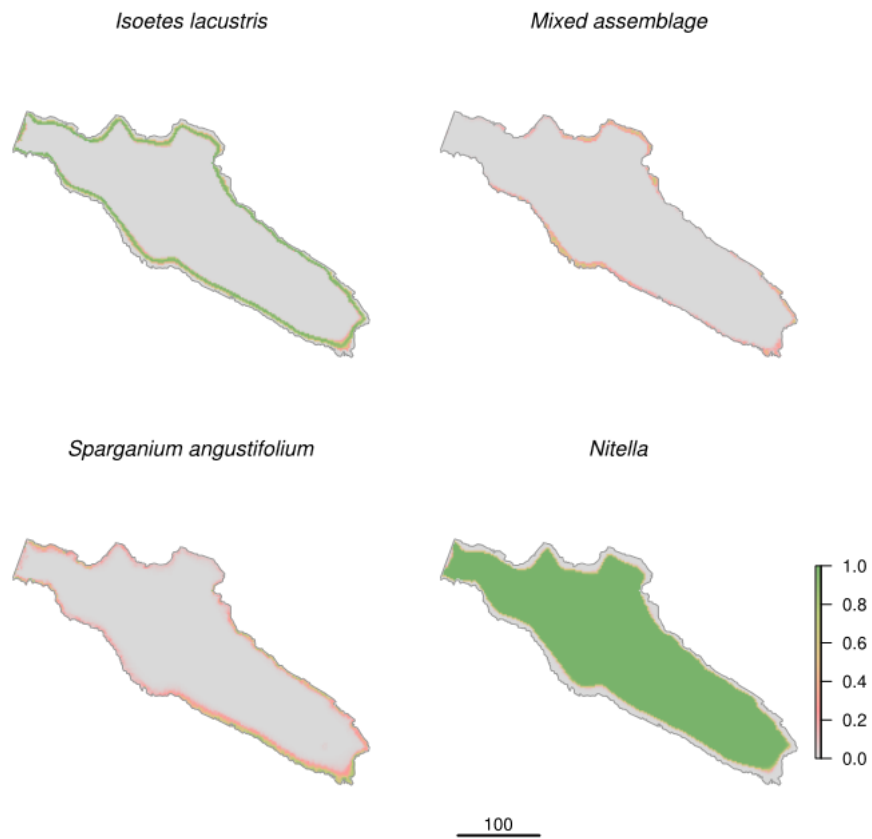
5
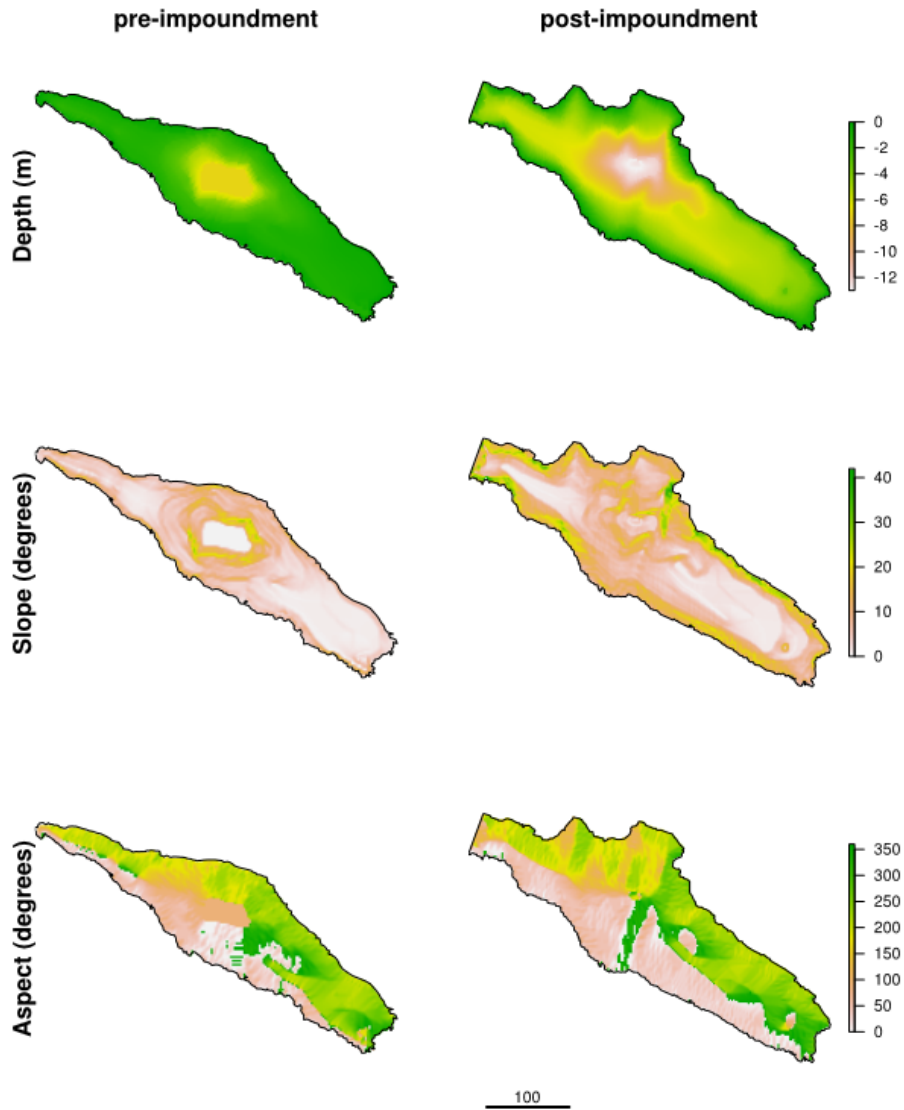
6

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.