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Decadal riparian forest evolution beside a regulated lake: a case study in the Swiss lowlands

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Abstract The consequences of lake level regulation on riparian forests have been little investigated in Europe, although they shelter a wide variety of habitats and species and are threatened in most European countries. This study therefore aims to improve our understanding of the past and future dynamics of wetland forests in Central Europe. Historical plant surveys (conducted around 1980) were compared with more recent surveys (2020) at the same locations in the Grande Cariçaie reserves, along the Lake Neuchâtel (Switzerland), regulated since 1962. The inventories were clustered into plant communities, and floristic diversities were compared. Changes in environmental conditions were evaluated using ecological indicator values. The species composition in tree and shrub layers was compared to predict the potential future evolution of these forests. Four types of forest communities have been identified and denoted as the *Alnus glutinosa*, *A. incana*, *Fraxinus excelsior* and *Pinus sylvestris* groups. Over the course of 40 years, some sites shifted between communities, particularly from the wet *A. incana* group to the drier *F. excelsior* group. We noticed a loss of hygrophilous and heliophilous species. Moreover, the regeneration of the dominant tree species is very low in the *A. glutinosa* and *F. excelsior* groups, and even absent in the *P. sylvestris* group. The riparian forests on the shores of the regulated lake are losing their characteristics, with significant changes in species composition. Over 40 years, the conditions have become drier, the canopy density has increased, and the understorey has suffered from shadier conditions, resulting in a loss of diversity at the landscape scale. The drier conditions are probably mainly following the lake regulation (lower variations of water level), but increasing evapotranspiration due to climate change cannot be excluded.

Keywords Wetland forest · Cover changes · Ecological indicator values · Ecosystem conservation · Forest dynamics · Quasi-permanent plots

Introduction

The effects of human activities on ecosystems and their changes need to be better understood to improve their conservation (Sutherland et al. 2013). Permanent plots are particularly efficient to assess changes in habitats (Bakker et al. 1996; de Bello et al. 2020).

Sarah Beuvier is diseased.

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Among the threatened communities, riparian forests are some of the most affected (Delarze et al. 2016; Klimo and Hager 2008). The term 'riparian' refers to biotic communities and the physical environment on the shores of streams, rivers, ponds, lakes and wetlands (Naiman et al. 1998). More precisely, riparian ecosystems exist at the interface between freshwater and terrestrial systems. Their composition is mainly influenced by the water level and they are maintained by periodic flooding or a high groundwater level (Mandžukovski et al. 2021). These ecosystems are often a mosaic of diverse habitats, from open wetlands to dense forests, with structured edges, depending on the water level and its variations, that encompass juxtaposed stages of ecological successions (Gallandat et al. 1993; Naiman et al. 1998; Finlayson et al. 2018; Maděra et al. 2008). Plants in these habitats are adapted to variable water regimes, ranging from submerged to dry conditions. The length of the respective hydrous states (submersion, water-saturated soil, etc.) controls the distribution of the species, particularly for trees. The 'hydric forest limit' is defined as the maximum length of flooding bearable for trees, *Salix alba* being the most tolerant species (190 days per year; Maděra et al. 2008). *Alnus* species show the typical necessary adaptations to tolerate high water levels, like a high leaf conductance gas transfer from stems to roots, the presence of lenticels and nitrogen-fixing symbiotic bacteria (Eschenbach and Kappen 1999; Große and Schröder 1984).

Riparian forest and other wetland have declined considerably in Central Europe. They were drained to gain agricultural and urban land in the wake of population growth (Delarze et al. 2015; Klimo and Hager 2008; Vischer 2003), as wetland soils are very productive once dried. Moreover, flooding often threatens infrastructure, and wetland may be reservoirs for diseases such as malaria (Vischer 2003). The few remaining vestiges continue to be threatened by pollution, agricultural and urban expansion and existing drains, inducing a loss of biodiversity (Bonnard et al. 2020; Klimo and Hager 2008; Pfadenhauer and Grootjans 1999; Vischer 2003). In Switzerland, the water level is regulated in 11 of the 15 large Swiss lakes (> 10 km^2; Vischer 2003). As a result, most of the remaining riparian forests have been qualitatively degraded, with a loss of typical species and colonization by late-successional species (Bonnard et al. 2020; Buttler et al. 1995; Gallandat et al. 1993). For these reasons, a large proportion of riparian forests are under legal protection, with management aiming to restore, or replace, natural water variations.

Riparian forests host different plant communities depending on the water level and dynamics, soil type and age of forest colonization (Prax et al. 2008). Natural vegetation dynamics along gravelly sections of rivers (braid plains) have long been an object of study in Central Europe (Middleton 2016; Naiman et al. 1998; Moor 1958). Other studies have also considered impacts of dams and channelling on vegetation (Breton et al. 2023; Friedman et al. 2022; Johnson et al. 2012). They concluded to a decrease in heliophilous and hygrophilous species after river regulation (Breton et al. 2023) and a change in tree species composition (Bejarano et al. 2011). Colonization by invasive exotic species or disease can also cause changes in communities (Johnson et al. 2012; Wilcox et al. 2005). Studies on the natural dynamics of alder carrs on peatland have shown a cyclical succession between alder groves and open *Carex* fens, mainly due to changes in the water regime and light-demanding alder regeneration (Barthelmes et al. 2010; Pokorný et al. 2000). However, there is more uncertainty about successions when water dynamics are calmer, for example along the lower sections of rivers or on lake shores (Wilcox et al. 2005).

The present study aims to describe the dynamics in riparian forests on the shores of a continental lake. These forests colonized wetland areas emerged after the lowering of the lake water level in the 19th century. Ninety-four exhaustive plant inventories performed between 1978 and 1988 were resurveyed. By means of a temporal comparison of species frequency and cover, and with the help of ecological indicator values (Landolt et al. 2010; Ellenberg et al. 1992) and other historical and environmental data, the following questions are addressed: (1) How have plant communities evolved over the last 40 years? (2) What environmental conditions can explain the observed changes? (3) How will these forests evolve in the near future? We hypothesized different evolutions according to the respective ecological conditions of the riparian forests, but generally a decrease in pioneer and hygrophilous species, replaced by mesophilic ones following the regulation of the lake 50 years ago. More competitive tree species have probably colonized the forests and replaced the species characteristic of the respective habitats, especially in the driest riparian forests. The results will improve our understanding of riparian forest dynamics in Central Europe and should help reserve managers to preserve the most valuable habitats and species.

Methods

Study Site

The study site is the riparian forests of the Grande Cariçaie nature reserves in Switzerland. These areas developed following the lowering of the lake level in 1878, which offered new shores for natural colonization processes, including forests that have been little influenced by humans since then. The name 'Grande Cariçaie' is derived from the French name of *Carex elata*, one of the dominant species in the open wetlands. These reserves are located along the southern shore of Lake Neuchâtel at 430 m.a.s.l. (Fig. 1). This region contains the largest lacustrine marshland in Switzerland, which is protected at the federal and international levels, with 42 km of shoreline and an area of 2,532 ha, including 647 ha of forests (Alfter et al. 2004; https://grande-caricaie.ch). The climate is temperate, attenuated by the lake (Sandoz 1949, in Buttler et al. 1995). The total annual rainfall is 854 mm, reaching its peak in June (92 mm). The average temperature is 9.8°C, with a minimum monthly average of 0.9°C in January and a maximum of 19.3°C in July (data for Payerne, 8 km from Lake Neuchâtel at 490 m.a.s.l., means for 1990–2020; www.meteosuisse.ch).

The southern shores of Lake Neuchâtel are mainly formed of Tertiary sandstone, built of alluvial deposits from the Alps, which forms an impermeable bedrock (map.geo.admin.ch; Buttler et al. 1995; Cornali 1992). Glaciers excavated it, and the lake finalized the erosion, leaving behind 30–70 m high cliffs (Fig. 2). The fine sediments (grain size between sands and silts) liberated by the waves eroding the cliffs contributed to the present wetland substrate sediments. Locally, thin morainic layers (around 30–50 cm) from the Würm period are present, attesting to Lake Neuchâtel's glacial origins (Buttler et al. 1995). Finally, thousand years of lake cover deposited limestone-rich lacustrine sediments (Verrecchia 2007). Most of the soils are now developed in the moraine or altered sandstone, mostly with organic rich horizons, but they all have a neutral to basic pH (not published, personal data).

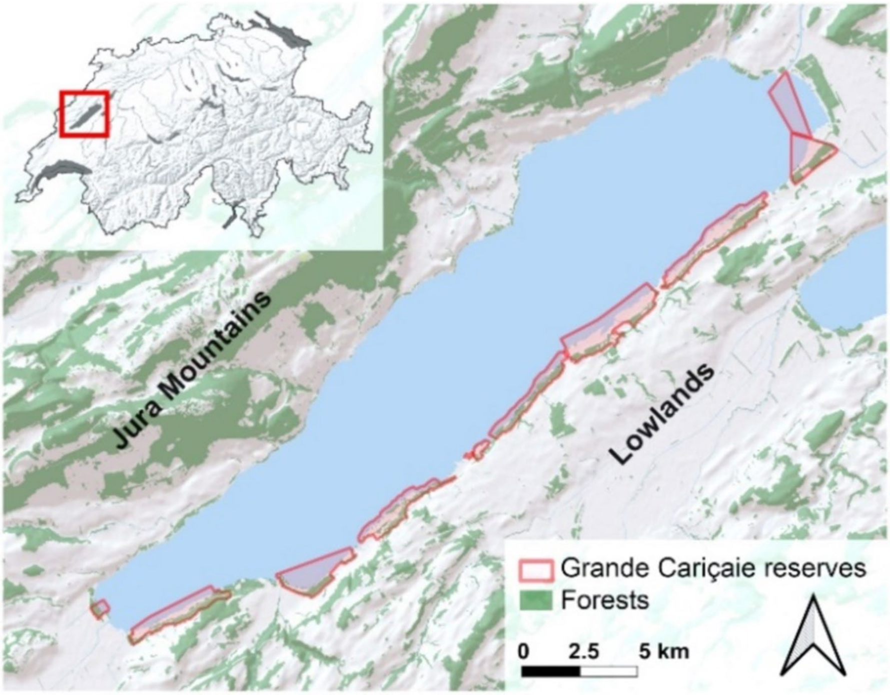


Fig. 1 Study area with the localization of the Grande Cariçaie reserves on the shores of Lake Neuchâtel in Switzerland (background map: Esri Topo; forests: Swisstopo)

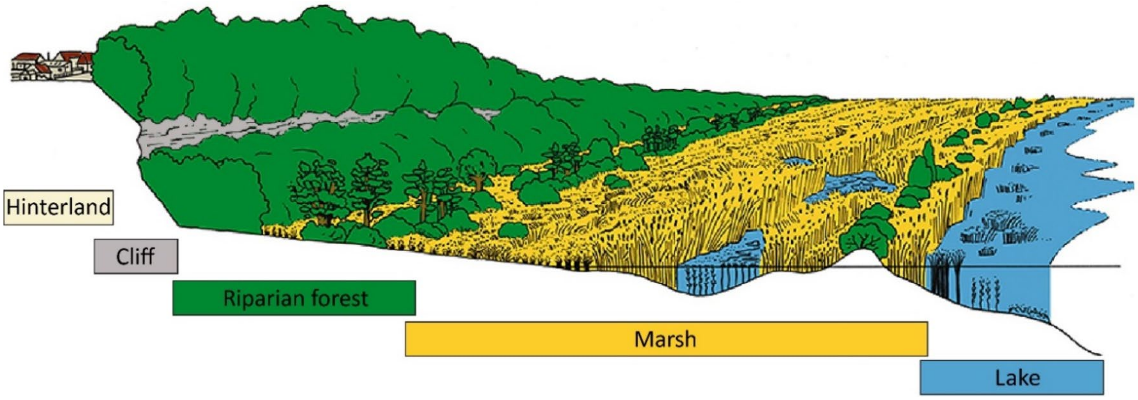


Fig. 2 Typical topographical section of the Grande Cariçaie reserves, with the lake on the right, the marshes, riparian forests and a 30–70 m high cliff on the left, separating wetlands from the hinterland. The hinterland consists mainly of crop fields, pastures and villages. Marshes and riparian forests have colonized the former lake bed, with the 1878 shore at the cliff foot (image modified from https://grande-caricaie.ch).

Lake Neuchâtel is connected to two other lakes at the foot of the Jura Mountains. They were previously surrounded by large, flat areas, close to the lake elevation and covered by 400 km^2 of wetlands. This largest continuous wetland in Switzerland was difficult to cultivate due to frequent floods, and it was also responsible for diseases (Buttler et al. 1995; Vischer 2003). To gain fields and protect the populations, the first correction of Jura waters (1868–1891) channelled several rivers, lowered the levels of the three lakes by 2.7 m (Fig. 3) and drained the surrounding wetlands (Buttler 1987). The recently emerged lake shoals were quickly colonised and served as a refuge for the specialized wetland flora and fauna (https://grande-caricaie.ch). A second correction of the Jura waters was carried out between 1962 and 1973 (Vischer 2003), which reduced the seasonal variations in the lake level from a maximal difference between high and low water of 3 m to one of 1.8 m, with average mean annual variations decreasing from 1.5 m to 0.85 m (Fig. 3; https://grande-caricaie.ch). From 1942, isolated protected areas were created, which were then grouped together in 1976 as the first Ramsar site (international convention for wetland

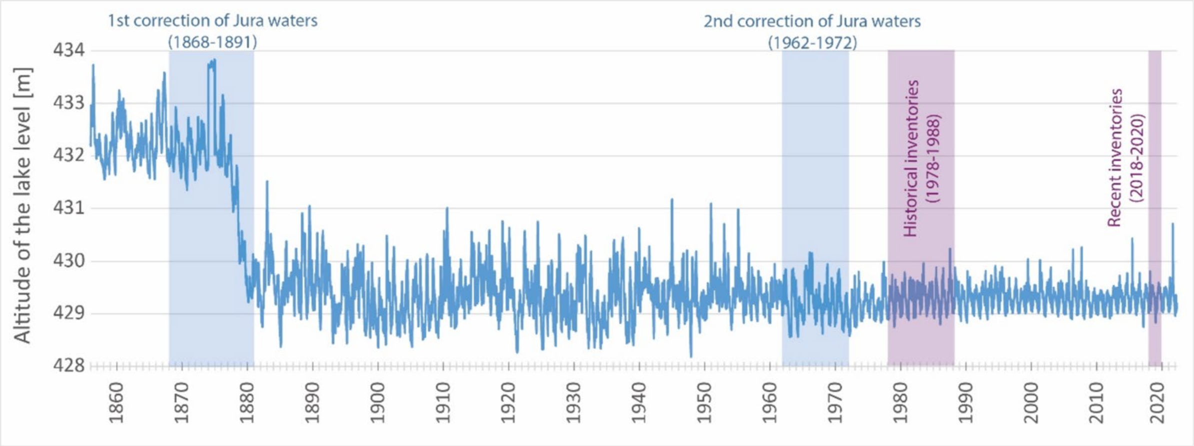


Fig. 3 Elevation variations of Lake Neuchâtel between 1856 and 2022. The two periods when the level of the Jura waters was modified are highlighted by blue columns. The second one reduced the seasonal variations (data: Federal Office for the Environment BAFU). The periods during which the two vegetation inventories were conducted are shown in violet

protection) in Switzerland. Since 1980, the managers aimed to conserve the open wetlands by preventing their colonization by trees, mainly by regular mowing or digging of small, temporary ponds.

Vegetation Inventories

Historical inventories were realized between 1978 and 1988 by three botanists in master or PhD thesis (Appendix I) in black alder forests (Roulier 1980), pine forests (Cornali 1992) and other broadleaved forests (Bueche's unfinished project). All the inventories are comparable in terms of approach and have been digitized by C. Roulier. The original location of the plots was reported in the field on a paper map, with an accuracy of 10–30 m, and converted to the Swiss geographic coordinate system (LV95).

For the recent survey, the historical plots were relocated using a GPS, on the basis of the historical data, particularly geographic coordinates, and tree species listed in historical inventories. Hence, these surveys can be considered quasi-permanent plots (Kapfer et al. 2017). In total, 94 historical exhaustive plant inventories were reconducted in 2018 and 2020, between May and August. The species were recorded on the same area as the historical inventories (between 30 and 1,000 m^2, Appendix I) and with the same method. The observed species were separated into three vegetation layers: trees (woody plants taller than 6 m), shrubs (woody plants 0.5–6 m tall) and herbs (herbaceous plants and woody plants shorter than 0.5 m). The cover of these three layers was visually estimated in percent. All species of vascular plants were identified in each layer (species nomenclature according to Eggenberg et al. 2018) and their respective cover estimated in cover classes (Braun-Blanquet 1964). Their red list status in Switzerland was extracted from Bornand et al. (2019).

The GPS coordinates of the four corners of each plot were measured with a precision of 3.5 ± 1.5 m (GPS Garmin Etrex 10; Appendix I). The elevation was retrieved from the MNT raster layer created from LiDAR data, with a horizontal precision of 2 m and vertical precision of 50 cm (Swisstopo – Federal Office of Topography). The relative height at lake level was calculated from the mean lake elevation from 1980 to 2021 (FOEN – Federal Office for the Environment). The date of forest colonization was estimated for each plot on the basis of historical topographic maps for the years 1887, 1891–94, 1899, 1911–15 and 1927–28 (Swisstopo; map.geo.admin.ch) and of aerial images available for the years 1934–38, 1946, 1954, 1968, 1979–81, 1985, 1990 and 2004.

Data Analyses

The Braun-Blanquet's scale (1964) was converted into numerical code to preserve the importance of the less abundant species (Wildi 2013; Appendix II). To structure the data, the inventories (historical and recent surveys) were grouped by clustering (Borcard et al. 2011) on the basis of the Bray–Curtis dissimilarity index and the Ward's minimum variance method. The number of groups retained was a compromise between several criteria, based on silhouettes, matrix correlations and species fidelity analyses (Appendix III; Borcard et al. 2011). Diagnostic species for each group were selected by calculating an indicator value for each species in each group, following Dufrêne and Legendre (1997). Species with a P-value < 0.05 were retained as diagnostic species.

To visualize the changes in floristic composition, a nonmetric multidimensional scaling (NMDS) was performed (Appendix IV). The Simpson diversity index was used to calculate alpha-diversity of the historical and recent surveys. Ecological indicator values for each species (Landolt et al. 2010) were used to assess environmental conditions in both sets of surveys. This semi-quantitative indirect measure, which comes from field experience, provides expert-based information about the ecological preferences and tolerance of plant species. These values, which vary between 1 and 5, express increasing species requirements in terms of light (L), soil humidity (F) and nutrient content (N), and between 1 and 3 for the moisture variability (W). The mean indicator values per plot were calculated, weighted by species cover (numerical code with a Hellinger transformation). Temporal changes between the surveys in Simpson diversity and mean ecological indicator values were tested using a linear mixed model with the Bonferroni correction (Appendix V). Plots that historically belonged to the same group were analysed together. Life strategy and growth form similarly extracted from Landolt et al. (2010).

To estimate the future dynamics of forest communities, the species composition of the tree and shrub layers was compared, as trees dominate ecosystem processes (Maděra et al. 2008). For this purpose, only tree species potentially exceeding 10 m in height at maturity were retained, because smaller species will never reach the canopy. The tree cover (> 6 m, tree layer) in the recent inventories (T) was compared with the tree cover in the historical inventories (HT) and with the cover of young trees (< 6 m, shrub layer) in the recent inventories (T < 6). This gives some indication of the rejuvenation of these forests and of the direction of their future evolution, but also highlights a possible floristic mismatch between vegetation layers (Gallandat et al. 1993).

Data processing and analyses were performed using R version 4.0.3 (R Core Team 2020) and SAS version 9.4 (SAS Institute Inc., Cary, NC, USA 2020). In R, the library 'vegan' was used to calculate the Simpson index, the Bray–Curtis index, for clustering and NMDS, whereas the *indval* was used to select diagnostic species. Linear mixed models were performed in SAS.

Results

Forest Communities

Ninety-four stands were inventoried, both historically and recently at the same location (Appendix VI). The clustering, including historical and recent data, led to the identification of four groups of forest communities. Each group was characterized by 23–39 diagnostic species and named after the most characteristic tree species (Table 1, Appendix VII). Thirty-nine surveys were included in the *Alnus glutinosa* (*A.g.*) group, 55 in the *A. incana* (*A.i.*) group, 45 in the *Fraxinus excelsior* (*F.e.*) group and 49 in the *Pinus sylvestris* (*P.s.*) group.

The first group have an almost total dominance of *Alnus glutinosa* in the tree layer, a low cover of the shrub layer and a herb layer codominated by hygrophilous species, such as *Caltha palustris*, *Solanum dulcamara* and *Galium palustre,* and by mesophilous species, such as *Hedera helix*, *Circaea lutetiana* and *Lamium galeobdolon* subsp. *montanum* (Table 1; Appendix VII). In the Grande Cariçaie reserves, the stands classified as *A. glutinosa* group were often located well above lake level (average 3.0 ± 1.0 m; Fig. 4A) and were among the latest to colonize the wetlands (mostly after 1945; Fig. 4B).

Alnus incana, *Rubus caesius*, *Cornus sanguinea*, *Prunus padus* (tree and shrub layer)*, Viburnum opulus* (shrub layer) and *Carex acutiformis* were the diagnostic species for the *A. incana* group (Table 1). On average, these forests were recent (mostly after 1945) and occupied areas close to the lake level (average 1.0 ± 0.3 m; Fig. 4).

The diagnostic species in the *F. excelsior* group included *F. excelsior, Quercus robur, Prunus padus* (herb layer), *Brachypodium sylvaticum* and *Viburnum opulus* (herb layer; Table 1). Many species were shared with the *A. incana group*, but with differences in frequency or cover between groups. Moreover, on average, the diagnostic species of the *F. excelsior group* were less hygrophilous than those of the *A. incana* group. These forests were 1.8 ± 1.0 m above lake level and occupied areas colonized by trees mostly between 1934 and 1968 (Fig. 4A).

The diagnostic species of the last group, *P. sylvestris*, were *P. sylvestris, Carex flacca, Ligustrum vulgare, Viburnum lantana, Molinia arundinacea* and *Calamagrostis varia*. These forests were the oldest (quick colonization between roughly 1927 and 1938, Fig. 4B; Appendix VIII) and occupied areas high above lake level (average 2.4 ± 0.9 m; Fig. 4A; Vischer 2003).

According to the Red List, seven species are considered threatened (endangered or vulnerable) in Switzerland (national or regional assessment; Bornand et al. 2019; Appendix VI and IX). *Ulmus laevis* is an endangered species that was observed in two stations in the historical inventories. Regionally vulnerable species (Swiss Midlands) include *Orchis palustris* and *Schoenus ferrugineus*, each was only recorded once in the historical inventory. Conversely, *Carex pseudocyperus*, *Thalictrum flavum* and *Thelypteris palustris* were also inventoried once in the recent inventories, and species of the genus *Callitriche* were recorded in two recent inventories. In addition, 25 supplementary species (21 in the historical inventories and 12 in the recent inventories) are considered near-threatened in Swiss or regional red lists (Appendix IX). The vast majority of the red list species had higher frequencies in the historical surveys than in recent ones. In regard to invasive alien species (FOEN 2022), only two species were recorded: *Solidago canadensis* with four observations

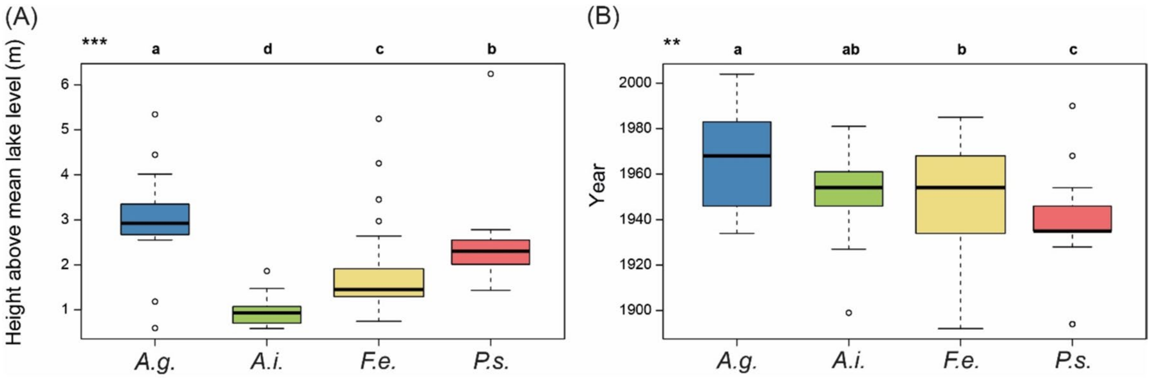


Fig. 4 **A** – Distribution of the height difference between the mean level of Lake Neuchâtel (1980–2021) and the elevation of the stands, classified in forest groups according to the recent survey. *A.g.* – *Alnus glutinosa* group, *A.i.* – *Alnus incana* group, *F.e.* – *Fraxinus excelsior* group, *P.s.* – *Pinus sylvestris* group. According to a global Kruskal–Wallis test, these groups are characterized by different heights to the lake level ($P < 0.001$). **B** – Distribution of the forest colonization in the Grande Cariçaie reserves (Appendix I). The years correspond to the first evidence of forests on topographic maps (1878–1928; Siegfried maps) or aerial photographs (after 1934; Swisstopo). However, the real colonization may have occurred up to ten years earlier than the retained year, because of the lapse time between available documents. According to a global Kruskal–Wallis test, periods of colonization are significantly different ($P = 0.003$). The boxplot width is proportional to the number of stands: 18, 17, 34 and 25 stands, respectively. The black line indicates the median whereas the limits of the boxes for the first and third quantiles. Different letters indicate significant differences between groups with a post-hoc comparison (Borcard et al. 2011).

in historical inventory and one recent occurrence of *Prunus laurocerasus*.

Floristic and Ecological *Indicator* Values

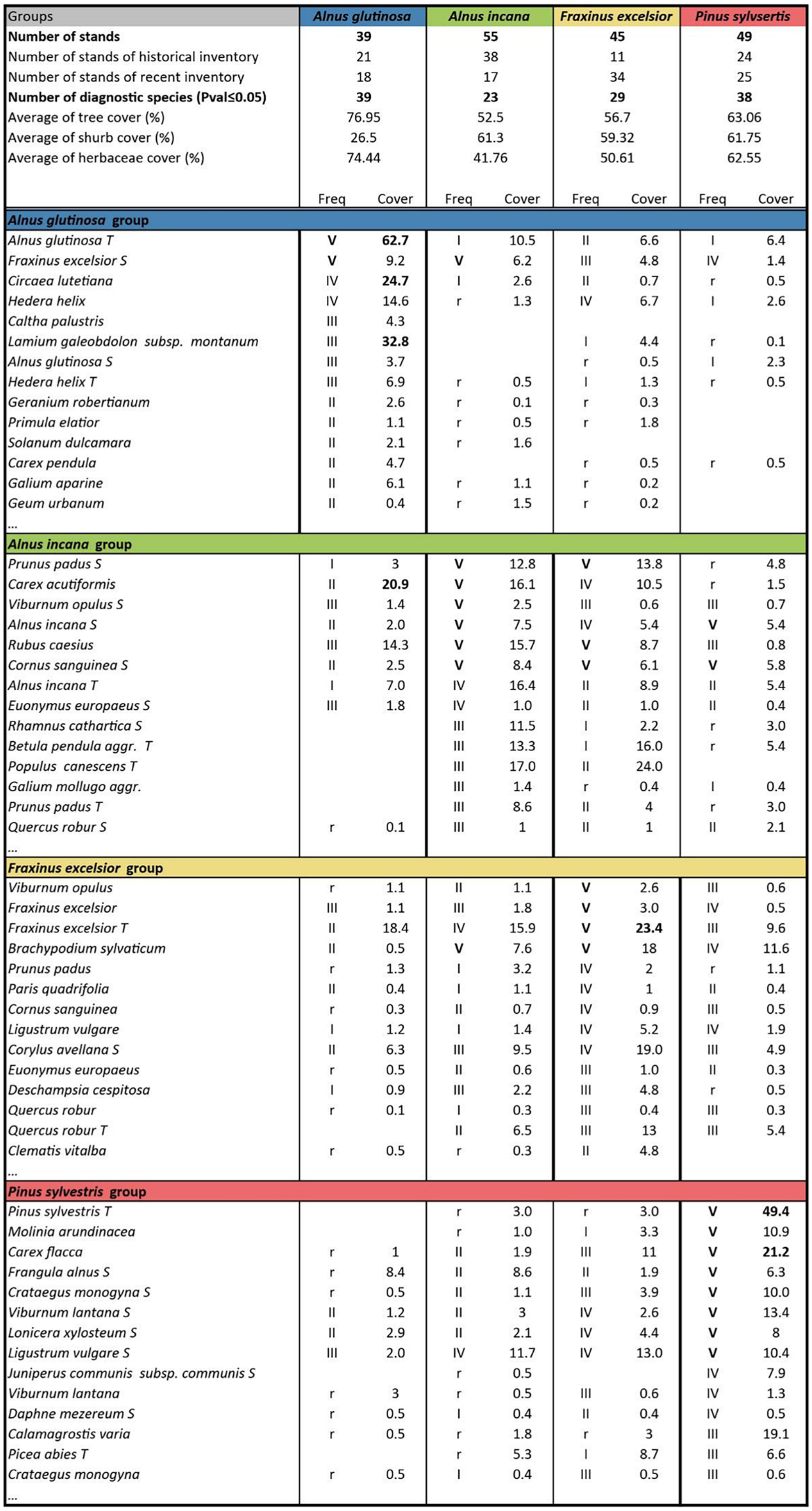
In the nonmetric multidimensional scaling analysis (NMDS; Fig. 5), the different stands appeared distributed according to the clustering, although the *F. excelsior* and *A. incana* groups plots were close in floristic composition. The floristic composition of all the groups changed significantly between the historical and recent inventories in terms of species and cover (arrows in Fig. 5). Moreover, for many stands, these changes were important enough that they led to a shift between two groups (Fig. 6). The *A. incana* group was the most affected, with 21 stands evolving towards the *F. excelsior* group.

Species richness increased in the *F. excelsior* group ($P = 0.039$) and statistically significantly in the *P. sylvestris* group ($P = 0.002$; Fig. 7A). The Simpson index increased in 67 stands and decreased in 27 between the two surveys (Appendix VI), but, at the group level, only the increase in the *P. sylvestris* group was significant ($P < 0.001$; Fig. 7B). A comparison of mean ecological indicator values (Landolt et al. 2010) showed that *A. incana* stands suffered the largest changes (Fig. 8; Appendix VI). The flora evolution corresponded to a decrease in available light (more sciophilous species; Fig. 8A) in all groups, significant in three of them. Only the *A. incana* group suffered a significant decrease in soil moisture (Fig. 8B). However, almost all groups showed a significant decrease in the moisture variability index, meaning that the present species are less tolerant of large variations in soil moisture. Finally, the change of the nutrient values showed that the flora of the *P. sylvestris group*, the most oligotrophic, and *A. glutinosa group*, the most eutrophic, evolved towards nutrient-richer soils whereas the opposite trend was observed in the *A. incana* group (Fig. 8D). The life strategy and growth form analyses showed little changes between the two surveys, except a replacement of graminoids (*Carex* species) by forbs in the *A. glutinosa* group (Appendix X).

Dynamics of Tree Species

In each group, the dominant tree species are less dominant than previously, either with the arrival of new woody species, or with the development of woody species that had a low cover in the historical survey (between HT and T; Fig. 9). This decrease

Table 1. Part of the synoptic table of the four plant community groups in riparian forests of the Grande Cariçaie reserves. Only the 14 most frequent diagnostic species ($P \leq 0.05$) are listed (the full table is provided in Appendix VII). Freq: frequency of the species in the groups (V – > 80%, IV– 60–80%, III – 40–60%, II – 20–40%, I– 10–20%, r – ≤ 10%). Cover: mean cover [%] of the species in the group. Constant species (frequency > 80%) and species with a mean cover > 20% are in bold. Species names are completed by the layer: T – tree, S – shrub; no letter – herbaceous layer



Groups	***Alnus glutinosa***		***Alnus incana***		***Fraxinus excelsior***		***Pinus sylvsertis***	
Number of stands	**39**		**55**		**45**		**49**	
Number of stands of historical inventory	21		38		11		24	
Number of stands of recent inventory	18		17		34		25	
Number of diagnostic species (Pval≤0.05)	**39**		**23**		**29**		**38**	
Average of tree cover (%)	76.95		52.5		56.7		63.06	
Average of shurb cover (%)	26.5		61.3		59.32		61.75	
Average of herbaceae cover (%)	74.44		41.76		50.61		62.55	
	Freq	Cover	Freq	Cover	Freq	Cover	Freq	Cover
***Alnus glutinosa* group**								
Alnus glutinosa T	**V**	**62.7**	I	10.5	II	6.6	I	6.4
Fraxinus excelsior S	**V**	9.2	**V**	6.2	III	4.8	IV	1.4
Circaea lutetiana	IV	**24.7**	I	2.6	II	0.7	r	0.5
Hedera helix	IV	14.6	r	1.3	IV	6.7	I	2.6
Caltha palustris	III	4.3						
Lamium galeobdolon subsp. montanum	III	**32.8**			I	4.4	r	0.1
Alnus glutinosa S	III	3.7			r	0.5	I	2.3
Hedera helix T	III	6.9	r	0.5	I	1.3	r	0.5
Geranium robertianum	II	2.6	r	0.1	r	0.3		
Primula elatior	II	1.1	r	0.5	r	1.8		
Solanum dulcamara	II	2.1	r	1.6				
Carex pendula	II	4.7			r	0.5	r	0.5
Galium aparine	II	6.1	r	1.1	r	0.2		
Geum urbanum	II	0.4	r	1.5	r	0.2		
…								
***Alnus incana* group**								
Prunus padus S	I	3	**V**	12.8	**V**	13.8	r	4.8
Carex acutiformis	II	**20.9**	**V**	16.1	IV	10.5	r	1.5
Viburnum opulus S	III	1.4	**V**	2.5	III	0.6	III	0.7
Alnus incana S	II	2.0	**V**	7.5	IV	5.4	**V**	5.4
Rubus caesius	III	14.3	**V**	15.7	**V**	8.7	III	0.8
Cornus sanguinea S	II	2.5	**V**	8.4	**V**	6.1	**V**	5.8
Alnus incana T	I	7.0	IV	16.4	II	8.9	II	5.4
Euonymus europaeus S	III	1.8	IV	1.0	II	1.0	II	0.4
Rhamnus cathartica S			III	11.5	I	2.2	r	3.0
Betula pendula aggr. T			III	13.3	I	16.0	r	5.4
Populus canescens T			III	17.0	II	24.0		
Galium mollugo aggr.			III	1.4	r	0.4	I	0.4
Prunus padus T			III	8.6	II	4	r	3.0
Quercus robur S	r	0.1	III	1	II	1	II	2.1
…								
***Fraxinus excelsior* group**								
Viburnum opulus	r	1.1	II	1.1	**V**	2.6	III	0.6
Fraxinus excelsior	III	1.1	III	1.8	**V**	3.0	IV	0.5
Fraxinus excelsior T	II	18.4	IV	15.9	**V**	**23.4**	III	9.6
Brachypodium sylvaticum	II	0.5	**V**	7.6	**V**	18	IV	11.6
Prunus padus	r	1.3	I	3.2	IV	2	r	1.1
Paris quadrifolia	II	0.4	I	1.1	IV	1	II	0.4
Cornus sanguinea	r	0.3	II	0.7	IV	0.9	III	0.5
Ligustrum vulgare	I	1.2	I	1.4	IV	5.2	IV	1.9
Corylus avellana S	II	6.3	III	9.5	IV	19.0	III	4.9
Euonymus europaeus	r	0.5	II	0.6	III	1.0	II	0.3
Deschampsia cespitosa	I	0.9	III	2.2	III	4.8	r	0.5
Quercus robur	r	0.1	I	0.3	III	0.4	III	0.3
Quercus robur T			II	6.5	III	13	III	5.4
Clematis vitalba	r	0.5	r	0.3	II	4.8		
…								
***Pinus sylvestris* group**								
Pinus sylvestris T			r	3.0	r	3.0	**V**	**49.4**
Molinia arundinacea			r	1.0	I	3.3	**V**	10.9
Carex flacca	r	1	II	1.9	III	11	**V**	**21.2**
Frangula alnus S	r	8.4	II	8.6	II	1.9	**V**	6.3
Crataegus monogyna S	r	0.5	II	1.1	III	3.9	**V**	10.0
Viburnum lantana S	II	1.2	II	3	IV	2.6	**V**	13.4
Lonicera xylosteum S	II	2.9	II	2.1	IV	4.4	**V**	8
Ligustrum vulgare S	III	2.0	IV	11.7	IV	13.0	**V**	10.4
Juniperus communis subsp. communis S			r	0.5			IV	7.9
Viburnum lantana	r	3	r	0.5	III	0.6	IV	1.3
Daphne mezereum S	r	0.5	I	0.4	II	0.4	IV	0.5
Calamagrostis varia	r	0.5	r	1.8	r	3	III	19.1
Picea abies T			r	5.3	I	8.7	III	6.6
Crataegus monogyna	r	0.5	I	0.4	III	0.5	III	0.6
…								

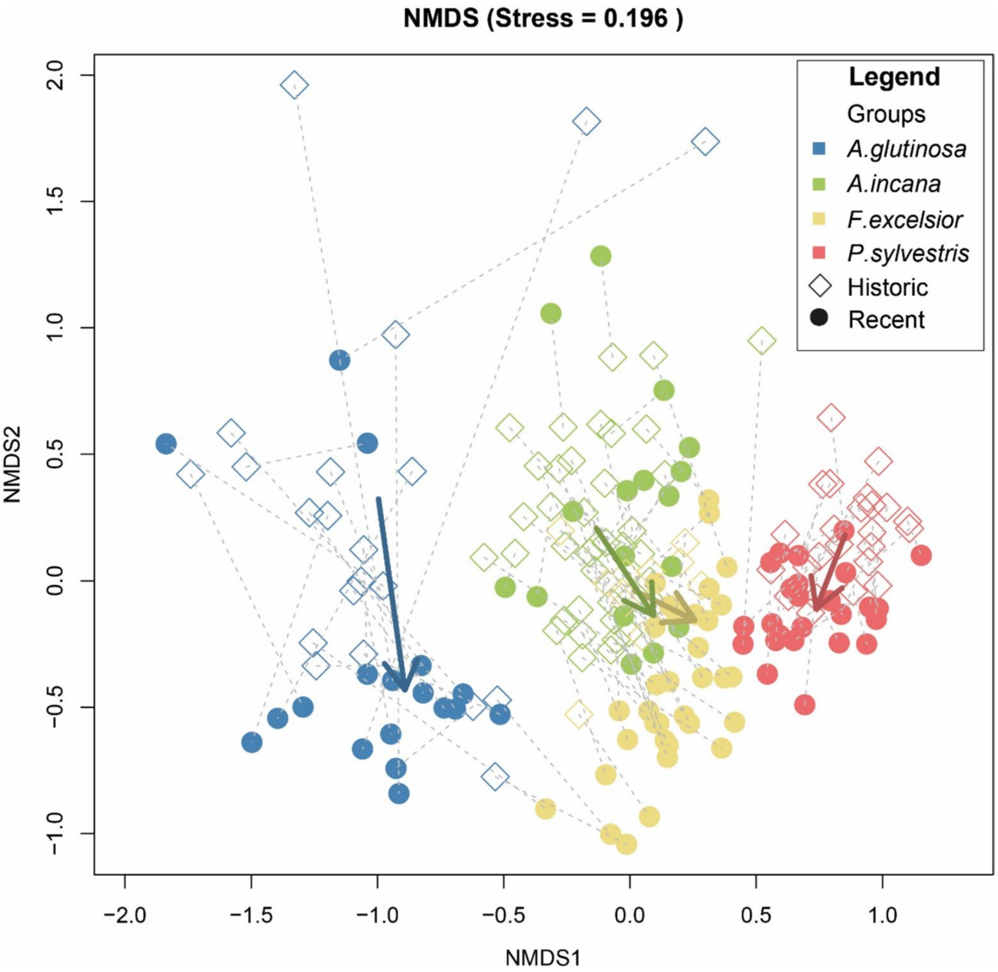


Fig. 5 Nonmetric multidimensional scaling (NMDS) based on species composition and cover, on two dimensions. The value of the stress is 0.196. Pairs of historical (empty square symbols) and recent (full circle symbols) inventories are connected with dotted lines. The arrows represent the significant mean shifts of the floristic composition, when stands are classified in groups according to the historical survey. Significance was calculated using a MANOVA function with *P*-values of 0.002 for *A. glutinosa* and *F. excelsior* groups and < 0.001 for the *A. incana* and *P. sylvestris* groups.

in dominance will probably continue, as these species were even less present among the young trees (< 6 m), with the exception of *A. incana* in the *A. incana* group. *Pinus sylvestris* was even completely absent among regeneration of the *P. sylvestris* group. Conversely, there was an important regeneration of *Fraxinus excelsior* in the *A. glutinosa* group. Other potentially important tree species in the future included *Acer pseudoplatanus* in the *A. glutinosa* group*,* *Ulmus glabra* in the *F. excelsior* group and *Fagus sylvatica* in the *A. incana, F. excelsior* and *P. sylvestris* groups. The emergence of the competitive, climactic *F. sylvatica* was accentuated by the absence of young *Betula pendula*, a pioneer species, which had a major presence in the tree layer of the *A. incana* group.

Discussion

This study has shown that major changes occurred in the species composition of the riparian forests of the Grande Cariçaie reserves: One hundred and fifty years after the lowering of the lake and 60 years after a strong reduction of lake level variations, the plant

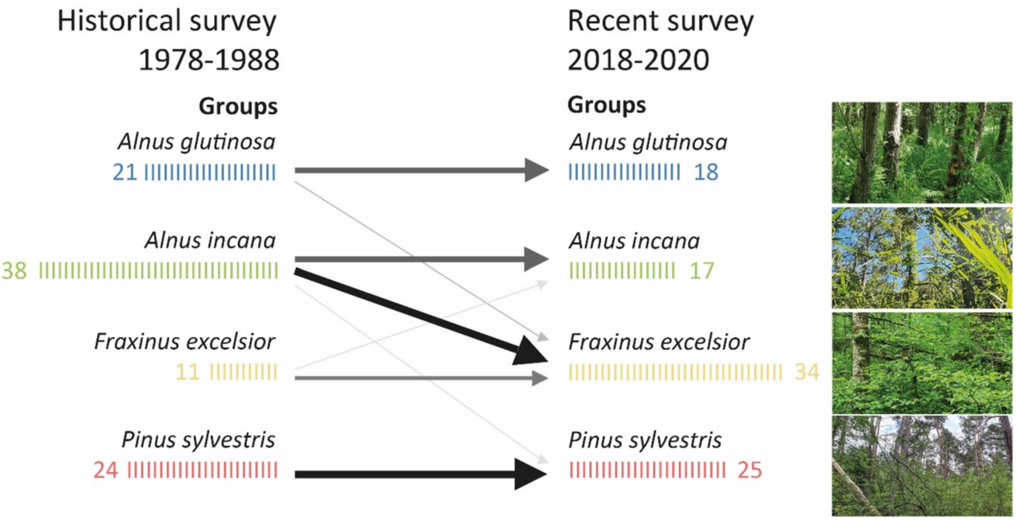


Fig. 6 Evolution of plant communities between the historical and recent surveys. The number of stands classified in each group is indicated under the names, while the thickness of the arrows is proportional to the number of stands that have shifted from one group to another. On the right, illustration of four forest communities in the Grande Cariçaie reserves

communities are still dynamic, with a general trend towards drier and darker forests.

Forest Communities

The division of plant inventories into groups is to some extent artificial with regard to the continuum of ecological conditions observed in an almost flat area like the Grande Cariçaie (e.g. Mucina 1997). However, it allows for a more detailed analysis by differentiating the respective dynamics of distinct habitats. The NMDS (Fig. 5) and some characteristic species (Table 1) showed the proximity of the *A. incana* and *F. excelsior* groups, which shared many species and were distinguished mainly by species dominance and frequency.

An attribution of the Grande Cariçaie forests to phytosociological alliances is complicated by the uncommon ecological conditions occurring in these wetlands and by the dynamics of these forests, with many stands in an intermediate stage of the evolution. Similar plant communities have rarely or never been described in Central Europe, and although it is possible to assign the inventories to alliances , the correspondence is not perfect. Compared with the descriptions of Delarze et al. (2015), the inventoried stands classified within the *A. glutinosa* group were on average drier than the *Alnion glutinosae* alliance (Malcuit 1929), with fewer hygrophilous species (e.g. absence of *Carex elongata* and rarity of other typical species) and more mesophilic ones (e.g. *Lamium galeobdolon* subsp. *montanum*). However, the dominance of *A. glutinosa* in the tree strata and the presence of other hygrophilous species, such as *Caltha palustris, Solanum dulcamara, Galium palustre* agg., *Cardamine amara* or *Scutellaria galericulata*, corresponded to this alliance (Appendix VII). Due to their topographic position, these forests are clearly disconnected of the lake (Fig. 4A), remaining out of reach of its fluctuations (Fig. 3), but they depend on small creeks, with water flowing or seeping down the cliffs (Roulier 1980; Fig. 2). This alliance is considered endangered according to the Swiss Red List of habitats (Delarze et al. 2016).

The *A. incana* group shared many species with previously published descriptions of the *Alnion incanae* alliance (Pawlowski 1928; Moor 1958; Delarze et al. 2015), although with some species indicating wetter conditions (e.g. *Carex acutiformis*). Indeed, the *Alnion incanae* is normally found along highly dynamic, braided rivers with periodic floods and sediment deposition (Delarze et al. 2015) whereas, in the Grande Cariçaie, the stands in the *A. incana* group were approximately 1 m above the lake (Fig. 4A). However, their soils allow for a good circulation of the groundwater,

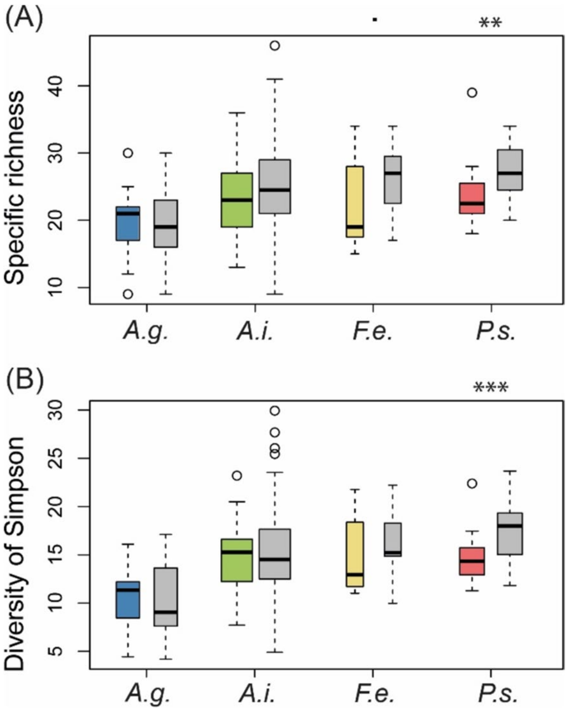


Fig. 7 Alpha-diversity with (A) species richness and (B) Simpson diversity index for historical (coloured boxes) and recent (grey boxes) surveys in the four groups, classified according to the historical survey. Stars above the boxes indicate a significant change between historical and recent inventories in the corresponding group, according to linear mixed models with the Bonferroni correction for the four forest communities (alpha = 0.05/4 = 0.0125): • – $P < 0.05$, * – $P < 0.0125$, ** – $P < 0.0025$, *** – $P < 0.00025$. Other abbreviations and symbols are as in Fig. 4.

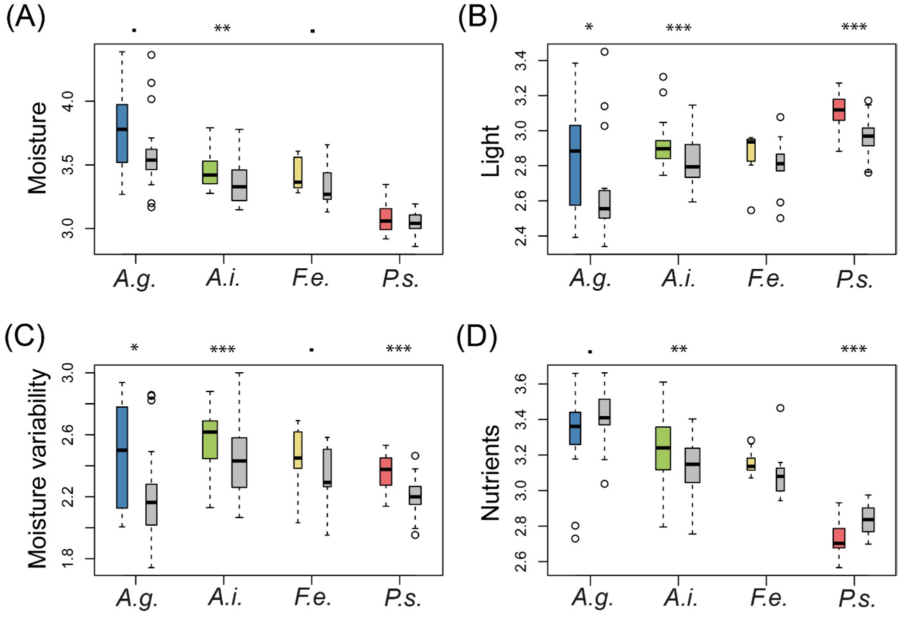
due to a draining substrate (personal observation; Delarze et al. 2015). Moreover, the water level changes quickly (hydrological measurements in three stands, not reported in this article), with the upper horizon rarely water-saturated during summer (Mandžukovski et al. 2020). As a result, oxygenation is probably good enough for most of the mesophilic species generally encountered in typical *Alnion incanae*. This alliance is considered vulnerable (Delarze et al. 2016).

Stands of the *F. excelsior* group were very similar to the description of the *Fraxinion* alliance (Moor 1976), with mesophilic species dominating, accompanied by species capable of tolerating a temporary high water table (Moor 1958; Delarze et al. 2015). In these forests, the water table is close to the soil surface in winter, but drops in summer, while rare and irregular floods may occur (Mandžukovski et al. 2020; unpublished personal observations).

Finally, the species composition of the *P. sylvestris* group was similar to the description of the *Molinio-Pinion* alliance (Ellenberg and Klötzli 1972), although some thermophilous and heliophilous species (e.g. *Aster amellus, Epipactis atrorubens, Anthericum ramosum*; Delarze et al. 2015) were missing. Indeed, these forests are normally found on sunny, unstable marly slopes with clayey substrate whereas in Grande Cariçaie they are located in flat areas, clearly above the lake level (> 2 m; Fig. 4A), with shallow soils limited by a slab (complete description of three stands, not reported in this article; see Cornali 1992). As a result of both the topography and substrates, soil humidity varies widely throughout the year, fluctuating between saturation in winter and early spring and extreme dryness in summer. This alliance is considered vulnerable in Switzerland (Derlaze et al. 2016).

All these forests are young, as they could not exist at these sites before 1878, when the lake level dropped by 2.7 m. Moreover, they did not develop immediately, because marshes were often mowed by farmers (Vaud Cantonal Archives). The first forests colonized the driest areas, high above lake level, with the drought tolerant *Pinus sylvestris* (Cornali 1992). The stands belonging to the *A. incana* and *F. excelsior* groups were approximately contemporary. All these sites were probably first colonized by species typical for the *A. incana* group, before slowly evolving towards the *F. excelsior* group, as observed along rivers according to the natural dynamics (Moor 1958) and many of our stands since the historical survey. It is very probable that the second correction of the Jura waters in the 1960s (Fig. 3), with a reduction in lake level fluctuations, accelerated the transition from the *A. incana* group towards the *F. excelsior* group, at least for the ones situated high above the lake level. Indeed, floods are now too rare to maintain the mesophilic species outside of these forests. This new control of lake level initiated a vigorous colonization of open wetlands by young *Alnus* as well (C. Clerc, pers. comm.). However, the regular mowing of most of these wetlands to conserve an open structure limited shrub encroachment and young forests are restricted to small areas.

Fig. 8 Mean ecological indicator values (Landolt et al., 2010) of the stands, calculated on the basis of plant composition, weighting by species cover, in the historical (coloured) and recent (grey) inventories, for soil moisture, light, soil moisture variability, and soil nutrient content. The stands were classified according to the historical survey, with 21 stands in the *A. glutinosa* group*,* 38 in the *A. incana group*, 11 in the *F. excelsior* group and 24 in the *P. sylvsetris* group. Symbols and significance thresholds are as in Fig. 7.



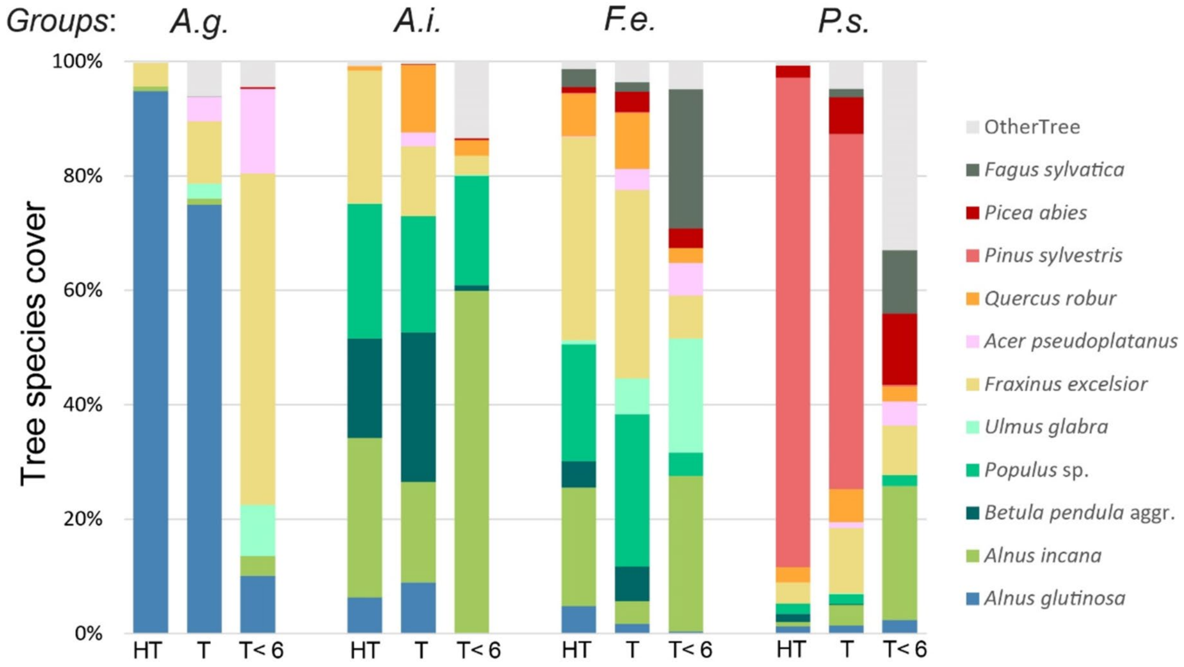


Fig. 9 Cover (in percent) of the main tree species in forest groups, classified according to the recent survey: HT – tree cover in the historical survey, T – tree cover in the recent survey, T < 6 – cover of the tree species in the recent shrub layer (0.5–6 m). Some rare species were grouped together to limit the number of categories. *Populus* sp.: *Populus ×canescens*, *P. alba*, *P. nigra* agg. and *P. tremula.* Other tree: *Abies alba*, *Acer campestre*, *A. opalus*, *Carpinus betulus*, *Juglans regia*, *Prunus avium*, *Pyrus pyraster*, *Salix alba*, *S. caprea*, *S. elaeagnos*, *Sorbus aria*, *S. aucuparia*, *Tilia cordata*, T. *platyphyllos*, *Ulmus laevis* and *U. minor*.

Species and Diversity Change

Diversity remained globally stable in both *Alnus* groups, explained by species replacement, with for example, the disappearance of *Stachys palustris*, *Gymnadenia conopsea* and *Epilobium hirsutum* and the arrival of *Adoxa moschatellina, Athyrium filix-femina* and *Ranunculus auricomus.* However, diversity increased between the historical and recent inventories in the *P.sylvestris* group. This was probably due to a decrease in ecological constraints (modification in soil humidity, soil development, etc.), which opened these sites to the establishment of more mesophilic, post-pioneer or late-successional species or to the increase of the populations of already present species. Species diversity is not necessarily related to habitat quality. Indeed, several studies conducted along rivers could not find any difference in species richness between flow-regulated and free-flowing rivers (Bejarano et al. 2011; Merritt and Wohl 2006). However, Wilcox et al. (2005) observed an indirectly link, with an increase in aggressive invasive alien plants, leading to a decrease in species richness after the regulation of Lake Ontario in North America. In our study, some species on the Swiss Red List (Appendix IX) disappeared, but they were anyway rare in the first survey, and they are more typical of open wetlands, where they are still common. Conversely, alien plant species are rare in Grande Cariçaie forests, and mostly limited to hedges (e.g. *Solidago canadensis* agg.).

Changes in Ecological Conditions

The decrease of the mean ecological indicator value for light in three groups (Fig. 8) corresponded to the replacement of heliophilous and/or pioneer species by late-successional species, with an increase in tree and shrub cover. The decrease in the moisture and in the moisture variability values pointed to a decline in hygrophilous species, probably due to lake regulation in 1962–1972 (Buttler et al. 1995; Vischer 2003). Prior to this, floods regularly reached 1.5 m above the mean lake level (429.3 m), meaning that currently existing *A. incana* stands were submerged. Nowadays, many of these stands are no longer reached by the lake, except in very exceptional high-water situations, such as in 2021, the largest flood in 66 years (Fig. 3). Drier and hotter summers resulting from climate change (www.meteoswiss.ch) is another potential explanation, as evapotranspiration is increasing. The moisture value did not change in the *P. sylvestris* group, probably because the sites were naturally dry and too high to be affected by lake regulation. These trends are coherent with a study by Breton et al. (2023) along an anthropized part of the river Rhône (France), where a decrease in hygrophilous and heliophilous species between historical and recent surveys has been observed.

The change of the nutrient value is more difficult to interpret because of contradictory developments (Fig. 8D). The increase in the *A. glutinosa* group may be due to stand fertilization by water run-off from the agricultural hinterland. In *P. sylvestris* group, the increase may follow the improved mineralization of the litter, with deciduous trees slowly replacing pine trees. Conversely, the decreasing mean in the *A. incana* group might follow the decrease in phosphates, as their concentration in Lake Neuchâtel was significantly reduced since 1980 (Liechti 1994), and the forests have now less contacts with the lake water. The second, more likely reason is that a large proportion of *A. incana* stands shifted towards the *F. excelsior* group, with a corresponding change in species composition (e.g. cover decrease of *Alnus incana*, *Rubus caesius* and *Carex acutifomis*, all with a nutrient value of 4; Landolt et al. 2010). As mentioned above, this evolution is probably due to the drier conditions, followed by an increase in canopy cover. In fact, the nutrient indicator reflects more the biomass productivity than the soil chemical composition (including N-mineralization and N-availability), although these two factors are linked (Bartelheimer and Poschlod 2016; Shaffers and Sýkora 2000). However, a study conducted by Halarewicz et al. (2021) showed that direct and indirect measurements (Ellenberg's indicator value) revealed similar results in a riparian ecosystem.

The Past and Future of the Riparian Forests in the Grande Cariçaie Reserves

Overall, the results show contrasting evolutions between the groups in the 20th century, and future dynamics will certainly differ as well. Most stands of the *A. glutinosa* group have been maintained since the last survey (Fig. 6), although their plant composition indicates significant reductions in light and water availability. These forests are young and some heliophilous wetland species, such as *Mentha aquatica*, *Cirsium palustre*, *Galium palustre*, *Filipendula ulmaria* and *Schoenus nigricans*, present in the historical survey, have decreased in presence and cover with the development of the tree canopy. In addition, the lack of light in mature *A. glutinosa* forests slowed the regeneration of *A. glutinosa*. This species can regenerate in forests where trees are low (2–3 m tall with little foliage), when a tree dies (creating a canopy gap) or in open wetlands (Douda et al. 2020; Pokorný et al. 2000). However, conditions got potentially drier following the shift in the exact position of the rivers (Roulier 1980), since these forests are only watered by small rivers. This change benefitted *F. excelsior*, which was already present in the historical tree layer and strongly colonized the understorey, followed by *Ulmus glabra* and *Acer pseudoplatanus* (Fig. 9). The conservation of this habitat, classified as endangered in the Swiss Red List (Delarze et al. 2016), is thus uncertain in the Grande Cariçaie, with its strong dependence on the river position and flow, and the availability of sufficiently open stands for the regeneration of *A. glutinosa*.

Forests of the *A. incana* group suffered the most important changes since the 1980s. In fact, 55% of the stands historically identified in this group were recently classified in the *F. excelsior* group (Fig. 6). At the Swiss scale, Gallandat et al. (1993) had already observed an accelerated evolution of *Alnion incanae* towards *Fraxinion* as the riparian forest. This shift reflects the natural dynamics of this alliance along rivers, where sediment deposit is elevating the banks and decreasing flood frequency (Gallandat et al. 1993; Maděra et al. 2008). However, such aggradation does not exist along lakes and the natural dynamics are less clear. In the Grande Cariçaie, the transition was certainly facilitated by the strong reduction of lake level variations after 1962 (Fig. 3). Close to the lake, many of these stands have afterwards stayed under the influence of water, with regular floods limiting mesohygrophilous species. Nevertheless, the highest stands have shifted towards the *F. excelsior* group. With drier conditions, species like *Picea abies* and *Quercus robur* colonized the canopy, shading the understorey. Surprisingly, the heliophilous and hygrophilous *P. incana* and *Populus* sp. are still dominating the shrub layer (Fig. 9), and there is an expectation that the ecological conditions of the remaining stands classified in this group will stay favourable for the conservation of this forest type. However, some young *Fagus sylvatica* have also colonized this area. These are unlikely to survive the next large flood (some died already in 2021; C. Clerc pers. comm.), but their presence might indicate that ecological conditions are now close to a critical threshold for the conservation of these communities.

In forests classified within the *F. excelsior* group, changes have apparently been less dramatic than in the other groups, although the moisture index has decreased significantly between the two surveys. This habitat may become the most common in the future. However, the dominant species may be changing, with *Fraxinus excelsior* mortality increasing over the last decade because of the invasive fungus *Hymenoscyphus fraxineus* (Pautasso et al. 2013; F. Ayer, pers. comm.). Young *Fraxinus excelsior* trees are extensively present in wetter habitats, notably in the *A. glutinosa* group, but their future is uncertain. The species that could replace it in the *F. excelsior* forests are already present as young trees: *Ulmus glabra*, *Acer pseudoplatanus, Quercus robur* and *Fagus sylvatica*. The growth of this last species into the canopy would mean that soil conditions are drying, corresponding to a shift of the *Fraxinion* towards a late-successional habitat, *Fagion sylvaticae*, the typical lowland forest alliance in Switzerland.

The forests in the *P. sylvestris* group are moving away from optimal conditions for *P. sylvestris*, with a decrease in light and an increase in soil nutrients. The replacement of this species, a pioneer in the lowlands of Central Europe, by broadleaved trees is part of the natural succession (Leuschner and Ellenberg 2017; Gallandat et al. 1993), as the light in the understorey is insufficient for *Pinus* regeneration. Moreover, the soil development in the Grande Cariçaie, with more organic matter, improved water capacity and facilitated colonization by mesophilic species (Cornali 1992). This has led to the replacement of *Pinus sylvestris* by broadleaf species and *Picea abies* (Fig. 9; Appendix VIII). Hence, *P. sylvestris* forests are only pioneer in these wetlands, in contrast to the *Molinio-Pinion* on clayey slopes, where substrate instability tends to maintain favourable conditions for this heliophilous plant community (Delarze et al. 2015; Brzeziecki et al. 1993; Cornali 1992).

Conservation of the Forest Communities

On the whole, the recent changes in the forests in the Grande Cariçaie have not been particularly favourable for the conservation of the most endangered riparian habitats in Switzerland. The least impacted stands belong to the *Fraxinion* alliance, which is the only one of these four forest types not considered threatened according to the Swiss Red List of habitats (LC; Delarze et al. 2016) and which has become the most common in the Grande Cariçaie following the regulation of the lake and the cessation of frequent large floods.

The rarefaction of hygrophilous species, particularly in the two *Alnus* forests, is in line with the general decline in frequency over the last 50 years in Switzerland of the wet forests of *Alnion glutinosae* and *Alnion incanae* (Delarze et al. 2016). Drought and the loss of alluvial dynamics are a real danger for these forests, which host red-listed plant species. To promote the conservation of *Alnion glutinosea* forests, it is important to have waterlogged soils for most of the year. Beavers, already present in the Grand Cariçaie, might help in this respect by retaining water behind their dams (Czerepko et al. 2009). However, too much water is not conducive to regeneration either, as young *A. glutinosa* cannot develop in submerged soil. They resprout at the base of mature trees or germinate on hummocks, elevated above the water (Barthelmes et al. 2006; Pokorný 2000). Sufficient light is also important for their regeneration. By consequence, *Alnion glutinosae* forests often alternate with more open communities dominated by *Salix* sp. (Barthelmes et al. 2020) or *Carex* sp. (dynamic cycle succession; Pokorný 2000) or young trees have to wait for a canopy gap. Small gaps, such as the area of a single canopy dead tree, are sufficient for successful regeneration of *A. glutinosa* (gap dynamic model; Douda et al. 2020). Naturally, new *Alnus* forests should colonize the wetlands, but the present management of the Grande Cariçaie maintains open marshes, dominated by *Carex* and reed, by mowing them every 3–4 years (https://grande-caricaie.ch). Hence, for a sustainable management of these forests, it is necessary to promote uneven age-structured forests (Douda et al. 2020) with moderate human intervention, such as felling of isolated trees in the stands, to increase diversity and help the regeneration of *A. glutinosa* (Natlandsmyr et al. 2016).

The best approach to conserve forests close to *Alnion incanae* would be to reintroduce regular major floods, but the economic issues connected with this regulation (buildings located next to the lake, control of the flow of the Rhine downstream, among other concerns) outweigh considerations about the conservation of habitats. An alternative way of promoting some heliophilous species typical of this habitat is to use coppicing to open the forests and stimulate *A. incana* resprouting (Delarze et al. 2008; Richardson 2000).

Natural ecological succession is also leading to a loss of landscape diversity (Buttler et al. 1995), with the probable, gradual replacement of *P. sylvestris* forests by deciduous forests (Cornali 1992). The disappearance of this habitat will not have a major impact on the floristic diversity of the Grande Cariçaie reserves, as most of the species lost in recent decades, such as *Dactylorhiza maculata* subsp. *fuchsii*, *Orchis palustris* and *Gymnadenia conopsea*, are still encountered in the open wetlands. However, this habitat is considered vulnerable in the Swiss Red List (Delarze et al. 2016) and the loss of *Pinus sylvestris* is detrimental to other groups of organisms, such as acidophilous bryophytes (e.g. *Dicranum montanum, D. scoparium*) and lichens (e.g. *Hypogymnia physodes, Lepraria incana*) that find on *Pinus sylvestris* the only acidic bark in the region (Vust et al. 2019). Hence, a management that is able to maintain this habitat, for instance by opening small gaps in canopy and reducing regeneration of broadleaf species in the gaps, or stripping topsoil to favour pine regeneration, could be considered. A test of this last method was conducted recently in Grande Cariçaie, but it is too soon to evaluate the results.

Conclusion

As hypothesized, we observed different changes in the species composition of the riparian forests in the Grande Cariçaie. According to ecological indicator values, these forests have suffered a decrease in humidity value following lake regulation. The resulting drier conditions and the induced natural succession are responsible for decreasing light availability in forest understorey. These species were partly replaced by mesophilic species. This induced a reduction in the surface area of *Alnus incana* forests and

A. glutinosa forests are slowly losing their specificity, with the replacement of *Alnus* by more competitive tree species in the new conditions. Both habitats are considered endangered in Switzerland. The general trend is towards *Fraxinus excelsior* forests, but with a decline in *F. excelsior* following the invasion of *Hymenoscyphus fraxineus*, an exotic pathogen. Hence, uncertainty remains high for these forests, too. The dry *Pinus sylvestris* forests, which colonized as pioneer communities the areas high above lake level, on shallow soils, are submitted to the natural succession, with soil development and replacement of *Pinus* by broadleaved tree species.

This study provides some ideas to conserve these riparian forests on the shores of a regulate lake, but they still need to be tested. However, it is important to note that in July 2021, one year after the recent surveys, the largest flood since 1955 occurred, leading to the deaths of many young individuals of *Picea abies* and *Fagus sylvatica*. No research has yet been carried out on this, but the consequences of this flood on future vegetation dynamics deserve to be studied. The same plots, now precisely localized, could be used in this purpose (Appendix I).

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In memory of Sarah Beuvier, whose commitment and passion for botany enabled a better understanding of these ecosystems.

Author Contributions LS and PV conceived of the research project; SB collected data in *P. sylvestris* stands and LS collected all other data; LS performed statistical analyses and discussed the results with PV. LS wrote the first draft of the manuscript and all authors completed and commented it.

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Declarations

Conflict of Interest The authors report there are no competing interests to declare.

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