Journal for Nature Conservation 78 (2024) 126574

Contents lists available at ScienceDirect

Journal for Nature Conservation

journal homepage: www.elsevier.com/locate/jnc

# Relict of riparian floodplain forests: Natural distribution and ecology of *Ulmus laevis* in Switzerland

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A R T I C L E I N F O

*Keywords:*
Alluvial forests
European white elm
Floodplain dynamics
Naturalness
Natural distribution range
Soil analysis
Vegetation plots

A B S T R A C T

European white elm (*Ulmus laevis* Pallas) is a typical species of riparian forest. In Switzerland, at the margin of its distribution range, this tree is rare and poorly known. Its naturalness was often debated, and the species was seen most often as only cultivated. We aimed to clarify its status, ecology and distribution with extensive field work and surveys in Switzerland, as well as historical investigations. *Ulmus laevis* has a scattered distribution along large rivers and lakes of Switzerland. It is found mainly on coarse, moderately calcareous soils with good fertility. It generally occurs in hardwood riparian forests and occasionally in softwood forests in more dynamic systems. Our findings indicate that *U. laevis* grows naturally in Switzerland. However, the channelization of the large rivers and stabilization of water levels of the main lakes during the 19th century have altered the alluvial dynamics necessary for *U. laevis'* natural regeneration and thus its long-term survival. Therefore, *U. laevis* occurs today mainly as a relict species in ancient floodplain forests with altered dynamics. In this context, regeneration occurs only to a very limited extent and is scarcely sufficient for species persistence. With a total population of less than 1000 naturally occurring individuals, it belongs to the rarest and most threatened trees of Switzerland. By demonstrating the fact that this species was actually present originally in this country, we exemplify the need for a multi-faceted approach to answering questions on the original occurrence versus introduced character of a species, which is very important in regard to land use planning, conservation, and wise use of local plant resources.

## 1. Introduction

Riparian zones belong to the most diverse, productive and dynamic systems in the world (Gregory et al., 1991). The riparian ecosystem can be defined as a water body (river or lake), plus the terrestrial landscape below the high-water mark, where vegetation may be influenced by elevated water tables or extreme flooding (Nilsson & Berggren, 2000). Riparian zones are also one of the habitats most impacted by human activities. For centuries, mankind has been trying to reduce or even eliminate the process responsible for the formation of alluvial landscapes, to protect itself from floods and to gain new agricultural land. In Switzerland, the first traces of river regulations date from Antiquity and the Middle Ages, but the peak was reached in approximately 1850 (Lachat, 2010). By 1900, the regulation of all the large rivers in Switzerland was completed. Eleven of the fifteen large lakes of Switzerland were also regulated to control periodic level fluctuations. It has been estimated that riparian zones have decreased from 81 000 ha to 23 275 ha (-71 %) in Switzerland (Lachat, 2010). This reduction not only affects surface area, but also implies a decline in quality: waterways have been confined to a minimal width between levees, preventing the natural processes of erosion and sedimentation inherent to alluvial dynamics. Additionally, dams now capture substantial amount of sediment that was previously transported downstream. The riparian forests located behind these levees are isolated from the adjacent water bodies, and floods no longer occur (Lachat, 2010; Nilsson & Berggren, 2000). This has a major impact on riparian forests that play a central ecological role and provide habitats for many species (Pielech, 2021). For example, the Rhine floodplain forest in the Alsace, close to Switzerland, is

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https://doi.org/10.1016/j.jnc.2024.126574
Received 26 September 2023; Received in revised form 10 January 2024; Accepted 9 February 2024
Available online 11 February 2024

considered one of the richest woody ecosystems of Western Europe (Carbiener, 1970).

European elms are a component of mixed broadleaved forests, showing a clear preference for water and nutrient-rich soils, distributed principally near rivers and streams or in floodplains, associated marshlands and ravines (Caudullo & De Rigo, 2016). The European white elm (*Ulmus laevis* Pallas, French: Orme lisse, German: Flatter-ulme), included in the section *Blepharocarpus*, is taxonomically and phylogenetically distinct from the two other native European elms, *Ulmus minor* Mill. and *Ulmus glabra* Huds., which belong to the *Ulmus* section (Whittemore et al., 2021). This taxonomic distance implies that *U. laevis* does not hybridize with the latter two species. At first glance, however, it may be difficult to distinguish *U. laevis* from *U. minor* and *U. glabra,* but several morphological characteristics allow a reliable identification of these European species (Fragnière et al., 2022). The most obvious are the long-stemmed flowers and fruits.

*Ulmus laevis* has a Central and Eastern European distribution to the Ural Mountains in the east. It ranges from South Finland at the northernmost boundary to its southernmost limits in Bulgaria, Caucasus and Crimea (Caudullo & De Rigo, 2016). At the margin of its distribution, the species today is always rare and considered locally endangered, for example, in southern Finland (Vakkari et al., 2009) or in Flanders (Belgium), where natural populations are mostly reduced to relict individuals due to the disappearance of riparian forests (Vander Mijnsbrugge et al., 2005). In Schleswig-Holstein (Germany), the same observation has been made (Janssen & Hewicker, 2006), also in a region that was not previously considered part of the natural range, which Müller-Kroehling (2003a) pointed out as an example of a common misconception about this species' occurrence in regions where it is scarce. In Western Europe, *U. laevis* is rare and its natural distribution is not very well known (Collin, 2003; Timbal, 1981). It has recently been recognized that the populations of northern and eastern France are natural, but it has also recently been proven that small scattered populations are native to southern France and Spain (Timbal & Collin, 1999; Venturas et al., 2015), which could be considered possible relicts of glacial refugia (Fuentes-Utrilla et al., 2014).

*Ulmus laevis* is generally considered a typical species of riparian lowland forests in its entire distribution range, for example, in Poland (Napierała-Filipiak et al., 2021) or in Estonia (Paal et al., 2007), where it is documented to occur on slightly elevated levees along rivers, on eutric gleysols or gleyic fluvisols. It is nevertheless also able to tolerate moderately dry soils (Caudullo & De Rigo, 2016). *Ulmus laevis* tolerates more than 80 days of water-logging (Leuschner & Ellenberg, 2017), and seedlings have a great resistance to flooding (Li et al., 2015). The annual mean temperature where *U. laevis* occurs (macroclimatic envelope) is between approximately 2° and 12 °C, with a yearly amount of precipitation between 400 and 1 000 mm (Fragnière et al., 2021; Thurm et al., 2019).

The tree is an anemophilous, self-incompatible and highly outcrossing species. Its fruits are samaras (winged nuts) with ciliated margins, which are dispersed by both wind and water (Collin, 2003; Guzmán-Delgado et al., 2017; Mittempergher & Porta, 1991). Wind allows mainly for short-range dispersal and water for long-range dispersal. Seeds are released at the beginning of the summer, just after springtime floods. Springtime flooding might favor germination by creating new suitable areas and by eliminating competitive herbaceous species (Deiller et al., 2003). Vegetative multiplication by root suckers and stump shoots in this species is a very sporadic phenomenon and is likely limited to situations where roots have been damaged (Müller-Kroehling, 2003b), for example, after flooding disturbance (Venturas, Nanos, et al., 2014).

*Ulmus laevis* is not solely a typical element of riparian hardwood communities, as often stated, but a species to place between the pioneer softwood forest (dominated by *Salix* and *Populus*) and the hardwood forest in the succession of a natural riparian system (Müller-Kroehling, 2003a). It seems that the seedlings need bare soils and a high level of humidity; hence, *U. laevis* is only able to establish itself in the pioneer stages of forest development. This could mostly explain why the species is naturally largely restricted to riparian forests and threatened as soon as the alluvial dynamic is disturbed.

*Ulmus laevis* itself is an important element of biodiversity. Many organisms from various taxonomic groups are found specifically on elms, and at least 8 species (from the following groups: cicadas, Psylloidea, aphids, microlepidopteras, mites, sawflies, gall wasps and beetles) are specialized on habitat provided by *U. laevis* (Müller-Kroehling, 2019a). It is also much less affected by Dutch elm disease, a fungal disease spread worldwide through the lumber trade. Although theoretically susceptible, reports of it having survived large-scale epidemic outbreaks that killed almost all other elm species are overwhelming evidence that earlier assumptions based on laboratory experiments with inoculated seedlings were not representative of the natural susceptibility (Müller-Kroehling, 2019c). It can survive the disease by an avoidance mechanism: the elm bark beetles that are the main propagation vectors (*Scolytus scolytus* and *S. multistriatus*) have been found to be little attracted to it due to the chemical components of the bark (Müller-Kroehling, 2003a, 2003b; Santini & Faccoli, 2015; Solla et al., 2005).

At the margin of its distribution, *U. laevis* is often poorly known. Because of its scarcity, it was frequently considered an introduced or alien species, with therefore a lack of interest for botanists and foresters in reporting its presence (Müller-Kroehling, 2003b; Venturas et al., 2015). The species was also often overlooked and confused with other elm species (Müller-Kroehling, 2003b). In Switzerland, the status of *U. laevis* is unclear. In the former distribution maps (e.g., Atlas Florae Europaeae), Switzerland was outside its distribution range (Jalas & Suominen, 1988). In the famous "Verbreitungsatlas der Farn-und Blütenpflanzen der Schweiz" (Welten & Sutter, 1982), the species is considered only cultivated. In the flora of Switzerland (Flora Helvetica), *U. laevis* is considered cultivated and rarely subspontaneous (Lauber et al., 2018). Whether the species has been truly planted in the past is doubtful. In Bavaria, for example, it does not seem that there has historically been much interest in cultivating it (Müller-Kroehling, 2019b). Despite its supposed non-native origin, the species was included in the Red List of vascular plants of Switzerland (Bornand et al., 2016) because some individuals in the canton of Basel are occurring near Alsace, where the species is considered native (Eggenberg S. personal communication). Nevertheless, it is evaluated as endangered (EN) in Switzerland. It is considered to be a characteristic species of hardwood riparian forests in the list of habitats of Switzerland (Delarze et al., 2015), as is generally also the case in Europe (Mandžukovski et al., 2021).

In the 1990s and 2000s, a project on rare forest trees was conducted, which included *U. laevis* (Schwab, 2001). It highlighted the lack of knowledge of the species and speculated that it could be spontaneous in Switzerland. The species could have reached Switzerland from the Upper Rhine in Alsace and was possibly more common along the main rivers in the past. It was considered very rare and threatened: the total population was estimated at 5 000 trees, assuming that 80 % of the trees were still not known, so that large parts of the often small populations may have been overlooked. This number was, however, hypothetical, as no true survey was conducted. The results were based on the opinions of foresters in different Swiss cantons. Since this project, to our knowledge, no studies have focused on *U. laevis* in Switzerland.

New investigation and data on *U. laevis* in Switzerland therefore seemed vital for a complete understanding and a new assessment. For the present publication, intensive fieldwork to clarify the status of this rare and fascinating species at the margin of its distribution range was launched. Our specific questions were as follows:

(1) What is the current distribution and status of the *U. laevis* population in Switzerland? (2) Can we consider that the species is native to Switzerland? (3) What is the exact ecological niche of *U. laevis* in Switzerland?

## 2. Materials and methods

### 2.1. Distribution

Different sources of information on existing *U. laevis* stands in Switzerland were explored. All existing occurrences of the National Data and Information Center on the Swiss Flora (Info Flora, 2023) were gathered. Existing factsheets were consulted (Delarze, 2009; Schwab, 2001), as well as some Herbaria (Bern, Lugano, Genève). Surveys were conducted in the cantonal forest services or other institutions (different cantons of the Swiss Plateau and Ticino), as well as the tree nursery of the canton of Bern in Lobsigen, which is known for its expertise of this species. Additionally, various foresters and local experts were consulted.

Based on the information collected, all stands that could potentially be considered natural were visited in the field. Furthermore, hundreds of kilometers were explored along the main rivers, deltas and lake shores of Switzerland. The exact GPS location of each observed *U. laevis* tree was recorded, as well as its diameter at breast height (DBH). Because the phenomenon of vegetative reproduction via root suckers sometimes occurs in this species, it is difficult to know if some close stems are of the same individual, so when stems were closely clustered (within a radius of up to about 3 m), we generally counted only one, and the DBH of the largest stem was recorded.

To assess the stand naturalness, the following criteria were used.

A) *Most likely natural stands*: match most of these criteria:

1) Mix of trees of different diameters: *U. laevis* trees of diverse diameters occurred in the same stand, which may indicate different ages, and thus more likely a natural population dynamic. For example, a mixture of trees with DBH less than 20 cm in diameter with others over 40 cm, and a few larger trees with DBH larger than 60 cm.
2) Dispersed trees, not clustered in one place and/or not aligned artificially: *U. laevis* trees were scattered, or in small groups where the trees were likely distributed randomly, indicating a probable natural dispersal. In contrast, plantings are typically done contiguously.
3) Several stands/individuals along a river/lake more or less distant: Several *U. laevis* trees or groups of trees along the same waterbody were located at varying distances, ranging from several hundred meters to several kilometers apart. This suggests a higher likelihood of natural colonization, making it unlikely that plantations have been established repeatedly, for example, along the same river.
4) Suitable habitat (riparian zone), at least historically: *U. laevis* trees were located in riparian forests, or in alluvial plains, with a flat topography, not far away from rivers or lakes. These areas were historically influenced by alluvial dynamics, subject to flooding, and characterized by high water tables, although these features have often been altered today. This indicates a likely suitable habitat for the natural establishment of *U. laevis* stands, at least historically.
5) Planting appearing unlikely given the circumstances: Plantations are generally established in locations ideal for cultivation. Observing trees on alluvial or pebble banks, nearly within the riverbed, etc. suggests that planting is improbable in such areas.

B) *Potentially natural stands*: Match part of the above criteria.

C) *Known or probable planted stands*: Stands that do not match the above criteria or that are known to be planted. Planted stands were not systematically investigated. For all the following steps, only the first two categories of stands (A and B) are considered.

### 2.2. Vegetation and soil analyses

Plots of 200 $m^2$ were designed in selected areas where *U. laevis* is present in most likely natural or in potentially natural stands, as defined above. A total of 29 circular plots were surveyed between May and September 2022. Their exact locations were chosen in the field by placing an *U. laevis* tree at the center of each plot. All vascular plant species were recorded, and their cover was evaluated using the Braun-Blanquet scale (Braun-Blanquet, 1932), without distinction between vegetation layers. For each species, the Landolt ecological indicator value was extracted (Landolt et al., 2010). Landolt values are an adaptation for the alpine region of the Ellenberg indicator values (Ellenberg, 1991) and range from 1 to 5. Indicator values, developed from expert assessments, are widely used in vegetation science as a proxy to estimate edaphic and climatic variables from lists of plant species. An arithmetic weighted mean of indicator values of all species was calculated for each plot, where the cover code of each species was used for the weights.

For 24 plots, the topsoil (0–20 cm) below the litter was sampled at 2 or 3 different locations and dried. The samples were analyzed in a professional laboratory, with the reference methods of the Swiss federal research station Agroscope (Agroscope, 2022). The following parameters were analyzed: soil texture (mineral materials, percentage of clay, silt, sand and gravel), total percentage of organic matter, total percentage of calcium carbonate ($CaCO_3$), soil pH, total percentage of nitrogen, carbon-to-nitrogen ratio (C/N), proportion of the main cations ($H^+$, $Na^+$, $Mg^{2+}$, $Ca^{2+}$, $K^+$), cation exchange capacity (CEC), and percentage of basic cations (base saturation). The R “soiltexture” package (Moeys, 2018) was used to plot the soil texture diagram.

### 2.3. Spatial analyses

Exact locations of *U. laevis* trees were used to extract elevational data from the Swiss high-resolution (0.5 m) LiDAR elevation model (Federal Office of Topography swisstopo, 2022). For each tree, the height above the water surface of the closest water body was calculated by adding a point at the edge of the closest main river or lake. Then, the difference in elevation was calculated. While the water level fluctuates throughout the year, it can be assumed that the elevation of the LiDAR model represents an average situation. The distance to the closest water body was also calculated from this point. All analyses were conducted in R and QGIS software (QGIS Development Team, 2021; R Core Team, 2018).

### 2.4. Historical information

Several online libraries and internet archives were used to find historical information on *U. laevis* in Switzerland and neighboring countries. A list and further details can be found in Appendix B. Along with the scientific name of the species, the names in French and German, including the numerous synonyms, were used for searching. General information concerning the planting, utilization or distribution of the species was recorded, mainly for the 18th, 19th and first half of the 20th century.

## 3. Results

### 3.1. Distribution

In Switzerland, a total of 819 *U. laevis* individuals were recorded that could be growing naturally. A total of 719 individuals met the criteria (see Materials and Methods) and were considered most likely natural (Fig. 1). Examples are shown in Fig. 2. The largest stands were situated along Lake Morat and Lake Neuchâtel. Many individuals were also present along the Aare River between Bern and Thun, principally along the levees. We also discovered many individuals along the Sarine River in the canton of Fribourg in areas where the species was never detected before. Another important stand was situated along the Wiese River, close to the Rhine, in the canton of Basel City, hosting the largest trees in Switzerland (Fig. 2d). Smaller stands in northern and eastern Switzerland, most likely natural, were located along the lower Aare, the Rhine close to Lake Constance and along the Thur River. One hundred additional trees were considered potentially natural, as they only partially met the criteria. This included, for example, a stand in Zürich close to the small Döltschibach and Chriesbach rivers, small stands close

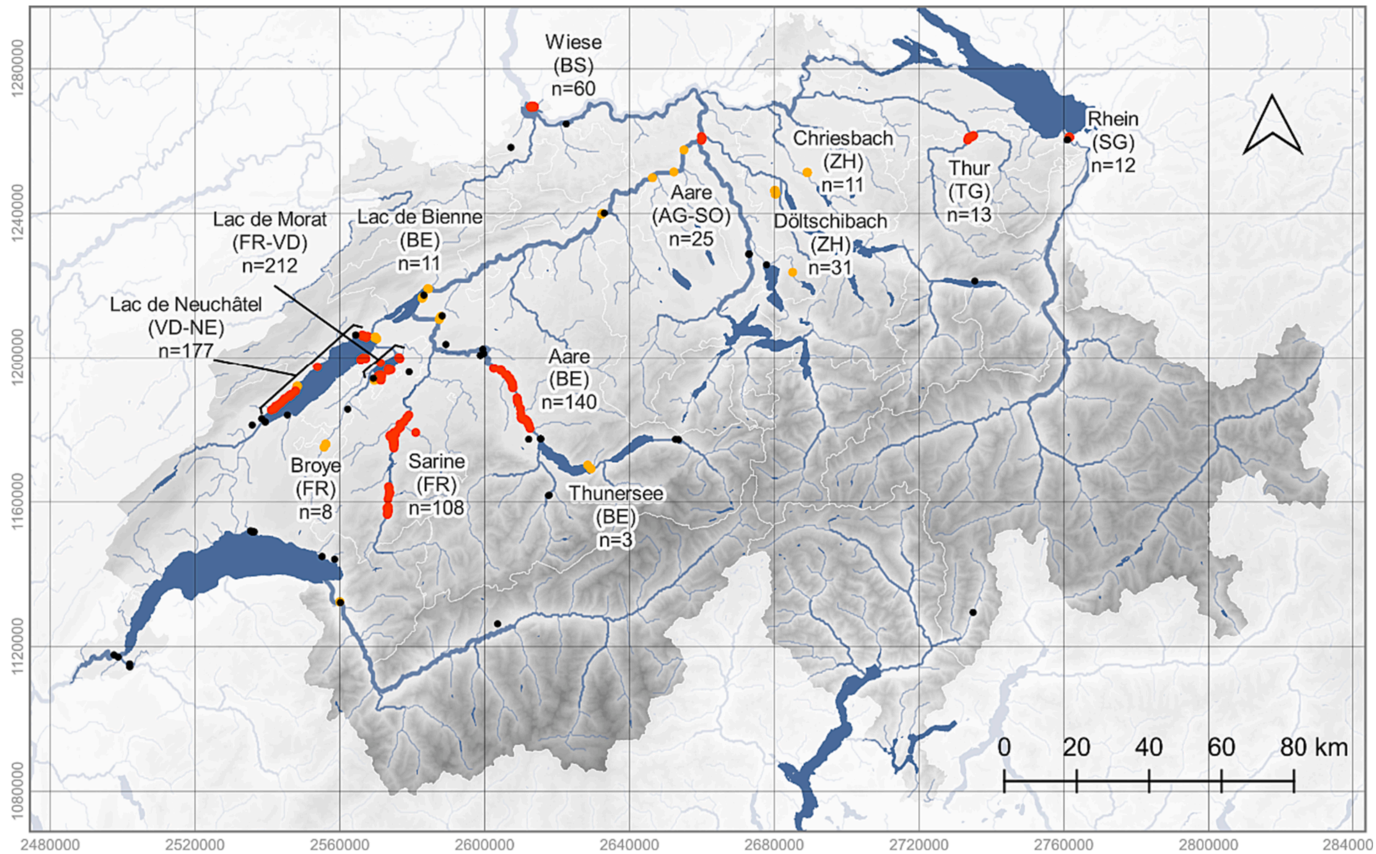


**Fig. 1.** Distribution of *U. laevis* in Switzerland. Red circles indicate most likely natural stands, and orange circles indicate potentially natural stands. The labels specify the name of the river/lake, the canton (AG: Aargau, BE: Bern, BS: Basel-City, FR: Fribourg, NE: Neuchâtel, SG: St. Gallen, SO: Solothurn, TG: Thurgau, VD: Vaud, ZH: Zürich) and the number of individuals for the main stands. Black dots show sites with planted trees. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to Lake Bienne, large trees close to a plantation next to the Rhône, scattered trees along the Aare and in other sites (Fig. 1). The elevation ranges from 253 (Wiese, canton of Basel-City) to 710 m a.s.l. (La Sarine, canton of Fribourg), see also Fig. S1 in Appendix A. Planted trees were not included and were not systematically recorded.

The mean DBH of the recorded trees was 31.6 cm (SD = 23 cm) and ranged from small trees with a DBH of 2 cm to large trees with a DBH of 180 cm. The frequency distribution of the DBH was quite similar in the different stands (Fig. S2). Small trees and seedlings seemed very rare to absent but were difficult to detect in the field. Vegetative propagation appeared to occur rather often (Fig. 2e). We tested the seed viability from different stands; they were fully able to germinate and produced seedlings (Fig. 2f).

*Ulmus laevis* trees were located on average close to water bodies (Fig. 3a). We calculated a mean distance of 44.2 m (SD = 61.3 m) to the closest main water body (river or lake). Trees were also very close to the water table. The elevation of individual trees above the water surface of the closest water body was on average 1.7 m (SD = 1.3 m). Differences are, however, noticeable in the different stands (Fig. 3b, Fig. S3).

### 3.2. Ecology

Soil analysis results are shown in Fig. 4, representing samples collected in 24 *U. laevis* stands in Switzerland. Data, including the proportion of the main cations, are available in Table S1. The data show that *U. laevis* was mainly found on coarse soils, including a high proportion of sand to sandy-silty soils. In approximately half of the samples, an important proportion of larger grained sediments (gravel, pebbles) was also present. Soils can be described as slightly alkaline and moderately calcareous to calcareous. However, two particular samples from Basel (along the Wiese) were slightly acidic with a very low carbonate content. The CEC, C/N ratio and organic matter indicated that in general, the soils can be considered fertile but with some variability.

The vegetation plots, 29 in total in the main *U. laevis* stands, allowed us to analyze the most frequent cooccurring species with *U. laevis* (Fig. 5, Table S2). Most of the plots can be considered *temperate hardwood riparian forest* (EUNIS habitat type code T13, Chytrý et al., 2020); however, some plots, mainly along the Sarine, should be classified as *Alnus glutinosa-Alnus incana forest on riparian and mineral soils* (EUNIS habitat type code T12) or as *temperate Salix and Populus riparian forest* (EUNIS habitat type code T11).

The mean ecological indicator values calculated from the vegetation plots (after removing *U. laevis*) indicated the following on average (Fig. 6): 1) moderately damp soils, 2) moderately alkaline soils, 3) intermediate to richly fertile soils, 4) semi-shade to shade light conditions, 5) low altitude to slightly montane zones, and 6) intermediate continentality to slightly sub-Atlantic climate. These values deviate from the ecological indicator values assigned to *U. laevis* in Switzerland by Landolt (2010) (red bars in Fig. 6).

### 3.3. Historical resources

Historical information on *U. laevis* is hard to find in Switzerland, but much information could be found in the surrounding countries, mainly in France and Germany (see Appendix B), which we used to cross-check our findings, especially relevant of course near the borders with Switzerland. The first obvious thing in the oldest references was the widespread confusion that existed between the different species of elms.


**Fig. 2.** *Ulmus laevis* in Switzerland: a) leaves and fruits, b) stand along the Sarine (canton of Fribourg), on coarse soil of pebbles, c) stand close to water along Lake Neuchâtel (canton of Vaud), d) the largest tree in Lange Erlen (canton of Basel-City), with a DBH of approximately 180 cm, e) two young root suckers, growing from the root of an old senescent large tree (top right of the image), near Lake Morat (canton of Fribourg), and f) viable germinating seeds collected from Swiss populations.

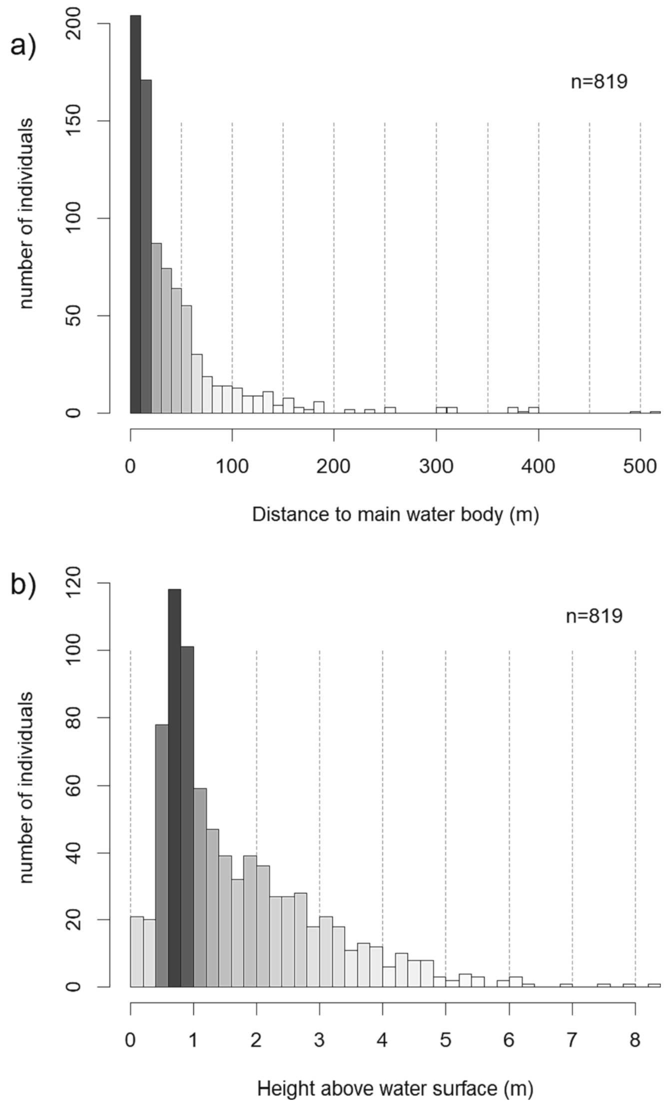


**Fig. 3.** Histograms of the spatial distribution of *U. laevis* in Switzerland in relation to the closest main water body (river or lake): a) distance of individual trees to the main water body; b) elevation of individual trees above the water surface of the closest water body.

It was not always clear which species authors were truly referring to. In Switzerland, it seemed that *U. laevis* was historically planted along roads and streets in some locations. No other information about plantings was found. In France, it seemed that the species was almost unknown before ~ 1800 or only locally known so that it did not appear in the literature. It was mentioned at this time as introduced and seen as an interesting tree. Later, since approximately 1850, it started to be reported in different places in France, especially in the riparian forests of Alsace. However, it seemed that people had completely changed their opinion about it, and it was now seen as a worthless tree, neither used as timber nor as firewood. The fertile surfaces where it was found deserved to be cleared of it. At the end of the 19th century and the beginning of the 20th century, it became evident that *U. laevis* was native in different forests in France. The negative opinion seemed to persist, as the species was apparently not cultivated, except along roads. In some parts of Germany, the species appeared to be relatively better known in the 19th century due to its wider distribution. Various uses were mentioned, but it was also generally considered low-quality wood. It is considered native, although not in all regions, at least until thorough field surveys and analyses are conducted, often only rather recently (e.g. Janssen and Hewicker, 2006). In Italy, its origin is unclear, but a native occurrence becomes more likely as new evidence is gathered (Pepori et al., 2013).

## 4. Discussion

Our investigations and results provide a new overview of *U. laevis* in Switzerland. The original data compiled here lead to a better understanding of the distribution, ecology and history of this rare species at the margin of its distribution range. Our results highlight that it belongs to the rarest tree species but deserves more attention, as several facts indicate that this species should be considered native, mainly as a relict of ancient floodplain forests.

### 4.1. Naturalness

Determining whether or not small marginal populations of a species are native is complicated (Venturas et al., 2015). Most likely because of its scarcity and because little is known about it, *U. laevis* is considered exclusively cultivated in Switzerland (Lauber et al., 2018; Welten & Sutter, 1982). However, we agree with Müller-Kroehling (2003) that many wrong beliefs exist for *U. laevis* and with Schwab (2001) that it should be considered native in Switzerland for the following reasons:

1) There is no historical evidence that *U. laevis* was commonly planted as a forest tree. The only available information was its planting along roads because of its fast growing capacity (Collin, 2003). In contrast, it seems that it is a species that in the 19th and 20th centuries enjoyed a negative appreciation among foresters in neighboring countries, considered "useless" in regard to forestry, and it was probably the same in Switzerland. In Bavaria, whose situation, close to the northern Alps, is comparable to Switzerland, *U. laevis* did not have a long tradition in silviculture. It has practically never been utilized commercially for forestry or only very regionally (Müller-Kroehling, 2019b), and until 20 years ago, it was basically not available through forest nurseries. Another study in Spain concludes similarly that there is no historic information supporting *U. laevis* introduction or its extensive use (Fuentes-Utrilla et al., 2014; Venturas et al., 2015).
2) Many stands surveyed were obviously not planted and thus likely are native, including scattered trees along rivers or lake shores, sometimes in very natural areas, sometimes very sparse, and including trees of very diverse DBH. Moreover, individuals were discovered in many areas of Switzerland in 62 different municipalities. It would be surprising if it had been cultivated in so many places without leaving a written record.
3) Switzerland is situated at the margin of its distribution range (considered native in Alsace and in southern Germany).
4) Genetic analysis (Dermelj, 2023) showed a homogeneous distribution of admixed genotypes within populations of Switzerland and throughout the upper Rhine, supporting gene flow with German and French populations. The genetic pattern of most Swiss populations seems therefore identical to neighboring countries where the species is considered natural.

Considering these different points, we argue that *U. laevis* must be considered native in Switzerland. Its colonization from the Rhine after the retreat of the glaciers seems plausible. Its distribution was potentially wider during some periods of the Quaternary. It was found in certain regions of Europe that *U. laevis* played an important role during the Atlantic period of the Holocene (Thomson, 1951).

### 4.2. Distribution

Our results show the actual scattered distribution of *U. laevis* in Switzerland, which at first sight may seem surprising. We consider that the actual stands were able to establish mainly in four different

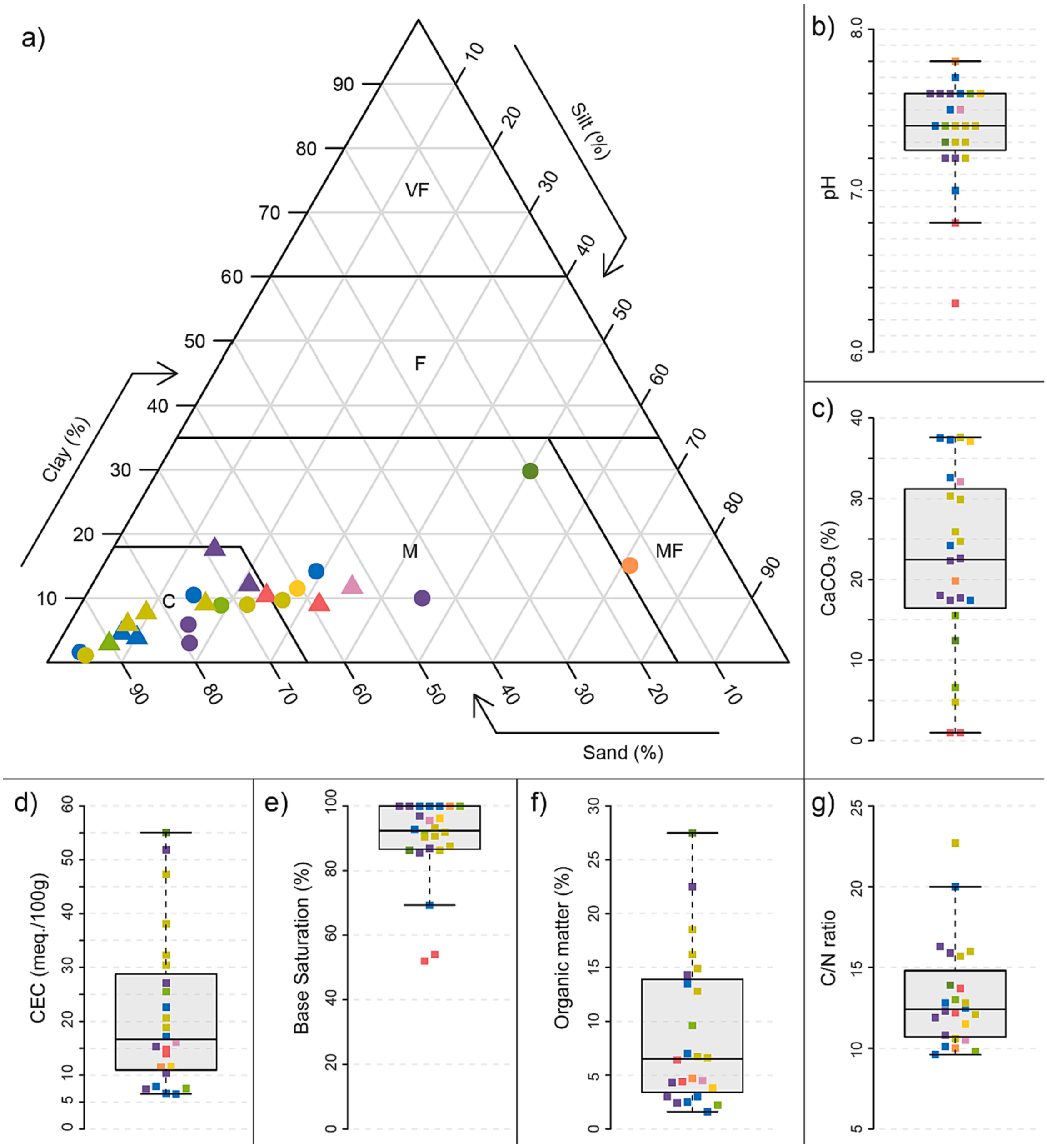


**Fig. 4.** Soil characteristics in *U. laevis* stands in Switzerland: a) Soil texture. Each colored point corresponds to a single sample. Triangles indicate soils with more than 30% gravels and large particles. The divisions correspond to the texture classification systems used for the European Soil Map (Moeys, 2018): coarse (C), medium (M), medium fine (MF), fine (F) and very fine (VF), b) soil pH, c) total percentage of calcium carbonate ($CaCO_3$), d) CEC, e) base saturation, f) total percentage of organic matter, and g) carbon-to-nitrogen ratio. The colors of the points correspond to different waterbodies: Lake Morat (green), Lake Neuchâtel (yellowish green), Lake Bienne (dark green), Aare (purple), Sarine (blue), Döltschibach (yellow), Thur (pink), Rhine (orange), and Wiese (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

circumstances:

1) *Ulmus laevis* regenerates through seeds only on bare soil, and unlike *U. minor,* it shows a limited tendency of regeneration through root suckers. Hence, a dynamic alluvial system is needed to persist (Fig. 7a). This dynamic is absent in the main rivers of Switzerland, with some exceptions where a weak dynamic is still occurring, for example, along unchannelized, meandering sections of the Sarine. In this context, scattered trees were found along the river, including young trees. This could represent the last self-sustaining stands of *U. laevis* due to river dynamics in Switzerland.
2) Some stands probably persist as relicts after the channelization of larger rivers (Fig. 7b). Riparian forests behind levees were isolated from the alluvial dynamic. Accelerated transition to post-pioneer communities occurs in this context (Janssen et al., 2020). Established *U. laevis* trees were able to persist and reproduce sporadically, but the absence of dynamics no longer allowed seedlings to establish. As this recruitment is absent, the species cannot expand to unoccupied but suitable patches anymore to regain territory within the patch dynamics of forest development and the alluvial soil mosaic. The remaining relict stands are threatened in the long term by this lack of regeneration possibilities. Examples include the Wiese and upper Sarine.
3) River regulations and the building of levees were huge construction works, with the consequence of artificially large areas of bare soil. Pioneer softwood forests were able to establish on these substitute

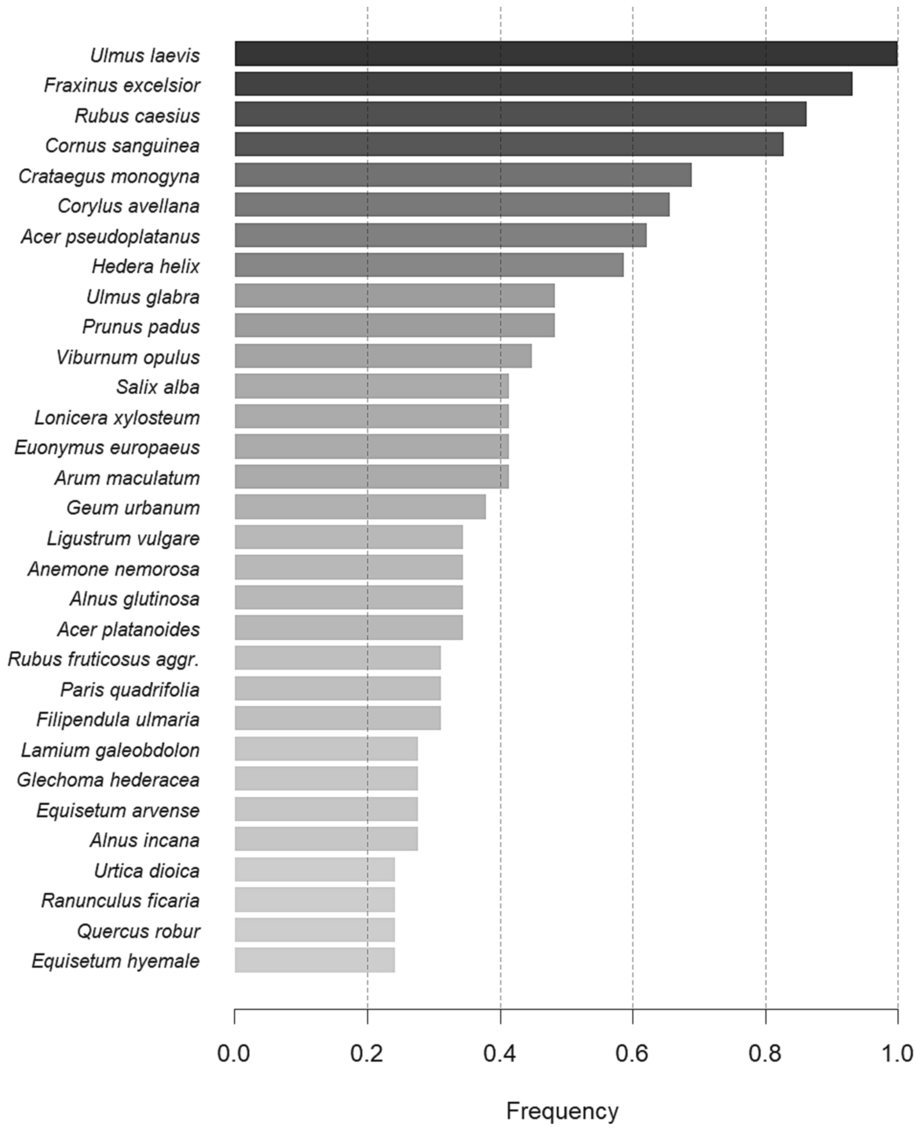


**Fig. 5.** Co-occurring species. Most frequent plant species in the vegetation plots.

habitats, and *U. laevis* probably also temporarily benefitted from this situation in some areas (Fig. 7b). Many trees are found along the Aare on levees. This colonization could have occurred after the Aare regulation in 1824 (Lachat, 2010). These stands are probably threatened in the long term, with recruitment today being rare or absent.

4) Large stands are found along Lake Neuchâtel and Lake Morat. These two lakes were largely impacted by the so called "Jura water correction" (1887), with a lowering of the water level of approximately 3 m and a significant decrease in fluctuation (Lachat, 2010). During this phase, large open surfaces emerged that were favorable for pioneer forest stages of bare soil germinating species. *Ulmus laevis* likely benefitted from this situation (Fig. 7c), although only temporarily. Areas where it occurs today were historically mostly under water (Fig. S4 in Appendix A). Today, the dynamics in such sites are low because of the reduced fluctuation, with probably only very limited recruitment for *U. laevis*. Finally, a few trees were also found along an artificial lake (Lake of Gruyère). It seems that the artificial and high fluctuations create an interesting substitutional habitat with secondary dynamics for *U. laevis*, although only in a limited area.

### *4.3. Population size*

With a population of 819 individuals detected in our study, *U. laevis* undoubtedly belongs to the rarest tree species in Switzerland. This number is based on an extensive field survey. All known stands today were visited based on all data collected in recent decades and expert information. Many extra suitable areas were explored (Fig. S5). Therefore, although some isolated trees were probably undetected as of yet, we are confident that most of the individuals (most likely native or potentially native) have now been recorded. It is unlikely that large populations are still unknown, as Switzerland is a small country where the forest is well surveyed throughout, especially at lower altitudes. The total native population in Switzerland could therefore be lower than 1 000 individuals, or not much more. This is significantly below the 5 000 individuals that were suggested approximately 20 years ago (Schwab, 2001). It should be pointed out, however, that this number does not include trees from plantations, which we have not inventoried. Their number may be of some importance, however, since we have observed some relatively large plantations and we have been informed of several recent plantations. These plantations, which are often located outside the species' natural habitat, cannot guarantee long-term survival of the species, but can play a temporary conservation role.

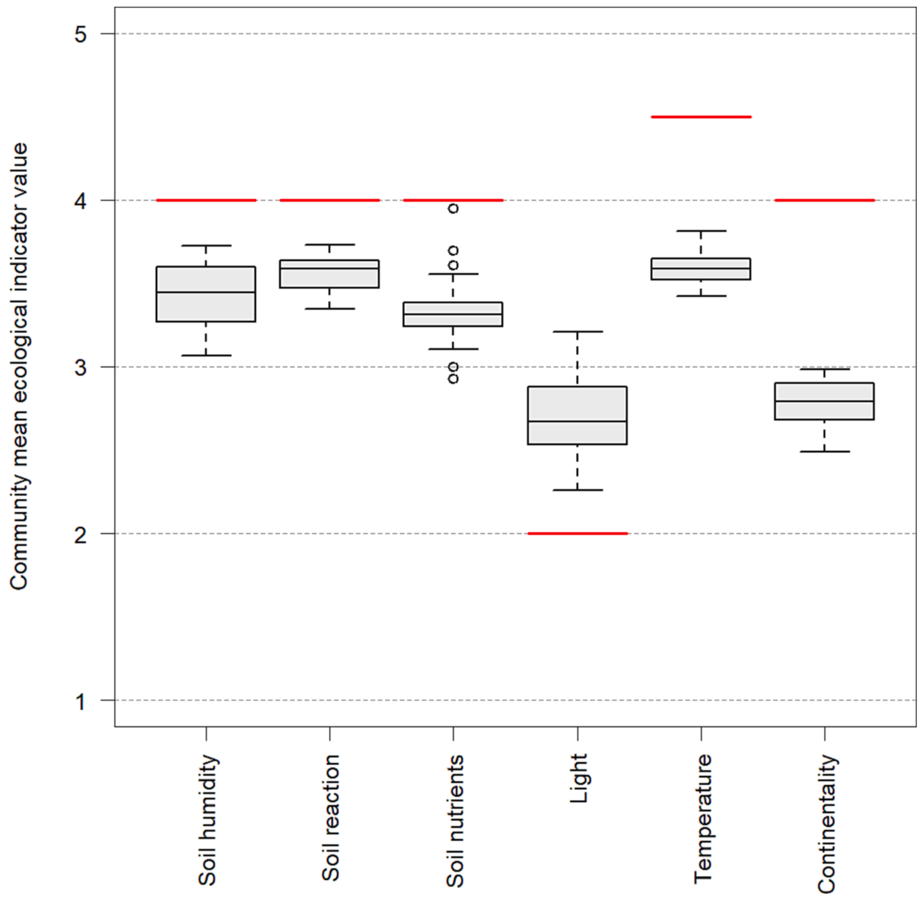


**Fig. 6.** Box plot of the mean ecological indicator value (Landolt et al., 2010) of the vegetation plots (community), excluding *U. laevis*. Six variables are shown: soil humidity, soil reaction, soil nutrients, light, temperature and continentality. The red bars indicate the Landolt ecological indicator value of *U. laevis*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### *4.4. Ecology*

*Ulmus laevis* is clearly linked to the close proximity of water bodies (Fig. 3) and located close to the water surface in terms of elevation, indicating the proximity of the water table. The communities where it occurs were, however, not especially hygrophilous, showing that the topsoil is only moderately damp. The coarse soils (Fig. 4a) do not allow for high water retention, and the channelization of rivers probably contributed to making these sites drier on average.

Community and soil analyses indicated a predominance of moderately alkaline, calcareous soils in *U. laevis* stands, with good fertility. In contrast, the samples from Basel (the Wiese) indicated more acidic soils with lower cation availability. The Wiese is the only river in our study not originating in the Alps but in the Black Forest, a siliceous massif. The soil pH and nutrient preferences of *U. laevis* are debated, and observations differ regionally (Caudullo & De Rigo, 2016; Napierała-Filipiak et al., 2021; Thurm et al., 2019; Venturas et al., 2015; Venturas, Fernández, et al., 2014; Venturas, Nanos, et al., 2014). Our results confirm that *U. laevis* has in fact a broad amplitude for these factors.

Our results are in line with the fact that the species is tolerant of calcareous soils (Müller-Kroehling, 2019a). Hesitations are sometimes voiced regarding the tolerance to calcareous soils, but the species does apparently have sufficient capabilities for uptake of all vital nutrients (i.e. iron and manganese) also on these soils once the root system taps into sufficiently wet soil depths or the trees grow on regularly flooded sites (Müller-Kroehling, 2019a). Hence, the fact that most Swiss occurrences are situated in calcareous floodplains is not a critical argument against the nativeness of the species, as had erroneously been put forth in Bavaria (Müller-Kroehling, 2019a).

Similarly, *U. laevis* has a large tolerance in terms of soil texture. In Switzerland, soils are mainly coarse, sometimes even very coarse (pebbles, see, e.g., Fig. 2b), typical of the middle course of rivers. However, in other regions, *U. laevis* can also tolerate heavy clay soils (Cicek et al., 2007; Köstler et al., 1968; Thurm et al., 2019).

*Ulmus laevis* is often seen as a thermophilous species that is frost sensitive and can only reach low elevations (e.g., 300 m a.s.l., Caudullo and De Rigo, 2016, or 500 m a.s.l., Delarze, 2009). We detected that it can grow up to 710 m a.s.l. in Switzerland and that the communities where it occurs are not composed of thermophilous species. Our results support the observations from Bavaria, where *U. laevis* occurs up to 600 to 800 m a.s.l. (Müller-Kroehling, 2019b) and should be considered neither very thermophilous nor very sensitive to frost.

Our observations also confirm that *U. laevis* should not be considered solely as a typical hardwood forest species but more as a species that establishes in an intermediate stage between the short-lived and dynamic pioneer softwood forests (“Weichholzaue”) and the more stable hardwood forests flooded less frequently (“Hartholzaue”). Some vegetation plots from the Sarine were closer to softwood forest communities than hardwood forest in terms of species composition. Similar observations were performed in Alsace along the Rhine (Schnitzler, 1995) and in Bavaria (Müller-Kroehling, 2003a). Adult trees can occur in both floodplain forest types, but pioneer stages with bare ground are necessary for seedlings to develop. It is interesting to observe that the American sister species, *U. americana*, has very similar habitat affinities (Marks, 2017). However, eliminating or reducing the perturbing effects of floods and lowered groundwater levels that follow river regulation changes the species composition of riparian forests to forest types more characteristic of unflooded upland areas (Décamps et al., 1988; Nilsson

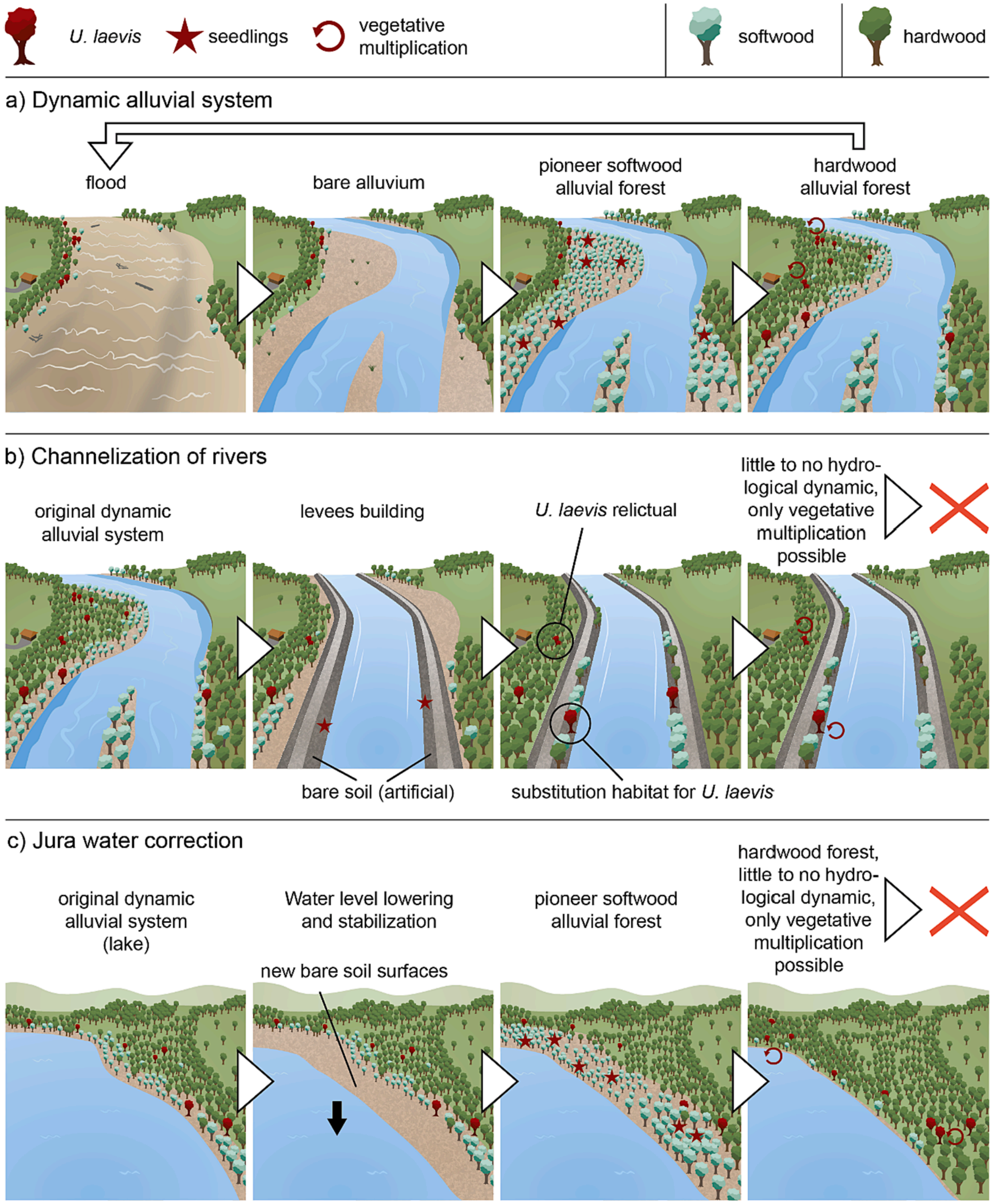


**Fig. 7.** Examples of ecological successions with a focus on *U. laevis*. a) Dynamic alluvial system, today almost absent in Switzerland. Natural habitat of *U. laevis*. b) Channelization of rivers, common in Switzerland during the 19th century. c) Jura water correction (1887), resulting in the lowering of the water level of large lakes of Switzerland where *U. laevis* is present.

& Berggren, 2000), somewhat masking the habitat affinities of true floodplain relicts, such as *U. laevis*.

In conclusion, we argue that the species should not be considered in Switzerland as a characteristic hardwood forest species but as a constant species of both softwood and hardwood riparian forests. Moreover, Landolt ecological indicator values (Landolt et al., 2010) should be revised for Switzerland, considering our results (Fig. 6).

### 4.5. Conservation and conclusion

Marginal populations are important for biodiversity conservation (Picard et al., 2022). In western Europe, river channelization, lowering of groundwater levels, deforestation and drainage of floodplains for agriculture and industry have severely diminished the area of suitable habitats for *U. laevis* (Müller-Kroehling, 2019b; Vander Mijnsbrugge et al., 2005). This is especially true for Switzerland (Lachat, 2010). Habitat fragmentation is a major threat for the mostly small and isolated populations. Among other things, such small and isolated populations are prone to the risk of genetic drift (Collin, 2003), although genetic depression seems not noticeable today in scattered populations of Switzerland (Dermelj, 2023). The pioneer stages, essential for *U. laevis*, are today very limited along water bodies (Lachat, 2010). Populations need minimum recruitment so that they do not go extinct (Hylander et al., 2015). With very poor seedling recruitment, no seed bank, vegetative multiplication, limited as it is in this species, apart from chance instances with small spots of bare soil or special occasions such as the lowering of lake water tables is one of the few mechanisms for *U. laevis* to sustain populations in Switzerland. Long-term conservation requires restoration of hydrological regimes and more space for pioneer communities (Venturas et al., 2015). *Ulmus laevis* is sometimes considered a tree that will benefit from climate change (Koch et al., 2022), but such predictions, based on the climatic envelope of the species, must be interpreted with caution, as the limiting factor is often not climate but habitat conditions. The species can be propagated in forest nurseries with ease (Müller-Kroehling, 2003a; Thurm et al., 2019), but maintaining dynamic natural populations seems a challenge in Switzerland unless great progress in alluvial landscape restoration is made. Considering the criteria of the Red List of Switzerland (Bornand et al., 2016), *U. laevis* deserves its current status as an endangered species (EN), principally because of its current population size and dependence on the reestablishment of semi-natural processes that can sustain natural populations in the floodplains.

*CRediT authorship contribution statement*

**Yann Fragnière:** Conceptualization, Formal analysis, Investigation, Methodology, Supervision, Visualization, Writing – original draft. **Lena Dermelj:** Investigation, Methodology, Supervision, Writing – review & editing. **Nicolas Küffer:** Investigation, Writing – review & editing. **Jacques Sciboz:** Investigation, Writing – review & editing. **Stefan Müller-Kroehling:** Validation, Writing – review & editing. **Christian Parisod:** Validation, Writing – review & editing. **Gregor Kozlowski:** Conceptualization, Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

## Declaration of competing interest

The authors declare no competing interests.

## Data availability

Data will be made available on request.

## Acknowledgement

We thank all the persons that kindly answered to our requests for information about *U. laevis* in their region: Adrian Aebischer, Canton de Fribourg; Peter Ammann, Bildungszentrum Wald Lyss; Franco Ciardo, Canton de Vaud; Christian Clerc, Association de la Grande Cariçaie; Pierre Cothereau, Kanton Solothurn; Romain Cottet, Canton de Fribourg; Raymond Delarze, bureau BEB, canton de Vaud; Stefan Eggenberg, Infoflora; Emmanuelle Favre, Canton de Genève; Laurent Fivaz, Canton de Vaud; Jean-Louis Gay, Canton de Vaud; Marcel Gigon, Kanton Luzern; Adrian Kempf, Kanton Luzern; Ruedi Lengweiler, Kanton Thurgau; Daniel Müller, Kanton Zug; Sofia Mangili, Cantone Ticino; Thomas Peter, Forstgarten Lobsigen; Andreas Rudow, ETH Zürich; Florence Rüegger, Kanton Aargau, Martin Schenk, Kanton Bern; Philippe Wohlhauser, Canton de Fribourg; Martin Ziegler, Kanton Zug. We also thank the Natural History Museum Fribourg (NHMF), especially Peter Wandeler, for his support in this project. Gregor Kozlowski and Nicolas Küffer were supported by the Fondation Franklinia. Finally, we would like to thank the anonymous reviewers for their constructive and helpful comments.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2024.126574.

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