Reviving Douro Basin

Task 3.1.4. Analysis of ecological impacts from dams in key Douro sub basins affected by the PLDP (Tua and Sabor), to be affected (Tâmega) or suitable to be affected (Paiva)

Manuel Lopes Lima
Project Coordinator

SUMMARY

Dams are known to have multiple nefarious effects on freshwater diversity. The impacts of large barriers or dams have been studied worldwide in many distinct freshwater taxa, especially on fish, freshwater mussels, and macroinvertebrate communities.

Within this project, almost 5,000 man-made physical barriers were detected in the Douro River basin that completely changed the hydrological regime of the entire catchment and, in synergy with other factors, strongly depleted its freshwater biodiversity from large areas of the basin.

Here we revised the ecological impacts and effects of larger barriers (higher than 5 meters) from the known scientific literature and carried out a study on ecological impacts of the smaller physical barriers on the biodiversity of the River Douro basin by comparing the biodiversity (fish, mussels and macroinvertebrates) patterns on 380 sampled sites. We also measured the genetic diversity patterns to investigate the connectivity and population structure of selected fish species to detect any effects of population fragmentation caused by dams. Fragmentation of populations, sediments and nutrients transport, changes in water quality, flow and hydrological regime, and habitat quality of the substrates are among the most important negative impacts of the larger barriers and dams. Smaller barriers have lower impacts that are difficult to discern. We have detected no major differences in the overall biodiversity on stretches affected by small barriers. However, these barriers may cause impacts on specific freshwater groups. For instance, reservoirs of small barriers presented a higher content of invasive species and may provide a refuge and bases for upstream dispersion and expansion. Most of the sessile and threatened freshwater mussels are also highly affected and cannot live in small reservoirs, probably due to the clogging of the substrate. Other groups of animals that are sessile or have low vagility are underrepresented in sites immediately downstream these smaller barriers. Most of the large dams of the Douro river basin were constructed during the

1970s and 1980s and all diadromous fish disappeared soon after. Due to the still recent presence of these dams we still have not detected any major fragmentation on the fish genetic structure. However, several species have shown an general upstream decrease in genetic diversity that coupled with the increased fragmentation, as shown in other tasks within the project, suggests that an accelerated genetic erosion is ongoing and will lead to the probable extirpation of small populations isolated by these dams. The results of the molecular data also detected several new linages/species in isolated regions that should be studied in detail to identify potential new species and reassess the conservation status of these potential taxonomic units.

The current report reaffirms the importance of the four river Douro sub-basins (Paiva, Sabor, Tâmega, and Tua) as the strongholds of most of the native fish and mussel fauna of the Douro basin. The dams already built on the Sabor, Tâmega and Tua already promoted the extirpation of most freshwater mussel communities under the influence of the reservoirs and isolated the populations of fish and mussels in small stretches. The fish communities are also changing rapidly in these areas with the native species being replaced by invasives. Therefore, it is crucial that no more dams or barriers are constructed in these basins, if we want to preserve what is left from the whole Douro freshwater diversity.

AIM OF THE TASK

The study was delineated to make a broad assessment of the ecological impacts of barriers on freshwater biodiversity on the River Douro basin.

TEAM

The assessments were made by a multi-disciplinary team composed by:

- Manuel Lopes Lima (CIBIO/InBio, University of Porto, Portugal, IUCN-SSC-Molluscs Sp. Group)
- Amílcar Teixeira (CIMO-ESA, Polytechnic Institute of Bragança, Portugal)
- Ronaldo Sousa (CBMA, University of Minho, Portugal)
- Simone Varandas (CITAB-University of Trás-os-Montes e Alto Douro, Portugal)
- Duarte Goncalves (CIBIO/InBio, University of Porto, Portugal)
- Aina Raventós (CIBIO/InBio, University of Porto, Portugal)
- Ana Filipa Filipe (CIBIO/InBio, University of Porto, Portugal)
- André Santos (CIIMAR-LA, University of Porto, Portugal)
- José Pedro Ramião (CIBIO/InBio, University of Porto, Portugal)
- Mário Ferreira (CIBIO/InBio, University of Porto, Portugal)
- Tiago Neves (CIBIO/InBio, University of Porto, Portugal)
- Francisco Carvalho (CBMA, University of Minho, Portugal)
- Elsa Froufe (CIIMAR-LA, University of Porto, Portugal)
- Fernando Teixeira (CIMO-ESA, Polytechnic Institute of Bragança, Portugal)
- Fernando Miranda (CIMO-ESA, Polytechnic Institute of Bragança, Portugal)
- Joana Nogueira (CIBIO/InBio, University of Porto, Portugal)
- Filipa Martins (ICETA/CIBIO), University of Porto, Portugal

Background

River fragmentation due to dams, weirs, and other anthropogenic barriers is one of the main threats to Iberian river habitats ecosystems. There almost 5,000 man-made physical barriers in the Douro River basin, with more than 1,000 in Portugal and more than 3,500 in Spain (Fig. 1. Cortes et al 2019; Confederación Hidrográfica del Duero). Of these, more than 250 are dams with a barrier height of more than 10 m tall, most of them completely avoiding the passage of most macro-organisms, being the most notorious fish.

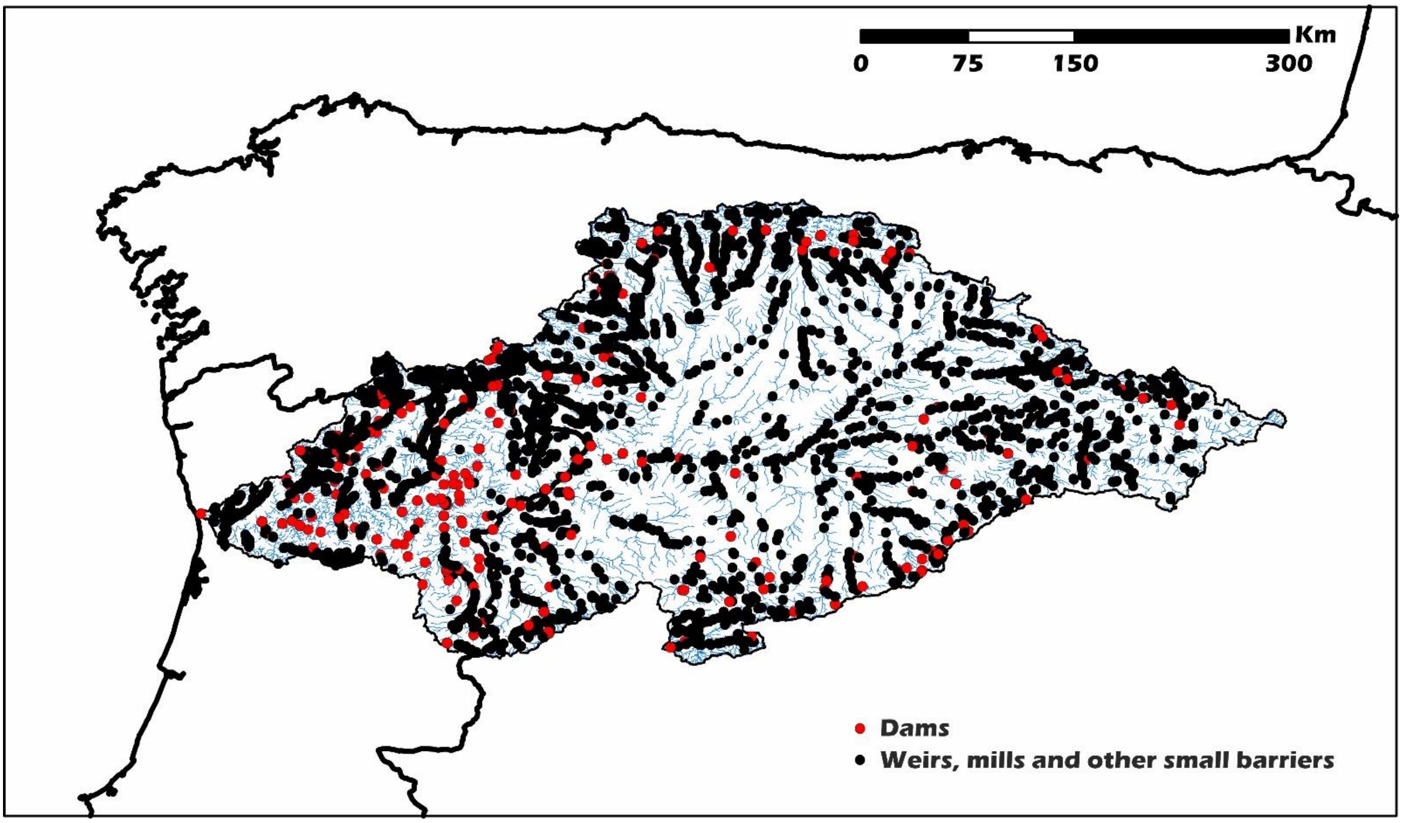

Figure 1. Map of known man-made physical barriers in the Douro River Basin according Cortes et al 2020 and public data from the Confederación Hidrográfica del Duero.

These river fragmentation effects are especially notorious for diadromous migratory fish as most of these animals almost disappeared from the Douro River basin since the inception of the first dam. However, other freshwater organisms may also be profoundly affected by these barriers due to the breakup of their population structure. Populations isolated by barriers are generally more vulnerable to extinctions by genetic erosion or from the occurrence of catastrophic events. The effects of large dams have already been shown to have an impact on the genetic structure of fish populations provoking the decrease of genetic diversity in isolated populations and exacerbating the usual upstream decrease in allelic diversity within river catchments, particularly when those dams lack fish-passes. Besides its effect on connectivity, large dams have also been shown to alter and considerably degrade suitable habitat for many species over vast areas. For instance, in reservoirs of big dams generally the fish fauna quickly changes to species prone to lentic environments and typically more resilient to increases in eutrophication and leads to the decrease in biodiversity. Reservoirs of large dams have already been shown to promote the taxonomic homogenization of fish communities within river basins and the source and refugia for invasive species expansion. On the other hand, other sessile species, such as many freshwater mussel species, that need a lotic or flowing water environment to survive, quickly die and disappear. Water stratification and oxygen depletion of the lower strata have also deep implications on the ability of organisms to survive, not only in the reservoir itself but downstream of the barrier where the release of cold, unoxygenated water may cause severe damage in many benthic organisms. The effects of smaller barriers like weirs and mills on habitat degradation and on the general biodiversity levels are less studied and it is not always obvious if the effects of these barriers, besides breaking the hydrological connectivity, have a negative impact on habitat quality. Therefore, the aim of the current task was to evaluate the diversity of selected freshwater organisms at variable distances from identified barriers to estimate their impacts and characterize the genetic structure of selected fish and freshwater mussel species to provide guidance for four of the biggest River Douro sub-basins in Portugal.

WORK PLAN

Site selection

A total of 205 river sites were surveyed on three of the target River basins (Tua N=96; Sabor N=60, and Paiva N=55) complemented by the 175 sampling sites surveyed for Task 3.2.1. Sites were selected based on its variable proximity to distinct barriers (dams an weirs) previously identified by the UTAD team and validated by our team.

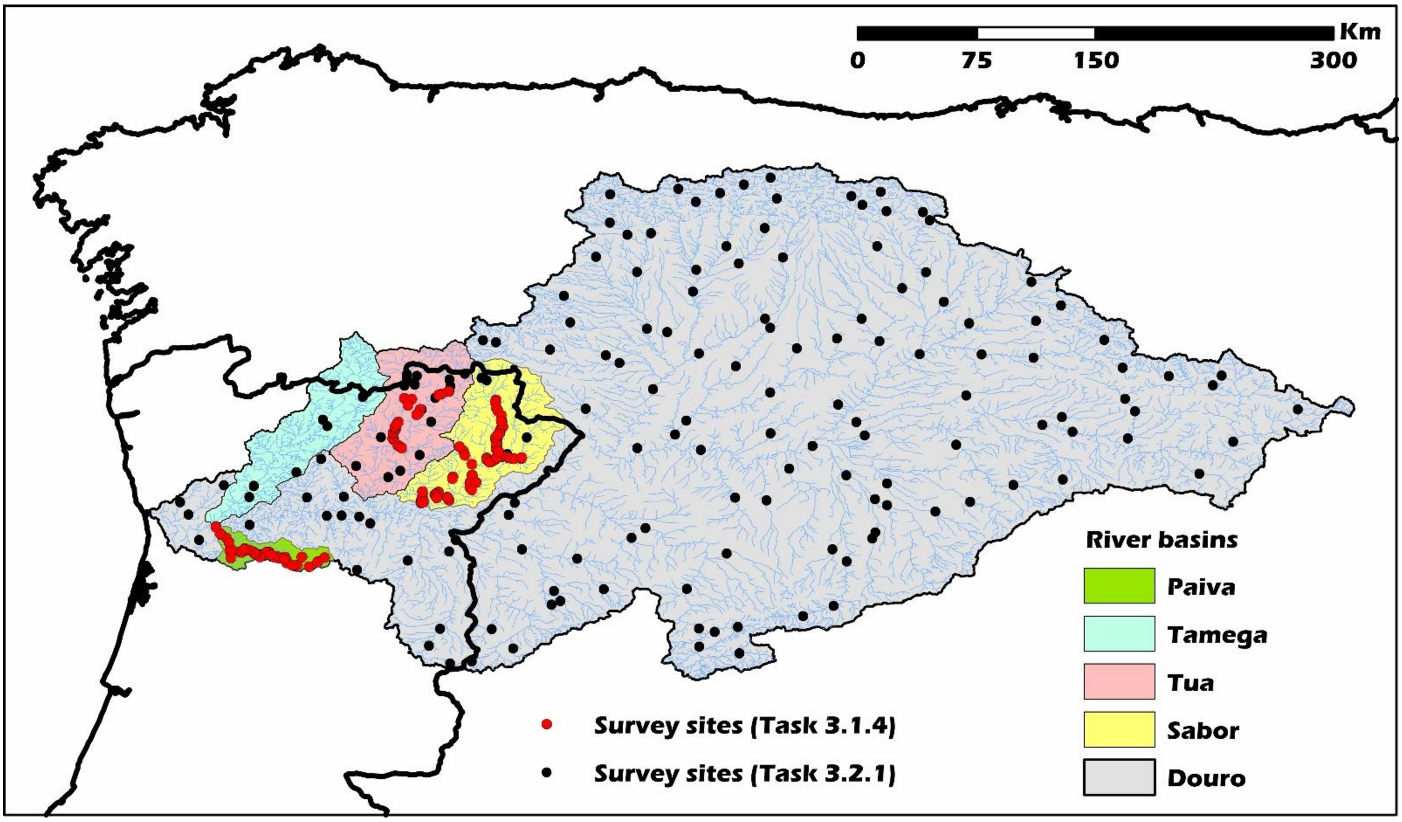

Figure 2. Study area and sampling points.

Fieldwork

The fieldwork was accomplished along the years of 2017, 2018 and 2019.

Surveys

All selected sites were surveyed for fish, macroinvertebrates including special surveys for crayfish, molluscs, and dragonflies. However, not all taxa were surveyed on all 380 sites but only those that could potentially be present in specific freshwater habitats (Supplementary Table 1).

Sites were categorized into distinct categories: Reservoir (inside the reservoir) and Outside reservoirs subdivided in Upstream (less than one Km upstream of the dam but outside the reservoir), Downstream (less than one Km downstream of the dam, and Free (more than 1 km to the nearest barrier).

Several of the selected sites were dry or partially dried and only suitable for very few taxonomic groups.

Methodologies

. Fish were assessed using electrofishing following INAG 2008.

. Freshwater molluscs were assessed using a Rapid Bioassessment for freshwater molluscs by Cummings et al. (2016) and complemented with the macroinvertebrates' assessment.

. Crayfish were assessed by the combined effort of macroinvertebrate sampling plus electrofishing for fish

. Adult Odonata were assessed by using the protocol for site count and complemented by the macroinvertebrates' assessment for the larval stages. All dragonflies present at the time of the assessment are counted for 1 hour. Not only dragonflies along and above the water, but also the adjacent vegetation is checked. Special attention is paid to micro-habitats which are sun-exposed and that give some protection against the wind.

. Macroinvertebrates were collected following the European Water Framework Directive protocol

. Genetic samples of tissue or fin clips were collected non-lethally from individuals of all fish and freshwater mussel species (N<20 individuals per species).

. Nuclear (Recombination-activating gene 1 (RAG1) and microsatellite markers) and mitochondrial (Cytochome oxidase subunit I (COI) and Cytochrome b (cytB)) markers were sequenced for selected populations of fish and mussels (up to 20 specimens per population) across its Douro River distribution.

. A case study about the impact of small hydropower plants on the abundance and size structure of the freshwater pearl mussel *Margaritifera margaritifera*, an umbrella and sentinel species, was accomplished by sampling 66 sites below, above and within dam reservoirs, in the Tua river basin.

RESULTS

Main effects of dams on the worldwide freshwater biodiversity

Artificial barriers for water regulation and management and the production of energy are pervasive worldwide, fragmenting streams and rivers into isolated habitats. Globally, 48% of rivers are impacted by either flow regulation, fragmentation, or both.
Man-made physical barriers or dams have been constructed with multiple purposes such as:

- Hydropower generation
- Drinking, industrial, and cooling water supplies
- Irrigation
- Flood control
- Navigation
- Recreation
- Fisheries

Unfortunately, dams are among the most destructive human activities in river basins, deeply altering the hydrology, geomorphology, and biodiversity of river catchments.
During and immediately after construction dam reservoirs follow a succession of physicochemical alterations, modifications in the structure and dynamics of primary producers, and changes in the community of consumers, especially invertebrates and fish. Subsequently, limnological stability increase in reservoirs but periodical occurrence of floods and draughts, caused by the dam operations, creates multiple disturbances to the systems. The negative effects of large barriers or dams (> 5 m of height) on freshwater biodiversity have been studied in detail in many parts of the world. The main impacts on biodiversity by dams are:

- Fragmentation of the hydrographic network (severely impacting fish and other freshwater species movements and hindering the transportation of sediments and nutrients)
- Sedimentation or siltation of river substrate in reservoirs leading to clogging of interstitial water with a huge impact on benthic sessile and rheophilic species and species that lay eggs or have periodical life-stages on the substrate.
- Homogenization of upstream habitats to lentic environments, being quite harmful for species that only occur or prefer lotic environments.

• Downstream exposure to extreme fluctuations of flow, with short strong discharges and long draught periods. This leads to the inability of fixation and survival of sessile or low vagility species such as freshwater mussels and smaller fish species.
• Changes of the river/groundwater exchange, altering geochemical cycles
• Downstream flow and water quality alterations, sometimes with dramatic changes on temperature and physical-chemical parameters of the water

These effects were summarized from the extensive bibliography gathered on the effects of dams on freshwater biodiversity worldwide, see dam effects bibliography section below.

Study on the small barriers of the Douro Basin

FISH

No diadromous fish was detected in any of the 380 sites with the exception of two European eels captured in Tera River in Spain likely introduced by man in Sanabria lake, and a single European Eel in the Sousa River, downstream of the first big dam. This once again confirms that diadromous fish are long gone from most of the Douro River Basin since the construction of the first large dams. The European eel (*Anguilla Anguilla*), two species of shad (*Alosa alosa* and *Alosa fallax*), the Atlantic Salmon (*Salmo Salar*), the European sturgeon (*Acypenser sturio*) and the sea lamprey (*Petromyzon marinus*) were commonly present and some of these species were known to reach high abundances in the Douro River basin.
The detailed survey confirmed these four basins as a stronghold for the native Douro basin fish and freshwater mussels, many of them highly threatened (Supplementary Table 1).
No significant differences in the fish species richness and abundance was detected between the distinct stretch categories, although invasive fish taxa and abundances are, in average, higher in reservoir sites (Fig. 3).

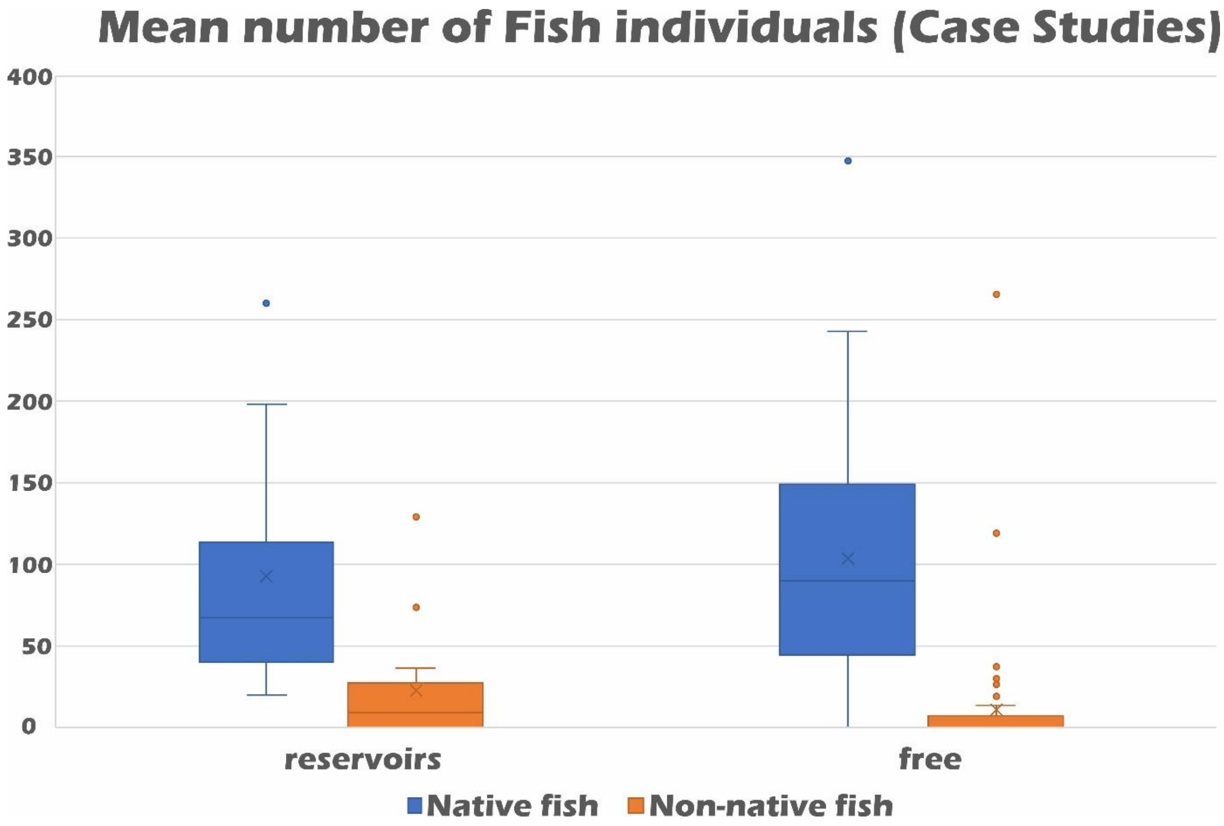

Figure 3. Average number of native and non-native fish individuals collected per reservoir and free river sites in the four studied river sub-basins (Paiva, Sabor, Tâmega and Tua).

Diversity metrics also do not seem to indicate any tendency to decrease in sites affected by these small barriers. An exception is made for sites downstream of barriers where fish species with lower dispersion rates (*Squalius*, *Achondrostoma* and *Cobitis* spp.) are less abundant than in reservoirs, upstream or free sites.

Contrary to what has been shown for large dams, the present results seem to suggest that the impacts of small barriers and weirs (< 5 m height) are smaller regarding the quality of the fish habitat and may even improve the heterogeneity of the hydrological regime allowing for a higher number of refugia for draught in the summer and high flows in the winter. Nevertheless, it also shows a higher affinity of invasive species to these lentic environments and may provide important refugia and sources for invasive species allowing for their long-term maintenance, and potentially increasing acclimation and expansion success.

Genetic diversity

There was no previous knowledge about the genetic structure of fish species within the Douro basin. We had predicted that similarly to the general trends, common to most river basins, genetic diversity would decrease from downstream to upstream areas. We also hypothesized that given the complex hydrological history of the Douro River basin, distinct sub-basins might harbour distinct and unique genetic lineages and or species. Dams potentially exacerbate this pattern leading to the isolation and higher exposure to gene erosion and extirpation of upstream or isolated populations. We firstly had selected threatened species from the genus *Pseudochondrostoma* with a higher dispersal ability and three with lower vagilities (genera *Achondrostoma*, *Cobitis* and *Squalius*).

Pseudochondrostoma duriense

The Northern straight-mouth nase (*Pseudochondrostoma duriense*) once abundant and widespread in the Douro River basin is now mainly restricted to the Portuguese populations, especially on the four target sub-basins (Paiva, Sabor, Tâmega and Tua: see report on Task 3.2.1). This species has a high vagility due to its long migration upstream to spawn. This was confirmed with the mitochondrial markers that have not revealed a strong genetic differentiation of the species across the basin (Fig. 4).

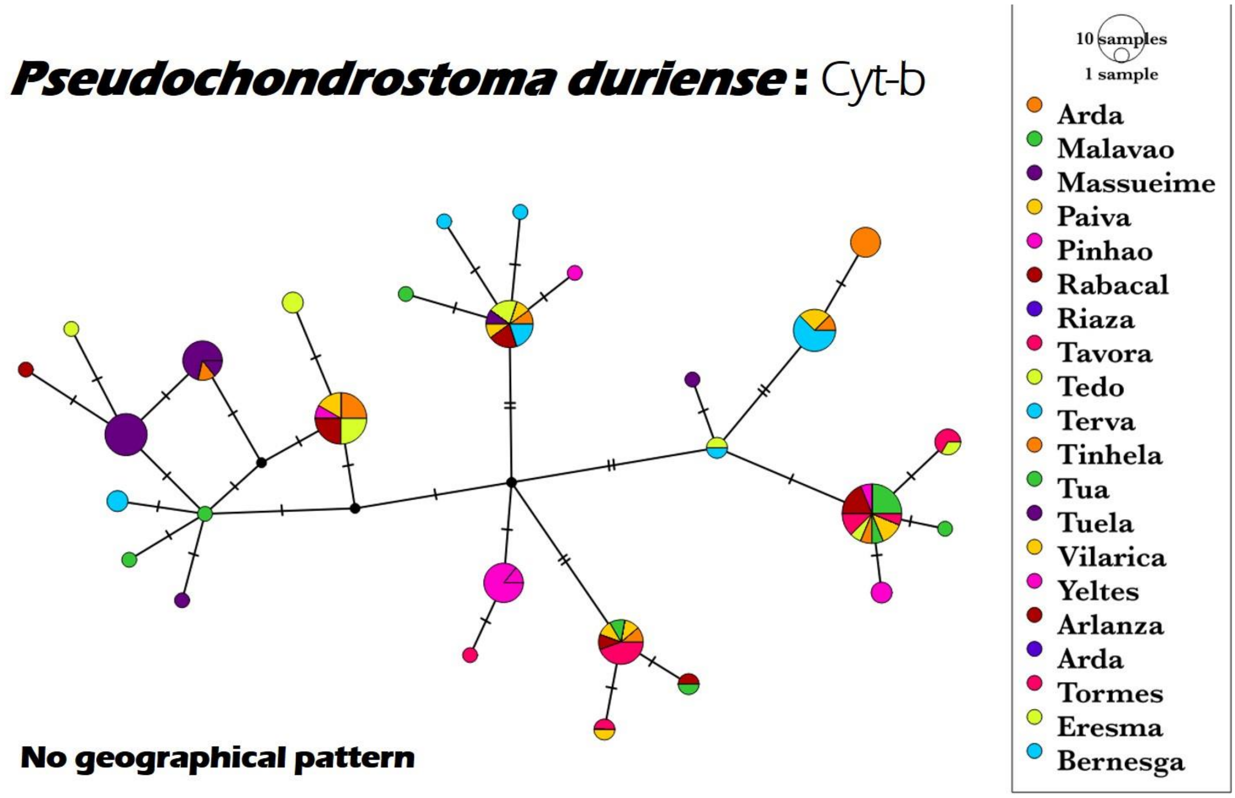

Figure 4. Median joining haplotype network of the Cyt-b gene of the Northern straight-mouth nase (*Pseudochondrostoma duriense*) across the whole Douro basin. Each circle consists of a distinct haplotype, size of the circle is proportional to the number of individuals with the same haplotype. Dashes between haplotypes consist of number of nucleotide substitutions.

Genetic diversity was generally lower than in *Achondrostoma* spp. (see below), which for a species with high vagility could mean that it has been suffering from genetic erosion possibly due to the lack of connectivity and the high number of physical barriers among the populations on the edges of distribution. Also, the few detected populations in Spain and those in Tâmega, Tormes and Esla sub-basins show a much lower genetic diversity indicating that upstream or populations isolated by dams are suffering from accelerated genetic erosion (Fig. 5). Again, the populations of Sabor, Paiva and Tua revealed to be the strongholds of the species with a higher genetic diversity and more abundant populations of this threatened species.

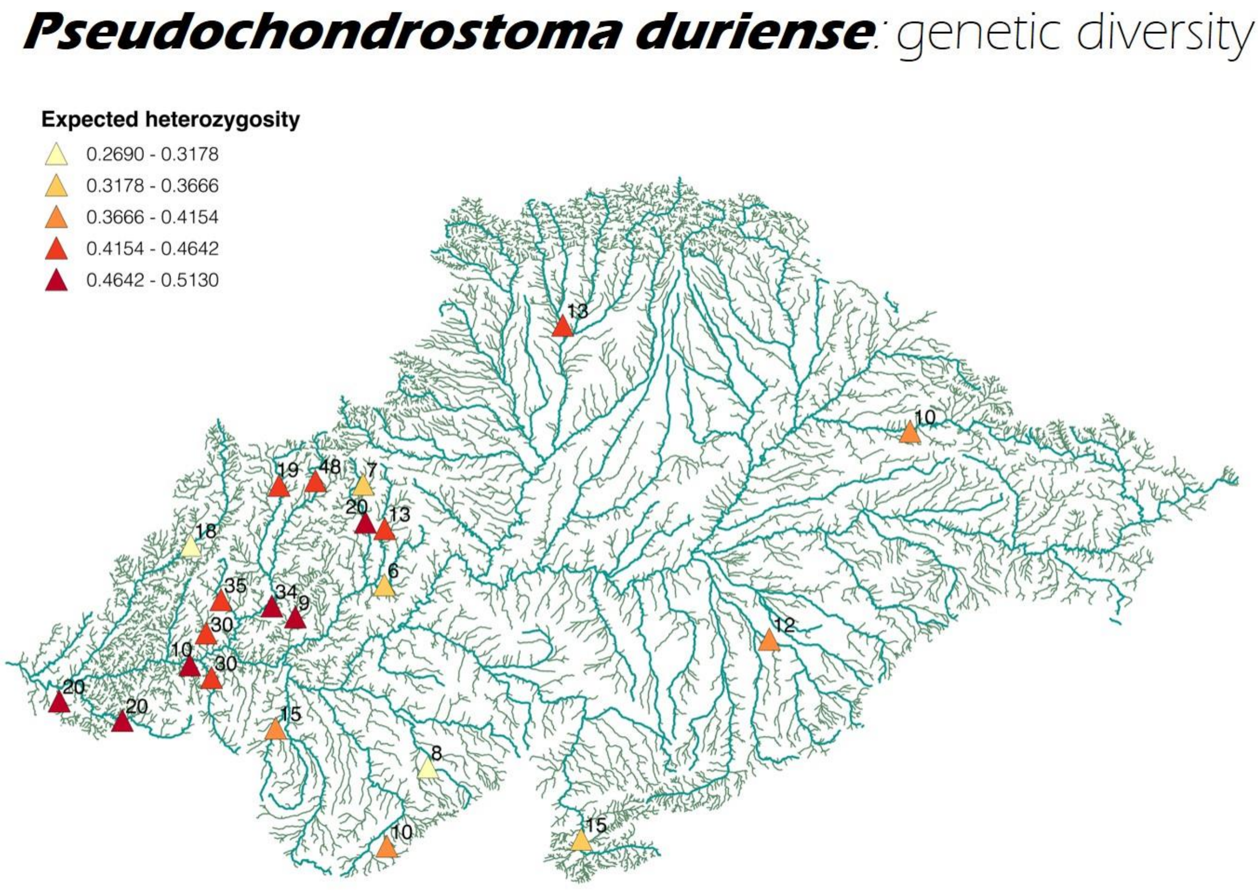

Figure 5. Map of the collected populations (coloured triangles) of the Northern straight-mouth nase (*Pseudochondrostoma duriense*) across the whole Douro basin selected for genetic analyses. The colour of each triangle is coded with the expected heterozygosity a standard genetic diversity metric. Expected heterozygosity was estimated by the microsatellite marker dataset. Number superscripts on the triangles mean the number of individuals sequenced.

Achondrostoma spp.

The genetic diversity found on this genus reveals an interesting mosaic of lineages or putative species coherent with distinct biogeographic regions (Fig. 6).

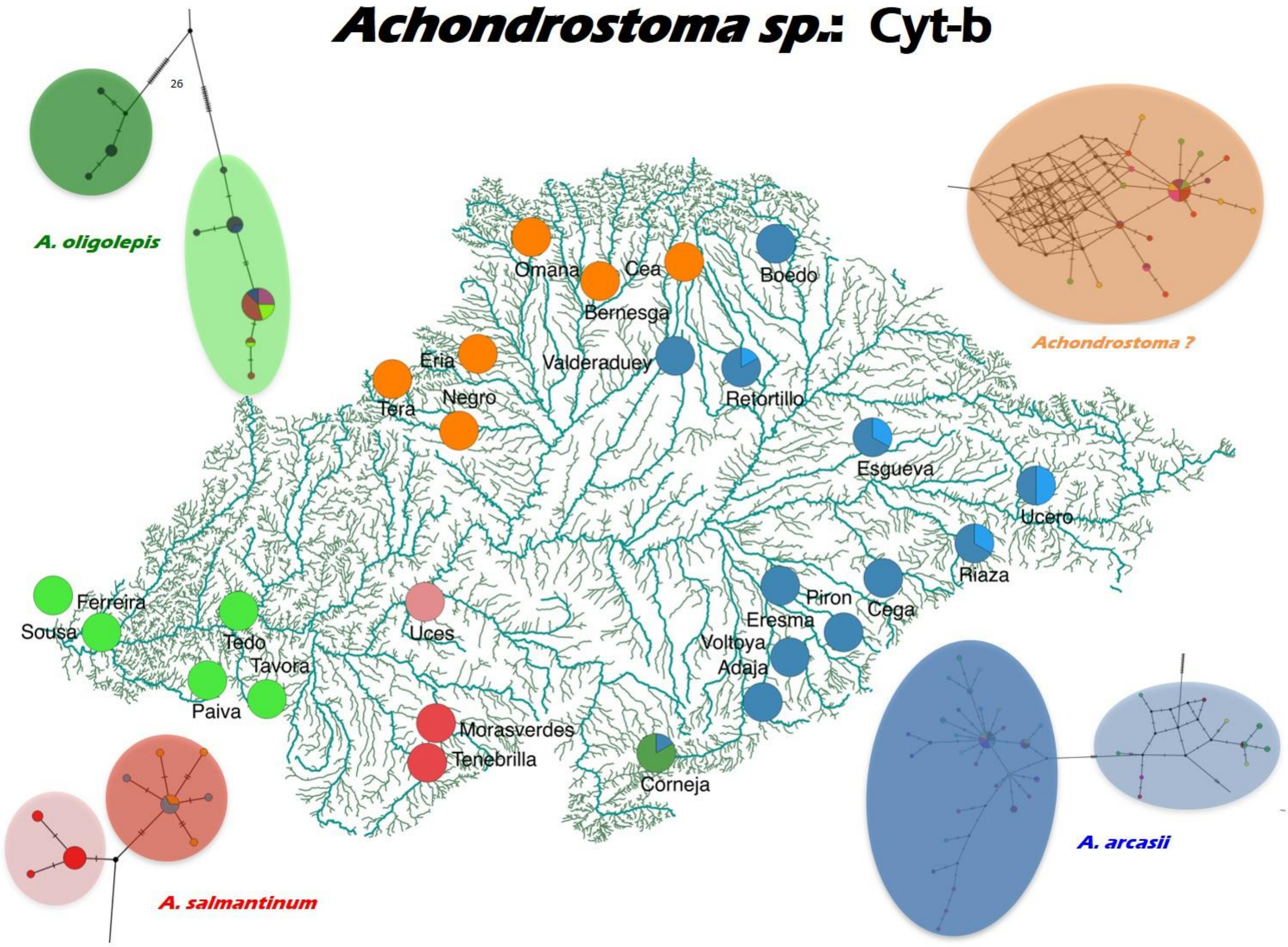

Figure 6. Map of the collected populations (coloured circles) of the four *Achondrostoma* species across the whole Douro basin selected for genetic analyses. The colour within each circle is coded with the corresponding species/lineage. The median joining haplotype network of the Cyt-b gene of each of these four species is presented on the corners.

The Western ruivaco (*Achondrostoma oligolepis*: green in Fig. 6) occupies the western region of the basin in Portugal, an undescribed lineage/species of *Achondrostoma* (orange in Fig. 6) occurs at the right Douro bank Esla and Sabor sub-basins, the Sarda (*Achondrostoma salmantinum*: red in Fig. 6) occurs in the Huebra and Tormes sub-basins on the left Douro bank and finally the Bermejuella (*Achondrostoma arcasii:* blue in Fig. 6) inhabits the inner eastern sections of the basin. These lineages are old divergent events and should not be related to the separation provoked by the more recent physical barriers. Genetic diversity of *A. oligolepis* and of the Douro endemic and highly imperilled *A. salmantinum* is much lower than the other two species (Fig. 7). This decrease of diversity could be an indication of increased fragmentation and genetic erosion of upstream populations of these species due to the high number of barriers. While *A. oligolepis* is restricted to small rivers trapped between the Douro large dam reservoirs and large dams within each of these rivers, *A. salmantinum*, is confined to the upper stretches of the Tormes and Huebra river basins being quite fragmented by dams and barriers and with the lower sections impacted by urbanization and mainly agriculture and water shortage.

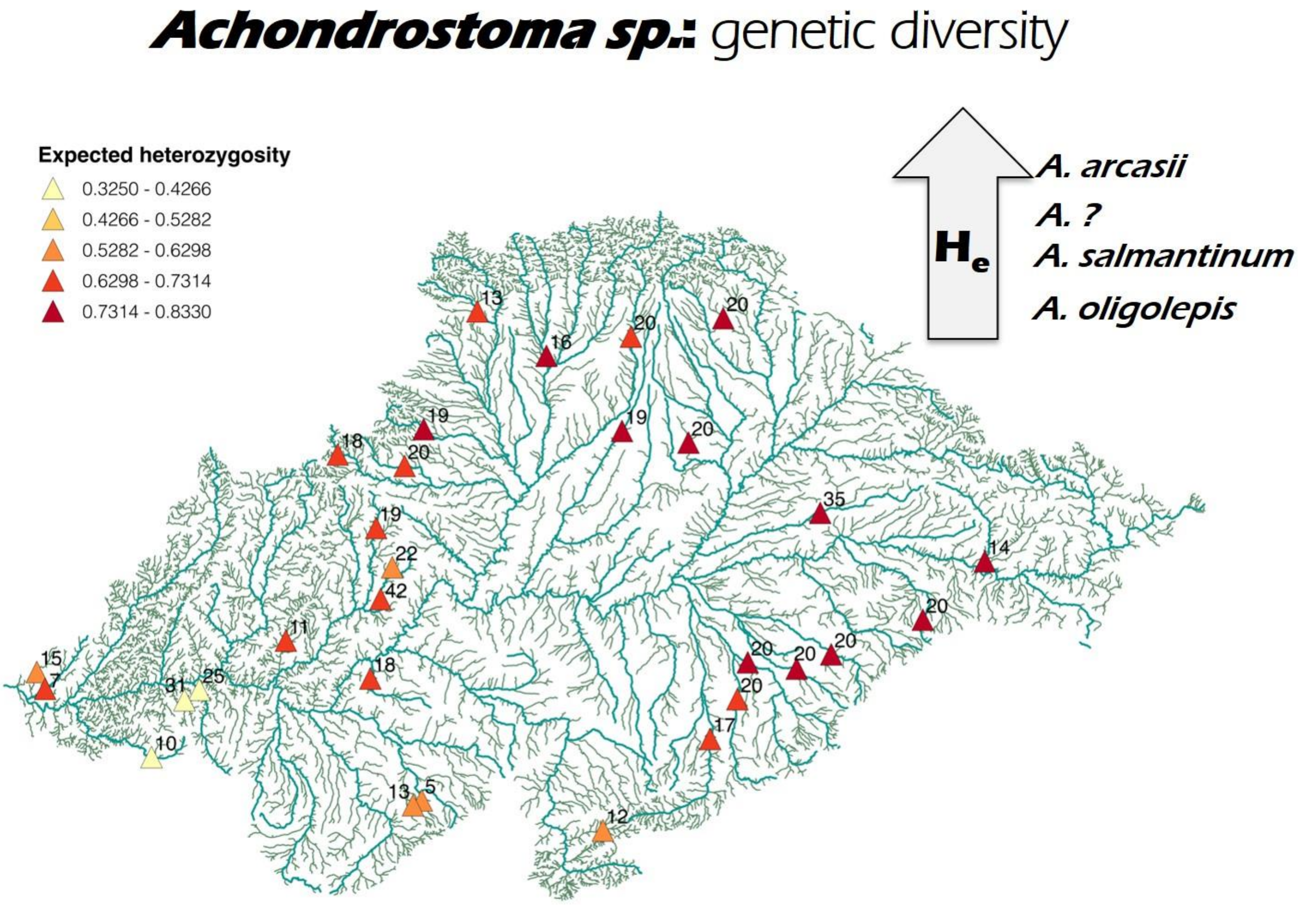

Figure 7. Map of the collected populations (coloured triangles) of the four *Achondrostoma* species across the whole Douro basin selected for genetic analyses. The colour of each triangle is coded with the expected heterozygosity (H_e), a standard genetic diversity metric. Expected heterozygosity was estimated by the microsatellite marker dataset. Number superscripts on the triangles mean the number of individuals sequenced.

Squalius carolitertii

Although the Northern Iberian chub (*Squalius carolitertii*) is less vagile than *P. duriense*, the genetic differentiation is very low across the basin, suggesting that the gene flow among populations of this species was high across the basin, previous to the construction of the man-made physical barriers to dispersion. In fact, a single haplotype was retrieved for COI for all populations and a shallow genetic structure with the faster marker Cyt-b (Fig. 8)

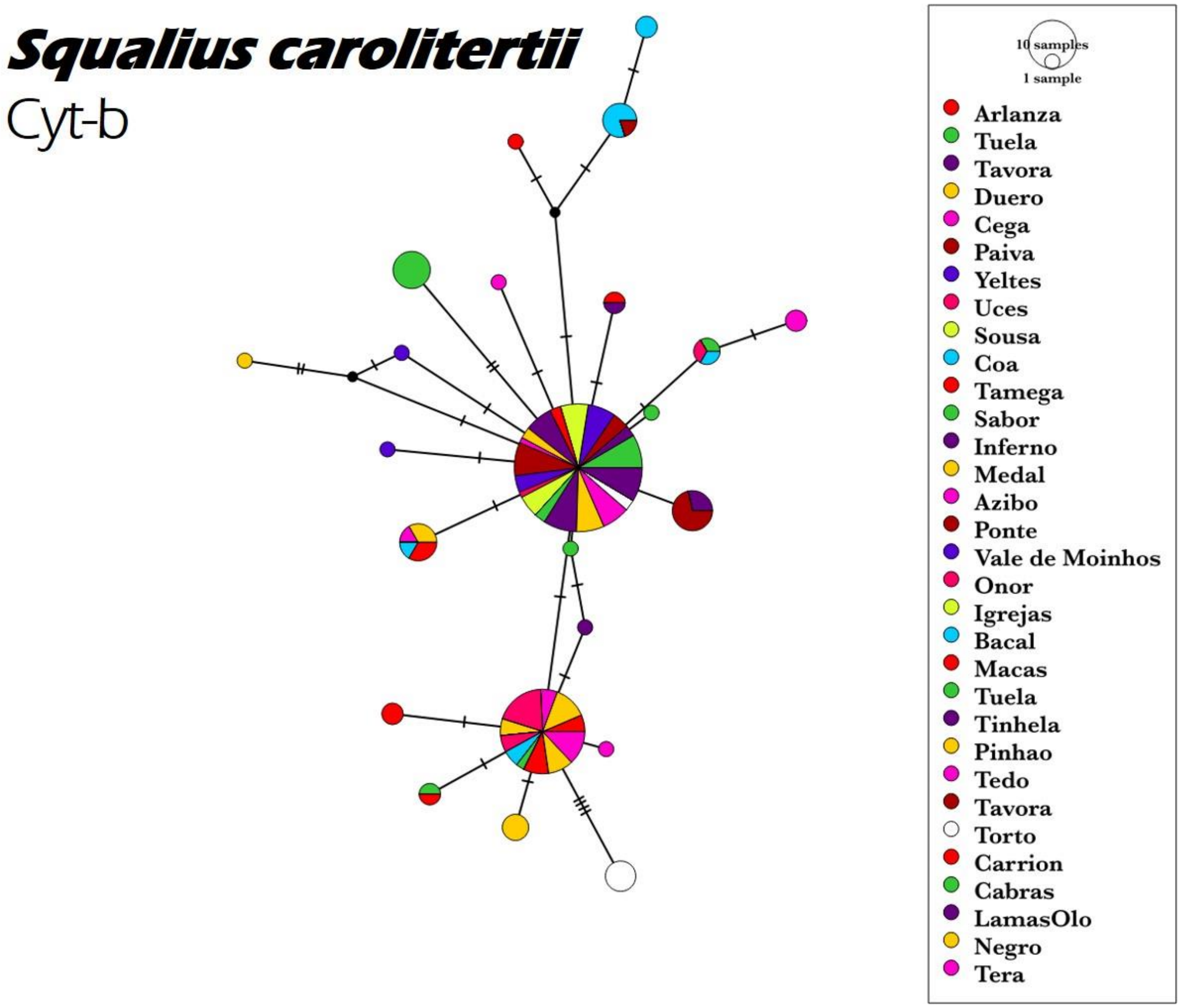

Figure 8. Median joining haplotype network of the Cyt-b gene of the Northern Iberian chub (*Squalius carolitertii*) across the whole Douro basin. Each circle consists of a distinct haplotype, size of the circle is proportional to the number of individuals with the same haplotype. Dashes between haplotypes consist of number of nucleotide substitutions.

The microsatellite work also revealed a lack of genetic differentiation among populations and still did not reveal genetic erosion on populations isolated by dams (Fig. 9). Again, the stronghold of the species is in the Portuguese sub-basins with higher abundances and genetic diversity (Fig. 10).

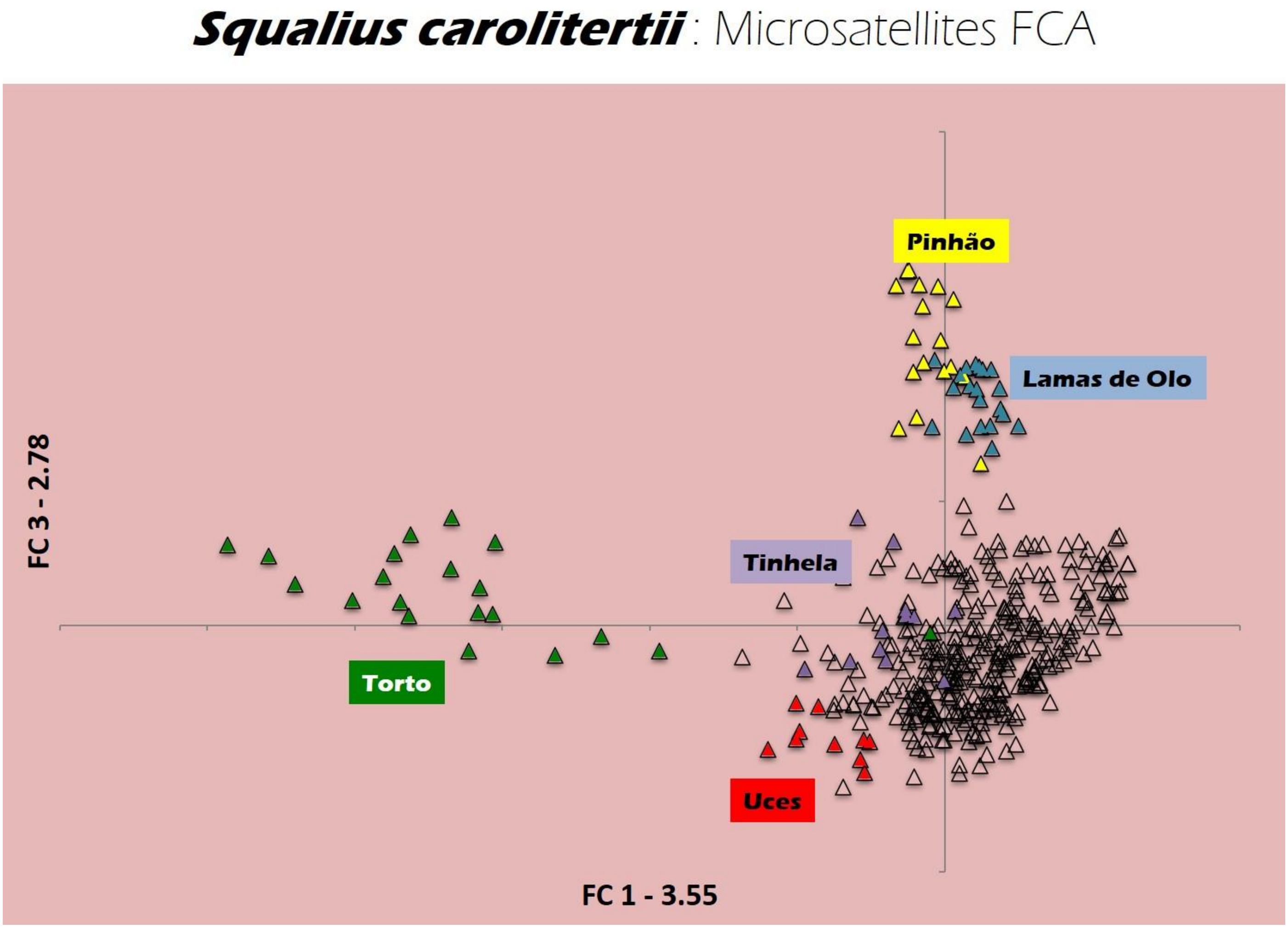

Figure 9. Factorial Correspondence Analysis (FCA) based on the Microsatellite loci used. Clustering patterns indicate genetic relatedness. The five more divergent populations are depicted in different colours.

Squalius carolitertii: genetic diversity

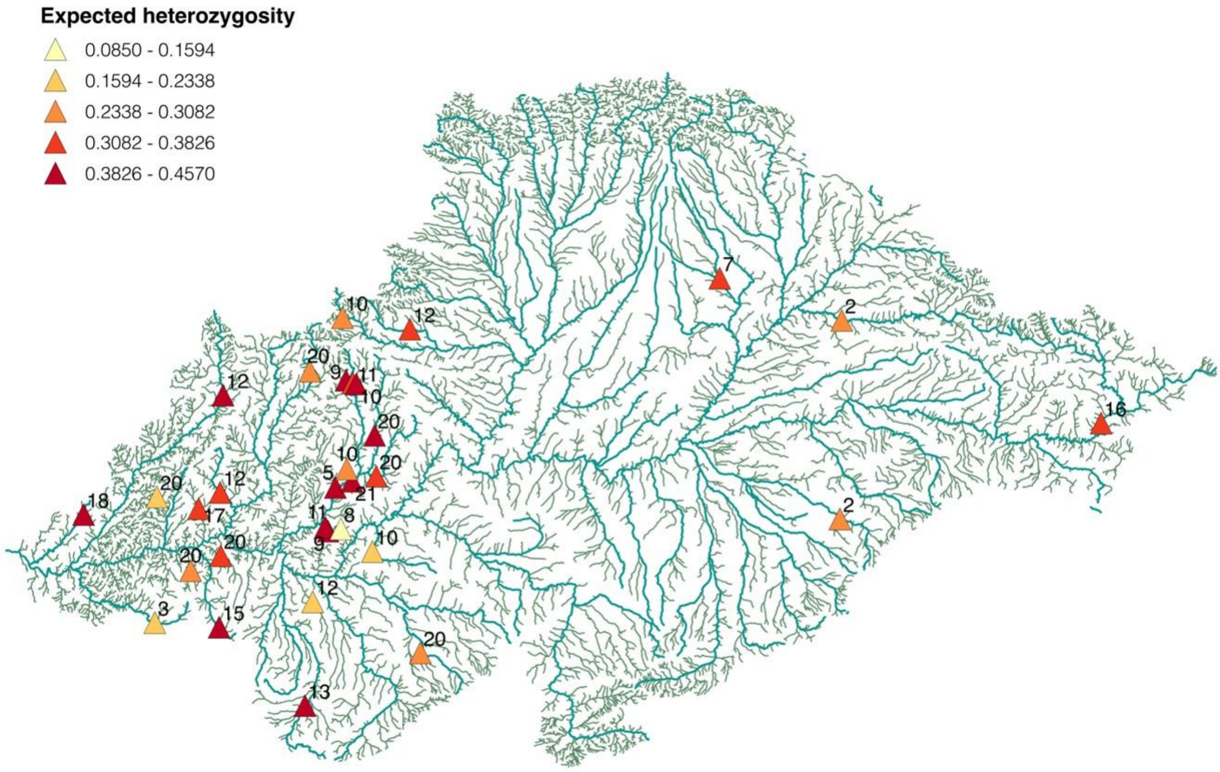

Figure 10. Map of the collected populations (coloured triangles) of the Northern Iberian chub (*Squalius carolitertii*) across the whole Douro basin selected for genetic analyses. The colour of each triangle is coded with the expected heterozygosity a standard genetic diversity metric. Expected heterozygosity was estimated by the microsatellite marker dataset. Number superscripts on the triangles mean the number of individuals sequenced.

Cobitis spp.

We found abundant populations of *Cobitis* in the central basins of the Douro, e.g. Esla, Sabor, Tua and Tormes, mainly in the middles and upper sections. These species are considered to have low dispersion and therefore gene flow among populations low. Previously to this study, only three species of *Cobitis* have been reported from the Douro River basin all of them highly threatened, i.e. the Northern Iberian spined-loach (*Cobitis calderoni*); the Vettonian spined-loach (*Cobitis vettonica*) and the Southern Iberian spined-loach (*Cobitis paludica*). The latter species has been hypothesized as being an introduction from southern basins, but a more detailed study is still needed to confirm this. We have detected all three species in the Douro basin, *C. paludica* in the Sabor, Huebra and Tormes Basins, *C. calderoni* in the Tua and Pisuerga basins, and *C. vettonica* in the Agueda and also in the Tormes basins (Fig. 11).

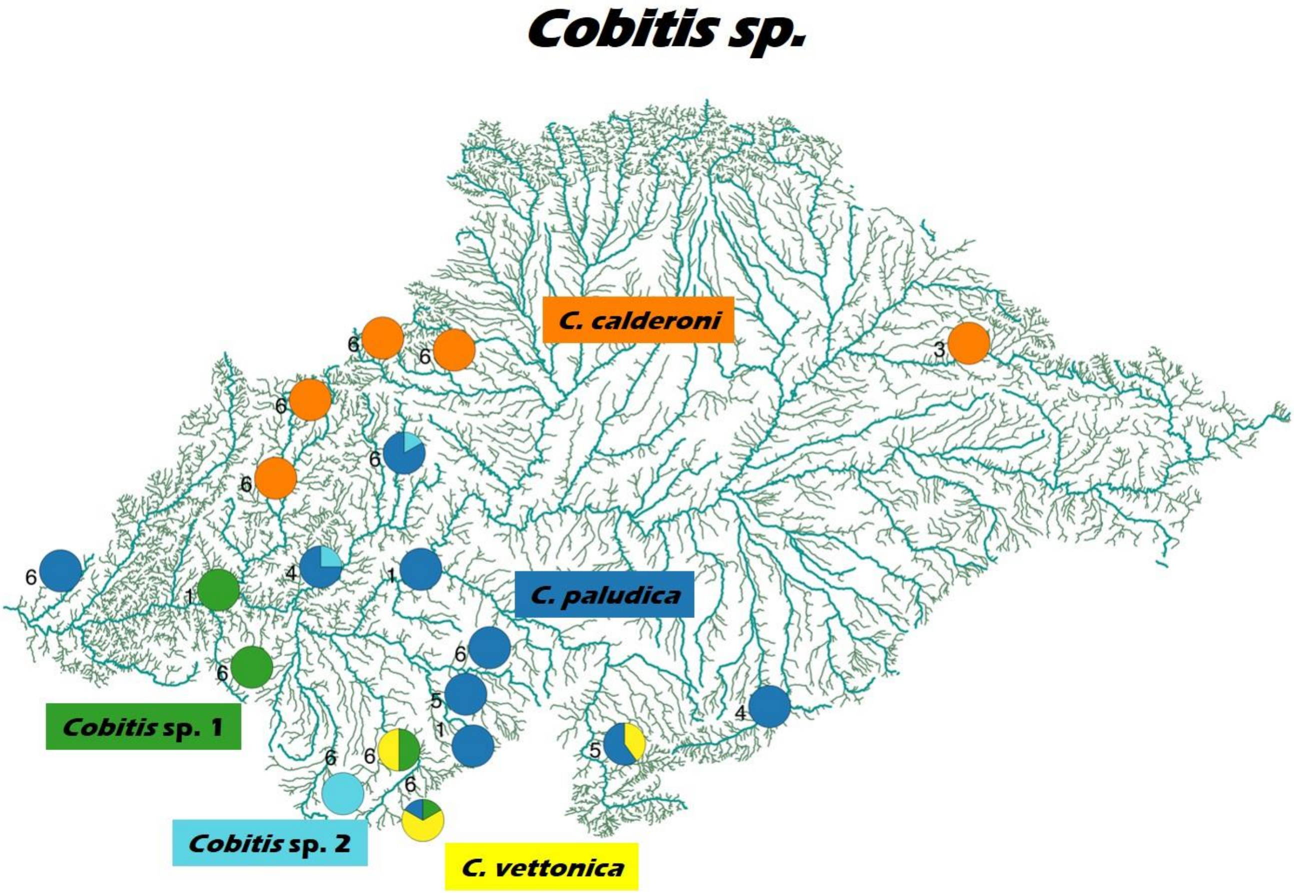

Figure 11. Map of the collected populations (coloured circles) of the four *Cobitis* species across the whole Douro basin selected for genetic analyses. The colour within each circle is coded with the corresponding species/lineage.

Besides these species and based on the genetics results we found two other undescribed species, one (*Cobitis* sp. 1) in Torto and Tavora sub-basins in Portugal and Agueda in Spain and the other (Cobitis sp. 2) in the Côa and Sabor River basins (Fig. 11). These new putative species are highly divergent genetically from the one previously described in all mitochondrial and nuclear markers used, suggesting that the systematics and taxonomy, and consequentially the conservation status of the species within this genus should be urgently revised (Fig. 12). We were unable to develop fast evolving markers to detect genetic diversity at a finer scale and therefore to estimate the impacts of physical barriers on their connectivity.

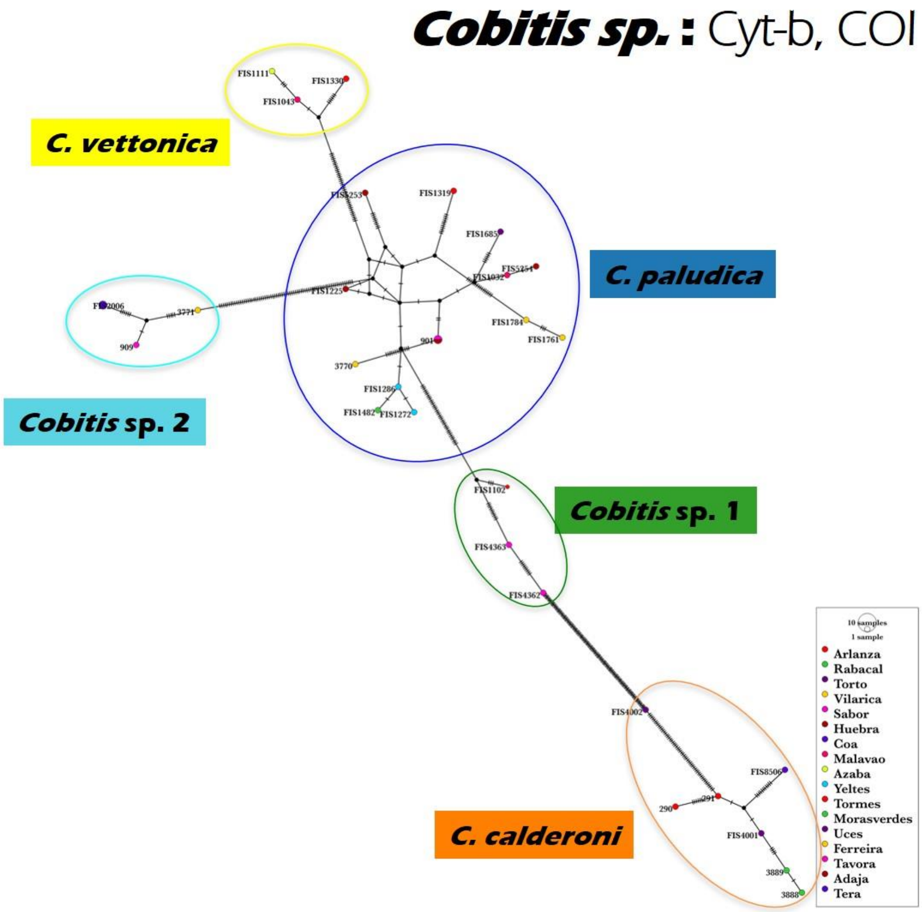

Figure 12. Median joining haplotype network of the concatenated Cyt-b + COI + RAG1 genes of the Iberian loach (*Cobitis*) species across the whole Douro basin. Each circle consists of a distinct haplotype, size of the circle is proportional to the number of individuals with the same haplotype. Dashes between haplotypes consist of number of nucleotide substitutions.

Freshwater mussels

Freshwater mussels are bivalves of the order Unionida that are strictly freshwater and have a parasitic stage of their life-cycle on fish. Their larvae must attach to a specific fish species to be able to complete their life-cycle and disperse upstream against the current. These organisms are extremely sensitive to environmental changes such as the degradation of water quality, substrate, and hydrological regimes. For these reasons, this group of organisms is among the most threatened worldwide (Lopes-Lima et al 2014; 2017; 2018). The extreme sensibility of these mussels to habitat perturbation also makes them an excellent warning system for impacts in the aquatic ecosystem and the adjacent terrestrial habitats.

Our study across the whole Douro River basin revealed that mussels, and especially those that prefer lotic habitats, are rarely found on reservoirs and immediately downstream of small physical barriers such as small dams and weirs. This results from the fact that sediment accumulation of fine sediments in the reservoir lead to unsuitable substrate for these mussels. Additionally, the slower flow of these changed habitats may also decrease oxygen exchange rates especially for species with high oxygen demand and more used to leave in lotic environments. Habitats downstream of dams usually have highly unstable water velocities and therefore unstable substrate, which does not enable mussels to settle during high flow. Nevertheless, some semi destroyed barriers and small weirs and water mills barriers have a beneficial effect, especially in Mediterranean climate intermittent rivers such as those east of the Tua River basin. One of the other major threats to aquatic biodiversity in the Douro River is the decrease of water quantity that has led to complete draught of many rivers and streams of the Douro River basin, especially those in the Mediterranean climate region. In these rivers, aquatic biodiversity persisted during summer months in temporary pools. The number and size of these pools or refuges have dramatically decreased or even disappeared in many watercourses during the past decades, provoking the extirpation of most populations of water dependent organisms, especially those that have low mobility, such as freshwater mussels and some small fish species. Very small barriers in these water-scarce habitats may provide refuge for aquatic taxa by the persistence of water in the reservoirs and therefore provide an artificial improvement for local biodiversity. Lotic species were specially affected by barriers due to their inability to withstand low water current and soft sediments.

Four species of these freshwater mussels are currently present in the Douro River basin: the freshwater pearl mussel *Margaritifera margaritifera*, the dolphin mussel *Unio delphinus*, the duck mussel *Anodonta anatina* and the dark mussel *Potomida littoralis*.

Margaritifera margaritifera

The freshwater pearl mussel *Margaritifera margaritifera* a species that is considered as Critically Endangered in Europe and can only survive in pristine flowing waters. This species has dramatically disappeared from most of the Douro basin and good recruiting populations persist only in remote or protected areas in the Tua, Paiva and Tâmega basins in Portugal.

The overall results from our case study on the small hydropower dams on this species show that even these small barriers can deeply affect pearl mussel populations: most specimens were almost extirpated from the areas within the reservoirs and sites located downstream only contained adults without any recent recruitment. In this study, already published in an international peer-reviewed scientific journal (Sousa et al 2020) we invoked that the need for future management measures devoted to the conservation of pearl mussels should consider these results. Particularly the improvement of flow management in areas downstream of dams. Additionally, this study strongly suggests that the construction of new dams in pearl mussel rivers should be avoided and that old or obsolete dams in these areas should be decommissioned and removed.

Unio delphinus

The Iberian dolphin mussel *Unio delphinus* was once widespread throughout the Douro River basin and is now mainly restricted to a few strongholds in the Tua, Sabor, Tâmega, Côa and Tormes basins although smaller populations can still be found in other basins. The species was assessed by IUCN as Near Threatened in 2011 but a recent study reassessed the conservation status of this mussel as Endangered given their short area of occupancy and decline rates. This species has been highly affected by the construction of the Sabor and Tua river dams, having lost considerable sections of their range. The species is now severely fragmented by dams and populations highly exposed to genetic erosion and local extirpation, especially those in the Mediterranean climate zone in Spain.

Potomida littoralis

This species only occurs in Southwest Europe and Northern Africa and is rapidly disappearing from the Iberian Peninsula and is now considered Endangered by the IUCN Red List. The species was quite common throughout the Douro River basin but is now restricted to very few locations with good populations only in the Sabor and Tua River basins. The construction of the Sabor and Tua basins had a high impact on both populations which had their habitat range reduced to less than half. This species can only survive in lotic environments, therefore, dams and changes in the hydrological regime may have a strong negative impact on their populations. This species is a habitat specialist, it occurs only in lotic habitats and changes on the hydrological regimes have strong impacts on its survival. The species was never detected in reservoirs, even of small dams and weirs.

Anodonta anatina

The duck mussel *Anodonta anatina* is widespread in Europe and although is still considered as Least Concern by the IUCN Red List its populations have been declining throughout its whole distribution. The same is happening in the Iberian Peninsula and in the Douro Basin where the species disappeared from most of its Spanish range. This species can better withstand changes in the hydrological regimes since it prefers slow moving waters and is able to survive in some dam reservoirs. In the lower section of the Tâmega basin and in the main River Douro in Portugal, this species replaced the other mussel species previously present like *Margaritifera margaritifera* and *Potomida littoralis*. Although this species is more plastic in its ability to withstand lentic environments, it already disappeared from most of its Spanish range, given that we were unable to find a single live specimen in this country. This fact was probably due to the synergistic effects of habitat degradation and water shortage together with the extensive fragmentation from dams and other barriers that avoided the recolonization of locally extirpated populations. Other threats such as the presence of invasive species promoted by the lentic environments is also a major impact given that these mussels are unable to complete their life cycle in most of invasive fish that now predominate in large areas of the basin.

Effects of dams on Freshwater Mussels

As in fish, dams and other physical barriers change the physical characteristics of mussel ecosystems and can disturb natural meta-population structure by blocking gene flow (Geist & Kuehn 2005). The consequent fragmentation is also a menace to long-term population persistence because it excludes the possibility of recolonization after an acute disturbance (e.g. drought, toxic spill etc…) due to the disconnection of fish-host migration from contiguous non-disturbed regions (Haag 2012). This condition may be more severe in freshwater mussels such as *M. margaritifera* that are contingent to vagile or migratory host-fishes, but less important in mussel species such as *A. anatina* that use less-mobile hosts (Douda et al 2013). Due to the changes of hydrologic regime on dam reservoirs, dams usually benefit lentic or habitat generalist taxa such as *A. anatina* and reduce or eradicate lotic species such as *M. margaritifera* or Potomida littoralis (Lopes-Lima et al 2017). Dams also negatively impact mussel habitat through changes in the substrate, flow, and temperature (Mueller et al., 2011). Increased siltation in dam reservoirs and decreases in substrate porosity are particularly harmful to rheophilic mussel species such as *M. margaritifera*, directly by increasing juvenile mortality due to the decrease in oxygen availability within the sediments (Osterling et al 2010), and also indirectly by decreasing hatching levels of salmonid hosts (Sternecker et al 2013). Other freshwater mussel species such as *Anodonta anatina* and *Unio delphinus* appear to be much more tolerant of fine sediments. Water releases from large dams repeatedly result in both unusually high and low flows (Vaughn & Taylor, 1999). Strong water currents can dislodge adults and juveniles and may impair recruitment. By contrast, prolonged periods of low flow downstream of dams may cause massive mussel mortality due to stranding and low oxygen levels. Changes to thermal regimes because of dams can have great effects on fish communities, and on the reproductive ability of freshwater mussels (Lopes-Lima et al 2017).

MACROINVERTEBRATES

Although the effects of large dams are already known to be very strong on the macroinvertebrate communities (e.g., Crosa et al 2009; Jones et al 2012; Krajenbrink et al 2019), the main biodiversity metrics (e.g., Shannon and evenness) presented no significant differences among sites, downstream, upstream and within reservoirs, when accounting for the small barriers study carried here (Fig. 13). Nevertheless, some macroinvertebrate groups with a strong preference for lotic conditions such as the Mollusca, Odonata and Trichoptera were in general less represented in reservoirs (supplementary table 1).

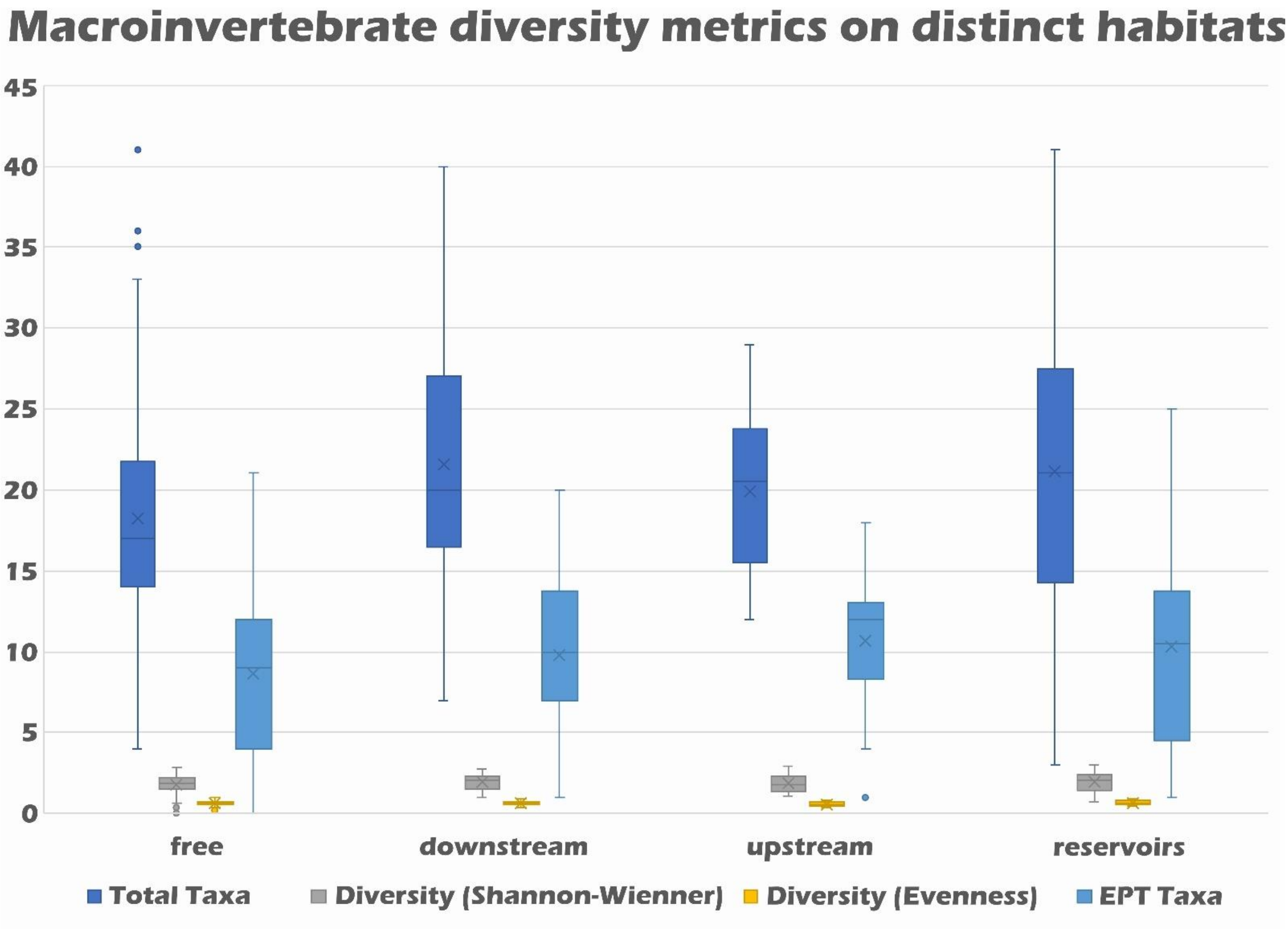

Figure 13. Macroinvertebrate communities' diversity metrics for stretches in distinct habitats: within reservoirs, upstream, downstream, and free from the barrier influence (<1 km from the reservoir). EPT refers to the macroinvertebrate reference groups Ephemeroptera, Plecoptera and Trichoptera.

Conclusions

Barriers higher than five meters have been shown to produce severe negative impacts on freshwater diversity. In the four target sub-basins, the Paiva is not affected by large dams but is still affected by several smaller ones with negative effects on the local diversity. The Tâmega, Tua and Sabor have large dams that fairly reduced the available habitat for the River Douro native species of fish and mussels. To notice that these basins are still the hotspot of diversity and the strongholds of fish diversity within the Douro Basin. Therefore, the construction of any additional dams should be avoided. Additionally, the decommissioning of all obsolete barriers higher than 5 meters should be pursued with urgency. In alternative, the construction of effective fish passes is a good mitigating measure to be applied. As for the ecological effects of small barriers (< 5 meters) should be considered on a case by case basis, given that some might benefit the local biodiversity by providing refuge for extreme changes in hydrological regimes such as draught and floods.

References:

Almaça C, Elvira B (2000). Past and Present distribution of *Acipenser sturio* L., 1758 on the Iberian Peninsula. Bol Inst Esp Oceanogr 16: 11-16.

Cortes R, Peredo A, Terêncio DP, Sanches Fernandes LF, Moura JP, Jesus JJ, Pacheco FA (2019) Undamming the Douro River catchment: A stepwise approach for prioritizing dam removal. Water 11: 693.

Cummings K, Jones H, Lopes-Lima M. 2016. Rapid Bioassessment Methods for Freshwater Molluscs. In Core Standardized Methods for Rapid Biological Field Assessment (Ed Trond H. Larsen), Conservation International, pp.185-207. ISBN: 978-1-934151-96-9

Douda K, Lopes-Lima M, Hinzmann M, Machado J, Varandas S, Teixeira A, Sousa R (2013) Biotic homogenization as a threat to native affiliate species: fish introductions dilute freshwater mussels's resources. Diversity and Distributions 19: 933-942.

Geist J, Kuehn R (2005) Genetic diversity and differentiation of central European freshwater pearl mussel (*Margaritifera margaritifera* L.) populations: implications for conservation and management. Molecular Ecology 14: 425–439.

Haag WR (2012) North American Freshwater Mussels: Natural History, Ecology, and Conservation. Cambridge University Press, Cambridge.

Lopes-Lima M, Teixeira A, Froufe E, Lopes A, Varandas S, Sousa R (2014) Biology and conservation of freshwater bivalves: past, present and future perspectives. Hydrobiologia 735: 1-13.

Lopes-Lima M, Sousa R, Geist J, Aldridge DC, Araujo R, Bergengren J, Bespalaja Y, Bódis E, Burlakova L, Van Damme D, Douda K, Froufe E, Georgiev D, Gumpinger C, Karatayev A, Kebapçi U, Killeen I, Lajtner J, Larsen BM, Lauceri R, Legakis A, Lois S, Lundberg S, Moorkens E, Motte G, Nagel KO, Ondina P, Outeiro A, Paunovic M, Prié V, von Proschwitz T, Riccardi N, Rudzīte M, Rudzītis M, Scheder C, Osterling ME, Arvidsson BL, Greenberg LA (2010) Habitat degradation and the decline of the threatened mussel Margaritifera margaritifera: influence of turbidity and sedimentation in the mussel and its host. Journal of Applied Ecology 47: 759–768.

Seddon M, Şereflişan H, Simić V, Sokolova S, Stoeckl K, Taskinen J, Teixeira A, Thielen F, Trichkova T, Varandas S, Vicentini H, Zajac K, Zajac T, Zogaris S. (2017). Conservation status of freshwater mussels in Europe: state of the art and future challenges. Biological Reviews 92: 572-607.

Lopes-Lima M, Burlakova LE, Karatayev AY, Mehler K, Seddon M, Sousa R (2018) Conservation of freshwater bivalves at the global scale: diversity, threats and research needs. Hydrobiologia 810: 1-14.

Sousa R, Ferreira A, Carvalho F, Lopes-Lima M, Varandas S, Teixeira A, Gallardo B (2020) Small hydropower plants as a threat to the endangered pearl mussel Margaritifera margaritifera. Science of The Total Environment 719: 137361.

Sternecker K, Geist J (2010) The effects of stream substratum composition on the emergence of salmonid fry. Ecology of Freshwater Fish 19: 537–544.

References for the effects of dams on freshwater diversity:

Agostinho AA, Pelicice FM, Gomes LC (2008) Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. Braz J Biol 68: 1119–1132

Basson G (2004) Hydropower dams and fluvial morphological impacts – an African perspective. The 10th United Nations Symposium on Hydropower and Sustainable Development. Beijing, pp 1–16

Basson G, Rooseboom A (1997) Dealing with reservoir sedimentation. Water Research Commission, Pretoria

Baumgartner MT, Piana PA, Baumgartner G, Gomes LC (2020) Storage or run-of-river reservoirs: exploring the ecological effects of dam operation on stability and species interactions of fish assemblages. Environmental Management 65: 220-231.

Baxter RM (1977) Environmental effects of dams and impoundments. Annu Rev Ecol Syst 8:255–283

Camargo JA (2017). Multimetric assessment of macroinvertebrate responses to mitigation measures in a dammed and polluted river of Central Spain. Ecological Indicators 83: 356-367.

Cooper AR, Infante DM, Daniel WM, Wehrly KE, Wang L, Brenden TO (2017) Assessment of dam effects on streams and fish assemblages of the conterminous USA. Science of the Total Environment: 586, 879-889.

Crosa G, Castelli E, Gentili G, Espa P (2009) Effects of suspended sediments from reservoir flushing on fish and macroinvertebrates in an alpine stream. Aquat Sci 72:85–95

Górski K, van den Bosch LV, van de Wolfshaar KE, Middelkoop H, Nagelkerke LAJ, Filippov OV, Zolotarev DV, Yakovlev SV, Minin AE, Winter HV, De Leeuw JJ, Buijse AD, Verreth JAJ (2012) Post-damming flow regime development in a large lowland river (Volga, Russian Federation): implications for floodplain inundation and fisheries. River Res Appl 28:1121–1134

Grill G, Lehner B, Lumsdon AE, MacDonald GK, Zarfl C, Reidy Liermann C (2015) An indexbased framework for assessing patterns and trends in river fragmentation and flow regulation by global dams at multiple scales. Environ Res Lett 10:15001

Hastings RP, Meiners SJ, Colombo RE, Thomas TE (2016) Contrasting impacts of dams on the metacommunity structure of fish and macroinvertebrate assemblages. North American Journal of Fisheries Management 36: 1358-1367.

Henley WF, Patterson MA, Neves RJ, Lemly AD (2000) Effects of sedimentation and turbidity on lotic food webs: a concise review for natural resource managers. Rev Fish Sci 8:125–139

Itsukushima R, Ohtsuki K, Sato T, Kano Y, Takata H, Yoshikawa, H (2019) Effects of sediment released from a check dam on sediment deposits and fish and macroinvertebrate communities in a small stream. Water 11: 716.

Jones JI, Murphy JFJ, Collins AL, Sear DA, Naden PS, Armitage PD (2012) The impact of fine sediment on Macro-Invertebrates. River Res Appl 28:1055–1071

Kang H, Choi B (2018) Dominant fish and macroinvertebrate response to flow changes of the Geum River in Korea. Water 10: 942.

Krajenbrink HJ, Acreman M, Dunbar MJ, Hannah DM, Laizé CL & Wood PJ (2019) Macroinvertebrate community responses to river impoundment at multiple spatial scales. Science of the Total Environment 650: 2648-2656.

Kemp P, Sear D, Collins A, Naden P, Jones I (2011) The impacts of fine sediment on riverine fish. Hydrol Process 25:1800–1821

Kimmel BL, Groeger AW (1984) Factors controlling primary production in lakes and reservoirs: a perspective. Lake Reservoir Manage 1:277–281

Kondolf GM (1997) Hungry water: effects of dams and gravel mining on river channels. Environ Manag 21:533–551

Kondolf GM, Gao Y, Annandale GW, Morris GL, Jiang E, Zhang J, Cao Y, Carling P, Fu K, Guo Q, Hotchkiss R, Peteuil C, Sumi T, Wang H-W, Wang Z, Wei Z, Wu B, Wu C, Yang CT (2014) Sustainable sediment management in reservoirs and regulated rivers: experiences from five continents. Earths Future 2:256–280

Kummu M, Varis O (2007) Sediment-related impacts due to upstream reservoir trapping, the Lower Mekong River. Geomorphology 85:275–293

Kown Y, Kim JY, Kim P, Kim J, Kim JK, Kong D (2020) Spatial Distribution of Benthic Macroinvertebrates at Three River Weirs in The Namhan River. Journal of Korean Society on Water Environment, 36: 36-47.

Liew JH, Tan HH, Yeo DC (2016) Dammed rivers: impoundments facilitate fish invasions. Freshwater Biology, 61: 1421-1429.

Likens GE (2010) River ecosystem ecology: a global perspective. Academic Press, Amsterdam

Newcombe CC, Jensen JOTJ (1996) Channel suspended sediment and fisheries: a synthesis for quantitative assessment of risk and impact. N Am J Fish Manag 16:693–727

Mattos LD, Kruger LD M, Affonso ALS, Perbiche-Neves G, Pressinatte Junior S (2017) Small dams also change the benthic macroinvertebrates community in rocky rivers. Acta Limnologica Brasiliensia 29.

Mihalicz JE, Jardine TD, Baulch HM, Phillips, ID (2019) Seasonal effects of a hydropeaking dam on a downstream benthic macroinvertebrate community. River Res and App 35: 714-724.

Nilsson C, Reidy CA, Dynesius M, Revenga C (2005) Fragmentation and flow regulation of the world's large river systems. Science 308:405–408

Oliveira AG, Baumgartner MT, Gomes LC, Dias RM, Agostinho AA (2018) Long-term effects of flow regulation by dams simplify fish functional diversity. Freshwater Biology 63: 293-305.

Pelicice FM, Agostinho AA (2008) Fish-passage facilities as ecological traps in large neotropical rivers. Conserv Biol 22:180–188

Pelicice FM, Pompeu PS, Agostinho AA (2015) Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. Fish Fish 16:697–715
Petts GE (1985) Impounded rivers – perspectives for ecological management. Wiley, Chichester

Poff NLR, Allan JD, Bain MB, Karr JR, Prestegaard KL, Richter BD, Sparks RE, Stromberg JC (1997) The natural flow regime; a paradigm for river conservation and restoration. Bioscience 47(11):769–784

van Puijenbroek, PJ, Buijse AD, Kraak MH, Verdonschot PF (2019) Species and river specific effects of river fragmentation on European anadromous fish species. River Research and Applications 35: 68-77.

Quevedo, L, Ibáñez, C, Caiola, N, Cid, N, & Hampel, H (2018) Impact of a reservoir system on benthic macroinvertebrate and diatom communities of a large Mediterranean river (lower Ebro river, Catalonia, Spain). Limnetica, 37: 209-228.

Singh P, Sharma K, Swami N, Rana JS, Gusain MP, Gusain OP (2019) Assemblages of Benthic Macroinvertebrate Communities Downstream of a Dam on River Alaknanda in Garhwal Himalaya, Uttarakhand, India. International Journal of Ecology and Environmental Sciences, 45: 403-412.

Straskraba M, Tundisi JG, Duncan A (1993) State-of-the-art of reservoir limnology and water quality management. In: Comparative reservoir limnology and water quality management. Kluwer Academic Publisher, Dordrecht, pp 213–288

Turgeon K, Turpin C, Gregory-Eaves I (2019) Dams have varying impacts on fish communities across latitudes: A quantitative synthesis. Ecology Letters 22: 1501-1516.

Wan Y, Yang JQ, Zou DW, Li JJ, Qiao YJ, An SQ, Leng X (2018) Effects of multiple dams on the metacommunity structure of stream macroinvertebrates. Marine and Freshwater Research, 69: 721-729.

Wu H, Chen J, Xu J, Zeng G, Sang L, Liu Q, Ye S (2019) Effects of dam construction on biodiversity: A review. Journal of Cleaner Production 221: 480-489.

Zarfl C, Lumsdon AE, Berlekamp J, Tydecks L, Tockner K (2014) A global boom in hydropower dam construction. Aquat Sci 77:161–170

Zeng L, Zhou L, Guo DL, Fu DH, Xu P, Zeng S, Li GF (2017) Ecological effects of dams, alien fish, and physiochemical environmental factors on homogeneity/heterogeneity of fish community in four tributaries of the Pearl River in China. Ecology and Evolution 7: 3904-3915.

Zhao W, Guo W, Zhao L, Li Q, Cao X, Tang X (2019) Influence of Different Types of Small Hydropower Stations on Macroinvertebrate Communities in the Changjiang River Basin, China. Water 11: 1892.

Zhong Y, Power G (1996) Environmental impacts of hydroelectric projects on fish resources in China. Regul Rivers Res Manag 12:81–98