Master's Thesis

Assessing the connectivity of and identifying potential restoration sites in river networks in Central Finland

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Freshwater ecosystems are some of the most endangered ecosystems in the world. Among the threats are water management practices and crossing structures, which encompasses culverts and dams. They have caused changes in abiotic and biotic processes of streams and are disrupting connectivity of river networks, which has led to impeded movement of aquatic biota. The first aim of this master's thesis was to assess how much the connectivity of the river networks in Central Finland has decreased due to culverts and dams. The second aim was to identify, which barriers affect connectivity the most and thus are the most efficient sites for connectivity restoration. The analysis was done by creating landscape graphs using pre-existing data and calculating connectivity metrics from the graphs. The results show that the connectivity of the river networks has decreased markedly as only 34–49% of the connectivity is left, and that dams have affected connectivity more than culverts. The barriers have decreased connectivity at varying degrees depending both on the passability and location of the barrier. Removing ca. 10 highest prioritized barriers, all of which are dams, leads to the fastest increase in the overall connectivity of the network and the connectivity of the river networks would increase to 63-71%. The results can be used to assess connectivity, but connectivity analysis should be supplemented with e.g. field studies when planning river restorations and barriers removals. The results provide an important selection criterion for decision-making capable of considering a whole network of rivers and streams, and the barriers in relation to each other. The state of rivers and streams is declining, and the species found in them are becoming endangered globally and their conservation requires restoration actions, including improving connectivity.

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Makeiden vesien ekosysteemit kuuluvat maailman uhanalaisimpien elinympäristöjen joukkoon. Yksi suurista vesistöjen tilaa heikentävistä tekijöistä ovat tierummut ja padot. Ne ovat aiheuttaneet muutoksia virtavesien abioottisessa ja bioottisissa ominaisuuksissa, ja heikentäneet kytkeytyneisyyttä, minkä vuoksi ne haittaavat akvaattisten lajien liikkumista elinympäristöjen välillä. Pro gradu -tutkielman tavoitteena oli arvioida patojen ja tierumpujen vaikutusta kytkeytyneisyyteen Keski-Suomen jokiverkostossa. Toisena tavoitteena oli tunnistaa vaellusesteet, jotka vaikuttavat kytkeytyneisyyteen eniten, koska poistamalla korkeasti priorisoituja esteitä jokiverkoston kytkeytyneisyyttä voidaan parantaa tehokkaasti. Analyysi suoritettiin aiemmin kerättyyn dataan perustuvilla aluegraafeilla ja niistä lasketuilla kytkeytyneisyysindekseillä. Tulokset osoittavat verkoston kytkeytyneisyyden heikentyneen merkittävästi, sillä kytkeytyneisyydestä on jäljellä enää vain noin 34–49 %. Patojen kytkeytyneisyyttä heikentävä vaikutus on tierumpujen vaikutusta suurempi. Yksittäisen vaellusesteen vaikutus kytkeytyneisyyteen vaihteli esteellisyydestä ja sijainnista riippuen. Poistamalla noin kymmenen korkeimmin priorisoitua estettä, jotka kaikki ovat patoja, jokiverkoston kytkeytyneisyys olisi 63–71 %. Tuloksia voidaan käyttää kytkeytyneisyyden ja sen parantamisen arvioinnissa, mutta kytkeytyneisyysanalyysi yksin ei riitä kunnostuksen ja esteiden poiston tehokkaaseen suunnitteluun, vaan analyysin tueksi tarvitaan esimerkiksi potentiaalisilla kunnostuspaikoilla suoritettuja kenttätutkimuksia. Kytkeytyneisyysanalyysi kuitenkin tarjoaa päätöksentekoon valintakriteerin, joka huomioi koko jokiverkoston kytkeytyneisyyden sekä muiden esteiden sijainnin. Jokien ja purojen tilan heikkeneminen ja niissä esiintyvien lajien uhanalaisuus ovat maailmanlaajuisesti ongelmia, joiden tehokas ratkaiseminen vaatii kunnostustoimenpiteitä, joihin myös kytkeytyneisyyden parantaminen kuuluu.

TABLE OF CONTENTS

TERMS AND ABBREVIATIONS

Terms

Connectivity	How landscape affects organisms′ ability to move between habitats
Fishway	A structure allowing fish to bypass a dam
Link	Represents an organism′s ability to migrate between habitat patches in a landscape graph
Node	Represents a suitable habitat patch in a landscape graph
Passability	Attribute of a barrier describing organisms′ ability to pass through the barrier
River	Flowing water course with catchment area more than 100 km^2
Stream	Small flowing water course with catchment area size 10-100 km^2

Abbreviations

EC	Equivalent connectivity
PC	Probability of connectivity

1 INTRODUCTION

Freshwater ecosystems are hotspots for biodiversity, but at the same time they are some of the most endangered ecosystems on Earth (Dudgeon et al. 2006). In addition to being important habitats for biota, streams and rivers offer many ecosystem services related to e.g. nutrient cycling and sediment formation (Ferreira et al. 2023). The major threats to freshwater ecosystems are changing climate, species invasion, habitat degradation and flow modification (Dudgeon et al. 2006, Reid et al. 2019). In riverine environment connectivity within the landscape can be defined as being longitudinal (headwater-estuarine), lateral (riverine-floodplain), or vertical (riverine-groundwater) connectivity (Pringle 2001). Especially longitudinal connectivity suffers from flow modification structures and road crossings. In a river network, they can act as barriers to movement of aquatic biota leading to disrupted ecological connectivity (Maitland et al. 2015). Often the laws protecting aquatic ecosystems do not include streams which is why they are not protected well enough (Ferreira et al. 2023).

In Europe, several fish species have been assessed to be at high risk of extinction with dams and water management structures being among of the biggest threats (Costa et al. 2021). In addition to dams, road crossings are another common structure threatening aquatic species in streams (Diebel et al. 2015). This is because both dams and culverts can cause fragmentation and act as barriers to movement of fish and other aquatic biota.

1.1 Impacts of barriers on abiotic and biotic properties

Culverts and dams are common structures in rivers and streams altering the abiotic processes and flow conditions. The physiochemical changes include higher water depth and temperature in streams with culverts compared to streams where road crossings are bridges (MacPherson et al. 2012, Maitland et al. 2015). Dams can also lead to shifts in water temperature (Chandesris et al. 2019). Both culverts and dams increase sediment accumulation in the upstream areas (MacPherson et al. 2012). Increased sedimentation has impacts on habitat quality and directly on health and behaviour of fish (Maitland et al. 2015) as negative changes in feeding behaviour and embryo development have been observed when sedimentation increases (Chapman et al. 2014). Culverts have been observed to both increase and decrease water velocity (MacPherson et al. 2012, Maitland et al. 2015). The velocity can be increased especially during high flows if slope is too high (Poplar-Jeffers et al. 2009) or if the culvert is much narrower than the stream channel (Clark et al. 2014). High water velocities can prevent upstream dispersal of organisms (including migrations). A culvert that has been installed too high can create a drop at the culvert outlet which also prevents upstream movement if the height is more than the jumping ability of the fish (Poplar-Jeffers et al. 2009).

If a culvert is not a barrier, the abundance of most fish species can be comparable to streams with bridges (MacPherson et al. 2012). When movement is impeded, the abundances of some fish species have been observed to be lower upstream of the culvert compared to species densities at downstream sites (MacPherson et al. 2012). Abundances of fish species are lower also when streams with culverts are compared to free-flowing reference streams meaning that culverts have effects both upstream and downstream (Favaro et al. 2014). Not all species are impacted the same way as the densities of some species may increase. Rather than the fish benefitting from the barriers, the higher density could be explained by stronger swimming fish being able to pass through culvert easier than weaker swimming fish and facing less competition and predation (MacPherson et al. 2012, Favaro et al. 2014). Even if some species or individuals can pass through a culvert, the species composition and richness can both decline because of them.

Dams also affect riverine fish communities because they often prevent upstream movement completely. Therefore, if a dam cannot be passed, the number of migrating fish species and their total density can become lower upstream of the dam (Katano et al. 2006). Fishways are constructed to enable fish to pass dams, but they often are not functional for all species (Januchowski-Hartley et al. 2013). The fish can also suffer from delayed passage through the fishway, or the individuals might not even attempt to enter the fishway (Ovidio et al. 2017).

Impacts of dams and culverts are not limited to fish. For example, the endangered, non-migratory freshwater pearl mussel (*Margaritifera margaritifera*) can be affected as well because they depend on migratory fish species such as brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) to ensure the survival of their larvae (Kestrup 2017). If the migration of the host fish is disrupted, the dispersal and recruitment of freshwater pearl mussels decreases threatening the population (Österling & Söderberg 2015, Kestrup 2017).

Migration barriers also have negative effects on other macroinvertebrates. Downstream of culverts the species composition changes due to lower numbers of native taxa and individuals compared to upstream sites (Gál et al. 2020). Endangered taxa, which are particularly sensitive to change, suffer from barriers more than some other species do (Gál et al. 2020). Culverts and dams can complicate species' conservation by altering vital habitats. Dams also decrease biodiversity of macroinvertebrates, replacing typical stream taxa with species that prefer stagnant or low flow conditions (Meißner et al. 2018). Dam construction increases zooplankton richness and abundance by promoting rotifers and crustaceans which are typically absent in flowing waters (Czerniawski & Domagała 2014). Despite barriers preventing movement, they can also sometimes increase the spread of alien species by altering riverbeds to provide suitable habitats (Gál et al. 2020).

Disrupted connectivity between habitats leads to movement of aquatic organisms decreasing, which threatens many species using streams and rivers as habitats or migration routes. Disconnected habitats prevent gene flow between populations leading to loss of genetic variation and thereby weakening the populations' ability to respond to environmental changes and increasing the risk of local extinction (Hamner et al. 2012). Barriers can also prevent some species from completing their lifecycles, because the barriers can block migrating fish from reaching their spawning habitats (Cote et al. 2009).

Climate change causes additional pressures on the survival of aquatic biota, and migration barriers can enhance the threat. For example, flow regimes can experience changes affecting connectivity of river networks (Franklin et al. 2024). Rising water temperatures can also force cool water adapted fish populations to migrate but barriers can prevent the migration to habitats that have more favourable conditions (Hari et al. 2006). Lack of connectivity can also lead to smaller populations as habitats are smaller (Hari et al. 2006).

Because culverts and dams are a major threat, mitigating their impact is important. In order to restore the lost connectivity, barrier removals have become a widely applied way to improve the status and functioning of streams. Due to high number of barriers in river networks (Belletti et al. 2020), effective tools are needed to map and compile data on the potential migration barriers as well as assess how they affect connectivity of river networks.

1.2 Prioritisation of connectivity restoration projects

In 2000, the EU Water Framework Directive was adopted setting a goal for achieving good ecological status in water bodies. For streams and rivers, one of the quality elements used in the classification is continuity which is affected by migration barriers. In addition, composition and abundance of fish, invertebrate and plant species are used in the evaluation of ecological status of freshwater ecosystems (Directive/200/60/EC). As culverts and dams can affect species composition by reducing connectivity, connectivity restoration projects, hereafter referred to as barrier removal, are important for achieving good ecological status. Restoring connectivity can be done by completely removing the barrier or by mitigating its impacts otherwise, such as by constructing bypasses or replacing road crossings with more passable structures. During the past decades, dam and culvert restoration projects have become more common (McManamay et al. 2019). Despite the efforts and data showing how migration barriers are lowering connectivity, culverts that impede movement are still in use, especially in small streams (MacPherson et al. 2012).

When only larger dams are considered in connectivity analysis, large rivers appear to be more fragmented than small rivers, which is not strictly true because barriers in smaller rivers are often poorly recorded (Duarte et al. 2021). The number of barriers found in field studies done in several European countries demonstrate that the true number of barriers is on average 2.5 times higher than recorded in the existing databases. Many of the barriers are no longer in use or they are small, making them good targets for removal (Belletti et al. 2020).

There are several ways to plan restoration actions and assess how removing a barrier improves connectivity depending on the aims of the restoration. One criterion commonly used for measuring the efficiency of restoration is the length of river sections opened. This means that the prioritisation is done based on where removal of a barrier opens the longest possible unimpeded river section (O'Hanley 2011). This does not always achieve the best results as gaining an access to habitat types, such as spawning grounds, that were previously absent or difficult to access can sometimes be more beneficial (Diebel et al. 2014). The financial cost of opening a barrier to be passable can be high and thus prioritisation is needed to select the barriers to be restored or removed (Favaro et al. 2014). One of the methods used in decision making is scoring and ranking scheme: the barriers are assigned attributes that can include habitat quality and quantity, and the cost of intervention, often ignoring how the barriers are located in the network in relation to each other (O'Hanley and Tomberlin 2005).

One way to prioritise barrier removal to achieve efficient results are landscape graphs where the effect that a single barrier has on connectivity can be analysed while also considering other barriers in the network. Benefits of prioritising barriers based on optimisation over, for example, ranking and scoring methods have been shown before as optimisation leads to higher habitat gains (O'Hanley & Tomberlin 2005). Prioritisation is one of the main purposes of landscape graphs in land use planning (Foltête et al. 2014). It allows re-connecting habitat patches effectively by restoring only the sites that are causing most of the fragmentation. Assessing the impacts of culverts and dams on catchment-level scale is more efficient than studying each watershed individually (Neeson et al. 2015).

1.3 Streams and restoration in Finland

It is estimated that in Finland there is 130 000 km of streams (catchment area 10–100 km^2) and 21 000 km of rivers (catchment area more than 100 km^2) (Rinnevalli et al. 2021). Most small streams are classified as endangered or threatened habitats (Kontula & Raunio 2018), which makes the protection and restoration of streams important. Streams have suffered e.g. from high nutrient loads, riverbed erosion, forestry, and various man-made structures (Aroviita et al. 2021). The connectivity of rivers can affect other ecosystems as well because they act as ecological corridors connecting other aquatic ecosystems to each other (Sarvilinna et al. 2012). Many of the dams in streams and rivers in Finland are no longer in use and these sites can be especially good options for dam removal (Rinnevalli et al. 2021). Some of the criteria used in prioritisation of dam removal in Finland are the occurrence of natural populations of migrating fish such as brown trout, the ecological quality of the water body and the use of the dams (Rinnevalli et al. 2021).

The exact number of culverts is not known, but there are approximately 90 000 culverts in Finland and approximately 5500 in Central Finland, of which one third are considered to be migration barriers for fish (Eloranta & Eloranta 2016). Only a fraction of the culvert construction projects are relayed to authorities, which has complicated knowing the exact number and impacts of culverts (Eloranta & Eloranta 2016). The total number of dams and other water regulation structures recorded in Finland is 5200 (Rinnevalli et al. 2021), but it is possible that this number does not include some of the older dams that are no longer in use or dams built without permits. In Finland, the Ministry of Environment's HELMI-program, and the Ministry of Agriculture and Forestry's NOUSU-program have included removing migration barriers from streams (Rinnevalli et al. 2021) as mitigation solutions to support the goals of the EU 2030 Biodiversity strategy (European Commission 2020). Dozens of problematic culverts and small dams have already been removed in Finland to restore connectivity and there are plans to continue this process (Rinnevalli et al. 2021).

1.4 Study objectives

The high number of potential culverts and dams in Central Finland necessitates restoration efforts to improve quality of rivers and streams. The objective of this master's thesis was to study how artificial barriers have affected the connectivity of river networks and to map potential targets for restoration projects. The research questions were:

1. How much dams and culverts decrease the connectivity of river networks in Central Finland?
2. Which barriers reduce connectivity the most and thus are the most efficient sites for connectivity restoration?

The study results can support efficient planning of barrier removals and restorations to improve connectivity of rivers and streams in Central Finland. By mobilising the underutilised barrier data to create landscape graphs, the study aimed at cost-efficient planning of connectivity. The restorations, that is barrier removal, are most beneficial when done in high quality streams and rivers, that offer migration routes to large, previously inaccessible habitats. The analysis allows assessing how the habitat gain can be maximised by increasing the length of free-flowing streams or connecting lakes.

2 MATERIALS AND METHODS

2.1 Materials

The spatial graph required data on catchment areas, regional borders and river networks which were obtained from the Finnish Environment Institute's (SYKE) open loading service (Finnish Environment Institute 2023). The river network used in the analysis was created by combining two map layers. The first layer was the river network, which is based on the topographic database of the National Land Survey of Finland at the scale of 1:5000–1:10 000 metres from

2000–2008. The data provided a continuous network with pseudo streams running through lakes. The pseudo streams are connecting rivers, creating a large undisrupted network of rivers, streams, and lakes. The second layer contained more rivers and streams, as the smallest streams are not included in the river network.

The national catchment data consists of five hierarchical levels and was also obtained from SYKE's open loading service. Only the second level describing the main watershed areas was used in defining the study area. The layer divided Finland into 109 catchments and coastal areas from which Kymijoki catchment was selected so that the analysis could be restricted to a single catchment area corresponding the most to the Central Finland region (Figure 1). The data on administrative borders was made by the National Land Survey in 2023 at the 1:10 000 m scale. Only the borders of the regions were used in the study to define the research area to Central Finland.

Culvert and dam records were obtained from ELY Centre of Central Finland containing the locations and assessed passabilities of the barriers as well as data on the condition and use some of the dams. The datasets contained 1263 culverts and 267 dams located in Central Finland (Figure 2). Some of the culverts and dams were in streams that could not be included in the graph (see below), or the barrier appeared to be located away from a river because of coordinate errors. The final number of barriers in the river network used was 645 culverts and 219 dams.

2.2 Methods

A landscape graph is a spatial model in which the habitat patches deemed favourable are represented by nodes surrounded by inhospitable matrix (Galpern et al. 2011). A habitat network G = (N, L) is defined by a set of N nodes connected to each other by L links (Segurado et al. 2013). Links among nodes represent the functional connectivity between the habitat patches (Foltête et al. 2014). The links between nodes can either be binary meaning that there is or is not functional connectivity between the nodes, or they can represent distance or the probability of dispersal (Urban 2009). A graph presents only the elements playing a role in the movement of species (Foltête et al. 2012).

One of the commonly used graph-based metrics is the probability of connectivity (PC), defined as the probability of two randomly placed points falling into habitat areas that are reachable from each other (Saura & Pascual-Hortal 2007). PC is based on a probabilistic connection model, where probability characterises an organism's ability to disperse in a defined area. Because PC is a probabilistic metric, it allows using several different probabilities for movement between different patches (Saura & Pascual-Hortal 2007). In this analysis the probability used was based on the estimated ability of fish being able to pass through a culvert or dam.

Equivalent connectivity (EC) is a modification of the PC metric that expresses connectivity as an equivalent habitat patch size and has therefore, an area unit (Saura et al. 2011). It is defined as the size of a single maximally connected habitat patch that would result in the same PC value as the habitat patches in the actual landscape. When comparing temporal changes or action scenarios within the same area, EC is more usable and offers easier interpretation (Saura et al. 2011). When the number of habitat patches or their size increases, the value of EC increases based on the size of the added habitat if the new patches are connected to the rest of the network. If an added habitat patch connects previously disconnected patches together, the value of EC can increase more than the size of the added habitat (Saura et al. 2011).

2.2.1 Data preparation

By using ArcMap (version 10.8.2), the study area was delimited as the overlap between the Kymijoki catchment and the Central Finland administrative region (Figure 1). The eastern part of Central Finland was excluded because it was a part of another catchment area and would have thus led to some of the river networks being separated from the main network. Part of the Kymijoki catchment outside of the Central Finland region was also excluded, as the dam and culvert data did not cover this area. To account for the edge effect, a 10 km wide buffer was created around Central Finland.

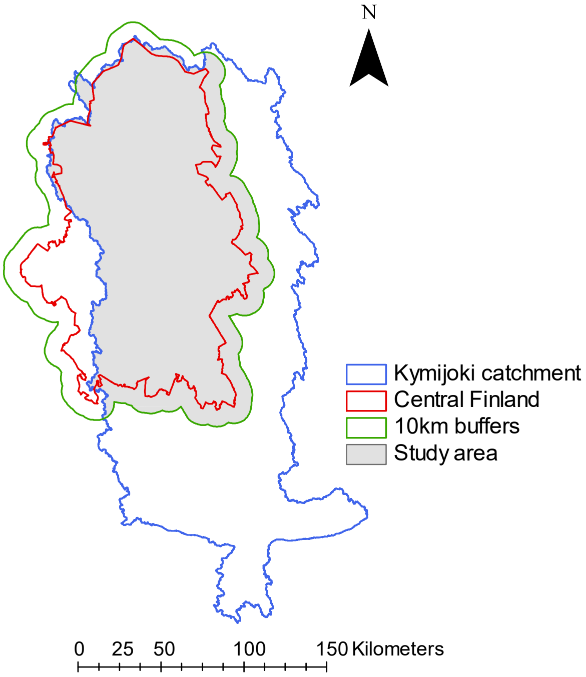

Figure 1. The study area based on the catchment area and regional borders.

The river network data contained only the centre line of each river. By creating a 3 m wide buffer around each river and stream, the lines were made into polygons, which also helped to correct for possible coordinate errors. Because the network was in two separate map layers, they were merged and dissolved to create a new layer where the river network layer and the smaller streams that were directly connected to the main networks created one large network. This extended the networks and allowed some of the smaller streams to be included in the analysis. The streams connected to the network through small lakes and ponds with no pseudo stream drawn through them, were excluded from the model as they appeared to be disconnected from the rest of the network. Only the seven largest networks were included in the analysis. Some parts of the network were not connected to each other as the study area did not include the whole catchment area.

The culverts and dams were recorded as points and transformed into polygons by creating a buffer around each barrier. To account for the errors in coordinates, all culverts and dams within 15 m of the central line of streams were included rather than only including the barriers that were inside the buffers (Figure 2). Size of the buffer around each barrier was adjusted to account for the width of the buffer around the central lines. Because the buffer around the rivers had to be clipped as well, the buffer around culverts and dams was set at 18 m (15 m + 3 m). For the connectivity analysis the rivers were split into sections at the sites where a culvert or dam was located by erasing a part of river with the buffer around a potential barrier.

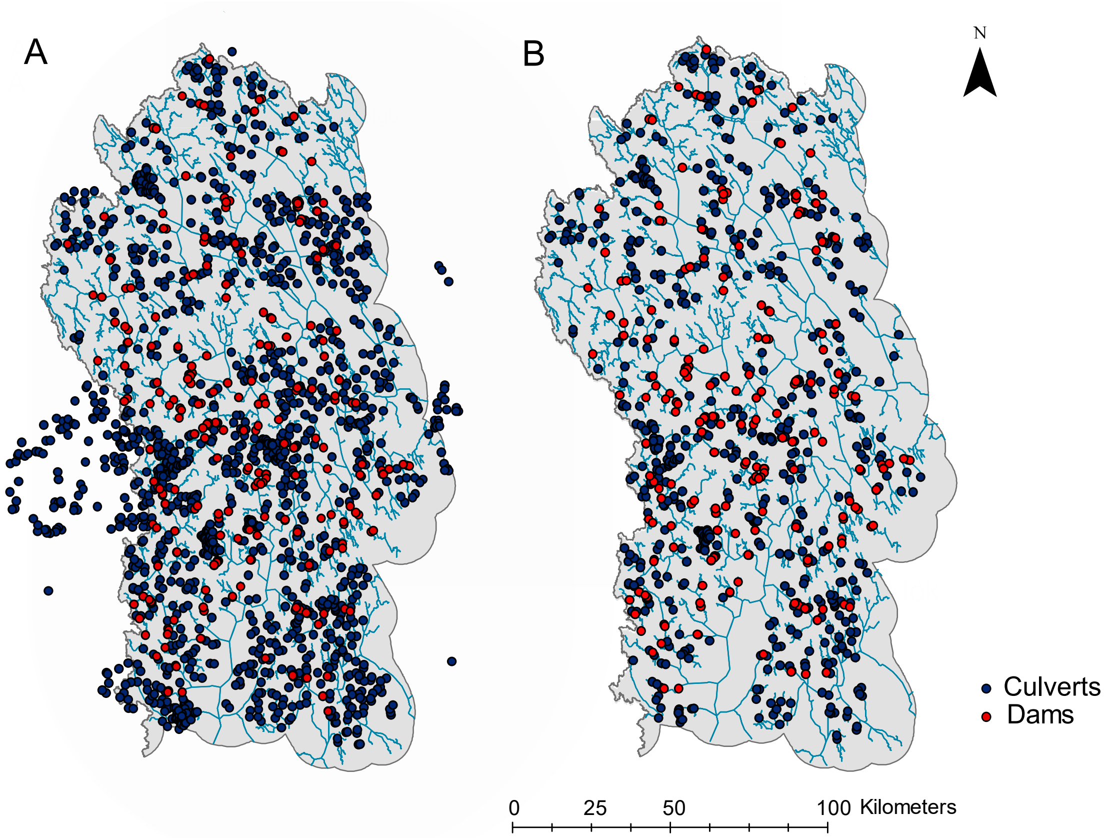

Figure 2. (A) All culverts and dams included in the records and (B) culverts and dams that are within 15 m of a river, and thus could fragment the network in connectivity analysis.

2.2.2 Conefor analysis

The connectivity metrics were calculated using Conefor (version 2.6) software package (Saura & Torné 2009). Conefor uses connectivity metrics to quantify landscape connectivity and the importance that habitat patches and links have on maintaining it (Foltête et al. 2012). In this study, a habitat patch was a river segment between two barriers and the links represented the barriers between the segments. Conefor includes an extension for ArcMap (Conefor Inputs) which was used to create the text files needed to calculate the metrics. To ensure that a link could be created only between connected river segments, the maximum distance at which two nodes could have a link between them was restricted to be the diameter of the buffers around culverts and dams. The layers containing barriers were joined with the created connection file so that the passability of each barrier could be used in the Conefor-analysis rather than using the distance between two nodes.

The probabilities of movement used were based on the previously assessed passability of each culvert and dam, including five classes: passable, partial barrier, total barrier, fishway and NoData. For the calculations, the distance between each segment was replaced with the probability of movement through that structure. The probability of movement through passable barriers was defined as 1, whereas total barriers were given the value of 0. The calculations were done three times using the passability values of 0.3, 0.5 and 0.7 for partial barriers to test how changing their estimated passability changed the connectivity and prioritisation. The barriers with no passability data or with fishways were given the same probability as the partial barriers.

The prioritisation ranking was based on equivalent connectivity metric (EC), which is defined as the size of single habitat patch that would give the same connectivity metric value as the actual habitat pattern. The equivalent connectivity is calculated as

$$EC = \sqrt{\sum_{i=1}^{n} \sum_{j=1}^{n} a_i \, a_j p_{ij}} \tag{1}$$

(1),

where a_i and a_j are the areas of habitat patches i and j, p_{ij} is the maximum probability of possible paths between areas i and j. For the connectivity assessment, only the overall connectivity was calculated. First, the original connectivity of the network was calculated without any barriers by giving the value of 1 for probability of movement through all culverts and dams. The impact of barriers on the connectivity was assessed by calculating connectivity of the network with culverts, with dams and with both barrier types. The results were compared to the original connectivity of the river network and percentage of intact network was calculated.

Link importance analysis was used to find barriers decreasing connectivity the most and thus being among the highest priority for barrier removals. Unlike overall connectivity, link importance can be used to calculate how each link and habitat patch affects connectivity, and to evaluate the importance landscape elements have on maintaining the overall connectivity (Pascual-Hortal & Saura 2006). For the analysis, all barriers were assigned a second passability value in addition to the current passability to test how removing a barrier would affect the connectivity. All barriers had a second probability of 1 and the change in passability was tested one barrier at the time meaning that only one of the barriers had the new probability and all the other barriers kept their original probabilities.

After establishing the ranking of barriers whose removal generated the highest gains, sequential barrier removals were simulated to evaluate the efficiency of such process. The passability of highly prioritised barriers was changed to 1 (simulating removal) and the overall network connectivity was recalculated. The process was repeated step by step through the 70 top ranked barriers.

3 RESULTS

The studied river networks in Central Finland had 315 culverts and dams that are at least partial barriers to fish movement. There were many more culverts than dams, however most culverts were assessed as passable while a large proportion of dams were assessed to impede at least some of the movement. The number of culverts is slightly higher than that of dams even when passable culverts and dams are excluded (Figure 3).

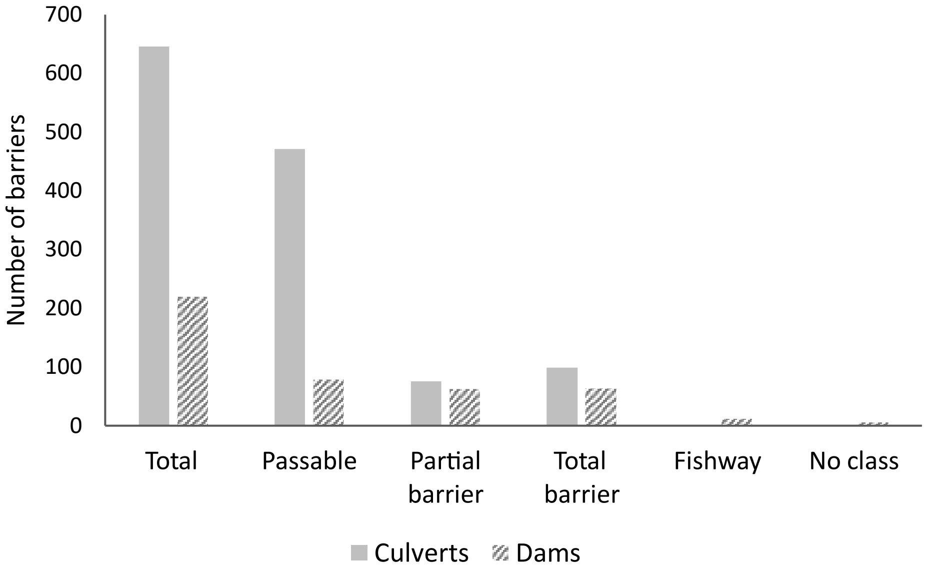

Figure 3. The barriers located within 15 m from the streams divided into passability classes. Barriers located in the smallest streams or too far away from the rivers were excluded.

When all rivers and streams were 6 m wide (i.e. 3 m buffers on each side), the equivalent connectivity metric (EC) of the river networks without any barriers was 34.7 km^2. EC indicated that dams decrease connectivity markedly more than culverts (Table 1). The proportion of connected network decreases only slightly (~3%) when both culverts and dams are considered in the analysis. The increased passability of partial barriers led to higher overall connectivity but did not change the relative impacts of culverts and dams. The amount of available habitat area (EC) as compared to the intact network was reduced by two thirds to a half depending on the passability used for partial barriers.

Table 1. The values of EC metric in km^2 of the whole river network calculated using different passability probability values (0.3, 0.5 and 0.7) for partial barriers. In the parenthesis is the size of the habitat area as compared to the original value calculated without any barriers in the network (percentage).

Barrier type	Connectivity of the river network		
	0.3	0.5	0.7
Culverts	31.9 (92%)	32.2 (93%)	32.5 (94%)
Dams	12.6 (36%)	14.9 (43%)	18.1 (52%)
Both	11.6 (34%)	13.9 (40%)	17.0 (49%)

The order of prioritisation shows that the effect of each barrier on connectivity varies greatly. Among the twenty barriers affecting connectivity the most, 17 were the same in all probabilities (Figure 4). Majority of the barriers decreasing connectivity the most were dams, as only one culvert was included in the highest prioritised barriers and only when the passability probability was 0.3 or 0.5. How much each barrier affected overall connectivity of the network varied when the passability of partial barriers was changed as each barrier had a bigger impact on connectivity when the passability was smaller. However, the highest prioritised barriers were very similar regardless of the used passability, showing stable prioritisation (Figure 4, comparing A, B, C). How much each barrier affected connectivity decreased as the passability used for partial barriers increased.

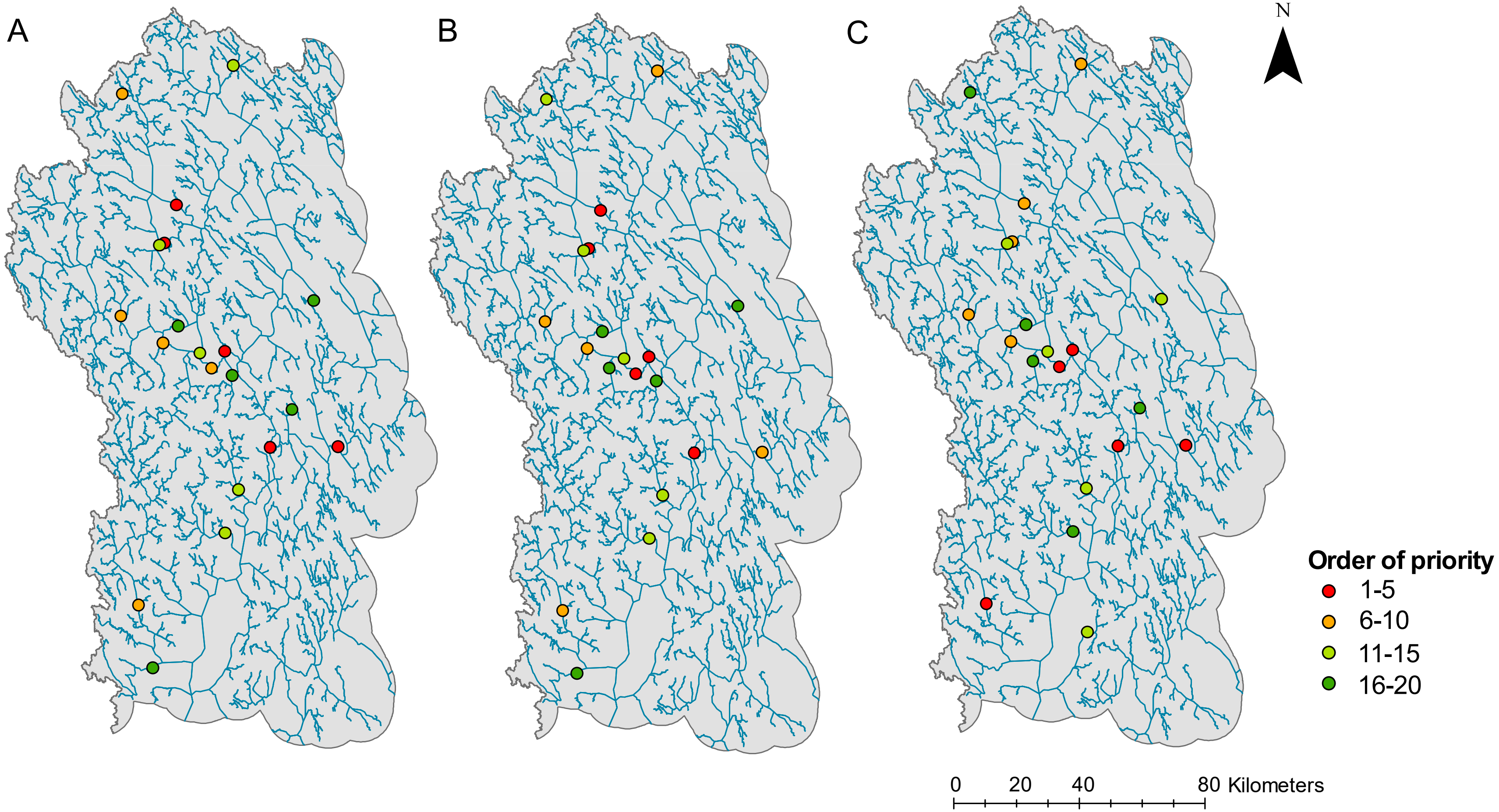

Figure 4. Twenty barriers affecting the connectivity the most calculated with passability probabilities 0.3 (A), 0.5 (B) and 0.7 (C) for partial barriers.

The removal of the highest prioritised barriers would still leave majority of the barriers in the network. Some of the streams have several barriers and thus a single barrier removal would not open an access to the whole river network. Most of highly prioritised barriers were in short rivers between lakes (Figure 5 and 6).

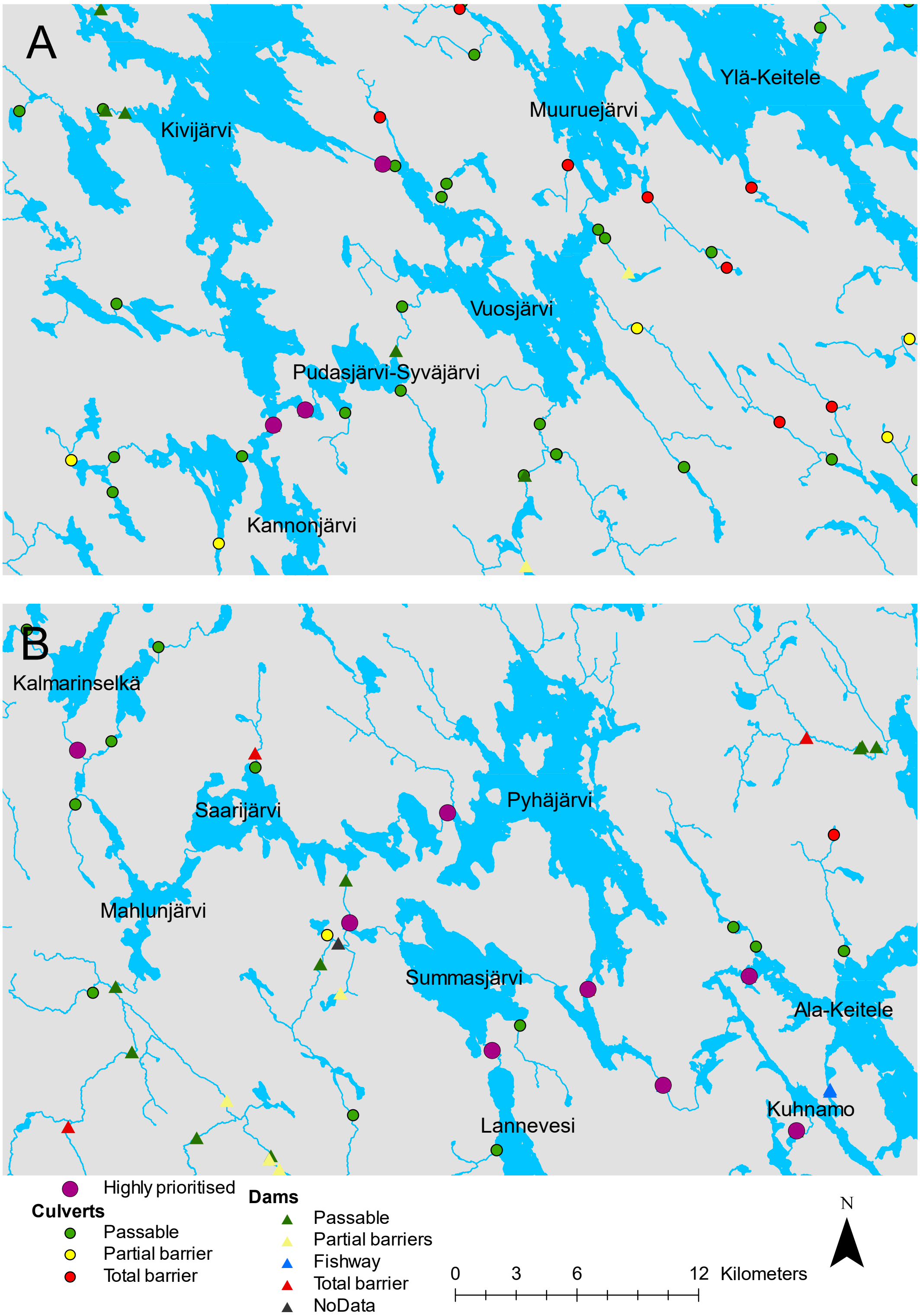

Figure 5. Highly prioritised barriers located in Kannonkoski (A) and Saarijärvi and Äänekoski (B).

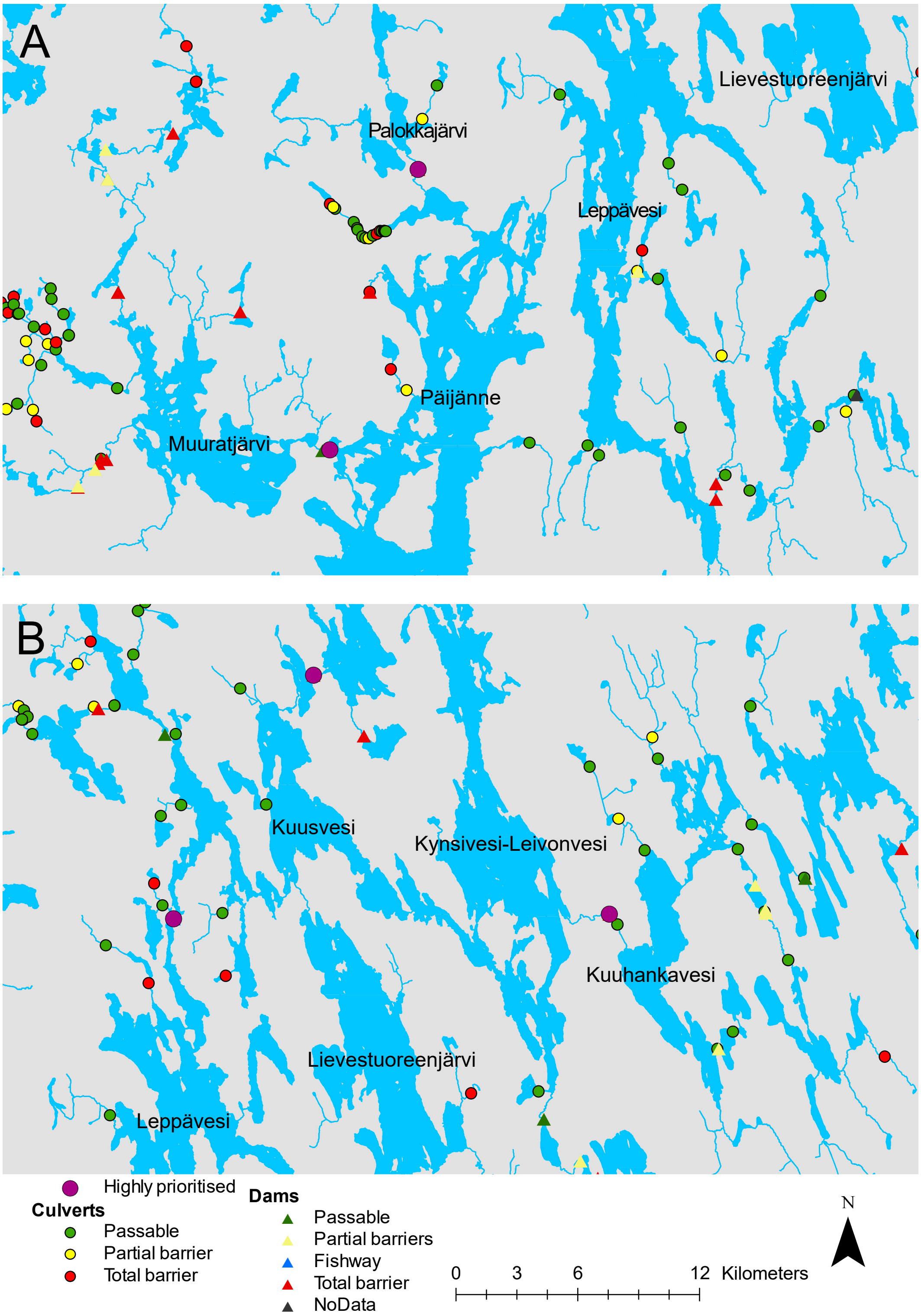

Figure 6. Highly prioritised barriers located in Jyväskylä and Muurame (A) and Hankasalmi and Laukaa (B).

A simulation of barrier removals shows that the connectivity increases the most after the removal of ca. 10 barriers of highest priority, after which the subsequent removals result in only moderate increase of connectivity (Figure 7). Removal of 10 high priority barriers would increase the value of EC to

21.7-24.8 km² depending on the passability probability used, which is 63-71% of the original value calculated without barriers in the network (34.7 km²).

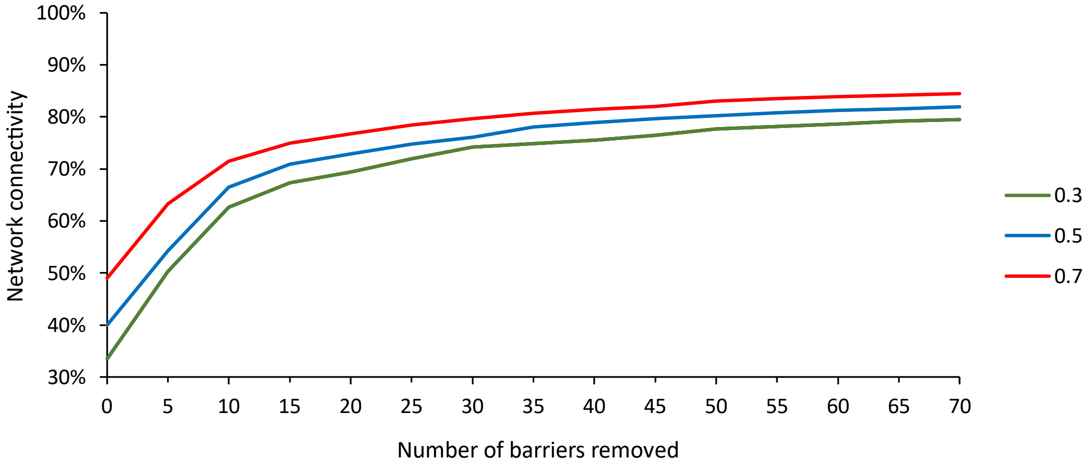

Figure 7. Percentage of change in the overall river network connectivity following barrier removal based on EC metric calculated with passability probabilities of 0.3, 0.5 and 0.7 for partial barriers. As barriers are removed and connectivity is improved, the value of the metric increases closer to the connectivity that the network would have without any barriers.

4 DISCUSSION

The results show that the river network connectivity in Central Finland has decreased substantially and less than half of connectivity is left, due to structures constructed by humans. However, dams had a much greater impact than culverts. The impact of barriers on connectivity varies greatly between locations whereas changing passability probability for partial barriers caused only minor changes in the prioritisation ranking of potential restoration sites. Removing ca. 10 highest prioritised barriers would increase connectivity to 63-71% of the original river network connectivity. Removing lower prioritised barriers increases connectivity less.

4.1 Decreased connectivity and barriers

Culverts exceeding the number of dams and having a higher cumulative impact on connectivity is commonly observed in river networks (e.g. Diebel et al. 2015), however in Central Finland the dams decrease connectivity more despite their lower number. The higher impact of dams could be explained by dams being located lower in the river network whereas culverts are mainly located in smaller headwater streams and thus contribute less to lost connectivity (Diebel et al. 2015). Road crossings in large mainstem rivers are usually bridges, which do not have the same barrier effect as culverts (Warren & Pardew 1998). Achieving the same improvement in connectivity requires opening markedly higher number of culverts compared to restoring connectivity by removing dams. Several highly prioritised dams had fishways, which means that enhancing their passability would increase connectivity without the need for entirely new structures.

The highly prioritised barriers are mainly found between two lakes or downstream in the river networks. This is likely caused by the objective of the analysis being maximising habitat area gain. Even though the actual area of lakes was not considered, they are large unobstructed habitats unlike most rivers and streams with numerous barriers that fragment and hinder movement. Therefore, opening access to another lake and its connected free flowing streams rather than aiming for long segments of free-flowing river was favoured. A barrier at the mouth of a river reduces connectivity more than the barriers in the tributaries and prevents reaching the habitats upstream (McKay et al. 2013). Even if the headwaters offer high quality habitats, restoring connectivity there without removing barriers downstream will not yield high results if the habitats remain unreachable. Therefore, extending the networks starting downstream first is an intuitive way to prioritise barrier removals. Corresponding with previous studies (e.g. O'Hanley et al. 2011, Branco et al. 2014), the findings show that the removal of barriers based on prioritisation increases connectivity more than removing randomly chosen barriers.

The location of a barrier in relation to other barriers can also explain why most of the highly prioritised barriers are dams. Previously, connectivity has been observed to be gained more efficiently when the removed barrier is not in a cluster with other barriers (de Leaniz & O'Hanley 2022). When barriers are in a cluster, removing one of them does not increase connectivity much because other barriers are preventing accessing it or the habitat area gained is small. Several streams had closely located culverts, whereas dams were usually located further away from each other and thus their removal would open larger areas.

The results indicate that barrier location influences prioritisation results more than the estimated passability. Approximately half of the highly prioritised barriers were partial barriers or had fish passages and thus they can be considered low-cost targets for future restorations (Cote et al. 2009, Diebel et al. 2015). The cost associated with removing total barriers or transforming them into partial barriers is often high, but it is highly important for opening large river areas for migratory fish and other biota (McKay et al. 2013). Repeating the calculations with different passabilities for partial barriers led only to minor changes in the prioritisation order, which has been observed earlier by Diebel et al. (2015). This means that being able to accurately assess passability of structures is not as important as being able to distinguish the partial barriers from passable structures and total barriers (Diebel et al. 2015).

To know more about the highly prioritised sites and their characteristics, data from VESTY database and Vesikartta containing important ecological data of migration barriers and the rivers where they were located, were used to describe the sites in more detail. In addition, data on observed salmonids in the streams collected by SYKE, and maps from Finnish Land Survey were used

(Appendix 1). Many high priority sites are in a good or high ecological quality class and inhabit salmonid stocks, meaning that there is ecological data supporting their high potential of being good restoration sites.

Some of the sites prioritised have already been or will soon be restored. For example, the Lohikoski dam in Tourujoki, Jyväskylä will be removed in the coming years. The new structures will allow fish passage while also retaining sufficient water level in the upstream lake Palokkajärvi (Kupiainen et al. 2018). The ecological status of the river is only moderate but other river restoration measures together with removal of the dam can have a major impact on the ecological quality. The results of the connectivity analysis show that this restoration site also improves the connectivity of the regional river networks. The highest prioritised barrier is a dam at Mämmenkoski in Äänekoski, where major restorations have already been conducted to support migratory fish populations (Metsä Board 2020). Barrier removals have also been done at Arvajankoski in Jämsä, where the passability of the previous fishway varied depending on the water flow, creating a partial barrier even after the dam became obsolete (Tähtö 2018). The old structures have been removed to improve fish passage (Leppänen 2022).

Focusing the restorations on highly prioritised barriers could improve connectivity efficiently, which highlights the importance of connectivity analysis as a part of restoration planning. The barriers affecting connectivity cannot be identified without considering all of them in relation to each other. Most of the barriers do not have a major impact on connectivity individually meaning that opening them does not affect the river network connectivity much.

4.2 Uncertainties of the analysis

The passable culverts could not be included in the analysis due to their high number slowing the calculation down. Their exclusion assumes complete passability, while in reality even passable culverts may hinder movement a little. Even though including all the barriers in the network might require using different type of analysis or modifying it, they should be accounted for in river monitoring and management.

Due to excluded passable culverts, the actual connectivity and movement between river sections may be lower than the results indicate. While it has not been extensively studied, it is possible that the darkness of the culverts can delay movement of fish (Ono & Simenstad 2014) and thereby increase the risk of predation (Jones & Hale et al. 2020). Even under favourable conditions, some fish might not even attempt to pass through the culvert (Goerig & Castro-Santos 2017). Given their high number the accumulation of these "mostly passable" barriers may however reduce connectivity more than total barriers do (Buddendorf et al. 2019). Because the passable culverts can reduce movement, the passability of passable culverts should have been less than 1 in the calculation and thus the overall connectivity of the network would have been lower. It should also be noted that assessing passability is an uncertain measure as it can vary due to seasonal fluctuations or depending on the swimming abilities of species (Kemp & O'Hanley 2010, MacPherson et al. 2012).

The number of barriers can also be higher than recorded. Achieving more exact results requires mapping all the barriers in the catchment areas. Knowing the locations and passabilities of structures requires field work, because especially small barriers are rarely recorded well (Belletti et al. 2020). Barriers might have also been removed, which means that restoration done elsewhere could increase connectivity more as a new passage has already been opened. It is also possible that including natural barriers, such as waterfalls, in addition to artificial barriers could affect the order of prioritisation (Diebel et al. 2015).

Several dams had fishways that, were assumed to be partial barriers, because they often are not passable for all species (e.g. Noonan et al. 2011, Januchowski-Hartley et al. 2013). For example, salmonids can pass fishways more efficiently than non-salmonid species, but their migration suffers as well. Not all individuals are able to locate the bypass entrance and less than half of the fish might be able to pass the barrier using fishways (Noonan et al. 2011). If the fishways are more passable than they were assumed to be in this study, they would have been prioritised lower.

4.3 Improving the connectivity analysis and future study needs

Iterative selection could have helped to refine the results (Foltête et al. 2014), but it was not done because of its complexity. In an iterative selection, the highest prioritised barrier is identified, and its removal is simulated after which the second highest prioritised barrier can be identified. This allows considering how removing barriers in the order of prioritisation changes connectivity and the prioritisation of other barriers. An iterative analysis could have led to different prioritisation order, because once a barrier is removed, the next one upstream can become highly prioritised especially if the barriers are located close each other (Martin 2018). Without iterative selection, the impact of a barrier removal on prioritisation and the relative priorities of remaining barriers cannot be assessed. Instead, the results show how much each barrier decreases connectivity currently before any barriers have been removed.

Order of priority could have also been affected by treating some of the barriers that are very close to each other as one restoration project. When two barriers are close to each other, individually they can both have low priority as removing the lower barrier does not open much stream-length upstream and removing the upper one does not aid in accessing headwaters as the lower barrier continues to block access (Martin et al. 2018). Therefore, neither barrier is prioritised highly even if removing both barriers would be the best option for improving connectivity.

This study did not consider the asymmetry in upstream and downstream passability of barriers, nor the habitat quality or specific characteristics of barriers. However, it should be noted that the barriers are particularly problematic for upstream migrations of fish and other biota (De Fries et al. 2023). Even though simple graphs without weights can be used to analyse fragmentation (Erös et al. 2011) these graphs might not be able to consider the characteristics of the habitat patches well enough. Thus, future connectivity analyses could assign different weights for upstream and downstream passabilities as well as for high- and low-quality habitats because weighting habitats can affect the prioritisation of individual barriers (Buddendorf et al. 2019). Such development would, however, require systematic assessment of river habitat quality, which is not available in Finland currently. Moreover, the use or condition of each barrier was not considered. Compared to large, operational hydropower dams, removal of old, abandoned, or small dams is usually more common and socio-economically feasible (Habel et al. 2020).

The objective of the analysis was to maximise habitat gain as larger and more connected habitats were assumed be the most beneficial for different species. However, it is not always the best measure as the most important sites for barrier removals can vary between life histories of aquatic species (McManamay et al. 2019). In Central Finland some freshwater resident species migrate between lakes and streams and several migratory fish species are endangered in Finland (Urho et al. 2019). Therefore, connectivity restorations that improve access to small headwater spawning streams are needed. As many highly prioritised barriers are in short rivers between lakes, the important small streams in the headwaters might remain unreachable even after restoration if the habitat types and lifecycles are not considered. Recolonisation of previously inaccessible habitats can take several years (Erkinaro et al. 2017) and other restoration measures, such as adding gravel to stream bed or creating river bends (Sarvilinna et al. 2012) might be needed to support survival and natural recruitment of migratory fish. In future studies the life histories of target species could be considered to assess how much connectivity has decreased and where connectivity restoration projects are the most important for species with varying life histories.

Barrier removal projects can have limitations also for economic and social reasons (Habel et al. 2020). The support that a barrier removal gets can vary and sometimes stakeholder groups oppose removal projects. This could be due to economic reasons or cultural (e.g. historical) significance of the structure (Habel et al. 2020). The connectivity analysis is not able to consider how stakeholders might react to barrier removals and if the landowner agrees to the restoration. The economic reasons limiting barrier removal usually mean having limited financial resources, which should be allocated as efficiently as possible. Cost-benefit analyses can support prioritisations (e.g. O'Hanley et al. 2013) but were not conducted here because the focus was only on connectivity. For example, the price of a dam removal can vary greatly depending on its size, with smallest dams being the cheapest to remove. In cost-benefit analysis low-cost barriers have been found to be prioritised higher than more expensive removals even when the low-cost barrier increases connectivity less (O'Hanley et al. 2013). Partial barriers have occasionally been prioritised in cost-benefit analysis due to their low replacement cost or high impact on connectivity (Diebel et al. 2015).

Monitoring of abiotic and biotic properties in restored streams is highly important but rarely implemented (Habel et al. 2020). The results of restoration vary at least in short term studies. After barrier removal, the fish have been observed to slowly recolonise the streams and become highly abundant (Kukula & Bylak 2022). There can also be variation between sites after connectivity restoration and restorations are not always effective by biological measures (Tummers et al. 2016, Mahlum et al. 2017). Therefore, monitoring the recovery of a restored site is important for planning future restorations because if restoring connectivity is not enough for aquatic species to recolonise opened habitats, other restoration actions are needed. It should also be noted that while barrier removals facilitate movement of native species, there are trade-offs as removing a barrier can facilitate the upstream spread of harmful, invasive species (Kerby et al. 2005, Fausch et al. 2009). If invasive species near barriers are known, it could be considered as a part of the analysis and those sites could be avoided.

Developing the connectivity analysis requires having precise data on the barriers including changes in their passability throughout the year. The passability of fishways would also have to be assessed to consider how much they affect connectivity and how functional they are for different fish species. In addition, knowing the biotic characteristics of rivers and streams could help to develop the analysis to become more efficient.

4.4 Conclusions

The connectivity of river networks in Central Finland has decreased showing the need to remove barriers or using other ways to mitigate the negative impacts. Even though some barriers have already been removed, it has not been enough to reconnect the river network meaning that more connectivity restorations are needed. Landscape graph is a tool that can be used in planning connectivity restoration actions, and to identify how the overall connectivity can be increased efficiently. The connectivity properties of a barrier, such as its passability and location in a river network, are not the only properties to consider in prioritisation. Therefore, connectivity and where to improve it cannot be assessed by focusing on one barrier. Instead, it requires a larger scale approach and considering how the barriers impede movement together. Even if the connectivity analysis does not provide full answers for connectivity restoration planning, the results offer a useful additional assessment criterion for barrier removal selection and help to focus prioritisation on the most disruptive barriers.

Disconnected rivers are a major problem worldwide (Dudgeon et al. 2006) and similar analysis could be applied elsewhere provided that barrier records exist. The national and international agreements such as Water Framework Directive require barrier removals to improve the state of rivers and streams. Running waters act as corridors connecting aquatic ecosystems to each other. Therefore, restoring connectivity can have positive impacts in other ecosystems as well and aid in supporting the function of these ecosystems. Improving the state of streams and rivers and protecting endangered species requires restorations actions and among them connectivity needs to be improved to protect some of the most threatened ecosystems in the world (Miyazono & Taylor 2013, Reid et al. 2019).

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APPENDIX 1. CHARACTERISTICS OF THE HIGHEST PRIORITISED SITES

Characteristics of highest prioritised sites based on data from VESTY, Vesikartta, showing the stream ecological qualities, Finnish Land Survey map, used to identify the riparian zone type, and SYKE's records on riverine salmonid stocks (Virtavesien lohikannat). The structures and passabilities listed are the same that were used in the analysis. The table includes the 20 highest prioritised barriers from of the calculations done with different passabilities for partial barriers (i.e. 0.3, 0.5 and 0.7) for partial barriers in descending order when the passability is 0.5. N/A means that there no data was available to describe a property of the site.

*For=forest, Agr=agricultural land, Urb=urban area

Location	Name of barrier	Barrier structure	Purpose	Effect	Ecological quality	Salmonids recorded	Riparian zone*	Other notes
Äänekoski	Mämmenkosken pato	Dam/ fishway	N/A	Partial	N/A	Yes	Fo	Restorations done and dam removed
Laukaa	Kuhankosken pato	Dam/ fishway	Hydropower	Partial	N/A	No	Fo, Agr	
Kannnonkoski	Potmonkosken pato	Dam/ fishway	Flood control	Partial	Good	No	Fo	
Kannonkoski	Hilmon voimalaitospato	Dam	Hydropower	Total	N/A	No	Fo	

Äänekoski	Hietamankosken voimalaitos	Dam/ fishway	Hydropower	Partial	Good	No	For, agr	
Hankasalmi	Venekosken voimalaitospato	Dam	Hydropower	Total	Moderate	Yes	Agr	
Jämsä	Patalankosken pato	Dam	Hydropower	Total	Moderate	No	Urb, agr	
Saarijärvi	Leuhunkosken voimalaitos	Dam/ fishway	Hydropower	Partial	Good	No	For, agr	
Saarijärvi	Haapakosken vesilaitospato	Dam	N/A	Partial	Good	Yes	Agr	
Pihtipudas	Elämäisjoen pato	Dam	Hydropower	Total	Moderate	No	For, agr	Dam is on the side of the river, so passage is possible
Jyväskylä	Lohikosken voimalaitospato	Dam	N/A	Total	Moderate	No	Urban	Dam removal ongoing
Kannonkoski	Kannonkosken myllypato	Dam	N/A	Total	Moderate	No	For, agr	
Äänekoski	Parantalankosken voimalaitos	Dam	Hydropower	Total	Good	No	Agr, for	

Kinnula	Savi-, Jäppä- ja Poikkeusjärvien säätöpato	Dam/ fishway	Flood control	Partial	Moderate	No	For, agr	
Muurame	Sahakosken voimalaitospato	Dam/ fishway	Hydropower	Partial	High	Yes	Urb	
Konnevesi	Enojoen myllypato	Dam	N/A	Total	N/A	No	For, agr	
Saarijärvi	Pyhäkosken pato	Dam/ fishway	Hydropower	Partial	Moderate	Yes	Agr, for	
Jämsä	Arvajankosken voimalaitos	Dam/ fishway	N/A	Partial	High	Yes	For, agr	Old dam structures removed
Saarijärvi	Hernesalmen myllypato	Dam	N/A	Partial	Good	Yes	For, agr	Dam deconstructed but not fully passable
Äänekoski		Culvert	Road crossing	Partial	Good	No	For, agr	
Laukaa	Myllykosken voimalaitos	Dam	Hydropower	Total	Moderate	No	For, agr	
Luhanka	Myllykosken pato	Dam	Fish farming	Total	Moderate	No	For, agr	