Co-occurrence patterns of fish in pre-alpine lakes in the light of habitat association and species interactions

Bachelor thesis in the Institute of Ecology and Evolution, Faculty of Science,
University of Bern

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2018

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Abstract

The composition of a lake fish community depends on biotic as well as abiotic factors. In this study, I investigated mechanisms creating co-occurrence patterns of fish species caught during the nation-wide sampling program “Projet Lac”. Twenty-seven lakes were sampled, most of which were Swiss lakes, though some were located in or adjacent to France, Germany, Austria, and Italy. Sampling methods were standardised (electrofishing, vertical and CEN gillnets) and a total of 48 littoral fish species were documented. However, investigation was limited to catches attained by electrofishing in this study.

The strength and direction of pairwise co-occurrence was assessed by comparing the proportions of actions in which the species were caught. Twenty-four pairs yielded statistically significant co-occurrence values, 13 of which were positive and 11 were negative. The ratios of positive and negative co-occurrences for each species were also compared. Trophic guilds and habitat associations were incorporated in order to explain the co-occurrence patterns observed. Additionally, the effects of a large piscivore, namely northern pike (*Esox lucius*), on local species assemblages were investigated. Community structure, species diversity, biomass and abundance were compared between pike-free and pike-containing biogenic habitats.

Piscivores tended to exhibit a comparatively high proportion of negative co-occurrences, whereas species feeding on vegetation, plankton, and detritus tended to be more positively co-occurring with other species. The proportion of positive co-occurrences decreased with an increase of the species’ trophic level. These patterns were largely created by the combined effects of biotic and abiotic factors. Invertivores showed no eminent patterns, however, this was most likely due to the limited resolution of this trophic guild. The significantly co-occurring pairs were dominated by members of the family Cyprinidae, whereas the pairs exhibiting significant negative co-occurrence consisted predominantly of predatory fish. In both cases, the main reasons were thought to be of biotic nature. Conspicuously, European perch (*Perca fluviatilis*) were negatively co-occurring with many native species, but exhibited positive co-occurrence with all invasive Perciformes. Competitive interactions appeared to be the main drivers of this pattern. However, I proposed that the aggressive behaviour of schooling perch may have played an additional role. The presence of pike did not have a significant effect on the number of species present, nor did it induce a relevant change in local species composition. However, local biomass and abundance were significantly lower in pike-containing habitats. Smaller fish tended to avoid pike to a larger extend than comparatively large fish.

Although sometimes difficult to differentiate between effects of biotic and abiotic factors, most co-occurrence patterns could be explained primarily by the habitat associations of the species in question. In some instances, however, the patterns suggest interspecific competition, predation, and (possibly) aggressive behaviour to be the main drivers in shaping local community assemblages.

Introduction

Community assembly theory – early concepts

Virtually every locality on earth, be it aquatic or terrestrial, is occupied by a particular set of species. The factors determining such species assemblages locally as well as regionally have been subject to heated debates between ecologists for the last five decades (e.g. Connor and Simberloff, 1979; Diamond, 1975; Jackson et al., 2001). The classical competition theory, initiated by Hutchinson (1959), was developed in order to explain the composition of species assemblages. It proposed that interspecific competition was the dominant ecological process limiting species diversity and underlying the observed patterns in community structure. Classic competition theory consisted of six key premises:

> (1) Certain species' life history characteristics, such as reproduction rate and success, can be adequately summarized by the per capita growth rate of the population,
>
> (2) Population growth can be modelled by deterministic equations as environmental fluctuations are negligible,
>
> (3) The environment is spatially homogenous,
>
> (4) Migration is unimportant,
>
> (5) The only relevant biotic interaction is competition, and
>
> (6) Long-term coexistence requires a consistent equilibrium point.

As competition only arises if resources are limited, the theory has to be viewed in the light of resource limitation. When incorporating this concept, these six premises underlie the prediction that a minimum amount of *n* limiting resources is required for the coexistence of *n* species. Further, in order for two species to co-exist, the principle of "limiting similarity" must be satisfied, i.e. the species must be sufficiently dissimilar in resource use, thereby reducing interspecific competition and facilitating coexistence. The idea behind this theory was that interspecific competition was a key driver of evolution. This coevolution, together with repeated invasions of new species and the subsequent extinction of some residents due to competitive exclusion, was thought to yield communities in which the theoretical upper limits to similarity are roughly achieved. In other words, species develop increasing dissimilarities until interspecific competition is reduced to a magnitude that enables co-existence. As further differentiation is not implicitly necessary, community members were thought to be as similar as possible but as dissimilar as required. Therefore, real-world communities should have highly predictable properties in terms of member dissimilarity and resource utilisation. They can therefore be described by models which assume consistent equilibria, given that chance factors, historical effects, and occasional environmental perturbations play a relatively small role (Chesson and Case, 1986).

Based on the premises of classic competition theory, Diamond (1975) used a list of bird species present on islands of the Bismarck Archipelago, Papua New Guinea to generate a number of general community assembly rules, including forbidden species combinations, checkerboard distributions, and incidence functions. Diamond's publication provoked a series of criticisms, the most common arguments being that 1) the rules he developed were only descriptions of data rather than predictions, 2) the mechanism behind the observed patterns was assumed to be competition without any proof or evidence, and 3) that randomness had not been taken into account (Connor and Simberloff, 1979). As the discussion among ecologist progressed, it became clear that predation needed to be recognised as another key biotic interaction (Jackson and Harvey, 1989; Roughgarden and Feldman, 1975). It was suggested that *n* species might be able to coexist on fewer than *n* resources, as predators represented another limiting factor.

Although non-random community assemblage was considered “obvious” by many ecologists early on (e.g. Diamond, 1975; Hairston, 1959), they failed to empirically show that real-world communities were structured as opposed to random. So in the subsequent two decades after Diamond’s publication, biologists have been discussing whether community structure does not evolve purely by chance. Simple tests for non-randomness have already been used beforehand, particularly the well-known chi-square test for association between pairs of species (e.g. Kershaw, 1965). The test determines whether or not the occurrences of two species are independent. The subsequent introduction of “null models”, which tested for more complex patterns, such as nestedness (e.g. Patterson and Atmar, 1986), sparked further controversy regarding the comparison between observed and randomized species assemblies, though the discussion focused increasingly on the methodical aspects of these models (see Gotelli and Gary, 1996). Overall, however, studies indicating non-random structuring of communities with various different types of null models accumulated (see Weiher and Keddy, 1995), steadily increasing consensus among ecologists. Finally, a large-scaled meta-analysis by Gottelli and McCabe (2002) on species presence-absence matrices yielded significant evidence that communities are, in fact, non-randomly assembled.

Modern community assembly theory

The premise that communities are in equilibria was also questioned by various studies. Niche differentiation, i.e. species becoming more dissimilar in their resource use to facilitate co-existence, did not seem sufficient to explain the observed coexistence patterns in some communities. The effect of predation on community structure was not as far-reaching as originally expected and many communities did not exhibit species compositions which would suggest that an equilibrium point has been attained (Connell, 1980; Hubbell, 1979). Approaches with more complex equilibrium concepts, such as spatially variable equilibria within one system (e.g. Hubbell, 1979), did not yield a satisfying explanation either. Further, the finding of vast temporal variation in environmental variables and population parameters, such as density (Grubb, 1977; Keough, 1983), went against the ideas of classic competition theory. This suggested that the structure of at least some communities might be better explained by non-equilibrium concepts.

Roughly a decade after Hutchinson (1959) initiated the development of the classic competition theory, an alternative explanation for community assemblage mechanisms was published by Smith and Powell (1971), though the publication failed to draw the attention of the ecologists debating the issue in the subsequent years. Examining fish communities in a North American creek during summer, Smith and Powell suggested that the local community may be viewed as the result of passing the global fish fauna through a series of screens. First, the gross physiological screen removes all species not adapted to freshwater. The second screen rejects species of other continents, further screens represent additional, continuously smaller-scaled factors such as climate barriers. Finally, tolerance to chemical, additional physical (e.g. current strength) and biological conditions eventually result in the observed local species assemblage. The concept first took root in the study of plant community assembly in the late 1970’s, thereon mainly referred to as “environmental filtering”, and grew in usage over the subsequent decades (Kraft et al., 2015).

During the more recent decades, the view that habitats (i.e. environments) act as filters to determine the species assembly by eliminating sets of traits that are unsuitable to the given conditions is now generally accepted (Keddy, 1992). The assumption that the composition of an assemblage is in equilibrium has largely been dismissed and replaced by the view that ongoing, repetitive filtering and sorting processes constrain community assembly and make some assemblages more likely to persist than others (Tilman, 2004; Weiher et al., 2011). At first sight, one might see a discrepancy between the earlier concepts, particularly that of “limiting similarity”, and environmental filtering. The former requires sufficient differences between coexisting species, whereas the second inevitably leads to clustering of species with similar traits by excluding those with other, unfitting traits. However, this comparison is oversimplified, given that the different filters select traits at different levels. The first group of filters cause overall similarity of trait values, more specifically of adaptations to the local physical conditions. The second group, however, leads to trait overdispersion associated with competition and resource partitioning. Therefore, communities are simultaneously constrained by both concepts; traits associated with (abiotic) environmental filtering may be clustered, whereas traits associated with biological interactions may be overdispersed (Weiher et al., 2011).

It is important to note that community assemblies likely vary with scale and along gradients. Community assembly “rules” should be less constrictive where both competitive and environmental adversity are weak, i.e. competition pressure is relatively low and environmental conditions are generally favourable and consistent. Trait overdispersion should be limited to small spatial scales over which species interactions actually take place. As scale increases, patterns of trait overdispersion should first become increasingly neutral and then should gradually shift to the opposite: trait underdispersion and/or the convergence of traits (Weiher and Keddy, 1995). However, such predictions have to be taken with caution, as biotic interactions (often resulting in trait overdispersion) are frequently neglected when assessing species distributions on broader scales and it remains unclear how these interactions scale-up from local to global scales (Kissling et al., 2012).

Numerous studies investigating biodiversity and community patterns emphasize that local, regional, and historical factors play a key role in structuring communities across ecosystems and organism groups, but assemblage structure can rarely be explained by abiotic factors alone (Stendera et al., 2012). While the importance of predation in shaping community structure has already been widely acknowledged by ecologists during the early stages of community assemblage research (Roughgarden and Feldman, 1975), the discussion concerning the relative role of competition was not as straight forward. Originally hypothesized to drive phenotypic (and/or phylogenetic) divergence, it has now become clear from both theory (Chesson, 2000; HilleRisLambers et al., 2012) and experiments (e.g. Godoy et al., 2014; Narwani et al., 2013) that competition may also result in phenotypic and/or phylogenetic convergence if the phenotypes in question are associated with competitive dominance. This means that the development of traits which offer an advantage over competitors, for example a larger mouth allowing larger prey to be swallowed, may be enhanced in both competing species, making them more similar. The outcome of competition depends on the average fitness differences that determine competitive dominance as well as the niche differences stabilising coexistence between different community members (Chesson, 2000). If the average differences in fitness are small, it is plausible that both species will develop traits necessary to outcompete the other species, e.g. both develop larger mouths. In contrast, if average fitness differs substantially between the two competitors, it is more likely that one (i.e. the weaker species) will enhance development of traits helpful to utilise other resources, thereby reducing competition pressure and resulting in a niche shift. The chance of success of the second strategy, however, depends on how different the two niches are. More distinct niches facilitate co-existence, but also require a more distinct change in morphology to be attained. Consequently, competitive exclusion is expected to be common among similar species, therefore theoretically resulting in an overdispersion in traits and/or phylogenetic relatedness (Cornwell et al., 2006). However, as suggested by Mayfield and Levine (2010), as high average fitness of a species depends on certain traits as well, competitive exclusion can result in trait and/or phylogenetic clustering. Given that both abiotic environmental filters and competition can lead to such clustering, it is often difficult to disentangle the relative role of each in forming community assemblages, and many community assembly analyses that report abiotic environmental filtering may in fact be describing the combined effect of both processes (Kraft et al., 2015). In summary, biotic and abiotic factors are not only interactive and complementary, but their effects can have similar roles in shaping communities (Jackson et al., 2001).

Fish community assembly theory

In terms of fish species assemblages, lakes have often been compared to islands by ecologists. Similar to islands, the degree of isolation, size, and habitat diversity have important effects on fish assembly and richness (Barbour and Brown, 1974; Tonn et al., 1990). Particularly in temperate zones where ice sheets covered most of the surface during the last glacial period, re-colonization patterns played a major role in structuring species compositions observed today (Hinch et al., 1991; Jackson and Harvey, 1989). For example, recolonization of today's Canadian highland lakes was only possible during a short post-glacial period, before isostatic rebound (i.e. the uplift of land due to a retreating glacier) quickly reduced the connectivity of these lakes. Consequently, these lakes currently exhibit lower fish diversity than the lowland lakes and consist mostly of cold-water species (Eschman and Karrow, 1985). Historical and regional processes must therefore be considered when interpreting local community patterns (Hinch et al., 1991).

Regional assembly patterns appear to be generally driven by large-scale factors, such as post-glacial dispersion and climate-induced thermal regimes of the lakes (lakes within a given region experience the same climatic conditions), whereas variation within regions is likely influenced by physico-chemical and morphological characteristics of the individual lakes, such as maximum depth and lake pH (Jackson and Harvey, 1989). As shown by Zalewski et al. (1984.), relatively low levels of dissolved oxygen decreases the abundance of large predators, as these fish need more oxygen than smaller species, while the latter often exhibit behavioural and morphological adaptations in order to tolerate low oxygen levels. In contrast, small-bodied species are more susceptible to increased acidity of the water (Harvey, 1974). Both examples emphasize the important role of lake characteristics in structuring community assembly.

Small lakes often experience lethal environmental conditions (e.g. hypoxia) and recolonization represents an important process in maintaining and structuring the fish community. Fish species differ in their ability to move through connected waterways and each river selects and filters species differently. This contributes to differences in community structure between the connected lakes, even where lakes are relatively similar in environmental conditions and habitat diversity (Jackson et al., 2001).

The mechanisms of fish community assemblages described above appear to be all in accordance with the initial concept of environmental filters proposed by Smith and Powell (1971). However, the importance of biotic interactions influencing community structure locally, particularly that of predation, has been increasingly emphasized in the subsequent decades (Jackson and Harvey, 1993; Jackson et al., 1992). In a comparison of fish community structure between Finnish and North American Lakes, Tonn et al. (1990) found that particularly in Finnish lakes, individual response to environment, rather than biotic interactions, played a major role in creating overall patterns of occurrence and assemblage composition in terms of species absence/presence. In contrast, biological interactions, namely predation by northern pike (*Esox Lucius*), determined a species' local presence or absence in the North American Lake Wisconsin. The authors proposed that the difference may be due to the different prey communities available to the pike. Whereas its prey in Finland were mainly cyprinids, capable of attaining size refuge from pike predation, the prey fish in Lake Wisconsin were considerably smaller, which meant that they were locally extirpated by predation. The authors added that predation was also influential in Finland, but only apparent in terms of abundance rather than species absence/presence.

Predation can also affect the choice of habitat by prey species and thereby influence fish assemblage composition (Gilliam and Fraser, 2001). In the presence of predators, prey fish may move to shallow waters, reside in complex habitats as they offer more protection, or leave the site all together (He and Kitchell, 1990). However, there does not seem to be a consensus regarding the role of interspecific competition in structuring freshwater fish assemblages (Jackson et al., 2001). Indeed, many studies suggest that the main outcome of competition is often niche segregation, rather than exclusion (Jackson et al., 2001). Robinson and Wilson (1994) similarly suggested that niche diversification is the main mechanism allowing fish species to coexist. Further, evolutionary responses to competition, for example character displacement, are much more common than previously considered and often result in the emergence of traits associated with a benthic and a pelagic/limnetic life style, respectively (Bernatchez et al., 1996; Crowder, 1984; McPhail, 1984; Schluter and McPhail, 1993). In addition, given that many freshwater fish species have similar habitat and diet requirements before fully maturing and often becoming more dissimilar, it is hypothesised that interspecific competition may be strongest among juvenile fish (Colby et al., 1987). It is evident that competition among freshwater fish species is ubiquitous, however, its role in shaping community structure relative to the role of abiotic factors and predation is hard to assess and differs profoundly between local systems.

The importance of biotic interactions is expected to be lower where physical disturbances reduce population densities. Given the higher environmental variability of small lakes, competition pressure should be correspondingly weaker (Jackson et al., 1992). In fact, large-scale studies find more abiotic factors governing fish community assemblage, whereas authors of small-scale studies put comparably more emphasis on competition. Predation effects, however, have been identified in both large- and small-scale studies, thus highlighting the importance of this biotic mechanism within as well as across scales (Jackson et al., 2001).

Aims of this study

The aim of this study was to investigate fish species co-occurrence in the littoral zone of pre-alpine lakes. I used information on trophic guild and habitat use in order to understand the role of interspecific competition in shaping assemblage composition through dietary overlap and shared habitat associations. I also assessed the relative importance of predation in shaping community assemblages, particularly focussing on the northern pike. I hypothesised that prey fish would avoid predators and that this would be revealed in a comparison of fish communities between similar habitats in the absence/presence of a predator.

Material & Methods

Data Collection – Projet Lac

My project was based on the data collected in Projet Lac, a program lead by Eawag in collaboration with the University Bern, the Federal Office of the Environment (FOEN), and the fishing authorities of the Swiss cantons, designed to assess fish diversity and composition across pre-alpine lakes. Data collection began in 2010 and ended in 2014. Twenty-seven lakes were sampled in Switzerland, France, Germany, Austria, and Italy. Sampling occurred between August and November and was standardised according to lake size and depth. Fish sampling methods included gillnet fishing (vertical and CEN) throughout the lake, as well as electrofishing in the littoral zone. Littoral habitats were mapped prior to fish sampling and each habitat type present in the lake was sampled at least three times. Each fish caught was identified to species level, measured in length and weight, photographed, and a tissue sample taken for genetic analysis. If identification to species level was not possible in the field, the specimen was categorized by genus (e.g. *Scardinius spp.*). Finally, notable features (e.g. parasite load) were recorded for each individual.

For three genera, namely Phoxinus, Scardinius, and Salmo, identification to species level was not always possible in the field. The first two, Phoxinus and Scardinius, were excluded from all analyses. These were formally described species that form hybrids and were therefore difficult to distinguish in some lakes. Relatively few specimens were only identified to genus-level. Due to taxonomic uncertainty, the genus of Salmo was converged to *Salmo trutta*, the brown trout, for analysis.

Morphological and behavioural differences mean that each fish species and body sizes have different likelihood to encounter, be caught and retained in gillnets (Hamley, 1975). Gillnet data are therefore not necessarily representative of the true fish community composition. Electrofishing, on the other hand, provides a substantially less biased representation of the relative abundance of fish species. That said, larger individuals may be underrepresented by electrofishing, as they are stronger and may be capable of escaping the electric field when it approaches. Size selectivity by electrofishing also varies between species (Anderson, 1995).

This study is therefore focused only on electrofishing catches. Due to the lack of electrofishing data in some lakes, analyses for this study included 19 Swiss lakes (Thun, Walen, Brienz, Lucerne, Neuchâtel, Upper Lake Constance [shared with Germany and Austria], Lower Lake Constance [shared with Germany], Upper Lake Zürich, Zürich, Lugano and Maggiore [shared with Italy], Joux, Hallwil, Murten, Geneva [shared with France] Zug, Brenet, Poschiavo, Sils), four French lakes (Chalain, Remoray, Saint-Point, Bonlieu), and one Italian lake (Garda).

The sampled area varied among electrofishing actions, so the number of fish caught and the total biomass were adjusted to a value per 100 m^2. Two habitats associated with rivers, namely inflowing and outflowing creeks and rivers, were excluded from the analysis. Although part of the lake, these habitats contain species which are more common in rivers (e.g. common barbel, *Barbus barbus*), and are therefore not necessarily part of the lake fish community.

Species co-occurrences

Within each lake, the spatial occurrence of each species was compared to the occurrence of every other species on a pairwise basis. The following formula was used to quantify the strength and direction of co-occurrence (positive/negative):

$$\frac{Sp1{,}2}{Act} - \left(\frac{Sp1}{Act} * \frac{Sp2}{Act}\right) = Co - occurrence\ value$$

Sp1,2 represents the number of actions in which the two focal species co-occurred within a given lake. *Act* represents the total number of electrofishing actions in the lake where at least one fish was caught, while *Sp1* and *Sp2* stand for the number of actions in which species 1 and species 2 were caught, respectively. The part of the formula in brackets thereby represents the proportion of actions that the two species would be expected to co-occur (i.e. both be present), relative to their frequency of occurrence, if the species were distributed randomly among actions. Subtracting the expected frequency of co-occurrence from the observed frequency of co-occurrence yields a number either above or below zero. If the observed frequency of co-occurrence is higher than expected by chance (i.e. the expected frequency of occurrence), the formula yields a positive result, indicating that the two species are positively co-occurring. In contrast, if the two species co-occurred in less actions than one would expect by chance, this results in a negative number, indicating negative co-occurrence. For species pairs coexisting in more than one lake, the mean of all lake-specific co-occurrence values was also calculated. Co-occurrence estimates were therefore based on species presence-absence data. The proportion of positive co-occurrences of each species to all other species was also calculated.

Trophic levels and guilds

The trophic level of each species was extracted from www.fishbase.org (2017). Trophic levels were calculated based on the trophic level of the food item(s), weighted by the importance of the prey item in the diet (Pauly et al., 1998). Each species was also assigned one or multiple trophic guilds according to Caussé et al. (2011) in the Wiser Report on Water Bodies in Europe. The abbreviations for the trophic guilds were also adopted from this report (see Table 1). It is important to note that the trophic guild of invertivores (INV) corresponds to fish feeding on benthic invertebrates, while fish feeding on invertebrates in the water column are defined as planktivores.

Table 1: Trophic guilds with their corresponding abbreviation

Abbreviation	Trophic guild
DETR	Detrivore
INV	Invertivore
PISC	Piscivore
PLANK	Planktivore
VEG	Herbivore

Due to the relatively low resolution of these trophic guilds, an attempt was made to compile more detailed data on diet items for each species. The objective was to further differentiate the trophic guilds to the level of phylum or even class. However, this task proved to be prohibitively complex. Very little diet data was available for rarer species and diet composition for common species varied strongly among regions and seasons.

Habitat Associations

Habitat associations for each species were adopted from Hefti (2017), who utilised the same Projet Lac data set. One difference, however, was that she also included catches obtained by vertical gillnets. In her thesis, she quantified lake-specific habitat association of each species with each habitat. She compared the expected proportion of actions where the species was recorded in a habitat if the species was distributed randomly among actions against the observed proportion. This was similar to the calculations applied in this thesis to quantify co-occurrence. An overall measure of association across all lakes for each species was calculated as a weighted mean. The measure for each lake was weighted by the number of fish sampling actions within a specific habitat. The association of each species to each habitat was then compared to a randomised distribution to determine significance. The habitat associations resulting from this overall weighted mean were used in this thesis.

Table 2: Habitat types with their corresponding code. Habitats comprised of rocks are marked grey, whereas biogenic habitats are marked green.

Habitat code	**Habitat**
BED	Rock slab
BLO	Blocks & boulders
COB	Cobbles
GGR	Gravel & cobbles
GRA	Gravel
BRA	Wood or trees
HEL	Reeds
HYD	Macrophytes
HYF	Floating plants
LIT	Leaf litter
SAB	Sand
SED	Fine sediment mineral

For simplicity, each habitat was assigned an abbreviation in the field. These codes were adopted in this study (see Table 2). Habitats, except SAB and SED, were further identified as being mainly formed by plants (biogenic habitats), or rocks (lithic habitats). Although sand is lithic, sandy habitats are often structured homogenously and offer little to no complex structures, making them more similar to habitats covered by sediments rather than rocky habitats, i.e. boulders.

Biotic interactions – predation by pike

In order to investigate the effect of a large piscivore, namely the northern pike, on the local fish community, assemblage composition was compared between sampling actions with and without pike. The analysis focused on actions associated with vegetated habitats (i.e. wood/trees, reeds, macrophytes, and floating plants), as pike, particularly as juveniles, use vegetation cover to ambush prey (Casselman and Lewis, 1996). Other habitats were not considered in the analysis as different habitat types are likely to differ in assemblage composition, consequently impeding comparison between different habitat types. Only lakes that yielded actions both with and without pike in vegetated habitats were analysed. The average number of other fish species and the community composition were compared with and without the presence of pike as well as the average total number and biomass of fish per 100 m^2. Pike was included in the number of species and individuals, but excluded from the total biomass comparison, because predators tend to be of larger size than their prey and disproportionally elevate biomass estimates.

The analysis was limited to pike, as this species was the most abundant piscivorous fish (caught in 16 lakes). Although perch (*Perca fluviatilis)* have been caught in 22 lakes, the most frequently caught size classes were unlikely to have already shifted to a piscivorous stage (Mann, 1978). Therefore, I did not expect perch to have a relevant effect on community assemblage by piscivory in the shallow littoral zone covered by electrofishing.

Statistical analysis

The statistical significance of co-occurrence was assessed by comparing the observed average co-occurrence of each species pair to a distribution of co-occurrences derived from randomisation. In each randomisation, the actions where each species was present were randomly shuffled and the average co-occurrence value for each species pair was recalculated. The randomisation was repeated one thousand times, creating a distribution of the resultant means. Observed co-occurrence values situated in either of the two 2.5% intervals on either side of the distribution (negative/positive co-occurrence) were defined as statistically significant.

To test whether commonly occurring fish species exhibited more positive co-occurrences with other species, the proportion of actions in which a species was caught was plotted against the proportion of positive co-occurrences. Significance was determined based on linear regression analysis.

In order to analyse differences in species richness, number of fish, and biomass per $100m^2$ between vegetated habitats with and without the presence of pike, a linear mixed-effects model (LME) was applied, with lake specified as a random factor. Statistical significance of the presence of pike was determined by comparing this model to a null model with a Chi-squared test.

All statistical analyses were conducted with the statistics software R (version 3.4.1).

Results

Across all possible pairs of species (Table 3), more negative co-occurrences (n=474, roughly 60%) were observed than positive co-occurrences (n=336, roughly 40%). However, the proportion of positive co-occurrence values varied substantially among species.

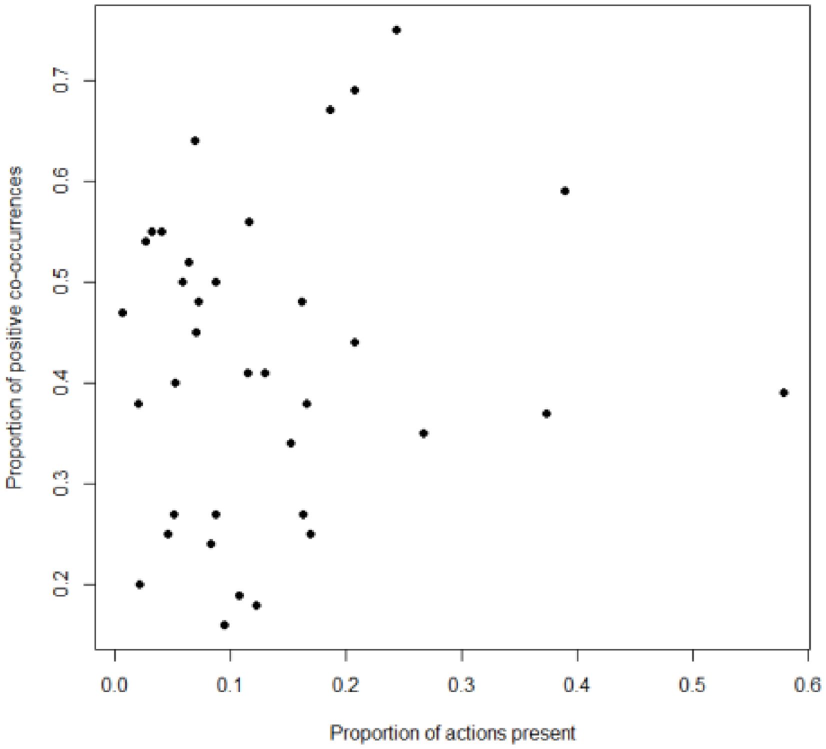

Figure 1: The proportion of positive co-occurrences plotted against relative abundance, as defined by the proportion of actions in which the species was caught.

Less common species (i.e. species caught in lower proportion of actions) did not seem to be less ikely to have a lower proportion of positive co-occurrences (Fig. 1). Linear regressioin also showed no significant effect of a species' prevalence on the proportion of positive co-occurrences ($F_{(1,34)}$=0.226, p=0.636).

Table 3: All possible species combinations with their corresponding co-occurrence values. Green and red cells indicate positive and negative co-occurrence values, respectively.

	Abramis brama	*Alburnus alborella*	*Alburnus alburnus*	*Anguilla anguilla*	*Barbatula barbatula*	*Barbus barbus*	*Blicca bjoerkna*	*Carassius gibelio*	*Cobitis bilineata*	*Cottus gobio*	*Cyprinus carpio*	*Esox lucius*	*Gasterosteus aculeatus*	*Gasterosteus gymnurus*	*Gobio gobio*	*Gymnocephalus cernua*	*Lepomis gibbosus*	*Leuciscus leuciscus*	*Lota lota*	*Micropterus salmoides*	*Padogobius bonelli*	*Perca fluviatilis*	*Phoxinus phoxinus*	*Rhodeus amarus*	*Rutilus aula*	*Rutilus rutilus*	*Salaria fluviatilis*	*Sander lucioperca*	*Scardinius erythrophthalmus*	*Scardinius hesperidicus*	*Silurus glanis*	*Squalius cephalus*	*Squalius squalus*	*Telestes muticellus*	*Tinca tinca*
Abramis brama			2.9	-0.7	-1.1	-0.2	2.0			0.8	4.5	0.0	-1.0	1.7	-0.7	-0.7	-0.9	0.7	-0.2			-1.3	-1.0			4.0	-1.7		8.5		-0.5	1.0			0.7
Alburnus alborella								-0.4									-0.6		2.4		3.4	-1.1		-0.4	2.3	-0.9	-2.1			2.4			1.9	6.2	
Alburnus alburnus	2.9			0.6	-2.0	-0.2	3.0		-0.2	-0.7	2.0	0.1	0.5	-0.2	-0.1	0.7	-0.4	-0.7	-0.9			-2.4	-1.9	-0.3		3.1	-3.6		1.6		-0.6	1.2			1.0
Anguilla anguilla	-0.7		0.6		0.1		-0.5			1.3	-0.3	-1.2	1.4		1.3	1.3	0.8	-3.0	1.7			1.8				-2.2			-0.8		-0.5	0.0			-0.4
Barbatula barbatula	-1.1		-2.0	0.1		1.7	0.9		1.5	2.9	1.5	-1.5	-1.5	-0.1	2.6	-0.6	-2.1	0.3	-0.9			-3.3	0.5	1.4		-0.2	2.6		-4.5		-1.6	0.2			-1.2
Barbus barbus	-0.2		-0.2		1.7							-0.5		0.0	-0.7			-2.4	-0.1			1.9		-0.9		-0.4	-0.6					5.7			0.7
Blicca bjoerkna	2.0		3.0	-0.5	0.9					-0.1	4.5	-0.4	-1.3		-0.1	-0.1	-0.3	1.6	-0.4			-0.1				2.0			3.5		-0.5	2.1			1.2
Carassius gibelio		-0.4															-0.9		-0.4			-0.4		6.2	4.9		-4.9			5.3			4.4	-0.4	
Cobitis bilineata			-0.2		1.5					-0.4	-0.2	-0.2			-0.6			-0.1	2.4			-0.8	-0.5	2.7		-0.5						-0.1			-0.7
Cottus gobio	0.8		-0.7	1.3	2.9		-0.1		-0.4		-1.2	-1.4	-0.3		-0.1	-0.5	-4.7	-0.5	-2.3			-5.3	1.4	-0.8		-1.5			-0.4		-0.1	-0.6			0.1
Cyprinus carpio	4.5		2.0	-0.3	1.5		4.5		-0.2	-1.2		-0.4	-1.3		6.9		-0.3	-0.9	0.6			-1.6	-1.5	2.4		4.2			4.3		-0.5	1.0			5.2
Esox lucius	0.0		0.1	-1.2	-1.5	-0.5	-0.4		-0.2	-1.4	-0.4		1.4	-0.1	-0.9	-1.1	-1.3	-0.6	-0.9	-1.8	-0.5	-4.3	-2.0	-0.3		-0.8	-1.8	-0.3	-0.8	-0.3	-0.4	-0.3	0.0	-0.3	0.3
Gasterosteus aculeatus	-1.0		0.5	1.4	-1.5		-1.3			-0.3	-1.3	1.4			-0.2	-0.2	-0.7	-2.2	-0.1			-1.6	-1.0			-0.3			-3.8		-1.3	-2.1			1.4
Gasterosteus gymnurus	1.7		-0.2		-0.1	0.0						-0.1			-0.4			1.8	-0.1			0.9				1.5	1.3					1.5			0.0
Gobio gobio	-0.7		-0.1	1.3	2.6	-0.7	-0.1		-0.6	-0.1	6.9	-0.9	-0.2	-0.4		-0.3	-2.3	1.4	-0.3			-1.9	-1.2	0.8		0.9	3.4		5.9		-0.1	0.7			1.5
Gymnocephalus cernua	-0.7		0.7	1.3	-0.6		-0.1			-0.5		-1.1	-0.2		-0.3		3.2	-0.6	0.7			4.0	-1.0			-2.0					-0.1	0.4			0.8
Lepomis gibbosus	-0.9	-0.6	-0.4	0.8	-2.1		-0.3	-0.9		-4.7	-0.3	-1.3	-0.7		-2.3	3.2		0.1	0.1	-0.3	3.2	4.5		-0.9	1.4	-0.7	-0.9	-0.8	-0.8	0.9	2.2	-1.5	-2.5	-0.8	0.9
Leuciscus leuciscus	0.7		-0.7	-3.0	0.3	-2.4	1.6		-0.1	-0.5	-0.9	-0.6	-2.2	1.8	1.4	-0.6	0.1		-0.9			-1.5	3.4	1.6		0.0	2.6		-2.6		0.5	-0.6			-2.2
Lota lota	-0.2	2.4	-0.9	1.7	-0.9	-0.1	-0.4	-0.4	2.4	-2.3	0.6	-0.9	-0.1	-0.1	-0.3	0.7	0.1	-0.9		1.5	1.2	1.2	1.2	2.1	-1.0	-3.0	2.4	-0.5	1.0	-0.8	2.1	1.7	-1.4	2.0	-0.2
Micropterus salmoides												-1.8					-0.3		1.5		-3.5	5.3				-9.0	-7.3	-1.8		3.3				-1.8	
Padogobius bonelli		3.4										-0.5					3.2		1.2	-3.5		2.6			3.4	2.8	0.1	-0.5		0.4			1.2	-0.5	
Perca fluviatilis	-1.3	-1.1	-2.4	1.8	-3.3	1.9	-0.1	-0.4	-0.8	-5.3	-1.6	-4.3	-1.6	0.9	-1.9	4.0	4.5	-1.5	1.2	5.3	2.6		-2.3	-0.5	4.3	-1.7	-2.3	0.8	2.7	0.4	1.3	-0.9	-0.2	-2.3	0.7
Phoxinus phoxinus	-1.0		-1.9		0.5				-0.5	1.4	-1.5	-2.0	-1.0		-1.2	-1.0		3.4	1.2			-2.3		-1.0		-2.1			-3.5			-2.0			-3.9
Rhodeus amarus		-0.4	-0.3		1.4	-0.9		6.2	2.7	-0.8	2.4	-0.3			0.8		-0.9	1.6	2.1			-0.5	-1.0		4.9	2.6	-4.9			5.3		-0.8	4.4	-0.4	0.5
Rutilus aula		2.3						4.9									1.4		-1.0		3.4	4.3		4.9		-0.9	-2.8			3.7			1.9	4.9	
Rutilus rutilus	4.0	-0.9	3.1	-2.2	-0.2	-0.4	2.0		-0.5	-1.5	4.2	-0.8	-0.3	1.5	0.9	-2.0	-0.7	0.0	-3.0	-9.0	2.8	-1.7	-2.1	2.6	-0.9		-3.3	-2.0	5.9	0.9	-0.2	-0.1	9.3	-2.0	-0.1
Salaria fluviatilis	-1.7	-2.1	-3.6		2.6	-0.6		-4.9				-1.8		1.3	3.4		-0.9	2.6	2.4	-7.3	0.1	-2.3		-4.9	-2.8	-3.3		3.3		-6.9		0.9	-7.7	-0.8	-0.6
Sander lucioperca												-0.3					-0.8		-0.5	-1.8	-0.5	0.8				-2.0	3.3			-0.3				-0.3	
Scardinius erythrophthalmus	8.5		1.6	-0.8	-4.5		3.5			-0.4	4.3	-0.8	-3.8		5.9		-0.8	-2.6	1.0			2.7	-3.5			5.9					-1.5	3.8			6.3
Scardinius hesperidicus		2.4						5.3				-0.3					0.9		-0.8	3.3	0.4	0.4		5.3	3.7	0.9	-6.9	-0.3					5.5	2.5	
Silurus glanis	-0.5		-0.6	-0.5	-1.6		-0.5			-0.1	-0.5	-0.4	-1.3		-0.1	-0.1	2.2	0.5	2.1			1.3				-0.2			-1.5			-2.9			-1.3
Squalius cephalus	1.0		1.2	0.0	0.2	5.7	2.1		-0.1	-0.6	1.0	-0.3	-2.1	1.5	0.7	0.4	-1.5	-0.6	1.7			-0.9	-2.0	-0.8		-0.1	0.9		3.8		-2.9				-1.0
Squalius squalus		1.9						4.4									-2.5		-1.4		1.2	-0.2		4.4	1.9	9.3	-7.7			5.5				4.4	
Telestes muticellus		6.2						-0.4				-0.3					-0.8		2.0	-1.8	-0.5	-2.3		-0.4	4.9	-2.0	-0.8	-0.3		2.5			4.4		
Tinca tinca	0.7		1.0	-0.4	-1.2	0.7	1.2		-0.7	0.1	5.2	0.3	1.4	0.0	1.5	0.8	0.9	-2.2	-0.2			0.7	-3.9	0.5		-0.1	-0.6		6.3		-1.3	-1.0			

Table 4: Species ordered from lowest to highest proportion of positive co-occurrence values with their corresponding number of electrofishing actions recorded, trophic level, and trophic guilds.

Number of Actions	Species	Proportion positive Co-occurrences	Trophic level	DETR	VEG	PLANK	INV	PISC
58	*Esox lucius*	0.13	4.35	0	0	0	0	1
2	*Sander lucioperca*	0.18	4.25	0	0	0	1	1
10	*Gasterosteus aculeatus*	0.19	3.51	0	0	0	1	0
3	*Silurus glanis*	0.20	4.37	0	0	0	0	1
1	*Cobitis bilineata*	0.21	-	1	0	0	1	0
59	*Cottus gobio*	0.22	3.15	0	0	0	1	0
100	*Salmo trutta*	0.25	3.16	0	0	0	1	1
44	*Phoxinus phoxinus*	0.26	3.11	0	0	0	1	
9	*Barbus barbus*	0.27	3.1	0	0	0	1	0
11	*Micropterus salmoides*	0.27	3.84	0	0	0	0	1
32	*Lepomis gibbosus*	0.35	3.12	0	0	0	1	0
95	*Rutilus rutilus*	0.35	2.79	1	1	1	1	0
60	*Salaria fluviatilis*	0.36	3.5	0	0	0	1	0
22	*Gymnocephalus cernua*	0.37	3.35	0	0	1	1	0
7	*Telestes muticellus*	0.38	-	0	0	0	1	0
42	*Gobio gobio*	0.38	3.13	0	0	0	1	0
3	*Carassius gibelio*	0.40	3.11	1	1	1	1	0
266	*Perca fluviatilis*	0.40	4.35	0	0	0	1	1
29	*Alburnus alburnus*	0.42	3.01	0	0	1	0	0
85	*Leuciscus leuciscus*	0.42	2.57	0	1	0	1	0
4	*Gasterosteus gymnurus*	0.43	3.51	0	0	0	1	0
6	*Blicca bjoerkna*	0.45	3.07	0	0	0	1	0
49	*Barbatula barbatula*	0.46	3.18	0	0	0	1	0
90	*Lota lota*	0.49	4.03	0	0	0	1	1
21	*Abramis brama*	0.50	2.94	0	0	1	0	0
3	*Alburnus arborella*	0.50	-	-	-	-	-	-
65	*Squalius cephalus*	0.50	3.03	0	1	0	1	0
4	*Scardinius erythrophthalmus*	0.50	2.89	0	1	1	1	0
6	*Cyprinus carpio*	0.52	2.96	0	1	0	1	0
5	*Rhodeus amarus*	0.52	2.95	0	1	0	1	0
32	*Tinca tinca*	0.54	3.49	1	1	0	1	0
11	*Anguilla anguilla*	0.55	3.53	0	0	0	1	1
9	*Squalius squalus*	0.62	-	0	1	0	1	0
13	*Padogobius bonelli*	0.64	3.5	0	0	0	1	0
7	*Scardinius hesperidicus*	0.69	-	0	1	0	1	0
6	*Rutilus aula*	0.75	2.8	-	-	-	-	-

Many piscivores (e.g. pike, wels [*Silurus glanis*], zander [*Sander lucioperca]*) exhibited comparably more negative than positive co-occurrences with other fish species (i.e. are positioned higher in the list; Table 4). Despite its relatively high trophic level (4.35), European perch displayed comparably more positive co-occurrences, even more so burbots (*Lota lota*), which were found in the lower third and exhibit a trophic level of 4.03. Both species are categorized as piscivores. The piscivore with the most positive co-occurrences was the European eel (*Anguilla anguilla*), which in turn also exhibited the lowest trophic level of all piscivores listed (3.53). In contrast, species feeding on plankton or vegetation tended to have higher proportions of positive co-occurrences. Species feeding on invertebrates, the trophic guild including by far the most fish species, tended to be spread evenly across the list.

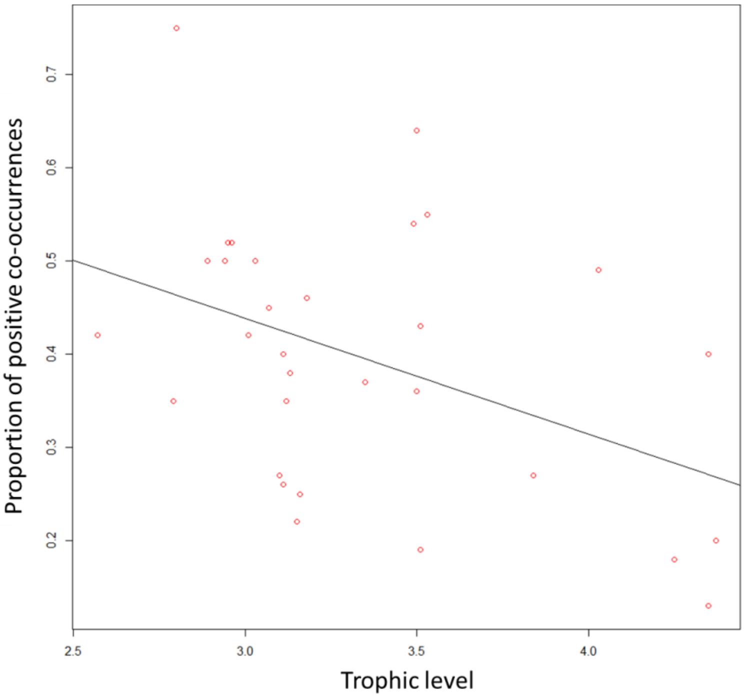

Figure 2: The relationship between trophic level and the proportion of positive co-occurrence values of each species.

Plotting trophic level against the proportion of positive co-occurrences of each species (*Fig. 2*) indicates a significant negative relationship; i.e. the proportion of species with which a particular species positively co-occurs decreases with increasing trophic level ($F_{(1,28)=}$6.531, R^2=0.189, p=0.016).

Table 5: Significantly negatively or positively co-occurring pairs along with their trophic guilds. Shared trophic guilds within each pair are highlighted in the trophic guild section with colours corresponding to the type of guild. The species names of perciformes and cyprinids are highlighted in brown and green, respectively. Piscivores are highlighted in red.

		Trophic guild									
POSITIVE CO-OCCURRENCE		**DETR**		**INV**		**PISC**		**PLANK**		**VEG**	
Species1	**Species2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**
Perca fluviatilis	*Lepomis gibbosus*			1	1	1					
Perca fluviatilis	*Gymnocephalus cernua*			1	1	1			1		
Rutilus rutilus	*Alburnus alburnus*	1		1				1	1	1	
Rutilus rutilus	*Squalius squalus*	1		1	1			1		1	1
Rutilus rutilus	*Abramis brama*	1		1				1	1	1	
Lota lota	*Salmo trutta*			1	1	1	1				
Alburnus alburnus	*Abramis brama*							1	1		
Squalius cephalus	*Barbus barbus*			1	1					1	
Abramis brama	*Scardinius erythrophthalmus*				1			1	1		1
Barbatula barbatula	*Gobio gobio*			1	1						
Gobio gobio	*Tinca tinca*		1	1	1						1
Gobio gobio	*Cyprinus carpio*			1	1						1
Cyprinus carpio	*Tinca tinca*		1	1	1					1	1
NEGATIVE CO-OCCURRENCE		**DETR**		**INV**		**PISC**		**PLANK**		**VEG**	
Species1	**Species2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**
Esox lucius	*Perca fluviatilis*				1	1	1				
Esox lucius	*Barbatula barbatula*				1	1					
Perca fluviatilis	*Salmo trutta*			1	1	1	1				
Perca fluviatilis	*Cottus gobio*			1	1	1					
Perca fluviatilis	*Alburnus alburnus*			1		1			1		
Perca fluviatilis	*Barbatula barbatula*			1	1	1					
Perca fluviatilis	*Gobio gobio*			1	1	1					
Rutilus rutilus	*Lota lota*	1		1	1		1	1		1	
Salaria fluviatilis	*Scardinius hesperidicus*			1	1						1
Squalius squalus	*Salaria fluviatilis*			1	1					1	
Tinca tinca	*Leuciscus leuciscus*	1		1	1					1	1

Of all possible pairs of species, a total of 24 exhibited significant co-occurrence (Table 5). Thirteen species pairs positively co-occurred, whereas eleven pairs exhibited negative co-occurrence. The positively co-occurring species pairs were largely dominated by cyprinids, with 9/13 pairs consisting entirely of members of this family. In contrast, 9/11 negatively co-occurring pairs contained piscivores.

Positively co-occurring species pairs were dominated by species in the family Cyprinidae (highlighted in green in Table 5). Nine of the positively co-occurring species pairs were both cyprinids. Another co-occurring pair was the cyprinid gudgeon (*Gobio gobio*; family Cyprinidae, order Cypriniformes) and the cypriniform stone loach (*Barbatula barbatula*; family Nemacheilidae, order Cypriniformes). The three remaining positively co-occurring pairs consisted of perch with two other representatives from the order of Perciformes (*Lepomis gibbosus* [pumpkinseed] and *Gymnocephalus cernua* [Eurasian ruffe]; highlighted in brown) and a pair of phylogenetically distant predators (*L. lota* and *Salmo trutta* [brown trout]).

In contrast, the negatively co-occurring species pairs are dominated by piscivores (highlighted in red), namely pike, perch, brown trout, and burbot. Eight of the eleven negatively co-occurring pairs contained at least one piscivore, most frequently perch, which were represented in six pairs.

All positively co-occurring species pairs shared at least one trophic guild. Three pairs shared two trophic guilds simultaneously. Comparing this to negatively co-occurring pairs, two pairs did not share a trophic guild, seven shared one trophic guild and two shared two trophic guilds.

The most commonly shared trophic guild in both groups was that of invertebrate feeders, shared by nine positively co-occurring and eight negatively co-occurring pairs. In contrast, fish species feeding on detritus showed neither positive nor negative co-occurrences with one another. Only one pair of piscivores (*L. lota* and *S. trutta*) yielded positive co-occurrence, compared to two pairs of piscivores (*E. lucius* and *P. fluviatilis, P. fluviatilis* & *S. trutta*) that negatively co-occurred. Plant feeders exhibited the opposite pattern with two pairs positively co-occurring (*Rutilus rutilus* [roach] and *Squalius squalus* [Italian chub], *Cyprinus carpio* [common carp] and *Tinca tinca* [tench]) and one pair negatively co-occurring (*Leuciscus leuciscus* [common dace] and *T. tinca*).

Planktivores tended to co-occur, with four planktivorous pairs exhibiting positive co-occurrence, and no negatively co-occurring planktivorous pairs. Of the six planktivorous species, all except Prussian carp (*Carassius gibelio*) and ruffe exhibited significant positive co-occurrence with other planktivores.

Table 5: Significant negatively and positively co-occurring species pairs with the corresponding habitat associations. Shared habitat associations are highlighted, with colours depending on the type of habitat: rocky habitats are indicated in brown, biogenic habitats in green. Pairs sharing the same habitat association and are highlighted in grey, while pairs where one species associates with rocky habitat and the other to biogenic habitats are coloured in orange.

		Positive habitat association																							
POSITIVE CO-OCCURRENCE		**BED**		**BLO**		**COB**		**GGR**		**GRA**		**BRA**		**HEL**		**HYD**		**HYF**		**LIT**		**SAB**		**SED**	
Species1	**Species2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**
Perca fluviatilis	Lepomis gibbosus			1	1																				
Perca fluviatilis	Gymnocephalus cernua			1	1																				
Rutilus rutilus	Alburnus alburnus													1		1	1								
Rutilus rutilus	Squalius squalus													1		1									
Rutilus rutilus	Abramis brama													1		1									
Lota lota	Salmo trutta			1	1																				
Alburnus alburnus	Abramis brama															1									
Squalius cephalus	Barbus barbus											1													
Abramis brama	Scardinius erythrophthalmus																								
Barbatula barbatula	Gobio gobio					1	1																		
Gobio gobio	Tinca tinca					1											1								
Gobio gobio	Cyprinus carpio					1																			
Cyprinus carpio	Tinca tinca																1								
NEGATIVE CO-OCCURRENCE		**BED**		**BLO**		**COB**		**GGR**		**GRA**		**BRA**		**HEL**		**HYD**		**HYF**		**LIT**		**SAB**		**SED**	
Species1	**Species2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**	**Sp1**	**Sp2**
Esox lucius	Perca fluviatilis				1									1		1		1							
Esox lucius	Barbatula barbatula						1							1		1		1							
Perca fluviatilis	Salmo trutta			1	1																				
Perca fluviatilis	Cottus gobio			1			1																		
Perca fluviatilis	Alburnus alburnus			1													1								
Perca fluviatilis	Barbatula barbatula			1			1																		
Perca fluviatilis	Gobio gobio			1			1																		
Rutilus rutilus	Lota lota				1									1		1									
Salaria fluviatilis	Scardinius hesperidicus	1				1																			
Salaria fluviatilis	Squalius squalus	1				1																			
Tinca tinca	Leuciscus leuciscus										1					1									

Among the thirteen positively co-occurring species pairs, five overlapped in their habitat association. Three pairs shared boulders (BLO), one pair cobbles (COB), and one pair macrophytes (HYD). In seven positively co-occurring pairs, either one or both members were not significantly associated with any habitat type. Only one species pair, *G. gobio* and *C. carpio*, exhibited a significantly positive co-occurrence, despite being associated with biogenic and rocky habitats, respectively.

Of the eleven negatively co-occurring species pairs, only one pair shared an association to the same habitat (*P. fluviatilis* and *S. trutta*; boulders). In five pairs, one member was associated with rocky habitats (highlighted in brown) and the other with biogenic habitats (highlighted in green). Three additional pairs were both associated with rocky habitats, and two other pairs included a species without any significant habitat association. There were no associates of biogenic habitats negatively co-occurring with one another.

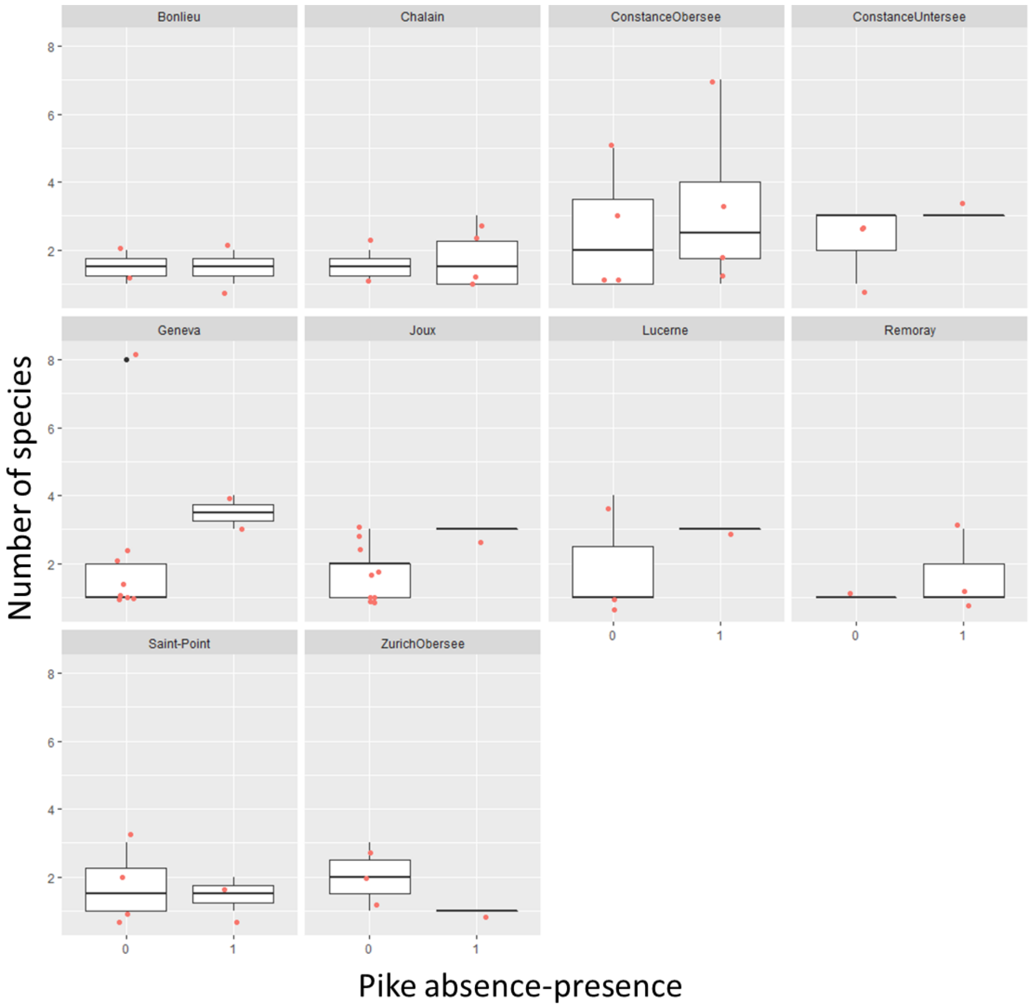

Figure 3: Average number of species per electrofishing action in each lake which yielded actions with and without pike presence in biogenic habitats.

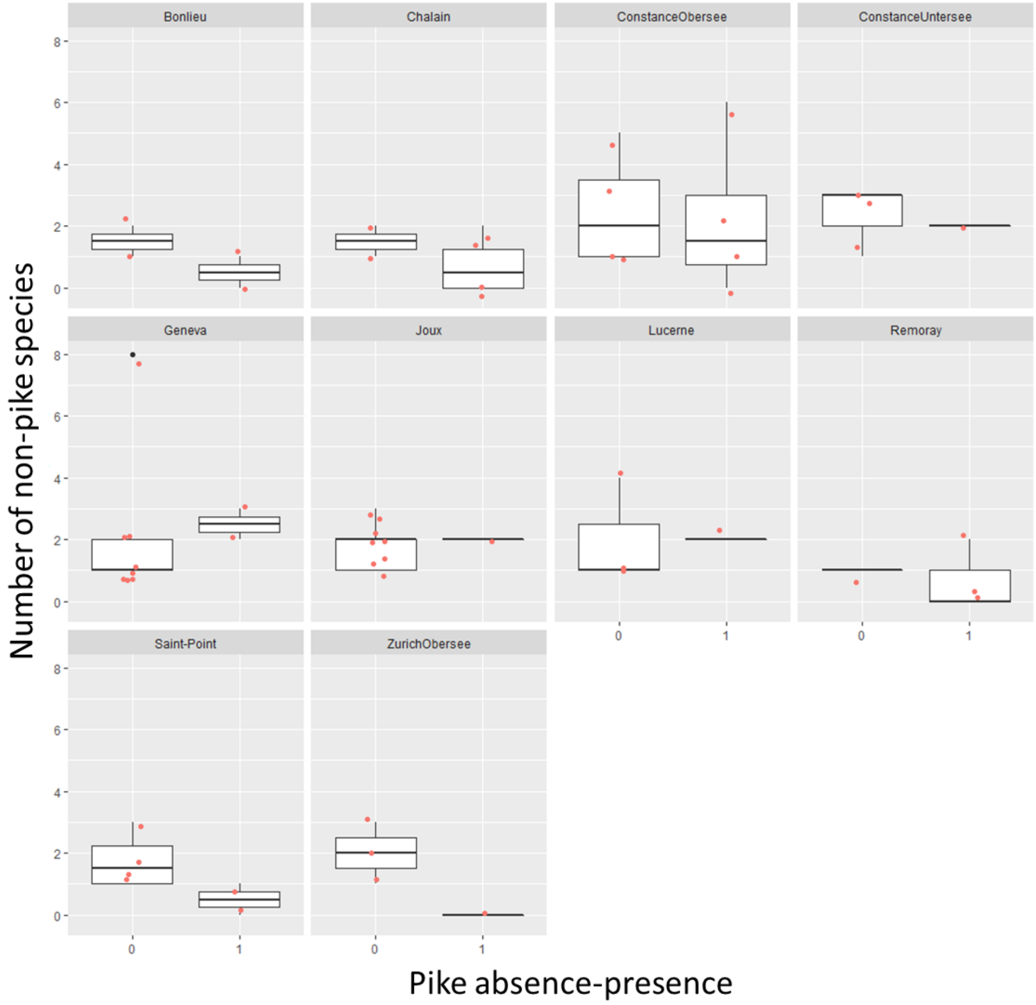

Figure 4: Average number of non-pike species per electrofishing action in each lake which yielded actions with and without pike presence in biogenic habitats.

A total of ten lakes yielded actions in biogenic habitats both with and without pike: Bonlieu, Chalain, Lower Constance, Geneva, Joux, Lucerne, Remoray, Saint-Point, and Upper Zurich. In these lakes, the presence of pike did not have a significant effect on the number of species present in biogenic habitats ($\chi^2_{(1)}$=0.782, p=0.377). However, it is important to mention that pike itself was included in the species count (Figure 3). When comparing the number of non-pike species between habitats with/without pike (Figure 4), there is a tendency albeit non-significant, towards a lower number of non-pike species in pike-containing habitats ($\chi^2_{(1)}$=2.971, p=0.085).

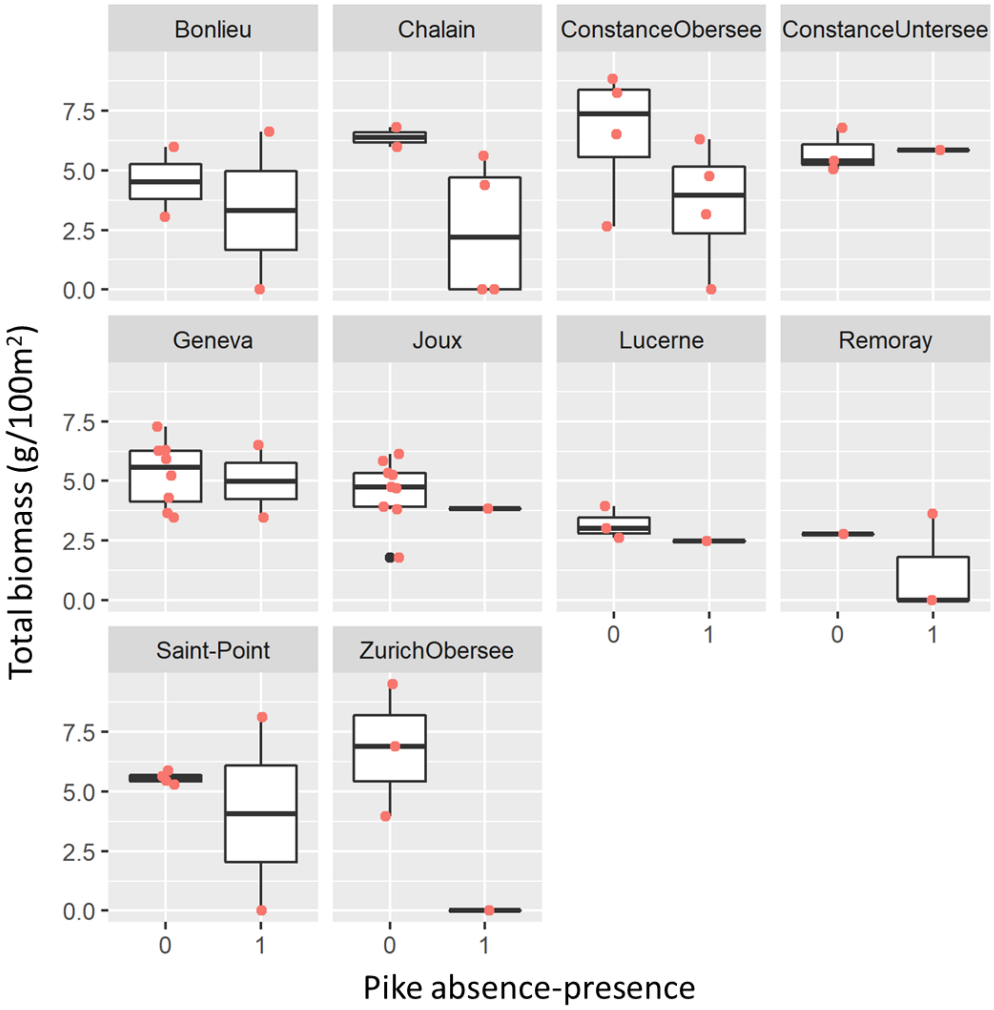

Figure 5: Average biomass per action in each lake which yielded electrofishing actions with and without pike presence in biogenic habitats.

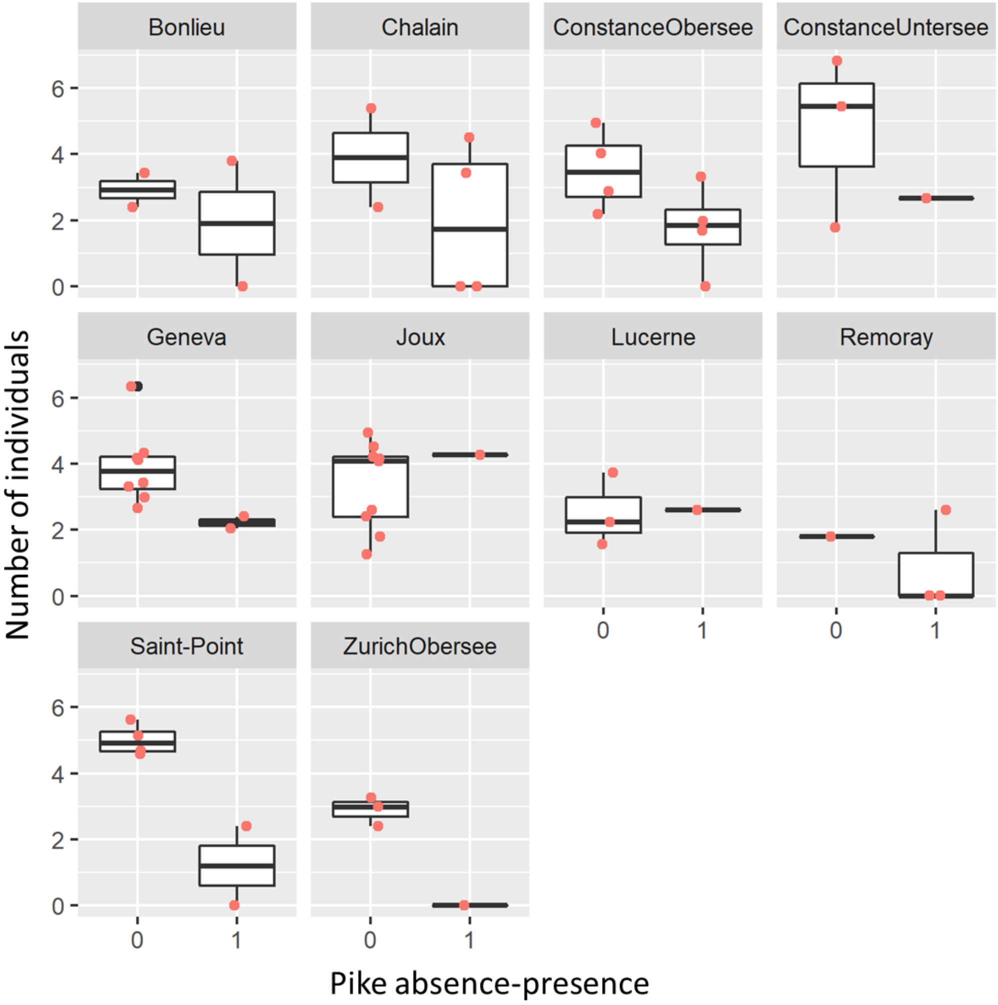

Figure 6: Average number of fish per action in each lake which yielded electrofishing actions with and without pike presence in biogenic habitats.

Average fish biomass was significantly higher in biogenic habitats without pike (Figure 5; $\chi^2_{(1)}$=12.588, $p < 0.001$). Local fish biomass was, on average, 66% lower in actions where pike was recorded (when the biomass of pike itself was excluded). Even when including pike, the difference remained significant. Similarly, the total number of fish in an action (Figure 6) was significantly higher in the absence of the predator ($\chi^2_{(1)}$=18.675, $p < 0.0001$). On average, actions in which a pike was caught yielded roughly 78% fewer fish than actions without pike. The abundance of pike was not excluded in the latter comparison as most actions contained only single pike.

Discussion

Trophic levels

As the prevalence of a species did not have any influence on its proportion of positive co-occurrences, the fact that overall more negative co-occurrences were found than positive co-occurrences may be explained by the various habitat associations of species. Each species occupies a particular ecological niche. A species' ecology is partially reflected by its habitat association, which results in a specific spatial distribution. With more habitat types in a system, more ecological niches will be available. This results in more species being dissimilar from each other, both in their ecology and their spatial distribution. The consequent differences in spatial distribution therefore often yielded negative co-occurrence values, as the proportion of actions containing a particular species pair is compared to a random distribution of both, independent of habitat association and their genuine spatial distribution throughout the lake. In other words, when focusing on one member within a lake community, it is expected that there will be fewer species with similar habitat associations than there will be species with decisively different habitat associations.

Large predators with higher trophic levels generally had more negative co-occurrences with other species. One might expect this pattern to arise as the result of biotic interactions (i.e. predation leading to active avoidance by prey). However, closer investigation suggests different mechanisms.

Pike, with one of the highest trophic positions, is strongly associated with biogenic habitats (particularly reeds, macrophytes, and floating plants) and negatively associated with habitats characterized by rocks (particularly rock slab, blocks & boulders, and pebbles). The effect resulting in a generally higher proportion of negative co-occurrences, as described in the paragraph above, is increasingly fortified the more restrictive the habitat associations of the species in question are. Indeed, when limiting the analysis to biogenic habitats, the proportion of positive co-occurrences increased from 0.13 to 0.4, suggesting that the high proportion of negative co-occurrences exhibited by pike can be chiefly explained by its strong habitat association. The two other piscivores with particularly high trophic positions, *S. lucioperca* and *S. glanis*, were caught in only two and three actions, respectively. Consequently, the high proportion of negative co-occurrences for these two species should be interpreted with caution, as the co-occurrence values may be unreliable due to low sample size.

The three-spined stickleback (*Gasterosteus aculeatus*) exhibited the highest proportion of negative co-occurrences of all non-piscivorous fish. Stickleback was not strongly associated with any habitats and was caught in many actions (in two lakes). Species interactions may therefore be the main driver of the pattern. Sticklebacks display aggressive behaviour towards both conspecifics and heterospecifics (Rowland, 1983a, b, 1989). Such behaviour is likely to result in the avoidance of sticklebacks by other species.

Despite its high trophic level (4.35), perch exhibited comparably high numbers of positive co-occurrences (0.41) for a piscivorous fish (positive co-occurrences with 41% of other species). However, this species undergoes a shift in diet from consuming plankton and invertebrates towards piscivory upon reaching 12-18 cm in length (Kottelat and Freyhof, 2007; Persson, 1988). Most perch caught in electrofishing actions were below 12 cm in length (see Appendix Figure 6), and where therefore probably not piscivorous. The trophic level is therefore overestimated for the perch considered in this study. Additionally, smaller perch feed predominantly on invertebrates; a trophic guild shared with many other fish species (Kottelat and Freyhof, 2007). Finally, perch were also significantly associated with boulders; the habitat to which many other fish species were also associated (overall 20/38 species were strongly associated with boulders (Hefti, 2017)). In summary, young perch exhibit ecological characteristics commonly found among fish of similar size, chiefly explaining the comparatively large proportion of positive co-occurrence values for the species characterized as a piscivore.

There were two predators which exhibited an even lower number of negative co-occurrences, namely burbot and European eel. Similar to perch, both were strongly associated with boulders, which may partially explain their high number of positive co-occurrences. Additionally, the trophic level of eel (3.53) may constitute an overestimate, as eels shift from feeding on invertebrates to a predominantly piscivorous diet at approximately 50 cm in size. Roughly half of the eels caught were below this size (see Appendix, Figure 6). Also, piscivory is more common during winter (Barak and Mason, 1992). Sampling took place between August and November, and it is therefore likely that many actions fell into a time interval when eels of all sizes still fed predominantly on invertebrates, consequently reducing their momentary trophic level.

Species feeding on vegetation tended to exhibit a relatively large number of positive co-occurrences. This may be explained to a large degree by their shared habitat association. All members of this trophic guild (except dace) were associated with biogenic habitats. This may not be surprising, as these habitats are defined by the presence of food for these species. However, the affiliation of dace into this trophic guild is not entirely certain. Other authors state that the species is feeding predominantly on invertebrates (see Kottelat and Freyhof, 2007). Of the 35 species caught, thirty were positively associated with biogenic habitats. The same number of species was associated with lithic habitats. However, I suspect the number of species to be overestimated in these habitats and underestimated in biogenic habitats. The majority of fish caught in electrofishing actions were juveniles (see Appendix, Figure 6), whereas habitat association was calculated on the basis of data obtained by both electrofishing and gillnetting (Hefti, 2017). Gillnetting yielded larger and, consequently, older fish, and therefore habitat associations were most likely biased when applied to data obtained by electrofishing alone. As shown by Hefti (2017), for example, perch of small sizes were more strongly associated with biogenic habitats, whereas the species was most strongly associated with boulders when fish of all sizes were incorporated. This is also in accordance with the common view that many fish species utilise complex vegetated habitats in their juvenile phase, both for attaining refuge from predation and the availability of food (e.g. Garner, 1996; Sass et al., 2006). In conclusion, fish species feeding on plant material are predetermined to forage in biogenic habitats, which in turn exhibit a high diversity of juvenile fish. This may explain the high number of positive co-occurrences observed in members of this trophic guild.

Similar to fish feeding on plant materials, planktivores also exhibited a high number of positive co-occurrences. Half of the six planktivorous species also fed on plant materials and a total of five species were positively associated with biogenic habitats. Consequently, I suspect their relatively high proportion of positive co-occurrences can be largely explained by the same mechanism yielding similar patterns in species feeding on plant materials, as explained above. However, ruffe appears to be an exception, as this species, in contrary to all other planktivores, is strongly associated with habitats containing boulders (BLO).

No clear patterns were apparent for detrivorous species. However, as spined loach (*Cobitis bilineata*) has been caught in only one single action, its correspondingly low proportion of positive co-occurrence values has to be interpreted with caution. When focusing on all other detrivores, the familiar pattern of species feeding on plant materials and being associated with biogenic habitats, as explained above, reappears.

Finally, invertivorous species exhibited a wide variety of positive co-occurrence proportions. Benthic invertebrates represent the most frequently shared food item among fish, as numerous species go through at least one life stage when they feed predominantly on arthropods or molluscs (Kottelat and Freyhof, 2007). More obvious patterns may be obtained by increasing the resolution of this trophic guild, i.e. to the level of phylum or even class. However, data on fish diet obtained from the literature varies fundamentally in resolution and quantity between species and differs highly between regions, thereby impeding more detailed comparison of invertivore diet in this study.

Apart from additional factors influencing a species' proportion of positive co-occurrences, for example the strength of habitat association (as shown in pike), these proportions displayed a strong tendency to decrease with increasing trophic level (Table 4). Trophic level is an indicator of a species' position within the food web, with higher trophic levels emphasizing a higher position (Pauly et al., 1998). One might expect fish to generally avoid species with high trophic levels, as these exhibit a propensity towards predatory behaviour and are therefore more dangerous. Although the proportions exhibited by zander and wels are to be interpreted with caution due to the low sample sizes, I believe they are relatively reliable. The two species are not nearly as strongly restricted to certain habitat types as pike, and it is therefore unlikely that their low proportion of positive co-occurrence values is the result of the same mechanism. Further, the two species exhibit a different hunting behaviour than pike, as they both hunt actively and don't rely on ambushing prey (Copp et al., 2009; Jepsen et al., 2000). Therefore, I hypothesise that zander and wels are visually detected quicker by other fish and potential prey is actively avoiding them more efficiently compared to a pike hidden in dense vegetation. Although olfactory cues play a role in the detection of a predator as well, it has been shown that visual detection alters prey behaviour to a higher degree (Mikheev et al., 2006). The inversed relationship between trophic level and proportion of positive co-occurrence values is further enhanced by species with low trophic levels. Their low trophic level is the result of a diet predominantly consisting of representatives positioned relatively low in the food web, i.e. plankton, vegetation, and detritus. As explained above, members of these trophic guilds exhibit high proportions of positive co-occurrence values due to their association with biogenic habitats, the type of habitat shared by juveniles of most species.

Significantly co-occurring species pairs

Comparing the habitat associations within species pairs emphasises its importance in creating species assemblages: many positively co-occurring pairs share a common habitat association. In contrast, members within negatively co-occurring pairs can often be separated into associates of lithic and biogenic habitats, respectively. This pattern fortifies when incorporating the non-significant habitat associations as well (see Hefti, 2017, for all habitat associations).

Although roughly half of the species caught in electrofishing actions were cyprinids (19 out of a total of 36 species), their incomparable prevalence within the positively co-occurring pairs is noteworthy nonetheless. The family of *Cyprinidae* is highly diverse, with members occupying numerous ecological niches and trophic guilds ranging from detrivory to piscivory (Kottelat and Freyhof, 2007; Winfield and Nelson, 1991). In Europe, many members of the family diversified in sympatry (Hanfling and Brandl, 2000). As sympatric speciation is often correlated with character displacement (e.g. Seehausen and Schluter, 2004) in order to reduce interspecific competition pressures (Brown and Wilson, 1956), I hypothesise that co-occurrence between different cyprinids is facilitated more frequently than the co-occurrence of cyprinids with members of other fish families, thus resulting in the vast overrepresentation of cyprinids in the positively co-occurring pairs observed.

Perch were positively co-occurring with ruffe and pumpkinseed. Both are members of the order Perciformes and are identified as invasive species in Swiss lakes. When also incorporating all non-significant co-occurrences for perch, the pattern fortifies. All invasive species, except Prussian carp, were positively co-occurring with perch and also belong to the Perciformes order. Zander, ruffe, and pumpkinseed were positively associated with boulders, analogous to perch. I therefore believe that the pattern can be largely explained by their shared habitat association. Due to the similar habitat preference and diet of these Perciformes (Kottelat and Freyhof, 2007), it appears natural to assume interspecific competition between these species to be relatively strong. However, as shown by Rezsu and Specziar (2006), perch, ruffe, and pumpkinseed show no biologically relevant diet overlap. This is likely to facilitate the co-occurrence pattern observed. Assumptions on whether weak dietary competition between these Perciformes is consistent when incorporating zander and largemouth bass (*Micropterus* salmoides) as well would require further investigation. However, their positive association with perch might indicate this to be the case.

Burbot and brown trout were the only co-occurring piscivores. Both species were positively associated with boulder habitats and are members of the same trophic guilds (invertivores and piscivores). Burbots commence benthic feeding at a size between 20-31 mm (Ryder and Pesendorfer, 1992) and feed predominantly on invertebrates during their juvenile life stage (Chen, 1969). Male burbots mature after two years and females after three years (Kottelat and Freyhof, 2007), which translates to a body length between 170 and 230 mm (Chen, 1969). As all specimens caught in electrofishing actions exceeded 30 mm in body size and most were smaller than 170 mm (see Appendix Figure 6), it can therefore be assumed that mainly juvenile burbots feeding on benthic invertebrates were investigated here. In contrast, aside from fish, brown trouts feed on benthic invertebrates as well as on insects on the water surface (Allen, 1938). However, they shift from invertivory to piscivory at a body length of approximately 130 mm, a size rarely exceeded by the trouts caught in the electrofishing actions (see Appendix Figure 6). Consequently, interspecific diet competition between burbot and brown trout may be expected to be relatively strong. As Jonsson (1989) stated, however, brown trouts exhibit a high foraging flexibility, as diet varied substantially between habitat and lake within the study area. It is therefore possible that they shift to more pelagic foraging strategies in the presence of burbots in order to reduce competition pressures and enable co-existence. This claim may be further supported by Carl (1992), who found no indication of biologically significant competition by investigating burbot ecology with changes in lake trout (*Salvelinus* namaycush) abundance.

Predators not only exhibited higher proportions of negative co-occurrences, but many of these negative co-occurrence values were also statistically significant. Conspicuously, all non-predatory species negatively co-occurring with piscivores are relatively small in size (Kottelat and Freyhof, 2007), i.e. may represent potential prey species, with the exception of roach (*R. rutilus*). However, the roaches caught did not differ essentially in size and might therefore still represent potential prey for larger predators, i.e. pikes.

As described earlier, it is unlikely that the perch caught in electrofishing actions had an influence on local species assemblage by predation. Predation effects can therefore hardly explain the large number of negative co-occurrences perch exhibited. Other biotic factors, such as interspecific competition, appear more likely to be creating the observed pattern. Interspecific competition of juvenile perch has been well investigated, particularly with roach (Persson, 1986, 1987). Perch are capable of shifting their diet, most frequently from zooplankton to benthic invertebrates (Persson, 1986), in order to reduce interspecific competition. Additionally, they may also alter their spatial distribution, given there is enough space to avoid competition geographically (Kahl and Radke, 2006). Spatial avoidance by perch may therefore play an important role in creating the co-occurrence patterns observed. Another biotic factor I investigated was the potential role of aggressive behaviour towards heterospecifics by perch. Perch tend to form large schools which exhibit high aggression, both towards other members of the school and other species nearby. Although individual perch which are comparatively more aggressive than other conspecifics have been shown to exhibit higher growth rates, indicating the advantage of aggressive behaviour in competition for food (Westerberg et al., 2004), the species also acts more aggressively in the presence of sheltering structures, which offer protection from large predators (Mikheev et al., 2005). Such constant aggressions may particularly cause small-bodied species, i.e. the species perch are negatively co-occurring with, to actively avoid locations where large schools of juvenile perch are present. This hypothesis is also in accordance with the fact that all Perciformes were positively co-occurring. All four Perciformes positively co-occurring with perch, namely ruffe, pumpkinseed, largemouth bass, and zander, exhibit a tendency towards aggressive behaviour (Almeida et al., 2014; Fleming and Johansen, 1984; Grozea et al., 2016; Savino et al., 2007). Consequently, I hypothesise that these species are less susceptible to physical aggression by perch, as they commonly experience such behaviour by conspecifics. Therefore, they may not react to the presence of schooling perch by spatial avoidance to the same extent many other species do. In summary, there are two biotic factors which may have caused the low number of positive co-occurrences observed in perch: First, perch may have spatially avoided advantaged competitors to reduce competition pressures. Second, perch may have also been actively avoided by other species, especially small individuals, due to their aggressive behaviour.

Trophic guilds

The vast majority of species pairs which yielded significant co-occurrence values, be it negative or positive, shared at least one trophic guild. It is therefore difficult to deduce biotic interactions shaping co-occurrence patterns by comparing the numbers of shared trophic guilds between positively and negatively co-occurring pairs, as they do not differ substantially between the two groups. In contrast, a trophic guild-specific approach may be more resolving.

Conspicuously, the trophic guild of invertivores is omnipresent throughout both lists. Benthic invertebrates play an important role in the diet of numerous fish species, particularly during early life stages (Kottelat and Freyhof, 2007). There is no eminent difference between positively and negatively co-occurring pairs regarding the prevalence of this shared trophic guild. However, as discussed earlier, more distinct patterns may be observed when increasing the resolution of the trophic guild, i.e. differentiating between classes or even orders of invertebrates.

In contrast to the trophic guild of invertivores, not a single species pair consisted of two detritivorous species. As only a total of six species are characterised as detritus feeders, one might expect this pattern to emerge simply by chance. However, though never to a significant extent, all detritivores yielded negative co-occurrence values with one another. Potentially, this pattern may be best explained by resource segregation between detritivores. Detritus is likely to differ regionally in content, for example with higher density of microfauna in one location and higher densities of diatoms in another location. The different feeding mechanisms of detrivores result in the available food items being consumed in different quantities (Whitfield and Blaber, 1978). It is therefore likely that species feed where the detritus composition best fits their requirements, consequently separating detritivorous species spatially.

There was only one positively co-occurring piscivorous pair, compared to two piscivorous pairs with negative co-occurrence values. Burbot and brown trout tended to co-occur, as explained earlier, likely due to their shared habitat association and relatively weak interspecific competition. In contrast, pike and perch were negatively co-occurring. Although predation, presumably more frequently by pike on perch than vice versa, is likely to play a role, I hypothesise that this may not be the sole mechanism creating this pattern. First, pike have been shown to prefer soft-rayed fish over perch as prey, most likely due to the lower handling time (Beyerle and Williams, 1968; Eklov and Hamrin, 1989; Wahl and Stein, 1993). Second, pike and perch exhibited strong associations with biogenic and boulder habitats, respectively. Despite the presumed underestimate of perch association with biogenic habitats, I hypothesise that the negative co-occurrence of pike and perch can be largely explained by their distinct habitat associations. The prey preference of pike may represent an additional factor, as they are unlikely to actively seek out inappropriate habitats with unfavourable prey. The second negatively co-occurring pair of piscivores consisted of perch and brown trout, although they were both associated with boulders. It is plausible that this is the result of strong interspecific competition. As shown by Thorpe (1974), the success and proliferation of brown trout was significantly reduced with increasing abundance of perch in a Scottish lake. Vast diet overlap between the two species indicated competition for food to be the main mechanism creating this pattern. Analogously, Fraser (1978) investigated the impact of newly introduced yellow perch (*Perca flavescens*), a close relative of the European perch, on local populations of salmonids in a small North American lake. The establishment of yellow perch caused a drastic change in the food habits of salmonids and a reduction of their growth rates of more than 50%. In addition to competition pressures, the aggressive behaviour exhibited by perch, as described earlier, may further diminish co-occurrence of perch and brown trout.

Of the three pairs consisting of species feeding on plant material and algae, only dace and tench were negatively co-occurring. Dace is strongly associated with rocky habitats, particularly gravel, whereas tench exhibits a strong association with biogenic habitats. Dace is often characterised as a more riverine species (Kottelat and Freyhof, 2007), with accordingly high requirements of dissolved oxygen in the water. In contrast, tench are extremely resistant to low oxygen concentrations and high water temperatures (Downing and Merkens, 1957). Consequently, the two species are separated spatially along an environmental gradient, resulting in the negative co-occurrence observed. In contrast, tench exhibited positive co-occurrence with the common carp. Although no significant habitat association of carp was found by Hefti (2017) in the lakes investigated, biogenic habitats are of major importance for carps. Both species are also highly resistant to low levels of dissolved oxygen and feed predominantly on benthic invertebrates (Kottelat and Freyhof, 2007), likely resulting in a comparable spatial distribution and thus creating the positive co-occurrence. Despite their similarity in biology, interspecific competition does not appear to be strong enough to cause local exclusion of either species. Conversely, the mechanism behind the positive co-occurrence value yielded by roach and the Italian chub is not as clear. Roaches are positively associated with biogenic habitats, particularly reeds, and so is the Italian chub, although not to a significant degree. Both cyprinids exhibit high diet flexibility (Kottelat and Freyhof, 2007), which may, on one hand, reduce interspecific competition for food and thus facilitate co-occurrence. On the other hand, they may have both been foraging for the most abundant food item available at the time of sampling (autumn), which would have led to temporally limited co-occurrence of the two species.

There were no planktivorous species pairs negatively co-occurring, as opposed to four pairs which yielded positive co-occurrences. Given that plankton is not homogeneously distributed on a horizontal scale throughout a lake, but dependant on water circulation patterns induced by wind (George and Edwards, 1976), one might expect planktivorous fish to be co-occurring where plankton accumulates. Indeed, when also incorporating the non-significant co-occurrence values between planktivores, the pattern fortifies, as 14/18 possible pairings were positively co-occurring. Zooplankton can be categorised into different size classes, and many planktivores are specialised in feeding on a particular size class (Keast, 1985). As the abundance of each size class depends on fluctuating external perturbations, the relative abundance of different zooplankton size classes is continuously altered (Gaedke, 1992). It is therefore plausible that certain planktivorous species may not benefit from the temporarily enhanced availability of their preferred size class long enough to effectively outcompete other planktivores. Alternatively, Gaedke (1992) also showed that the larger size classes of zooplankton are most abundant during late summer. As Brooks (1968) concluded from experimental investigations, many planktivorous fish species prefer the larger size classes if sufficiently available. It can thus be hypothesised that during autumn, when sampling took place, the zooplankton community was dominated by comparably large individuals. Consequently, most planktivorous fish focused on such. Due to the vast availability of the larger zooplankton, interspecific competition may have therefore been minimised and co-occurrence facilitated, at least during this time of the year.

Effects of pike on community assemblages

To investigate the influence the presence of a large predator has on local species assemblage, actions which yielded pike were compared to actions without pike in biogenic habitats. The number of species present did not differ significantly between the two groups, however, pike was included in the species count. When excluding pike, the difference remained non-significant, but the number of species tended to be reduced in the presence of pike. Although this might be interpreted as an indication that pike replaced another species, no patterns as to which species is most frequently replaced became evident. It is therefore plausible that this pattern is simply a reflection of the general carrying capacity of a local habitat. On the other hand, given the non-significant difference in species numbers, this pattern may have evolved purely by chance.

Over all actions considered here, substantially more species were caught in the absence of pike. A total of 16 different species were caught in pike-free actions, compared to a subset of nine species caught in actions with the predator. This represents a reduction in fish diversity of 46% in the presence of pike, indicating its crucial effect on local species composition. The fact that the same species caught in the presence of pike were also present in pike-free actions emphasises that some species tend to avoid pike more drastically than others. However, as the number of species between actions with/without pike did not differ significantly, species exhibiting comparably strong avoidance behaviour must have been replaced by other species, which are less susceptible to predation by pike. Unfortunately, the pattern is vastly distorted by the distinct quantity of actions with and without pike, respectively. Twenty-one electrofishing actions in biogenic habitats yielded pike, compared to 39 actions without pike. As a higher number of actions is expected to yield more species, it is difficult to deduce the relative role of pike in shaping community composition. Further, of the seven species never co-occurring with pike in biogenic habitats, five have only been caught in a single action. The two remaining species, namely largemouth bass and burbot, were caught in three and six actions, respectively. However, they did not exhibit extraordinarily negative co-occurrence values with pike, indicating that the substantial difference in overall diversity between the two groups is largely due to the vast variation in sample size.

In contrast to the number of species, relative biomass and abundance were significantly lower in the presence of a pike in biogenic habitats. Given that the biomass decreased on average by 66% and the number of fish by 78%, it appears unlikely that a pike would directly reduce a local population to such an extent purely by predation. Rather, despite the pike's successful specialisation as an ambush predator, I suspect that it is detected and identified as a potential threat by most fish, either by olfactory or visual cues. Active avoidance by potential prey fish may be further enhanced by attacks already performed by a pike, which are likely to be observed by other fish in the nearby surroundings. In experiments conducted by Turesson and Bronmark (2004), it has been shown that pike neither suffer from a confusion effect in high prey densities, nor do they catch comparably more prey. This might indicate that foraging success of pike does not necessarily have to decrease analogously to a reduction in local fish abundance.

The fact that fish abundance was reduced to a larger extent than biomass emphasises that predominantly smaller bodied fish avoided local habitats where a pike was present. Indeed, when comparing the influence of pike on fish assemblages between North American and Finnish lakes, Tonn et al. (1990) found strong evidence that some North American prey species are locally excluded purely by pike predation, whereas no similar patterns could be found in Finish lakes. However, similar to my results, a significant reduction in relative abundance was evident. The authors hypothesised the reason for this pattern to be the biological differences between the North American and European prey species, more specifically their body sizes. Many North American prey species, such as the central mudminnow (*Umbra limi*) and the northern redbelly dace (*Chrosomus eos*), are relatively small-sized and prone to pike predation at virtually any life stage. In contrast, European freshwaters are dominated by comparably larger cyprinid species (e.g. common bream, roach, chub), which can grow large enough to attain a size refuge from predation by pike. This explanation is in accordance with my findings, as smaller sized fish avoided habitats where a pike was present more frequently compared to their larger conspecifics, i.e. the proportional reduction in relative abundance was higher than in biomass.

Conclusion

Most species yielded predominantly negative co-occurrences. Piscivores generally exhibited a higher proportion of negative co-occurrences, emphasising that predation plays an important role in structuring fish communities. Most co-occurrence estimates, however, could be explained by comparing habitat associations of the species in question. As a species' habitat association is a reflection of both biotic and abiotic factors, the distinction of patterns created by either one may be difficult.

When additionally taking species-specific affiliations of trophic guilds into account, the patterns of some negatively co-occurring species suggest that competitive pressures play a role not to be underestimated. For instance, the relationship between perch and brown trout, sharing both habitat association and diet, is largely dominated by competitive interactions likely to result in the local exclusion of brown trout. In fact, perch were most commonly co-occurring with other, invasive Perciformes, and were negatively co-occurring with many native species. Although strong competitive interactions between perch and cyprinids have been found in many studies, competition between Perciformes appears to be relatively low. However, I hypothesise that the co-occurrence pattern of perch is not the result of interspecific competition alone. Perciformes have been shown to exhibit aggressive behaviour, both towards conspecifics and heterospecifics, and may therefore be capable of actively driving other species away. As other Perciformes may be more accustomed to aggressive behaviour, it is plausible that they tend to avoid habitats with schooling perch to a lesser extent than, for example, many cyprinid species. However, the relative role of aggressive behaviour towards heterospecifics in shaping community assemblages has not been nearly as closely examined as other biotic interactions and assessing the relative impact such behaviour has on local community assemblage would require further investigation.

I was, however, able to detect the effect a large predator, namely northern pike, has on a local community. Although no alteration in community composition was evident, electrofishing actions in biogenic habitats where a pike was present yielded significantly lower values of relative biomass and abundance than in biogenic habitats where no pike was caught. Conspicuously, the local biomass was reduced on average by 66% in the presence of a pike and the number of fish even decreased by 78%. Consequently, smaller-bodied individuals exhibited a higher tendency to avoid pike-containing habitats than their larger conspecifics, which appeared to be able to attain size refuge from pike predation. Due to inadequate sample size, investigation on predation effects was limited to pike. Whether this pattern is consistent among freshwater piscivores, particularly large-sized species such as wels and zander, would require additional sampling effort in habitats with which these piscivores are positively associated.

Acknowledgements

I would like to thank the entire Projet Lac team, particularly Pascal Vonlanthen and Guy Périat, whose vast data set on pre-alpine fish fauna I was able to use for the purpose of my thesis. I was also able to join the fieldwork for two weeks, providing me with valuable insights which were greatly appreciated and of fundamental importance to me. Special thanks to Professor Ole Seehausen for making it possible to work on this project at Eawag and his constructive feedbacks during the progress of my thesis. Last but not least, I would like to thank my supervisor Dr. Timothy Alexander, whose knowledge on freshwater systems, teaching skills, and patience enabled me to gain an incredible amount of new knowledge and skills, without which this work would have been impossible to conduct.

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Appendix

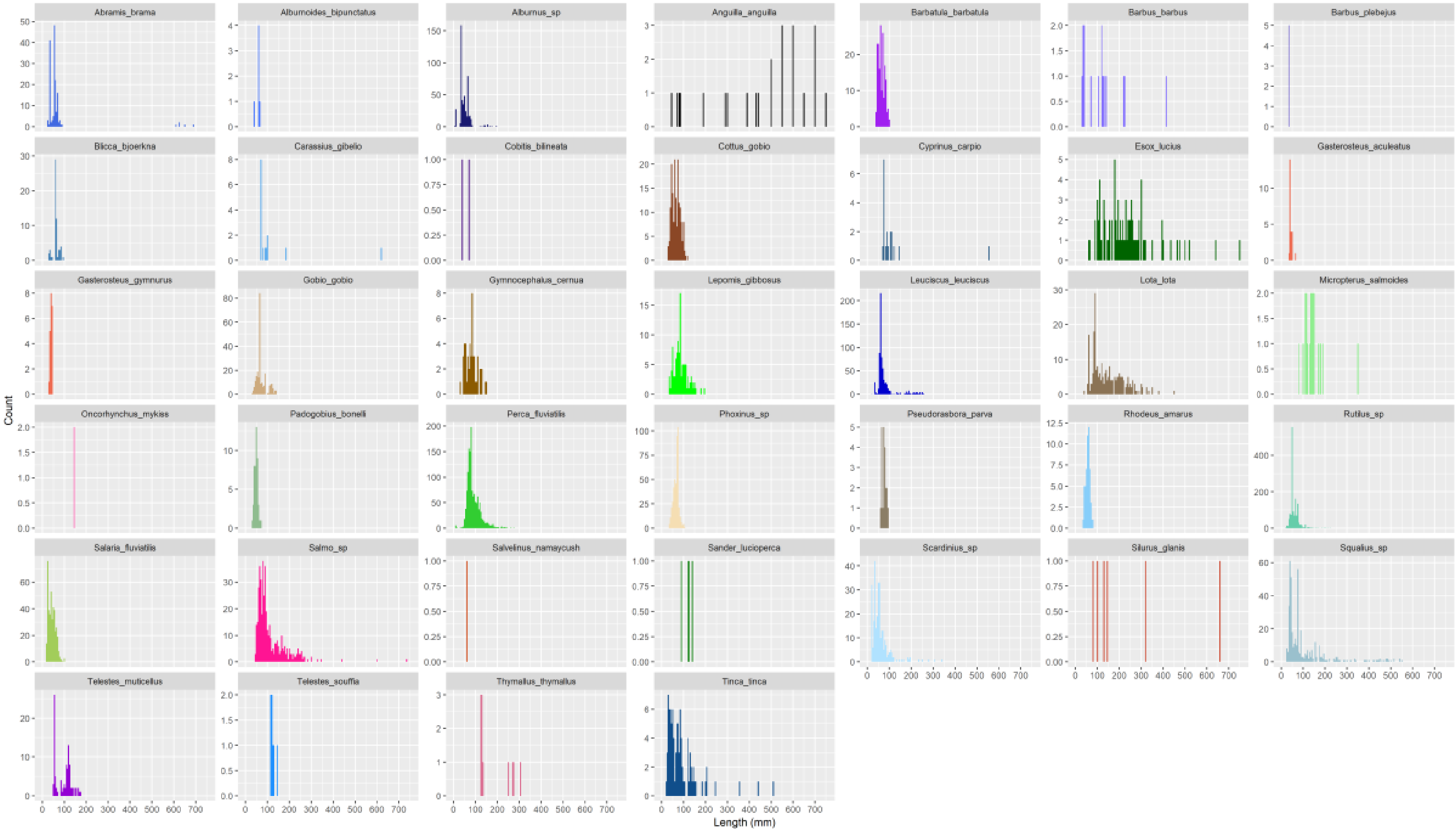

Figure 6: Size-frequency distribution of every species caught in electrofishing actions across all lakes.

Table 7: Latin, English, and German name of all species caught in electrofishing actions and investigated in this study.

Latin Name	English Name	German Name
Abramis brama	Common bream	Brachse
Alburnus arborella	Alborella	Alborella
Alburnus alburnus	Bleak	Laube
Anguilla anguilla	European eel	Aal
Barbatula barbatula	Stone loach	Bartgrundel
Barbus barbus	Barbel	Barbe
Blicca bjoerkna	White bream	Blicke
Carassius gibelio	Prussian carp	Giebel
Cobitis bilineata	Italian spined loach	Südlicher Steinbeisser
Cottus gobio	Bullhead	Groppe
Cyprinus carpio	Common carp	Karpfen
Esox lucius	Northern pike	Hecht
Gasterosteus aculeatus	Three-spined stickleback (armoured)	Stichling
Gasterosteus gymnurus	Three-spined stickleback (naked)	Stichling
Gobio gobio	Gudgeon	Gründling
Gymnocephalus cernua	Ruffe	Kaulbarsch
Lepomis gibbosus	Pumpkinseed	Sonnenbarsch
Leuciscus leuciscus	Dace	Hasel
Lota lota	Burbot	Trüsche
Micropterus salmoides	Largemouth bass	Forellenbarsch
Padogobius bonelli	Padanian goby	
Perca fluviatilis	European perch	Flussbarsch
Phoxinus phoxinus	Minnow	Elritze
Rhodeus amarus	Bitterling	Bitterling
Rutilus aula	Triotto	Triotto
Rutilus rutilus	Roach	Rotauge
Salaria fluviatilis	Freshwater blenny	Blenny
Salmo trutta	Brown trout	Forelle
Sander lucioperca	Pike-perch	Zander
Scardinius erythrophthalmus	Rudd	Rotfeder
Scardinius hesperidicus	Southern Rudd	Schwarzfeder
Silurus glanis	Wels catfish	Wels
Squalius cephalus	European chub	Alet
Squalius squalus	Italian chub	Südlicher Alet
Telestes muticellus	Italian riffle dace	Südlicher Strömer
Tinca tinca	Tench	Schleie