How barriers shape freshwater fish distributions: a species distribution model approach

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Abstract

Aim

Barriers continue to be built globally despite their well-known negative effects on freshwater ecosystems. Fish habitats are disturbed by barriers and the connectivity in the stream network reduced. We implemented and assessed the use of barrier data, including their size and magnitude, in distribution predictions for 20 species of freshwater fish to understand the impacts on freshwater fish distributions.

Location

Central Germany

Methods

Obstruction metrics were calculated from barrier data in three different spatial contexts relevant to fish migration and dispersal: upstream, downstream and along 10km of stream network. The metrics were included in a species distribution model and compared to a model without them, to reveal how barriers influence the distribution patterns of fish species. We assess impacts of barriers by estimating species' specific range gains and losses due to barrier inclusion in the model.

Results

Barriers were important for the predictions of many fish species with the metric upstream barriers being the most relevant barrier predictor across the fish community. With the inclusion of barriers, most species saw a reduction in their predicted range and habitat suitability decreased, particularly species with small ranges or considered as threatened.

Main conclusions

Predictions from this SDM application point out how and where barriers influence fish distributions in the studied catchment. Our results indicate a reduction in suitable habitat due to barriers and suggest a higher extirpation risk. This species-specific and spatially-explicit

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information is highly valuable for target-oriented river restoration measures, biodiversity conservation efforts and catchment management in general.

Keywords: brook lamprey, connectivity, habitat suitability, long-term ecological research, obstruction metric, stream network

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A - Introduction

Water resource development measures are important threats to freshwater biodiversity at a global scale, as their modifications of the hydrological regime negatively influence freshwater fish communities. These development measures consist of various types of barriers in streams and rivers (i.e. culverts, weirs, slides, dams, etc.) that continuously increase in number with urbanization and the infrastructure associated to widespread and rising water scarcity issues (Park *et al.* 2008; Strayer & Dudgeon 2010).

Freshwater ecosystems are true biodiversity hotspots: an estimated 13,000 freshwater fish species alone inhabit rivers and lakes, which in turn cover less than 1% of the earth's surface (Lévêque *et al.* 2007). These ecosystems are hierarchically structured in stream networks, which ultimately place them in a "receiver position" of effluents from the landscape (Dudgeon et al. 2006). Thus, freshwater ecosystems are highly vulnerable to anthropogenic disturbances, making them one of the most impaired ecosystems globally (Allan & Flecker 1993; Sala *et al.* 2000). Furthermore, barriers play a leading role in freshwater ecosystem impairment as they hydrologically modify habitats and reduce or entirely disrupt connectivity along the stream network (Fullerton *et al.* 2010). This connectivity loss and the resulting habitat fragmentation have negative impacts on fish populations, diminishing freshwater biodiversity and threatening ecosystem function (Cardinale *et al.* 2012*;* Perkin & Gido 2011; Rolls *et al.* 2013).

As water quality has started to improve in some regions of the world (e.g. Europe; Azimi & Rocher 2016) concerns have shifted to barriers as the main anthropogenic impairment. Barriers are a priority of the European Water Framework Directive (WFD) agenda to improve the ecological status of streams (Reyjol *et al.* 2014) and their removal is already a frequent river

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restoration measure at the global scale. This fact is supported by an increasing number of studies dealing with dam prioritization and removal (Palmer, Hondula & Koch 2014; Branco *et al.* 2014). Some studies have thoroughly documented the effect of large dams on freshwater fish (e.g. Gehrke, Gilligan & Barwick 2002; Wofford, Gresswell & Banks 2005), but the impact of different barrier types and sizes on their distribution poses an interesting, yet surprisingly understudied question. Culverts, weirs and slides are mostly small and far more abundant structures than dams, reducing but not always fully block connectivity along the stream network. While previous studies have related such structures to stream fragmentation, extinction risk and recolonization success in benthic macroinvertebrates, fish, crayfish and turtles (Dodd 1990; Morita & Yokota 2002; Perkin & Gido 2011; Foster & Keller 2011; Tonkin *et al.* 2014), their impact on the distribution of freshwater fish communities has not been addressed in detail.

We applied high resolution species distribution models (SDMs) to the fish community of a German catchment, to shed light on the role barriers play in their distribution patterns by including them as a further predictor in the model. SDMs have been applied to model freshwater fish distributions in relation to climate scenarios (Bond *et al.* 2011; Filipe *et al.* 2013) or for conservation purposes (Domínguez-Domínguez *et al.* 2006; Esselman & Allan 2011) but, to our knowledge, no SDM approach has incorporated barriers into their set of predictors. Furthermore, we calculated three different, spatially explicit metrics based on ecological criteria related to fish migration and dispersal in order to determine how barrier obstruction affected their distribution in the catchment. Two obstruction metrics accounted for number and magnitude of barriers along migration routes (upstream & downstream), while one was

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conceived to represent obstruction to dispersal movements (10 km in every possible direction along the stream network).

In a first step, we calibrated SDMs for 19 fish and one lamprey species from the Kinzig River catchment, as applied by Kuemmerlen et al. (2015) for benthic macroinvertebrates. For this purpose, environmental datasets at very high spatial resolutions (25m x 25m, *sensu* Domisch *et al.* 2015) from the long term ecological research site (LTER) Rhine-Main-Observatory (RMO) were used as predictors representing the categories climate, hydrology, land use, geology and topography. In a second step, we additionally included the three obstruction metrics. Based on this two-step approach, our aims were (i) to assess the effect of including barriers on the SDM performance, (ii) to determine the relative importance of the three obstruction metrics in the model, (iii) to explore how the different obstruction metrics influence the predicted distributions of individual fish species and (iv) to derive possible patterns in the fish responses related to the barrier predictors.

Model results are analyzed in detail for three different species, each one being mostly affected by a different obstruction metric: the threatened brook lamprey (*Lampetra planeri*), the threatened grayling (*Thymallus thymallus*), as well as the exotic and formerly stocked rainbow trout (*Oncorhynchus mykiss*). Establishing the spatial context in which barriers have the strongest influence on the distribution of specific species (i.e. upstream or downstream) and highlighting areas where fish distribution is being hampered by barriers, is highly valuable information for freshwater fish conservation and watershed management. Hence, we anticipate a broad applicability of SDMs using key anthropogenic disturbance factors such as barriers, as a valuable method in the field of freshwater ecosystem restoration.

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A - Methods

A SDM was set up for the freshwater fish of the Kinzig catchment (~1060 km^2), which is located in the German central mountain ranges (98-731 m a.s.l.). The Rhine-Main Observatory (RMO) operates in this catchment as a long-term ecological research site (LTER) focused on river and floodplain ecosystems (e.g. Tonkin *et al.* 2016). The RMO provides detailed data on a broad variety of biotic and abiotic variables, particularly useful to build SDMs (Kuemmerlen *et al.* 2015).

B - Biological & Environmental Data

Fish occurrences were sourced from the Hessian authorities for Environment and Geology (Hessisches Landesamt für Naturschutz, Umwelt und Geologie [HLNUG] and Hessen Forst; both unpublished data) comprising samples taken between 2005 and 2012 at 94 locations. A total of 20 species with at least ten occurrences were modeled (Table 1). Some species are considered critically endangered or vulnerable by regional, national or global red lists (RL), while others are listed in either annex II or IV of the European Habitats Directive (EHD; Freyhof 2009; Dümpelmann & Korte 2013; Table 1). RL indicate conservation status estimates, while EHD defines concrete measures, such as habitat conservation and management strategies. Environmental predictors were pre-processed to fit the spatial scale (25m) and extent of the model (28 205 grid cells in the stream network) using ArcMap 10.1 (ESRI, Redlands CA, USA) and the raster package for R (R Development Core Team 2014; Hijmans 2015). Predictor selection was based on correlation ($r < |0.7|$; Dormann *et al.* 2013), predictor ranking in previous model runs, as well as on expert knowledge. The bioclimatic predictors temperature annual range and mean temperature of wettest quarter were calculated for the period 2003-2012 from the Land Surface Temperature (LST) dataset for Europe with a 250 m spatial resolution (Metz, Rocchini & Neteler 2014) and monthly precipitation dataset at 1 km spatial resolution from the worldclim dataset (Hijmans *et al.* 2005). The topographical predictor slope was derived from a digital elevation model of the German Federal Agency for Cartography and Geodesy (DEM; ©GeoBasis-DE; BKG, 2011). Hydrology was represented by the mean annual discharge for the years 2001 to 2010 at 51 subcatchment outlets, obtained from a hydrological model set up for the Kinzig catchment (Schmalz *et al*., 2012) using the Soil and Water Assessment Tool (Arnold *et al.* 1998) and extrapolated to the gridded stream network using flow accumulation (average R^2= 0.89). The land use predictors agriculture and pasture were derived from a national vectorized dataset (©GeoBasis-DE; BKG, 2011). The geological predictors’ fine and coarse sediment, as well as basalt and sandstone were obtained from the GÜK300 geological database for the federal state of Hesse (HLNUG, 2007). Relative land use and geology for each grid cell in the stream network were calculated using a subcatchment specific approach (Kuemmerlen *et al.* 2014).

Barrier point data was obtained from the local authority (HLNUG; unpublished data) and comprised 718 relevant anthropogenic structures of different sizes such as culverts, drops, slides, weirs and dams. These structures are recorded in a standardized survey that covers all water bodies in segments of 100m, is known in German as Gewässerstrukturgütekartierung and is implemented as part of the WFD. Each barrier has an assigned value of 0, 3, 4, 6 or 7, depending on its capacity to hinder sediment transport, as well as the migration and dispersal of fish, according to German standards of structural integrity of streams and rivers (LAWA 2000). In

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the specific case of culverts, those originally classified with values of zero were modified and assigned the lowest possible barrier value (Value = 3), as we also considered them a significant obstacle for fish. In a further step, three obstruction metrics were calculated for every grid cell in the stream network: (i) upstream barriers (Fig. 1), (ii) downstream barriers and (iii) up- and downstream barriers within 10 km stream network distance, along all possible tributaries (hereafter referred to as upstream, 10 km and downstream barriers). The network distance of 10 km was based on previous research in the RMO (Tonkin *et al.* 2014). Each metric consisted of the sum of all barrier values in the relevant stream network segment (Fig. 1), divided by the number of grid cells each calculated segment is comprised of, to obtain a value that reflected the relative influence of the spatially relevant barriers for each single grid cell, in each one of the obstruction metrics.

The three metrics were designed to capture possible pathways in which barriers hinder two specific ecological processes: migration and dispersal. Migration is a directed movement, either up or down stream networks, which can happen at different life-stages of freshwater fish: upstream to spawn or downstream for mating. The upstream and downstream obstruction metrics are intended to account specifically for the impairment of migration. Dispersal, on the other hand, is an undirected, often short to intermediate-distance movement (Radinger & Wolter 2014) which allows for recolonization and exchange of individuals between populations. Restrictions to movements in this restricted spatial setting where are accounts for through the 10 km stream network obstruction metric.

B - Model setup

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An ensemble model framework was implemented using the R package “biomod2” (Thuiller, Georges & Engler 2014) using default settings, unless described otherwise below. The ensemble comprised five algorithms (generalized linear model: GLM, generalized boosted model: GBM, classification tree analysis: CTA, artificial neural network: ANN, maximum entropy: MAXENT), three different pseudo-absence runs with 7000 randomly distributed pseudo-absences each and 10 repetitions, totaling 150 models per species. Every single model was cross-validated using a subset of the occurrence data (30%; Thuiller et al., 2009). The large number of repetitions and pseudo-absences were chosen according to the recommendations of Barbet-Massin et al. (2012). Predicted probabilities were converted to binary predictions by applying a threshold that maximized the true skill statistic TSS (Allouche, Tsoar & Kadmon 2006). From the resulting models, those with TSS above 0.6 were selected and weighted according to their score to obtain the final ensemble model (Araújo & New 2007). For each species, variable importance, predicted probability of occurrence, binary predicted occurrence and a coefficient of variation across predictions were recorded, as well as the performance measures TSS, AUC, Sensitivity and Specificity.

Two sets of ensemble models were run: one with all environmental predictors, but excluding barriers and one including all environmental and barrier predictors. To assess whether the inclusion of barriers improved the model outcome, a paired Wilcoxon signed rank test with continuity correction, was used to compare TSS, AUC, Sensitivity, Specificity, number of cells with predicted occurrences and coefficient of variance between the two model runs.

B - Analysis of Predictions

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All further analyses on predictions were performed on the results of the model including barriers. The predicted probability of occurrence for each species was plotted (i) against mean annual discharge to check whether predictions of species were ecologically meaningful (i.e. species occurrences are assigned to stream orders as expected from literature) and (ii) against the barrier predictor found to be most relevant, to assess the interaction of the species with the barrier. Binary predictions of occurrence for each species were mapped showing occurrences (i) as predicted by both models (suitable habitat with and without barriers; i.e. stable range); (ii) as predicted by the model without barriers, but not by the model with barriers (i.e. suitable habitat lost due to the inclusion of barriers); and (iii) viceversa (i.e. suitable habitat gained through the inclusion of barriers).

From the range predicted to be suitable for each species in presence of barriers, the maximum obstruction metric value for the barrier predictors was extracted and determined how much area with values above this threshold was predicted as unsuitable. These thresholds were calculated individually for each species, barrier predictor and stream order (one through four), as well as the entire stream network and across all barrier predictors.

Finally, Spearman's rank correlation analyses and Wilcoxon rank sum tests were performed to assess whether the effects of including barriers on the predicted occurrences were related to habitat preferences, conservation concerns (Table 1) or vulnerability to obstruction metrics.

A - Results

Models calibrated without barriers performed very well with average TSS values of 0.89 ± 0.05 and 0.97 ± 0.02 for AUC (mean ± standard deviation; Fig. 2; see Table S1 in Supporting

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Information). Their occurrence predictions matched the expected distribution of fish, increasing in predicted richness along the stream network, from streams of order one, to streams of order four (1, 15, 20, 20 species per stream order respectively). The smallest streams were predicted as unsuitable habitat for fish, with the exception of minnow (*Phoxinus phoxinus*) but only in a very small proportion (< 0.1% of all stream segments, Table S2). Streams of order two were predicted to be the main suitable habitat for brook lamprey (62.8%; Fig. 4a) and those of order three for stone loach (*Barbatula barbatula*), bullhead (*Cottus gobio*), three-spined stickleback (*Gasterosteus aculeatus*), topmouth gudgeon (*Pseudorasbora parva*) and brown trout (*Salmo trutta*). The remaining species were predicted to occur primarily in streams of order four (Table S2).

On average, all performance indicators rose only very slightly when barrier predictors were included in the model, with significant differences for TSS ($p > 0.05$) and AUC ($p > 0.01$), as indicated by the pairwise Wilcoxon test.

The average relative importance of the environmental predictors remained mostly unaffected by the inclusion of barriers, dominated by hydrology, geology and climate (Fig. 3). The hydrological predictor mean annual discharge was the most important in the model including barriers, accounting for 52.4% of the variation and followed in decreasing importance by geological, climatic, barrier, land use and topographic predictors (Table 2). Barrier predictors had an average relative importance in the model of 4.9% across all species, but in the cases of brook lamprey, rainbow trout, stone loach and grayling, barriers reached variable importances exceeding 10%. Out of the three barrier metrics, upstream barriers was the most relevant for 14 fish species, while 10 km barriers played a major role for five species (brook lamprey, pike [*Esox*

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lucius], barbel [*Barbus barbus*], nase [*Chondrostoma nasus*] and topmouth gudgeon) and downstream barriers only for one species (grayling).

Furthermore, the inclusion of barriers in the model reduced the area of predicted occurrence by an average of 3.8%, but showed very diverse responses among the fish community: 13 species lost and seven species gained predicted range (-35.5% max. loss; 51.2% max. gain; Table S2). Most of the suitable habitat loss was located in middle sized streams of orders two and three; however, independent of range losses or gains, the prevailing stream order for each species remained the same in the two models. Further, the size of ranges predicted with barriers was found to be inversely correlated with the relative number of cells above the combined barrier threshold ($\rho = -0.55$; $p < 0.05$). This indicates that barriers significantly influence range predictions, particularly those of species with small predicted ranges. This pressure was found to be exerted by upstream ($\rho = -0.53$; $p < 0.05$) and 10 km barriers ($\rho = -0.47$; $p < 0.05$), but not to downstream barriers ($\rho = 0.04$; $p = 0.85$). EHD-listed species (Annexes II and V; Table 1), those requiring management or conservation measures, were also found to be under significant pressure of barriers in general, when compared to non-EHD-listed species ($W = 57$, $p < 0.1$).

In the particular case of brook lamprey, the predicted range increased by 13.8% with the addition of barriers to the model, with gains being located in streams of order three and four (Fig. 4c; Table S2). The obstruction metric 10 km barriers was the most relevant for this species (Table 2), becoming absent at intermediate and high values (Fig. 4b). Such values were recorded in 32.8% of the grid cells in streams of order two, where the brook lamprey was most frequently predicted to occur (Fig. 4a, b, c).

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The rainbow trout saw an overall contraction of its predicted range by 13.2%, with losses taking place in streams of order three and four, but expansions in streams of order two (Fig. 5c; Table S2). The most relevant obstruction metric for this species was upstream barriers, which restricted its occurrence only marginally, as predictions were projected nearly throughout the entire stream network (Fig. 5b, c; Table 2).

Predictions resulted in range reductions across all stream orders for grayling, totaling a range loss of 12.3% (Table 2). This was the only species primarily influenced by downstream barriers becoming absent at high values, like those detected at 24.8% grid cells in the stream network (Fig. 6.b, c).

A - Discussion

In concordance with the literature (Huet 1949), the model without barriers predicted fish to be distributed according to the European river zonation: brown trout, brook lamprey, stone loach and bullhead primarily in the trout region, represented in this model by streams of order two and three (Epi- and Metarhithral); further downstream grayling, nase, chub (*Squalius cephalus*), dace (*Leuciscus leuciscus*) and gudgeon in the grayling zone, in streams of order four (Hyporhithral). The remaining species were predicted to occur either in both zones, such as the minnow, or primarily in the grayling zone while belonging to other zones further downstream and beyond the RMO. This first step served as a fundamental validation of the SDM projections, reinforcing further analysis.

B - Effects of barriers on the distribution of the fish community

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The marginal improvement of model performance by barriers may be due to the high indicator values already attained by the initial model. However, many fish distributions were affected by barriers as indicated by the relevance of barrier predictors for many species and the observed changes in predicted occurrence (Figs. 4-6).

The distribution of the fish community in the RMO was primarily shaped by hydrology, geology and climate, variables unlikely to be influenced at the local or regional scale through management or conservation measures, as they are controlled by larger scale natural regimes (hydrology and climate), or cannot be modified at all (geology). Conversely, small barriers such as culverts, weirs and slides are much more relevant for regional management as they are comparatively easy to remove through local restoration measures. Thus, barriers are the most important management-relevant predictor category, highlighting them as optimal candidates for stream restoration projects in the RMO. These results strengthen current practice for river ecosystems, where barrier removal has become one of the most frequent restoration measures (Simaika *et al.* 2015; Thomas *et al*. 2015). Land use, moreover, ranked fifth in this model after barriers. While the potential of a modification in land use regimes as a supplementary restoration measure in the RMO is undisputed, it should be considered as secondary when compared to barrier removal. This may differ in other catchments, with lower barrier densities and a different land use composition.

Barriers reduced predicted fish ranges, mainly where upstream barrier density was high. It is remarkable that vulnerable species, those with small predicted distributions or EHD-listed, lost significantly more range to barriers than less vulnerable species. This supports barriers as a major concern for freshwater fish conservation. Habitat suitability was also compromised by the combination of all obstruction metrics in 19% of the RMO stream network, as indicated by barrier thresholds. Combined with connectivity reduction, fish populations experienced elevated fragmentation, a state stream networks are very prone to because of their linear, hierarchical structure. Such a mosaic of disconnected habitats has serious consequences for metapopulation persistence (Fagan 2002), as local extinction risk is inversely related to fragment size and possible re-colonization events are impeded by barriers. This situation has been documented at similar spatial scales for freshwater fish in Japan (Morita & Yokota 2002) and North America (Perkin & Gido 2011).

Threats stemming from barriers are predominantly associated to potamadromous fish that migrate long distances (e.g. Marschall *et al.* 2011). However, barriers also affect non- or short-distance- migrating fish, particularly at small spatial scales (Mahlum *et al.* 2014). This is likely the case of some species studied here: brook lamprey, stone loach and bullhead, which showed an above-average variable importance of barrier predictors. The narrow niches of these species are well depicted by the environmental conditions considered in the model and because it is unlikely that local populations perform regular movements beyond the RMO, their predictions should be amongst the most reliable.

B - Heterogeneous responses of fish species to barriers

Fish populations in the RMO have been under the influence of barriers for a considerable amount of time (i.e. decades). Thus, their impact is embedded in the occurrence data used to predict their distributions. The three barrier metrics used, reflect connectivity along three different movement paths, critical to many species' life histories (Binder, Cooke & Hinch 2011).

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The fact that 10 km barriers was the most important obstruction metric for brook lamprey, is supported by the rather short movements that are part of its life cycle: upstream to spawn and downstream to disperse (Maitland 2003). With the inclusion of barriers, considerable range gains were predicted in large streams for this species. This may be related to increased sediment retention and habitat stability upstream of barriers, which are required for its larval stage (ammocoete; Malmqvist 1980). Nevertheless, this gain is overshadowed by a range contraction of 10% in streams of order two, the species' spawning grounds.

Grayling displayed a more complex response to barriers, being affected by both upstream and downstream barriers and loosing range throughout the catchment with the inclusion of barriers (Fig. 6.c; Table 2). Its elaborate migration habits support these results: it requires access to headwaters for spawning (Lucas & Batley 1996; Fredrich *et al.* 2003) and free passage downstream during winter migration (Cunjak 1996). Grayling has been found to move up to 20 km, well beyond the 10 km stream network distance used to calculate the obstruction metric and making it the least important to this species. In contrast to brook lamprey, the rheophilic grayling avoids stagnant water bodies likely to be created behind barriers. Thus, both habitat unsuitability and fragmentation could be mayor reasons for its predicted range loss (Mallet *et al.* 2000).

The distribution of the introduced rainbow trout was mostly influenced by upstream barriers. While it experienced a strong loss of predicted range under consideration of barriers, the high obstruction metric values at which it occurs, suggest high resilience to barriers. Considering its stocking history for fishing, it is possible that rainbow trout may have been released in confined stream segments (i.e. between two barriers) on purpose, as to block their dispersal throughout

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the stream network. Recreational fishing is popular and widespread in the Kinzig catchment, which combined with low reproductions rates, made the regular but costly stocking necessary to maintain the population. Furthermore, our results for the exotic species (topmouth gudgeon and rainbow trout) suggest they may profit from the presence of barriers in the RMO, as reported by Johnson et al. (2008).

Other species such as bream (*Abramis brama*), barbel, perch (*Perca fluviatilis*) and chub, have wide niches that extend downstream beyond the Kinzig River and are not fully covered by the extent of this model. Barriers considered here were of low importance for these species and had only slight effects when comparing predictions with and without barriers. However, those barriers affecting their distributions are probably located further downstream, outside of the RMO, where their critical habitats lie.

B - Implications

Precise information on barrier location and magnitude, such as the one available for the RMO, is generally rare and its high relevance for applications as the one presented here, echoes recent calls to expand barrier inventories (Januchowski-Hartley et al. 2013). The obstruction metrics applied in this study refer to the ecological relevance of barriers in a stream network, including their number and magnitude. In combination with the derived barrier thresholds, they provide spatially-explicit and species-specific guidance to understand how the effect of barriers affects freshwater fish distributions. The application of SDMs to gain this valuable information is of great interest to both river managers and freshwater biodiversity conservationists, while being universally applicable in any given stream network.

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Recent research increasingly emphasizes on freshwater biodiversity conservation, exploring various methods to identify and quantify threats or to prioritize restoration measures. Studies have incorporated the cost of proposed interventions using decision networks (Mantyka-Pringle *et al.* 2016), integrated longitudinal connectivity in an open-source, conservation planning software (Hermoso *et al.* 2011), estimated passability of culverts for fish with various swimming abilities (Januchowski-Hartley *et al.* 2014) or developed a decision tool for barrier removal that maximizes habitat availability (O'Hanley *et al.* 2013). The approach presented in this study, however, is based on the well-established SDMs, which can be applied to further understand distribution patterns of freshwater fish, as influenced by barriers.

For the RMO it was possible to infer that 10 km barriers are the major anthropogenic constraint for brook lamprey in streams used for spawning. Also, to secure seasonal migration routes for the grayling, downstream barriers in streams of order three and upstream barriers in streams of order four should be addressed. Further, rainbow trout occurrence is strongly related to barriers, which may be containing this exotic species to a certain extent from spreading in the catchment. Finally, barrier pressure is highest for EHD-listed fish, and those with small ranges. These indications could be used as a baseline to prioritize barrier removal, to manage fish populations, or to guide conservation initiatives at the catchment level. However, considering the fact that these conclusions rely on distribution predictions, a validation through additional assessments or methods would greatly increase their certainty.

Barriers are abundant and widespread in European freshwaters, causing demographic isolation and species loss in fish populations, among many other negative effects (Gehrke, Gilligan & Barwick 2002; Wofford, Gresswell & Banks 2005). Thus, recent policy developments in Europe,

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motivated by the WFD, have urged European countries to engage in costly restoration projects to improve the structure and connectivity of lotic aquatic ecosystems, ultimately enhancing biodiversity. Yet, some barriers will remain because of their economic significance (Hering *et al.* 2010). Either way, free passage for fish is now a major focus in freshwater ecosystem restoration and its success depends largely on catchment-wide connectivity, particularly when regional species pools are fragmented and impoverished (Stoll *et al.* 2014).

In our study, barriers show a strong signature on predicted fish distributions. Moreover, our results prove that, beyond simple fragmentation, fish distributions are affected heterogeneously by different types and magnitudes of barriers. Their cumulative effects impair habitat suitability, restrict movement possibilities and increase local extirpation risk, factors frequently ignored when global change scenarios are considered. Our approach highlights the importance of barriers and provides precise information on them for the effective conservation of freshwater fish.

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Biosketch

Mathias Kuemmerlen is a postdoctoral researcher interested in studying the impact of anthropogenic disturbances to natural systems, in order to understand, prevent and mitigate biodiversity loss and ecosystem impairment. His past work has focused on the application of species distribution models in freshwater ecosystems at high temporal and spatial resolutions.

Stefan Stoll is the head of Eußerthal Ecosystem Research Station (EERES) at the University of Koblenz-Landau and leads a research group on fish and freshwater ecology. He is interested in developing strategies and tools that help to make stream restorations more effective for aquatic communities.

Peter Haase is full professor at the University of Duisburg-Essen and head of the Department of River Ecology and Conservation at Senckenberg. He is a freshwater ecologist focusing on river restoration and global change effects on riverine ecosystems. Long-term ecosystem research (LTER) is a further core topic in his research.

Author contributions: M.K. and S.S. conceived the ideas; M.K. P.H. and S.S. collected the data; M.K. and S.S. analysed the data; M.K. led the writing, with contributions of all authors.

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Tables

Table 1. Modelled fish species with code, conservation status according to different Red Lists (NA = not assessed, LC = least concern, V = early warning, VU = vulnerable, EN = endangered) and consideration in the European Habitats Directive and Bern Convention (Annex number).

					Red List Status				EU Habitats Directive (Annex)	Bern Convention (Annex)
code	**Species**	**English name**	**Origin**	**Occurrences**	**IUCN 2015**	**EU 2011**	**Germany 2009**	**Hesse 2014**		
abr_bra	*Abramis brama*	Common bream	native	27	LC	LC	LC	LC		
ang_ang	*Anguilla anguilla*	European eel	native	61	CR	CR	NA	CR		
bar_bar	*Barbus barbus*	Common barbel	native	19	LC	LC	LC	LC	5	
bat_bat	*Barbatula barbatula*	Stone loach	native	56	LC	LC	LC	LC		
cho_nas	*Chondrostoma nasus*	Common nase	native	10	LC	LC	V	V		3
cot_gob	*Cottus gobio*	Bullhead	native	39	LC	LC	LC	LC	2	
eso_luc	*Esox lucius*	Northern pike	native	28	LC	LC	LC	V		
gas_acu	*Gasterosteus aculeatus*	Western stickleback	native	19	LC	LC	LC	LC		
gob_gob	*Gobio gobio*	Gudgeon	native	60	LC	LC	LC	LC		
lam_pla	*Lampetra planeri*	European brook lamprey	native	13	LC	LC	LC	LC	2	3
leu_leu	*Leuciscus leuciscus*	Common dace	native	47	LC	LC	LC	LC		
onc_myk	*Oncorhynchus mykiss*	Rainbow trout	exotic	10	NA	NA	NA	NA		
per_flu	*Perca fluviatilis*	European perch	native	56	LC	LC	LC	LC		
pho_pho	*Phoxinus phoxinus*	Eurasian minnow	native	11	LC	LC	LC	LC		
pse_par	*Pseudorasbora parva*	Topmouth gudgeon	exotic	13	LC	NA	NA	NA		
rut_rut	*Rutilus rutilus*	Roach	native	59	LC	LC	LC	LC		
sal_tru	*Salmo trutta*	Brown trout	native	61	LC	LC	LC	LC		
squ_cep	*Squalius cephalus*	Chub	native	48	LC	LC	LC	LC		
thy_thy	*Thymallus thymallus*	Grayling	native	29	LC	LC	EN	VU	5	3
tin_tin	*Tinca tinca*	Tench	native	10	LC	LC	LC	LC		

Table 2. Relative variable importance (%) by species. Gray columns show predictor category sums, or a single predictor value when only one was used by category. See text for full predictor names.

	Barriers				Hydrology	Geology	Climate	Landuse	Topography
Spp code	**SUM**	**Upstream**	**10km Net.**	**Downstream**	**Ann. Dis.**	**SUM**	**SUM**	**SUM**	**Slope**
lam_pla	**15.8**	*1.0*	*14.4*	*0.3*	**20.9**	**35.1**	**24.6**	**2.8**	**0.9**
onc_myk	**12.0**	*7.5*	*3.8*	*0.8*	**38.3**	**21.0**	**23.5**	**3.1**	**2.1**
bat_bat	**10.6**	*8.7*	*0.5*	*1.4*	**32.8**	**38.7**	**4.5**	**10.1**	**3.4**
thy_thy	**10.2**	*3.6*	*1.1*	*5.5*	**48.6**	**17.3**	**13.1**	**9.5**	**1.3**
cot_gob	**5.5**	*4.2*	*0.6*	*0.8*	**45.6**	**29.4**	**5.8**	**11.3**	**2.5**
rut_rut	**5.3**	*4.4*	*0.6*	*0.2*	**55.4**	**9.9**	**26.6**	**1.2**	**1.7**
pho_pho	**4.8**	*3.1*	*1.4*	*0.3*	**11.9**	**29.5**	**17.9**	**18.4**	**17.5**
sal_tru	**4.8**	*3.9*	*0.5*	*0.4*	**49.2**	**37.9**	**0.5**	**5.0**	**2.7**
leu_leu	**4.5**	*3.0*	*0.8*	*0.7*	**52.8**	**9.9**	**27.7**	**2.6**	**2.5**
gas_acu	**3.9**	*3.6*	*0.2*	*0.1*	**39.2**	**13.5**	**17.1**	**6.1**	**20.2**
eso_luc	**3.5**	*1.2*	*2.2*	*0.1*	**74.2**	**11.1**	**3.9**	**2.7**	**4.7**
squ_cep	**3.2**	*2.6*	*0.5*	*0.1*	**65.9**	**6.4**	**20.1**	**1.8**	**2.6**
per_flu	**3.1**	*2.0*	*0.6*	*0.4*	**54.6**	**14.4**	**23.7**	**2.3**	**1.9**
gob_gob	**3.1**	*2.6*	*0.2*	*0.2*	**55.0**	**6.9**	**29.3**	**4.4**	**1.3**
tin_tin	**2.9**	*2.2*	*0.1*	*0.7*	**51.3**	**18.8**	**12.0**	**1.9**	**13.0**
ang_ang	**2.5**	*1.2*	*0.6*	*0.7*	**47.4**	**23.6**	**21.7**	**2.2**	**2.6**
abr_bra	**1.3**	*0.7*	*0.2*	*0.3*	**86.0**	**4.9**	**5.2**	**0.8**	**1.8**
bar_bar	**0.7**	*0.1*	*0.5*	*0.1*	**67.3**	**6.5**	**24.0**	**0.9**	**0.7**
pse_par	**0.6**	*0.1*	*0.3*	*0.1*	**82.2**	**3.5**	**11.5**	**1.7**	**0.6**
cho_nas	**0.5**	*0.2*	*0.2*	*0.1*	**69.2**	**4.6**	**24.6**	**0.4**	**0.8**
Mean	**4.9**	*2.8*	*1.5*	*0.7*	**52.4**	**17.1**	**16.9**	**4.5**	**4.2**

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Figure legends

Fig. 1 Scheme for the calculation of three obstruction metrics in a stream network for one single cell: from the starting grid (circle) and along the stream network a) downstream until the outlet from the catchment of interest; b) upstream along all possible tributaries; c) 10km in all possible directions. Arrows indicate stream segment relevant for the calculation of the metric for one grid cell in the stream network.

Fig. 2 Boxplots (bar – median; box – 1st and 3rd interquantile range (IQR); whiskers – 1.5 × IQR; outliers > 1.5 × IQR) for performance indicators for models with (grey boxes) and without (white boxes) barrier predictors: on the left vertical axis area under curve (AUC) and true skill statistic (TSS); on the right vertical axis sensitivity (Sens.) and specificity (Spec.). Significant differences indicated by asterisks: * $p = 0.1$; ** $p = 0.05$.

Fig. 3 Boxplots (bar – median; box – 1st and 3rd interquantile range (IQR); whiskers – 1.5 × IQR; outliers > 1.5 × IQR) for variable importance for models with (grey boxes) and without (white boxes) barrier predictors, with predictors grouped into categories.

Fig. 4 Brook lamprey (a) predicted probability of occurrence along the river continuum, depicted here by mean annual discharge with approximate location in the stream network indicated through discharge maxima by stream order (O1 = stream order one); (b) predicted probability of occurrence along the obstruction gradient of 10 km stream network barriers; (c) comparison of predicted distributions in the RMO with and without barriers as predictors.

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Fig. 5 Rainbow trout (a) predicted probability of occurrence along the river continuum, depicted here by mean annual discharge with approximate location in the stream network indicated through discharge maxima by stream order (O1 = stream order one); (b) predicted probability of occurrence along the obstruction gradient of upstream barriers; (c) comparison of predicted distributions in the RMO with and without barriers as predictors.

Fig. 6 Grayling (a) predicted probability of occurrence along the river continuum, depicted here by mean annual discharge with approximate location in the stream network indicated through discharge maxima by stream order (O1 = stream order one); (b) predicted probability of occurrence along the obstruction gradient of downstream barriers; (c) comparison of predicted distributions in the RMO with and without barriers as predictors.

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Figures

Fig. 1

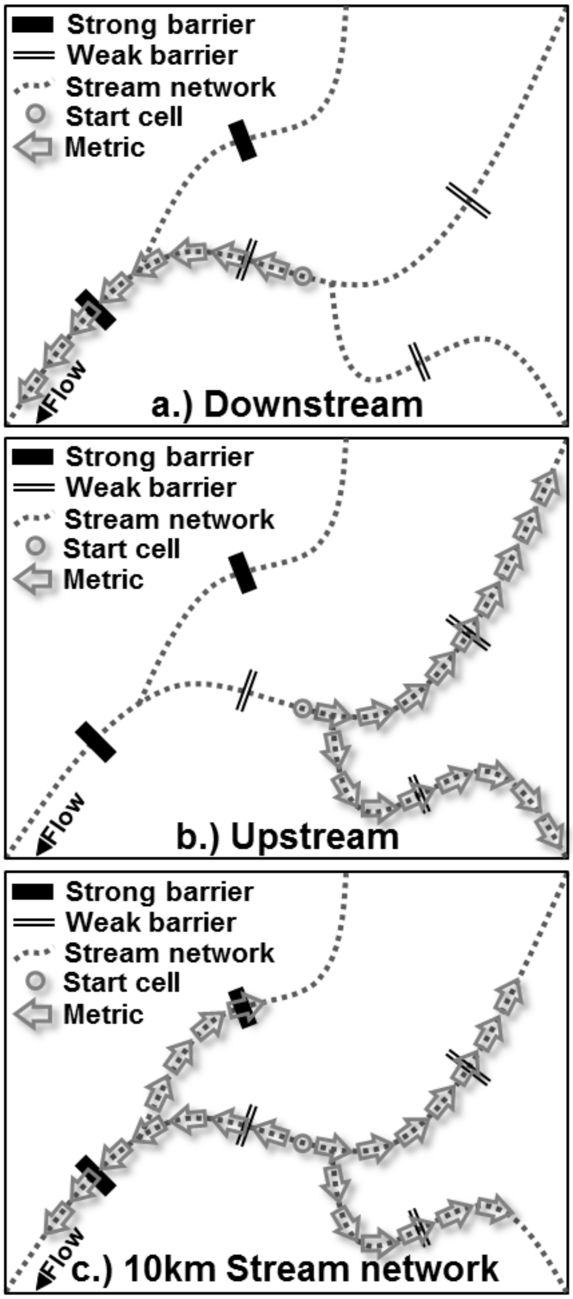

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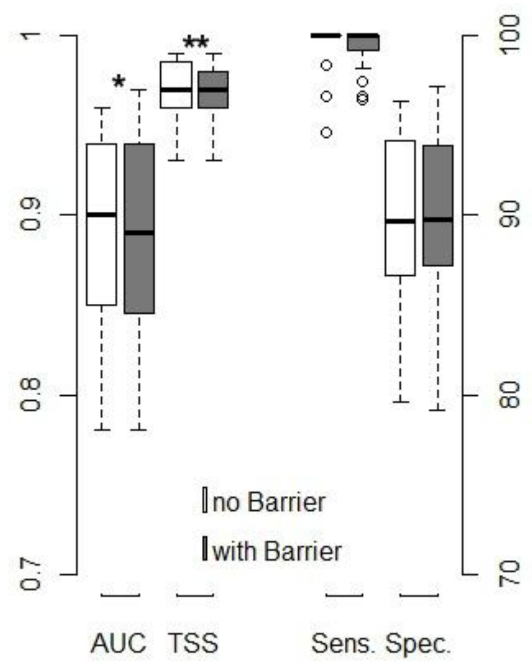
Fig. 2



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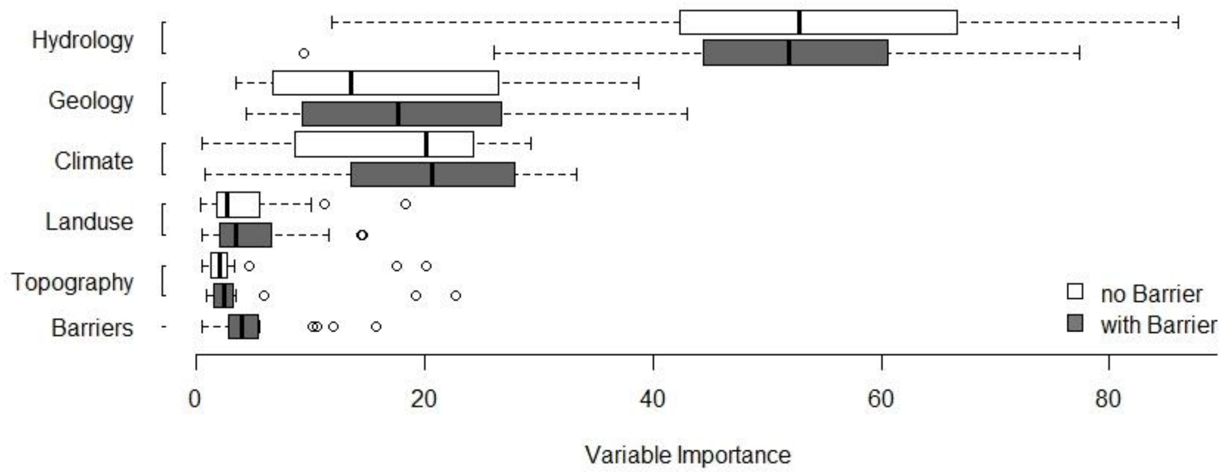
681 **Fig. 3**



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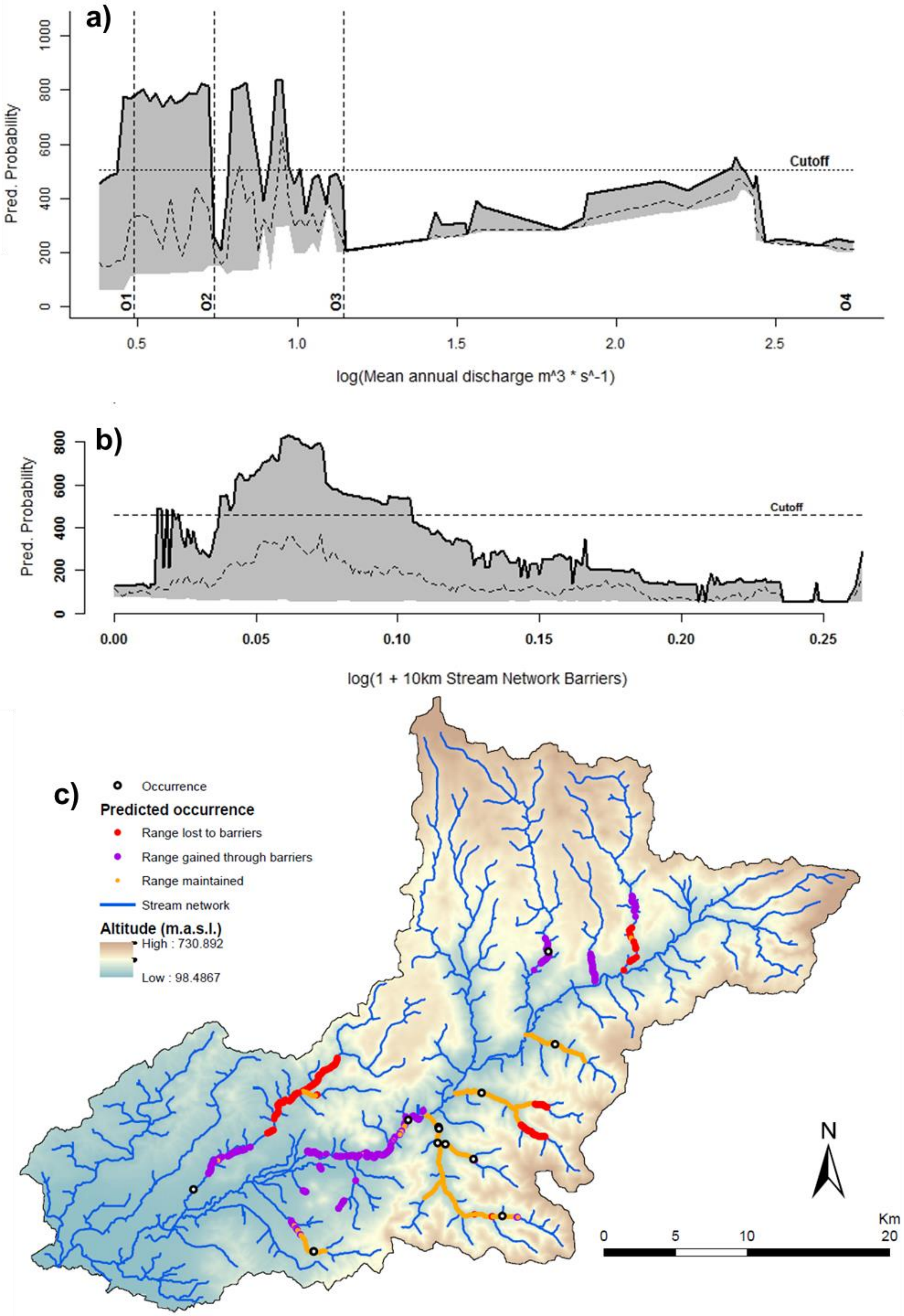
684 **Fig. 4 *Brook Lamprey*** *(Lampetra planeri)*



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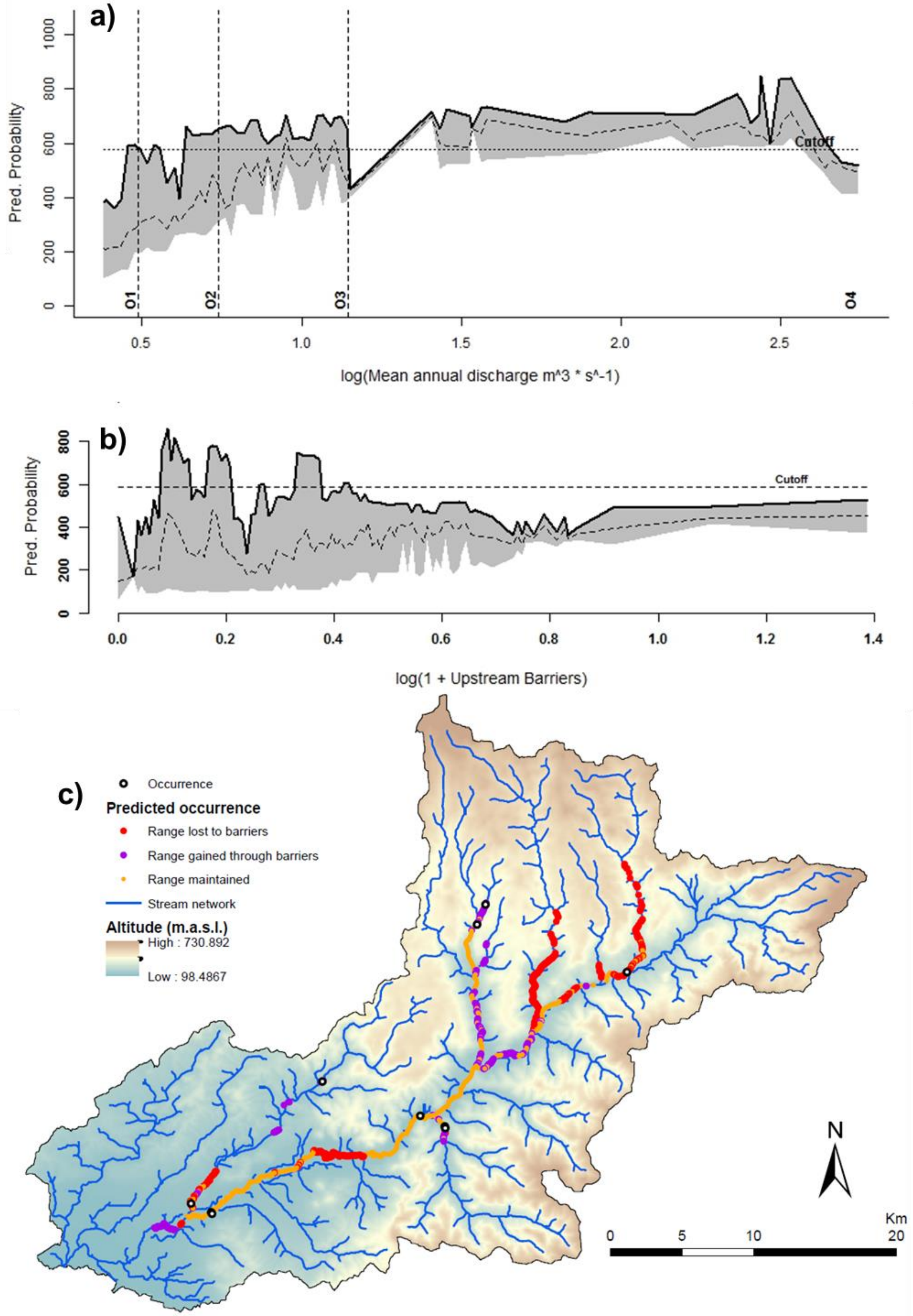
686 **Fig. 5 Rainbow Trout** (*Oncorhynchus mykiss*)



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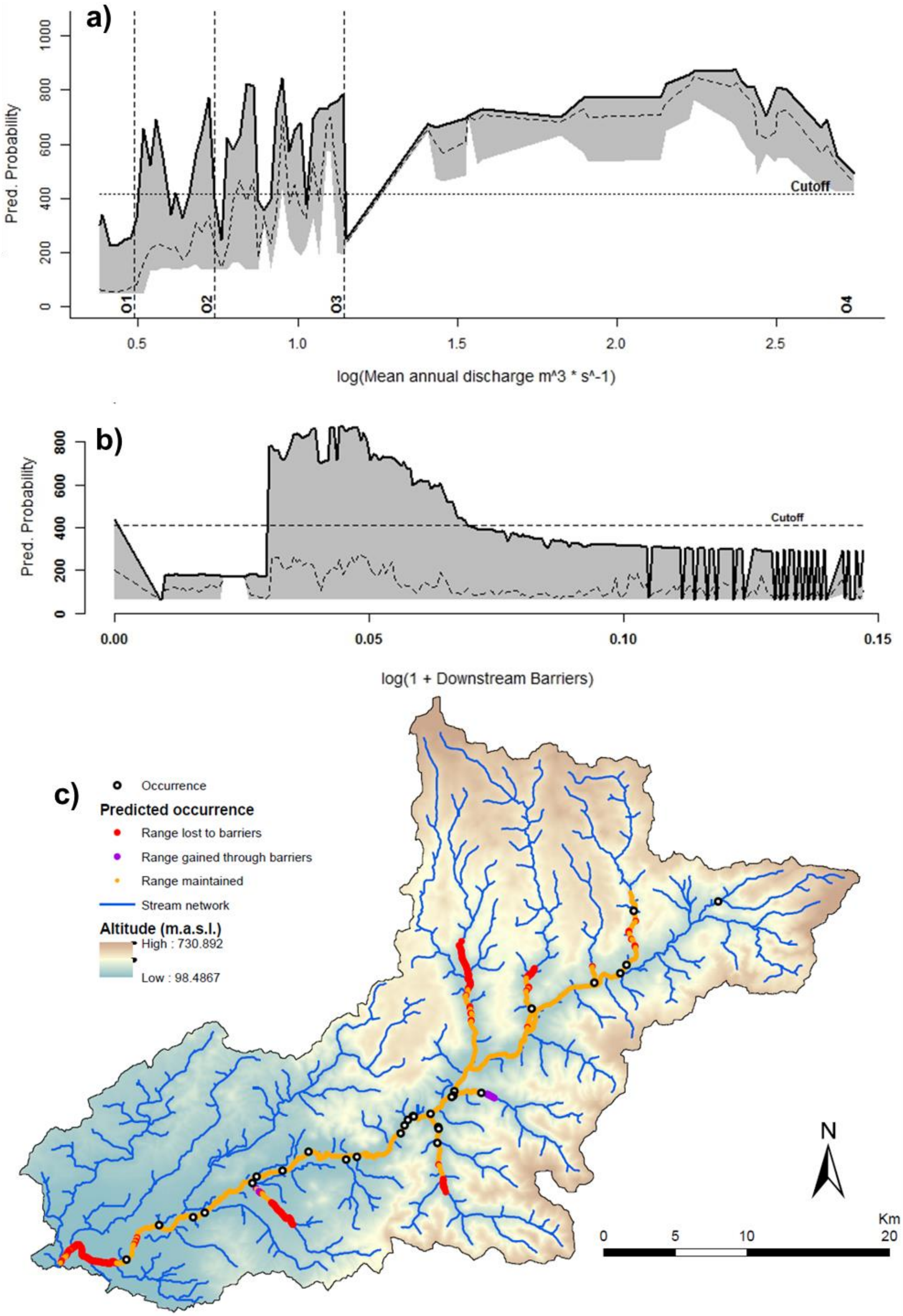
689 **Fig. 6 Grayling** (*Thymallus thymallus*)



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Supporting Information

Table S1 Performance indicators by species and model

Species code	without Barriers				with Barriers			
	TSS	AUC	Sens	Spec	TSS	AUC	Sens	Spec
abr_bra	0.94	0.98	100.0	93.6	0.93	0.98	100.0	93.2
ang_ang	0.84	0.95	100.0	84.2	0.85	0.96	100.0	84.9
bar_bar	0.97	0.99	100.0	96.5	0.96	0.99	100.0	96.3
bat_bat	0.81	0.94	100.0	81.0	0.79	0.94	94.6	84.2
cho_nas	0.95	0.99	100.0	95.1	0.96	0.99	100.0	95.9
cot_gob	0.85	0.95	97.4	87.6	0.85	0.95	100.0	84.5
eso_luc	0.91	0.98	96.4	94.3	0.92	0.98	100.0	91.6
gas_acu	0.93	0.98	100.0	93.3	0.95	0.99	100.0	95.0
gob_gob	0.84	0.96	100.0	84.2	0.85	0.97	100.0	84.8
lam_pla	0.94	0.98	100.0	93.7	0.93	0.99	100.0	92.8
leu_leu	0.89	0.97	100.0	88.9	0.90	0.97	100.0	89.7
onc_myk	0.91	0.97	100.0	91.4	0.93	0.99	100.0	92.5
per_flu	0.88	0.97	98.2	89.7	0.89	0.97	100.0	88.4
pho_pho	0.97	0.99	100.0	97.1	0.96	0.99	100.0	95.6
pse_par	0.94	0.99	100.0	94.0	0.96	0.99	100.0	96.1
rut_rut	0.83	0.96	96.6	86.8	0.85	0.96	96.6	88.7
sal_tru	0.78	0.93	98.4	79.1	0.78	0.93	98.4	79.5
squ_cep	0.88	0.97	100.0	87.9	0.89	0.97	100.0	88.5
thy_thy	0.88	0.97	100.0	87.9	0.89	0.97	100.0	89.4
tin_tin	0.94	0.98	100.0	94.0	0.96	0.98	100.0	96.2
Mean	**0.894**	**0.969**	**99.35**	**90.01**	**0.900**	**0.970**	**99.48**	**90.40**
SD	**0.053**	**0.016**	**1.19**	**5.01**	**0.060**	**0.020**	**1.37**	**4.81**

696 **Table S2** Predicted probability of occurrence and predicted occurrence by species and
697 stream order for models with and without barriers, as well as the relative changes
698 between them.

		Prediction without Barriers			*Change*		Prediction with Barriers			Barrier Analysis						
		Occ.		Prob.	*Occ.*	*Prob.*	Occ.		Prob.	Treshold			Habitat unsuitability			
Species	Stream Order	Absolute	Relative [%]	Mean (± SD)	*Relative [%]*	*Relative [%]*	Absolute	Relative [%]	Mean (± SD)	10 km Network	Downstream	Upstream	10 km Network [%]	Downstream [%]	Upstream [%]	All combined [%]
abr_bra	1	0	0.0	45 (5)	*0.0*	*40.0*	0.0	0.0	63 (10)	NA	NA	NA	-	-	-	-
	2	0	0.0	46 (9)	*0.0*	*39.1*	0	0.0	64 (14)	NA	NA	NA	-	-	-	-
	3	24	1.3	117 (101)	*204.2*	*12.0*	73	3.8	131 (97)	0.072	0.056	0.092	43.3	47.1	48.2	79.1
	4	1802	98.7	567 (241)	*3.5*	*4.9*	1865	96.2	595 (216)	0.095	0.162	0.116	9.9	0.0	27.1	27.2
	All	1826	100.0	104 (171)	*6.1*	*17.3*	1938	100.0	122 (170)	0.095	0.162	0.116	33.5	0.0	23.4	42.5
ang_ang	1	0	0.0	64 (34)	*0.0*	*-7.8*	0.0	0.0	59 (27)	NA	NA	NA	-	-	-	-
	2	365	8.1	129 (98)	*-16.7*	*2.3*	304	7.1	132 (100)	0.219	0.098	0.496	3.7	2.0	1.5	5.8
	3	1931	43.0	323 (191)	*-7.5*	*-1.9*	1786	41.6	317 (186)	0.205	0.087	0.228	0.0	0.4	2.2	2.6
	4	2199	48.9	633 (231)	*0.3*	*-0.3*	2206	51.4	631 (231)	0.095	0.162	0.135	9.8	0.0	12.0	12.0
	All	4495	100.0	174 (206)	*-4.4*	*-1.7*	4296	100.0	171 (205)	0.219	0.162	0.496	2.5	0.0	1.9	3.7
bar_bar	1	0	0.0	51 (10)	*0.0*	*0.0*	0	0.0	51 (9)	NA	NA	NA	-	-	-	-
	2	0	0.0	52 (9)	*0.0*	*1.9*	0	0.0	53 (10)	NA	NA	NA	-	-	-	-
	3	72	7.1	89 (109)	*5.6*	*5.6*	76	7.2	94 (111)	0.076	0.060	0.094	39.7	36.3	45.9	70.9
	4	936	92.9	530 (224)	*4.9*	*0.9*	982	92.8	535 (222)	0.079	0.162	0.115	18.8	0.0	28.0	31.6
	All	1008	100.0	101 (159)	*5.0*	*1.0*	1058	100.0	102 (160)	0.079	0.162	0.115	43.3	0.0	23.6	49.6
bat_bat	1	0	0.0	64 (46)	*0.0*	*-15.6*	0	0.0	54 (33)	NA	NA	NA	-	-	-	-
	2	871	16.1	190 (155)	*-26.5*	*1.1*	640	14.3	192 (161)	0.225	0.091	0.221	2.8	10.0-6	12.3	21.7
	3	2379	44.1	440 (220)	*-19.1*	*-0.9*	1925	42.9	436 (224)	0.205	0.087	0.228	0.0	0.4	2.2	2.6
	4	2150	39.8	568 (186)	*-10.5*	*2.8*	1925	42.9	584 (183)	0.095	0.080	0.135	9.8	5.2	12.0	17.3
	All	5400	100.0	202 (220)	*-16.9*	*-1.5*	4490	100.0	199 (225)	0.225	0.091	0.228	1.9	7.7	8.0	14.3
cho_nas	1	0	0.0	65 (17)	*0.0*	*-10.8*	0	0.0	58 (16)	NA	NA	NA	-	-	-	-
	2	0	0.0	68 (17)	*0.0*	*-8.8*	0	0.0	62 (19)	NA	NA	NA	-	-	-	-
	3	2	0.1	108 (85)	*-50.0*	*-3.7*	1	0.1	104 (89)	0.075	0.060	0.091	40.2	36.3	50.9	73.2
	4	1384	99.9	552 (230)	*-15.8*	*-1.4*	1165	99.9	544 (225)	0.090	0.162	0.115	11.7	0.0	29.3	30.5
	All	1386	100.0	117 (159)	*-15.9*	*-5.1*	1166	100.0	111 (159)	0.090	0.162	0.115	36.4	0.0	23.9	44.9

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cot_gob	1	0	0.0	66 (38)	*0.0*	*-12.1*	0	0.0	58 (36)	NA	NA	NA	-	-	-	-
	2	856	24.3	231 (190)	*52.1*	*3.5*	1302	29.7	239 (199)	0.265	0.100	0.450	0.0	0.3	2.0	2.0
	3	1828	51.8	430 (256)	*11.5*	*-2.3*	2039	46.5	420 (256)	0.205	0.087	0.267	0.0	0.4	0.0	0.4
	4	844	23.9	399 (221)	*23.2*	*-0.5*	1040	23.7	397 (235)	0.095	0.050	0.135	9.8	32.0	12.0	36.7
	All	3528	100.0	198 (214)	*24.2*	*-1.5*	4381	100.0	195 (218)	0.265	0.100	0.450	0.2	2.2	2.3	4.2
eso_luc	1	0	0.0	52 (11)	*0.0*	*26.9*	0	0.0	66 (9)	NA	NA	NA	-	-	-	-
	2	0	0.0	55 (17)	*0.0*	*23.6*	0	0.0	68 (14)	NA	NA	NA	-	-	-	-
	3	326	20.0	180 (166)	*32.8*	*8.3*	433	18.2	195 (168)	0.106	0.068	0.189	17.3	21.7	8.4	31.5
	4	1301	80.0	556 (211)	*49.3*	*4.0*	1943	81.8	578 (197)	0.095	0.162	0.124	9.9	0.0	18.3	18.3
	All	1627	100.0	118 (172)	*46.0*	*12.7*	2376	100.0	133 (173)	0.106	0.162	0.189	26.0	0.0	11.1	30.1
gas_acu	1	0	0.0	107 (59)	*0.0*	*0.0*	0	0.0	107 (53)	NA	NA	NA	-	-	-	-
	2	288	15.2	194 (147)	*-37.5*	*-3.6*	180	12.8	187 (133)	0.221	0.100	0.118	3.2	0.3	36.8	37.0
	3	975	51.6	391 (200)	*-29.8*	*-2.6*	684	48.5	381 (187)	0.123	0.096	0.112	12.6	0.0	25.1	29.3
	4	627	33.2	482 (142)	*-12.8*	*3.3*	547	38.8	498 (130)	0.093	0.053	0.116	10.3	25.2	27.4	49.8
	All	1890	100.0	209 (180)	*-25.3*	*-1.0*	1411	100.0	207 (174)	0.221	0.100	0.118	2.2	2.2	22.7	24.0
gob_gob	1	0	0.0	48 (17)	*0.0*	*-4.2*	0	0.0	46 (7)	NA	NA	NA	-	-	-	-
	2	346	7.7	78 (87)	*-4.3*	*2.6*	331	7.6	80 (87)	0.169	0.099	0.118	15.1	0.6	36.9	39.8
	3	1922	42.8	312 (233)	*-6.2*	*0.3*	1802	41.6	313 (229)	0.163	0.096	0.202	4.2	0.0	4.9	6.4
	4	2226	49.5	627 (214)	*-1.0*	*-0.8*	2203	50.8	622 (213)	0.095	0.162	0.135	9.8	0.0	12.0	12.0
	All	4494	100.0	149 (214)	*-3.5*	*0.0*	4336	100.0	149 (212)	0.169	0.162	0.202	8.4	0.0	10.1	15.2
lam_pla	1	0	0.0	152 (112)	*0.0*	*-3.3*	36	1.8	147 (109)	0.060	0.068	3.000	65.1	33.5	0.0	66.3
	2	1121	62.8	242 (204)	*-9.9*	*-7.4*	1010	49.8	224 (184)	0.110	0.087	0.351	32.8	14.0	3.9	36.4
	3	602	33.7	324 (184)	*10.5*	*-6.2*	665	32.8	304 (169)	0.091	0.077	0.179	29.8	5.8	10.8	31.1
	4	61	3.4	291 (89)	*423.0*	*11.3*	319	15.7	324 (93)	0.070	0.049	0.108	30.0	37.3	34.9	63.7
	All	1784	100.0	216 (167)	*13.8*	*-3.2*	2030	100.0	209 (158)	0.110	0.087	3.000	23.0	10.3	0.0	26.7
leu_leu	1	0	0.0	51 (16)	*0.0*	*-2.0*	0	0.0	50 (4)	NA	NA	NA	-	-	-	-
	2	108	3.4	71 (69)	*-62.0*	*0.0*	41	1.4	71 (65)	0.054	0.036	0.077	73.5	93.3	54.4	95.0
	3	887	28.0	275 (201)	*-16.5*	*-3.6*	741	25.2	265 (188)	0.148	0.081	0.197	6.6	2.7	6.6	9.2
	4	2169	68.6	652 (214)	*-0.5*	*-2.6*	2159	73.4	635 (205)	0.095	0.162	0.135	9.8	0.0	12.1	12.1
	All	3164	100.0	145 (209)	*-7.0*	*-2.1*	2941	100.0	142 (201)	0.148	0.162	0.197	11.7	0.0	10.6	17.9
onc_myk	1	0	0.0	210 (47)	*0.0*	*-25.2*	0	0.0	157 (65)	NA	NA	NA	-	-	-	-
	2	10	0.4	273 (73)	*460.0*	*-20.1*	56	2.7	218 (100)	0.209	0.093	0.532	5.8	6.7	1.3	11.6
	3	836	34.4	433 (131)	*-30.6*	*-20.6*	580	27.5	344 (182)	0.205	0.087	0.228	0.0	0.4	2.2	2.6
	4	1586	65.2	593 (108)	*-7.1*	*-3.0*	1474	69.9	575 (131)	0.095	0.069	0.135	9.8	6.8	12.0	18.8
	All	2432	100.0	296 (144)	*-13.2*	*-18.6*	2110	100.0	241 (163)	0.209	0.093	0.532	3.7	5.9	1.6	9.7
per_flu	1	0	0.0	68 (23)	*0.0*	*2.9*	0	0.0	70 (17)	NA	NA	NA	-	-	-	-

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	2	209	7.1	106 (79)	*83.7*	*3.8*	384	11.6	110 (82)	0.214	0.098	0.520	4.9	2.0	1.3	6.6
	3	589	20.1	225 (156)	*16.8*	*-5.3*	688	20.8	213 (154)	0.205	0.087	0.228	0.0	0.4	2.2	2.6
	4	2137	72.8	625 (231)	*4.5*	*3.0*	2234	67.6	644 (228)	0.095	0.162	0.135	9.8	0.0	12.0	12.0
	All	2935	100.0	154 (189)	*12.6*	*0.6*	3306	100.0	155 (192)	0.214	0.162	0.520	3.2	0.0	1.7	4.3
pho_pho	1	1	0.1	156 (79)	*0.0*	*5.8*	1	0.1	165 (80)	0.075	0.048	0.000	49.6	67.9	16.7	72.1
	2	1	0.1	193 (102)	*600.0*	*4.7*	7	0.6	202 (92)	0.224	0.091	0.125	2.9	8.9	33.3	38.1
	3	304	37.1	300 (185)	*29.3*	*-0.3*	393	31.7	299 (166)	0.109	0.062	0.184	14.4	29.7	9.4	34.9
	4	514	62.7	454 (165)	*63.2*	*5.5*	839	67.7	479 (150)	0.094	0.050	0.135	10.1	32.0	12.0	36.9
	All	820	100.0	215 (147)	*51.2*	*4.2*	1240	100.0	224 (142)	0.224	0.091	0.184	2.0	7.2	11.5	16.9
pse_par	1	0	0.0	173 (53)	*0.0*	*-4.6*	0	0.0	165 (49)	NA	NA	NA	-	-	-	-
	2	349	20.8	283 (147)	*-55.6*	*-1.4*	155	14.1	279 (150)	0.218	0.090	0.166	3.9	11.1	19.2	28.6
	3	1264	75.2	500 (118)	*-29.0*	*1.6*	898	81.8	508 (115)	0.149	0.096	0.190	6.4	0.0	8.0	8.2
	4	68	4.0	496 (23)	*-33.8*	*4.6*	45	4.1	519 (27)	0.092	0.050	0.116	10.5	32.0	27.5	52.8
	All	1681	100.0	283 (163)	*-34.7*	*-0.7*	1098	100.0	281 (170)	0.218	0.096	0.190	2.6	4.0	11.1	14.4
rut_rut	1	0	0.0	65 (26)	*0.0*	*-9.2*	0	0.0	59 (10)	NA	NA	NA	-	-	-	-
	2	42	1.1	106 (77)	*-71.4*	*6.6*	12	0.4	113 (94)	0.207	0.090	0.109	6.3	11.5	39.8	45.2
	3	1558	41.3	350 (174)	*-28.0*	*5.4*	1121	34.7	369 (165)	0.198	0.096	0.206	1.1	0.0	3.7	4.4
	4	2176	57.6	649 (206)	*-3.8*	*0.8*	2094	64.9	654 (199)	0.095	0.162	0.135	9.8	0.0	12.1	12.1
	All	3776	100.0	173 (207)	*-14.5*	*1.7*	3227	100.0	176 (211)	0.207	0.162	0.206	4.0	0.0	9.7	11.8
sal_tru	1	0	0.0	46 (23)	*0.0*	*-8.7*	0	0.0	42 (22)	NA	NA	NA	-	-	-	-
	2	1640	27.8	240 (219)	*-1.9*	*0.4*	1609	27.7	241 (224)	0.228	0.100	0.450	2.5	0.3	2.0	3.9
	3	2461	41.7	446 (251)	*-7.6*	*-2.2*	2274	39.2	436 (260)	0.205	0.087	0.265	0.0	0.4	0.2	0.6
	4	1803	30.5	521 (211)	*6.4*	*0.8*	1918	33.1	525 (215)	0.095	0.119	0.135	9.8	1.4	12.0	13.4
	All	5904	100.0	205 (240)	*-1.7*	*-1.5*	5801	100.0	202 (243)	0.228	0.119	0.450	1.7	1.0	2.3	4.4
squ_cep	1	0	0.0	49 (19)	*0.0*	*12.2*	0	0.0	55 (7)	NA	NA	NA	-	-	-	-
	2	0	0.0	60 (43)	*0.0*	*11.7*	0	0.0	67 (37)	NA	NA	NA	-	-	-	-
	3	1253	36.3	272 (218)	*-12.3*	*-0.7*	1099	33.5	270 (208)	0.147	0.096	0.197	6.7	0.0	6.6	6.9
	4	2201	63.7	650 (194)	*-0.8*	*-2.3*	2184	66.5	635 (191)	0.095	0.162	0.135	9.8	0.0	12.0	12.0
	All	3454	100.0	141 (208)	*-5.0*	*2.1*	3283	100.0	144 (200)	0.147	0.162	0.197	11.8	0.0	10.6	18.0
thy_thy	1	0	0.0	61 (40)	*0.0*	*11.5*	0	0.0	68 (19)	NA	NA	NA	-	-	-	-
	2	24	0.7	94 (72)	*-100.0*	*8.5*	0	0.0	102 (63)	NA	NA	NA	-	-	-	-
	3	1167	33.8	322 (197)	*-17.7*	*-11.2*	960	31.7	286 (174)	0.167	0.066	0.264	3.9	25.9	0.2	27.4
	4	2259	65.5	625 (183)	*-8.5*	*-5.8*	2066	68.3	589 (186)	0.095	0.071	0.135	9.8	6.4	12.0	18.5
	All	3450	100.0	161 (202)	*-12.3*	*-1.9*	3026	100.0	158 (182)	0.167	0.071	0.264	8.7	24.8	5.6	29.1
tin_tin	1	0	0.0	199 (61)	*0.0*	*3.5*	0	0.0	206 (61)	NA	NA	NA	-	-	-	-
	2	180	10.7	280 (106)	*-76.1*	*1.8*	43	4.0	285 (97)	0.209	0.093	0.439	5.8	6.7	2.1	12.1

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	3	542	32.2	420 (121)	*-48.2*	*-5.0*	281	25.9	399 (104)	0.205	0.087	0.228	0.0	0.4	2.2	2.6
	4	961	57.1	579 (113)	*-20.8*	*-2.8*	761	70.1	563 (103)	0.119	0.162	0.164	5.0	0.0	1.7	5.0
	All	1683	100.0	290 (150)	*-35.5*	*0.0*	1085	100.0	290 (138)	0.209	0.162	0.439	3.7	0.0	2.5	5.3
All species (mean)	1	0	0.0	90 (37)	-	*-3.3*	2	0.0	87 (32)	0.000	0.000	2.000	57.0	51.0	8.0	69.0
	2	321	10.0	150 (96)	*-5.3*	*-0.7*	304	9.0	149 (96)	0.000	0.000	0.000	12.0	12.0	18.0	27.0
	3	1046	34.0	313 (175)	*-11.5*	*-2.9*	926	32.0	304 (172)	0.000	0.000	0.000	11.0	10.0	12.0	21.0
	4	1470	56.0	552 (182)	*1.9*	*0.7*	1498	59.0	556 (179)	0.000	0.000	0.000	11.0	9.0	17.0	25.0
	All	2837	100.0	183 (186)	*-3.8*	*-1.1*	2730	100.0	181 (185)	0.000	0.000	0.000	12.0	3.0	10.0	19.0