TITLE

Dead wood can mediate effects of large and small-scale drivers of fish abundances in stream ecosystems

Or

Large and small-scale drivers of fish abundances in stream ecosystems: direct and indirect effects mediated by woody debris

Manuscript type: Article

**ABSTRACT**

Theoretical knowledge and empirical evidence show that both large and local-scale environmental factors and biotic interactions determine the structure and distribution of freshwater fish species. As restoration measures typically focus on the modification of local conditions, it is crucial to understand the relative importance of drivers of species abundance, and their potential interactive effects. This is especially challenged by high environmental variation in running waters at multiple spatial and temporal scales. Rivers typically encompass gradients in climatic and geographic factors as well as highly diverse adjacent habitats, where e.g. water velocity, depth, and substrate, vary within few meter and from day to day. Among the local-scale factors affecting fish abundance, the occurrence of woody debris has been reported to boost salmonid fish population growth. However, what species benefit from woody debris, to what extent relative to other biotic and abiotic drivers, and what factors influence woody debris quantity is not clear yet, which limits our ability to use woody debris as an effective restoration measure.

We applied path analyses to time series data collected between 1993 and 2016 from 3653 rivers (total of ca 7000 sampling sites) all over Sweden to investigate 1) the relative importance of large- and local-scale environmental drivers, as well as biotic factors and their interactions with environmental drivers, for the abundance of brown trout (*S. trutta*), salmon (*Salmon salar*), and sculpin fish (*Cottus* spp.), 2) beneficial effects of woody debris on these three species after accounting for other factors, and 3) the drivers of woody debris abundance and persistence.

We found that overall, large scale-factors, i.e. average air temperature and latitude, had larger weight than local-scale factors for sculpin fish population, while the opposite is true for trout and salmon population, with stream width and depth being the stronger drivers. Abundances of predators such as burbot and pike only (negatively) affected trout population, while no evidence of competition or interactions with other drivers was found. Woody debris appeared to benefit trout, but not salmon or sculpin fish populations. The quantity of woody debris strongly decreased with stream width, but also depended, albeit to a lesser extent, on stream bed slope and depth, forest age and cover, altitude, and mean air temperature. Our study suggests that the weight of large- and local-scale factors on fish abundances in streams varies strongly with species, and that effectiveness of woody debris as a restoration measure depends on both the targeted species and local environmental conditions.

**Keywords**:

**INTRODUCTION**

Both economically and non-economically valuable fish population provides a range of ecosystem services for human societies (Holmlund et al. 1999). Fish populations are however undergoing increasing pressures (e.g. overfishing, habitat loss, climate change REF) in both marine and freshwater ecosystems, and is therefore crucial to understand drivers of abundance and distribution to aid management and conservation.

It is commonly accepted that large-scale factors and processes structure species assemblages by determining the potential range that any given species can occupy (Ricklefs 1987, Tonn 1990, Poff 1997, Morán-López et al. 2012). On the other hand, behavioral, morphological, and physiological adaptations to local conditions, as well as biotic interactions (competition and predation), further constrain the available pool of species and ultimately determine where and when a species will be found (Tonn 1990, Thrush 1991, Grossman et al. 1998, Jackson et al. 2001). A number of studies has addressed fine-scale habitat use of fish in freshwater systems, often in relation to competition and predation (e.g. Gilliam 2001, Marchetti and Moyle 2001), while others have focused on major abiotic constraints at large scales (e.g. Magalhães et al. 2002). So far, however, a unified approach for understanding the relative importance of large- and local-scale drivers has been often prevented by the availability of resources to data collection, as well as the questions considered (Jackson et al. 2001). An integrated framework is especially needed given that habitat restoration measures typically focus on the modification of local conditions (e.g. restoration of natural flow regimes, rehabilitation of spawning habitats) and their effectiveness may be conditional on the specific abiotic and biotic context (Roni et al. 2008). It is therefore important, for both our ecological understanding and management purposes, to evaluate together the relative weight of large-scale, local-scale and biotic factors in driving species distribution, and to assess potential context-dependent (interactive) effects.

The assessment of drivers of fish abundance in running waters is often challenged by broad variation in environmental conditions at multiple spatial and temporal scales (Cooper et al. 1998, Jackson et al. 2001). Rivers typically form vast interconnected networks that include strong longitudinal gradients of climatic and geographic factors (Vannote et al. 1980) . While the occurrence of some species is restricted to specific environmental conditions (e.g. colder temperatures), other fish species migrate long distances upstream and downstream (Pont et al. 2005). Moreover, streams offer a multitude of adjacent habitats, where local conditions such as depth, water velocity, and substrate composition can vary widely within tens of meters and from day to day, due to fluctuations in stream flow (Grossman and Freeman 1987, Cooper et al. 1998, Benda et al. 2004). Many freshwater fish species show basic habitat preferences, i.e. trout tend to occupy shallower areas, while graylings deeper areas, that are often conditional to the presence of competitors or predators (Grossman and Freeman 1987, Degerman et al. 2000, Gilliam and Fraser 2001). Overall, such spatial and temporal variability in abiotic and biotic factors is not easily accounted for in monitoring programs, and ultimately challenges our understanding of the effect size of significant drivers.

Among the local-scale factors affecting fish abundance, the occurrence of woody debris is suggested to benefit fish population growth by providing refugia from predators and elevated flow, and substrate for spawning and feeding (Crook and Robertson 1999, Dolloff and Warren 2003, Degerman et al. 2004, Sievers et al. 2017). Beneficial effects of woody debris are mostly reported for juvenile and adult salmonids, while evidence for non-salmonid fish is equivocal (Langford et al. 2012, Roni et al. 2014). Furthermore, most studies have not accounted for other potential drivers of fish abundances when investigating the influence of woody debris (e.g. Degerman et al. 2004, Langford et al. 2012). Therefore, what species benefit from woody debris and to what extent relative to other biotic and abiotic drivers is not clear yet. Finally, several knowledge gaps remains on the factors affecting woody debris abundances and persistence (Seo et al. 2010), which limits our ability to use woody debris as an effective restoration measure.

In the current study we analyzed time series data from 3653 rivers (total of ca 7000 sampling sites) across Sweden to investigate 1) the relative importance of large-scale, local-scale and biotic factors for the abundance of three key freshwater fish species: salmon (*Salmon salar*), brown trout (*S. trutta*), and sculpin fish (*Cottus* spp.). Specifically, we asked 2) whether local abundance of woody debris had beneficial effects on these three species, and 3) what drivers determined woody debris persistence. We used path analyses (Grace 2006), a statistical technique that allows not only to evaluate simultaneously the relative strength of multiple causal links, but also to assess indirect effects, hence the significance of woody debris as a mediator factor for fish abundances.

**METHODS**

*Data*

The dataset was extracted from the Swedish Electrofishing Register (SERS) and consisted of 33278 records from 9096 sites spread in 3641 rivers across Sweden. Each site was sampled up to t wenty times but at least once between 1993 and 2016. Electrofishing was performed mostly between July and October along sections on average 45 ± 23m (SD) long and spanning the whole width of the river, by using DC-equipment from LUGAB or BIOWAVE (Sweden). The abundance of each fish species was estimated through successive removals according to Bohlin et al. (1989), and expressed as number per 100 m2. For the current study we used abundances of three key species: salmon (*Salmon salar*), brown trout (*S. trutta*), and sculpin fish (*Cottus* spp.). Brown trout and salmon were classified either as migrating or resident based on.., and type of migration was coded as 0 for resident and 1 for migrating fish for statistical analyses.

In each sampling occasion, stream width, average depth, and maximum depth were measured. The date of fishing was expressed as Julian date (ranging from 1 to 354). The bottom substratum was classified into 5 categories, from 1 to 5, according to increasing particle size (fine: <0.2mm, sand: 0.2–2mm, gravel: 2–20mm, stones: 20–200mm, boulders: >200mm). Water velocity was scored from 0 to 3 with 1 being slow flow and 3 being rapids. Woody debris with diameter ≥ 10 cm and length ≥ 50 cm were counted and given as number per 100 m2.

For each site altitude, latitude, stream bed slope, upstream catchment area, and forest data were estimated in a GIS environment using ArcMap 10.2. Forest data were collected in 2000, 2005 and 2010, and were used for electrofishing data collected respectively before and during 2000, between 2001 and 2005, and from 2006 onwards. Coverage, mean forest age, and total forest volume from 25mx25m squares were averaged over an area of 700m diameter and 150 hectares surface around each sampling site. Average annual air temperatures between 1960 and 1990 were provided by the Swedish Meteorological and Hydrological Institute ([www.smhi.se](http://www.smhi.se)).

*Statistical analyses*

We consider rivers rather than sites as replicates to simplify the hierarchical structure of the data and overcome potential issues related to sites mislabeling. However, we wanted to retain the year-to-year variation to investigate changes over time. Hence, averages by rivers and year for all variables were calculated. Preliminary data exploration where fish and woody debris abundances were plotted against total water volume sampled (calculated as width\*length\*average depth of the sampled section of each site) did not reveal any issues related to samples size.

We used path analyses to evaluate 1) the relative contribution of drivers of abundance of salmon, brown trout and sculpin, 2) potential beneficial effects of woody debris on the abundance of these three species after accounting for the effects of other explanatory variables, and 3) drivers of woody debris abundance, which could indirectly affect fish abundance. We first formulated hypotheses based on current empirical and theoretical knowledge (Fig. 1). We expected large-scale factors (factors that vary on large-scales) such as latitude, altitude, and average air temperature, to set the limits of species distribution (Poff 1997, Trigal and Degerman 2015). Local-scale factors (factors that vary on local scales) such as stream width and bed slope, upstream catchment area (which correlates with the river size), average and maximum depth, water velocity, and substrate type, were expected to further constrain species habitat use (e.g. Pont et al. 2005), together with biotic interactions, i.e. predation from pike and burbot, and competition between brown trout, brook trout, grayling, salmon and sculpin fish (e.g. Näslund et al. 1997, Degerman et al. 2000, Öhlund et al. 2008). Type of migration was included as explanatory factor of trout and salmon abundance. We expected the abundance of woody debris to be affected by the above-mentioned large-scale factors as well as forest coverage, age and volume (Dolloff and Warren 2003, Ekbom et al. 2006), and factors related to stream size and hydrology, i.e. stream width and bed slope, upstream catchment area, average and maximum depth, water velocity (Harmon et al. 1986, Seo et al. 2010, Ruiz-Villanueva et al. 2014). Finally, abundances of fish and woody debris were hypothesized to vary within and between years. To test the hypothesis that woody debris are especially important as shelter when predators are abundant (Enefalk et al. 2017), we incorporated an interaction between woody debris and predators (pike and burbot). Also, the interaction between stream bed slope or depth and competitors was included to investigate whether habitat partitioning is more likely to show when species occur in sympatry (Degerman et al. 2000). Finally, we included an interaction between average air temperature and competitors to test potential effects of temperature on the outcome of competitive interactions (Öhlund et al. 2008).

After formulating the conceptual model, we used path analysis to test the significance of causal links (paths) corresponding to our hypotheses for each fish species separately. Models included 20 or 21 exogenous variables (i.e. not caused by other variables) and 2 endogenous variables (i.e. caused by other variables) (Table 1). Due to the hierarchical nature of our data we used the *piecewiseSEM* package, version 1.1.1 (Lefcheck 2015) in R 3.2.3 (R Development Core Team, 2015) to construct our path models as sets of hierarchical linear mixed models, each of which included a two-nested random-effect structure, taking into account catchments and rivers within a catchment, and a lag-1 autoregressive correlation structure accounting for repeated measures. Collinearity in each component model was checked by calculating the variance inflation factor (VIF) for each predictor. As latitude and average air temperature were collinear (VIF ≥ 2), as well as average and maximum depth, and forest coverage and volume, they were included in separate models. Abundances of each fish species and woody debris were log-transformed to attain normal error distribution.

Finally, we compared the relative fit of alternative piecewise models to the data, first using the test of directional separation (Shipley 2009), which produces a Chi-square distributed Fisher’s C statistic, where *P* values > 0.05 indicate adequate fit, and second, through comparison of AIC values (Shipley 2013). For the best-fitting (final) models, we calculated standardized path coefficients (scaled by subtracting the minimum and dividing by the difference of the range) to compare the relative importance of predictors (Lefcheck 2015). Marginal R2 values for endogenous variables were estimated following (Nakagawa and Schielzeth 2013). Model validation was performed visually by plotting residuals versus fitted values for each component model.

**RESULTS**

Our path analyses suggest that large-scale, local-scale and, to a minor extent, biotic factors affected the abundances of the studied fish populations, but their relative importance varied with species. Overall, large scale-factors had larger weight than local-scale factors for sculpin fish population, while the opposite is true for trout and salmon population. This is also confirmed by a more prominent latitudinal gradient apparent in the geographic distributions of sculpin fish abundances compared to trout and salmon abundances (FIG. 2).

Our best-supported models fit the data well (trout: Fisher's C = 21.50, *P* = 0.255, salmon: Fisher's C =6.06, *P* = 0.641, sculpin fish: Fisher's C =13.81, *P* = 0.313, Fig. 3). The total explained variation was respectively 0.79 for trout, 0.69 for salmon and 0.82 for sculpin fish abundance, while it was 0.52 for woody debris abundance. The relatively large differences between conditional R squared (which is associated to the sum of fixed and random effects) and marginal R squared (which is associated to the fixed effects), in general indicated strong variation between catchments. The many zeros in salmon abundances (FIG 2) may have partly contributed to the especially low variation explained by fixed effects (FIG 3).

Among the large-scale factors, average air temperature was preferred over latitude as it gave a better overall fit (AIC = … vs …). Average air temperature was the stronger predictor of sculpin fish abundance, with negative effects, while it had weaker positive effects on trout abundance and no effects on salmon abundance (FIG. 3, Table 2). Both sculpin fish and salmon, but not trout, abundances decreased with altitude (FIG. 3, Table 2).

Local-scale factors especially contributed to explained variation in trout and salmon abundances. Stream width was the most important driver, though with opposite effects; trout was more abundant in smaller streams, while salmon in larger streams (FIG. 3, Table 2). All three studied species preferred shallower areas, with trout showing the strongest effect size of maximum depth (preferred over average depth according to the overall model fit: AIC = … vs …, FIG. 3, Table 2). Stream bed slope had weak positive and negative effects on trout and sculpin fish abundances respectively, while water velocity moderately increased salmon abundance. Trout was the only species affected by substrate type, with higher abundances associated to finer sediments (FIG. 3, Table 2). Abundances of predators such as burbot and pike only affected trout population (negative effects), while no evidence of competitive interactions between brown trout, salmon, sculpin fish, grayling and brook trout was found (FIG. 3, Table 2). Temporal variation had overall little bearing on our models, which revealed a slight seasonal decrease of salmon and trout abundances, and an average year-to-year increase of salmon abundance (FIG. 3, Table 2). No significant effects of interactions (see hypotheses) was found.

Woody debris appeared to benefit trout but not salmon and sculpin fish populations (FIG. 3, Table 2). The abundance of woody debris strongly decreased with stream width, and to a lesser extent with depth, while it slightly increased with stream bed slope and water velocity (FIG. 3, Table 2). Forest coverage, which gave a better overall fit than forest volume (AIC = … vs ..), boosted the number of woody debris, which instead lessened with forest age (FIG. 3, Table 2). Average air temperature and altitude showed moderate negative effects on woody debris abundances (FIG. 3, Table 2). These results, together with the evidence presented above, suggest that many of the large- and local-scale factors considered affected trout abundance both directly and indirectly, i.e. by controlling woody debris abundance.

**DISCUSSION**

Our analyses of data from more than 3000 rivers across Sweden showed that (1) the importance of large-scale, local-scale, and biotic factors for fish abundances in streams varies strongly with species, and that (2) environmental drivers that control the abundance of woody debris can ultimately affect fish, i.e. trout, populations./ (2)Woody debris benefitted trout but not sculpin or salmon population and (3) woody debris abundances depended on … which therefore had an indirect effect on trout populations

We found that large-scale factors, i.e. average air temperature and latitude, had larger weight than local-scale factors on sculpin fish populations, while local conditions such as stream width and depth were the stronger predictors of trout and salmon abundance. Sculpin fish abundance were higher in the Northern part of Sweden, where temperature are on average lower, and at lower altitude (i.e. closer to the sea), in line with existing literature (REF). Among the local-scale drivers, only stream slope and width had weak negative effects on sculpin fish abundance. On the opposite/In contrast/Meanwhile, salmonids appeared to respond promptly to variations in local conditions. Both trout and salmon preferred shallow environments, which likely provide refuge from predation to juveniles (REF), however trout were more abundant in smaller streams and salmon in larger streams (as also shown by…REF). In line with current knowledge (REF), trout abundance increased with stream slope and coarser bottom sediment, and salmon abundance correlated positively with water velocity. Such fine scale habitat use of trout and salmon, contrasted to the evidence of the importance of large-scale factors for sculpin fish abundance, suggests that salmonids may undergo higher interspecific competition and/or predation pressure than sculpin fish. The fact that we did not find any indication of competitive interactions affecting trout or salmon would rather confirm that niche separation is a successful evolutionary strategy.

1. Our analyses showed that many environmental factors, by determining the abundance of woody debris, indirectly affected fish populations. Woody debris had beneficial effects on trout, and its abundance and persistence depended on local conditions such as stream width, slope and depth, as well as large-scale variables such as forest age and cover, altitude, and mean air temperature. This indicates that local and large scale factors can affect fish population through both direct and an indirect effects mediated by woody debris. Discuss factors, i.e. temperature, that had contrasting direct and indirect effects on fish. Discuss factors that have only indirect effect on fish – implication for management
2. Woody debris, a tool often used in restoration programs, had beneficial effects on trout, but not salmon or sculpin fish populations. Discuss in light of previous evidence. Consider factors affecting woody debris abundance and discuss implications for management, i.e. what species will benefit, what conditions make it a useful tool for restoration (smaller shallower streams..)
3. On a more conceptual ecological level: Fine scale habitat use for trout and salmon may indicate higher competition: By looking at data it seems like Cottus distribution is mainly determined by large scale factors, while salmonids respond promptly to variation in local conditions. As large-scale drivers typically define the fundamental niche of species, while small-scale factors define the applied niche of species, our results suggest that salmonids may undergo higher competition/predation pressure than Cottus.
4. Discuss potential flaws in the analyses: the presence of feedbacks or misspecification of directions of causal links. Woody debris can potentially influence many abiotics, such as depth and width by creating pools. However our link is negative, which exclude the possibility that causation goes from woody debris to such variables.
5. Maybe paragraph on biotic interactions, our evidence agfaiunst current evidence
6. conclusions

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TABLES

Table 1. Variables included in the path analyses. Means, standard deviations and variable types are given.

Table 2. Path coefficients from the best-supported structural equation models for trout, salmon and sculpin fish abundance (Figure 3).



FIGURES

Fig. 1. Schematic representation of all variables and paths included in the models. Interactive effects are not shown. Average and maximum depth were considered in separate models. White and grey boxes indicate exogenous and endogenous variables, respectively. Type of migration was included only in models for trout abundance.

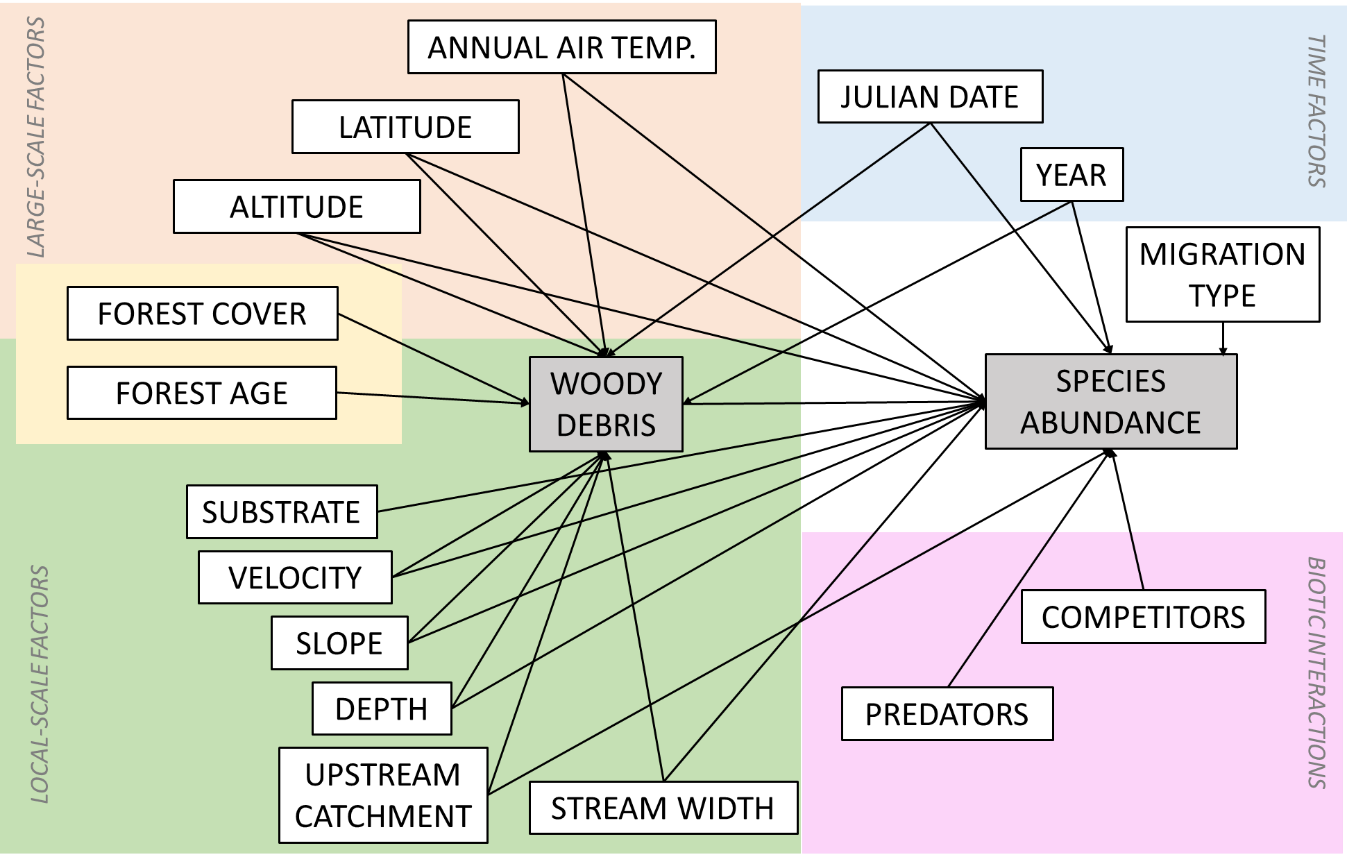


Fig. 2. Maps showing abundances of trout (A), salmon (B), sculpin fish (C) and woody debris (D) as averages over the years and rivers within 25×25km squares.

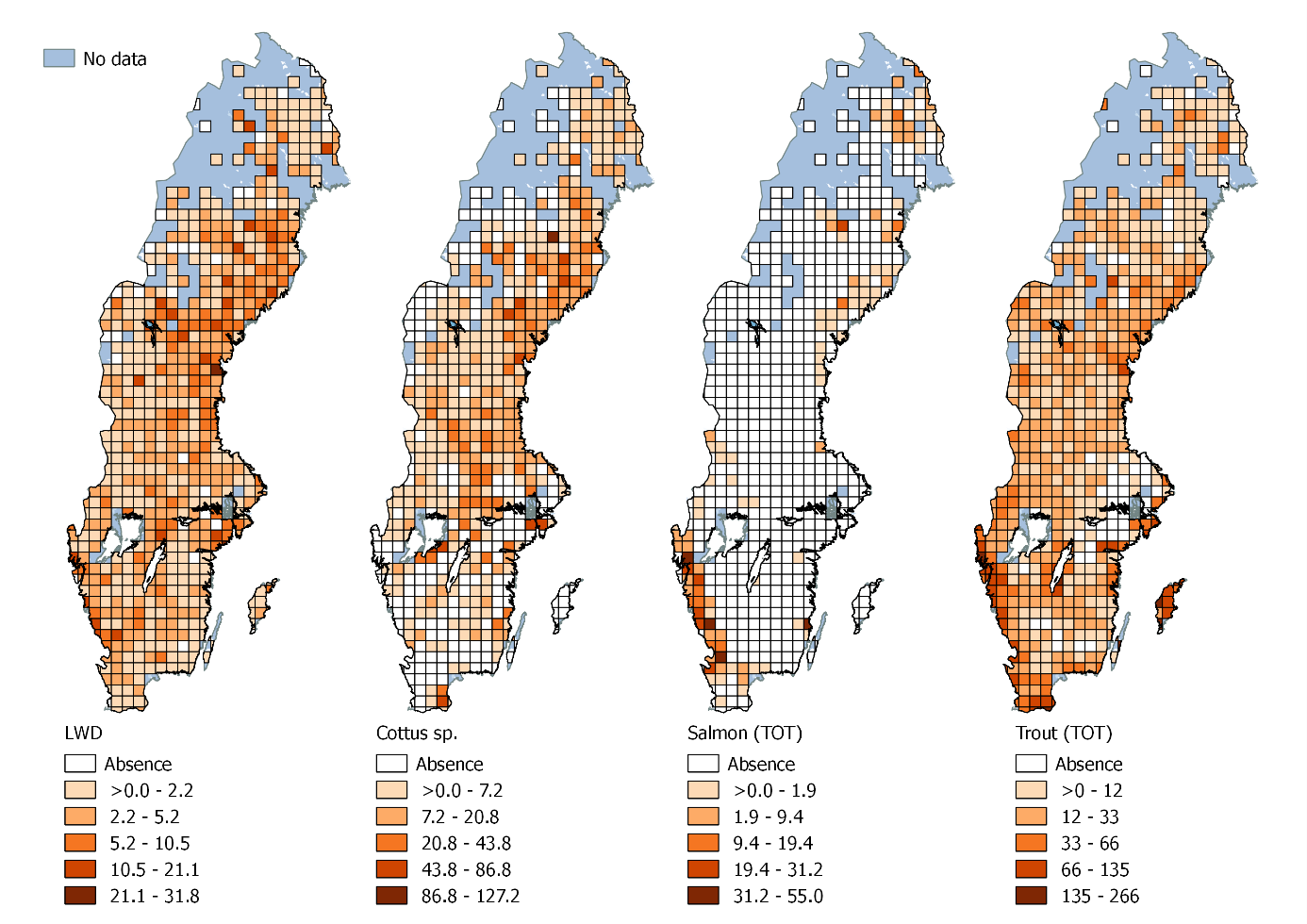


Fig. 3. Best-supported structural equation models representing significant relationships between all predictors and abundances of trout (A), salmon (B), and sculpin fish (C). Blue arrows indicate positive effects while red arrows indicate negative effects. Arrow widths are proportional to the standardized path coefficients. Conditional and marginal R2 values are shown for endogenous variables.

