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TITLE

Country-wide analysis of large wood as a driver of fish abundance in Swedish streams: who benefits and where?

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ABSTRACT

1. Rivers are heavily affected by anthropogenic impacts that threaten many fish species. Among restoration measures, the addition of large wood (LW) in streams has been showed to increase fish abundance. However, what species benefit from LW, to what extent relative to other drivers, and what factors influence LW quantity is not clear, which limits our ability to use LW as an effective restoration measure.
2. Here, time series (from 1993 to 2016) of electrofishing data including 3641 streams across Sweden were used to investigate 1) beneficial effects of LW on the abundance of juvenile brown trout *Salmo trutta*, juvenile Atlantic salmon *S. salar*, and juvenile and adult sculpins *Cottus gobio* and *C. poecilopus*, while accounting for other abiotic and biotic factors, and 2) the drivers of LW abundance at country-wide scale.
3. LW benefitted brown trout, and the effects were larger with decreasing shaded stream surface. LW effects were comparable in magnitude to the positive effects of average annual air temperature and the negative effects of stream depth and predator abundance, factors whose influence was second only to the negative effects of stream width. LW did not benefit salmon abundance, which correlated positively with stream width and negatively with altitude, nor did it benefit sculpin abundances, which mainly decreased with annual average air temperature and altitude.
4. The quantity of LW strongly diminished with stream width, and, to a lesser extent, with stream depth, altitude, annual average air temperature and forest age, while it increased with stream velocity, slope and forest cover.
5. The results suggest that LW can be used as an effective restoration tool for brown trout in shallow and narrow streams, especially in areas with little shade. Here, the addition of large wood could help alleviate the impacts of forest clearance and climate change.

Keywords: *Cottus gobio*, *Cottus poecilopus*, path analysis, river restoration, *Salmo salar*, *Salmo trutta*

1. INTRODUCTION

Riverine ecosystems support rich and endemic biota, and provide vital resources for humans, yet they are directly threatened by an increasing number of human activities (Strayer & Dudgeon, 2010; Vörösmarty et al., 2010). Habitat loss and degradation are classified as the third major stressor to freshwater fish, imperiling ca 40% of freshwater fish species globally (Arthington, Dulvy, Gladstone, & Winfield, 2016). This makes conservation and restoration of riverine and freshwater ecosystems a high priority for society.

In streams and rivers, the occurrence of fully or partially submerged large wood (LW) supplied by riparian forests plays an important role for the biota by affecting ecological, hydro-morphological and biogeochemical processes. LW constitutes the substrate for plants and invertebrates that are food for many aquatic organisms (Benke, Henry, Gillespie, & Hunter, 1985; Cashman, Pilotto, Harvey, Wharton, & Pusch, 2016). It also provides refuges to fish from predators and elevated flow, and substrate for spawning and feeding (Crook & Robertson, 1999; Degerman, Sers, Törnblom, & Angelstam, 2004; Dolloff & Warren, 2003; Sievers, Hale, & Morrongiello, 2017). Besides stabilizing stream banks and channels (Collins, Montgomery, Fetherston, & Abbe, 2012; Gregory & Davis, 1992; Gurnell, Tockner, Edwards, & Petts, 2005), LW increases habitat diversity by generating scour pools in areas of flow convergence and sediment deposition within jams (Harvey, Henshaw, Parker, & Sayer, 2018; Montgomery, Buffington, Smith, Schmidt, & Pess, 1995). Such increase in deposition of fine sediments and debris promotes microbiological activity and nutrient uptake, as well as the development of vegetated ledges, which further contribute to nutrient attenuation and habitat diversity (Krause et al., 2014; Valett, Crenshaw, & Wagner, 2002).

However, despite scientific recognition of the beneficial effects of LW on riverine ecosystems, LW often remains an unwanted feature that is thought to disrupt the aesthetic value of riverscapes and enhance the risk of flood damages (Chin et al., 2014; Piégay et al., 2005; Wohl, 2015). This perception partly derives from a long history of management practices in river ecosystems, where LW was deliberately removed from rivers to improve drainage, together with landscape changes and river engineering that decreased quantities of wood in streams over timescales of 1000 years (White, Justice, Kelsey, Mccullough, & Smith, 2017; Wohl, 2015). Furthermore, management policies led to the disappearance or reduction of old highly productive forests in the riparian areas in many countries, which contributes to reduce the supply of LW (Lazdinis & Angelstam, 2005, Valett et al., 2002).

In the last decades, strong focus has been put on the conservation and restoration of water bodies (e.g. Council of the European Communities, 2000), and LW has been increasingly used to improve riverine fish habitats. However, some controversies and knowledge gaps still remain on the use of wood in river restoration (Roni, Beechie, Pess, & Hanson, 2015). For example, beneficial effects of LW are mostly reported for juvenile and adult salmonids, species favored by the public as targets for recreational fishery, while knowledge on the effects of LW on other fish species is lacking (Langford, Langford, & Hawkins, 2012; Roni et al., 2015). Furthermore, most studies investigating the influence of LW have not accounted for other potential drivers of fish abundances, which can undermine the robustness of the results (e.g. Degerman et al., 2004, Langford et al., 2012). In fact, the high spatial and temporal variability in abiotic and biotic factors in riverine ecosystems, together with the strong collinearity among environmental factors, challenge our understanding on the effect size of LW on response variables. Therefore, what species benefit from LW and to what extent relative to other biotic and abiotic drivers is not clear yet. Finally, several knowledge gaps remain on the factors affecting LW abundances and persistence on local and regional scales (Seo, Nakamura, & Chun, 2010). It is therefore important, for both our ecological understanding and management purposes, to gain a better understanding of the factors affecting LW abundance and persistence to improve our ability to use LW as an effective restoration measure.

In the current study, time series data (from 1993 to 2016) from 3641 rivers (total of ca 9000 sampling sites) across Sweden were analyzed to investigate 1) effects of LW on the abundance of three key freshwater fish taxa: Atlantic salmon *Salmo salar*, brown trout *S. trutta*, and sculpins *Cottus poecilopus* and *C. gobio*, in relation to other abiotic and biotic factors, and 2) drivers of LW quantity at a country-wide scale. We hypothesized that LW has beneficial effects on lotic fish populations, and that the quantity of LW is strongly influenced by climate-related factors, as well as stream and forest attributes (see specific hypotheses in the Methods). Ultimately, the current study aimed at understanding whether and when LW can be a valuable restoration tool. Analyses were performed using path analysis (Grace, 2006), a statistical technique that allows simultaneous evaluation of the relative strength of multiple causal links, while overcoming the problem of collinear explanatory factors that is usually encountered in multiple regression frameworks.

2. METHODS

2.1 Data

The dataset was extracted from the Swedish Electrofishing RegiSter (SERS) and consisted of 33278 electrofishing records from lotic (run-riffle) habitat from 9096 sites in 3641 streams across Sweden. Individual sites were sampled up to twenty times, but at least once between 1993 and 2016. Electrofishing by wading was performed mostly between July and October along sections 45 ± 23 m (mean ± SD) long and spanning the whole width of the stream (5.5 ± 4.3 m, mean ± SD), by using DC-equipment from LUGAB or BIOWAVE (Sweden). All fish were handled according to the national guidelines and returned to the streams alive (Bergquist et al., 2014). The abundance of each fish species was estimated through successive removals according to Bohlin et al. (1989) or from average catch probability of the given species and age class (Degerman & Sers, 1999), and expressed as number per 100 m^2. For the current study abundances of three frequent taxa in lotic habitat were used: Atlantic salmon *Salmo salar*, brown trout *S. trutta*, and sculpins *Cottus gobio* (European bullhead) and *C. poecilopus* (Alpine bullhead). Atlantic salmon and brown trout are the target species for recreational and commercial fishing (e.g. Armstrong et al., 2003), and the European bullhead is protected under the terms of Annex II of the European Union Habitat Directive. Brown trout and Atlantic salmon caught by electrofishing were mostly juveniles (fry and parr), while all age classes were caught for sculpins. While Atlantic salmon is an obligate anadromous species, brown trout can either spend the whole life in the same river or perform migration to the sea or to a lake. As migration can have strong effects on the local abundance and structure of fish populations, brown trout in each site were classified either as migrating (to the sea or to lakes) or resident based on information from regional fisheries officers at the County boards. Type of migration was coded as 0 for resident and 1 for migrating trout for statistical analyses.

On each sampling occasion, stream wetted width (hereafter 'width') and average depth were measured, and the percentage of stream surface shaded from the sun at midday was estimated. The date of fishing was expressed as Julian date (ranging from 1 to 365). The dominating bottom substratum was classified into 5 categories, from 1 to 5, according to increasing particle size (fine: <0.2 mm, sand: 0.2–2 mm, gravel: 2–20 mm, stones: 20–200 mm, boulders: >200 mm) and was point-measured in transects laid out each five meters along the length of the electrofishing site. Water velocity was scored from 1 to 3 with 1 being slow flow (circa <0.2 m/s) and 3 being rapids (broken water surface, velocity above circa 0.7 m/s). Pieces of wood with diameter ≥ 10 cm and length ≥ 50 cm (hereafter large wood; 'LW') were counted individually and given as number per 100 m^2.

For each site, altitude, latitude-longitude, stream bed slope and upstream catchment area were estimated from maps (1:50 000 Terrängkarta, Sweden), and forest data (SLU Forest Map, Dept. of Forest Resource Management, Swedish University of Agricultural Sciences) were extracted in a GIS environment using QGIS 2.14.6. Forest data were collected in 2000, 2005 and 2010, and were paired in the analyses to electrofishing data collected respectively before and during 2000, between 2001 and 2005, and from 2006 onwards. Forest coverage, mean forest age, and total forest volume from 25x25 m squares were averaged over an area of 700 m diameter (ca 150 hectares surface) around each sampling site. Average annual air temperatures between 1961 and 1990 were provided by the Swedish Meteorological and Hydrological Institute (http://www.smhi.se).

2.2 Statistical analyses

Streams rather than sites were considered as replicates to simplify the hierarchical structure of the data. However, the year-to-year variation was retained to investigate changes over time. Hence, averages by streams and year for all variables were calculated. Preliminary data exploration where fish and LW 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 sample-size issues.

Path analyses were used to evaluate 1) potential beneficial effects of LW on the abundance of the taxa after accounting for the effects of other explanatory variables, and 2) drivers of LW abundance at a country-wide scale. Path analyses allow to simultaneously handle many explanatory variables in order to identify the effects of LW, given the extremely high geographical and environmental variation between sampling sites. Also, unlike multiple regression techniques, path analyses can overcome the problem of collinearity between variables by modelling intermediate factors and indirect effects (Grace, 2006). Causal links between variables were modelled based on current empirical and theoretical knowledge (Fig. 1). LW was hypothesized to affect fish abundance and in turn be affected by climate-related factors such as latitude, altitude, and average annual air temperature, forest attributes, such as coverage, age and volume (Dolloff & Warren, 2003; Ekbom, Schroeder, & Larsson, 2006), and stream attributes, such as upstream catchment area, stream width and slope, average depth, and water velocity (Harmon et al., 2004; Ruiz-Villanueva, Díez-Herrero, Ballesteros, & Bodoque, 2014; Seo et al., 2010). All these variables, except forest coverage, age and volume, possibly affect fish distribution (e.g. Armstrong, Kemp, Kennedy, Ladle, & Milner, 2003; Pont, Hugueny, & Oberdorff, 2005; Trigal & Degerman, 2015) and were therefore included as explanatory factors of fish abundance. Furthermore, additional covariates potentially affecting fish abundance were substrate type, percentage of shaded water surface, abundance of predators, i.e. pike and burbot, and competitors, i.e. brook trout (*Salvelinus fontinalis*), European grayling (*Thymallus thymallus*), salmon and sculpins (Degerman, Näslund & Sers, 2000; Louhi, Mäki-Petäys, Huusko, & Muotka, 2014; Näslund, Degerman, & Nordwall, 1997; Öhlund, Nordwall, Degerman, & Eriksson, 2008). Type of migration was included as explanatory factor of trout abundance, and both fish and LW abundances were hypothesized to vary within and between years, therefore year and Julian date were used as covariates. Finally, the model included the effects, on fish abundance, of the interactions between: i) LW and predators, and ii) shaded water surface and LW, as large wood can be especially important as shelter when predator abundance is high or shaded surface is little (Enefalk, Watz, Greenberg, & Bergman, 2017), and iii) competitors and stream depth, and competitors and bed slope, to account for potential stronger habitat partitioning when species occur in sympatry (Degerman et al., 2000).

After formulating the conceptual model, path analysis was used to test the significance of causal links (paths) corresponding to the hypotheses for each fish taxa separately. Models included 21 or 22 exogenous variables (i.e. whose values are not determined by other variables in the model) and 2 endogenous variables (i.e. whose values are assumed to depend on other variables in the model) (Table 1). Due to the hierarchical nature of the data the *piecewiseSEM* package, version 1.1.1 (Lefcheck, 2015) in R 3.2.3 (R Core Team, 2015) was used to construct the path models as sets of hierarchical linear mixed models. Each linear mixed models included a random factor ‘catchment’, and a lag-1 autoregressive correlation structure accounting for repeated measures. Abundances of each fish taxa and LW were log-transformed to attain normal error distribution. Collinearity in each component model was checked by calculating the variance inflation factor (VIF) for each predictor, and a threshold value equal to 2 was used. Annual average air temperature, collinear with latitude, was preferred over the latter as it gave a slightly better overall fit (the differences in AIC values were < 4). For the same reason, stream width was preferred over upstream catchment area, and forest coverage was preferred over forest volume.

Finally, the relative fit of alternative models to the data was compared by using the test of directional separation (Shipley, 2009), which produces a Chi-square distributed Fisher’s C statistic, where P values > 0.05 suggest adequate fit, and by comparing AIC values (Shipley, 2013). For the best-fitting models, standardized path coefficients (scaled by subtracting the minimum and dividing by the difference of the range) were calculated to investigate the relative importance of predictors (Lefcheck, 2015). Marginal and conditional R^2 values for endogenous variables were estimated following Nakagawa and Schielzeth (2013). Model validation was performed visually according to standard procedure (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) by plotting residuals versus fitted values and versus significant explanatory factors, and residual frequency distributions, for each component model.

For both salmon and trout abundances, additional analyses were performed to exclude false zeros caused by the presence of dams that could prevent fish migration. The conceptual model (see above) was tested on a subset of data including only the samples where migrating trout were found and the results were compared to the outcome of the model that used the whole dataset. Although the explained variation in endogenous variables was lower compared to what found when using the whole dataset, the results were very similar (Appendix A).

3. RESULTS

Large wood (LW) benefitted brown trout but not salmon and sculpin abundance (Fig. 2, Table 2). The positive effect of LW abundance on trout abundance was stronger in sites that were less shaded (Fig. 3), as indicated by the significant interaction between LW abundance and percentage of shaded water surface (Table 2). The effects of LW on trout abundance were comparable in magnitude to the positive effects of average annual air temperature and the negative effects of stream depth and burbot abundance. Stream width was the most important driver of brown trout and salmon abundances, though with opposite effects; brown trout was more abundant in smaller streams, while salmon in larger streams (Fig. 2, Table 2). Instead, sculpin abundance was mostly explained by negative effects of average annual air temperature, as also confirmed by the prominent latitudinal gradient in their geographic distributions (Fig. 4). Both sculpin and salmon, but not brown trout abundances decreased with altitude (Fig. 2, Table 2). All three studied taxa preferred shallower areas (Fig. 2, Table 2). Stream bed slope had weak positive and negative effects on brown trout and sculpin abundances respectively, while water velocity moderately increased salmon abundance. Brown trout was the only species affected (negatively) by abundances of predators, i.e. burbot and northern pike, and by substrate type, where higher trout abundance correlated to finer particle sizes (Fig. 2, Table 2). The results did not suggest that competition occurred between any of the studied taxa (Fig. 2, Table 2). Temporal variation had overall little bearing on our models, which revealed a slight seasonal decrease of salmon and brown trout abundances, and an average year-to-year increase of salmon abundance (Fig. 2, Table 2). Except for the effect of the interaction between shaded water surface and LW on trout abundance, no significant effects of other interactive terms (see methods) were found.

The abundance of LW strongly decreased with increasing stream width and altitude, andincreased with increasing stream bed slope. (Fig. 2, Table 2). Forest coverage boosted the quantity of LW, which instead decreased with forest age (Fig. 2, Table 2). Average annual air temperature and stream depth had moderate negative effects on LW abundances, while water velocity had minor positive effects (Fig. 2, Table 2). Also, the abundance of LW increased over time (Fig. 2, Table 2).

The best-supported models fit the data well (brown trout: Fisher's C = 21.50, P = 0.255, salmon: Fisher's C =6.06, P = 0.641, sculpins: Fisher's C =13.81, P = 0.313, Fig. 2). The conditional R squared, which indicates the total explained variation, i.e. including the variation explained by the random factor ‘catchment’, was 0.79 for trout, 0.69 for salmon and 0.82 for sculpin abundances, respectively, and it was 0.52 for large wood (LW) abundance. The marginal R squared, which relates to the variation explained only by the predictors (fixed effects) was 0.21, 0.06 and 0.18 for the three taxa, respectively, and 0.14 for LW. The relatively large differences between conditional and marginal R squared in general indicated strong variation between catchments (Fig. 2).

4. DISCUSSION

The analyses of data from more than 3000 streams across Sweden showed that (1) large wood (LW) benefitted brown trout, and the effects were stronger in sites that were less shaded, and (2) the amount of LW in the streams mainly depended on stream and forest attributes, as well as altitude and average annual air temperature.

LW had positive effects on brown trout, but not on Atlantic salmon or sculpin abundances. The results of the current study apparently contrast with those from a meta-analysis showing an average increase in Atlantic salmon density of more than 200% after large wood placement in streams (Roni et al., 2015; Whiteway, Biron, Zimmermann, Venter, & Grant, 2010). However, ths study uses correlations from field data. Atlantic salmon typically inhabit large (wide) streams, where the amount of LW is generally low. Therefore, it cannot be ruled out that the natural quantities of LW in salmon-inhabited sites were generally too low to result in a significant effect on salmon abundance, or that other environmental factors were more important in explaining the variation in salmon abundance at such large scales, thus hiding beneficial effects of LW. Also, the outcome of restoration measures is context dependent (Roni, Hanson, & Beechie, 2008), and while the current study conducted at a country-wide scale do not show effects of LW on Atlantic salmon at such a large scale, local and regional factors may result in different site-specific outcomes. On the other hand, the results confirm previous findings that sculpins are not favored by LW (Trigal & Degerman, 2015). While LW often accumulate at the stream surface (Inoue & Nunokawa, 2005), sculpins are strictly benthic species that lack swim-bladder and use cavities underneath stones in hard bottom substrates for spawning (Knaepkens, Bruyndoncx, Coeck, & Eens, 2004). Overall, the results warn about the general effectiveness of LW as a restoration tool for different species of fish.

LW can benefit fish populations via several mechanisms, i.e. by increasing habitat diversity, by providing spawning substrate, food, cover from predators and competitors, and refuge from water flow that allow the fish to minimize their energetic costs (Crook & Robertson, 1999; Dolloff & Warren, 2003; Harmon et al., 2004). As fish grow, the relative importance of these mechanisms can shift. For example, the invertebrates that thrive on stream wood constitute an important food source for juvenile fish, while adults mainly benefit from the sheltering effects of large wood (Quist & Guy, 2001). Although the current study cannot provide conclusive evidence on the mechanisms underlying the positive effects of LW on trout, the significant interaction between shaded water surface and LW abundance suggests that large wood plays a key role in the provision of shelter from diurnally active predators, so that beneficial effects are larger in less shaded areas. This is in line with previous experimental evidence of brown trout increasing time spent on the streambed and under stream wood in daylight compared to darkness (Enefalk et al., 2017). In larger rivers, where water surface is often disturbed, this beneficial effect of dead wood is likely less important. Furthermore, the occurrence of LW potentially cool down and buffer the stream temperature (Arrigoni et al., 2008), a variable with a large influence on different life stages of salmonids (Crisp, 1996), and such effect can be especially important in the absence of shade provided by riparian vegetation (Malcolm, Hannah, Donaghy, Soulsby, & Youngson, 2004). From a management perspective, this implies that large wood could be used to buffer the negative effects on fish associated to forest clearance along streams (Allan, 2004). Also, the addition of large wood in streams, possibly together with other restoration measures, has the potential to mitigate climate change impacts under warmer climate scenarios (Justice, White, McCullough, Graves, & Blanchard, 2017; Turschwell et al., 2017).

The analyses highlight several environmental factors that control the abundance of LW at a country-wide scale. LW was found less frequently in larger and deeper streams compared to smaller streams. Previous studies show that LW interact with the beds and banks in smaller streams, and is therefore more likely to be retained, while the occurrence of LW in larger streams is minimized because of the lower wood piece-length to channel-width ratio and the higher stream power (Marcus, Marston, Colvard, & Gray, 2002; Seo & Nakamura, 2009). However, this pattern is probably partly due to long-term changes in the riparian landscape, and past and current land use practices, for example the removal of wood from large streams to prevent flood damages (Anlauf et al., 2011; Montgomery et al., 1995; White et al., 2017;

Wohl, 2018). LW abundance also increased with forest cover (as in Paula, Ferraz, Gerhard, Vettorazzi, & Ferreira, 2011), and declined with average annual air temperature, likely because of the slower decay rate of conifer species (*Pinus sylvestris* and *Picea abies*), which dominated at lower temperatures (Ekbom et al., 2006), compared to deciduous forest. In contrast to other studies (e.g. Warren et al. 2007), the amount of LW decreased with forest age and altitude. This may be caused by LW being estimated in the current study as number of pieces rather than total volume: old forests as well as forests at higher altitude are dominated by pine (*P. sylvestris*), which typically die standing and form long lasting snags, instead of being snapped in many branches like deciduous trees (Siiltonen, 2001). Hence, estimating abundances potentially underestimate the LW biomass produced in conifer-dominated forests.

Most studies that reported positive responses of fish to LW come from small streams (Roni et al. 2014, Degerman et al. 2004) and have not accounted for the effects of multiple abiotic and biotic drivers on fish abundance. By using data from more than 3000 streams spanning broad gradients in width and depth, and by using path analyses, a statistical technique that is able to solve complex multivariate relationships among interrelated variables, this study brings sound evidence of beneficial effects of LW for brown trout populations, and gives insights into the relative importance of multiple environmental drivers on fish. This knowledge can help refine predictions of the effects of changes in environmental conditions at local and large spatial scales on fish populations, and can aid decisions in conservation and restoration plans for targeted species. For example, the strong preference of brown trout for narrow and shallow streams makes the addition of large wood a useful restoration tool, given the higher probability of retention in smaller than larger streams for wood pieces of equal size. Also, a negative effect of burbot and northern pike was found on brown trout abundance, as observed earlier (Degerman & Sers, 1993), but not on salmon, which utilize fast-flowing waters that are normally devoid of these predators. Both burbot and northern pike are often found in the vicinity of lakes and in lentic habitats (Degerman & Sers, 1994). Hence, restoration efforts focusing on brown trout should take into consideration the occurrence of lakes and lentic habitats in the vicinity of target areas and the potential presence of predators. The results from the present study may thus help to design appropriate restoration measures depending on target species.

Overall, the current study highlights the importance of large wood in sustaining trout populations and its potential to buffer negative effects of loss of riparian vegetation, as well as of a future warmer climate. Furthermore, because land use practices affecting forest attributes and stream morphology have strong impacts on the supply and persistence of LW in streams, they should be the target of restoration and conservation policies at both local and regional spatial scale.

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SUPPLEMENTAL MATERIAL

Appendix A

Results of the best-supported structural equation models for migrating trout and salmon.

TABLES

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

Variables	**Mean**	**SD**	**Variable type**
Latitude (DD)	60.260717	3.028914	exogenous
Altitude (m a.s.l.)	169	157	exogenous
Average annual air temperature (°C)	5	2	exogenous
Stream width (m)	5.5	4.3	exogenous
Stream slope (%)	1.49	1.67	exogenous
Shaded water surface (%)	57.76	25.91	exogenous
Upstream catchment area (squared km)	144.9	1023.7	exogenous
Average depth (m)	0.23	0.11	exogenous
Maximum depth (m)	0.55	0.22	exogenous
Water velocity	2.1	0.5	exogenous
Substrate type	4.1	1.0	exogenous
Forest age (years)	54.80	16.63	exogenous
Forest cover (ha)	102.32	39.29	exogenous
Forest volume (cubic m)	13292.07	7183.10	exogenous
Year	2008	5	exogenous
Julian date	237	27	exogenous
Migration type	0.44	0.50	exogenous
Northern Pike (#/100 squared m)	0.23	0.95	exogenous
Burbot (#/100 squared m)	0.43	2.50	exogenous
European Grayling (#/100 squared m)	0.08	0.88	exogenous
Brook trout (#/100 squared m)	0.46	6.61	exogenous
Atlantic Salmon (#/100 squared m)	2.99	18.94	endogenous or exogenous
Brown trout (#/100 squared m)	30.61	56.80	endogenous or exogenous
Sculpins (#/100 squared m)	8.09	27.54	endogenous or exogenous
LW (#/squared m)	3.77	8.24	endogenous

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

	Unstandardized coefficients		Standardized coefficients		P value
	estimate	**SE**	**estimate**	**SE**	
BROWN TROUT MODEL					
Average annual air temperature -> Trout abundance (log)	0.13	0.02	0.21	0.03	<0.001
Substrate type -> Trout abundance (log)	0.09	0.02	0.04	0.01	0.003
Stream slope -> Trout abundance (log)	0.05	0.02	0.11	0.04	0.001
Average depth -> Trout abundance (log)	-2.03	0.16	-0.23	0.02	<0.001
Stream width -> Trout abundance (log)	-0.09	0.01	-0.43	0.04	<0.001
LW abundance -> Trout abundance (log)	0.24	0.05	0.18	0.04	<0.001
Shade -> Trout abundance (log)	3.E-03	1.E-03	0.03	0.02	0.024
LW abundance * Shade -> Trout abundance (log)	-3.E-03	7.E-04	-0.18	0.06	0.001
Burbot abundance -> Trout abundance (log)	-0.05	0.01	-0.22	0.05	<0.001
Pike abundance -> Trout abundance (log)	-0.08	0.02	-0.09	0.03	0.003
Migration type -> Trout abundance (log)	0.90	0.06	0.12	0.01	<0.001
Julian date -> Trout abundance (log)	-5.E-03	7.E-04	-0.08	0.01	<0.001
Average annual air temperature -> LW abundance (log)	-0.07	0.01	-0.09	0.03	<0.001
Altitude -> LW abundance (log)	-2.E-03	4.E-04	-0.13	0.04	<0.001
Forest cover -> LW abundance (log)	4.E-03	5.E-04	0.10	0.02	<0.001
Forest age -> LW abundance (log)	-5.E-03	1.E-03	-0.10	0.03	<0.001
Water velocity -> LW abundance (log)	0.08	0.02	0.03	1.E-02	<0.001
Stream slope -> LW abundance (log)	0.06	0.01	0.13	3.E-02	<0.001
Average depth -> LW abundance (log)	-0.52	0.11	-0.08	2.E-02	<0.001
Stream width -> LW abundance (log)	-0.06	5.E-03	-0.34	3.E-02	<0.001
Year -> LW abundance (log)	0.02	3.E-03	0.07	1.E-02	<0.001

ATLANTIC SALMON MODEL					
Altitude -> Salmon abundance (log)	-3.E-03	3.E-04	-0.27	0.03	<0.001
Water velocity -> Salmon abundance (log)	0.10	0.02	0.04	0.01	<0.001
Average depth -> Salmon abundance (log)	-0.56	0.12	-0.07	0.02	<0.001
Stream width -> Salmon abundance (log)	0.04	0.01	0.29	0.03	<0.001
Year -> Salmon abundance (log)	0.01	2.E-03	0.04	0.01	<0.001
Julian date -> Salmon abundance (log)	-3.E-03	5.E-04	-0.06	0.01	<0.001
Average annual air temperature -> LW abundance (log)	-0.07	0.01	-0.14	0.02	<0.001
Altitude -> LW abundance (log)	-2.E-03	4.E-04	-0.18	0.03	<0.001
Forest cover -> LW abundance (log)	4.E-03	5.E-04	0.12	0.02	<0.001
Forest age -> LW abundance (log)	-5.E-03	1.E-03	-0.10	0.02	<0.001
Water velocity -> LW abundance (log)	0.08	0.02	0.04	0.01	<0.001
Stream slope -> LW abundance (log)	0.06	0.01	0.12	0.03	<0.001
Average depth -> LW abundance (log)	-0.52	0.11	-0.09	0.02	<0.001
Stream width -> LW abundance (log)	-0.06	5.E-03	-0.37	0.03	<0.001
Year -> LW abundance (log)	0.02	3.E-03	0.05	0.01	<0.001
SCULPINS MODEL					
Average annual air temperature -> Sculpins abundance (log)	-0.32	0.02	-0.43	0.03	<0.001
Altitude -> Sculpins abundance (log)	-4.E-03	5.E-04	-0.25	0.03	<0.001
Average depth -> Sculpins abundance (log)	-0.45	0.10	-0.06	0.01	<0.001
Stream slope -> Sculpins abundance (log)	-0.05	0.01	-0.08	0.03	0.002
Average annual air temperature -> LW abundance (log)	-0.07	0.01	-0.09	0.03	0.002
Altitude -> LW abundance (log)	-2.E-03	4.E-04	-0.14	0.03	<0.001
Forest cover -> LW abundance (log)	4.E-03	5.E-04	0.11	0.02	<0.001
Forest age -> LW abundance (log)	-5.E-03	1.E-03	-0.09	0.03	0.003
Water velocity -> LW abundance (log)	0.08	0.02	0.03	0.01	<0.001
Stream slope -> LW abundance (log)	0.06	0.01	0.13	0.04	<0.001

Average depth -> LW abundance (log)	-0.52	0.11	-0.08	0.02	<0.001
Stream width -> LW abundance (log)	-0.06	5.E-03	-0.33	0.03	<0.001
Year -> LW abundance (log)	0.02	3.E-03	0.07	0.01	<0.001

FIGURE LEGENDS

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

Fig. 2. Best-supported structural equation models representing significant relationships between all predictors and abundances of brown trout (A), Atlantic salmon (B), and sculpins (C). Black arrows indicate positive effects while red arrows indicate negative effects. Arrow widths are proportional to the standardized path coefficients.

Fig. 3. Partial regression plots showing the effects on brown trout abundance (log transformed) of the interaction between percentage of shaded surface and abundance of large wood (log-transformed) after accounting for other significant explanatory factors (see Results). The panels show partial residuals and regression lines at three levels of shaded water surface (low, medium and high), centered respectively around a value of 20, 60 and 90% shaded water surface (corresponding to the 10^{th}, 50^{th} and 90^{th} quantiles respectively).

Fig. 4. Maps showing abundances of brown trout (A), Atlantic salmon (B), sculpins (C) and large wood (D). For illustration purposes, averages of sites and years within 25×25km squares were used.

Fig.1

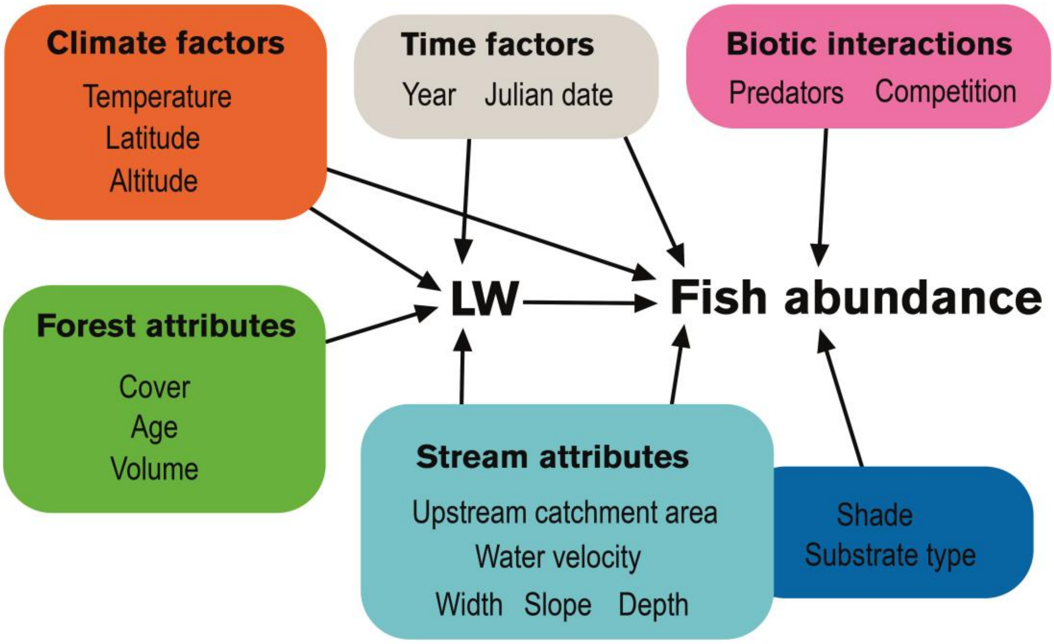

Climate factors
Temperature
Latitude
Altitude
Time factors
Year Julian date
Biotic interactions
Predators Competition
Forest attributes
Cover
Age
Volume
LW
Fish abundance
Stream attributes
Upstream catchment area
Water velocity
Width Slope Depth
Shade
Substrate type

Fig.2

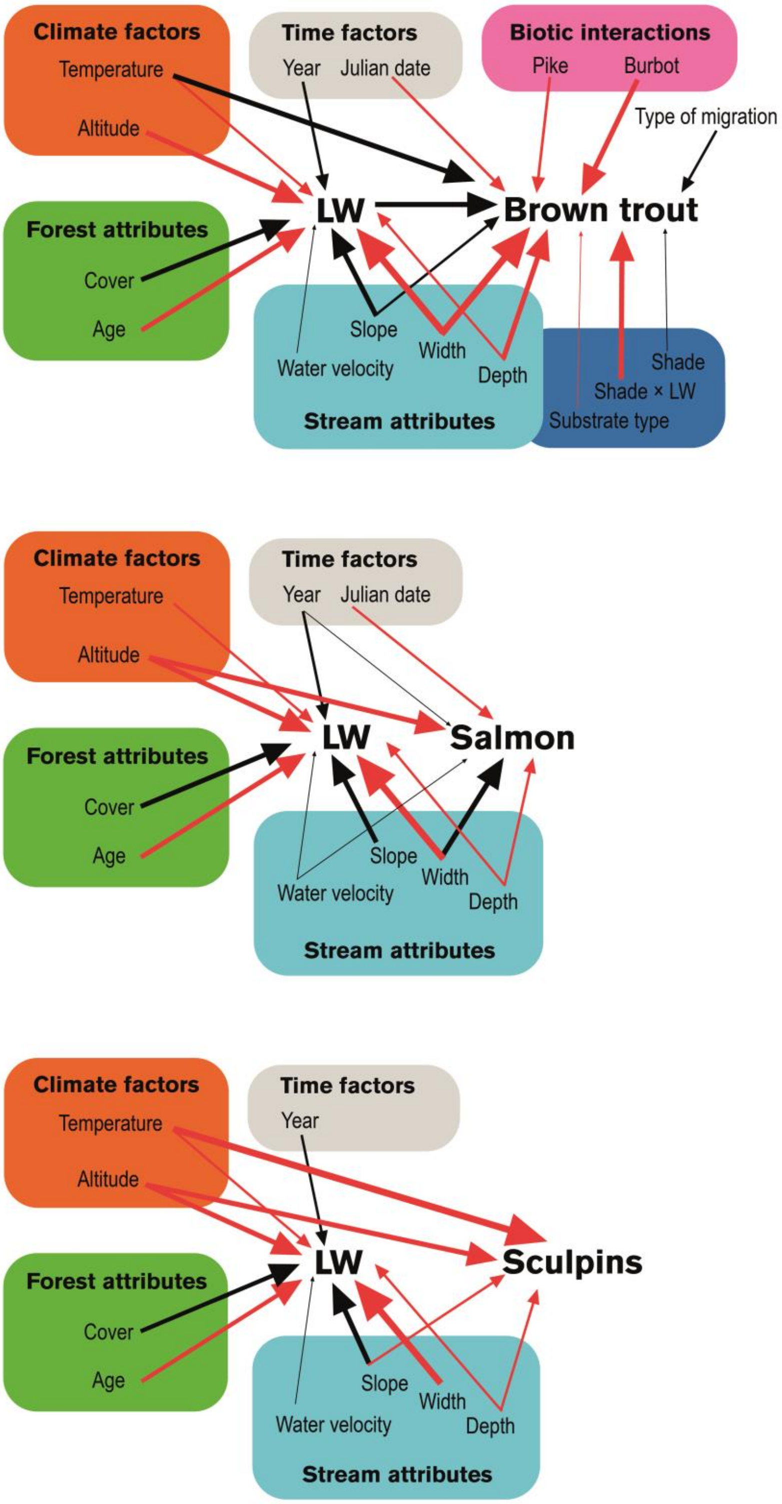
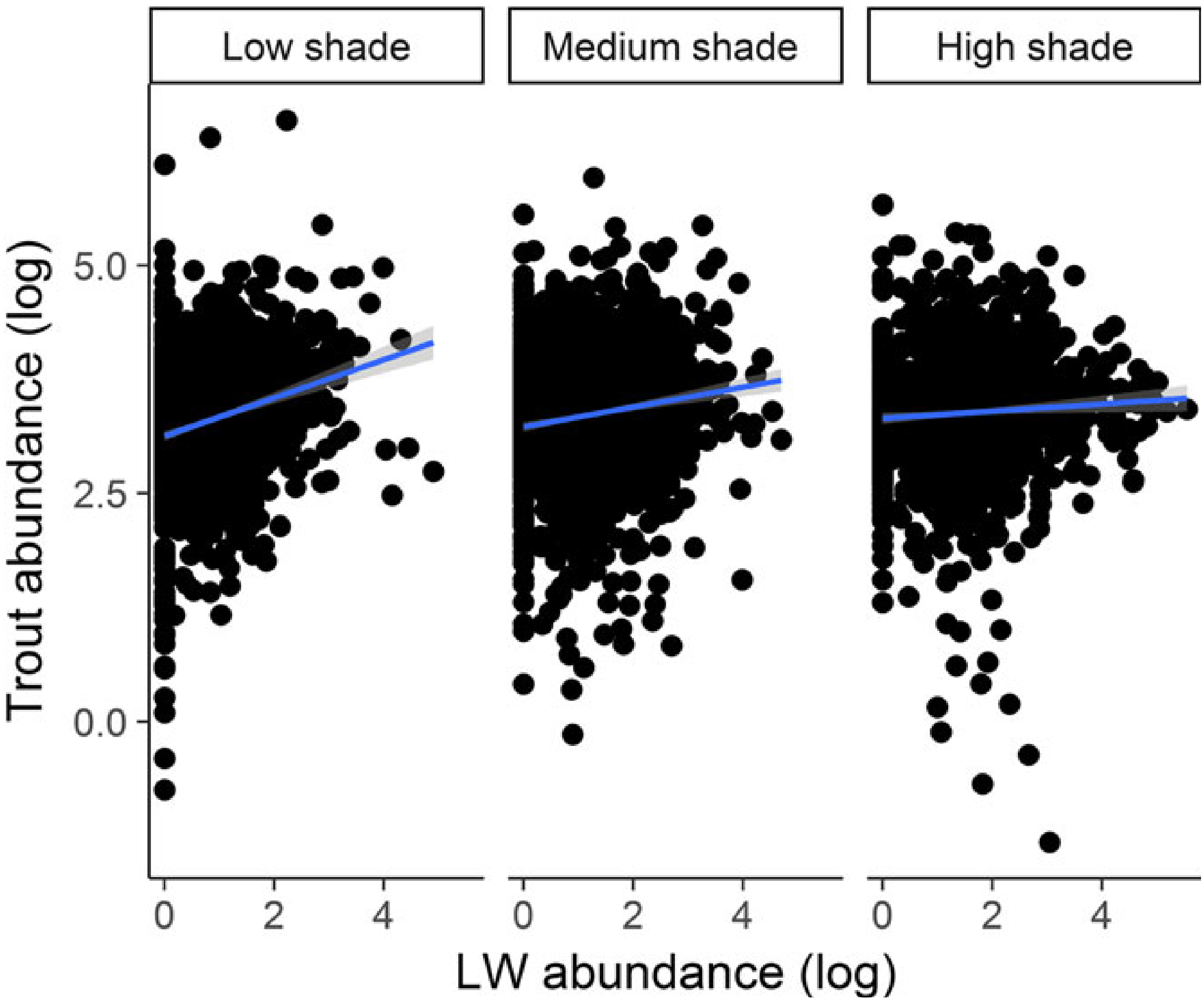
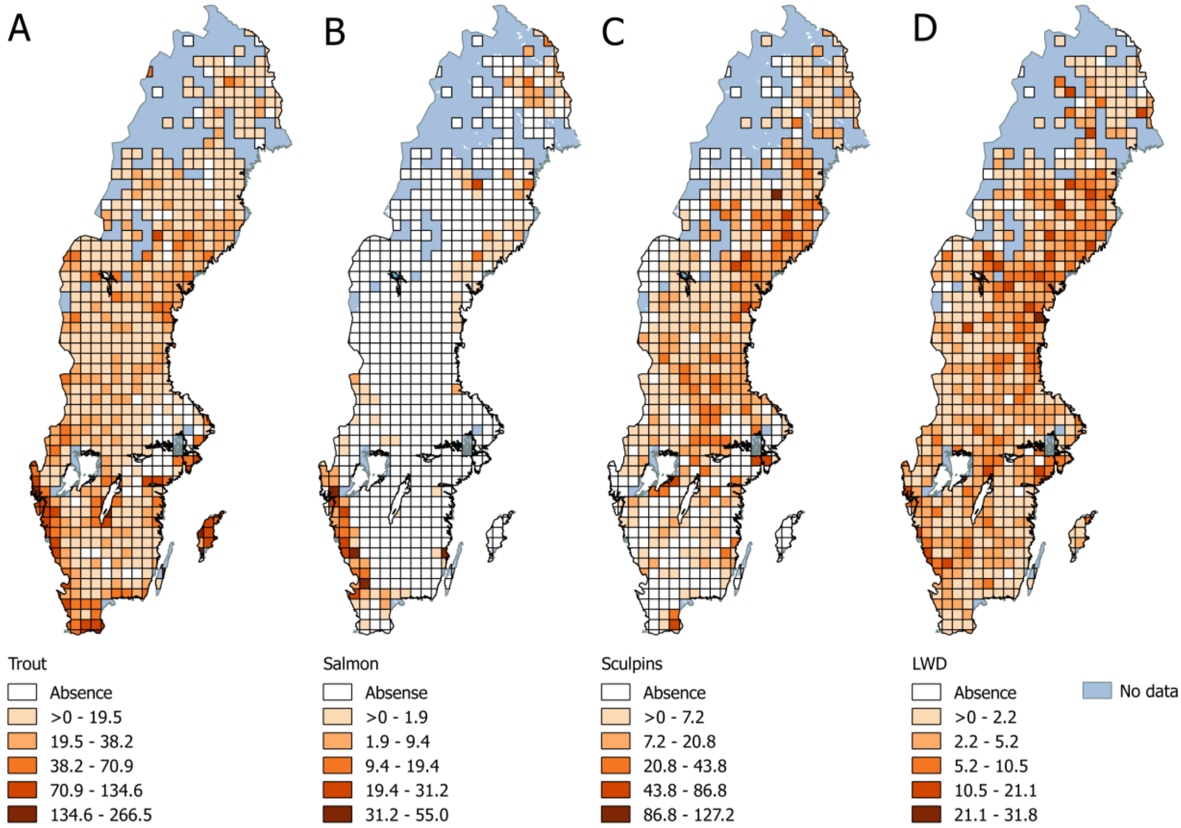

Climate factors
Temperature
Altitude
Time factors
Year
Julian date
Biotic interactions
Pike
Burbot
Type of migration
LW
Brown trout
Forest attributes
Cover
Age
Slope
Width
Water velocity
Depth
Shade
Shade × LW
Substrate type
Stream attributes
Climate factors
Temperature
Altitude
Time factors
Year
Julian date
LW
Salmon
Forest attributes
Cover
Age
Slope
Width
Water velocity
Depth
Stream attributes
Climate factors
Temperature
Altitude
Time factors
Year
LW
Sculpins
Forest attributes
Cover
Age
Slope
Width
Water velocity
Depth
Stream attributes

Fig.3



Low shade
Medium shade
High shade
Trout abundance (log)
5.0
2.5
0.0
0
2
4
LW abundance (log)

583 Fig.4


A
B
C
D
Trout
Absence
>0 - 19.5
19.5 - 38.2
38.2 - 70.9
70.9 - 134.6
134.6 - 266.5
Salmon
Absense
>0 - 1.9
1.9 - 9.4
9.4 - 19.4
19.4 - 31.2
31.2 - 55.0
Sculpins
Absence
>0 - 7.2
7.2 - 20.8
20.8 - 43.8
43.8 - 86.8
86.8 - 127.2
LWD
Absence
>0 - 2.2
2.2 - 5.2
5.2 - 10.5
10.5 - 21.1
21.1 - 31.8
No data

584