

# Biotic resistance in freshwater fish communities

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*Till min familj*



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# List of papers

This thesis is a summary of the following papers that are referred to in the text by their Roman numerals:

- I. **Henriksson, A.**, Yu, J., Wardle, D. A., and Englund, G. 2015. Biotic resistance in freshwater fish communities: species richness, saturation or species identity?  
*Oikos*, 124: 1058-1064.
- II. **Henriksson, A.**, Yu, J., Wardle, D. A., Trygg, J., and Englund, G. Weighted species richness outperforms species richness as predictor of biotic resistance.  
*Ecology*, in press
- III. **Henriksson, A.**, Wardle, D. A., Trygg, J., Diehl, S., and Englund, G. Strong invaders are strong defenders – implications for the resistance of invaded communities.  
*In review for Ecology Letters*
- IV. **Henriksson, A.**, Rydberg, C., and Englund, G. Failed and successful introductions of fish species into 821 Swedish lakes.  
*In review for Ecology*

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# Author contributions

**Paper I:** GE, JY and DAW conceived the study. Data collection and quality control was done by AH. AH performed all analyses with support from GE and JY. AH wrote the first draft of the manuscript. All authors contributed significantly to the revision of the manuscript.

**Paper II:** GE, JY and DAW conceived the study. Data collection and quality control was done by AH. AH performed all analyses with support from GE, JY and JT. AH wrote the majority of the manuscript. All authors contributed significantly to the revision of the manuscript.

**Paper III:** AH, GE and SD conceived the study. AH and GE wrote the first draft of the manuscript. AH and GE collected data. JT assisted in the statistical analyses. AH performed all data analyses. All authors contributed significantly to the revision of the manuscript.

**Paper IV:** Data collection and quality control was done by CR, AH and GE. AH wrote the first draft of the metadata text. All authors contributed significantly to the revision of the metadata text.

**Author abbreviations:** Anna Henriksson (AH), Göran Englund (GE), Jun Yu (JY), David A. Wardle (DAW), Johan Trygg (JT), Sebastian Diehl (SD), and Cecilia Rydberg (CR).

# Abbreviations and glossary

**Abiotic resistance** – The physical environments' ability to repel new invaders.

**Biotic resistance** – The resident species' ability to repel new invaders.

**Complementarity effect** – The more complete use of resources as species richness increases.

**Interaction hierarchy** – A scenario where some species are strong in both the role as an invader and as a resident species while other species are weak in both roles. This creates a negative feedback that will make the biotic resistance grow stronger as new species accumulates in the community.

**Invasion -/introduction -/establishment success** – These are used interchangeably for when a species that has not been present in the habitat before, establishes.

**Invasional meltdown** – The phenomenon named by Simberloff and Van Holle (1999) where facilitative effects between introduced species leads to decreasing biotic resistance as introduced species accumulates in an accelerating manner.

**Invasive species** – A non-native species that causes damage to the invaded habitat.

**O-PLS** – Orthogonal projections to latent structures. The abbreviation PLS stands for projections to latent structures here, which is different from what PLS stands for in PLS-GLR (see below), however, the models are both built upon the same PLS method it is only a change in name. The biggest difference between the two models is that O-PLS can remove variation from X that is not correlated to Y and store the variation that is correlated to Y in just one component (Trygg & Wold 2002). The PLS-GLR is here a logistic model while O-PLS is a linear model.

**Performance traits** – Traits of species that describe their success in their role as an invader and as a resident species.

**PLS-GLR** – Partial least squares generalized linear regression (Bastien et al. 2004). See O-PLS for more information.



**Propagule pressure** –In this thesis it refers to the number of individuals arriving at the same introduction event.

**Sampling effect** – The increased probability of including a species that have a strong effect on the invader as species richness increases.

**Saturation hypothesis** –The hypothesis that biotic resistance is best described by the saturation level of the habitat, i.e., the number of resident species relative to the maximum number of species that the habitat can support.

**Species identity hypothesis** – The hypothesis that one or just a few species can resist invaders on their own, because they are strong competitors with the invader or efficient predators.

**Species richness hypothesis** –The hypothesis that species rich communities are more resistant to invaders than species poor communities. Elton (1958) is often cited as the founder of this hypothesis.

**Weighted species richness** – A novel hypothesis stating that species' different contributions to resistance in terms of strength and sign needs to be accounted for to describe the biotic resistance of a community.

# Sammanfattning

Introduktioner av nya arter i ekologiska samhällen kan medföra stora skador på ekosystemet genom förluster av inhemska arter och ekosystem funktioner. Nya arter kan också medföra stora ekonomiska förluster t.ex. i form av skador på grödor och förlorade ekosystemtjänster. I denna avhandling använder jag data på mer än 1000 lyckade och misslyckade introduktioner av fisk i svenska sjöar för att testa hypoteser kring biotisk resistens. Biotisk resistens är det residenta samhällets förmåga att förhindra att nya arter etablerar sig, antingen genom stark konkurrens mellan de residenta arterna och den nya arten eller genom att de residenta arterna prederar på den nya arten. En viktig hypotes inom biotisk resistens är artrikedomshypotesen, den predikterar att ett artrikt samhälle bör ha större resistensförmåga än ett artfattigt då fler arter kan använda upp en större andel av resurserna. Hypotesen har inte så stort stöd i empiriska studier och ett viktigt skäl är att den förutsätter att alla arter bidrar till resistensen lika mycket och att alla har en negativ påverkan på den nya artens förmåga att etablera sig. I denna avhandling presenteras en ny metod att estimerar artrikedom på som bättre återspeglar samhällets resistensförmåga. Metoden, som vi kallar viktad artrikedom, tar hänsyn till att residenta arter bidrar med olika styrka till resistensen, men också att arter inte bara har en negativ påverkan på etableringen av den nya arten utan också kan ha en positiv påverkan. Våra resultat visar att denna metod att estimerar resistensförmåga predikterar introduktionsframgång bättre än klassisk artrikedom. Detta innebär att de specifika interaktionerna de residenta arterna har med den nya arten bestämmer utgången av introduktionen.

Vidare utforskar vi hur resistensen i ett ekologiskt samhälle utvecklas över tid genom att analysera arters prestation i rollen som den invaderande arten och den residenta arten. Olika scenarier har olika betydelse för resistensen, till exempel om arters förmåga att etablera sig är stark men deras förmåga att stå emot nya arter är låg kommer resistensen att minska över tid. Om istället arter med god etableringsförmåga också bidrar mycket till att stå emot etableringen av nya arter, så kommer resistensen att byggas upp över tid. Vi fann att arters etableringsförmåga och resistensförmåga korrelerar positivt. Vi fann också att arter med låg resistensförmåga och etableringsförmåga är känsligast för utrotning när nya arter etablerar sig. Detta har betydelse för naturvården: Samhällen som består av svaga arter är mer känsliga för etablering av nya arter samt är svårare att återintroducera när de är förlorade. Våra resultat visar också att resistensen kommer att byggas upp över tid genom att de arter som har lättast för att etablera sig också bidrar mest till resistensen mot andra arter.

# Abstract

Invasions of non-native species cause problems in ecosystems worldwide, and despite the extensive effort that has been put into research about invasions, we still lack a good understanding for why some, but not other, communities resist these invasions. In this doctoral thesis I test hypotheses on biotic resistance using a large dataset of more than 1000 both failed and successful introductions of freshwater fish into Swedish lakes. We have found that the classic species richness hypothesis is a poor descriptor of introduction success because it fails to acknowledge that resident species contribute to the resistance in different ways. We developed a new measure of biotic resistance, the weighted species richness, which takes into account that the resident species contributes to the resistance with different strength and sign. Further, we correlated performance traits of species in their role as an invader and as a resident species to predict how the biotic resistance of these communities would develop over time. We found a positive correlation between performance traits: Some species have high introduction success, they make a large contribution to the resistance, and they cause extinctions when introduced but do not go extinct themselves when other species establishes, whereas other species are weak performers in these respects. Thus, the biotic resistance of these communities should grow stronger as non-native species accumulates. These results give us clues about what type of communities that should be most sensitive to further invasions, i.e., communities harboring species weak performers.

My results show that the biotic resistance of communities is an important factor in determining invasibility of a community. They also show that methods for quantifying resistance must take into account how interactions are structured in nature. What determine the biotic resistance of a community is the type of interactions that the resident species have with the invader and not the species richness of the community.

**Key words:** biotic resistance; freshwater fish; introductions; invasions; invasion success; invasibility; invasiveness; species richness; saturation; species identity; weighted species richness

# Introduction

Invasions of non-native species are considered a major threat to ecosystems through both biodiversity loss and loss of ecological functions (Clavero & García-Berthou 2005, Ehrenfeld 2010, Simberloff *et al.* 2013). Newly established species have caused the extinction of many animal species world-wide (Clavero & García-Berthou 2005) and has altered ecosystem functions (Ehrenfeld 2010, Simberloff *et al.* 2013). By studying invasions registered in the IUCN red list, Clavero and García-Berthou (2005) found that 54 % of the analyzed extinctions were partly caused by invasive species and that 20 % of the extinctions were caused by invasive species alone. Invasive species are the leading cause of bird extinctions and the second leading cause for extinctions of fish and mammals (Clavero & García-Berthou 2005). Invasive plant species have been reported to cause few extinctions of native plants (Gilbert & Levine 2013). However, there could be a time lag of hundreds of years from the invasion event to the actual extinction event and thus the full impact of plant invasions might not be observable yet (Gilbert & Levine 2013). The spread of invasive species does not only have strong ecological impact, it also costs billions of dollars and euros every year (Pimentel *et al.* 2005, Kettunen *et al.* 2008). The costs can be divided into two categories; cost of damage and cost of control. The cost of damage, which is the larger of the two categories, results mostly from the spread of non-native pests (e.g. plant diseases and insects) (Kettunen *et al.* 2008).

The majority of the problems are believed to be caused by humans due to both deliberate and accidental spread of non-native species. Invasive species can be spread accidentally with ballast water, as contaminants among crop seeds, by seeds attached to motor vehicles or shoes, or as a result of the trade with pets and garden plants. However, many introductions have been deliberate such as fish, crop species and livestock (Hodkinson & Thomsen 1997, Mack *et al.* 2000).

One of the major objectives in invasion biology is to understand why some ecosystems can resist the invasion of non-native species while others cannot (Fridley *et al.* 2007). An ecosystem can be resistant to invasions both due to abiotic limitations of the invader and biotic interactions with the resident species (D'Antonio *et al.* 2002, Shea & Chesson 2002). Abiotic factors can slow the process of an invasion or even restrict an invader completely if the physical environment is outside of the invaders tolerance limit (D'Antonio *et al.* 2001). The biotic factors can prevent new invaders to establish due to strong competition over similar resources or due to predation on the invader (Shea & Chesson 2002, Kennedy *et al.* 2002, DeRivera *et al.* 2005). In this

thesis the major focus is on biotic resistance, and I used introduction data on freshwater fish to test established hypotheses as well as novel hypotheses on biotic resistance.

### **Biotic resistance and invasion success**

Charles Elton, often acknowledged as the father of invasion biology, is attributed the classic hypothesis that states that more species rich communities should be better at resisting invasions (hereafter called the species richness hypothesis). In his book *'The Ecology of Invasions by Animals and Plants'* from 1958 he sets out examples of how small islands are vulnerable to invasions and how the species rich tropical forests are relatively stable, he writes on page 145: "...the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones; that is, more subject to destructive oscillations in populations, especially of animals, and more vulnerable to invasions". The underlying idea is that more species-rich communities can use up resources more completely in both space and time, leaving little niche space for new invaders (Elton 1958, Case 1990, Kennedy et al. 2002), this is sometimes referred to as a complementarity effect (Fargione & Tilman 2005, Hooper & Dukes 2010). The idea seems to be based on the assumption that competition is the only important interaction structuring biotic resistance, which might be due to that plants have been the main study organism within the field (Pyšek et al. 2008). Except for the complementarity effect, support for the hypothesis can also be due to a sampling effect which is the increased probability to include a species with a strong effect on the invader with increasing species richness (Huston 1997, Fargione & Tilman 2005, Hooper & Dukes 2010, Oakley & Knox 2013). The species richness hypothesis is one of the most tested hypotheses within invasion biology (Lowry et al. 2013) and has support in small-scale experiments, particularly in plant communities (Levine et al. 2002, Kennedy et al. 2002, Mwangi et al. 2007). However, the support from studies of invasions is rather weak (Jeschke et al. 2012). Thus, there is a disagreement between the popularity of the hypothesis and the support for it. In paper **I** and **II** we examined the species richness hypothesis and modified the hypothesis to better fit empirical data by testing alternative hypotheses.

As a first alternative hypothesis we postulated that biotic resistance is best described by the saturation of the habitat, i.e., the number of species present relative to the maximum number of species that the habitat can support. Saturation should be a more accurate description of a communities' resistance because the amount of species that can be supported vary widely between habitats of different size, productivity and spatiotemporal heterogeneity (Kohn & Walsh 1994, Davies et al. 2007). In the second alternative

hypothesis, the species identity hypothesis, we considered individual species' contributions to resistance and asked whether one species alone can resist invasions better than the total richness of the community. Single resident species can effectively reduce invader success both through predation and competition (DeRivera et al. 2005, Emery & Gross 2006, Dzialowski 2010).

The third alternative hypothesis was developed within this thesis. In the original species richness hypothesis, it is implicitly assumed that all resident species have a similarly strong and negative effect on the invader. However, communities are typically structured by a mixture of negative and positive interactions, including competition, predation and facilitation (Stachowicz 2001, Chase et al. 2002). Species interactions are also known to be of different strength in nature (Wootton & Emmerson 2005). Therefore, we postulated in paper **II** that the invasibility of a community is best described by a weighted sum of all resident species where the weights are of different strength and sign depending on the type of interaction the resident species have with the invader. We termed this hypothesis the weighted species richness hypothesis.

### **Biotic resistance and performance traits**

In paper **III** we investigated whether the establishment of new species makes communities more vulnerable to further invasions or if they become increasingly resistant to additional invaders (Simberloff & Von Holle 1999, Collin & Johnson 2014). By studying how performance traits of invaders and resident species correlate we can predict how biotic resistance of invaded communities develops over time. The performance traits we used were: (1) invasion success - the ability to establish successfully, (2) impact - the ability to cause extinctions of residents, (3) defense capacity - the contribution to resistance of the resident community to invasion, and (4) persistence - a resident's ability to persist and maintain high population densities after the establishment of invaders.

Different scenarios of how the biotic resistance of communities will develop can be linked to patterns of correlation between invader performance and resident performance. If they are positively correlated then the biotic resistance should grow stronger over time, since the successful invaders also will contribute strongly to the future resistance. These communities would then be structured as an interaction hierarchy (Shipley 1993; Shipley & Keddy 1994), where some species are good in all respects – they are good at invading, they cause extinctions, are strong defenders and are persistent. However, if the correlation is negative then the resistance of the community should erode with time as weak defenders will establish. The scenario where

the biotic resistance of invaded communities decrease as species establishes has been termed an invasional meltdown, which has been described by Simberloff & Von Holle (1999). Other scenarios includes Darwin's naturalization hypothesis, where he proposes that closely related species will compete more with each other than more distant species and thus invading congeners of the resident species will be less likely to establish (Darwin 1859). Hence, it predicts that successful invaders will have little niche overlap with residents, which implies that high invasion success is associated with low impact on resident species (Ricciardi et al. 2013). The species richness hypothesis, which is based on the assumption that all resident species makes the same contribution to resistance (paper **II**), will hence predict that there is no correlation between invader performance traits and resident performance traits.

## Objectives

This thesis consists of four papers with the overall objective to gain better understanding of the contribution of resident species to the resistance of invading species. Data on freshwater fish introductions into Swedish lakes are used to test established hypotheses within invasion biology and to develop new hypotheses. The objectives of each of the four papers included in this thesis are as follows;

- I.** To investigate whether species richness, saturation or species identity explain the introduction success of Arctic char (*Salvelinus alpinus*) best.
- II.** To further investigate if species richness, saturation or species identity explain the introduction success best for additionally three species. Furthermore, to develop and test a new hypothesis on introduction success, called weighted species richness.
- III.** To investigate the correlation between performance traits of invaders and resident species and the implications it has for the development of biotic resistance in invaded communities.
- IV.** To make the dataset used in the thesis available for other researchers and to discuss benefits and limitations of the dataset.

# Abstracts of the papers

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## **Paper I** – *Oikos* (2015) 124: 1058-1064

Biotic resistance in freshwater fish communities: species richness, saturation or species identity?

**Anna Henriksson**, Jun Yu, David A. Wardle and Göran Englund

### **Abstract**

Some communities are susceptible to invasions and some are not. Why? Elton suggested in 1958 that the ability of the community to withstand invading species – its biotic resistance – depends on the number of resident species. Later contributors have emphasized the habitat's ability to support species, as well as the contribution of individual species to the resistance. In this study we use information from 184 introductions of Arctic char into Swedish lakes to study both abiotic and biotic aspects of the resident community's ability to resist introductions. We find that the best model included the proportion of forest cover and the proportion of agricultural land cover in the watershed in combination with the presence versus absence of northern pike. Thus, the most important biotic factor to explain the outcome of introductions of Arctic char is the presence of northern pike, a large piscivore. This means that one single species explains the outcome of the introductions better than does the species richness or the saturation level of the community.

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## **Paper II** – *Ecology*, in press

Weighted species richness outperforms species richness as predictor of biotic resistance

**Anna Henriksson**, Jun Yu, David A. Wardle, Johan Trygg and Göran Englund

### **Abstract**

The species richness hypothesis, which predicts that species-rich communities should be better at resisting invasions than species-poor communities, is one of the most tested hypotheses within invasion biology. However, it has been found to be poorly supported in empirical studies. In this paper we contrast the species richness hypothesis with four alternative hypotheses with the aim of finding better descriptors of the relationship between invasion resistance and community composition. The four alternative hypotheses states that a community's resistance to invasions is determined; by abiotic conditions, by community saturation, i.e., the number of resident species relative to the maximum number of species that can be supported, by the presence/absence of key species, or by weighted species richness. The weighted species richness is a weighted sum of the number of species, where each species' weight describes its contribution to resistance. We tested these hypotheses using data on the success of 571 introductions of four freshwater fish species into lakes throughout Sweden (i.e., Arctic char (*Salvelinus alpinus*), tench (*Tinca tinca*), zander (*Sander lucioperca*), and whitefish (*Coregonus lavaretus*)). We found that the weighted species richness best predicted invasion success. The weights describing the contribution of each resident species to community resistance varied considerably in both strength and sign. Positive resistance weights, which indicate that species repel invaders, were as common as negative resistance weights, which indicate facilitative interactions. This result can be contrasted with the basic assumption of the original species richness hypothesis, that all resident species have identical and negative effects on invader success. We argue that this assumption is unlikely to be true in natural communities, and thus that we expect that weighted species richness is a better predictor of invader success than the actual number of resident species in most natural communities.

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### **Paper III** – *In review for Ecology Letters*

Strong invaders are strong defenders – implications for the resistance of invaded communities

**Anna Henriksson**, David A. Wardle, Johan Trygg, Sebastian Diehl and Göran Englund

#### **Abstract**

Many ecosystems receive a steady stream of non-native species. How biotic resistance develops over time in these ecosystems will depend on how established invaders contribute to subsequent resistance. If species that are more successful as invaders also have a greater defense capacity, then the resistance of the community to subsequent invasion should build up as species accumulate. In contrast, if successful invaders have weak defense capacity, this resistance would erode with time, as proposed by the invasional meltdown hypothesis. We analyzed 1158 introductions of freshwater fish in Swedish lakes and found that invasion success was positively correlated with defense capacity, thus, some species are both good invaders and good defenders while others are neither. This suggests that these communities will develop stronger resistance to invasions as more invaders establish. These insights about assembly rules can further be used to identify scenarios where invading species are expected to cause large impact.

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### **Paper IV** – *In review for Ecology*

Failed and successful introductions of fish species into 821 Swedish lakes

**Anna Henriksson**, Cecilia Rydberg and Göran Englund

#### **Abstract**

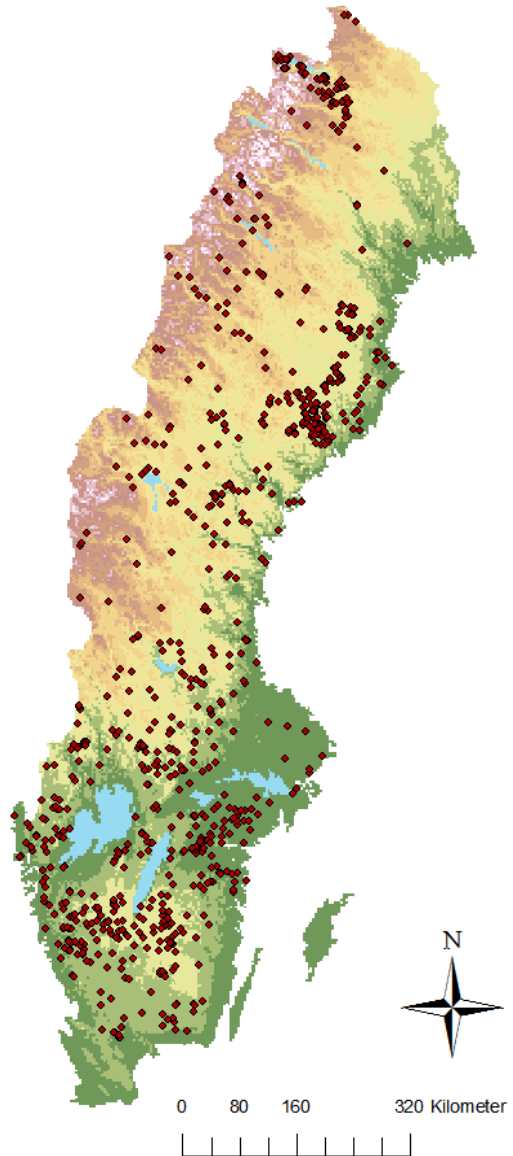
Introductions of fish into lakes can be viewed as whole system experiments, which can be used to study the principles of community assembly and factors determining the outcome of species invasions. Freshwater fish species have been translocated by humans for centuries in Sweden and this activity has been documented by national and regional authorities starting at the end of the 19<sup>th</sup> century. Based on this documentation and additional interviews with local fishermen we have compiled a dataset that includes 1158 introductions of 26 freshwater fish species into 821 Swedish lakes. The data includes both successful and failed introductions; where a successful introduction means that the introduced fish species was present in the lake for  $\geq 20$  years or that reproduction was observed earlier than that. The oldest introduction is from 1658 and the latest from 2002. Additionally, the dataset includes species composition, temperature sum, maximum temperature, lake area, elevation, longitude and latitude for all lakes. This data has been used to test hypotheses about biotic resistance and invasion success in three papers. We found the presence or absence of specific species predicted invasion success better than the species richness of the lakes. We also found that species with high invasion success tend to make a large contribution to biotic resistance, which will make communities more resistant in the future as they are invaded by additional species.

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# Methods

## Dataset and study system

In paper **I**, **II** and **III** we used data from a database that contains occurrence records and introduction data for fish species in Swedish lakes. In paper **IV**, which is a data paper, we present this database. Information about introductions and species compositions was compiled from both published and unpublished surveys made by the Institute of Freshwater Research at the Swedish University of Agricultural Sciences, county administration boards, municipalities, local fishery managers, and the Department of Ecology and Environmental Science at Umeå University. The introduction data that were included met the following criteria: 1) No presence of the introduced species were recorded prior the introduction. 2) There was data available that allowed us to characterize species composition of the lakes. 3) The outcome of the introduction was known. Introductions were considered successful if reproduction was observed or if the species was present at least 20 years after the introduction. They were considered failed if records of the species composition after the introduction did not in-



**Figure 1** Map of the distribution of the data used. *Modified from paper IV.*

clude the introduced species. 4) There were no additional introduction attempts of the species during the establishment period.

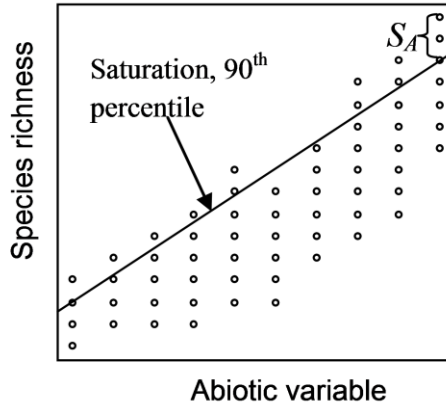
In paper **I** we analyzed 184 introductions of Arctic char (*Salvelinus alpinus*), of which 32% were successful. In paper **II** we included introductions of three species in addition to Arctic char, i.e., 203 introductions of whitefish (*Coregonus lavaretus*, 56% successful), 129 introductions of tench (*Tinca tinca*, 59% successful), and 55 introductions of zander (*Sander lucioperca*, 38% successful). In paper **III** we extended the data even more and used the full database that is presented in paper **IV**. This includes 1158 introductions of a total of 26 different species, 50.2 % of which were successful. This data is distributed from the north to the south of Sweden (Fig. 1).

In paper **III** we correlated introduction success with contribution to resistance for species that had been introduced at least 10 times (13 species). Further, to obtain data on the persistence and the impact of each introduced species, we used extinction data collected from local fishermen and published surveys. This dataset is separate from the data used to estimate invasion success and contribution to resistance. It consists of 118 cases where a species were introduced and another species went extinct following the introduction. Most of this data comes from local fishermen's observations of a native resident species going extinct within few years after the introduction of another species, and a few of these observations comes from standardized gillnet surveys. Since the total number of introductions that the extinction data was based on was unknown we were unable to calculate extinction probabilities. Thus, two binary variables were constructed from this data for each focal species: if extinction of a resident species had been observed after an introduction of the focal species or not, and whether or not the focal species had gone extinct following the introduction of another species.

## **Statistical analyses**

### *Abiotic resistance hypothesis*

In paper **I** and **II** we used abiotic variables to test the effect of abiotic resistance and to compare the importance of abiotic versus biotic factors to explain establishment success. We used a logistic regression model with the outcome of introductions as the response and the following abiotic variables as predictors: maximum temperature, temperature sum, lake area, and land cover data.



**Figure 2** Illustration of how the degree of saturation was quantified. Each point represents an individual lake and the 90<sup>th</sup> percentile represents the species richness at which a lake is saturated. Thus, lakes below the 90<sup>th</sup> percentile are under-saturated with species and lakes above the line are over-saturated with species. The residuals ( $S_A$ ) were used as a measure of the degree of saturation. *Modified from paper II.*

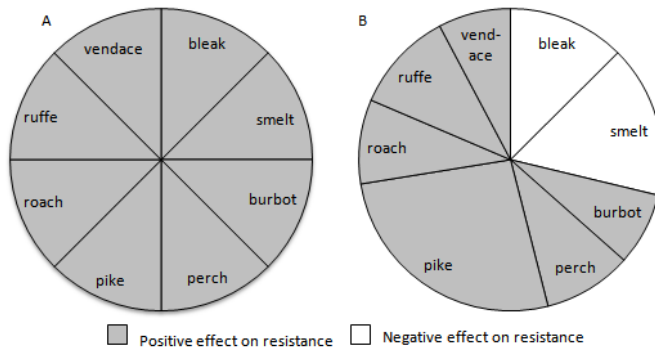
### *Biotic resistance hypotheses*

In paper **I** we tested three hypotheses on biotic resistance: 1) the species richness hypothesis, 2) the saturation hypothesis, and 3) the species identity hypothesis. In paper **II** we also tested 4) the weighted species richness hypothesis. Logistic regression models were used to fit each hypothesis to data on the outcome of the introductions and Akaike's information criterion (AIC) were used to compare the different models. For the saturation model we needed a measure on the degree of saturation of the lakes, which was quantified using quantile regression. We plotted species richness against abiotic variables that we found to best describe species richness and used the residuals from the 90<sup>th</sup> percentile as a measure on saturation level (Fig. 2).

When testing the weighted species richness hypothesis we quantified each species contribution to resistance and summed all contributions as an alternative measure of species richness. We used partial least squares generalized linear regression (PLS-GLR; Bastien et al. 2005, Bertrand et al. 2014) to extract the species contribution to resistance. This measure takes into account that species contribute both with different strength and sign to the resistance. In comparison, the original species richness hypothesis assumes that all species contribute with equal strength and sign to the resistance (Fig. 3).

## Performance traits

In paper **III** we correlated species' introduction success with their contribution to resistance. Introduction success was simply measured as the percent successful introductions. We used orthogonal projections to latent structures (O-PLS) to quantify contribution to resistance (Trygg & Wold 2002). This is a similar method to the PLS-GLR used to quantify the weighted species richness in paper **II**. The main motivation for using the O-PLS is that it partitions the variance in a matrix of predictors into variation that is associated with a response 'Y' and variation that is unrelated to Y. Thus it only produces one interpretable component that we can use to correlate with invasion success, in comparison with the PLS-GLR that produces many interpretable components.



**Figure 3** An example from the lake Ljusnaren where Arctic char has been introduced that illustrates the contribution to resistance for each resident species under the species richness hypothesis (A) and the weighted species richness hypothesis (B). Under the species richness hypothesis all species have an equally strong and positive contribution to resistance. Under the weighted species richness hypothesis species have different effects on resistance both in terms of sign and strength. Positive effect on resistance means that the resident species has a negative effect on the invader, and negative effect on resistance means that the resident species has a positive effect on the invader. *Modified from paper II.*

# Results and discussion

## Biotic resistance and invasion success

In paper **I**, we show that species richness and saturation poorly explains the outcome of introductions of Arctic char and that species identity best predicts the outcome. Specifically, it is northern pike (*Esox lucius*) that determines the invader success for Arctic char. In paper **II** we extend our introduction data to include three more species, tench, zander and whitefish and we include a novel hypothesis, the weighted species richness. We also here find that species richness and saturation are poor predictors of invasion success. Only one species had a significant negative relationship between establishment success and species richness. Further, models that accounts for species identity were better than those using species richness for all species. For three of the four species the novel descriptor, the weighted species richness, was the best, and for one species, zander, the species identity and the weighted species richness models had similar fit (paper **II**).

The weighted species richness was constructed using a multivariate regression model, from which we estimated a weight for each resident species that describes its contribution to invasion resistance (Fig. 4). The sign of the weights depend on the type of interaction the invader has with the resident species. Interactions that are associated with positive contribution to resistance can either be competition by the resident species or predation by the resident species. Negative contribution to resistance is instead expected if, for example, the resident species is a prey of the invader. We found that ruffe (*Gymnocephalus cernua*) contributed positively to the resistance when whitefish was introduced; ruffe is known to predate on whitefish eggs (Etheridge et al. 2011, Rösch & Schmid 1996, Winfield et al. 1996). Ide (*Leuciscus idus*) and bleak (*Alburnus alburnus*) were found to contribute negatively to the resistance when zander was introduced, probably because they are important prey species of zander (Biró 1973, Kottelat & Freyhof 2007).

Thus, the weighted species richness model acknowledges that resident species can either promote establishment or restrict establishment. In the original species richness hypothesis it is assumed that all resident species has a negative and equally strong effect on establishment success. In nature, interaction strengths tend to have a skewed distribution with many weak and few strong interactions (Wootton & Emerson 2005) and communities are typically structured by a combination of competitive, predatory and facilitative interactions (Stachowicz 2001, Chase et al. 2002). Therefore, we should not expect that the species richness hypothesis fits empirical data very well,

which is in line with the general findings (Jeschke et al. 2012). Even though most ecologists should know that communities are structured by different interaction strengths and by both positive and negative interactions in nature, the species richness hypothesis has been a very popular hypothesis (Lowry et al. 2013).

Estimating the weighted species richness requires data on failed and successful introductions of the invader and information on the species composition prior the introductions, which is rarely available. The classic species richness is easier to estimate, and in some cases it might work fairly well. The invasion success of a species that is negatively affected by the presence of almost all species will be reasonably well described by the species richness of the invaded community. Arctic char appears to be such a species (Fig. 4), as it is known to be a weak competitor and a prey of other species (Filipson & Svårdsson 1976). Furthermore, we found species richness to have a significantly negative effect on the invasion success of Arctic char; however, the weighted species richness model was better. On the other hand, the species richness hypothesis will be misleading for invading species that are positively affected by most other species, e.g., piscivores, and species that have similar number of positive and negative interactions with other species. We propose that the findings that the weighted species richness best describes biotic resistance should be widely applicable to communities that are structured by interactions varying in both strength and sign (Stachowicz 2001, Chase et al. 2002, Wootton & Emmerson 2005), which should be most natural communities.

In addition to biotic resistance, abiotic resistance can also influence a species invasion success. In fact, it has been argued that abiotic factors are more important than biotic interactions in temperate fish communities (Moyle & Light 1996). However, our findings show that the biotic interactions better describe invasion success on their own than does the abiotic factors in our relatively species poor study system (paper I and II), although the best models includes both abiotic and biotic predictors. In neo-tropical fish communities biotic factors were also found to be more important than abiotic factors (Skóra et al. 2015). However, it is important to note that the weights in the weighted species richness model might not all be reflecting biotic interactions. Some weights could also emerge due to correlations between species' response to abiotic factors (Alofs & Jackson 2015), that we were unable to include in the analyses. We found for example, that tench were positively affected by the presence of rudd (*Scardinius erythrophthalmus*) (Fig. 4), which we suspect is due to that both prefer well vegetated shallow, waters (Kottelat & Freyhof 2007). We do not know how many of the correlations this could affect, but, biotic interactions - predation in particular - have been

documented to be a highly structuring factor in high latitudinal lakes (Vander Zanden et al. 1999, Persson et al. 2007, Byström et al. 2007, Spens & Ball 2008, Alofs & Jackson et al. 2014) and probably also in neo-tropical fish communities (Skóra et al. 2015). We found that predator-prey interactions could explain the strongest correlations for three out of four introduced species (paper II).

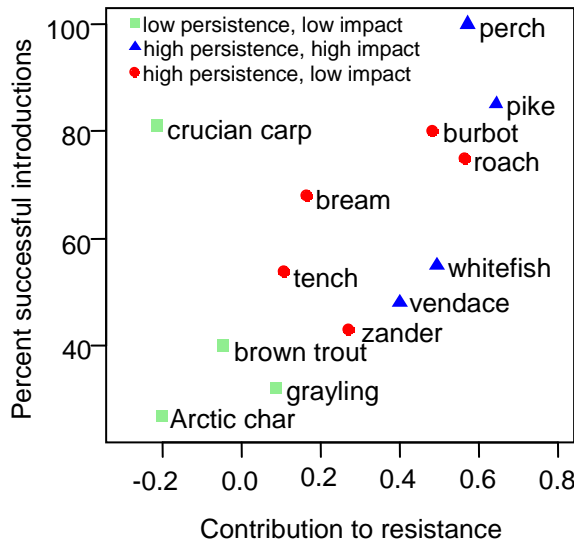


**Figure 4** Figure showing the coefficients that estimates the contribution to resistance of each resident species. Resident species with positive coefficients increase community resistance when present and species with negative coefficients facilitates invader establishment. The negatives of the coefficients are plotted to facilitate interpretation. Very common resident species were excluded from the analysis and rare species were lumped in a variable called “other”. Depending on the identity of the invader the resident species have different effects on the invader in terms of both strength and sign. E.g., zander is a piscivore (Kottelat & Freyhof 2007) and is positively affected by all resident species. While Arctic char, which is known to be a weak competitor and a prey species (Filipsson and Svårdson 1976), has mostly negative interactions with resident species. *Modified from paper II.*



## Biotic resistance and performance traits

We found that species that are strong invaders are also strong defenders, persistent and cause impact (Fig. 5), while other species are weak in all performance traits. Thus we find that the correlation pattern in Swedish lakes is consistent with the hypothesis of an interaction hierarchy (paper III). The only exception from this pattern was crucian carp (*Carassius carassius*) which had high establishment success but low contribution to resistance (Fig. 5). When we excluded the crucian carp, the species that had suffered extinctions (green data points in Fig. 5) and the species that cause extinctions (blue data points) are perfectly separated in the introduction success-contribution to resistance space (Fig. 5). Competitively structured interaction hierarchies have been found for vascular plant, algae and bacteria communities (Shipley 1994, Roxburgh & Wilson 2000, Zhang & Zhang 2010).



**Figure 5** The contribution to resistance by each species plotted against the percentage of successful introductions. Positive contribution to resistance means that they have a negative effect on the invader, while a negative contribution to resistance means a positive effect on the invader. Low persistence denotes species that are known to go extinct after the establishment of new species; high persistence denotes species that are not known to go extinct. Low impact denotes species that are not known to cause any extinction when introduced, and high impact denotes species that are known to cause extinctions when they are introduced. *Modified from paper III.*

As these communities are invaded they are expected to grow more resistant to invasions since species that invade successfully also make large contributions to resistance, and possibly also replace weaker species. Thus, from the hierarchy we can predict which communities that will be the most sensitive to future invasions, that is, those that consists of weak species low in the hierarchy. In Scandinavia we would for example expect that the relatively cold mountain lakes, inhibited mostly by weak species, such as Arctic char and brown trout (*Salmo trutta*), would be highly sensitive to invasions by species high up in the hierarchy. Species such as pike, a strong interactor, are expected to invade these mountain communities as climate change will eliminate temperature barriers that hinder these invaders today, and as a consequence extensive extinctions are predicted (Hein et al. 2012, 2014).

Invading species that have a majority of negative interactions with other resident species are expected to be positioned low in the hierarchy since they are inferior to most other species, e.g., Arctic char in our data (Fig. 4 & 5). Whitefish has about the same amount of positive as negative interactions with other species (Fig. 4) and is hence placed in the middle of the hierarchy (Fig. 5). However, both zander and tench has a majority of positive interactions with other species but are still placed in the middle of the hierarchy (Fig. 4 & 5). This could be due to that we only had data to evaluate a few of the interactions that these species has with resident species, or that factors other than biotic interactions restrain these species. Unfortunately, we did not have data to estimate the weighted species richness of the invaded communities for any of the species high up in the hierarchy, but it is expected from the hierarchy that they will mostly be positively or neutrally affected by other species.

The classification of strong versus weak performers that we make here might be context-dependent. Species classified as weak species in our communities could be a strong performer in other biogeographical regions. For example, brown trout which is classified as a weak performer in our study system is considered an invasive species with high impact in other parts of the world (Ault & White 1994, Townsend 1996, Young et al. 2010). Thus, the classification made here might not be globally applicable.

## **The data**

The dataset used for paper **I-III** is unique in its extent and the inclusion of both successful and failed introductions of freshwater fish (paper **IV**). Datasets that includes failed invasions are rare but without such data it is impossible to distinguish communities that are resistant from those where few

non-native species have attempted to invade (Gido & Brown 1999, Kolar & Lodge 2001).

There are however, some limitations to the data; we have for example not data on some important environmental variables such as lake depth, productivity and water color. Propagule pressure is another variable that is lacking that has gained much attention in the last decade (Leprieur et al. 2008, Simberloff 2009). An invading population with a large propagule supply will suffer less from competition and predation by resident species, while one with a smaller propagule is more likely to be affected by both demographic and environmental stochasticity (Simberloff 2009).

Another limitation is that some of the resident species are present in almost all analyzed lakes. This limits our ability to estimate the contributions of these species to resistance; although it does not affect the estimation of other resident species contribution to resistance as these species can be viewed as background variables that were held constant. What it can affect is the level at which invading species are successful.

## **Concluding remarks**

In this thesis I have studied biotic resistance in freshwater fish communities in Sweden. By doing so, I have contributed to the general understanding of biotic resistance and specifically of the studied fish communities. I have demonstrated that a measure on biotic resistance needs to include that interactions between species are of both different strength and sign. Further, I have demonstrated that information on species performances as invaders and residents give us important clues about how invaded communities will develop in the future. This information can also be used to identify communities that will be most sensitive to future invasions.

The main aims of invasion biology are to understand why some systems are resistant to invaders while others are susceptible to them, and what ecosystems that will suffer most impact from non-native species. Although it might be impossible to estimate weighted species richness for each potential invader in all type of communities the insights into biotic resistance provided here will contribute to the understanding of the complexity of biotic resistance and its importance. In fact, biotic resistance might be more important than believed before, since it often has been estimated in a way that does not reflect how interactions are structured in nature. Further, if the interactions of the community are structured as a hierarchy, and that hierarchy is known, it is straightforward to identify communities that are vulnerable to invasions.

Communities dominated by weak species (i.e., those with low invasion success, low persistence, low defense capacity and low impact) will be more vulnerable to future invasions and will also be harder to re-introduce once they are lost. Thus, it is not the number of species present in a community that determines its susceptibility or resistance against non-native species but the interactions the resident species have with the invader.

Future studies should involve testing the generality of the weighted species richness hypothesis as well as how common interaction hierarchies are in nature. Furthermore, the underlying characteristics of species that make up weak and strong performers in these communities should be an interesting follow up.

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