**Project description**

1. **Summary**

Human-driven activities greatly affect ecosystems worldwide, contributing to biodiversity loss and profound shifts on ecological systems and services. Hence, there is an urgent need to understand and predict biodiversity and ecosystems dynamics. Currently, a big gap exists between theoretical and empirical ecologists. Surprisingly, scarce studies have been conducted in ecology to integrate theoretical development and empirical testing. In this 1-year proposal we explore how to combine observational and experimental data, together with theory to explore the effects of functional diversity on direct and indirect interactions among individuals because of speciation from a keystone species in Alp lakes with three different regimes of perturbation (grossly polluted, mildly polluted and pristine). One of the **innovative approaches of this project is working with functional diversity, based on ecological traits of each fish species (body size, trophic group, etc.).** We combine data from existing **fish database (FISHBASE), experiments and field surveys** conducted by researchers of the host institution, **together with modelling tools, i.e. Approximate Bayesian Computing (ABC).**

We develop a model based on direct (predation and competition) and indirect (facilitation and inhibition) interactions between the keystone species, i.e. whitefish (*Coregonus* spp.), and the remaining fish in Alp lakes. The proposed modelling scenarios may reveal the interactions between species traits that define functional diversity depending on the rate of disturbance in Alp lakes. The expected results may show consistent differences between pristine and grossly polluted lakes, since pristine are identified as no perturbed. The present proposal encourages collaboration between several research groups at the host institution, providing an excellent opportunity of **exchange of ideas and experiences between empirical and theoretical scientists**, by integrating empirical, experimental and theoretical data from modelling tools. This project has an important scalable component, being a complement for future proposals in the host institution concerning field databases, experimental data and theoretical approaches.

1. **Current state of the research in the field**

Keystone species are pivotal in all ecosystems (Mills et al. 1993), since they exert top-down influence on lower trophic levels and prevent species at lower trophic levels from monopolizing critical sources, e.g. competition for space or capital food producers. In freshwater systems a high variety of fish are considered keystone species because of their importance on the ecosystem processes (e.g. Willson & Halupka, 1995). For example, whitefish of the genus *Coregonus* spp. is a valuable component of water ecosystems (Kirczuk et al., 2018) being keystone species in Alp lakes since other species depend on their survival, abundances and diversity. Thus, ecological implications are of utmost importance if loss or sharp variations of whitefish populations occur in lakes where they inhabit.

In the European Alps, 1 to 5 whitefish species (*Coregonus* spp.) coexist in at minimum 25 lakes (Kottelat & Freyhof, 2007; Hudson et al., 2011). A phenotypically differentiation within these genetically differentiated (Douglas et al., 2005) Alpine whitefish species has been observed resulting in speciation, with differences in traits related to trophic guild (e.g. gill-raker number, growth rate, shape and colour), as well as, reproductive aspects (e.g. time of spawning, location/depth of spawning, egg size) (Steinmann, 1950; Douglas et al., 2005). Furthermore, whitefish exhibit differences in resource use along the benthic-limnetic resource axis (Harrod et al. 2010), with adaptation to different trophic niches (Lundsgaard-Hansen et al. 2013). The divergence in whitefish underpinned top-down effects through trophic cascades as occur to other freshwater fish (Bassar et al. 2012). At ecosystem level, these effects may alter consumer-resource dynamics and ecosystem functions (Lundsgaard-Hansen et al. 2014). In contrast, pollution effects (eutrophication) showed to affect greatly the speciation of these species in lakes, underpinning a reversal in speciation processes (Vonlanthen et al. 2012; Alexander et al. 2017). Former ecological studies observed that speciation processes affect species interactions, trophic cascades and population dynamics (Seehausen 2009).

A better understanding of the network of traits that underlie specific ecosystem functions and the genomic underpinning of trait variation and species differentiation are needed to estimate the possibility and potential rates of recovery, re-divergence and the restoration of associated ecosystem function (Alexander et al. 2017). Thus, knowledge of how variation in the traits underlying ecosystem functions influences the services that these functions provide to society is required (Alexander et al. 2017). Interaction strength among species depends on ecological and evolutionary processes underlying complex traits and trait distributions (Melián et al., 2018), showing that species traits are feasible tools to determine species interactions, as well as, the ecosystem effects of keystone species on the remaining diversity (Goldstein & Meador, 2005).

Scarce studies have been focused on the effects of whitefish in the remaining fish of Alp lake ecosystems. To our knowledge, no approach has been developed involving the study of the whole fish community considering functional traits. Species traits have shown to be feasible tools to identify species interactions, as well as, the ecosystem effects of keystone species on the remaining diversity (Goldstein & Meador 2005). Functional traits have several advantages (Noble et al. 2007; Ibáñez et al. 2009): (i) higher correlation to environmental variables, (ii) trait variations are not dependent to individual abundances, (iii) not geographically limited to a certain ecosystem.

In this proposal, experimental and observational data are combined with theory to contrast the effects of keystone species (whitefish) in Alp lakes ecosystems. These effects are explored in different rates of human-induced disturbances (grossly polluted, mildly polluted and pristine) in formerly studied Swiss lakes. Thus, we can contrast the empirical and experimental data with theoretical models with different degrees of complexity.

The combination of field data at multiple scales of spatial and biological integration, from performance of individual organisms in the laboratory (Lundsgaard-Hansen et al. 2013; Roesch et al. 2013), as well as theoretical modelling is of utmost importance to understand complex interactions in natural ecosystems (Alexander et al. 2017). Surprisingly, there is an enormous gap of knowledge integrating theory and real data from biodiversity where most of studies have been focused on taxonomic and ecologic diversity. No integrative works have been published dealing with functional diversity, though it has been extensively demonstrated its importance as a reliable biodiversity in natural ecosystems, from rain forests to coral reefs (Mouillot et al. 2013). Thus, the novelty of this research is working in functional terms, not previously being done with the FISHBASE global database considering the factor “pollution” (grossly polluted, mildly polluted and pristine) in Swiss lakes.

Modelling approaches have been criticized by the difficulties to be interpreted in an ecologic manner. However, a recent modelling tool (Bayesian techniques) has the possibility to integrate prior information from field or even experimental data (Beaumont, 2010). Approximate Bayesian Computation (ABC) techniques can be fitted to natural observations and thus, can be utilized to infer mechanisms controlling species traits in natural ecosystems considering functional and morphological diversity.

The present approach constitutes an initial step to fill this gap on the driving mechanisms that affect the functional diversity in ecosystems, based on species traits from natural and experimental observations. ABC are used to fit the models to data in order to infer mechanisms that best explain data from previous field surveys conducted in Swiss Alp lakes and experimental data carried out in the host institution facilities.

Previously, several studies have been conducted combining empirical data and theoretical models to understand trophic relationships within ecosystems, but most of these were limited to a single species or a pool of species integrated in one category (e.g. Aebischer 2013, Lundsgaard-Hansen et al. 2013, 2014). However, complex effects occurring in ecosystems are extremely complicated to be understood through the inference of one single species belonging to the ecosystem. Nevertheless, no integrative works have been published dealing with functional diversity, though it has been extensively demonstrated its importance as a reliable biodiversity in natural ecosystems, from rain forests to coral reefs (Mouillot et al. 2013). Thus, a step forward would be to integrate several species from ecosystems occupying different ecological niches based on their functional traits (body size, trophic guild, etc.).

A theoretical framework contrasting prediction from different models is of outmost importance. For this reason, we will use empirical data from a worldwide fish database (FISHBASE, www.fishbase.org). The combination of data from previous field surveys conducted in Swiss Alp lakes, as well as, data from experiments carried out in the host Institute facilities will provide an excellent opportunity to lead an exchange of ideas and experiences between empirical and theoretical scientists. Moreover, the results of the present proposal are of priority interest for conservationists and stakeholders since the experimental and theoretical approaches are based on functional traits that contribute to the conservation and persistence of ecosystem properties and services.

1. **Detailed project description**

**c1. Goals**

The **main aim** of the present proposal is to **evaluate the consequences of keystone species (whitefish) speciation in functional properties** of the Alp lakes ecosystems **through direct** (top-down and bottom-up) **and indirect** (facilitation and inhibition) **interactions with the remaining fish**. Specifically, we intend to explore general functional patterns in Alp lakes ecosystems from experimental and observational data, as well as, FISHBASE database, and develop modelling scenarios to test the mechanisms underpinning changes in functional diversity of Alp lakes.

This objective is carried out by three approaches:

1. **Patterns from previous field surveys conducted in Swiss lakes, and the FISHBASE database**, using functional diversity and redundancy in traits in grossly polluted, mildly polluted and pristine lakes.
2. **Analysis of experimental data** conducted in the host Institute facilities, analyzing morphometric and functional diversity of whitefish, as well as, other fish species used in previous experiments that cohabit with it in Alp lakes.
3. **Modelling tools** to infer interactions using ABC (Approximate Bayesian Computation) methods through IBM (Individual-based models) models in order to disentangle mechanisms occurring between species interactions and to identify species traits that best predict data from mesocosms, lakes and FISHBASE global database.

**c2. Methodology**

The present proposal is divided in two parts: (i) General functional patterns from fields surveys and large databases; (ii) Modeling scenarios.

1. General functional patterns from field surveys and large databases

We will analyse patterns of functional diversity on a series of data sources:

* Host Institute database containing Fish communities from the majority of lakes of Switzerland. This database contains information on spatial coordinates, morphological traits, species abundances, habitats and DNA data.
* Whitefish community database from most lakes of North Alps containing information on the sampling locations, morphological, ecological and genetic data.
* Laboratory experiments conducted at the host Institute.
* FISHBASE database (Froese & Pauly 2019).

We specifically address these questions: (i) **What** are the global patterns of functional diversity in pristine ecosystems; (ii) **Do** they significantly differ from disturbed (e.g. eutrophized) lakes? (iii) **How** keystone species affect functionally the ecosystem? (iv) Effects are the same in all lakes or they differ? **Why**?

**Functional diversity assessment** can be determined with the use of indices that summarize community diversity with respect to species’ traits. Here, we propose to explore a suite of functional diversity index incorporating **eight traits** that contain most of the species ecological characteristics (Noble et al. 2007; Frimpong & Angermeier 2009; Stuart-Smith et al. 2013). These traits contain at least the following variables that will be obtained from FISHBASE (Froese & Pauly 2019):

1. Body size (e.g. maximum length);
2. Feeding ecology (e.g. trophic group, trophic breadth);
3. Behaviour (e.g. daily activity pattern, gregariousness or other related traits);
4. Habitat use (e.g. preferred substratum, habitat complexity or other related traits).

**Three functional diversity indices** are estimated from a multidimensional approach, **functional richness** (FRic), **functional evenness** (FEve) and **functional divergence** (FDiv).

The functional richness is assessed through the functional dispersion index (FDis, Laliberté & Legendre 2010). FDis accounts for not only the trait space filled by a community (convex hull volume), but also dispersion and species relative abundance. FEve may be seen as the degree to which the biomass of a community is distributed in niche space to allow effective utilisation of the entire range of available resources. FDiv defines how far high species abundances are from the centre of the functional space. High functional divergence indicates a high degree of niche differentiation, and thus low resource competition.

1. Modelling scenarios

We will build **Individual-based models** (IBM) to test the mechanisms that best predict the loss or gain of functional diversity. Three models are developed representing an experimental scenario (grossly polluted, mildly polluted and pristine) for alp lakes ecosystems. Fish populations are represented by mean and variance for each functional trait. Fitting direct and indirect interactions are made by comparing the matrix of functional traits and individual abundances from each model scenario with data collected from experimental and observational works. This is made by using the community matrix starting with varying competition and antagonistic coefficients terms. We also start with different mean and variance for each functional trait to understand the effect of trait variance on functional diversity and whether variance influences the rate of trait loss or gain.

**Which model scenario best predict the empirical data? Do we find a match between model and experimental and observational scenarios?** We will use ABC methods to fit the simulation scenarios to the experimental data. This approach is ideally suited for parameter estimation and inference using dynamical models. The output of our model will be a matrix of functional traits and individual abundances. The difference between model output and observations can be evaluated as the absolute distance between predicted and observed values with traits and abundances. Posterior parameter distribution minimizing the model data distance is obtained using ABC through two algorithms: (i) Rejection sampling (Melián et al. 2015), and (ii) Simulated annealing ABC (Albert et al. 2014). Parametrising and fitting the model separately in experimental and observational experiences, we can test how disturbance regimes affect functional diversity through direct and indirect interactions and how they affect to ecosystem processes in Alp lakes. Lastly, to demonstrate the feasibility of the model, we fit the model to experimental and observational databases collected by the host institute researchers. Figure 1 shows a representation of all components (Empirical Data, Model Fitting and Simulations) and processes regarding the model developed in the present proposal. For the model, most of the simulations used will be numerical. The present model is implemented in **JULIA** (julialang.org).

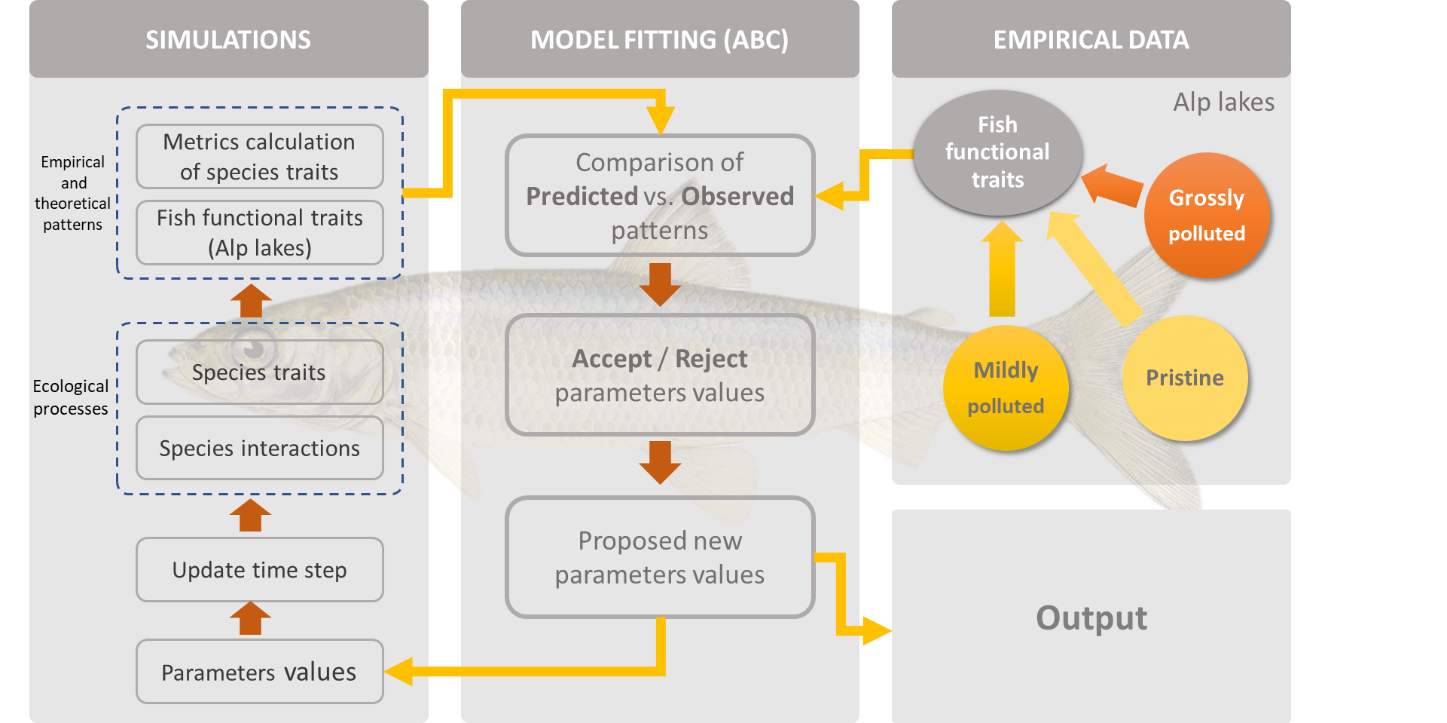


Figure 1 - Components and phases involved in the development of the model.

**c3. Approach**

The project is planned for the duration of 12 months, which includes the development of the model, and the fitting to experimental and observational data, as well as, the analysis of FISHBASE global database.

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Tasks | Month | | | | | | | | | | | |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| Start-up meeting |  |  |  |  |  |  |  |  |  |  |  |  |
| Collecting information |  |  |  |  |  |  |  |  |  |  |  |  |
| Formulation of the model structure and Implementation of the model |  |  |  |  |  |  |  |  |  |  |  |  |
| Parametrisation of the model |  |  |  |  |  |  |  |  |  |  |  |  |
| Model-data comparisons |  |  |  |  |  |  |  |  |  |  |  |  |
| Advanced draft of paper to be submitted |  |  |  |  |  |  |  |  |  |  |  |  |

* **Start-up meeting** (Month 1)

During this task, several informal meetings are expected with the supervisor and other research scientists from the host institution that are implicated directly to the present proposal.

* **Collecting information from experimental and observational data and FISHBASE global database** (Months 1-4)

An exhaustive compilation of bibliography on fish assemblages from Alp lakes will be conducted. Papers related to trophic guilds or other certain traits from freshwater fishes will be considered for the present approach. Moreover, a compilation of all experiments conducted in ponds and mesocosms by researchers from the host institution will be carried out, with special emphasis on those regarding whitefish.

* **Formulation of the model structure and Implementation of the model** (Months 4-6)
* **Parametrisation of the model** (Months 7-9)

Through parametrising and fitting the model for lakes considering different disturbance regimes (grossly polluted, mildly polluted and pristine). Each model will be tested for the “targeted” species (whitefish).

* **Model-data comparisons** (Months 10 and 12)

Final steps in model-data comparisons.

* **Advanced draft of paper to be submitted** (Months 11 and 12)

At least one advanced draft of paper to be submitted to SCI journals is expected at the end of the year or just right after. A possible first paper will be related to the fish functional diversity subjected to different rates of disturbance (grossly polluted, mildly polluted and pristine) in lakes. A second paper will explore in a multidisciplinary approach the interactions in species traits between keystone species (whitefish) and the remaining fish of the Alp lakes ecosystems, considering experimental and observational data, as well as, modelling scenarios.

**c4. Expected outcomes**

The main purpose is to explore the effects of functional diversity on direct and indirect interactions among individuals because of speciation from keystone species (whitefish) in Alp lakes. This will be tested by using experimental and observational data, as well as, FISHBASE global database. The proposed modelling scenarios will reveal the interactions between species traits that define functional diversity depending on the rate of disturbance (grossly and mildly polluted and pristine) in Alp lakes. We expect consistent differences between pristine and grossly polluted lakes, since pristine are identified as no perturbed. As a short-term aim, we expect to publish one scientific contribution in a top-ranked ecological journal reporting the results of the present proposal. We also aim to make the code implement freely available and easily reusable by other researchers at the host institute.

1. **Risks and gains of the research project**

**Gains:** reliable knowledge; excellent opportunity of exchange of ideas and experiences between empirical and theoretical scientists, by integrating empirical, experimental and theoretical data from modelling tools.

**Risks:** The plan does not present high risks as it is feasible to be done throughout the planned schedule, given that all empirical data needed for this project are already available.

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