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Methodological and Ideological Options

Quantification of the Indirect Use Value of Functional Group Diversity Based on the Ecological Role of Species in the Ecosystem

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A B S T R A C T

An important issue in biodiversity valuation is gaining a better understanding of how biodiversity conservation affects economic activities and human welfare. Quantifying the economic benefits of biodiversity for human well-being is not straightforward. Here, we expand the ecosystem service cascade by (i) attributing a methodology to the different steps of the cascade to assess the effects of changes in functional group diversity on economic activities; (ii) including multiple attributes for defining functional diversity and (iii) integrating a dynamic ecological model simulating complex interactions and feedbacks between species with an economic model assessing the effects of changes in functional group diversity for gross revenues. The stepwise methodological framework integrates a production function approach with a market price-based approach in order to investigate the indirect use value of functional group diversity based on the ecological role of species in the ecosystem. The methodology is applied to estimate the relationship between the gross economic value of Chinook salmon (Pacific Northwest, United States) and the diversity of freshwater macroinvertebrates. The results of our analysis emphasize the importance of biological diversity for sustaining ecosystem goods and services. The analysis provides a tractable framework for quantitatively exploring the economic consequences of changes in functional group diversity.

1. Introduction

Biodiversity plays a key role in ecological processes and the delivery of ecosystem services, and its importance has been widely recognized (MA, 2005). Most of the central issues facing conservation involve understanding the effects of economic activity on biodiversity and ecosystems, whilst finding solutions to conservation problems requires demonstrating the benefits of conservation for the wellbeing of people (Polasky, 2009). Although the costs for biodiversity conservation measures are generally well known, the quantification of economic benefits is less straightforward (Christie et al., 2006). Economic valuation is increasingly being recognized as an indispensible tool to target biodiversity protection (Polasky, 2009) with scarce budgets and to determine damages for losses of biodiversity in liability regimes (Christie et al., 2006; OECD, 2001). It is believed to be a suitable means to facilitate their recognition, demonstration and consideration in decision making (Lienhoop et al., 2015).

At the same time, economic valuation is heavily criticized due to, among others, the lack of the inclusion of the respondent's motives or the lack of social embeddedness or social formation of preferences, and therefore the use of more deliberative approaches to valuation have been advocated (Lienhoop et al., 2015). While the motivation for increased knowledge on the economic impact of biodiversity losses on human welfare is clear (Polasky, 2009), assessments of the role of biodiversity for the generation of human welfare remain ambiguous (Barbier, 2012; TEEB, 2010). Several key challenges predominate the scientific discourse: (i) The plurality and multiplicity of valuation languages (Cardoso, 2018) as well as the ambiguity on the definition of biodiversity and the object of valuation (Bartkowski, 2017; Bartkowski et al., 2015) weakens the credibility of the use of economic values of non-marketed goods for decision-making purposes, (ii) no established framework has been agreed upon that effectively assesses biodiversity losses for their effects on economic performances (Farnsworth et al., 2015; Nijkamp et al., 2008), (iii) ecological uncertainty (Tilman et al., 2014) and ambiguity (Jax and Heink, 2015) exist on the relationship between species diversity and ecosystem services and (iv) biodiversity is a multi-dimensional concept and requires multiple proxies for quantifying it (Bartkowski et al., 2015; Nijkamp et al., 2008).

In the literature, many sources of value derived from biodiversity have been identified. They can be found in the use value and existence value of individual species (Mace et al., 2012; Polasky et al., 2005) as a source of bioprospecting revenues or knowledge values (Heal, 2000;

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Polasky et al., 2005), as an integral part of the provision of ecosystem services via their contribution to ecosystem functions (Cardinale et al., 2012; Polasky et al., 2005), as a source of indirect use value (Costanza et al., 1997; de Groot et al., 2002; Farnsworth et al., 2015), insurance value (Baumgärtner, 2007; Heal, 2000; Henselek et al., 2016) or intrinsic value (Sandler, 2012). Sometimes, ecosystem resilience is considered an asset in itself for valuation (Walker et al., 2010). Recently, it has been argued that biodiversity has an economic value extending beyond these values, including an option value and a spill-over value (Bartkowski, 2017).

Hamilton (2013) recognized that, as a consequence of the fact that the majority of ecosystem services are provided to the economy as externalities, these values are already capitalized in other values such as farmland or as the economic benefits to their owners who benefit from the supply of (costless) environmental services. In this respect, adding up the values of the ecosystem services and including them as separate values in a national balance sheet would be considered double-counting (Hamilton, 2013).

Economic valuation of biodiversity as defined in natural sciences is yet unfulfilled and methodologies that provide a strong link between economic theory and ecological research (i.e. a production function analogy that describes how ecosystems generate services and expressing the relationships between the quantities of production factors used and the amount of goods or services produced) remain largely unexplored (Bartkowski et al., 2015; Daily et al., 2000; Farnsworth et al., 2015). Farnsworth et al. (2015) emphasize a refocusing of economists for the economic valuation of biodiversity towards production-based methods whereby biodiversity is considered as an input in a production function, thereby generating products or services that are used directly by humans. The production function estimates the contribution of biodiversity for the production of marketable goods or services (Bertram and Rehdanz, 2013). The use of a production function approach therefore recognizes functional group diversity as an essential production factor so that changes in functional group diversity indirectly affect the production of a marketable good. “A production function estimates the value of a non-marketed resource or ecological function in terms of changes in economic activity by modeling the physical contribution of the resource or function to economic output. It generally uses scientific knowledge on cause-effect relationships between the ecosystem service(s) being valued and the output level of marketed commodities and relates to objective measurements of biophysical parameters” (TEEB, 2010). The ecological functions are considered “emergent properties of a system and inherent to it, on different system levels, not artifacts or social constructs made and controlled by humans. They are relevant for the ecosystem, its functioning and development, regardless of any human recognition or valuation and in this sense objectively valuable for the ecosystem…” (Spangenberg et al., 2014). “Production function approaches estimate how much a given ecosystem service contributes to the delivery of another service or commodity which is traded on an existing market… The PF approach generally uses scientific knowledge on cause-effect relationships between the ecosystem service(s) being valued.” (TEEB, 2010). In this respect, production functions have the advantage that they rely on objective measurements of biophysical parameters and can therefore quantify the physical effects of changes in a biological resource on an economic activity (Barbier, 1994, 2012; TEEB, 2010). Diversity might increase output by supporting landscape-level ecosystem functions that help to enhance productivity (Omer et al., 2007; Pascual et al., 2013; Tscharntke et al., 2005). The impact of these changes is valued in terms of the corresponding change in marketed output (Barbier, 1994; TEEB, 2010). For example, natural predators have been shown to perform important biological pest control services, thereby reducing crop damages and indirectly contributing to farmer's income (Daniels et al., 2017). Similarly, through consumer-resource interactions, the diversity of insects and other invertebrates in streams and rivers serve as the food source for economically valuable fishes (Bellmore et al., 2017), which in turn, fishing industries and local economies rely upon.

The strength of production functions as a viable methodology for policy analysis (Barbier, 2007) stems from the potential to relate measurements of cause-effect relationships to changes in economic activities. In doing so, they provide justification when making a case for environmental protection by providing supporting scientific information on the effects of changes in biological resources for human welfare (Polasky, 2009).

Strengthening a production-based method could be achieved by stressing the functionality of biodiversity in valuation studies. The recent biodiversity valuation literature emphasizes that the ecological and broader biological role that biodiversity plays in human well-being should be at the centre of valuation studies (Bakhtiari et al., 2014; Bartkowski et al., 2015; Daniels et al., 2017; Farnsworth et al., 2015). Meta-analyses have shown that ecosystem services - the benefits humans receive from ecosystems – are tightly linked to the performance of ecosystem functions and the level of biodiversity (Wall and Nielsen, 2012). A loss of biodiversity may directly and indirectly affect ecosystem functions and services, as well as human welfare (Chapin Iii et al., 2000; Hooper et al., 2005). Functional groups of species provide a link between species diversity and ecosystem function (Cleland, 2011), and are the main units to investigate the consequences of global environmental change on ecosystem function and the delivered services (Carmona et al., 2016). It has been estimated that indirect use values may constitute the largest source of total economic value in biodiversity valuation (Costanza et al., 1997; de Groot et al., 2012; Farnsworth et al., 2015). The indirect use value can be derived from the regulation services provided by species and ecosystems (TEEB, 2010) or can be defined as the support and protection provided to economic activity by regulatory environmental services (Barbier, 1994). It is safe to assume that biodiversity has a large indirect use value to humans when it is considered as an input in a production function, thereby influencing the provision of products or services that are used directly by humans.

Bartkowski et al. (2015) presented an overview of needs for the proper valuation of biodiversity among which the need to formulate a coherent framework for the valuation of biodiversity based on the functional roles it plays. Studies on biodiversity require a pluridisciplinary approach (Nijkamp et al., 2008), requiring integrated valuation methodologies combining disciplines (ecology and economics) and methods (production function approach and market-based technique) and aiming at assessing real life impact (Jacobs et al., 2016). The Ecosystem Services Cascade introduced by Haines-Young and Potschin (2010) provides a cascade of consequent events leading to monetary valuation. The cascade starts from (i) Ecosystem Properties (EP) leading to (ii) Ecosystem Functions (EF), (iii) Ecosystem Services (ES), (iv) Benefits (B) and (v) Values (V) (see Fig. 1) (Boerema et al., 2017; Haines-Young and Potschin, 2010; Potschin and Haines-Young, 2011). Recently, it has been argued that a cascade is both “an oversimplification of a complex reality” as well as “an unnecessary complication” since “ecosystem services equal benefits by definition” and a better representation was suggested, including complex interactions and feedbacks among built, social, and natural capital in order to produce ecosystem services (Costanza et al., 2017).

Here, the use of production functions is explored whereby the flow of benefits provided by a functional diversity can be conceived as the result of a ‘natural production function’. Functional diversity (quantified by multiple attributes) is the input to the production function, resulting in marginal changes in the flow of benefits (Barbier, 2012; Hamilton, 2013). In line with Costanza et al. (2017), we here expand the ecosystem service cascade by (i) attributing a methodology to the different steps of the cascade to assess the effects of changes in functional group diversity on economic activities; (ii) including multiple attributes for defining functional diversity and (iii) integrating a dynamic ecological model simulating complex interactions and feedbacks between species with an economic model assessing the effects of changes in functional group diversity for gross revenues. The stepwise

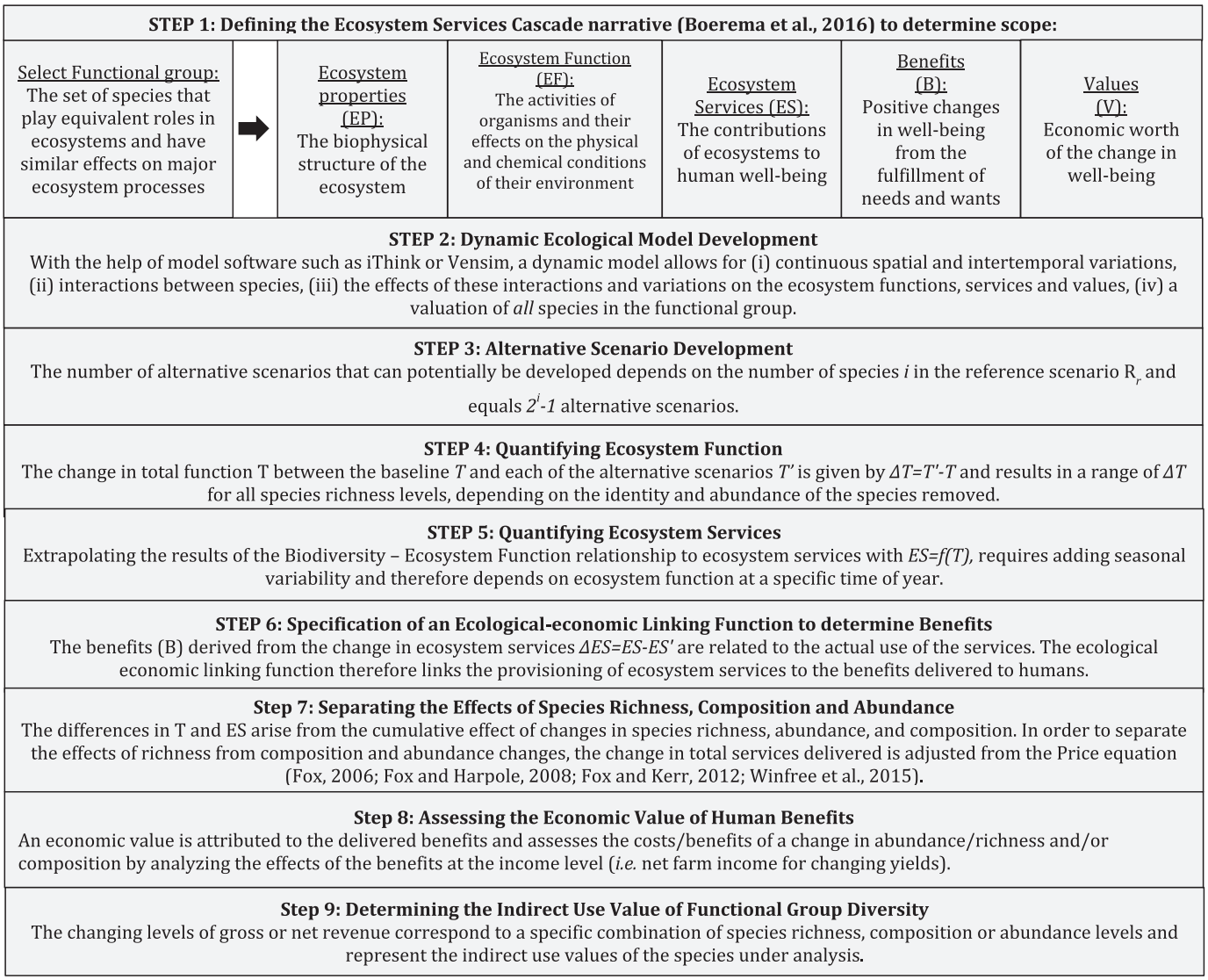

Fig. 1. Overview of the stepwise methodological framework to quantify the effects of changes in non-marketable species diversity for their impact on economic activities through the delivery of ecosystem services, attaching an indirect use value to species diversity.

methodological framework integrates a production function approach with a market price-based approach in order to investigate the indirect use value of functional group diversity based on the ecological role of species in the ecosystem. It serves to quantify the effects of changes in non-marketable species diversity for their impact on economic activities through the delivery of a selected set of ecosystem services and as such attaches an indirect use value to functional group diversity. The methodological framework both (a) quantifies the contribution of functional group diversity to gross revenues through the use of a production function, and (b) attributes an indirect use value to functional group diversity by employing a direct market based technique based on the changes in the provision of a marketable good.

2. Extending the Ecosystem Service Cascade for the Incorporation and Valuation of Functional Group Diversity

In the following, the stepwise methodological approach is investigated as an extension of the ecosystem service cascade. An overview of the methodological framework is represented in Fig. 1.

2.1. Step 1: Definition of the Ecosystem Services Cascade Narrative to Determine Scope

Describing the five key concepts of the Ecosystem Service Cascade (Haines-Young and Potschin, 2010) sets the scope and boundaries for the analysis. Filling out the cascade starts by identifying the functional group to be valued. A functional group is defined as a set of species that have similar effects on major ecosystem processes (Blondel, 2003). Daniels et al. (2017) examined the effect of natural predators (i.e., functional group), which act as biological pest control of pear psylla (*Cacopsylla pyri* L.), on pear quality and net farm income. Other examples are the contribution of plankton to the (regional or global) commercial fishing industry or the contribution of wild pollinators to changes in net farm income from fruit or crop production. The analysis can contain one or more functional groups that will be valued, whereby each functional group can consist of an unlimited number of species performing a similar function. For example, to determine the consequences of a reduction of bacterial diversity on soil functions and bioremediation, functional groups of bacteria were identified (i.e. denitrifying or nitrifying bacteria, photosynthetic bacteria and organic carbon degraders) (Jung et al., 2016).

Next, the endpoint is identified which directly or indirectly depends on the services delivered by the functional group of species. This endpoint is a marketable good or service, defined as a good or service that is sold and has a market value. The identification of the endpoint follows from either (i) in-depth ecological research that reveals trophic interactions up to the point where a marketable good or service can be linked (see case study below), or (ii) a hypothesis to be verified empirically. Last, the ecosystem function (EF), ecosystem service (ES) and benefits (B) are the different cascade components linking the marketable good identified to the functional group of species to be valued and are explained in detail in step 3, 4 and 5 (see Fig. 1).

2.2. Step 2: Dynamic Ecological Model Development

A dynamic ecological model starts from a multi-attribute approach taking into account the complexity, abstractness and multi-dimensionality of biodiversity. Since biodiversity is a multi-dimensional concept 'spanning genes and species, functional forms, adaptations, habitats and ecosystems, as well as the variability within and between them' (Laurila-Pant et al., 2015), biodiversity proxies should not reduce biodiversity to one single aspect, should not cover more than biodiversity, and the connection between the proxy and the contribution of biodiversity to human well-being should be clear. Therefore, it is suggested to use a multi-attribute approach (Bartkowski et al., 2015), meaning that multiple variables are required to describe and quantify biodiversity. By choosing a multi-attribute approach to account for complexity, we propose that the choice of variables representing biodiversity should encompass at least the species richness, species composition and species abundance (or biomass) since they are essential for ecological model construction. Added to the variables describing biodiversity are the population dynamic parameters, expressed on a continuous scale. A dynamic model allows for (i) continuous spatial and intertemporal variations, (ii) interactions between species, (iii) the effects of these interactions and variations on the ecosystem functions, services and values and therefore (iv) comparison of realistic alternative scenarios of species richness, composition and abundance (Letourneau et al., 2015), and (v) a valuation of *all* species in the functional group. System dynamic software packages such as Stella (iThink) or Vensim can provide valuable tools for building dynamic ecological models (Ford, 2009).

2.3. Step 3: Alternative Scenario Development

Once biodiversity is incorporated into a dynamic modeling framework, the model can be used to test alternative scenarios that evaluate the implication of species loss (or species replacement). Alternative scenarios are defined as "hypothetical species assemblages that may occur under changing environmental conditions". In the case where future projections of species assemblages are not known, (most cases), the creation of hypothetical future species assemblages can be utilized to explore the potential effects of changing environmental conditions that result in the loss, gain or replacement of species within a functional group. The number of alternative scenarios that can potentially be developed depends on the number of species i in the reference scenario R_r and equals $2^i - 1$ alternative scenarios. The alternative scenarios all differ in species richness and/or species composition from the baseline scenario: some scenarios may have the same species richness (number of species) but may differ in the composition (identity) of the species present. For each alternative scenario, one or more species can be removed from the system in order to assess the individual and cumulative effects of removal. An example of the different scenarios for a functional group consisting of i species is represented in Table 1.

Table 1
Schematic overview of the reference scenario ($R_r = R_1$) and potential alternative different scenarios (R_2, R_3, …, $R_2{}^{i}{}_{-1}$) to be developed, indicating the presence (x) or absence (0) of a species i. The reference scenario $R_r = R_1$ includes all species i, each of the alternative scenarios reduce species richness or share the same species richness but a different species composition and the last scenario $R_2{}^{i}$ contains no species.

Species (s = i)	R_1	R_2	R_3	…	$R_2{}^{i}$
Species 1	x	0	x	…	0
Species 2	x	x	0	…	0
Species 3	x	x	x	…	0
…	…	…	…	…	…
Species i	x	x	x	…	0

2.4. Step 4: Quantifying Ecosystem Function

The ecosystem function was defined as "all the activities of plants, animals and bacteria and their effects on the physical and chemical conditions of their environment" (Tilman et al., 2014).

The reference scenario contains s species (species richness) with species composition $i = 1, 2\ldots, s$ and species abundance a_i. The alternative scenarios contain s' species with species composition $j = 1,2,\ldots s'$ and species abundance a'_j. The number of species that both the reference scenario and the alternative scenarios have in common is denoted as s_c. The functional contribution of species i is denoted as z_i with $\sum_{i=1}^{s} z_i = s\overline{z} = T$ for the reference scenario and $\sum_{j=1}^{s'} z_j = s'\overline{z'} = T'$ where T and T' represent the total function (EF) for all species s or s'.

The change in total function T between the baseline T and each of the alternative scenarios T' is then given by $\Delta T = T' - T$ with the number of $\Delta T_{2^i} - 2 = 1, 2, \ldots, 2^i - 3, 2^i - 2$. This results in a range of ΔT for all species richness levels and depends on the identity of the species removed (since alternative scenarios can have the same species richness but can differ with regards to the identities of the species involved and therefore can also differ with regards to total function T).

2.5. Step 5: Quantifying Ecosystem Services

After a quantification of the total ecosystem function T, the ecosystem services delivered can be quantified. As an example, the increase in pollen grain deposition by pollinators, will be closely linked to an increase in pollination and hence yields. Therefore, extrapolating the results of the Biodiversity–Ecosystem Function relationships (step 4) to ES is an essential step in the valuation process that requires establishing a quantitative relationship between EF and ES. The relationship ES = $f(T)$ is highly specific and depends on the nature of the Ecosystem Function T and the ES. The nature of the EF-ES relationship can be determined by seasonal variability and hence depends on ecosystem function at a specific time of year. For example, for pollination different types of relationships have been found between June pollen concentrations and the yields of dryland cereals on the one hand and between mean cereal yields and mean annual pollination on the other (Muñoz et al., 2000). A time-specific effect is also encountered for biological pest control services when pest populations at a crucial stage of the growth process are more significant than at other periods of the year (Daniels et al., 2017). Carbon sequestration has also been shown to exhibit seasonal variation patterns (Zhao et al., 2016). For the dynamic approach explained here, the existence of a specific time-dependent relationship does not pose any issues for establishing the relationship, due to the continuous nature of the model outputs.

2.6. Step 6: Specification of an Ecological-Economic Linking Function to Determine Benefits

The economic-ecological linking function links the ecosystem services quantified for each scenario to the benefits delivered to humans. It links the ecological model (from EPs to ES) to the economic model (from B to V). The benefits (B) derived from the change in ecosystem services $\Delta ES = ES - ES'$ are related to the actual use of the services (i.e. pollination is linked to yields ($kgha^{-1}\,yr^{-1}$; $numbersha^{-1}\,yr^{-1}$), gross energy ($GJha^{-1}$) or food consumed ($ton\,household^{-1}\,yr^{-1}$)) (Boerema et al., 2017). If the economic-ecological linking function is not known, a number of functions can be simulated, resulting in a range of benefits (Daniels et al., 2017) (i.e. linear, logistic, logarithmic, exponential, …).

2.7. Step 7: Separating the Effects of Species Richness, Composition and Abundance

One of the key questions for maintaining continued provision of ecosystem services is whether the EF and ES depend on the number of species present, on key species, species traits or on composition of the communities (Wall and Nielsen, 2012). The difference in T and ES as a consequence of the changes in biodiversity arises from the cumulative effect of changes in species richness, abundance, and composition. Therefore, the change in total services delivered (ES) is not only due to losses in species richness, but also depends on the number of individuals lost and the composition of the species that remain. In order to separate the effects of richness from composition and abundance changes, the change in total services delivered stems from the Price equation (Fox, 2006; Fox and Harpole, 2008; Fox and Kerr, 2012; Winfree et al., 2015) according to:

$$\Delta ES = ES - ES' = (s_c - s)\overline{x} + (s' - s_c)\overline{x'} + \mathrm{Sp}(w_{\cdot}^{I}, x) + [-\mathrm{Sp}(w_j^{\cdot}, x')] + \sum_{i=1}^{s}\sum_{j=1}^{s'} w_j^i (x'_i - x_i) \quad (1)$$

where Sp denotes the sum of products operator, $w_{\cdot}^{I} = \sum_{j=1}^{s'} w_j^i$, and $w_j^{\cdot} = \sum_{i=1}^{s} w_j^i$. The variable $w_{\cdot}^{I} = 1$ if species i is present at both sites and 0 otherwise, while the variable $w_j^{\cdot} = 1$ if species j is present at both sites and 0 otherwise. The variable w_j^i indicates whether a species is present at both sites, so that $w_j^i = 1$ if $i = j < s_c$ and 0 otherwise so that:

$$\Delta ES = ES - ES' = (RICH\text{-}L) + (RICH\text{-}G) + (COMP\text{-}L) + (COMP\text{-}G) + (ABUN) \quad (2)$$

The first term of Eq. (2) is a measure of the fraction of change in total ES due to species losses from the baseline site (RICH-L) and is analogue to the second term, which represents the fraction of change in ES due to increased species richness (RICH-G). The third term (COMP-L) captures the effects that depend on the identity of the species lost. If species with a low functional contribution are absent from alternative scenario, this will increase average functional contribution. Similarly, the fourth term (COMP-G) captures the effects that depend on the identity of the species gained. The last term (ABUN) captures differences in abundance effects for the species common to both sites. Depending on the ultimate goal of the analysis, the effect of changes in species richness, composition, abundance or functionality can be singled out as a proportion of ΔES delivered and the corresponding values calculated for each component of biodiversity. (i.e. if the goal is to analyse the effect of the loss of species: the ΔES in function of RICH-L (ΔES_{RICH-L}) can be singled out and the benefits and values calculated based on them. For mathematical details or proof of the additionality of the five terms, we refer to appendix S1 in Winfree et al. (2015).

2.8. Step 8: Assessing the Economic Value of Human Benefits

Through employment of the Ecosystem Services Cascade (see Fig. 1), the relationship between a functional group of species and a marketable good can be established. In order to have a realistic representation of the contribution of diversity to changes in welfare, an economic value is attributed to the benefits delivered whereby not just the changes in gross revenues but also the changes in net revenues are to be analyzed. The economic model assesses the costs/benefits of a change in abundance/richness and/or composition by analyzing the effects of the benefits at the income level (i.e. net farm income for changing yields).

The net income for each scenario is defined as $I_N = I_G - TC$ with I_G the gross revenue (price × quantity) and TC the total costs (equaling the sum of all variable and fixed costs). A sensitivity analysis takes into account uncertainty in the data. This results in confidence intervals for the net income for each scenario, which is a function of changes in species richness, composition and/or abundance changes.

2.9. Step 9: Determining the Indirect Use Value of the Functional Group of Species

Throughout the methodology and for each step of the Ecosystem Services Cascade, the contribution of more or less biodiversity for the delivery of economic value can be traced back to changing levels of species richness, composition, and abundance. The changing levels of gross or net revenue therefore correspond to a specific combination of richness, composition or abundance levels and make up the indirect use values of the species under analysis.

3. Applying the Methodological Framework: the Indirect Use Value of Freshwater Aquatic Macroinvertebrate Diversity

In this illustrative example we examine (i) the relationship between the diversity of aquatic macroinvertebrate prey and juvenile Chinook salmon (*Oncorhynchus tshawytschas*) in rivers and streams, (ii) the quantity of adult Chinook salmon that are later available to the commercial salmon fishery, and ultimately, (iii) the economic value of freshwater macroinvertebrate diversity.

Chinook salmon, also referred to as “king” or “Tyee” salmon, are the largest species of Pacific salmon (Fig. 2).

Due to their large size and high fat content, adult Chinook salmon are a prized and highly sought-after resource by commercial, recreational and subsistence fisherman. The importance of Chinook salmon for the economy – in part - stems from the annual commercial Chinook salmon landings and values.[1] For the period 2000–2015, commercial Chinook salmon landings in the United States averaged 8176 tons per year with an average total yearly value of 4,3 million $ (or $5,24\$kg^{-1}$).[2]

Like other salmon species, Chinook salmon have a complex life cycle that spans oceans, estuaries and rivers. Although Chinook salmon generally spend a majority of their life in salt water where they are commonly targeted by commercial fisheries, the first one to two years of their life is spent in freshwater environments, generally streams and rivers. During their freshwater residence salmon consume a variety of food resources, but aquatic macroinvertebrates species—especially insects (Fig. 3)—make up a majority of their diet. For example, Bellmore et al. (2013) observed 37 different aquatic macroinvertebrate taxa in juvenile Chinook salmon diets, and found that most of these taxa were important for fish growth. Although aquatic invertebrates have no

[1] https://www.st.nmfs.noaa.gov *Fisheries of the United States*, issued annually by the National Marine Fisheries Service (NMFS) and the National Oceanic and Atmospheric Administration (NOAA) (last updated June 15th, 2017).

[2] http://www.st.nmfs.noaa.gov (last updated April 4th 2017).

Fig. 2. Chinook salmon (left) are the largest species of Pacific salmon, and have long been harvested for commercial purposes (photo courtesy of Gregg Morgan). The photograph on the right shows seine netters catching salmon on the Columbia River, Oregon, USA, circa 1914.

Fig. 3. Chinook salmon primarily forage on aquatic insects and other macroinvertebrates during their freshwater residence. The images above are common aquatic insects consumed by juvenile Chinook, which include (from left to right): mayflies (Ephemeroptera; photo courtesy of Colden V. Baxter), stoneflies (Plecoptera) and caddisflies (Trichoptera).

Table 2
Defining the Ecosystem Services Cascade to examine the relationship between freshwater aquatic macroinvertebrate diversity and their contribution to the commercial fishing industry.

Functional group (FG)		Ecosystem properties (EP)	Ecosystem function (EF)	Ecosystem service (ES)	Benefit (B)	Value (V)
Freshwater aquatic macroinvertebrates in salmon streams	➔	1) Diversity and population parameters of the aquatic macroinvertebrates 2) Consumer-resource interactions 3) Inputs of energy, nutrients and organic matter 4) Environmental conditions	Food availability for juvenile salmon in fresh water	Edible salmon	Availability of salmon for salmon fishing industry	Annual revenues of the commercial fishing industry

direct value to humans, this and other studies suggest that changes in aquatic macroinvertebrate diversity could impact the capacity for streams to support juvenile salmon, which in turn, could impact the number and total value of adult salmon caught by the commercial fishing industry.

3.1. Defining the Relationship Between Macroinvertebrate Diversity and Their Contribution to the Fishing Industry (Step 1)

In a first step, the Ecosystem Services Cascade defines the scope and sets the boundaries for the analysis, linking the diversity of macroinvertebrates in freshwater river systems to the economic value created for the commercial fishing industry. This ultimately results in an indirect use value for freshwater macroinvertebrates (Table 2).

The functional group to be valued is the macroinvertebrates in freshwater rivers and streams along the north Pacific coast where juvenile Chinook salmon reside. These flowing water-bodies generally contain a diversity of different macroinvertebrate species that are consumed by juvenile salmon (Bellmore et al., 2013; Nielsen, 1992; Reece and Richardson, 2000).

The four main ecosystem properties (EP) determining ecological function are:

1) Diversity and population parameters of the aquatic macroinvertebrates: i.e. species richness $s = 25$, species composition $i = 1,2,3\ldots, 25$, biomass a_i (g/m^3) and functional contribution z_i. These macroinvertebrates provide a functional contribution z_i to the overall ecosystem function (EF) of interest, which is the availability of food resources necessary for the growth and survival of juvenile salmon (step 3).
2) Consumer - resource interactions i.e. predator-prey interactions
3) Inputs of energy, nutrients and organic matter
4) Environmental conditions: i.e. river discharge, water temperature, water clarity, dissolved nutrient concentrations, light availability, and channel hydraulics

The ecosystem services provided to humans are provisioning services in terms of the number juvenile Chinook salmon that survive to

adulthood. The benefits from the ecosystem services stem from the availability of these adult Chinook salmon for the commercial fishing industry and human consumption. The value of benefits is derived from the annual revenues of the commercial fishing industry. Ultimately, the indirect use value is determined by the change in annual revenues due to changes in aquatic macroinvertebrates.

3.2. Quantitatively Linking Macroinvertebrate Diversity to Salmon Survival (Step 2)

The dynamic ecological model explores the relationship between freshwater macroinvertebrate diversity and the presence of Chinook salmon, by examining the food web responses to changes in macroinvertebrate diversity. Because populations of many macroinvertebrates observe strong seasonal fluctuations in abundance, a dynamic ecological model is capable of accounting for these seasonal dynamics. The model used here is the Aquatic Trophic Productivity (ATP) model (Bellmore et al., 2017).

The ATP model represents the generalized trophic structure of river food webs (Fig. 4), whereby aquatic macroinvertebrate populations are linked to the dynamics of upper (fish) and lower trophic levels (periphyton and terrestrial detritus such as leaf litter) via a series of linked consumer-resource equations (see Bellmore et al., 2017). In turn, the strength of these consumer-resource interactions, are connected to the environmental conditions of the stream and the adjacent riparian zone. These environmental conditions include: river discharge, water temperature, water clarity, dissolved nutrient concentrations, light availability, and channel hydraulics (i.e., water depth, width and velocity). Water temperature, for example, influences consumption and respiration rates for all the members of the food web, including macroinvertebrates. The model simulates the biomass-dynamics of aquatic macroinvertebratres on a daily time-step in units of grams of ash-free-dry-mass per square meter of stream bed (g AFDM m^{-2}). For further details on the model see Bellmore et al. (2017).

As invertebrate populations fluctuate, either due to top-down predation by fish or variation in other environmental conditions, fish switch to forage on those macroinvertebrates that are most abundant. Fish consumption and growth is linked to juvenile fish survival in two ways: (1) starvation mortality, if food is limiting fish lose mass and succumb to starvation, and (2) size-based mortality, smaller fish have higher mortality rates than larger fish, thus, when fish grow faster (i.e., when macroinvertebrate food resources are plentiful) they "escape" higher mortality rates. Following this logic, reductions in macroinvertebrate diversity may result in longer periods of low food availability, higher juvenile salmon mortality, and ultimately, fewer salmon that grow to adulthood and are available for the commercial fishery.

The ATP model was used to simulate the dynamics of 25 different aquatic macroinvertebrate species, which were coded into the model as 25 separate biomass stocks. Stocks were not coded to represent any specific set of macroinvertebrate species, but rather, physiology parameters (e.g., consumption and respiration rates, food preferences, foraging efficiencies, temperature sensitivity, etc.) were adjusted, via a randomization process, to create a diverse assemblage of macroinvertebrates that respond differently to environmental and food web conditions. Details on coding of the 25 macroinvertebrate species are in Annex A.

We parameterized the model with environmental conditions (i.e., water temperature, discharge, channel hydraulics) representative of Pacific Northwestern streams where juvenile Chinook salmon rear before migrating to the ocean. We chose this location because the environmental inputs need to parameterize the model were readily available, and because this river system is representative of snow-melt fed rivers where Chinook salmon commonly spawn and rear. That said, we acknowledge that the relationship between macroinvertebrate diversity and salmon survival could vary significantly across the range of Chinook salmon.

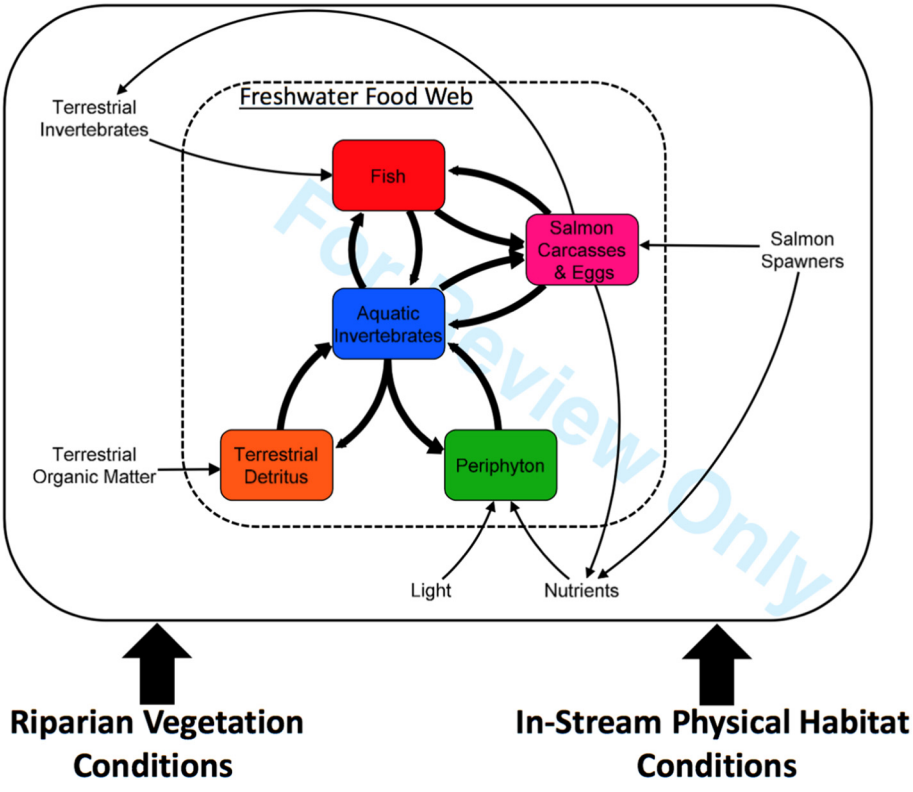

Fig. 4. The Aquatic Trophic Productivity Model is a system dynamic model consisting of (i) biomass stocks (fish, aquatic invertebrates, salmon carcasses & eggs, periphyton and terrestrial detritus) (ii) consumer-resource interactions (arrows among the biomass stocks), (iii) inputs of energy (light), nutrients and organic matter (terrestrial organic matter and invertebrates, salmon spawners) and (iv) linkages to in-stream physical habitat conditions and riparian vegetation conditions (figure from Bellmore et al., 2017).

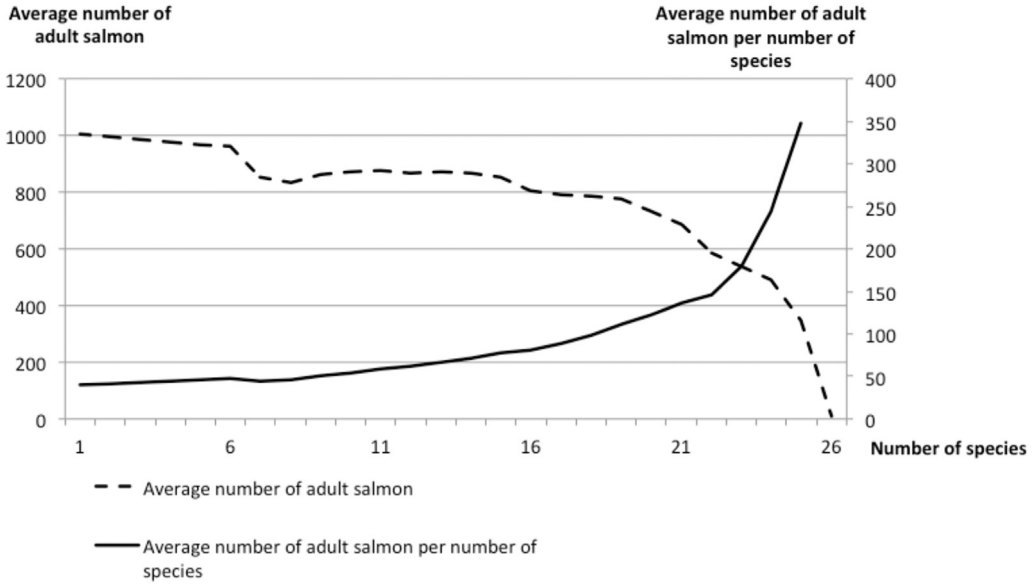

Fig. 5. Represents the average total number of edible adult salmon $\overline{Y}$ and the average number of salmon per number of aquatic invertebrate species $\overline{Y}/s$ for $s = 1,2\ldots 25$.

3.3. Alternative Scenario Development (Step 3)

Alternative scenarios were created by conducting removal experiments by iteratively removing one aquatic macroinvertebrate species at a time from the freshwater food web. A total of 100 removal experiments were conducted, each starting from the reference scenario R_r containing all 25 aquatic invertebrates ($s = 25$). Each experiment randomly removed one species at a time until no species were left, resulting in 25 alternative scenarios per experiment. Therefore a total of 100 experiments and 2500 alternative scenarios were developed.

3.4. Quantifying Changes in Ecosystem Function With Reduction of Macroinvertebrate Diversity (Step 4)

Aquatic macroinvertebrates provide many important ecological functions EFs (e.g., organic matter processing, nutrient cycling, etc.) in stream ecosystems. However, the EF of interest in this analysis is the amount of prey or food resources macroinvertebrates provide to juvenile salmon. As stated in Section 3.2, more macroinvertebrate biomass equates to higher juvenile salmon growth and survival. Thus, the change in total ecosystem function between the baseline scenario T and each alternative species removal scenario T' is the difference in total macroinvertebrate biomass (summed across all species). In this analysis we assume that each invertebrate species has the same nutritional value (i.e., digestibility) for juvenile Chinook salmon.

3.5. Effects of Macroinvertebrate Diversity on Adult Salmon Abundance (Step 5)

The relationship between the ecosystem function, macroinvertebrate biomass, and the ecosystem service, adult salmon abundance was quantified using the dynamic equations contained within the ATP model (see Section 3.2 and Bellmore et al., 2017). For the reference scenario (S_r) and each removal experiment whereby successively one species at random was removed, the resulting average number of edible adult salmon Y was modeled (Fig. 5). The reference scenario, including all 25 aquatic invertebrate species reveals 1005 individual adult salmon. The average number of salmon $\overline{Y}$ for decreasing aquatic invertebrate richness was calculated resulting in $\overline{Y}$ for each level of species richness (i.e. $\overline{Y}$ for 24 random aquatic invertebrate species equals 996 and $\overline{Y}$ for 23 random aquatic invertebrate species equals 988). Also, the average number of salmon per number of aquatic macroinvertebrate species ($\overline{Y}/s$) with $s = 1,2, \ldots 25$ was analyzed (Fig. 5).

For each scenario developed, the individual functional contribution x_i of each aquatic invertebrate species s_i to the total number of adult salmon Y is calculated and standardised per gram of biomass per m^2 for species s_i (Fig. 6).

Table 3 represents an overview of the results with column (1) to (4) the results from the dynamic ecological model, and column (5) to (14) the extrapolation of these results for their effect on the commercial fishing industry. They show that a reduction in species diversity of 1 decreases adult salmon abundance by 0,88% (column 4). A decrease of species diversity of 2 reduces salmon abundance by 1,67% up until the complete loss of aquatic species diversity would result in the loss of all adult salmon. The decrease in species diversity results in non-linear losses with relatively higher losses under lower species diversity, indicating the importance of a high species diversity.

3.6. Benefits of Aquatic Invertebrate Species Richness for Salmon Availability (Step 6)

The benefits (B) derived from the change in ecosystem services $\Delta ES = ES - ES'$ are the related changes in catch by the commercial fishing industry. The decrease in aquatic invertebrate species diversity reduces the number of adult salmon, thereby reducing the potential for commercial catch. For the period 2000–2015, commercial Chinook salmon landings averaged 8176 kton per year. The ecological economic linking function therefore links the provisioning of ecosystem services to the benefits delivered to humans. The relationship between abundance and catch per unit effort is represented by a logarithmic relationship (Guzzo et al., 2014) (Fig. 7; Table 3).

Reducing the species diversity by 1 resulted in a decrease of 8,88% in the number of adult salmon, thereby reducing catch from 8,18 to 8,14 kton per year. Due to the logarithmic shape of the function, the losses in catch have a higher impact when the decrease in salmon abundance is higher (see Table 2 column (5)).

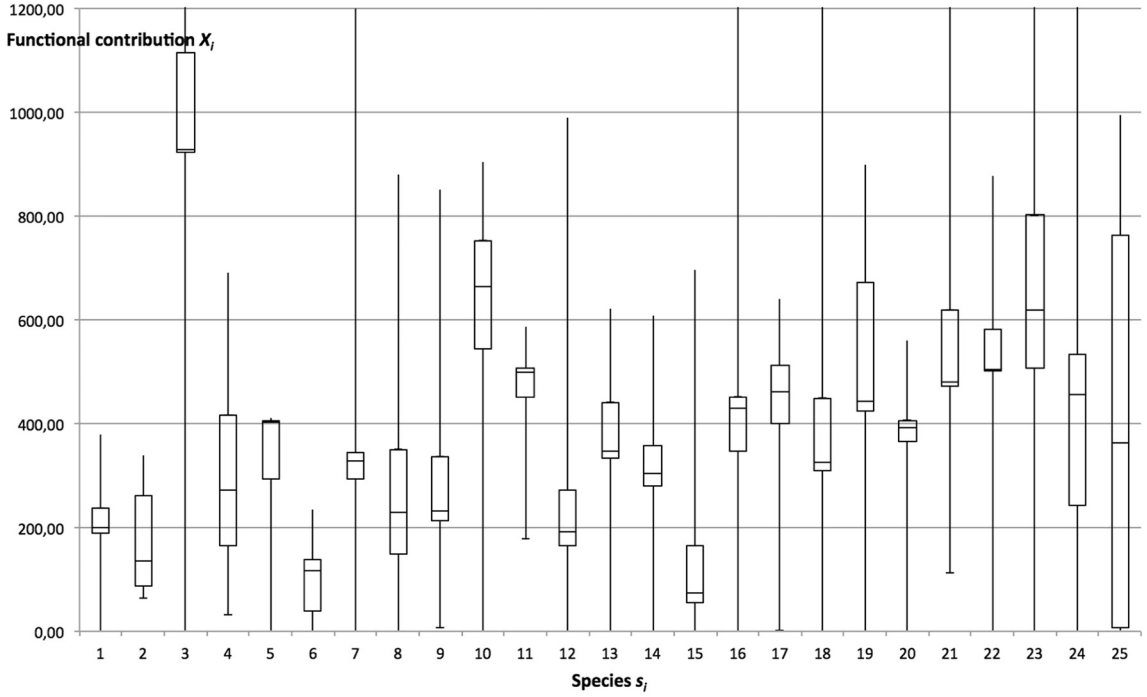

Fig. 6. Boxplot showing the functional contribution x_i of species i to adult salmon abundance Y.

3.7. Separating the Effects of Macroinvertebrate Species Richness, Composition and Abundance (Step 7)

In order to separate the effects of richness, composition and abundance on the number of edible adult salmon Y, all components of the Price equation are calculated according to Eq. (2) (Fig. 8).

RICH-G and COMP-G = 0 for all scenarios since no species were added. The results show that with high species diversity, the effect of species loss on the total number salmon is relatively low (2%) and that the composition (50%) and abundance (48%) of species are the main determinants for functioning. However, when species diversity decreases, the effect of species loss becomes increasingly important (48%) while the effect of composition (4%) decreases in importance.

3.8. The Economic Value of Salmon (Step 8)

A reduction in catch due to reduced salmon presence has important effects for the commercial fishing industry's income generation and annual total catch value losses (Table 3 column 7).

Column 12, 13 and 14 (Table 3) represent the total catch value losses which can be attributed to changes in species diversity, changes in species composition and changes in species abundance and is represented in Fig. 9. The separation of effects reveal that species composition effects are the most important factor under high species diversity but ceases to be the most important factor when > 13% of ecosystem services provisioning (salmon abundance) is lost, after which species richness becomes the most important factor. Only at extreme low levels of diversity (and when > 50% of ES are lost), species abundance becomes the most important factor to which value losses can be attributed.

3.9. The Indirect Use Value of Aquatic Invertebrates (Step 9)

The cost of losing species increases with decreasing species diversity. The marginal value of species (Table 3 column 8) is defined as the total catch value loss divided by the total number of species lost. The marginal value varies from 0,19 million $ per species lost at high species diversity, to 1,79 million $ at low species diversity. For example, in the case when only 10 species out of 25 remain, we found an average annual gross value loss of 5,22 million $ representing a loss of 0,35 million $ per species lost. Under high species richness ($20 < s < 25$), the loss of a single aquatic invertebrate species represents an average gross revenue loss of 0,19–0,25 million $. When species diversity is lower ($19 < s < 5$), average gross annual loss are higher amounting to 0,24–0,55 million $ per species lost, and increase to 1,79 for the loss of all species, irrespective of the identity of the species lost (see Fig. 10). Separating the effect of species richness from composition and abundance changes (see Section 3.6) also indicated that the importance of species richness increased with declining species diversity. The richness effect for the loss of the first species accounted for 2,07% of the value lost and increased gradually to 48,78% for the loss of the last species (see Table 3). Hence, the effects of species richness represent a gross revenues loss of 0,004 million $ for the loss of the first species and increases under high species diversity to 21 million $ for the loss of a single species under low species diversity (Table 3 column 12).

4. Discussion

Integrating a market-based approach with a production function approach relies on actions that occur in the market and makes use of market prices for products or services that rely on renewable natural resources as inputs into a production process. Market-based methods usually focus on private costs and benefits, thereby neglecting the social costs and benefits of changes at the ecosystem level. Future research could examine how the social costs and benefits can be included in the methodology to result in a more holistic value for biodiversity. Also, problems may arise from multi-specification of the ecological-economic relationship or double counting (TEEB, 2010).

Therefore, and agreeing with Hamilton (2013), the aggregation of different values derived from functional diversity may give rise to issues of double counting. The marginal values derived here are not to be used in cost benefit analysis or national accounting, since the marginal values are already capitalized in the marketable goods from which they were estimated. The marginal value estimates derived here can provide information to be included in financial risk analysis, when private

Table 3
Overview of the results. The underlined numbers in column 12, 13, 14 indicate which aspect of diversity (richness, composition or abundance) contributes most to value losses encountered.

Model outputs				Extrapolation to pacific northwest river systems										
Species richness (1)	Salmon (2)	Delta ES (3)	Delta ES (%) (4)	Catch (kton/y) (5	Total catch value (million $) (5,24$/kg) (6)	Total catch value loss (million $) (7)	(%)	Value lost (million $) per species lost (8)	RICH-L % (9)	COMP-L % (10)	ABUN % (11)	Total value loss due to species richness losses (12)	Total value loss due to species composition changes (13)	Total value loss due to species abundance changes (14)
												(million $)	(million $)	(million $)
25	1004,61			8,18	42,84									
24	995,74	8,88	0,88	8,14	42,65	0,19	0,44	0,19	2,07	50,22	47,70	0,004	0,095	0,090
23	987,85	16,77	1,67	8,06	42,23	0,61	1,42	0,30	4,31	50,42	45,27	0,026	0,306	0,275
22	975,27	29,34	2,92	8,02	42,02	0,82	1,91	0,27	6,71	50,74	42,55	0,055	0,415	0,348
21	966,75	37,86	3,77	7,98	41,82	1,03	2,40	0,26	9,33	50,96	39,71	0,096	0,523	0,408
20	963,04	41,58	4,14	7,94	41,61	1,24	2,89	0,25	12,22	51,05	36,72	0,151	0,631	0,454
19	854,73	149,89	14,92	7,90	41,40	1,45	3,38	0,24	19,03	55,28	25,69	0,275	0,799	0,372
18	835,20	169,42	16,86	7,86	41,19	1,66	3,86	0,24	24,27	56,32	19,41	0,402	0,933	0,321
17	860,68	143,94	14,32	7,82	40,98	1,87	4,35	0,23	28,43	55,05	16,52	0,530	1,027	0,308
16	871,88	132,73	13,21	7,74	40,56	2,28	5,33	0,25	33,61	54,54	11,85	0,768	1,246	0,271
15	874,58	130,03	12,94	7,66	40,14	2,70	6,31	0,27	39,79	54,43	5,78	1,076	1,472	0,156
14	866,32	138,29	13,76	7,58	39,72	3,12	7,29	0,28	45,39	52,65	1,96	1,418	1,644	0,061
13	872,27	132,34	13,17	7,50	39,30	3,54	8,27	0,30	46,21	45,60	8,19	1,637	1,615	0,290
12	865,35	139,26	13,86	7,42	38,88	3,96	9,25	0,30	46,55	38,54	14,92	1,844	1,527	0,591
11	852,59	152,02	15,13	7,30	38,25	4,59	10,71	0,33	46,73	33,19	20,08	2,145	1,523	0,922
10	804,20	200,42	19,94	7,18	37,62	5,22	12,18	0,35	46,17	26,87	26,96	2,410	1,402	1,407
9	793,01	211,60	21,06	7,06	36,99	5,85	13,65	0,37	46,51	22,59	30,89	2,720	1,321	1,807
8	785,15	219,47	21,84	6,90	36,16	6,69	15,61	0,39	46,92	18,29	34,79	3,137	1,223	2,326
7	777,15	227,47	22,64	6,70	35,11	7,73	18,05	0,43	47,31	15,04	37,65	3,659	1,163	2,912
6	732,42	272,20	27,09	6,46	33,85	8,99	20,99	0,47	47,23	12,43	40,34	4,247	1,118	3,627
5	686,65	317,96	31,64	6,18	32,38	10,46	24,41	0,55	47,27	10,43	42,31	4,944	1,090	4,425
4	586,52	418,09	41,60	5,78	30,29	12,56	29,31	0,63	46,83	7,54	45,63	5,879	0,947	5,729
3	536,67	467,94	46,56	5,22	27,35	15,49	36,15	0,74	47,20	5,81	46,98	7,312	0,900	7,278
2	488,55	516,06	51,35	4,50	23,58	19,26	44,96	0,88	47,82	3,96	48,22	9,211	0,763	9,288
1	347,53	657,08	65,39	3,30	17,29	25,55	59,64	1,11	48,30	2,69	49,01	12,340	0,688	12,522
0	10,05	994,57	98,97	0,00	0,00	42,84	100,00	1,79	48,78	2,20	49,02	20,898	0,941	21,001

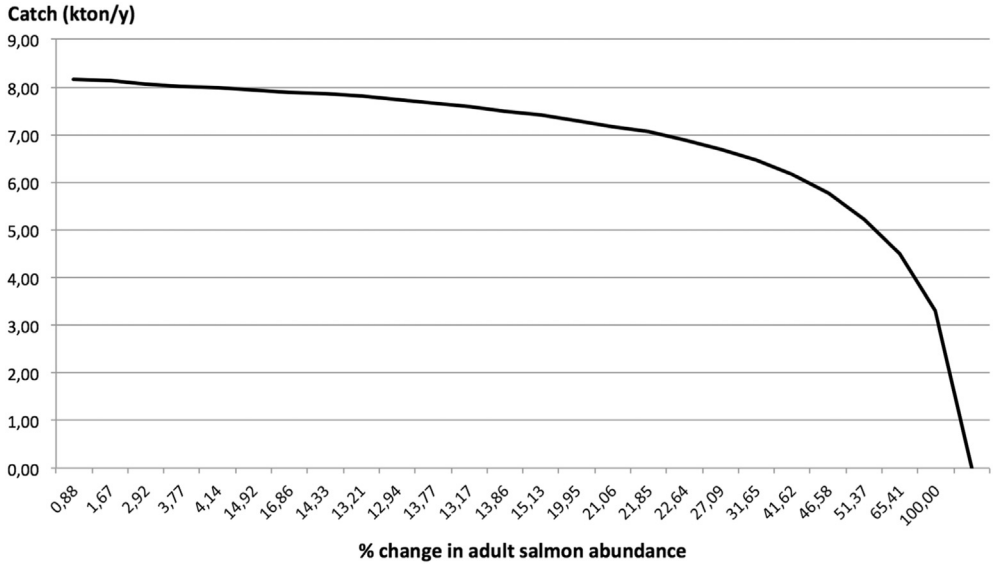

Fig. 7. The ecological economic linking function shows the effect of a change in adult salmon abundance on the catch of salmon.

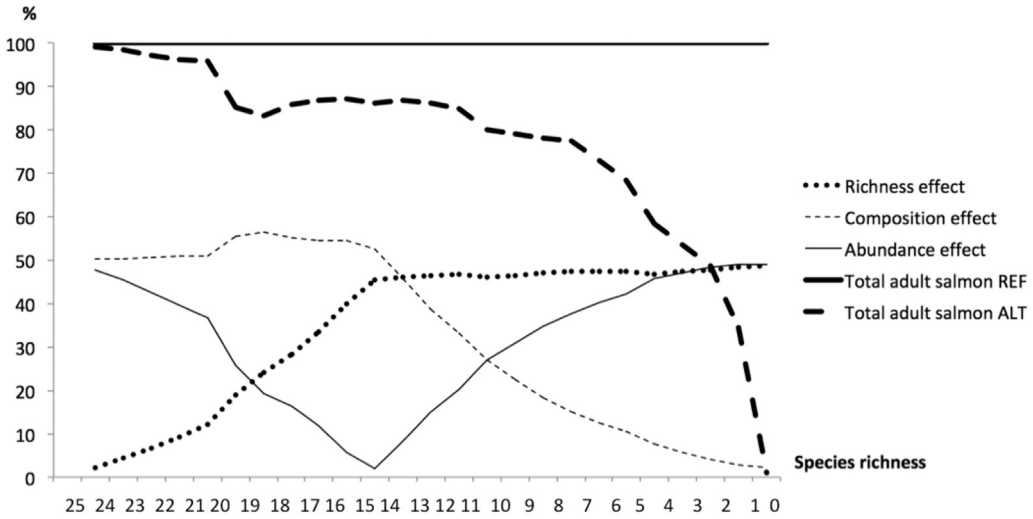

Fig. 8. Shows the effect of richness, composition and abundance on the number of adult salmon Y at each level of macroinvertebrate species richness.

companies are dealing with uncertainty over natural resources and the provision of marketable goods depending on functional diversity.

The case study application presented here illustrates the potential grave economic consequences of the loss of freshwater biodiversity for the commercial salmon fishing industry. No external costs of the effects of macroinvertebrate losses in other parts of the ecosystem were included in the analysis. The analysis focused on gross revenue losses for the commercial fishing industry since this is the first market price encountered in the production chain. Other valid endpoints further down the production process include consumer values such as nutritional value, taste and health benefits. Other values such as for the recreational fisherman, tourism and spiritual values are also likely to be affected by a change in macroinvertebrate diversity but have not been included in this analysis.

The results confirm earlier findings that "the impact of biodiversity on any single ecosystem process is nonlinear and saturating, such that change accelerates as biodiversity loss increases" (Cardinale et al., 2012). In this analysis, the decrease in species diversity results in nonlinear losses with relatively higher losses under lower species diversity, indicating the importance of a high species diversity. This also suggests that ecosystems with higher macroinvertebrate diversity may be more resilient to environmental alternations that result in species extirpations, versus those with already low diversity. Also, the results support other studies in that functional traits, such as richness and diversity, display a predominantly positive relationship and species level traits such as species abundance were found to benefit a number of services (Harrison et al., 2014). Overall, the results in this analysis are in line with global consensus that "diverse communities are more productive because they contain key species that have a large influence on productivity, and differences in functional traits among organisms increase total resource capture" (Cardinale et al., 2012). In their analysis, Winfree et al. (2015) state that it is species abundance of common species that drives ecosystem service delivery whereas richness changes are relatively unimportant because they primarily involve rare species that contribute little to function. In our analysis, this statement can only partly be supported at extreme low levels of diversity (i.e. when 2 species or less out of 25 remain).

The results in this analysis could further provide an indication of how the importance of functional or species traits might gradually decrease or increase as a function of the number of species encountered in the ecosystem. It might be that the V-shaped curve of the abundance effect represented in Fig. 8 is related to the compositional response driven by the presence of certain "dominant species" that are highly abundant and that strongly compete with the other species. The

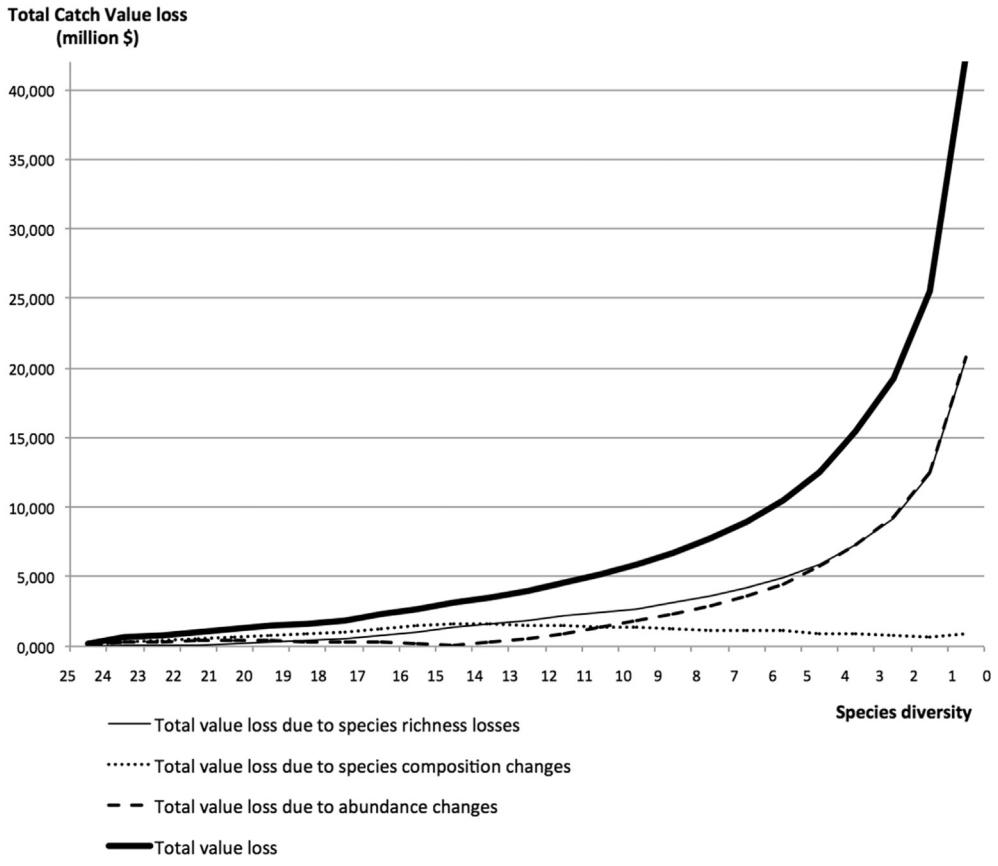

Fig. 9. Shows the total value losses of salmon catch in terms of gross revenues, as well as the total value losses due to changes in species richness, composition and abundance.

removal of important dominant species early on influences the abundance of other species because they are released from strong competition. However, as more species are randomly removed, the impact of removing a dominant competitor decreases (because there are less species to release from their competitive effects). Eventually, this switches as the removal of the few species that remain are more likely to be important to maintaining adult salmon abundance.

Nevertheless, modeling complex relationships is subject to large uncertainties due to the large uncertainties encountered in modeling food web dynamics, market dynamics and human preferences. We acknowledge the need for a larger number of case studies applying the methodology in other ecosystems with other functional groups and other ecosystem services in order to gain insight on the potential wider applicability of the methodology.

Last, the methodology could be extended to include the effect of management practices. Steps 1 to 9 of the methodology did not specify

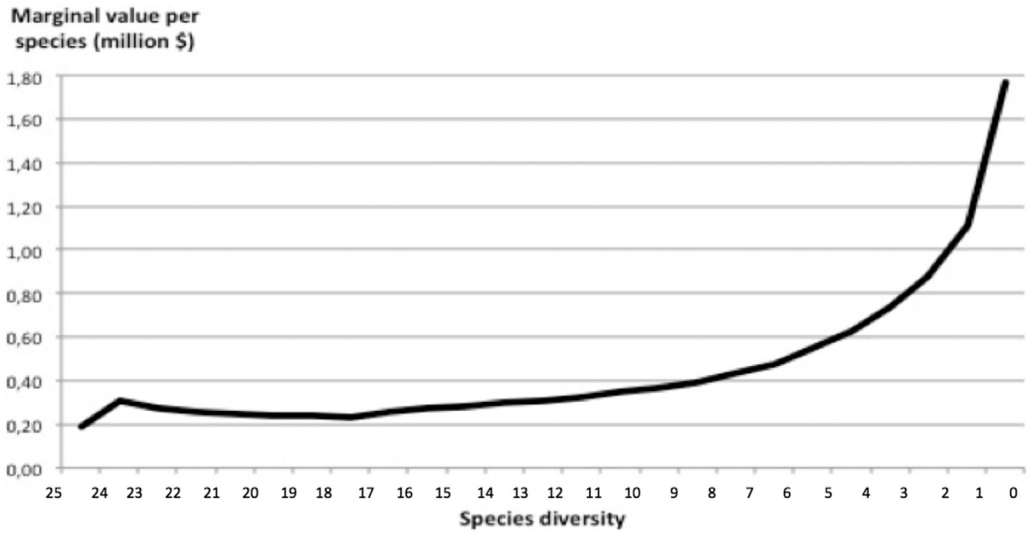

Fig. 10. Shows the cost of losing species (marginal value per species) in function of the level of species richness encountered, irrespective of the identity of the species.

any cause(s) for changing biodiversity levels. However, the framework can be extended to include the valuation of management practices by examination of their effects on biodiversity and hence of their effects on the marketed goods or ecosystem services. With the proposed methodology, we hope to facilitate and encourage further research on the effect of changes in biodiversity for the economy and human well-being that effectively take into account the importance of species diversity for ecological function, with the ultimate aim of assessing the effects of ecosystem management for the well-functioning of ecosystems.

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Appendix A. Creating Invertebrate "Pseudo-species"

We 'created' 25 different aquatic invertebrate species for the model analysis by randomly selecting the values of 11 parameters in the Aquatic Trophic Productivity (ATP) model that control invertebrate physiology and population dynamics (Table A1). These "pseudo-species" were created via Latin hypercube sampling (LHS). In LHS, the specified range for each parameter is divided into N strata of equal width (where $N = 10{,}000$), and a random parameter value is selected within each strata. From the 10,000 possibilities for each parameter, LHS randomly selected one of these values (without replacement). We did this 10,000 times, to create 10,000 randomly selected parameter combination that represents 10,000 'potential' aquatic invertebrate species. These parameter combinations were then simulated in the ATP model to create modeled biomass dynamics for 10,000 aquatic invertebrate species. However, many of these parameter combinations produced species that were unrealistic. Many parameter combinations, for example, produced invertebrate biomasses that quickly crashed (or approached zero), or were unrealistically high. To account for this, we removed those species those maximum modeled biomass for the year was (after reaching equilibrium) < 0.02 and > 1.9. Removing these species left 1281 species that we deemed to be "realistic"; i.e., produced invertebrate biomasses that are similar to those reported in the literature (Water, 1977; Huryn and Wallace, 2000; Bellmore et al., 2013). From those 1281 species we randomly selected 25 to include in our analysis.

Table A1
Parameters used to code aquatic invertebrates in the ATP model, including: a description of each parameter, parameter units, the range of values used in the Latin hypercube analysis to create alternative species, and literature source(s).

Parameter	Parameter description	Units	Value range	Sources
$cons_{max,I}$	Maximum rate of consumption when temperature is optimum	$g\,g^{-1}\,day^{-1}$	0.05–0.8	(D'Angelo et al., 1997; Grafius and Anderson, 1979; McIntire, 1996; Rutherford et al., 2000)
$Temp_{opt,I}$	Optimum temperature for consumption	°C	5–25	(McIntire, 1996; Rutherford et al., 2000)
γ_I	Dimensionless self-interaction parameter	Unitless	1–10	(Bellmore et al., 2017)
k_I	Prey biomass half saturation level	g AFDM m^{-2}	1–15	(Bellmore et al., 2017)
$r_{ref,I}$	Rate of respiration at 20 °C	$g\,g^{-1}\,day^{-1}$	0.01–0.1	(D'Angelo et al., 1997; McIntire, 1996; Rutherford et al., 2000)
m_I	Daily mortality rate	$g\,g^{-1}\,day^{-1}$	0.005–0.07	(Bellmore et al., 2017)
a_I	Shape parameter for export rate equation	Unitless	2–15	(Bellmore et al., 2017)
B_I *	Refuge biomass that is invulnerable to predation	g AFDM m^{-2}	0–1	Assumed
$Pref_{carcass}$	Preference of aquatic invertebrates to consume salmon carcass material	Unitless	0–1	Assumed
$Pref_{periphyton}$	Preference of aquatic invertebrates to consume perphyton	Unitless	0–1	Assumed
$Pref_{detritus}$	Preference of aquatic invertebrates to consume terrestrial detritus	Unitless	0–1	Assumed

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