Modelling the Response of a Terrestrial Food Web to a Change in Aquatic Subsidies through Environmental Stress

Stephen Esosa Osakpolor

from Benin City, Nigeria

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Thesis examiners:

Prof. Ralf B. Schäfer, Rheinland-Pfälzische Technische Universität Kaiserslautern-Landau

Prof. Shawn J. Leroux, Memorial University of Newfoundland and Labrador

Fachbereich: Natur- und Umweltwissenschaften

Rheinland-Pfälzische Technische Universität Kaiserslautern-Landau

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Summary

Ecosystems are interconnected through the exchange of resources known as subsidies. Subsidies have the potential to affect the receiving ecosystem, altering its productivity and trophic cascade. The boundary between aquatic and terrestrial ecosystems provides a clear distinction between aquatic and terrestrial organisms and is a particularly interesting location for studying resource subsidies. Process-based models can aid in predicting the effects of anthropogenic stressors on food webs and understanding the functioning of meta-ecosystems. The goal of this thesis is to contribute to the development of theories on how changes in subsidies affect recipient ecosystems using aquatic-terrestrial interface as a case study.

In this thesis, a review of process-based food web models applied to the aquatic-terrestrial interface (aquatic-terrestrial models) and theoretical meta-ecosystems (theoretical models) was carried out (**chapter 2**). Results show that the models have enhanced our understanding of how terrestrial subsidies affect aquatic ecosystem. General understanding of how subsidies affect the stability and functions of meta-ecosystems was also enhanced. However, existing aquatic-terrestrial models focused primarily on how subsidies from terrestrial ecosystems affect aquatic ecosystems, with none considering reciprocal flows. Furthermore, the quality characteristics of subsidies were not taken into account, despite potential differences from alternative local resources. Therefore, **chapters 3 and 4** developed theories using terrestrial ecosystems with aquatic subsidies as a case study. **Chapter 3** focused on how changes in subsidy quality affect the recipient ecosystem and hypothesized that changes in subsidy quality have a cascading effect on the recipient ecosystem (subsidy quality hypothesis). However, the model predictions were most sensitive to the input rate of inorganic nutrients in the recipient ecosystem, indicating that ecosystems are controlled by both top-down (TD) and bottom-up (BU) processes. **Chapter 4** shows that the TD and BU processes of ecosystems interact antagonistically.

The generated theories can be integrated into empirical research by testing predictions, assumptions, using model equations, and adopting the framework. This thesis improves our understanding of the impacts of subsidies on recipient ecosystems. Future meta-ecosystem models may consider the cross-ecosystem flow of information to further enhance our understanding of meta-ecosystems. Additionally, aquatic-terrestrial models developed to predict algae blooms may consider developing trait-based models to improve predictions.

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Chapter 1: Introduction and objectives

1.1 Aquatic-terrestrial linkage

The concept of ecosystems has evolved over time, with early views suggesting that ecological systems were largely self-contained and that their dynamics were determined by local processes (Forbes, 1887). However, this narrow understanding changed with a growing recognition of the importance of energy flows and movements of energy, organic and inorganic material across ecosystems (e.g., Levin, 2005; Lindeman, 1942; Polis and Strong, 1996). This changed the concept of ecosystems from being independent to being interconnected via multiple linkages of varying strength (Holt, 2008; Loreau et al., 2003; Knight et al., 2005). One of the key processes that links ecosystems and crosses ecosystem boundaries is resource subsidies, which are flows of biologically fixed energy and nutrients from one ecosystem to another (Richardson et al., 2010). Subsidies have effects on recipient habitats at individual, population, community and ecosystem level (Baxter et al., 2005), and can potentially alter the productivity of recipient systems (Nakano and Murakami, 2001), and the impact they have depends on several factors. For example, the timing of the subsidy is an important consideration (Leroux and Loreau, 2012), as well as the ability of top predators to exploit it (McCary et al., 2021). The impact of resource subsidies can also be influenced by the ratio of subsidies to comparable resources in the recipient system and its spatial and temporal extent (Marczak et al., 2007).

Some of the most striking examples of resource subsidies occur at the boundary between aquatic and terrestrial ecosystems. This is likely due to the well-defined physical boundary between these ecosystems, which allows for a clear distinction between aquatic and terrestrial organisms (Richardson et al., 2010). Aquatic-terrestrial linkages have been found to exist in various ecosystems including streams (Kato et al., 2003; Kowarik et al., 2021), lakes (Twining et al., 2021), and ponds (Fehlinger et al., 2022). These linkages involve the transfer of subsidies from terrestrial to aquatic ecosystem and vice versa (see Richardson et al., 2010 for examples). For instance, terrestrial leaves and invertebrates fall into streams subsidizing its consumers, while emerging aquatic insects can be consumed by terrestrial-dwelling birds, bats, and spiders (Baxter et al., 2005) with potential indirect effect on the whole terrestrial system (Bultman et al., 2014; Henschel et al., 2001). The magnitude of these cross-ecosystem subsidies varies based on several factors including the cover of riparian vegetation (Edwards and Huryn, 1995), catchment geomorphology (Iwata, 2007), land use (Krell et al., 2015), and climate (Boulton et al., 2008; Freitag, 2004).

The quantity of terrestrial subsidies to aquatic ecosystem is greater than aquatic subsidies to terrestrial ecosystem (Bartels et al., 2012) due to the concave profile of aquatic ecosystem (i.e., gravity induced cross-ecosystem flows). This is also reflected in most researches focusing on how terrestrial subsidies affect aquatic ecosystems than vice versa. However, recent studies have begun to focus more on subsidy flow from aquatic to terrestrial ecosystem (Schulz et al., 2015). Nonetheless, these studies have mostly looked at the first recipient in the terrestrial food web (e.g., Graf et al., 2020; Kowarik et al., 2021). Therefore, the extent to which aquatic subsidies translate to effects cascading top-down or bottom-up on the terrestrial food webs remains largely unknown (but see Henschel et al., 2001; Graf et al., 2017) (figure 1a) (**objectives 2 and 3**).

1.2 Effect of anthropogenic stressors on aquatic to terrestrial subsidies

Aquatic subsidies can flow into terrestrial ecosystem via biotic (e.g., emergent aquatic insects) and abiotic (i.e., flooding) pathways that are subjected to anthropogenic stressors (Schulz et al., 2015). In terms of abiotic pathways, construction of dams has been shown to alter abiotic pathways by reducing the intensity and frequency of floods (Beechie et al., 2010). Conversely, channelization of aquatic ecosystems can increase flow velocity, leading to channel incision and a subsequent decrease in flood events (Schindler and Smits, 2016). These changes in flood intensity and frequency can impact the composition of adjacent terrestrial communities (Li et al., 2012) and plant density (Stave et al., 2003). Additionally, reduced flood events can create a favorable environment for the spread of invasive species that are less tolerant to flooding, such as *Tamarax sp.* (Lovell et al., 2009).

In regards to biotic pathways, stressors can affect different aspects of the emergent aquatic insects (e.g., *Ephemeroptera*). For example, contaminants can reduce the quantity of the emergent aquatic insects affecting the terrestrial food webs (Kolbenschlag et al., 2023; Kraus et al., 2014; Paetzold et al., 2011). Specifically, species richness and the spider densities in affected terrestrial food webs can be reduced (Graf et al., 2020). Invasive species (amphipod *Dikerogammarus villosus*) led to reduced emergence of emergent aquatic insects (chironomids) in the upper river Rhine floodplains resulting in altered food sources of terrestrial tetragnathid spiders (Gergs et al., 2014). Land use also had a long-term effect (one year) on the quantity of emergent aquatic insects (Ohler et al., 2022). The timing of emergent aquatic insects can also be affected by stressors. Artificial lights

(Perkin et al., 2011) and contaminants (Kolbenschlag et al., 2023) can affect emerging insects' phenology, with a consequent effect on the composition of riparian predators and scavenger communities (Manfrin et al., 2017). Recently, more studies are focusing on documenting the quality (long chain polyunsaturated fatty acids) of emergent aquatic insects (Parmar et al., 2022; Shipley et al., 2022), their transfer to terrestrial food web (Kowarik et al., 2021; Twining et al., 2021; Martin-Creuzburg, 2016) and how they are affected by stressors (Shipley et al., 2022; Kowarik et al., 2023; Pietz et al., 2023; Fehlinger et al., 2022). This may be as a result of the findings that the quantity of terrestrial-to-aquatic subsidies exceeds that of aquatic-to-terrestrial subsidies, but causes equal contribution to animal carbon (Bartels et al., 2012).

Emergent aquatic insects have higher quality relative to the alternative terrestrial prey irrespective of season (Parmar et al., 2022), thereby providing necessary energy for terrestrial predators (Kowarik et al., 2021; Twining et al., 2021). Long chain polyunsaturated fatty acids have been linked to positive effects on the immune (Fritz et al., 2017) and fitness of their consumers (Gladyshev et al.,2009; Twining et al., 2016; Závorka et al., 2022). However, the long chain polyunsaturated fatty acids of emergent aquatic insect can be reduced by up to 80% by contaminants (metals) (Pietz et al., 2023). Emergent aquatic insects clearly transfer important resources to riparian areas, but the question remains how stressor-induced change in the quality of aquatic emergent insects affects the terrestrial food webs (figure 1c) (**objective 2**).

1.3 Meta-ecosystem theory

Ecological theory is a crucial tool in explaining ecological events (Pickett et al., 2010; Rossberg et al., 2019) and are often developed with mathematical models (Otto and Rosales, 2020). Mathematical models present a more definite and objective representation of the relationships between ecological processes and patterns. Additionally, mathematical models bring out any implicit assumptions or logical flaws that could be hidden in verbal hypotheses form (Grimm, 1994; Kokko, 2007; Marquet et al., 2014; Otto and Rosales, 2020).

The use of mathematical models in the development of meta-ecosystem theory (i.e., aquatic-terrestrial interface and other ecosystems) is a common approach that helps to formulate ideas and hypotheses into a scientifically useful format. By meta-ecosystem, we mean single or more ecosystems connected by subsidy flow. For example, the theoretical models predicted that the cross-ecosystem flow of primary producers or primary consumers has either neutral or stabilizing effects (Gounand et al., 2014), whereas the cross-ecosystem flows of nutrients (Gounand et al., 2014; Marleau et al., 2010) and detritus (Gounand et al., 2014) destabilize meta-ecosystems. Cross-ecosystem predator subsidies can increase the strength of top-down trophic cascades (Leroux and Loreau, 2008), with such food web interactions (for lakes) playing a key role in its eutrophication state (Janse et al., 1995; Puijenbroek et al., 2004). These models can be reused or adapted to improve our understanding of meta-ecosystems, but a comprehensive review and classification of existing subsidy-recipient ecosystem models and their applications is currently lacking (figure 1b) (**objective 1**). Subsidy-recipient ecosystem theories generally have assumed that subsidies and local resources are of comparable quality, thus the impact of the subsidy quality on recipient ecosystems has received little attention. Further theoretical study into how changes in subsidy quality affect recipient ecosystems can deepen our understanding of meta-ecosystems (figure 1c) (**objective 2**). Additionally, most meta-ecosystem theory assumes the patches are from the same ecosystem. This assumption is generally made because flows of organisms are the same in both patches, which is unrealistic for most meta-ecosystems that are coupling different ecosystems. Predictions from theory that models connections between different types of ecosystems may be different (**objectives 2 and 3**).

The scientific inquiry process in ecology operates as a feedback loop between theory and empirical research. The theory provides a framework for inquiry, experimental design and interpretation, while empirical research supports, refutes or revises theoretical predictions. The scientific process is important for ecological understanding and for addressing global challenges like climate change, biodiversity loss and emerging diseases (Ferrier et al., 2016).

The relationship between empirical and theoretical studies in aquatic-terrestrial interface research is limited due to a mismatch in measurements. Empirical studies tend to focus on how the usage of emergent aquatic insects (subsidies) by its consumers affect the terrestrial ecosystem (recipient ecosystem) (e.g., Krell et al., 2015; Lam et al., 2013). Theoretical studies, on the other hand, measure how the input of subsidies affect the recipient ecosystem (e.g., McCary et al., 2021). However, the rate of subsidy input into an ecosystem does not always accurately reflect the subsidy consumed by the recipient consumer, and consumer preferences for subsidies can determine its effect on the ecosystem (Abrams et al., 1998; Leroux and Loreau, 2008). Additionally, theoretical studies often concentrate on endpoints such as stability (Gounand et al., 2014) that are empirically difficult to measure, while empirical studies focus on measures such as efficiency and production (Mehner et al., 2022). Therefore, developing and applying empirical friendly metrics in the development of theories will enhance the connection between empirical and theoretical aquatic-terrestrial interface studies (figure 1b) (**objective 3**).

1.4 Objectives and structure of thesis

The aim of this thesis is to contribute to the development of theories on how changes in subsidies affect recipient ecosystems using aquatic-terrestrial interface as a case study. The thesis addresses the following objectives:

Objective 1: to review the applicability of current meta-ecosystem models (type, structure, and code accessibility) and to summarize the results from the application of the models. Furthermore, we aim to identify research gaps and future research topics that may improve our understanding of food webs in meta-ecosystems (**chapter 2**).

Objective 2: to study the effects of subsidy quality on the stocks and functions of recipient ecosystem (**chapter 3**).

Objective 3: to study how differential subsidy-recipient ecosystem coupling pathways independently and interactively affect the equilibria stocks and functions of recipient ecosystem (**chapter 4**).

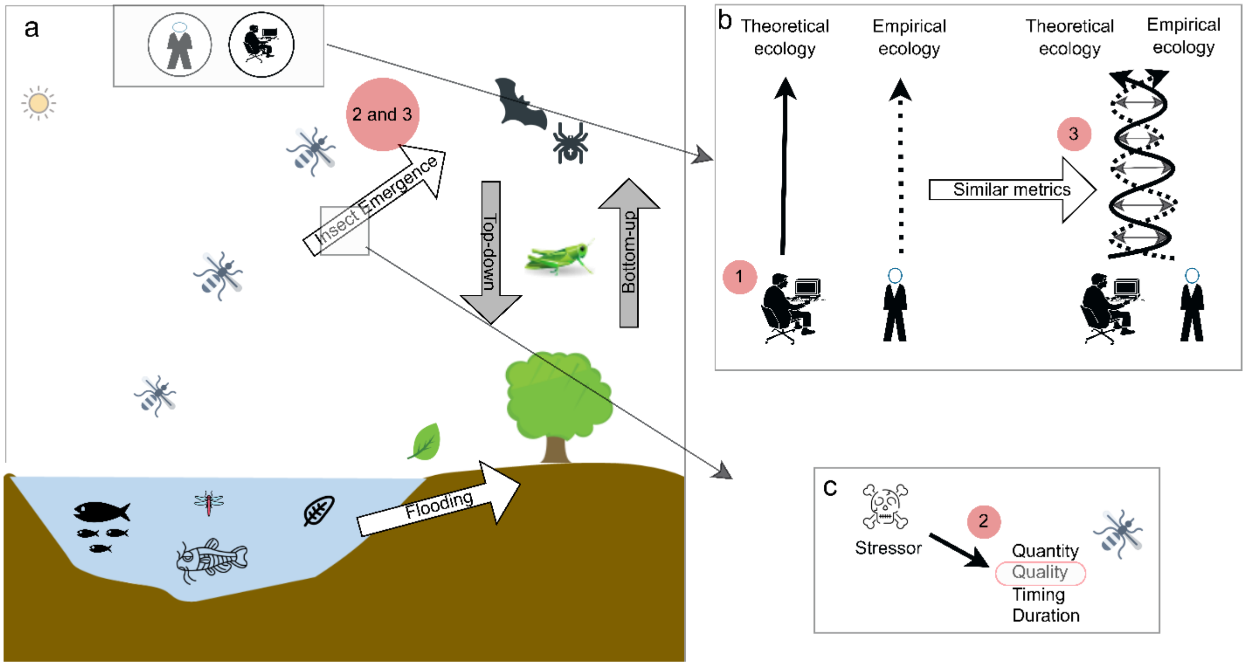

Figure 1.1: Overview of the thesis based on the thematic background in the introduction. The red circles refer to the thesis objectives as highlighted in section 1.4. Fig. a shows the case study, fig. b shows the two major ecological approaches and fig. c highlights the second objective.

1.5 References

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Chapter 2: Mini-review of process-based food web models and their application in aquatic-terrestrial meta-ecosystems*

Abstract

In a meta-ecosystem, spatially separated ecosystems are linked by biotic and abiotic cross-ecosystem flows. Hence, food webs in a meta-ecosystem are functionally linked. They are susceptible to multiple stressors threatening ecosystem functions and associated services. Although empirical studies can help understand stressor effects on meta-ecosystem food webs, they are often limited by their narrow spatial and temporal scales. This limitation may be overcome by process-based food web models, which allow variable spatial and temporal scales. We reviewed process-based food web models and their application to aquatic-terrestrial and theoretical meta-ecosystems. We refer to theoretical models as food web models based on theoretical considerations rather than describing a particular natural system. We found nineteen aquatic-terrestrial models that represented aquatic food webs with flows from terrestrial to aquatic ecosystems. Most of the aquatic-terrestrial models can be applied to study the environmental stressors of eutrophication (15 models) and climate change (10 models). Eight theoretical models were found that study ecosystem stability, trophic cascades, source-sink dynamics, co-nutrient limitation and co-existence of primary consumers. The theoretical models are more similar in terms of types of state variables and model complexity (i.e., number of state variables) than the aquatic-terrestrial models. Generally, the applications of the models have shown that environmental changes cause cross-scale effects on food webs in aquatic-terrestrial and theoretical meta-ecosystems. Finally, we outline major research gaps regarding the directionality of cross-ecosystem flows, anthropogenic stressors, and accessibility of models' codes.

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2.1 Introduction

Over the last decades, ecology has increased our understanding of the significance of processes operating on multiple temporal and spatial scales (Loreau et al., 2003). This resulted in the development of theoretical concepts like meta-population (Levins, 1969), meta-community (Hanski and Gilpin, 1991), and meta-ecosystem (Loreau et al., 2003), which have enhanced environmental management actions (Schiesari et al., 2019). The meta-population and meta-community concepts represent spatially structured populations of single or multiple species, respectively, linked by the flow of biotic components of the ecosystem. However, ecosystems are characterized by the cross-ecosystem flows of both biotic and abiotic components (Polis et al., 1997).

Therefore, the meta-ecosystem concept extends the meta-population and meta-community approach through explicit consideration of the cross-ecosystem flows of abiotic and biotic components of ecosystems (Loreau et al., 2003). For example, aquatic emerging insects are food subsidies for many terrestrial consumers such as insects and birds, whereas litter inputs from terrestrial ecosystems support productivity in adjacent aquatic ecosystems (Nakano and Murakami, 2001; Sabo and Power, 2002). These aquatic-terrestrial flows have the potential to affect top-down and bottom-up food web control (Menge et al., 1997), thereby establishing the aquatic-terrestrial interface (Richardson et al., 2009; Sabo and Power, 2002) and ensuring ecosystem functions (Trzcinski et al., 2016).

Food webs, especially at the aquatic-terrestrial interface, are affected by multiple anthropogenic stressors including climate change (Harper and Peckarsky, 2006; Li et al., 2011; Mosner et al., 2011), habitat degradation (Mikolajewski et al., 2015; Rowe and Ludwig, 1991), water pollution (Graf et al., 2019), and invasive species (Baxter et al., 2007; Finlay and Vredenburg, 2007; Mineau et al., 2012). By anthropogenic stressor, we mean any human pressure that causes a change in biological responses outside the range of their natural variation (Crain et al., 2008). Understanding the ecological effects of multiple anthropogenic stressors can be challenging because they can lead to non-additive ecological responses, such as antagonistic and synergistic responses (Côté et al., 2016).

Empirical studies (i.e., laboratory, mesocosm, and field studies) focusing on meta-ecosystems have deepened our understanding of multiple anthropogenic stressors' effects on food webs (e.g., McCormick et al., 2020). However, anthropogenic stressor interactions can change over time and spatial scale, whereas most empirical studies focus on narrow temporal and spatial scales (Allesino, 2020; Leuzinger et al., 2011). Process-based food web models can allow the prediction of anthropogenic stressor interactions and food web responses over variable temporal and spatial scales, as well as the testing of hypotheses and mechanistic assumptions (Cramer et al., 2001; Cuddington et al., 2013). They may thereby contribute to understanding the functioning of meta-ecosystems, filling and identifying observation gaps, and developing management strategies.

Considering that process-based food web models are re-usable, a review of the type, structure, and code accessibility of existing models can inform their application for different research questions. Moreover, a synthesis of the results from the application of process-based food web models in meta-ecosystems can inform the current understanding of meta-ecosystems, especially because recent reviews on meta-ecosystems have focused on empirical studies. Specifically, recent reviews focused on the effect of global change on resource flow between terrestrial and aquatic ecosystems (Larsen et al., 2016) and the importance of alteration of aquatic ecological and biogeochemical linkages to the surrounding terrestrial ecosystems (Schulz et al., 2015).

We reviewed process-based food web models applied to the aquatic-terrestrial interface (aquatic-terrestrial models) and theoretical meta-ecosystems (theoretical models). By theoretical meta-ecosystems, we mean meta-ecosystems where the system types are not explicitly stated. We provide a general description of the models and analyze their similarity. Subsequently, we summarize the results from the applications of the models. Finally, we identify research gaps and derive recommendations for future research topics with process-based food web models that may improve our understanding of food webs in meta-ecosystems.

2.2 Material and Methods

We performed a literature search in June 2020 using the search engine ISI Web of Knowledge supplemented by footnote chasing (White, 2009). The search was conducted in the advanced tab using the keywords: “TS=((meta ecosystem OR meta population OR meta community OR aquatic to terrestrial OR terrestrial to aquatic OR aquatic terrestrial OR terrestrial aquatic OR "aquatic to terrestrial" OR "terrestrial to aquatic" OR meta habitat) AND ("model" OR "simulation") AND (subsid* OR linkage* OR coupl* OR organismal movement OR migration OR food web OR trophic OR dispersal))”. The search returned 1009 publications. We evaluated these 1009 publications based on the following criteria: 1. contained process-based food web models 2. focused on aquatic-terrestrial or theoretical meta-ecosystems, 3. captured flows between the ecosystems. By food web model, we mean a model of organism groups within an ecosystem that are linked by trophic interactions. This therefore includes food chains and food webs irrespective of their linkage to an abiotic component (e.g., inorganic nutrients).

To quantify the similarity between models, we conducted a similarity analysis following the method of Janssen et al. (2015). As in the analysis of ecological similarity between communities of two sites, the method treats models as study sites and scores for the presence of state variables as if they were species. The resulting binary table is analyzed for model similarity using the Sørensen similarity index. The index varies between 0 (no overlap between the models) and 1 (models are completely identical) (appendix 1: text s1).

2.3 Description of the models

2.3.1 General overview

We found 19 aquatic-terrestrial models developed to study how flows from terrestrial ecosystems affect aquatic food webs, while none considered how flows from aquatic ecosystems affect terrestrial food webs (figure 2.1). The models covered food web interactions in various marine and freshwater ecosystems. Eutrophication was the main application area of the aquatic-terrestrial models (15 models), while other application areas include climate change (10 models), carbon cycle (8 models), biodiversity loss (2 models), toxicants (2 models), invasive species (1 model), residential development (1 model), windstorm (1 model) (table 2.1).

We found 8 theoretical models that were developed to study how cross-ecosystem flows affect ecosystem stability (3 models), trophic cascade (2 models), source-sink dynamics (1 model), co-nutrient limitation (1 model) and the co-existence of primary consumers (1 model) (table 2.1).

Individual organisms were not considered in both the aquatic-terrestrial and theoretical models as they used the aggregate population approach, which was implemented with either ordinary differential equations (25 models), difference equations (1 model), or structural dynamic equations (1 model). A diversity of programming languages was used in coding the aquatic-terrestrial and theoretical models: Matlab (5 models), R (3 models), Fortran (3 models), Java (1 model), Delphi (2 models), C/C++ (2 models), Phyton (1 model), Pascal (1 model), Visual Basic (1 model), Stella (1 model), and Advanced Continuous Simulation Language (2 models). Of the 27 models (i.e., 19 aquatic-terrestrial and 8 theoretical models), only 11 aquatic-terrestrial models are publicly available and for 7 models the language was not reported (appendix 1: table 6.1).

Table 2.1: Overview of aquatic terrestrial models (ATM) and theoretical models (TM) with information on scope, model names (if available) and food web system.

Reference	**Model Names (Model Type)**	**Model Application**	**Food web System**
Atlas and Palen (2014)	- (ATM)	Trophic cascade and prey vulnerability	Streams
Baretta et al. (1995)	ERSEM (ATM)	Eutrophication, climate change, carbon cycle, biodiversity loss	Estuaries, seas, oceans
Bartell et al. (2020)	CASM (ATM)	Toxicants, eutrophication	Stream, pond, wetland
Petzoldt and Siemens (2002)	SALMO (ATM)	Eutrophication, climate change	Lakes, reservoirs
Bellmore et al. (2017)	ATP (ATM)	Habitat restoration, invasive specie	Rivers
Billen et al. (1994)	RIVERSTRAHLER (ATM)	Eutrophication, climate change, carbon cycle	Rivers
Carpenter et al. (2016)	- (ATM)	Eutrophication	Lake
Cole and Wells (2003)	CE-QUAL-W2 (ATM)	Eutrophication, climate change, carbon cycle	Lakes, reservoirs, ditches/canals, rivers, estuaries
Gurkan et al. (2006)	Pamolare (ATM)	Eutrophication	Lakes
Hipsey et al. (2006)	CAEDYM (ATM)	Eutrophication, fisheries, climate change, carbon cycle, adaptive processes	Lakes, reservoirs, rivers, estuaries, seas, oceans
Park et al. (2008)	AQUATOX (ATM)	Eutrophication and toxicants	Pond, lake, stream, reservoir, estuary
Weijerman et al. (2014)	GACREM (ATM)	Eutrophication, fisheries, climate change, biodiversity loss, adaptive processes, carbon cycle	Lakes, reservoirs, ditches/canals, rivers, estuaries, coastal, seas, oceans
Zouiten et al. (2013)	EnvHydrEM (ATM)	Eutrophication	Coastal lagoons
Roth et al. (2017)	- (ATM)	Residential development, windstorm	Lake
Vasconcelos et al. (2018)	- (ATM)	Browning, climate change	Lake
Janse and Aldenberg (1990)	PCLoos (ATM)	Eutrophication	Temperate shallow lake
Janse et al. (1995)	PCLake (ATM)	Eutrophication, climate change, carbon cycle	Temperate shallow lake

Janssen et al. (2019)	PCLake$^+$ (ATM)	Eutrophication, climate change, carbon cycle	Lake across climatic zones
Kong et al. (2016)	- (ATM)	Eutrophication, climate change, carbon cycle	Sub-tropical shallow lakes
Gravel et al. (2010)	- (TM)	Source-sink dynamics	Hypothetical ecosystems
Gounand et al. (2014)	- (TM)	Ecosystem stability	Hypothetical ecosystem
Leroux and Loreau (2008)	- (TM)	Trophic cascade	Hypothetical ecosystem
Leroux and Loreau (2012)	- (TM)	Trophic cascade	Hypothetical ecosystem
Marleau et al. (2010)	- (TM)	Ecosystem stability	Hypothetical ecosystem
Marleau et al. (2014)	- (TM)	Ecosystem stability	Hypothetical ecosystem
Marleau et al. (2015)	- (TM)	Nutrient co-limitation	Hypothetical ecosystem
Marleau and Guichard (2019)	- (TM)	Co-existence of primary consumers	Hypothetical ecosystem

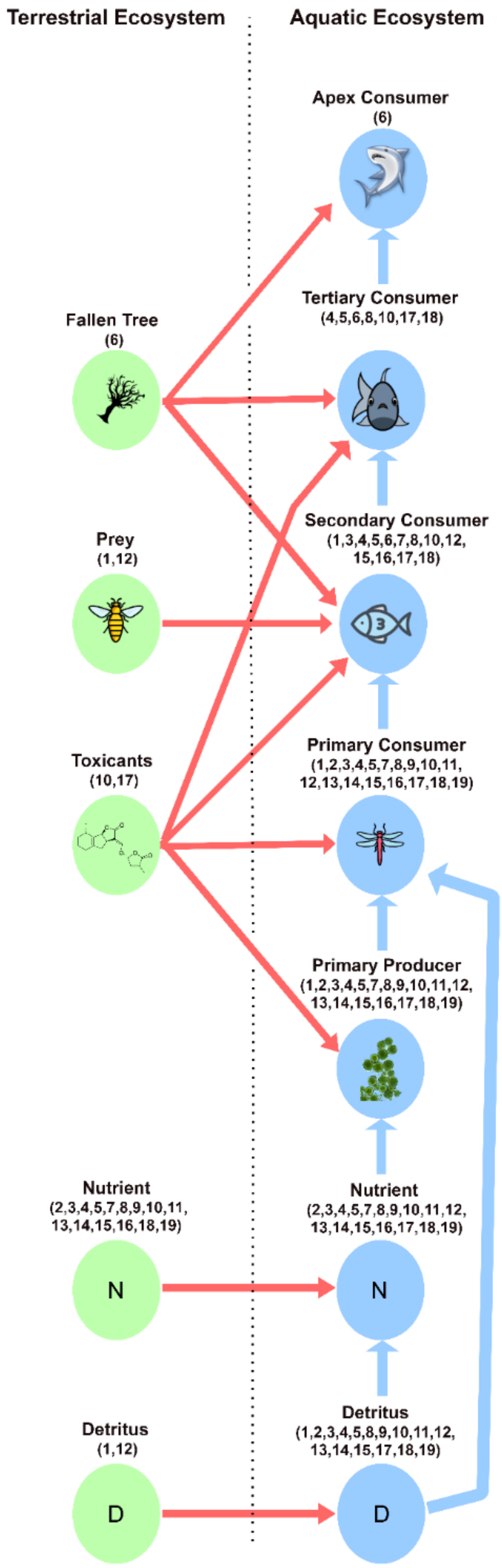

Figure 2.1: Conceptual diagram of the components of the aquatic-terrestrial models. Components (blue circles) were grouped into classical food web compartments of nutrients, primary producer, primary consumer, secondary consumer, tertiary consumer, and apex consumer. The red arrows indicate terrestrial-to-aquatic flows (green circles) and the aquatic food web component directly affected. Numbers refer to 1: Atlas and Palen (2014), 2: Carpenter et al (2016), 3: Janse and Aldenberg (1990), 4: Janse et al. (1995), 5: Janssen et al (2019), 6. Roth et al. (2017), 7: Vasconcelos et al. (2018), 8: Kong et al. (2016), 9: Baretta et al. (1995), 10: Bartell et al. (1999), 11: Petzoldt and Siemens (2002), 12: Bellmore et al. (2017), 13: Billen et al. (1994), 14: Cole and Wells (2003), 15: Gurkan et al. (2006), 16: Hipsey et al. (2006), 17: Park et al. (2008), 18: Weijerman et al. (2014), 19: Zouiten et al. (2013).

2.3.2 Similarity of the models

The aquatic-terrestrial models had a mean similarity of 0.05 and a total of 850 unique state variables (figure 2.2a). Generic state variables such as dissolved oxygen, phosphate, particulate inorganic phosphorus, zooplankton increased the similarity between the models. Considering the low similarity, the existing aquatic-terrestrial models cover a diverse set of ecosystems and food webs. The minimum number of state variables per model was 4 (Carpentel et al., 2016), and the maximum was 291 (Park et al., 2008). The theoretical models had a mean similarity of 0.66 and a total of 19 unique state variables. The number of state variables ranged from 6 to 10 (figure 2.2b). The high similarity of the theoretical models was expected as they do not specify particular organisms (organism groups) as state variables but categorize organism groups according to their function (e.g., primary producers).

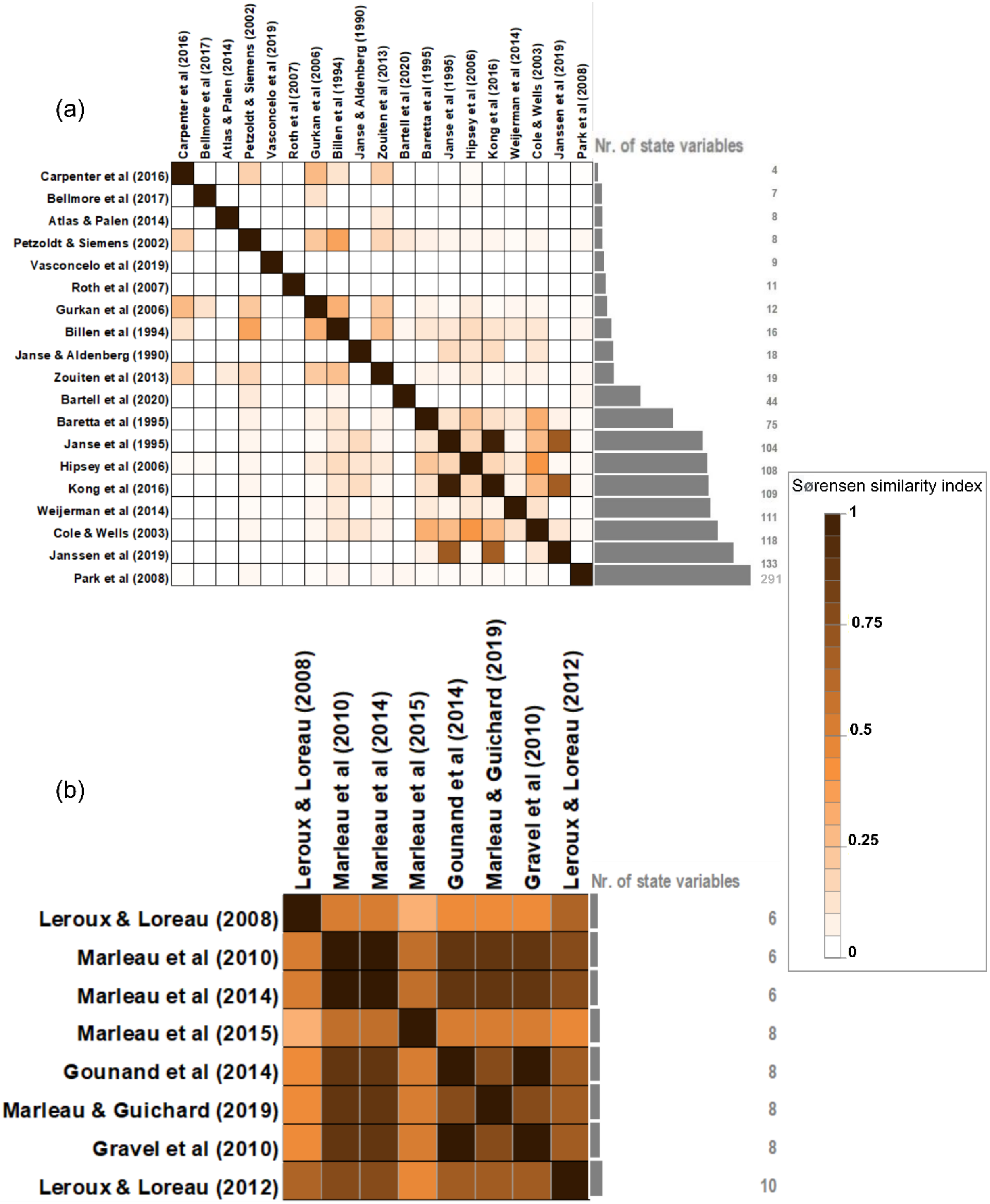

Figure 2.2: Model similarity based on the Sorensen similarity index of a) aquatic-terrestrial models and b) theoretical models. The references of the models are used as labels given that some models lack names. The Marleau et al. (2014; 2015), Marleau and Guichard (2019) models can be applied to more than two ecosystems but we used two ecosystems for the similarity analysis (same for other models).

2.4 Application of the models

Sections 2.4.1 and 2.4.2 provide summary results of the application of some of the models. In the application studies of the models, simulations were done to study how general system components (e.g., changes in predator composition) and anthropogenic stressors (e.g., eutrophication and warming) affect food webs in meta-ecosystems. The aquatic-terrestrial models were applied to study the effects of system components and anthropogenic stressors on food webs, whereas the theoretical models were only applied to study the effect of changes in system components on food webs. Hereafter, we refer to both changes in system component and in anthropogenic stressor as environmental change. The studies that applied the aquatic-terrestrial models in sections 2.4.1 and 2.4.2 were parameterized through field measurement/experimental data or literature data, while studies that applied the theoretical models were mostly parameterized through expert knowledge. Validation was also carried out for some of the aquatic-terrestrial models application studies (table 2.2).

Table 2.2: Overview of the parameterization and validation of highlighted model application studies

Parameterization Methods	**References**	**Validated Studies[4] References**
Empirical data (specific experiment/field study)[1]	Janse et al. (1992; 1995; 1998), Janssen et al. (2017), Janse and Aldenberg (1990; 1991), Atlas and Palen (2014), Vasconcelos et al. (2018), Carpenter et al. (2016).	Janse et al. (1995), Puijenbroek et al. (2004), Janse et al. (2008), Janssen et al. (2017), Janse and Aldenberg (1990), Janse et al. (1992), Vasconcelos et al. (2018), Bellmore et al. (2017).
Empirical data (literature)[2]	Puijenbroek et al. (2004), Janse et al. (2001; 2008), Mooij et al. (2007; 2009), Nielsen et al. (2014), Lischke et al. (2014), Roth et al. (2007), Bellmore et al. (2017), Gravel et al. (2010), Marleau and Guichard (2019).	
Expert knowledge[3]	Gounand et al. (2014), Marleau et al. (2010; 2014), Leroux and Loreau (2008; 2012).	

[1] Empirical data (specific experiment/field study): if the study is partly or fully parameterized based on field observation or experiment specific to the modelling study. [2] Empirical data (literature): if the study is fully or partly parametrized without field observation or experiment specific to the modelling study, but with literature data (e.g., existing databases). [3] Expert knowledge: If the study

is parametrized without any empirical data. ^{4}*Validated studies: if the modelling results from the study were compared against empirical data.*

2.4.1 Aquatic-terrestrial models

The application of some of the aquatic-terrestrial models can be grouped into studies that applied the eutrophication models to investigate the effects of nutrient flows on the clear/turbid state of lakes, and studies that applied the non-eutrophication models to investigate the effect of other stressors on the aquatic food web.

2.4.1.1 Effect of eutrophication on clear/turbid state of lakes

The eutrophication models contributed to our current understanding that food web interactions play an essential role in the distribution of nitrogen (N) and phosphorus (P) in lakes (Janse et al., 1995; Puijenbroek et al., 2004). Lakes are either in a clear (macrophytes dominated) or turbid (phytoplankton dominated) state. Both states are self-stabilizing, while the nutrient (N and P) levels at which a switch occurs from turbid to a clear state is much lower than the opposite switch (hysteresis), according to a model application by Janse et al. (1998). The critical nutrient level (CNL) for the transition of a lake between the turbid and clear states depends on both biological and physicochemical factors (Janse et al., 2008) and could vary within a lake (Janssen et al., 2017). The CNL for eutrophication (CNL_{eu}) (i.e., switch from clear to turbid state) decreases with an increase in bird herbivory (Janse et al., 1998), temperature (Mooij et al., 2007; 2009; Nielsen et al., 2014), terrestrial particulate organic matter (Lischke et al., 2014), lake fetch (Janse et al., 2008), lake depth (Janse et al., 2008), and a decrease in marsh area (Janse et al., 2001; 2008) or water levels (Janse et al., 2008; Kong et al., 2016).

The critical nutrient level for oligotrophication (CNL_{oligo}) (i.e., switch from turbid to clear state) decreases with an increase in terrestrial particulate matter (Lischke et al., 2014), lake fetch (Janse et al., 2008), and lake depth (Janse et al., 2008), and a decrease in marsh area (Janse et al., 2008). Another model-based study on remediation of turbid lakes predicts a reduction in the phosphorus/carbon (P/C) ratio of phytoplankton and detritus as a result of a reduction in P flux mobilization from the sediment (Janse and Aldenberg, 1990), resulting in P deficiency of algae (Janse and Aldenberg, 1991). The higher P/C ratios of zooplankton and fish remained unchanged, causing a delay in the response of the lake ecosystem to remediation measures (Janse and Aldenberg, 1990;1991). A high internal P recycling and assimilation efficiency of the phytoplankton can also cause a delay in lake response to remediation measures (Janse et al., 1992).

2.4.1.2 Effect of other stressors on the aquatic food web

Atlas and Palen (2014), Roth et al. (2007), and Vasconcelos et al. (2018) examined the effects of environmental change at different ecosystem response levels. At the community level, Vasconcelos et al. (2018) predicted that browning (flow of terrestrially derived dissolved organic matter) decreases benthic and increases pelagic primary production, which leads to more pelagic primary and secondary consumers due to active habitat choice. This increases the trophic cascade (i.e., indirect top-down food web control) in the aquatic pelagic zone, which was reduced by an increase in temperature due to higher temperature-related loss of secondary consumers. Similarly, Atlas and Palen (2014) predicted that an increase in the flow of terrestrial prey led to an increased trophic cascade in streams through higher secondary consumer biomass, which was reduced by an increase in the proportion of armored prey in the stream food web. At the population response level, Roth et al. (2007) predicted that reduction of fallen trees into lakes caused by residential development led to a reduction of benthic invertebrate prey. However, an increase in fishing (caused by increased proximity of residential areas) led to an increase of benthic invertebrate prey, whereas reduction of fallen trees into lakes caused by windstorm had little effect on lake food webs. This can be attributed to the differences in the implementation of windstorm and residential development effects during model simulations. Both disturbances (i.e., windstorm and residential development) were initiated at year 50 of 300-year simulations. However, for residential development, the thinning of adult trees occurred at a constant rate per year, whereas for windstorm it was implemented as a single event of 65% windfall of adult trees (one-time pulse stressor).

Beyond the effects of environmental change at various ecosystem response levels, Carpenter et al. (2016) predicted that the effects of terrestrial flows were dependent on the lake trophic levels. They predicted that P flow increased phytoplankton and zooplankton biomass. However, terrestrial particulate organic carbon (TPOC) decreased phytoplankton biomass and had a weak effect on zooplankton biomass. The negative effect of TPOC on phytoplankton was due to increased shading caused by dissolved organic carbon. Overall, the above studies show that stressors propagating from terrestrial ecosystems have cross-scale effects on food webs in aquatic ecosystems. Furthermore, model predictions by Bellmore et al. (2017) showed that strategies to restore aquatic food webs linked to terrestrial flows should consider the aquatic food web structure (e.g., the presence of invasive species).

2.4.2 Theoretical models

Equilibrium and stability analysis are done to analyze food web models. A food web model is in equilibrium if the state variables remain unchanged (Otto and Day, 2007). Stability analysis on a food web model in equilibrium, which is done by analyzing the dynamics of populations near equilibrium, can inform on stabilizing or destabilizing effects of environmental change on the modelled system. An environmental change destabilizes if it pushes the system away from equilibrium, whereas it stabilizes if it pushes the system towards equilibrium (Otto and Day, 2007). At the ecosystem response level, the theoretical models predicted that cross-ecosystem flows of nutrients (Gounand et al., 2014; Marleau et al., 2010) and detritus (Gounand et al., 2014) destabilize meta-ecosystems, whereas the cross-ecosystem flow of primary producers or primary consumers has either neutral or stabilizing effects (Gounand et al., 2014). Even though the cross-ecosystem flow of primary consumers can stabilize meta-ecosystems, in combination with nutrients, it can cause a destabilizing effect. However, the onset and spatial scale of the destabilizing effect depends on the meta-ecosystem's spatial structure (Marleau et al., 2014). Overall, according to models, meta-ecosystems were more stable at a combined cross-ecosystem flow of nutrients, primary producers, primary consumers, and detritus compared to a single flow (Gounand et al., 2014).

Cross-ecosystem flow also interacted with various meta-ecosystem stabilizing or destabilizing characteristics. For example, meta-ecosystems that are stabilized by ecosystems with different nutrient fertility are further stabilized by the cross-ecosystem flow of primary consumers (Gounand et al., 2014). Meta-ecosystems destabilized by local enrichments of nutrients can be stabilized if the cross-ecosystem flow of primary producers or primary consumers are sufficiently strong to redistribute enrichment to the nutrient-deficient ecosystem, whereas meta-ecosystems destabilized by regional enrichments of nutrients can only be stabilized by the intermediate cross-ecosystem flow of primary consumers (Gounand et al., 2014). Gravel et al. (2010) showed that the cross-ecosystem flow of nutrients, detritus, primary producers, or primary consumers can reverse the source-sinks dynamics of meta-ecosystems.

Community-level responses were also investigated. Marleau and Guichard (2019) predicted that the cross-ecosystem flow of primary consumers with nutrient recycling could generate spatial heterogeneity to allow the coexistence of primary producers where the well-mixed system predicts competitive exclusion. In terms of top-down control in food webs, the cross-ecosystem flow of nutrients, primary producers, primary consumers, or secondary consumer causes an increased top-down control in the recipient ecosystem (Leroux and Loreau, 2008). Meta-ecosystems that exhibit reciprocally pulsed cross-ecosystem flow of primary consumers lead to spatial and temporal variability in the strength of top-down control in both local and meta-ecosystems. However, top-down control is strongest when the reciprocally pulsed cross-ecosystem flow of primary consumers is temporally concentrated (Leroux and Loreau, 2012). Overall, similar to the application of the aquatic-terrestrial models, the above studies have shown that changes in cross-ecosystem flows have cross-scale effects on food webs in hypothetical meta-ecosystems, but their effects are often context-dependent.

2.5 Outlook and Recommendations

In summary, our study found that various process-based food web models have been developed, which has led to a greater understanding of aquatic-terrestrial and meta-ecosystems in general. Specifically, the reviewed studies have provided predictions that can form the basis of experiments on the effects of environmental change on aquatic-terrestrial and meta-ecosystem food webs. However, relative to the theoretical models, the aquatic-terrestrial models provide a greater diversity of model state variables and complexity. Not surprisingly, owing to its generality, the theoretical models have been applied to study the effect of change in system components (e.g., change in cross-ecosystem flows, heterogeneity of ecosystems) not explicitly linked to an anthropogenic stressor on food webs in meta-ecosystems. In contrast, the aquatic-terrestrial models were also used to study anthropogenic stressors. Below we outline major research gaps that limit our understanding of food webs in an aquatic-terrestrial interface or meta-ecosystem context.

2.5.1 Flows and stressors from aquatic to terrestrial food webs

The reviewed aquatic-terrestrial models focused on how flows from terrestrial ecosystems affect aquatic food webs, with none focusing on reciprocal flows. Similarly, only anthropogenic stressors propagating from terrestrial ecosystems to aquatic food webs were considered, for example, the effects of the reduction in fallen trees (caused by residential development and windstorm) on lake food webs (Roth et al., 2007). The focus on an aquatic ecosystem is not surprising as aquatic ecosystems generally receive higher cross-ecosystem flows (Ballinger and Lake, 2006; Power et al., 2004) caused by the difference in terrain profiles. The concave terrain profile of aquatic ecosystems makes them spatial attractors of many flows from terrestrial ecosystems due to gravity, unlike the terrestrial ecosystems that exhibit convex terrain profiles. Consequently, the effects of terrestrial flows on aquatic ecosystems have been a major theme in ecosystem ecology for decades (Likens, 1992; Schindler and Smits, 2016).

However, empirical studies have shown that physically and biologically mediated flows from aquatic ecosystems overcome gravity to affect terrestrial food webs (Schindler and Smits, 2016; Schulz et al., 2015). Biologically mediated flows from aquatic to terrestrial ecosystems involve animal movements. Specifically, such flows include the emergence of aquatic insects (Bartels et al., 2012; Muehlbauer et al., 2014; Richardson et al., 2009) and the distribution of fish-derived energy by foraging terrestrial predators (Helfield and Naiman, 2006) in the terrestrial ecosystem. Physically mediated flows from the aquatic ecosystem involve the movements of nutrients, sediments, and detritus through floods and subsurface water flows into terrestrial ecosystems (Schindler and Smits, 2016; Schulz et al., 2015; Wölz et al., 2011).

Empirical studies have also shown that anthropogenic stressors propagate from the aquatic ecosystem to terrestrial food webs through physically and biologically mediated pathways. In the context of anthropogenic stressors propagation via physically mediated pathways, dam construction reduces flood intensity and frequency (Beechie et al., 2010), while channelization of an aquatic ecosystem can increase flow velocity leading to channel incision and reduction of flood events (Schindler and Smits, 2016). The effects on flood intensity and frequency can reduce adjacent terrestrial community composition (Li et al., 2012) and plant density (Stave et al., 2003). Moreover, a reduction in flood events can support the spread of less flood tolerant invasive species in an adjacent terrestrial ecosystem (e.g., *Tamarax sp.)* (Lovell et al., 2009). Examples of anthropogenic stressors propagating via biological mediated pathways include, the reduction of the quantity of emerging insects or the bioaccumulation of pollutants in emerging insects with consequent effects on terrestrial food webs (Kraus et al., 2014; 2019; Paetzold et al., 2011). Specifically, species richness and the spider densities in affected terrestrial food webs can be reduced (Graf et al., 2019). Similarly, artificial lights can affect emerging insects' phenology and physiology (Perkin et al., 2011), with a consequent effect on the composition of riparian predators and scavenger communities (Manfrin et al., 2017). Even though the impacts of flows and stressors from aquatic ecosystems on terrestrial food webs are now being quantified, the impacts on terrestrial food web trophic interactions are understudied (Schindler and Smits, 2016).

Also, the relative importance of physically and biologically mediated pathways in the propagation of anthropogenic stressors from aquatic to terrestrial ecosystems remains unclear. For example, quantitative comparisons between biologically and physically mediated pathways of the pollutant transport from aquatic to terrestrial ecosystems and associated effects on food webs are lacking (Schulz and Bundschuh, 2020). Therefore, process-based food web modelling studies (based on empirical evidence) focusing on flows and anthropogenic stressors propagating from aquatic to terrestrial ecosystems could help in understanding the relative effects of biologically and physically mediated pathways on terrestrial food webs through model simulations. They could also provide clarity on how aquatic-to-terrestrial anthropogenic stressors and effects on food webs change across various temporal and spatial scales. Moreover, such studies will enable freshwater scientists to convey the relevance of their work to terrestrial managers (Sullivan and Manning, 2019).

2.5.2 Anthropogenic stressors affect the time, space, and quality characteristics of aquatic-terrestrial flows

The reviewed studies focused on how anthropogenic stressors affect the quantity of aquatic-terrestrial flows. However, anthropogenic stressors can also shift the timing, quality, and spatial characteristics of such flows (Larsen et al., 2016) and consequently affect the recipient's food web. For example, rising temperature can lead to early emergence and faster development of merolimnic insects (Harper and Peckarsky, 2006; Reading, 1998) and conceivably lead to temporal mismatches with the dietary need of terrestrial consumers. Similarly, climate change can shift the distribution of species poleward (e.g., riparian vegetation), conceivably affecting recipient aquatic organisms (e.g., stream detritivores) through spatial mismatch (Doi, 2008). In terms of resource quality, climate warming of 2.5°C can reduce fatty acids (8.2% to 27.8%) in algae (Hixson and Arts, 2016), which may indirectly affect terrestrial consumers via an altered nutritional quality of the aquatic subsidy in terms of merolimnic insects. Consequently, future process-based food web modelling studies should also focus on how anthropogenic stressors affect the above-mentioned characteristics of aquatic-terrestrial flows.

2.5.3 Models accessibility

Publicly sharing code increases the reproducibility and transparency of scientific studies (Gallagher et al., 2020; McKiernan et al., 2016). Scientific journals are adopting guidelines that require scientists to publish their codes (Stodden and Guo, 2013). This is crucial for models, because it avoids the inefficiency of "reinventing the wheel" and encourages their reusability (Mooij et al., 2010). Recently, Culina et al. (2020) found that only 27% of eligible ecology publications shared their code, and they called for increased code availability. It matches approximately our case, as only 11 out of 27 models (approximately 41%) had their models/model codes publicly available. Hence, we second their call for an increase in code availability of process-based food web models for meta-ecosystems.

2.6 References

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Chapter 3: Cascading impacts of changes in subsidy quality on recipient ecosystem functioning*

Abstract

The quantity and quality of resources can differ between adjacent ecosystems and these differences can impact subsidies exchanged between ecosystems. The quantity and quality of subsidies are rapidly changing in response to stressors associated with global environmental change, but while we have models to predict the effects of changes in subsidy quantity, we currently lack models to predict the effects of changes in subsidy quality on recipient ecosystem functioning. We developed a novel model to predict the effects of subsidy quality on recipient ecosystem biomass distribution, recycling, production, and efficiency. We parameterized the model for a case study of a riparian ecosystem subsidized by pulsed emergent aquatic insects. With this case study, we focus on a common measure of subsidy quality which differs between riparian and aquatic ecosystems; the higher content of long-chain polyunsaturated fatty acids (PUFAs) in aquatic ecosystems. We analyze how changes in the PUFA concentration of aquatic subsidies affect the dynamics in biomass stocks and functions of the riparian ecosystem. We also conducted a global sensitivity analysis to identify key drivers of subsidy impacts. Our analysis shows that subsidy quality increases the functioning of the recipient ecosystem. Recycling increases stronger than production per unit subsidy quality increase, which means there is a threshold where an increase in subsidy quality led to stronger effects of subsidies on recycling relative to production of recipient ecosystem. Our predictions were most sensitive to basal nutrient input, highlighting the relevance of recipient ecosystem nutrient levels to understanding the effects of ecosystem connections. We argue that recipient ecosystems that rely on high quality subsidies, such as aquatic-terrestrial ecotones are highly sensitive to changes in subsidy-recipient ecosystem connections. Our novel model unifies the subsidy hypothesis and food quality hypothesis and provides testable predictions to understand the effects of ecosystem connections on ecosystem functioning under global changes.

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3.1 Introduction

Ecosystems are coupled via the flows of nutrients, energy, and organisms (Loreau et al., 2003; Polis et al., 1997; Reiners and Driese, 2001). Meta-analyses demonstrate that these flows are often subsidies (i.e., resources of external origin) that influence the food webs in recipient ecosystems (Allen and Wesner, 2016; Marczak et al., 2007; Montagano et al., 2019). For example, terrestrial arthropod subsidies reduce the predation of headwater stream fish on aquatic arthropods (Nakano et al., 1999). In addition to subsidy quantity, subsidy quality can vary relative to local resources (Larsen et al., 2016). Subsidy quality can relate to different characteristics of the subsidy (e.g., body size or nutritional value) and is not a fixed characteristic but may vary with the predator preference (Chapin et al., 1990; Moyes et al., 2009). Subsidy quality can also impact the dynamics of coupled ecosystems (Marcarelli et al., 2011). For example, emergent aquatic insects have higher nutritional value to riparian predators, because they have a higher content of essential fatty acids relative to riparian prey (Twining et al., 2019). At equal quantity relative to local prey, terrestrial invertebrates are preferred by stream fish over aquatic invertebrates due to their larger size, reducing foraging costs (Baxter et al., 2005; Wipfli, 1997). Therefore, ignoring quality when studying cross-ecosystem subsidies may bias the estimation of the subsidy effects on recipient ecosystems (Twining et al., 2019).

Ecological models have been proposed as a tool to identify the mechanisms of how subsidies affect the stability and functioning of recipient ecosystems (Loreau et al., 2003; Marleau et al., 2014; Polis et al., 1997). These theories make quantitative predictions, but they also contribute to the synthesis of related concepts (Grainger et al., 2022). Mathematical models (e.g., Huxel and McCann, 1998; Leroux and Loreau, 2008; McCary et al., 2021; Takimoto et al., 2009) have identified some of the key mechanisms of subsidy effects. For example, the trophic level of the consumer (Huxel and McCann, 1998; Leroux and Loreau, 2008; McCary et al., 2021) and its relative preference for subsidy and local resources (Leroux and Loreau, 2008) drives the response of the recipient ecosystem.

Theoretical approaches, however, have largely assumed equal quality of subsidies and local resources. Consequently, they have been limited to an examination of the role of subsidy quantity in cross-ecosystem studies. Additionally, most previous theories focus on the effects of subsidies on the stability of local and meta-ecosystems (see review in Osakpolor et al., 2021). For example, Leroux and Loreau (2008) studied how subsidies affect the strength of trophic cascades, and

Takimoto et al. (2009) studied how factors such as the subsidy input rate and the responses of consumers influence the direction of the subsidies indirect effects on in-situ resources. While these and other studies may have indirectly considered recipient ecosystem/consumer functions, the effects of subsidies on ecosystem functions such as recycling, production, and efficiency have rarely been directly explored in models of connected ecosystems. Filling this gap can foster our understanding of how subsidies influence recipient ecosystem functions which may be particularly critical as ecosystem connections shift with global changes (Larsen et al., 2016).

Here, we introduce a novel ecosystem model that incorporates quality of subsidies to examine the effect of changes in subsidy quality on stocks, recycling, production, and efficiency of the recipient ecosystem. The model was applied to a common case study of a riparian ecosystem subsidized by emergent aquatic insects (e.g., Diptera, Ephemeroptera, Plecoptera). We focus on transient dynamics (i.e., changes in short-term dynamics) in the riparian ecosystem because the emergent aquatic insects' subsidies are episodic, short-duration events of resource availability (Yang et al., 2008).

3.2 Methods

3.2.1 General Model

The state variables in existing ecosystem models are exclusively representing quantity (e.g., biomass, population size). Here, we propose the use of a complementary state variable to capture the quality of subsidies. Based on this quantity-quality approach, we developed a general ecosystem model with different qualities of subsidy and local prey for the recipient ecosystem predator.

The ecosystem model consists of three biotic compartments: plants (A), herbivores (H), and predators (P), and one abiotic compartment: inorganic nutrients (N). All the compartments describe biomass except the inorganic nutrient compartment, which describes the mass of inorganic nutrients. The ecosystem model is open at the basal level through constant input of inorganic nutrient, I, and its loss at constant rate k. Biotic modules recycle nutrients at rates d_i but only a fraction, $1- \delta_i$, of recycled nutrients reach the soil nutrient pool, where i is A, H, P or E. We use Type II functional responses (Murdoch, 1969) for each consumer with attack rate, a_i, total available time, T_i, and handling time, V_i. Consumer uptake is converted to stock i with efficiency, e_i. The recipient ecosystem predator (P) is subsidized by the flow of subsidy (E). The recipient ecosystem predator, therefore, has two resources, subsidy (E) and the local prey (H). We model recipient ecosystem predator preference for the local prey as $\boldsymbol{\pi}_p$ (where $1-\ \boldsymbol{\pi}_p$ is the preference for the subsidy) (Huxel et al., 2002; McCann et al., 2005).

The quality of the subsidy relative to the local prey is captured in the model by an additional state variable (Q_E). The subsidy quality is passed via consumption to the recipient ecosystem predator and is also tracked by an additional state variable of the recipient ecosystem predator (Q_P). We used a Type II functional response (with a consumption efficiency e_F) to model the consumption of subsidy quality by the predator. The quality of the predator is reduced via density dependent mortality (i.e., $d_P Q_P$) and determines its consumption ability of both subsidy and local prey via a rational function (Otto and Day, 2007). With the rational function, the recipient ecosystem predator can still consume even when the predator quality is 0 (Otto and Day, 2007). The quantity and quality of subsidy input to the recipient ecosystem are represented by a step-function (equations 1 and 2), with *s* denoting the start of the pulse, *w* denoting the duration of the pulse, *m* denoting the rate of subsidy quantity input, and *q* denoting the subsidy quality during the pulse. The rate of subsidy quality input is $m * q$. The subsidy either enters the soil nutrient pool via recycling ($(1-\delta_E)d_E E$) or the predator pool via consumption (modelled in the functional response of the predator) of the recipient ecosystem. The model is described by the dynamical equations as shown in equations 3 - 9.

$$\mathrm{iE_t} = \begin{pmatrix} \mathrm{m\ for\ s<t\leq s+w} \\ \mathrm{0\ otherwise} \end{pmatrix} \tag{1}$$

$$\mathrm{iQE_t} = \begin{pmatrix} \mathrm{m*q\ fors<t\leq s+w} \\ \mathrm{0\ otherwise} \end{pmatrix} \tag{2}$$

$$\frac{dN}{dt} = I + (1-\delta_A)\ d_A A + (1-\delta_H) d_H H + (1-\delta_P) d_P P + (1-\delta_E) d_E E - A\left(\frac{a_A T_N N}{1+a_A V_A N}\right) - kN \tag{3}$$

$$\frac{dA}{dt} = A\left(\frac{a_A T_N N}{1+a_A V_A N}\right) - H\left(\frac{a_H T_A A}{1+a_H V_H A}\right) - d_A A \tag{4}$$

$$\frac{dH}{dt} = e_H H\left(\frac{a_H T_A A}{1+a_H V_H A}\right) - P\left(\frac{a_P T_H H \pi_P}{1+a_P V_P H \pi_P + a_P V_p E(1-\pi_P)}\right)\frac{a\left(\frac{Q_P}{P}\right)+c}{b\left(\frac{Q_P}{P}\right)+d} - d_H H \tag{5}$$

$$\frac{dP}{dt} = e_P P\left(\frac{a_P T_H H \pi_P + a_P T_E E(1-\pi_P)}{1+a_P V_P H \pi_P + a_P V_p E(1-\pi_P)}\right)\frac{a\left(\frac{Q_P}{P}\right)+c}{b\left(\frac{Q_P}{P}\right)+d} - d_P P \tag{6}$$

$$\frac{dE}{dt} = iE_t - P\left(\frac{a_P T_E E(1-\pi_P)}{1+a_P V_P H \pi_P + a_P V_p E(1-\pi_P)}\right)\frac{a\left(\frac{Q_P}{P}\right)+c}{b\left(\frac{Q_P}{P}\right)+d} - d_E E \tag{7}$$

$$\frac{dQ_E}{dt} = iQE_t - P\left(\frac{a_P T_E Q_E(1-\pi_P)}{1+a_P V_p Q_E(1-\pi_P)}\right)\frac{a\left(\frac{Q_P}{P}\right)+c}{b\left(\frac{Q_P}{P}\right)+d} - d_E Q_E \tag{8}$$

$$\frac{dQ_P}{dt} = e_F P\left(\frac{a_P T_E Q_E(1-\pi_P)}{1+a_P V_p Q_E(1-\pi_P)}\right)\frac{a\left(\frac{Q_P}{P}\right)+c}{b\left(\frac{Q_P}{P}\right)+d} - d_P Q_P \tag{9}$$

3.2.2 Model case study

Riparian ecosystems are functionally linked to the adjacent aquatic ecosystem across all major biomes (Allen and Wesner, 2016; Baxter et al., 2005; Montagano et al., 2019). Riparian predators (e.g., spiders and bats) depend on emergent aquatic insects, especially in resource-poor riparian ecosystems (Sabo and Power, 2002). For example, along different environmental gradients in the Central South Island, New Zealand, the abundance of predatory riparian arachnids correlated with emergent aquatic insect subsidies (Burdon and Harding, 2007), and stable isotope studies revealed that emergent aquatic insect subsidies contribute to the diet of riparian predators (Kato et al., 2004; Sanzone et al., 2002). It has been shown at both field and mesocosm scales that emergent aquatic insects can trigger cascading effects in the riparian ecosystem. Henschel et al. (2001) showed at the field scale that emergent aquatic insect subsidies had a cascading effect (via riparian spiders) on a riparian plant species (i.e., *Urtica dioica*). They speculated that this effect may propagate to the plant community as both aquatic insects and generalist riparian predators tend to be abundant along shores. Moreover, stinging nettles (i.e., *Urtica dioica*) often dominate riparian plant communities in Europe suggesting that this effect may occur widely (Sommaggio et al., 1995; Zabel and Sommaggio, 1998). Graf et al. (2017) demonstrated in a mesocosm experiment that aquatic insect subsidies had a cascading effect (via riparian spiders) on riparian plants (*Urtica dioica*). Bultman et al. (2014) showed at the field scale that aquatic insect's deposition in riparian ecosystem affects riparian plants (via nutrient availability), with effects propagating to riparian herbivores. Riparian ecosystems receive on average a higher quantity of subsidies from aquatic ecosystems than aquatic ecosystems receive from riparian ecosystems (Bartels et al., 2012). Surprisingly, despite the difference in quantity, the contribution of these subsidies to animal carbon is similar between aquatic and riparian ecosystems, which is most likely explained by the difference in the quality of riparian and aquatic subsidies (Bartels et al., 2012). This difference is reflected in a higher content of long-chain omega-3 polyunsaturated fatty acids (n-3 LC-PUFAs) in aquatic subsidies relative to riparian resources (Hixson et al., 2015). The n-3 LC-PUFAs (i.e., eicosapentaenoic acid, α-linolenic acid and docosahexaenoic acid) are synthesized by primary producers (e.g., diatoms, dinoflagellates) at the base of aquatic food webs. By contrast, primary producers (e.g., *Urtica dioica*) in riparian ecosystems cannot synthesize n-3 LC-PUFAs (Sayanova and Napier, 2004). The n-3 LC-PUFAs have been linked to positive effects on the fitness (Gladyshev et al.,2009; Twining et al., 2016) and immune response of their consumers (Fritz et al., 2017).

Environmental stressors affect the production of n-3 LC-PUFAs in aquatic ecosystems. For example, eutrophication can increase the proportion of cyanobacteria in algal communities (Paerl and Paul, 2012), which do not produce n-3 LC-PUFAs (Caramujo et al., 2007). Moreover, the widespread growth of cyanobacteria can increase water turbidity, thereby reducing the penetration of light, which in turn can impede the synthesis of n-3 LC-PUFAs in other algae (Paerl and Paul, 2012). Hence, eutrophication can reduce the n-3 LC-PUFAs concentrations in the emergent aquatic insects that feed on algae, resulting in lower n-3 LC-PUFAs concentrations propagating to the riparian ecosystem.

3.2.3 Adaptation of the general model to case study

In our case study, the recipient ecosystem model represents the riparian ecosystem, while the subsidy represents the emergent aquatic insects. We represent the flow of quality (n-3 LC-PUFAs) between state variables as concentration mass (in g) since mass-balance models such as ours are realized through the flow of mass, while the parameter describing the quality of subsidy (q) is in concentration of n-3 LC-PUFAs (g g^{-1}) of total fatty acids. As discussed above, an increase in the consumption of local riparian prey can reduce the concentration of n-3 LC-PUFAs and fitness of riparian predators. This was captured in our model, by linking the fitness of the riparian predator to its n-3 LC-PUFAs concentration (Q_P/P). We used higher consumption of the predator to represent its fitness because this implicitly captures the positive effects of n-3 LC-PUFAs.

3.2.4 Equilibrium state and parameter values

Following McCary et al. (2021), we used a mixed approach to parameterize our model for the case study. For the ecosystem model (i.e., without the subsidy), we first defined parameter values that were available from the literature (Kainz et al., 2004; Leroux and Loreau, 2008; Marcarelli et al., 2011; McCary et al., 2021). Then we randomly selected other parameter values which were not available from the literature from a uniform distribution (appendix 2: table 7.3). Specifically, parameters describing proportions (e.g., the proportion of materials lost from herbivores) were drawn from a uniform distribution between (0,1), whereas all other parameters (e.g., the consumption rate of herbivore) were drawn from a uniform distribution between (0,10). The process of selecting parameters from a uniform distribution was iterated 200,000 times. From the 200,000 parameter combinations generated, we used our ecosystem model and rootSolve package (Soetaert et al., 2014) for R Version 4.0.5 (R Core Team, 2021) to calculate equilibrium stocks (i.e., stock values when changes over time is 0) of the recipient ecosystem. Next, we randomly selected a set of equilibrium stocks of the recipient ecosystem that are feasible (i.e., all stocks > 0) and stable (i.e., negative dominant eigenvalue of the Jacobian matrix; appendix S1: section S2). We also ensured that the selected equilibrium stock values are consistent with the common pattern of an ecological biomass pyramid (see review in Trebilco et al., 2013), i.e., biomass decreases with increasing trophic levels (figure 3.1b). The approach of sampling parameters from the uniform distribution is similar to Leroux and Schmitz (2015). This is the standard approach for ecosystem models that are modelled at functional group level and we also explored the effects of parameters change via sensitivity analysis. For the remainder of the paper, we use * to denote variables and/or function values at feasible and stable equilibrium. After determining the equilibrium stock values and associated parameters for the recipient ecosystem, we determined the parameter values of the subsidy in comparison to similar parameter values of the recipient ecosystem. For example, the mortality rate of the subsidy is 0.2 similar to the compartments of the recipient ecosystem, while the proportion of nutrient lost from the subsidy 0.48 similar to the recipient ecosystem predator. The rational function describing the fitness of the recipient ecosystem predator was parameterized to cause a maximum consumption effect of 5.7-fold at maximum quality. The 5.7-fold effect is consistent with the meta-analysis result of Bartels et. al (2012), which showed that terrestrial subsidies to aquatic ecosystems were 5.7-fold greater than aquatic subsidies to terrestrial ecosystems, causing equivalent effects in recipient ecosystems. We also examined how a 50% lower (2.85-fold) or higher (8.55-fold) consumption effect influences the results. Finally, we explored our model across various levels of subsidy quality (see appendix 3: table 7.3 for the equilibrium and parameter values). Considering that recipient predators rely differently on subsidy (Kato et al., 2004), we examined how low (20%, $\boldsymbol{\pi}_p = 0.8$), intermediate (60%, $\boldsymbol{\pi}_p = 0.4$) and high (80%, $\boldsymbol{\pi}_p = 0.2$) preference for subsidy relative to local alternative prey influences the results.

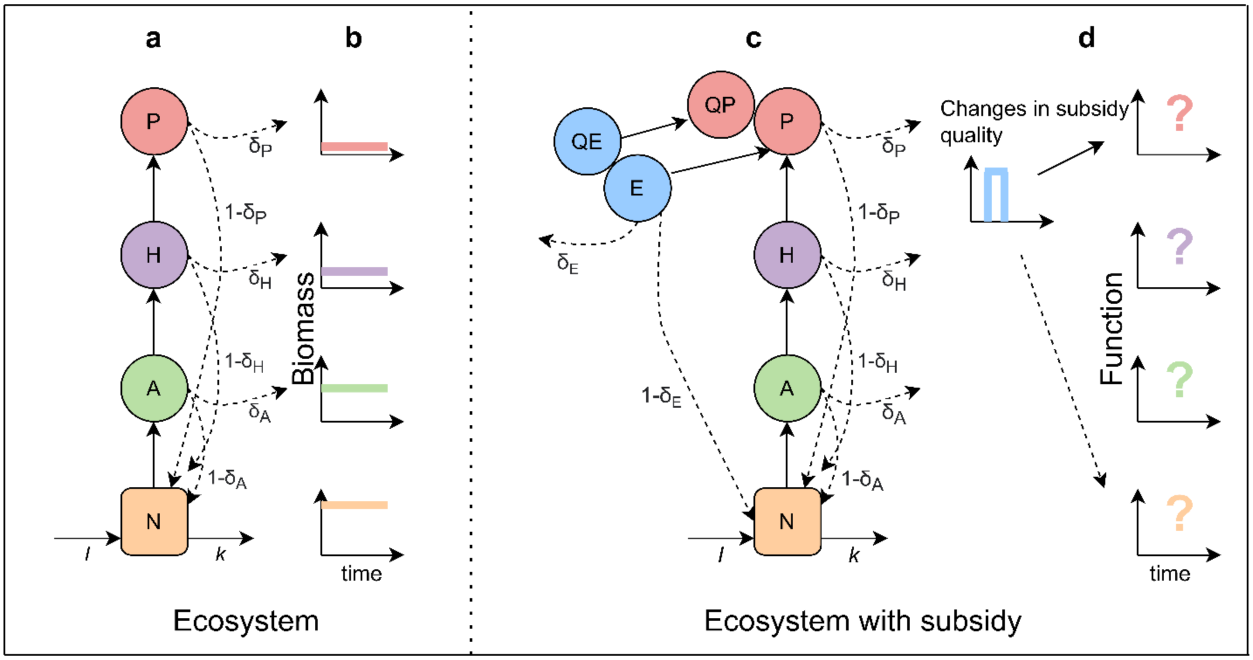

Figure 3.1: Overview of ecosystem models and research goal. Panels a and c are the model structures without subsidy and with subsidy, respectively. Panel b shows the equilibrium stocks of the ecosystem compartments, while panel d shows our research goal.

3.2.5 Analysis

To study the effects of changes in subsidy quality, we numerically solved our model using the R deSolve package (Soetaert et al., 2010) for varying values of the subsidy quality parameter (q) (0.1, 0.3, 0.5, 0.7, and 0.9 g g^{-1} of n-3 LC-PUFAs), where other model parameters were kept constant. Shipley et al. (2022) reported about 64% of total fatty acids in emergent aquatic insects (Ephemeroptera) is n-3 LC-PUFAs. However, we chose a wide range of subsidy quality values (i.e., up till 90%) because we aim to provide general insight on how change in subsidy quality affects the recipient ecosystem. For all simulations, the model stocks were initialized at the equilibrium stocks without the subsidy. Because the non-subsidized ecosystem was in a state of stable equilibrium, the subsidized ecosystem eventually returned to equilibrium stocks after it was perturbed by subsidy inflow. We ran the model for the period until the perturbed stocks and functions of the recipient ecosystem returned to the equilibrium (120 days, figure 3.2 and appendix 2: figure 7.1). To analyze the transient dynamics, we subtracted our simulated values from the values at equilibrium (i.e., no subsidy).

3.2.5.1 Effect of change in subsidy quality on time series of stocks and top-down trophic cascade of recipient ecosystem

Subsidies can increase the abundance of predators, thereby reducing herbivores and herbivory (Henschel et al., 2001). Hence a reduction in the herbivore's consumption of plant stock results in a stronger predator-mediated trophic cascade. Therefore, similar to McCary et al. (2021), we calculated top-down trophic cascade as the difference between herbivore consumption of plant in response to subsidy and at equilibrium (i.e., no subsidy) at time t (equation 10) and reported the cumulative values. In addition, proportional changes in recipient ecosystem stocks (i.e., nutrient, plant, herbivore or predator stocks; see Appendix 2 for quantitative definitions) were calculated (equation 11) and we report the values over the whole simulated period.

3.2.5.2 Effect of change in subsidy quality on the functions of recipient ecosystem

The recipient ecosystem functions were calculated following analytical expressions for production, efficiency, and recycling in Loreau (2010) and Leroux and Schmitz (2015) (appendix 2: equations S5-S16). Specifically, for a particular trophic level, production was defined as the amount of stock gained by consumption, ecological efficiency was defined as the ratio of its production to the production of the next lower trophic level, while recycling was defined as the quantity of stock recycled to the nutrient pool (Loreau, 2010). We calculated proportional change in recipient ecosystem functions as the recipient ecosystem function at time t relative to recipient ecosystem function at equilibrium (equation 12), and reported the cumulative values for the simulated period. Generally, the functions are key to the ecosystem (Chapin et al., 2011), for example, high recycling increases the nutrient pool, thereby enhancing energy flow up the food web. Ecological efficiency can reveal bottlenecks in energy transfer between trophic levels (Leroux and Schmitz, 2015). We obtained the relative effect of subsidy quality on total (i.e., the sum across trophic levels, see appendix 2 for quantitative definitions) ecosystem recycling and production by calculating the decadal logarithm of the ratio of cumulative total ecosystem recycling to the cumulative total ecosystem production (equation 13) along the subsidy quality gradient. A value above 0 on the y-axis means that the subsidy has a greater effect on ecosystem recycling than ecosystem production and vice versa.

$$\text{herbivore consumption of plant} = H_{(t)}\left(\frac{a_H T_A A_{(t)}}{1+a_H V_H A_{(t)}}\right) - H^{*}\left(\frac{a_H T_A A^{*}}{1+a_H V_H A^{*}}\right) \qquad (10)$$

$$\text{proportional change in ecosystem stock} = \frac{(\text{Stock}_{(t)} - \text{Stock}^{*})}{\text{Stock}^{*}} \tag{11}$$

$$\text{proportional change in ecosystem function} = \frac{(\text{Function}_{(t)} - \text{Function}^{*})}{\text{Function}^{*}} \tag{12}$$

$$\text{comparison of total ecosystem functions} = \log_{10}\left(\frac{\text{cumulative total recycling function}}{\text{cumulative total production function}}\right) \tag{13}$$

3.2.5.3 Sensitivity Analysis

Following Bellmore et al. (2014), we performed a global sensitivity analysis (GSA) to identify the most influential parameters on our model predictions. In GSA, all parameters are changed simultaneously. The GSA ranks parameters according to their relevance, taking into account both model structure and parameter variability. We randomly selected 20,000 parameter combinations from a uniform distribution, with a minimum and maximum of -50% and +50% of the default parameter values respectively. The 20,000 parameter combinations were then used to predict recipient ecosystem stocks. With the input of the parameter combinations and predicted recipient ecosystem stocks, we applied a random forest algorithm to calculate the residual sum of squared errors for each parameter (node impurity metric), which is a common method for ranking parameters of ecological models (Bellmore et al., 2014; Harper et al., 2011). The residual sum of squared errors for each factor was normalized by the sum of the total. To check the robustness of our model predictions, we varied the five most important parameters (-50% and +50%) and predicted recipient ecosystem functions. For the proportion of nutrient lost from the herbivores (δ_H), efficiency of predators (e_P), efficiency of herbivores (e_H), efficiency of predators for n-3 LC-PUFAs consumption (e_F) adding 50% would have exceeded the proportion of 1, which is not meaningful. Hence, we limited the upper boundary to 0.9 for these parameters. We then checked whether the predictions from the adjusted top five parameters were qualitatively similar to the predictions from the default parameters.

3.3 Results

3.3.1 Effect of change in subsidy quality on time series stocks and top-down trophic cascade of the recipient ecosystem

The inflow of subsidy causes an initial increase in the predator and plant stocks but a decrease in herbivore and nutrient stocks before they eventually return to equilibrium values. The effects of the subsidy increase with an increase in the subsidy quality (figure 3.2). Relative to other recipient ecosystem compartments, it had more effect on the maximum (i.e., the difference between the maximum stock at 0 subsidy quality and 0.9 subsidy quality) of plants (0.76) and the minimum (i.e., the difference between the minimum stock at 0 subsidy quality and 0.9 subsidy quality) of herbivores (-0.41). The subsidy quality effects on the minimum and maximum stocks of recipient ecosystem increase with the parameter maximum effect of subsidy quality on predator consumption (appendix 2: figure 7.3). The minimum and maximum stocks of the recipient ecosystem was most affected by subsidy quality at an intermediate predator preference for local prey (0.4) (appendix 2: figure 7.5). Increasing subsidy quality causes an increase in the strength of top-down trophic cascade (i.e., reduction of in situ plant consumption by herbivores) (appendix 2: figure 7.2).

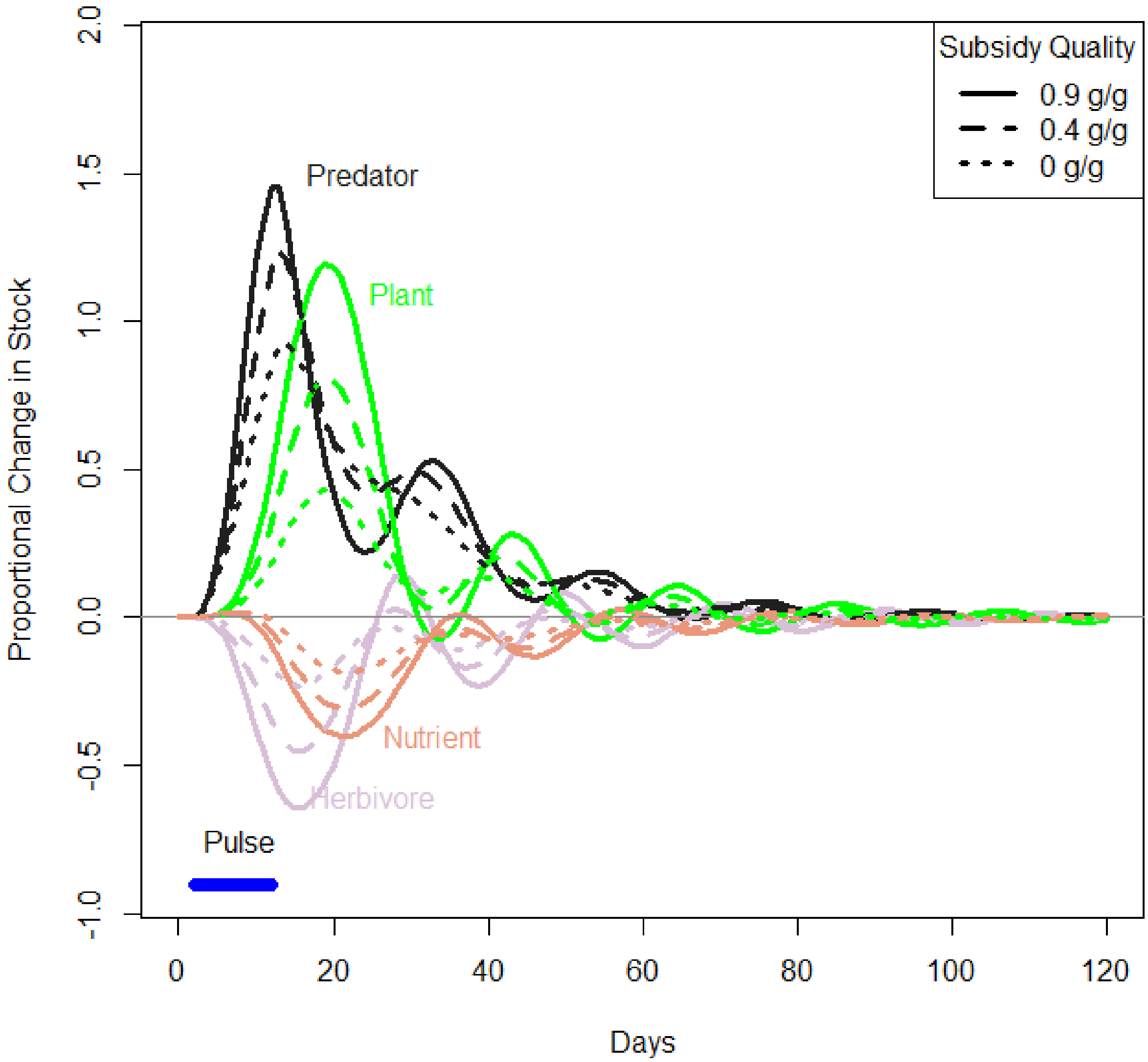

Figure 3.2: Time series of proportional changes in recipient ecosystem stocks. Lines indicate the stock content at time t relative to that at equilibrium (equation 11). See appendix 2: table 7.3 for the parameter values.

3.3.2 Effect of change in subsidy quality on functions of the recipient ecosystem

Increasing the subsidy quality caused an increase in the functions of plants and predators but a decrease in the functions of herbivores (figures 3.3a, 3.3b, 3.3c). The effects of subsidy quality are strongest on the production (figure 3.3a), efficiency (figure 3.3b) of predators, and the recycling of plants (figure 3.3c). Overall, changes in subsidy quality had a stronger effect on the total (i.e., sum across trophic levels – see appendix 2 for quantitative definitions) efficiency and total (i.e., sum across trophic levels) recycling of the recipient ecosystem in comparison to its production (figure 3.3d). Specifically, increasing subsidy quality seems to increase total ecosystem efficiency (i.e., reduce total bottlenecks of material transfer). The stronger influence of subsidy quality on total production over total recycling is until a subsidy quality of 0.4 (about 50% quality), which if exceeded, switches recycling to be more responsive to the subsidy than production (figure 3.4). The 0.4 threshold reduced to 0.22 when the maximum effect of subsidy quality on predator consumption was increased by 50% (i.e., 5.7-fold to 8.55-fold). However, a 50% reduction of this parameter (i.e., 5.7-fold to 2.85-fold) caused a stronger effect of subsidy quality on total production in comparison to total recycling across subsidy quality (i.e., no switch) (appendix 2: figure 7.4). Similarly, the 0.4 threshold reduced to 0.2 when the predator preference for local prey decreased from 40% to 20%, while it increases to 0.7 when the predator preference for local prey increased from 40% to 80% (appendix 2: figure 7.6).

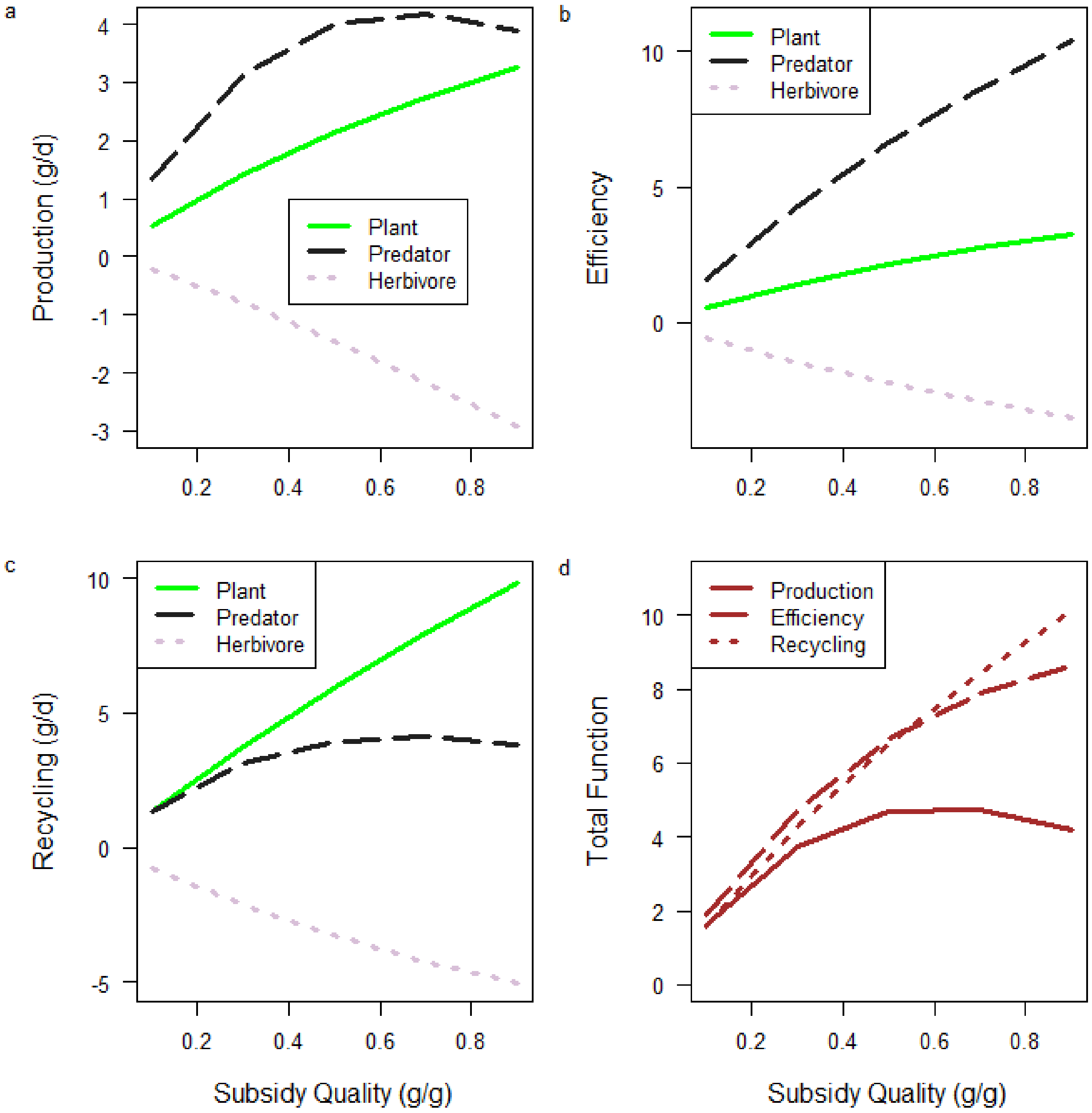

Figure 3.3: Cumulative ecosystem functions over the simulated period. The lines represent the difference between the cumulative functions at various subsidy quality and when the subsidy quality is 0. See appendix 2: table 7.3 for the parameter values and appendix 2: equations S5-S16 for the mathematical expressions of each function.

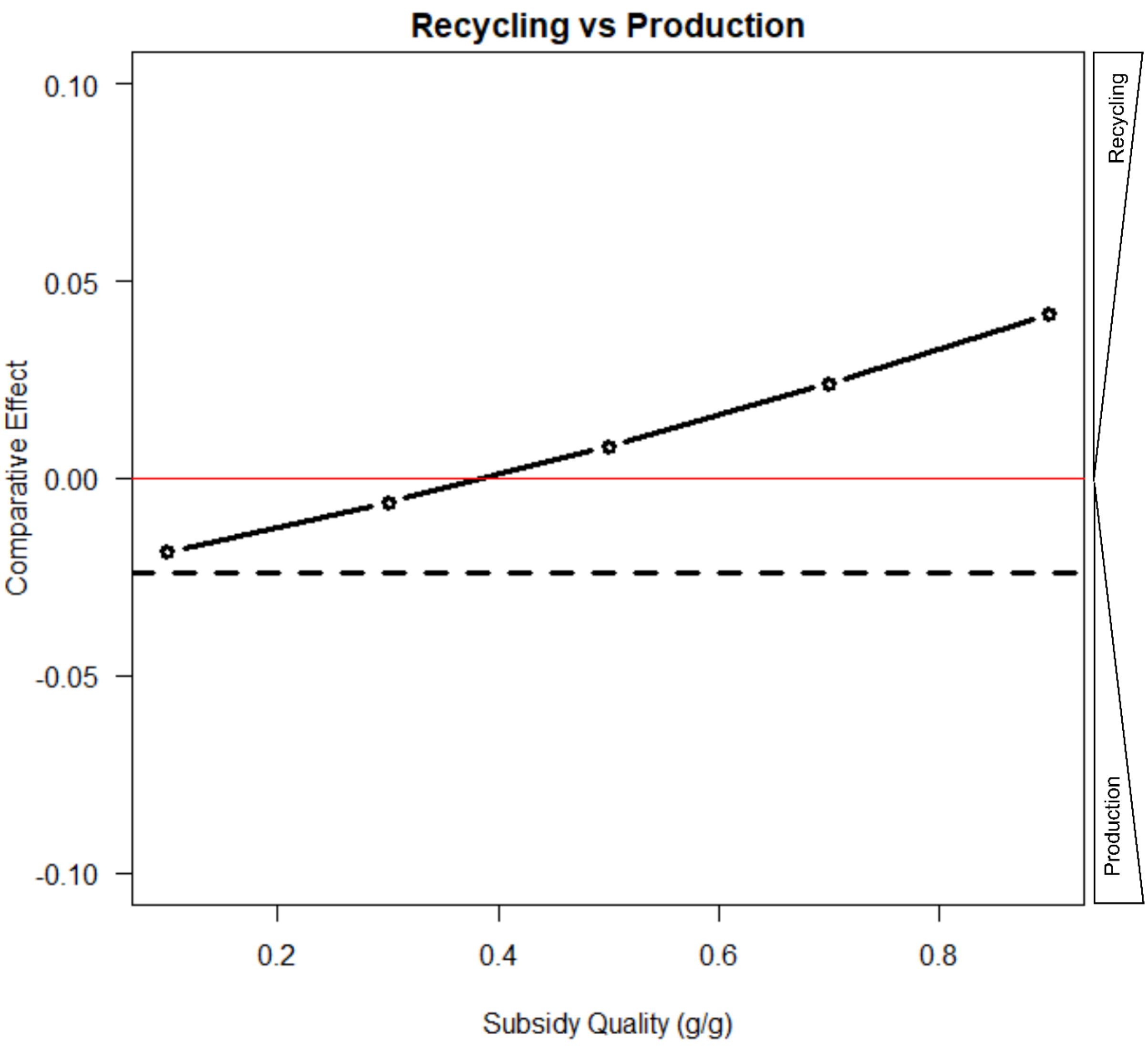

Figure 3.4: Comparison of total recycling and production of the recipient ecosystem (equation 13). The dash line represents 0 subsidy quality, while the points represent model with varying subsidy quality specified in the x-axis. Points greater than 0 on the y- axis means that the subsidy has a greater effect on ecosystem recycling than ecosystem production (effect increases northwards) for a given subsidy quality (x-axis), while points less than 0 means that the subsidy has a greater effect on ecosystem production than recycling (effect increases southwards) for a given subsidy quality (x-axis). See appendix 2: table 7.3 for the parameter values and appendix 2: equations S8 and S12 for the mathematical expressions of each function.

3.3.3 Sensitivity Analysis

The modelled recipient ecosystem compartments varied in their sensitivity to the model parameters. For example, the nutrient compartment was most sensitive to the total available time of the nutrient (T_N), while the herbivore and predator compartments were most sensitive to basal input of inorganic nutrient (I). Overall, the top 5 most influential parameters of the recipient ecosystem are basal input of inorganic nutrient (I), total available time of the nutrient (T_N), total available time of plants (T_A), efficiency of herbivore (e_H), mortality rates of plants (d_A) (figure 3.5). Model predictions of the effect of subsidy quality on recipient ecosystem functions were 90% qualitatively robust to changes in the five most important parameters. Specifically, it was 97.5% for efficiency, 92.5% for recycling, and 80% for production (appendix 2: table 7.4).

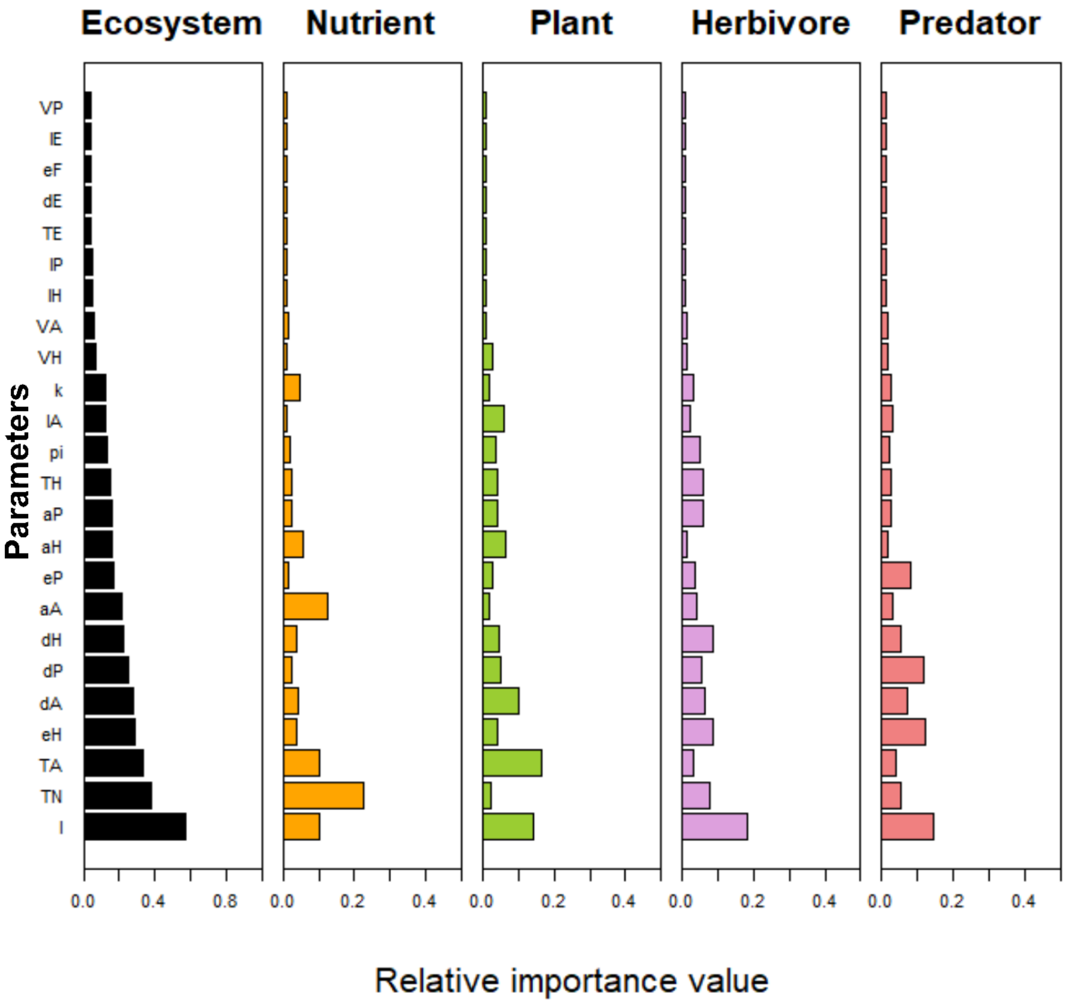

Figure 3.5: Relative importance of different model parameters in determining changes to cumulative recipient ecosystem stocks and its compartments determined from Random Forest analysis.

3.4 Discussion

We derived an ecosystem model that captures differential qualities of subsidies and local resources to study how changes in subsidy quality affects the stocks and functions of recipient ecosystem. This is motivated by the fact that current models of recipient ecosystem responses to subsidies (e.g., Huxel and McCann, 1998; Leroux and Loreau, 2008; Takimoto et al., 2009) or meta-ecosystems (i.e., coupled donor and recipient ecosystem models, Gravel et al., 2010; Leroux and Loreau, 2012; Marleau et al., 2014) assume resources flowing across ecosystem boundaries are of the same quality as local resources. This assumption contrasts with empirical evidence that subsidy quality differs from local resources (e.g., Elser et al., 2000; Hixson et al., 2015). We demonstrate that incorporating subsidy quality to predict recipient ecosystem functions is critical to understand ecosystem connections.

Our study is also novel in that we focus on how subsidy quality affects recipient ecosystem functions (i.e., production, recycling and efficiency), thereby providing model predictions in metrics that are often measured by empiricists (see Mehner et al., 2022). Hence, we improve on connections or testability of existing theory that tends to focus on measures of stability (e.g., leading eigenvalue of Jacobian matrix); a metric that is not often measured empirically. In addition, our model predictions are made at short time scales (transients) which matches the time scales of most empirical studies of subsidies. As above, the focus on short time scales, stands in contrast to most theory of connected ecosystems being done for long-term equilibrium dynamics (e.g., Huxel and McCann, 1998; Leroux and Loreau, 2008; Takimoto et al., 2009 but see McCary et al., 2021). By studying short-term dynamics, we increase the relevance of our predictions with related empirical works which tend to occur over short time frames (Hasting, 2004). Marczak et al.'s (2007) meta-analysis revealed that empirical studies of food web effects of subsidies range from one to 36 months in duration (median = three months). For example, Graf et al. (2017) studied how aquatic subsidies affect terrestrial food webs with a six-week experimental duration, and Kato et al. (2004) studied the effects of aquatic insects on spider dynamics with a three-month field study duration.

The model analysis shows that an increase in the quality of subsidies can have important cascading effects on the recipient ecosystem. Specifically, it causes an increase in the production, recycling, and efficiency of the plants and predators but a decline in these functions for herbivores (figure 3.3). In our model, the increase in subsidy quality reduces material transfer at the herbivore-plant level therefore compounding this common ecological bottleneck. The total (i.e., sum across trophic levels – see appendix 2 for quantitative definitions) production, recycling and efficiency of the recipient ecosystem increase with subsidy quality. Our model predictions are consistent with components of existing theoretical work investigating the impacts of resource quality on local ecosystems (i.e., models not focused on subsidies or meta-ecosystems). Specifically, Hall et al. (2007) predicted that higher quality plants (i.e., easy digestibility) promote stronger trophic cascades in local ecosystems, though their models' lacked predictions on other ecosystem functions such as production and recycling. Empirically, Rigg and Bommarco (2019) found that the addition of high-quality (i.e., easily decomposable) organic fertilizer caused higher predator top-down effects on plants relative to low quality organic fertilizer.

Overall, our model predictions provide a unification of the food quality hypothesis (Hall et al., 2007) and the subsidy hypothesis (Leroux and Loreau, 2008). The food quality hypothesis ignores subsidies and states that higher quality plants should promote stronger trophic cascades (Hall et al., 2007). The subsidy hypothesis states that an increase in subsidy rates causes an increase in the strength of trophic cascades in ecosystems receiving subsidies (Leroux and Loreau, 2008). Our predictions demonstrate how these two hypotheses may interact, in that, increasing the quality of subsidies increases the strength of trophic cascades of a recipient ecosystem. A general explanation of the variation in the strength of trophic cascade among ecosystems remain elusive (Leroux and Loreau, 2008). Current hypotheses include: primary producer diversity hypothesis (Hillebrand et al., 2007), foraging-predation risk trade-off hypothesis (Schmitz et al., 2004; Schmitz, 2008), primary producers quality hypothesis (Borer et al., 2005; Hall et al., 2007), primary consumer efficiency hypothesis (Borer et al., 2005), primary productivity hypothesis (Shurin and Seabloom, 2005), body size hypothesis (Shurin and Seabloom, 2005), subsidy hypothesis (Leroux and Loreau, 2008). Our subsidy quality hypothesis integrates components of two existing hypotheses (i.e., quality and subsidy) and states that, the effect of subsidy on recipient ecosystem functions can be stronger when the subsidy quality is higher than that of *in-situ* resources. Marczak et al. (2007) found that the consumer response in a recipient ecosystem was significantly related to the ratio of subsidy resources to equivalent *in-situ* resources in terms of quantity. Our study complements these results with a focus on quality. Our hypothesis may provide higher explanatory power, considering that all ecosystems are open and that subsidies may differ in quality from local alternative resources.

We uncovered a threshold where an increase in subsidy quality can eventually lead to weaker effects of subsidies on total production of recipient ecosystem relative to its total recycling (figure 3.4). An explanation for this is that production is often less or differentially affected by top-down forces (e.g., consumption) than other functions (Loreau, 2010). For example, Cargill and Jeffries (1984) shows how snow geese herbivory can decrease plant biomass but increase plant production in tundra ecosystems, a phenomenon commonly referred to as grazing optimization. Production may also be affected by bottom-up influences because physical mass balance constraints require that an increase in bottom-up inflow must eventually be offset by an increase in bottom-up outflow. An increase in bottom-up outflow will propagate upwards through the food chain and in turn spread throughout the entire ecosystem. Consequently, the subsidy effect might be stronger on ecosystem production than ecosystem recycling if the dominant process is bottom-up. We expect other systems in which top predators receive high quality subsidies to also follow our predictions, i.e., subsidy causing a top-down cascading effects with stronger effects on recycling than production (e.g., terrestrial invertebrates' subsidies for fish). Our quality-quantity modelling framework can be applied to diverse cases in which subsidy qualities vary. Further examples include: high quality lake food in seston (i.e., high growth-producing nutrient per unit of food intake) for filter feeding animals in streams at the outflow of lakes (Richardson and Mackay, 1991), and high-quality riparian leaf litter (i.e., decomposability) for aquatic invertebrates (Richardson et al., 2004) (see Richardson et al., 2009 for other potential examples). Our findings that model predictions are most sensitive to the basal input rate of inorganic nutrients (I) (figure 3.5), demonstrates that ecosystems are controlled by both top-down and bottom-up processes. Future empirical and theoretical work on the impacts of subsidy quality on recipient ecosystem function should measure or incorporate both biotic and abiotic components of the recipient ecosystem in order to capture key bottom-up and top-down feedbacks that emerge from such an ecosystem perspective (see Loreau and Holt, 2004; Leroux and Loreau, 2015).

Feedbacks between our predictions and empirical research can advance our understanding of ecosystem connections under global changes. For example, theory provides a framework to guide experimental design and interpretation of observation, while empirical research can be used to test model predictions, assumptions, and identify missing model processes (Grainger et al., 2022). Recent advances in spatial stoichiometry provide the methods to map empirical patterns in limiting nutrients at an ecosystem level (Leroux et al., 2017; Soranno et al., 2019). Consequently, even at a field scale, our predictions on ecosystem functions can be tested across field sites with varying quality of subsidies. Empirical methods to measure production exist for marine (Nishijima et al., 2021), terrestrial (Zheng et al., 2003), and freshwater ecosystems (Puts et al., 2022). In some instances (e.g., Eggert and Wallace, 2003), empirical studies of subsidies measure these ecosystem functions and in others (e.g., Barrett et al., 2005, Bomkamp et al., 2004); it would be a small addition to do so. Measuring such functions is key as we know many ecosystem functions have different responses to global changes (Giling et al., 2018; Larsen et al., 2016).

Our model and simulations are not without limitations. First, based on a meta-analysis of Bartels et. al (2012), we assume that subsidy quality causes a maximum predator consumption effect of 5.7-fold (but see appendix 2: figure 7.4 for results when we vary this by +/- 50%). This calls for additional experimental evidence to characterize the relationship between n-3 LC-PUFAs and consumer fitness. This requires experiments with treatments across n-3 LC-PUFAs gradients, i.e., rather than just two levels. The processes that underpin how n-3 LC-PUFAs affect the consumption of predator will more accurately be identified, and thus will enhance the prediction of ecological outcomes in the riparian ecosystem. Second, based on our research goal (i.e., focus on transient dynamics) and following McCary et al. (2021), the unsubsidized recipient ecosystem was formulated to have a fixed equilibrium. However, ecological systems are rarely at a fixed equilibrium (Burton et al., 2020) because model parameters often fluctuate with environmental variability, which implies that the theoretical equilibrium state is constantly fluctuating and never settles at a fixed point (Coulson, 2020). Nevertheless, our results are quite robust as in many different parameter values with different equilibria, the results were qualitatively similar in most cases (90%). Third, the ecosystem variables were modelled at the functional group level (i.e., herbivores, predators). This approach is consistent with other ecosystem models (e.g., Leroux and Loreau, 2008; McCann et al., 1998), however, variabilities exist within the functional groups which could reflect differences between ecological system types. For example, Kowarik et al. (2021) showed that n-3 LC-PUFAs content differ in different orders of emergence aquatic insects. Graf et al. (2017) showed that the effects of aquatic subsidies on riparian ecosystems depend on the herbivore composition of the riparian ecosystem. However, the current level of complexity of our model enabled us gain general insights into how changes in subsidy quality affect the recipient ecosystem, and the model can easily be applied to other ecosystems.

Based on our findings, we suggest that ecosystems that rely on high quality subsidies (relative to local alternative resources), are sensitive to the removal or degradation of their connections to subsidies (e.g., due to eutrophication, climate change, see Larson et al., 2016). Examples are nutrient-poor ecosystems and ecosystems that are located in remote locations (e.g., arctic and alpine lakes, and their surrounding terrain). This is because such ecosystems have clear ecosystem boundaries and thus are more sensitive to subsidy changes resulting from rapid environmental change (Burpee and Saros, 2020). Our study also highlights the importance of considering multiple dimensions of subsidies (e.g., pulse duration, timing, quality). Temporal and spatial heterogeneity in subsidies likely translates to variable responses in the recipient ecosystems. For the example of streams and riparian ecosystems, the strength of the subsidy effect likely depends on the distance from the shore and the stream and riparian species composition (Muehlbauer et al., 2019; Schindler and Smits, 2016). Future empirical studies could investigate the patchiness of subsidy effects.

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Chapter 4: Top-down and Bottom-up coupling effects of subsidy on recipient ecosystem*

Abstract

A subsidy can directly enter a recipient ecosystem by either being consumed or being recycled to the nutrient pool with both pathways causing multiple indirect and potentially conflicting effects. Subsidy pathways are prone to anthropogenic stressors, which can impact the relative strength of the recycling and direct consumption fluxes. Current studies have mainly focused on a single coupling pathway, limiting our knowledge of subsidy effects on recipient ecosystems. We derive a series of models to predict the relative and interactive effects between consumption and recycling subsidy coupling pathways on the biomass and functions of a recipient ecosystem. We solved the models for analytical equilibria, and compared model predictions with and without each subsidy pathway. Our results show that the direct consumption and recycling coupling pathways of subsidies interact antagonistically, as the feedbacks between both pathways led to lower stocks and functions of the recipient ecosystem than a model which omits these feedbacks. These subsidy effects are consistent for each trophic level of the recipient ecosystem. Our models also predicted that consumption and recycling pathways of subsidies had differential effects on the recipient ecosystem. Recycling coupling pathway always led to equal or higher stocks and functions across recipient ecosystem trophic levels, whereas consumption couplings had alternating positive and negative effects depending on trophic level and characteristic of a trophic cascade. We suggest that future empirical and theoretical research on subsidies should consider various coupling pathways to provide a more mechanistic understanding of the effects of subsidies.

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4.1 Introduction

Ecosystems are interconnected through the flow of energy, materials, and organisms (Loreau et al., 2003; Polis et al., 1997). These flows, often referred to as subsidies (i.e., resources of external origin), can alter the recipient ecosystem by changing the spatial distribution of resources (Gravel et al., 2010) and cause trophic cascades (Leroux and Loreau, 2008). The impact of such subsidies is influenced by the timing (Leroux and Loreau, 2012) and quality (Osakpolor et al., 2023) of the subsidy, the ability of top predators to exploit the subsidy (McCary et al., 2021), the ratio of subsidies to comparable resources in the recipient system, and its spatial and temporal extent (Marczak et al., 2007).

Understanding the impact of subsidies on recipient ecosystems is hampered by the subsidy affecting multiple trophic levels. In many cases, a single subsidy can have direct effects on consumers and detritus in the recipient ecosystem through processes like direct consumption and recycling. For example, migratory salmon provide marine-derived subsidies to streams (Gende et al., 2002), which are consumed by various organisms (direct consumption) and their carcasses can end up in the stream's nutrient pool (recycling) to benefit primary producers (Wipfli et al., 1998). Terrestrial leaf subsidies are directly consumed by larval caddisflies, while also providing subsidies for algae through recycling (Holgerson et al., 2016).

The challenge of understanding subsidy impacts on recipient ecosystem is additionally complicated by the multiple indirect effects that a subsidy can exert on the recipient ecosystem. For example, emergent aquatic insects can subsidize the riparian secondary consumers (Kowarik et al., 2021), potentially resulting in increased predation pressures on the riparian herbivores, and ultimately increasing riparian plant productivity. Hence, emergent aquatic insects can indirectly affect plant productivity (Henschel et al., 2001; Holgerson et al., 2016). Simultaneously, those emergent aquatic insects can increase the input of subsidies into the riparian nutrient pool (Dreyer et al., 2015) causing an increase in herbivore biomass (Bultman et al., 2014), and potentially resulting in an increase in riparian secondary consumer biomass. Hence, measuring the degree of ecosystem coupling by a single subsidy becomes quite challenging as pathways of recycling and direct consumption involve multiple indirect and potentially contrasting effects in the recipient ecosystem. One of the challenges of understanding subsidy impacts on recipient ecosystems is therefore to determine the interaction between the direct consumption and recycling subsidy pathways (Allen and Wesner, 2016). Mathematical models can be a useful tool to tackle this challenge.

Ecological understanding gained through feedbacks between theory and empirical studies can be valuable in addressing how anthropogenic stressors affect the subsidy dependent functioning of recipient ecosystems (Simberloff and Wilson, 1969; Tilman, 1977). The connection between empirical and theoretical research in subsidy-recipient ecosystem studies, however, has been missing due to a mismatch in what is measured. Empirical studies typically measure the interaction between subsidies and the recipient ecosystem in terms of the utilization of subsidies and their transfer in the recipient food web (e.g., using stable isotopes- Lam et al., 2013). Meanwhile, theoretical studies measure the input of subsidies into the recipient ecosystem (see review in Osakpolor et al., 2021). However, the input rate of subsidies does not necessarily reflect the actual energy consumed by the recipient ecosystem. Consumer preferences for subsidies can impact the stability (Abrams et al., 1998; Huxel and McCann, 1998) and functioning (Leroux and Loreau, 2008) of the recipient ecosystem, so a high subsidy input rate may be insufficient to determine subsidy impact if it is not a preferred resource. Moreover, theoretical studies often focus on endpoints such as stability (Gounand et al., 2014), which differ from the functional measures used in empirical studies like efficiency and production (Mehner et al., 2022).

Our aim is to develop theories on how subsidies affect the recipient ecosystem using metrics that are compatible with empirical research. To do this, we will derive and analyze a series of models to explore how subsidy-recipient ecosystem coupling pathways can impact, both independently and interactively, the equilibria stocks (i.e., biomass) and functions (i.e., recycling, efficiency and production) of the recipient ecosystem. First, we will examine the predictability of how the two different subsidy-recipient ecosystem coupling pathways (direct consumption and recycling) interact to impact the equilibria stocks and functions of the recipient ecosystem. Then we will investigate how different subsidy-recipient ecosystem coupling pathways affect the equilibria stocks and functions of the recipient ecosystem.

4.2 Methods

4.2.1 Model case studies

Riparian areas are a globally common and specific area of concern as they are important hotspots and hot moments of biogeochemical processes and biodiversity, supporting ecosystem functions (Costanza et al., 1997; Williamson et al., 2008). Riparian ecosystems are functionally linked to aquatic ecosystems through subsidy flows. The permeability of the boundary between aquatic and riparian ecosystems has been well documented, suggesting the examination of these ecosystems by analyzing cross-ecosystem resource exchange (Soininen et al., 2015). We will achieve our research goals using two case studies featuring a riparian ecosystem subsidized by aquatic resources. The riparian ecosystem is constituted by inorganic nutrient (e.g., nitrogen), plants (e.g., stinging nettles), herbivores (e.g., leafhoppers), and predators (e.g., spiders) subsidized by emergent aquatic insects. In case study 1, the aquatic subsidy (emergent aquatic insects) is directly consumed by the riparian predator (fig. 4.1a), while in case study 2 the aquatic subsidy (flood-driven deposition of macrophytes, e.g., reeds) is directly consumed by the riparian herbivore (fig. 4.1b). For both case studies, the subsidy can also be recycled to the nutrient pool.

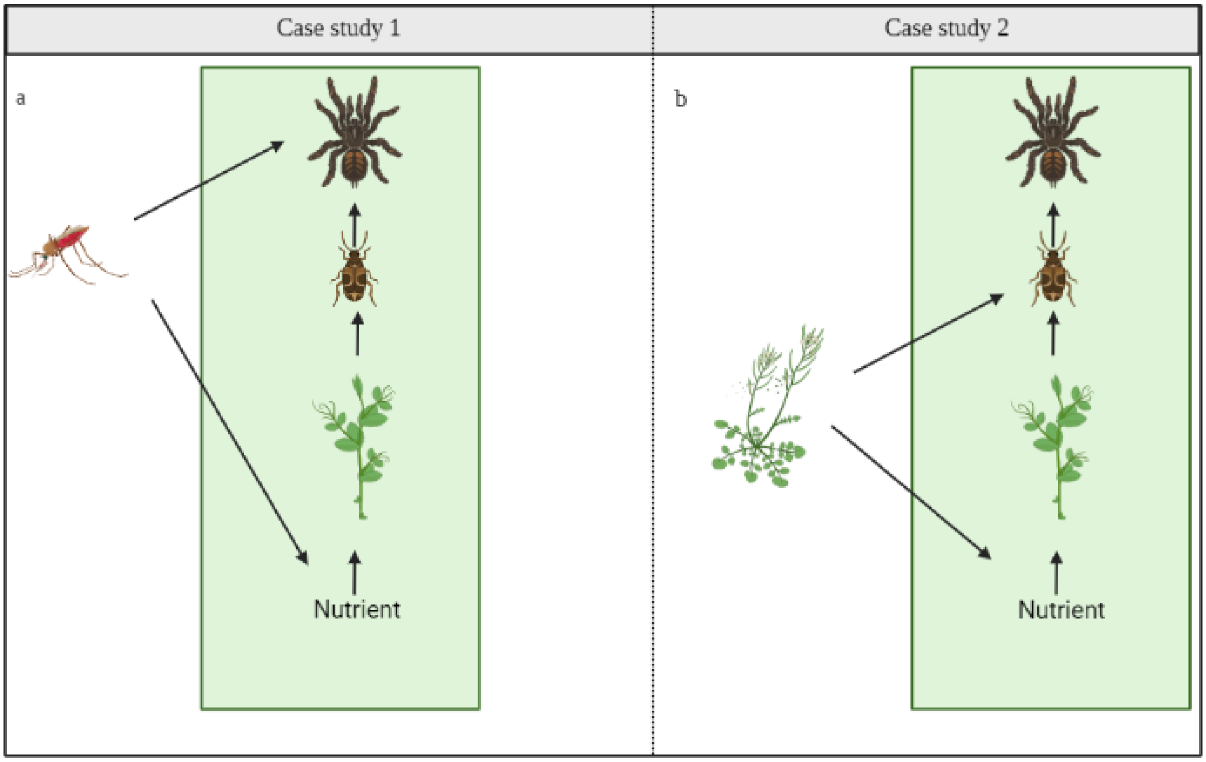

Figure 4.1: Case studies

4.2.2 Model

We derived models for each case study that allowed us to investigate how each subsidy pathway (i.e., direct consumption or recycling to the nutrient pool) and the combined pathway (i.e., both direct consumption and recycling to the nutrients pools) impacts the recipient ecosystem. Specifically, we had a total of seven models consisting of (1) base model: non-subsidized recipient ecosystem, (2) full model for case study 1, (3) full model for case study 2, (4) direct consumption model for case study 1, (5) direct consumption model for case study 2, (6) recycling model for case study 1, (7) recycling model for case study 2 (figs. 4.2a-4.2g respectively for diagram depictions of each of these models).

The complete model equations consist of one abiotic compartment: inorganic nutrients (N) and five biotic compartments: plant (A), herbivore (H), predator (P), H subsidy (L), and P subsidy (E). L and E are subsidies while N, A, H, P are in the recipient ecosystem. The recipient ecosystem model is open at the basal level through constant input of inorganic nutrient, I, and constant loss of inorganic nutrient, l. Biotic modules recycle nutrients at rates d_i but only a fraction, $1- \delta_i$, of recycled nutrients reach the soil nutrient pool whereas the remainder (δ_i) is lost from the system, where i is L, E, A, H, or P. We use Type I functional responses for each consumer with an attack rate, a_i, and consumption efficiency, e_i.

The donor ecosystem-controlled subsidy (E) (with constant input rates w_E) (eq. 5) serves as a subsidy for P (Equation 4) and also enters the soil nutrient pool via recycling ($(1 - \delta_E)\ d_E E$) (eq. 1). P, therefore, has two resources, subsidy (E) and herbivore (H). Following Huxel et al. (2002) and McCann et al. (2005), we model P preference for H as $\boldsymbol{\pi}_p$ (where 1- $\boldsymbol{\pi}_p$ is the preference for E) (eq. 4). Similarly, the donor ecosystem-controlled subsidy (L) (with constant input rates w_L) (eq. 6) serves as a subsidy for H (eq. 3) and also enters the soil nutrient via recycling ($(1 - \delta_L)\ d_L L$) (eq. 1). As above, we also model H preference for the local plant as $\boldsymbol{\pi}_h$ (where 1- $\boldsymbol{\pi}_h$ is the preference for E) (Huxel et al., 2002; McCann et al., 2005) (eq. 3). The models are described by the dynamic equations as shown in eqs. 1 – 6. The seven models can be derived from the complete set of model equations as stated in table 4.1.

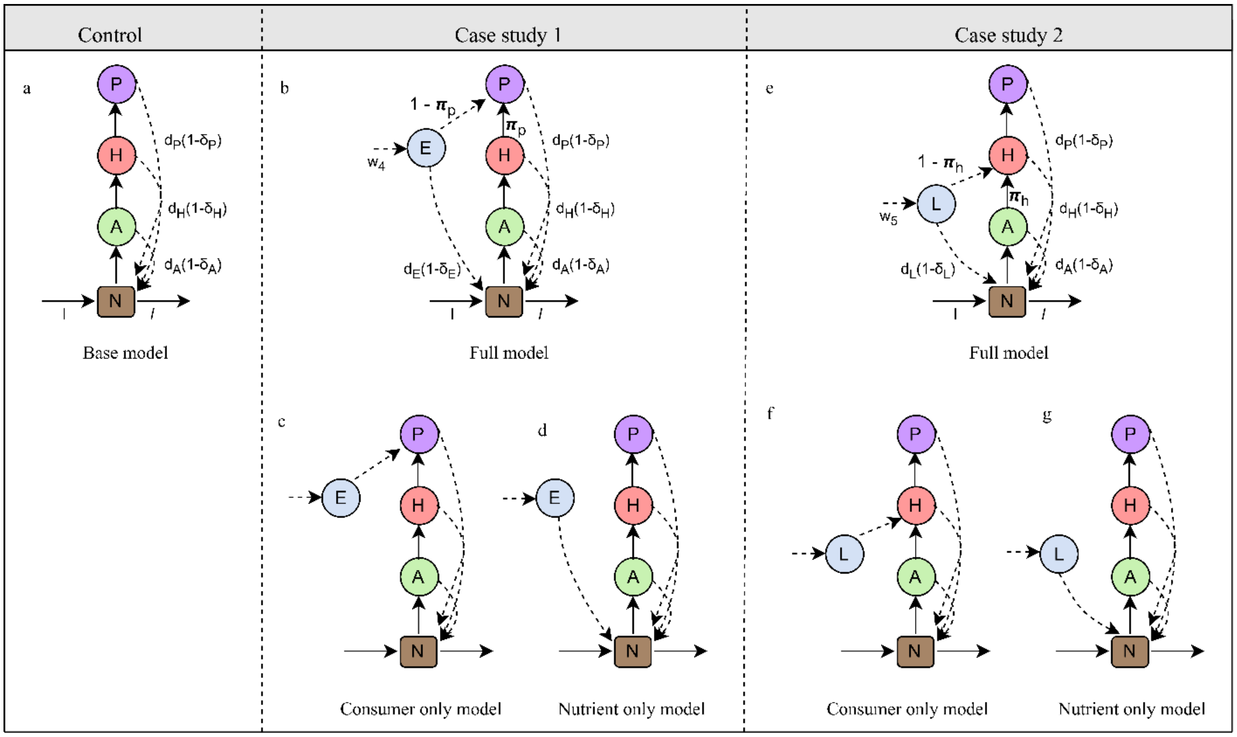

Figure 4.2: Analyzed models

$$\frac{dN}{dt} = I + (1-\delta_L)\, d_L L + (1-\delta_E)\, d_E E + (1-\delta_A)\, d_A A + (1-\delta_H) d_H H + (1-\delta_P) d_P P - a_A NA - lN \tag{1}$$

$$\frac{dA}{dt} = a_A NA - a_H \pi_h AH - d_A A \tag{2}$$

$$\frac{dH}{dt} = e_H a_H \pi_h AH + e_H a_H LH(1-\pi_h) - a_P \pi_P HP - d_H H \tag{3}$$

$$\frac{dP}{dt} = e_P a_P \pi_P HP + e_P a_P EP(1-\pi_P) - d_P P \tag{4}$$

$$\frac{dE}{dt} = w_E - e_P a_P EP(1-\pi_P) - d_E E \tag{5}$$

$$\frac{dL}{dt} = w_L - e_H a_H LH(1-\pi_h) - d_L L \tag{6}$$

Table 4.1: derivation of the models from the model equations

Model Type	**Derivation**
Full model for case study 1	set $w_L = 0$, $\pi_h = 1$
Full model for case study 2	set $w_E = 0$, $\pi_p = 1$
Direct consumption model for case study 1	set $w_L = 0$, $\delta_E = \pi_h =1$
Direct consumption model for case study 2	set $w_L = 0$, $\delta_L = \pi_p = 1$
Recycling model for case study 1	set $w_L = 0$, $\pi_p = \pi_h = 1$
Recycling model for case study 2	set $w_E = 0$, $\pi_p = \pi_h = 1$
Base model	set $w_E = w_L = 0$

4.2.3 Analysis

We compared the models (fig. 4.2) using the same parameter sets. First, we solved the models for equilibrium (denoted with *) using *Mathematica 12.3*. Then, we randomly selected 150,000 parameter sets whereby all parameters were simultaneously varied between 0 and 10 according to a uniform random distribution (as per Leroux and Schmitz, 2015) with the exception of δ_i, e_i, w_L, and w_E, which are proportions and were simultaneously varied between 0 and 1 according to a uniform random distribution (appendix 3: table 8.2). Next, using the 150,000 parameter sets and analytical equilibria solutions, we calculated equilibria stocks and functions for each parameter set retaining only feasible parameter sets (i.e., where $N^*, A^*, H^*, P^* > 0$). We follow Loreau (2010) in the derivation and measurement of analytical expressions for ecosystem functions including production, efficiency, and recycling (appendix 3: eqs. s1-s12).

4.2.3.1 Subsidy coupling metrics

Based on our case studies, we have three distinctive subsidy-recipient ecosystem coupling pathways. Specifically, coupling by the direct consumption of subsidy (E) by predator (P) (eq. 7), coupling by the direct consumption of subsidy (L) by herbivore (H) (eq. 8), and recycling coupling of subsidy (E or L) (eq. 9 or 10) which were derived following Tunney et al. (2012). The coupling by the direct consumption of E by P is defined as the ratio of subsidy (E) to an alternative local resource (H) consumed by P, the coupling by the direct consumption of L by H is defined as the ratio of subsidy (L) to an alternative local resource (A) consumed by H, while the nutrient coupling is defined as the proportion that subsidy E or L recycling, respectively, contributes to the overall nutrient pool.

Consumption coupling for case study 1 = $(e_p a_p EP(1-\pi_P))/(e_P a_P \pi_P HP)$ (7)

Consumption coupling for case study 2 = $(e_H a_H LH(1-\pi_h))/(e_H a_H \pi_h AH)$ (8)

Recycling coupling for case study 2 = $((1-\delta_L)\, d_L L)/((1-\delta_A)\, d_A A + (1-\delta_H) d_H H + (1-\delta_P) d_P P)$ (9)

Recycling coupling for case study 1 = $((1-\delta_E)\, d_E E)/((1-\delta_A)\, d_A A + (1-\delta_H) d_H H + (1-\delta_P) d_P P)$ (10)

4.2.3.2 *Interactions and effects of subsidy-recipient ecosystem coupling pathways on recipient ecosystem functions*

We studied the interaction of the subsidy-recipient ecosystem coupling pathways for our case studies using attenuation plots. For the attenuation plots we plotted the ratio of the full model (i.e., consisting of all pathways; figs. 4.2b and 4.2e) to the base model vs the ratio of the sum model (i.e., a sum of the direct consumption of the subsidy only model and the direct recycling of the subsidy to the nutrient pool only model) to the base model for a given metric (e.g., recycling) for each case study. In this way, we determined the interaction between the coupling pathways by examining where the points sit relative to the one-to-one line. If the points are above the line that means that recycling and direct consumption interact synergistically, i.e., are greater than the sum of their parts (the one-to-one line), while if they sit below the one-to-one line, they interact antagonistically, i.e., are less than the sum of their parts (see appendix 3: fig. 8.1 for cartoon representation).

4.2.3.3 Effects of subsidy-recipient ecosystem coupling pathways on stocks and function of the recipient ecosystem

To assess the independent effect of each subsidy-recipient ecosystem coupling pathway on the recipient ecosystem, we measured the natural logarithm of each equilibrium stock and function in the independent coupling models (i.e., consumption coupling by P, consumption coupling by H, and recycling coupling models) divided by the base model equilibrium stock and function. We report these coupling metrics along a coupling gradient to determine how coupling affects recipient ecosystem functions (see appendix 3: fig. 8.2 for cartoon representation). Specifically, the coupling gradient measures the extent to which the recipient ecosystem relies on subsidy. In this way, a value greater than 0 on the y-axis implies that subsidy coupling led to greater stocks or functions relative to a non-subsidized ecosystem for a given subsidy-recipient ecosystem coupling (x-axis).

4.3 Results

4.3.1 General Overview

We obtained two feasible equilibria solutions for the full model for case study 1, direct consumption model for case study 1, and one feasible equilibrium solution for the full model for case study 2, base model, recycling model for case studies 1 and 2, and direct consumption model for case study 2. We randomly selected one feasible equilibria solution in cases where we obtained two solutions (e.g., full model for case study 1). Out of the 150,000 parameter sets, a range of 3143 – 4055 parameter sets across the models were retained because they led to N*, A*, H*, and P* > 0 (appendix 3: table 8.1).

4.3.2 How do subsidy-recipient ecosystem coupling pathways interact and affect recipient ecosystem functions?

The full model incorporating both direct subsidy pathways (i.e., direct consumption of the subsidy and direct recycling of the subsidy to the nutrient pool) results in lower total ecosystem stocks and lower total ecosystem functions (i.e., sum across trophic levels) than the sum model (i.e., a sum of the direct consumption of the subsidy only model and the direct recycling of the subsidy to the nutrient pool only model) (fig. 4.3). Therefore, the coupling pathways interact antagonistically, i.e., feedbacks between the coupling pathways result in lower stocks and functions relative to a model which omits these feedbacks. Moreover, this difference between the full model and the sum model is dependent on the strength of the subsidy effect. As the impact of the subsidy becomes stronger (i.e., the total stocks or functions becomes much greater in the presence of the subsidy) the difference between the full and sum models decreases. The above relationship also holds at the various trophic levels of the recipient ecosystem (appendix 3: figs. 8.3 – 8.6).

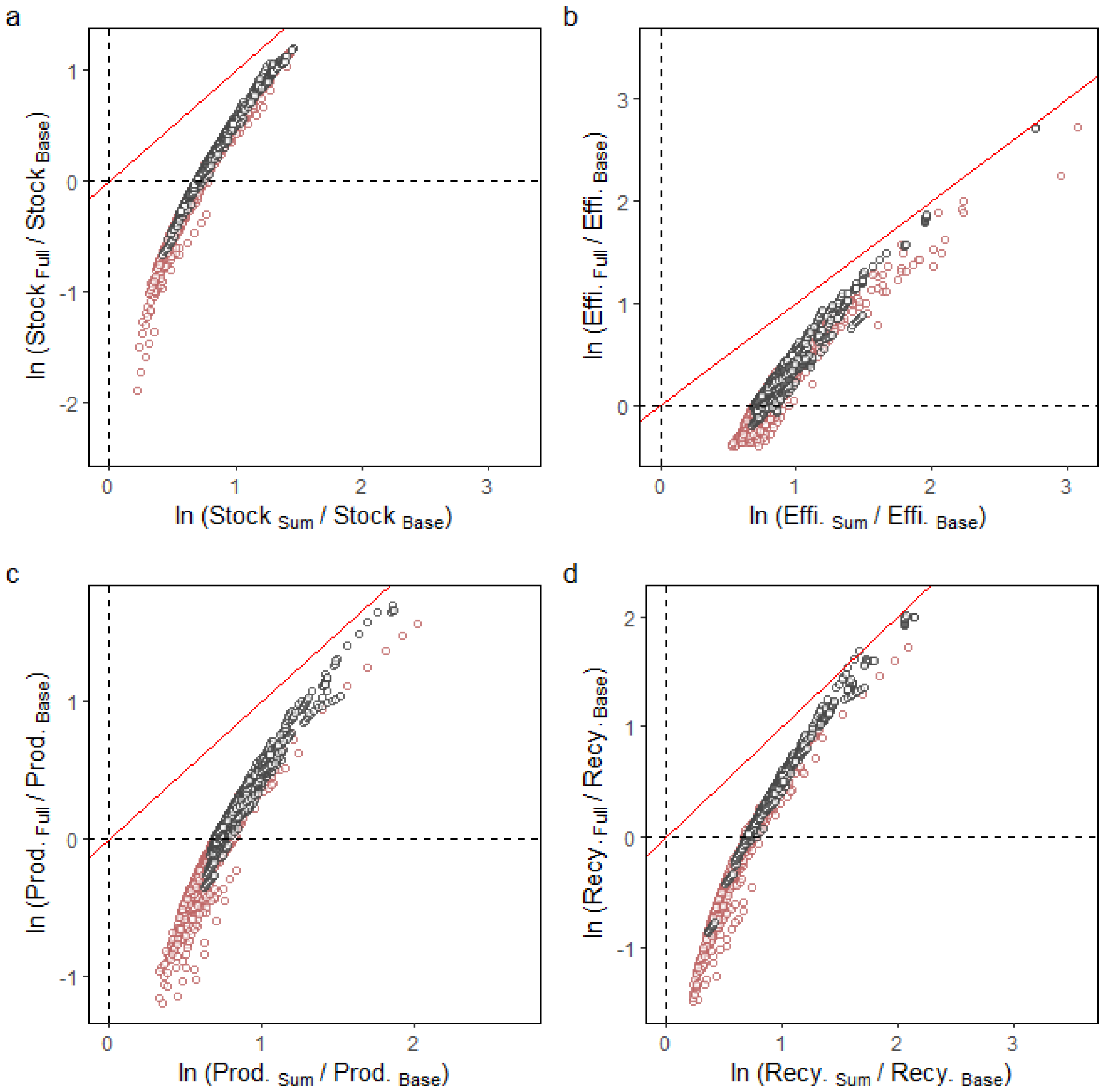

Figure 4.3: Interaction of subsidy-recipient ecosystem coupling pathways and effects on total stocks and total functions of the recipient ecosystem (i.e., sum across trophic levels). The red points represent case study 1, while the black points represent case study 2. Effi., Prod., Recy. represents the efficiency, production and recycling functions, respectively. The red line is the one-to-one line where points below the line indicate that direct subsidy pathways (i.e., direct consumption or recycling into nutrient pool) interact antagonistically, while points above the line indicate that direct subsidy pathways interact synergistically. See appendix 3: fig. 8.1 on how to interpret the figure.

4.3.3 How do different subsidy-recipient ecosystem coupling pathways affect recipient ecosystem stocks and functions?

Increasing the subsidy couplings led to an increase in stocks and functions of the recipient ecosystem (i.e., sum across trophic levels) (fig. 4.4). But the intensity of the increase differs between recipient ecosystem functions and coupling pathways. For example, the efficiency of the recipient ecosystem increased stronger in case study 1 consumption coupling than case study 2 consumption or recycling coupling (figs. 4.4a-4.4c). This difference occurs when the top predator depends more on subsidy than on local alternate resource (i.e., C1 coupling > 0) (fig. 4.4b). Recycling coupling always led to equal or higher stocks and functions of the recipient ecosystem relative to a non-subsidized ecosystem (base model) (figs. 4.4a, 4.4d, 4.4g, 4.4j), while consumption couplings may cause lower stocks and functions of the recipient ecosystem, but the stocks and functions increase with coupling (fig. 4.4). This is because recycling coupling always led to equal or higher stocks and functions across the recipient ecosystem trophic levels, while consumption couplings had cascading effects on the recipient ecosystem trophic levels (appendix 3: figs. 8.7-8.10). The positive cascading effects of case study 1 consumption coupling on the stock and functions of plant is more evident when the top predator depend more on subsidy than local resource (appendix 3: figs. 8.7e, 8.8b, 8.9b, 8.10b).

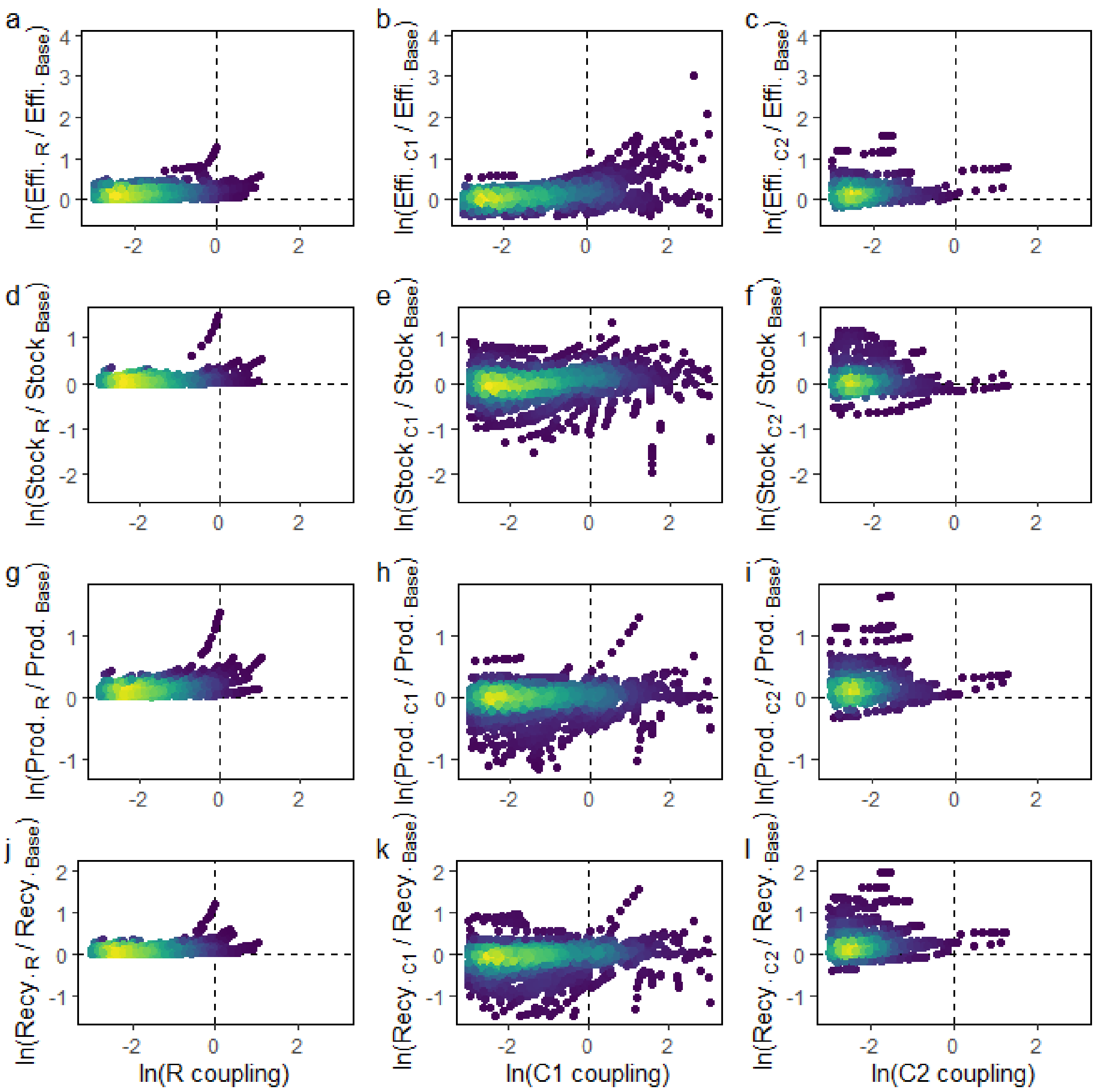

Figure 4.4: Subsidy coupling effects on stocks and functions of recipient ecosystem (i.e., sum across trophic levels). The y-axis shows a comparison between the coupling and the base models for a particular function/stock. Note: because of the way the parameter sets were chosen for the two case studies the recycling models for both case study 1 and case study 2 end up being identical. R, C1, and C2 represent the recycling model, and the consumption model for case study 1 and 2, respectively, while R coupling, C1 coupling, and C2 coupling are the coupling metrics for these different models (eqs. 9 and 10 for R coupling and eqs. 7 and 8 for C1 and C2 coupling). Base is the base model. Effi, Prod., Recy represents the efficiency, production and recycling functions respectively. See subsidy coupling metrics section for definition of the x-axis and appendix 3: fig. 8.2 on how to interpret the figure.

4.4 Discussion

We derived ecosystem models that enabled us to study how subsidy-recipient ecosystem coupling pathways independently and interactively affect stocks and functions of a recipient ecosystem. This is because subsidies are often coupled to recipient ecosystems via direct consumption and recycling, with both pathways causing multiple direct and indirect effects with different strengths and directions. We aimed to understand how the different couplings interact and generate feedbacks in recipient ecosystems (Allen and Wesner, 2016).

The theoretical study was conducted using metrics that are compatible with empirical research. This is motivated by the mismatch in terms of what is being measured in empirical and theoretical subsidy-recipient ecosystem research studies. For example, empirical scientists often study subsidy effects in terms of its usage (e.g., Hambäck et al., 2016), while the theoreticians study subsidy effects in terms of its availability (see review in Osakpolor et al., 2021). The assumption of most subsidy models contradicts evidence that subsidy preference over local resource has an impact on the effect of subsidy (Abrams et al., 1998; Leroux and Loreau, 2008).

How do subsidy-recipient ecosystem coupling pathways interact and affect recipient ecosystem functions?

The model analysis shows that the direct consumption and recycling coupling pathways of subsidy interact antagonistically, as the feedbacks between both pathways led to lower stocks and functions of recipient ecosystem (i.e., sum across trophic levels) and the various trophic levels relative to a model which omits these feedbacks. Previous studies have attempted to study how changes in multiple trophic levels interactively affect food webs. For example, a meta-analysis found that the presence of predators leads to a decline in herbivore biomass and an increase in plant biomass, regardless of plant productivity (Borer et al., 2006). On the other hand, an increase in nutrient levels increased plant biomass, but not herbivore biomass irrespective of the presence of predators. In particular, the minimal impact of increasing nutrient levels on higher trophic levels demonstrates the importance of bottom-up effects and the difficulties in teasing out the impacts of bottom-up and top-down effects in empirical systems. These results were consistent across different ecosystems, including marine, freshwater, and terrestrial, and were independent of study size and duration (Borer et al., 2006). In another meta-analysis of experimental studies, the effect of nutrient and herbivory changes on producer biomass showed limited support for statistical interactions (Gruner et al., 2008). However, a synergism of nutrient enrichment and herbivore removal on producer biomass in marine temperate rocky reef systems was found.

The above studies demonstrate some of the fundamental difficulties in attempting to tease out the interactive effects of bottom-up and top-down effects in experimental settings. By using a modeling approach, we were able to explicitly quantify these interactive effects. Our study defined interaction similar to the definition of stressors interaction, whereby combined effects are compared to the sum of individual effects (Brook et al., 2008). An interaction is antagonistic when the sum of individual effects is greater than the combined effects and synergistic when the sum of effects is less than then combined effects (Brook et al., 2008). Our model predictions provide profound insight on how subsidies can impact recipient ecosystems and the need to study the effects of the different subsidy-recipient ecosystem pathways on the recipient ecosystem. This is because the subsidy coupling pathways are also prone to anthropogenic stressors, which can change the relative importance of the recycling link and the direct consumption link. For example, a degraded riparian habitat (i.e., less vegetation structure) can reduce the accessibility of emergent aquatic insects to riparian consumers (Hunt et al., 2020; Muehlbauer et al., 2014), which could increase the input of emergent aquatic insects into the riparian nutrient pool. A degraded riparian soil (i.e., low nutrient levels) can enhance the impacts of recycling linkage of emergent aquatic insects on the riparian food web (Burpee and Saros, 2020), because nutrient enrichment represents a relative relief from nutrient limitation (Hillebrand, 2002).

How do subsidy-recipient ecosystem coupling pathways affect recipient ecosystem stocks and functions?

Our models also predict that consumption and recycling coupling pathways of subsidy had differential effects on the stocks and functions of the recipient ecosystem trophic levels. Recycling coupling pathway always led to equal or higher stocks and functions across the recipient ecosystem trophic levels, whereas consumption couplings had cascading effects. Specifically, the nutrient and herbivore trophic levels of the recipient ecosystem remained similar for recycling coupling, whereas the plant and predator trophic levels slightly increased. Our predictions support the trophic theory that predicts that an increase in the nutrient levels of an ecosystem consisting of plants, herbivores and predators will cause the plant biomass to increase, whereas herbivore biomass remains unchanged (Oksanen et al., 1981). The cascading (indirect) effect predicted by our model is more pronounced when the consumer of the recipient ecosystem consumes more of the subsidy than local resource. Our results have also been corroborated by previous studies focusing on different ecological systems. For example, fish predators induced a significant increase in the biomass of phytoplankton, whereas nutrient addition promoted phytoplankton growth without significantly elevating the biomass of zooplankton (Brett and Goldman, 1997). Another study revealed that predators demonstrate strong top-down effects throughout entire food chains, whereas the bottom-up influence of eutrophication primarily affects plant productivity (Borer et al. 2006). Thus, the asymmetry in the effects of direct consumption and recycling coupling pathways have far-reaching implications: reduction of the consumption coupling pathway of subsidy may have more extensive multi-trophic implications for communities than will the recycling coupling pathway.

Our study acts as a bridge between empirical and theoretical fields. In particular, our predictions on ecosystem functions (production, efficiency and recycling) can be empirically tested at a field scale. Empirical methods for measuring production exist for various types of ecosystems, including marine (Nishijima et al., 2021), terrestrial (Zheng et al., 2003), and freshwater ecosystems (Puts et al., 2022). In some instances (e.g., Eggert and Wallace, 2003), empirical studies of subsidies measure these ecosystem functions and in others (e.g., Barrett et al., 2005) it would require minimal additional effort. Measuring such functions is key as we know many ecosystem functions have different responses to global changes (Giling et al., 2018; Larsen et al., 2016) and forecasting the responses of these ecosystem functions is becoming more imperative.

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Chapter 5: General discussion and future perspective

In this thesis, the main aim is to contribute to the development of theories on how changes in subsidies affect recipient ecosystems using aquatic-terrestrial interface as a case study. This led to further sub-objectives: (1) to review current meta-ecosystem models (type, structure, and code accessibility) and to summarize the results from the application of the models (**chapter 2**), (2) to quantify the effects of subsidy quality on the stocks and functions of recipient ecosystem (**chapter 3**), (3) to examine how differential subsidy-recipient ecosystem coupling pathways independently and interactively affect the equilibria stocks and functions of recipient ecosystem (**chapter 4**).

5.1 Existing subsidy-ecosystem models and their application

The review study performed in **chapter 2** showed that mechanistic models has enhanced our understanding of how terrestrial subsidies affect aquatic ecosystems. For example, it was predicted that flows of nitrogen and phosphorus can cause a lake to switch from clear to turbid (i.e., to phytoplankton dominated) state. The alternative states (clear and turbid) are self-stabilizing, but different physicochemical and biological factors can affect the critical nutrient level (CNL) for cross-state transition (figure 5.1). General understanding of how cross-ecosystem subsidies affect the stability and trophic cascade of meta-ecosystems were also enhanced. For example, Leroux and Loreau (2008) confirmed the subsidy hypothesis, which states that ecosystems with high amount of subsidy will experience strong trophic cascades. Some of the above predictions have been corroborated by empirical studies. For example, Ho and Michalak (2020) found empirical evidence that summer temperature drives the transition from clear to turbid state of lakes. Henschel et al. (2001) found that emergent aquatic insect subsidies had a cascading effect on a riparian plant species.

Another goal of the literature review in **chapter 2** was to compare the structure of existing models, their code availability and identify research gaps. The result showed that the theoretical models had more similar state variables than aquatic-terrestrial models (mean similarity of 0.66 against 0.05). The diversity of the aquatic-terrestrial models points to the wide range of its models, which can be re-used or adapted for future research. Of the 27 models, only 11 models had their codes publicly available. This supports the call by Culina et al. (2020) for increased code availability in ecological research, as this will increase the reproducibility and transparency of scientific studies (Gallagher et al., 2020; McKiernan et al., 2016). We also found that existing aquatic-terrestrial models focused on how flows from terrestrial ecosystems affect aquatic food webs, with none focusing on reciprocal flows (**chapter 2**). This is because, due to the concave terrain profile of aquatic ecosystems (making them spatial attractors), the effects of terrestrial flows on aquatic ecosystems have been a major theme in ecosystem ecology for decades (Likens, 1992; Schindler and Smits, 2016). Also, the quality characteristics of subsidies were not considered in the current models, even though they might differ from alternative local resources (Baxter et al., 2005; Wipfli, 1997). Consequently, **chapters 3 and 4** developed theories using terrestrial ecosystem with aquatic subsidies as case study, while **chapter 3** also focused on how changes in subsidy quality affect recipient ecosystem.

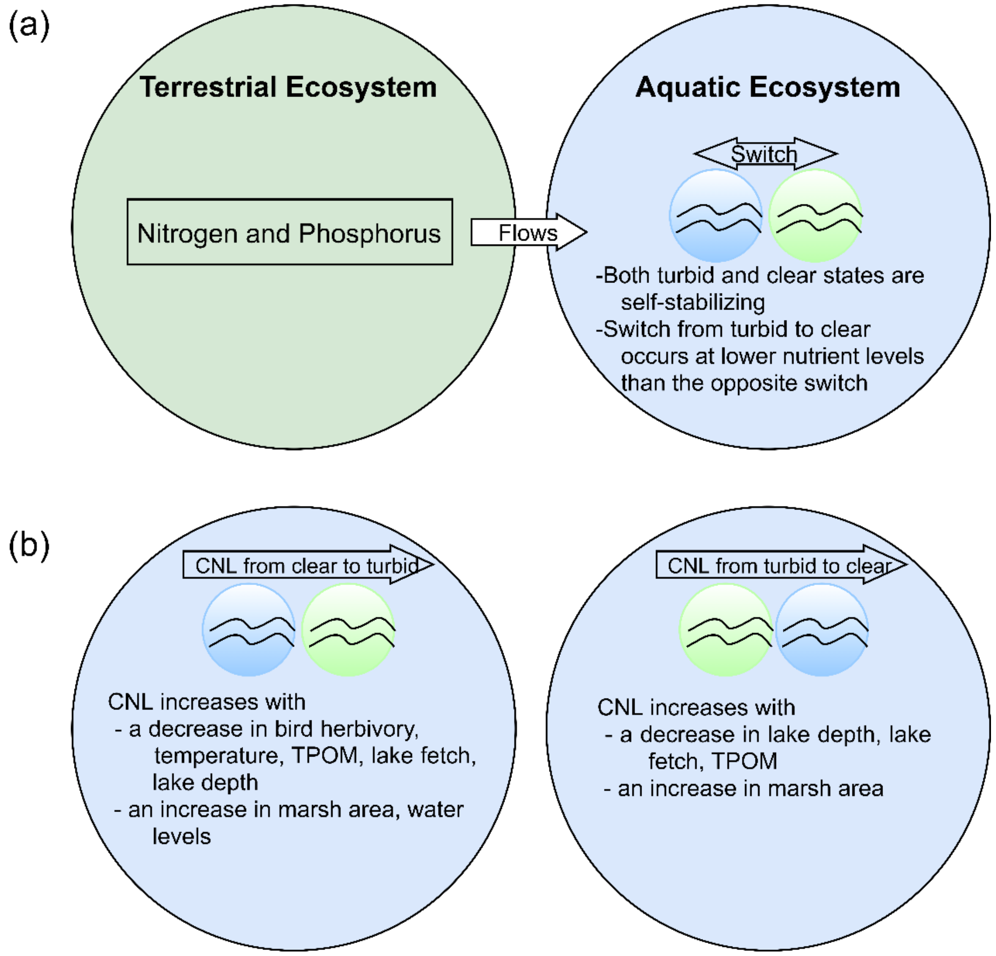

Figure 5.1: (a) Effect of nutrients on lake states and (b) factors influencing state shifts. CNL is critical nutrient level, TPOM is terrestrial particulate organic matter.

5.2 Subsidy-recipient ecosystem theories and how they can be linked to empirical studies

Recent studies have shown that emergent aquatic insects have higher quality (measured as long-chain omega-3 polyunsaturated fatty acids) than terrestrial herbivores (alternative local resource for terrestrial predators) (Parmar et al., 2022). It has also been shown that aquatic-derived long-chain omega-3 polyunsaturated fatty acids (n-3 LC-PUFAs) are exported to terrestrial consumers consequently increasing their fitness and immunity (Kowarik et al., 2021; Twining et al., 2016). Environmental stressors (e.g., eutrophication) (Paerl and Paul, 2012) can reduce n-3 LC-PUFAs export from aquatic to terrestrial ecosystem with potential cascading effects on the terrestrial ecosystem. According to the conclusion in **chapter 3**, changes in subsidy quality had a cascading effect on the recipient ecosystem. Specifically, it caused an increase in the production, recycling, and efficiency of the plants and predators but a decline in these functions for herbivores. Our new hypothesis (**subsidy quality hypothesis**) is an addition to existing hypotheses (highlighted in discussion section of **chapter 3**) attempting to provide a general explanation of the variation in the strength of trophic cascade among ecosystems. Specifically, our hypothesis unifies the subsidy (Leroux and Loreau, 2008) and food quality hypotheses (Borer et al., 2005; Hall et al., 2007), and states that the effect of subsidy on recipient ecosystem functions can be stronger when the subsidy quality is higher than that of in-situ resources.

Another goal of **chapter 3** was to check the key parameter that drives our model findings. The results in **chapter 3** showed that model predictions were most sensitive to the basal input rate of inorganic nutrients, demonstrating that ecosystems are controlled by both top-down and bottom-up processes. This further points to the relevance of top-down and bottom-up pathways in which terrestrial ecosystem are coupled to aquatic flows as reported by Schulz et al. (2015).

A single subsidy (e.g., emergent aquatic insects) can directly enter a recipient ecosystem (e.g., terrestrial ecosystem) by either being consumed (i.e., direct consumption by spiders) or being recycled to the nutrient pool (i.e., direct recycling) with both pathways causing multiple indirect and potentially conflicting effects. Given that the increase in nutrient levels can potentially cause bottom-up effects as reported by the sensitivity analysis in **chapter 3**, **chapter 4** focused on how subsidy induced top-down (direct consumption) and bottom-up (direct recycling) forces interactively and independently affect the stocks and functions of the recipient ecosystem. The need for such research was also highlighted by Allen and Wesner (2016). According to the conclusion in **chapter 4**, direct consumption and recycling coupling pathways of subsidy interact antagonistically, causing lower stocks and functions of the recipient ecosystem relative to an ecosystem that omits these feedbacks. In the past, empirical studies have investigated the interactions between bottom-up and top-down effects by manipulating the presence of top consumers and basal resources (Borer et al., 2006; Gruner et al., 2008; Hillebrand, 2002). However, their definition of interaction is different from that of **chapter 4**. Interaction was defined in **chapter 4** similar to stressor interactions, whereby combined effects were compared to the sum of individual effects. With this definition, dynamic feedbacks, which is often the goal of interaction studies, may be identified. Another goal of **chapter 4** was to study how the different pathways independently affect the stocks and functions of the recipient ecosystem. The results in **chapter 4** predict that consumption and recycling coupling pathways of subsidy had differential effects on the stocks and functions of the recipient ecosystem trophic levels. Specifically, recycling coupling did not cause a change in the nutrient and herbivore trophic levels of the recipient ecosystem, but slightly increased plant and predator trophic levels. The cascading (indirect) effect reported in **chapter 4** is more pronounced when the consumption coupling is by the predator (top consumer), while recycling induced cascading effects were minimal. The results corroborate previous studies on similar processes. For example, it supports the trophic theory of Oksanen et al. (1981) and the empirical works of Brett and Goldman (1997) and Borer et al. (2006). The above predictions have implications on how subsidies affect the structure and functioning of recipient ecosystems.

Scientific feedbacks between theory and empirical research are important for ecological understanding and for addressing global challenges (Ferrier et al., 2016). Consequently, the theories in **chapters 3 and 4** were generated in an empirically-friendly way. For example, model predictions in **chapter 3** were made at transient time scale (i.e., short term time scale), which matches the time scales of most empirical studies (Hasting, 2004). Consequently, increasing the relevance of the model predictions. Additionally, model predictions on effect of changes in subsidy on recipient ecosystem functions in **chapters 3 and 4** were done in metrics (i.e., production, efficiency, and recycling) that are often measured by empiricists (see Baruch et al., 2023; Mehner et al., 2022). Consequently, improving the connections or testability of existing theory that tends to focus on measures of stability (e.g., leading eigenvalue of Jacobian matrix); a metric that is not often measured empirically.

Grainger et al. (2022) outlined four ways theory can be integrated into empirical research. The reported ways are: (1) test predictions, (2) test assumptions, (3) use model equations, (4) adopt the framework. Clear examples of how the generated models and theories can be integrated into empirical research are highlighted in table 5.1.

Table 5.1: Hints on how theoretical works in the thesis can be applied in empirical research. n-3 LC-PUFAs is long-chain omega-3 polyunsaturated fatty acids.

Integration method	**Theory**	**Empirical research**
Test predictions	Subsidy quality hypothesis (**chapter 3**)	Empirical methods for measuring production (Zheng et al., 2003) and efficiency (Baruch et al., 2023) exist.[1]
Test assumptions	n-3 LC-PUFAs content of subsidy had a maximum predator consumption effect of 5.7-fold (**chapter 3**)	Empirical characterization of the relationship between n-3 LC-PUFAs and consumer fitness.[2]
Adopt the framework	Quantity-quality subsidy framework (**chapter 3**)	Emphasizes a new way of thinking about subsidies.[3]
Use equations	Subsidy-recipient ecosystem coupling metrics (**chapter 4**)	Empirical utilization of the metrics helps to standardize measurement of recipient ecosystem dependence on subsidies.[4]

[1] *The stated endpoints can be calculated at various scales. At a field scale, a gradient of stressors (e.g., stream degradation) can result to subsidies of different quality (Kowarik et al., 2023). At lower scales (e.g., laboratory), subsidies of different qualities can be cultured as per Twining et al. (2016) and then be used in a mesocosm study as per Graf et al. (2017).*

[2] *This requires experiments with treatments across n-3 LC-PUFAs gradients, i.e., rather than just two levels.*

[3] *That is, in addition to subsidy quantity, subsidy quality can differ from in-situ resource. The term "quality" can be dynamic and have different interpretations (e.g., body size, fatty acid content, etc.).*

[4] *Empirical studies usually measure dependence of recipient ecosystem on subsidies (e.g., emergent aquatic insects) based on quantity consumed by the consumer. This approach may not truly reflect dependence, as it does not take into account the quantity of in-situ resources consumed. This therefore may affect comparability across studies. The coupling metrics derived in chapter 4 is the*

ratio of subsidy to in-situ resources used by the consumer. Such metric can truly reflect dependence and is comparable across studies.

5.3 Future perspectives

5.3.1 Integrating traits into aquatic-terrestrial models

The reviewed studies that applied aquatic-terrestrial models predominantly examined the effect of eutrophication on algae bloom in lakes. They utilized taxon-based models that do not take into account the functional traits of phytoplankton (e.g., defense strategy, light dependent growth) (**chapter 2**). In contrast, trait-based models offer a framework for predicting trait combinations under different conditions (Klausmeier et al., 2020). Such models have the potential to identify the mechanisms that contribute to the turbid state of lakes across varying environmental conditions (Litchman, 2022). While taxon-based models can be useful when based on reliable empirical trait data and relevant mechanisms such as resource-dependent growth and grazing mortality, they may not be sufficient in predicting the emergence of novel harmful phytoplankton taxa that were not accounted for in the models (Litchman, 2022). Therefore, there is a need for novel models that can enhance our predictive capabilities of the turbid state of lakes (Wells et al., 2020). Hence, future models aimed at studying algae bloom may consider the trait-based approach. Klausmeier et al., (2020) highlighted ways to set-up trait-based models.

5.3.2 Integrating information flows into meta-ecosystem theory

Theories regarding ecosystems that receive subsidies place great emphasis on the spatial movement of matter. However, matter can exist in various forms, each representing distinct properties, including energy source, material, and environmental information (Marleau et al., 2020). Although ecological theories have traditionally treated matter solely as energy or material resources, such as phosphorus and nitrogen (**chapter 2**), it is important to recognize that organisms sense their environment and utilize environmental information to modify their behaviors and physiologies (Aartsma et al., 2017; O'Connor et al., 2019).

For instance, organisms can change their movement patterns in response to environmental cues and alter their interactions with other organisms (O'Connor et al., 2019). Moreover, external information, originating from ecosystems beyond their boundaries, can have a significant impact on the dynamics of recipient ecosystems (Little et al., 2022). This is particularly evident when considering the export of resources or detritus from one ecosystem to another, which also contains valuable information (Marleau et al., 2020). Furthermore, vocalizations and info-chemicals, such as pheromones and kairomones, can cross ecosystem boundaries and have important implications for the dynamics of recipient ecosystems. For instance, vocalizations of male frogs can attract females from distant habitats (Buxton et al., 2015), impacting ecosystem dynamics by adding gametes that contribute to trophic energy flux (Little et al., 2022). Conversely, less attractive vocalizations can deprive ecosystems of these inputs. Little et al. (2022) generated some hypotheses arising from the integration of information flow in meta-ecosystem theory and suggested ways of theoretically testing them. Consequently, future meta-ecosystem theoretical studies should consider incorporating cross-ecosystem information flow in their studies.

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Appendix 1 - chapter 2 supporting information

Text S1: Similarity Analysis

The method of Janssen et al. (2015) is based on the Sørensen index (Sørensen, 1948). Similar to biodiversity research, each model is treated as study site and scored for the presence of different state variables as if they were species using the equation:

$$Qs = \frac{2|M \cap N|}{|M|+|N|} \qquad \text{(Equation S1)}$$

Where;

$|M|$ is the number of state variables in model 1,

$|N|$ is the number of state variables in model 2,

$|M \cap N|$is the number of state variables shared by model 1 and 2,

| | denote the cardinality of the sets,

Qs is the Sørensen index varying between 0 (no overlap between the models) and 1 (models are complete identical).

Table 6.1: Programming language, code availability, type of models

Model Reference	**Programming Language**	**Model code/program availability**	**Model Type**
Vasconcelo et al. (2018)	Matlab	Not available	ODE
Roth et al. (2007)	Matlab	Not available	ODE
Atlas and Palen (2014)	Visual basic and Excel	Not available	Difference equation
Carpenter et al. (2016)	R	Available[1]	ODE
Janse et al. (1990)	Pascal programming language	Not available	ODE
Janse et al. (1995)	Advanced continuous simulation language	Available[2]	ODE
Kong et al. (2016)	Not stated	Not available	ODE
Janssen et al. (2019)	Advanced continuous simulation language	Available[3]	ODE
Baretta et al. (1995)	Fortran	Available[4]	ODE
Bartell et al. (2020)	Not stated	Available[5]	ODE
Petzoldt and Siemens (2002)	Java, Delphi and C	Available[6]	ODE
Bellmore et al. (2017)	Stella	Available[7]	ODE
Billen et al. (1994)	Phyton & Visual Basic	Not available	ODE
Cole & Wells (2003)	Fortran	Available[8]	PDE
Gurkan et al. (2006)	Not stated	Available[9]	Structural dynamic
Hipsey et al. (2006)	Fortran	Not available	ODE
Park et al. (2008)	Delphi	Available[10]	ODE
Weijerman et al. (2014)	C++	Available[11]	ODE
Zouiten et al. (2013)	Not stated	Not available	PDE
Gravel et al. (2010)	Not Stated	Not available	ODE
Leroux and Loreau (2008)	Not Stated	Not available	ODE
Leroux and Loreau (2012)	R	Not available	ODE
Gounand et al. (2014)	R	Not available	ODE
Marleau et al. (2010)	Matlab	Not available	ODE
Marleau et al. (2014)	Not Stated	Not available	ODE
Marleau et al. (2015)	Matlab	Not available	ODE
Marleau and Guichard (2019)	Matlab	Not available	ODE

ODE is ordinary differential equations, PDE is partial differential equations

URL for model code/program

[1] *https://github.com/SRCarpen/ATZ_Cascade/*

[2] *https://github.com/pcmodel/PCModel/tree/master/Licence_agreement/I_accept/PCModel1350/PCModel/3.00/Models/PCLake/6.13.16*

[3] *https://github.com/pcmodel/PCModel/tree/master/Licence_agreement/I_accept/PCModel1350/PCModel/3.00/Models/PCLake%2B/6.13.16*

[4] *https://www.pml.ac.uk/Modelling_at_PML/Access_Code*

[5] *https://GitHub.com/StevenMBartell/CASM_access*

[6] *available upon request: http://simecol.de/getas/*

[7] *trial freely available: https://stella-trial.software.informer.com/10.1/*

[8] *http://www.ce.pdx.edu/w2/*

[9] *https://pamolare-2.software.informer.com/*

[10] *https://www.epa.gov/ceam/aquatox-32-download-page#download*

[11] *available upon request: https://www.coris.noaa.gov/activities/ecosystem_model_guam/*

Table 6.2: State variables of the aquatic-terrestrial models (the model references are sorted based on number of state variables).

State variable	Carpenter et al (2016)	Bellmore et al (2017)	Atlas & Palen (2014)	Petzoldt & Siemens (2002)	Vasconcelo et al (2019)	Roth et al (2007)	Gurkan et al (2006)	Billen et al (1994)	Janse & Aldenberg (1990)	Zouiten et al (2013)	Bartell et al (2020)	Baretta et al (1995)	Janse et al (1995)	Hipsey et al (2006)	Kong et al (20x6)	Weijerman et al (2014)	Cole & Wells (2003)	Janssen et al (2019)	Park et al (2008)
2,4D Acid																			x
4Nonvlphenol isomer																			x
Acipenser fulvescens											x								
Acrolein																			x
Adult fish carbon													x		x			x	
Adult fish nitrogen													x		x			x	
Adult fish phosphorus													x		x			x	
Adult piscivore_Water						x													
Aerobic bacteria/carbon												x							
Alachlor																			x
Aldicarb																			x
Alevwife																			x
Algae (generic)			x																
Alkalinity																	x		
Alkalinity sediment																	x		
Aluminium (total)														x					
Ammonia										x									x
Ammonium							x	x				x		x		x	x		

Ammonium marsh water													x		x			x	
Amphipod, FL																			x
Amphipod, marine																			x
Amphipods											x								x
Anaerobic bacteria/carbon												x							
Anchow																			x
Anthracene																			x
Armored algivores_Water			x																
Armored detritivores_Water			x																
Asian clam																			x
Asian mud snail																			x
Atrazine																			x
Available dissolved silica										x									
Azinphos																			x
Bacteria																x	x		
Bacteria sediment														x		x			
BacteriaC												x							
BacteriaN												x				x			
BacteriaN sediment																x			
BacteriaP												x							
Bacterioplankton										x									
Benthic bluegreen algae carbon																	x		
Benthic bluegreen algae nitrogen																	x		
Benthic bluegreen algae Phosphate																	x		
Benthic bluegreen algea generic														x					
Benthic Chlorophytes														x					
Benthic Chlorophytes Nitrogen													x		x		x	x	
Benthic Chlorophytes Phosphate													x		x		x	x	
Benthic Cryptophutes														x					
Benthic diatoms Carbon																	x		

Benthic diatoms fresh (Generic)														x					
Benthic diatoms marine (Generic)														x					
Benthic diatoms Nitrogen													x		x		x	x	
Benthic diatoms Phosphate														x			x		
Benthic Dinoflagelate														x					
Benthic grazer biomass					x														
Benthic macroalgaeCarbon														x					
Benthic macroalgaeNitrogen														x					
Benthic macroalgaePhosphate														x					
Benthic Nodularia														x					
Benthic piscivore fish																x			
Benthic piscivore fish Individual reserve N																x			
Benthic Piscivore fish total N																x			
Benthic piscivores Individ structural N																x			
Benthic primary producer					x														
Benthivore						x													
Benthivore_N_Water									x										
Benthivore_P_Water									x										
Bivalves														x					
Bluegreens_DW_in_epilimnion_lake_water																		x	
Bluegreens_DW_in_hypolimnion_lake_water																		x	
Bluegreens_DW_in_marsh_water													x		x			x	
Bluegreens_DW_in_surface_layer																		x	
Bluegreens_DW_on_lake_sediment													x		x			x	
Bluegreens_N_in_epilimnion_lake_water																		x	
Bluegreens_N_in_hypolimnion_lake_water																		x	
Bluegreens_N_in_marsh_water													x		x			x	
Bluegreens_N_in_surface_layer																		x	
Bluegreens_N_on_lake_sediment													x		x			x	
Bluegreens_P_in_epilimnion_lake_water																		x	

Bluegreens_P_in_hypolimnion_lake_water																		x	
Bluegreens_P_in_marsh_water													x		x			x	
Bluegreens_P_in_surface_layer																		x	
Bluegreens_P_on_lake_sediment													x		x			x	
Blueqill																			x
Blueqill CR																			x
Blueqill, YOY																			x
Bosmina lon.											x								
Bosmina Lonqirostris																			x
Broadstripe Shiner																			x
Bromoxvnil																			x
Brornacil																			x
Brown Trout, Lq																			x
Brown Trout, YOY																			x
Browsing herbivore fish Individual reserve N																x			
Browsing herbivore fish																x			
Browsing herbivores Individ structural N																x			
Bubble snail																			x
Buffalofish																			x
Buffalofish, iuv.																			x
Bullhead																			x
Bumphead parrotfish																x			
Bumphead parrotfish Individual reserve N																x			
Bumphead parrotfish total N																x			
Bumphead parrotfish Individ structural N																x			
Buried matter/carbon												x							
Buried matter/nitrogen												x							
Buried matter/phosphorus												x							
Butvlate																			x
C in lake sediment									x										

Caddisflv																			x
Caddisflv/Trichopter																			x
Calcite												x							
Calcite												x							
Carban/I																			x
Carbofuran																			x
Carbon Dioxide																			x
Carbonaceous biochemical oxygen demand (generic)																			x
Carbonaceous biochemical oxygen demandCarbon dissolved																	x		
Carbonaceous biochemical oxygen demandCarbon particulate																	x		
Carbonaceous biochemical oxygen demandNitrogen dissolved																	x		
Carbonaceous biochemical oxygen demandNitrogen particulate																	x		
Carbonaceous biochemical oxygen demandPhosphorus dissolved																	x		
Carbonaceous biochemical oxygen demandPhosphorus particulate																	x		
Carex											x								
Carnivore_Water					x														
Carnivorous Zooplankton Nitrogen																x			
Carp																			x
Carp, Lq																			x
Carp, YOY																			x
Carrion																x			
Catfish																			x
Catostomus catostomus											x								
Catostomus commersoni											x								
CephalopodN																x			
Ceratophyllids Carbon																	x		
Ceratophyllids Nitrogen																	x		
Ceratophyllids Phosphate																	x		
Chaoborus																			x
Chara																			x

Characeans Carbon																	x		
Characeans Nitrogen																	x		
Characeans Phosphate																	x		
Chinook Salmon																			x
Chinook Salmon, Juv																			x
Chir.Thienemannimvia																			x
Chironomid CR																			x
Chironomid FL																			x
Chironomids											x								x
Chiselmouth																			x
Chlamydomonas											x								
Chlordane																			x
Chlorophylla																x			
Chlorophytes freshwater (single pool)				x							x								
Chlorophytes carbon freshwater									x				x	x	x		x		
Chlorophytes chlorophylla freshwater														x					
Chlorophytes Nitrogen freshwater													x	x	x		x		
Chlorophytes Phosphate freshwater									x				x	x	x		x		
Chlorpvrifos																			x
Chlorpvrifos pond																			x
Chlorpvrifos a																			x
Chlorpvrifos stream																			x
Chn/sophvte																			x
Chromulina											x								
Chronomid IPolvped.l																			x
Chrvsene																			x
Chrysophytes											x								
Cisco																			x
Cladoceran																			x
Cladophora																			x

Cladophora CR																			x
Clams														x					
Cn/Ptomonas CR																			x
Colored Dissolved Organic Matter																	x		
Concentration of detrital nutrients in the surface sediment					x														
Concentration of dissolved nutrient in the benthic habitat					x														
Concentration of dissolved nutrient in the pelagic habitat					x														
Concentration of mineral nutrients in the surface sediment					x														
Copepod																			x
Copper Sulfate																			x
Coralivore fish																x			
Coralivore fish Individual reserve N																x			
Coralivore fish total N																x			
Coralivores Individ structural N																x			
Coregonus artedii											x								
Coregonus clupeaformis											x								
Couesius plumbeus											x								
Crab																			x
Crappie																			x
Cravfish																			x
Cricotopus																			x
Croaker																			x
Crustacean Grazers														x					
Crustose coraline algae																x			
Crvptomonad																			x
Crvptomonad DR																			x
Crvptomonas																			x
Crvptomonas Cloern																			x
Crvptomonas Onon																			x
Crypotophytes carbon														x					

Crypotophytes chlorophyll														x					
Crypotophytes Nitrogen														x					
Crypotophytes Phosphate														x					
Cvanazine																			x
Cvclotella nana																			x
Cvlindrospermopsis																			x
Cyanophytes											x								
Cyclonexis											x								
Cyclops scu.											x								
Dace																			x
Daphnia											x								x
DBOC										x									
DDT																			x
deposit feeder/carbon												x							
Depth_of_hypolimnion_lake_water																		x	
Depth_of_lake_water													x		x				
Depth_of_marsh_water													x		x			x	
Depth_of_mixing_layer																		x	
Dermersal Zooplankton Nitrogen																x			
Detrital silicate (single pool)								x					x		x	x	x		
Detrital silicate in sediment													x		x		x	x	
Detritivore fish																x			
Detritivore fish Individual reserve N																x			
Detritivore fish total N																x			
Detritivores Individ structural N																x			
Detritus			x							x									
Detritus_DW_in_epilimnion_lake_water																		x	
Detritus_DW_in_hypolimnion_lake_water																		x	
Detritus_DW_in_lake_sediment													x		x			x	
Detritus_DW_in_lake_water									x				x		x				

Detritus_DW_in_marsh_sediment													x		x			x	
Detritus_DW_in_marsh_water													x		x			x	
Detritus_N_in_epilimnion_lake_water																		x	
Detritus_N_in_hypolimnion_lake_water																		x	
Detritus_N_in_lake_water													x		x				
Detritus_N_in_marsh_sediment													x		x			x	
Detritus_N_in_marsh_water													x		x			x	
Detritus_P_in_epilimnion_lake_water																		x	
Detritus_P_in_hypolimnion_lake_water																		x	
Detritus_P_in_lake_water									x				x		x				
Detritus_P_in_marsh_sediment													x		x			x	
Detritus_P_in_marsh_water													x		x			x	
Detritus_Si_in_epilimnion_lake_water																		x	
Detritus_Si_in_hypolimnion_lake_water																		x	
Detritus_Si_in_marsh_sediment													x		x			x	
Detritus_Si_in_marsh_water													x		x			x	
Diatoms_DW_in_epilimnion_lake_water																		x	
Diatoms_DW_in_hypolimnion_lake_water																		x	
Diatoms_DW_in_marsh_water													x		x			x	
Diatoms_DW_on_lake_sediment													x		x			x	
Diatoms_N_in_epilimnion_lake_water																		x	
Diatoms_N_in_hypolimnion_lake_water																		x	
Diatoms_N_in_marsh_water													x		x			x	
Diatoms_P_in_epilimnion_lake_water																		x	
Diatoms_P_in_hypolimnion_lake_water																		x	
Diatoms_P_in_marsh_water													x		x			x	
Diatoms_P_on_lake_sediment													x		x			x	
Diazinon																			x
Dicamba																			x
Dieldrin																			x

Different size fractions														x					
Dinitrogen gas												x							
Dinobryonbav											x								
Dinobryondiv											x								
Dinobryonser											x								
Dinoflagellates																	x		
Dinoflagellates Carbon marine														x					
Dinoflagellates Chlorophylla marine														x					
Dinoflagellates Nitrogen marine														x					
Dinoflagellates Phosphorus marine														x					
Dinoflaqellate																			x
Dinoflaqellate, Mar.																			x
Dissolved aluminum														x					
Dissolved Inorganic Carbon												x		x		x	x		
Dissolved Inorganic Carbon in pore water												x		x					
Dissolved Inorganic Matter													x		x		x		
Dissolved Inorganic Nitrogen (single pool)				x															
Dissolved manganese														x					
Dissolved Organic Carbon (labile)												x		x					
Dissolved Organic Carbon (refractory)														x					
Dissolved Organic Carbon (similabile)												x							
Dissolved Organic Carbon (single pool)																	x		x
Dissolved Organic Carbon in pore water (labile)														x					
Dissolved Organic Carbon in pore water (refractory)														x					
Dissolved Organic Carbon in pore water (total)												x					x		
Dissolved Organic Matter								x							x				x
Dissolved Organic Nitrogen (labile)												x		x			x		
Dissolved Organic Nitrogen (refractory)														x			x		
Dissolved Organic Nitrogen (single pool)										x						x			
Dissolved Organic Nitrogen in pore water												x							

Dissolved Organic Nitrogen in porewater (labile)														x			x		
Dissolved Organic Nitrogen in porewater (refractory)														x			x		
Dissolved Organic Phosphorus (labile)												x		x			x		
Dissolved Organic Phosphorus (refractory)														x			x		
Dissolved Organic Phosphorus in pore water (labile)												x		x			x		
Dissolved Organic Phosphorus in pore water (refractory)														x			x		
Dissolved oxygen				x				x		x		x	x	x	x	x	x		x
Dissolved Phosphorus (total)							x												
Dissolved_Si_in_epilimnion_lake_water																		x	
Dissolved_Si_in_hypolimnion_lake_water																		x	
Dissolved_Si_in_marsh_water													x		x			x	
Dixie chub																			x
Duckweed ILemna]																			x
Early succession CWH						x													
Early succession saplings						x													
Early succession snags						x													
Early succession trees						x													
Eleocharis											x								
Elodeids Carbon																	x		
Elodeids Nitrogen																	x		
Elodeids Phosphate																	x		
Epischura lac.											x								
EPTC																			x
Equisetum flu											x								
Esfenvalerate																			x
Esox lucius											x								
Eunotia																			x
Eunotia 002																			x
Excavating herbivore fish																x			
Excavating herbivore fish Individual reserve N																x			

Excavating herbivores Individ structural N																x			
Fecal Bacteria								x											
Ferric Iron																	x		
Ferrous Iron										x				x			x		
Fish (generic)		x					x							x					
Fish_C_Water									x										
Fish_N_Water									x										
Flagellates											x								
Fluridone																			x
Fonofos																			x
Fontinalis																			x
Fontinalis a																			x
Freshwater bluegreen algae (single pool)				x															
Freshwater bluegreen algae carbon									x				x	x	x		x		
Freshwater bluegreen algae Chlorophylla														x					
Freshwater bluegreen algae nitrogen													x	x	x		x		
Freshwater bluegreen algae Phosphate									x				x	x	x		x		
Freshwater diatoms Carbon									x				x	x	x		x		
Freshwater diatoms Chlorophylla														x					
Freshwater diatoms Nitrogen													x	x	x		x		
Freshwater diatoms Phosphate									x				x	x	x		x		
Freshwater diatoms single pool (single pool)				x				x			x								x
Freshwater Drum																			x
Freshwater Drum YOV																			x
Gar																			x
Gastropod [Florida]																			x
Gastropod Cahabal																			x
Gastropod, marine																			x
Gastropods											x								x
Gizzard Shad																			x

Glyphosate																			x
Golden Shiner																			x
Grazing herbivore fish Individual reserve N																x			
Grazing herbivore fish															x	x			
Grazing herbivores Individ structural N																x			
Grazing herbivores Individ structural N																x			
Green Sunfish, Adult																			x
Green Sunfish, YOY																			x
Green_algae_DW_in_epilimnion_lake_water																		x	
Green_algae_DW_in_hypolimnion_lake_water																		x	
Green_algae_DW_in_marsh_water													x		x			x	
Green_algae_DW_on_lake_sediment													x		x		x	x	
Green_algae_N_in_epilimnion_lake_water																		x	
Green_algae_N_in_hypolimnion_lake_water																		x	
Green_algae_N_in_marsh_water													x		x			x	
Green_algae_P_in_epilimnion_lake_water																		x	
Green_algae_P_in_hypolimnion_lake_water																		x	
Green_algae_P_in_marsh_water													x		x			x	
Greens																			x
Guthion																			x
Height_of_vegetation																		x	
Helophytes Carbon																	x		
Helophytes Nitrogen																	x		
Helophytes Phosphate																	x		
Herbivore Browser fish total N																x			
Herbivore_C_in_Lake_Water									x										
Herbivore_P_in_Lake_Water									x										
Herbivores Excavator fish total N																x			
Herbivores Grazer fish total N																x			
Herbivores Grazer fish total N																x			

Herbivorous Zooplankton Nitrogen																x			
Heterotrophic Bacteria								x						x					
Humphead wrasse																x			
Humphead wrasse Individual reserve N																x			
Humphead Wrasse total N																x			
Humphead wrasse Individ structural N																x			
Humus Carbon in sediment (single pool)													x		x			x	
Humus Organic Nitrogen in sediments (single pool)													x		x			x	
Humus Phosphorus in sediment (single pool)													x		x			x	
Humus_DW_in_marsh_sediment													x		x			x	
Humus_N_in_marsh_sediment													x		x			x	
Humus_Pin_marsh_sediment													x		x			x	
Hydrilla																			x
Hybrid Str Bass Juv																			x
Hybrid Striped Bass																			x
Hydrogen sulfide																	x		
Inorganic Matter													x		x			x	
Inorganic Matter in marsh sediment													x		x			x	
Inorganic Matter marsh water													x		x			x	
Inorganic Nitrogen sediments (single pool)														x					
Inorganic phosphorus										x									
inorganic soil																			x
Inorganic_matter_in_epilimnion_lake_water																		x	
Inorganic_matter_in_hypolimnion_lake_water																		x	
Ints P									x										
Invertebrates		x																	
Invertivore fish																x			
Invertivore fish Individual reserve N																x			
Invertivore fish total N																x			
Invertivores Individ structural N																x			

Iron (Total)										x				x					
Jellyfish														x					
Juvenile fish carbon													x		x			x	
Juvenile fish nitrogen													x		x			x	
Juvenile fish phosphorus													x		x			x	
Juvenile piscivore_Water_Water						x													
Kellicottia											x								
Labile detritus																			x
Lake Trout LG																			x
Lake Trout, YOY																			x
Lamprey, adult																			x
Lamprey, larval																			x
Large zoo benthos															x				
Largesize Particulate Organic Matter/carbon												x							
Largesize Particulate Organic Matter/nitrogen												x							
Largesize Particulate Organic Matter/phosphorus												x							
LargesizeParticulate Organic Matter/silicate												x							
Larqemouth Bass, Lq																			x
Larqemouth Bass, YOY																			x
Lemnacaea Carbon																	x		
Lemnacaea Nitrogen																	x		
Lemnacaea Phosphate																	x		
light																			x
Lonqear Sunfish																			x
Loqperch																			x
Macroalgae																x			
Macrophytoplankton																x			
Macrophytoplankton Nitrogen																x			
Macrophytoplankton Silicon																x			
Malathion																			x

Manganese (total)														x			x		
Manganous ion										x									
Marine diatoms chlorophyll												x		x			x		
Marine diatoms intracellular carbon												x		x			x		
Marine diatoms intracellular nitrogen												x		x			x		
Marine diatoms intracellular phosphorus												x		x			x		
Marine diatoms intracellular phosphorus												x							
Mayfly [Florida)																			x
Mayfly [Isonychial																			x
Mayfly Baetisl																			x
Mayfly Baetisl CR																			x
Mediumsize Particulate Organic Matter/carbon												x							
Mediumsize Particulate Organic Matter/nitrogen												x							
Mediumsize Particulate Organic Matter/phosphorus												x							
Mediumsize Particulate Organic Matter/silicate												x							
MeiofaunaC												x							
MeiofaunaN																x			
Melosira isl											x								
Menhaden																			x
Mesozooplankton carbon												x							
Methane																	x		
Methomvl																			x
Methvl parathion																			x
Metolachlor																			x
Microcystis																	x		
Micronutrients																x			
Microphytobenthos (benthic microalgae) chlorophyll																	x		
Microphytobenthos Nitrogen																	x		
Microphytobenthos Phosphorus																	x		
Microphytobenthus Carbon																	x		

Microphytoplankton/carbon												x							
Microphytoplankton/chlorophyll a												x							
Microphytoplankton/nitrogen												x							
Microphytoplankton/phosphorus												x							
Microzooplankton carbon												x			x		x		
Microzooplankton nitrogen												x					x		
Microzooplankton phosphorus												x					x		
Mid succession CWH						x													
Mid succession saplings						x													
Mid succession snags						x													
Mid succession trees						x													
Midwater Piscivore fish total N																x			
Midwater piscivores fish																x			
Midwater piscivores fish Individual reserve N																x			
Midwater piscivores Individ structural N																x			
Minnow																			x
Monosigma											x								
Mtn. whitefish adult																			x
Mtn. whitefish YOY																			x
Mullet																			x
Mussel																			x
Mussel, sensitive																			x
Mussel, tolerant																			x
Mvriophvllum																			x
Mvsid																			x
N in NH4 in marsh sediment pore water													x		x			x	
N in NO3 in marsh sediment pore water													x		x			x	
N_in_NH4_in_epilimnion_lake_water																		x	
N_in_NH4_in_hypolimnion_lake_water																		x	
N_in_NH4_in_lake_water													x		x				

N_in_NO3_in_epilimnion_lake_water																	x	
N_in_NO3_in_hypolimnion_lake_water																	x	
N_in_NO3_in_marsh_water												x		x			x	
Naidid worm																		x
Nanoflagellates/carbon											x							
Nanoflagellates/nitrogen											x							
Nanoflagellates/phosphorus											x							
Nanophytoplankton															x	x		
Nanophytoplankton chlorophyll											x					x		
Nanophytoplankton intracellular carbon											x					x		
Nanophytoplankton intracellular nitrogen											x				x	x		
Nanophytoplankton intracellular phosphorus											x					x		
Nitrate						x	x		x		x	x	x	x	x	x		x
Nitrate in porewater											x	x	x	x		x	x	
Nitrifying Bacteria							x											
Nodularia carbon													x					
Nodularia Chlorophylla													x					
Nodularia Nitrogen													x					
Nodularia phosphate													x					
Nonnative Fish		x																
Nonnative Snail		x																
Nonsiliceous algae							x											
Nonviphenol QSAR																		x
Nonvlphenol																		x
Northern Pike																		x
Nymphaeids Carbon																x		
Nymphaeids Nitrogen																x		
Nymphaeids Phosphate																x		
Odonata																		x
Oligochaetes										x								

Oliqochaete																			x
Omnivorous fish															x				
Organic Phosphorus								x		x									
Ostracode																			x
Oxygen_in_epilimnion_lake_water																		x	
Oxygen_in_hypolimnion_lake_water																		x	
Oxygen_in_marsh_water													x		x			x	
Oyster																			x
Oyster Drill																			x
P in lake sediment									x										
P_adsorbed_onto_IM_in_epilimnion_lake_water																		x	
P_adsorbed_onto_IM_in_hypolimnion_lake_water																		x	
P_adsorbed_onto_IM_in_marsh_sediment													x		x			x	
P_adsorbed_onto_IM_in_marsh_water													x		x			x	
P_in_PO4_in_epilimnion_lake_water																		x	
P_in_PO4_in_hypolimnion_lake_water																		x	
P_in_PO4_in_marsh_sediment_pore_water													x		x			x	
P_in_PO4_in_marsh_water													x		x			x	
Pacific giant salamander			x																
Paraquat																			x
Parathion																			x
Particulate biogenic silica										x									
Particulate Inorganic Nitrogen (single pool)														x					
Particulate Inorganic Nitrogen in sediment (single pool)														x					
Particulate Inorganic Phosphorus (adsorbed)								x					x	x	x		x		
Particulate Inorganic Phosphorus (immobilised)																	x		
Particulate Inorganic Phosphorus in sediment (adsorbed)													x		x		x	x	
Particulate Inorganic Phosphorus in sediment (immobilised)																	x		
Particulate Inorganic Phosphorus in sediment (single pool)														x					
Particulate organic carbon (labile)														x					

Particulate organic carbon (refractory)														x					
Particulate organic carbon (single pool)																	x		
Particulate Organic Carbon in sediment (labile)														x					
Particulate Organic Carbon in sediment (refractory)														x					
Particulate Organic Carbon in sediment (single pool)												x					x		
Particulate Organic Matter (fixed stoichiometry; single pool)				x			x	x											
Particulate Organic Matter (refractory, fixed stoichiometry)																	x		
Particulate Organic Nitrogen (labile)														x		x	x		
Particulate Organic Nitrogen (refractory)														x		x	x		
Particulate Organic Nitrogen (single pool)																x			
Particulate Organic Nitrogen in marsh water													x						
Particulate Organic Nitrogen in sediments (labile)														x			x		
Particulate Organic Nitrogen in sediments (refreactory)														x			x		
Particulate Organic Nitrogen in sediments (single pool)												x	x		x		x	x	
Particulate Organic Phosphorus (labile)														x			x		
Particulate Organic Phosphorus (refractory)														x			x		
Particulate Organic Phosphorus in sediment (labile)														x			x		
Particulate Organic Phosphorus in sediment (refractory)														x			x		
Particulate Organic Phosphorus in sediment (single pool)												x	x		x		x	x	
Particulate Organic Silicate												x							
Particulate Phosphorus (total)														x					
Pathogens														x					
PCB x0x																			x
PCB x05																			x
PCB xx0																			x
PCB xx8																			x
PCB x254																			x
PCB x254 Hartwell																			x
PCB x254 toxic																			x
PCB x38																			x

PCB x49																			x
PCB x53																			x
PCB x8																			x
PCB x80																			x
PCB x87+x82																			x
PCB x94																			x
PCB 203+x96																			x
PCB 28+3x																			x
PCB 66																			x
PCB 70+76																			x
PCB 84																			x
pCresol																			x
Pelagic grazer biomass					x														
Pelagic primary producer					x														
Pelecypods											x								
Pendimethalin																			x
Pentachlorophenol																			x
Perca flavescens											x								
Peri Diatom, Marine																			x
Peri HiNut Dia CR																			x
Peri HiNut Dia wrm																			x
Peri HiqhNut Diatom																			x
Peri LowNut Dia CR																			x
Peri LowNut Dia wrm																			x
Peri LowNut Diatom																			x
Peri LowNut Diatoma																			x
Peri, BlueGreen CR																			x
Peri, BlueGreen FL																			x
Peri, BlueGreen hot																			x
Peri, BlueGreen wrm																			x

Peri, BlueGreens																			x
Peri, Chlorococcum																			x
Peri, Fraqilaria																			x
Peri, Green																			x
Peri, Green CR																			x
Peri, Green FL																			x
Peri, Green wrm																			x
Peri, Navícula																			x
Peri, Nitzschia																			x
PeriDhvton,Cocconeis																			x
Periphyton		x																	
Permethrin																			x
PFOA ÍNH4x																			x
PFOS																			x
PFOS no toxicity																			x
PH														x		x	x		
pH																			x
pH sediment																	x		
Phorate																			x
Phosphate				x								x	x		x		x		x
Phosphate in pore water (or DIP or FRP)												x	x	x	x		x	x	
Photosynthetically Active Radiation														x					
Photosynthetically Active Radiation epibenthic																	x		
Phvt BlueGreen HiLt																			x
Phvt BlueGreens																			x
Phvt BlueGreens CR																			x
Phvt Diatom, Marine																			x
Phvt HiqhNut Dia CR																			x
Phvt HiqhNut Diat																			x
Phvt HiqhNut Diatom																			x

Phvt LowNut Dia CR																			x
Phvt LowNut Diatom																			x
Phvt, BlGreens, Mar																			x
Phvt, BlueGreen max																			x
Phvt, BlueGreens DR																			x
Phvt, BlueGreens JC																			x
Phvto Greens																			x
Phvto Greens Lownut																			x
Phvto, Diatom max																			x
Phvto, Diatom wrm																			x
Phvto, Green																			x
Phvto, Green CR																			x
Phvto, Green LowNut																			x
Phvto, Green, Marine																			x
Phvto, HiNut Diatom																			x
Phvto, Navícula																			x
Phytoplankton (single pool)	x						x			x									
Phytoplankton detritus	x																		
PhytoplanktonC (generic)																	x		
PhytoplanktonN (generic)																	x		
PhytoplanktonP (generic)																	x		
Picophytoplankton/carbon												x							
Picophytoplankton/chlorophyll a												x							
Picophytoplankton/nitrogen												x							
Picophytoplankton/phosphorus												x							
Pikeminnow																			x
Pirate Perch																			x
Planktivore fish Individual reserve N																x			
Planktivore fish total N																x			
Planktivore fish (generic																x			

Planktivores Individ structural N																x			
Polychaetes														x					x
Porewater ammonium												x	x	x	x		x	x	
Potamogeton spp.											x								
Predatory_fish_DW_in_lake_water													x		x			x	
Prosopium cylindraceum											x								
Pumpkinseed																			x
Rainbow Trout																			x
Rainbow Trout YOY																			x
Ray fish																x			
Ray fish Individual reserve N																x			
Ray fish total N																x			
Rays Individ structural N																x			
Red drum																			x
Redear Sunfish																			x
Redfin pickerel																			x
Redhorse																			x
Reef shark																x			
Reef shark Individual reserve N																x			
Reef shark Individual structural N																x			
Reef turf																x			
Refactoy Detritus																			x
Refractory matter/carbon												x							
Refractory matter/nitrogen												x							
Refractory matter/phosphorus												x							
Reptile																x			
Reptile Individ structural N																x			
Riffle beetle																			x
Root_biomass_DW_in_marsh_sediment													x		x			x	
Root_biomass_N_in_marsh_sediment													x		x			x	

Root_biomass_P_in_marsh_sediment													x		x			x	
Rotifer x																			x
Rotifer, Brachionus																			x
Rotifer, Keratella																			x
Rotifer, marine																			x
Roving Piscivore fish total N																x			
Roving piscivores fish																x			
Roving piscivores fish Individual reserve N																x			
Roving piscivores Individ structural N																x			
Salinity																x			
Salmo salar											x								
Salmon carcass		x																	
Salmonid																			x
Saltwater copepod																			x
Salvelinus fontinalis											x								
Salvelinus namaycush											x								
Scraping herbivore fish																x			
Scraping herbivore fish Individual reserve N																x			
Sculpin																			x
Seagrass (generic)														x					
Seatrout																			x
Seatrout, small																			x
Sediment carbon										x									
Sediment dissolved oxygen												x		x			x		
Semotilus corporalis											x								
Shad																			x
Shad, iuv																			x
Shad, juvenile																			x
Shiner																			x
Shiner, redside																			x

Shoot_biomass_DW_in_marsh_water													x		x			x	
Shoot_biomass_N_in_marsh_water													x		x			x	
Shoot_biomass_P_in_marsh_water													x		x			x	
Shrimp																			x
Silicate (dioxide) sediment												x		x					
Silicate dioxide								x				x	x	x	x	x	x		
Silverside																			x
Simazine																			x
Smallmouth Bass, Lq																			x
Smallmouth Bass, YOY																			x
Smallsize Particulate Organic Matter /carbon												x							
Smallsize Particulate Organic Matter/nitrogen												x							
Smallsize Particulate Organic Matter/phosphorus												x							
Smelt																			x
Soluble P									x										
sopod																			x
Sparganium											x								
Sphaerid																			x
Steelhead trout			x																
Stiqeoclonium, peri.																			x
Stizostedion vitreum											x								
Stoneflv																			x
Stoneflv CR																			x
Stoneroller																			x
Sulfur (total)																	x		
Sunfish, Adult																			x
Surf clam																			x
Suspension feederC												x							
Synechococcus											x								
Synechocystis											x								

Target benthic piscivore fish																x			
Target benthic piscivore fish Individual reserve N																x			
Target Benthic Piscivores fish total N																x			
Target benthic piscivores Individ structural N																x			
Target browser fish																x			
Target browser fish Individual reserve N																x			
Target browsers Individ structural N																x			
Target Fish Browsers total N																x			
Target Fish Grazer total N																x			
Target grazer fish																x			
Target grazer fish Individual reserve N																x			
Target grazers Individ structural N																x			
Target invertivore fish																x			
Target invertivore fish Individual reserve N																x			
Target Invertivore fish total N																x			
Target invertivores Individ structural N																x			
Tefluthrin																			x
temperature																			x
Terbufos																			x
Terrestrial detritus		x																	
Terrestrial particulate organic matter	x																		
Total inorganic carbon										x									
Total manganese										x									
Total Nitrogen in pore water (single pool)							x												
Total Nitrogen sediments (single pool)							x												
Total Phosphorus in the sediment (single pool)							x												
Total Phosphorus pore water (single pool)							x												
Total Suspended Solids								x						x					
Total_amount_of_DW_moved_into_or_out_from_the_system													x		x			x	
Total_amount_of_N_moved_into_or_out_from_the_system													x		x			x	

Total_amount_of_O2_moved_into_or_out_from_the_system																		x	
Total_amount_of_P_moved_into_or_out_from_the_system													x		x			x	
Total_amount_of_Si_moved_into_or_out_from_the_system													x		x			x	
Toxin Chlorophytes														x					
Toxin Cryptophutes														x					
Toxin cyano														x					
Toxin Dinoflagelate														x					
Toxin Freshwater Diatoms														x					
Toxin marine Diatoms														x					
Toxin Nodularia														x					
Tracer																	x		
Trichodesmium chlorophyll																	x		
Tricorvthodes																			x
Tubifex tubifex																			x
Turtles Individual reserve N																x			
Turtles total N																x			
Vegetation (generic)							x												
Vegetation_DW_in_lake_water													x		x			x	
Vegetation_N_in_lake_water													x		x			x	
Vegetation_P_in_lake_water													x		x			x	
Vulnerable algivores_Water			x																
Vulnerable detritivores_Water			x																
Walleve																			x
Water Volume																			x
White Bass, Lq																			x
White Bass, YOY																			x
White Perch																			x
White Perch, Juv																			x
White Sucker																			x
White Sucker, Sm																			x

Whitefish adult																			x
wind loading																			x
Yellow Perch																			x
Yellow Perch, Lq																			x
Yellow Perch, YOY																			x
Zebra Mussels																			x
Zoobenthos carbon													x		x			x	
Zoobenthos nitrogen													x		x			x	
Zoobenthos phosphate													x		x			x	
Zooplankton (generic)	x			x			x	x		x				x					x
Zooplankton_DW_in_epilimnion_lake_water																		x	
Zooplankton_DW_in_hypolimnion_lake_water																		x	
Zooplankton_DW_in_lake_water													x		x				
Zooplankton_DW_in_marsh_water													x		x			x	
Zooplankton_N_in_epilimnion_lake_water																		x	
Zooplankton_N_in_hypolimnion_lake_water																		x	
Zooplankton_N_in_lake_water															x				
Zooplankton_N_in_marsh_water													x		x			x	
Zooplankton_P_in_epilimnion_lake_water																		x	
Zooplankton_P_in_hypolimnion_lake_water																		x	
Zooplankton_P_in_lake_water													x		x				
Zooplankton_P_in_marsh_water													x		x			x	

Table 6.3: State variables of the theoretical models (the model references are sorted based on number of state variables).

State variable	Leroux et al (2008)	Marleau et al (2010)	Marleau et al (2014)	Marleau et al (2015)	Gounand et al (2014)	Marleau et al (2019)	Gravel et al (2010)	Leroux et al (2012)
Autochthonous primary producers_ecosystem 1	x	x	x	x	x	x	x	x
Autochthonous primary producers_ecosystem 2		x	x	x	x	x	x	x
Autochthonous primary consumers_ecosystem 1	x	x	x	x	x	x	x	x
Autochthonous primary consumers_ecosystem 2		x	x	x	x	x	x	x
Autochthonous predators_ecosystem 1	x							x
Autochthonous predators_ecosystem 2								x
Autochthonous inorganic nutrients_ecosystem 1	x	x	x		x	x	x	x
Autochthonous inorganic nutrients_ecosystem 2		x	x		x	x	x	x
Autochthonous primary consumers 2_ecosystem 1						x		
Autochthonous primary consumers 2_ecosystem 2						x		
Allochthonous primary producers_ecosystem 1	x							
Allochthonous primary consumers_ecosystem 1	x							x
Allochthonous primary consumers_ecosystem 2								x
Autochthonous detritus_ecosystem 1					x		x	
Autochthonous detritus_ecosystem 2					x		x	
Nutrient element R_ecosystem 1				x				
Nutrient element R_ecosystem 2				x				
Nutrient element S_ecosystem 1				x				
Nutrient element S_ecosystem 2				x				

References (not in chapter 2)

Sørensen, T., 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. Biologiske Skrifter 5:1-34.

Appendix 2 – chapter 3 supporting information

Section S1: Quantitative definitions (i.e., equations) for the ecosystem stocks and ecosystem functions

Ecosystem stocks:

Nutrient stock = N^* (Equation S1)

Plant stock = A^* (Equation S2)

Herbivore stock = H^* (Equation S3)

Predator stock = P^* (Equation S4)

where * is equilibrium value

Ecosystem functions:

Plant production = $A\left(\frac{a_A T_N N}{1+a_A V_A N}\right)$ (Equation S5)

Herbivore production = $e_H H\left(\frac{a_H T_A A}{1+a_H V_H A}\right)$ (Equation S6)

Predator production = $e_P P\left(\frac{a_P T_H H\pi_P + a_P T_E E(1-\pi_P)}{1+a_P V_P H\pi_P + a_P V_p E(1-\pi_P)}\right)\frac{a\left(\frac{Q_P}{P}\right)+c}{b\left(\frac{Q_P}{P}\right)+d}$ (Equation S7)

Total production = plant production + herbivore production + predator production (Equation S8)

Plant recycling = $(1-\delta_A)d_A A$ (Equation S9)

Herbivore recycling =$(1-\delta_H)d_H H$ (Equation S10)

Predator recycling =$(1-\delta_P)d_P P$ (Equation S11)

Total recycling = plant recycling + herbivore recycling + predator recycling (Equation S12)

Plant efficiency = $\left(A\left(\frac{a_A T_N N}{1+a_A V_A N}\right)\right)/I$ (Equation S13)

$$\text{Herbivore efficiency} = (e_H H \left(\frac{a_H T_A A}{1+a_H V_H A}\right))/A \left(\frac{a_A T_N N}{1+a_A V_A N}\right) \qquad \text{(Equation S14)}$$

$$\text{predator efficiency} = (e_P P \left(\frac{a_P T_H H \pi_P + a_P T_E E(1-\pi_P)}{1+a_P V_P H \pi_P + a_P V_p E(1-\pi_P)}\right) \frac{a\left(\frac{Q_P}{P}\right)+c}{b\left(\frac{Q_P}{P}\right)+d})/(e_H H \left(\frac{a_H T_A A}{1+a_H V_H A}\right)) \qquad \text{(Equation S15)}$$

Total efficiency = plant efficiency + herbivore efficiency + predator efficiency (Equation S16)

Section S2: Stability analysis

Table 7.1: Jacobian matrix of recipient ecosystem at equilibrium for parameter values provided in table S3.

	Nutrient	**Plant**	**Herbivore**	**Predator**
Nutrient	-0.4088+0.4488i	-0.4088-0.4488i	-0.8414+0i	-0.7486+0i
Plant	0.7139+0.0000i	0.7139+0.0000i	0.4783+0i	0.5891+0i
Herbivore	-0.05368-0.3376i	-0.0536+0.3376i	-0.2226+0i	-0.2133+0i
Predator	-0.0670+0.0181i	-0.0670-0.0181i	0.1167+0i	0.2165+0i

Table 7.2: Eigenvalues

Eigenvalues
-0.0323+0.3025i
-0.0323-0.3025i
-0.1177+0.0000i
-0.0609+0.0000i

The dominant eigenvalue is -0.03231549 indicating that the recipient ecosystem is locally stable (parameters in table S3). We also confirmed that the dominant eigenvalue is still negative when we vary predator preference (see specific parameters sets in figures S5 and S6). The dominant eigenvalue is -0.03979754 and -0.03090648 when predator preference for local prey is 0.2 and 0.8 respectively.

Sections S3: Supplementary figures

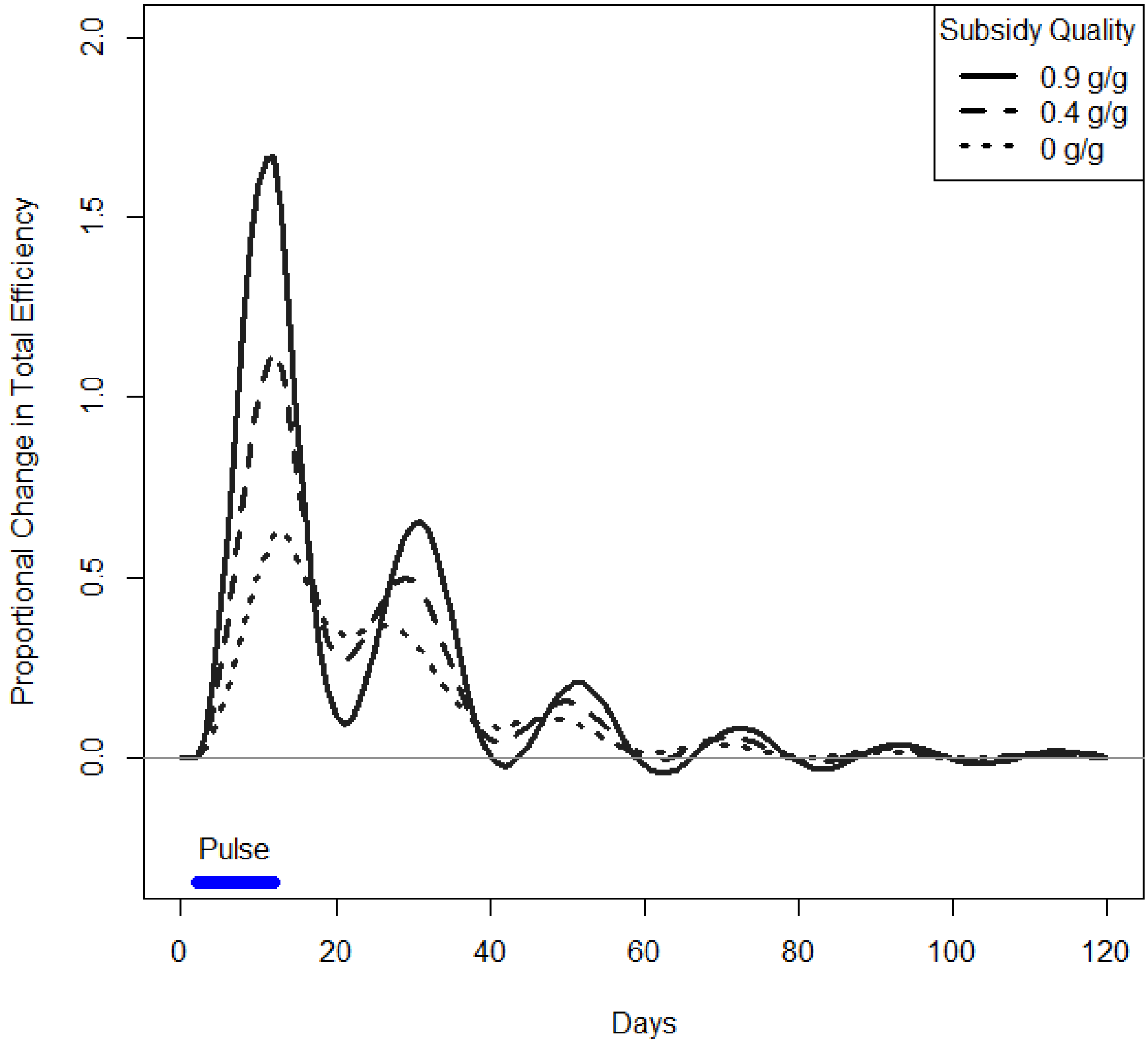

Figure 7.1: Proportional change in total efficiency over time. The change in the recipient ecosystem function (efficiency) is almost indistinguishable from equilibrium after approximately 120 days. See appendix 2: table 7.3 for the parameter values and appendix 2: equation S16 for the mathematical expressions for total efficiency.

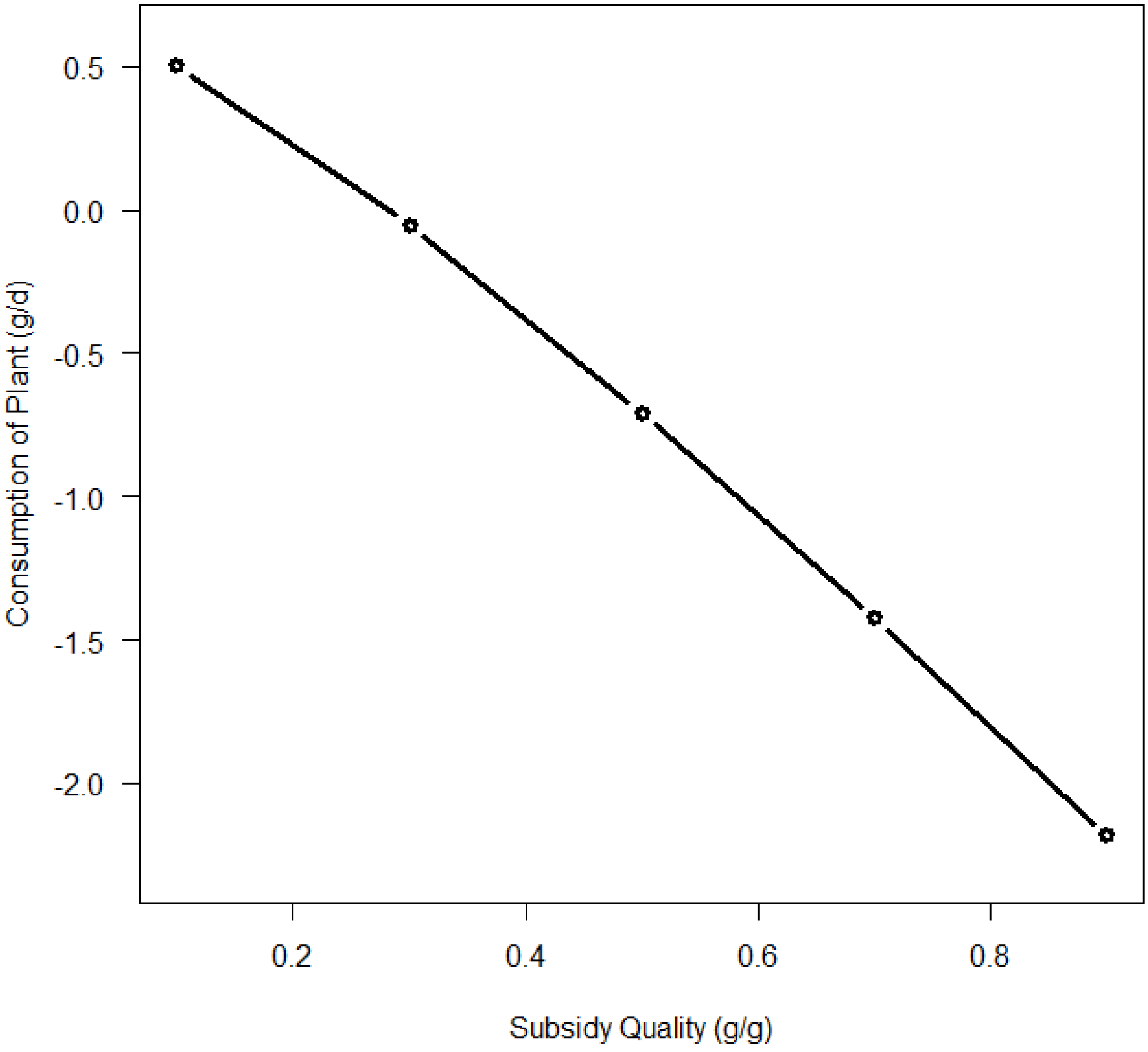

Figure 7.2: Cumulative subsidy quality effect on herbivore consumption of plants. See appendix 2: table 7.3 for the parameter values and equation 10 for the mathematical expressions.

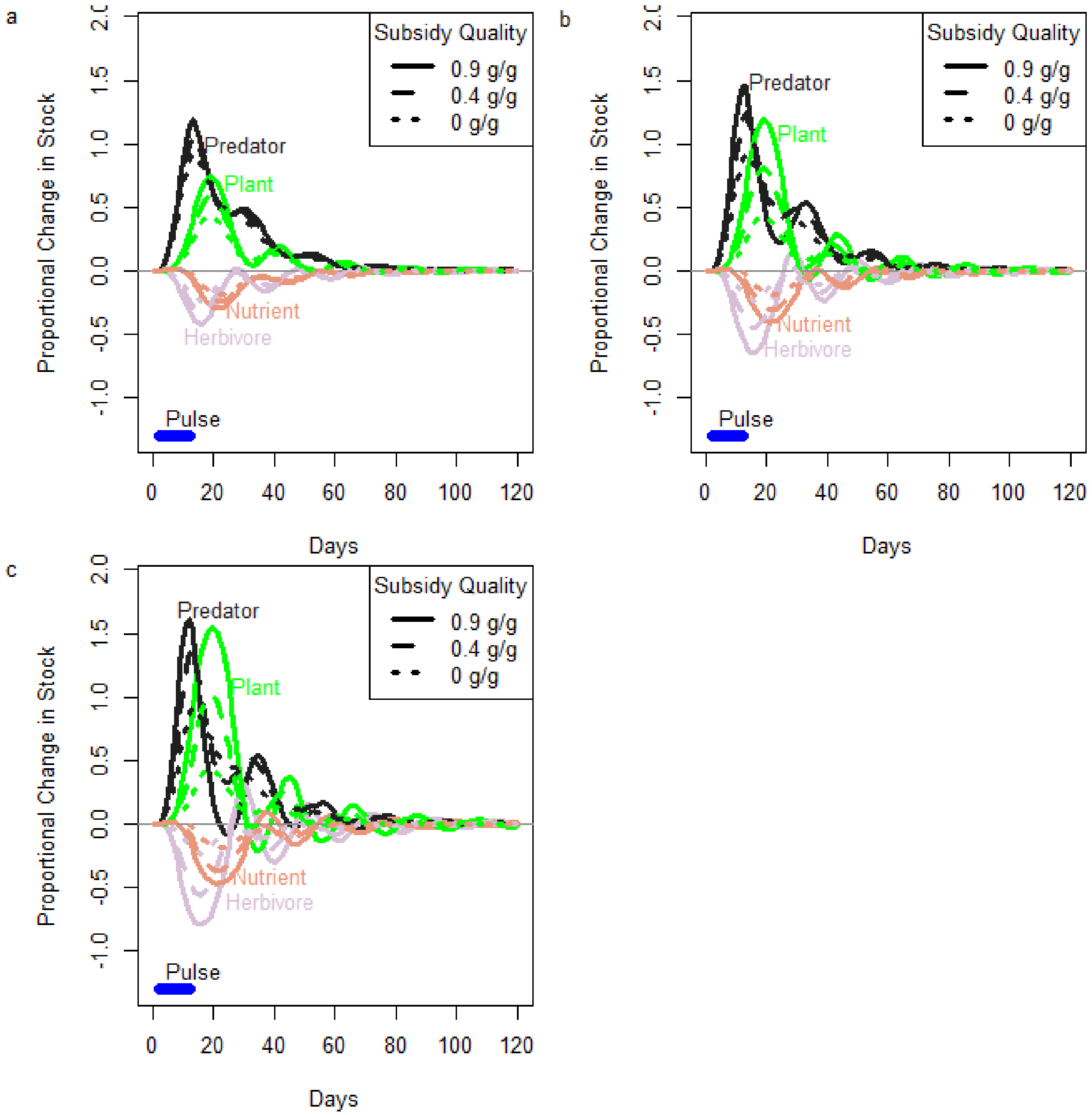

Figure 7.3: Time series of proportional changes in recipient ecosystem stocks for the differential effect of subsidy quality on recipient ecosystem predator. Maximum consumption effect is 2.85-fold for fig. a, 5.7-fold for fig. b, and 8.55-fold for fig. c. See appendix 2: table 7.3 for the parameter values.

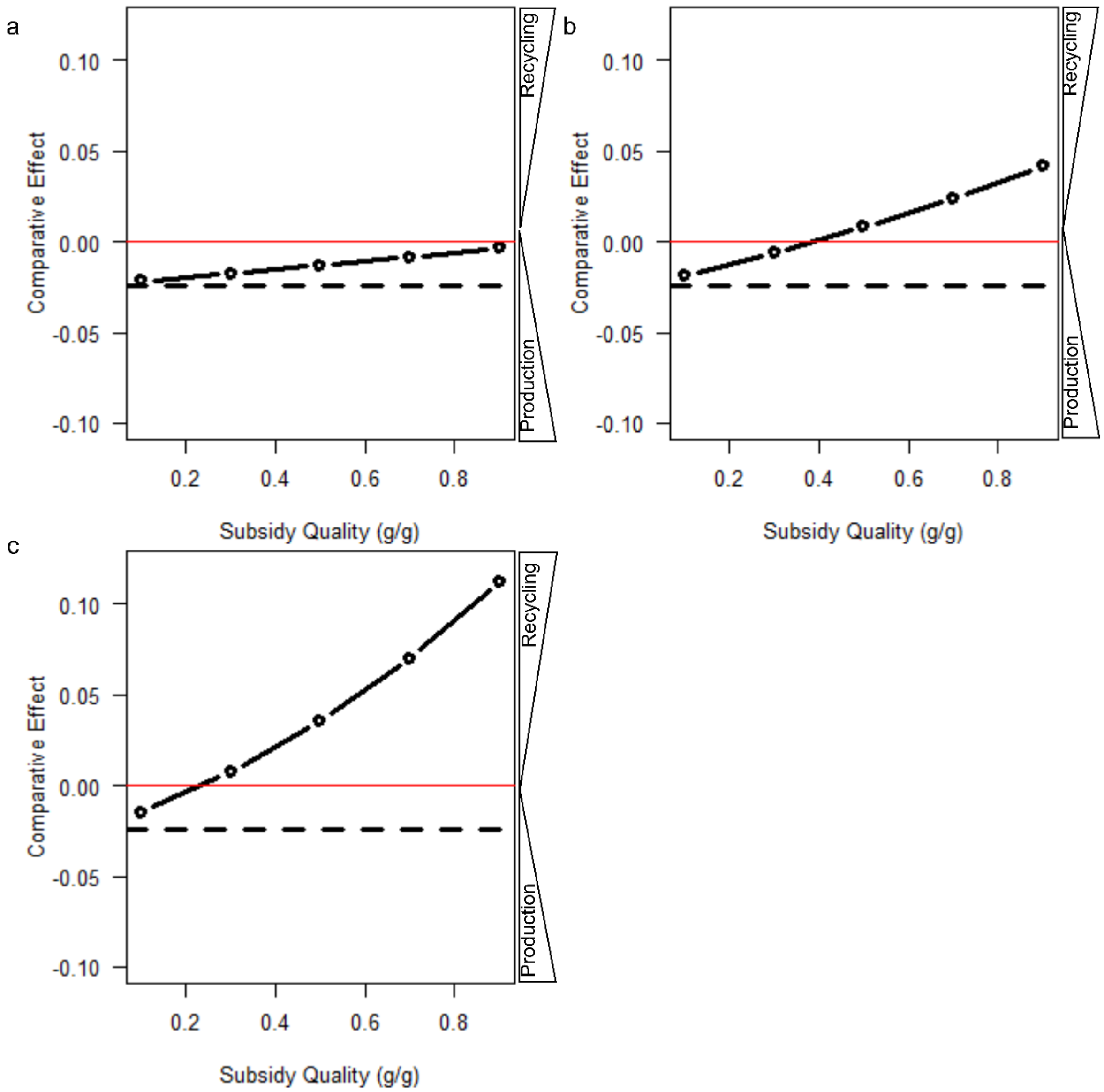

Figure 7.4: Comparison of total recycling and production of the recipient ecosystem (equation 13) for the differential effect of subsidy quality on recipient ecosystem predator. Maximum consumption effect is 2.85-fold for fig. a, 5.7-fold for fig. b, and 8.55-fold for fig. c. The dashed line represents 0 subsidy quality, whereas the points represent the results from a model with varying subsidy quality as specified on the x-axis. See appendix 2: table 7.3 for the parameter values and appendix 2: equations S8 and S12 for the mathematical expressions of each function.

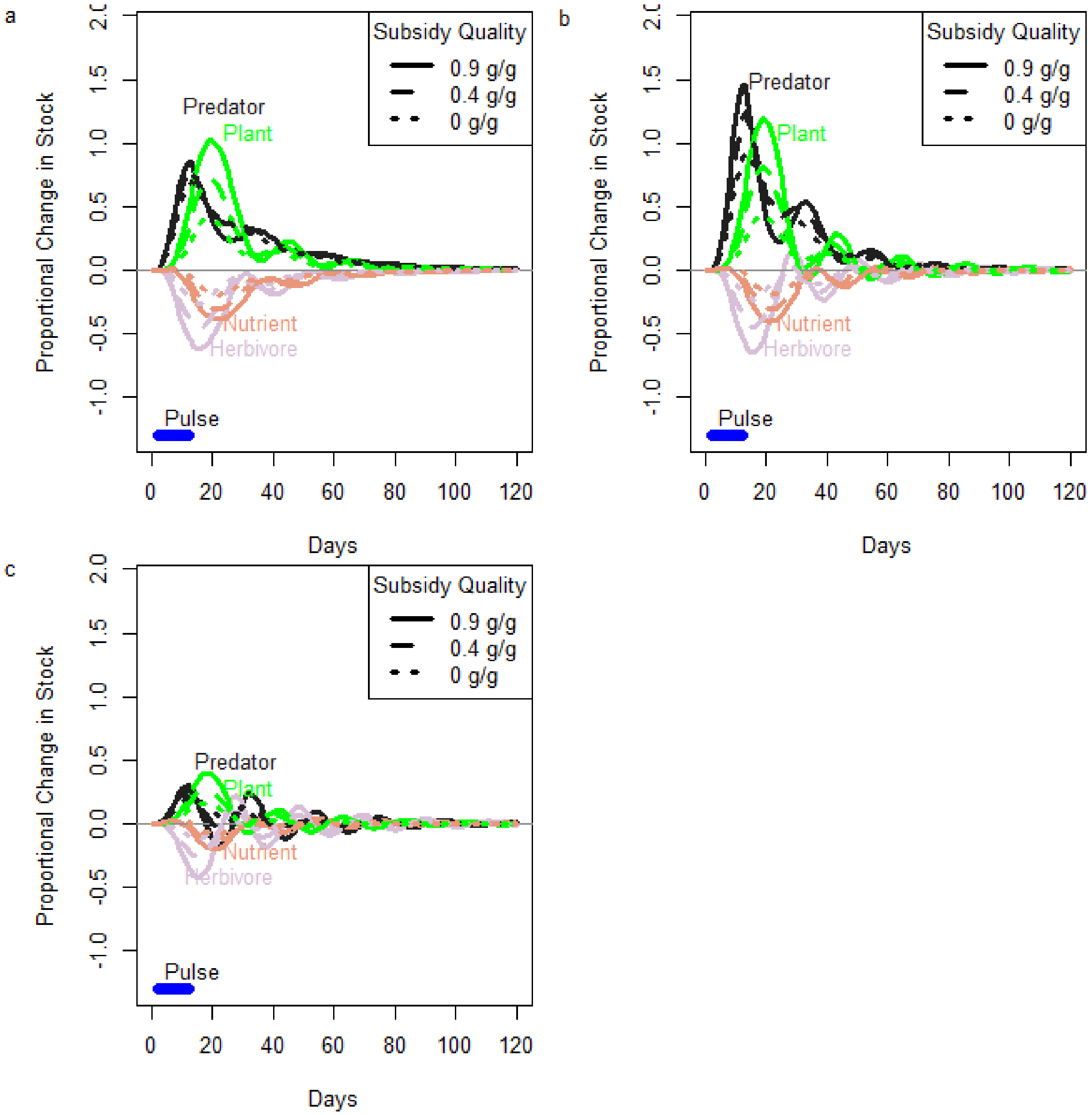

Figure 7.5: Time series of proportional changes in recipient ecosystem stocks for the differential recipient ecosystem predator relative preference for local prey and subsidy. Recipient ecosystem predator preference for local prey is 0.2 for fig. a, 0.4 for fig. b, and 0.8 for fig. c. Points greater than 0 on the y-axis means that the subsidy has a greater effect on ecosystem recycling than ecosystem production (effect increases northwards) for a given subsidy quality (x-axis), while points less than 0 means that the subsidy has a greater effect on ecosystem production than recycling (effect increases southwards) for a given subsidy quality (x-axis). See appendix 2: table 7.3 for the parameter values but note that we had to change some other parameters to ensure a return to equilibrium, specifically, $k = 0.08$ and $dP = 0.1$ for fig. a., $k = 0.1$ and $dP = 0.2$ for fig. b, and $k = 0.1$ and $dP = 0.26$ for fig. c.

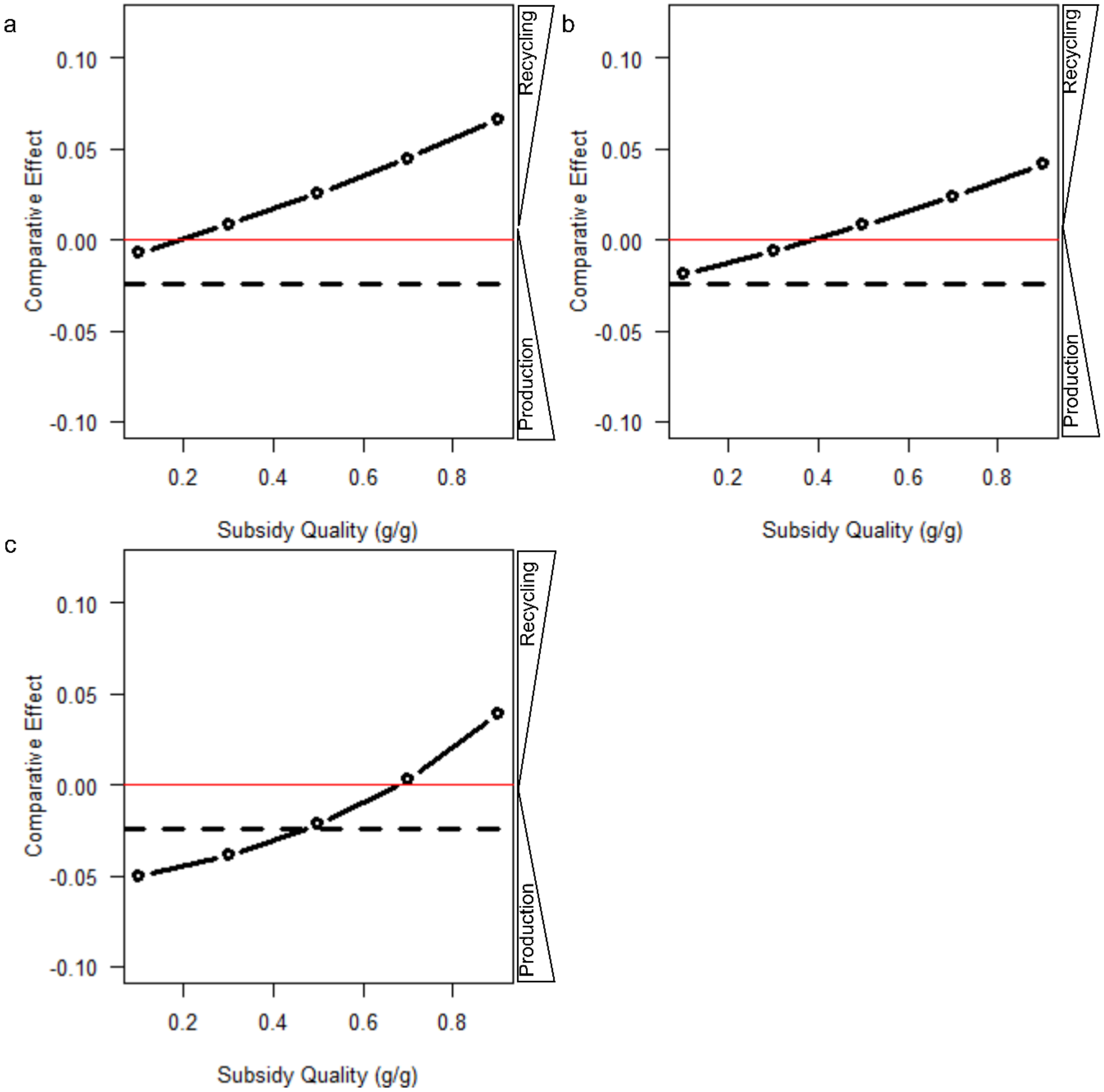

Figure 7.6: Comparison of total recycling and production of the recipient ecosystem (equation 13) for the differential recipient ecosystem predator relative preference for local prey and subsidy. Recipient ecosystem predator preference for local prey is 0.2 for fig. a, 0.4 for fig. b, and 0.8 for fig. c. The dashed line represents 0 subsidy quality, whereas the points represent the results from a model with varying subsidy quality as specified on the x-axis. Points greater than 0 on the y-axis means that the subsidy has a greater effect on ecosystem recycling than ecosystem production (effect increases northwards) for a given subsidy quality (x-axis), while points less than 0 means that the subsidy has a greater effect on ecosystem production than recycling (effect increases southwards) for a given subsidy quality (x-axis). See appendix 2: table 7.3 for the parameter values but note that we had to change some other parameters to ensure a return to equilibrium, specifically, k=0.08 and dP=0.1 for fig. a., k = 0.1 and dP = 0.2 for fig. b, and k = 0.1 and dP = 0.26 for fig. c and appendix 2: equations S8 and S12 for the mathematical expressions of each function.

Sections S4: Supplementary tables

Table 7.3: Model state variables and parameter definitions. Parameter q was varied during simulations.

	Variable	Equilibrium Value	Dimension (Constraints)	Biological meaning of parameters
N	Stock of inorganic nutrients	7.8[i]	g	-
A	Stock of plants	4.7[i]	g	-
H	Stock of herbivores	2.6[i]	g	-
P	Stock of predators	0.8[i]	g	-
Q_E	n-3 LC-PUFAs Stock of the subsidy	NA	g	-
Q_P	n-3 LC-PUFAs Stock of the predators	NA	g	-
	Parameters			
I	Basal input of inorganic nutrients	2.19[ii]	g d^{-1}	Amount of constant inorganic nutrient gained by the soil nutrient pool per day
k	Loss rate of inorganic nutrients	0.1[iii]	d^{-1}	Rate of inorganic nutrient loss, e.g., via hydrological loss

a_A	Consumption rate of plants	0.14[ii]	$g^{-1}d^{-1}$	The rate at which the plant accumulates nutrients per unit of nutrient density
a_H	Consumption rate of herbivores	0.68[ii]	$g^{-1}d^{-1}$	The rate at which the herbivores accumulate plant per unit of plant density
a_P	Consumption rate of predators	0.15[ii]	$g^{-1}d^{-1}$	The rate at which the predators accumulate herbivore per unit of herbivore density
V_A	handling time of soil nutrients by plants	0.25[ii]	$d\ d^{-1}$	The rate at which the plants consume and digest the soil nutrients
V_H	handling time of plants by herbivores	0.10[ii]	$d\ d^{-1}$	The rate at which the herbivores consume and digest the plants
V_P	handling time of herbivores and subsidy by predators	0.12[ii]	$d\ d^{-1}$	The rate at which the predators consume and digest the herbivores
d_A	Mortality rate of plants	0.2[iii]	d^{-1}	Rate of non-predation mortality of plants, e.g., via disease, natural death
d_H	Mortality rate of herbivores	0.2[iii]	d^{-1}	Rate of non-predation mortality of herbivores, e.g., via disease, natural death
d_P	Mortality rate of predators	0.2[iii]	d^{-1}	Rate of non-predation mortality of predators, e.g., via disease, natural death

d_E	Mortality rate of subsidy	0.2[vii]	d^{-1}	Rate of non-predation mortality of subsidy, e.g., via disease, natural death
π_P	Predator preference for local prey	0.4[v]	- $(0 < \pi_P < 1)$	Proportion of local prey consumed by the predator, when local prey and subsidy are available to the predator
δ_A	Proportion of material lost from plants	0.59[ii]	- $(0 < \delta_A < 1)$	Proportion of dead plants not recycled into the soil nutrient pool
δ_H	Proportion of material lost from herbivores	0.89[ii]	- $(0 < \delta_H < 1)$	Proportion of dead herbivores not recycled into the soil nutrient pool
δ_P	Proportion of material lost from predators	0.48[ii]	- $(0 < \delta_P < 1)$	Proportion of dead predators not recycled into the soil nutrient pool
δ_E	Proportion of material lost from subsidy	0.48[vii]	- $(0 < \delta_E < 1)$	Proportion of dead subsidy not recycled into the soil nutrient pool
e_P	Efficiency of predators	0.75[iii]	- $(0 < e_P < 1)$	Proportion of prey consumed by the predators that is converted to biomass
e_H	Efficiency of herbivores	0.75[iii]	- $(0 < e_H < 1)$	Proportion of plant consumed by the herbivores that is converted to biomass
e_F	Efficiency of predators for n-3 LC-PUFAs consumption	0.8[v]	- $(0 < e_F < 1)$	Proportion of plant consumed by the herbivores that is converted to biomass

T_N	Total available time of nutrients	0.49[ii]	d^{-1}	The rate at which the nutrients are available for the plant
T_A	Total available time of plants	0.16[ii]	d^{-1}	The rate at which the plants are available for the herbivore
T_H	Total available time of herbivores	1.77[ii]	d^{-1}	The rate at which the herbivores are available for the predator
T_E	Total available time of subsidy	2[vii]	d^{-1}	The rate at which the subsidies are available for the predator
w	Pulse duration	10[iv]	d	Temporal duration of subsidy input into the recipient ecosystem
m	Rate of subsidy quantity input	-	$g\ d^{-1}$	Rate of subsidy input into the recipient ecosystem
q	n-3 LC-PUFAs concentration of the subsidy	-	$g\ g\text{-}^{1}$	Concentration of long chain PUFA of total fatty acids in subsidy
s	Start of the pulse	2	d	Temporal start of the subsidy input into the recipient ecosystem
a	Parameter of rational function	5.7[vi]	-	Parameter for the maximum consumption effect of subsidy quality
b	Parameter of rational function	1[vi]	-	Parameter for the maximum consumption effect of subsidy quality
c	Parameter of rational function	2.4[vi]	-	Parameter for the maximum

				consumption effect of subsidy quality
d	Parameter of rational function	2.4[vi]	-	Parameter for the maximum consumption effect of subsidy quality

[i] *values are obtained from the solved model.*

[ii] *values are samples from a uniform distribution. Proportion values from U(0,1), while non-proportion values from U(1,10).*

[iii] *values from Leroux and Loreau (2008).*

[iv] *values from McCary et al. (2021).*

[v] *values are based on empirical approximation from the literature. The preference of the riparian predator was based on Marcarelli et al. (2011), while the n-3 LC-PUFAs consumption efficiency was based on Kainz et al. (2004).*

[vi] *values from Bartels et al. (2012).*

[vii] *values determined in comparison to similar values of other model components.*

Table 7.4: Qualitative and quantitative effect of parameters changes on cumulative recipient ecosystem functions.

Parameters	*Plant efficiency*	*Herbivore efficiency*	*Predator efficiency*	*Ecosystem efficiency*
Default	Increases (2.72)	Reduces (-2.99)	Increases (8.76)	Increases (8.50)
I (50% less)	Increases (1.99)	Reduces (-4.37)	Increases (16.46)	Increases (14.08)
I (50% more)	Increases (2.69)	Reduces (-2.48)	Increases (4.31)	Increases (4.52)
T_N (50% less)	Increases (7.75)	Reduces (-0.82)	Increases (21.95)	Increases (28.88)
T_N (50% more)	Increases (1.22)	Reduces (-4.39)	Increases (5.98)	Increases (2.81)
T_A (50% less)	Increases (2.26)	Reduces (-8.26)	Increases (2.19)	**Reduces (-3.80)**
T_A (50% more)	Increases (4.34)	Reduces (-1.30)	Increases (27.44)	Increases (30.48)
e_H (50% less)	Increases (4.82)	Reduces (-7.20)	Increases (7.73)	Increases (5.36)
e_H (50% more)	Increases (2.59)	Reduces (-2.37)	Increases (9.94)	Increases (10.16)
d_A (50% less)	Increases (2.45)	Reduces (-2.19)	Increases (8.26)	Increases (8.52)
d_A (50% more)	Increases (3.12)	Reduces (-3.54)	Increases (10.26)	Increases (9.83)
Parameters	*Plant recycling*	*Herbivore recycling*	*Predator recycling*	*Ecosystem recycling*
Default	Increases (8.52)	Reduces (-4.27)	Increases (2.48)	Increases (6.72)
I (50% less)	Increases (6)	Reduces (-3.33)	Increases (3.70)	Increases (6.37)
I (50% more)	Increases (9.53)	Reduces (-4.14)	**Reduces (-1.70)**	Increases (3.68)
T_N (50% less)	Increases (8.50)	Reduces (-2.35)	Increases (4.81)	Increases (10.96)
T_N (50% more)	Increases (7.66)	Reduces (-3.96)	**Reduces (-1.86)**	Increases (1.82)
T_A (50% less)	Increases (11.93)	Reduces (-6.47)	**Reduces (-5.01)**	Increases (0.44)
T_A (50% more)	Increases (7.66)	Reduces (-3.91)	Increases (14.98)	Increases (18.73)
e_H (50% less)	Increases (18.76)	Reduces (-6.35)	Increases (3.20)	Increases (15.61)
e_H (50% more)	Increases (7.41)	Reduces (-4.03)	Increases (2.80)	Increases (6.19)
d_A (50% less)	Increases (13.48)	Reduces (-4.05)	Increases (5.16)	Increases (14.59)
d_A (50% more)	Increases (6.51)	Reduces (-4.62)	Increases (2.21)	Increases (4.10)
Parameters	*Plant production*	*Herbivore production*	*Predator production*	*Ecosystem production*
Default	Increases (2.72)	Reduces (-2.69)	Increases (2.53)	Increases (2.56)
I (50% less)	Increases (1.99)	Reduces (-1.77)	Increases (3.72)	Increases (3.95)
I (50% more)	Increases (2.69)	Reduces (-3.70)	**Reduces (-1.63)**	**Reduces (-2.64)**
T_N (50% less)	Increases (7.75)	Reduces (-0.44)	Increases (4.83)	Increases (12.14)
T_N (50% more)	Increases (1.22)	Reduces (-3.65)	**Reduces (-1.83)**	**Reduces (-4.26)**
T_A (50% less)	Increases (2.26)	Reduces (-13.02)	**Reduces (-5.23)**	**Reduces (-16)**
T_A (50% more)	Increases (4.34)	**Increases (0.86)**	Increases (15.12)	Increases (20.33)
e_H (50% less)	Increases (4.82)	Reduces (-8.28)	Increases (3.22)	Reduces (-0.23)
e_H (50% more)	Increases (2.59)	Reduces (-1.90)	Increases (2.86)	Increases (3.55)
d_A (50% less)	Increases (2.45)	Reduces (-1.60)	Increases (5.13)	Increases (5.98)
d_A (50% more)	Increases (3.12)	Reduces (-3.12)	Increases (2.22)	Increases (2.22)

In the bracket, is the difference between the cumulative recipient ecosystem functions at 0.1 $g\ g^{-1}$ *subsidy quality and 0.9* $g\ g^{-1}$ *subsidy quality. Values in boldface indicate cases where changes in parameters resulted in qualitatively dissimilar predictions as the default parameters.*

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Kainz, M., M. T. Arts, and A. Mazumder. 2004. "Essential fatty acids in the planktonic food web and their ecological role for higher trophic levels." Limnology and Oceanography, 49(5), 1784–1793. doi:10.4319/lo.2004.49.5.1784.

Appendix 3 - chapter 4 supporting information

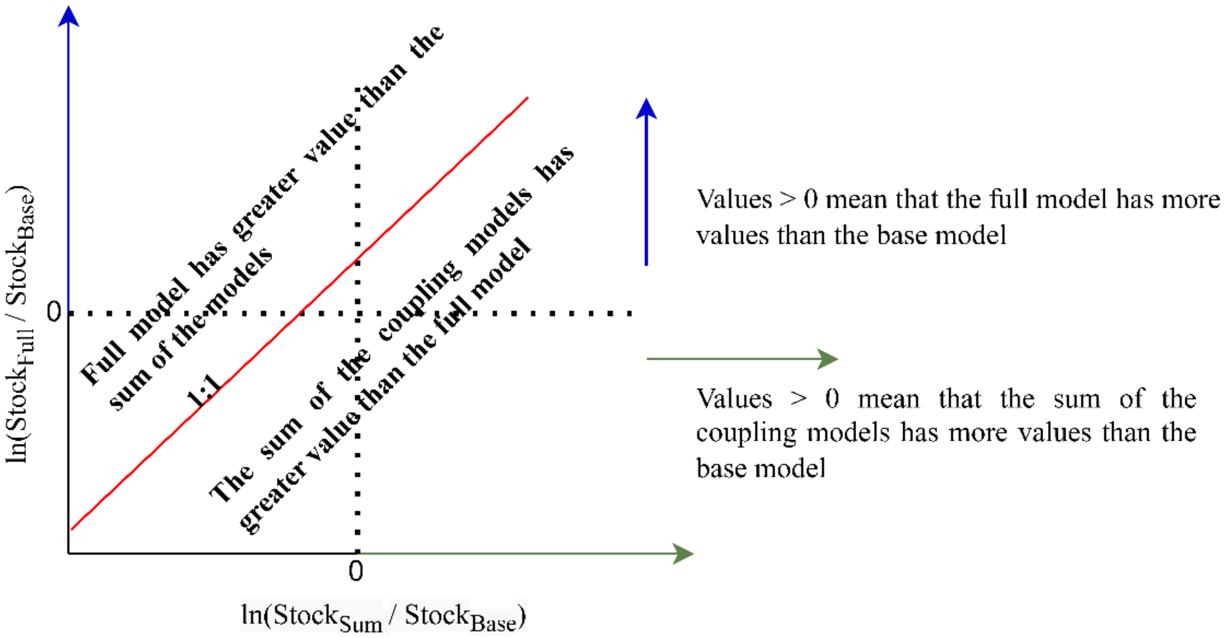

Figure 8.1: A cartoon depiction of how to interpret the interaction between subsidy-recipient ecosystem coupling pathways and their effects on stocks and functions of recipient ecosystem.

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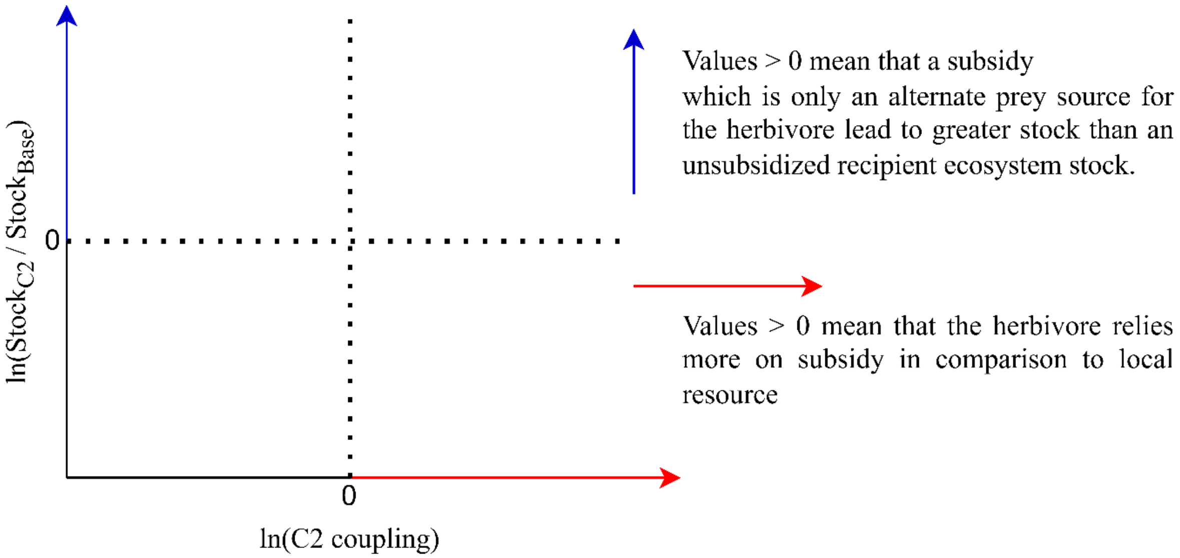


Figure 8.2: A cartoon depiction of how to interpret the effects of subsidy coupling on stocks and functions of recipient ecosystem. This is a case for consumption coupling for case study 2 (C2). The C2 coupling is defined as the ratio of subsidy to an alternative local resource consumed by the herbivore.

Plant production = $a_A NA$ (s1)

Herbivore production = $e_H a_H \pi_h AH$ (s2)

Predator production = $e_P a_P \pi_P HP$ (s3)

Ecosystem production = Plant production + Herbivore production + Predator production (s4)

Plant recycling = $(1-\delta_A)d_A A$ (s5)

Herbivore recycling = $(1-\delta_H)d_H H$ (s6)

Herbivore recycling = $(1-\delta_P)d_P P$ (s7)

Ecosystem recycling = Plant recycling + Herbivore recycling + Predator recycling (s8)

Plant efficiency = $(a_A NA)/I$ (s9)

Herbivore efficiency = $(e_H a_H \pi_h AH)/(a_A NA)$ (s10)

Predator efficiency = $(e_P a_P \pi_P HP)/(e_H a_H \pi_h AH)$ (s11)

Ecosystem efficiency = Plant efficiency + Herbivore efficiency+ Predator efficiency (s12)

Table 8.1: Overview of the models with information on feasible equilibria, parameter sets retained and their stability.

Model	**Feasible equilibrium**	**Parameter sets retained**	**No. of stable equilibrium parameter sets**	**No. of unstable equilibrium parameter sets**
Full model for case study 1	2	1136	1136	0
Full model for case study 2	1	871	456	415
Direct consumption model for case study 1	2	961	961	0
Recycling model	1	979	979	0
Direct consumption model for case study 2	1	857	429	428
Base model	1	979	979	0

Table 8.2: Overview of variables and parameters

	Variable	***Equilibrium Value***	***Dimension (Constraints)***
N	Stock of inorganic nutrients	-	g *($N > 0$)*
A	Stock of plants	-	g *($A > 0$)*
H	Stock of herbivore	-	g *($H > 0$)*
P	Stock of predator	-	g *($P > 0$)*
L	Stock of herbivore subsidy	-	g *($L > 0$)*
E	Stock of predator subsidy	-	g

			(E > 0)
	Parameters		
I	Basal input of inorganic nutrients	*U(1,10)*	g t^{-1}
l	Loss rate of inorganic nutrients	*U(1,10)*	t^{-1}
a_A	Consumption rate of plants	*U(1,10)*	$g^{-1}t^{-1}$
a_H	Consumption rate of H	*U(1,10)*	$g^{-1}t^{-1}$
a_P	Consumption rate of P	*U(1,10)*	$g^{-1}t^{-1}$
d_A	Mortality rate of plants	*U(1,10)*	t^{-1}
d_H	Mortality rate of H	*U(1,10)*	t^{-1}
d_P	Mortality rate of P	*U(1,10)*	t^{-1}
d_E	Mortality rate of P subsidy	*U(1,10)*	t^{-1}
d_L	Mortality rate of H subsidy	*U(1,10)*	t^{-1}
π_P	P preference for local resource	*U(0,1)*	- $(0 < \pi_P < 1)$
π_h	H preference for local resource	*U(0,1)*	- $(0 < \pi_P < 1)$
δ_A	Proportion of material lost from plants	*U(0,1)*	- $(0 < \delta_A < 1)$
δ_H	Proportion of material lost from H	*U(0,1)*	- $(0 < \delta_H < 1)$
δ_P	Proportion of material lost from P	*U(0,1)*	- $(0 < \delta_P < 1)$

δ_E	Proportion of material lost from P subsidy	*U(0,1)*	- $(0 < \delta_E < 1)$
δ_L	Proportion of material lost from H subsidy	*U(0,1)*	- $(0 < \delta_E < 1)$
e_P	Efficiency of P	*U(0,1)*	- $(0 < e_P < 1)$
e_H	Efficiency of H	*U(0,1)*	- $(0 < e_H < 1)$
w_E	Rate of P subsidy quantity input	*U(0,1)*	$g\ t^{-1}$
w_L	Rate of H subsidy quantity input	*U(0,1)*	$g\ t^{-1}$

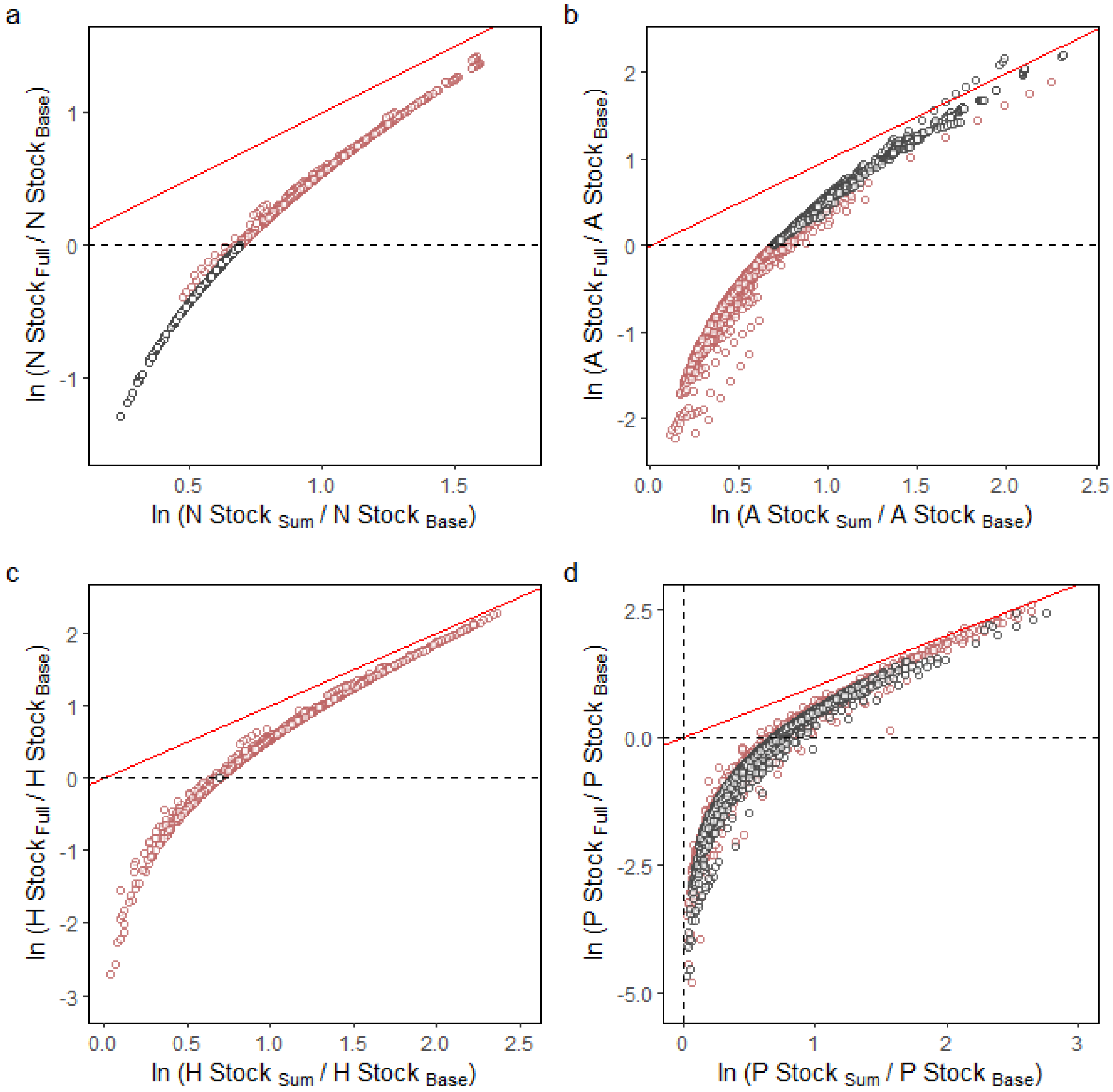


Figure 8.3: Interaction of subsidy-recipient ecosystem coupling pathways and effects on trophic levels stocks. The red points represent case study 1, while the black points represent case study 2. See appendix 3: figure 8.1 on how to interpret the figure.

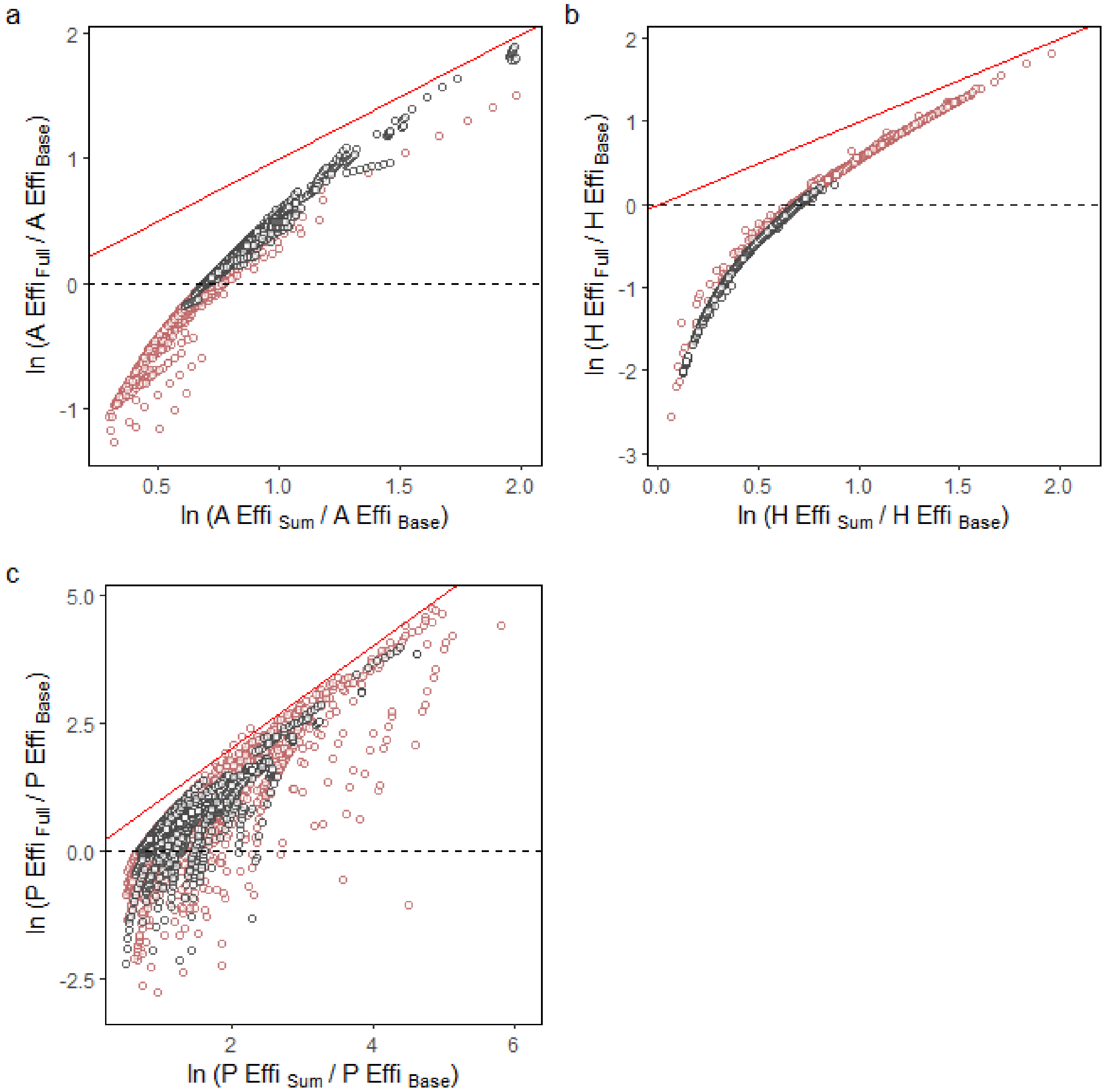


Figure 8.4: Interaction of subsidy-recipient ecosystem coupling pathways and effects on trophic levels efficiency (Effi). The red points represent case study 1, while the black points represent case study 2. P is predator, H is herbivore, and A is plant. See appendix 3: figure 8.1 on how to interpret the figure.

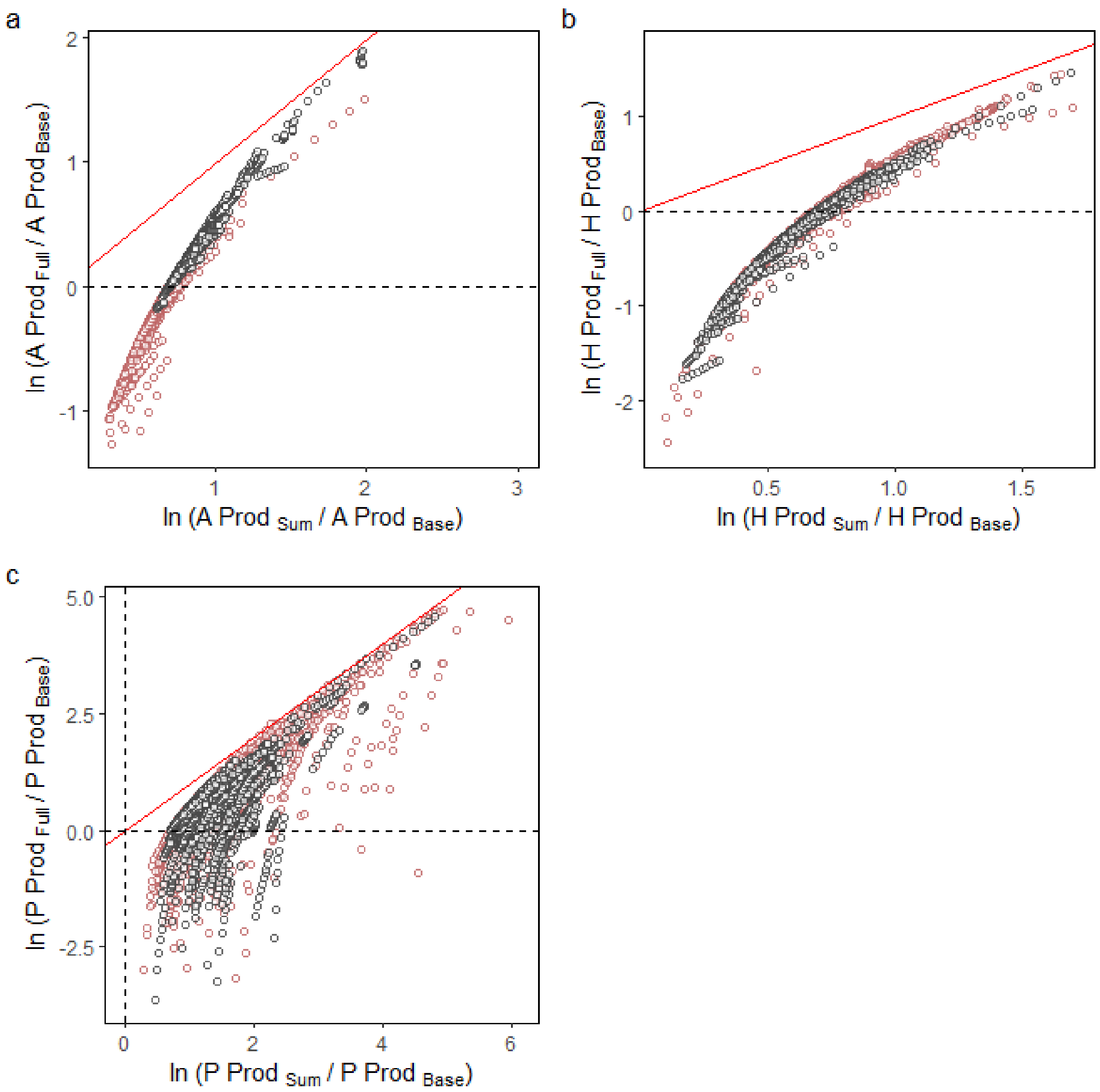


Figure 8.5: Interaction of subsidy-recipient ecosystem coupling pathways and effects on trophic levels <u>*production*</u> *(prod). The red points represent case study 1, while the black points represent case study 2. See appendix 3: figure 8.1 on how to interpret the figure.*

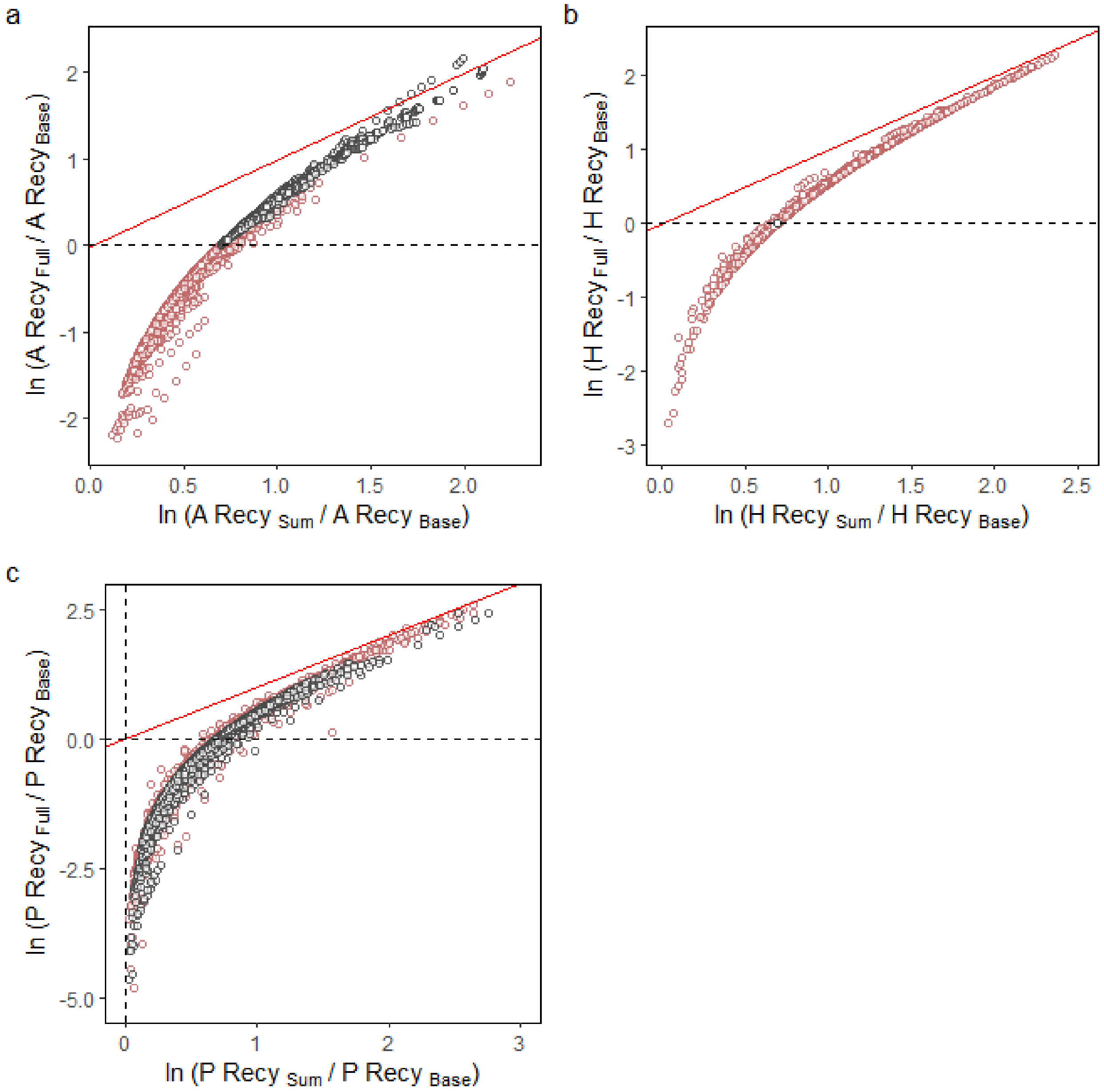


Figure 8.6: Interaction of subsidy-recipient ecosystem coupling pathways and effects on trophic levels recycling (Recy). The red points represent case study 1, while the black points represent case study 2. See appendix 3: figure 8.1 on how to interpret the figure.

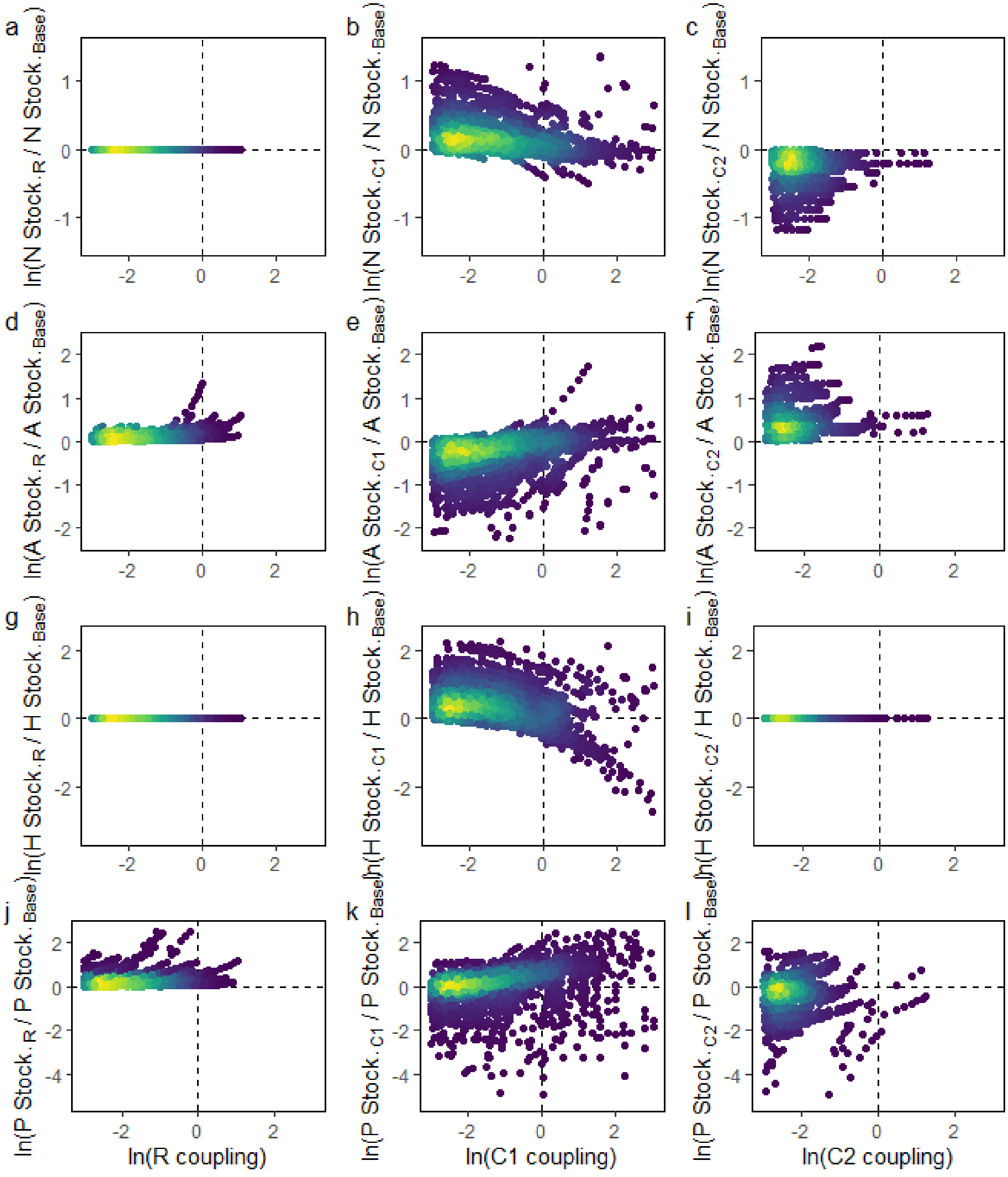


Figure 8.7: Subsidy coupling effects on trophic levels stocks. R, C1, C2 are recycling, consumption coupling for case study 1 and consumption coupling for case study 2 respectively. Base is the base model. See chapter 4: section 4.2.3.1 for definition of the x-axis and appendix: figure 8.2 on how to interpret the figure.

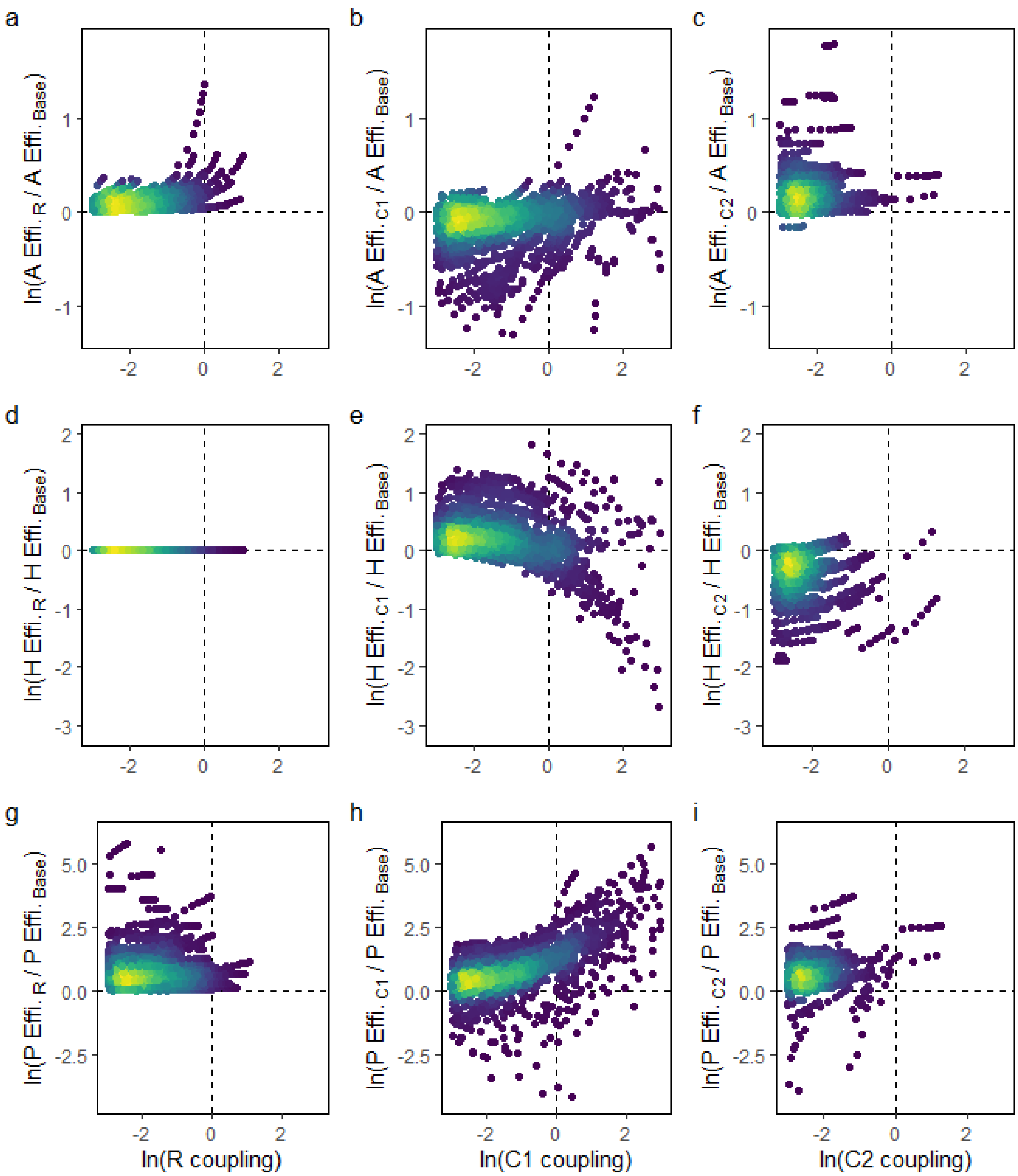


Figure 8.8: Subsidy coupling effects on trophic levels <u>*efficiency*</u> *(Effi). R, C1, C2 are recycling, consumption coupling for case study 1 and consumption coupling for case study 2 respectively. Base is the base model. See chapter 4: section 4.2.3.1 for definition of the x-axis and appendix: figure 8.2 on how to interpret the figure.*

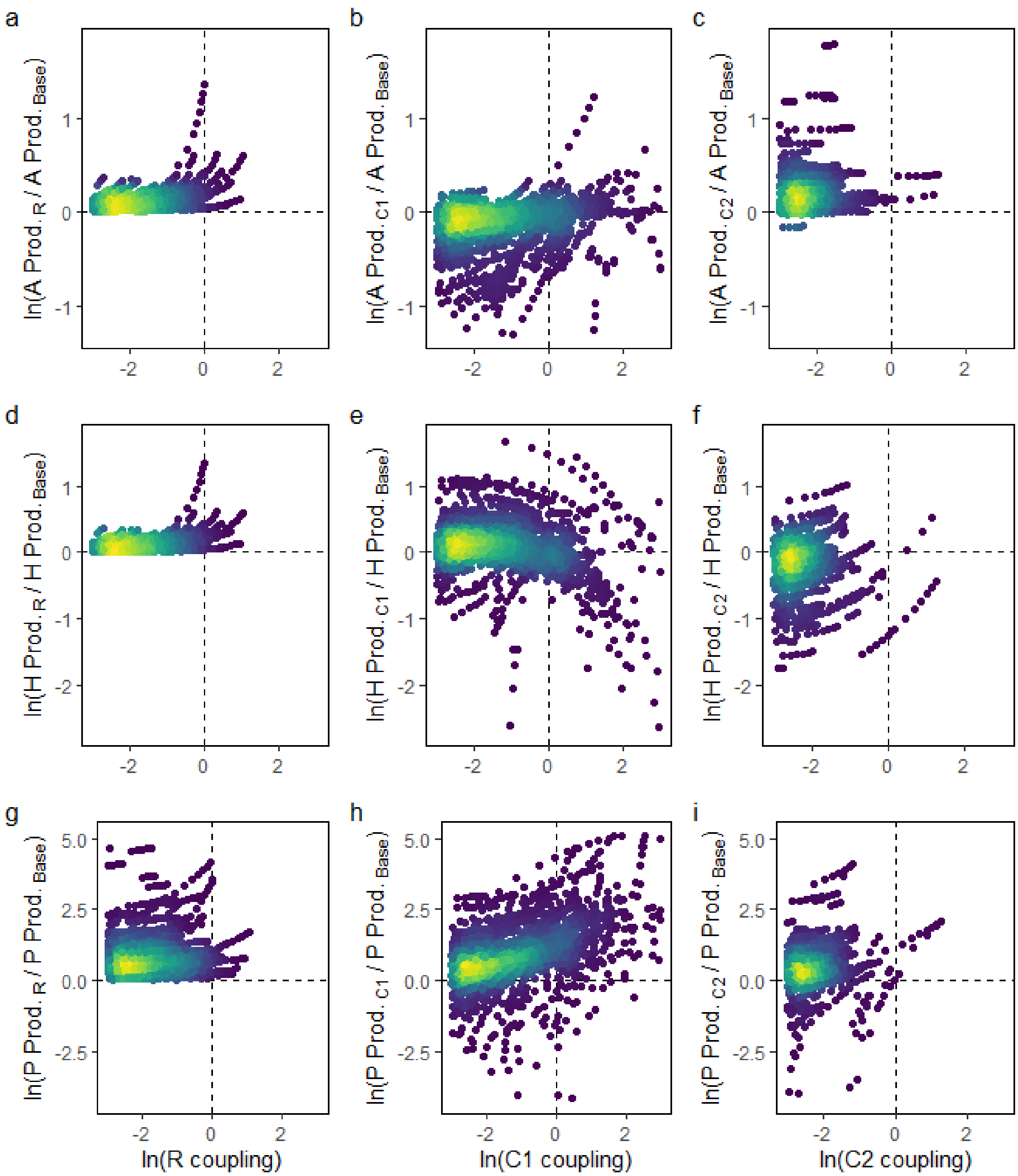


Figure 8.9: Subsidy coupling effects on trophic levels <u>*production*</u> *(prod). R, C1, C2 are recycling, consumption coupling for case study 1 and consumption coupling for case study 2 respectively. Base is the base model. See chapter 4: section 4.2.3.1 for definition of the x-axis and appendix: figure 8.2 on how to interpret the figure.*

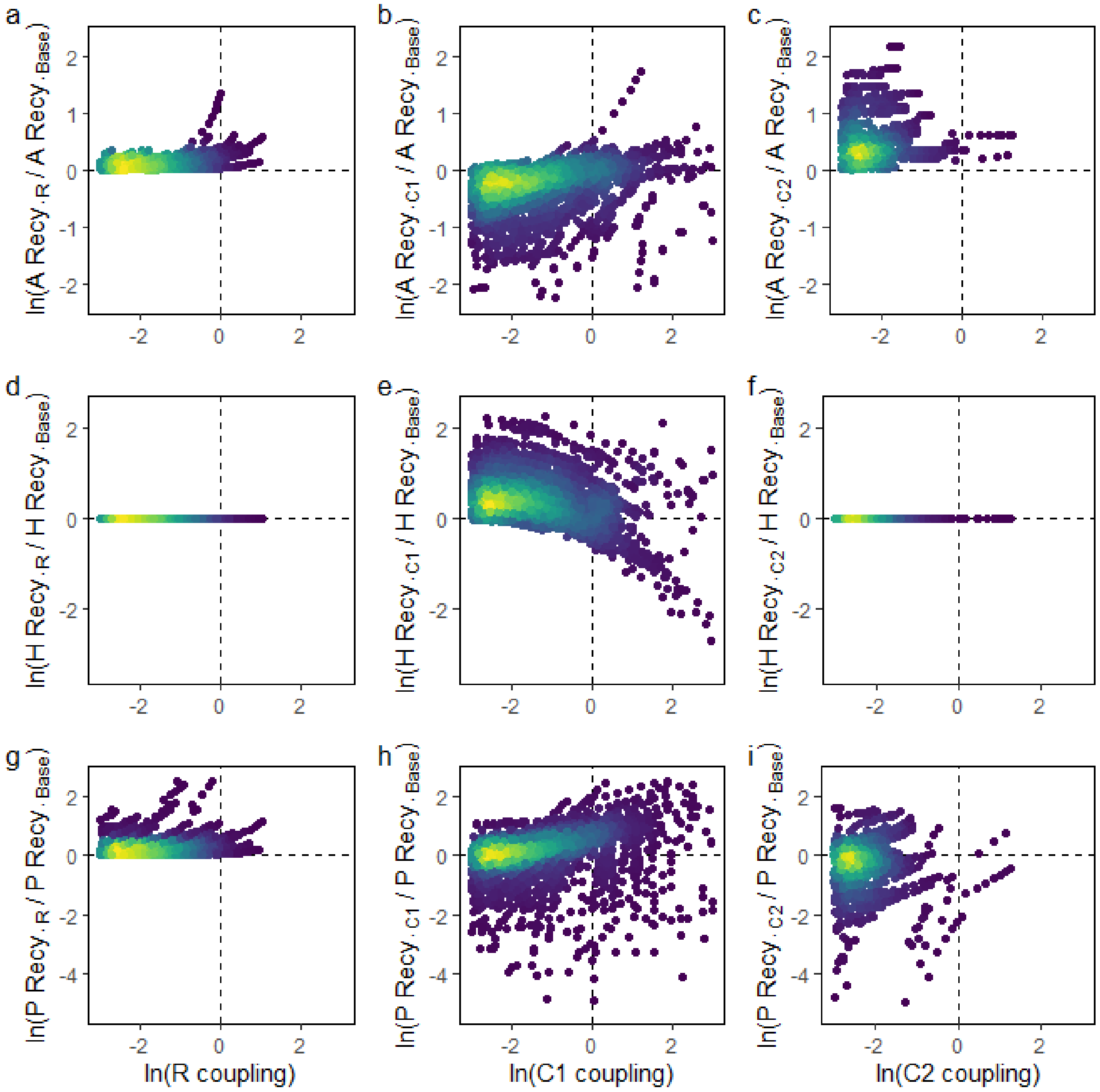


Figure 8.10: Subsidy coupling effects on trophic levels recycling (Recy). R, C1, C2 are recycling, consumption coupling for case study 1 and consumption coupling for case study 2 respectively. Base is the base model. See chapter 4: section 4.2.3.1 for definition of the x-axis and appendix: figure 8.2 on how to interpret the figure.

Author Contribution

This is a cumulative dissertation containing 2 published articles in peer-reviewed international journals and one article in preparation.

I, Stephen Esosa Osakpolor (SEO) was the main author of the publications. The publications were co-authored by Mira Kattwinkel (MK), Jens Schirmel (JS), Alexander Feckler (AF), Anne M. McLeod (AMM), Alessandro Manfrin (AM), Shawn J. Leroux (SJL), Ralf B. Schäfer (RBS).

Publication 1: Osakpolor, S. E., M. Kattwinkel, J. Schirmel, A. Feckler, A. Manfrin, and Schäfer, R. B. 2021. "Mini-review of process-based food web models and their application in aquatic-terrestrial meta-ecosystems." Ecological Modelling, 458, 109710. doi:10.1016/j.ecolmodel.2021.109710.

SEO: Conceptualization, Investigation, Writing – original draft, Writing – review & editing, Visualization.

MK: Conceptualization, Investigation, Writing – review & editing, Supervision.

JS: Conceptualization, Investigation, Writing – review & editing, Supervision.

AF: Writing – review & editing.

AM: Writing – review & editing.

RBS: Conceptualization, Investigation, Writing – review & editing, Supervision, Visualization.

Publication 2: Osakpolor S. E., A. Manfrin, S. J. Leroux, and Schäfer, R. B. 2023. "Cascading impacts of changes in subsidy quality on recipient ecosystem functioning." Ecology, e4023. https://doi.org/10.1002/ecy.4023.

SEO: Conceptualization, Writing – original draft, Writing – review and editing, Model implementation – coding and simulation.

AM: Writing – review and editing.

SJL: Supervision, Conceptualization, Writing – review and editing.

RBS: Supervision, Conceptualization, Writing – review and editing.

Publication 3: Osakpolor S. E., A. Manfrin, S. J. Leroux, R. B. Schäfer, and McLeod A. 2023 (Under review in theoretical ecology).

SEO: Conceptualization, Writing – original draft, Writing – review and editing, Model implementation – coding and simulation.

AM: Supervision, Writing – review and editing, Model implementation – coding and simulation.

AMM: Supervision, Conceptualization, Writing – review and editing, Model implementation – coding and simulation.

SJL: Supervision, Conceptualization, Writing – review and editing.

RBS: Supervision, Conceptualization, Writing – review and editing.

Declaration

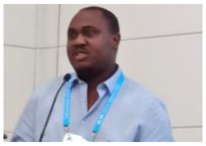
I hereby declare that I independently conducted the work presented in this thesis entitled 'modelling the response of a terrestrial food web to a change in aquatic subsidies through environmental stress'. All used assistances are mentioned and involved contributors are either co-authors of or are acknowledged in the respective publication.

This thesis has never been submitted elsewhere for an examination, as a thesis or for evaluation in a similar context to any department of this university or any scientific institution. I am aware that a violation of the aforementioned conditions can have legal consequences.

Place, date Signature

Curriculum Vitae

Nationality: Nigerian



Education

Ph.D. Environmental Science
Rheinland-Pfälzische Technische Universität Kaiserslautern-Landau
10.2019 – Date *Germany*
Thesis: Ecological-stress response modelling (short title)

MSc. Environmental Science
University of Koblenz-Landau
10.2016 – 09.2019 *Germany*
Thesis: Statistical modelling of pesticides in small streams

MTech. Geo-Information Technology
Federal University of Technology, Akure
10.2010 – 09.2012 *Nigeria*
Thesis: Geo-spatial modeling of quality of life in Benin City

BSc. Geography & Regional Planning
University of Benin
10.2003 – 09.2008 *Nigeria*
Thesis: Urban poverty in Benin City

Publications

Osakpolor, S. E., Manfrin, A., McLoed, A., Leroux S., & Schäfer, R. B. (2023). Bottom-up and top-down effects of subsidy on recipient ecosystem. Under review (Theoretical ecology).

Schäfer R.B., ..., **Osakpolor S**.**E**, ..., Vinebrooke R. (2023). Chemical mixtures and multiple stressors – Same but different? Environmental Toxicology and Chemistry, https://doi.org/10.1002/etc.5629.

Manfrin A., ..., **Osakpolor S.E.**, ..., Schulz R. (2023). SystemLink: moving beyond aquatic-terrestrial interactions. Limnology and Oceanography Bulletin, https://doi.org/10.1002/lob.10557.

Osakpolor, S. E., Manfrin, A., Leroux S., & Schäfer, R. B. (2023). Cascading impacts of changes in subsidy quality on recipient ecosystem functioning. Ecology, e4023. https://doi.org/10.1002/ecy.4023.

Fehlinger L., Benjamin Misteli, ..., **Stephen E. Osakpolor**, ..., Rimcheska B. (2022). The ecological role of permanent ponds in Europe: a review of dietary linkages to terrestrial ecosystems via emerging insects. Inland Waters, DOI: 10.1080/20442041.2022.2111180

Anke Schneeweiss, Noel P.D. Juvigny-Khenafou**, Stephen Osakpolor**, Andreas Scharmüller, Sebastian Scheu, Verena C. Schreiner, Roman Ashauer, Beate I. Escher, Florian Leese, Ralf B. Schäfer (2022). Three perspectives on the prediction of chemical effects in ecosystems. Global Change Biology, doi:10.1111/gcb.16438

Osakpolor, S. E., Kattwinkel, M., Schirmel, J., Feckler, A., Manfrin, A., & Schäfer, R. B. (2021). Mini-review of process-based food web models and their application in aquatic-terrestrial meta-ecosystems. Ecological Modelling, 458, 109710. doi:10.1016/j.ecolmodel.2021.1097

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