Received: 19 July 2022 | Revised: 30 January 2023 | Accepted: 13 February 2023

DOI: 10.1002/ecy.4023

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Cascading impacts of changes in subsidy quality on recipient ecosystem functioning

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Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: 326210499/GRK2360; Natural Sciences and Engineering Research Council of Canada Discovery Grant

Handling Editor: Daniel E. Schindler

Abstract

Resource quantity and quality 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. In this case study we focused on a common measure of subsidy quality that differs between riparian and aquatic ecosystems: the higher content of long-chain polyunsaturated fatty acids (PUFAs) in aquatic ecosystems. We analyzed 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 showed that subsidy quality increased the functioning of the recipient ecosystem. Recycling increased more strongly than production per unit subsidy quality increase, meaning there was a threshold where an increase in subsidy quality led to stronger effects of subsidies on recycling relative to the production of the 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.

KEYWORDS
allochthonous input, aquatic–terrestrial linkages, ecosystem function, meta-ecosystem, model, polyunsaturated fatty acids, recipient ecosystem, theory

INTRODUCTION

Ecosystems are coupled via the flows of nutrients, energy, and organisms (Loreau et al., 2003; Polis et al., 1997; Reiners & 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 & 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 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 & McCann, 1998; Leroux & 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 & McCann, 1998; Leroux & Loreau, 2008; McCary et al., 2021) and its relative preference for subsidy and local resources (Leroux & Loreau, 2008) drive 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 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 affected the strength of trophic cascades, and Takimoto et al. (2009) studied how factors such as the subsidy input rate and the responses of consumers influenced the direction of 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).

METHODS

General model

The state variables in existing ecosystem models exclusively represent 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

nutrients, I, and their 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) (Figure 1c). 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 & Day, 2007). With the rational function, the recipient ecosystem predator can still consume even when the predator quality is 0 (Otto & 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 the duration of the pulse, m the rate of subsidy quantity input, and q the subsidy quality during the pulse. The rate of subsidy quality input is $m \times q$. The subsidy either enters the soil nutrient pool via recycling, $(1-\delta_E)d_E E$, or the predator pool via consumption (modeled in the functional response of the predator) of the recipient ecosystem. The model is described by dynamical equations as shown in Equations (3)–(9):

$$iE_t = \begin{pmatrix} m & \text{for} \quad s < t \le s+w \\ 0 & \text{otherwise} \end{pmatrix}, \tag{1}$$

$$iQE_t = \begin{pmatrix} m \times q & \text{for} \quad s < t \le s+w \\ 0 & \text{otherwise} \end{pmatrix}, \tag{2}$$

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

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

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

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

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

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

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

Model case study

Riparian ecosystems are functionally linked to the adjacent aquatic ecosystem across all major biomes (Allen & 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 & 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 & Harding, 2007), and stable isotope studies revealed that emergent aquatic insect subsidies contributed 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 & Tscharntke, 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 insects' 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. In contrast, primary producers (e.g., *Urtica dioica*) in riparian ecosystems cannot synthesize n-3 LC-PUFAs (Sayanova & 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 & 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 & Paul, 2012). Hence, eutrophication can reduce n-3 LC-PUFA concentrations in the emergent aquatic insects that feed on algae, resulting in lower n-3 LC-PUFA concentrations propagating to the riparian ecosystem.

Adaptation of 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 earlier, 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-PUFA concentration (Q_P/P). We used a higher consumption of the predator to represent its fitness because this implicitly captures the positive effects of n-3 LC-PUFAs.

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) (Figure 1a), we first defined parameter values that were available from the literature (Kainz et al., 2004; Leroux & Loreau, 2008; Marcarelli et al., 2011; McCary et al., 2021). Then we randomly selected other parameter values that were not available from the literature from a uniform distribution (Appendix S1: Table S3). Specifically, parameters describing proportions (e.g., the proportion of materials lost from herbivores) were drawn from a uniform distribution in the range (0, 1), whereas all other parameters (e.g., the herbivore consumption rate) were drawn from a uniform distribution in the range (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 the rootSolve package (Soetaert, 2014) for R version 4.0.5 (R Core Team, 2021) to calculate the 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 were feasible (i.e., all stocks >0) and stable (i.e., negative dominant eigenvalue of Jacobian matrix; Appendix S1: Section S2). We also ensured that the selected equilibrium stock values were consistent with the common pattern of an ecological biomass pyramid (see review in Trebilco et al., 2013), that is, biomass decreases with increasing trophic levels (Figure 1b). The approach of sampling parameters from a uniform distribution is similar to that of Leroux and Schmitz (2015). This is the standard approach for ecosystem models that are modeled at a functional group level, and we also explored the effects of parameter 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

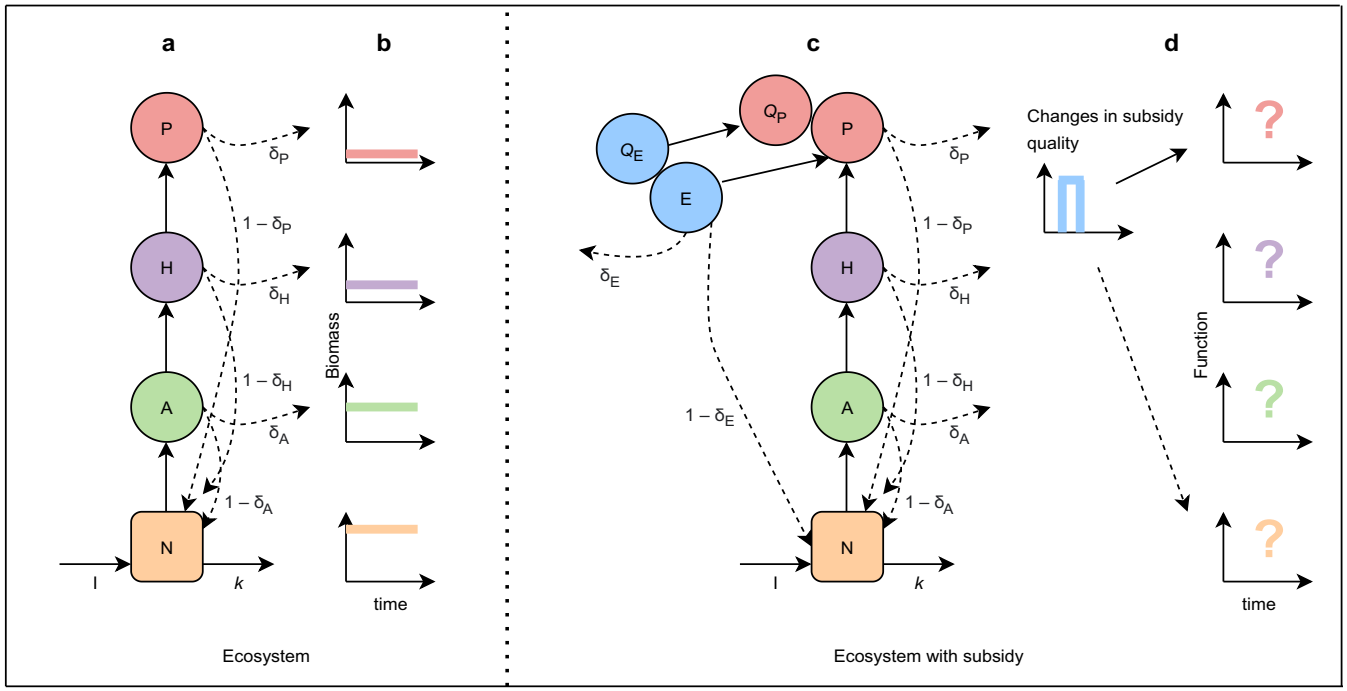

FIGURE 1 Overview of ecosystem models and research goal. Panels (a) and (c) are the model structures without subsidy and with subsidy, respectively. Panel (b) shows the equilibrium stocks of the ecosystem compartments, while panel (d) shows our research goal.

ecosystem. For example, the mortality rate of the subsidy is 0.2, similar to the compartments of the recipient ecosystem, while the proportion of nutrients lost from the subsidy is 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 affected the results. Finally, we explored our model across various levels of subsidy quality (see Appendix S1: Table S3 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 affected the results.

Analysis

To study the effects of changes in subsidy quality (Figure 1d), 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) are n-3 LC-PUFAs. However, we chose a wide range of subsidy quality values (i.e., up to 90%) because we aimed to provide general insight on how change in subsidy quality affected the recipient ecosystem. For all simulations, the model stocks were initialized at the equilibrium stocks without the subsidy. Because the nonsubsidized 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 equilibrium (120 days, Figure 2 and Appendix S1: Figure S1). To analyze the transient dynamics, we subtracted our simulated values from the values at equilibrium (i.e., no subsidy).

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).

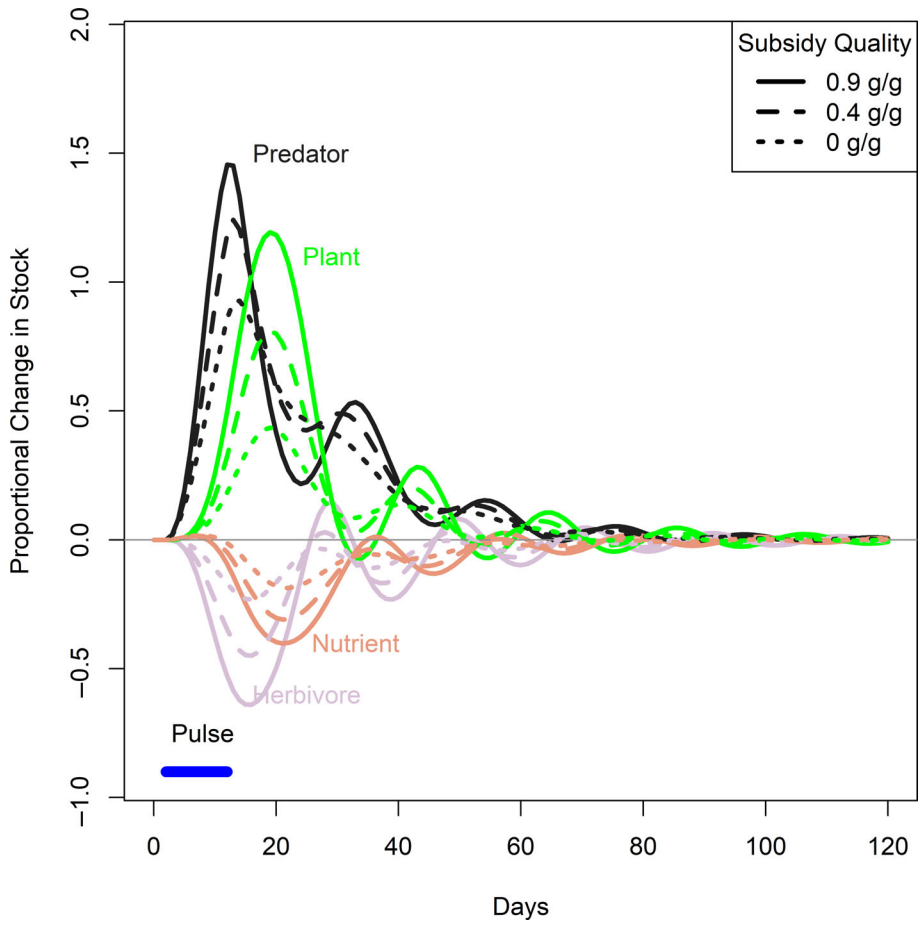

FIGURE 2 Time series of proportional changes in recipient ecosystem stocks. Lines indicate stock content at time t relative to that at equilibrium (Equation 11). See Appendix S1: Table S3 for the parameter values.

Hence, a reduction in the herbivore's consumption of plant stock results in a stronger predator-mediated trophic cascade. Therefore, like McCary et al. (2021), we calculated top-down trophic cascade as the difference between herbivore consumption of plants 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 S1 for quantitative definitions) were calculated (Equation 11), and we report the values over the whole simulated period.

Effect of change in subsidy quality on 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 S1: 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 III 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 & Schmitz, 2015). We obtained the relative effect of subsidy quality on total (i.e., the sum across trophic levels, see Appendix S1 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 meant that the subsidy had a greater effect on ecosystem recycling than ecosystem production and vice versa:

$$\text{Herbivore consumption of plant} = \mathrm{H}_{(t)}\left(\frac{a_{\mathrm{H}}T_{\mathrm{A}}\mathrm{A}_{(t)}}{1+a_{\mathrm{H}}V_{\mathrm{H}}\mathrm{A}_{(t)}}\right) - \mathrm{H}^{*}\left(\frac{a_{\mathrm{H}}T_{\mathrm{A}}\mathrm{A}^{*}}{1+a_{\mathrm{H}}V_{\mathrm{H}}\mathrm{A}^{*}}\right), \quad (10)$$

$$\text{Proportional change in ecosystem stock} = \frac{\left(\mathrm{Stock}_{(t)} - \mathrm{Stock}^{*}\right)}{\mathrm{Stock}^{*}}, \quad (11)$$

$$\text{Proportional change in ecosystem function} = \frac{\left(\mathrm{Function}_{(t)} - \mathrm{Function}^{*}\right)}{\mathrm{Function}^{*}}, \quad (12)$$

$$\text{Comparison of total ecosystem functions} = \log_{10}\left(\frac{\text{Cumulative total recycling function}}{\text{Cumulative total production function}}\right). \quad (13)$$

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-PUFA 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.

RESULTS

Effect of change in subsidy quality on time series stocks and top-down trophic cascade of 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 2). Relative to other recipient ecosystem compartments, it had a greater 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 increased with the parameter maximum effect of subsidy quality on predator consumption (Appendix S1: Figure S3). The minimum and maximum stocks of the recipient ecosystem were most affected by subsidy quality at an intermediate predator preference for local prey (0.4) (Appendix S1: Figure S5). Increasing subsidy quality caused an increase in the strength of the top-down trophic cascade (i.e., reduction of in situ plant consumption by herbivores) (Appendix S1: Figure S2).

Effect of change in subsidy quality on functions of recipient ecosystem

Increasing the subsidy quality caused an increase in the functions of plants and predators but a decrease in the functions of herbivores (Figure 3a–c). The effects of subsidy quality were strongest on the production (Figure 3a) and efficiency (Figure 3b) of predators and the recycling of plants (Figure 3c). Overall, changes in subsidy quality had a stronger effect on the total (i.e., sum across trophic levels; see Appendix S1 for quantitative definitions) efficiency and total (i.e., sum across trophic levels) recycling of the recipient ecosystem in comparison to its production (Figure 3d). Specifically, increasing subsidy quality seemed 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 appears up to a subsidy quality of 0.4 (about 50% quality), which, if exceeded, causes recycling to be more responsive to the subsidy than production (Figure 4). The 0.4 threshold reduced to 0.22 when the

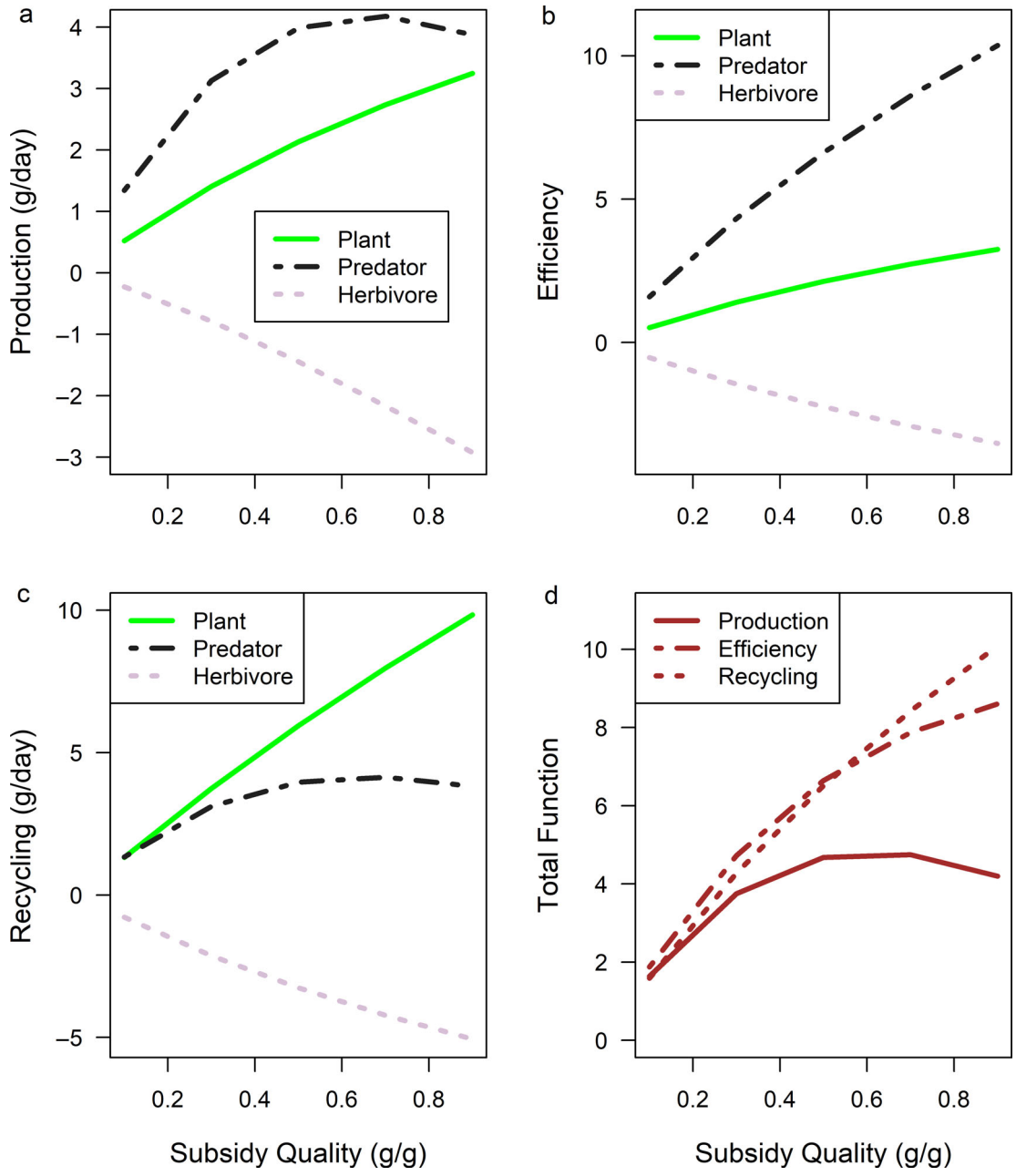

FIGURE 3 Cumulative ecosystem functions over simulated period. Lines represent difference between cumulative functions at various subsidy qualities and when subsidy quality is 0. See Appendix S1: Table S3 for parameter values and Appendix S1: Equations S5–S16 for mathematical expressions of each function.

maximum effect of subsidy quality on predator consumption was increased by 50% (i.e., 5.7- to 8.55-fold). However, a 50% reduction of this parameter (i.e., 5.7- 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 S1: Figure S4). Similarly, the 0.4 threshold reduced to 0.2 when the predator preference for local prey decreased from 40% to 20%, while it increased to 0.7 when the predator preference for local prey increased from 40% to 80% (Appendix S1: Figure S6).

Sensitivity analysis

The modeled 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 five most influential parameters of the recipient ecosystem were basal input of inorganic nutrients (I), total available time of nutrients (T_N), total available time of plants (T_A),

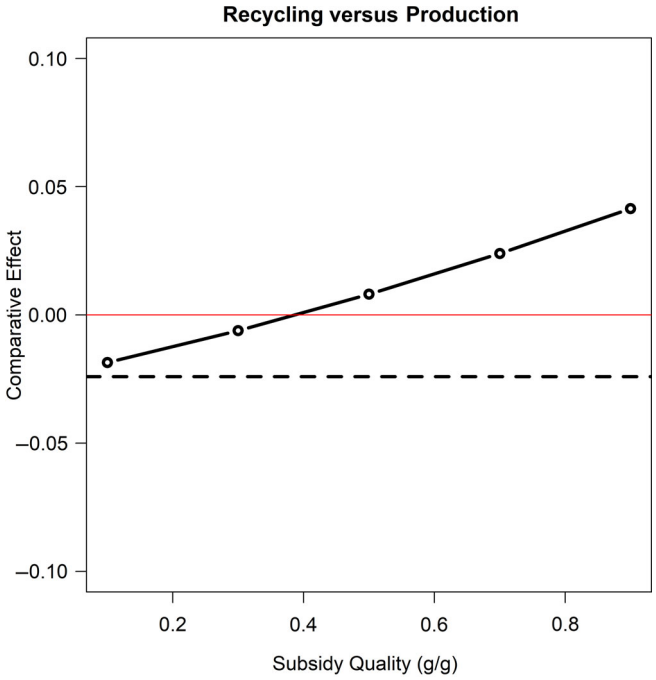

FIGURE 4 Comparison of total recycling and production of recipient ecosystem (Equation 13). Dashed line: 0 subsidy quality; points: model with varying subsidy quality specified on *x*-axis. Points greater than 0 on *y*-axis signify that the subsidy has a greater effect on ecosystem recycling than ecosystem production (effect increases northward) for a given subsidy quality (*x*-axis), while points less than 0 indicate that the subsidy has a greater effect on ecosystem production than recycling (effect increases southward) for a given subsidy quality (*x*-axis). See Appendix S1: Table S3 for the parameter values and Appendix S1: Equations S8 and S12 for the mathematical expressions of each function.

efficiency of herbivores (e_H), and mortality rates of plants (d_A) (Figure 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 S1: Table S4).

DISCUSSION

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

Our study was also novel in that we focused on how subsidy quality affected recipient ecosystem functions (i.e., production, recycling, and efficiency), thereby providing model predictions in metrics that are often measured by empiricists (Mehner et al., 2022). Hence, we improved on the connections or testability of existing theory, which 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 were made at short time scales (transients), which matches the time scales of most empirical studies of subsidies. As discussed previously, the focus on short time scales stands in contrast to most theory of connected ecosystems applied to long-term equilibrium dynamics (e.g., Huxel & McCann, 1998; Leroux & Loreau, 2008; Takimoto et al., 2009 but see McCary et al., 2021). By studying short-term dynamics, we increased the relevance of our predictions with related empirical works that were generally carried out over short time frames (Hastings, 2004). Marczak et al.'s (2007) meta-analysis revealed that empirical studies of food web effects of subsidies ranged from 1 to 36 months in duration (median = 3 months). For example, Graf et al. (2017) studied how aquatic subsidies affected terrestrial food webs over the course of 6 weeks, and Kato et al. (2004) studied the effects of aquatic insects on spider dynamics in a study that lasted 3 months.

The model analysis showed that an increase in the quality of subsidies could have important cascading effects 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 (Figure 3). In our model, the increase in subsidy quality reduced material transfer at the herbivore–plant level, thereby compounding this common ecological bottleneck. The total (i.e., sum across trophic levels; see Appendix S1 for quantitative definitions) production, recycling, and efficiency of the recipient ecosystem increased with subsidy quality. Our model predictions were 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) would promote stronger trophic cascades in local ecosystems, though their models lacked predictions

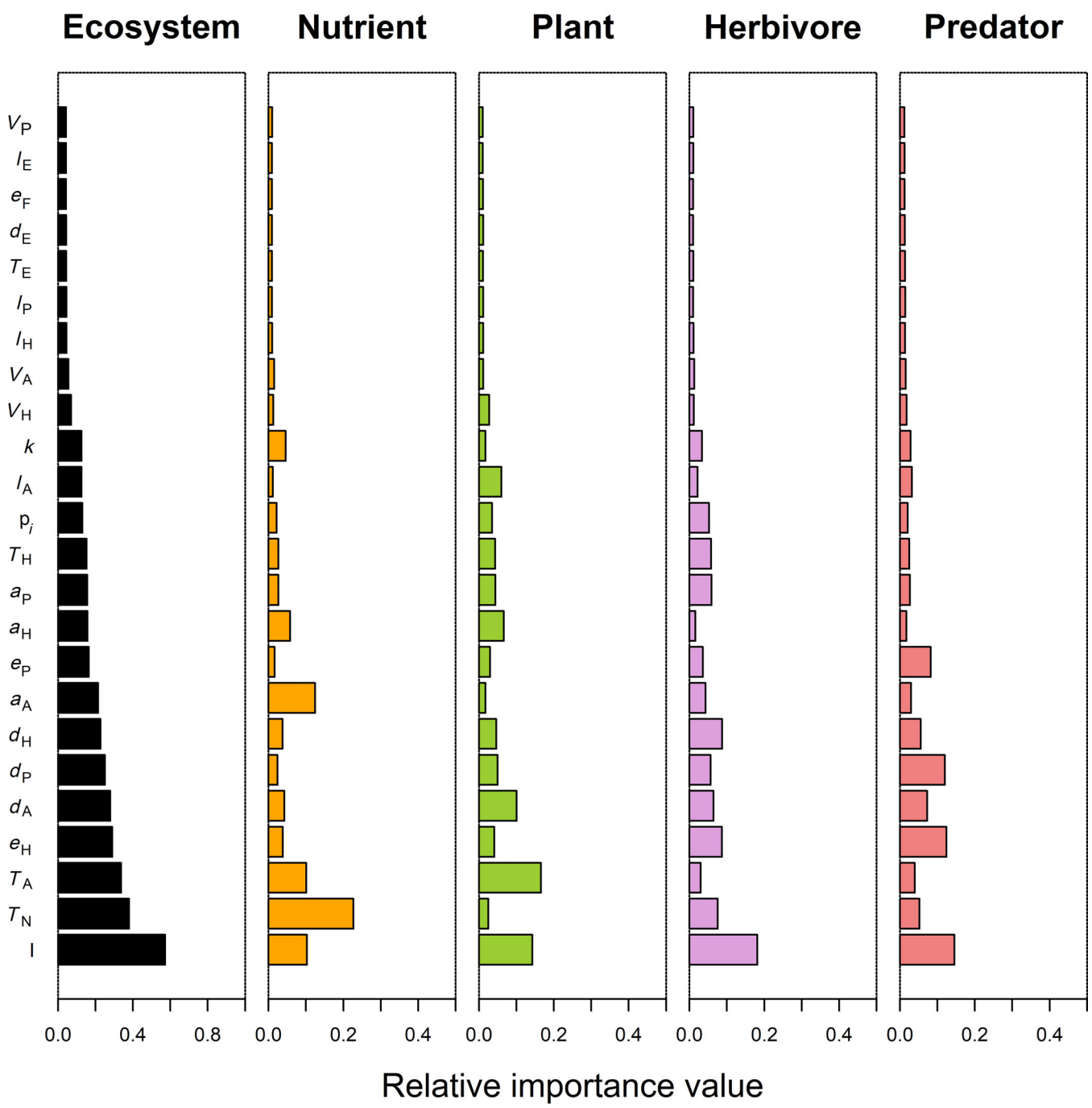

FIGURE 5 Relative importance of various model parameters in determining changes to cumulative stocks of recipient ecosystem and its compartments determined from random forest analysis.

for other ecosystem functions, such as production and recycling. Empirically, Riggi 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 represent a unification of the food quality hypothesis (Hall et al., 2007) and the subsidy hypothesis (Leroux & 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 & Loreau, 2008). Our predictions demonstrated how these two hypotheses may interact, in that increasing the quality of subsidies increased the strength of trophic cascades of the recipient ecosystem. A general explanation of the variation in the strength of trophic cascade among ecosystems remains elusive

(Leroux & Loreau, 2008). Current hypotheses include primary producer diversity hypothesis (Hillebrand et al., 2007), foraging-predation risk trade-off hypothesis (Schmitz, 2008; Schmitz et al., 2004), primary producer quality hypothesis (Borer et al., 2005; Hall et al., 2007), primary consumer efficiency hypothesis (Borer et al., 2005), primary productivity hypothesis (Shurin & Seabloom, 2005), body size hypothesis (Shurin & Seabloom, 2005), and subsidy hypothesis (Leroux & Loreau, 2008). Our subsidy quality hypothesis integrates components of two existing hypotheses (i.e., quality and subsidy) and states that the effect of subsidies 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 greater 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 could eventually lead to weaker effects of subsidies on the total production of the recipient ecosystem relative to its total recycling (Figure 4). One 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 Jefferies (1984) showed how snow geese herbivory could 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 upward through the food chain and in turn spread throughout the entire ecosystem. Consequently, subsidies might affect ecosystem production more than ecosystem recycling if the dominant process is bottom-up. We expect other systems in which top predators receive high-quality subsidies would also follow our predictions, that is, subsidies will cause top-down cascading effects, with stronger effects on recycling than production (e.g., terrestrial invertebrates' subsidies for fish). Our quality–quantity modeling framework can be applied to diverse cases in which subsidy quality varies. Further examples include high-quality lake food in seston (i.e., high growth-producing nutrients per unit of food intake) for filter feeding animals in streams at the outflow of lakes (Richardson & 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 examples). Our findings that model predictions are most sensitive to the basal input rate of inorganic nutrients (I) (Figure 5) demonstrate 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 Leroux & Loreau, 2015; Loreau & Holt, 2004).

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 and assumptions and identify missing model processes (Grainger et al., 2022). Recent advances in spatial stoichiometry provide methods for mapping 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 & Wallace, 2003), empirical studies of subsidies measured these ecosystem functions, while in others (e.g., Barrett et al., 2005; Bomkamp et al., 2004), it would be a small additional step to do so. Measuring such functions is key because 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 assumed that subsidy quality caused a maximum predator consumption effect of 5.7-fold (but see Appendix S1: Figure S4 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 will require experiments with treatments across n-3 LC-PUFA gradients, that is, not just two levels. The processes that underpin how n-3 LC-PUFAs affect the consumption of predators will more accurately be identified and, thus, will enhance the prediction of ecological outcomes in a 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 since, at many different parameter values with different equilibria, the results were qualitatively similar in most cases (90%). Third, the ecosystem variables were modeled at the functional group level (i.e., herbivores, predators). This approach is consistent with other ecosystem models (e.g., Leroux & Loreau, 2008; McCann et al., 1998); however, variabilities exist within the functional groups, which could reflect differences among ecological system types. For example, Kowarik et al. (2021) showed that n-3 LC-PUFA contents differ in different orders of emerging aquatic insects. Graf et al. (2017) showed that the effects of aquatic subsidies on riparian ecosystems depended on the herbivore composition of the riparian ecosystem. However, the current level of complexity of our model gave us general insights into how changes in subsidy quality affected the recipient ecosystem, and the model could 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 Larsen et al., 2016). Examples are nutrient-poor ecosystems and ecosystems located in remote areas (e.g., Arctic and alpine lakes and their surrounding terrain). This is because such ecosystems have clear boundaries and so are more sensitive to subsidy changes resulting from rapid environmental change (Burpee & 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 & Smits, 2016). Future empirical studies could investigate the patchiness of subsidy effects.

AUTHOR CONTRIBUTIONS

Stephen E. Osakpolor: Conceptualization, writing—original draft, writing—review and editing, model implementation—coding and simulation. **Alessandro Manfrin**: Writing—review and editing. **Shawn J. Leroux**: Supervision, conceptualization, writing—review and editing. **Ralf B. Schäfer**: Supervision, conceptualization, writing—review and editing.

ACKNOWLEDGMENTS

This work was funded by the Deutsche Forschungsgemeinschaft (German Research Foundation)—326210499/GRK2360 to Stephen E. Osakpolor, Alessandro Manfrin, and Ralf B. Schäfer and a Natural Sciences and Engineering Research Council of Canada Discovery Grant to Shawn J. Leroux. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Osakpolor, 2022) are available in Figshare at https://doi.org/10.6084/m9.figshare.20324043.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Osakpolor, Stephen E., Alessandro Manfrin, Shawn J. Leroux, and Ralf B. Schäfer. 2023. "Cascading Impacts of Changes in Subsidy Quality on Recipient Ecosystem Functioning." *Ecology* 104(5): e4023. https://doi.org/10.1002/ecy.4023