Received: 13 June 2022 | Revised: 20 March 2023 | Accepted: 23 March 2023

DOI: 10.1002/ecy.4101

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Food webs coupled in space: Consumer foraging movement affects both stocks and fluxes

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Funding information
H2020 European Research Council, Grant/Award Number: 856506; Vetenskapsrådet, Grant/Award Numbers: 2016-06872, 2018-05523

Handling Editor: Caz M. Taylor

Abstract

The exchange of material and individuals between neighboring food webs is ubiquitous and affects ecosystem functioning. Here, we explore animal foraging movement between adjacent, heterogeneous habitats and its effect on a suite of interconnected ecosystem functions. Combining dynamic food web models with nutrient-recycling models, we study foraging across habitats that differ in fertility and plant diversity. We found that net foraging movement flowed from high to low fertility or high to low diversity and boosted stocks and flows across the whole loop of ecosystem functions, including biomass, detritus, and nutrients, in the recipient habitat. Contrary to common assumptions, however, the largest flows were often between the highest and intermediate fertility habitats rather than highest and lowest. The effect of consumer influx on ecosystem functions was similar to the effect of increasing fertility. Unlike fertility, however, consumer influx caused a shift toward highly predator-dominated biomass distributions, especially in habitats that were unable to support predators in the absence of consumer foraging. This shift resulted from both direct and indirect effects propagated through the interconnected ecosystem functions. Only by considering both stocks and fluxes across the whole loop of ecosystem functions do we uncover the mechanisms driving our results. In conclusion, the outcome of animal foraging movements will differ from that of dispersal and diffusion. Together we show how considering active types of animal movement and the interconnectedness of ecosystem functions can aid our understanding of the patchy landscapes of the Anthropocene.

KEYWORDS

cross-habitat foraging, metacommunity, meta-ecosystem, nutrient recycling, nutrient stocks, optimal foraging, plant diversity, productivity, spillover predation

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Kate L. Wootton and Alva Curtsdotter contributed equally.

INTRODUCTION

Land-use conversion and habitat fragmentation have led to patchy forestry and agricultural landscapes globally. This leaves remnant biodiversity-rich ecosystems, such as natural and seminatural grasslands, adjacent to intensively managed lands, such as croplands (Fahrig et al., 2011; Ramankutty et al., 2018; Watson et al., 2005). As a consequence, adjacent ecosystems frequently differ sharply in fertility (i.e., plant nutrient availability) as well as biodiversity (Fahrig et al., 2011; Mendenhall et al., 2016) while remaining connected through the exchange of materials and individuals (Rand et al., 2006). Such exchanges can affect local richness and dynamical stability (McCann et al., 2005; Ryser et al., 2021), and we might expect that it would also affect ecosystem functions such as biomass production and nutrient dynamics (Gounand et al., 2018; Massol et al., 2011). However, there is a lack of theory integrating active animal movement (as opposed to more frequently studied passive flows), food web complexity, and nutrient recycling and their effect on ecosystem functions rather than stability.

Here we take a dynamic approach to investigate the effects of habitat fertility and basal species richness on ecosystem functions both within a focal habitat and on adjacent habitats linked by the active movement of foraging consumers. We consider the whole loop of matter transformation, which intimately links many ecosystem functions. The loop of matter transformation encapsulates the process of inorganic compounds being turned into living biomass, transferred through food chains, and ultimately recycled through decomposition and mineralization back into inorganic compounds (Gounand et al., 2014, 2020). This loop ties together stocks of living biomass through fluxes such as primary productivity and predation, as well as stocks of detritus (dead biomass) and inorganic nutrients through fluxes such as decomposition and nutrient uptake (Figure 1). Adopting this perspective of stocks tied by fluxes in a cycle emphasizes that ecosystem compartments and functions are interdependent, so that changes in one can cascade onto others.

Adjacent habitats, especially in patchy, human-altered landscapes, can differ strongly in fertility and basal species richness, leading to vastly different ecosystems. While we know a lot about how fertility and basal species richness can affect ecosystems in isolation, we know much less about how they might spill over to affect adjacent ecosystems through the active movement of foraging consumers. On its own, basal species richness increases primary productivity and biomass stocks (Cardinale et al., 2012) and can have positive, cascading effects on consumer richness (Ebeling et al., 2017; Welti et al., 2017) and consumption (Ebeling et al., 2017; Hertzog et al., 2017; Loranger et al., 2014). However, food web structure also plays a role and can strengthen (Albert et al., 2022), neutralize (Thébault & Loreau, 2003, 2005), or even invert (Worm & Duffy, 2003) the relationship between plant species richness and productivity. Fertility increases productivity and biomass across trophic levels (Gruner et al., 2008; Spivak et al., 2009) and increases food chain length (Post, 2002). However, high fertility can lead to competitive exclusion in plant communities (Hautier et al., 2009) and, in food webs, to strong top-down control, resulting in dynamic instability and species loss (Rosenzweig, 1971; Ryser et al., 2021).

While studies of both nutrient dynamics and food web dynamics have a long history in ecology, dating back to the works of Lotka (1925), Volterra (1931), Lindeman (1942), Odum (1957), and Hutchinson (1964), for a long time they represented rather separate disciplines in ecology, despite clearly being interrelated. In a landmark publication, DeAngelis (1992) summarized knowledge in both these fields and set the stage for a more synthetic approach that connects nutrient dynamics and food web dynamics. Adding nutrient recycling to food webs or food chains, that is, closing the loop of matter transformation, increases primary productivity and the total amount of nutrients stored in the ecosystem (Barot et al., 2007; de Mazancourt et al., 1998; DeAngelis, 1980). The increased nutrient availability from recycling can exacerbate the paradox of enrichment, producing instability earlier, that is, at lower levels of external nutrient input (Quévreux et al., 2021). However, nutrient recycling can also have the opposite effect, reducing nutrient availability by locking nutrients into the detritus pool (Gounand et al., 2014). Overall, it is clear that the effects of nutrient recycling are variable and depend on both food web structure and the particular dynamics of the nutrient recycling processes themselves (Quévreux et al., 2021; Zou et al., 2016).

The spatial flow of organisms between habitats can have profound effects on their stability and functioning (Loreau et al., 2003; McCann et al., 2005; Polis et al., 1997). In heterogeneous landscapes, flows of organisms from high- to low-quality habitats provide rescue effects (Brown & Kodric-Brown, 1977)—bolstering populations in low-quality habitats—as well as drainage effects (Ryser et al., 2021)—stabilizing the dynamics in high-fertility habitats—thereby supporting higher species richness than is otherwise locally possible in both low- and high-quality habitats (Heinrichs et al., 2016; Ryser et al., 2021). Spatial coupling of

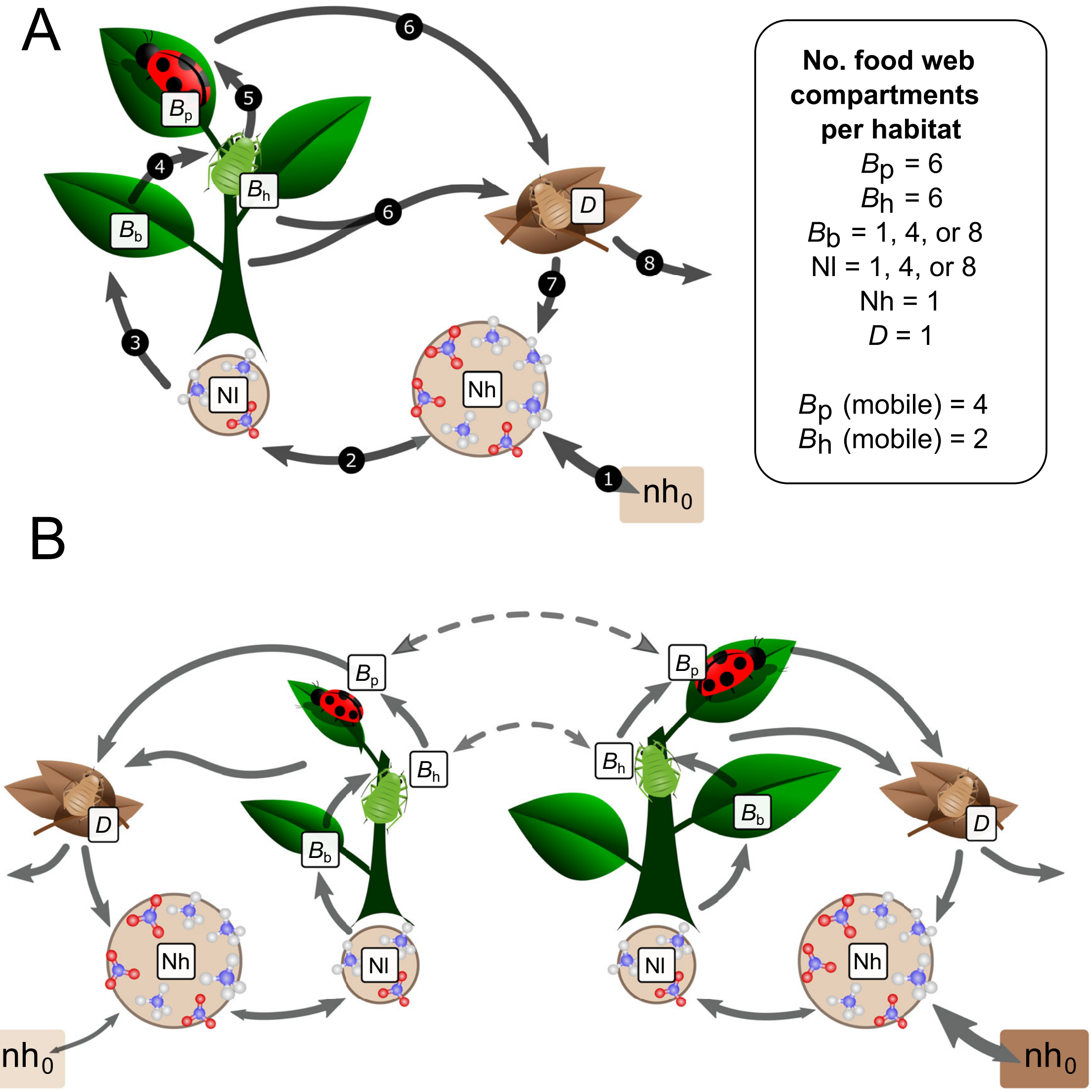

FIGURE 1 Representations of the model in (A) a single habitat and (B) two habitats of differing fertility (nh_0) coupled by consumer foraging movement. The habitat on the right has higher fertility (as shown by the darker saturation of nh_0), while the habitat on the left has low fertility. Letters in rectangular boxes represent stocks: nutrient concentration in habitat pool (Nh), nutrient concentration in plant's resource depletion zone (Nl), basal species biomass (B_b), herbivore species biomass (B_h), predator species biomass (B_p), and detritus (D). Note that there are multiple basal species (one, four, or eight, each with its own depletion zone), six herbivores, and six predators per habitat, but only one habitat nutrient pool and detritus pool per habitat. Fluxes connect the stocks and are represented by numbers in black circles: Plants are consumed by herbivores (4: herbivory), which in turn are consumed by predators (5: predation). The mortality of plants, herbivores, and predators contributes to the detritus pool, as does waste from consumption (6: waste and mortality). Detritus decomposes and releases nutrients, some of which are lost from the habitat (8: nutrient loss), and some of which replenish the habitat nutrient pool (7: decomposition). The habitat nutrient pool also draws nutrients from the surrounding environment (1: environmental nutrient exchange). Plants grow by taking up nutrients from the soil immediately surrounding their roots (3: plant growth), creating a resource depletion zone that is replenished by nutrients from the habitat nutrient pool (the soil not in immediate vicinity of plant roots) (2: nutrient influx to depletion zones). Thus, plant competition for the nutrients in the habitat pool is indirect, and its strength is mediated by the rate of nutrient transport from the habitat pool to the plant depletion zones. Arrows 1 and 2 are double headed, indicating that these fluxes are driven by the difference in nutrient concentration between the two stocks and sometimes flow in the opposite direction. Mobile consumers (two of the herbivores and four of the predators), finally, link ecosystem functions in neighboring habitats by feeding in both. Note that this means their waste and mortality contribute to both detritus pools, in proportion to the amount of time they spend feeding in each.

habitats via consumer movements can enhance dynamical stability (Guichard, 2017; McCann et al., 2005; Ryser et al., 2021), but it can also create apparent competition between resources in the different habitats (Frost et al., 2016), leading to resource overexploitation and extinction as a consequence (Holt & Hochberg, 2001;

Rand et al., 2006). Metaecosystem research adds nutrient recycling to simple food chains (Loreau et al., 2003) or food web modules (Massol et al., 2011) in a spatial context, making it possible to include the indirect effect on ecosystems that consumer movement can have by bringing nutrients into the ecosystem in the form of the consumers' bodies and their waste (excrement). Consumer influx can represent substantial nutrient subsidies (Abbas et al., 2012; Subalusky et al., 2015) and generate spatial trophic cascades that can either promote or undermine coexistence depending on consumer behavior (Marleau & Guichard, 2019; Peller et al., 2022).

While the importance of combining food web and nutrient dynamics has been highlighted at least since DeAngelis (1992), and metaecosystem ecology later focused on the importance of nutrient flows between habitats (Loreau et al., 2003), we still lack an understanding of how food web and nutrient dynamics interact with active animal movement across habitats and, particularly, what the effect is on ecosystem functions rather than stability and coexistence. Given that the models of both food web and metaecosystem ecology are explicit about the stocks and fluxes of biomass and, in the latter case, of nutrients, they represent an overlooked tool to holistically study the ecosystem functions of the matter transformation loop. Furthermore, the tendency in many fields has been to conceptualize the spatial flow of organisms as long-distance dispersal between similar habitat patches in an otherwise uninhabitable landscape or as a passive process, like diffusion, across a continuous landscape (Gounand et al., 2018; Massol et al., 2011). But organism movement is more diverse than that; for example, organisms may change habitat as part of an ontogenetic shift, others perform seasonal migrations, and many move between habitats as part of their daily foraging. The effect of habitat coupling is likely to depend not only on the characteristics of the habitats but on the type of organism movement involved (Gounand et al., 2018) and the way in which it links habitats. Lundberg and Moberg (2003) define three categories of mobile links that mobile animals can provide: resource linkers that transfer resources such as nutrients, genetic linkers that are important for cross-habitat reproduction, such as moving seeds or pollen, and process linkers that provide important process such as pest control. Animal foraging movement between adjacent habitats is ubiquitous and can cover all three of these linkage categories (Lundberg & Moberg, 2003; Rand et al., 2006; Subalusky et al., 2015). It can have profound impacts on biomass and nutrient stocks as well as coexistence (Abbas et al., 2012; Peller et al., 2022; Subalusky et al., 2015). Even so, there is a dearth of theory for active animal movement between adjacent ecosystems and its consequences for their functioning.

We propose to address this gap in ecological theory by combining dynamic food web models with models for nutrient recycling across habitats differing in fertility and plant diversity. We explore how neighboring ecosystems, linked through animal foraging movements, affect multiple food web characteristics and processes, including species persistence and the following ecosystem functions: standing stocks of living biomass at each trophic level, biomass fluxes between trophic levels (primary, secondary, and tertiary production), the stock and flux of detritus, and the size of soil nutrient pools and fluxes. Specifically, we use computer simulations of coupled tri-trophic food webs, with explicit nutrient recycling, to study the effect of cross-habitat animal foraging movement on the suite of ecosystem functions and processes in the matter transformation loop. Because the model includes both food web and nutrient dynamics, our animal foragers can be classified as both resource and process linkers (sensu Lundberg & Moberg, 2003). We parameterize the model for grassland–arthropod systems (small body sizes) but expect it will generalize to most terrestrial systems that include herbivory. To establish a baseline for comparison, we first determine how (1) fertility and (2) plant species richness affect isolated food webs. We then ask how habitats coupled by the movement of consumers influence each other and how this depends on the differences in fertility and plant diversity between the communities.

Based on existing research, we may expect that fertility and basal species richness will increase production across trophic levels but that they may have conflicting effects on species' richness. Foraging movement may allow effects to spill over to support diversity or biomass. We do not, however, know how these effects may be moderated as they are recycled through the loop of matter transformation.

MATERIALS AND METHODS

We used a dynamic model to simulate the matter transformation loop (i.e., food web and soil nutrient cycle) in habitats varying in soil fertility and plant diversity. Our model is a combination of the ecosystem model of Thébault and Loreau (2005) (hereafter the TL model) and the Allometric Trophic Network model (Berlow et al., 2009; Otto et al., 2007; Schneider et al., 2012, hereafter the ATN model). The TL model describes the flow of nutrients between detritus, nutrient pools, and plant species within an ecosystem and models their dynamics.

The ATN model uses consumer and resource body sizes to parameterize the functional response of consumers, quantify the strength of trophic interactions, and model their dynamics. Body size underlies the parameterization of the functional response because many parts of the interaction, including movement speed, consumption rate, and mortality, scale nonlinearly in a predictable way with body size due to the relationship between body size and metabolism (Brown et al., 2004). The ATN model therefore allows us to easily and efficiently parameterize relatively realistic interactions with few variables. Our hybrid TL-ATN model describes both food web and nutrient dynamics (Figure 1). We first focused on food webs in isolated habitats, exploring the effect of fertility (nh_0) and basal species diversity. We then extended this model to two habitats (Figure 1B), where each habitat had its own habitat nutrient pool and detritus pool. The habitats were coupled through the movements of optimally foraging consumers.

The model

Our model describes a 13- to 20-species tritrophic food web with nutrient recycling through decomposition and nutrient exchange with the environment. In the food web portion of the model, we have one to eight basal species, six herbivores, and six predators, with no omnivory or intraguild predation. When linked to another habitat, two of the herbivore species and four of the predator species have a population in both habitats and redistribute each time step according to available food resources.

For all scenarios we modeled the dynamics for the following stocks in a given habitat x (Figure 1): each species' biomass, B_{jx} (Equation 1), the nutrient concentration in each plant species' resource depletion zone, Nl_{jx} (Equation 2), the nutrient concentration of the habitat nutrient pool, Nh_x (Equation 3), and the nutrient concentration in the detritus pool, D_x (Equation 4). The dynamics of these stocks depended on the fluxes between them: environmental nutrient exchange (Equation 6, Figure 1A arrow 1), nutrient influx to each plant's depletion zone (Equation 7, arrow 2), plant growth/primary productivity (Equation 8, arrow 3), consumption (both herbivory and predation, Equation 9, which was then assimilated to secondary and tertiary productivity, Equation 10, arrows 4 and 5), waste from consumption (Equations 11 and 12), mortality (Equation 13, arrow 6), decomposition (Equation 14, arrow 7) and nutrient loss (Equation 15, arrow 8), and consumer foraging movement (Equation 16).

Stocks were modeled as follows:

$$\begin{aligned}\frac{dB_{jx}}{dt} &= \text{plant growth}_{jx} + \sum_{i \in R_j} \text{assimilation}_{jix} \\ &\quad - \sum_{l \in C_j} \text{consumption}_{jlx} - \text{mortality}_{jx} \\ &\quad + \text{ consumer movement}_{jx},\end{aligned} \tag{1}$$

$$Vl_{jx}\frac{dNl_{jx}}{dt} = \text{nutrient influx}_{jx} - \text{plant growth}_{jx}, \tag{2}$$

$$\begin{aligned}Vh_x\frac{dNh_x}{dt} &= \text{environmental nutrient exchange}_x \\ &\quad + \text{decomposition}_x - \sum_{j \in S_x} \text{nutrient uptake}_{jx},\end{aligned} \tag{3}$$

$$\begin{aligned}\frac{dD_x}{dt} &= \sum_{j \in S_x} \phi_{jx}(\text{mortality}_{jx} + \text{waste}_{jx}) \\ &\quad - \text{decomposition}_x - \text{nutrient loss}_x.\end{aligned} \tag{4}$$

Here, i was a given resource and l a given consumer of species j, and Vl_{jx} and Vh_x were the volumes of species j's resource depletion zone in habitat x (nonzero for plant species only) and habitat x's habitat nutrient pool, respectively, R_j is the set of resources of species j, C_j is the set of consumers of species j, and S_x is the set of species in habitat x. Some terms were equal to zero depending on the type of species. Mobile species foraged optimally by continuously redistributing between habitats in response to prey availability, following an ideal free distribution (Fretwell, 1972; Fretwell & Lucas, 1969; Williams et al., 2013). More specifically, mobile consumers redistributed between two habitats x and y in proportion to expected consumption rates, as determined by average historical per-capita consumption rates in the different habitats over a set time window, in our case five timesteps (days). Expected consumption rate in habitat x was quantified by the parameter ϕ_{jx} (and correspondingly ϕ_{jy} for habitat y):

$$\phi_{jx} = \frac{\sum_{i \in R_j} \frac{\text{consumption}_{ijx}}{B_{jx}}}{\sum_{i \in R_j} \frac{\text{consumption}_{ijx}}{B_{jx}} + \sum_{i \in R_j} \frac{\text{consumption}_{ijy}}{B_{jy}}}. \tag{5}$$

Here, $\sum_{i \in R_j} \text{consumption}_{ijx}$ is the consumption by species j of all resources i in habitat x and is described subsequently by Equation (9). Note that in Equation (5), each term was averaged over the previous five timesteps. ϕ_{jx} can be interpreted as the proportion of consumer j's nutrient intake (consumption) across all resource species i that occurred in habitat x as opposed to habitat y.

Net dispersal is then based on the difference between ϕ_{jx} and the proportion of species j's total biomass that is in habitat x rather than y. If, for example, 80% of a species' consumption comes from habitat x ($\phi_{jx} = 0.8$), but 90% of its biomass is in habitat x, then we would see a foraging outflux of 10% of the biomass to habitat y. We use the simplifying assumption that mortality and waste will occur in the habitat where consumption occurs. This may not be true if consumers do not reside in the areas they feed in (see, e.g., Peller et al., 2022 for an exploration of this assumption using different values for a "sheltering" parameter), and in such a situation, we would see that many of the effects on nutrient recycling (i.e., the resource link, sensu Lundberg & Moberg, 2003) would be shifted to the sheltering habitat, while the effects of consumption (i.e., the process link) are likely to remain as they are. Links between mobile predators and their prey that existed in one habitat also existed in the other habitat if both predator and prey were present there as well.

The unit for detritus pools as well as plant depletion zones and habitat nutrient pools was grams of nitrogen per habitat, while the unit for all species was grams of live (wet) biomass per habitat. Conversion between amount of nitrogen and amount of biomass was achieved by assuming that the average nitrogen content of plants, herbivores, and predators was 1%, 3.21%, and 3.68%, respectively (Fagan et al., 2002; Sage, 1982; Scriber & Slansky, 1981). The processes of plant growth and mortality refer to live biomass in Equation (1) and nitrogen content in Equations (2) and (4). See Appendix S1: Section S1.5 for further details.

Equations governing fluxes in habitat x were as follows (and correspondingly for habitat y):

$$\text{environmental nutrient exchange}_x = q \times Vh_x(nh_0 - Nh_x), \tag{6}$$

$$\text{nutrient influx}_{jx} = Vl_{jx} \times k \times (Nh_x - Nl_{jx}), \tag{7}$$

$$\text{plant growth}_{jx} = \frac{g_j \times Vl_{jx} \times Nl_{jx} \times B_{jx}}{[N]_j}, \tag{8}$$

$$\text{consumption}_{ijx} = \frac{a_{ij} B_{jx} B_{ix}}{1 + c_j B_{jx} + \sum_{l \in R_j} a_{lj} h_j B_{lx}}, \tag{9}$$

$$\text{assimilation}_{jx} = e_0 \times \sum_{i \in R_j} \text{consumption}_{ijx}, \tag{10}$$

$$\text{waste}_{jx}(\text{biomass}) = (1 - e_0) \times \sum_{i \in R_j} \text{consumption}_{ijx}, \tag{11}$$

$$\text{waste}_{jx}(\text{nitrogen}) = \sum_{i \in R_j} \left(1 - \frac{e_0 \times [N]_j}{[N]_i}\right) \times [N]_i \times \text{consumption}_{ijx}, \tag{12}$$

$$\text{mortality}_{jx} = m_j \times B_{jx}, \tag{13}$$

$$\text{decomposition}_x = Df_x \times D_x, \tag{14}$$

$$\text{nutrient loss}_x = q \times D_x, \tag{15}$$

$$\text{consumer movement}_{jx} = \left(\phi_{jx} - \frac{B_{jx}}{B_{jx} + B_{jy}}\right) \times (B_{jx} + B_{jy}), \tag{16}$$

where q is the rate of nutrient flux, nh_{0x} the fertility of habitat x, and Vh_x and Nh_x the volume and nutrient concentration respectively of the regional nutrient pool for habitat x. Vl_{jx} is the volume of the resource depletion zone for species j in habitat x, k the rate of nutrient uptake from the habitat nutrient pool to plants' resource depletion zones, Nl_{jx} the concentration of nutrients in depletion zone, and g_j the intrinsic growth rate of species j. Vl_{jx}, Nl_{jx}, and g_j were nonzero for plant species only. $[N]_j$ is the nitrogen content of species j. Dividing by $[N]_j$ (e.g., Equation 8) converts from nitrogen content to living biomass. Equation 12 shows how the nitrogen content of waste excreted from consumption after nitrogen assimilation of resource i by consumer j (i.e., the waste will have a lower nitrogen content than the resource it was derived from). a_{ij} is the per-milligram-of-biomass attack rate of herbivore or predator j on plant or herbivore i. For herbivores, the attack rate depends on herbivore body mass and plant growth rate, while for predators it is determined by the predator–prey body-mass ratio. c_j scales intraspecific interference, and h_{ij} is time spent attacking and handling prey. All of these ATN model parameters (a_{ij}, c_j, and h_{ij}) were first parameterized on a per-capita basis using allometric relationships with body size (as in Jonsson et al., 2018; Schneider et al., 2012) and then rescaled to per unit biomass. e_0 is the biomass assimilation efficiency, which equaled 0.24 for herbivores and 0.67 for predators. The intrinsic mortality rate, m_j, is a constant for basal species and for consumers depends on body mass (Appendix S1: Equations S6 and S7). Df_x is the rate of decomposition in habitat x. Herbivore body masses were assigned by drawing them from a uniform distribution between 0.2 and 1 mg, after which predator body masses could be assigned by multiplying a predator-specific predator–prey body-mass ratio (drawn from a log-normal distribution with a mean of 1.5 and SD of 0.4) by the mean body size of its prey.

Further details on building the local food webs and coupling habitats, parameter values, and the simulations can be found in Appendix S1: Section S1.

Running the model

For the single-habitat simulations each habitat had low, medium, or high fertility (mean value 0.09, 0.9, or 9 mgN/L, respectively) and low, medium, or high diversity (one, four, or eight basal species, respectively) in a fully factorial design, producing nine plant diversity–fertility combinations. These combinations can be conceptualized as encompassing a range of scenarios, for example, a nutrient-poor, species-rich grassland to a fertilized monoculture. Each food web had six herbivore species and six predator species.

For the simulations with two coupled habitats, each of the nine fertility–diversity combinations studied in isolated habitats was coupled to a second habitat of either (1) low diversity and low fertility or (2) low diversity and high fertility. Habitats were coupled by the movement of two herbivore and four predator species. In addition to the mobile species, each habitat had four resident herbivore and two resident predator species. We chose these numbers to give a roughly realistic community within the limits of what we could feasibly simulate. Six herbivores and consumers allowed a community where most consumers could coexist in many scenarios, while still allowing some amount of diversity and food web dynamics. We chose to allow more predators than herbivores to be mobile, because generally predators are larger and more mobile than herbivores, but both trophic levels have some (but not all) species that would forage in adjacent habitats. Overall, we do not expect that these choices would qualitatively affect our results, and indeed we found that a "low-mobility" scenario with fewer mobile consumers gave similar, but weaker, results compared to the "high-mobility" scenario (results not shown).

These combinations produced $3 \times 3 \times 2 \times 2 = 36$ combinations of two habitats differing in fertility, diversity, and consumer movement (in addition to the nine single-habitat combinations). Each combination was replicated 1000 times by drawing parameters from specified distributions and ranges (Appendix S1: Section S1.6). For each replicate, we ran the model for 1000 timesteps (days) to allow the dynamics to stabilize (i.e., pass from any transient state dynamics to stable dynamics).

RESULTS

In isolated webs, fertility and diversity increased all stocks and fluxes (Figures 2 and 3A) and changed the distribution of biomass among trophic levels (Figure 4A). When coupled, the foraging movement of consumers also caused substantial changes to fluxes, stocks, and biomass distributions (Figures 3B, 4B, and 5B). These latter changes especially concerned the low-fertility habitats coupled with high-fertility habitats, whereas the higher-fertility habitats were largely unaffected. For brevity and clarity, we highlight key outcomes in the main text and provide more detail on results in Appendix S1: Section S2.

Stocks and fluxes increase with fertility and diversity in isolated habitats

All stocks and fluxes, as well as species persistence, increased with both fertility and diversity in isolated webs (Figure 3A). All fluxes increased at the same rate, and stocks largely followed the same pattern, but with some variation among specific quantities. Total nutrient stock in depletion zones increased with fertility and, more strongly, with diversity. This latter result is simply because with higher diversity there were more plants, hence more depletion zones, and therefore a higher cumulative stock of nutrients. This can be considered analogous to a complementarity effect with plants having roots at different depths and, thus, more effectively exploiting the regional nutrient pool. Habitat nutrient stocks increased with fertility but actually weakly decreased with diversity because there were more plants depleting nutrients. Biomass and detritus were the stocks that increased most strongly with both diversity and fertility. All species persisted except at low fertility, where persistence was lowest at a combination of low fertility with low diversity.

Mobile consumers flow from high to low fertility or diversity, increasing stocks and fluxes in the receiving habitat

When habitats were coupled, net foraging movement was usually directed from high- to low-fertility habitats (Figure 6). The magnitude of this consumer flux increased with the difference in diversity between habitats but did not change direction. If both habitats had the same fertility, net movement was from high- to low-diversity habitats.

The foraging movement of consumers between habitats increased stocks and fluxes, primarily in low-fertility habitats coupled to high-fertility habitats (a pattern shown by the blue points in the upper panels and green points of the lower panel of Figure 3B). The effect of influx on the low-fertility habitat was strengthened when the high-fertility habitat was also characterized by high

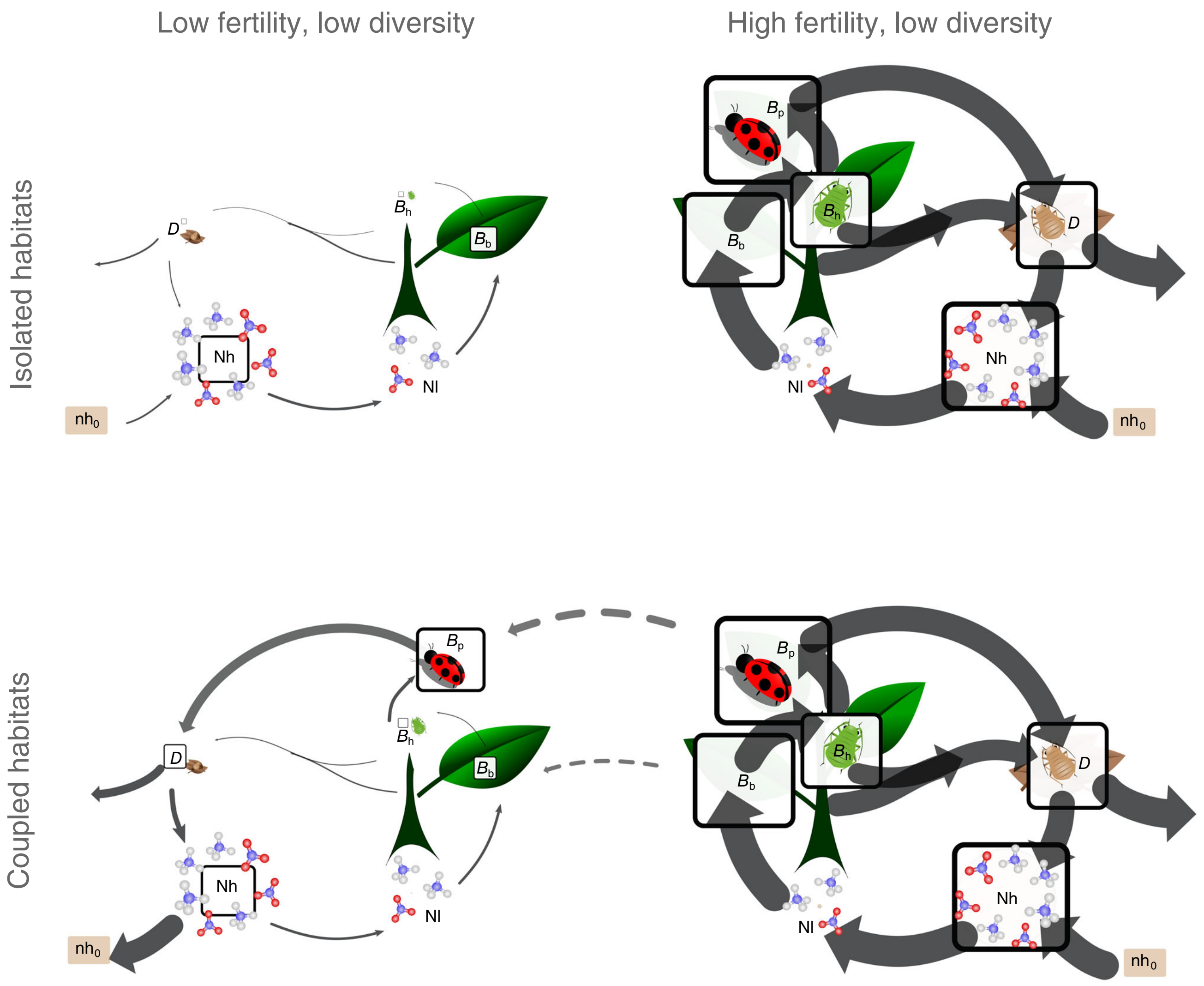

FIGURE 2 An example of how stocks (boxes) and fluxes (arrows) change with soil fertility and with foraging movement. Results are shown for a low-fertility, low-diversity habitat coupled with a high-fertility, low-diversity habitat. Arrows and boxes are scaled relative to the amount of nutrients (converted from biomass for living stocks) present in each stock or flux. We show median values across 1000 simulations, and B_h and B_p here represent the cumulative biomass across six species. Note that in all cases the box for Nl is so small it is not easily visible. For variance and results from other scenarios, see Appendix S1: Figures S3–S23.

diversity (compare solid [high diversity] to dashed [low diversity] green lines of the lower panels of Figure 3B). In contrast, the effect was weakened if the lower-fertility habitat showed high diversity (compare solid to dashed blue lines in the upper panels of Figure 3B).

Biomass stocks, particularly of consumers, also increased as a result of consumer influx (circles in right-hand panels of Figure 3B), as did the in situ biomass influx from plant growth, herbivory, and predation within the same habitat, albeit to a lesser extent (circles in left-hand panels of Figure 3B). This suggests that foraging movement increased stocks in the low-fertility habitat beyond what it could support when isolated. Despite the increase in biomass stocks in the low-fertility habitat, there was no noticeable change in biomass stocks in the higher-fertility habitat, but this may be because the substantial increase in the low-fertility habitat was still within the natural range of variation for the high-fertility habitat (Figure 4 and Appendix S1: Figure S1). Species persistence increased in low-fertility habitats receiving consumer foraging influx from high-fertility habitats (green asterisks in lower, right-hand panel of Figure 3B).

Foraging movement can reverse environmental nutrient exchange

The most notable change in a flux was environmental nutrient exchange (Figure 5). The strength of this flux was driven by the difference between environmental

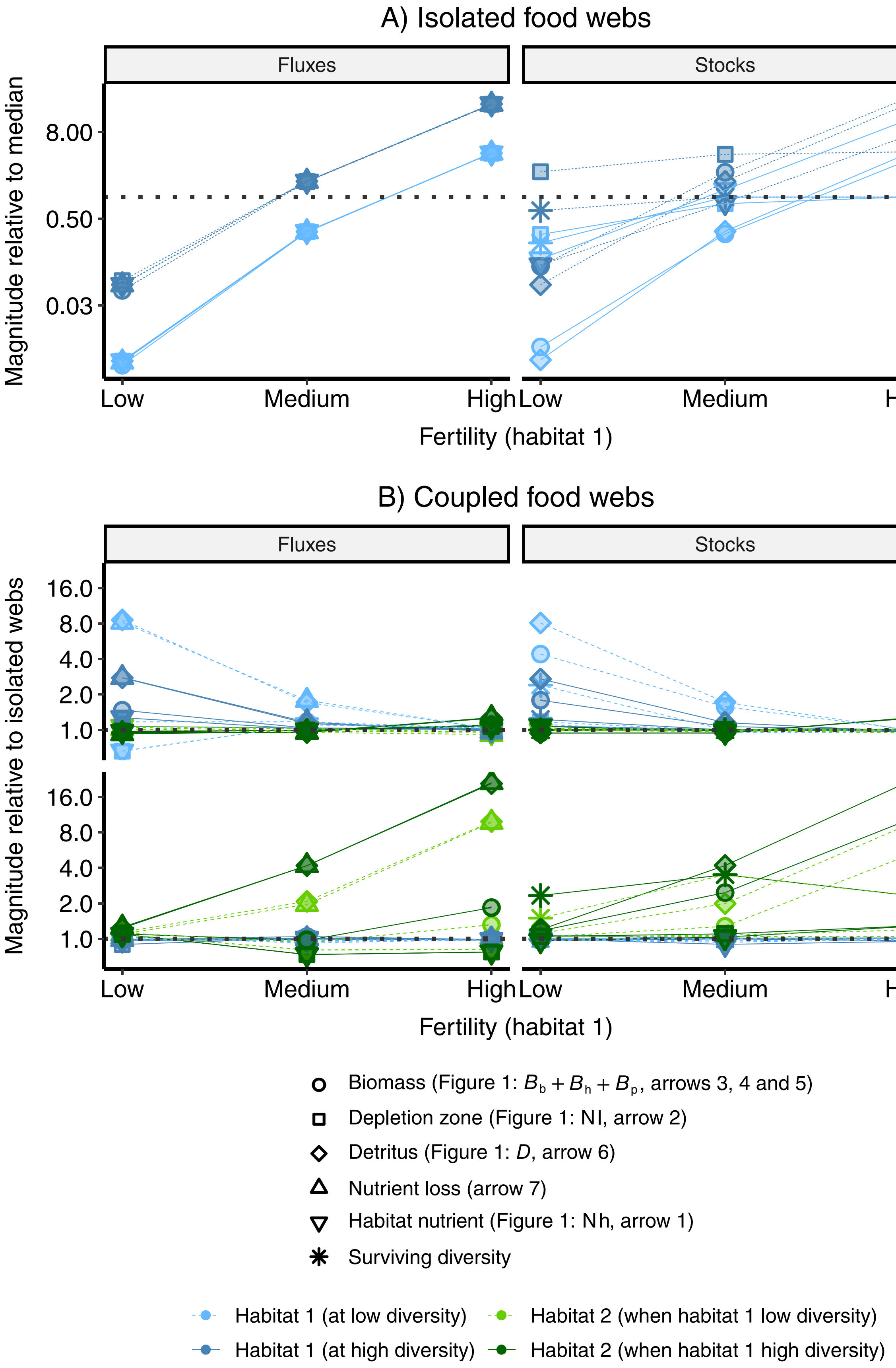

FIGURE 3 Legend on next page.

fertility and the stock of the habitat nutrient pool (Equation 6). When habitats were coupled, the movement of consumers provided a substantial boost to the detritus pool through consumption and mortality (Figure 3). This increased decomposition, which supplemented the habitat nutrient pool, in some cases to the point that the habitat nutrient pool had a higher nutrient concentration than environmental fertility, resulting in a net outflow of nutrients (Figures 2 and 5). This mechanism prevented the buildup of nutrients from the detritus pool from substantially supplementing the total nutrients in the system, especially in low-diversity habitats. In higher-diversity, low-fertility habitats, plants were able to take up some of the extra nutrients such that environmental nutrient exchange remained an influx (Figure 5) and the total nutrients in the system increased (Appendix S1: Table S6).

Diversity, fertility, and foraging movement change biomass distributions

Fertility, diversity, and foraging movement changed the distribution of biomass among the three trophic levels (Figure 4). In isolated food webs, both cumulative and per-species plant biomass increased with fertility and with diversity (green bars in Figure 4A, Appendix S1: Tables S8 and S9). At low fertility and diversity, there were very few predators, and biomass was distributed in a classical pyramid (Figure 4A). As productivity and plant diversity increased, predators took up an increasing proportion of the biomass distribution. The biomass distribution changed considerably for habitats coupled by foraging consumers to higher-fertility habitats and, to a lesser extent, for habitats coupled to higher-diversity habitats (Figure 4B). This change was driven by a substantial increase in predators (red bars), whose biomass in some scenarios outweighed that of plants (green bars). Herbivores (blue bars) also increased in low-fertility habitats coupled to high-fertility habitats relative to uncoupled webs, but, due to heavy predation pressure, the increase was more modest.

DISCUSSION

Our results showcase the wide-ranging impacts that consumer foraging movement can have on functioning in neighboring ecosystems. Coupled ecosystems can differ drastically in levels of functioning compared to equivalent, isolated ecosystems. However, a look at the interconnected functions in the loop of matter transformation reveals that the effects of ecosystem coupling can attenuate in surprising ways. We found that active foraging movement primarily affected stocks and fluxes in the arc spanning from secondary production through to decomposition (Figure 2) but that nutrient loss from the detritus pool and habitat nutrient pool prevented effects from cascading around the rest of the loop. The effects of ecosystem coupling were strongest in low-fertility habitats linked to high-fertility habitats or, for habitats of similar fertility, in low-diversity habitats linked to high-diversity habitats. By examining both stocks and fluxes, we revealed how the interdependence of ecosystem functions could lead to cascades as well as attenuation of effects, with implications for community and ecosystem dynamics in patchy landscapes.

Asymmetric consumer flows have asymmetric impacts

Greater subsidy (nutrient or organism) flows and, hence, greater impacts have been proposed to occur between habitats with a greater difference in productivity (Gravel et al., 2010; Marczak et al., 2007; Rand et al., 2006)—a proposition for which there is both theoretical (Gravel et al., 2010; Oksanen, 1990) and empirical support (Frost et al., 2015; Marczak et al., 2007). In line with this, we

FIGURE 3 Changes in fluxes and stocks as a result of diversity, fertility, and consumer foraging movement. All fluxes are influxes, and in the legend we note the corresponding stocks and fluxes from Figure 1. Values plotted are the median across 1000 replicates. In (A) isolated food webs, we plot the ratio of the magnitude of the flux or stock relative to the median value (across all isolated food webs) for low diversity (lighter, dashed lined) or high diversity (darker, solid lines) and low to high fertility (*x*-axis). A value of 1 (shown by the horizontal dashed line), therefore, indicates that the magnitude for that combination of fertility and diversity is equal to the median; values larger (smaller) than 1 mean that scenario has a higher (lower) value than the median. In (B) coupled food webs, we plot the magnitude of each stock and flux relative to the equivalent isolated food web (i.e., same fertility and diversity). A value of 1 means that the stock or flux is the same magnitude in both coupled and isolated food webs; values larger (smaller) than one mean that the stock or flux has increased (decreased) in magnitude as a result of coupling. Darker and solid lines represent high-diversity habitats, while lighter and dashed lines represent low-diversity habitats. Blue shapes and lines represent Habitat 1, and green Habitat 2. Different stocks and their equivalent fluxes are shown by different shapes. In the upper panels of (B), we show scenarios where Habitat 2 is high fertility, and in the lower panels we show scenarios where Habitat 2 is low fertility. Habitat 2 is always low diversity. Surviving diversity is also shown on the stocks panels. Note that the scale of the *y*-axis in both (A) and (B) is logarithmic. For variance and further detail, see Appendix S1: Figures S3–S19.

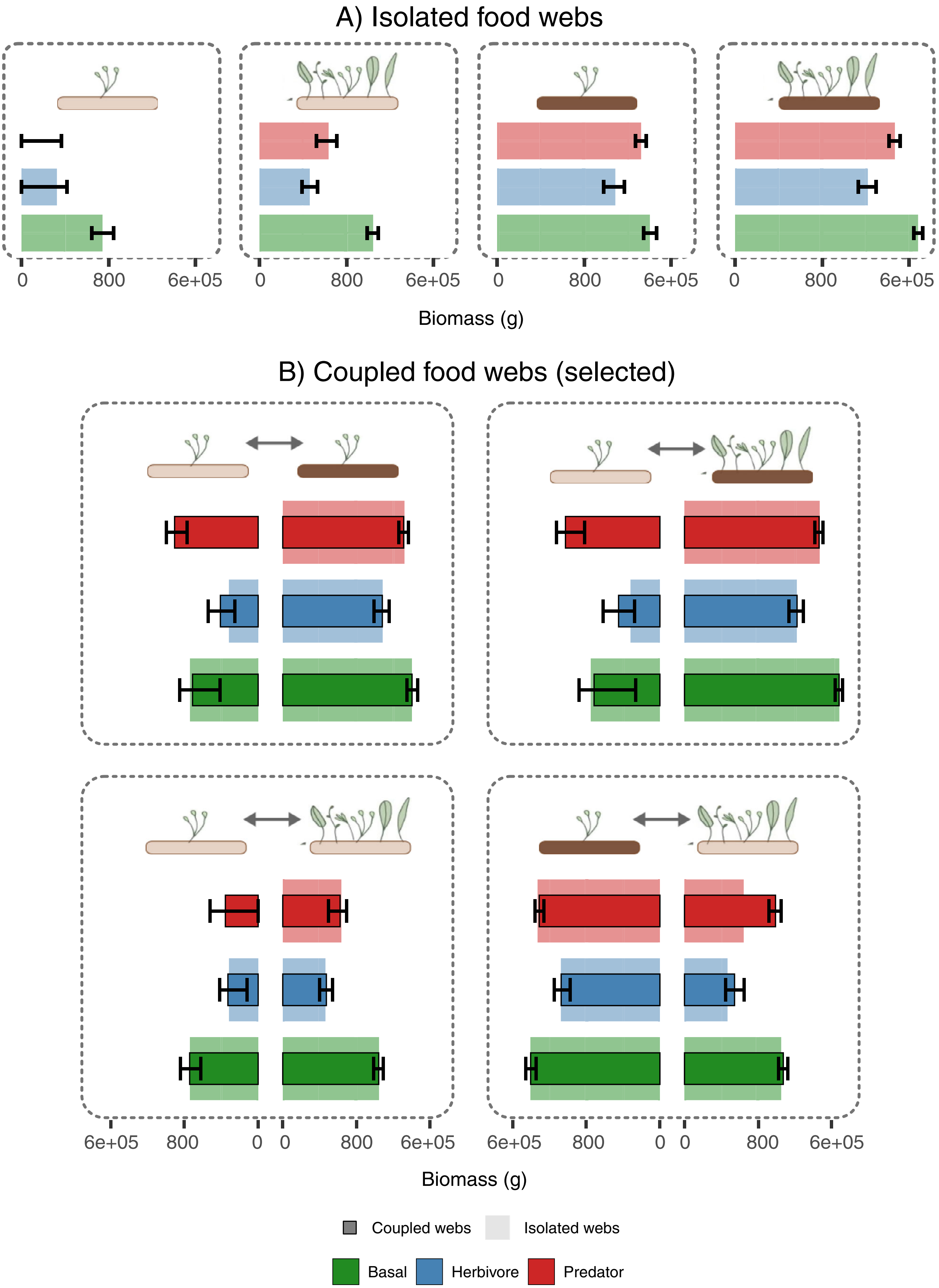

FIGURE 4 Legend on next page.

found that the effects of consumer movement were asymmetric, with large effects on low-fertility habitats and no substantial effects on high-fertility habitats. In our model, consumers foraged optimally, so movement occurred from habitats with a high consumer:resource biomass ratio to those with a lower consumer:resource biomass ratio (Figure 4). Usually, this was directed from high-fertility habitats—where high plant biomass was met by an equally high consumer biomass—to low-fertility habitats—where the lower plant biomass supported fewer herbivores (both biomass and number of species) and, thus, less competition. When habitats were at the same level of fertility but differing in diversity, we saw movement from high-diversity to low-diversity habitats. In this case, consumer movement was driven by predators. The low-diversity habitat had a lower predator:herbivore ratio, so predators moved to the habitat with less competition. Without herbivore influx, this would drive down herbivore population sizes, leading to a lower herbivore:plant ratio. As a result, we observed herbivore influx, even though the herbivore stock in the receiving habitat did not change.

Nonetheless, in real landscapes, greater productivity contrasts may not always predict greater fluxes. When consumer movement between habitats is driven by optimal foraging behavior, consumers do not simply “spill over” from high- to low-consumer-density habitats; if a neighboring ecosystem lacks important resources, then optimally foraging consumers will fail to move into it (Charnov & Orians, 2006; Wiens, 1976; Williams et al., 2013). In our results, this was demonstrated by the habitat with intermediate fertility receiving a larger influx of consumers from the high-fertility habitat than did the low-fertility habitat (Figure 6). This also demonstrates the fundamental difference between active animal movement, such as optimal foraging, and passive movement, such as diffusion. Although the outcomes from the two can be similar, resulting in source–sink-type patterns of animal movement (Amarasekare, 2004; Pulliam, 1988), the magnitude of the flows follow different rules. Passive movement will tend to increase with increasing productivity differences, as net consumer flux is typically proportional to the difference in a consumer’s population size between two habitats (Gounand et al., 2014; Gravel et al., 2010). Movement due to optimal foraging, on the other hand, is a product of not just consumer but also resource biomass (Fretwell, 1972; Fretwell & Lucas, 1969; Williams et al., 2013), and therefore consumer flux does not always increase with increasing productivity contrasts, as shown here. Our results therefore add to the evidence that to predict the magnitude of animal movement and, hence, its impact in metaecosystems, we need to account for a greater variety of types of animal movement and behavior (García-Callejas et al., 2019; Gounand et al., 2018; Peller et al., 2022).

Foraging movement shifts biomass patterns

We found contrasting effects on ecosystem functioning of nutrients derived from local fertility versus from increased decomposition of incoming consumers. An increase in local fertility increased all ecosystem functions relatively evenly around the loop of matter transformation (Figure 2). Foraging, in contrast, shifted the balance of stocks and fluxes by primarily boosting fluxes and stocks around only half the loop, from herbivore biomass to decomposition. Consumer flow between neighboring habitats increased predator biomass more than herbivore biomass. Looking only at biomass stocks, we might conclude that this was because there were more mobile predator species (four) than mobile herbivore species (two) in our simulations. However, examining biomass fluxes revealed that predator biomass increased from both inward foraging movement and increased in situ tertiary productivity as a result of higher prey availability (Figure 2, Appendix S1: Figures S1 and S2). Thus, even if predators were not mobile, they would still increase due to herbivore influx.

Relative productivity at different trophic levels became increasingly top-heavy as consumer influx supported more consumer growth, but because nutrient loss from the detrital and habitat nutrient pools prevented the influx of nutrients from reaching plants, we saw very different biomass distributions across trophic levels in coupled compared

FIGURE 4 Biomass pyramids in (A) isolated food webs and (B) selected coupled food webs. Icons at top of each panel show whether that food web is in a high-fertility (dark brown) or low-fertility (light brown) habitat and whether it is high diversity (many plants) or low diversity (one plant). Bars show the median biomass per habitat for plants (green), herbivores (blue) and predators (red) across all replicates of that scenario. In the interest of readability, in (B) we only show the four scenarios where coupling by foraging movement of consumers caused the greatest difference in biomass distribution (other scenarios showed little change relative to equivalent isolated food webs, see Appendix S1: Figure S1). Narrower, darker bars show the biomass distribution in the coupled food webs, while the wider, faded bars they overlie show the equivalent isolated food web, for reference purposes (the background bars are therefore the same as for the equivalent scenario in [A]). Bars show median results across 1000 replicates, with error bars showing 25th and 75th quantiles. For variance and further scenarios, see Appendix S1: Figures S3–S5.

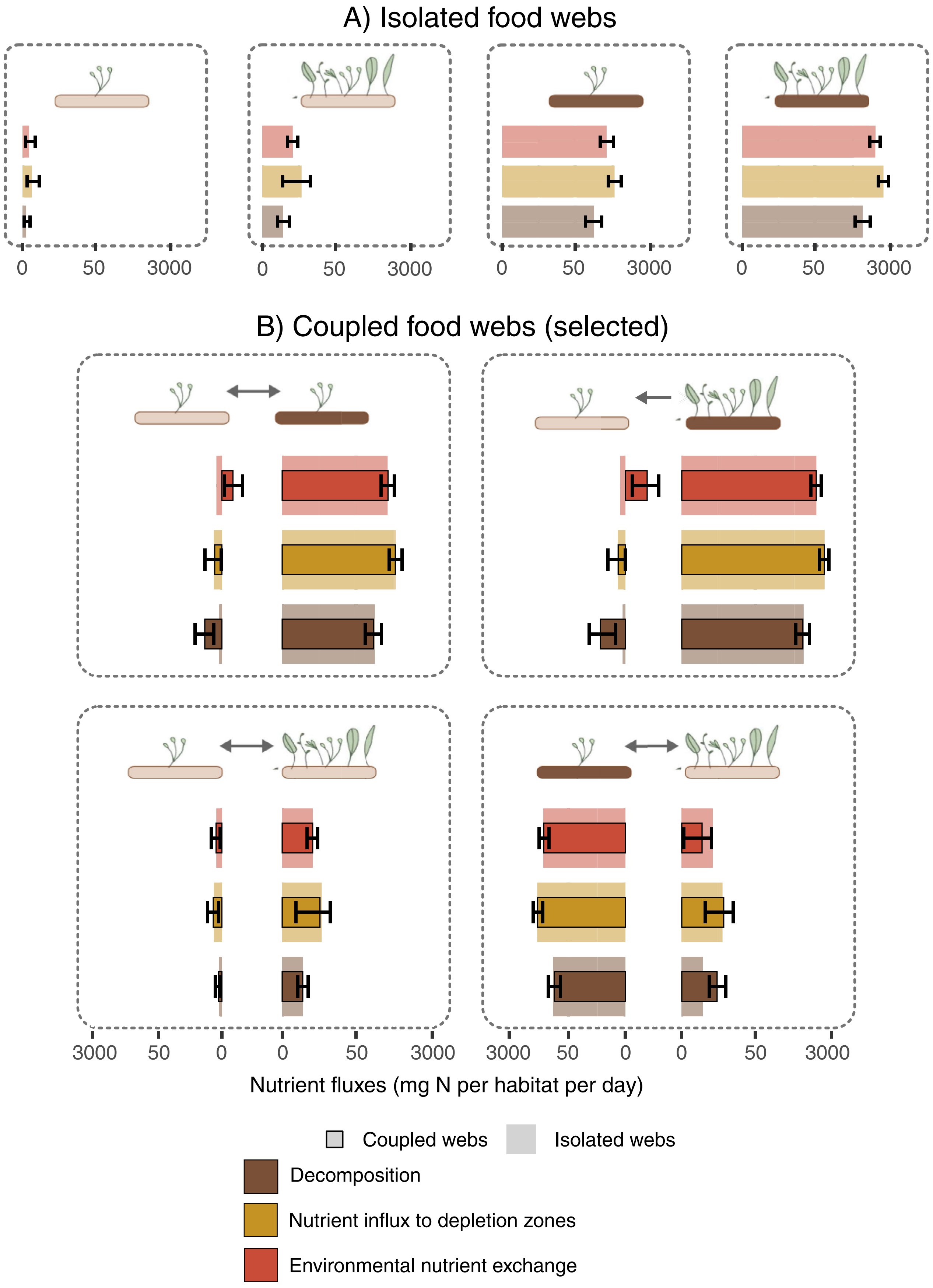

FIGURE 5 Legend on next page.

with isolated food webs. Theoretical predictions state that classic pyramids or stacks, such as we see in isolated, low-fertility habitats, should dominate in nature (Trebilco et al., 2013). Such biomass distributions should occur unless the efficiency of energy transfer between trophic levels and/or consumer–resource body-mass ratio is large (Jonsson, 2017). Yet, with consumer foraging movements, we see a shift toward top-heavy distributions, consistent with previous work on systems with energy subsidies or mobile consumers (McCauley et al., 2018; Trebilco et al., 2013, 2016). Thus overall, we see a clear signature of foraging movements on biomass distributions across spatially structured landscapes.

The matter transformation loop links it all

In ecosystems, matter constantly cycles in the loop of matter transformation; inorganic nutrients are absorbed from the soil by plants, then transferred by consumption to increasingly higher trophic levels of the food web, and finally returned via decomposition and mineralization of dead biomass and animal waste back to the soil (Gounand et al., 2020). In this loop of interconnected ecosystem functions, the effects of spatial subsidies to any of the various biomass or nutrient compartments (Figure 1) can either be propagated to neighboring compartments and onward or fade out. We found examples of both scenarios. For example, we found that consumer influx resulted in larger consumer biomass stocks—an effect that propagated, via a larger detrital pool, to a larger decomposition flux (Figure 2). However, this had little effect on the habitat nutrient pool. In our model, nutrient uptake from the environment was driven by the difference in nutrient levels between the environment (nh_{0x}) and the habitat nutrient pool (Nh_x) (Equation 6). This meant that no matter how much nutrient was added to the system through decomposition of foraging consumers, the nutrient concentration in the habitat nutrient pool never increased above the level of environmental fertility, so the effect of the allochthonous resources attenuated at this point (Figure 2 and Equations 3, 6, and 14). Therefore, the cascading effect of consumer influx was attenuated and had little effect on the plants' nutrient pools, productivity, and biomass. In high-diversity habitats, however, the influx of nutrients did have a weakly positive effect on plant biomass. More plant species pulling nutrients from the habitat nutrient pool kept its nutrient concentration low enough that it still took up nutrients from the environment, leading to a boost in total nutrients in the system (Appendix S1: Table S6) and in plant biomass.

The attenuation hinges on the dynamics assumed for the nutrient loop, in particular on the passive diffusion determining the nutrient exchange between the habitat nutrient pool and the external environment. In other metaecosystem models, where the external nutrient input is modeled as a constant influx rate, increased detritus flows would not be attenuated at the habitat nutrient pool but would instead substantially boost primary productivity (Gravel et al., 2010; S. Leroux & Loreau, 2010). Thus, from the viewpoint of ecological theory, the attenuation effect we observed here was unexpected. Similarly, from a theoretical viewpoint, we could have expected to see an increase in plant biomass with consumer influx, as the resulting larger predator population intensifies top-down control, indirectly benefiting the plant population in a tri-trophic food web like ours (Leroux & Loreau, 2008; Oksanen et al., 1981; Polis et al., 1997). These theoretically predicted effects were either absent or of negligible magnitude in our results. We can interpret these results in light of the different kinds of mobile links we have in our system. Of the three types described by Lundberg & Moberg, 2003—resource, genetic, and process—animal foraging in our system provides both resource and process links. Mobile consumers die and produce waste in the habitat they move to (resource link) and increase grazing and predation (process link). We had both

FIGURE 5 Soil fluxes changed magnitude and, in some cases, direction with diversity, fertility, and consumer foraging movement. Here we show decomposition (dark brown, corresponding to arrow 7 in Figure 1), nutrient influx to depletion zones (i.e., nutrients taken up by plants, arrow 2 from Figure 1, yellow), and environmental nutrient exchange (red, arrow 1 in Figure 1) for different combinations of diversity, fertility, and consumer foraging movement. Negative values indicate that the flux has switched direction, that is, in the case of environmental nutrient exchange has become an outflux rather than an influx. Note that, while decomposition and environmental nutrient exchange change substantially in some scenarios, nutrient influx rarely changes, because it is buffered by the habitat nutrient pool. As in Figure 4, the icons at the top of each panel indicate whether the food web was in a low-fertility (light brown) or high-fertility (dark brown) habitat and low-diversity (one plant species) or high-diversity (many plant species) habitat. We first show (A) isolated food webs. In (B) coupled food webs, the fluxes for the coupled food webs are shown by the narrower, more saturated bars. The wider, faded bars underlying the narrow bars indicate the fluxes in the equivalent, isolated food web, for reference purposes (the wider, faded bars are therefore the same as the equivalent diversity and fertility combination in [A] isolated food webs). For readability, we only show the four coupled scenarios where there was a substantial change in fluxes as a result of foraging movement. Other scenarios can be seen in Appendix S1: Figures S2, S9, S10, and S20. Bars show median results across 1000 replicates, with error bars showing 25th and 75th quantiles.

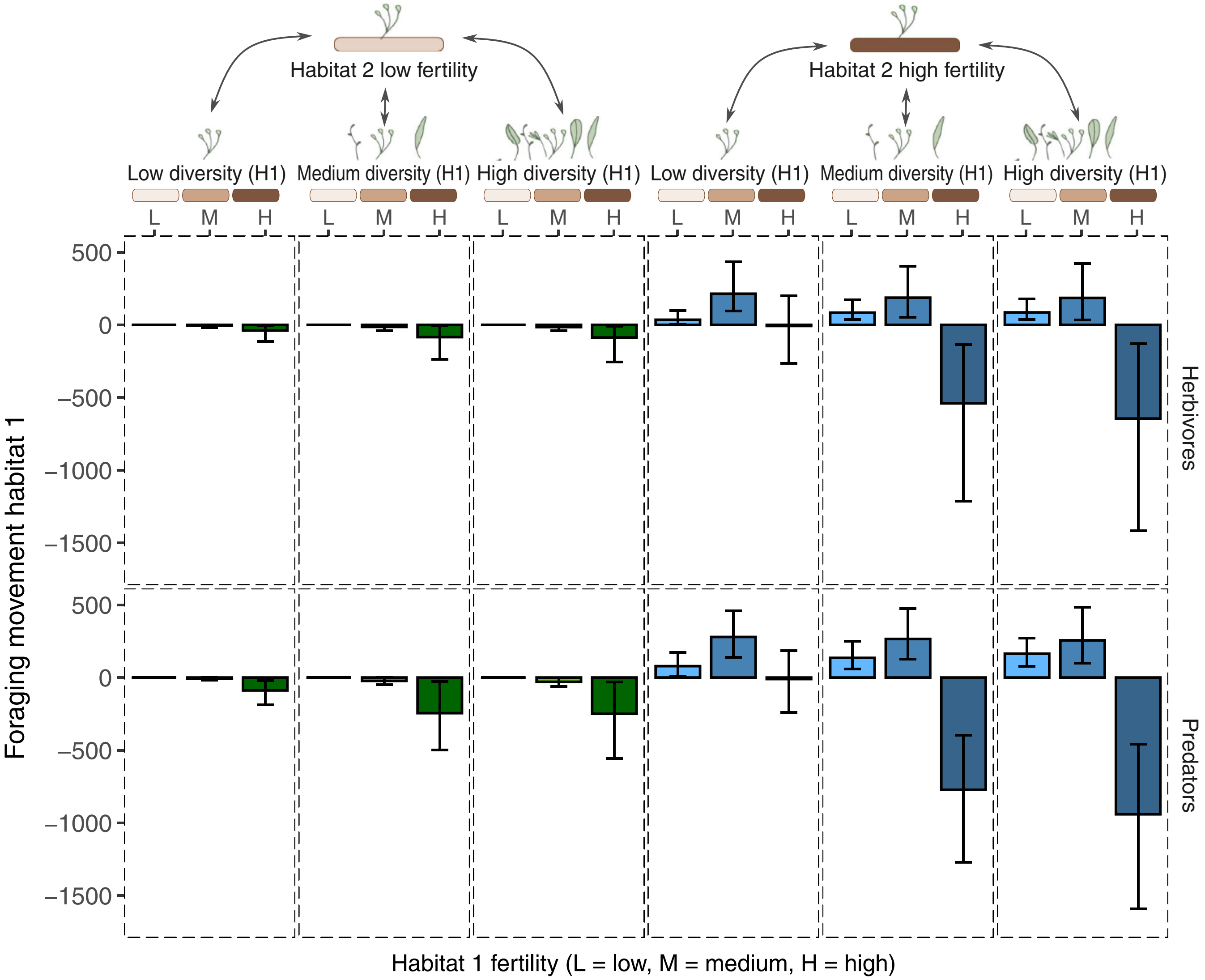

FIGURE 6 Net foraging movement of herbivores (top row) and predators (bottom row) into (positive values) or out of (negative values) Habitat 1. Green bars show movement out of Habitat 1 (all negative values) when Habitat 2 is low fertility. Blue bars show movement in (positive values) or out (negative value) of Habitat 1 when Habitat 2 is high fertility. Habitat 2 is always low diversity. Bars show median results across 1000 replicates, with error bars showing 25th and 75th quantiles. For further detail, see Appendix S1: Figures S22 and S23.

mobile herbivores and predators, so increased top-down control from a larger predator population (process link) was balanced by herbivore influx, maintaining the herbivore population (resource link) and herbivory pressure (process link). If only predators were mobile, we might have seen the process link indirectly facilitating the effect propagation of the resource link; if top-down control increased plant biomass and therefore the demand for nutrients from the regional nutrient pool, it might have prevented the attenuation effect we observed.

Although at first glance unexpected, the observed attenuation effects can thus be explained through the interplay of stocks and fluxes in the matter transformation loop. Furthermore, the attenuation of effects that we see for consumer influx, but not for fertility, echoes what occurs in the real world (Allen & Wesner, 2016). The strong direct effects that the influx of predators, or of their prey, have on local predator numbers is on par with the direct effect that nutrient subsidies have on primary producers—but the top-down cascading effects are weak and attenuate quickly, whereas the bottom-up effects of nutrient subsidies do not (Allen & Wesner, 2016).

Animal movement behavior has implications for patchy landscapes

The consumer movement patterns observed in our simulations have direct implications for community and ecosystem dynamics in patchy agricultural landscapes interspersed by remnants of natural habitat. Consumer movement from high-fertility croplands to diverse natural habitats can result in high predation pressures (Andrén et al., 1985; Blitzer et al., 2012; Rand & Louda, 2006) and to overexploitation (Holt & Hochberg, 2001; Oksanen, 1990; Polis et al., 1997). In this context, our results contrast with previous theoretical research (Guzman et al., 2019; Holt & Hochberg, 2001; Polis et al., 1997; Schneider, 2001 but see Plitzko & Drossel, 2015) and empirical research (Blitzer et al., 2012; Suarez et al., 1998), which suggests that mobile consumers are detrimental to the survival of their resources due to a high risk of strong apparent competition between prey in consumer-coupled habitats (Callaway & Hastings, 2002; Frost et al., 2016; Peller et al., 2022; Polis et al., 1997) and of direct overexploitation (Oksanen, 1990; Oksanen et al., 1992; Polis et al., 1997). In stark contrast to this prediction, we found that the effect of consumer influx was either positive or neutral for overall species persistence of both plants and herbivores. Two of our modeling choices are likely to be key to this discrepancy: higher vertical and horizontal trophic complexity compared to most previous studies (e.g., Holt & Hochberg, 2001; Oksanen, 1990; Peller et al., 2022; Schneider, 2001) and animal movement driven by optimal foraging. In terms of higher trophic complexity, our inclusion of three trophic levels, as compared to two in many other studies (e.g., Callaway & Hastings, 2002; Holt & Hochberg, 2001; Peller et al., 2022; Polis et al., 1997; Schneider, 2001), may provide top-down control of herbivores and positive indirect effects between plants and predators. Furthermore, multiple co-occurring plant species can together better tolerate the influx of herbivores. This was shown by the high-diversity scenarios, where herbivory pressure was distributed across several plant species and where plants had a greater aggregate nutrient uptake efficiency, resulting in augmented primary productivity.

In terms of animal movement, the choice of using optimal foraging to drive active animal redistribution may be of even greater importance, as it provides a rescue mechanism for the resources. As resource levels become low in one habitat, consumer movement into that habitat will decrease (Wiens, 1976), thus promoting consumer–resource coexistence (Křivan, 1996). This kind of rescue mechanism is missing from the passive movement models, such as passive diffusion (Guzman et al., 2019; T. Oksanen, 1990; Polis et al., 1997; M. F. Schneider, 2001) and/or long-distance, cross-matrix dispersal, which have been more commonly used in spatial food web and metaecosystem research (Gounand et al., 2018; Guzman et al., 2019; Massol et al., 2011).

The type and scale of animal movement involved in linking ecosystems is also important in driving local nutrient dynamics. Dispersal for settlement often involves long-distance movement between similar habitats. In contrast, large cross-ecosystem subsidies occur when animals move from one habitat type to another, during their life cycle or daily foraging. Examples include the emergence of aquatic insects (Gratton et al., 2008) and anadromous fish coming up-river to spawn (Gende et al., 2002), which in both cases constitute both prey and detritus subsidy flows to terrestrial ecosystems (Gende et al., 2002; Gratton et al., 2008). Examples of large nutrient flows, via consumer waste, have also been documented when consumers move daily between a foraging habitat and a sheltering habitat (Abbas et al., 2012; Maron et al., 2006; Stukel et al., 2013; Subalusky et al., 2015). Such large subsidies likely affect local nutrient dynamics more than nutrient flows from long-distance dispersal (Gounand et al., 2018). Animal foraging movement, as we model it, sits somewhere in between these extremes. On the one hand, our two habitats are of similar type, with overlapping species composition and with both habitats being able to provide food and shelter for the consumers. On the other hand, the two habitats can differ substantially in quality, producing a unidirectional net flux of consumers of a magnitude, which is large relative to the biomass stocks in the receiving habitat.

Whether an animal feeds and shelters in the same or in different habitats can have great implications for nutrient flows and consumer–resource dynamics (Maron et al., 2006; Peller et al., 2022; Stukel et al., 2013). When animals have strong preferences for feeding and sheltering in different habitats, large amounts of nutrients can be transferred from the feeding to the sheltering habitat (Abbas et al., 2012; Stukel et al., 2013; Subalusky et al., 2015), resulting in spatial cascades (García-Callejas et al., 2019; Maron et al., 2006), stronger apparent competition, and lost coexistence (Peller et al., 2022). When animals prefer one habitat over another for both feeding and sheltering, there is no nutrient transfer and no spatial cascades (Peller et al., 2022). Consumer behavior in our model is most similar to the latter case, as waste and dead biomass are assigned to the habitat in which the consumer is foraging. But nutrient flow behavior is more similar to the former case, as our model produces unidirectional net consumer and, hence, nutrient flux from a donor habitat to a receiver habitat. In line with this, we do see a spatial cascade, with a stronger top-down control in the receiving habitat. Yet, in our case, this cascade is due to the direct effect of consumer influx rather than to the nutrients that they bring with them, due to the attenuation effect in the nutrient dynamics.

All in all, our results serve to highlight how changes in ecosystem functioning can be understood by examining the interplay of stocks and fluxes in driving the matter transformation loop and how different mechanisms driving movement and nutrient dynamics can lead to different outcomes (Gounand et al., 2018, 2020; Peller et al., 2022; Zou et al., 2016). The discrepancy in outcomes highlights the need to understand not only nutrient flow within and between food webs but also the mechanisms whereby nutrients are recycled and returned to living biomass.

CONCLUSIONS

Understanding ecosystem dynamics in current, fragmented landscapes requires that we lift our gaze to the patchwork of habitats and to the flow of organisms and matter between them. In this paper, we have elucidated some of the ways that animal foraging movement between adjacent ecosystems can affect ecosystem functioning. By combining an allometric dynamic food web model with a model for plant–nutrient dynamics, we found that the fertility and plant species richness of the local ecosystems affected the direction, magnitude, and effect of consumer foraging movement. Furthermore, by explicitly modeling the dynamics of the entire matter transformation loop, we traced how the trophic interactions determined the effect of consumer influx on food web biomass stocks and how these effects were propagated or attenuated through the matter transformation loop to other ecosystem functions. Where our study lacks in realism is in our focus on only two adjacent and stable habitats; real landscapes consist of a patchwork of habitats, all of which exchange organisms and materials on multiple spatiotemporal scales (Gounand et al., 2018; Guzman et al., 2019; Rand et al., 2006). Nonetheless, by examining patterns across a small subset of the landscape, we offer a start for the spatiotemporal explorations needed to understand ecosystem functioning in a human-dominated world.

AUTHOR CONTRIBUTIONS

All authors conceived the project. Kate L. Wootton and Alva Curtsdotter led the writing of the manuscript. Kate L. Wootton and Tomas Jonsson led the development of the modeling framework, with support from Alva Curtsdotter. Kate L. Wootton led the analysis and presentation of results. All authors contributed to the development of ideas, writing, and editing of the manuscript.

ACKNOWLEDGMENTS

We thank Kevin McCann, David Gilljam, and Yuval Zelnick for helpful comments on an earlier version of this manuscript. Kate L. Wootton, Tomas Roslin, and Tomas Jonsson were funded by Vetenskapsrådet (VR) Grant 2016-06872, and Tomas Jonsson was also partially funded by VR Grant 2018-05523. Tomas Roslin was funded by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (Grant Agreement 856506; ERC-synergy project LIFEPLAN). Open access publishing facilitated by University of Canterbury, as part of the Wiley - University of Canterbury agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Wootton et al., 2023a) are available in Dryad at https://doi.org/10.5061/dryad.59zw3r2cs. Code (Wootton et al., 2023b) is available in Zenodo at https://doi.org/10.5281/zenodo.7796629.

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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: Wootton, Kate L., Alva Curtsdotter, Riccardo Bommarco, Tomas Roslin, and Tomas Jonsson. 2023. "Food Webs Coupled in Space: Consumer Foraging Movement Affects Both Stocks and Fluxes." *Ecology* 104(8): e4101. https://doi.org/10.1002/ecy.4101