

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

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Abstract

The exchange of material and individuals between neighbouring food webs is ubiquitous, but theory remains scarce for how such spatial flows affect ecosystem functioning. Here, we combine dynamic food web models with models for nutrient recycling to explore how animal foraging movement, between habitats of contrasting fertility and plant diversity, affects species persistence as well as the stocks and fluxes of biomass, detritus, and nutrients. We found that the net flow of consumers went from the habitat of higher fertility or diversity to the habitat with lower fertility or diversity, boosting ecosystem functioning in the receiving habitat. By explicitly modelling stocks and interconnecting fluxes we could replicate empirically observed effects of spatial subsidies, such as biomass distribution shifts and effect attenuation, and elucidate the underlying mechanisms. Our results demonstrate how foraging movement can drastically alter local functioning. Overall, our approach offers a start toward understanding ecosystem function in human-dominated landscapes.

1 Introduction

Spatial heterogeneity is known to affect ecological systems (Gounand et al. 2018; Polis et al. 1997; Wiens 2002). Globally, human land-use conversion has led to habitat fragmentation and patchy forestry and agricultural landscapes in which remnant biodiversity-rich habitats border intensively managed habitats (Fahrig et al. 2011; Ramankutty et al. 2018; Watson et al. 2005). Thus, adjacent habitats will frequently differ sharply in fertility (i.e. nutrient availability) as well as biodiversity (Fahrig et al. 2011; Mendenhall et al. 2016). Although it is well understood that organisms and abiotic resources are frequently exchanged between habitat patches (Loreau et al. 2003; Polis et al. 1997; Rand et al. 2006), there is a lack of theory for how spatial flows between adjacent ecosystems affect local ecosystem functions (Gounand et al. 2018; Massol et al. 2011).

In response to long-standing calls, food-web ecology is increasingly being applied to improve understanding of biodiversity-ecosystem functioning relationships (Cardinale et al. 2012; Duffy 2002; Hines et al. 2015), something that is particularly relevant for understanding ecosystem functions driven by trophic interactions such as consumption (Hines et al. 2019). Most approaches have been theoretical, taking advantage of dynamic food-web models explicitly describing the biotic interactions that drive several ecosystem functions and processes, such as biomass stocks, productivity, and consumption, at multiple trophic levels. This has improved our understanding of how ecosystem functioning is affected by food-web structure, animal and plant diversity, and feeding niche complementarity (Allhoff and Drossel 2016; Poisot et al. 2013; F. D. Schneider et al. 2016; Wang and Brose 2018). However, the effects of spatial flows between food webs remain to be taken into account.

The spatial flow of organisms or abiotic resources between habitats can have profound effects on their stability and functioning (Loreau et al. 2003; Lovett et al. 2005; Polis et al. 1997). For example, meta-community ecology has shown that spatial flows of organisms can fundamentally change the relationship between complexity or nutrient enrichment and food web stability (Guichard 2017; McCann et al. 2020). Metaecosystem research has added yet another layer, by adding nutrient dynamics to simple food chains (Loreau et al. 2003) or food web modules (Massol et al. 2011), allowing us to examine how nutrient flows within and between habitats affect their functioning. Nonetheless, the focus has mainly been on stability and co-existence rather than on ecosystem functions (Massol et al. 2011). Furthermore, in both fields, the spatial flow of organisms is typically conceptualized as dispersal (*sensu* the tendency of organisms to settle away from their birthplace) occurring between distant but similar habitats (Gounand et al. 2018; Guzman et al. 2019; Massol et al. 2011). Therefore, theoretical predictions remain scarce for how other types of organ-

ism movement affect ecosystem functioning in typical situations in nature, including the effects of ubiquitous animal foraging movements across nearby but dissimilar habitats (Gounand et al. 2018; Rand et al. 2006).

Many ecosystem functions are intimately linked to the loop of matter transformation - the process of inorganic compounds being turned into living biomass, transferred through the food chains, and ultimately recycled through decomposition and mineralization back into inorganic compounds (Gounand et al. 2020). This loop ties together stocks of living biomass through fluxes such as primary productivity and predation. It also ties together stocks of detritus (dead biomass) with stocks of inorganic nutrients through fluxes of decomposition, etc. (for a visual illustration, see Fig. 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. An inescapable conclusion resulting from this view is that ecosystem functions ought to be studied through a comprehensive approach that considers the whole loop of matter transformation and is explicit about the processes that drive functioning (Gounand et al. 2020; Hines et al. 2019).

We propose that such a process-explicit and comprehensive approach can be achieved by combining spatially explicit, dynamic food-web models with models for nutrient recycling. Here, we adopt this approach to explore how neighbouring ecosystems, linked through animal foraging movements, affect each other's stocks and flows. 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 a suite of ecosystem functions and processes in the matter transformation loop. For tractability, we limit our study to assess impacts of cross-habitat movements of animals but not direct nutrient movements. To establish a baseline for comparison, we first determine how (i) fertility and (ii) 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.

To achieve a versatile understanding of how spatial coupling affects multiple food web characteristics and processes, we examine responses from species persistence, through the standing stock of living biomass at each trophic level, the biomass fluxes between trophic levels (primary, secondary and tertiary production), the standing stock and flux of detritus, to the size of soil nutrient pools and fluxes. For aggregate fluxes, we assess how the relative contribution by the constituting fluxes are affected; for instance how the relative contribution to plant biomass loss emanates from consumer-inflicted versus intrinsic mortality.

Our findings illustrate how exchange of individuals and, hence, matter among neighbouring food webs can fundamentally alter dynamics in spatially structured landscapes. We find that when adjacent ecosystems are coupled through animal foraging movement, there is a net flow of consumers from the habitat with higher

fertility to the habitat with lower fertility or, when habitats are of the same fertility, from the habitat with higher diversity to that with lower diversity. This flow generally boosts ecosystem functioning in the receiving habitat, but without inflicting adverse effects on the donor habitat. As a result, the total species richness, biomass, nutrient stocks and fluxes in low-productive food webs tend to be substantially larger when coupled to high-productive neighbouring webs than when isolated, implying that local food web functioning will be propped up in landscapes where low-productive habitats intersperse with more high-productive sources.

2 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 Thebault and Loreau (2005, hereafter TL model), and the Allometric Trophic Network model (Berlow et al. 2009; Otto et al. 2007; F. D. Schneider et al. 2012, hereafter 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. Our hybrid TL-ATN model describes both food web and nutrient dynamics (Fig. 1). We first focus on food webs in isolated habitats, exploring the effect of fertility (nr_0) and basal species diversity. We then extended this model to two habitats (Fig. 1B), where each habitat had its own regional nutrient pool and detritus pool. The habitats were coupled through the movements of optimally foraging consumers.

The model

For all scenarios, we modeled the dynamics for the following stocks (Fig. 1): each species' biomass, B_j (Eq. 1), the nutrient concentration in each plant species' resource depletion zone, Nl_j (Eq. 2), the nutrient concentration in the regional nutrient pool of habitat x , Nr_x (Eq. 3), and the nutrient concentration in the detritus pool, D_x (Eq. 4). The dynamics of these stocks depended on the fluxes between them: environmental nutrient exchange (Eq. 5), nutrient influx to each plant's depletion zone (Eq. 6), plant growth/primary productivity (Eq. 7), consumption (both herbivory and predation, Eq. 8, which was then assimilated to secondary and tertiary productivity, Eq. 9), waste from consumption (Eqs. 10 and 11), mortality (Eq. 12), decomposition (Eq. 13) and nutrient loss (Eq. 14) and consumer foraging movement (Eq. 15).

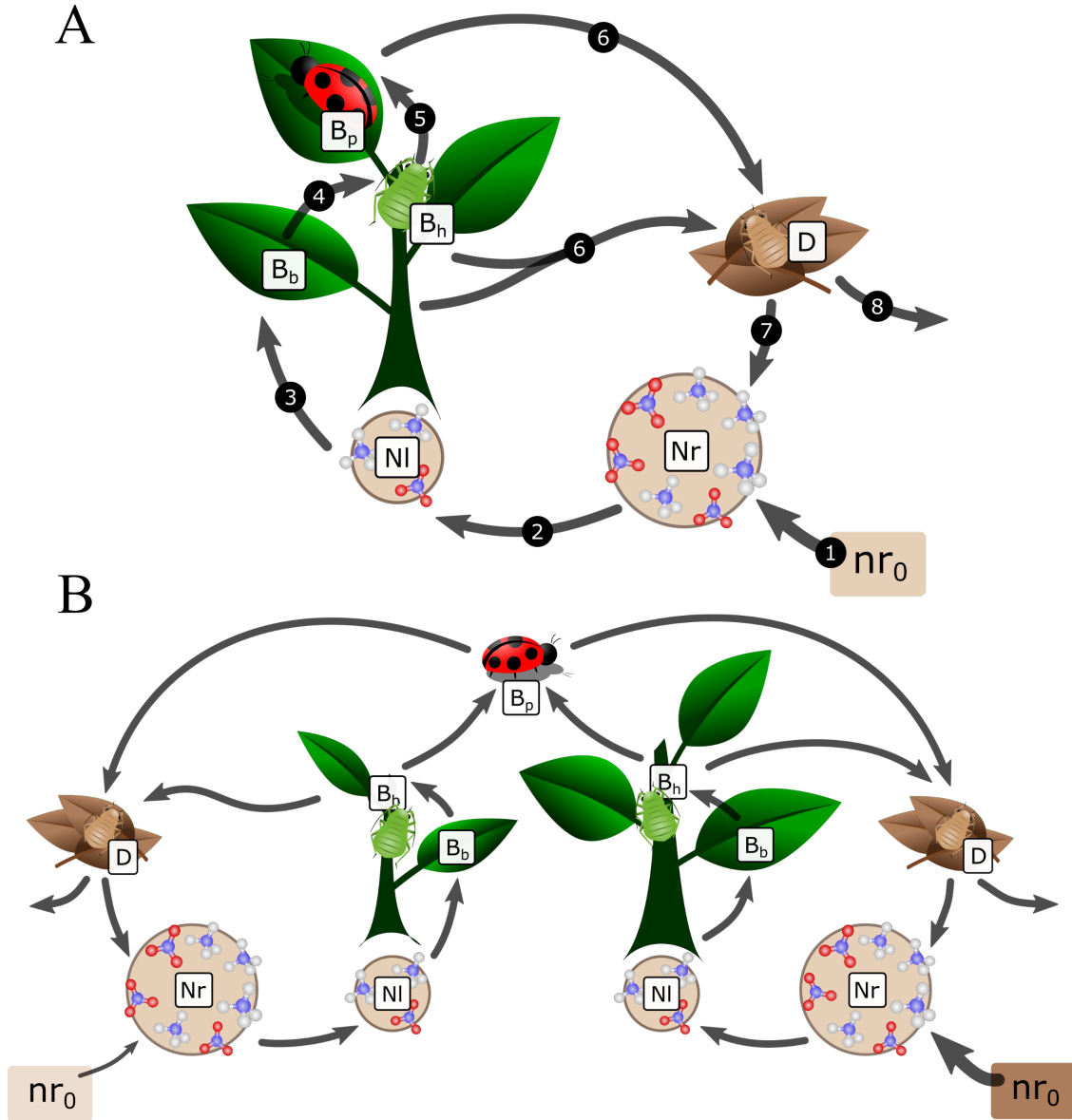


Figure 1: Representations of the model in (A) a single habitat, and (B) two habitats of differing fertility (nr_0) coupled by consumer foraging movement. The habitat on the right has higher fertility (as shown by the darker saturation of nr_0), while the habitat on the left has low fertility. Letters in rectangular boxes represent stocks: nutrient concentration in the regional pool (Nr), nutrient concentration in the 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 (each with its own depletion zone), herbivores and predators, but only one regional 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). Mortality of plants, herbivores, and predators contribute 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 replenishes the regional nutrient pool (7. decomposition). The regional 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 which is replenished by nutrients from the regional 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 regional pool is indirect, and its strength mediated by the rate of nutrient transport from the regional pool to the plant depletion zones. Mobile consumers, finally, link ecosystem functions in neighbouring 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. Furthermore, although not illustrated here, if habitats are coupled, each habitat hosts one or more mobile herbivore as well as several 'local' non-mobile predators (in addition to the 'local' non-mobile herbivore and mobile predator included here).

Stocks were modeled as follows:

$$\begin{aligned} \frac{dB_j}{dt} = & \text{plant growth} + \sum_i \text{assimilation}(ji) - \sum_l \text{consumption}(jl) - \text{mortality} \\ & + \text{consumer movement} \end{aligned} \quad (1)$$

$$Vl_j \frac{dNl_j}{dt} = \text{nutrient influx} - \text{plant growth} \quad (2)$$

$$Vr_x \frac{dNr_x}{dt} = \text{env. nutr. exch.} + \text{decomposition} - \sum_j \text{nutrient uptake}(j) \quad (3)$$

$$\frac{dD_x}{dt} = \sum_j \phi_{jx} (\text{mortality}(j) + \text{waste}(j)) - \text{decomposition} - \text{nutrient loss} \quad (4)$$

Where i was a given resource and l a given consumer of species j , and Vl_j and Vr_x were the volumes of species j 's resource depletion zone (non-zero for plant species only) and habitat x 's regional nutrient pool respectively. Some terms were equal to zero depending on the type of species. For mobile species, the proportion of their mortality and waste that occurred in habitat x , ϕ_{jx} , was equal to the proportion of their expected consumption (based on prey population sizes and interaction strengths) that occurred in habitat x (Eq. 4).

The unit for detritus pools as well as plant depletion zones and regional nutrients pools was amount of limiting nutrient (here assumed to be nitrogen), while the unit for all species was live (wet) biomass. 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 and Slansky 1981). The processes *plant growth* and *mortality* refer to live biomass in Eq. 1 and nitrogen content in Eqs. 2 and 4. See section 1.4 of the supplementary material for further details.

Equations governing fluxes were as follows:

$$env. \text{ nutr. } exch. = q \cdot Vr_x(nr_0 - Nr_x) \quad (5)$$

$$nutrient \text{ influx} = Vl_j \cdot k \cdot (Nr_x - Nl_j) \quad (6)$$

$$plant \text{ growth} = \frac{g_j \cdot Vl_j \cdot Nl_j \cdot B_j}{[N_j]} \quad (7)$$

$$consumption = \frac{a_{jl}B_jB_l}{1 + c_lB_l + \sum_i a_{il}h_{il}B_i} \quad (8)$$

$$assimilation = e_0 \cdot consumption \quad (9)$$

$$waste(biomass) = (1 - e_0) \cdot consumption \quad (10)$$

$$waste(nitrogen) = (1 - \frac{e_0 \cdot [N_{cons}]}{[N_{res}]}) \cdot [N_{res}] \cdot consumption \quad (11)$$

$$mortality = m_j \cdot B_j \quad (12)$$

$$decomposition = Df_x \cdot D_x \quad (13)$$

$$nutrient \text{ loss} = q \cdot D_x \quad (14)$$

$$cons. \text{ movement} = \phi_{jx} \cdot (B_{j,x} + B_{j,y}) \quad (15)$$

Where g_j was the intrinsic growth rate of species j , Vl_j was the volume of the resource depletion zone for species j and Nl_j was the concentration of nutrients in the depletion zone, all of which were non-zero for plant species only. $[N_j]$ was the nitrogen content of the species, dividing by this value converted from nitrogen amount to living biomass (Eq. 7), while Eq. 11 shows the nitrogen content of waste excreted from consumption after nitrogen assimilation by the consumer (i.e. the waste will have a lower nitrogen content than the resource it was derived from). a_{jl} was the per-mg-of-biomass attack rate of herbivore or predator l on plant or herbivore j . For herbivores, the attack rate depended on herbivore body mass and plant growth rate, while for predators it was determined by the predator-prey body-mass ratio. c_l scaled intraspecific interference and h_{il} was time spent attacking and handling prey. All of these ATN model parameters (a_{jl} , c_l , and h_{il}) were first parameterized on a per capita basis using allometric relationships with body size (as in Jonsson et al. 2018; F. D. Schneider et al. 2012) and then rescaled to per unit biomass. e_0 was the biomass

assimilation efficiency, which equaled 0.24 for herbivores and 0.67 for predators. The intrinsic mortality rate, m_j was a constant for basal species and for consumers depended on body mass (see supplementary material). Df_x was the rate of decomposition in habitat x , q was the rate of nutrient flux, and k was the rate of nutrient uptake from the regional nutrient pool to plants' resource depletion zones. 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 mean of 1.5 and standard deviation of 0.4) by the mean body size of its prey.

Mobile consumers were assumed to attempt to forage optimally by continuously redistributing between habitats in response to prey availability, following an ideal free distribution (Fretwell 1972; Fretwell and Lucas 1969; Williams et al. 2013). More specifically, mobile consumers redistributed between habitats 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, 5 timesteps (days). Links between predators and their prey which existed in one habitat also existed in the other habitat if both predator and prey were present there as well.

Further details on building the local food webs and coupling habitats, parameter values, and running the simulation can be found in the supplementary material.

Running the model

For the single habitat simulations each habitat had either low, medium or high fertility (mean value 0.09, 0.9 or 9 mgN/10cm³ respectively), and low, medium or high diversity (1, 4 or 8 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, from e.g. a nutrient-poor, species-rich grassland to a fertilized monoculture. 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 (i) low diversity and low fertility, or (ii) low diversity and high fertility. Habitats were coupled by the movement of one herbivore and one predator species (low movement level), or two herbivore and four predator species (high movement level). This produced $3 \times 3 \times 2 \times 2 = 36$ combinations of two habitats differing in fertility, diversity, and consumer movement (in addition to the 9 single-habitat combinations). Each combination was replicated 1000 times by drawing certain parameters at random from specified distributions (see supplementary material). 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).

Analysis

As our response variables, we measured the following ecosystem functions: species persistence (number of remaining species), aggregated biomass stock at each trophic level, aggregated productivity of each trophic level, and magnitude and direction of consumer movement between adjacent habitats. We also measured nutrient stocks in detritus, at a regional level, and in the resource depletion zones, as well as influxes to each. Although we reached a stationary stable state in the vast majority of cases, there might be cases of cyclic dynamics. To ensure representative response values we averaged across the final 100 time steps (except for persistence).

We used binomial (for species persistence) and linear (for stocks and fluxes) regression analysis to first analyse the effect of fertility and plant diversity on the response variables in isolated habitats, and then to analyse the effect of fertility, plant diversity, and consumer foraging movement on the response variables in coupled habitats. Full details of the statistical analysis can be found in the supplementary material.

3 Results

In isolated webs, fertility and diversity increased all stocks and fluxes (Fig. 2A), as well as changing the distribution of biomass among trophic levels (Fig. 4A) and changing the composition of fluxes (Fig. 5A). When coupled, the foraging movement of consumers also caused substantial changes to fluxes, stocks, biomass distributions, and flux composition (Figs. 2B, 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 detailed regression results and figures in the supplementary material.

3.1 Changes to stocks and fluxes

All stocks and fluxes, as well as species persistence, increased with both fertility and diversity in isolated webs (Fig. 2A). All fluxes increased at the same rate, and stocks largely follow the same pattern, but with some variation among specific quantities. Nutrient stocks in depletion zones were little affected by fertility, but increased with diversity. This latter result is simply because with higher diversity there were more plants, and therefore more depletion zones, and therefore a higher cumulative stock of nutrients. Regional

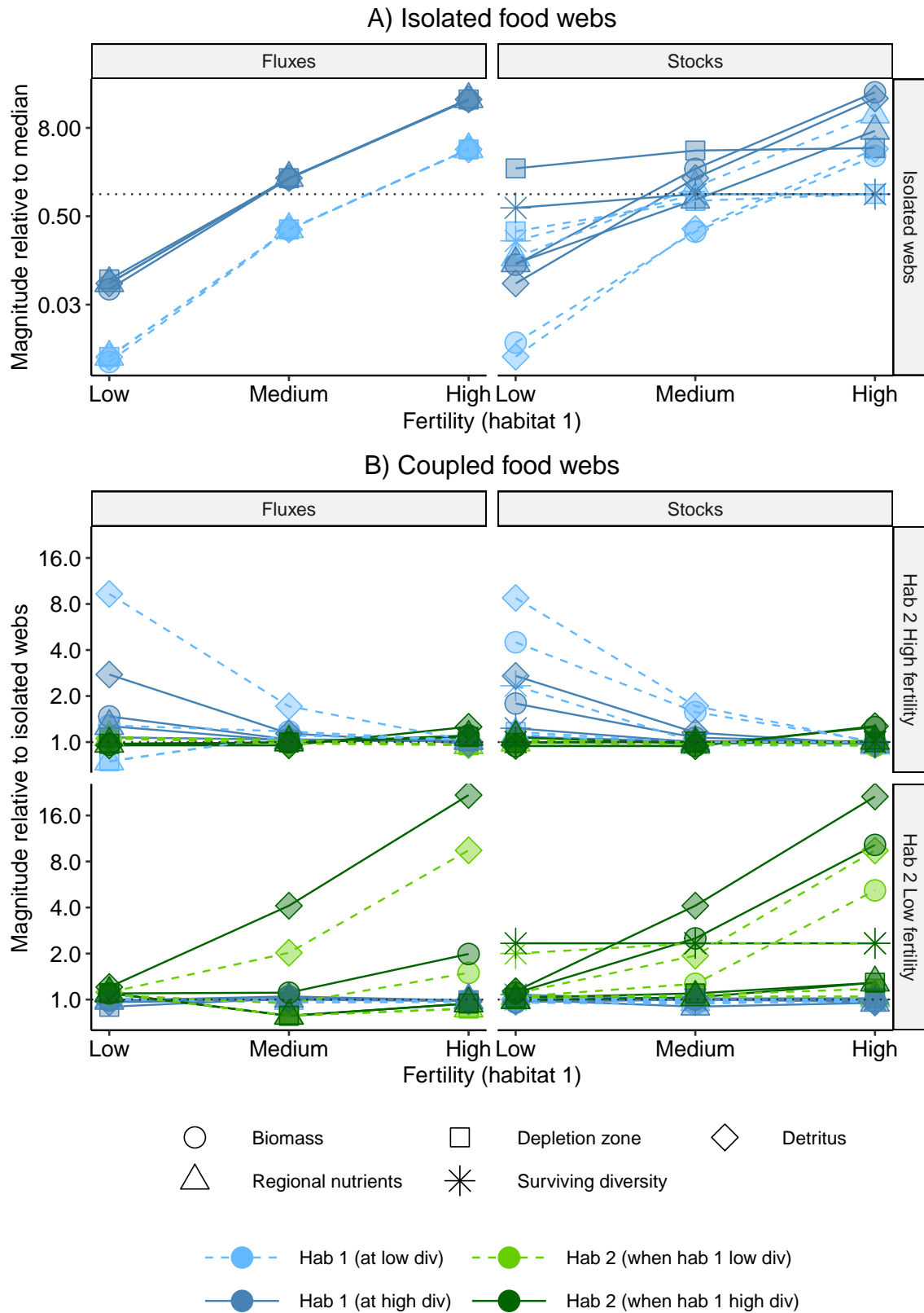


Figure 2: (Continued on the following page)

Figure 2: Changes in fluxes and stocks as a result of diversity, fertility, and consumer foraging movement. In A) Isolated food webs, we plot the difference in 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 one 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 two 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.

nutrient stocks increased with fertility, but actually weakly decreased with diversity. 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.

When habitats were coupled, net foraging movement was usually a spillover from high- to low-fertility habitats (Fig. 3). The magnitude of this spillover 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 Fig. 2B). The effect of influx on the low fertility habitat was strengthened when the high fertility habitat was also characterized by high diversity (compare solid (high diversity) to dashed (low diversity) green lines of the lower panels of Fig. 2B). 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 Fig. 2B).

The stock and flux most affected by movement was detritus and its influx (diamonds in Fig. 2B). These changes were caused by the spillover and subsequent mortality of foraging consumers from a higher fertility habitat, where they were abundant, to a lower fertility habitat. Biomass stocks also increased as a result of spillover through foraging movement (circles in right-hand panels of Fig. 2B), even though the in situ biomass influx from plant growth, herbivory, and predation within the same habitat was little affected (circles in left-hand panels of Fig. 2B). Despite the increase in biomass stocks in the low fertility habitat, there was no corresponding decrease in biomass stocks in the higher fertility habitat. This lack of effect suggests

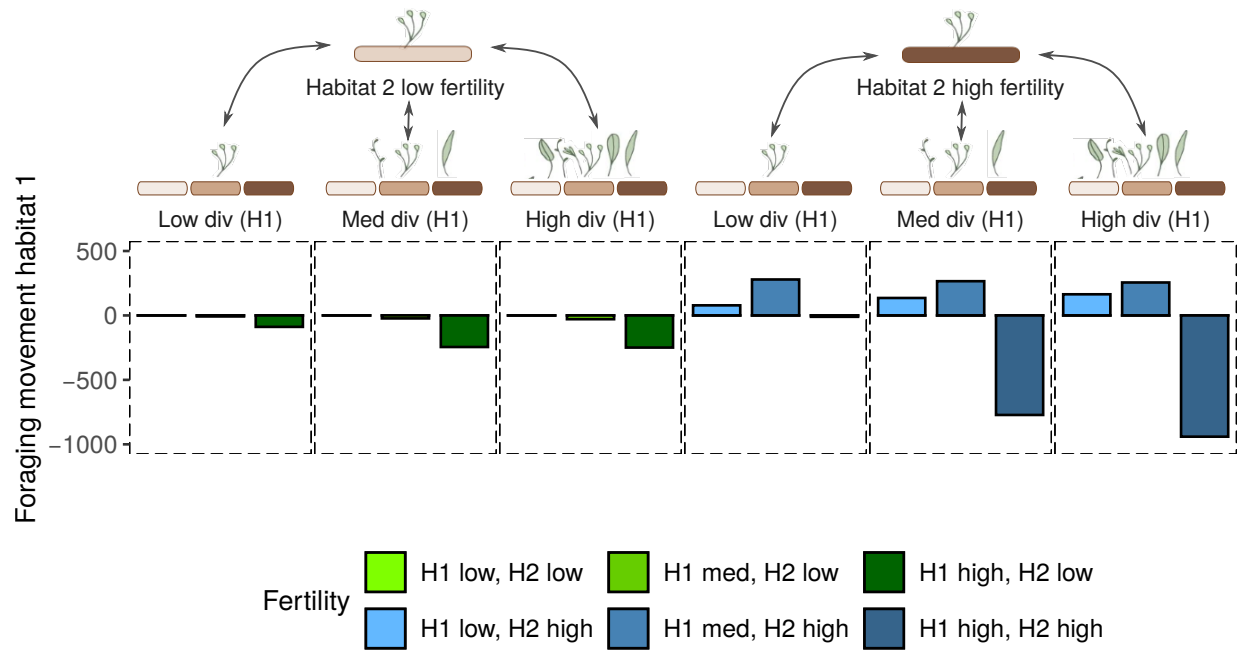


Figure 3: Net foraging movement of consumers into (positive values) or out of (negative values) habitat 1. Green bars show movement out of habitat 1 (all negative values) when habitat 2 is low fertility. Blue bars show movement in (positive values) or out (negative value) of habitat 1 when habitat 2 is high fertility. Habitat 2 is always low diversity.

that the foraging movement increased stocks in the low-fertility habitat beyond what it could support when isolated. Species persistence increased in low fertility habitats receiving consumer foraging spillover from high fertility habitats (green asterisks in lower, right-hand panel of Fig. 2B).

3.2 Biomass distribution

Fertility, diversity, and foraging movement changed the distribution of biomass among the three trophic levels (Fig. 4). In isolated food webs, plant biomass increased with fertility and, to a lesser extent, with diversity (green bars in Fig. 4A). At low fertility and diversity, there were very few predators, and biomass was distributed in a classical pyramid (Fig. 4A). As productivity and diversity increased, predators took up an increasing proportion of the biomass distribution. The biomass distribution of habitats coupled by foraging consumers to higher fertility and/or diversity habitats changed considerably (Fig. 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 relative to uncoupled webs, but due to heavy predation pressure, the increase was more modest.

3.3 Composition of fluxes

Both in- and outfluxes to or from each stock were composites of multiple fluxes; for example, influx to herbivore biomass came from both herbivory and foraging movement, while outfluxes consisted of both intrinsic mortality and loss to predation. The makeup of composite fluxes depended on fertility, diversity, and foraging movement. Here we highlight three examples: (i) the outflux of plant biomass to intrinsic mortality versus herbivory (green bars in Fig. 2), (ii) the outflux of herbivore biomass to intrinsic mortality versus predation (blue bars), and (iii) the influx to the regional nutrient pool from environmental exchange versus decomposition (brown bars).

In isolated webs with a healthy predator population, approximately three-quarters of herbivore biomass was lost to predation (dark blue section of bars in Fig. 2A) rather than intrinsic mortality (light blue section). Low fertility and diversity habitats, however, could not support predators and all herbivore biomass was lost to intrinsic mortality (left hand panel of Fig. 2A). When habitats were coupled by foraging movement, the boosted predator populations in these low fertility habitats could dramatically increase the proportion of herbivore biomass lost to predation (left hand panels in Fig. 2B, compare narrower bars representing the coupled webs to the wider bars they overlay which represent the equivalent isolated web).

The proportion of plant biomass lost to herbivory increased with fertility, but decreased with diversity

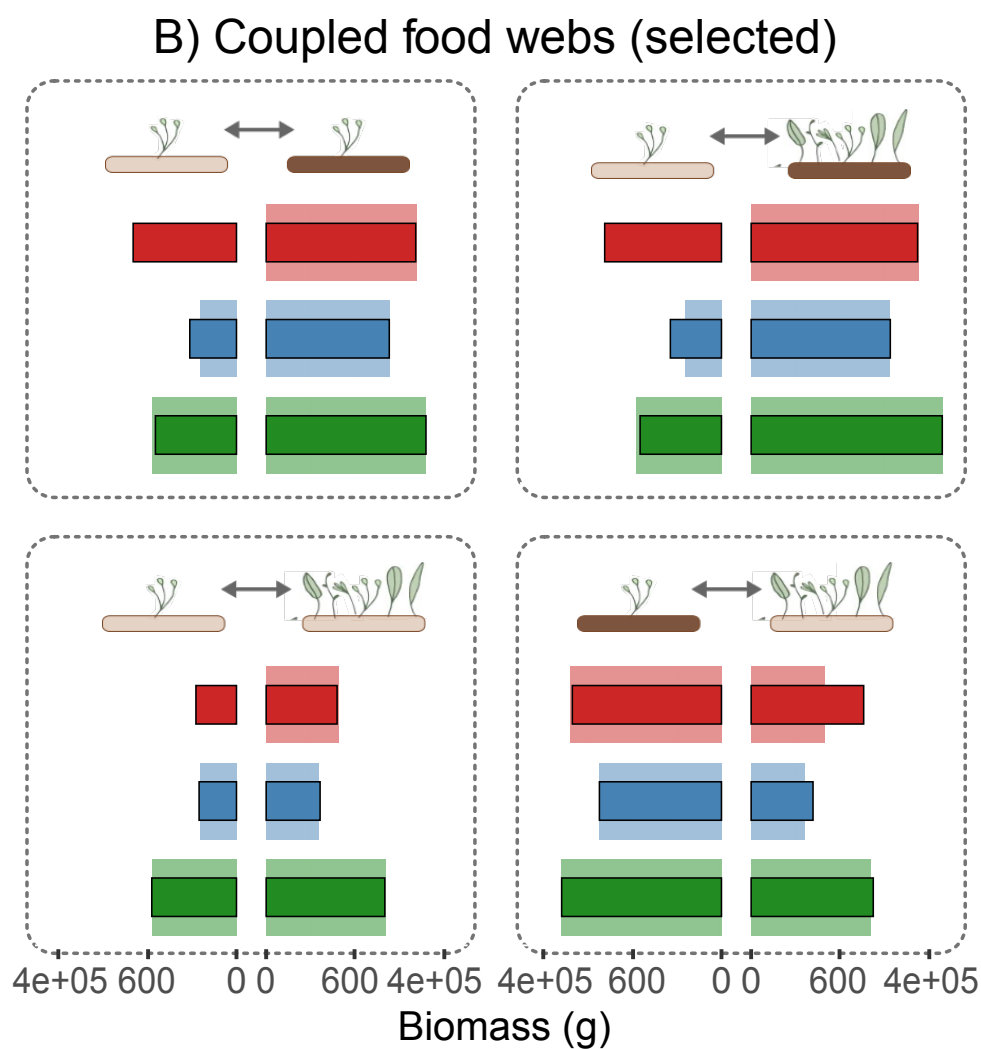
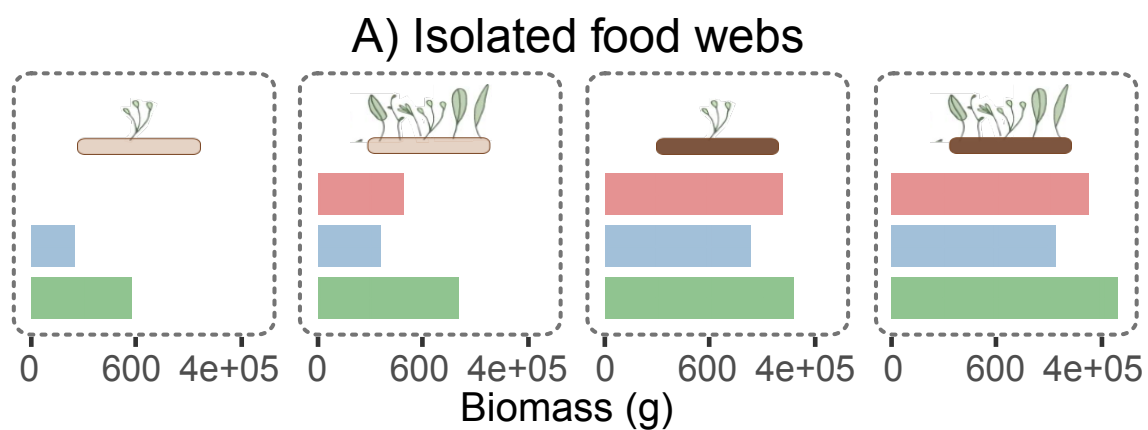


Figure 4: (Continued on the following page)

Figure 4: Biomass pyramids in A) isolated food webs and B) selected coupled food webs. Icons at the 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). Narrower, darker bars show the biomass distribution in the coupled food webs, while the wider, faded bars they overlay show the equivalent isolated food web, for reference purposes (the background bars are therefore the same as for the equivalent scenario in A).

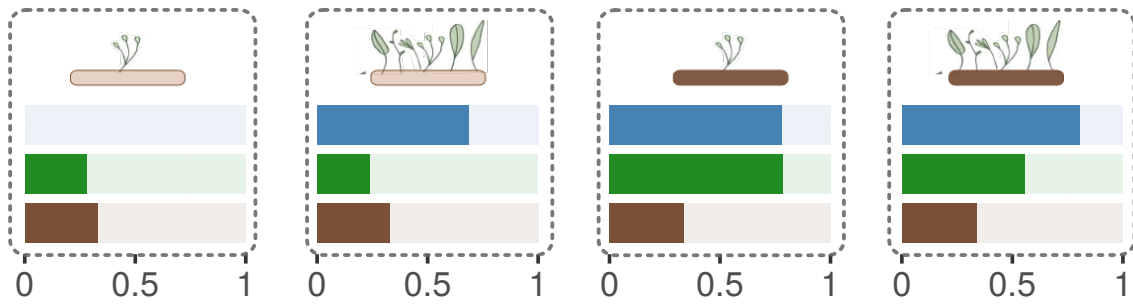
(green bars in Fig. 5A). When coupled by foraging movement, the influx of herbivores from high fertility habitats increased the proportion of plant biomass lost to herbivory in low fertility habitats (Fig. 5B). The effect was less marked than the effect on herbivores, because predation pressure prevented the herbivore population from exploding.

When isolated, the relative contribution of decomposition and environmental nutrient exchange to the regional nutrient pool was fixed at approximately 1:3 regardless of fertility and diversity (brown bars in Fig. 5A). When coupled, however, the contribution of decomposition increased dramatically in low fertility habitats linked to high fertility habitats (Fig. 2B). This increase was especially marked if the low fertility habitat was also characterized by low diversity (upper panels of Fig. 2B) where decomposition provided 100% of the nutrients to the regional nutrient pool.

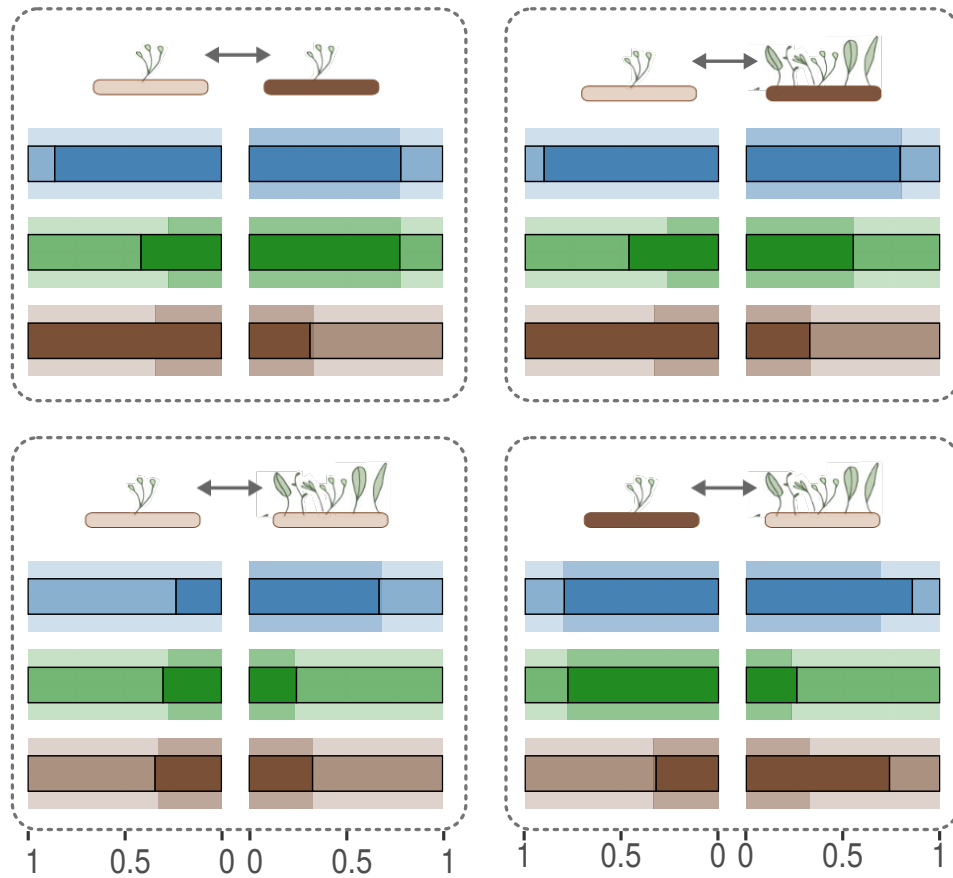
4 Discussion

Our results showcase the wide-ranging impact that consumer foraging movement can have on functioning in neighbouring ecosystems. Based on our simulations of isolated versus coupled food webs in contrasting habitats, we found that effects 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 reveal how the interdependence of ecosystem functions can lead to cascades as well as attenuation of effects, with implications for patchy landscapes. Below, we first summarise the effects of consumer coupling on ecosystem functioning, and then turn to effects on stocks and fluxes in particular. We conclude with implications for the spatially structured landscapes of the Anthropocene.

A) Isolated food webs



B) Coupled food webs (selected)



Coupled webs
 Isolated webs



Figure 5: (Continued on the following page)

Figure 5: The composition of composite fluxes changed with diversity, fertility, and consumer foraging movement. Here we show the proportion of regional nutrient influx coming from decomposition (dark brown) relative to the environment (light brown); the proportion of plant outflux going to herbivory (dark green) versus intrinsic mortality (light green); and the proportion of herbivore outflux to predation (dark blue) versus intrinsic mortality (light blue) for different combinations of diversity, fertility, and consumer foraging movement. As in Fig. 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 (1 plant species) or high diversity (many plant species). 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 under-laying 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 the appendix.

Changed functioning in coupled ecosystems

Our results reveal how ecosystems, when coupled, can exhibit drastically differing levels of functioning than when isolated. For the short-distance foraging movements at the core of our analysis, movement had net effects on species persistence, the standing stock of living biomass at each trophic level, the biomass fluxes between trophic levels (primary, secondary and tertiary production), the standing stock and flux of detritus, and the size of soil nutrient pools and fluxes. It also affected the composition of aggregate fluxes, such as the relative contribution to plant biomass loss by consumer-inflicted vs intrinsic mortality.

The current result supports the proposition that consumer flow and effects in patchy landscapes are likely to be asymmetric, and particularly pronounced when a high-fertility habitat is linked to one of low fertility (Oksanen 1990; Rand et al. 2006). 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 relation for which there is both theoretical (Gravel et al. 2010; Oksanen 1990) and empirical support (Marczak et al. 2007). Indeed, in our simulations, the effect of cross-habitat movement depended on the difference in fertility and plant species richness. The imprints of movement proved the strongest in low-fertility habitats neighbouring high-fertility habitats. In this case, net consumer flow was strongly toward the low-fertility habitat, increasing biomass and, hence, nutrients.

Nonetheless, in real landscapes greater productivity contrasts may not always predict greater fluxes. First, 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 neighbouring ecosystem lacks important resources, then optimally foraging consumers will fail to move into it. In our results, this was demonstrated by a higher flux of consumers from the high fertility habitat to the intermediate than to the low fertility habitat (Fig. 3). Second, in natural landscapes additional features of the habitat patches, as neglected by

us, may override the effects of differences in habitat productivity. Among such additional features is habitat geometry and the permeability of habitat boundaries (Marczak et al. 2007; Ries et al. 2004).

Importantly, input from local sources (henceforth "local fertility") versus spill-over from elsewhere differed in their effects on local ecosystem functioning. An increase in local fertility increased all ecosystem functions, but their relative magnitudes remained unchanged. Spill-over, in contrast, shifted the balance of stocks and fluxes. As a result, spillover changed the relative productivity at different trophic levels, resulting in different biomass distributions across trophic levels in coupled as compared with isolated food webs. These changes all occurred in the low fertility habitat, with little effect on the high fertility habitat actually providing the consumer spill-over.

The patterns observed enrich our understanding of realised biomass distributions. Where theoretical predictions state that classic pyramids or stacks should dominate (Trebilco et al. 2013) (unless the efficiency of energy transfer between trophic levels and/or consumer-resource body-mass ratio is large (Jonsson 2017)), such predictions are based on isolated food webs. In systems with energy subsidies or mobile consumers, we may find even inverted biomass pyramids (McCauley et al. 2018; Trebilco et al. 2013; Trebilco et al. 2016). Consistent with the latter prediction, we found a shift towards predator-dominated biomass distributions where the influx of mobile consumers was high relative to the predator standing stock (Fig. 4). Thus, flows of organisms can fundamentally shift the local balance between trophic levels.

Stocks versus fluxes in coupled food webs

To reveal mechanisms and implications of changes in ecosystem functions, we need to consider stocks and fluxes in parallel (Gounand et al. 2020). This is because fluxes connect stocks, and because the same stocks can result from highly dissimilar combinations of fluxes. Stocks are the standing crop of organisms or nutrient, i.e. the amounts observable at any one point in time. Fluxes connect stocks, through flows of individuals, biomass, and/or nutrients. A low stock can result from either small fluxes of production and consumption, or large fluxes of both - yielding an entirely different understanding of the underlying dynamics. Here, linking the concepts through the matter transformation loop serves to clarify their relationship (Gounand et al. 2020; Hines et al. 2019, see also Fig. 1).

We found that foraging movement affected both stocks and fluxes. For instance, consumer flow between neighbouring 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 discloses that predator

biomass increased both from inward foraging movement and from increased *in situ* tertiary productivity as a result of higher prey availability. Even if predators were not mobile, they would still increase due to herbivore influx. Here, our results for consumer biomass stocks, as well as the small effect of consumer inflow on primary producer biomass, are in agreement with empirical evidence: recently, Allen and Wesner (2016) showed that inflows of predators and prey have a strong effect on local predators (prey) but cascading effects are weak and do not travel far.

The matter transformation loop links it all

Importantly, in real ecosystems, matter constantly cycles between the living and non-living components of the matter transformation loop. As inorganic compounds are turned into living biomass, transferred through the food chains, and ultimately recycled through decomposition and mineralization back into inorganic compounds (Gounand et al. 2020), effects of spatial subsidies on local ecosystem functions can either propagate or fizz out. For example, we found that consumer spill-over resulted in larger consumer biomass stocks — an effect which cascaded, via a larger detrital pool, to a larger decomposition flux. But this increased nutrient influx satiated the soil with nutrients, which in turn led to a counterbalancing decrease in nutrient uptake via the environmental nutrient exchange (see Eqs. 3, 5, 13). Therefore, the cascading effect of higher consumer biomass stocks was attenuated and had little effect on the regional nutrient pool.

The above result hinges on the dynamics assumed for the nutrient loop, in particular on the passive diffusion determining the nutrient exchange between the regional nutrient pool and the external environment. In other metaecosystem models, where the external nutrient input is instead modelled as a constant influx rate, increased detritus flows would not be attenuated at the level of the nutrient pool and would rather provide a substantial boost to primary productivity (Gravel et al. 2010; Leroux and Loreau 2010). However, the attenuating effect that we observe for consumer spill-over, but not for fertility, echoes what occurs in real systems, where the effect of consumer flows quickly attenuate, whereas those of nutrient subsidies do not (Allen and Wesner 2016). 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 (Gounand et al. 2020).

Implications for community dynamics in patchy landscapes

The consumer spill-over patterns observed in our simulations have direct implications for ecosystem functioning in patchy, human impacted landscapes. Here, consumer movement between neighbouring habitats may

affect species persistence and ecosystem functions (Andrén et al. 1985; Chaplin-Kramer et al. 2011; Duelli et al. 1990; Dyer and Landis 1997; Rand et al. 2006), the establishment of pest herbivores (Roschewitz et al. 2005; Tscharntke et al. 2016) and their control by natural enemies (Bianchi et al. 2006; Chaplin-Kramer et al. 2011). Consumer flux in the opposite direction, from croplands of high fertility, can result in high predation pressures (Andrén et al. 1985; Blitzer et al. 2012; Rand and Louda 2006) and over-exploitation (Oksanen 1990; Polis et al. 1997) in the neighboring (semi-)natural habitats.

In this context, our results contrast with previous theoretical (Guzman et al. 2019; Polis et al. 1997; M. F. Schneider 2001 but see Plitzko and 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. We found that, despite the risk of strong apparent competition between prey in different habitats (Callaway and Hastings 2002; Frost et al. 2016; Polis et al. 1997) and of direct over-exploitation (Oksanen 1990; Oksanen et al. 1992; Polis et al. 1997), the effect of consumer spill-over was either positive or neutral for overall species persistence of both plants and herbivores. This finding may partly reflect our focus on the impacts of short-range foraging movement between neighbouring habitats of different fertility, where consumers distribute themselves across the landscape to optimise their foraging success (Fretwell 1972; Fretwell and Lucas 1969; Williams et al. 2013) (see Methods, Eq. 15) — a scenario which contrasts with a previous focus in metacommunity and metaecosystem research on long-distance, cross-matrix dispersal between similar habitats (Gounand et al. 2018; Guzman et al. 2019; Massol et al. 2011) and/or on passive diffusion (Guzman et al. 2019; Oksanen 1990; Polis et al. 1997; M. F. Schneider 2001).

5 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 spill-over. Furthermore, by explicitly modelling the dynamics of the entire matter transformation loop, we traced how the trophic interactions determined the effect of consumer spill-over on food web biomass stocks, and how these effects were propagated or attenuated through the matter transformation loop to the 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, which all exchange organisms and materials on multiple spatiotemporal scales (Gounand et al. 2018; Guzman et al. 2019; Rand et al. 2006). 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.

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