DR. SHAOPENG WANG (Orcid ID : 0000-0002-9430-8879)

Intraguild predation enhances biodiversity and functioning in complex food webs

Shaopeng Wang[1*], Ulrich Brose[2,3], Dominique Gravel[4]

[1] Institute of Ecology, College of Urban and Environmental Science, and Key Laboratory for Earth Surface Processes of the Ministry of Education, Peking University, 100871 Beijing, China

[2] EcoNetLab, German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, 04103 Leipzig, Germany

[3] Institute of Biodiversity, Friedrich Schiller University Jena, 07743 Jena, Germany

[4] Département de Biologie, Universite de Sherbrooke, Sherbrooke, Québec, Canada

[*] Email: shaopeng.wang@pku.edu.cn

Type of contributions: Article

Running head: Intraguild predation in complex food webs

Abstract

Intraguild predation (IGP), i.e. feeding interaction between two consumers that share the same resource species, is commonly observed in natural food webs. IGP expands vertical niche space and slows down energy flows from lower to higher trophic levels, which potentially affects the diversity and dynamics of food webs. Here, we use food web models to investigate the effects of IGP on species diversity and ecosystem functioning. We first simulate a five-species food web module with different strengths of IGP at the herbivore and/or carnivore level. Results show that as the strength of IGP within a trophic level increases, the biomass of its resource level increases because of predation release; this increased biomass in turn alters the energy fluxes and biomass of other trophic levels. These results are then extended by subsequent simulations of more diverse food webs. As the strength of IGP increases, simulated food webs maintain (1) higher species diversity at different trophic levels, (2) higher total biomasses at different trophic levels, and (3) larger energy fluxes across trophic levels. Our results challenge the intuitive hypothesis that food web structure should maximize the efficiency of energy transfer across trophic levels; instead, they suggest that the assembly of food webs should be governed by a balance between efficiency (of energy transfer) and persistence (i.e. the maintenance of species and biomasses). Our simulations also show that the relationship between biodiversity and ecosystem functioning (e.g. total biomass or primary production) is much stronger in the presence of IGP, reconciling the contrast from recent studies based on food-chain and food-web models. Our findings shed new light on the functional role of IGP and contribute to resolving the debate on structure, diversity and functioning in complex food webs.

Introduction

Understanding the mechanisms underlying the diversity and functioning of ecosystems is a major goal in ecology. Although numerous studies have developed theories and experiments to uncover the mechanisms of species coexistence (Chesson 2000; Levine 2010) and the functioning and stability of ecosystems (Loreau et al. 2001; Tilman et al. 2014), they focused mainly on competitive communities. Species at higher trophic levels bear a higher risk of extinction (Binzer et al. 2011), and their extinction might have a strong negative impact on ecosystem functioning (Estes et al. 2011; Brose et al. 2017; Wang & Brose 2018). There is, therefore, an urgent need to improve our understanding of the mechanisms governing species diversity and ecosystem functioning in complex food webs.

Network structure has long been suggested to play an important role in regulating the dynamics and stability of food webs (Pimm 1982; McCann 2012). In particular, the stability of food webs could be enhanced by weak trophic interactions (McCann et al. 1998), modularity (Stouffer and Bascompte 2011), and correlation between interaction strengths (Jansen & Kokkoris 2003; Tang et al. 2014). Recently, theoreticians also started to investigate the effect of network structure on energy fluxes (deBruyn et al. 2007), ecosystem productivity (Poisot et al. 2013; Wang & Brose 2018) and species diversity (Barbier et al. 2018). Despite these advances, a comprehensive understanding of the effect of network structure on the diversity and functioning of food webs, remains far from complete.

One important element of natural complex food webs is intraguild predation (IGP), which characterizes feeding interactions between two consumers that share the same resource (Holt & Polis 1997). IGP increases the vertical niche breadth of a consumer species and consequently increases complexity of the whole food web (Duffy et al. 2007). Without IGP, all species have integer trophic levels along trophic chains, making the structure and dynamics of food webs easier to understand. However, IGP is commonly found at all trophic

levels in natural ecosystems (Arim & Marquet 2004; Riede et al. 2010). However, the effects of IGP on the diversity and functioning, especially in complex food webs, remains largely unexplored (Irigoien & de Roos 2011).

Food webs comprise feeding links between species, through which nutrients and energy flow from the bottom to the top of the network. Network structures that slow down this upward flux, can dampen top-down control (deBruyn et al. 2007). IGP acts as such a structure, keeping energy within the same trophic level and thus slowing down energy flows between trophic levels (Mylius et al. 2001; deBruyn et al. 2007). The reduced top-down control can release species at lower trophic levels and enhance their efficiency of transforming energy inflows into biomass (Holt & Polis 1997; Finke & Denno 2005; Schneider et al. 2012). The increased biomasses at lower trophic levels may in turn affect the build-up of biomass at higher trophic levels, as the bottom-up effect becomes the major driver of food web dynamics following the weakening of top-down effect. Taken together, IGP may remarkably re-shape energy fluxes and biomass distributions in food webs by altering trophic control.

Very few studies have discussed the effect of IGP on species diversity. Earlier theoretical research investigated how IGP might influence the coexistence of two consumers that compete for the same resource (Holt & Polis 1997). In the absence of the IGP link, the two consumers cannot coexist due to resource competition (Tilman 1982). However, their coexistence is possible when IGP exists between the two consumers, under the additional condition that the IG prey is superior in exploitative competition for the resource (Holt & Polis 1997; Kondoh 2008). In this sense, IGP contributes to maintaining a higher diversity among competitors, but it is largely unclear whether similar effects occur in complex food webs (but see Stouffer & Bascompte 2010).

The presence of IGP may also alter the relationship between diversity and functioning in food webs. In food chains without IGP, the strong trophic cascade results in a non-monotonic relation between food chain length and primary productivity (Oksanen et al. 1981; Loreau 2010). In complex food webs, however, the primary productivity increases exponentially with the maximum trophic level (Wang & Brose 2018). One explanation for this contrast is that, in complex food webs, IGP links can significantly weaken the strength of trophic cascades by mixing chains of various lengths between any pair of basal and top species. The weakened trophic cascades then generate a smooth relation between the maximum trophic level and primary productivity (Wang & Brose 2018), but this hypothesis has yet to be explored rigorously.

In this study, we use dynamical food web models to examine the effect of IGP on species diversity, biomass and energy fluxes across trophic levels. We start with a simple food web module with five species and investigate how IGP links at different trophic levels alter species biomass and energy flows. We then simulate complex food webs and examine how IGP affects the diversity and functioning of multitrophic ecosystems. Our simulations demonstrate that IGP increases species diversity, biomass, and energy fluxes across trophic levels, and it strengthens the relation between biodiversity and ecosystem functioning. Our results demonstrate the fundamental importance of IGP and contribute to reconciling the structure, diversity and functioning in complex food webs.

Methods

We start with a five-species module that consists of one plant (P), two herbivores (H_1 and H_2), and two carnivores (C_1 and C_2) (Figure 1a). The plant is consumed by both herbivores, and the two herbivores are in turn consumed by both carnivores. We investigate the effect of IGP by adding IGP links: (i) at the herbivore level, i.e. H_2 consuming H_1; (ii) at the carnivore

level, i.e. C_2 consuming C_1; and (iii) at both herbivore and carnivore levels. We simulate population dynamics before and after the addition of IGP links, and the temporal dynamics of species biomass and energy fluxes are recorded. In addition, we also investigate the effects of IGP by gradually increasing the strength of IGP, i.e. the feeding preference of H_2 on H_1 or that of C_2 on C_1 and examine how the equilibrium species biomass and energy fluxes change accordingly. To facilitate coexistence of all species, we assume that H_1 is a better competitor than H_2 (i.e. H_1 has a higher attack rate than H_2 when feeding on P) and C_1 and C_2 are better competitors on H_1 and H_2, respectively. Population dynamics are governed by differential equations of species biomass, which will be described later.

We then simulate complex food web models to investigate the effects of IGP on species diversity and ecosystem functioning. Network structure is generated with an allometric variant of the niche model (Schneider et al. 2016). Briefly, a number of plant (20) and animal (60) species are first sampled from preassigned body size ranges; these body size values determine the feeding probability between any two species and thus the food-web topology (see details in Schneider et al. 2016). The resulting food webs usually contain a considerable number of IGP links (Figure 1b). Here we define IGP links as follows: we first calculate the shortest-chain based trophic level for each species, i.e. the length of the shortest chain connecting the focal species and the abiotic resource; then IGP links are identified as feeding interactions within the same trophic level (Figure 1b). Under this definition, the simulated food webs include a proportion of 20 - 46% IGP links. Again, we manipulate a gradient of IGP in two ways. (i) We simulate the loss of IGP by randomly removing different proportions of all IGP links that were generated by the allometric niche model. Note that the removal of IGP links will simultaneously reduce the food web connectivity and generality of consumers. (ii) We gradually decrease the strength of IGP links by reducing the feeding preference of consumers (i.e. the fraction of their diet) on resource species that belong to the

same (shortest-chain based) trophic level. In doing so, the preference of consumers on resource species at lower trophic levels (i.e. non-IGP) is increased, leading to stronger top-down controls.

The dynamics of the five-species module and complex food webs are governed by multi-species predator-prey interactions. Specifically, the biomass dynamics of a plant species i (P_i) and an animal species j (A_j) are described as follows:

$$\frac{dP_i}{dt} = r_i G_i P_i - \sum_k A_k F_{ki} - x_{Pi} P_i \tag{1}$$

$$\frac{dA_j}{dt} = e_1 A_j \cdot \sum_{\substack{i:plant \\ resource}} F_{ji} + e_2 A_j \cdot \sum_{\substack{k:animal \\ resource}} F_{jk} - \sum_l A_l F_{lj} - x_{Aj} A_j \tag{2}$$

Here, $G_i = \frac{N}{k_i+N}$ is the growth factor that is determined by the nutrient concentration (N), the dynamics of which follow:

$$\frac{dN}{dt} = D(T - N) - \sum_i r_i G_i P_i \tag{3}$$

The functional response, F_{ji}, describes the consumption rate of consumer species j on its resource species i: $F_{ji} = \frac{\omega_{ji} a_{ji} R_i^q}{1 + cA_j + \sum_k \omega_{jk} a_{jk} h_{jk} R_k^q}$, where R_i is the biomass of resource species i (either plants or animals) and A_j is the biomass of consumer species j. The parameter c controls the strength of predator interference (Skalski & Gilliam 2001; Lang et al. 2011) and q determines the type of functional response (type II: $q=1$; type III: $q=2$). ω_{ji} represents the feeding preference of consumer j on resource species i, which is manipulated to change the strength of IGP links. Given any predator species, we restrict its preference for the intraguild prey to be no larger than that for the shared resource species based on two considerations: (1) empirical studies reported that intraguild predation formed 1 - 49% of the diet of predator species in different taxa (Polis et al. 1989); (2) in the case that the intraguild prey is preferred over the resource species, the predator is shifted to a higher trophic level and thus the system becomes an omnivory module (McCann & Hastings 1997). See Table 1 for explanations of all other parameters and their values in our simulations. Note that the parameterization has

not incorporated size constraints suggested by recent theory (Schneider et al. 2016). This is because body size affects both structure and dynamics, but our objective here is to manipulate network structure (as our explanatory variable) and investigate its effect on dynamics and functioning (as our response variables).

Under each level of IGP, we run food web dynamics to reach equilibrium and record species diversity and total biomass within three trophic groups: plants, herbivores (species that feed exclusively on plants or on both plants and animals, thus including true herbivores as well as omnivores), and carnivores (species that feed exclusively on animals). Species are assumed to be extinct once their biomass fell below 10^{-6}. We derive the energy fluxes (i.e. the total feeding rate) between these three trophic groups based on equilibrium species biomass. Specifically, we calculate the feeding rate of consumer j on resource k by $A_j F_{jk}$, and then the total energy fluxes between two trophic levels l and $l+1$ is obtained by the sum of feeding rates for all predator-prey pairs between these two trophic levels: $\sum_{j \in level\ l+1, k \in level\ l} A_j F_{jk}$. The primary productivity is defined as the total nutrient flow from the abiotic pool to the plant community: $\sum_i r_i G_i P_i$. We investigate how species diversity, biomass and energy fluxes change along the gradient of IGP. In simulations of complex food webs, we simulate 500 food webs under each of the four levels of nutrient supply rates (very low: 5, low: 20, intermediate: 100, and high: 500; see Table 1) and the two types of functional responses (type II and III) to test the robustness of our results. With two ways of simulating IGP loss (removing or weakening IGP links) and nine IGP gradients, we simulate a total of 72000 (=500×4×2×2×9) food webs. All simulations are performed in Matlab (codes are available by request).

Lastly, we examine the relationships between ecosystem functioning (total biomass and primary productivity) and diversity metrics (total species richness and vertical diversity) across simulated food webs. Note that in our simulations, all these variables are determined

by lower-level processes (e.g. network structure, nutrient supply, etc.). The vertical diversity was measured by the food web's maximum trophic level; to match the prediction of Wang & Brose (2018), we calculate the trophic level using the prey-averaged approach, which is different from the aforementioned shortest-chain definition. To test the hypothesis that IGP could alter the relationship between biodiversity and ecosystem functioning in food webs (Wang & Brose 2018), we calculate the coefficients of determinants (r^2) of these relationships and compare them between food webs with strongest (i.e. original food webs generated from the niche model) and weakest (i.e. food webs with 99% original IGP links were removed or with lowest preference, i.e. 1%, on intraguild preys) IGP.

Results

IGP in a five-species module

We first investigate the effect of IGP by monitoring the change of species biomasses and energy fluxes before and after adding the IGP link between H_1 (as prey) and H_2 (as predator). Immediately after the IGP link is added, the feeding rate of H_2 on P (i.e. the energy flux from P to H_2) is greatly decreased due to the reduced feeding preference of H_2 on P; this decreased feeding rate releases P and causes its biomass to increase and total herbivore biomass to decrease (Fig. 2). Following the increase in plant biomass, the total feeding rate of herbivores on plants increases (Fig. 2b), and the biomass of herbivores stops declining and starts to increase (Fig. 2a). The increase in herbivore biomass results in an increase in energy flow from herbivores to carnivores (Fig. 2b), which causes the total biomass of carnivores to increase and that of herbivores to decrease accordingly (Fig. 2a). Overall, adding the IGP link between H_1 and H_2 increases the biomass of the plant and carnivores, decreases the nutrient concentration, alters the biomass distribution across trophic levels (i.e. from middle-heavy to

top-heavy), and increases the total energy fluxes between trophic levels (Figs. 2, Appendix S1: Figs. S2, S3).

Similar results are found if the strength of the IGP link is increased in a continuous way. As the strength of the IGP link between H_1 and H_2 increases, the biomasses of the plant and carnivores both increase, and the energy fluxes between different trophic levels all increase (Fig. 3, Appendix S1: Fig. S4). Note that the herbivore biomass remains constant.

Similarly, the IGP at the carnivore level releases the herbivore species and increase their biomass; this increased herbivore biomass in turn suppresses the plant species P and causes its biomass and primary productivity to decrease (Figs. 3b, Appendix S1: Figs. S1 & S4). The IGP at the carnivore level also results in a reduced total biomass of carnivores as a consequence of decreased energy fluxes from herbivores to carnivores (Fig. 3b). Finally, as IGP links are added or enhanced at both herbivore and carnivore levels, the biomasses of the plant, herbivores and carnivores all increase, and the energy fluxes between different trophic levels also increase (Figs. 3c, Appendix S1: Figs. S1 & S4).

IGP in complex food webs

We investigate species diversity and ecosystem functioning along a gradient of enhanced IGP in complex food webs. Overall, our simulations show generally consistent results between the two ways of manipulating IGP, i.e. changing either the number or the relative strength of IGP links, and under different types of functional responses and nutrient supply rates (Figs. 4, Appendix S1: Figs. S5 & S6).

The total species richness, total biomass and ecosystem productivity of the food web all increase with IGP (Figs. 4, Appendix S1: Figs. S5 & S6). As the number or strength of IGP links increases, the species richness and total biomass of all three trophic groups (i.e. plants, herbivores and carnivores) generally increase, except for the plant species richness

which remains constant. But at very low nutrient supply, the richness and biomass of carnivores exhibit slightly decreasing trends with increased IGP (Fig. 4d,e). The primary (i.e. energy flux from the abiotic nutrient to plants) and secondary (i.e. energy flux from plants to herbivores) productivities both increase, and the total energy fluxes within the herbivore level also increase. However, the energy fluxes from herbivores to carnivores and those within the carnivore level stay roughly constant at intermediate or high nutrient supply and slightly decrease at lower nutrient supply (Figs. 4, Appendix S1: Figs. S5 & S6).

Across simulated food webs, ecosystem functioning as calculated by either total community biomass or primary productivity exhibits a strong positive correlation (r^2 = 0.48~0.57; slope = 0.098~0.11) with vertical diversity in food webs with many and strong IGP links. But their correlations are significantly reduced in food webs with much less (r^2 = 0.09~0.17; slope = 0.031~0.052) or weaker (r^2 = 0.33~0.38; slope = 0.075~0.088) IGP links (Figs. 5, Appendix S1: Fig. S7).

Discussion

IGP is ubiquitous in natural ecosystems (Arim & Marquet 2004; Riede et al. 2010); however, we have a poor understanding of its implications. Our study demonstrates the fundamental importance of IGP for biodiversity and functioning of complex food webs. Our models show that IGP increases the species diversity, biomass, and energy fluxes across trophic levels in complex food webs, as well as enhancing the relation between biodiversity and ecosystem functioning.

Early studies on the three-species IGP module showed that IGP can increase the biomass of the shared resource through a trophic cascade effect (Holt & Polis 1997). Our analysis confirmed and extended this classic result with a multi-species IGP module. It shows that IGP at one trophic level could increase the biomass of its resource level, and this

increased biomass in turn have cascading effects on the biomass and energy fluxes at even higher and lower trophic levels (Fig. 2). In particular, IGP at the herbivore level increases the primary productivity of the whole ecosystem. These results were further extended by our simulations of complex food web models, which showed that IGP across the whole food web enhanced the capacity of ecosystems in exploiting abiotic resources and building biomasses across trophic levels (Fig. 4). All these observations could be explained by the reduced top-down control with IGP. By strengthening feeding interactions within trophic levels relative to those between levels, IGP links impede the vertical flow of energy and weaken the top-down control (DeBruyn et al 2007), which releases species at lower trophic levels and enhance the build-up of their biomasses.

Our simulations also show that IGP could increase species diversity across trophic levels. This result is consistent with recent findings that the persistence of species in complex food webs increases with the number of three-species IGP modules (Stouffer & Bascompte 2010). One explanation could be the expanded vertical niche space with IGP, which decreases exploitative competition between consumers (Holt & Polis 1997) and creates new niches for species coexistence compared to the simplified, discrete niche space (Duffy et al. 2007; Brose 2008). Furthermore, the presence of IGP splits the feeding activities of predators to more prey or resource species, which, on the one hand, creates many weak interactions and, on the other hand, slows down energy fluxes between trophic levels and weakens top-down pressures. Both patterns were demonstrated to promote community persistence (McCann et al. 1998; Neutel et al. 2002; Rip & McCann 2011). In this case, a positive feedback may be created because a higher diversity also potentially enhances the productivity and biomass of food webs (Schneider et al. 2016; Wang & Brose 2018). Distinguishing cause and effect between biodiversity and functioning is beyond the scope of this study. That said, our results show that the presence of IGP could result in a much stronger correlation between

them. This confirms the recent hypothesis that IGP could weaken the strength of trophic cascades and result in a stronger relation between diversity and productivity in complex food webs, compared to that in simple food chains (Wang & Brose 2018).

Our findings challenge the intuitive hypothesis that the assembly of food webs may be governed by constraints that promote the efficiency of energy delivery across trophic levels (Garlaschelli et al. 2003; Bellingeri and Bodini 2016). In our simulations, as the efficiency of energy transfer increased, i.e. by removing or weakening IGP links, food webs nevertheless have lower diversity, productivity and total biomass. In other words, a higher efficiency could be detrimental for the complexity and functioning of food webs, simply because strong top-down control and trophic cascades can impair the persistence of species (Rosensweig 1971; McCann 2012). This leads us to heuristically propose a balance hypothesis: the assembly of food webs is an outcome of trade-offs between efficiency and persistence. In nutrient-rich conditions, maintenance is more important, and thus IGP contributes to increasing diversity and biomass across trophic levels. In nutrient-limited conditions, energy transfer efficiency is essential for biomass production, and the presence of IGP may cause a decrease of diversity and biomass at higher trophic levels. Our simulation results seem to be consistent with these hypotheses (Fig. 4, Appendix S1: Figs. S5 and S6), but further investigations are needed for a rigorous test.

In his seminal monograph, May (1973) concluded that complexity impaired stability, in contrast with the high diversity and complexity observed in natural ecosystems. While May's prediction was derived in randomly structured ecosystems, many later studies have shown that non-random structures of food webs can enhance the persistence and diversity of species in ecological communities (Jansen & Kokkoris 2003; Brose et al. 2006; Thébault & Fontaine 2010; Tang et al. 2014; Jacquet et al. 2016). Our results add to this discussion by demonstrating the positive effect of another commonly observed structure in natural

communities, namely IGP, which also increased species persistence and yielded higher food-web diversity.

Natural food webs are susceptible to structural changes in the face of global changes, e.g. by species extinction, invasion, and extinction of ecological interactions (Tylianakis et al. 2008; Jordano 2016). This calls urgently for an advanced understanding of the functional implications of food web structure. Our study that reveals the positive role of IGP in the maintenance of biodiversity and functioning, is a new step towards reconciling the structure, diversity and functioning in food webs. Our findings inspire us to develop a balance hypothesis for understanding the assembly of food webs, which emphasizes a balance between energy-transfer efficiency and species persistence, rather than any single aspect. From a thermodynamical point of view, the successional development of systems tends to increase their complexity and the exploitation of energy (Schneider & Kay 1994; Nielsen & Ulanowicz 2000; Neutel et al. 2007), thus species traits that affect IGP, e.g. body size and life stage (Irigoien & de Roos 2011; Schneider et al. 2012), may be selected in the long-term development of ecosystems. Understanding the origination and functional importance of IGP by incorporating evolutionary processes should be a promising direction for future research.

Reference

Arim, M., & Marquet, P. A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecology Letters*, *7*(7), 557-564.

Barbier, M., Arnoldi, J. F., Bunin, G., & Loreau, M. (2018). Generic assembly patterns in complex ecological communities. *Proceedings of the National Academy of Sciences*, 201710352.

Bellingeri, M., & Bodini, A. (2016). Food web's backbones and energy delivery in ecosystems. *Oikos*, *125*(4), 586-594.

Binzer, A., Brose, U., Curtsdotter, A., Eklöf, A., Rall, B. C., Riede, J. O., & de Castro, F. (2011). The susceptibility of species to extinctions in model communities. *Basic and Applied Ecology*, *12*(7), 590-599.

Brose, U. (2008). Complex food webs prevent competitive exclusion among producer species. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1650), 2507-2514

Brose, U., Blanchard, J. L., Eklöf, A., Galiana, N., Hartvig, M., R Hirt, M., *et al*. (2017). Predicting the consequences of species loss using size- structured biodiversity approaches. *Biological Reviews*, 92(2), 684-697.

Brose, U., Williams, R. J., & Martinez, N. D. (2006). Allometric scaling enhances stability in complex food webs. *Ecology Letters*, *9*(11), 1228-1236.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, *31*(1), 343-366.

DeBruyn, A. M., McCann, K. S., Moore, J. C., & Strong, D. R. (2007). An energetic framework for trophic control. In *From energetics to ecosystems: the dynamics and structure of ecological systems* (pp. 65-85). Springer, Dordrecht.

Duffy, J. E., Cardinale, B. J., France, K. E., McIntyre, P. B., Thébault, E., & Loreau, M. (2007). The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters*, *10*(6), 522-538.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... & Marquis, R. J. (2011). Trophic downgrading of planet Earth. *Science*, *333*(6040), 301-306.

Finke, D. L., & Denno, R. F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*, *8*(12), 1299-1306.

Garlaschelli, D., Caldarelli, G., & Pietronero, L. (2003). Universal scaling relations in food webs. *Nature*, *423*(6936), 165.

Holt, R. D., & Polis, G. A. (1997). A theoretical framework for intraguild predation. *The American Naturalist*, *149*(4), 745-764.

Irigoien, X., & de Roos, A. (2011). The role of intraguild predation in the population dynamics of small pelagic fish. *Marine Biology*, *158*(8), 1683-1690.

Jacquet, C., Moritz, C., Morissette, L., Legagneux, P., Massol, F., Archambault, P., & Gravel, D. (2016). No complexity–stability relationship in empirical ecosystems. *Nature Communications*, 7, 12573.

Jansen, V. A., & Kokkoris, G. D. (2003). Complexity and stability revisited. *Ecology Letters*, *6*(6), 498-502.

Jordano, P. (2016). Chasing ecological interactions. *PLoS Biology*, *14*(9), e1002559.

Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the National Academy of Sciences*, *105*(43), 16631-16635.

Levine, J. M., & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, *461*(7261), 254.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., *et al.* (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, *294*(5543), 804-808.

Loreau, M. (2010). *From populations to ecosystems: Theoretical foundations for a new ecological synthesis (MPB-46)*. Princeton University Press, Princeton NJ, USA.

May, R. M. (1973). *Stability and complexity in model ecosystems.* Princeton University Press, Princeton NJ, USA.

McCann, K., & Hastings, A. (1997). Re–evaluating the omnivory–stability relationship in food webs. *Proceedings of the Royal Society of London B: Biological Sciences*, *264*(1385), 1249-1254.

McCann, K., Hastings, A., & Huxel, G. R. (1998). Weak trophic interactions and the balance of nature. *Nature*, *395*(6704), 794.

McCann KS (2012) *Food webs.* Princeton University Press, Princeton NJ, USA.

Mylius, S. D., Klumpers, K., de Roos, A. M., & Persson, L. (2001). Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *The American Naturalist*, *158*(3), 259-276.

Neutel, A. M., Heesterbeek, J. A., & de Ruiter, P. C. (2002). Stability in real food webs: weak links in long loops. *Science*, *296*(5570), 1120-1123.

Neutel, A. M., Heesterbeek, J. A., Van de Koppel, J., Hoenderboom, G., Vos, A., Kaldeway, C., ... & De Ruiter, P. C. (2007). Reconciling complexity with stability in naturally assembling food webs. *Nature*, *449*(7162), 599.

Nielsen, S. N., & Ulanowicz, R. E. (2000). On the consistency between thermodynamical and network approaches to ecosystems. *Ecological Modelling*, *132*(1-2), 23-31.

Oksanen, L., Fretwell, S. D., Arruda, J., & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, *118*(2), 240-261.

Pimm, S. L. (1982). *Food webs*. Springer, Dordrecht.

Poisot, T., Mouquet, N., & Gravel, D. (2013). Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecology Letters*, *16*(7), 853-861.

Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual review of ecology and systematics*, *20*(1), 297-330.

Riede, J. O., Rall, B. C., Banasek-Richter, C., Navarrete, S. A., Wieters, E. A., Emmerson, M. C., *et al.* (2010). Scaling of food-web properties with diversity and complexity across ecosystems. In *Advances in Ecological Research* (Vol. 42, pp. 139-170). Academic Press.

Rip, J. M. K., & McCann, K. S. (2011). Cross- ecosystem differences in stability and the principle of energy flux. *Ecology letters*, *14*(8), 733-740.

Rosenzweig, M. L. (1971). Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science*, *171*(3969), 385-387.

Schneider, E. D., & Kay, J. J. (1994). Complexity and thermodynamics: towards a new ecology. *Futures*, *26*(6), 626-647.

Schneider, F. D., Scheu, S., & Brose, U. (2012). Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters*, *15*(5), 436-443.

Schneider, F. D., Brose, U., Rall, B. C., & Guill, C. (2016). Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications*, *7*, 12718.

Stouffer, D. B., & Bascompte, J. (2010). Understanding food- web persistence from local to global scales. *Ecology Letters,* 13(2), 154-161.

Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, *108*(9), 3648-3652.

Tang, S., Pawar, S., & Allesina, S. (2014). Correlation between interaction strengths drives stability in large ecological networks. *Ecology Letters*, *17*(9), 1094-1100.

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, *329*(5993), 853-856.

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*(12), 1351-1363.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Princeton NJ, USA.

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*.

Wang, S., & Brose, U. (2018). Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters*, *21*(1), 9-20.

Wang, S. (2018) Simplicity from complex interactions. *Nature Ecology & Evolution,* 2, 1201–1202

Table 1. Parameters and their values used in the simulation.

Parameters	Explanation	Values in the five-species module	Values in complex food webs
T	Nutrient supply concentration	100	5, 20, 100, 500
D	Nutrient turnover rate by which the nutrient is refreshed	0.25	0.25
r_i	Mass-specific maximum growth rate of plant species i	0.15	$U[0.05, 0.15]$
k_i	Half-saturation density for the growth rate of plant species i	5	$U[1, 5]$
x_{Pi}	Mass-specific metabolic rate of plant species i	0.02	$U[0.01, 0.03]$
x_{Aj}	Mass-specific metabolic rate of animal species j	0.02	$U[0.01, 0.03]$
e_1	Assimilation efficiency when consuming plants	0.45	0.45
e_2	Assimilation efficiency when consuming animals	0.85	0.85
a_{ji}	The attack rate of consumer species j on resource species i	$a_{ji} = 0.01$, except: $a_{H_1P} = 0.032, a_{H_2P} = 0.03,$ $a_{C_1H_1} = 0.02, a_{C_2H_2} = 0.025$	$U[0.05, 0.1]$ or $U[0.01, 0.02]$, when the resource is plant or animal.
h_{ji}	The handling time of consumer species j on resource species i	10^{-3}	$U[0.5, 1.5]\times10^{-3}$
q	A parameter that determines functional response: type II ($q=1$) and type III ($q=2$)	2	1, 2
c	A parameter that determines the strength of predator interference	0	0.05
ω_{ji}	The preference (i.e. the fraction of time) of consumer species j on resource species i	$\omega_{ji} = \frac{1}{number of resource of j}$, except otherwise specified in figures 2 & 3	$\omega_{ji} = \frac{1}{number of resource of j}$, except otherwise specified in figures 4

Figure 1. IGP in a five-species module (a) and a complex food web (b). The vertical positions of species are mainly determined by the shortest chain length between the focal species and plants, adjusted by their prey-averaged trophic levels. Dashed boxes depict different trophic levels in different colors: plants (green), herbivores (red), carnivores (blue), and secondary carnivores (yellow). Trophic links within each dashed box represent IGPs at different trophic levels.

Figure 2. The dynamics of species biomass (a) and energy fluxes (b) before and after adding an IGP link at the herbivore level, i.e. between H_1 and H_2. In the simulation, we first ran the dynamics of the five-species module without IGP until it reaches equilibrium (on the left of the grey dashed vertical line). Then we add a feeding link between the two herbivores H_1 and H_2, such that H_2 has the same feeding preference on H1 and P ($\omega_{H_2H_1} = \omega_{H_2P} = 0.5$). Food web dynamics were simulated until it reached a new equilibrium (on the right of the grey dashed vertical line). See Appendix S1: Fig. S1 for results under other scenarios of IGP and Appendix S1: Fig. S2 for same data as in (b) exhibited on a logarithmic scale.

Figure 3. The equilibrium species biomass (a-c) and energy fluxes (d-f) with gradually increased strength of IGP: (a,d) IGP at the herbivore level, (b,e) IGP at the carnivore level, and (c,f) IGP at both herbivore and carnivore levels. In the simulation, we simulated the dynamics of the five-species module under different feeding preference on the IGP link (e.g. $\omega_{H_2H_1}$ in (a,d), $\omega_{C_2C_1}$ in (b,e), $\omega_{H_2H_1}$ and $\omega_{C_2C_1}$ in (c,f)). Grey arrows in the five-species modules depict the IGPs, the strength of which was manipulated along the x-axis. See Figure S4 for same data in (d,e,f) exhibited on a logarithmic scale.

Figure 4. Effects of IGP on species diversity (a,d), biomass (b,e) and energy fluxes (c,f) across trophic levels in complex food webs under intermediate ($T = 100$; a,b,c) and very low ($T = 5$; d,e,f) nutrient supply. We manipulated IGP in two ways: (i) randomly removing a proportion of IGP links from the complex food web model generated by the niche model (solid lines), and (ii) gradually reducing the strength of IGP by decreasing the relative feeding preference on IGP resources compared to non-IGP resources for each consumer species (dashed lines). In the first case, all links (either IGP or non-IGP) have same feeding preference. In the second case, the feeding preference on IGP resources is at most as high as that on non-IGP resources (see main text). The x-axis represents the proportion or relative strength of IGP. Each line represents the median value for respective metrics across 500 simulated food webs. The functional response follows Type III (q=2). See Appendix S1: Figs. S5 and S6 for results under other parameters ($T = 20$, 500 and $q = 1$).

Figure 5. Relationships of primary productivity (a,b,c) and total community biomass (d,e,f) with vertical diversity in food webs with many (a,d), few (b,e) and weak (c,f) IGPs. Food webs with many IGP links were originally generated by the food web model (parameters: $T = 100$ and q=2), those with few IGP links were obtained by removing 99% of original IGP links, and those with weak IGP links were obtained by reducing the feeding preference on intraguild preys to 1% of that on the shared resources (see our simulation methods). The vertical diversity is represented by the food web's maximum trophic level. Note that the y-axes are on a logarithmic scale. Lines represent least-square fits, and the coefficient of determinants (r^2) and slopes (b) were shown. See Appendix S1: Fig. S7 for results under parameters $T = 100$ and $q = 1$.

Figure 1

(a)

(b)
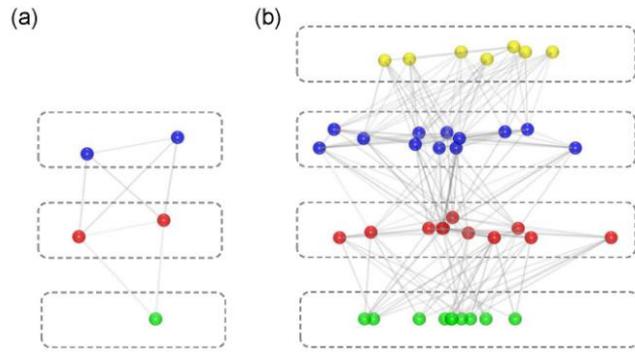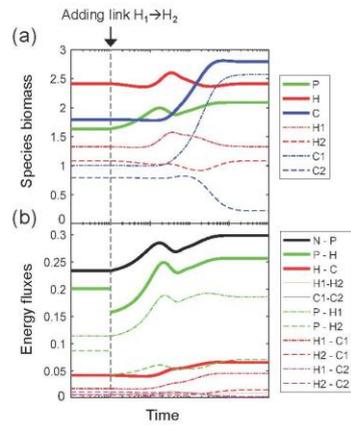
Figure 2

Figure 3

Figure 4

Figure 5