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Weak intra-guild predation facilitates consumer coexistence but does not guarantee higher consumer density

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ABSTRACT

In plant communities, resource partitioning has been shown to facilitate species coexistence and, in turn, enhance community density. Such positive effects of resource partitioning in higher trophic levels are not as obvious possibly due to the occurrence of intra-guild predation (IGP). We thus built a model to explore the joint effects of IGP and resource partitioning on consumer coexistence and their collective density as rarely have studies investigated this joint effect. The model consists of two prey resources that do not directly compete with each other and two consumers that are engaged in IGP and can partition their use of the two prey resources. This model shows that the effects of IGP on consumer coexistence depend on which consumer requires the lower resource density to persist. When the IG predator is the inferior competitor, weak IGP enhances coexistence by lowering the minimum degree of partitioning that is required for coexistence; otherwise, IGP always constrains coexistence. In addition, the effects of IGP on total consumer density (Z_{tot}) depends on which consumer has the lower maximum growth potential, defined as the difference between their maximum growth rate and mortality. Weak IGP increases Z_{tot} when the IG predator has lower maximum growth potential; otherwise, IGP always decreases Z_{tot}. Last, the criterion for IGP to have positive effects on consumer coexistence and Z_{tot} are different. Our results show that weak to intermediate strengths of intra-guild predation can facilitate consumer coexistence and total community density, but consumer coexistence does not guarantee higher consumer density.

1. Introduction

Competition among species for limited resources is thought to be one of, if not the most, important inter-specific interactions that lead species to partition their resources in space or time in order to coexist (Chesson, 2000; Hutchinson, 1961, 1957). When competing species minimize competition through resource partitioning, theoretical studies - most of which developed for plant communities - have demonstrated that the communities with more species can attain higher community functions like more efficient resources use or higher total biomass (Tilman et al. 1997, Loreau 1998, Loreau and Hector 2001). Positive effects of resource partitioning on both species coexistence and community function are believed to also exist in consumer communities (MacArthur, 1958; Schluter, 1993). For example, studies of eel grass systems have shown that more coexisting herbivores species often consumes more algae and thus leads to higher total herbivore biomass (Duffy et al., 2015, 2003; Stachowicz et al., 2007). This positive effect of diverse herbivore species on biomass is believed to result from the fact that different grazer species tend to partition their resource use by occupying different microhabitats and, in turn, allowing them to partition space by foraging on different parts of the eel grass.

While there is evidence that resource partitioning influences both consumer coexistence and the function of a consumer community, it is important to recognize that resource partitioning is not the only factor. Other factors include predator-predator interaction modifications (Sih et al., 1998), predator-predator facilitation (Losey and Denno, 1998), intra-guild predation (Polis et al., 1989; Polis and Holt, 1992) and other forms of omnivory (Pimm and Lawton, 1978). Among these, intra-guild predation is particularly widespread type of interaction, with 86% or more of the taxa in a food web involved in intra-guild predation (Arim and Marquet, 2004). Intra-guild predation (IGP) occurs when one species (the intra-guild (IG) predator) feeds on another one (the intra-guild (IG) prey) with which it also competes for a shared resource (Polis et al., 1989; Polis and Holt, 1992).

Some theoretical studies suggest that IGP can promote the coexistence of consumers, but only under specific conditions. For example,

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the classic IGP model consisting of one basal resource, an IG prey and IG predator, has shown that the IG prey must be superior in resource competition in order for both species to coexist (assessed by the species' R*, defined as the resource level at which population growth rate is zero) (Holt and Polis 1997). This prediction has been supported by more complicated IGP models (Mylius et al. 2001; Kuijper et al. 2003; Tanabe and Namba 2005) as well as by empirical studies that have focused on simple food web configurations (Morin 1999; Diehl and Feißel 2000, 2001).

Theoretical studies further suggest that IGP may be detrimental to the function of a consumer community. The function of a consumer community is often measured as the summed density of consumers (or their resources) in many modeling studies so that predictions are not subject to specific assumptions about how densities are converted to biomass. Most models predict that IGP reduces total consumer density and, in turn, basal resources are relieved from consumption (Holt and Polis, 1997; Revilla, 2002; Rosenheim et al., 1995 and references therein). This prediction makes intuitive sense as predation pressure on IG prey releases the basal resource from top-down control due to a trophic cascade, which is a prediction that has generally been supported by the balance of empirical studies (Vance-Chalcraft et al., 2007). In the current study, we also use the total density of consumers as a proxy for ecological 'function', as this is how prior studies have examined IGP influence on community-level properties of the consumers and their top-down control over prey.

To date, the joint impacts of resource partitioning and IGP on consumer coexistence and density have not been explicitly studied theoretically (but see Holt and Huxel 2007). In fact, coexistence predictions of the classic IGP model were developed under the assumption that the IG prey and predator overlap completely in their resource usage (Holt and Polis 1997). Yet, when resource partitioning has been allowed to occur in empirical studies, either via the use of alternative prey species (Liess and Diehl 2006; Novak 2013) or via spatial-temporal separation of habitat (Amarasekare, 2007a, 2007b), predictions about consumer coexistence from the classic IGP model have not been supported. This suggests that impacts of IGP on coexistence depend on how resource partitioning influences competition among the IGP prey and predator. When resource partitioning is allowed, empirical evidence also lies at odds with the prediction of the classic IGP model regarding the detrimental effect of IGP on total consumer density. Several studies suggest that when the IG prey and IG predator partition their resources, detrimental effects of IGP on the IG prey can be alleviated to the point that the IG predator reaches higher density and suppresses the basal resources more (Janssen et al. 2007; Messelink and Janssen, 2014). Consequently, it is important to study the relative importance of resource partitioning versus IGP in mediating consumer coexistence as well as density if we were to manage the population dynamics and ensuing functions of consumer community (Duffy et al., 2007).

Currently, there are few theoretical studies that explicitly bring together resource partitioning and IGP into a single model to determine how they jointly impact consumer coexistence and total consumer density (but see Daugherty et al. 2007, Holt and Huxel 2007). To this end, we built a model with two consumers engaged in IGP and resource competition for two basal prey species. By doing so, we were able to vary the strength of IGP and resource partitioning simultaneously, which allowed us to accomplish two objectives. First, it allowed us to understand how species coexistence is simultaneously affected by the strength of IGP and by resource partitioning. Based on the general conclusion of most studies of IGP, we anticipated that IGP would constrain consumer coexistence, and that the minimum degree of resource partitioning required for coexistence would monotonically increase IGP strength. Resource partitioning, on the other hand, was expected to alleviate the detrimental effects of IGP on species coexistence. The second objective is to understand the joint effects of IGP strength and resource partitioning on total consumer density at equilibrium where species coexist. We anticipated that the strength of IGP would always suppress total consumer density, but such negative effect would diminish with the increase of resource partitioning.

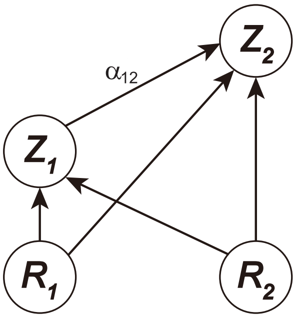

Fig. 1. A schematic diagram showing the interaction among resources and consumers. As described by Eq. 1 to 4, R1 and R2 are the resources and are being consumed by Z_1 (IG prey) and Z_2 (IG predator). Z_1 is then being consumed by Z_2 due to intra-guild predation.

2. Model and analyses

2.1. Model description

The model contained two resource species (R_1 and R_2) as well as two consumer species, IG prey (Z_1) and IG predator (Z_2), that are engaged in IGP (Fig. 1).

The population dynamics of the four species were described by four ordinary differential equations.

$$\frac{dR_1}{dt} = r_1R_1\left(1 - \frac{R_1}{K_1}\right) - s_1c_1R_1Z_1 - (1 - s_2)c_2R_1Z_2, \tag{1}$$

$$\frac{dR_2}{dt} = r_2R_2\left(1 - \frac{R_2}{K_2}\right) - (1 - s_1)c_1R_2Z_1 - s_2c_2R_2Z_2, \tag{2}$$

$$\frac{dZ_1}{dt} = e_1s_1c_1R_1Z_1 + e_1(1 - s_1)c_1R_2Z_1 - \alpha_{12}Z_1Z_2 - m_1Z_1, \tag{3}$$

$$\frac{dZ_2}{dt} = e_2(1 - s_2)c_2R_1Z_2 + e_2s_2c_2R_2Z_2 + f_{12}\alpha_{12}Z_1Z_2 - m_2Z_2\ . \tag{4}$$

Eqs. (1) and (2) described the dynamics of the two shared resource species (R_1 and R_2), which grow logistically with intrinsic growth rates r_1 and r_2 and carrying capacities K_1 and K_2. Both shared resource species were consumed by IG prey (Z_1) and IG predator (Z_2) following a linear functional response with maximum consumption rate, c_i. The s_i parameter manipulated the degree of resource partitioning. For example, when $s_1 = s_2 = 0$ (or 1), the IG prey and predator were complete specialists consuming resource R_2 (or R_1) and R_1 (or R_2), respectively. When $s_1 = s_2 = 0.5$, both IG prey and predator are complete generalists consuming equal amount of both resource species.

Eqs. (3) and (4) described the dynamics of IG prey (Z_1) and IG predator (Z_2). The per capita growth rate of the two consumers were linearly related to consumption rate (c_i) times the assimilation efficiency (e_i). IG prey was also consumed by IG predator with the intraguild predation rate of α_{12} and the assimilation efficiency of f_{12}. Both animal consumer species had a density independent mortality (m_i).

2.2. Model analyses

2.2.1. Species coexistence

Our first objective is to understand the interactive effects of intraguild predation and resource partitioning on species coexistence. We began by analytically solving Eq. (1) through 4 for the non-trivial equilibrium where all four species coexist at positive densities. We then numerically studied the sign of the leading eigenvalue of the Jacobian matrix of the non-trivial equilibrium in a parameter space consisting of

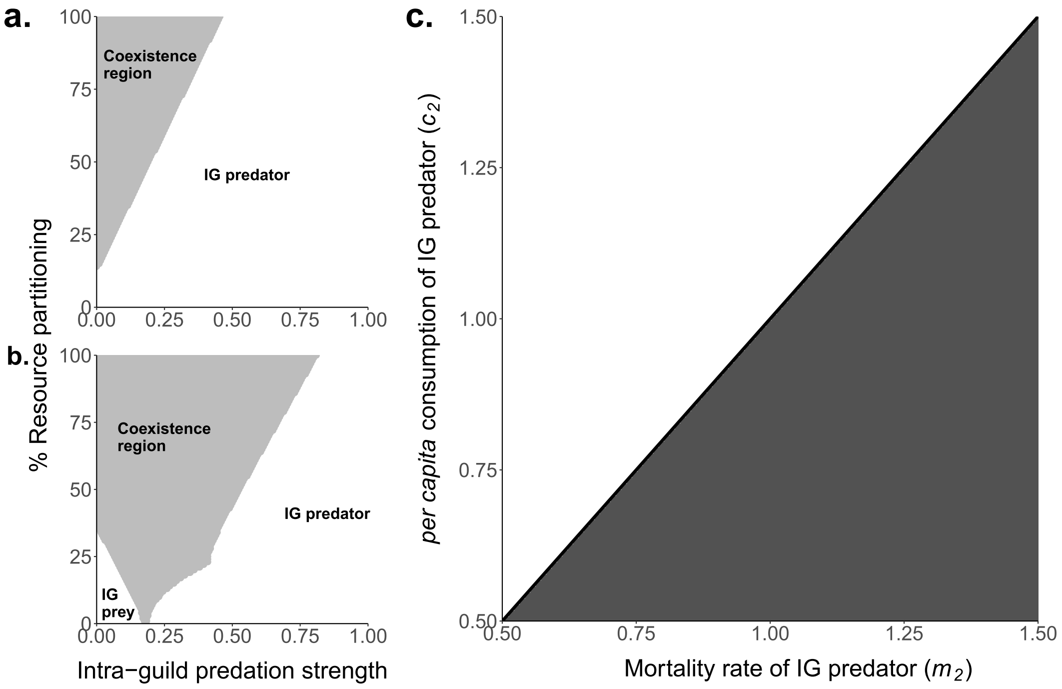

Fig. 2. Panel a. and b. show examples of always negative and first positive and negative effect of IGP (α_{12}) on consumer coexistence. Panel c. shows the region where parameter combinations of IG predator *per capita* consumption rate (c_2) and mortality rate (m_2) lead to either always-negative effect of IGP on coexistence (white region) or first positive and then negative effect of IGP (gray region). In panel a, the *per capita* consumption and mortality of IG predator are 1.2 and 1, which represent the white region of panel c., so that IG prey is the inferior competitor and IGP is always negative to coexistence. In contrast, in panel b. the *per capita* consumption and mortality of IG predator are 0.7 and 1.5, which represent the gray region of panel c., so that weak IGP can facilitate coexistence by lowering the degree of resource partitioning that is required for coexistence. The *per capita* consumption and mortality of IG prey in these two panels are also 1. Text in panel a. and b. represent the competitive outcome between the IG prey and predator. In panel c., the *per capita* consumption (c_1) and mortality (m_1) of IG prey are fixed to be 1, and c_2 and m_2 are varied independently from 0.5 to 1.5. Other parameters are that $r_1 = r_2 = 2.5$, $K_1 = K_2 = 50$, $e_1 = e_2 = 0.3$ and $f_{12} = 1$.

IGP strength (α_{12}; from 0 to 1) and the resource partitioning (s_i; from 0 to 0.5, indicating 100% to 0% partitioning). Specifically, we studied how increasing α_{12} affects the minimum degree of s_i needed to generate negative real parts for the leading eigenvalue (and thus guarantee stable coexistence). If α_{12} always increase the minimum degree of s_i that guarantees stable coexistence, then IGP has detrimental impacts on consumer coexistence because resource partitioning (s_i) is required.

We then performed the above analysis under different competitive hierarchy scenarios among the two consumers because the competitive hierarchy is known to determine species coexistence (Holt and Polis, 1997). Consumers' competitive hierarchy determines which consumer can outcompete the other one if competition is the only interaction among consumers. Therefore, consumers' competitive hierarchy is defined as their R* (i.e., the minimum resource level that still allows consumers to persist) such that the consmer with lower R* reguires lower resource level to persist and thus can outcompete the other one. Consequently, the consumer with lower R* is regard as the superior competitor. To manipulate competitive hierarchy, we assumed that the two shared resource species are identical to the two consumers, $e_1 = e_2$ and $s_1 = s_2$. Making this assumption allowed us to focus only on the benefits of reducing competition via resource partitioning. If two resource species were not identical, the consumer who prefers the resource with high growth rate may gain additional benefits by consuming that resource. Under these assumptions, $\frac{m_i}{e_i c_i}$ directly determined the competitive hierarchy. By fixing the consumption (c_1) and mortality (m_1) of the IG prey and varying that of the IG predator, we manipulated competition hierarchy and then investigated how IGP strength affects consumer coexistence.

2.2.2. Total consumer density (Z_{tot})

To address how intra-guild predation and resource partitioning affects total consumer density (Z_{tot}), we performed a two-step analysis. First, we mathematically analyze how the sum of the two consumer densities at the equilibrium (Z_{tot}) responds to IGP (α_{12}). To do so, we took the derivative of Z_{tot} with respective to the α_{12}, i.e. $\frac{dZ_{tot}}{d\alpha_{12}}$, and used this derivative to describe how total consumer density changes with IGP. If the derivative is negative (positive), then α_{12} will decrease (increase) Z_{tot}. Note that in addition to analytically calculating $\frac{dZ_{tot}}{d\alpha_{12}}$, we also numerically make sure that IG prey and IG predator can stably coexist by performing linear stability analysis (see above). We performed these analyses across the same parameter space of c_2 and m_2.

2.2.3. Parameter value selection

First, to study the effects of IGP strength (α_{12}) and resource partitioning (s_i) on species coexistence, we created the competitive hierarchy by fixing both c_1 and m_1 at 1, and varying c_2 and m_2 between 0.5 and 1.5, respectively. For the parameters related to resources, we picked values that are similar to a ciliate-bacteria system, i.e. $r_1 = r_2 = 2.5$, $K_1 = K_2 = 50$, $e_1 = e_2 = 0.3$ (Laybourn and Stewart 1975, Ratkowsky et al. 1982, Fedrigo et al. 2011). We also set $f_{12} = 1$ as it should not affect the competitive hierarchy. Second, we used the same parameter set ($r_1 = r_2 = 2.5$, $K_1 = K_2 = 50$, $e_1 = e_2 = 0.3$, and $f_{12} = 1$) to assess whether IG prey and IG predator can stably coexist when calculating $\frac{dZ_{tot}}{d\alpha_{12}}$ to study the effects of IGP on consumer density. Finally, to confirm that model results were robust to the above parameter values, we individually increased and decreased c_1 and m_1 by 50% as well as increased and decreased r_i, K_i, e_1, e_2, and f_{12} by 30% in order to relax the identical resource assumption (Appendix B).

3. Results

3.1. Species coexistence

When resource partitioning is explicitly considered in the model, we show that the effects of intra-guild predation (α_{12}) on consumer coexistence is not always disruptive and depends on the competitive hierarchy among consumers.

In Fig. (2)a, we show that the minimum degree of resource partitioning required for consumer coexistence (light gray region) increases monotonically with intra-guild predation, which means IGP always constrains consumer coexistence. On the other hand, in Fig. (2)b, the minimum degree of resource partitioning required for consumer coexistence first decreases and then increases with intra-guild predation. This indicates that IGP first facilitates consumer coexistence by lowering the minimum degree of resource partitioning required for stable coexistence but then constrains coexistence. The two different effects of IGP in Fig. (2)a and b depend on the competitive hierarchy between IG prey and predator (Fig. (2)c). In the upper triangle of Fig. (2)c (white region), the IG predator is the superior competitor because $\frac{m_1}{e_1c_1} > \frac{m_2}{e_2c_2}$. When the IG predator is the superior competitor, some degree of resource partitioning is required to prevent the IG prey from being excluded without intra-guild predation. Allowing intra-guild predation will impose additional negative effects on the IG prey, so more resource partitioning is required to prevent the IG prey from exclusion. Consequently, the minimum degree of resource partitioning required for consumer coexistence always increases with intra-guild predation.

In contrast, in the lower triangle of Fig. (2)c (dark gray region), the IG prey is the superior competitor ($\frac{m_1}{e_1c_1} < \frac{m_2}{e_2c_2}$). In this scenario, the IG prey can outcompete the IG predator without intra-guild predation. Therefore, allowing weak to intermediate intra-guild predation relaxes the IG predator from competition, so that less resource partitioning is required for the IG prey and IG predator to coexist. However, as intra-guild predation increases, the negative impacts of predation on the IG prey becomes too severe so that a higher degree of resource partitioning is required to prevent the IG prey from exclusion. As a result, the minimum degree of resource partitioning required for coexistence first decreases and then increases with intra-guild predation.

3.2. Total consumer density (Z_{tot})

Total consumer density (Z_{tot}) changes with intra-guild predation strength (α_{12}) in two different fashions (Fig. 3a and b).

As we derived in Appendix A, under the assumption that $e_1 = e_2$ and $f_{12} = 1$, the effects of intra-guild predation (α_{12}) on total consumer density (Z_{tot}) depends on the sign of the following expression:

$$[e_1s_1c_1K_1 + e_1(1 - s_1)c_1K_2 - m_1] - [e_2s_2c_2K_2 + e_2(1 - s_2)c_2K_1 - m_2] \tag{5}$$

When Eq. (5) is negative, the sign of $\frac{dZ_{tot}}{d\alpha_{12}}$ is first negative and then positive, indicating that IGP strength (α_{12}) should first decrease and then increase total consumer density (Z_{tot}); otherwise, the sign of $\frac{dZ_{tot}}{d\alpha_{12}}$ is first positive and then negative, indicating that IGP strength should first increase and then decrease total consumer density (see Appendix A for detailed derivation). In Fig. 3a and b, we visualize the two effects of IGP strength (α_{12}) on the total consumer density (Z_{tot}). Note that the patterns shown in Fig. (3)a and (3)b are truncated because the two consumers cannot coexistence if α_{12} is beyond a certain threshold (as shown in Fig. 2). For example, Eq. (5) is negative in Fig. (3)a, so theoretically Z_{tot} should first decrease and then increase with α_{12}; yet, we do not see the increasing part because IG prey and predator cannot coexist when α_{12} starts to increase Z_{tot}.

The criterion differentiating the two effects of IGP strength on total consumer density, i.e. Eq. (5), can be interpreted as the difference between the maximum growth potential of IG prey and IG predator. The maximum growth potential is defined as the highest growth rate a consumer can potentially attain. As shown in Fig. (3)c, Eq. (5) is negative in the upper white region, so that IG prey has lower maximum growth potential and intra-guild predation (α_{12}) will first decrease and then increase total consumer density (Z_{tot}). On the other hand, Eq. (5) is positive in the lower dark gray region of Fig. (3)c, so that IG prey has higher maximum growth potential and intra-guild predation (α_{12}) will first increase and then decrease total consumer density (Z_{tot}). Finally, from different line types in both Fig. (3)a and b, we show that degree of resource partitioning (s_i) diminishes the effect of IGP strength. The more that consumers partition their resource use, the less severe intra-guild predation always decreases (Fig. 3a) or first increase and then decrease (Fig. 3b) total consumer density.

3.3. Effects of IGP on coexistence and consumer density is decoupled

The criteria for the positive effects of IGP on consumer coexistence and on total consumer density are different (Fig. 4).

For consumer coexistence, the criterion is the competitive hierarchy between IG prey and predator (the dashed diagonal line in Fig. 4), while the criterion for total consumer density is the maximum growth potential, i.e. Eq. (5) (the solid slightly sloped line in Fig. 4). Accordingly, region 1 and 4 in Fig. (4) correspond to the dark gray region of Fig. (2)c, where the IG prey is the superior competitor (i.e. $\frac{m_1}{e_1c_1} < \frac{m_2}{e_2c_2}$) and weak to intermediate intra-guild predation facilitates consumer coexistence. In the opposite two regions (2 and 3), intra-guild predation always constrains coexistence. On the other hand, region 3 and 4 in Fig. (4) correspond to the gray region in Fig. (3)c, where the IG prey has higher maximum potential growth rate (Eq. 5 is positive), so that weak to intermediate intra-guild predation positively affect total consumer density. In the two contrasting regions (1 and 2), intra-guild predation always has negative effects on total consumer density. In conclusion, weak to intermediate intra-guild predation can have positive effects on consumer coexistence, but this positive effect does not guarantee higher total consumer density (e.g. in region 1 in Fig. 4).

3.4. Model results robustness

First, for the consumer coexistence, we confirm that competitive hierarchy between IG prey and predator remains the primary criteria distinguishing the two effects of IGP on consumer coexistence after varying c_1, m_1, e_1, e_2, and f_{12} (Fig. B1 and Fig. B2) and relaxing the identical resource assumption (left figure of each panel of Fig. B3 and Fig. B4). Second, for the two types of IGP effects on total consumer density (Z_{tot}), the distinguishing criterion remains to be Eq. (5) after relaxing the identical resource assumption (right figure of each panel of Fig. B3 and Fig. B4). Finally, the two criteria are fundamentally different because the criterion separating effects of IGP on coexistence is about consumer's R* and the other criterion is about consumer's maximum growth potential. Consequently, the effects of IGP on consumer coexistence and density are decoupled and should remain robust to parameter value selection.

4. Discussion

Resource partitioning and intra-guild predation have been proposed to be two prominent factors that govern consumer coexistence and their collective density (Duffy et al., 2007; Schluter, 1993). However, seldom have theoretical studies simultaneously taken these two factors into account to study their joint impacts on consumer coexistence and total consumer density. Our model explicitly considers the two factors simultaneously and show that weak to intermediate levels of intra-guild predation can make consumers more to coexistence more easily (Fig. 2b) and can increase total consumer density (Fig. 3b). However, the model also shows that the positive effect of IGP on consumer coexistence does not guarantee higher collective consumer density (Fig. 4). In the following sections, we compare the positive effect of intra-guild predation on consumer coexistence in our model to previous theoretical studies that also show positive effects of intra-guild predation on consumer population dynamics. We then discuss the synergistic effects of intra-guild predation and resource partitioning on total

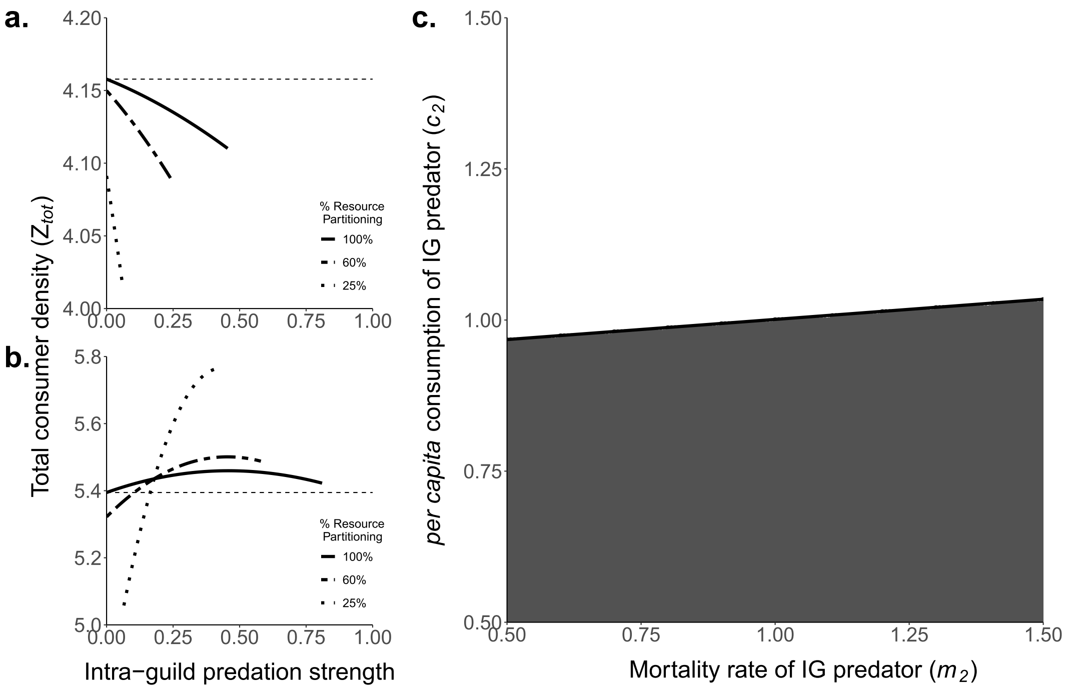

Fig. 3. Panel a. and b. show examples of always negative and first positive and then negative effect of IGP on total consumer density with the horizontal dashed lines representing the Z_{tot} when IGP is zero and resource partitioning is 100%. Panel c. shows parameter combinations leading to always-negative effect of IGP on total consumer density (Z_{tot}; white region) and those leading to first positive and then negative effect of IGP (gray region). In panel a., the *per capita* consumption and mortality of IG predator are 1.3 and 1, which represent the white region of panel c., so that the IG predator has higher maximum growth potential (Eq. 5 is negative) and IGP will always decrease Z_{tot}. On the other hand, in panel b., the *per capita* consumption and mortality of IG predator are 0.7 and 1.5, weak IGP can increase Z_{tot} because IG prey has higher maximum growth potential (Eq. 5 is positive). The *per capita* consumption and mortality of IG prey in these two panels are also 1. In panel c., the *per capita* consumption (c_1) and mortality (m_1) of IG prey are fixed to be 1, and c_2 and m_2 are varied independently from 0.5 to 1.5. Other parameters are the same as listed in Fig. 1.

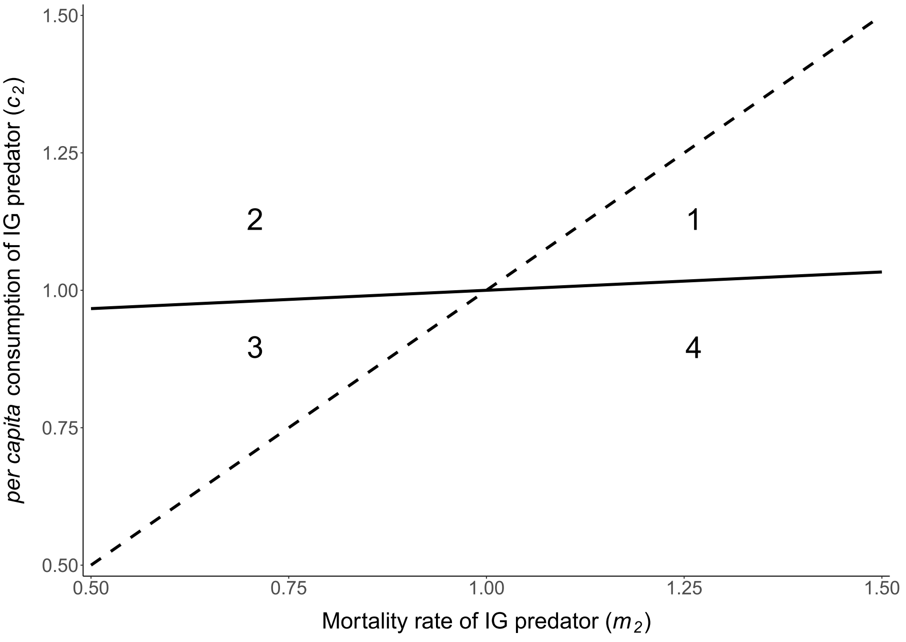

Fig. 4. Schematic figure summarizing decoupled effects of intra-guild predation (IGP) strength on both consumer coexistence and total consumer density at equilibrium (Z_{tot}). Under fixed *per capita* consumption (c_1) and mortality (m_1) of IG prey, IG predator with combinations of c_2 and m_2 in region 1 and 2 would have higher competition free growth rate. Therefore, in region 1 and 2, IGP strength has always-negative effect on Z_{tot}, while in region 3 and 4, IGP strength has first positive and then negative effect on Z_{tot}. In addition, IG predator with combinations of c_2 and m_2 in region 2 and 3 would be competitive inferior. Therefore, in region 2 and 3, IGP strength has always-negative effect on four species coexistence, but in region 2 and 3, IGP strength has first positive and then negative effect.

consumer density as no study has yet reported a positive effect of intra-guild predation on consumer density. Lastly, we discuss implications of the effects of intra-guild predation on consumer coexistence being decoupled from its effect on consumer density (Fig. 4).

4.1. Species coexistence

Our model shows that weak intra-guild predation is not always a stabilizing factor for consumer coexistence (Fig. 2). Only when the IG prey is the superior competitor, weak intra-guild predation becomes a stabilizing factor because it lowers the minimum degree of resource partitioning that is required for coexistence (Fig. 2b); otherwise, intra-guild predation is always destabilizing (Fig. 2a). Both our model and the classic IGP model (Holt and Polis 1997) demonstrate the importance of a competitive hierarchy in determining consumer coexistence. In addition, our finding that intra-guild predation can be

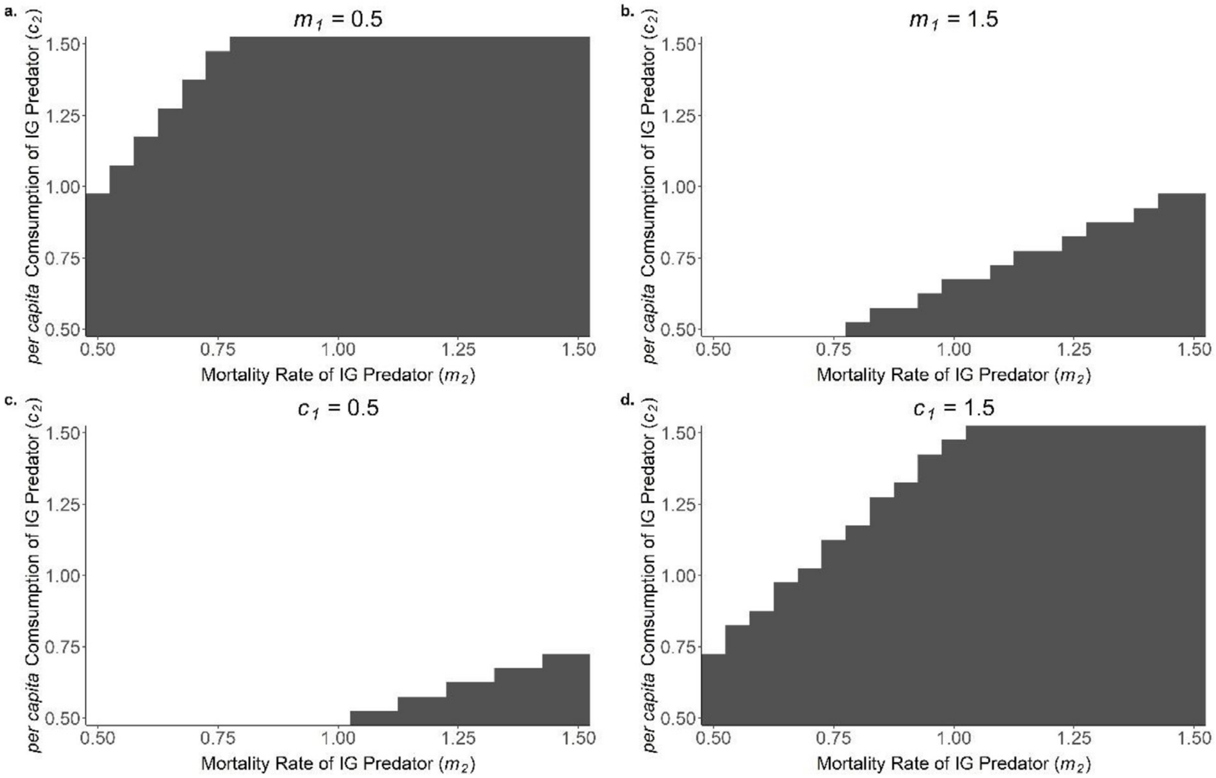

Fig. B1. In this figure, we increase and decrease m_1 and c_1 by 50%. i.e. $m_1 = 0.5$ (panel a) or 1.5 (panel b); $c_1 = 0.5$ (panel c) or 1.5 (panel d), but set other parameter value the same as those in the main text ($r_1 = r_2 = 2.5$, $K_1 = K_2 = 50$, $e_1 = e_2 = 0.3$, $f_{12} = 1$). The grid size of the figure is 0.05 by 0.05. In the unshaded (white) region, IG prey is the inferior competitor ($\frac{m_2}{e_2C_2} < \frac{m_1}{e_1C_1}$), so that IGP is always detrimental to consumer coexistence. In contrast, in the shaded region, IG predator is the inferior competitor ($\frac{m_2}{e_2C_2} > \frac{m_1}{e_1C_1}$), so that IGP can first enhance and then undermine coexistence.

stabilizing is in line with previous theoretical studies that have analyzed the community matrix or implemented bifurcation analyses to demonstrate that intra-guild predation can first stabilize and then destabilize the food web dynamics (McCann and Hastings 1997; McCann et al. 1998; Gellner and McCann 2012).

The positive effects of intra-guild predation on consumer coexistence might also be supported by some empirical studies, although rarely do empirical studies explicitly manipulate the strength of intra-guild predation. Some experiments that show IG prey and predator can coexist when intra-guild predation is weakened by certain mechanisms, such as IG prey taking advantage of habitat refuges from predators (Wissinger et al., 2006) or IG prey defense behavior (Kratina et al., 2010). Based on our model and some implicit empirical evidence, it seems plausible that weak to intermediate intra-guild predation may be a stabilizing factor in food webs when the IG prey is the superior competitor. The positive effect of weak intra-guild predation on consumer coexistence might help explain why intra-guild predation is common in diverse food webs (Arim and Marquet 2004; Thompson et al. 2007).

4.2. Total consumer density (Z_{tot})

Intra-guild predation can also be beneficial to the total density of consumers in our model. We show that weak to intermediate intra-guild predation will increase total consumer density when the IG prey has higher maximum growth potential, i.e. when Eq. 5 is positive. When the IG prey has higher growth potential, the IG prey can recover faster from consumption. By moderately consuming the IG prey, the IG predator can both directly increase its own density and release itself from resource competition. However, the more the IG prey and predator partition their resource use, the less the IG predator will benefit from being released from competition. More resource partitioning will, therefore, diminish the positive effects of IGP on IG predator density. Consequently, the total consumer density at the equilibrium will increase with weak to intermediate intra-guild predation, but such effects diminish as the degree of resource partitioning increase.

However, the positive effect of intra-guild predation on total consumer density should be interpreted with some caution. To the best of our knowledge, no other theoretical study has found a positive effect of intra-guild predation on total consumer density. Theoretical works have long focused on the coexistence of IG prey and predator, but have not focused on the density of consumers or their consumption on basal resources (e.g. Holt et al., 1997, McCann et al., 1998). Second, empirical studies rarely manipulate the strength of intra-guild predation, although non-disruptive effects of intra-guild predation total consumer density have sometimes been reported (Vance-Chalcraft et al., 2007). However, few empirical studies have demonstrated that the same animal species composition consumes more prey and attend higher collective density in structurally complex habitats where IGP is less likely to occur (Snyder et al., 2006) but not in structurally simple habitats (Straub and Snyder, 2006). This empirical evidence implies that intra-guild predation may have a positive impact on total consumer density. To better understand how intra-guild predation strength impacts the density of consumers, theoretical studies should focus more on the responses of consumer density and not just the stability of the food web. Moreover, more empirical studies are needed to examine the effects of intra-guild predation strength *per se*, and not just the occurrence of intra-guild predation on the density of the consumer community.

4.3. Effects of IGP on coexistence and community density are decoupled

According to our model, the criterion for intra-guild predation to have a positive impact on consumer coexistence differs from that for total consumer density (Fig. 4). The separate criteria for coexistence

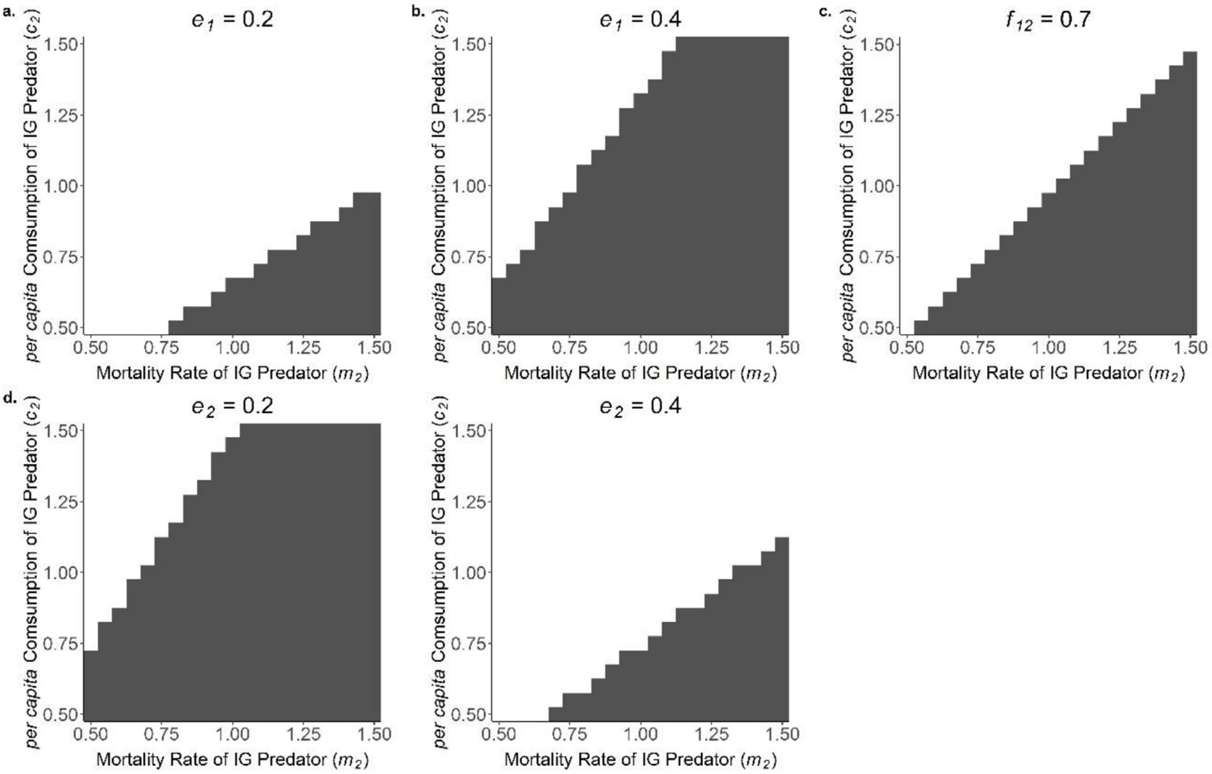

Fig. B2. In this figure, we increase and decrease e_1 and e_2 by 30% (panel a to d) and decrease f_{12} by 30% (panel e), but set other parameter value the same as those in the main text ($m_1 = 1$, $c_1 = 1$, $r_1 = r_2 = 2.5$, $K_1 = K_2 = 50$). The grid size of the figure is 0.05 by 0.05. In the unshaded (white) region, IG prey is the inferior competitor ($\frac{m_2}{e_2 C_2} < \frac{m_1}{e_1 C_1}$), so that IGP is always detrimental to consumer coexistence. In contrast, in the shaded region, IG predator is the inferior competitor ($\frac{m_2}{e_2 C_2} > \frac{m_1}{e_1 C_1}$), so that IGP can first enhance and then undermine coexistence.

and total consumer density suggest that coexistence does not guarantee higher density. By decoupling consumer coexistence and their community density, our study offers an important view to understand species coexistence and their collective density. Modern coexistence theory (Chesson, 2000) predicts that when species coexist, either through increasing "niche difference" or through decreasing "relative fitness difference", higher total density should be attained in a system (Carroll et al., 2011; Turnbull et al., 2013). However, modern coexistence theory assumes that competition is the only inter-specific interaction that occurs among species. When intra-guild predation occurs in a community, the belief that species coexistence always leads to a higher density of the community needs to be re-evaluated. Our model demonstrates that weak intra-guild predation can facilitate species coexistence, but will either increase or decrease total animal density depending on the biological characteristics of the IG prey and predator. It is, therefore, important to consider these complex interactions or other complex feeding behaviors that cannot be accurately modeled by a linear functional response when studying the factors mediating the density of animal communities. Consequently, we call for a closer combination of theoretical and empirical works to better link consumer coexistence and the density of a consumer community with the underlying complex inter-specific interactions among animals.

Author credit

Feng-Hsun Chang: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - original draft preparation and Editing

Po-Ju Ke: Formal analysis, Investigation, Writing-Original draft preparation and Reviewing

Bradley Cardinale: Supervision, Writing-reviewing

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A: Deduction of Eq. 5

In this document, we show the analyses of the summed density of IG prey and predator at the coexistence equilibrium (Z_{tot}) and investigate how it is affected by intra-guild predation (α_{12}). To do so, we first show the analytical solution of the four species at the equilibrium as follow:

$$R_1^* - \frac{K_1}{r_1}[r_1 - s_1 c_1 Z_1^* - (1 - s_2) c_2 Z_2^*] = 0, \tag{A.1}$$

$$R_2^* - \frac{K_2}{r_2}[r_2 - s_2 c_2 Z_2^* - (1 - s_1) c_1 Z_1^*] = 0, \tag{A.2}$$

$$e_1 s_1 c_1 R_1^* + e_1 (1 - s_1) c_1 R_2^* - \alpha_{12} Z_2^* - m_1 = 0, \tag{A.3}$$

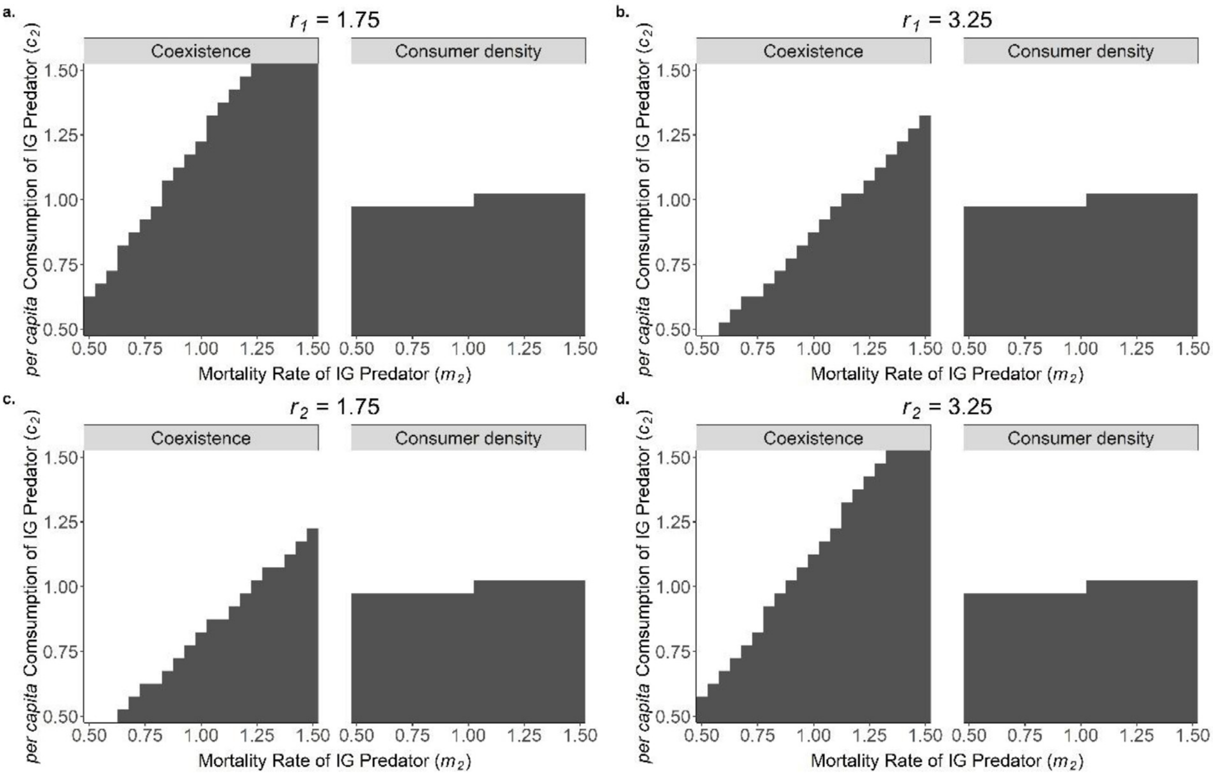

Fig. B3. In this figure, we increase and decrease r_i by 30%, i.e. $r_1 = 1.75$ (panel a), $r_1 = 3.25$ (panel b), $r_2 = 1.75$ (panel c), $r_2 = 3.25$ (panel d), but set other parameter value the same as those in the main text ($m_1 = 1$, $c_1 = 1$, $K_1 = K_2 = 50$, $e_1 = e_2 = 0.3$, $f_{12} = 1$). The grid size of the figure is 0.05 by 0.05. In the left figure of each panel, the unshaded (white) region is where IGP (α_{12}) always increase the minimum degree of resource partitioning needed to allow stable coexistence. On the other hand, in the shaded region, IGP (α_{12}) first decrease and then increase the minimum degree of resource partitioning needed to allow stable coexistence. In the right figure of each panel, the unshaded (white) region is where IG predator has higher maximum growth potential, i.e. Eq. 5 is negative, so that IGP is always decrease total consumer density. In contrast, the shaded region is where IG predator has lower maximum growth potential, i.e. Eq. 5 is positive. IGP therefore first increase and then decrease total consumer density in this region.

$$e_2 s_2 c_2 R_2^* + e_2(1 - s_2)c_2 R_1^* + f_{12}\alpha_{12} Z_1^* - m_2 = 0. \tag{A.4}$$

From Eq. A.1 and A.2, we can express the resource density at the coexistence equilibrium as $R_i^* = \frac{K_i}{r_i}[r_i - s_i c_i Z_i^* - (1 - s_j)c_j Z_j^*]$, where $i = 1$ or 2. We substitute R_1^* and R_2^* in Eq. A.3 and A.4 with our expression and derive the following two equations:

$$e_1 s_1 c_1 K_1 + e_1(1 - s_1)c_1 K_2 - m_1 - \frac{e_1 s_1^2 c_1^2 K_1 Z_1^*}{r_1} - \frac{e_1 s_1(1 - s_2)c_1 c_2 K_1 Z_2^*}{r_1} - \frac{e_1(1 - s_1)s_2 c_1 c_2 K_2 Z_2^*}{r_2} - \frac{e_1(1 - s_1)^2 c_1^2 K_2 Z_1^*}{r_2} = \alpha_{12} Z_2^*, \tag{A.5}$$

$$e_2 s_2 c_2 K_2 + e_2(1 - s_2)c_2 K_1 - m_2 - \frac{e_2 s_2^2 c_2^2 K_2 Z_2^*}{r_2} - \frac{e_2(1 - s_1)s_2 c_1 c_2 K_2 Z_1^*}{r_2} - \frac{e_2 s_1(1 - s_2)c_1 c_2 K_1 Z_1^*}{r_1} - \frac{e_2(1 - s_2)^2 c_1^2 K_1 Z_2^*}{r_1} = -f_{12}\alpha_{12} Z_1^*. \tag{A.6}$$

Let $e_1 s_1 c_1 K_1 + e_1(1 - s_1)c_1 K_2 - m_1 = \mu_1$ and $e_2 s_2 c_2 K_2 + e_2(1 - s_2)c_2 K_1 - m_2 = \mu_2$, so that we can rewrite Eq. A.5 and A.6 as:

$$\mu_1 = Z_1^*\left[\frac{e_1 s_1^2 c_1^2 K_1}{r_1} + \frac{e_1(1 - s_1)^2 c_1^2 K_2}{r_2}\right] + Z_2^*\left[\frac{e_1 s_1(1 - s_2)c_1 c_2 K_1}{r_1} + \frac{e_1(1 - s_1)s_2 c_1 c_2 K_2}{r_2}\right] + \alpha_{12} Z_2^*, \tag{A.7}$$

$$\mu_2 = Z_1^*\left[\frac{e_2 s_1(1 - s_2)c_1 c_2 K_1}{r_1} + \frac{e_2(1 - s_1)s_2 c_1 c_2 K_2}{r_2}\right] + Z_2^*\left[\frac{e_2(1 - s_2)^2 c_1^2 K_1}{r_1} + \frac{e_2 s_2^2 c_2^2 K_2}{r_2}\right] - f_{12}\alpha_{12} Z_1^*. \tag{A.8}$$

We then redefine the terms within brackets as $A = \frac{e_1 s_1^2 c_1^2 K_1}{r_1} + \frac{e_1(1 - s_1)^2 c_1^2 K_2}{r_2}$ and $B = \frac{e_1 s_1(1 - s_2)c_1 c_2 K_1}{r_1} + \frac{e_1(1 - s_1)s_2 c_1 c_2 K_2}{r_2}$ for Eq. A.7, and as $C = \frac{e_2 s_1(1 - s_2)c_1 c_2 K_1}{r_1} + \frac{e_2(1 - s_1)s_2 c_1 c_2 K_2}{r_2}$ and $D = \frac{e_2(1 - s_2)^2 c_1^2 K_1}{r_1} + \frac{e_2 s_2^2 c_2^2 K_2}{r_2}$ for Eq. A.18. From here, the density of IG prey, IG predator, and their total density (i.e., Z_1^*, Z_2^*, and Z_{tot}, respectively) can be solved in terms of A, B, C, D, μ_1, and μ_2 as:

$$Z_1^* = \frac{\mu_2(B + \alpha_{12}) - \mu_1 D}{(C - f_{12}\alpha_{12})(B + \alpha_{12}) - AD}, \tag{A.9}$$

$$Z_2^* = \frac{\mu_1(C - f_{12}\alpha_{12}) - \mu_2 A}{(C - f_{12}\alpha_{12})(B + \alpha_{12}) - AD}, \tag{A.10}$$

$$Z_{tot} = F(\alpha_{12}) = Z_1^* + Z_2^* = \frac{\mu_1(C - f_{12}\alpha_{12} - D) + \mu_2(B + \alpha_{12} + A)}{(C - f_{12}\alpha_{12})(B + \alpha_{12}) - AD} \tag{A.11}$$

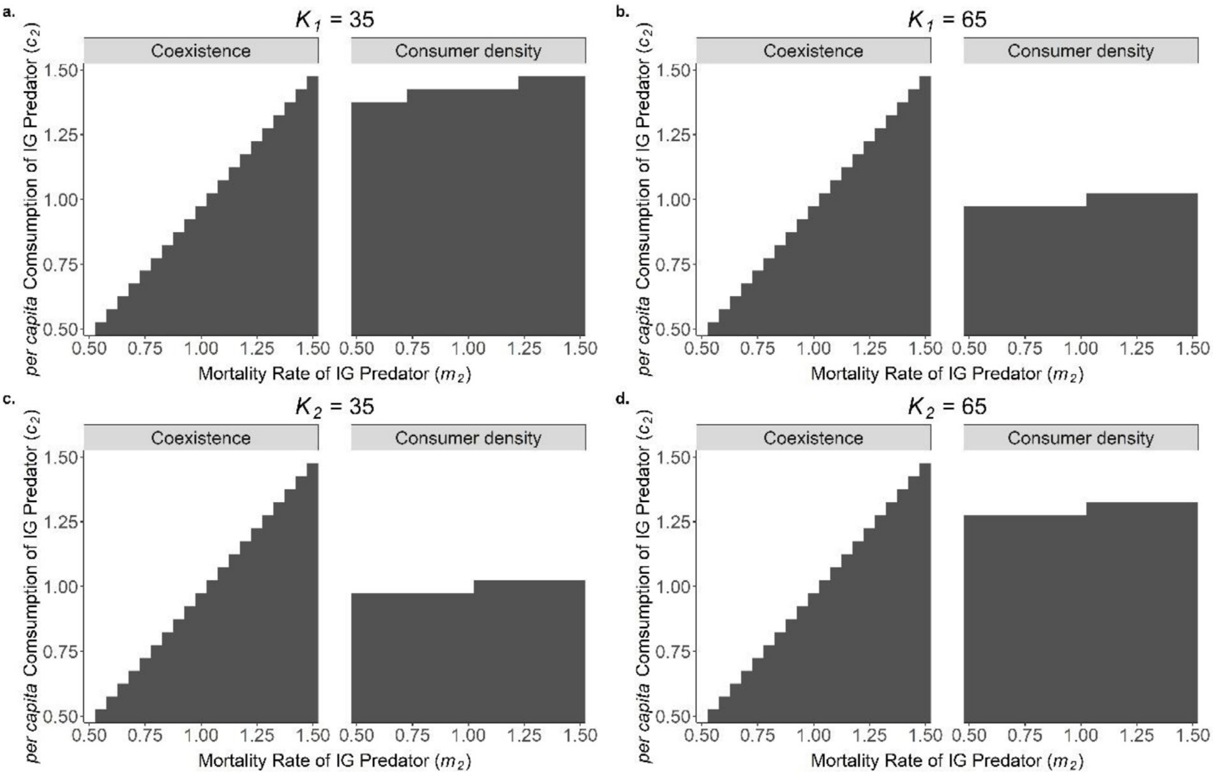

Fig. B4. In this figure, we increase and decrease K_i by 30%, i.e. $K_1 = 35$ (panel a), $K_1 = 65$ (panel b), $K_2 = 35$ (panel c), $K_2 = 65$ (panel d), but set other parameter value the same as those in the main text ($m_1 = 1$, $c_1 = 1$, $r_1 = r_2 = 2.5$, $e_1 = e_1 = 0.3$, $f_{12} = 1$). The grid size of the figure is 0.05 by 0.05. In the left figure of each panel, the unshaded (white) region is where IGP (α_{12}) always increase the minimum degree of resource partitioning needed to allow stable coexistence. On the other hand, in the shaded region, IGP (α_{12}) first decrease and then increase the minimum degree of resource partitioning needed to allow stable coexistence. In the right figure of each panel, the unshaded (white) region is where IG predator has higher maximum growth potential, i.e. Eq. 5 is negative, so that IGP is always decrease total consumer density. In contrast, the shaded region is where IG predator has lower maximum growth potential, i.e. Eq. 5 is positive. IGP therefore first increase and then decrease total consumer density in this region.

The key of our analytical treatment is that we set A, B, C, D, μ_1, and μ_2 independent to α_{12} and f_{12}, which simplifies later calculations. As we are interested in how total consumer density (Z_{tot}) is affected by the strength of intra-guild predation (α_{12}), we can define Z_{tot} as a function of α_{12}, i.e., $F(\alpha_{12})$, and take its derivative in respect to α_{12}:

$$\frac{dZ_{tot}}{d\alpha_{12}} = \frac{dF(\alpha_{12})}{d\alpha_{12}} = \frac{-f_{12}(f_{12}\mu_1 - \mu_2)\alpha_{12}^2 + 2f_{12}[(C-D)\mu_1 - (B-A)\mu_2]\alpha_{12} + \{(f_{12}\mu_1 - \mu_2)(AD - BC) - (Bf_{12} - C)[(C-D)\mu_1 - (B-A)\mu_2]\}}{[(C - f_{12}\alpha_{12})(B + \alpha_{12}) - AD]^2}. \tag{A.12}$$

Mathematically, Z_{tot} will increase with α_{12} in the range of α_{12} that lets Eq. A.(12) > 0, but will decrease with α_{12} if Eq. A.12 < 0. To address our second hypothesis regarding the effects of α_{12} on Z_{tot}, we need to study the sign of Eq. A.12, which is determined by its numerator because the denominator is always positive. In addition, Eq. A.(12) will not have vertical asymptotes if $e_1 = e_2$ and $f_{12} = 1$. This is because B = C under these simplifications and the denominator becomes $[-f_{12}\alpha_{12}^2 - (AD - BC)]^2$. Since the term within the bracket will always be negative because $AD - BC = \frac{K_1K_2}{r_1r_2}e_1e_2c_1^2c_2^2(1 - s_1 - s_2)^2 > 0$, it will have no real roots and the denominator of Eq. A.12 will always be defined (i.e., no vertical asymptotes). For analytical tractability, we follow the assumption that $e_1 = e_2$ and $f_{12} = 1$ and focus on the numerator of Eq. A.12, which from here we define as $G(\alpha_{12})$.

The next step is to judge 1) if $G(\alpha_{12})$, which is a quadratic function of α_{12}, has two real roots, 2) the sign of these two roots, and 3) the opening of $G(\alpha_{12})$. If $G(\alpha_{12})$ does not have two real roots, its direction of opening determines whether Eq. A.12 will be always positive or always negative: if $G(\alpha_{12})$ concaves up (or down), it will be always positive (or negative) so that Z_{tot} will always increase (or decrease) with α_{12}.

If $G(\alpha_{12})$ does have two real roots, the opening of $G(\alpha_{12})$ determines how the sign of Eq. A.(12) changes with α_{12}: if $G(\alpha_{12})$ is a concave upward function, Eq. A.(12) will first be positive, then negative, and finally positive again with increasing α_{12}; if $G(\alpha_{12})$ is a concave downward function, Eq. A.(12) will first be negative, then positive, and finally negative again. Therefore, the opening of $G(\alpha_{12})$ determines how Z_{tot} is being affected by α_{12}. If $G(\alpha_{12})$ concaves up, increasing α_{12} will first cause Z_{tot} to increase, then decrease, and finally increase again. In contrast, if $G(\alpha_{12})$ concaves down, increasing α_{12} will cause Z_{tot} to first decrease, then increase, and finally decrease again. Finally, in addition to the opening direction of $G(\alpha_{12})$, we also need to consider the sign of its two roots because the domain of $G(\alpha_{12})$ should be restricted to $\alpha_{12} > 0$ (i.e., the strength of intra-guild predation cannot be negative).

First, we can judge if the two roots are real numbers with the discriminant of $G(\alpha_{12})$. The two roots are real numbers when the discriminant is positive. Let $a' = -f_{12}(f_{12}\mu_1 - \mu_2)$, $b' = 2f_{12}[(C-D)\mu_1 - (B-A)\mu_2]$, and $c' = (f_{12}\mu_1 - \mu_2)(AD - BC) - (Bf_{12} - C)[(C-D)\mu_1 - (B-A)\mu_2]$. The discriminant can be expressed as follow:

$$b'^2 - 4a'c' = 4f_{12}^2[(C-D)\mu_1 + (B-A)\mu_2]^2 + 4f_{12}(f_{12}\mu_1 - \mu_2)[(f_{12}\mu_1 - \mu_2)(AD - BC) - (Bf_{12} - C)[(C-D)\mu_1 - (B-A)\mu_2]]. \tag{A.13}$$

With the assumption that $e_1 = e_2$ and $f_{12} = 1$, Eq. A.13 can be simplified (because $Bf_{12} - C = 0$) as:

$$b'^2 - 4a'c' = 4[(C - D)\mu_1 + (B - A)\mu_2]^2 + 4(\mu_1 - \mu_2)^2(AD - BC). \tag{A.14}$$

Eq. A.14 is always positive because both the squared terms and $AD - BC$ are positive. This means that $G(\alpha_{12})$ will always have two real roots, which means α_{12} will either increase, decrease and then increase Z_{tot}, or decrease, increase, and then decrease Z_{tot}, depending on the opening of $G(\alpha_{12})$. We then went on to judge the sign of the two real roots. The sign of the two roots can be judged by the product of the two roots, $\frac{c'}{a'} = \frac{AD - BC}{-f_{12}}$, which is negative since $AD - BC$ is positive. This means $G(\alpha_{12})$ has one positive (α') and one negative real root (α''). However, negative α_{12} are beyond our discussion because intra-guild predation cannot be negative. Accordingly, increasing α_{12} will cause Z_{tot} to either first increase and then decrease (if $G(\alpha_{12})$ concaves down), or first decrease and then (if $G(\alpha_{12})$ concaves up). Finally, the opening direction of $G(\alpha_{12})$ is determined by the sign of a′: $G(\alpha_{12})$ concaves down if $f_{12}\mu_1 > \mu_2$ but concaves up if $f_{12}\mu_1 < \mu_2$.

Replacing μ_1 and μ_2 with the parameters of the model, when $f_{12}\mu_1 > \mu_2$, which means $f_{12}[e_1S_1C_1K_1 + e_1(1 - S_1)C_1K_2 - m_1] > [e_2S_2C_2K_2 + e_2(1 - S_2)C_2K_1 - m_2]$, intra-guild predation (α_{12}) will first increase and then decrease total animal density (Z_{tot}). However, there must exist a threshold of α_{12} beyond which the intra-guild predation is too strong to allow the four species to coexist (i.e., the coexistence equilibrium is no longer stable). On the other hand, when $f_{12}\mu_1 < \mu_2$, which means $f_{12}[e_1S_1C_1K_1 + e_1(1 - S_1)C_1K_2 - m_1] < [e_2S_2C_2K_2 + e_2(1 - S_2)C_2K_1 - m_2]$, intra-guild predation (α_{12}) will first decrease and then increase total animal density (Z_{tot}). Similarly, there must exist a threshold of α_{12} beyond which the intra-guild predation is too strong to allow the four species to coexist. Therefore, it is possible that for the intra-guild predation (α_{12}) to only decrease total animal density (Z_{tot}).

Appendix B

In this appendix, we show a serious of figures demonstrating sensitivity analyses mentioned in Section 2.3 (Parameter value selection). First, we assess whether the competitive hierarchy is still the criterion distinguishing always negative and first positive and then negative effect of IGP on consumer coexistence when increasing and decreasing m_1 and c_1 by 50% and e_i and f_{12} by 30% ($m_1 = 0.5$ or 1.5; $c_1 = 0.5$ or 1.5; $e_1 = 0.2$ or 0.4, $e_2 = 0.2$ or 0.4, and $f_{12} = 0.7$). From Fig. B1 and Fig. B2, we see that boundary in these figures all correspond to the competition hierarchy between IG prey and predator. The unshaded upper triangle is where IG prey is the inferior competitor ($\frac{m_2}{e_2C_2} < \frac{m_1}{e_1C_1}$), so that IGP is always detrimental to consumer coexistence. In the shaded triangle, IG predator is the inferior competitor ($\frac{m_2}{e_2C_2} > \frac{m_1}{e_1C_1}$), so that IGP can first enhance and then undermine coexistence.

In addition, in Fig. (B3) and Fig. (B4), we relaxed the identical resource assumption by varying r_i and K_i. Specifically, we independently increase and decrease r_i and K_i by 30% ($r_1 = 1.75$ or 3.25, $r_2 = 1.75$ or 3.25, $K_1 = 35$ or 65, and $K_2 = 35$ or 65) to see if competitive hierarchy is still the criterion separating two types of IGP effects on coexistence (left figure of each panel) and maximum growth potential is still the criterion separating two types of IGP effects on consumer density (right figure of each panels). Regarding consumer coexistence, competitive hierarchy is still the primary criterion separating always negative and first positive and then negative effect of IGP (left figure of each panel). However, because the resources are not identical, the competitive hierarchy is determined by resources' rates along with consumers' consumption and mortality. For the two types of IGP effects on consumer density, the distinguishing criterion was not affected by resources' growth rate (r_i; right figure of each panel of Fig. B3) but their carrying capacity (K_i; right figure of each panel of Fig. B4). This indicated that Eq. (5) remains the criterion separating the two effects of IGP on total consumer density (Z_{tot}).

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