Title

Prey preference of top predators manipulates the functioning and stability of multi-trophic ecosystems

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Declarations of interest

None

Abstract

The relationship between biodiversity and ecosystem functioning, and the mechanisms underpinning the food web stability, have been intensively investigated in ecological research. The ubiquities of generalists in natural food webs and its important role in dictating these ecosystem properties have been generally recognized. However, how competition between multiple top predators shape these ecosystem properties and determine the success of invasive predators remain largely unexplored. Here, we use a well-developed food web model to investigate the effects of prey preference of top predators on ecosystem functioning and food web stability in both local and invasive conditions. We design several modeling scenarios to mimic combinations of different types of top predators (specialist/generalist) and their origins (local/invasive). Our model theoretically shows that lower exploitation competition for prey between top predators (with distinct prey preferences featured by higher attack rates) would be beneficial for the ecosystem functioning and food web stability. We also demonstrate that the success of top predator invasion depends on the prey preference of both local and invasive top predators. Sensitivity analysis on the model further supports our findings. Our results highlight the importance of prey preference of multiple top predators in manipulating the properties of multi-trophic ecosystems. Our findings may have important implications because the current ongoing global changes profoundly change the phenology of many biological systems and create trophic mismatch, which may manipulate prey preference of top predators and in turn deteriorate ecosystem functioning and food web stability.

Keywords: Prey preference; Top predator; Invasive species; Food web stability; Ecosystem functioning

1. Introduction

The relationship between biodiversity and ecosystem functioning is one of the fundamental topics in ecological research for a long history (Hooper et al., 2005; Loreau, 2010; Loreau et al., 2001). One general consensus is that biodiversity positively affects ecosystem functioning in terms of indicators such as ecosystem productivity and energy efficiency (Tilman et al., 2014). However, this critical finding is limited in one single trophic level, particularly in the plant community. Recent advances in theoretical research have extent the scope of this framework towards multi-trophic systems and complex food webs. Key findings are such that there is an exponential relationship between primary production and maximum trophic level in multi-trophic systems (Wang and Brose, 2018), and that intraguild predation in complex food web is beneficial for biodiversity and ecosystem functioning, as well as their relationships (Wang et al., 2019).

Another central topic in ecology is to address the mechanisms underlying how the food web stability responses to food web structure and complexity (Kéfi et al., 2019; May, 1972). Here we follow the definition of the 'resistance stability' (as reviewed in McCann (2012)) that the stability of a food web quantifies the change of the system after a perturbation. One major finding is that trophic interaction in food webs is composed of a few strong and many weak interactions, and food web stability is governed by those weak interaction strengths in long trophic loops, such as omnivore cycles characterized by biomass pyramids (McCann et al., 1998; Neutel et al., 2002; O'Gorman and Emmerson, 2009). Increasing complexity in food webs does not necessarily relate to changing stability because of the low predator-prey biomass ratios in the omnivorous loops (Neutel et al., 2007). On the other hand, diversity in both horizontal and vertical trophic levels influence food web stability (Zhao et al., 2019). Predator-prey body mass

ratios, which determine the interaction strength, are also critical in stabilizing natural ecosystems (Brose et al., 2006a; Brose et al., 2006b; Kalinkat et al., 2013). Furthermore, coupling of fast and slow energy channels by top predators is demonstrated to be crucial to confer food web stability (Moore et al., 2004; Rooney et al., 2006).

Intriguingly, in both research topics aforementioned, generalists are always involved by mechanisms e.g. intraguild predation, omnivore cycles, and fast/slow channels of top predators. In fact, the role of generalists in shaping biodiversity, food web stability and ecosystem functioning has been extensively investigated. Omnivores in food webs, as typical generalists, slow down the energy flow between trophic levels, thereby dampening top-down control (DeBruyn et al., 2007). As a result, species at low trophic levels are released from predations and become more efficient in building up biomass. However, contrast findings are demonstrated that multi-chain omnivorous fish in lakes stabilize the food web via enabling strong and persistent top-down control (Vadeboncoeur et al., 2005). In addition, omnivore mechanisms, namely, the changes in the degree of trophic omnivore between preys, is one of the three structural mechanisms that determine the changes in food-chain length (Post and Takimoto, 2007). Furthermore, as a key feature of generalist predators, prey preference is also found as the key to eliminate chaos and to induce food web stability (Post et al., 2000). Overall, effects of generalists on food webs are presumably drastic but currently far from conclusive.

One major challenge for current ecological research is to improve our understanding on the role of generalist predators in mediating properties of food webs with more than one carnivore predator, regarding food web stability and ecosystem functioning (Wang and Brose, 2018). Previous theoretical studies usually consider only one top carnivore predator (Attayde et al., 2010; Post et al., 2000), whereas the situations of more than one top carnivore predators are

generally overlooked. However, in natural ecosystems, it is common to have more than one top predators, which act as either specialists or generalists. It is still unclear how the prey preference of predators at the same trophic level (top) may shape their competition and how this competition may in turn affect the ecosystems. In addition, competition of predators exists among local predators and also between local and invasive predators. It remains debatable which factors fundamentally determine the success of invasion (Romanuk et al., 2009; Zhang and van Kleunen, 2019). As a key trait of the top predators, the role of prey preference in driving their invasive success to local habitats remains unexplored.

We hypothesize that prey preference has significant impact on the ecosystems driven by local or invasive carnivore top predators. We refer to ecosystem functioning as ecosystem productivity (i.e. biomass of species) and material/energy flux (Tilman et al., 2014). Specifically, our hypotheses are: 1) ecosystem functioning and food web stability will all increase if top generalist predators have distinct prey preference from their specialist counterparts (i.e. higher preference on other preys); 2) ecosystem functioning and food web stability will be maximized if top carnivore predators have distinct preference on different preys of higher attack rates; and 3) the success of invasive carnivore predators depends on the prey preference of both invasive and local top predators.

To address our hypotheses, we use a food web model adopting well-acknowledged principles of trophic interactions to theoretically investigate the effects of prey preferences of top carnivore predators on multi-trophic ecosystems. We design several scenarios to mimic combinations of different types of top predators (specialist/generalist) and their allocations (local/invasive). We found significant role of prey preference in dictating ecosystem functioning and food web stability in most scenarios. Our results may contribute to recognizing the role of

generalist top predators in food webs and may provide implications for more complex ecosystems.

2. Materials and methods

2.1 The food web model

We use a food web model (Wang et al., 2019) that adopts the widely accepted principles in literature. The model is composed of one nutrient (*N*), one plant species (*P*) at trophic level I, two herbivores (H_1 and H_2) at trophic level II, and two carnivores (C_1 and C_2) at trophic level III.

In particular, the dynamic of the nutrient (*N*) is described by:

$$\frac{dN}{dt} = D(T - N) - rGP \quad (1)$$

where *D* is the nutrient refresh rate, *T* is the nutrient supply rate, and *r* is the mass-specific maximum growth rate of plant *P*. *G* is the growth correction factor of the plant by the nutrient *N*, which is calculated as:

$$G = \frac{N}{N + k} \quad (2)$$

where *k* is the half-saturation nutrient concentration of plant growth.

The dynamic of the plant species (*P*) is described by:

$$\frac{dP}{dt} = rGP - \sum_i H_i F_{iP} - x_P P \quad (3)$$

where functional response F_{iP} denotes the consumption rate of herbivore H_i on the plant *P*:

$$F_{iP} = \frac{\omega_{iP}\alpha_{iP}P^q}{1 + c \cdot H_i + \omega_{iP}\alpha_{iP}h_{iP}P^q} \quad (4)$$

where ω_{iP}, h_{iP} and α_{iP} quantify the feeding preference, handling time, and attack rate of consumer H_i on plant *P*, respectively. *c* represents the strength of predator interference, *q* denotes

the type of functional response (Type II: q=1; Type III: q=2), and x_P is the mass-specific metabolic rate of the plant P.

The dynamics of the two herbivore species (H_1 and H_2) are described by:

$$\frac{dH_i}{dt} = e_1 H_i F_{iP} - \sum_k e_2 C_k F_{ki} - x_{Hi} H_i \quad (5)$$

where e_1 and e_2 are the assimilation efficiency when consuming plant and animals, respectively, x_{Hi} is the mass-specific metabolic rate of the herbivore H_i. Functional response F_{ki} denotes the consumption rate of consumer carnivore C_k on the herbivore H_i:

$$F_{ki} = \frac{\omega_{ki}\alpha_{ki}H_i^q}{1 + c \cdot C_k + \sum_i \omega_{ki}\alpha_{ki}h_{ki}H_i^q} \quad (6)$$

The dynamics of the two carnivore species (C_1 and C_2) are described by:

$$\frac{dC_k}{dt} = \sum_i e_2 C_k F_{ki} - x_{Ck} C_k \quad (7)$$

where x_{Ck} is the mass-specific metabolic rate of the carnivore C_k.

Definitions and values of all parameters in the food web model are provided in Table 1. Following Wang et al. (2019), we assume that H_1 has a higher attack rate than H_2 when feeding on plant P, and C_1 and C_2 are better predator on H_1 and H_2, respectively.

2.2 Model simulations

We design four food web configurations with different combinations of top predators: (A) one local generalist, one local specialist, (B) two local generalists, (C) one local specialist, one invasive generalist and (D) one local generalist, one invasive generalist. We perform five groups of model scenario simulations (#S1-#S5) to investigate how prey preference of predators

manipulates the food web structure, stability and ecosystem functioning under different food web configurations (A-D) (Fig. 1).

For #S1, we change the prey preference of C_1 on H_1 ($\omega_{C_1H_1}$) from 0.1 to 0.9 at a step of 0.1, while prey preference of C_1 on H_2 ($\omega_{C_1H_2}$) is assigned as the value subtracting $\omega_{C_1H_1}$ from 1.0. Meanwhile, C_2 remain as the specialist that that prey on H_2 only ($\omega_{C_2H_2}$= 1.0 and $\omega_{C_2H_1}$ = 0.0). This simulation corresponds to the configuration 'A' in order to test the impact of prey preference in a relatively simple food web architecture.

For #S2, similar simulation is conducted, whereas we change the prey preference of C_2 on H_2, and we keep C_1 as the specialist and the prey preference of C_1 on H_1 as constant ($\omega_{C_1H_1}$= 1.0). #S2 is designed to confirm the outcomes from #S1 so that it is part of configuration 'A'.

For #S3, this simulation corresponds to the configuration 'B'. With two generalists (C_1 and C_2), prey preferences of C_1 and C_2 on H_1 ($\omega_{C_1H_1}$ and $\omega_{C_2H_1}$) are varied from 0.1 to 0.9 at a step of 0.1. All combinations of $\omega_{C_1H_1}$ and $\omega_{C_1H_2}$ are used for individual model simulations.

For #S1-S3, the model is run for 5,000 time steps when the model outcomes are considered to reach equilibrium. The values of all the state variables and fluxes between each pair of functional groups are extracted as the representative of the equilibrium.

For #S4 and #S5, C_1 is considered as the local predator. C_2 is provided as the invasive predator but initially not exists by assigning the prey preferences of C_2 on both H_1 and H_2 to zero. In #S4, this simulation corresponds to the configuration 'C', and C_1 is a specialist that only preys H_1 ($\omega_{C_1H_1}$= 1). Meanwhile, in #S5, this simulation corresponds to the configuration 'D'. C_1 is a generalist that preys on both H_1 and H_2 ($\omega_{C_1H_1}$= $\omega_{C_1H_2}$= 0.5). For #S4 and #S5, the model is first run for 5,000 time steps, which results in zero biomass of C_2 at equilibrium. The final values for the state variables for the 5,000 steps are used as the initial values of the subsequent

simulation. Then, the prey preferences of C_2 on H_1 and H_2 are assigned as (1) $\omega_{C_2H_1}$ = 1.0, $\omega_{C_2H_2}$ = 0.0; (2) $\omega_{C_2H_1}$ = 0.5, $\omega_{C_2H_2}$ = 0.5; and (3) $\omega_{C_2H_1}$ = 0.0, $\omega_{C_2H_2}$ = 1.0. The model is run for another 5,000 time steps. The outputs at the last time step are used as the final equilibrium.

All model simulations, stability calculation and sensitivity analysis (see below) are performed in MATLAB (MathWorks, 2010) using the GRIND for MATLAB (http://www.sparcs-center.org/grind).

2.3 Food web stability analysis

We use eigenvalue as the indictor for food web stability. We consider the (Jacobian) community matrix $A=[a_{ij}]$ of the food web model, in which the elements (a_{ij}) quantify the interaction strengths between species i and j. The maximum eigenvalue (S_{max}) is the eigenvalue of matrix A with the largest real part, which determines the dynamics of the community near the equilibrium. The equilibrium is stable when the real part of S_{max} is negative, i.e. the system always moves back to equilibrium after perturbations. The smaller the real part of S_{max}, the more stable the system is. On the other hand, the complex part of the S_{max} determine whether the system fluctuates near the equilibrium. It has been widely used to determine the local stability of a modeled ecosystem (Neutel et al., 2002; Nilsson et al., 2018). For each simulation above, we first calculate the Jacobian matrix for the system at equilibrium. Then, we calculate the eigenvalues of the Jacobian matrix. In this way, we assess the variation of the local stability of the system among different simulations with distinct prey preference as described above.

2.4 Sensitivity analysis

196 To better understand the impact of prey preference on model predictions, we perform
197 sensitivity analysis for all the parameters in the food web model. The Morris classification
198 screening method, a widely applied local sensitivity analysis method (Morris, 1991), is used for
199 the present study. In specific, we implement a 'perturbation' near the value of a parameter by
200 multiplying the value with a factor randomly sampled between 0.9 and 1.1 with uniform
201 distribution, while we keep other parameters unchanged. We use the variations of model outputs
202 at the equilibrium to evaluate the sensitivity. For each parameter, we perform the 'perturbation'
203 with 1,000 iterations. The coefficient of sensitivity (*Cs*) for one parameter is calculated by a
204 multivariate analysis of the parameter sensitivity (Klepper, 1997). The model is simulated for
205 5,000 time steps in each individual run, and the outputs at the final time step are used to calculate
206 *Cs*.
207

208 # 3. Results and discussion

209 ## *3.1 One local generalist and one local specialist as top predators*

210 From #S1, we find profound effects of the prey preferences of the top predator on the
211 ecosystem (Fig. 2). We assume that C_1 is a generalist and C_2 is a specialist on H_2. When C_1 has a
212 higher preference on H_2 rather than H_1 ($\omega_{C_1H_1}$=0.1), the food web is dominated by P and H_1. The
213 competition between C_1 and C_2 on H_2 ends up in the absence of all of the three components.
214 Intriguingly, with increasing preference of C_1 on H_1, biomass of C_1, C_2, H_2 and P start to grow.
215 In particular, the increasing P denotes an enhanced ecosystem productivity. Due to increasing
216 predation pressure from C_1, biomass of H_1 starts to decline. The system reaches a state with the
217 coexistence of all the components when $\omega_{C_1H_1}$ becomes higher than 0.8. In addition, our model
218 indicates that when $\omega_{C_1H_1}$ increases, flux from P to H_2 becomes higher whereas the flux from P

to H_1 remains relatively stable. These two fluxes approach to an equivalent level. Flux from H_1 to C_1 surpasses the input from H_2 to C_1. Meanwhile, flux from H_2 to C_2 gradually increases. In terms of food web stability, we find an evident increase trend with increasing $\omega_{C_1H_1}$, suggesting that the food web is more stable when preference of C_1 on H_1 becomes higher. Likewise, in the #S2 where the prey preference of C_2 ($\omega_{C_2H_2}$) is manipulated, similar patterns are observed as those in #S1 (Fig. 3).

Our model suggests that when a food web has two top predators, i.e. one specialist and one generalist, the ecosystem functioning and food web stability all become higher when the generalist predates on the prey other than the one for the specialist. Our results imply that an ecosystem with higher species richness could be more stable as long as the system is configured in a way that different predators consume the preys with relatively higher attack rate than other predators. That is to say, the complex system can be stable when all species find their own ecological niche. Our results therefore highlight the importance of prey preferences by top predators in dictating the food web properties.

3.2 Two local generalists as top predators

From #S3, we observe significant impact of the prey preference of C_1 and C_2 (as two local generalists) to their preys (H_1 and H_2) on the ecosystem, in terms of biomass distribution at equilibria (Fig. 4) and food web stability (Fig. 5). We find that different components show maximum biomass at different combinations of $\omega_{C_1H_1}$ and $\omega_{C_2H_1}$, while the maximum total biomass and food web stability occur when $\omega_{C_1H_1}$ is the maximum (0.9) and $\omega_{C_2H_1}$ is the minimum (0.1). This finding implies that when C_1 and C_2 predominately predate on separate

preys of higher attack rate (H_1 and H_2, respectively), the ecosystem exhibits the highest ecosystem functioning (total production) and food web stability.

#S3 is considered as the extension of #S1 and #S2, because #S1 and #S2 are simply the approximation of the very left column (when $\omega_{C_2H_2} = 1$) and very bottom row (when $\omega_{C_1H_1} = 1$) of the model outcomes in Fig. 3 and Fig. 4, respectively. Serving as a global evaluation, we find interesting patterns in #S3, such that the maximum biomass of P and C_1 occur when $\omega_{C_1H_1}$ is the maximum value (0.9) and $\omega_{C_2H_1}$ is the minimum (0.1), whereas maximum biomass of H_1, H_2 and C_2 occur at other different parameter combinations. In specific, H_1 peaks when both C_1 and C_2 mainly prey on H_2 ($\omega_{C_1H_1} = \omega_{C_2H_1} = 0.1$), and H_2 peaks when both C_1 and C_2 mainly prey on H_1 ($\omega_{C_1H_1} = \omega_{C_2H_1} = 0.9$). For C_2, the biomass is high when C_1 mainly preys on H_1 so that the competition for resource would be low. However, the peak values occur when C_1 mainly preys on H_2 and C_2 has roughly an equivalent preference between H_1 and H_2 ($\omega_{C_2H_1} = 0.6$). In this case, biomass of C_1 becomes very low primarily because the advantage of C_2 on predating H_2. As a result, C_1 is outcompeted by C_2 and more resource become available to C_2 to support its maximum biomass.

Another interesting pattern is that food web stability is generally higher among the lower triangular matrix of the heat map than that on the upper triangular matrix (Fig. 5). The lower triangular matrix represents conditions when the top predators (generalists) predates more on the preys with higher attack rates. On the contrary, the upper triangular matrix corresponds to those scenarios when the top predators (generalists) have to predate on the preys with low attack rates. Food web stability therefore become lower in general on the upper triangular matrix, but still could become equivalent to those at the lower triangular matrix, only when one predator is predating the unfavored prey and the other predator has an equal preference among the preys.

We observe that food web stability undergoes a shift along the main diagonal of the matrix (Fig. 5), so does the food web composition (Fig. 4). This outcome is in concert with previous finding in shallow lake ecosystems using theoretical modeling by PCLake (Kuiper et al., 2015), in which a critical transition in food web stability occur with increase nutrient loading into the lake. Our results therefore confer the existence of nonlinear shift in food web stability, and further imply that prey preference of top predators may be an important driver of shifts in food web stability in general.

Our results partially comply with earlier findings that weak links in the food web are the main mechanisms for the stability in complex systems (Neutel et al., 2002; Neutel et al., 2007), but we suggest that prey preference should be also considered in dictating food web stability. As our model shows, the weak links are not influential on the food web stability when the predators have higher preference on their favored preys (i.e. higher attack rates). We reconcile the relation between prey preference, interaction strength and food web stability as follows: one food web is stable when weak links in the long loops exist. However, the food web could be more stable when top predators (C_1 and C_2 here) focus on one prey, ignore the others, and thereby has less but strong links within the food web. Nevertheless, when one predator have to switch its prey preference to the unfavored prey, the weak link theory come into play, as the food web stability will become higher when the other predator has a more diverse prey preference and thereby establishing more weak links in the food web. Our results may make a step forward to a more comprehensive understanding on the relation between stability and other features of food webs such as interaction strength.

It is worth noting that distribution of the stability is not completely symmetric (Fig. 4), primarily due to the asymmetric distributions of attack rates on H_1 and H_2 from C_1 and C_2,

287 respectively (Table 1). The highest stability is when $\omega_{C_1H_1}$ = 0.9 and $\omega_{C_2H_1}$ = 0.1 (the bottom left
288 point in Fig. 5), whereas the lowest stability is when $\omega_{C_1H_1}$ = 0.1 and $\omega_{C_2H_1}$ = 0.8. Our model
289 suggests that the food web become most vulnerable when the top predators start to predate on
290 preys with relatively low attack rates.
291
292 ***3.3 Invasive generalists as top predators***
293 We find that the success of invasive species depends on the prey preference of both the
294 invasive species and the local species. For #S4 (Fig. 6), C_1 acts as a local specialist on H_1. Before
295 the invasion of C_2, the food web is oscillating as a typical Lokta-Volterra type predator-prey
296 interaction, which is featured by low biomass of C_1, and approximately two times higher of H_2
297 than H_1 likely due to the predation by C_1. Our model predicts that the food web remains
298 unchanged if C_2 invades the food web at t=5,000 with exactly the same prey preference as C_1,
299 which is attributed to the lower attack rate of C_2 on H_1 and therefore lower competitively of C_2.
300 This implies that top predator invasion will not be successful if the invasive species has exactly
301 the same ecological niche as the local predator.
302 However, one invasive predator (C_2) with the equal preference on H_1 and H_2, or with the
303 total preference on H_2, ends up in successful invasions (Fig. 6). We observe substantial increases
304 in not only the invasive species C_2, but also in *P* and C_1. The new node in the food web (C_2)
305 increases the primary production of the ecosystem. This is because *P* is more efficient in
306 exploring the nutrient sources and therefore has a higher biomass, which in turn increase the
307 biomass at higher TLs including C_1. Simultaneously, a significant decline in the biomass of H_2 is
308 observed, possibly due to predation from C_2. This result indicates that invasive species do not

necessarily replace the local species. Instead, they could co-exist and ultimately increase the local ecosystems functioning.

On the other hand, from #S5, we find that the change in local biomass of one successful invasion would be lower when the local top predator (C_1) is a generalist that has equivalent preference on both preys (Fig. 7). When the invasive predator (C_2) has a full preference on H_1, or equivalent preference on both H_1 and H_2, the invasion ends up in failure. The invasion only become successful when C_2 has a total preference on H_2. However, the magnitude of changes among different components is much lower comparing to the results in #S4, e.g. the increase in P after the invasion of C_2 is much less significant.

Intriguingly, shifts in the food web dynamics do not occur immediately after the invasion of C_2, but rather lag behind after the invasion. For example, in #S4, the shift in food web takes place at time step of ~8,000 and ~6,000 when the invasive C_2 is a generalist and specialist, respectively (Fig. 6). In #S5, the shift occurs at ~8,000 (Fig. 7). The length of the time lag in shifts of food web composition in response to the invasion of C_2 could be attributed to both the prey preference of the invasive and the local predators. Our results also imply that the ecosystems exhibit resilience before final collapse when being confronted with external stresses.

3.4 Sensitivity analysis

Sensitivity analysis on all the model parameters (excluding c due to zero value, and C_1H_2 and $\omega_{C_2H_1}$ because they are subtracted values of $\omega_{C_1H_1}$ and $\omega_{C_2H_2}$ from 1.0, respectively) shows that those parameters denoting prey preference of top predators ($\omega_{C_1H_1}$ and $\omega_{C_2H_2}$) both impose significant impact on the biomass of most model components at ecological equilibrium (Fig. 8). Nonetheless, $\omega_{C_1H_1}$ and $\omega_{C_2H_2}$ do not rank the top influential ones comparing to other parameters

such as r and x_{C1}. Summary of absolute *Cs* values of $\omega_{C_1H_1}$ and $\omega_{C_2H_2}$ are 0.33 and 0.24, while the highest value is 0.55 (r). Besides, these two parameters in general have higher influence on the preys (H_1 and H_2) than the predators (C_1 and C_2). Intriguingly, our analysis shows that the absolute *Cs* of $\omega_{C_1H_1}$ and $\omega_{C_2H_2}$ are relatively higher for H_1 and H_2, respectively (Fig. 8), suggesting that the prey preference of top predators would be more influential to their preys with higher attack rate than the other preys. Overall, the results of sensitivity analysis further support our findings on the importance of prey preference of top predators on the food webs.

3.5 Limitations and perspectives

There are several limitations in our modeling approach. First, our model does not take into account the effect of predator-prey body-mass ratio on the prey preference allometry, which in turn becomes critical in dictating the functional response parameters in food web models (Kalinkat et al., 2011). Body-mass ratio between predator and prey manipulates handling time, attack rates and ultimately the type of functional response. Consequently, given the myriads of interactions in natural ecosystems, our model may be oversimplified in terms of functional response. Body-mass-ratio-inclusive food web model (Brose et al., 2006a) needs to be considered for the generality of our conclusions. Second, our modelling approach represents a relatively simple configuration of a food web, whereas networks in natural ecosystems could be far more complex. Whether our findings on the impact of prey preference would apply in complex food webs remains uncertain. Generator of theoretical food webs based on an allometric variant of the niche model (Schneider et al., 2016) would be critical to generalize our findings to more complex food webs, which is a promising direction for future research. Third, for the complex food web modeling, it would be highly valuable to adopt the emerging concept of

355 community weighted mean (CWM) of body-size (or body-mass) as the community trait
356 composition within the multi-trophic ecosystems. Defined as the average of each trait value
357 weighted by relative abundance (Garnier et al., 2004; Laigle et al., 2018), CWM of trait values is
358 found better in predicting ecosystem functions than other functional metrics (Cohen et al., 2014;
359 Laughlin, 2011).

360 Our results highlight the importance of prey preference of top predators in manipulating
361 the properties of multi-trophic ecosystems. We show that theoretically, lower exploitation
362 competition for prey between top predators, and top predators with distinct prey preferences that
363 in favor of preys with higher attack rates, would be beneficial for the ecosystem in all aspects.
364 We also demonstrate that the success of top predator invasion depends on the prey preference of
365 both local and invasive top predators.

366 Our modeling results comply with empirical approaches showing the predominant effects
367 of prey preference of generalist predators on the population dynamics of multi-trophic systems
368 (Venzon et al., 2001). In practice, overlap in prey preference could trigger negative interactions
369 among predators when used together in biological control of pests in agroecosystems (Buitenhuis
370 et al., 2010). Effective natural enemy should exhibit a high degree of prey preference
371 (Manwaring et al., 2020), and our findings here imply that such prey specificity is beneficial to
372 the local ecosystem because the target pest communities are usually weakly preyed before the
373 introduction of their natural enemy. Apparently, more experimental studies are needed to allow
374 for more general conclusions on the effects of prey preference of generalist predators. Besides, it
375 would be interesting to explore the regime when a local generalist predator switches its
376 preference between local and invasive alien prey (Jaworski et al., 2013) and the model behavior
377 under a gradient of nutrient input and primary productivity (Faria and da Silveira Costa, 2010).

Our approach may have important implications because the current ongoing global changes, including both habitat loss due to human activities and climate warming, may profoundly change the phenology of many biological systems and creating trophic mismatch in a seasonal scale. For example, human activities increase trophic niche overlap of carnivores and thereby trigger interspecific competition (Manlick and Pauli, 2020). Besides, on-going global change may substantially manipulate the phenology of plant community at lower trophic levels (Cleland et al., 2007; Fei et al., 2014) and enhance the systematic predator preference allometry (Kalinkat et al., 2011), which may impose pressure to switch prey preference of predators at higher trophic levels. Consequently, specialist species may have to extend their diet compositions to become generalists, generalists need to change their prey preference, and invasion of external species may be stimulated. As we have shown here, switch in the prey preference of the top predators (when they compete with other top predators) may end up with tremendous effects on the multi-trophic ecosystems regarding food web stability and ecosystem functioning.

4. Conclusion

Our theoretical modeling approach implies that prey preference of top predators pose profound effects on multi-trophic ecosystems in both local and invasive conditions. We demonstrate that ecosystem functioning and food web stability will all increase if top predators have distinct prey preference from their specialist counterparts (i.e. higher preference on other preys), and will be maximized if top predators have full preference on different preys of higher attack rates. In addition, we show that the success of top predator invasion depends on the prey preference of both local and invasive top predators. For many multi-trophic ecosystems

confronting ongoing global changes, in particular the agroecosystems, the ubiquities of multiple generalist predators and the impending need for biological control of pests via introducing natural enemy call for more in-depth understanding of the generalist predators, for which our findings on the importance of the prey preference could be highly relevant.

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Table 1 List of parameters and values in the food web model

Parameters	Definition	Value
ω_{ji}	Feeding preference of predator *j* on prey *i*	Specified in this study
T	Nutrient supply rate	100
D	Nutrient turnover rate	0.25
r	Mass-specific maximum growth rate of plant *P*	0.15
k	Half-saturation nutrient concentration of plant growth	5
x_P	Mass-specific metabolic rate of the plant *P*	0.02
x_{Hi}	Mass-specific metabolic rate of the herbivore H_i	0.02
x_{Ci}	Mass-specific metabolic rate of the carnivore C_i	0.02
e_1	Assimilation efficiency when consuming plant	0.45
e_2	Assimilation efficiency when consuming animals	0.85
C	Strength of predator interference	0
Q	Type of functional response (Type II: q=1; Type III: q=2)	2
h_{ji}	Handling time of predator *j* on prey *i*	10^{-3}
a_{ji}	Attack rate of predator *j* on prey *i*	$a_{H_1P} = 0.032$; $a_{H_2P} = 0.03$; $a_{C_1H_1} = 0.02$; $a_{C_1H_2} = 0.01$; $a_{C_2H_1} = 0.01$; $a_{C_2H_2} = 0.02$;

Figure

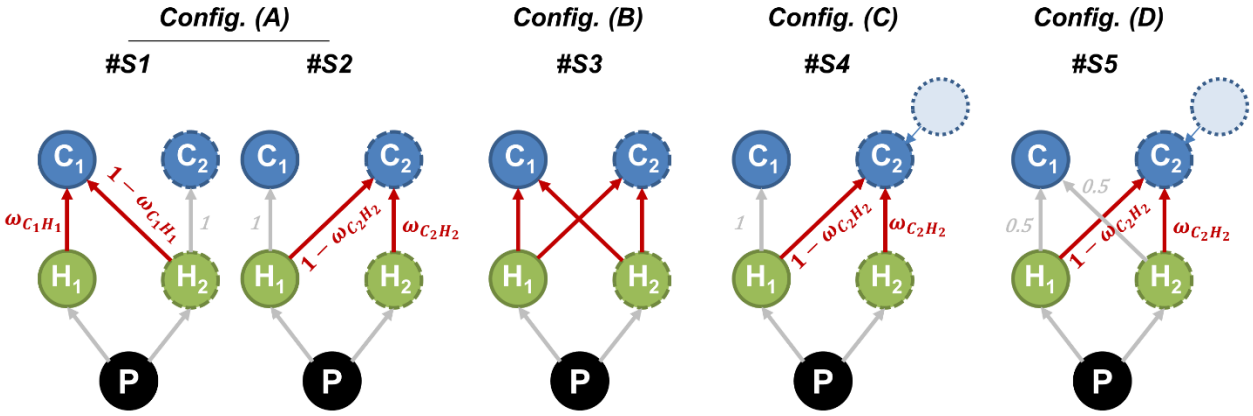
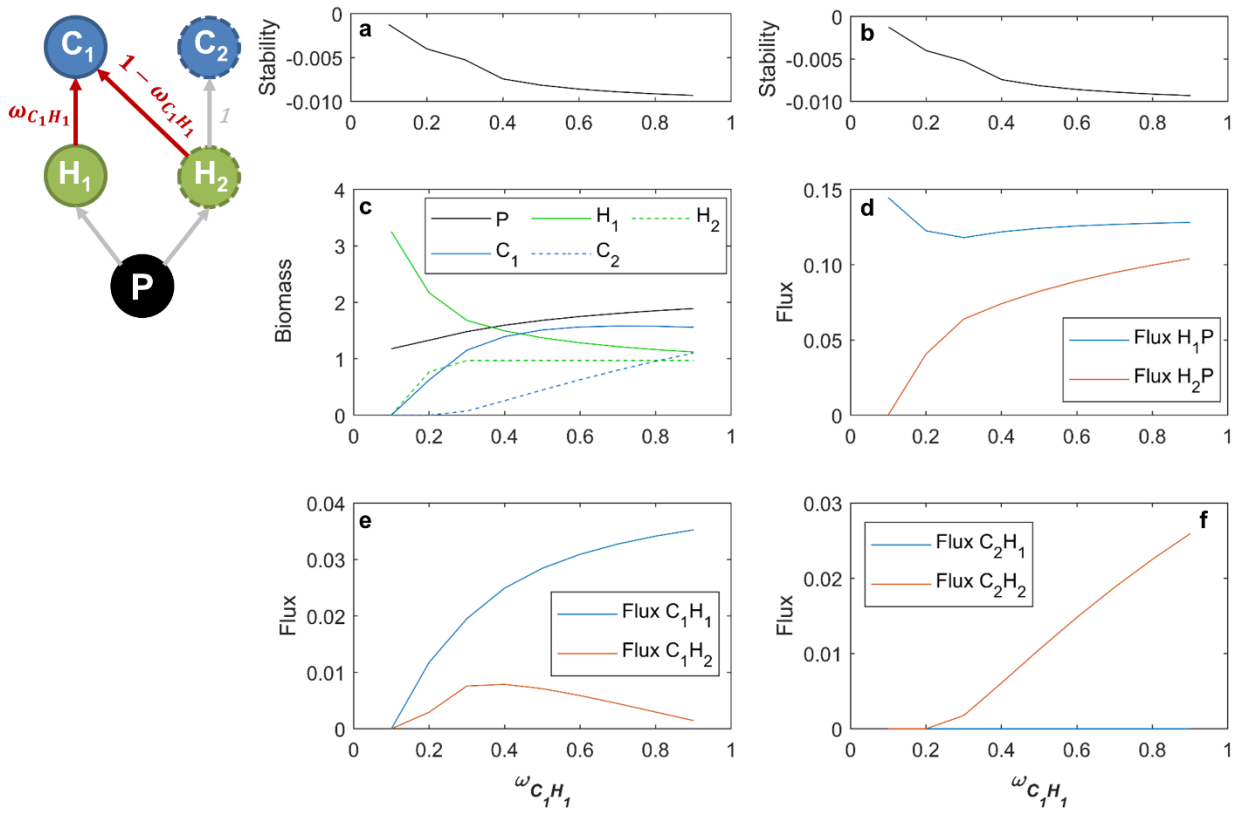


Figure 1. Diagram of the food web model configuration (A-D) and simulation (#S1-#S5) in the present study. The circles represent the components in the food web including top predators (C_i), herbivore (H_i) and plant species (P), colored depending on the trophic level. The parameter $\omega_{C_iH_i}$ denotes the prey preference of C_i on H_i. The arrows in red are varied in the simulation, while the arrows in grey remain constant.



524

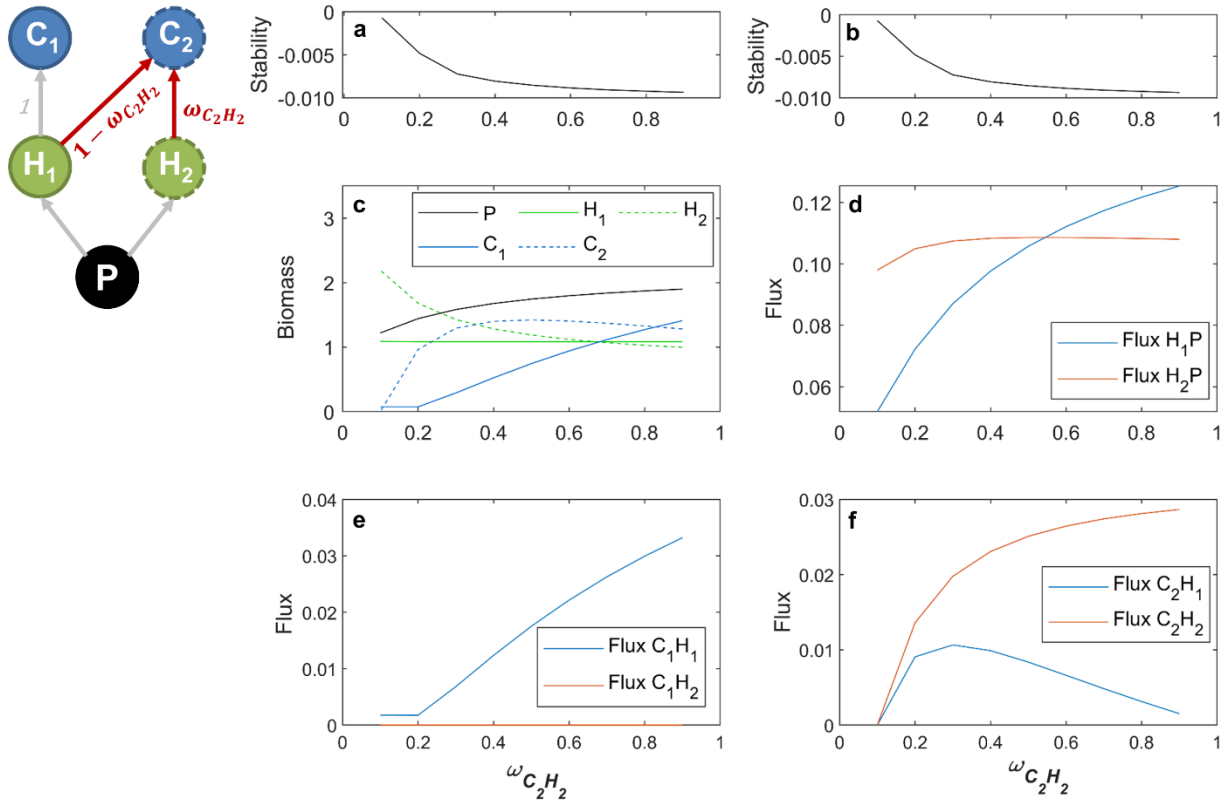
525 **Figure 2. Effects of prey preference of *C1* on the ecosystem.** Here *C1* is a generalist, and

526 $\omega_{C_1H_2}$ is kept as (1- $\omega_{C_1H_1}$). $\omega_{C_2H_2}$ remains constant (equals 1) implying that *C2* is a specialist on

527 *H2*. Modeling results are provided for **(a-b)** food web stability (the same), **(c)** biomass of

528 different components, and **(d-f)** flux between each pair of components, all at ecological

529 equilibria with different $\omega_{C_1H_1}$ values simulated by the model.



530

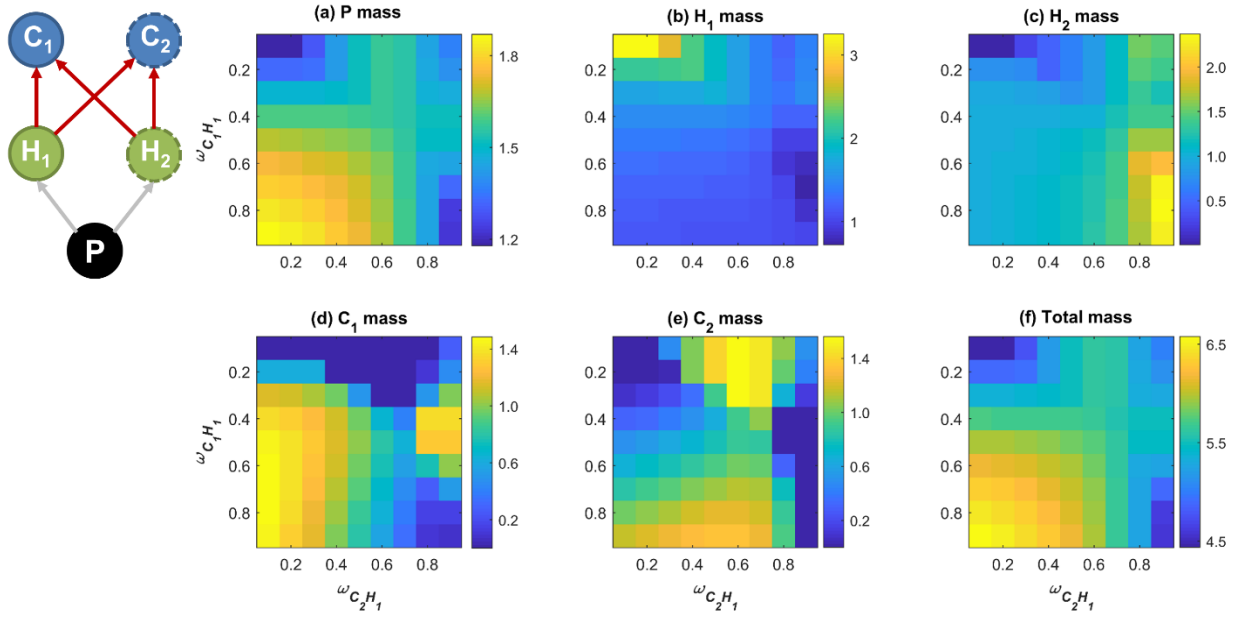
531 **Figure 3. Effects of prey preference of *C₂* on the ecosystem.** Here *C₂* is a generalist, and

532 $\omega_{C_2H_1}$ is kept as (1- $\omega_{C_2H_2}$). $\omega_{C_1H_1}$ remains constant (equals 1) implying that *C₁* is a specialist on

533 *H₁*. Modeling results are provided for **(a-b)** food web stability (the same), **(c)** biomass of

534 different components, and **(d-f)** flux between each pair of components, all at ecological

535 equilibria with different $\omega_{C_2H_2}$ values simulated by the model.



536

537 **Figure 4. Effects of prey preference of *C₁* and *C₂*, both as generalists, on the biomass of**

538 **different groups, when they change their prey preferences on *H₁* and *H₂* simultaneously.**

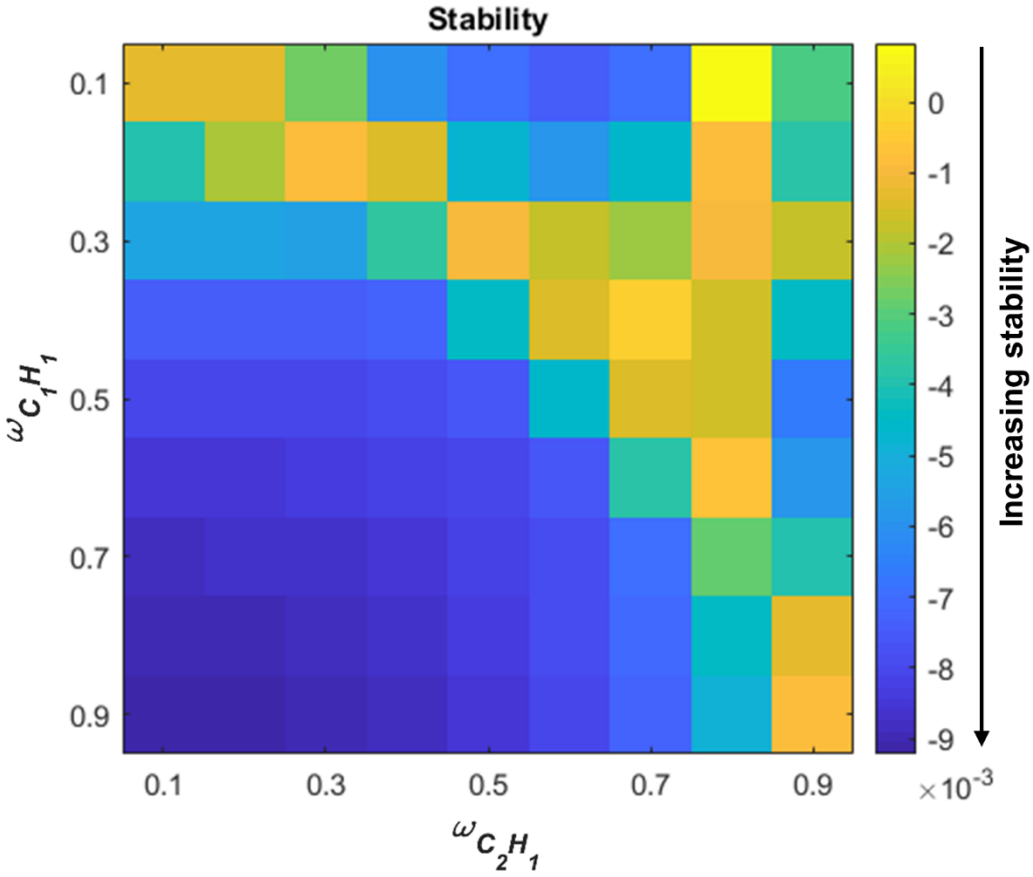
539 Prey preferences on H_1 ($\omega_{C_1H_1}$ and $\omega_{C_2H_1}$) range from 0.1 to 0.9 at a step of 0.1, and prey

540 preferences on H_2 ($\omega_{C_1H_2}$ and $\omega_{C_2H_2}$) equal the value subtracted by 1 ($\omega_{C_1H_2} = 1 - \omega_{C_1H_1}$, and

541 $\omega_{C_2H_2} = 1 - \omega_{C_2H_1}$). Results are presented as heat-maps, showing the biomass of **(a-e)** different

542 components and **(f)** the total biomass, at ecological equilibria under different combination of

543 $\omega_{C_1H_1}$ and $\omega_{C_2H_1}$ values simulated by the food web model.



544

545 **Figure 5. Effects of prey preference of *C₁* and *C₂*, both as generalists, on the food web**

546 **stability when they change their prey preferences on *H₁* and *H₂* simultaneously.** Prey

547 preferences on H_1 ($\omega_{C_1H_1}$ and $\omega_{C_2H_1}$) range from 0.1 to 0.9 at a step of 0.1, and prey preferences

548 on H_2 ($\omega_{C_1H_2}$ and $\omega_{C_2H_2}$) equal the value subtracted by 1 ($\omega_{C_1H_2} = 1 - \omega_{C_1H_1}$, and $\omega_{C_2H_2} = 1 -$

549 $\omega_{C_2H_1}$).

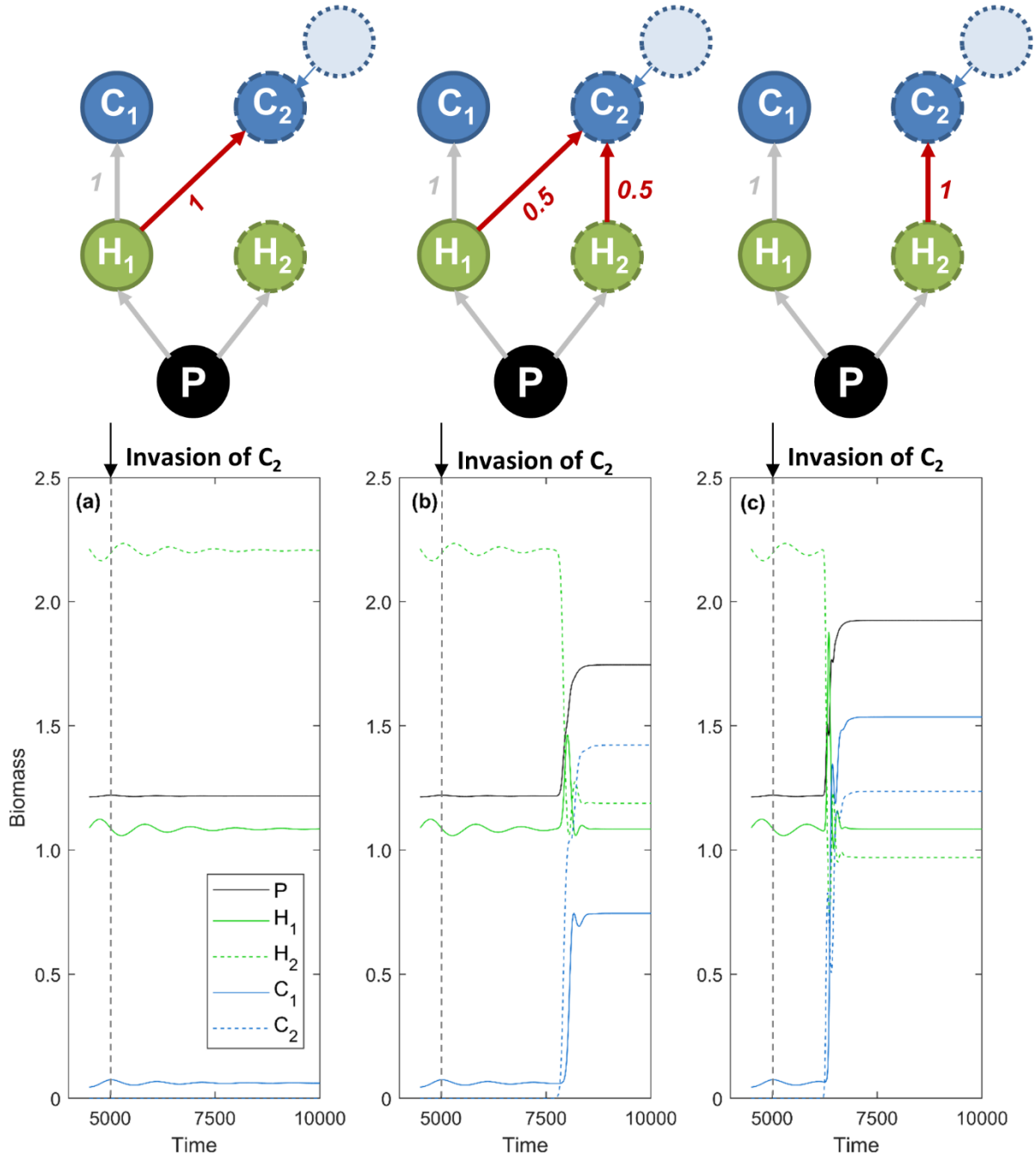


Figure 6. Response of ecosystem dynamics (with one local specialist C_1) to the invasion of C_2 with contrasting prey preference. (a) C_2 has the same prey preference as C_1 towards H_1 ($\omega_{C_2H_1}$ = 1); **(b)** C_2 has the equivalent prey preference on H_1 and H_2 ($\omega_{C_2H_1}$ = $\omega_{C_2H_2}$ = 0.5); **(c)** C_2 has the completely different prey preference as C_1 towards H_1 ($\omega_{C_2H_2}$ = 1). The model simulations

555 have two parts, each for 5,000 time steps, and the invasion of C_2 occurs at t= 5,000. Biomass of
556 different components are simulated by the model representing ecological equilibrium after t =
557 5,000.
558

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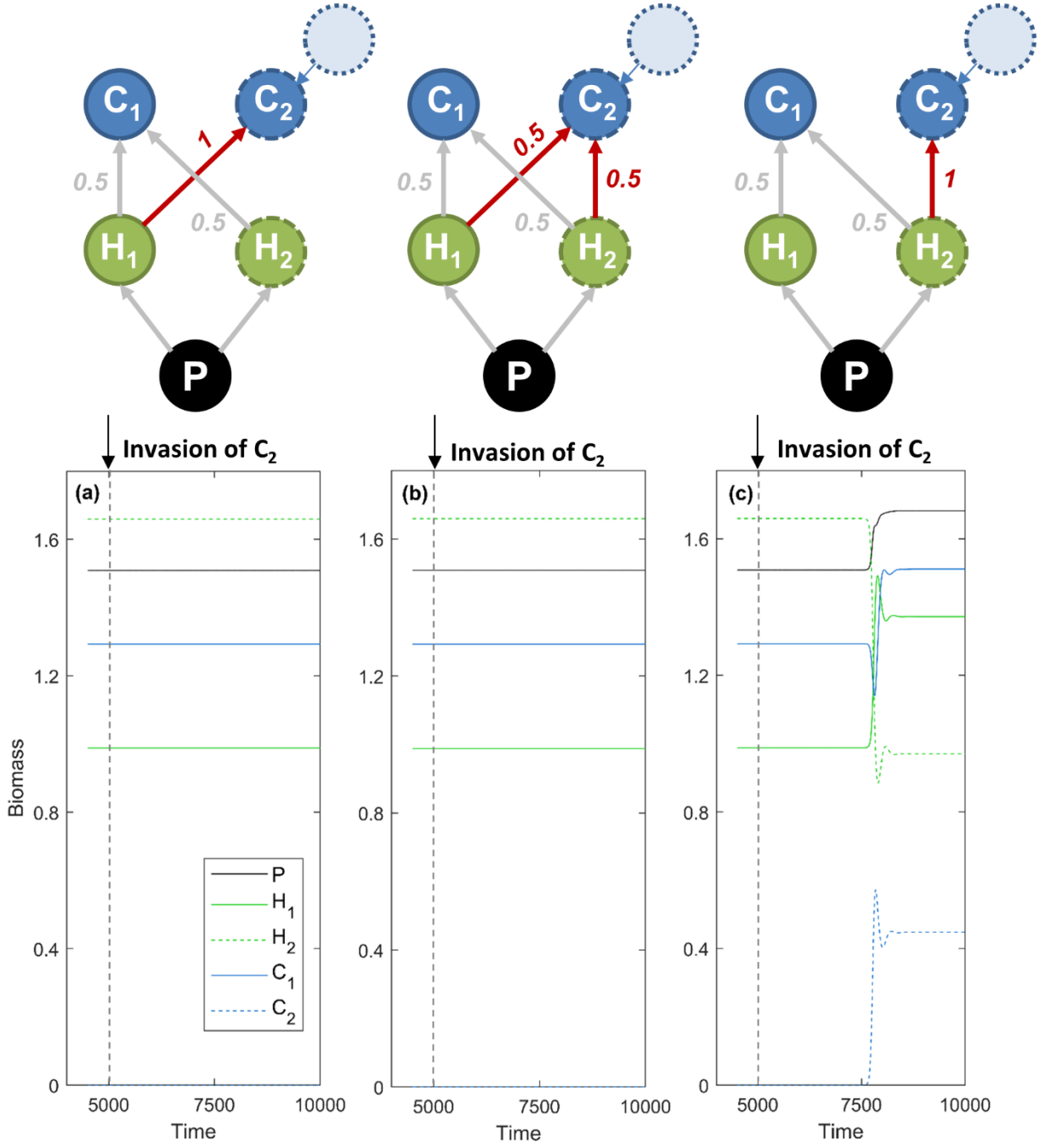


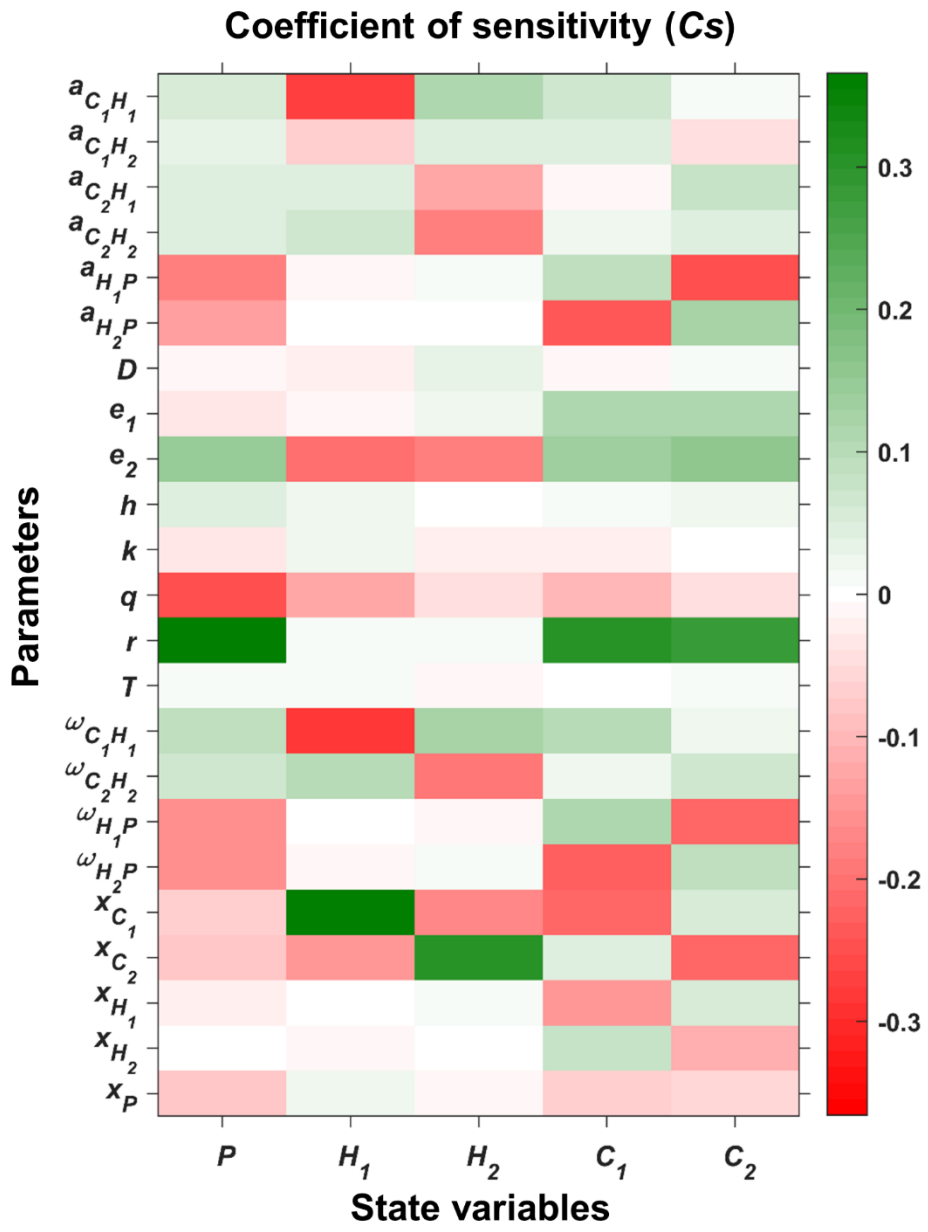
560

561 **Figure 7. Response of ecosystem dynamics (with one local generalist C_1) to the invasion of**

562 **C_2 with contrasting prey preference. (a)** C_2 has the full prey preference on H_1 ($\omega_{C_2H_1} = 1$); **(b)**

563 C_2 has the equivalent prey preference on H_1 and H_2 ($\omega_{C_2H_1} = \omega_{C_2H_2} = 0.5$); **(c)** C_2 has the

completely different prey preference as C_1 ($\omega_{C_2H_2}$ = 1). The model simulations have two parts, each for 5,000 time steps, and the invasion of C_2 occurs at t= 5,000. Biomass of different components are simulated by the model representing ecological equilibrium after t = 5,000.



568

569 **Figure 8. Sensitivity analysis on the model.** Each grid in the heat map represents the *Cs* value

570 of one certain model parameter to one certain state variables among *P*, H_1, H_2, C_1 and C_2. *Cs* is

571 calculated based on model simulation outputs at t = 5,000, representing ecological equilibrium.