Superadditive and subadditive dynamics are not inherent to the types of interacting threat

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Abstract

Species and ecosystems usually face more than one threat. The damage caused by these multiple threats can accumulate nonlinearly: either subadditively, when the joint damage of combined threats is less than the damages of both threats individually added together, or superadditively, when the joint damage is worse than the two individual damages added together. These additivity dynamics are commonly attributed to the nature of the threatening processes, but conflicting empirical observations challenge this assumption. Here, we provide a theoretical demonstration that the additivity of threats can change with different magnitudes of threat impacts. We use a harvested single-species population model to integrate the effects of multiple threats on equilibrium abundance. Our results reveal that threats do not always display consistent additive behavior, even in simple systems. Instead, their additivity depends on the magnitudes of the two threats, and the population parameter that is impacted by each threat. In our model specifically, when multiple threats impact the growth rate of a population, they display superadditive dynamics at low magnitudes of threat impacts. In contrast, threats that impact the carrying capacity of the environment are always additive or subadditive. These dynamics can be understood by reference to the curvature of the relationship between a given parameter (e.g., growth) and equilibrium population size. Our results suggest that management actions can achieve amplified benefits if they target threats that affect the growth rate, and low-magnitude threats, since these will be in a superadditive phase. More generally, our results suggest that cumulative impact theory should focus on the magnitude of the impact on the population parameter, and should be cautious about attributing additive dynamics to particular threat combinations.

Keywords

threat interactions, superadditivity, subadditivity, multiple threats, threat management, prioritization

Introduction

Species and ecosystems across the globe are exposed to a large variety of threats. When considering an ecosystem, for example, coral reefs, there can be a variety of threat sources, including local, direct impacts such as fishing; land-based impacts such as water quality; and global impacts such as coral bleaching (1, 2). The damages caused by these threats are rarely straightforward since they can interact and display nonlinear behaviors (3), which can either magnify, reduce, or erase the benefits of management actions (2, 4, 5).

When multiple threats occur simultaneously (6), the damage they cause to an ecosystem feature (e.g., a species' population) is a result of each individual threat, and the interaction between them (5, 7). Interactions can occur in a variety of ways; here, we focus solely on interactions that occur within a single population. The accumulated effects of multiple threats are not always additive, meaning two threats aren't always twice as bad as one, but rather can display super- or subadditive behavior. The existence of non-additive threat interaction dynamics has been shown repeatedly (7-10). Subadditivity occurs when the damages caused by the combined threats, D(A&B), are smaller than the sum of the effects of the individual threats, D(A&B) < D(A)+D(B) (11). Similarly, superadditivity is defined as the joint damage being larger than the sum of the individual effects, D(A&B) > D(A)+D(B) (11). To give an example: in a controlled laboratory experiment, a mollusk *Dolabrifera brazier* experienced a decrease in population size of 10% at high salinity, and a decrease in population size of 25% when exposed to high UV radiation. If the joint damage of these two threats was additive, then we would expect a decrease of 35% when both threats are present. However, the decrease in the presence of both threats was measured at a superadditive 80% (12).

The majority of studies on threat interactions rely on experimental or observational methods. The main aim of these studies is to identify which threat combination (e.g., salinity and light, or salinity and temperature) displays which type of additivity. However, the studies often disagree about the type of additivity, even when considering the same study species and threats. As with the *D. brazier* example, interacting threats are generally investigated using field or laboratory experiments (7). Crain, Kroeker (7) reviewed 202 studies on these interaction types in marine systems and found that 26% of threat combinations are additive, while 36% are superadditive and 38% are subadditive. There was also variation within threat combinations: all threat combinations that had been thoroughly investigated displayed all three additivity types (7). For example, 34 independent factorial experiments that investigate the impact of UV light and fishing found additive impacts in 17 cases, subadditive impacts in 5 cases and superadditive impacts in 12 cases (7). So far, this variation is explained by context dependence (7), including the number of threats considered and the trophic level of the species experiencing the threat. Here, we investigate an alternative explanation for the observed variation: additivity of joint damages of threats can change with varying magnitude of threat impacts.

Investigating different magnitudes of threat impacts is difficult in both observational and experimental studies because any experiment would need to be structured factorially, with the species or community being exposed to the threats individually and in combination, across a range of magnitudes. For example, Schlöder and D'Croz (13) investigated the effect of temperature and nitrate on two coral species, *Pocillopora damicornis* and *Porites lobate*. In this experiment, 60 coral pieces were grown for 30 days in isolation and the frequency and volume of their zooxanthellae was measured. The magnitude of the threat was only classified in two (nitrate) or three (temperature) categories, resulting in six possible scenarios and leaving five replicates per species. Even an increase to three levels in nitrate would result in an increase of the combinations to nine combinations and 90 coral fragments if keeping the replication constant. This makes the investigation of many different magnitudes of threat impacts very challenging; modelling studies need to be used to address these kind of questions more holistically. Simulations of threats at many trophic levels, including all of their impacts and magnitudes, as well as utilising large sample sizes can be analysed to draw conclusions that are more generalizable. In contrast, models can evaluate threats and their management in situations where manipulation or experimentation is challenging (5, 14, 15).

When a threat on a population occurs it passes through several stages before we see the damage (Fig.1). In this paper, we distinguish between impact and damage. The impact is defined as the actual reduction of a population parameter that the threat causes (Table 1). For example, we could have a cyclone (a threat) occurring at a reef. This cyclone might reduce the amount of habitat available for the fish population, i.e. the carrying capacity is reduced. This reduction of the fishes carrying capacity is the actual impact on the population. Damage on the other hand is the effect of the cyclone that we can measure at some point after the threat has occurred, usually this is a population reduction.

Figure 1. Schematic diagram of threats impacting on populations

Table 1. Definition and connection of commonly used terms in this paper

Term	**Definition**

Impact	Impact is the proportion of the population parameter that is reduced by the threat.
Joint impact	Joint impact is the combined impact that two threats have on one population parameter.
Damage (D)	Damage is the change in the population equilibrium that is caused by one or more threats. This damage is what is measured in observational studies.
Joint damage ($D_{1,2}$)	Joint damage is the reduction in population equilibrium size that can be measure after two threats have occurred.
Additivity index	The additivity index gives a characteristic of the joint damage in relation to the dame caused by a single threat. It ranges from -1 to 1 and can be categories as additivity types: superadditive ($-1 \leq A < 0$), additive ($A = 0$) or subadditive ($0 < A \leq 1$).

In this study, we analyse the conditions within a population and threats that lead to superadditive and subadditive behaviour. Our aim is to theoretically investigate the additivity of joint threats, and to offer a more nuanced understanding of the factors that influence additivity. We are especially interested in understanding how additivity varies with different magnitudes of threat impacts, and how it depends on the parameters impacted by the threats. We use a suite of single-species population models to simulate damages caused by threats in isolation and combination to identify the interaction behaviour. Then, we identify and explain the conditions that lead to super- and subadditivity. Finally, possible management actions are simulated and their relative benefits depending on the additivity are compared.

Methods

Our analyses are based on a single-species population model – the harvested logistic model (Eq. 1) – which allows us to derive some results analytically, and to more easily interpret them in the context of cumulative threat theory. Threats are modelled as proportional reductions (*a* and *b*) in two population parameters: the growth rate (*r*), and the carrying capacity (*K*) respectively. So the logistic model

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - hN \qquad \text{(Eq. 1)}$$

becomes

$$\frac{dN}{dt} = (1 - a_i)rN\left(1 - \frac{N}{(1 - b_i)K}\right) - hN \qquad \text{(Eq. 2)}$$

in the presence of threat i.

We note that in this model, a single threat i can affect both our population parameters. For example, in coral reef ecosystems sedimentation simultaneously reduces the habitat available to corals (*K*), and increases coral mortality (*r*). Our approach would therefore allow this single threat to interact with itself. In Eq. 1 and Eq. 2, $r =$ growth rate, $(1 - a_i)$ $=$ impact on the growth rate, $K =$ carrying capacity, $(1 - b_i) =$ impact on carrying capacity, $h =$ harvest rate, also $0 \leq a_i, b_i, r, h \leq 1$ and $h < r$. A value of zero for either *ai* or *bi* therefore indicates no impact of the threat on the parameter, while a value of one indicates a total loss of the process represented by the parameter. Our analyses focus on the equilibrium population in the face of multiple threats that each impact the population to form a new population equilibrium,

$$N^*(a_i,b_i) = \left(1 - \frac{h}{(1-a_i)r}\right)(1-b_i)K. \qquad \text{(Eq. 3)}$$

If $N^*(a_i,b_i) < 0$, we consider the population to be extinct and set $N^*(a_i,b_i) = 0$. In the figures a line is added that separates extinct populations.

Furthermore, we define the damage (D) to be the reduction in population size caused by the threat:

$$D = N^*(0,0) - N^*(a_i,b_i). \qquad \text{(Eq. 4)}$$

Two threats acting upon one parameter could be modelled in two ways: multiplicative $(1-b_1)*(1-b_2)$ or additive $(1-b_1)+(1-b_2)$. Both of these are reasonable. Additive impacts would indicate that the two impacts occur independently with no influence on one another, while multiplicative would indicate that they change the impact of one another. One example for non-independence is if they act consecutively, i.e. the impact of threat 2 affects the parameter that has already been impacted by threat 1. Which one is most appropriate could be dependent on the actual threats and how they affect the physiologic state of the modelled organisms. However, this is not something that is usually investigated, so it is hard to determine which one is more appropriate in a given situation.

Additivity of multiple threats

Here we present the results of the additive model, however the analysis for the multiplicative version can be found in the supplementary materials. Furthermore, the supplementary materials also provide the results for the equivalent analysis for the Beverton-Holt (S2) and the Ricker model (S3).While there are slight differences in the actual results, all major conclusions in this paper are supported by the results of both analyses.

To categorise the joint damage caused by multiple threats we have created an additivity index (A). It is based on the population equilibria in the presence and absence of the threats. Basically the additivity index is equal to the sum of the damage caused by each threat separately, minus the damage caused by both threat simultaneously,

$$A = D_1 + D_2 - D_{1,2}. \qquad \text{(Eq. 5)}$$

When A is negative the joint damage is superadditive; when A is positive then the joint damage is subadditive.

We consider four different types of interacting threats (Table 2). In our first two cases, both threats impact only one parameter, either the carrying capacity ($a_1 = a_2 = 0, b_1,b_2 \neq 0$) or the growth rate ($a_1,a_2 \neq 0, b_1 = b_2 = 0$). In case three and four, threats impact both parameters. Case three only considers interactions between parameters ($a_1,b_1 \neq 0, a_2 = b_2 = 0$) while case four considers both interactions between and within both parameters ($a_1, a_2,b_1,b_2 \neq 0$).

Table 2. Analytical conditions for the four special cases with r=growth rate, a=impact of the threat on growth rate, h=harvest rate and b=impact on carrying

Case	**Parameters**	**Additivity index (logistic model)**
Both threats only impact the carrying capacity	$a_1 = a_2 = 1$ $0 < b_1{,}b_2 < 1$	$K(b_2 - 1)(b_1 - 1)\left(1 - \frac{h}{r}\right)$ ⇨ Always positive
Both threats only influence the growth rate	$0 < a_1{,}a_2 < 1$ $b_1 = b_2 = 1$	$\left(\frac{1}{a_1} - \frac{1}{a_1 a_2} - \frac{1}{a_2} - 1\right)K\frac{h}{r}$
One threat of the growth rate and one on the carrying capacity	$a_2 = b_1 = 1$ $0 < a_1{,}b_2 < 1$	$K\left(\frac{h}{r}\left(\frac{b}{a} - 1\right)^2 + (b - 1)^2\right)$ ⇨ Always positive
Both threats influence both parameters	$0 < a_1{,}a_2 < 1$ $0 < b_1{,}b_2 < 1$	$(1 + a_1 b_2 - b_2 - a_1)K\frac{h}{r}$

We first analytically analyse the additivity index for the different cases. However, since the interaction is not consistent for each case, we cannot find one overall condition rather a set of conditional statements that depend on the case (Table 2). While correct, these statements are difficult to interpret, consequently, we use simulations to further investigate the conditions for additivity through simulations. We simulate 10^6 random populations (randomly chosen values for r) at different magnitudes (0 to 1) of the threat impact over 1000 timesteps, to reach the equilibrium population size. Since the ratio of $\frac{h}{r}$ changes the magnitude of the threat impact at which the additivities occur, we have chosen specific values for $\frac{h}{r}$ and split the simulations according to those values, to enable better visualisation. Those values are $\frac{h}{r} = 0.2$, $\frac{h}{r} = 0.5$ or $\frac{h}{r} = 0.8$. Since r is chosen randomly, h is assigned to each simulation so that $\frac{h}{r}$ equals the value specified for each group. Equilibria are re-calculated three times for each random population with three different treatments: each one of the threats acting separately, and then the two threats interacting. The additivity index of the two threats for each population is calculated (Eq. 4).

Finally, we simulated the effects of management by decreasing one or both threats by 5% and recalculating the long-term population equilibrium. Management actions could be designed to reduce the threat as a whole, for example reducing fishing pressure, or to reduce the impact on one population parameter, for example fishing technique is changed so that less habitat destruction is caused. For simplicity, it is assumed here that a management action reduces the impact of a threat on both population parameters simultaneously and equally. The benefit is recorded for random populations and across the magnitude of threat impacts of all cases (~100,000 data points per case)

$$Benefit = \frac{N^*(a\_managed, b\_managed) - N^*(a,b)}{N^*(1,1)} \qquad \text{(Eq. 6)}$$

Results

The results of the simulations agree with the results of the analytical analysis; consequently both are appropriate for analysing the threat interactions. However, caution has to be given to the defined parameter space to prevent negative population sizes.

Cases 1 and 2 both concentrate on one of the population parameters (Fig 2). These two cases show very different patterns in the joint damages. Two threats on the carrying capacity always cause a joint damage that is additive until the extinction line (at which point at least one threat can cause extinction) where the joint damage becomes necessarily subadditive. The threats on the growth rate, however, display a joint damage that is additive at low magnitudes of threat impacts and superadditive at high magnitudes of threat impacts. Within the area of extinctions there will again be subadditive joint damage. Generally, it can be said that the additivity index decreases from zero towards negative one until it hits the extinction line, then the additivity index starts to increase until it reaches positive 1. As harvest levels increase (Fig 2), the extinction line moves closer towards the origin, as extinction occurs at lower threat levels.

Figure 2. Additivity indices for 10^6 simulations of random values for h and r split into three cases depending on the parameter impacted by the threats. The four cases represent: a-c: Case 1; Two threats that only influence the carrying capacity ($\boldsymbol{a_1 = a_2 = 0, b_1, b_2 \neq 0}$); d-f: Case 2; Two threats that only influence the growth rate ($\boldsymbol{a_1, a_2 \neq 0, b_1 = b_2 = 0}$); g-i: Case 3; Each parameter is only influenced by one threat ($\boldsymbol{a_1, b_1 \neq 0, a_2 = b_2 = 0}$) ; j-l: Case 4; Both threats influence both parameters($\boldsymbol{a_1, a_2, b_1, b_2 \neq 0}$). The columns indicate the level of harvest relative to the population growth rate. Between the origin and the extinction line, the population of organisms persists in the present of the threats, from the extinction line onwards, the population will go extinct in the presence of at least one threat in isolation. The interpretation of an additivity

index of zero has to be done carefully, since the graph aligns all values in the range $-0.02 < 0 < 0.02$ as zero. While there are truly additive impacts, the line from additive to subadditive is less distinct and more like a gradual decrease in A.

Case 3 demonstrates the joint damage when both parameter are impacted. This case shows only additive and subadditive damage similar to case 1. However, subadditivity now also occurs without the presence of extinction. Furthermore, it is interesting to note that changes to the impact on the growth rate (a_1) and changes to the impact on the carrying capacity (b_1) do not cause the same change in the additivity index.

In case 4, both threats impact both the carrying capacity and the growth rate. This means that we can compare it directly with case 1 and 2, since they are basically a subset of the simulations displayed within case 4. The only difference is that the results are collapsed into a lower dimensional space. For example, case 1 shows the impact of threat 2 on the carrying capacity on the y-axis and the impact of threat 1 on the carrying capacity on the x-axis. In case 4, both impacts are displayed on the y-axis by simple addition. This means that when the impact on the growth rate is very low in case 4 ($a_1 + a_2 = 0$), then case 4 is equivalent to case 1. Similarly we can find the results from case 2 in case 4 buy setting the impact on the carrying capacity close to zero ($b_1 + b_2 = 0$). The rest of the case 4 compromises a mixture of sub- and superadditivity. Superadditivity occurs only at high impacts on the growth rate, while subadditivity mainly occurs at medium impacts on both the growth rate and carrying capacity. The absolute magnitude of the additivity index still increases towards the extinction line and decreases after the extinction line with increasing impacts of one or either population parameters.

Next, we consider the relationship between the population parameter and the population equilibrium (Fig 3). When increasing the threats (e.g. from 0 to 1) on the growth rate we can see a decrease in the population equilibrium (Fig 3A). This decrease is first slow then becomes steeper resulting in a concave relationship. On the other hand, when increasing the threat impacts on the carrying capacity the population equilibrium decreases linearly (Fig 3B). Finally, when we increase the impact on both parameters at different levels (Fig 3C), we can identify all three; convex (red line), linear (blue lines) and concave (green line) relationships (Fig 3D).

Figure 3. Relationships between the threats on (A) growth rate, (B) carrying capacity, (C&D) growth rate and carrying capacity and the population equilibrium. Part A. shows a concave relationship between the threats impacting the growth rate and the population equilibrium for all levels of the carrying capacity. Part B shows a linear relationship between the threats impacting the carrying capacity and the population equilibrium for all magnitudes of the growth rate. Part C shows a contour graph of the population equilibrium with varying threats impacting the growth rate and the carrying capacity. Furthermore, slices are highlighted (lines) that are displayed in Part D. The x-axis in part D represents the magnitude of the impact of the threats on the growth rate. The threats impacting the carrying capacity are also varied and can

be identified using the appropriate linear function to calculate b. Part D shows that depending on the slice we choose from Part C both concave and convex relationships can be found when all threat impacts are varied.

Management benefit per 5% threat impact change displays a large variation from as low as 0% increase of the no threat population equilibrium up to 4300% increase (Table 3). Both extremes occur when the equilibrium populations are close to zero before management.

Table 3. Statistics summarising all of the simulations used for Fig. 4 divided according to the cases and extinction status after the management on the threats

Statistic	**Case 1**	**Case 2**	**Case 3**	**Case 4**
Including extinct populations				
Minimum	0.28	0	0	0
Q1	3.773	0	0	0
Median	5.25	0	4.48	0
Q3	6.71	003.153	6.71	2.22
Maximum	100	2894.1	4374.7	295.59
Excluding extinct populations				
Minimum	0.28	$4*10^{-4}$	$4*10^{-4}$	$1.5*10^{-3}$
Q1	3.773	5.63	4.31	3.191
Median	5.25	12.17	5.41	5.499
Q3	6.71	18.95	7.79	8.912
Maximum	100	2894.1	1803.7	186.74

Several factors influence the management benefit experienced by a population when particular threats are decreased. First, there is the magnitude of the threat impact. The impact on the parameter growth rate shows some variation with benefit being higher in the extreme case (high and low magnitude) versus the medium magnitude (Fig 4a). On the other hand, the threat impact of the carrying capacity shows a clear decrease of management benefit with a decrease in magnitude. The lowest threat impact doubles or even triplets the management benefit experienced (Fig 4b). The largest amount of variation is explained when we consider the additivity together with the benefit (Fig 4c). More superadditive behavior lead to over ten times the benefit compared to cases where very subadditive damage is displayed.

Figure 4. Management benefit (±1.96*SE) when reducing both threats simultaneously according to the four cases. Panel a) splits the benefit for different magnitudes of threat impact on the parameter carrying capacity. Panel b) splits the benefit for different magnitudes of threat impacts on the growth rate. Low impact < 0.25; 0.25< Medium-Low impact < 0.5; 0.5 < Medium-High impact < 0.75; High impact > 0.75. Panel c) splits the benefit depending on the additivity type. High superadditivity < -0.5; -0.5 < Low superadditivity < 0; 0 < Low subadditivity < 0.5; High subadditivity > 0.5.

Discussion

This study explored the interaction behaviour of two threats acting upon two population parameters in theoretical populations. We found that, contrary to orthodox assumptions, the joint damage of threats is not inherent to the particular threat combination (7, 9). Even in a simple, one-species model, the additivity can exhibit qualitative changes, depending on the affected parameter, and the magnitude of the impact on a threat. Our results therefore suggest that studies or reviews should be careful when they attribute the qualitative type of additivity to particular combinations of threats (4), and be aware that the parameters affected and the magnitude of the impact could be driving the threat behaviour.

In our models, superadditivity only occurs if there are several impacts on the growth rate. This can be explained by the concave relationship between the intrinsic growth rate and the equilibrium population size (Fig. 3a). Following this curve toward the origin, we see that the slope increases in response to increasing threats. A threat with twice the impact will therefore cause more than double the damage to the equilibrium population size. In contrast, the joint damage of threats will be additive when the slope is constant, i.e. a linear relationship between the population parameter and the population equilibrium. On the other hand, the additive joint damage when only the carrying capacity is impacted can be related to the linearity of its relationship to the equilibrium population size (Fig. 3b).

During this study, we found a few occasions where concavity does not predict all of the interactions that we can find, i.e. this generalization seems to contradict our results. For example, at high magnitude of threat impacts there are subadditive interactions. On closer examination, we found that all of these subadditive data points resulted in extinction. This subadditivity can only be found in the simulation results, the analytical analysis results in negative population sizes, which are not ecologically defined. Consequently, the data points resulting in extinction (negative population sizes, subadditivity) lay outside the realm of definition of the concave function.

Interestingly, reducing both parameters simultaneously can cause both super- and subadditivity at varying magnitudes of threat impacts. This is also reflected in the parameter-equilibrium relationships that can be both convex and concave (Fig. 3c-d). This means that at high levels of the growth rate and the carrying capacity the curve is concave, causing superadditivity and at low levels convex, causing subadditivity without extinction. This confirms our results and leads to the conclusion that we can infer the additive behavior from the curvature of the applicable curve.

Additivity of multiple threats has been considered in terms of conservation and management of populations repeatedly. In many cases, the opinion is that superadditivity is the worst case for the population (16, 17). However, superadditivity can also be the best case scenario when considered from the perspective of management (18). Our results support this since superadditive threats result in the largest proportional management benefit. This can be especially true when we consider local versus global, manageable versus unmanageable, threats. Superadditivity can mean that by reducing a manageable threat we can simultaneously achieve a reduction in the damage caused by the unmanageable threat (5). On the other hand subadditivity would mitigate the benefit from the management of a single threat and, consequently, the management action could be of small use. Following from here is that the management benefits are easiest to predict for an additive threat combination (9).

These results in combination with the commonly-conducted cumulative threat mapping (6, 19) can be used to prioritise management actions. Prioritising management is especially important in ecosystems that spread over large areas where it is impossible to protect the full extent of a species (20). In such systems prioritising management actions is crucial. When prioritising there are many aspects to consider, such as cost, risk, suitability and resulting benefit (21). The analysis shown here can aid in the assessment of the suitability for management of different areas and likely benefit that can be achieved. Global threats are always difficult to manage for local government so are less suitable. So if a global threat impacts all areas of conservation concern, but different local threats impact specific areas, then according to the analysis here, we might want to protect the areas that are impacted by superadditive threats. Furthermore, the actual benefit that a management action can result in is influenced by all threats to this system. The analysis conducted here, i.e. knowledge of the parameters impacted by each threat can help to estimate likely benefits. Therefore, these findings could streamline some aspects of management prioritisations.

The study utilises a simple logistic model that considers one population is isolation. This is not particularly realistic since all species interact with other species and threats can also interact with each other through those species. However, for this study a simple model is used to highlight the complexities that interactions introduce. It is important to note here that a more complex model will result in more complexities in the result not less. The simple model also provides a framework to interpret and explain some of the phenomena that are likely to still play role in more complex communities. The applicability of these results for many populations is also confirmed through the use of the Beverton-Holt and the Ricker model that both showed the same patterns of additivity (S1). Future work will aim to transfer the conclusions and explanations from a single population in this study to more complex community level models.

Conclusions

This study has provided an overview of the complexity of behaviors that interacting threats can display. Overall, the traditional idea of assigning types of interactions to threat combinations is re-conceptualized to a fluid concept of interactions depending on the parameters impacted. Besdies the large complexities found in this study, clear conclusions can be drawn about the origins of superadditive behavior; several threats that impact the growth rate of a population. Furthermore, this characteristic, superadditivity, can be connected to more efficient management and inform a prioritization of locations with different interacting threats.. More generally, the interaction behavior can be predicted by the curvature of the relationship between the impacted parameter and the equilibrium population size; a convex relationship implies subadditivity, and a concave relationship implies superadditivity. Finally, this study urges ecologists to focus on identifying the parameter and relative magnitude of threat impacts rather than the additivity type as a result of the threat combination.

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SUPPORTING INFORMATION

S1 Multiplicative impact on the logistic model

S2 Additive and multiplicative impact on the Beverton-Holt model

S3 Additive and multiplicative impact on the Ricker model

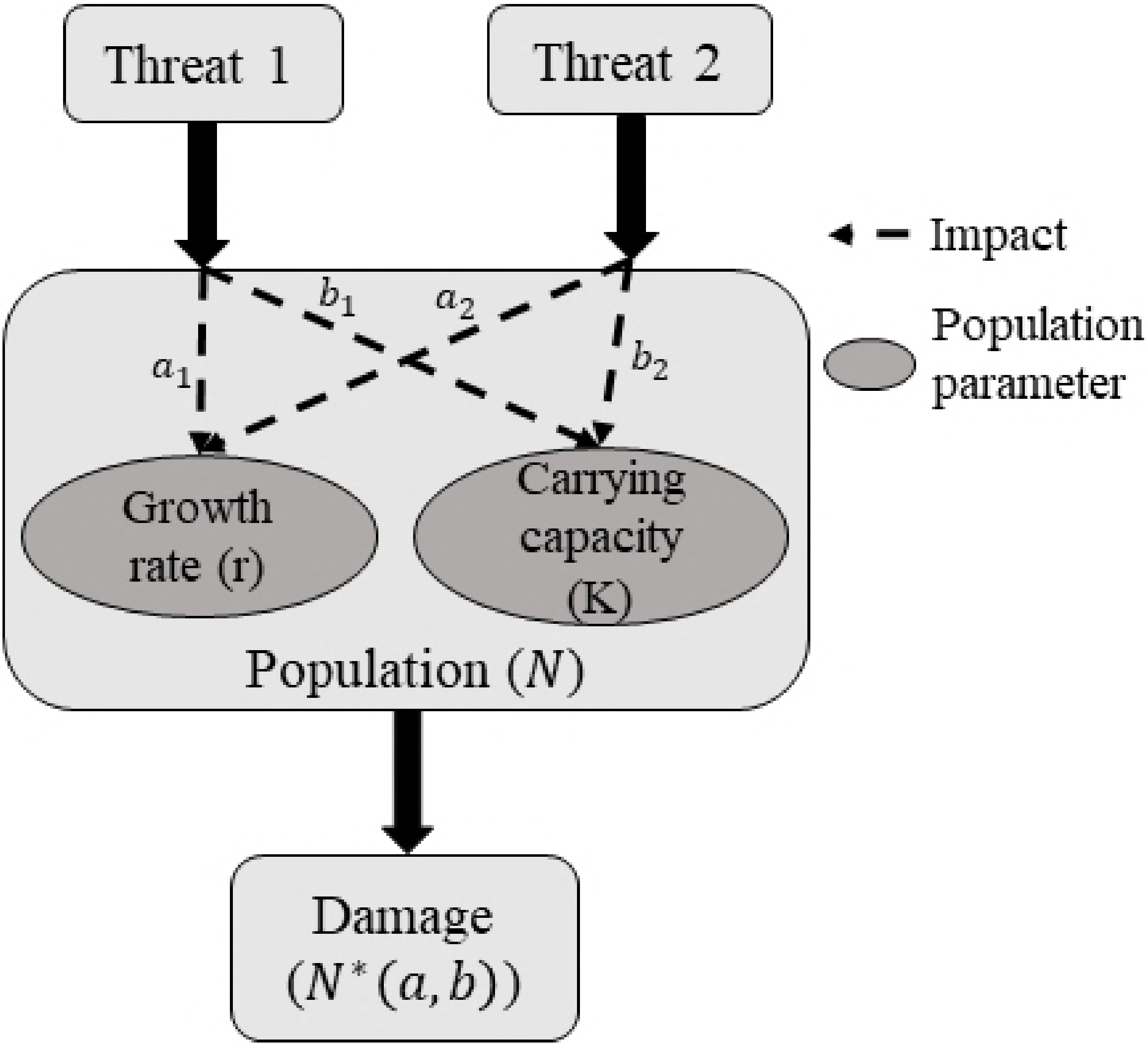

Threat 1
Threat 2
Impact
Population parameter
b_1
a_2
a_1
b_2
Growth rate (r)
Carrying capacity (K)
Population (N)
Damage ($N^*(a,b)$)

Figure 1

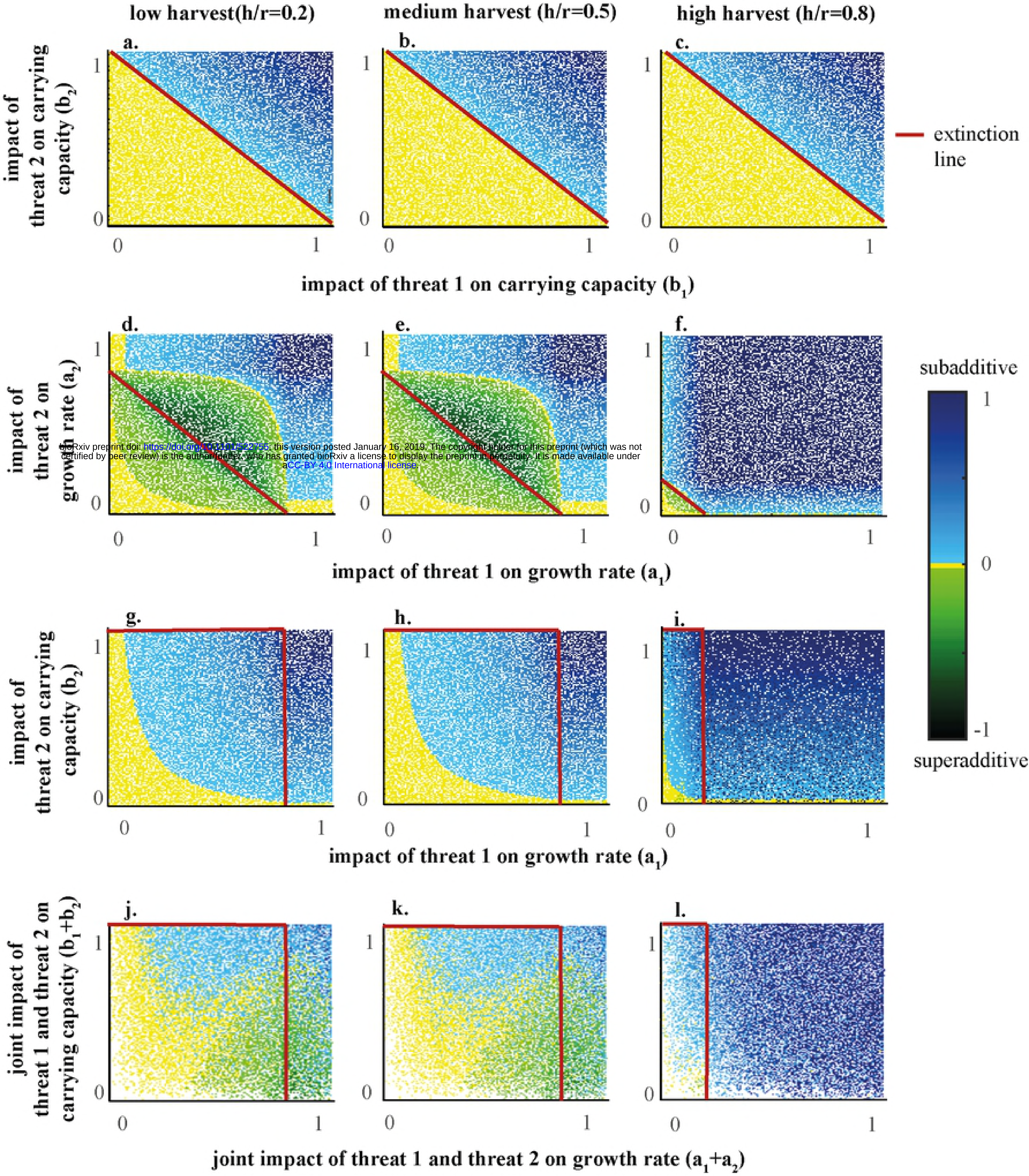

low harvest(h/r=0.2)
medium harvest (h/r=0.5)
high harvest (h/r=0.8)
a.
b.
c.
impact of threat 2 on carrying capacity (b_2)
impact of threat 1 on carrying capacity (b_1)
extinction line
d.
e.
f.
impact of threat 2 on growth rate (a_2)
impact of threat 1 on growth rate (a_1)
subadditive
superadditive
1
0
-1
g.
h.
i.
impact of threat 2 on carrying capacity (b_2)
impact of threat 1 on growth rate (a_1)
j.
k.
l.
joint impact of threat 1 and threat 2 on carrying capacity (b_1+b_2)
joint impact of threat 1 and threat 2 on growth rate (a_1+a_2)
0
1

Figure 2

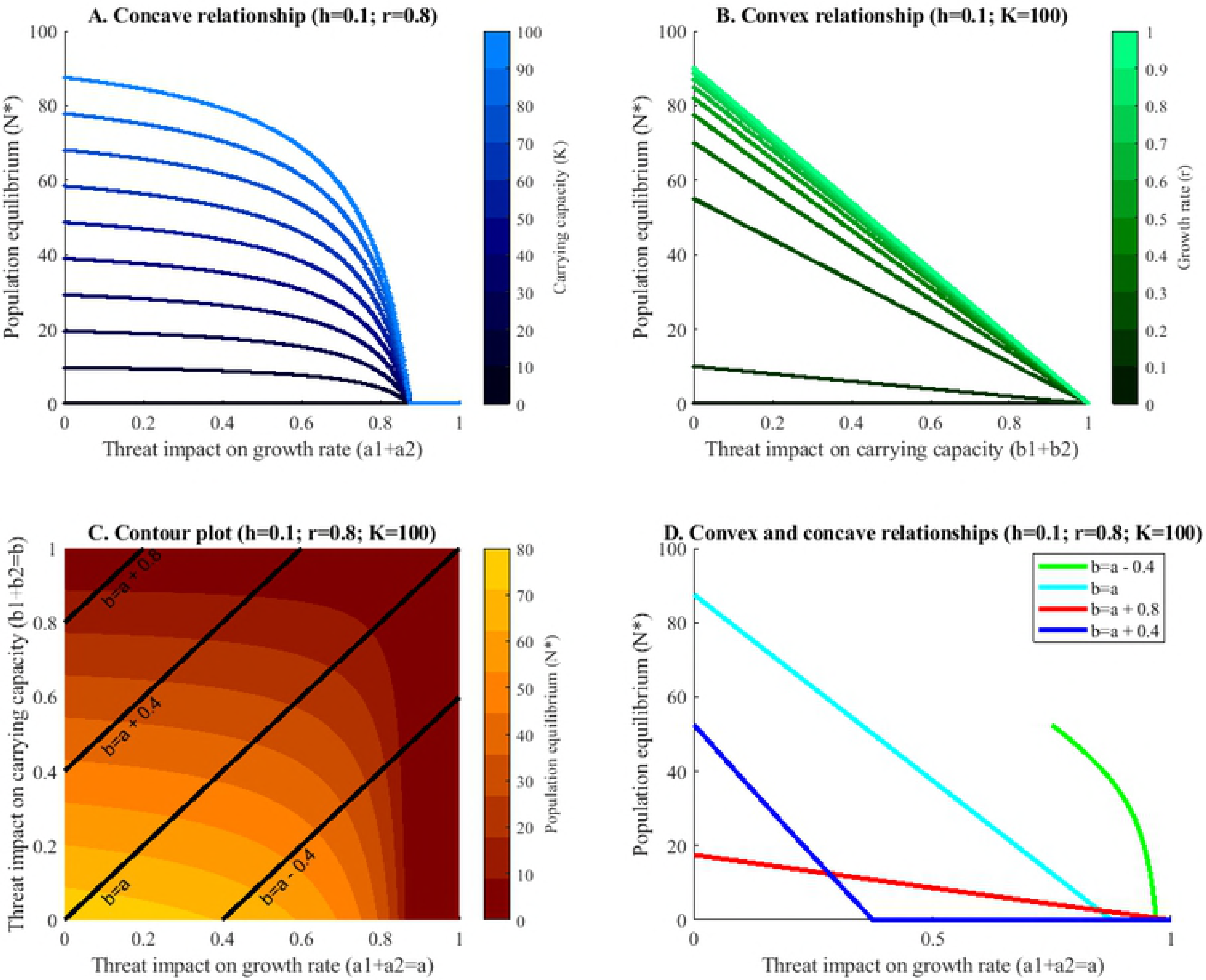
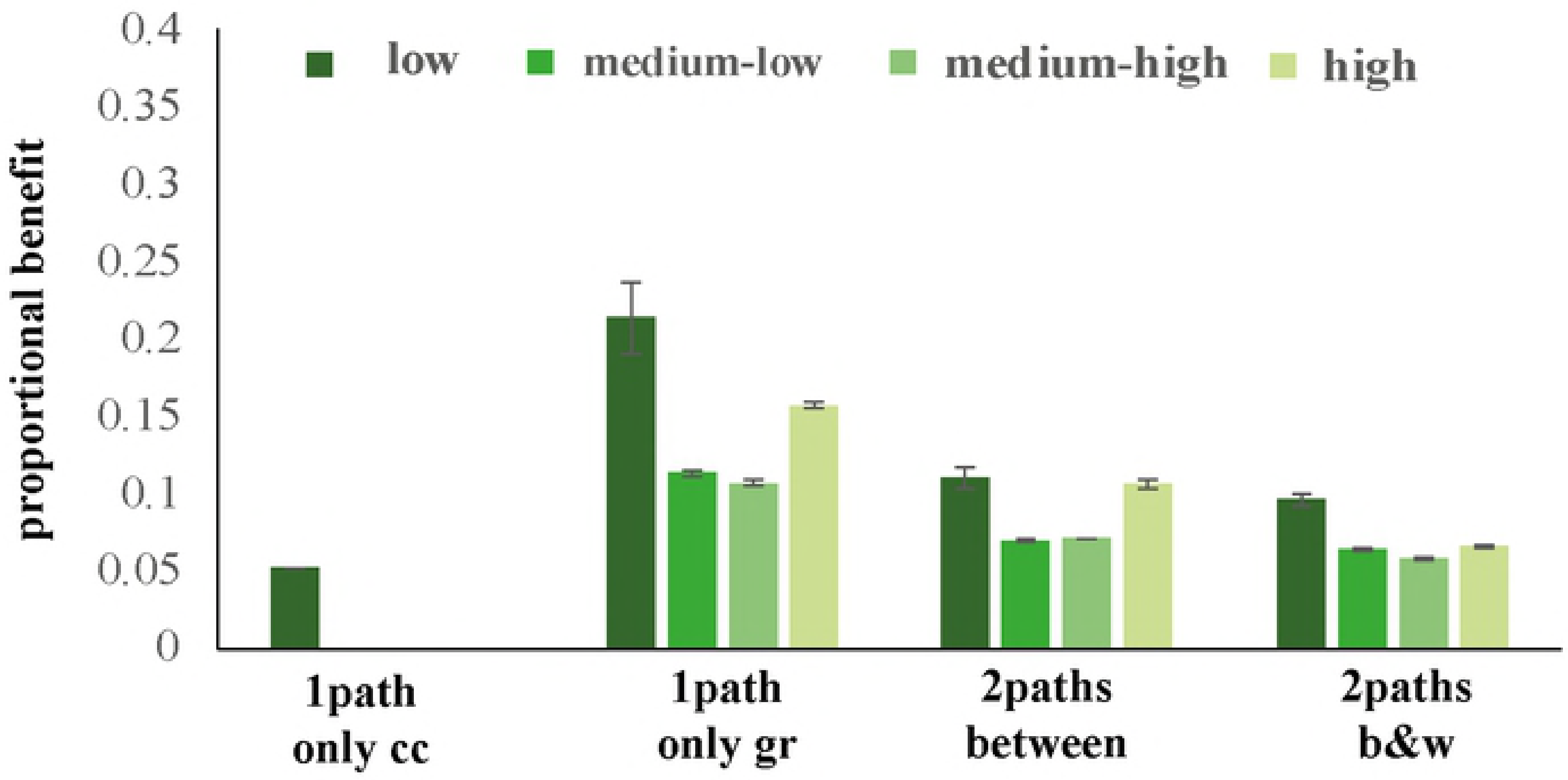
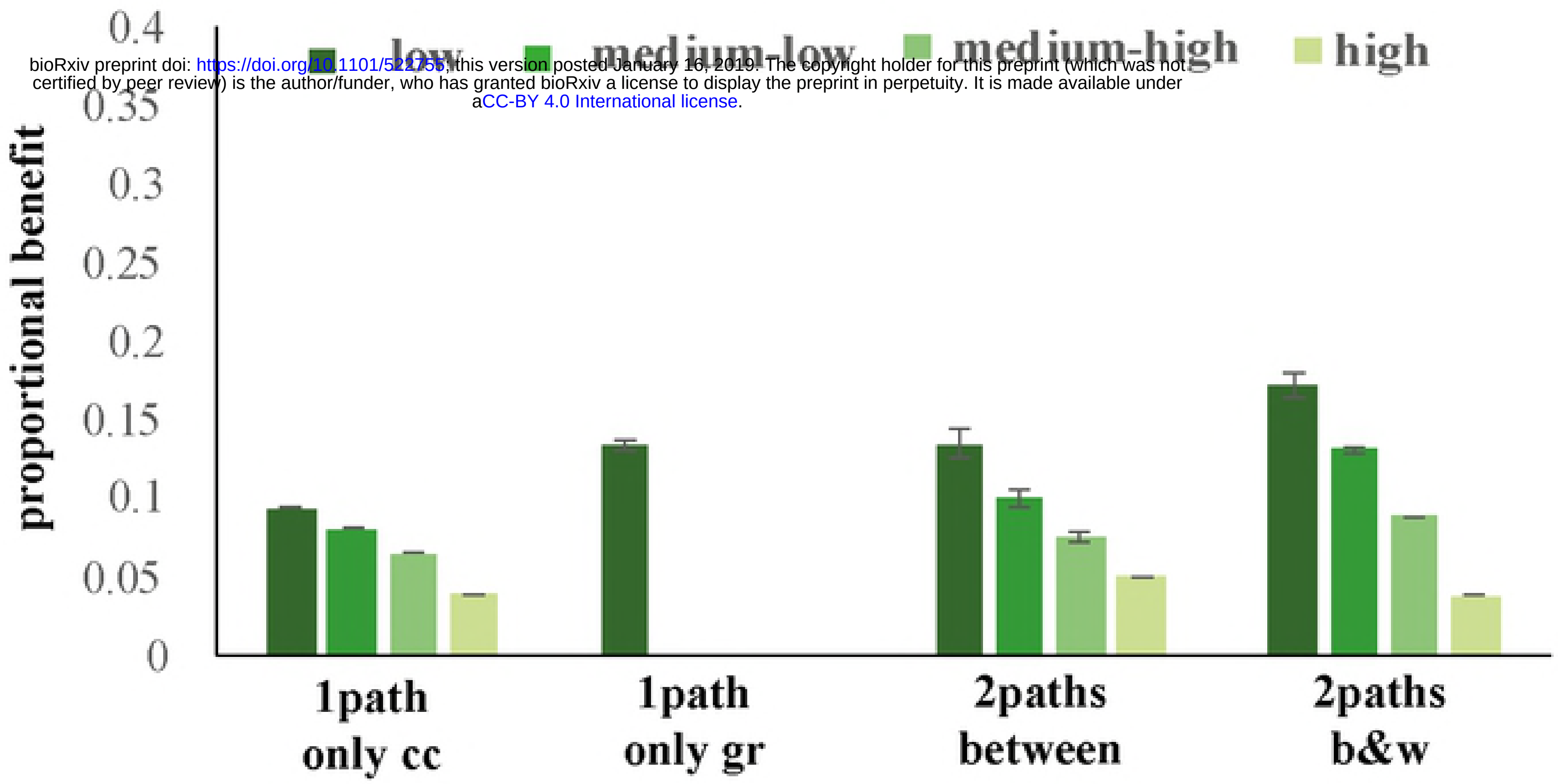

A. Concave relationship (h=0.1; r=0.8)
Population equilibrium (N*)
Threat impact on growth rate (a1+a2)
Carrying capacity (K)
0
10
20
30
40
50
60
70
80
90
100
0
0.2
0.4
0.6
0.8
1
B. Convex relationship (h=0.1; K=100)
Population equilibrium (N*)
Threat impact on carrying capacity (b1+b2)
Growth rate (r)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
C. Contour plot (h=0.1; r=0.8; K=100)
Threat impact on carrying capacity (b1+b2=b)
Threat impact on growth rate (a1+a2=a)
Population equilibrium (N*)
b=a + 0.8
b=a + 0.4
b=a
b=a - 0.4
D. Convex and concave relationships (h=0.1; r=0.8; K=100)
Population equilibrium (N*)
Threat impact on growth rate (a1+a2=a)
b=a - 0.4
b=a
b=a + 0.8
b=a + 0.4
0
0.5
1

Figure 3

a) threat impact on the growth rate



b) threat impact on the carrying capacity



c) aditivity type

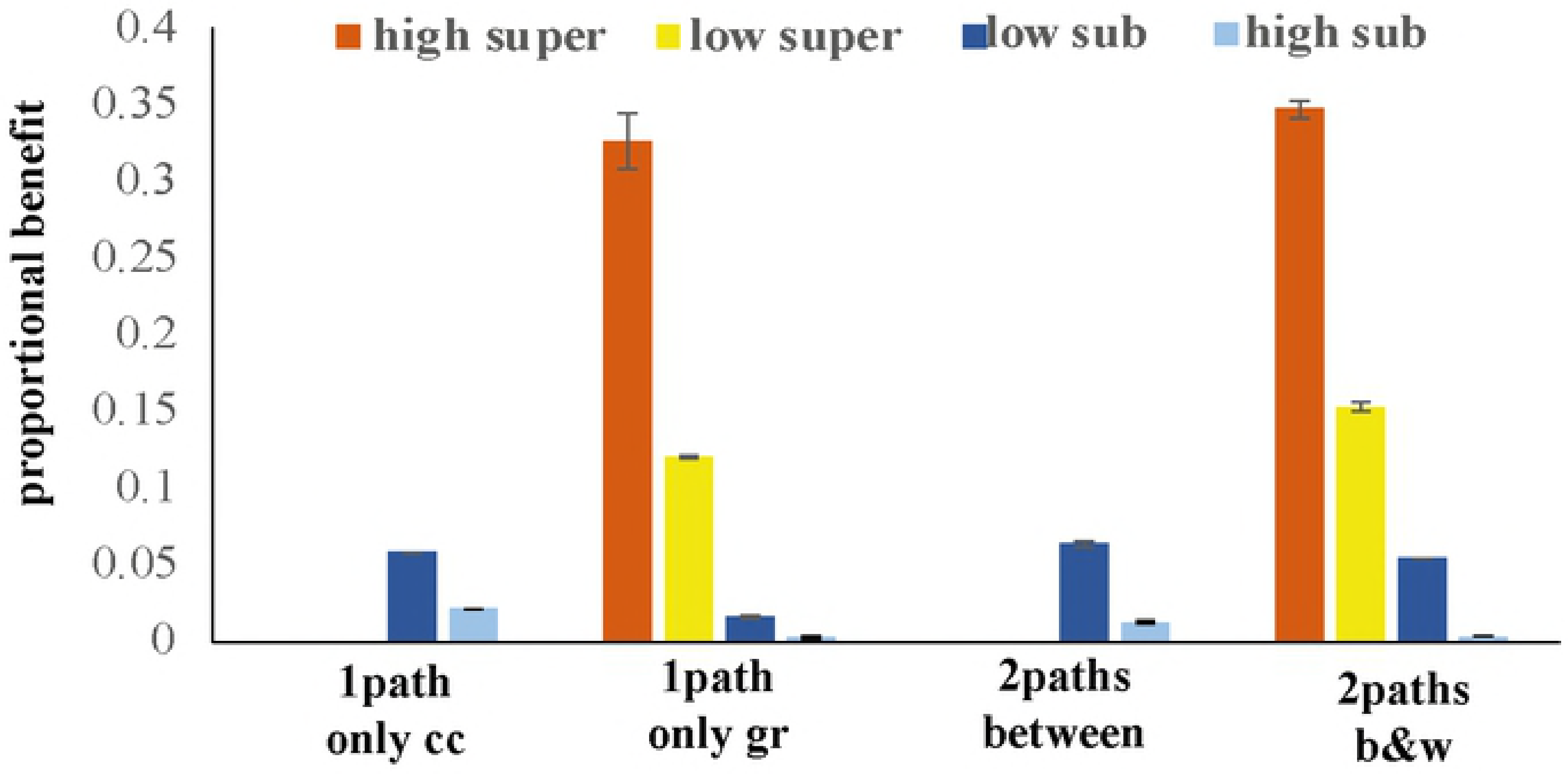


Figure 4