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種內合作如何與資源共同影響族群動態

**Cooperation and lateral forces: moving beyond bottom-up
and top-down drivers of animal population dynamics**

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誌謝


韶光荏苒，轉眼間已在 ESS lab 待了近四年。

四年是一段不短的時間，在 ESS lab，我從大二大三的懵懂天真逐漸成長為現在自己還算滿意的樣子，這中間實在發生過太多事。大三時投身於系上活動，大四、碩一時憂鬱纏身，研究上的進展始終起伏不定。加上焦慮性格使然，總覺得未知的太多，能發揮的精力太過有限，惶惶惑惑之時曾不認為自己未來能從事科學研究。幸好這些分神與低潮都被 ESS lab 接納了，尤其感謝老師聖峰給予我充分的空間與彈性，儘管他的想法總是跳躍得很快，但允許我像烏龜一樣慢慢的爬。

做理論研究是有點孤獨的，畢竟同行的人少之又少，不會有一起在蟲室做實驗的閒話家常，也少有機會和其他夥伴討論資料與分析。幸而在這路上還是有人給我及時的指點或珍貴的建議，使我少了一點卡關、多了一點探索的可能性。謝謝昌祐在我進實驗室之初領我入門，給我一些畫圖上的建議，這些建議在我日後呈現結果的時候非常有用。我也感謝劉銘時不時與我討論我的模式的細節，指出其中我未曾細想過但可能不合理之處，經過數次的修改，模式才變成現在所呈現的樣子。此外，劉銘也會推薦我一些重要的科學文章，分享自己所知以及申請學校的經驗，這些都幫助我在研究上或申請學校上有更明確的方向，十分感謝！

我也很慶幸在做理論研究之餘，有去四川做實驗的機會，讓我能親身體會如何為了一個科學問題設計實驗，以及其中現實的限制與困難，並在做理論研究之時能與現實的生物做連結，更可貴的是，在這三年夏天的四川野外，我認識了一群很棒的共事夥伴。謝謝彥廷在第一年的四川野外帶著毫無經驗的我做實驗，小至如何接電線，大至如何解決所關心的科學問題，彥廷都一一詳盡解說。還記得在彥廷車上吹著風聽著有點年代的搖滾的逍遙，因為交通管制徒步上山收陷阱的暢快的疲累，還有某次探險到擋巴溝頂端見識到宏偉瑰麗的山勢，或許是這些經驗讓我更喜歡山的吧。我也要謝謝老師聖峰在坐鎮四川之時常常協助我出野外，





開車開過最危險刁鑽的地形，並教了我許多野外技巧，讓我走在山上不在那麼跌跌撞撞。謝謝崇凡時常跟我討論箱子實驗（及至研究）的大小事，因為工作性質類似、常常得晚上標蟲，所以讓我有比較不孤單的感覺。謝謝詩蘋在第二年四川野外成為我很有力的搭檔，非常清楚我的實驗規劃，所以每次出野外都有效率，也謝謝她在我第三年因病撐不下去的時候接手我的工作。謝謝仕凡時常給予心理上的支持，並在我撐不下去時分擔了不少野外工作。謝謝郁盟載著當時還不會開車的我去了好幾趟險惡的炳陽溝。謝謝宗佑、勳承讓野外變得更有趣～最後，也謝謝大家都願意犧牲自己的時間幫忙餵蟲，包括前面未提及的憶晴、宇恆、佑得、陳鈺。

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心，謝謝室友亦盈，謝謝亞錚、以莊在我生病的時候給予我建議，謝謝宣凱總是最主動聯絡大學同學相聚。謝謝你們陪伴我度過這段研究生生活！



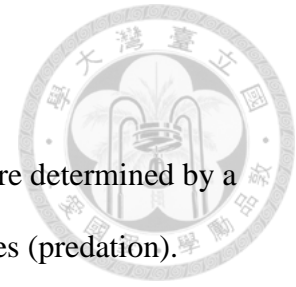


摘要

生態學家早已知道，動物的族群動態是由上行力 (bottom-up forces) (例如資源可利用性) 和下行力 (top-down forces) (例如捕食) 所共同決定的。然而，一些經濟學家指出人口動態也受到合作的影響，這是生態學家很少考慮的概念。在這裡，我們透過建構將環境條件、合作和族群大小結合在一起的個體為本模式 (individual-based model)，來考慮「橫向力量」(例如作用於族群內的種間合作) 對族群動態的作用。在證明環境質量同時影響合作和資源可利用性之後，我們發現由於資源可利用性對合作和族群大小的對比影響，在中等資源水平下社會性生物的族群大小會大於非社會性生物。最終，我們的結果顯示，社會性族群比非社會性族群對環境變化的適應力更強，這是因為合作的好處可能大於資源匱乏的影響。在氣候變化時代，了解環境如何影響包括我們自己在內的社會物種的族群動態至關重要。

關鍵字：合作、族群動態、恢復力

Abstract



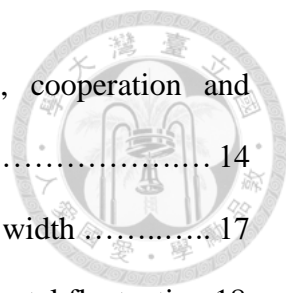
Ecologists have long known that animal population dynamics are determined by a combination of bottom-up (resource availability) and top-down forces (predation). However, some economists have shown that human population dynamics are also influenced by cooperation, a concept seldom considered by ecologists. Here we consider the role of “lateral forces” on population dynamics by constructing an individual-based model linking environmental conditions, cooperation, and population size. After showing that environmental quality influences both cooperation and resource availability, we find that sizes of social populations will be greater than those of non-social populations under intermediate resources levels due to the contrasting effects that resource availability has on cooperation and population size. Ultimately, we show that social populations are more resilient to environmental change than non-social ones because the benefits of cooperation can outweigh the effects of low resource availability. Understanding how the environment influences population dynamics of social species, including our own, is critical in era of climate change.

Keywords: cooperation, population dynamics, resilience

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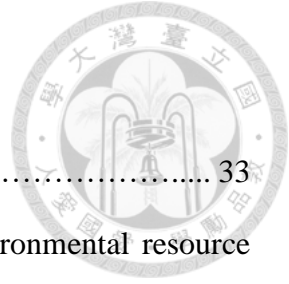


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1. Introduction



1.1 Two contrasting views on the relationship between resource availability and population dynamics


The abundance or carrying capacity of animal populations is often determined by top-down forces like predation pressure or bottom-up forces like resource availability (Anne & Rudy, 1997; Berryman, 2004; Hopfenberg, 2003; Melis et al., 2009; Rutz & Bijlsma Rob, 2006; Schluter & Repasky, 1991; Walankiewicz, 2002), both of which can be influenced by environmental conditions. The role of bottom-up forces extends the view of resource-constrained populations proposed by the economist Thomas Malthus over two centuries ago (Malthus, 1798). Not only is Malthus' view on resource-constrained population dynamics still widely held in ecology (Gotelli, 2008; Lomnicki, 1988; May & McLean, 2007; Molles, 2016), his view on the human struggle for existence remains central to the theory of evolution by natural selection (Darwin, 1859). After the industrial revolution, however, the growth of the world's population prompted economists to reconsider the role of resources in human population dynamics (Brown, 1954; Cépède, Houtart, & Grond, 1964; Cohen, 1995). More than a half century ago, the economist Esther Boserup (Boserup, 1965) further proposed that high population density stimulated human cooperation in order to improve agricultural efficiency, thereby increasing resource supply to match the needs of a growing population. In



contrast to the views of Malthus, Boserup hypothesized that human populations can overcome resource constraints and thrive through cooperation. Whether human populations can actually escape from resource limitation by cooperating remains a topic of great debate to this day (Decker & Reuveny, 2005; Demont, Jouve, Stessens, & Tollens, 2007; Lipton, 1989; Richerson & Boyd, 1997; Urdal, 2005).

1.2 Intraspecific cooperation: an overlooked “lateral force” acting within populations


As an extension of Boserup’s ideas, intraspecific cooperation can be considered to be a “lateral force” that acts within populations and interacts with external top-down and bottom-up forces to regulate population size. Although the role of cooperation has been widely discussed in studies of human population dynamics (Ellis, Magliocca, Stevens, & Fuller, 2018; Hamilton et al., 2009), it is rarely considered in studies of population dynamics in other animals. One exception comes from studies of microbes (de Vargas Roditi, Boyle, & Xavier, 2013; Gore, Youk, & van Oudenaarden, 2009; Sanchez & Gore, 2013) that have explored the impact of cooperation on population growth (Gore et al., 2009; Rainey & Rainey, 2003) or the interaction between cooperation and population dynamics (Sanchez & Gore, 2013). Yet, given that harsh environments are thought to favor cooperation in microbes (Bottery, Wood, &



Brockhurst, 2016; Frost et al., 2018; Yurtsev, Chao, Datta, Artemova, & Gore, 2013), as they do in other social animals (Firman, Rubenstein, Moran, Rowe, & Buzatto, 2020; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017; Rubenstein & Lovette, 2007), how environment-associated cooperation affects population dynamics remains largely unstudied in any organism.

1.3 Brief review on the relevant theoretical studies

Although initial theoretical work on cooperative behavior tended to focus on the emergence and maintenance of cooperation by studying the dynamics of cooperators and free riders in populations of fixed size (Axelrod & Hamilton, 1981; Ohtsuki, Hauert, Lieberman, & Nowak, 2006; Traulsen & Nowak, 2006; Weitz, Eksin, Paarporn, Brown, & Ratcliff, 2016), more recent studies have begun to consider populations that vary in size (Epstein, 1998; Zhang & Hui, 2011). Indeed, eco-evolutionary feedbacks between cooperative behavior and population dynamics often induce coexistence of cooperators and defectors (Hauert, Holmes, & Doebeli, 2006; Sanchez & Gore, 2013). Yet, the role of resource availability in driving these eco-evolutionary feedbacks remains poorly known. Environmental harshness, which reduces resource availability (Allison, 2005; Wang & Goldenfeld, 2011) and increases mortality (Yurtsev et al., 2013; Zhang & Hui, 2011), tends to favor cooperation (Smaldino, Schank, & McElreath,



2013). Yet, clarifying the interactions between resource availability (a bottom-up force) and intraspecific cooperation (a lateral force) on population dynamics remain a challenge for theoretical biologists. Simultaneous consideration of the relationships among population dynamics, cooperation, and resource availability is necessary to more fully understand how social species and populations respond to resource constraints and other environmental challenges.

1.4 Research aims

To capture the essence of a social population and formulate the theory about the relationships among population dynamics, cooperation, and resource availability, it is necessary to construct a model to address this subject. Individuals' cooperative behaviour and their interactions with each other and with other elements of their environment play an important role in impacting the properties of a social population. Most importantly, individuals are adaptive, and adaptation, from which population-level properties emerge, occurs at individual-level, not higher levels. Therefore, individual-based modeling is a suitable approach to explore the emergent properties at the population level in which we are interested. Here, we model how environmental conditions and the benefits of cooperation shape the evolution of asexual and structured populations with overlapping generations. We assume that there are two types of



individuals in the population: free-riders, who do not contribute to creating group benefits, and cooperators, who invest in creating benefits that are shared by all group members at the cost of decreasing the cooperator's own fitness. Groups interact in the population through random offspring dispersal. Population size is not externally assumed, but instead emerges from the dynamics of birth and death processes that are influenced by both environmental conditions and individual behavioral strategies (Fig.

1). We first consider environments of differing quality (harsh environments with low resource availability versus benign environments with high resource availability) to elucidate the relationship between environmental quality and the evolution of cooperation. To tease out the ecological consequences of cooperation, we then compare the population size and the niche breadth of social and non-social populations.

Ultimately, we model population dynamics in a fluctuating environment with varying levels of resources to explore how social populations respond to environmental changes.


2. The model



2.1 General description

We use an individual-based model to simulate the dynamics of structured populations consisting of cooperators and noncooperators (free riders). Cooperators produce benefits (group resources that are shared equally by the group members) at a cost to themselves. Individuals have different genetically-determined levels of cooperative investment, which determine the group resources that they generate. Group resources are essential for individual's reproduction. In other words, more cooperators generate greater group resources, which leads to a higher average reproduction rate of the group members. In contrast, noncooperators provide no benefit to their groups and bear no cost; they simply consume the group resources.

For a comparison with social populations, we also model nonsocial populations consisting exclusively of noncooperators. For simplicity, we consider asexual populations with a mutation rate equal to 0.001, which means the probability that every newborn offspring born from cooperators (noncooperators) mutate into noncooperators (cooperators) is 0.001. At the beginning of each simulation, population size is set to 300, proportion of cooperators is set to 0.01 (to ensure that), and all cooperators and free-riders are randomly divided into 90 groups, which is a level of social structure between individual and population levels. We assume that the interaction among



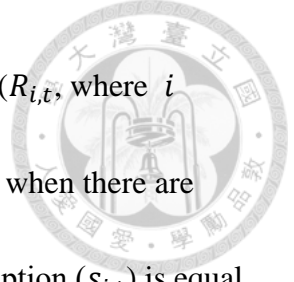
individuals happens only within groups. That is, the group resources generated by the cooperators are only shared by the individuals in the same group. For comparison, we also model the scenario of non-structured populations and found that cooperation cannot evolve in such a scenario (Fig. S1), as has been found in other studies (Zhang & Hui, 2011).

Within every simulation time step, cooperators generate group resources, all individuals consume resources and reproduce, and some individuals die. After individuals produce offspring, the offspring disperse and randomly join a group. The total number of time steps in a simulation is 10,000, which means that the evolutionary process lasts 10,000 years (roughly several thousand generations), to ensure that the system settles into relatively stable dynamics (Strogatz, 2001). We record the proportion of cooperators in populations, the average degree of cooperation that an individuals exhibits, the population size, and the total and per capita reproductive output of each group throughout the process. These properties spontaneously emerge from individual-level interactions.

All variables and parameters are summarized in Table 1.

2.2 Life cycles of individuals

The individuals will undergo the following process during a time step:



At the beginning, individuals equally share the group resources ($R_{i,t}$, where i denotes the i^{th} group and t denotes the t^{th} time step). Therefore, when there are $N_{i,t}$ individuals in the i^{th} group, each individual's resource consumption ($s_{i,t}$) is equal to $R_{i,t}/N_{i,t}$.

Group resources is determined by environmental resource availability (R_0) and cooperation benefits ($b_K \sum_j \phi_{K,i,j}$). b_K denotes cooperation efficiency, and $\phi_{K,i,j}$ with eleven levels (0.0, 0.1, 0.2, ..., 1.0) denotes the j^{th} individual's degree of cooperation, which is genetically-determined and affects the individual's level of cooperative investment, in the i^{th} group. Group resources is a saturating function of cooperation benefits ($b_K \sum_j \phi_{K,i,j}$), which is analogous to Monod equation (Monod, 1949):

$$R_{i,t} = R_0 \left(1 + I \cdot \frac{b_K \sum_j \phi_{K,i,j}}{\frac{IR_0}{2} + b_K \sum_j \phi_{K,i,j}} \right),$$

where I is the maximum resource increment rate. For the groups without cooperators generating group benefits, $R_{i,t} = R_0$.

Next, individuals produce offspring, and the offspring disperse and randomly join a group. The number of offspring the j^{th} individual can produce (reproduction rate $F_{i,j,t}$) is a saturating function of the amount of resource it consumed in the form of Monod equation (Monod, 1949) and also depends on the cost of cooperation:

$$F_{i,j,t} = \alpha \left(1 - \beta \phi_{K,i,j} \right) \cdot \frac{s_{i,t} - M}{K_s + (s_{i,t} - M)},$$

where α denotes the maximum reproduction rate of an individual, β ($0 < \beta \leq 1$) is



defined as the percentage decrease in reproduction rate caused by per unit cooperation degree ($\emptyset_{K_{i,j}}$), M is a constant and represents the metabolic consumption of an individual, which is a threshold for reproduction, and K_s is the “half-saturation constant”, which is the value of the individual energy for reproduction ($s_{i,t} - M$) at which reproduction rate ($F_{i,j,t}$) is half of its maximum.

Finally, the system determines whether individuals survive. The survival rate ($r_{i,j,t}$) of the j^{th} individual in the i^{th} group decreases as it gets older:

$$r_{i,j,t} = c \cdot \exp\left(-\frac{age_{i,j,t}}{age_{const}}\right),$$

where c is a constant between 0 and 1. For the offspring born at the t^{th} time step, $r_{i,j,t} = c$ because $age_{i,j,t} = 0$.

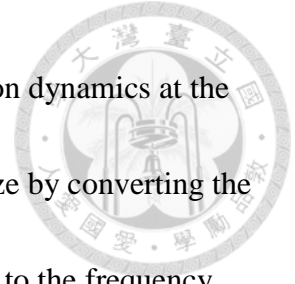
2.3 Populations in fluctuating environments

Ultimately, we introduce environmental fluctuation into the system. Environmental resource availability (R_{0_t}) periodically fluctuates in a sine function:

$$R_{0_t} = R_{0_0} + A \sin\left(\frac{2\pi t}{P}\right),$$

where A denotes the amplitude and P denotes the period. We record the time series of the proportion of cooperators, the average degree of cooperation, and the population size. To derive the trend in population dynamics, we average the time series from 500 replicates of simulations. We further use time-lagged cross-correlation (TLCC) to

quantify synchrony between environmental fluctuation and population dynamics at the relatively stable state, and evaluate the variation of the population size by converting the time series of the population size variation standardized by the mean to the frequency spectra using a fast Fourier transformation (Dillon et al., 2016).



3. Results




3.1 Environmental quality and the evolution of cooperation

We found that the evolution of cooperative behavior is determined jointly by the amount of available environmental resources and the benefits of cooperation. Cooperation, in terms of both the proportion of cooperators in the population and the average degree of cooperation that each individual exhibits, is more likely to evolve when environmental conditions are harsh (i.e. low resource availability) and when the benefits of cooperation are large (Figs. 2 and 3). This is because individuals are generally unable to produce offspring with the few resources generated by cooperators in harsh environments (Fig. 4a). Thus, free riders cannot persist without cooperators under harsh environmental conditions. In addition, although both cooperators and free riders share the group resources generated by cooperators (but only the cooperators have to pay personal costs), cooperators in groups with more group resources can still have more offspring than individuals in groups with fewer cooperators and group resources in harsh environments (Fig. 4a). However, resources generated by cooperators play a smaller role in impacting reproduction in benign environments because available environmental resources are already abundant (Fig. 4b). As a consequence, cooperation is maintained in harsh environments, particularly when the benefit of cooperating is high.



3.2 Joint influence of environmental quality and cooperation on population dynamics

Next, we explored how environmental quality and cooperation jointly influence population dynamics. We found that population size in social organisms is affected by environmental quality both directly in terms of resource availability and indirectly by its effect on the number of cooperators and the degree of cooperation within the population. When the benefit of cooperating is small, population size is largely determined by environmental quality, resulting in a population that is similar in size to one without cooperators (Fig. 5a). However, as the benefit of cooperating becomes greater, population size is determined by both environmental quality and cooperation (Fig. 5b). When the benefit of cooperating becomes very large, population size increases abruptly with an increase in environmental quality (i.e. an increase in resources) and then stays relatively constant (Fig. 5c). This result can be explained by the fact that the average degree of cooperation is also modulated by environmental quality in such a way that individuals are less cooperative in benign than in harsh environments (Fig. 2). Therefore, the positive effect of additional resources in benign environments is canceled out by the negative effect of additional free riders. Moreover, additional cooperators in harsh environments compensate for any negative effects of resource scarcity. Furthermore, we showed that social populations possess an advantage in harsh



environments with low resource availability when the benefit of cooperating is great enough to outweigh any effects of resource limitation on population size. This result implies that social populations can have wider ecological niches (i.e., can occur in environments with a wider range of resource availability) than non-social populations due solely to the fact that individuals cooperate.

3.3 Stability of population dynamics in a fluctuating environment

Finally, we compared the population dynamics of cooperative and noncooperative populations in a changing environment. We found that the dynamics of noncooperative populations tend to synchronize with environmental fluctuation (Fig. 6a and 6c), whereas the dynamics of cooperative populations do not (Fig. 6b and 6d). Population size increases after environmental conditions become extremely harsh, but decreases as conditions become more benign. In addition, the values of peaks in the frequency spectra of population size variation in noncooperative populations are higher than in cooperative populations (Fig. 6e and 6f), which indicates that cooperative populations are more stable than noncooperative ones in a changing environment because the pattern of cooperation is also modulated by environmental conditions (i.e., they are more cooperative in harsher environments), which can buffer the effect of changing environmental conditions on population size (Fig. 7).

4. Discussion




4.1 The significance of the research

Our results show that environmental conditions have an impact on the size and carrying capacity of social species in complex ways (Fig. 5) by affecting both the degree of cooperation and the dynamics between cooperators and noncooperators (i.e. free riders) (Fig. 3). Our model therefore provides a theoretical framework for understanding the ecological causes (e.g., environmental harshness) and consequences (e.g. niche width) of cooperation. Three main results emerge from our model: (1) there will be complex relationships among environmental conditions, cooperation, and population dynamics (Fig. 5); (2) cooperation can facilitate social species to expand their niche width in terms of resource abundance (Fig. 5) and stability (Fig. 6); and (3) social species have greater population resilience to environmental fluctuation than non-social ones (Fig. 6). We explain these results in greater detail below.


4.2 Complex relationships among environmental conditions, cooperation and population dynamics

Our results show an unexpected relationship between environmental quality and population size in social organisms (Fig. 5). Despite resource scarcity, the size of a social population can be larger in harsh environments than in benign ones if the benefit



of cooperating is high enough. This pattern contradicts the Malthusian view of resource-constrained population dynamics, which does not consider the impact of cooperation on population size. It also differs from Boserup's idea that high population density drives cooperation to facilitate population growth, since the degree of cooperation is also determined by environmental conditions. In a benign environment, free-riders account for the majority of individuals in a population, and thus there is little benefit of cooperating for further population growth. Therefore, our model synthesizes Malthus' view of resource-constrained population dynamics (Malthus, 1798) with Boserup's idea that cooperation drives population growth (e.g. via agricultural innovation in humans) (Boserup, 1965). We show that environmental quality influence population dynamics both directly (via resource availability) and indirectly (via the degree of intraspecific cooperation within the population).

The magnitude of the benefit of cooperating play an important role in shaping the relationship between environmental quality and population size. When the benefit of cooperating is low, the impact of cooperation on population size is weak, and thus the size of a social population—similar to that of non-social one—is mainly determined by environmental conditions (Fig. 5a). However, when the benefit of cooperating is high, cooperation can strongly influence population size (Fig. 5c). In addition, the degree to which cooperators invest in creating group resources depends on the environmental



conditions, such that they contribute more in harsh environments and less in benign environments (Fig. 3). Consequently, the direct relationship between environmental quality and population size is less clear than has been previously assumed.

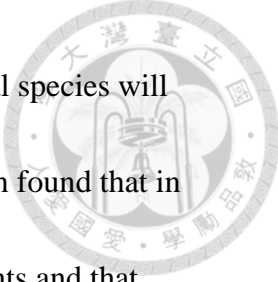
Two important implications can be drawn from this observation. First, ecologists often assume that better environmental conditions lead to larger populations (Gotelli, 2008; Molles, 2016). Yet, to the best of our knowledge, few empirical studies examine the relationship between resource availability and size of social populations. Our finding highlights the need to empirically test such assumptions in social species by quantifying lateral forces—the degree of intraspecific cooperation—to understand their impact on population size. Second, the booming human population sizes of the past century are often considered as evidence that human populations are not limited by resources (Kögel & Prskawetz, 2001; Steinmann, Prskawetz, & Feichtinger, 1998). However, we caution against such a view (Boserup, 1965), since our model suggests that the effect of resource availability on the degree of cooperation within a population can also influence population dynamics and constrain population sizes. Thus, empirically testing the direct and indirect relationships among environmental quality, cooperation, and population dynamics is urgently needed in social species, including our own.



4.3 Cooperation can facilitate social species to expand their niche width

If we consider resource availability as a dimension of niche space, we can deduce that social species have a wider fundamental niche breadth than non-social ones (Fig. 5). However, it should be noted that this study has not considered the confounding effects of body size and thermal affinity on niche breadth. Despite its limitation, this study does suggest cooperation helps social species to maintain positive population growth even when the environments are harsh, i.e. with scarce resources if the benefit of cooperation is large. This result supports and provide a more complete theoretical foundation for the social conquest hypothesis. The ecological consequences of cooperation, such as how cooperation influences the abundance and the niche width, has been rarely tested empirically. Although Wilson has long argued that ants and human are the two most dominant species on earth because of their ability to cooperate and form groups (Wilson, 1987, 2012), to our knowledge, few formal analyses or evidence exist. One exception is a study in Asian burying beetles, it has been found that social groups are more cooperative in harsher, hotter environments with more intense inter-specific competition than in benign environments (Sun et al., 2014). As a consequence, social groups are able to expand their thermal niche to harsher, hotter environments than the solitary groups.


Since wider niche width often leads to larger geographic range size and higher



abundance (Slatyer, Hirst, & Sexton, 2013), we also predict that social species will likely have larger geographic range size of species. Indeed, it has been found that in starlings, cooperation occurs more frequently in the harsh environments and that cooperative species have larger range sizes than non-cooperative ones (Lin, Chan, Rubenstein, Liu, & Shen, 2019). However, they also found that cooperation does not influence range size of species in hornbills and that hornbills cooperate only when resources are abundant, presumably due to the habitat saturation caused by high population density, which are different from the scenario described in our model. In short, more studies comparing the niche width and geographic range size of social and non-social species will help us understand the generality of this prediction.

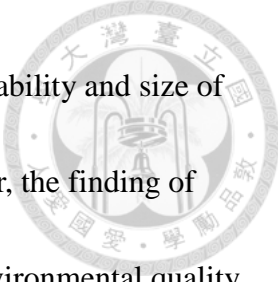
4.4 Social species have greater population resilience to environmental fluctuation

We found that in fluctuating environments, the size of social populations is more stable than that of non-social populations (Fig. 6) because environment-associated cooperation buffers the impact of environmental fluctuations on social populations. In other words, the key mechanism leading to population resilience of social species is that they are more cooperative in harsh than benign environments (Fig. 2, 3, and 7). A study of social microbes also found that social populations are more resilient to environmental disturbance (i.e. experimentally lower population density) than non-social ones because



more cooperators generate greater public resources (public goods) (Sanchez & Gore, 2013). However, this study assumed that environmental resource availability was stable and the only change in the experiment was lowering the population density. Thus, population resilience in this study meant that populations could survive through periods of low density but not environmental harshness per se, and the population dynamics were driven by density-dependent processes such that more cooperators in the population generated greater public goods. Several theoretical studies have investigated this density-dependent process (Epstein, 1998; Hauert et al., 2006; Zhang & Hui, 2011), showing similar patterns of dynamics: abundant public goods generated by cooperators favor the rise of free-riders who do not invest in producing public goods, eventually resulting in an overall reduction of public goods. As public goods became scarce, cooperators are favored by selection again. However, since environmental conditions such as resource availability are assumed constant, these studies cannot determine how bottom-up forces influence the interaction between population and evolutionary dynamics. In contrast, our model suggests that environmental quality can influence both the evolution of cooperation and population dynamics, a result that should be incorporated in future empirical studies.


4.5 Model limitations



Our model indicates that the relationship between resource availability and size of social population is more complex than previously assumed. However, the finding of this study has been primarily concerned with the indirect effect of environmental quality via degree of intraspecific cooperation on population growth. This model has not considered other individual traits related to population growth.

Some studies show that cooperation is more likely to evolve in benign environments (Leticia Avilés et al., 2007), which contrasts our results. This inconsistency may be due to the differences in the benefits of forming social groups. Dual-benefit hypothesis suggest that animals form social groups for two main reasons: coping with environmental harshness or intraspecific competition and outcompete conspecifics (Shen, Emlen, Koenig, & Rubenstein, 2017). Some animals are more likely to form social groups to overcome environmental challenges, whereas others are more likely to do so to compete with their conspecifics. In our model, we have only considered that individuals cooperate to coping with environmental harshness (i.e., low resource availability). Therefore, the lack of consideration of both dual benefits means that we cannot be certain that cooperation must evolve under certain conditions.

4.5 Concluding remarks



As the earth continues to warm, its climate is becoming increasingly unpredictable (Salinger, 2005; Schär et al., 2004). Some studies have argued that climate change-driven resource scarcity will lead to increased armed conflict in human societies, a truly neo-Malthusian perspective (Nordås & Gleditsch, 2007; Raleigh & Kniveton, 2012; Scheffran & Battaglini, 2011). Yet, other studies have argued that the environmental problems caused by climate change will not exacerbate violent conflict (Benjaminsen, Alinon, Buhaug, & Buseth, 2012; Gleditsch, 2012), and may even promote peace and greater cooperation (Slettebak, 2012). Based on our models exploring environmental quality, social interactions, and population dynamics, we predict that harsh environments—those with low resource availability—will also promote more cooperation in human societies depending on the types of cooperative benefits that can be generated under different environmental conditions. Empirical studies testing our model predictions by comparing patterns of cooperation under different environmental scenarios, as well as those examining population fluctuation and stability between social and non-social species, will be of great importance for understanding the future dynamics of social species, including our own.

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6. Tables



Table 1: Summary of model parameters.

Name	Value	Description
R_0	[1, 20]	Environmental resource availability
b_K	[0.1, 6.5]	Cooperation efficiency
ϕ_K	{0.0, 0.1, 0.2, ..., 1.0}	Degree of cooperation
I	40	Maximum resource increment rate
α	3	Maximum reproductive rate of an individual
β	0.5	The percentage decrease in the reproductive rate caused by per unit cooperation degree
M	1.0	Metabolic consumption of an individual
K_s	2	Half-saturation constant
c	0.7	Maximum survival rate
age_{const}	2	A constant related to age
A	5	The amplitude of environmental fluctuation
P	1000	The period of environmental fluctuation

7. Figures

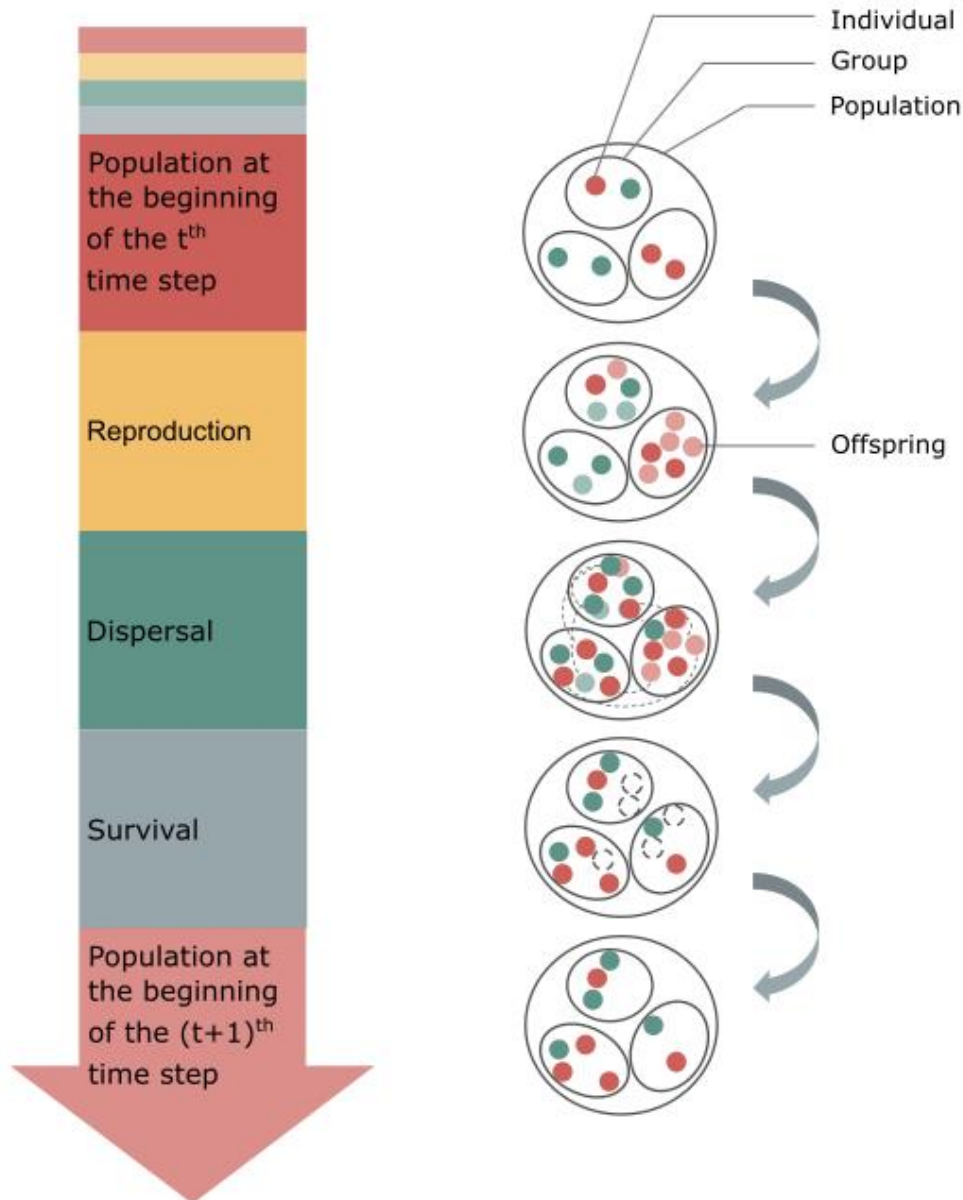


Fig. 1: A schematic diagram for the model. The diagram shows the process a population undergoes within one simulation time step. The red, yellow, green, and grey portions in the arrow on the left represent reproduction, dispersal, and survival stages in

individual life cycle, respectively. Red and green dots represent cooperators and noncooperators, respectively, and lighter colors represent newborn individuals.



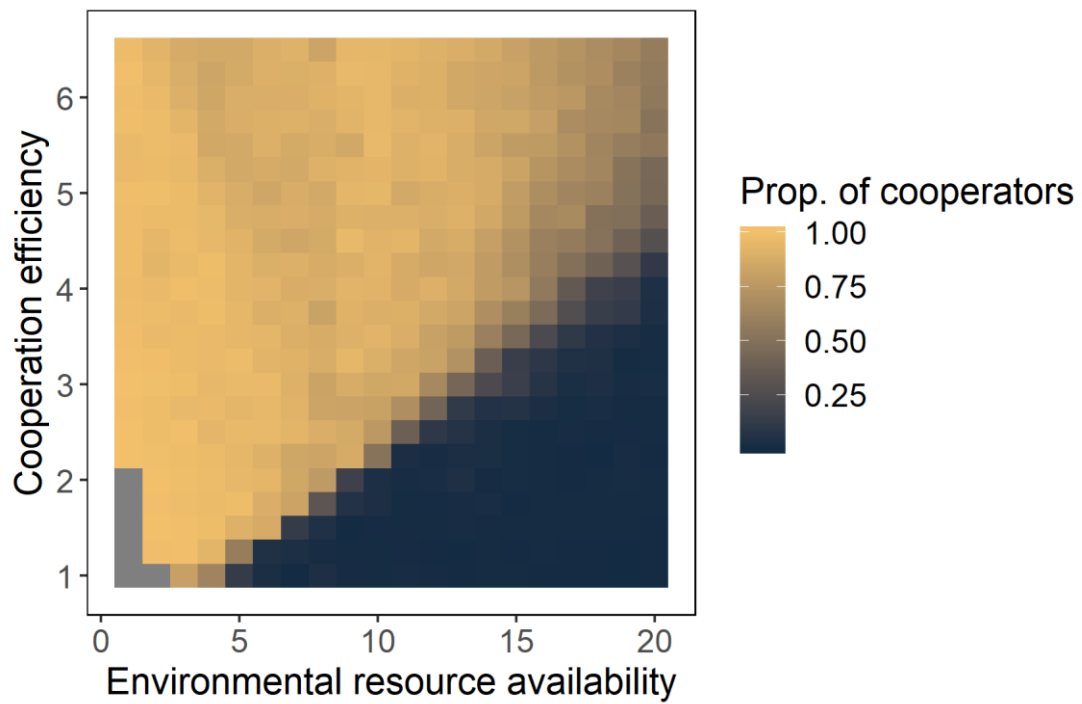


Fig. 2: Proportion of cooperators in populations in relation to environmental resource availability and cooperation efficiency. Cooperative behavior is more likely to evolve when environmental conditions are harsh (i.e. low environmental resource availability) and when cooperation efficiency, an intrinsic property of individuals, is high.

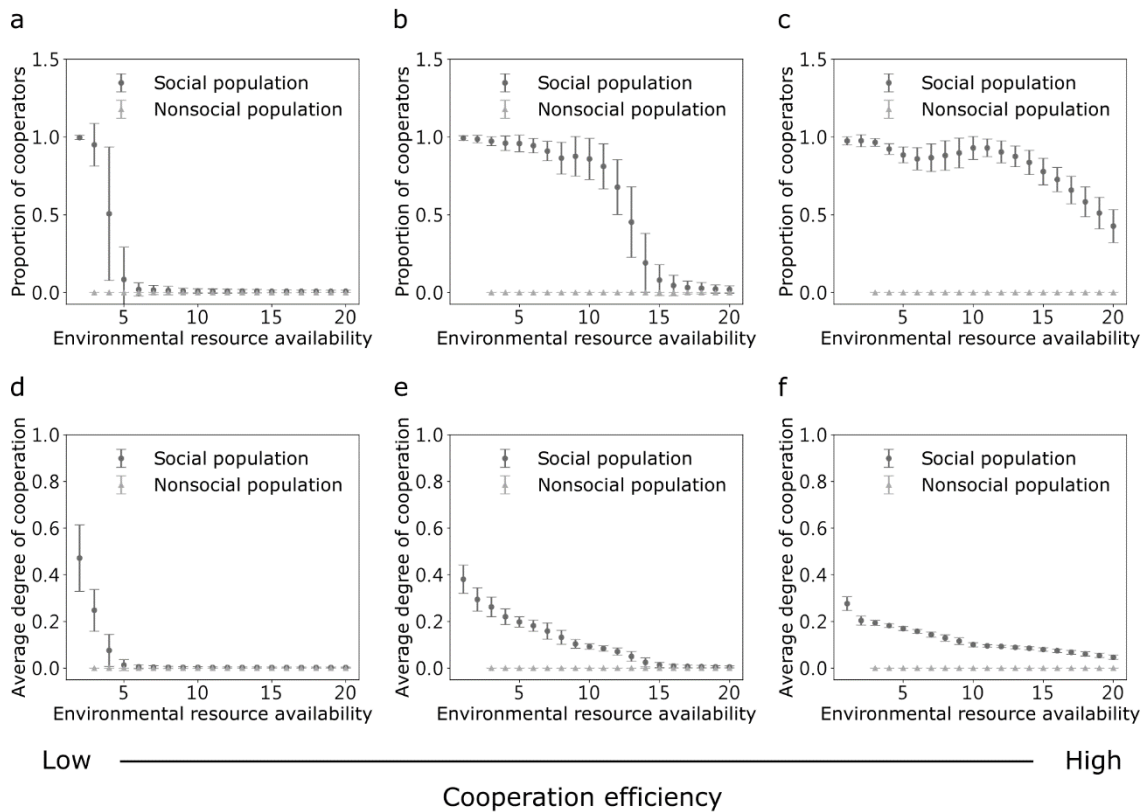


Fig. 3: The outcome of the evolution of cooperation influenced by varying

environmental resource availability. (a)-(c) Mean proportion of cooperators in populations in relation to environmental resource availability as cooperation efficiency is **(a)** low ($b_K = 1$), **(b)** medium ($b_K = 3$), and **(c)** high ($b_K = 5$). **(d)-(f)** Mean degree of cooperation that individuals exhibit in relation to environmental resource availability as cooperation efficiency is **(d)** low ($b_K = 1$), **(e)** medium ($b_K = 3$), and **(f)** high ($b_K = 5$). Points represent means and bars represent standard deviations. Each mean and standard deviation is calculated on the output data of 500 simulations.

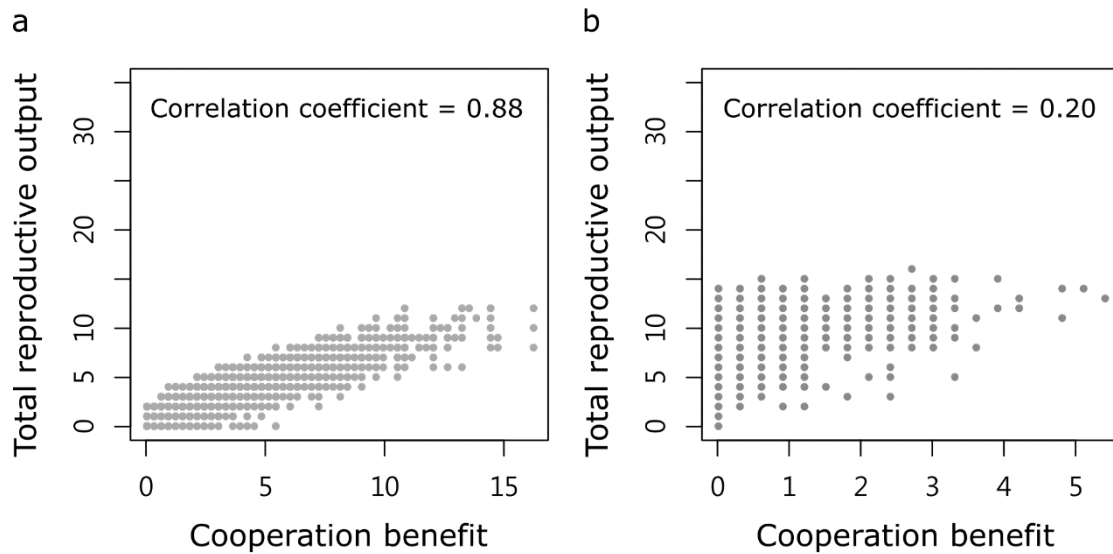


Fig. 4: Comparison of the relationship between total reproductive output and cooperation benefit of groups in different environments. (a)-(b) Total reproductive output of groups in relation to their cooperation benefit in **(a)** harsh and **(b)** benign environments. Each point represents a group's condition. The results are extracted from the early stage (the end of the 100th time step) of the simulations to see how cooperation benefits influence the reproductive output at the evolving stage.

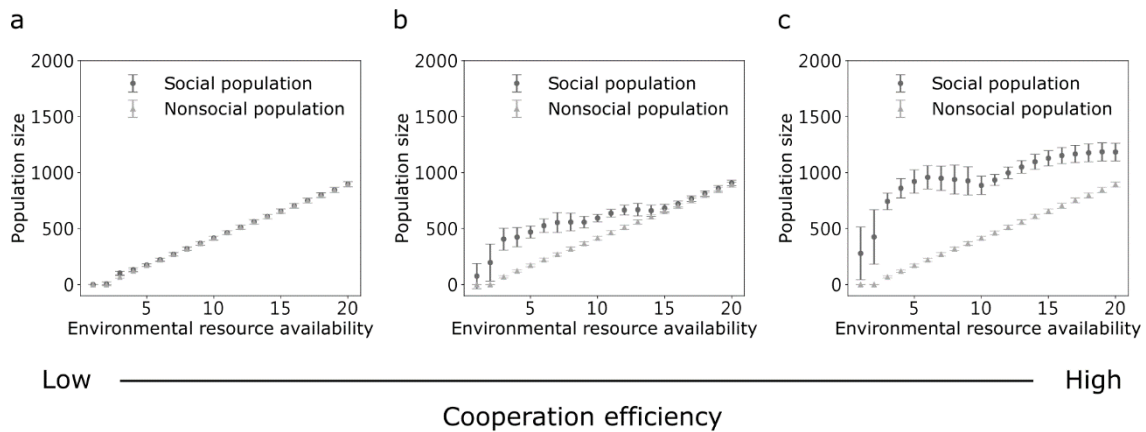


Fig. 5: The combined effects of environmental resource availability and degree of cooperation on population size. (a)-(c) Population size in relation to environmental resource availability when cooperation efficiency is **(a)** low ($b_K = 1$), **(b)** medium ($b_K = 3$), and **(c)** high ($b_K = 5$). Points represent means and bars represent standard deviations. Each mean and standard deviation is calculated on the output data of 500 simulations.

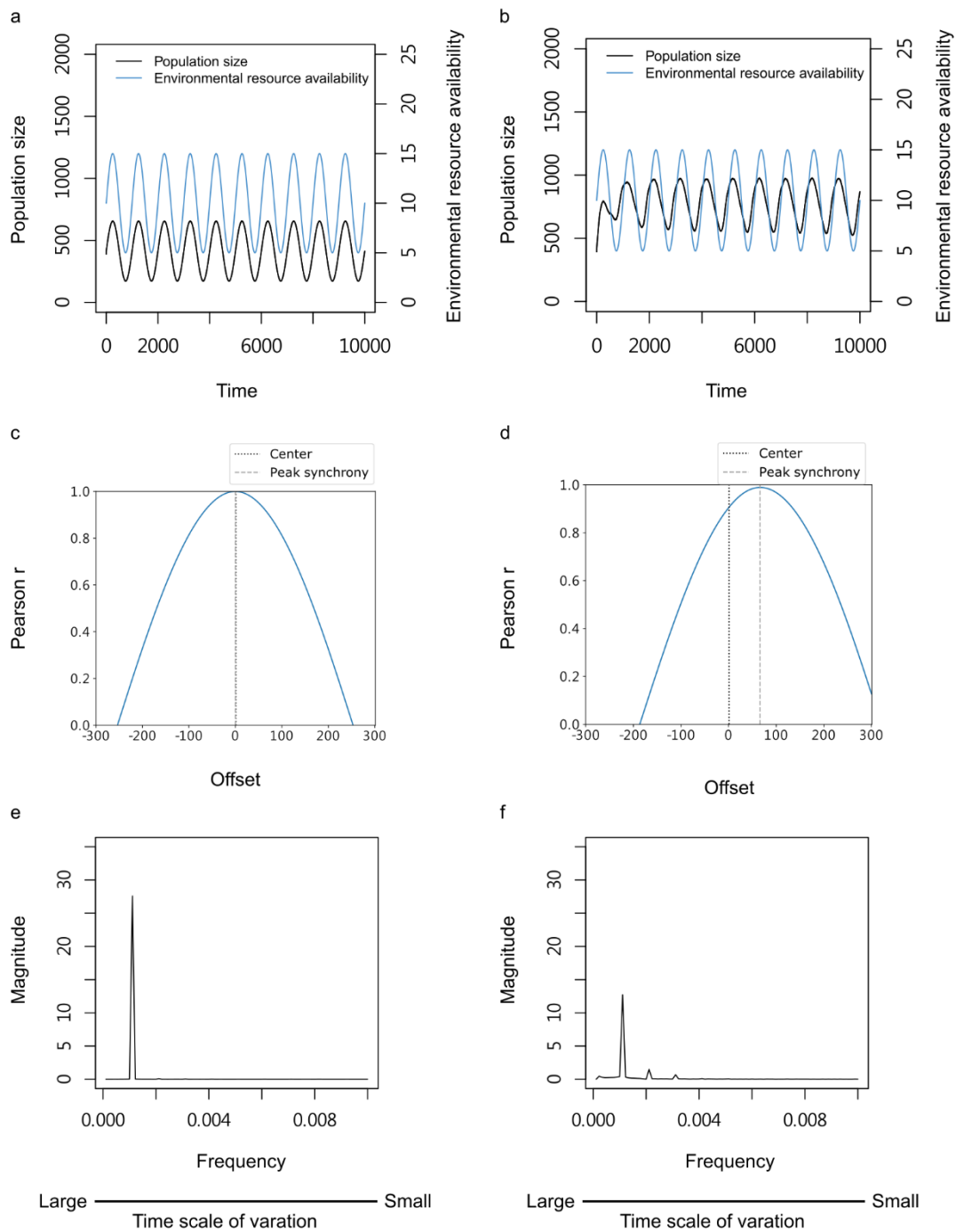
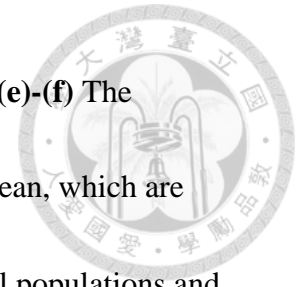


Fig. 6: Population dynamics and relative variability in population size in a fluctuating environment. (a)-(b) Time series of the population size of **(a)** non-social populations and **(b)** social populations in the fluctuating environment. **(c)-(d)** The time-lagged cross correlation between the population dynamics and the environmental

fluctuation for **(c)** nonsocial populations and **(d)** social populations. **(e)-(f)** The frequency spectra of the population size variation standardized by mean, which are derived from fast Fourier transformation, are shown for **(e)** nonsocial populations and **(f)** social populations. Each line is the average of the output data of 500 simulations.



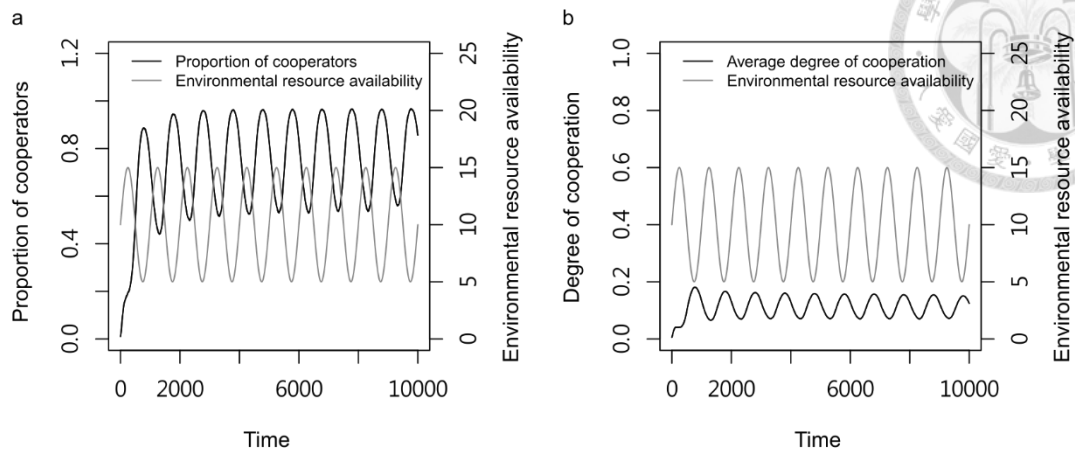


Fig. 7: Degree of cooperation changes with the fluctuation of environmental resource availability. Time series of (a) the proportion of cooperators and (b) the individual average degree of cooperation of social populations in a fluctuating environment. Each line is the average of the output data of 500 simulations.

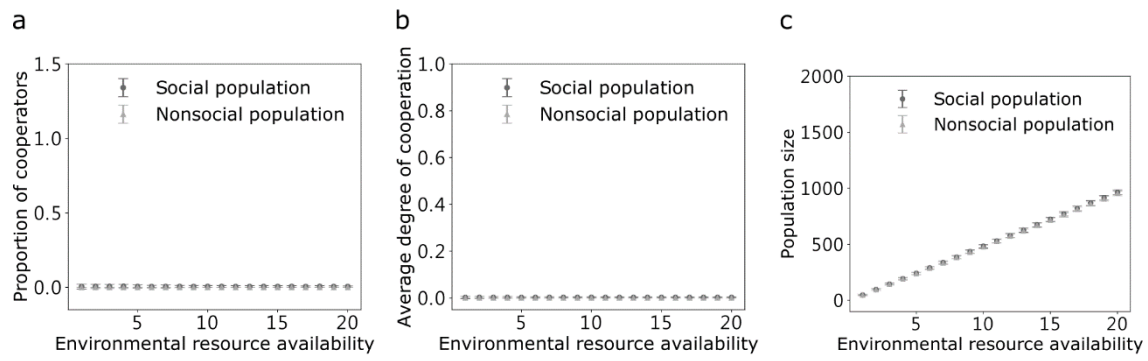


Fig. S1: The evolutionary outcome and the population size of non-structured

populations. (a) The proportion of cooperators, **(b)** the individual average degree of cooperation, and **(c)** the population size in relation to the environmental resource availability as the populations are not structured.