Cash, crowds, and cooperation: The effects of population density and resource scarcity on cooperation in the dictator game

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Abstract: The adaptive benefits of cooperation among humans have been widely studied. However, is being cooperative always adaptive across various combinations of ecological conditions? Existing work has focused on cultural, inter-, and intra-individual predictors of cooperation yet there is a lack of research on how an individual's ecology may come into play. In this work, we focus on the interaction of two ecological factors—population density and resource scarcity—on cooperation. Population density is often accompanied by social competition for limited resources. We hypothesise that in response to cues of high (versus low) population density, people facing resource-scarcity would adaptively lower their cooperativeness, more so than those with resource abundance. Results from two studies support our hypothesis—population density lowers cooperation, but only for people who perceive lower resources or social status. Our findings provide insights that cooperation varies adaptively as a function of interacting ecological factors.

Keywords: Population density, Resource scarcity, Socio-economic status, Cooperation, Dictator game

1. Introduction

In a world that is becoming increasingly populated, we are often faced with a common social dilemma—do we hoard resources for our own use, or do we try to sacrifice our personal needs for the collective instead? Indeed, such behaviors that involve cost to oneself but can benefit others has been defined as "cooperation" (Balliet, Mulder and Van Lange, 2011, Balliet, Wu and van Lange, 2020; Rand & Nowak, 2013).

The large body of literature on cooperation has largely been focused on identifying cultural, group, inter- and intra-individual predictors such as the nature of incentives (i.e., reward or punishment) (Balliet et al., 2011), norms of helping, expectations of reciprocity (Keltner et al., 2014), communication methods (Balliet, 2010) and being compassionate (Piff, Kraus, Cheng, et al., 2010). Meanwhile, the influence of ecological conditions on cooperation has received less attention, with present research typically focusing on singular aspects such as historical interdependence for sustenance (e.g., Talhelm et al., 2014) or access to resources (e.g., Piff, et al., 2010). Yet, individuals are typically situated in environments with multiple ecological dimensions (see Sng et al., 2018) that influences their social behavior (Koohgard et al., 2024; Tan et al., 2023). This leads to questions of whether from an evolutionary perspective, does the adaptive value of cooperation vary across different combinations of ecological conditions?

In particular, we focused on the interactive influence of two ecological factors—population density and resource scarcity—on cooperative behaviors, which we earlier defined as the act of benefitting another party (or group), sometimes at a cost to oneself (Balliet, Mulder and Van Lange, 2011, Balliet, Wu and van Lange, 2020). From an ecological perspective, population density could serve as a cue that many people are vying for the available resources afforded by a certain geographic region (Sng et al., 2018). Higher density could lead to greater competition and an amplified need to protect one's resources.

While some evidence suggests that higher population density predicts lower helping behaviors[1, 2, 3, 4, 5, 6 and 7] (Levine et al., 1994), researchers have not yet investigated how the effect of density on cooperation differs across levels of resource scarcity. Having more resources facilitates the pursuit of adaptive goals. In the face of high density, having more resources might buffer against the need to hoard resources selfishly since there is enough to go around. Moreover, resource scarcity reflects ecological harshness and unpredictability, promoting immediate self-serving responses (Griskevicius, Tybur, et al., 2011; Tan et al., 2022). Hence, we aimed to shed light on why individuals might choose to compete or cooperate in different combinations of density and resource conditions.

1.1. Population density and cooperation

Human populations have experienced fluctuations in population sizes throughout ancestral history (Hu et al., 2023; Schiffels & Durbin, 2014). It is plausible that organisms evolved to display behavioral plasticity to respond adaptively to ecological changes. For instance, animals of the same species from urban (versus nonurban) ecologies display large differences in habitation preferences, personality differences and social behavior (Caspi et al., 2022). Likewise, humans also experience more negative affect in interpersonal interactions (Griffit & Veitch, 1971) and different navigation strategies or threat responses (Haghani & Sarvi, 2018) when their surroundings are crowded (versus not crowded). In a similar manner, we believe humans have adaptations in social behavior in response to population density cues.

There are many economic advantages to living in urban regions with high population densities (especially in urbanised areas), such as enhanced accessibility to necessary lifestyle amenities, higher efficiency in usage of resources (e.g., land, natural resources), increased education and employability, and higher affordability of housing options and quality of life (refer to Tables 2–8; Boyko & Cooper, 2011). However, despite potential economic gains and improvements to quality-of-life, crowded environments may be psychologically perceived as threatening to our evolved brains.

In ancestral times, high population density meant more people vying for the same pool of resources within a given geographic area, thereby subjecting people to the possibility of having insufficient resources for survival or reproduction. Accordingly, human brains may have evolved to interpret population density as an adaptive threat (the savannah principle; Kanazawa, 2004). Indeed, data on well-being are consistent with this view: people living in higher population densities or urban areas consistently report lower happiness (e.g., Berry & Okulicz-Kozaryn, 2009; Li & Kanazawa, 2016) than those living in lower densities or rural areas. Humans have evolved to deal with the threat from increased population density by having lowered motivation to cooperate with others due to several reasons, (1) an increased sense of threats to one's resource availability and (2) lowered sense of genetic relatedness.

First, when a large population is concentrated in a small geographic area, there is a decrease in available resources per individual. High density objectively leads to lower land-space for agriculture (Kyalo Willy et al., 2019) and shortage of basic resources for survival (e.g., clean water; Mekonnen & Hoekstra, 2016). It is possible that our evolved brain construes this as a sense of scarcity and a threat to one's survival needs. Supporting this, people report higher levels of stress in conditions of high density (Aiello et al., 1977; Hassan, 1977). Without first meeting self-preservation needs, it is difficult to be motivated to pursue other adaptive goals such as affiliation (Maslow, 1970). As such, people tend towards being more competitive to secure limited resources (Ho et al., 1999). Using experimental designs, after being exposed to high (vs. low) population density cues, participants reported a significantly higher sense of social competition (Koo et al., 2022).

Behavioral evidence supports this notion. When resources are scarce, there is a higher motivation to prioritise individual needs at the expense of other individual or group goals (Pitesa & Thau, 2018; Roux et al., 2015). Additionally, people facing resource scarcity tend to view resource distribution in a zero-sum manner (Shah et al., 2012); every unit of one's limited pool of resources given to others comes at a cost to oneself. At the group level, we observe that countries go to war over scarce resources (Pinker, 2012). People even adopt life strategies that helps them sustain a competitive edge in the long run (Sng et al., 2018). Thus, it is plausible that due to the sense of scarcity which accompanies population density, people are less cooperative[2] and prioritise self-preservation over others' needs.

The second psychological effect of high population density is that it increases the likelihood of interacting with people who are genetically unrelated to us (Dunbar, 1992; Gonzalez-Cabrera, 2018), which decreases the gains from cooperation afforded by kin altruism (Hamilton, 1963) and hence, lowers our tendency to cooperate with others (Sng et al., 2018). Taken together, our brain has evolved to perceive population density as a threat to adaptive fitness and thus, humans may be less motivated to be cooperative with others. Indeed, across states in the US, cities with higher population density is associated with lower cooperation and helping behaviors (Levine et al., 1994).

Notably, an alternative perspective is that cooperation might be adaptive under high competition (Katz et al., 2021), which accompanies high densities. However, cooperation is only adaptive in helping people band together against high competition when social settings do not exceed the capacities of the human mind. Social networks operate optimally within a group size of 150 (Dunbar, 1992), which mirrors the

[1] Helping behavior towards strangers are consistent with our conceptualization of cooperativeness because it involves benefitting another party while incurring a cost to the self (e.g. time, energy, money etc.).

[2] Notably, there is evidence that population density might *increase* cooperation (Katz et al., 2021). It has been proposed that the association between population density pro-social behaviors might be curvilinear—although population density increases aggressiveness and competitiveness, at extremely high levels of density, it is counter-productive (and chaotic) to be aggressive (Sng et al., 2018). This highlights that people may have potentially evolved mechanisms that allows for social orientations to adjust adaptively in response to ecological demands. Nonetheless, our research does not focus on the extremities of population density.

[3] Although we propose that scarcity should reduce cooperation as a means of self-preservation, there is some research supporting the opposite, negative effect of resources on cooperation. Afterall, humans evolved to live in groups that heavily rely on reciprocal relationships for survival; in the ancestral past, people share resources as a means of reducing net variance in resources necessary for survival and this increases overall odds of survival. Indeed, some empirical work suggests that people facing scarcity (versus abundance) are more cooperative and other-oriented (Kraus et al., 2012; Piff, Kraus, Côté, et al., 2010). Given these mixed directions associations between resource availability and cooperation, we will explore both these plausible direction of effects in our Singaporean student sample. Nonetheless, our research focus is on testing our hypothesis that people facing scarcity are more likely to change their cooperativeness in response to ecological cues.

[4] Note that Singapore is a small, developed city with especially high population density and high GDP per capita. Moreover, university students are more likely to be wealthier. We acknowledge that there may be some range restriction effects. Nonetheless, we sought to test our hypotheses based on the premise that subjective perceptions of population density and resource availability might influence cooperativeness in the dictator game.

[5] For further information about different measures of socio-economic status or perceived resource availability, please refer to Table 1 of Antonoplis (2023) that documents various definitions of socio-economic status across different research work.

[6] While our current work provides preliminary evidence for a population density x resources interaction effect on cooperation in the dictator game, future work can adopt alternative statistical methods such as Bayesian statistics to verify the null hypothesis—that there is no effect of density on cooperation among people with more resources.

[7] In accordance with our debriefing form approved by the IRB, participants were clearly informed that the dictator game was a fictitious paradigm used in our study for research purposes.

size of our ancestor's social networks. The human brain had not evolved capacities to manage reciprocal exchanges beyond this group size (Dunbar, 2010; Dunbar, 2011). In our modern world, unprecedented rates of population growth results in humans residing among communities that are psychologically perceived to exceed the social network sizes that our brains evolved to manage. Thus, given the extremely large size of populations and proximity of residences today, it is likely that high densities translates into acting competitively under high densities.

Current research on how population density influences cooperation is sparse. Furthermore, existing studies have focused on the effects of population density on cooperation, without accounting for the potential interactive effects of other ecological factors, such as resource availability. In line with arguments that human behavior results from the simultaneous influence of ecological conditions (Ellis et al., 2009a; Sng et al., 2018), we believe that resource availability can potentially mitigate the perceived threats that come with population density. As such, in this work, we examine the effects of both population density and resource availability on cooperation.

1.2. The interaction of resource availability and population density

While there is a negative influence of population density on cooperation, the heightened competition for resources accompanying higher density may only pose a severe threat or stressor to people with fewer resources who already face challenges due to their state of scarcity. Resource scarcity has always posed a severe threat to mortality. For the majority of mankind's evolutionary history, humans have relied on acquiring resources from their environment for survival (Orians & Heerwagen, 1992). Large fluctuations in resource availability led to mass extinctions of some hominin populations (Shea, 2008). Even after mankind's agricultural revolution, many human societies constantly faced falling short of having sufficient harvest for biological sustenance (Harari, 2017). Thus, it is likely that recurring selection pressures due to resource scarcity throughout mankind's ancestral past has led to psychological adaptations to overcome these threats. One of these adaptations against scarcity involves the how one might distribute available resources with others (i.e., the tendency to cooperate or compete).

Scarcity induces an inclination to be competitive, rather than cooperative. Economic and evolutionary biology theories contend that competition always involves scarce resources (Keller, 1992). Resource scarcity drives a motivation to compete with others for the appropriation of the relevant resources that facilitates survival (Grossman & Mendoza, 2003). Extending this idea to the mating domain, when there is a scarcity of opposite sex members, intra-sexual competition intensifies (Griskevicius et al., 2012). People who lack resources tend to fixate on resolving the scarcity (Cannon et al., 2019) and construe resource acquisition as a self-other tradeoff (Shah et al., 2015). If presented with the option of a self- versus other-gain, scarcity tends to induce a prioritization of self-goals. This is adaptive because when resources are scarce, it is not logistically possible to simultaneously protect self-needs and those of others. This concurs with other theories that without first meeting self-needs, it is difficult to extend help to others or pursue affiliative goals (Maslow, 1970). Thus, resource scarcity increases a prioritization of self over others' needs.

Indeed, empirical studies have supported that scarcity drives a motivation to prioritise individual needs at the expense of other individual or group goals.[3] In times of poor economic outlook, people perceived success in a zero-sum manner (i.e., others' gains are one's losses), which led to lowered helping behavior (Sirola & Pitesa, 2017). Further, when primed with a sense of scarcity (versus a control condition), people became more competitive, less willing to donate $1, and behaved more selfishly in resource-distribution paradigms (Roux et al., 2015). Even in workplaces, perceived resource scarcity reduces effort in getting work done cooperatively (Pitesa & Thau, 2018).

This heightened sense of threat faced by people with pre-existing resources scarcity is compounded in the presence of high population density. With heightened social competition for limited resources in each geographic region, people facing scarcity experience dual sources of threats—(1) their pre-existing shortages and (2) needing to compete with others to maintain access to necessary resources for their livelihood (i.e., survival)—both of which increase the tendency to behave non-cooperatively.

In addition to experiencing relative scarcity, the presence of high social competition would increase a sense of threat to one's livelihood and promote competition for self-preservation (Ellis et al., 2009a). This is especially so due to an evolved psychology that is adapted to the EEA (Tooby & Cosmides, 1990) and resultantly, directs humans to interpret the presence of competitors as a threat to access to limited resources (Kanazawa, 2004). Thus, the heightened threats arising from social competition may incline people with resource scarcity to be less cooperative and instead, enhance their tendency to ensure self-gains. In contrast, people who are resource abundant do not face resource constraints and thus, it is likely that they are unfazed by the presence of social competition since they have a surplus of resources to cope with potential challenges; they have the luxury of affording to spend some resources on benefitting others at their own expense.

Due to the larger adaptive threat of having insufficient resources for survival among those with resource scarcity, we propose that financially poorer people or of lower SES have evolved to be more sensitive to ecological cues when people have scarce resources than when they have plentiful resources. Specifically, the negative effect of population density on cooperative behaviors would be stronger among people who are resource-scarce and they would behave less cooperatively under cues of high population density, compared to low population density.

Overall, we hypothesise that under cues of high (versus low) density, people with resource scarcity will be significantly less cooperative (H1). In contrast, among those who are resource-abundant, population density cues are less likely to reduce cooperation as they can afford to weather high social competition. This leads us to our second hypothesis that among people with resource abundance, cooperation rates would be similar under cues of either high or low population density (H2).

Importantly, there is recent work that investigates the link between life history strategy and cooperation across various economic games (Wu et al., 2017). While this comprehensive package of studies finds no such association, in our General Discussion section, we highlight how our findings might suggest that their lack of hypothesized effects could be qualified by ecological conditions.

2. Research overview

Across two studies, we test our hypotheses. In Study 1, we measured perceptions of population density and examined whether it negatively influences cooperation in an economic game among those with low (but not high) resource availability. In Study 2, we retain the same approach while experimentally manipulating population density.

In this work, we operationalize cooperation in the form of choosing to prioritise others' benefit over oneself. Other work has also used this economic paradigm to assess cooperation or self-orientedness (e.g., Benenson et al., 2007; Chen et al., 2013; Piff, Kraus, Cheng, & Keltner, 2010; Piff, Kraus, Côté, et al., 2010). Across two studies, we adopt choices made in the dictator's game (Engel, 2011) as the key dependent variable, which reflects a resource distribution paradigm where a self-other trade-off has to be made. We operationalize cooperation in the form of a one-shot resource-distribution paradigm because it reflects self-other trade-off (Dawes, 1980; Van Lange & Joireman, 2008) that lies on a linear scale where the choice to benefit oneself is directly proportionate to the cost to the other party (Engel, 2011). Moreover, we chose a one-shot paradigm because the advent of any cooperative alliance requires an initial other-benefitting act (tit-for-tat; Axelrod & Hamilton, 1981).

Our moderator—resource scarcity—is assessed across several measures as perceptions of childhood scarcity (which might have long-lasting imprinting effects; Mittal et al., 2015), current scarcity, and self-inferred social status relative to one's society.

All datasets and analysis codes are uploaded to Open Science Framework (OSF) (https://osf.io/67gvb/?view_only=cbc6607c287643d5bc418845493336f7). All manipulations, measures, and exclusion criteria are reported in these studies. The research methods have met the ethical standards of the Institutional Review Board from Singapore Management University (code number: IRB-20-133-A086(1020)).

3. Study 1

In Study 1, as an initial test of our hypotheses, we measured perceptions of population density and use several measures of perceived resource availability. We operationalized resource scarcity using three measures: (1) childhood resource availability, (2) current resource availability, and (3) subjective SES on the MacArthur ladder (Adler et al., 2000). All these measures reflect subjective perceptions of having sufficient resources to meet one's livelihood needs, or general socio-economic ranking relative to one's community. We chose not to assess objective measures because subjective measures of perceived wealth and SES (versus objective measures) reflect relative standing in one's perceived ecology and are likely to be linked to people's psychology. Indeed, such measures appear to have higher predictive power of life outcomes (Tan, Kraus, Carpenter, & Adler, 2020).

4. Method

4.1. Participants and procedure

Participants are recruited from undergraduate courses in a major Singapore university.[4] After eliminating incomplete responses ($N = 23$ had <55% of the study completed), the final sample size collected was $N = 148$ (28 male, 120 female), with a mean age of $M = 23.89$, $SD = 1.77$. A post-hoc power analysis based on the averaged f^2 of three *population density x resource availability* interaction terms revealed that our sample yielded a statistical power of 85.29%.

After acknowledging the informed consent form, participants completed a four-item measure of perceived population density. Next, they completed questions about their perceptions of resource availability during their childhood and at present. Finally, they completed demographic measures (gender, age, subjective SES) and were awarded course credit as compensation.

4.2. Measures

Resource availability. Resource availability was measured in three ways. Past work suggests that the effects of resource scarcity in childhood can extend later into life (Griskevicius, Delton, et al., 2011; Griskevicius, Tybur, et al., 2011). Thus, we explore whether childhood resource availability may be associated with current cooperative tendencies. However, this research also finds that long-lasting impacts are isolated to childhood resources, but not current resources. Yet, other work suggests that perceptions of current resources relative to others predicts prosociality (Gheorghiu et al., 2021; Korndörfer et al., 2015).

We adopted measures assessing both childhood and current resource availability. The three items for childhood resource availability include “My family usually had enough money for things when I was growing up”, “I grew up in a relatively wealthy neighborhood”, and “I felt relatively wealthy compared to the other kids in my school” ($\alpha = 0.81$). The three items for current resource availability were “I have enough money to buy things I want”, “I don't need to worry too much about paying my bills”, and “I don't think I'll have to worry about money too much in the future” ($\alpha = 0.81$). Responses were made on a 7-point Likert scale from 1 = *strongly disagree* to 7 = *strongly agree*. The mean of the response scores was calculated to form a composite scale. For both measures, higher scores reflect perceived resource abundance while lower scores reflect perceived resource scarcity.

Additionally, we adopted the MacArthur scale of subjective SES[5] (Adler et al., 2000). as another operationalization of resource scarcity. People who perceived themselves to be higher in social rank tend to enjoy higher access to resources, while those of lower social rank feel deprived of opportunities to gain resources (Zhou et al., 2021). In this measure, people place themselves on a ladder with 10 rungs (1 = *lowest*, 10 = *highest*) in terms of where they perceive their wealth, job prestige, and education level to be relative to others in their community (i.e., within Singapore society).

Perceived population density. We measured perceptions of population density using four items created to assess perceived population density, namely “I feel like my surroundings are crowded with people”, “I feel like where I live is highly populated”, “I feel like I am often in places packed with people”, and “I often feel squeezed among people” ($\alpha = 0.77$). Responses were made on a Likert scale of 1 = *strongly disagree* to 7 = *strongly agree*. The items were averaged to form a composite score for perceived crowdedness.

Dictator game. The dictator game is a commonly used assessment of resource distribution between oneself and another (Engel, 2011). This resource distribution paradigm ostensibly randomly assigns participants as a “dictator” who has the autonomy of deciding how much of a given pool of resources (10 Singapore dollars) to keep or give to the assigned partner, the “recipient”. The participants were told that in this hypothetical game, his/her identity would be kept anonymous, and that the recipient cannot reject the offer, nor retaliate. Higher scores (i.e., the amount of money given to the recipient at the cost to the self) reflect higher cooperative tendencies.

Table 1
Means, standard deviations, and correlations among all independent, dependent, and moderator variables.

	Variable	*M*	*SD*	1	2	3	4	5
1	Dictator game	4.07	1.93	–				
2	Perceived population density	4.81	1.19	-0.06	–			
3	Early childhood resources	4.57	1.35	-0.05	-0.08	–		
4	Current resources	4.69	1.35	0.08	-0.13	**0.35****	–	
5	Subjective SES	6.05	1.42	0.07	-0.09	**0.51****	**0.54****	–

Note. M and *SD* denote mean and standard deviation respectively. Significant correlations are bolded. A * indicates $p < .05$, and ** indicates $p < .01$.

5. Results

There were no significant effects of gender and age on the amount given to the recipient in the dictator game ($ps > 0.30$). The descriptive statistics are reported in Table 1. We note that our three resource availability measures are correlated and thus, for hypothesis testing, we also created a composite measure by averaging the standardised versions of these scales.

5.1. Hypothesis testing

To test our hypothesis, we used SPSS PROCESS (Hayes et al., 2010) for our moderation analysis (Model 1). We ran the analysis with perceived population density as the independent variable. Four measures of resource availability were entered as moderators (each in separate models)—early childhood resource availability, current resource availability, the MacArthur ladder and the composite of all three resource measures ($M = 0.00$, $SD = 0.81$). Finally, the dictator game amounts were included as the dependent variable.

Descriptive statistics are reported in Table 1.

In all four models, there were no significant main effects of population density, or any of the measures of resource availability, on cooperation in the dictator game. Most importantly, there were consistent interaction effects such that H1 was supported across all four models and H2 was supported across two models[6] (early childhood resource availability and the MacArthur ladder), but not on the model where resource availability was measured as current resource availability or the composite measure of resources. Table 2 shows the regression coefficients for the moderation analyses. For a depiction of these interaction effects, refer to Figs. 1 to 4.

We expected that the cooperation rates of those who perceive resource scarcity will be negatively affected by perceptions of high (versus low) population density (H1). On all four models (with different measures of resource availability), we found support for this prediction. Among those with low early childhood resources, low current resource availability, and low relative SES within their communities (−1 *SD*), there was a significant negative effect of population density on cooperation rates. As expected, people who rated having lower resources had lower cooperation in the dictator game when they perceive population density as high (versus low). This supports our theories that people with resource scarcity are sensitive to ecological cues.

Next, we also expected that the cooperation rates of those who perceive resource abundance (versus scarcity) will be less affected by cues of population density (H2). On two measures of resource availability, we found support for this prediction. Supporting H2, among those with high early childhood resources and high relative SES within their communities (+1 *SD*), there was no significant effect of population density on cooperation rates. However, contrary to our prediction, among those with higher perceived current resource availability and higher scores on the composite measure of resources (+1 *SD*), population density had a positive significant effect on cooperation. In other words, only when resource availability is measured as current resource availability and on the composite measure, the cooperation rate of people with higher resources was influenced positively by population density cues.

Table 2
Results from PROCESS output showing the significant resource availability x perceived population density moderation analysis on cooperation in the dictator game.

	β	*SE*	*t*	*p*
Perceived population density x Early childhood resource availability				
Main effect of condition	−0.07	0.13	−0.54	*n.s.*
Main effect of early childhood resource availability	−0.14	0.12	−1.15	*n.s.*
Interaction	**0.22***	0.09	2.45	<0.05
Simple slopes				
-1SD	**−0.37***	0.17	−2.16	<0.05
0 (mean)	−0.07	0.13	−0.54	*n.s.*
+1SD	0.23	0.19	1.22	*n.s.*
Perceived population density x Current resource availability				
Main effect of condition	−0.15	0.13	−1.13	*n.s.*
Main effect of current resource availability	−0.08	0.12	−0.68	*n.s.*
Interaction	**0.39*****	0.10	3.90	<0.001
Simple slopes				
-1SD	**−0.68****	0.20	−3.37	<0.01
0 (mean)	−0.15	0.13	−1.13	*n.s.*
+1SD	**0.38***	0.17	2.19	<0.05
Perceived population density x Subjective SES (MacArthur ladder)				
Main effect of condition	−0.07	0.13	−0.55	*n.s.*
Main effect of subjective SES	0.02	0.12	0.15	*n.s.*
Interaction	**0.24***	0.10	2.36	<0.05
Simple slopes				
-1SD	**−0.41***	0.19	−2.13	<0.05
0 (mean)	−0.07	0.13	−0.55	*n.s.*
+1SD	0.26	0.20	1.32	*n.s.*
Perceived population density x Composite resource measure				
Main effect of condition	−0.09	0.13	−0.69	*n.s.*
Main effect of composite resource measure	−0.19	0.20	−0.90	*n.s.*
Interaction	**0.65*****	0.17	3.83	<0.001
Simple slopes				
-1SD	**−0.61****	0.19	−3.24	<0.01
0 (mean)	−0.09	0.13	−0.69	*n.s.*
+1SD	**0.43***	0.19	2.30	<0.05

Note. Significant regression coefficients are bolded. A * indicates $p < .05$, a ** indicates $p < .01$, and a *** indicates $p < .001$. Coefficients of simple slopes are reported at various levels of resource availability.

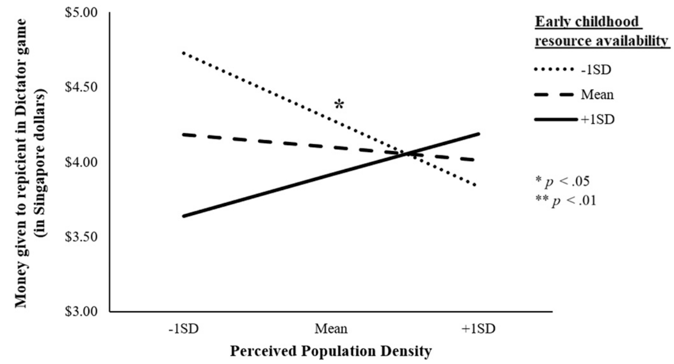

Fig. 1. Interaction effects of early childhood resource availability and perceptions of population density on cooperation in the dictator game.

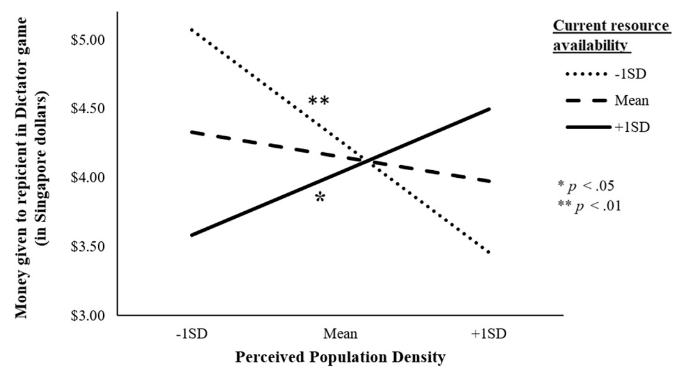

Fig. 2. Interaction effects of current resource availability and perceptions of population density on cooperation in the dictator game.

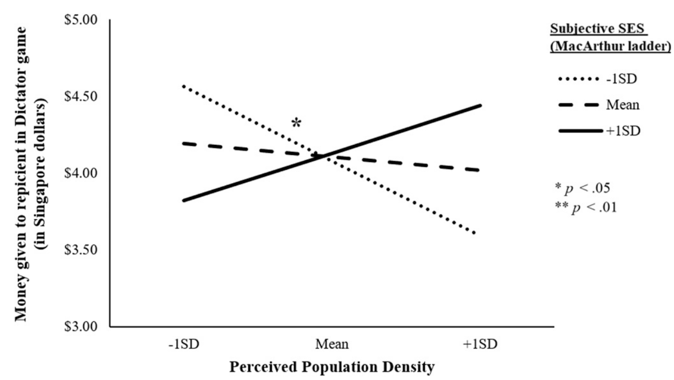

Fig. 3. Interaction effects of subjective SES and perceptions of population density on cooperation in the dictator game.

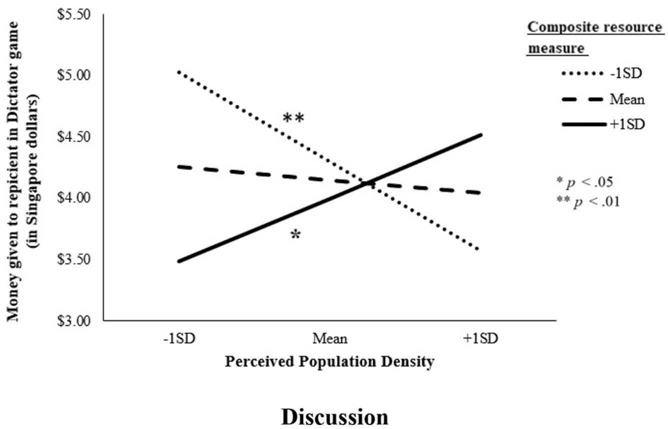

Fig. 4. Interaction effects of composite of three resource measures and perceptions of population density on cooperation in the dictator game.

6. Discussion

The results of Study 1 support both our hypotheses. Across three measures of resource availability and the composite resource scale, people who perceived resource scarcity were less cooperative when they perceived higher (versus lower) population density (supporting H1). In contrast, the cooperation rate of people who perceived resource abundance was unaffected by perceptions of population density (supporting the attenuated effects we expected; H2), with the exception of one measure of resource availability, current resources, and the composite resource scale.

Surprisingly, when resource availability was measured as current resource availability and on the composite resource scale, we found an unexpected positive association between population density and cooperation in the dictator game. This may be explained by the potential reputational and status gains that come with being a cooperator in densely populated societies. While people with resource scarcity tend to focus on resolving their financial deficits (Shah et al., 2012), which is especially crucial when social competition is present, people with resource abundance may focus on establishing higher status in the presence of a large social network where reputational information spreads fast (Romano et al., 2021). Indeed, people from cities with higher population density are more concerned with status signals (Otterbring et al., 2021) and acts of altruism effectively improve status perceptions (Griskevicius et al., 2010; Mifune et al., 2010). We further explore whether this pattern is replicated in Study 2.

7. Study 2

A key limitation of Study 1 was that population density was measured, disallowing us from drawing causal inferences. Hence in Study 2, we experimentally manipulated population density and expect that cues of high (versus low) population density will negatively influence cooperation rates for those with low resource availability (H1), but to a smaller extent for those with high resource availability (H2). We retained the same measures of resource availability and cooperation as in Study 1.

8. Method

8.1. Participants and procedure

Using the results from Study 1 to determine effect size of the interaction effects, we calculated the average f^2 from the three population density x resource availability interaction terms. We yielded an average f^2 of 0.062, which reflects a small-moderate effect size (Cohen, 2013).

We then conducted a power analysis on G*Power. To achieve 80% power with an effect size of 0.062; a sample of 129 participants is needed. Study 2 had a sample size of $N = 228$ undergraduate students (46 male, 182 female) with a mean age of $M = 24.86$, $SD = 1.91$. Participants first completed an informed consent form. Next, they were randomly assigned to view either the high or low population density cues, where they were exposed to the passage and photoshopped images of crowds (versus no crowds) and completed an essay writing task. Next, they completed the PANAS, the dictator game, and answered questions about their resource availability in their childhood and at the current moment. Then, they completed demographic questions (which included measures of gender, age, and the MacArthur ladder of subjective SES). Finally, they were debriefed,[7] thanked, and given course credit as compensation.

8.2. Measures

The measures used in Study 2 are similar to Study 1, except that population density was manipulated.

Resource availability and cooperation. Similar to Study 1, the dictator game and the same three measures of resource availability were used: (1) childhood resource availability ($\alpha = 0.64$), (2) current resource availability ($\alpha = 0.67$), and (3) subjective SES on the MacArthur ladder (Adler et al., 2000).

Manipulated population density. Participants were randomly assigned to the high or low population density conditions (see Appendix for details about the manipulation). First, participants read a passage describing conditions of high or low population density. These passages describe a typical commute to work in the city center on public transportation; the key difference is the focus on a crowded commute during peak hours versus a spacious commute during off-peak hours. To strengthen the manipulation of population density, participants were shown 12 images of crowded versus empty public spaces. The locations shown are standardised and the crowdedness was manipulated using Photoshop to superimpose crowds into the scene. The order of these images was randomized between participants. As a final manipulation booster, participants were tasked to write an essay for 2 min about living in a densely versus sparsely populated place. This manipulation was adapted from past work which effectively manipulated scarcity perceptions using essay writing (Mehta & Zhu, 2016; Roux et al., 2015).

Pilot. In a separate sample, we conducted a pilot study to examine if our manipulation of population density effectively changes perceptions of crowdedness in the intended direction. We recruited 72 undergraduates (male = 16, female = 56; $M_{age} = 22.99$, $SD_{age} = 1.48$) and randomly assigned them to either condition and were subsequently asked two questions about their perceptions of population density around them. These items included “How crowded do you think your surrounding is?” (Response scale: 1 = *Not crowded at all*, 7 = *Very crowded*) and “To what degree do you feel that you are surrounded by people?” (Response scale: 1 = *Very few people around me*, 7 = *Lots of people around me*). After compositing these items, the condition had a significant effect on perceived population density in the expected direction ($\alpha = 0.85$) ($t(70) = 5.93$, $p < .001$) (High population density: $M = 5.55$, $SD = 0.80$; Low population density: $M = 3.46$, $SD = 2.04$). This demonstrates the effectiveness of our population density manipulation.

Affect. The positive affect and negative affect schedule (PANAS) (Watson et al., 1988) was used to check whether participants' state affect was influenced by the population density manipulations (passage, images, and 3-min essay). If so, affect would pose as a confounding factor and should be controlled for during analysis. This scale has 20 items, each naming an affective state. Participants responded on a scale of 1 = *not at all*, to 5 = *extremely*, reflecting the extent to which they felt that emotion in that current moment.

9. Results

Similar to Study 1, there were no significant effects of gender and age on cooperation in the dictator game (*ps* > 0.70). The descriptive statistic of each variable is shown in Table 3.

9.1. PANAS

Participants exposed to high population density cues reported significantly lower positive affect ($t(226) = 2.32$, $p < .05$) (high population density: $M = 22.21$, $SD = 6.96$; low population density: $M = 24.42$, $SD = 7.40$), and significantly higher negative affect ($t(226) = -2.77$, $p < .01$) (high population density: $M = 18.74$, $SD = 7.12$; low population density: $M = 16.17$, $SD = 6.86$) than participants exposed to low population density cues.

We explored the associations between positive and negative affect on cooperation in the dictator game. Using linear regression, both positive and negative affect was not associated with higher amounts of money given to the recipient in the dictator game (positive: $\beta = -0.014$, $SE = 0.016$, $t(227) = -0.88$, $p = .377$; negative: $\beta = 0.014$, $SE = 0.016$, $t(227) = 0.87$, $p = .386$). Nonetheless, to rule out affect as an alternative explanation for our findings, we controlled for affect in our main hypothesis testing.

9.2. Hypothesis testing

An independents sample *t*-test revealed that the population density manipulation did not influence any of the three resource availability measures (all *ps* > 0.40).

The moderation analyses were conducted on SPSS using PROCESS Model 1 (Hayes et al., 2010) (refer to Table 4 for the output). Similar to Study 1, we included the measures of subjective SES (MacArthur ladder), childhood resource availability, and perceived current resource availability as the moderator in three separate models, as well as an additional model with the composite of the standardised versions of all three resource measures ($M = 0.00$, $SD = 0.75$). Population density condition (0 = *low density*, 1 = *high density*) was the independent variable, and the dictator game amounts were the dependent variable (higher scores reflect giving more money to the recipient).

The results yielded a negative main effect of perceived current resources ($\beta = -0.21$, $SE = 0.10$, $t(227) = -2.19$, $p < .05$). There was no main effect of population density condition ($\beta = -0.16$, $SE = 0.23$, $t(227) = -0.72$, $p = .475$). Most importantly, there was a significant interaction ($\beta = 0.43$, $SE = 0.14$, $t(227) = 3.06$, $p < .01$) (refer to Fig. 6 for the depicted interaction).

Examining simple slopes, we found support for H1. Similar to Study 1, among those who perceived lower current resource availability (−1 *SD*), there was a negative effect of population density on the amount of money given to the recipient in the dictator game ($\beta = -0.86$, $SE = 0.32$, $t(227) = -2.68$, $p < .01$). Further, H2 was also supported as there was no effect of population density on cooperation in the dictator game for those who perceived high current resource availability (+1 *SD*) ($\beta = 0.54$, $SE = 0.32$, $t(227) = 1.66$, $p < .10$). Notably, this is unlike Study 1 where people who perceived higher current resources showed an inclination to be more cooperative as their perceptions of population density increased. There was no significant effect of population density on cooperation at the mean level of current resource availability.

For the other models tested (i.e., where resource scarcity is measured as early childhood resources, subjective SES, and the composite of the three resource measures), none of the main effects of population density, resource availability, nor the interaction effects on cooperation were significant (refer to Figs. 5, 7 and 8). We further elaborated on a plausible explanation for this in the general discussion section.

Table 3
Means, standard deviations, and correlations among all independent, dependent, and moderator variables.

	Variable	*M*	*SD*	1	2	3	4	5
1	Dictator game	5.37	1.75	–				
2	Manipulated population density (0 = *low*, 1 = *high*)	0.49	0.50	-0.05	–			
3	Early childhood resources	5.16	1.83	0.04	0.03	–		
4	Current resources	5.23	1.63	0.00	-0.06	**0.28****	–	
5	Subjective SES	5.81	1.34	-0.13	0.03	**0.34****	**0.39****	–

Note. *M* and *SD* denote mean and standard deviation respectively. Significant correlations are bolded. A * indicates $p < .05$, and a ** indicates $p < .01$.

Table 4
Results from PROCESS output showing the resource availability x manipulated population density moderation analysis on cooperation in the dictator game.

	β	*SE*	*t*	*p*
Manipulated population density x Early childhood resource availability				
Main effect of condition	−0.17	0.23	−0.73	*n. s.*
Main effect of early childhood resource availability	0.01	0.09	0.17	*n. s.*
Interaction	0.05	0.13	0.42	*n. s.*
Simple slopes				
-1SD	−0.27	0.33	−0.81	*n. s.*
0 (mean)	−0.17	0.23	−0.73	*n. s.*
+1SD	−0.07	0.33	−0.22	*n. s.*
Manipulated population density x Current resource availability				
Main effect of condition	−0.16	0.23	−0.72	*n. s.*
Main effect of current resource availability	**−0.21***	0.10	−2.19	<0.03
Interaction	**0.43****	0.14	3.06	<0.01
Simple slopes				
-1SD	**−0.86****	0.32	−2.68	<0.01
0 (mean)	−0.16	0.23	−0.72	*n. s.*
+1SD	0.54	0.32	1.66	*n. s.*
Manipulated population density x Subjective SES (MacArthur ladder)				
Main effect of condition	−0.15	0.23	−0.66	*n. s.*
Main effect of subjective SES	−0.16	0.12	−1.36	*n. s.*
Interaction	−0.02	0.17	−0.11	*n. s.*
Simple slopes				
-1SD	−0.13	0.33	−0.39	*n. s.*
0 (mean)	−0.15	0.23	−0.66	*n. s.*
+1SD	−0.18	0.33	−0.55	*n. s.*
Manipulated population density x Composite resource measure				
Main effect of condition	−0.17	0.23	−0.71	*n. s.*
Main effect of composite resource measure	−0.32	0.21	−1.48	*n. s.*
Interaction	0.47	0.31	1.51	*n. s.*
Simple slopes				
-1SD	−0.52	0.33	−1.58	*n. s.*
0 (mean)	−0.17	0.23	−0.71	*n. s.*
+1SD	0.19	0.33	0.57	*n. s.*

Note. Significant regression coefficients are bolded. A * indicates $p < .05$, a ** indicates $p < .01$, and a *** indicates $p < .001$.

9.3. Affect as a covariate

Given that the population density manipulation led to significantly different affective states, we tested this moderation model again with positive and negative affect included as covariates to rule of affect as a potential explanation for our findings.

First, we analysed the same four moderation models with positive affect from the PANAS as a covariate. The results remained consistent. The positive main effect of current resources on cooperation remained significant ($\beta = -0.20$, $SE = 0.10$, $t(227) = -2.01$, $p < .05$). Again, there was no main effect of condition on cooperation. The interaction effect

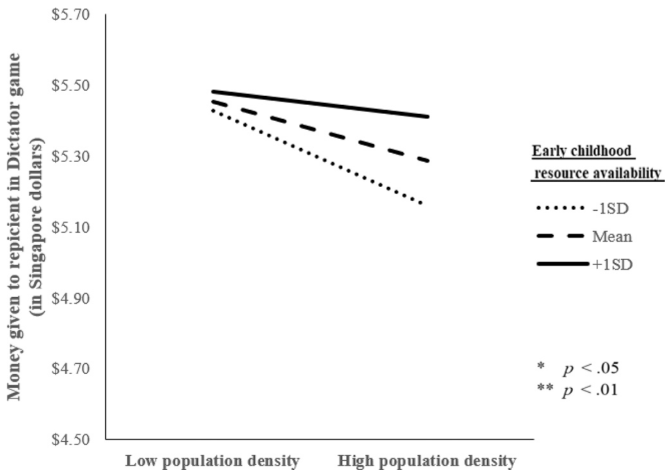

Fig. 5. Interaction effects of perceived childhood resource availability and manipulated population density on cooperation in the dictator game.
Note. All main effects and interaction effects are non-significant (*ps* > 0.40). All simple slopes are non-significant (*ps* > 0.40).

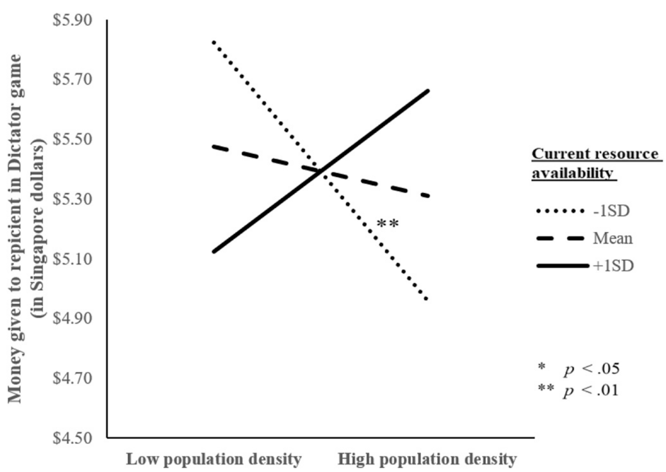

Fig. 6. Interaction effects of perceived current resource availability and manipulated population density on cooperation in the dictator game.
Note. The negative main effect of current resource availability is significant ($p < .05$). At +1 SD of current resources availability, the slope is marginally significant ($p = .098$).

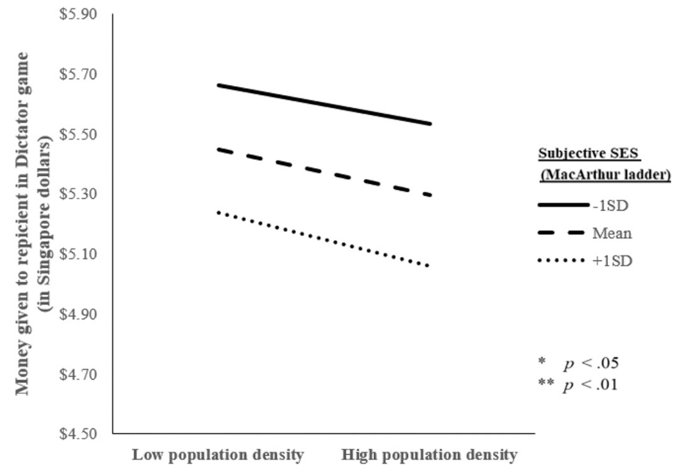

Fig. 7. Interaction effects of perceived childhood resource availability and manipulated population density on cooperation in the dictator game.
Note. All main effects and interaction effects are non-significant (*ps* > 0.15). All simple slopes are non-significant (*ps* > 0.50).

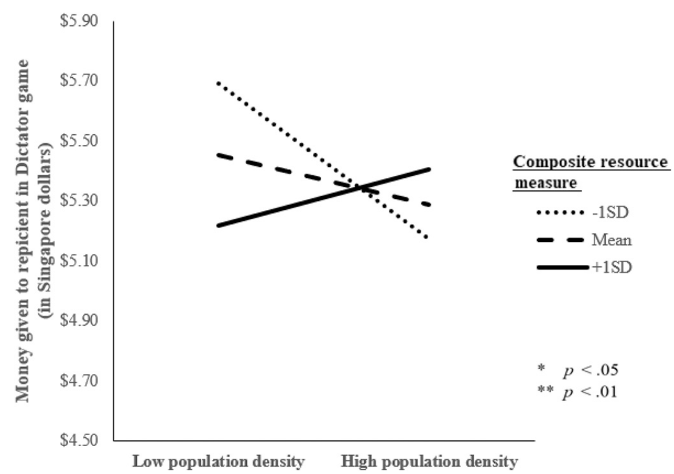

Fig. 8. Interaction effects of composite resource measure and manipulated population density on cooperation in the dictator game.
Note. All main effects and interaction effects are non-significant (*ps* > 0.13). All simple slopes are non-significant (*ps* > 0.11).

also remained significant ($\beta = 0.42$, $SE = 0.14$, $t(227) = 2.95$, $p < .01$). Most importantly, H1 remains supported—at lower current resource availability (-1*SD*), population density negatively affects cooperation ($\beta = -0.87$, $SE = 0.32$, $t(227) = -2.68$, $p < .01$). Further, H2 was also supported. At higher current resource availability (+1*SD*), population density has no effect on cooperation ($\beta = 0.50$, $SE = 0.33$, $t(227) = 1.50$, $p = .134$).

Next, we repeated our hypotheses testing with negative affect as a covariate. Again, the original results were held consistent. There was a positive main effect of current resources on cooperation ($\beta = -0.20$, $SE = 0.10$, $t(227) = -2.03$, $p < .05$), and the main effect of condition on cooperation was non-significant. The interaction effect also remained significant ($\beta = 0.43$, $SE = 0.14$, $t(227) = 3.06$, $p < .01$). Both H1 and H2 remain supported—at lower resource availability (-1*SD*), population density negatively affects cooperation ($\beta = -0.91$, $SE = 0.33$, $t(227) = -2.78$, $p < .01$); and at higher resource availability (+1*SD*), population density has no effect on cooperation ($\beta = 0.50$, $SE = 0.33$, $t(227) = 1.52$, $p > .13$). In summary, all original effects (or lack of effects) were maintained even after positive or negative affect had been included into the moderation analyses as covariates.

10. Discussion

In Study 2, we manipulated population density using a pre-tested manipulation and replicated the findings from Study 1. Supporting H1, the cooperation rate of people who reported lower current resource availability was negatively influenced by cues of high population density. Supporting H2, the cooperation rate of people with higher current resources was not influenced by either high or low population density cues. Notably, the unexpected positive resource-cooperation slope for those with high current resource availability from Study 1, presumably for status gains, was not replicated when population density salience is manipulated. Given that our manipulation of population density influenced positive and negative affect, we included both measures as covariates. The results remained consistent, ruling out changes in affect as a confounding factor in our findings. Overall, both studies support our prediction that the cooperation rate of people with resource scarcity, but not those with resource abundance, is susceptible to ecological cues.

11. General discussion

While existing literature has identified many cultural, intra-, and inter-individual differences that may explain cooperative tendencies (e.g., Keltner et al., 2014; Piff, Kraus, Cheng, & Keltner, 2010; Piff, Kraus, Côté, et al., 2010), there is a shortage of research investigating how broader ecological factors may simultaneously interact to influence the cooperation (for a review on key ecological dimensions, refer to Sng et al., 2018). The adaptive value of cooperation varies across ecological conditions. In this work, we examined the interactive effects of resource availability and population density on cooperation. Specifically, we hypothesized that the adaptive costs and benefits of cooperation might be less favorable for people facing resource scarcity and high population density.

We proposed that the cooperation levels of people with resource scarcity would be negatively influenced by population density (H1), while that of people with resource abundance are relatively less affected by density (H2). From an evolutionary perspective, human ancestors had to adopt adaptive strategies to deal with recurring problems of securing resources from their environment (Orians & Heerwagen, 1992). With added pressures of social competition from high population density, self-preservation instincts are likely to kick in among people who are already facing scarcity. In contrast, people with resource abundance are unthreatened by social competition as they have more resources to serve as a buffer. Using a correlational and experimental design, we find support for both hypotheses.

In Study 1, across three measures of resource scarcity and the composite measure of these measures, people who have lower resources were less cooperative in the dictator game as their perception of population density increased. This supports H1. We also find support for H2 on two of the three measures of resource availability—among people with higher childhood resources and higher subjective SES, perceptions of population density did not influence their cooperation rates. However, on two measures of resource availability—perceived current resources and the composite of all resource measures—increasing perceptions of population density led people with higher resources to be more cooperative. This finding contradicts H2.

In Study 2, we experimentally manipulated cues of population density while retaining the same measures of resource availability and cooperation. Again, we found support for H1, albeit only for one measure of resource scarcity. The cooperation level of people who report lower current resources was negatively affected in the high (versus low) density condition. Furthermore, H2 was also supported. Among people with higher childhood resources, current resources, lower perceived SES, and the composite of these measures, there was no effect of high (versus low) population density on cooperation in the dictator game. This pattern is consistent with the general pattern in Study 1; notably, the positive significant effect of population density on cooperation for people with abundant resources in Study 1 was not replicated in Study 2. No main effects, interactions, or simple slopes were significant for the other measures of resource availability (early childhood resources, subjective SES, and the composite scale). These results remained consistent after controlling for affect.

Comparing both studies, we made an interesting observation that when population density is measured (Study 1), we find evidence across all three measures of resource scarcity supporting our hypothesis that people with perceived scarcity are negatively influenced by perceived population density. However, when population density is manipulated (Study 2), this hypothesis was only supported on one measure of resource scarcity (i.e., current resources). A plausible explanation could lie in the compatibility of the types of measures—in Study 1, population density and all three measures of scarcity are measured variables that arguably reflect chronic ecological perceptions. In Study 2, participants' sense of population density is temporarily manipulated, and our hypothesis was only supported for the measure of scarcity that is closest to capturing temporarily malleable perceptions (i.e., perceived current scarcity) but not on the other two measures that are more chronic or non-malleable (i.e., early childhood resources and subjective SES). Other scholars have argued that in testing a theory, it is important that the temporal nature of the measures involved are compatible (Ajzen, 1991, 2020). It is plausible that we would have found stronger support for our hypotheses in Study 2 if we included other measures of scarcity that are more sensitive to temporary manipulations.

Our findings contribute to the existing literature in several ways. First, most research on cooperation has accounted for intra-personal, inter-personal, and group processes (Balliet et al., 2011; Keltner et al., 2014; Kraus et al., 2012) without understanding the predictors of cooperation from an ecological perspective. More specifically, we address the lack of research that simultaneously accounts for the interactive effects of population density and resource availability on cooperation. Finally, our findings suggest that population density is a crucial factor that may potentially resolve the existing mixed findings on the resource-cooperation association (Stamos et al., 2021).

11.1. Differences in cooperation strategies among the rich and poor

Importantly, we do not contend that people facing scarcity are always less cooperative. After all, in ancestral times, scarcity encourages sharing of food and caretaking services to increase the odds of survival (Trivers, 1971). Instead, we believe that those with scarce resources may still dedicate resources towards cooperation, but only when they perceive that the self-gains confer fitness gains (i.e., status or future reciprocation). Indeed, within the same investigation, which finds that people primed with scarcity (versus control) tend to be more selfish and competitive, those in a scarcity mindset still showed generosity in publicly-made (but not privately-made) donations (Roux et al., 2015). This suggests that while a state of scarcity promotes self-serving motivations, it does not invariantly discourage cooperative or other-oriented behaviors; instead, scarcity can promote cooperativeness or other-orientedness if it entails some form of self-gain. Afterall, people facing scarcity cannot afford expending resources on social alliances who have low reciprocal abilities or tendencies. Each unit of resource weighs heavier on their overall adaptiveness compared to people with abundant resources. Thus, those facing scarcity are more likely to be very selective and careful with their level of cooperation with others to minimise risk of making the wrong social investment out of their limited resources.

In both studies of our investigation, we used an anonymous one-shot dictator game where people with limited resources have no opportunity to gain status or future reciprocation. In short, although our findings show that population density lowers cooperation among people of lower SES (but not those of high SES), scarcity may not necessarily discourage cooperation; instead, scarcity makes people more discerning and pragmatic with the decision to cooperate (i.e., only cooperate if it confers adaptive gains).

We do not rule out the idea that people with abundant resources also use cooperation for adaptive gains. It is likely that resource-abundant or resource-scarce people have cooperative tendencies, but they differ in the type of people they choose to cooperate with. From an evolutionary standpoint, it is adaptive if people only cooperate with others who affords them fitness gains. Resource-abundant people would benefit from having reciprocal relationships with other wealthy people with high reciprocal power, or from reputations gains from helping the less fortunate. In contrast, as per our results, people facing scarcity should be more discerning with their "social investments" and only focus on building reciprocal alliances with people whom they can trust would reciprocate (i.e., their ingroup) or in situations with high guarantees of fitness gains (e.g., reputation gains).

11.2. Reconciling past findings

An important recent work by Wu et al. (2017) theorises that a slow (versus fast) life strategy, as well as childhood SES as a proxy, should predict higher cooperativeness. Across a series of studies and various operationalisations of cooperativeness (see Table 1; Wu et al., 2017), this expected association was not supported by their data.

While their research focuses on life history strategy as a predictor of cooperation, our work focuses on the interactive effects of ecological factors (population density and resource availability) as predictors of cooperation. Ecological conditions do predispose individuals towards specific life strategies (Ellis et al., 2009b). For instance, higher density adaptively promotes slower strategy behaviors (Sng et al., 2017). Pertaining to resource availability, childhood socioeconomic conditions, but not current socioeconomic conditions, polarises behaviors according to the individual's predisposed life strategy (Griskevicius, Delton, et al., 2011; Griskevicius, Tybur, et al., 2011). We believe it is possible that resource availability serves as a catalyst or inhibitor for the pursuit of an individual's life strategy, rather than being an antecedent factor of life strategy.

Integrating our findings with those of Wu et al. (2017), our work shed light on the importance of specific combinations of ecology conditions that might qualify the emergence of different cooperative tendencies. It is possible that despite the overall null associations between life strategy and cooperativeness across various economic games, specific ecological conditions (and various combinations) could serve as crucial moderators.

Interestingly, while past work finds that childhood resources, but not current resources, interacts with ecology cues (i.e., mortality threats) to predict resource management strategies life (Griskevicius, Delton, et al., 2011; Griskevicius, Tybur, et al., 2011), our results find the opposite pattern in Study 2—current resources, but not childhood resources, interacts with ecology cues (i.e., population density) to predict resource distribution. Notably, in Study 1, all resource measures qualified the effects of population density on cooperation. This means that both childhood versus current resources can both influence resource management decisions in response to various ecological cues.

Thirdly, our findings provide insight into the unresolved debate in the mixed findings for the resource-cooperation association (Stamos et al., 2021). While we discussed earlier that a large body of work documents a positive resource-cooperation relationship (e.g., Benenson et al., 2007; Gittell & Tebaldi, 2006; Korndörfer et al., 2015; Prediger et al., 2014), other evidence suggests the opposite effect. For example, people from low (versus high) SES were more cooperative in the dictator game (Chen et al., 2013), and displayed more group-oriented behaviors (Guinote et al., 2015). In contrast, wealthier people behaved more selfishly across various helping scenarios (Piff, Kraus, Cheng, et al., 2010), and cheated more (Dubois et al., 2015; Piff et al., 2012). Some plausible explanations are that people of higher SES have higher solipsistic and individualistic values (Kraus et al., 2012) or harbour a higher sense of power (Dubois et al., 2015). Likewise, other evidence shows that people of higher SES tend to have more self-oriented emotions of pride and contentment, while those of lower SES tend to have more other-oriented emotions such as compassion and love (Piff & Moskowitz, 2018). Furthermore, some work found a U-shaped association between SES and prosociality (James & Sharpe, 2007; Liddell & Wilson, 2010).

Concurring with past evidence for a positive resource-cooperation association (e.g. Korndörfer et al., 2015), while there is no main effect of resource scarcity on cooperation in Study 1, Study 2 finds a negative main effect of resources on cooperation—people who reported higher current resources gave less to their partner in the dictator game. Our data appears to support the idea that humans indeed evolved to rely on each other in times of scarcity, rather than being more self-serving.

Moreover, we found evidence that the influence of resources on cooperation cannot be considered in isolation from another ecological dimension, population density. Specifically, people with lower resources were less cooperative in higher (versus lower) population density, while people with higher resources remained relatively unaffected. Plausibly, this is because unlike wealthier people who have abundant resources that easily extinguish challenges to their mortality (e.g., dealing with high social competition), poorer people have to be more careful with the allocation of their scarce resources. Since people with fewer resources are more sensitive to ecological cues such as population density, it is possible that some of the mixed findings in the resource-cooperation association are explainable by differences in poorer peoples' cooperativeness as ecological conditions vary in harshness (e.g., high-density) across the studies.

Next, one of our key premises is that higher density would predict lower cooperation. There is an alternative perspective with accompanying findings, however, that cooperation is adaptive under high population density and thus, high competition (Katz et al., 2021). Likewise, others have suggested that in extremely high densities, cooperation is necessary to facilitate social order (Sng et al., 2018). One possible explanation of the discrepancy is that there are variables that influence whether people become more competitive or cooperative. For instance, if social complexities, which accompanies high density, does not exceed the capacities of the human brain (Dunbar, 1992), it is plausible that people cooperate to deal with competitors.

Furthermore, the optimal strategy depends on the nature of the resource distribution paradigm. In the case of a one-shot dictator game, which we employed, it is adaptive for people in population dense areas with resource scarcity to act in a self-protective manner because every unit of resources is crucial to their self-sustenance and must be wisely invested. Indeed, other work finds that it is adaptive to act in self-serving manners in a one-shot resource sharing game (Kanazawa & Fontaine, 2013) given that it is an opportunity for exploitation and self-gain without incurring losses due to anonymity. On the other hand, it is possible that population density and competition may increase cooperativeness when the time horizon is longer, as exemplified by iterated dictator games, or in other resource-distribution paradigms that offer other situational affordances (refer to Thielmann, Spadaro and Balliet, 2020). Future work could examine how the population density x resource interaction might differ between such contexts.

11.3. Limitations and future directions

In this investigation, cooperation was only measured with a single resource distribution paradigm—an anonymous dictator game. Several challenges may arise from using this measure. Firstly, this game allows recipients to be exploited with no backlash. Real-world cooperation has historically involved the possibility of retaliation, reciprocity, and future dependence on the other party (see Table 3; Thielmann et al., 2020). In contrast, the anonymous nature of our dictator game departs significantly from the face-to-face dealings that characterized human evolutionary history. It is possible that while people facing resource scarcity may be less cooperative to invisible strangers, they may be more cooperative among friendly, familiar faces from their community. This would be compatible with evolutionary theories indicating that reciprocal altruism evolved among fellow villagers exactly because people did not have enough resources (e.g., meat) to survive or thrive on their own. Imparting resources on invisible strangers is evolutionarily novel (Folwarczny et al., 2022), not likely to lead to reciprocated benefits, and something that only wealthy individuals can even afford to do. Future research can examine these ideas by investigating how people with high versus low levels of resources treat strangers versus friends.

Additionally, although we have documented evidence of lowered cooperativeness among resource-scarce people under high density, we take caution in concluding that lower cooperation objectively confers more adaptive gains for people facing scarcity under conditions of high density. This would require computer simulation studies, showing that such a response under conditions of high (versus low) densities produces a net gain for the resource-scare individual. Future work can consider these directions.

It is worth noting an inherent confound in using a monetary-based measure of cooperation—the value placed on each dollar qualitatively differs by income group. Wealthier people may value $10 less (Andreoni et al., 2017). Future replications of this investigation are necessary to demonstrate whether the lowered cooperativeness of people facing resource-scarcity in response to population density cues extends to other operationalizations of cooperation that capture other resource distribution paradigms that are non-monetary, entail other situational affordances (e.g., opportunity for backlash), naturalistic measures (e.g., helping a colleague/ stranger) or even a broader sense of other-orientedness.

Our study appears to contradict past evidence of a main effect of resources on cooperation (e.g., positive effect: Benenson et al., 2007; negative effect: Chen et al., 2013; Piff, Kraus, Cheng, & Keltner, 2010, Piff, Kraus, Côté, et al., 2010). This is potentially because our sample is limited to students in an interdependent society (i.e., Singapore). Recent work has identified that in interdependent cultures such as Japan (as well as Singapore), higher SES is associated with both higher self- and other-orientation; whereas in independent cultures such as the US, higher SES is only associated with higher self-orientation (Miyamoto et al., 2018). This alludes to the idea that the main effect of SES on cooperation in the dictator game found in prior work with independent cultures such as the US (Piff, Kraus, Cheng, et al., 2010) or the UK (Benenson et al., 2007) (but not in our interdependent sample) may reflect the absence of a contradicting motivation to be both self-oriented and other-oriented on the dictator game which directly captures a self-other trade-off. Future work can consider delineating these potential cultural differences in how resources may influence cooperation when it is operationalized as a self-other trade-off (i.e., dictator game).

Finally, our investigation did not provide direct tests of our proposed mechanisms. We had theorized that high density is accompanied by social competition for limited resources and that people with scarce resources are likely to face higher mortality threats (Ellis et al., 2009a); resultantly, they prioritise self-preservation and are less likely to cooperate. However, we did not assess participants' sense of competition, sense of control, self-preservation concerns, or the perception of mortality threats induced by high population density. Future work can consider assessing these constructs for mediating effects. Existing studies suggest that a scarcity mindset (versus control) promotes a competitive orientation which manifests in the form of prioritizing benefits to oneself over others (Roux et al., 2015). We expect that for people with resource scarcity, the negative effect of high (versus low) density on cooperation would be mediated by perceptions of higher competition.

12. Conclusion

The current literature has rarely considered the simultaneous influence of ecological factors when examining predictors of cooperation. Our work bridges this gap by investigating how two such factors—perceived resource scarcity and population density—interact to influence cooperative behaviors. While high population density negatively influences the cooperation levels of people who perceive resource scarcity, those with perceived abundance in resources remain relatively unaffected by population density. This evidence provides further insight that cooperation strategies do change as individuals maximise adaptiveness in their given ecology—those facing scarcity (vs abundance) are more likely to change their resource allocation strategies in response to external cues of population density.

CRediT authorship contribution statement

Lynn K.L. Tan: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Norman P. Li:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Kenneth Tan:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Declaration of Competing Interest

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

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