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Fear of supernatural punishment can harmonize human societies with nature: an evolutionary game-theoretic approach

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Human activities largely impact the natural environment negatively and radical changes in human societies would be required to achieve their sustainable relationship with nature. Although frequently overlooked, previous studies have suggested that supernatural beliefs can protect nature from human overexploitation via beliefs that supernatural entities punish people who harm nature. Studies of folklore and ethnology have shown that such supernatural beliefs are widely found. However, it remains unclear under which conditions such supernatural beliefs prevent people from harming nature, because overexploiting natural resources without supernatural beliefs produces the greatest benefits. The current study aimed to build a mathematical model based on the evolutionary game theory and derive the conditions under which supernatural beliefs can spread in society, thereby preserving natural resources. To maintain supernatural beliefs, the fear of supernatural punishment invoked by scarce natural environments would, on one hand, be strong enough to prevent overexploitation but, on the other, be weak enough for the supernatural belief to spread in society via missionary events. Our results supported that supernatural beliefs would facilitate sustainable relationships between human societies and nature. In particular, the study highlighted supernatural beliefs as an essential driver for achieving sustainability by altering people's interaction with nature.

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Introduction

Negative human impacts on natural environments have been widely recognized (Cardinale et al., 2012; Dirzo et al., 2014; Malhi et al., 2014), and fundamental changes in human societies are considered necessary to achieve a sustainable relationship with nature (McPhearson et al., 2021; Pascual et al., 2023). Beliefs in supernatural entities that punish people who harm nature may play an important role in harmonizing human societies with nature (Purzycki et al., 2022). Previous folklore and ethnological studies have shown that such supernatural beliefs exist across human societies and may protect nature from human overexploitation (Hartberg et al., 2016). For example, Frazer (1890) recorded the taboos of plant abuse worldwide. Ethnographic data analysis revealed that Japanese folklore includes episodes where spirits of nature (e.g., mountains and trees) punish or avenge people who develop or overuse natural resources (Nakawake and Sato, 2022). Similarly, the Batak people of Palawan Island in the Philippines believe in the forest spirits that punish people who overexploit or waste forest resources (Eder, 1997). Itza' Maya, Guatemala, also views forest spirits as punitively protecting local forests against exploitation (Atran et al., 2002). It remains unclear, however, under which conditions human society can maintain the beliefs in supernatural punishment and when such beliefs can protect nature from human overexploitation.

The problem of overusing natural resources is referred to as the tragedy of the commons (Hardin, 1968) in the context of the evolution of cooperation. If a society is composed of cooperators who self-regulate the usage of nature, natural resources can remain abundant, and people can continue to earn great benefits therefrom. Such a society is, however, vulnerable to invasion by selfish individuals who overexploit natural resources since the selfish people gain more benefits than the cooperators. Previous studies have shown that cooperation can evolve if cooperative individuals interact more frequently with other cooperators than with selfish ones via kin selection, multi-level selection, direct reciprocity, and indirect reciprocity (Apicella and Silk, 2019; Rand and Nowak, 2013). For example, punishing selfish individuals is a form of direct or indirect reciprocity that facilitates the evolution of cooperation (Brandt et al., 2006; Fowler, 2005; Hauert et al., 2007). Although humans can spontaneously punish selfish individuals (Fehr and Fischbacher, 2004; Fehr and Gächter, 2002; Henrich et al., 2006; Raihani and Bshary, 2019; Rand et al., 2009; Yamagishi, 1988), such punishments are accompanied by the problem of costs. Punishers need to spend time or energy to monitor and punish others, and they may be retaliated upon by the punished individuals (Denant-Boemont et al., 2007; Janssen and Bushman, 2008). As a result, cooperation collapses due to the increase of individuals who do not contribute to the costly punishment (Sigmund, 2007). This remains a central problem in the evolution of cooperation and punishment.

In human societies, beliefs in supernatural punishment may solve the problem of costly punishments (Bourrat and Viciana, 2016; Fitouchi et al., 2023; Johnson and Krüger, 2004; Lightner and Purzycki, 2021; Schloss and Murray, 2011), although scholars have debated whether such beliefs drove the evolution of social complexity (Turchin et al., 2023a,b; Whitehouse et al., 2023). Supernatural punishment is advantageous over "real" punishment because people do not have to bear the costs of the punishments (Johnson and Bering, 2006). Thus, the fear of supernatural punishment can prevent believers from behaving selfishly; but see Lenfesty and Morgan (2019) for an alternative hypothesis on how supernatural beliefs facilitate the evolution of human cooperation. The moralizing gods hypothesis associates the cooperation in human societies with the belief in moralizing gods, who monitor human activities and enforce moralistic behaviors (Bayramoglu et al., 2018; Johnson, 2005; Lang et al., 2019; Purzycki et al., 2016; Singh et al., 2021; Watts et al., 2015). Although the relationship between humans and nature was not considered in this hypothesis, some scholars argue that supernatural beliefs can also regulate human behaviors toward nature (Bendixen and Grant Purzycki, 2023; Bendixen et al., 2023). To clarify the conditions under which supernatural beliefs contribute to sustainability, we must examine the conditions that allow these beliefs to persist in human societies and regulate the human usage of natural resources.

Here, we built and investigated a mathematical model to reveal whether and how beliefs in supernatural punishment facilitate the sustainable relationship between human societies and nature. We used evolutionary game theory to analyze the co-evolutionary dynamics of three elements as follows: (i) the belief in supernatural punishment, (ii) the intensity of human exploitation of nature, and (iii) the amount of natural resources. Recent advances in the evolutionary game theory have introduced the environmental feedback games (Ito and Yamamichi, 2024; Tilman et al., 2020; Weitz et al., 2016), in which the payoffs depend on the individuals' strategies (for example, how many trees people cut) and current environmental states (for example, the abundance of trees in a forest). At the same time, the environment also changes depending on the strategies individuals apply. This is an ideal framework for investigating how the evolution of both human behaviors and beliefs affects natural resources as public goods. We mathematically derived two conditions under which the beliefs in supernatural punishment could spread in human society and protect nature from overuse. Intuitively, the first condition indicates that the fear of supernatural punishment should exceed the net benefits of overexploiting natural resources so that believers stop the overexploitation. The second condition represents that the fear of supernatural punishment should be small so that people can accept the supernatural beliefs through the missionary events. Our study could provide a theoretical foundation for how and when supernatural beliefs can facilitate the sustainable relationship between human societies and nature.

Model

In this study, we considered the public goods game, including the environmental feedback (Ito and Yamamichi, 2024; Tilman et al., 2020; Weitz et al., 2016) and the positive or negative missionary events (Fig. 1). We considered an infinite human population in which each individual was characterized by two binary independent aspects. The first aspect distinguishes the usage of natural resources (Fig. 1a). We call individuals cooperators if he/she exploits only a small amount of the natural resource so that the resource is conserved. In contrast, selfish people are those who exploit the natural resources more than the cooperators to earn larger benefits. The second aspect represents whether each individual believes in supernatural punishment when he/she overexploits natural resources (Fig. 1b). We assumed that selfish believers (SB) bore the cost of fearing supernatural punishment even when they were not really punished, because studies suggested that religious guilt can damage mental health: see the meta-analysis by Aggarwal et al., (2023).

Combining the benefits of natural resources and the fear of supernatural punishment, the payoffs of the four strategies—cooperative believers (CS), SB, cooperative non-believers (CN), and selfish non-believers (SN)—were represented as follows:

$$f_{\mathrm{CB}}(R) = (aR)^{w}, \tag{1a}$$

$$f_{\mathrm{SB}}(R) = (bR)^{w} - P(R), \tag{1b}$$

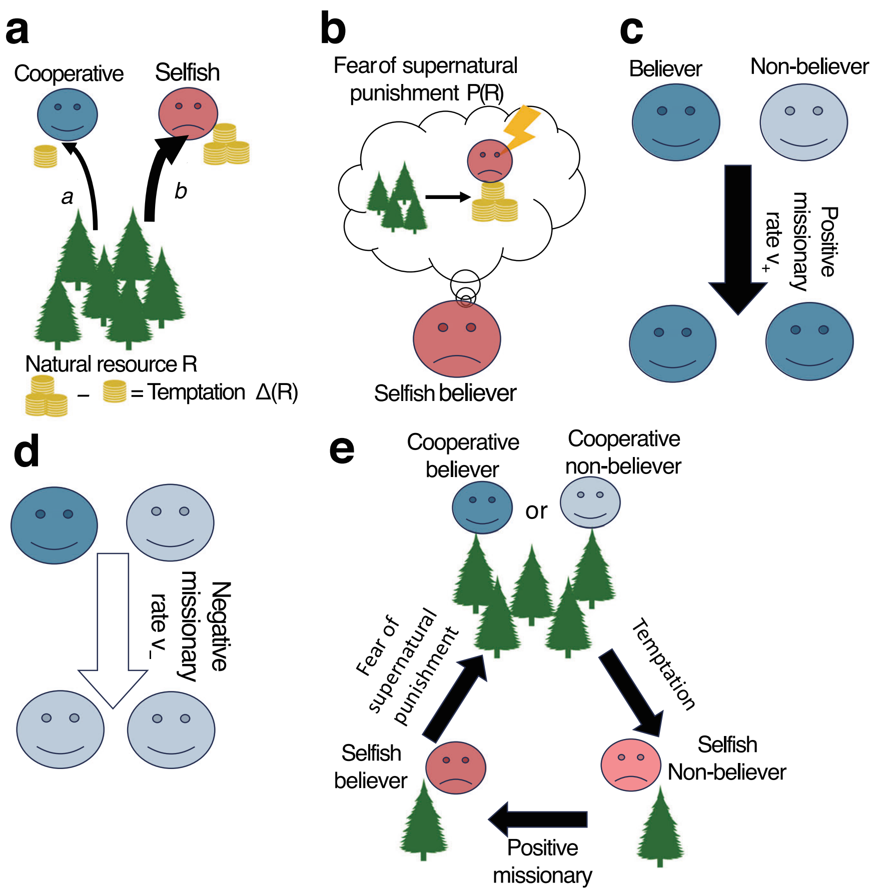

Fig. 1 Schematic representation of the model. a Local people play the public goods game by exploiting natural resources (e.g., woods). Cooperative strategies regulate the exploitation of natural resources (cooperative exploitation rate a), wheares selfish strategies do not (selfish exploitation rate $b > a$). As a result, the selfish strategies yield more benefits than the cooperative ones; the difference in the benefits represents the temptation to selfishness $\Delta(R)$. **b** The selfish believers (SB), however, are afraid of supernatural punishment, which damages their health and decreases their payoffs by $P(R)$. **c**, **d** The individuals change whether they believe in supernatural punishment or not, following the positive and negative missionary rates, v_+ and v_-, respectively. The events occurred in accordance with the proportions of believers and non-believers. **e** Due to the environmental feedback, the amount of natural resources depends on the fractions of the four strategies. If either cooperative believers (CB) or non-believers (CN) dominate, the amount of natural resources remains high. This leads to a strong temptation to selfishness, and selfish non-believers (SN) can become dominant. Once this occurs, the amount of natural resources declines due to overexploitation. However, SN may be replaced by SB via positive missionary events. Although SB has an identical exploitation rate to SN, the fear of supernatural punishment can turn SB into CB (or CN), which can then recover the amount of natural resources.

$$f_{\mathrm{CN}}(R) = (aR)^w, \tag{1c}$$

$$f_{\mathrm{SN}}(R) = (bR)^w, \tag{1d}$$

where a and b were the rates of natural resource exploitation by cooperative and selfish individuals ($b > a > 0$), respectively, and $P(R)$ is the fear of supernatural punishment when the amount of natural resource is R. Here, $w > 0$ determines how the benefit increases over R; $w = 1$ corresponds to a linear function, $0 < w < 1$ corresponds to a concave function, and $w > 1$ corresponds to a convex function. Regardless of the value of w, the selfish strategy always had greater benefits than the cooperative strategy, which led to the tragedy of the commons (Hardin, 1968). The fear of supernatural punishment $P(R)$ differs in two aspects from the models of real punishments. First, no individual in our model pays costs for punishing others since no one punishes selfish individuals in our model. Second, selfish people bear the costs of the fear of supernatural punishment $P(R)$ only if he/she believes in supernatural punishment; SN do not bear this cost. This highlights the difference from typical real punishment systems, in which all selfish individuals are punished.

The payoff functions (Eqs. 1a–1d) clarified that we did not assume that believing in supernatural punishment was adaptive, although supernatural beliefs could motivate individuals to cooperate. The payoffs of the cooperators did not change regardless of whether they believed in supernatural punishment. For selfish individuals, on the other hand, believing in supernatural punishment decreased their payoffs since the fear of supernatural punishment damaged their mental health.

The strength of supernatural beliefs was assumed to positively correlate with the extent of nature. In other words, we assumed that people may be more likely to perceive spiritual entities in richer natural elements, fostering religious beliefs grounded in awe and fear (Frazer, 1890). Based on this idea, we assumed that the amount of natural resources increased the perceived fear of the supernatural punishment (and the associated costs) P. Similar to the benefits obtained from natural resources, the fear of supernatural punishment was formulated using the following equations:

$$P(R) \equiv (pR)^u, \tag{2}$$

where p^u is the fear of supernatural punishment when $R = 1$, and $u > 0$ determines the shape of the function $P(R)$ over a natural resource. In Supporting Information (SI) 6, we relaxed this assumption and analyzed the cases when the fear of supernatural punishment decreased over R, which did not qualitatively alter our findings.

Our model considered the public goods game with environmental feedback so that the dynamics of the natural resources were explicitly represented (Estrela et al., 2019). This allowed us to incorporate the difference in time scales between the evolution of human behavior and the recovery of natural resources. Here, we assumed that the natural resource was recovered following a logistic growth model, but was consumed by the local people whose exploitation rates were either a or b. The dynamics of the natural resource followed a classical consumer-resource model (MacArthur, 1970) with four parameters: the intrinsic growth rate (per-capita growth rate when the natural resource is scarce) μ, the carrying capacity (the maximum amount of natural resource) K, and the consumption rates by the cooperative or selfish individuals (a and b, respectively). Sethi and Somanathan (1996) analyzed a similar model that combined resource dynamics with the evolution of cooperation and real punishment. On the other hand, our model analyzed the role of belief in supernatural punishment and whether such beliefs could be maintained in a population.

Further, we assumed that whether an individual believed in the supernatural punishment changed due to the positive and negative missionary events (Fig. 1c and d); non-believers became believers when they frequently interacted with the latter at the rate ν_+ (the positive missionary rate), and vice versa (the negative missionary rate ν_-). This formulation follows a typical epidemiological analogy (Olsson and Galesic, 2024). Positive and negative missionary events can be justified by combining the positive frequency-dependent biases (i.e., mimicking the majority) and the content biases (i.e., difference in cognitive attractiveness) (Mesoudi, 2016). If most people believe in supernatural punishment and the beliefs are readily transmitted, for example, the non-believers can immediately become believers.

The governing dynamics of human behavior and natural resources are composed of the replicator dynamics (Nowak, 2006) with positive and negative missionary events and the consumer-resource model:

$$\epsilon \dot{x}_{\mathrm{CB}} = x_{\mathrm{CB}}\left(f_{\mathrm{CB}}(R) - \bar{f}(R)\right) + \nu_+\left(x_{\mathrm{CB}} + x_{\mathrm{SB}}\right)x_{\mathrm{CN}} - \nu_-\left(x_{\mathrm{CN}} + x_{\mathrm{SN}}\right)x_{\mathrm{CB}}, \tag{3a}$$

$$\epsilon \dot{x}_{\mathrm{SB}} = x_{\mathrm{SB}}\left(f_{\mathrm{SB}}(R) - \bar{f}(R)\right) + \nu_+\left(x_{\mathrm{CB}} + x_{\mathrm{SB}}\right)x_{\mathrm{SN}} - \nu_-\left(x_{\mathrm{CN}} + x_{\mathrm{SN}}\right)x_{\mathrm{SB}}, \tag{3b}$$

$$\epsilon \dot{x}_{\mathrm{CN}} = x_{\mathrm{CN}}\left(f_{\mathrm{CN}}(R) - \bar{f}(R)\right) + \nu_-\left(x_{\mathrm{CN}} + x_{\mathrm{SN}}\right)x_{\mathrm{CB}} - \nu_+\left(x_{\mathrm{CB}} + x_{\mathrm{SB}}\right)x_{\mathrm{CN}}, \tag{3c}$$

$$\epsilon \dot{x}_{\mathrm{SN}} = x_{\mathrm{SN}}\left(f_{\mathrm{SN}}(R) - \bar{f}(R)\right) + \nu_-\left(x_{\mathrm{CN}} + x_{\mathrm{SN}}\right)x_{\mathrm{SB}} - \nu_+\left(x_{\mathrm{CB}} + x_{\mathrm{SB}}\right)x_{\mathrm{SN}}, \tag{3d}$$

$$\dot{R} = \mu R\left(1 - \frac{R}{K}\right) - R\left\{a\left(x_{\mathrm{CB}} + x_{\mathrm{CN}}\right) + b\left(x_{\mathrm{SB}} + x_{\mathrm{SN}}\right)\right\}, \tag{3e}$$

where x_i is the fraction of strategy i ($i = \mathrm{CB, SB, CN, SN}$), $\bar{f}(R) = \sum_i x_i f_i(R)$ is the average payoff in the population, ϵ changes the time scales of the dynamics of the human behavior and the natural resources: $1 > \epsilon > 0$ indicates that the evolutionary dynamics of the human behavior to be faster than that of the natural resources. In contrast, $\epsilon > 1$ represents that the evolution of human behavior to be slower than the dynamics of the natural resources. The dynamics of human behaviors and beliefs affect the dynamics of natural resources, while the amounts of natural resources affect the payoffs by changing the benefits from the natural resources and the fear of supernatural punishment; our model investigates the public goods game accompanying the environmental feedback and cultural evolution of supernatural beliefs (Fig. 1e).

Table 1 List of variables and parameters.

Symbol	Description
$x_i(t)$	Fraction of strategy i in a local population at time t
$R(t)$	Amount of natural resources at time t
a	Exploitation rates of cooperative strategies
b	Exploitation rates of selfish strategies
$\Delta(R)$	Temptation to selfishness, see Eq (4)
μ	Intrinsic growth rate of the natural resource
K	Carrying capacity of the natural resource
$P(R)$	Fear of supernatural punishment, see Eq (2)
ν_+	Positive missionary rate
ν_-	Negative missionary rate
ϵ	Time-scale parameter

For ease of analysis, we define the temptation to selfishness (i.e., the difference in the benefits between selfishness and cooperation) as follows:

$$\Delta(R) \equiv (bR)^w - (aR)^w \geq 0. \tag{4}$$

Table 1 lists the key variables and parameters.

A strategy is evolutionarily stable if it is not invaded by any other strategy (Maynard Smith and Price, 1973). The temptation to selfishness $\Delta(R)$, the fear of supernatural punishment $P(R)$, the positive missionary rate ν_+, and the negative missionary rate ν_- determined whether a strategy was evolutionarily stable in our model (see SI 1 for derivation).

Numerical simulations were performed by the solve_ivp function with the RK45 method in Scipy version 1.11.3 (Virtanen et al., 2020) in Python 3.11.5. To analyze how parameter values affected the dynamics, we fixed the step size as 0.01 so that the solve_ivp function would not change the step size depending on the parameter values. We evaluated the average density of each strategy and natural resource at time $T_f - 100 \leq t \leq T_f$, where the simulation finished at $t = T_f$. If the average density of a strategy was equal to or smaller than 10^{-4}, we regarded it as extinct; otherwise, it persisted. For a persistent strategy, we evaluated the coefficient of variation at time $T_f - 100 \leq t \leq T_f$. For strategies that went extinct, the coefficient of variation was set to 0. If the mean of the coefficient of variation across the four strategies exceeded 0.1, the dynamics were considered to be oscillating.

Results

Selfish non-believers are stable without positive and negative missionary events. We first began by analyzing the simplest model without the positive and negative missionary events ($\nu_+ = \nu_- = 0$). SN was evolutionarily stable without the missionaries because the payoff of SN was the highest when $R > 0$. The amount of the natural resource, in this case, remained at its minimum value $R_b^* \equiv K(1 - b/\mu)$. By incorporating the positive and negative missionary events in the following subsections, we aimed to determine the conditions under which the cooperators evolved and the amount of the natural resources exceeded R_b^*.

Introduction of positive missionary events stabilizes cooperative believers and conserves the natural resource. Next, the positive missionary events were introduced into the model ($\nu_+ > 0$) while the negative missionary events were not ($\nu = 0$). This led to the fixation of CB, and we investigated how the parameter values changed the evolutionary fate.

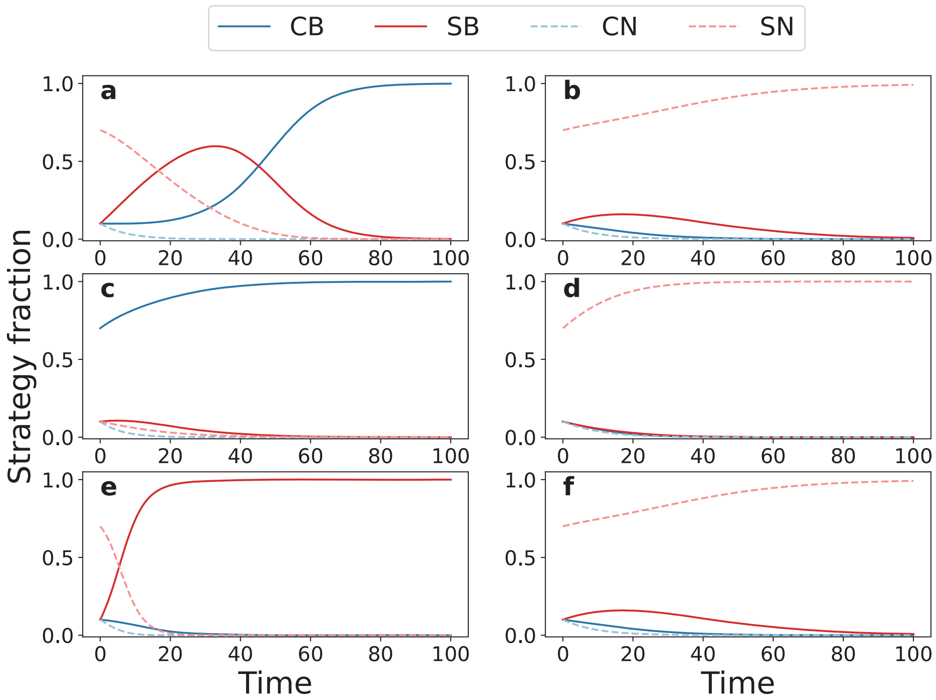

Fig. 2 Each of the three strategies was fixed under the constant natural resources and positive missionary events. Examples of human behavior dynamics under constant natural resources and positive missionary events. Negative missionary events were not allowed in these examples ($v_- = 0$). The dynamics depended on the inequality across the temptation to the selfishness $\Delta = (bR)^w - (aR)^w$, of the supernatural punishment $P = (pR)^u$, and the positive missionary rate v_+. Each panel differed in the values of p and v_+, resulting in changes in the relationship among the three parameters. The remaining parameter values were fixed as follows: $a = 0.5$, $b = 0.8$, $w = 1.7$ (thus $\Delta \approx 0.116$), $u = 2$, and $R = 0.5$. **a** $p = 1$ and $v_+ = 0.3$ result in $v_+ > P > \Delta$. The CB was fixed and evolutionarily stable in this condition. **b** $p = 1$ and $v_+ = 0.1$ resulted in $P > \Delta > v$. SN was then fixed and evolutionarily stable. **c**, **d** $p = 1$ and $v_+ = 0.2$ resulted in $P > v_+ > \Delta$. This condition stabilized both the CB (**c**) and SN (**d**). These two panels differed in the initial fractions of the four strategies. **e** $p = 0.1$ and $v_+ = 0.3$ resulted in $v_+ > \Delta > P$. In this case, the SB was evolutionarily stable. $\Delta > P > v_+$ also stabilized the SB. **f** $p = 0.1$ and $v_+ = 0.1$ resulted in $\Delta > v_+ > P$. In this case, SN was evolutionarily stable.

When the evolutionary dynamics of human behaviors were much faster than that of the natural resources $\epsilon \longrightarrow 0$, we assumed that the amount of the natural resource R, the temptation to the selfishness Δ, and the fear of the supernatural punishment P were constant over time. Then, either the CB, SB, or SN was evolutionarily stable depending on the inequality among Δ, P, and v_+:

- $v_+ > P > \Delta$: CB was evolutionarily stable (Fig. 2a).
- $P > v_+ > \Delta$: Both CB and SN were evolutionarily stable (Fig. 2c, d).
- $v_+ > \Delta > P$ or $\Delta > v_+ > P$: SB was evolutionarily stable (Fig. 2e).
- $P > \Delta > v_+$ or $\Delta > P > v_+$: SN was evolutionarily stable (Fig. 2b, f).

In other words, the dynamics always converged to one of the three equilibria (fixation of CB, SB, or SN). The initial conditions and the parameter values determined the strategy that was ultimately fixed.

When the amount of natural resources changed over time, we derived similar conditions for the evolutionarily stable strategies by replacing Δ and P with $\Delta(R)$ and $P(R)$, respectively, at equilibrium (see SI 1 for details). In other words, the CB (Fig. 3a), SB (Fig. 3b), and SN (Fig. 3c) would be evolutionarily stable under evolving the amount of the natural resources. Figure 3 shows that the amount of the natural resource at the equilibrium was the highest ($R_a^* \equiv K(1 - a/\mu)$) when the CB was evolutionarily stable.

Unlike the constant resource scenario (Fig. 2), none of these strategies could be evolutionarily stable when the amount of the natural resources changed over time. Furthermore, this scenario stabilized the coexistence of multiple strategies in two types of equilibria, one where CB coexisted with SB (Fig. 3d), and the other when CB coexisted with SB and SN (Fig. 4a, b). The local stability conditions of the equilibria were analytically derived assuming that a fraction of CN remained negligible ($x_{CN} \approx 0$; see SI 2 for details). Remarkably, the time-scale parameter ϵ affected the stability of the equilibrium where CB, SB, and SN coexisted (Fig. 4c). We further observed this oscillatory dynamics when none of the equilibria was stable (Fig. 4d).

Conversely, CN could not coexist with any other strategy since the payoffs of CB and CN were identical for any R and the negative missionary events were not allowed in the current setting (see SI 3 for mathematical details).

A small negative missionary rate allows the evolution of cooperation and the maintenance of the natural resources. The full model included the dynamics of the natural resources, positive missionary events, and negative missionary events (v_+, $v_- > 0$). Due to its high dimensionality and nonlinearity, it was challenging to derive complete analytical solutions for this model. However, we derived the conditions under which the selfish strategies cannot be fixed, resulting in the amount of natural resources exceeding its minimum (R^*_b).

From the calculation in SI 1, neither SB nor SN is evolutionarily stable if and only if

$$v_+ - v_- > P\left(R_b^*\right) > \Delta(R_b^*). \quad (5)$$

Intuitively, this inequality means that the fear of the supernatural punishment needs to be stronger than the temptation to

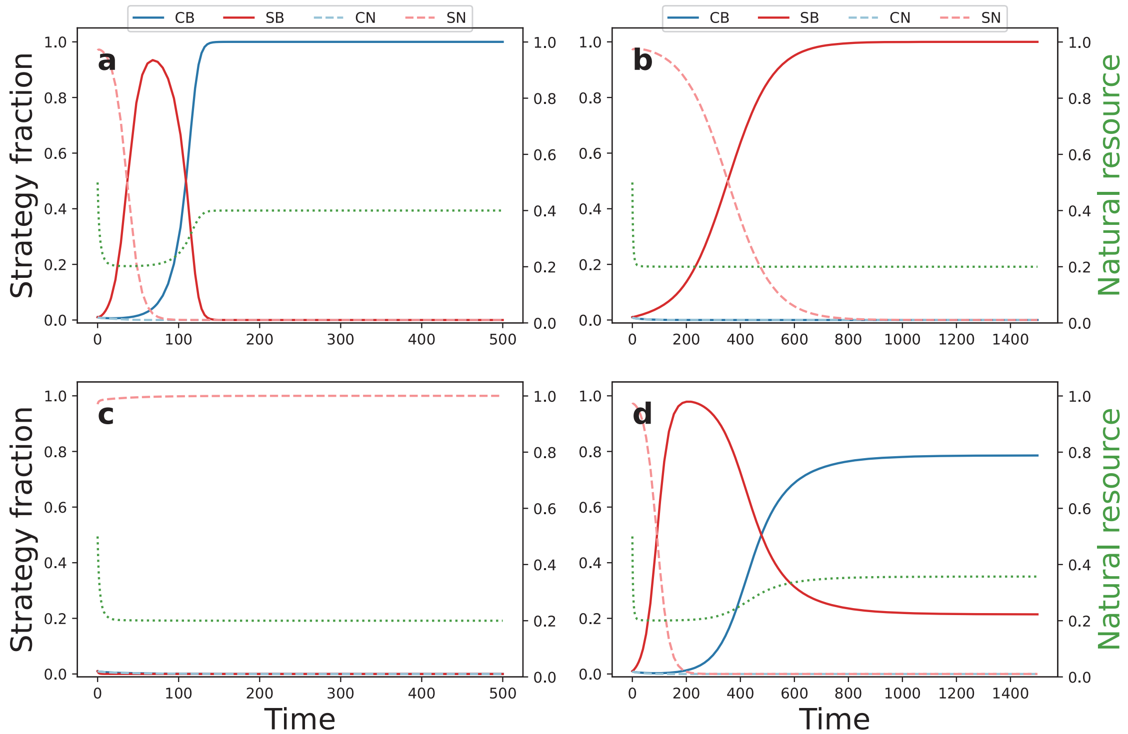

Fig. 3 The positive missionary events increased cooperative believers and selfish believers. Four examples of the dynamics of human behaviors and beliefs co-evolving with the amount of natural resources are shown (the dotted green lines). Here, only positive missionary events occur ($v_+ > 0$); no negative missionary events ($v_- = 0$). The parameter values changed the evolutionary fate, although all four dynamics started from the identical initial condition $(x_{CB}, x_{SB}, x_{CN}, x_{SN}, R) = (0.01, 0.01, 0.01, 0.97, 0.5)$. **a** CB was fixed. **b** SB was fixed. **c** SN was fixed. **d** CB stably coexisted with SB. The four panels differed in the values of (v_+, p, u). **a** $(v_+, p, u) = (0.1, 1, 2)$. **b** $(v_+, p, u) = (0.01, 0.02, 1)$. **c** $(v_+, p, u) = (0.01, 1, 1)$. **d** $(v_+, p, u) = (0.042, 0.1, 1)$. The remaining parameter values were fixed at: $a = 0.6$, $b = 0.8$, $\mu = 1$, $K = 1$, $v_- = 0$, $w = 2$, and $\epsilon = 0.5$.

selfishness (i.e., allowing the CB to invade the SB) while it needs to be smaller than the positive missionary rate minus the negative missionary rate (so that the SN is not evolutionarily stable). It should be noted that the coexistence of SB and SN was unstable in the presence of the negative missionary events (see SI 4). When the inequalities (5) are satisfied, the cooperators can, therefore, evolve, and the amount of the natural resources can be higher than its minimum value R_b^*.

Figure 5 shows how the negative missionary rate ν_- and the exploitation rate of cooperators a affect the evolutionary dynamics. The horizontal and vertical dashed vertical lines in Fig. 5a represent the two thresholds $P(R_b^*) = \Delta(R_b^*)$ and $\nu_+ = \nu_- + P(R_b^*)$, respectively. When the negative missionary rate was sufficiently high, the dynamics converged to the fixation of SN (the black areas on the right in Fig. 5a) in most cases since it was evolutionarily stable. When the exploitation rate of the cooperators was large and close to that of the selfish strategies while the negative missionary rate remained high (the top-right skyblue area surrounded by the gray line in Fig. 5a), the CB could also be fixed; both CB and SN were evolutionarily stable in these parameter ranges and thus the initial conditions determined which strategy was fixed (Fig. 5c, d). When the negative missionary rate was low and the exploitation rate of the cooperators was below the threshold, the SB was fixed (the bottom-left orange areas in Fig. 5a) since the temptation to selfishness was so large that the fear of the supernatural punishment did not allow the invasion by CB. If the exploitation rate by the cooperators was sufficiently large and the negative missionary rate was low, CB could persist and potentially coexist with other strategies (the top left blue, green, or pink areas in Fig. 5a). Further, we also observed the oscillations when multiple strategies coexisted (the cross marks in Fig. 5a).

The average amounts of the natural resources at time $T_f - 100 \le t \le T_f$ are shown in Fig. 5b. The persistence of CB resulted in a higher amount of natural resources than its minimum R_b^*. In particular, the amount of natural resources reached its maximum R_a^* when CB was fixed. Although the parameter space where CB was fixed increased over the exploitation rate of the cooperators a, increasing a resulted in fewer resource availabilities since R_a^* decreased linearly over a. Overall, the highest natural resource was achieved when the negative missionary rate was lower than the threshold and when the exploitation rate of the cooperators was the lowest value that fixated CB.

Next, we also examined how the evolutionary fate changed when the temptation to selfishness or the fear of supernatural punishment was a nonlinear function of R (Figs. S1–S4). SI 5 shows that the nonlinear functions of the $P(R)$ decreased the area where the CS persisted. In contrast, the CS remained in a broader parameter space when the temptation $\Delta(R)$ was a convex function. We also examined the cases when the fear of supernatural punishment decreased over the amount of natural resources (Figs. S5 and S6). In all cases, inequality (5) provided the information on when the CB could persist and when the natural resource remained higher than the minimum.

Discussion

Previous studies have discussed how supernatural beliefs affect human activities, including achieving sustainability (Rakodi, 2012; Rolston, 2006). While the moralizing gods hypothesis associates the norms in human relationships with complex

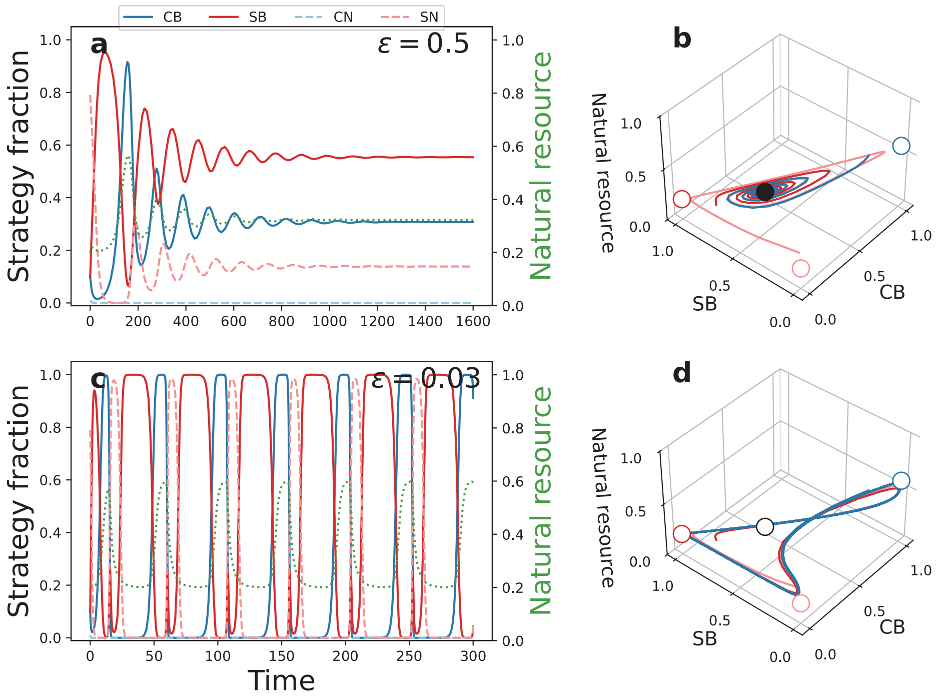

Fig. 4 Faster evolution of the human behavior destabilized the coexistence of the three strategies. The CB, SB, and SN can coexist when human behavior evolves slowly; however, their coexistence is unstable under rapid human evolution. **a** When the evolution of human behavior was slow ($\epsilon = 0.5$), the dynamics converged to the equilibrium where CB (the solid blue line), SB (the solid red line), and SN (the dashed pink line) coexisted. The CN (the dashed sky-blue line) remained small, wheares the dynamics of the natural resource (the dotted green line) converged to a moderate value. **b** A phase-space diagram of the system is shown. Since the fraction of CN remained small, we omitted its dynamics and simplified the phase-space diagram into three dimensions. In the current parameter values, either CB (the open blue dot), SB (the open red dot), or SN (the open pink dot) was not evolutionarily stable. The three dynamics, starting from different initial conditions (shown in different colors), converged to the coexistence of the three strategies (the black dot). **c** The evolution of human behavior and beliefs was faster ($\epsilon = 0.03$) in this panel than in (**a**), while maintaining the rest of the parameter values. The dynamics exhibited the oscillations. **d** The phase-space diagram and the three examples of the dynamics started from different initial conditions (shown by different colors) under the fast human evolution. Since all four equilibria were unstable, the dynamics oscillated regardless of the initial conditions. Parameter values were as follows: $a = 0.4$, $b = 0.8$, $p = 0.5$, $\mu = 1$, $K = 1$, $v_+ = 0.15$, $v_- = 0$, $w = 1$, $u = 1$, and $\epsilon = 0.5$ (**a**, **b**) or $\epsilon = 0.03$ (**c**, **d**). In (**a**, **c**), the initial condition is $(x_{CB}, x_{SB}, x_{CN}, x_{SN}, R) = (0.1, 0.1, 0.01, 0.79, 0.2)$. In (**b**, **d**), the initial conditions were as follows: $(x_{CB}, x_{SB}, x_{CN}, x_{SN}, R) = (0.1, 0.1, 0.01, 0.79, 0.2)$ for the pink lines, (0.1, 0.79, 0.01, 0.1, 0.2) for the red lines, and (0.79, 0.1, 0.01, 0.1, 0.2) for the blue lines.

human societies (Purzycki et al., 2016; Watts et al., 2015), supernatural beliefs may also impose norms on the relationship between humans and nature (Bendixen and Grant Purzycki, 2023; Bendixen et al., 2023; Purzycki et al., 2022). However, it remains unclear when beliefs in supernatural punishment can spread in human society and whether such a belief can harmonize human society with nature. We built a formal mathematical model to investigate the coevolutionary dynamics of human exploitation of natural resources, belief in supernatural punishment, and the amount of natural resources. The mathematical analysis revealed two conditions under which supernatural beliefs can be maintained in human society while sustaining abundant natural resources: the fear of supernatural punishment should be larger than the temptation to selfishness and be smaller than the positive missionary rate minus the negative one. While a previous study shows the natural impact on human beliefs (Nakadai, 2023), our results suggest how supernatural beliefs affect natural environments.

Inequality (5) show the two conditions under which beliefs in supernatural punishment could facilitate sustainability. These conditions clarified the similarity and difference between the systems with real punishment and beliefs in supernatural punishment. The first condition, $P(R_b^*) > \Delta(R_b^*)$, implies that the fear of supernatural punishment needs to be stronger than the temptation to selfishness so that CS are more adaptive than SB. Studies on the evolution of cooperation under real punishment derived similar conditions; cooperation can evolve if the punishment is strong enough to make selfish behaviors maladaptive (p. 283 Broom and Rychtar, 2013; Fowler, 2005; Nakamaru and Iwasa, 2006). Both real punishment and beliefs in supernatural punishment can facilitate the sustainable relationship between human society and nature if they invoke strong (fear of) punishment on those who harm nature. The second condition in inequality (5), $v_+ - v_- > P(R_b^*)$, argued that supernatural beliefs should spread more efficiently via positive missionary events than it is lost via negative missionary events. This condition highlights the difference between real punishment and beliefs in supernatural punishments. The systems of real punishment need to compensate the costs of punishing others (Boyd et al., 2003; Dos Santos et al., 2011; Gardner and West, 2004); otherwise, punishing systems collapse. In the current model, such conditions do not exist because no one pays the cost for punishing selfish individuals. Instead, supernatural beliefs should easily spread in human society because only believers would be afraid of supernatural punishment. If this condition is not satisfied, individuals selfishly behave and natural resources remain scarce (e.g., the bottom-right area in Fig. 5a, b). In short, real punishment and beliefs in supernatural punishment have different obstacles to facilitating sustainable relationships between human society and nature.

It is beyond the scope of this manuscript to formally test our theoretical prediction with empirical data. Nevertheless,

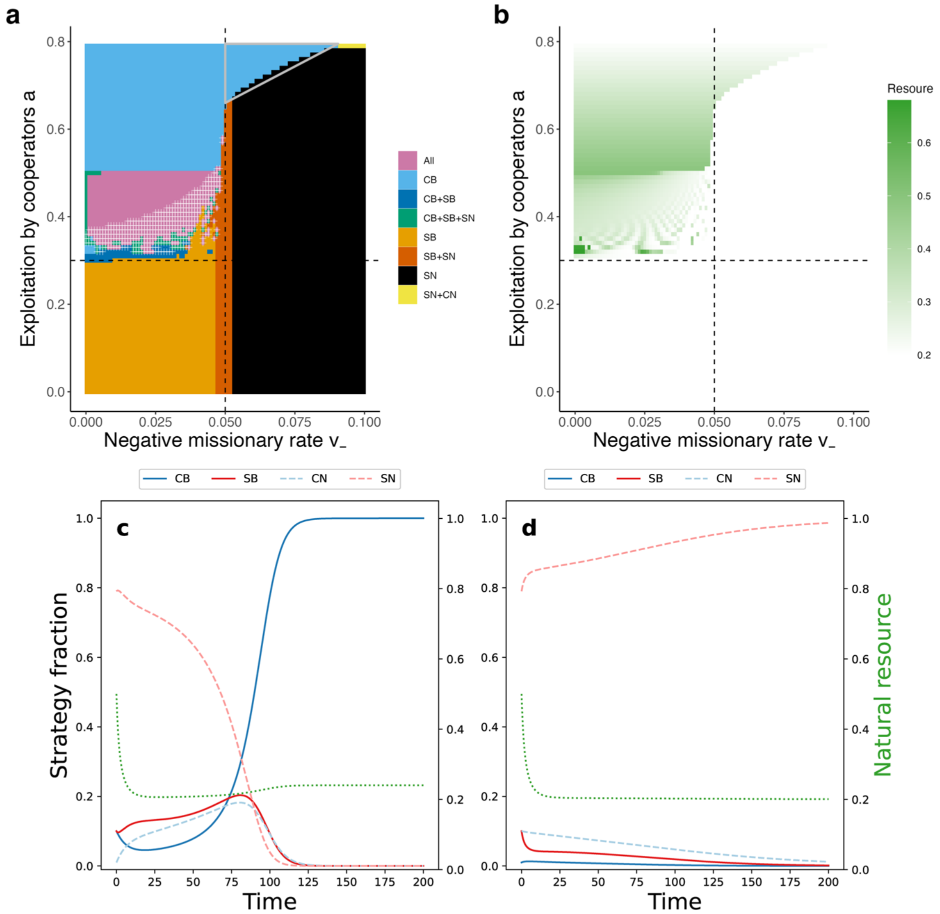

Fig. 5 Negative missionary rate and the exploitation by cooperators affected the evolutionary fates and natural resources. a Increasing the negative missionary rate v_- and the exploitation rate by the cooperators a (i.e., decreasing the temptation to selfishness $\Delta(R)$) affect the evolutionary fates (represented by different colors). When the negative missionary rate is high (the right area of the vertical dashed line $v_- = v_+ - P(R_b^*)$), the SN is fixed unless the exploitation by the cooperators is close to that of the selfish strategies. When the negative missionary rate is low (the left area of the vertical dashed line), the cooperators' exploitation rate a determines the evolutionary fate. The SB is fixed below the horizontal dashed line $P(R_b^*) = \Delta(R_b^*)$. Above the horizontal dashed line, the CB is maintained alone or with other strategies. Cross symbols in the panel indicate the oscillations. **b** The average natural resource availability at time $T_f - 100 \le t \le T_f$ is shown over the negative missionary rate v_- and exploitation rate by the cooperators a. The extinction of cooperative strategies resulted in minimum natural resource availability $R_b^* = 0.2$ (i.e., the white areas). However, the persistence of the cooperators increased the natural resources. Greener areas retain more natural resources. **c**, **d** When $v_- > v_+ - P(R_b^*)$ but a is close to b (the skyblue area surrounded by the gray line in (**a**)), both CB and SN are evolutionarily stable (**c**, **d**, respectively). In such cases, the initial condition determines which strategy is fixed. The values of fixed parameters are as follows: $b = 0.8$, $p = 0.5$, $\mu = 1$, $K = 1$, $v_+ = 0.15$, $w = 1$, $u = 1$, $\epsilon = 0.5$, and $T_f = 1600$. We used $a = 0.76$ and $v_- = 0.07$ on (**c**, **d**). All simulations started from $(x_{CB}, x_{SB}, x_{CN}, x_{SN}, R) = (0.1, 0.1, 0.01, 0.79, 0.5)$ in (**a**, **b**, **c**), while (**d**) started from $(x_{CB}, x_{SB}, x_{CN}, x_{SN}, R) = (0.01, 0.1, 0.1, 0.79, 0.5)$. See also Figs. S1–S4 for the cases where either the temptation to selfishness or the fear of the supernatural punishment is a nonlinear function of R.

ethnological and psychological studies suggest that inequality (5) seems reasonable. Consistent with our first condition, previous studies have shown that certain supernatural beliefs invoke a strong fear of supernatural punishment. Nakawake and Sato (2022) quantitatively showed that severe supernatural punishment (e.g., the death of members of a village, kinship, or family of individuals who harm nature) is typical in Japanese folklore. A global meta-analysis by Hartberg et al. (2016) shows that one-third of supernatural punishment results in the death of those who harm nature.For example, cutting trees on a mountain was believed to cause a flood that could wash away all houses in a village (Sakurai, 1999). When and how could a belief in supernatural punishment spread efficiently in human society via missionaries and satisfy the second condition in inequality (5)? One possibility is that supernatural or religious beliefs are a by-product of cognitive adaptation and thus likely to be accepted (Boyer, 2003). For example, the minimally counterintuitive theory suggests that many religious concepts violate an optimal number of our expectations, which increases their memorability and helps them spread (Barrett and Nyhof, 2001; Boyer, 2003). Another possibility is the prestige bias; if prestigious people believe in supernatural punishment for any reason, other people would also start believing in the one-to-many transmission of supernatural beliefs. In fact, in many religious traditions, religious leaders tend to gain power in non-religious domains, such as political or juridical domains (Winkelman, 1990), which might strengthen their prestige as religious leaders. Further, costly religious rituals practised by religious leaders might also help spread religious beliefs (Norenzayan et al., 2016; Sosis, 2003). To test our theoretical prediction, future studies are encouraged to compare the degree of fear of supernatural punishments, transmission rates of such beliefs, and abundance of natural resources.

Our results may be generalized to non-supernatural belief systems that impose norms on human-nature relationships without punishment or sanction (e.g., environmental ethics). In such cases, $P(R)$ should be regarded as the strength of guilt when an individual feels in overexploiting nature, and ν_+ and ν_- represent the rates of acquisition and loss of such morality through interaction with others, respectively. In this framework, inequality (5) represents the conditions under which such moral systems—whether supernatural beliefs or ethics—can facilitate the sustainable relationship between human society and nature. This inequality suggests that moral systems invoking a too strong feeling of guilt fail in achieving a sustainable relationship because the second condition, $\nu_+ - \nu_- > P(R_b^*)$, cannot be met. Instead, increasing the transmission rate of the moral systems (ν_+) would successfully lead to sustainable resource usage because $\nu_+ - \nu_-$ becomes larger. These conditions suggest how to design environmental moral systems to contribute to sustainability successfully. In a society with a belief in supernatural punishment, for example, incorporating environmental ethics in the supernatural belief (i.e., introducing $P(R)$) may be more effective than trying to spread the environmental ethics through secular approaches, because the supernatural belief would have a large ν_+. Alternatively, using non-rational narratives that are easy to accept, including supernatural beliefs, may facilitate the transmission of environmental ethics among individuals because these narratives would increase ν_+ of the environmental ethics.

Our model could also be extended to a quantitative model by formulating the evolution of the exploitation rate of natural resources and the strength of belief in supernatural punishment. However, we focused on the current qualitative strategies because, to the best of our knowledge, the current model is the first rigorous formulation of the coevolutionary dynamics of human behaviors, beliefs in supernatural punishment, and natural resources. Future studies should investigate whether the results in this manuscript are valid for quantitative models because such models would be easier to compare with empirical data than our current model.

In conclusion, our model provides a theoretical foundation for supernatural beliefs to facilitate sustainability. While the moralizing gods hypothesis argues that some supernatural beliefs impose norms on human relationships, others regulate the relationship between humans and nature. Our mathematical model suggested two conditions under which such supernatural beliefs could prevent humans from overexploiting nature through the fear of supernatural punishment: the fear of supernatural punishment should be larger than the temptation to selfishness and be smaller than the positive missionary rate minus the negative one. Although believing in supernatural punishment is not adaptive, positive missionary events can stabilize cooperative individuals who believe in supernatural punishment and self-regulate the exploitation of nature. Even if they are not evolutionarily stable, CS can coexist with SB and non-believers when the two conditions are met. Therefore, the current results supported the idea that supernatural beliefs harmonize human societies and nature, and that supernatural beliefs could play an important role in achieving sustainability. Future studies are encouraged to empirically test our theoretical prediction by examining the association among the degree of fear of supernatural punishments, transmission rates of such supernatural beliefs, and abundance of natural resources.

Data availability

The codes and simulation data used in this study are available from the Zenodo repository: https://doi.org/10.5281/zenodo.16548844.

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