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From information free-riding to information sharing: how have humans solved the cooperative dilemma at the heart of cumulative cultural evolution?

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Cumulative cultural evolution, where populations accumulate ever-improving knowledge, technologies and social customs, is arguably a unique feature of human sociality and responsible for our species' ecological dominance of the planet. However, at the heart of cumulative cultural evolution is a cooperative dilemma. Assuming asocial learning is more costly than social learning, social learners can act as 'information free-riders' by copying innovations from asocial learners without paying the cost. This cost asymmetry will reduce innovation, inhibiting cumulative culture. Innovators might respond by protecting their knowledge and keeping the benefits to themselves – 'information hoarding' - but then others cannot build on their discoveries and again cumulative culture is inhibited. Here we formally model information free-riding and information hoarding within a cumulative cultural evolution framework using both analytical and agent-based models. Model 1 identifies the conditions under which information sharing can evolve in the face of information free-riding and hoarding. Models 2-4 then show how three mechanisms known to favour cooperation in non-informational contexts - kin selection, partner choice and cultural group selection – can also solve the informational cooperative dilemma and facilitate cumulative cultural evolution, each with distinct signatures potentially detectable in historical, ethnographic and other empirical data.

1. Introduction

Cumulative cultural evolution (CCE), where populations accumulate ever-improving knowledge, technologies and social customs, is arguably a unique feature of human sociality and responsible for our species' ecological dominance of the planet [1,2]. Yet at the heart of CCE lies a cooperative dilemma. CCE requires both asocial learning (aka 'innovation') to create new knowledge, and social learning (aka 'cultural transmission') to preserve and accumulate knowledge across generations [3]. Asocial learning is assumed to be more costly than social learning; it takes more time and effort to invent something new than copy it from someone else. If innovators freely share their knowledge, then social learners can become 'information free-riders' by copying beneficial knowledge from innovators without bearing the costs of innovation. All else being equal, social learners will therefore outperform and replace all innovators. However, if everyone copies, then no-one is innovating, and CCE stops.

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Innovators might respond by protecting their knowledge and keeping the benefits to themselves – 'information hoarding' – although then others cannot build on their discoveries, and again CCE stops.

While humans have clearly to some extent solved this cooperative dilemma given that we exhibit CCE, a glance through history and across societies shows how pervasive and challenging information free-riding and information hoarding are. Amongst West Papuan hunter-gatherers, expert male adze-makers transmit their skills exclusively to their sons or nephews via apprenticeships [4]. In medieval Venice, expert glassmakers were legally prohibited from leaving the city to prevent their skills spreading to rival states [5]. In such cases, while specific actors benefit (adze-makers' kin; the Venetian Republic), overall CCE is inhibited due to the reduced pool of innovators [6,7]. Sometimes, however, widespread information-sharing emerges. Mokyr [8] attributes the exponential accumulation of knowledge during the 17th–18th century Enlightenment to a 'Republic of Letters', a network of innovators such as Francis Bacon and Isaac Newton who openly shared ideas, data and methods. Mokyr attributes this to a process of 'competitive patronage', where powerful families or governments protected and rewarded innovators in exchange for reputational benefits. The recent 'open science' movement also represents a shift from scientists hoarding information for their own benefit to the open release of data and methods, aiding the identification of replicable results that can be more reliably built upon by others [9]. Patent and copyright systems provide financial benefits to innovators to offset the costs of innovation [10], although there is little consensus on their effectiveness [11], and practices such as patent thicketing or patent hoarding can block innovation, illustrating the fragility of information sharing.

Our aim here is to formally model information free-riding and information hoarding in a CCE context, to (i) explore when and why these phenomena inhibit CCE, and (ii) whether solutions to free-riding from the evolution of cooperation literature [12], originally designed for material cooperative dilemmas, also apply to informational cooperative dilemmas. Formal models can clarify verbal arguments and historical case studies such as those of Mokyr [8], highlight often hidden underlying assumptions, and generate unexpected insights or predictions not apparent to the unaided mind [13].

While previous models have touched on the cooperative dilemma at the heart of CCE, none have directly addressed it, nor fully examined potential solutions to it. Rogers [14] modelled the evolution of social learning as a producer-scrounger dilemma where innovators generate knowledge at higher cost than social learners can copy that knowledge. This generates a dilemma where, in constant environments, social learners entirely replace innovators because they bear lower costs. When environments change, an equilibrium exists between social learners and innovators due to the added advantage to innovators of discovering newly adaptive knowledge when previous knowledge is obsolete. In this model and its extensions [15,16], social learning constitutes information free-riding. However, these models are not directly relevant to the context described above. Rogers' model does not allow the accumulation of knowledge, only alternation between one of two behaviours. Environmental change renders all existing knowledge useless, again preventing CCE. Furthermore, innovators have no control over whether others can copy them, thus excluding the possibility of information hoarding, nor solutions to the cooperative dilemma.

One study that incorporated both CCE and information hoarding modelled the accumulation of technology in a producer-scrounger game, with a parameter controlling the excludability of the technology produced by innovators [17]. Generally, social learners facilitated CCE by acquiring multiple beneficial technologies from different innovators and passing them all to the next generation. Excludability acted against this: when innovators could prevent social learners copying them, fewer social learners persisted, inhibiting CCE. While this model demonstrates the negative consequence of information hoarding for CCE, it does not model cooperative solutions to information hoarding. A more recent model allowed innovators to either teach, i.e. facilitate social learning, or mask, i.e. inhibit social learning, equivalent to information hoarding [18]. This and other models of teaching [19] and language/communication [20,21] find that teaching evolves due to kin selection, as both genes for teaching and adaptive information are transmitted together from parent to offspring. Yet these models are designed to explore the evolution of teaching across different species rather than the emergence of information sharing within human CCE, and make assumptions (e.g. that teaching and masking are genetically transmitted) that are inconsistent with the diversity and sporadic emergence and loss of information sharing through human history.

The following models build up in complexity to first formally analyse the informational dilemma at the heart of CCE (Model 1) before exploring how kin selection (Model 2), partner choice (Model 3) and cultural group selection (Model 4) might solve this dilemma and facilitate CCE. Figure S1 presents a schematic of all models. Models were written in R [22] and all code is available at https://doi.org/10.5281/zenodo.14771184.

2. Model 1: The dilemma

The aim of Model 1 is to formalise the informational public goods dilemma described above. This is intended as a clarification of the logic using many simplifying assumptions, not a realistic simulation of specific historical processes. Model 1a is an analytic population-level model. Model 1b introduces an agent-based version of Model 1a with explicit agents, traits and transmission events which recreates and confirms the findings of Model 1a and serves as a basis for Models 2-4.

Model 1a formalises two processes: information free-riding and information hoarding. Assume three types of individual. Open Innovators innovate at cost c to generate a cultural trait that yields a benefit b (see Table S1 for parameter definitions). Open Innovators then freely and unconditionally share their trait with others. They receive a benefit x for sharing their trait, via a mechanism which for now remains unspecified. Later we replace x with explicit mechanisms of cooperation, but for now it is a placeholder to clarify the general logic of informational cooperative dilemmas. Non-Innovators never innovate and benefit from others' (open) innovation. They can be seen as information free-riders. Closed Innovators innovate at cost c with benefit b, and bear an additional cost d to hoard their trait from others. With probability p_h this hoarding is successful, otherwise the innovation is released to the community just like those of Open Innovators. If their innovation is released, they also get the benefits of sharing x. Closed Innovators can be seen as information hoarders. Our guiding question is under what conditions do Open Innovators displace Closed Innovators and Non-Innovators.

Assume the number of Open, Closed and Non-Innovators in the population are X, Y and Z respectively. The payoff to an Open Innovator, $W(OI)$, is then:

$$W(OI) = w_0 + bX + bY(1 - p_h) + x - c$$

In addition to baseline payoff w_0, Open Innovators receive a payoff b from each of the innovations generated by the X Open Innovators in the population (including themselves), a payoff b from the $Y(1 - p_h)$ Closed Innovators who unsuccessfully protect their innovation such that it becomes openly known, a benefit x for releasing their innovation, and they bear a cost of innovation c. The payoff to a Closed Innovator, $W(CI)$, is:

$$W(CI) = w_0 + bX + bY(1 - p_h) + bp_h + x(1 - p_h) - c - d$$

Closed Innovators receive the same benefits as Open Innovators from the open knowledge generated by Open Innovators and unsuccessful Closed Innovators, $bX + bY(1 - p_h)$. Closed Innovators also receive, with probability p_h, another benefit b from their successfully protected innovation, and with probability $1 - p_h$ a benefit x from sharing their unsuccessfully protected innovation. Finally, Closed Innovators bear a cost of innovation c and a cost of attempting to protect their knowledge d. The payoff to a Non-Innovator, $W(NI)$, is:

$$W(NI) = w_0 + bX + bY(1 - p_h)$$

Non-Innovators pay no costs of innovating, and receive the benefits of open innovation from Open Innovators and unsuccessful Closed Innovators. Note that in this formulation, innovation is a perfectly *non-rival* good via its benefit b. Every Open Innovator and unsuccessful Closed Innovator generates a benefit b which is received by (not divided amongst) every individual in the population. This captures the notion that, unlike for material goods, one person can transmit knowledge to another without themselves losing that knowledge or the knowledge being depleted [23]. Innovation is *excludable* for Closed Innovators via parameter p_h: with probability p_h, Closed Innovators generate private knowledge, and with probability $1 - p_h$ it is non-excludable. For Open Innovators, innovation is always non-excludable.

Open Innovators can invade Non-Innovators when $x > c$. This is when the benefits to Open Innovators of releasing their innovation outweigh the cost of producing that innovation. Note that b is not present in this inequality. It does not matter how big the benefit is of the innovation, because both Open Innovators and Non-Innovators receive that benefit. Closed Innovators can invade Non-Innovators when $bp_h + x(1 - p_h) > c + d$. This is when the benefit to Closed Innovators of private innovation, bp_h, plus the reputational benefit of unsuccessfully protected innovation, $x(1 - p_h)$, outweigh the costs to Closed Innovators of innovation and of protecting their innovation. Here the benefit of innovation, b, does matter, because when Closed Innovators are successful then only they receive their private benefit. Open Innovators can invade Closed Innovators when $d > p_h(b - x)$. This occurs when d is large (imposing high costs on Closed Innovators), when p_h is small (low probability of Closed Innovators generating private knowledge) and when x is large relative to b (because Open Innovators benefit uniquely from x and not b). Assuming $d > 0$, when $x > b$ Open Innovators will always outperform Closed Innovators. Note that c is not present in this inequality, as both Open Innovators and Closed Innovators pay innovation costs.

Consider how to get to a population of Open Innovators from a mix of Non-Innovators and Closed Innovators. Consider first a situation when $p_h = 1$, i.e. Closed Innovators are always successful in protecting their knowledge. This is perhaps due to poor communication and limited social networks. This means that Open Innovators will do better than Non-Innovators when $x > c$ and better than Closed Innovators when $x > b - d$. Only when both of these conditions are met will Open Innovators spread. Collectively, then, for Open Innovators to spread, x and/or d need to increase relative to c and/or b (figure 1*a-c*). Note the apparent paradox related to b. Open Innovators are more likely to emerge if the benefit from innovation b is small. Yet CCE by definition surely *increases* b in absolute terms, as technology becomes more effective and knowledge more accurate. So the consequence of open innovation - larger benefits of innovation - paradoxically make it harder for open innovation to emerge.

Consider now the case when $p_h < 1$, i.e. when Closed Innovators sometimes fail to protect their knowledge. This might be due to inventions or institutions such as the printing press, postal services, cheaper transportation or the internet making it harder to keep innovations secret. Reducing p_h does not affect whether Open Innovators outcompete Non-Innovators, which remains when $x > c$. Benefits of sharing still need to outweigh the costs of innovation. However, it does reduce the parameter space within which Closed Innovators can outcompete Open Innovators, assuming $x > c$. At the extreme when $p_h = 0$, Open Innovators will replace Closed Innovators whenever $d > 0$ (figure S2). This confirms the notion that making it harder to protect or conceal knowledge favours open innovation.

Finally, we implement a crude form of CCE by assuming that the benefits to innovation, b, increase with accumulating knowledge. A steel axe is more effective and durable than a stone axe, but only appeared after the accumulation of prior axe manufacturing and steelworking knowledge. Accumulated knowledge must be openly available in order to accumulate, otherwise it dies with the innovator. We therefore assume that every timestep the parameter b increases by an amount

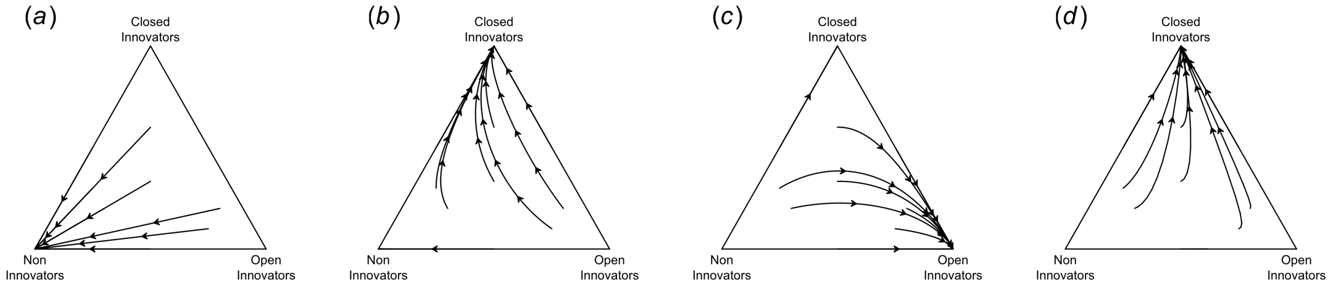

Figure 1. Conditions in Model 1a in which Non Innovators, Closed Innovators and Open Innovators are favoured. (*a*) When the benefits of sharing fail to exceed the cost of innovation ($x < c$) and when the benefits of innovation fail to exceed the cost of innovation and hoarding ($b < c + d$), then Non-Innovators spread at the expense of Open Innovators and Closed Innovators. Parameter values: $b = 0.15, c = 0.1, x = 0.05, d = 0.1, p_h = 1, \gamma = 0$. (*b*) Increasing the benefit of innovation b and reducing the cost of hoarding d favours Closed Innovators. Parameter values: $b = 0.2, c = 0.1, x = 0.05, d = 0.05, p_h = 1, \gamma = 0$. (*c*) Increasing the unspecified benefit of sharing x such that $x > c$ and $x > b - d$ favours Open Innovators. Parameter values: $b = 0.2, c = 0.1, x = 0.2, d = 0.05, p_h = 1, \gamma = 0$. (*d*) Allowing benefits from innovation to accumulate by setting $\gamma = 1$ favours Closed Innovators where Open Innovators would otherwise be favoured. Parameter values: $b = 0.2, c = 0.1, x = 0.2, d = 0.05, p_h = 1, \gamma = 1$. Plots created using a modified version of package *baryplot* [24].

$\gamma(bX + bY(1 - p_h))$, where γ is a constant controlling the extent to which b increases, and the term in brackets is the benefit from public knowledge. Figure 1*d* shows the same parameter values as figure 1*c* where Open Innovators were favoured, but with $\gamma = 1$. Now Closed Innovators are favoured. This is because increasing b favours Closed Innovators by increasing their benefit from private innovation (bp_h). The increased benefits generated by Open Innovators and unsuccessful Closed Innovators are shared by all agents and therefore do not affect the dynamics.

Model 1b replicates and extends Model 1a to incorporate explicit agents, interactions and traits. This added complexity and need to explicitly model social interactions favours an agent-based modelling approach [25,26]. Model 1b assumes N agents each of whom can learn any number of L traits. Traits are sequences of L ones and zeroes where a 1 in position l indicates that the lth trait has been learned and a 0 indicates no knowledge of the trait. For example, 00110 denotes $L = 5$ traits of which this agent only knows the third and fourth. Each learned trait gives a benefit b each timestep; this agent would receive $2b$ from their two learned traits. As in Model 1a, agents are Open Innovators, Closed Innovators or Non-Innovators. In each timestep, each Open and Closed Innovator innovates by randomly picking one of its L traits and setting it to 1 with probability p_i. Innovation costs c whether successful or not. Following innovation, there is sharing/copying. As before, Closed Innovators successfully hoard their traits with probability p_h. Each agent copies each trait known by at least one non-hoarding agent with probability p_c per trait. When $p_c = 1$, each agent acquires all the traits known by all non-hoarding agents in the population. This extreme case matches Model 1a, with $p_c < 1$ the more realistic case when only some traits are copied due to time constraints or copying error. As before, Open Innovators and unsuccessfully-hoarding Closed Innovators who innovated on that timestep receive a benefit x for openly releasing their innovation. Closed Innovators pay a hoarding cost d whether hoarding is successful or unsuccessful. Closed Innovators who fail to innovate (because $p_i < 1$) do not pay the cost d as they have nothing to hoard.

After fitnesses are calculated, there is payoff-biased copying of strategies (Open Innovation, Closed Innovation or Non-Innovation). Each agent picks another random agent and if the chosen agent has higher fitness than the focal agent, the focal agent adopts the strategy of the chosen agent with probability p_s. Then there is agent turnover. With probability p_d, each agent 'dies' and is replaced with a naive, unknowledgeable agent whose traits are all zero but who keeps the same strategy as its parent. The parameter p_d therefore controls how much timesteps overlap. When $p_d = 1$, all agents die each timestep and are replaced with unknowledgeable agents, recreating Model 1a. When $p_d = 0$, agents never die. This resembles a fixed population of agents engaging in repeated cycles of innovation and copying, allowing the accumulation of learned traits over time. Finally, it is unrealistic to assume that if a population learns all L possible traits then cultural evolution stops. Consequently we assume that when the mean proportion of traits known across all agents in the population reaches 0.9, then a new set of L unknown traits are added to the set of possible traits. This can be seen as the opening up of a new space of possibilities once knowledge in one domain has reached a certain point. This generates realistic patterns of punctuated equilibria with rapid increases in cultural knowledge followed by stasis, then rapid increases again [27,28]. This makes Model 1b resemble genuine sequential cumulative cultural evolution, rather than the crude implementation in Model 1a.

Model 1b replicated the findings of Model 1a with equivalent parameter values (figures S3-S5), supporting the conclusions drawn by the analytical model. We additionally find that reducing the probability of innovation p_i favours Non-Innovators given that Open and Closed Innovators pay a cost for innovation that increasingly yields no benefits (figure S6). We also find that when the informational dilemma is eliminated by making innovation easier than social learning ($p_c < p_i$), then Open Innovators do best, as expected (figure S6). Finally, Model 1b shows a clear link between scenarios in which parameter values favour open innovation and CCE (figure S7): more open innovation means more traits are accumulated, and when combined with overlapping timesteps ($p_d < 1$) generates open-ended CCE.

In summary, Model 1 shows that there are two ways in which Open Innovators who freely share information can be exploited, resulting in the disruption of CCE. First, when Non-Innovators can copy cultural traits from Open Innovators without paying the cost of innovation, and when any benefits accrued to Open Innovators for information sharing fail to compensate for this (i.e. when $x < c$). Second, when Closed Innovators can generate and successfully hoard their own private knowledge, and the benefits of this private knowledge exceed the benefits to Open Innovators of information sharing minus the cost of hoarding (i.e. when $x < b - d$). The latter is increasingly likely as knowledge accumulates, which increases the benefits of innovation b. Overall, crucial to the emergence of CCE is the currently-unspecified benefit of openly releasing information, x. In Models 2-4 we replace this parameter with three mechanisms from the evolution of cooperation literature which endogenously direct benefits back to Open Innovators: kin selection (Model 2), partner choice (Model 3) and cultural group selection (Model 4).

3. Model 2: Kin selection

A widespread solution to cooperative dilemmas in nature is kin selection [29]. Individuals direct helping behaviour towards kin who share genes with the helper due to common ancestry. On average, relatives will share the genes underlying kin-directed cooperation, and so such genes will increase in frequency as a result of the cooperation. Kin selection explains the vast majority of cooperative behaviour in non-human species [30], as well as various forms of human cooperation [12].

Here we do not model the evolution of cooperation via kin selection, which has been extensively modelled in evolutionary biology [29,31]. We assume kin selection has already evolved in our species, and provides motivation to preferentially help genetic relatives, in this context to preferentially share beneficial information with relatives. We focus on parent-to-offspring transmission (i.e. vertical cultural transmission [32]), given that parents will typically have greater knowledge than, and spend considerable time with, their children. This resembles the case of father-son adze making apprenticeships amongst West Papuans [4]. (Note however that there is extensive evidence of learning from non-parents across societies [33–37], both obliquely from unrelated elders and horizontally from unrelated peers.) However, while kin selection may be one solution to the informational dilemma, it has downsides. Learning from just two parents - or one, for sex-specific skills and knowledge - provides a far smaller pool of demonstrators and teachers than learning from any member of society. Fewer demonstrators means slower CCE [6,7].

Model 2 implements kin-directed information sharing in the above framework. Model 2 is identical to Model 1b except for the social learning stage. We no longer assume social learning from all non-hoarders, i.e. horizontal transmission, nor Open Innovators who indiscriminately share with all other agents. Instead, social learning takes the form of vertical transmission and occurs at the start of each timestep (except the first, when there are no parents from whom to learn). Open Innovators are replaced with Kin-directed Innovators who share traits exclusively with their offspring. Each agent produces one offspring via asexual reproduction. While humans are obviously not asexual reproducers, this resembles sex-specific transmission of skills, and provides a simple test case. Parents transmit their strategies (Kin-directed Innovator, Closed Innovator or Non-Innovator) to their one offspring. This could be via either genetic or cultural inheritance. Non-hoarding agents also transmit each of their known cultural traits to their offspring with probability p_c per trait. There is then innovation amongst Kin-directed Innovators and Closed Innovators, fitness calculations, and payoff-biased copying of strategies, as in Model 1b. There is now no agent mortality via p_d because all agents are assumed to die every timestep and replaced with their offspring. Unlike Model 1, there are now no direct benefits of openness ($x = 0$) given that kin selection is explicitly modelled as a mechanism providing those benefits. Initially we assume copying and innovation are both errorless ($p_c = p_i = 1$) and hoarding always successful ($p_h = 1$).

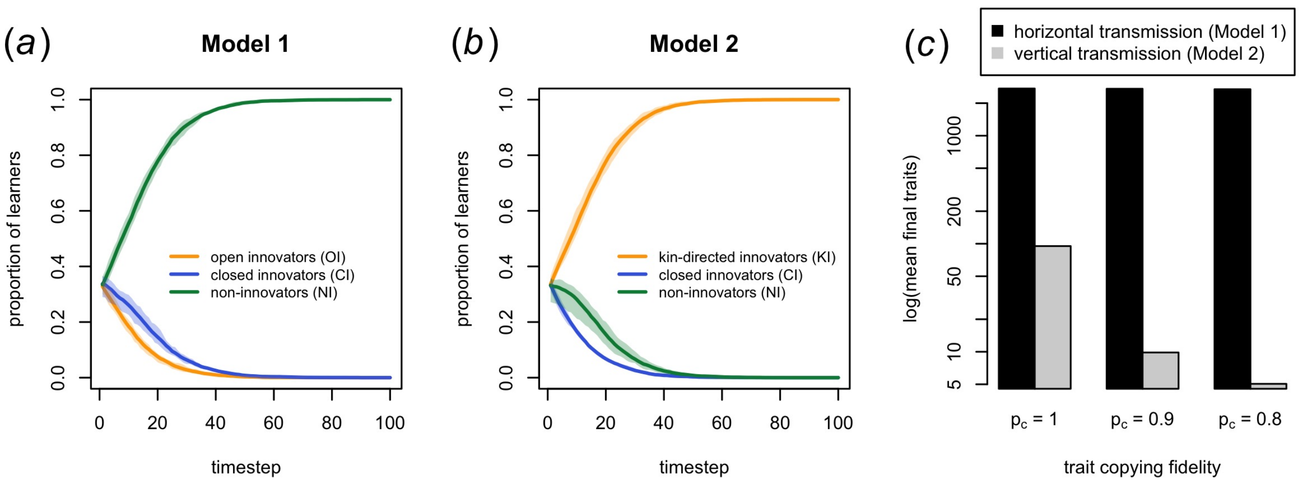

Figure 2. (*a*) Time series for the agent-based version of Model 1 (Model 1b) with no benefits to Open Innovators for sharing knowledge ($x = 0$), favouring Non-Innovators (other parameter values: $b = 0.15$, $c = 0.1$, $d = 0.1$, $p_h = p_i = p_c = p_d = 1$; thick lines are means of 10 independent runs with shaded areas showing the range). (*b*) Time series with the same parameter values for Model 2, now favouring Kin-directed Innovators who share traits exclusively with kin (offspring). (*c*) Logged mean final number of traits accumulated at $t = 100$ for Model 1b and Model 2 in populations entirely composed of Open Innovators or Kin-directed Innovators respectively, showing that horizontal transmission in Model 1b supports orders of magnitude more traits than vertical transmission in Model 2, and is far less vulnerable to reduced trait copying fidelity ($p_c < 1$).

Figure 2 shows that under parameter values that would not have favoured Open Innovators in Model 1b (figure 2*a*), Kin-directed Innovators go to fixation (figure 2*b*). Kin selection favours agents who preferentially share traits with offspring. This is because both strategies and cultural traits are inherited vertically together. Only Kin-directed Innovator parents will innovate and pass on beneficial knowledge to their offspring. Closed Innovators innovate but do not pass on knowledge to their offspring, while Non-Innovators do not innovate so have nothing to pass on. This is the same mechanism that explains the evolution of teaching in other models [18,19], where both genes for teaching and the superior taught knowledge that results from teaching are passed on together from parents to offspring.

Figure 2*c* shows the downside of Kin-directed Innovation. Compared to the horizontal transmission of Model 1b with 100% Open Innovators, Model 2 with 100% Kin-directed Innovators accumulates far fewer cultural traits. Learning from a single parent creates a bottleneck that inhibits CCE compared to horizontal transmission from all N individuals. Figure 2*c* also shows that reducing the probability of copying p_c by a small amount severely inhibits CCE in Model 2, while has a negligible effect in Model 1b. Vertical transmission is far more vulnerable to copying error given that there is only a single demonstrator, compared to horizontal transmission from the entire population. This effect of demonstrator number on CCE is known from other models [6,7]. This might explain why real world cases of kin-directed information sharing involve lengthy apprenticeships: the West Papuan adze making example from [4] involved apprenticeships of five years or more. Such lengthy apprenticeships may be one way to reduce copying error and maximise the probability of successfully copying cultural traits.

Figure S8 shows two alternative versions of Model 2. Model 2b assumes sexual reproduction where agents mate and produce offspring who inherit the strategy and traits of one randomly chosen parent. This yields almost identical results to Model 2 with Kin-directed Innovators favoured (figure S8*a*), again because traits and strategies are inherited together. Model 2c assumes that offspring combine the traits of both parents, while inheriting their strategy from just one. This reduces the success of Kin-directed Innovators, who now co-exist with Non-Innovators (figure S8*b*). This is because the inheritance link between strategy and cultural traits has been partially broken. If a Kin-directed Innovator and a Non-Innovator mate and produce a Non-Innovator offspring, this offspring will inherit the cultural traits of its Kin-directed Innovator parent without paying the cost of innovation that Kin-directed Innovator offspring do. Figure S8*c* further confirms the trade-off between selective information sharing and the speed of CCE: when Kin-directed Innovators are less favoured in Model 2*c*, traits accumulate slower, especially when copying fidelity is less than perfect.

4. Model 3: Reputation-based partner choice

Partner choice, aka competitive altruism [38,39], involves individuals selecting interaction partners based on the partners' past history of cooperation (their 'reputation'). If individuals who cooperate are subsequently more likely to be selected as recipients of cooperation, then cooperators are paired with cooperators and free-riders are excluded. This mechanism can favour cooperation amongst non-kin as individuals compete to be the most cooperative partner and thus benefit by being chosen to receive help.

Model 3 implements partner choice as a potential mechanism for maintaining open innovation and facilitating CCE. Model 3 is identical to Model 1b except that we relabel the previously indiscriminate Open Innovators as Reputational Innovators, and modify the social learning phase. Each agent now selects n_c candidates to be learners at random from the $N-1$ other agents in the population. When $n_c = 1$ partner choice is random and should not favour information sharing. When $n_c > 1$, the candidate with the highest reputation is chosen to be the learner for that agent, who acts as the demonstrator in their interaction. The larger n_c, the stronger the partner choice. If $n_c = N-1$, then the agent with the highest reputation in the entire population is guaranteed to be picked. Once demonstrators and learners are paired up, if the demonstrator is not successfully hoarding their knowledge, the chosen learner copies each known trait of the demonstrator with probability p_c per trait. Demonstrators receive a reputation increase of r_s per trait shared. This should lead to sharing demonstrators (Reputational Innovators, Non-Innovators and sometimes Closed Innovators when $p_h < 1$) acquiring higher reputations than non-sharing demonstrators, and so in subsequent timesteps being more likely to be chosen as learners. In addition, if the demonstrator was the first agent to innovate and share that trait - i.e. they were its inventor - then the demonstrator gets an additional reputation increase of r_i per trait shared (so $r_s + r_i$ in total, where r_s and r_i are independent and additive). The r_i bonus represents the 'priority advantage' often seen for scientific or technological discovery, where originators of ideas (e.g. Newton, Edison) receive higher reputation increases for sharing what they have originated than those who share others' inventions or discoveries. Frequent fights over priority (e.g. Newton vs Leibniz; Edison vs Tesla) indicate the potential importance of priority advantage [40]. We added this assumption because it should lead to Reputational Innovators receiving higher reputations than Non-Innovators, given that only Reputational Innovators can originate (and then share) ideas.

Finally, we model two different ways in which reputations are acquired, local and global. For global partner choice, every agent has a single reputation known by every other agent in the population which is updated whenever they share knowledge with any other agent. For example, if agent i shares knowledge with agent j, then agent i's reputation increases in the eyes of all N agents in the population. This resembles reputation-based models of indirect reciprocity [41,42] where reputations are globally known, and might represent a modern situation where mass communication or the internet allows the rapid spread of reputational information. For local partner choice, every agent has a specific and potentially different reputation score for each other agent which is only updated when knowledge is shared with that specific agent. For example, if agent i shares knowledge with agent j, then only agent j increases their reputation score associated with agent i. This resembles previous models of partner choice [43], and might represent a fragmented community with infrequent, face-to-face communication.

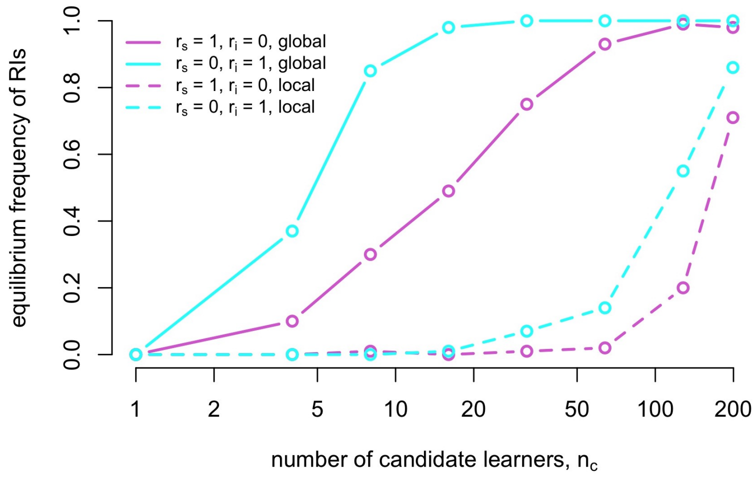

Figure 3. The proportion of 100 simulation runs in which Reputational Innovators (RIs) go to fixation, as a function of the number of candidate learners (n_c), for the case when sharing any trait yields reputation rewards ($r_s = 1$; purple lines) or when only sharing traits that that agent invented yields reputation rewards ($r_i = 1$), and for global (solid lines) or local (dotted lines) reputations. Other parameters are set to values that ordinarily favour Non-Innovators: $N = 200$, $L = 1000$, $p_c = 0.8$, $p_i = 0.1$, $p_h = 0.9$, $p_s = 1$, $b = 0.2$, $c = 0.1$, $d = 0.05$, $p_d = 0.001$.

Figure 3 shows the likelihood of Reputational Innovators going to fixation as a function of the number of candidate learners (n_c), whether reputations increase when any trait is shared ($r_s = 1$) or only traits that that agent invented are shared ($r_i = 1$), and for local vs global reputations, under parameter values that in Model 1 would have favoured Non-Innovators. As expected, when partner choice is random ($n_c = 1$), Reputational Innovators are not favoured under any condition. As n_c increases and partner choice gets stronger, Reputational Innovators are increasingly favoured. At the maximum ($n_c = N - 1$), Reputational Innovators are virtually guaranteed to go to fixation when reputations are global, and likely (but not guaranteed) to go to fixation when reputations are local. Also as expected, increasing reputations only when agents share traits that they themselves invented ($r_i = 1$) is more effective at promoting information sharing than increasing reputations due to sharing any trait ($r_s = 1$). However, even the latter still favours Reputational Innovators at high values of n_c especially when reputations are global, even though Non-Innovators can receive reputation increases for sharing Reputational Innovators' invented traits without bearing the costs of innovation. This is because while Non-Innovators initially increase in frequency due to this advantage, few new traits are then being innovated, and rare Reputational Innovators gain an advantage by sharing traits that only they know (figure S9). Finally, Figure 3 shows that it takes much higher values of n_c, i.e. much stronger partner choice, for Reputational Innovators to be favoured under local partner choice than for global partner choice. This is expected, given that localised, agent-specific knowledge of reputations acquired through direct interactions is inevitably less reliable than universally-known reputations acquired indirectly via every interaction in the population.

5. Model 4: Cultural group selection

Another hypothesis for human cooperation amongst non-kin is cultural group selection [44,45]. Generally, group selection is where groups of cooperators out-compete groups of non-cooperators. Genetic group selection is unlikely given that migration breaks down the between-group genetic variation that is required for selection to operate at the group level, and group-wide cooperation will be undermined by selection within groups for selfish free-riders. However, *cultural* group selection rests on the assumption that cultural evolution generates better conditions for group-level selection. Processes like conformity [46], punishment [47] and reciprocity [48] can maintain group-wide norms of cooperation and thus between-group variation in cooperation that is then subject to selection via direct (e.g. warfare) or indirect (e.g. economic) inter-group competition. In the context of information sharing, we might imagine groups of innovators who freely share information exclusively within their group to accumulate more beneficial knowledge, and consequently out-compete, both groups of Non-Innovators who have nothing to share and accumulate, or groups of Closed Innovators who never share information and thus fail to accumulate information.

Here we model this scenario, adapting a previous agent-based simulation of cultural group selection [47]. Assume g groups each containing n agents, giving $ng = N$ agents in total. Agents can be Non-Innovators, Closed Innovators or Group Innovators. The latter are innovators who only share traits with other members of their own group. To test the above logic, and assuming that Non-Innovators are the 'ancestral' state, we start with one group of Group Innovators, one group of Closed Innovators, and the rest (i.e. the majority) Non-Innovators. Each timestep Closed Innovators and Group Innovators innovate with probability p_i as before, then social learning occurs where each agent acquires each trait known by every non-hoarding agent in their group with probability p_c per trait. Then, following [47], there is costly punishment, an empirically supported within-group mechanism of cooperation [49,50]. Each Group Innovator reduces each Non-Innovator and hoarding Closed Innovator's payoff by u/n, and bears a cost of k/n per punished agent. Then there is payoff-biased copying of strategies as before, followed by migration. With

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probability p_m, each agent moves to a randomly chosen group, taking their traits and strategy with them [51]. Finally there is group selection. Groups are paired at random and with probability p_g enter into a contest. The group with more traits wins the contest. The losing group's strategies and traits are replaced with those of the winning group. Unlike previous models where intergroup conflict success is determined by frequencies of agent types [47], here we make the more plausible assumption that group success is determined by number of cultural traits; hence group selection does not act directly on the Group Innovator phenotype, it acts only via the Group Innovators' ability to generate and accumulate knowledge.

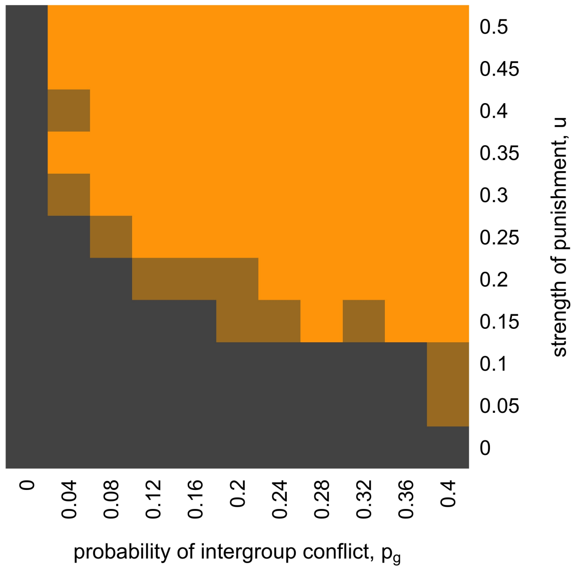

Figure 4. The frequency at equilibrium of Group Innovators in Model 4 (cultural group selection), for different values of the probability of intergroup conflict p_g, and the within-group punishment penalty u of agents with other strategies (Non-Innovators and Closed Innovators). Colours indicate the mean frequency at equilibrium of Group Innovator agents across 20 independent simulation runs; orange = frequency greater than 2/3, black = frequency < 1/3, grey = intermediate frequencies. Other parameter values: $n = 50$, $g = 20$, $L = 1000$, $p_c = 0.8$, $p_i = 0.2$, $p_h = 0.9$, $p_s = 0.2$, $p_d = 0.1$, $b = 0.2$, $c = 0.1$, $d = 0.05$, $p_m = 0.01$, $k = 0.2$.

Figure 4 shows how Group Innovators are favoured as the probability of intergroup competition p_g increases, and the fitness cost of punishment imposed by Group Innovators on the other two types within groups u also increases, given a low migration rate of $p_m = 0.01$. As in previous models [47], cultural group selection alone is not sufficient to spread group-beneficial behaviour in the face of migration. Punishment within groups is also required. Figure S10 confirms that intergroup conflict is vulnerable to migration. Figure S11 shows the effect of population structure, with information sharing (like cooperation in general) less likely to emerge in larger populations, either via the number (g) or size (n) of groups.

6. Discussion

Here we formally explored the factors that affect the cooperative dilemma at the heart of cumulative cultural evolution, as well as solutions to the dilemma borrowed from evolutionary biology. Model 1 formalised the essential cooperative dilemma of CCE: if innovation (i.e. asocial learning) is more costly than copying (i.e. social learning), then it is optimal to be the latter, an information free-rider acquiring costly information from others at no cost. Yet if everyone is copying, no-one is innovating, and CCE halts. Alternatively, innovators might try to protect their knowledge from being copied ('information hoarding'), but this again prevents the spread and accumulation of information, and CCE stops.

The notion that social learning can be seen as information free-riding has been modelled previously [14], yet not within the context of CCE where beneficial traits can accumulate over time. In fact, Model 1 found that making culture cumulative makes the informational cooperative dilemma even more pronounced. As culture accumulates, its benefits increase. As culture accumulates, therefore, information hoarders (Closed Innovators in our models) can increasingly benefit from private knowledge, out-competing Open Innovators who freely release their knowledge to others and have no private knowledge. Model 1 also shows that information hoarding is more likely to emerge when the cost of hoarding is low, and when hoarders have a high probability of successfully hoarding their knowledge. Information free-riding (Non-Innovators in our models) is more likely to emerge when innovation is costly or difficult, which reduces the fitness of both Open and Closed Innovators.

In Model 1, Open Innovators only emerge when unspecified benefits to openness outweigh the benefits of information free-riding and information hoarding. Models 2, 3 and 4 unpacked this unspecified benefit, replacing it with mechanisms known in evolutionary biology to promote cooperation more generally. Model 2 showed that kin selection can favour information sharing when that sharing is preferentially directed to kin, specifically offspring. This is because strategies and traits are inherited together: individuals who share knowledge with their kin produce offspring who inherit a propensity to share with kin and also inherit their parent's beneficial cultural traits. This resembles models of the evolution of teaching, where costly teaching is inherited together with cultural traits whose acquisition is facilitated by that teaching [18,19]. Model 2 also showed that the downside of kin-directed innovation is a notable decrease in the rate of CCE due to the reduction in effective sample size of demonstrators from potentially the entire population down to one or two parents. This reflects general findings related to population size and CCE [6,7]. This downside is particularly pronounced when copying fidelity is even slightly less than perfect, and when transmission is biparental rather than uniparental, which partially unlinks the inheritance of strategies and traits. All this suggests that kin-directed information sharing is viable, but more likely for hard-to-acquire traits that are uniparentally transmitted. This fits with empirical cases such as male-kin adze-making apprenticeships in West Papuan hunter-gatherers [4].

Model 3 showed that reputation-based partner choice is another viable solution to the informational dilemma. If sharers acquire reputations by sharing, and others preferentially direct sharing to those with high reputations, then the benefits of sharing return back to the sharer. Partner choice is more effective when high reputation individuals can be more easily identified and when reputations are global (known by everyone) rather than local (acquired via direct interaction). Such factors are more likely as populations become more interconnected and communication improves. This supports Mokyr's [8] suggestion that letter writing, postal services, the printing press and international travel led to the formation of the Republic of Letters in which open innovation bloomed during the Enlightenment. Partner choice is also more likely to favour information sharing when there is a 'priority advantage' such that the inventor of an idea receives a higher reputation increase for sharing that idea than someone who shares it second-hand and did not invent it. This sheds light on frequent and sometimes fierce priority battles in the history of science and technology [40]. Nevertheless, this was not an absolute condition, and even when reputations increased for sharing information irrespective of provenance, partner choice was still effective. Overall, the robustness of partner choice supports suggestions from historians pointing to the importance of reputation and partner choice in the emergence of open knowledge sharing in periods such as the Enlightenment [8].

Finally, Model 4 showed that cultural group selection is another viable solution to the informational dilemma. Here individuals preferentially share costly innovations exclusively with other members of their group, and groups of such group-biased innovators out-compete groups of Non-Innovators or Closed Innovators due to the former's superior culturally accumulated knowledge. However, as in previous non-informational models, cultural group selection acting alone is highly vulnerable to migration breaking down between-group variation and preventing group-based information sharers from assorting. Adding punishment greatly increases the range of conditions under which cultural group selection favours information sharing.

These findings yield several novel predictions of qualitative signatures to look for in historical and ethnographic data which may be indicative of the different cooperation mechanisms. While most complex, hard-to-acquire cultural traits are transmitted obliquely or horizontally via success or prestige biases [33–37], Model 2 suggests that where such traits *are* transmitted vertically, and especially uniparentally, we would expect to see lengthy apprenticeships that function to reduce copying error, as in the aforementioned West Papuan adze makers [4]. Furthermore, such vertically transmitted traits should accumulate more slowly than widely shared horizontally transmitted traits. While this has already been shown for non-cumulative traits [32], Model 2 shows that this also extends to CCE. Historically, we might predict an increase in the rate of CCE as societies shift from vertical transmission to mass forms of horizontal transmission such as formal education systems. Model 3 suggests that innovators should be concerned with and foster their reputations for sharing (consistent with theories of reputation management more broadly: [52]), and that reputations for sharing are associated with the preferential acquisition of knowledge from others (or potentially other benefits, such as material or financial rewards or protection from persecution). Furthermore, reputation-based partner choice should support more information sharing when reputational information is globally rather than locally known. This suggests that improvements in communication such as postal services, the printing press and the internet are important for CCE not just in facilitating the transmission of knowledge, but also in transmitting information about reputations. Model 3 also showed that priority advantage is important but not crucial for partner choice to work. While priority advantage has been explored previously [40], Model 3 suggests that non-priority-advantage reputational systems may have emerged first, followed by the more specific priority advantage, and that the shift to priority advantage is associated with increases in the rate of CCE. Model 4 predicts that any group-wide advantage due to group-directed sharing is likely to covary with within-group mechanisms of cooperation such as punishment. Potentially the latter is needed before the former, which could be tested historically. Given that migration is a major obstacle to cultural group selection working, we might also expect specific mechanisms to have evolved to deal with either the immigration of non-sharing free-riders, or the emigration of knowledgeable individuals intending to share expertise with rival groups, such as the aforementioned ban on glassmakers leaving the Venetian Republic. Finally, population size has long been known to facilitate CCE [6,7], but Model 4 suggests that large population sizes also intensify the cooperative dilemma at the heart of CCE. This might explain previous inconsistent results relating to population size and CCE. Potentially, population size might only facilitate CCE when mechanisms to ensure information sharing (e.g. partner choice, punishment) are present.

There are several limitations of our models that warrant caution in our conclusions and should stimulate further modelling work. First, we assumed for simplicity discrete behavioural strategies (Open Innovators, Non-Innovators, etc.). It is clearly unrealistic to assume that individuals either always innovate or never innovate, and always share or never share. Allowing innovation or sharing to be a continuous probability may well change the dynamics of our models, as has been found for non-informational models of cooperation [48]. Second, we implemented only a crude form of cumulative culture. In the analytic Model 1a, the benefits of knowledge increase in proportion to the amount of openly-shared knowledge. In the agent-based Models 1b-4, traits accumulate within a large trait-space that expands once 90% of traits have been discovered. More realistic implementations of CCE might allow for path-dependence and parallel lineages [3]. We might also assume that the benefit of traits reduces over time according to a discount factor such that knowledge gradually becomes out-of-date, akin to Schumpeterian 'creative destruction' [53]. Alternatively, the benefits of knowledge might increase with the number of users of that knowledge (i.e. network effects: [54]). Both of these factors might favour more open innovation than in our current models. Conversely, innovation might become harder as knowledge accumulates [55], increasing the cost of innovation over time and favouring less open innovation. Third, the cooperation mechanisms implemented in Models 2-4 are all first steps that can be extended in many ways. Kin selection in Model 2 is implemented as vertical cultural transmission, but this can be extended by incorporating non-parental kin transmission, kin competition, assortative mating and paternity certainty [31]. Model 3 could incorporate the explicit transmission and perhaps dishonest faking of reputations, while Model 4 could incorporate preferential rather than random migration [56], and other within-group mechanisms such as reciprocity [48] or conformity [46]. Fourth, while these models are generic, intended to clarify the logic of how cooperation mechanisms might apply to informational dilemmas, models might also be developed for specific historical scenarios, such as Mokyr's [8] competitive patronage hypothesis for the Enlightenment which resembles a bidirectional version of our partner choice in Model 3. Finally, an additional non-cooperative mechanism that we did not implement is information theft, where individuals might pay an initial cost, and also risk costly punishment, for accessing another individual's knowledge against their will.

The questions raised here have parallels in other literatures. In economics, endogenous growth theory views technological change as a cumulative process [23], sharing our assumptions that knowledge is nonrivalrous such that its benefits replicate rather than deplete when shared, that people behave rationally to maximise benefits relative to costs, and that knowledge is partially excludable such that innovation occurs when the benefits returned to innovators exceed the costs of innovation. However, endogenous growth theory is typically concerned with economic growth in contemporary industrialised societies rather than the broader process of CCE itself across societies and throughout history, and seldom considers mechanisms of cooperation drawn from evolutionary biology and cultural evolution theory, as we do. Elsewhere, scholars have transferred theory designed for managing material commons such as irrigation systems or fisheries to 'knowledge commons' [57], with parallels to our models. Again, however, there is little engagement with mechanisms of cooperation from evolutionary biology (although see [58]), and little formal modelling.

Analysing patent systems through the lens of cultural evolution is a fruitful avenue for future research. Patent systems can be seen as culturally evolved, legally enforced institutions for solving the problem of information free-riding in capitalist societies. They work by giving innovators exclusive rights to an innovation's use, or a share in the profits from that innovation, for a fixed time period. Yet patents come with a fundamental trade-off [10]: longer patents provide higher incentives to innovators so make innovation more likely, facilitating CCE, yet longer patents also prevent other innovators building on the patented knowledge, inhibiting CCE. There is no theoretical or empirical consensus on how this trade-off can be optimally balanced [11]. In our models, Closed Innovators are essentially permanent patent-holders, so time-limiting their ability to hoard information could provide a way to incorporate patents into our framework. The priority advantage in Model 3 where only the first inventor of a trait gets a reputational reward also resembles the patent system, where likewise only the first to patent an idea receives benefits [59]. Unlike patents, however, there is no trade-off inherent in reputation-based priority advantage systems, where ideas or discoveries can be immediately used or learned by others [59].

In conclusion, our models clarify the exact nature of the informational dilemma at the heart of CCE - information free-riding and information hoarding - and present potential mechanisms known from evolutionary biology that might solve this dilemma in different ways. We hope that these simple models will stimulate further modelling and empirical work to further identify the conditions under which information is likely to be shared or hoarded, and the consequences for cumulative cultural evolution.

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