Optimal population turnover regimes for cultural evolution depend on network size, density and behavioral transmissibility

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Abstract

Culture's substrate is the social network, linking social factors and dynamics to cultural evolution in a variety of ways. Yet while extensive attention has been given to the effects of population size and network structure, little is known of the effect of population turnover—the cyclic replacement of individuals in fission-fusion social systems. Here, we present a generative model to explore how population turnover affects a core criteria for cultural evolution, the selective retention of more adaptive traits. We let a novel, high payoff behavior compete against an established, low payoff behavior in populations of networked agents who can socially learn behavior and make behavioral decisions. We simulate this process across different turnover regimes, varying the intervals between replacement events and the number of agents replaced. We find that there are optimal turnover regimes that promote selection for higher payoff behaviors beyond what's possible in static populations. The optimal regime depends on network size, density, behavioral transmissibility, as well as characteristics of the learners. Our model demonstrates that information loss, combined with the enhanced ability of incoming naive agents to sample the behavior space, are key mechanisms that link turnover to cultural outcomes. Our study provides theoretical support and predictions for the important role of naive learners for cultural evolution, identified by previous experimental studies.

1 Introduction

The capacity for culture, broadly defined as socially learned traits that persist over generations, is widespread across taxonomic groups [1, 2], including birds [3], cetaceans [4, 5] and primates [6]. Culture exhibits key features of Darwinian evolution (variation, competition, inheritance) and cultural traits can change over time to become more adaptive in a process of cultural evolution [7, 8, 9, 10, 11]. The adaptive plasticity made possible by cultural evolution [12, 13] is often cited as the defining reason behind human success in the occupation and exploitation of the planet's niches [14, 15, 16, 11]. However, the past decade of evidence has shown that cultural evolution can occur in non-human animals, as well [11, 17].

Critical to the adaptiveness of culture is the selective retention of higher payoff behavior, or cultural selection [18, 11]. The exploration of mechanisms that allow improved variants supplant established behaviors has often centered on the evolution of specialized transmission biases [19, 20, 21, 22], teaching and high-fidelity transmission [23, 24, 25], or meta-cognitive abilities [26, 27]. Yet cultural selection can also rely on simpler mechanisms present "for free" as part of the phenotypes of many social species, such as the introduction of naive learners through a general social process of population turnover [28, 29, 30], and the reinforcement learning that occurs during the maintenance of socially acquired behavior [31, 32]. To date, hypotheses linking population turnover to cultural evolution have relied on verbal models drawn from limited experimental data. In this study, we use a mechanistic computational model to conduct a theoretical exploration of turnover, with the aim of providing robust predictions under minimal assumptions.

As culture persists through social networks, it is widely recognized that social structure and processes influence many aspects of cultural evolution [33, 34]. Recently, more attention has been given to social processes, such as demographic structure, immigration and population growth. In age-structured populations, different social learning strategies such as copy-the-young or copy-the-old, can evolve depending on environmental variability [35]. In evolutionary linguistics, social processes such as immigration and population growth have also been linked to the reduction of morphological diversity [36, 37, 38, 39], as new learners provide selection pressure for simpler, more structured languages. Despite the critical role that new generations of naive learners have been hypothesized to play in cultural evolution [40], population turnover, or the gradual replacement of individuals in a population, is perhaps one of the most understudied social processes in the field. Turnover may be caused by movement between social groups, or fission-fusion dynamics, which is a common feature of nearly all animal social systems [41, 42]. Further, cultural diffusion experiments are often designed to include the introduction of naive learners (reviewed in [43, 44]) through transmission chains of individuals or groups, but the rate or magnitude of replacement is not varied. Prior computational models have implemented population turnover (e.g. [45, 46]), but similarly as a necessary requirement for cultural transmission, not the object of study. Additionally, these explorations of the topic have remained limited to human behavioral contexts. Thus, it is of great importance to further our understanding of how turnover may influence cultural evolution in socially learning species, given its ubiquity in social species and central role in cultural evolution.

To our knowledge, there have been only 3 empirical studies that have explicitly investigated the effect of turnover on animal culture. First, Blue-headed wrasse (*Thalassoma bifasciatum*), a species that culturally inherits spawning sites, chose more suitable spawning sites when populations were entirely replaced by naive individuals [28]. These sites were chosen again after a second replacement event [47], suggesting that the original preferences were the sub-optimal result of cultural inertia. Another study found that successive replacement of pairs of homing pigeons (*Columba livia*) increased route efficiency [29]. Finally, our recent study directly compared static and turnover micro-populations of captive great tits (*Parus major*), showing that turnover populations were much more likely to adopt a more efficient foraging behavior over an established, inefficient tradition [30]. These studies hypothesized that naive individuals introduced new innovations [29], or improved the sampling of behavior space [28, 47, 30]. However, these were proposed hypotheses drawn from experimental data. To our knowledge, no theoretical work exists that explores turnover.

In order to better understand how turnover might affect cultural evolution, we used a computational model to explore the effect of turnover in structured populations. We simulated the diffusion of a novel, higher payoff behavior, which competed against an established, low payoff behavior. We varied two parameters of turnover: the magnitude, or what percentage of the population was replaced, and the tempo, or how frequently replacement events occurred. We varied network size, density, the transmissibility of behaviors, as well as the rules that agents used to make behavioral decisions, with the expectation that the effect of turnover might depend on these variables. We found that as turnover changed the overall composition of populations, it changed the composition of repertoires in the population, as well as agents' beliefs about their own behavioral choices. These changes could lead to positive, negative or neutral consequences for the relative proportion of adaptive behavior that a population used, compared to static populations. Our model

illustrates how cultural selection does not necessarily need to occur between individuals, but can occur within individuals, assuming that they learn from reward.

2 Methods

Our model simulated dynamic social networks of size N, populated by socially learning agents. Agents present in the first time-step were initialized with knowledge of a low-payoff behavior a, which was intended to represent an established tradition. In each time-step, agents could acquire knowledge about a novel high-payoff behavior b, and also chose one behavior from their repertoire to produce, for which they received a payoff ($\pi_a = .5$ or $\pi_b = 1$). We manipulated population turnover by either leaving populations as static, or by replacing a certain number of agents (turnover magnitude) at a set interval (turnover tempo). Each combination of turnover magnitude and tempo was a turnover regime. Agents were replaced by naive agents, who had no knowledge of a or b, with a probability proportional to their age. These naive agents inherited the network connections of the agent that they replaced. To understand the cultural dynamics that emerged from different turnover regimes, over the course of the $5{,}000$ time-step simulation we measured behavioral frequencies, repertoire states, and the expected payoffs that agents held about the behaviors in their repertoire.

Our model was adapted from our previously described generative agent based model of cultural evolution that linked a sub-model of acquisition with a sub-model of behavioral production [32]. We assumed that agents could acquire knowledge of behaviors either through asocial innovation, or from observation of neighboring agents, defined by a social network, via a process of social transmission. Acquisition was conditioned on association and production: the more productions of a novel behavior an agent observed, the more likely it was to acquire knowledge of that behavior. When choosing which behavior to produce, agents were reinforcement learners, and chose behaviors from their repertoire depending on personal information (previously received payoffs), as well as social information (observation of neighbors). The equations of both sub-models are defined below, with further detail in Chimento *et al.* [32].

2.1 Sub-model of acquisition

Each time-step, an agent i could independently innovate or socially learn behavior a or b from their neighbors, as defined by the social network. This probability of acquisition was defined by Equation 1, where it was influenced by a base learning rate (λ) and a transmission function T that accounted for the associates of i defined by the social network (binary vector a_i where $a_{i,j} = 1$ if associated, else 0) and their behavioral productions ($w_k(t)$) where $k \in \{a, b\}$.

$$P(\text{individual } i \text{ acquires } k|t) = 1 - exp(-\lambda(T(a_i, w_k(t)) + 1)) \tag{1}$$

The $+1$ accounts for asocial innovation of the behavior by an agent. We were primarily interested in cultural behaviors spread by social transmission, so we set the probability of independent innovation to a very low value for both behaviors ($\lambda = 0.001$, resulting in innovation probability of $.00099$ per time-step). The transmission function T (Equation 2) contained the social transmission rate s, which defined how easily an agent might socially acquire knowledge of a behavior (transmissibility). This multiplied the sum of associates' behavioral productions, defined by transmission weight $w_{k,j}(t)$.

$$T(a_i, w_k(t)) = s \sum_{j=1}^{N} a_{i,j} w_{k,j}(t) \tag{2}$$

The transmission weight (Equation 3) was the proportion of an agents productions that were of behavior k over memory window m. If an agent j produced only behavior b for the last m, timesteps, $w_{b,j}(t) = 1$

$$w_{k,j}(t) = \frac{\sum_{r=t-m}^{t} n_{k,j}(r)}{m} \tag{3}$$

The transmission weight was an important connection between the sub-model of acquisition and the sub-model of behavioral production. The acquisition of behavior depended on agents observing its production, with more frequent productions resulting in a higher probability of acquisition.

2.2 Sub-model of behavioral production

The production sub-model was adapted from Experience Weighted Attraction models [48], a extended reinforcement learning model that has been commonly used in social learning studies [49, 50, 51, 52]. It assumes that behavioral choices depended on personal experience of payoffs from behaviors, as well as social information observed from their neighbors.

In each time-step, agents produced one behavior k from their repertoire using the sub-model of production, for which they received a payoff π_k. Their convex combination was recorded as $E_{i,k}(t)$, representing an agent's current expected payoff for behavior k.

$$E_{i,k}(t) = \rho\pi_k(t-1) + (1-\rho)E_{i,k}(t-1). \tag{4}$$

In the first time-step of the simulation, all agents in all conditions were assumed to be knowledgeable of the low payoff behavior, yet held no expectations about its payoff $E_{i,a}(0) = 0$. One agent j was seeded with knowledge about high-payoff behavior b to eliminate noise at the beginning of simulations due to stochastic innovation events. This seed agent held $E_{j,b}(0) = 0$, giving it an equal chance of producing either behavior. In turnover conditions, naive agents entered populations without knowledge of either behavior. Upon acquisition of behavior k, $E_{i,k}(t_{acq}) = 0$, conservatively assuming that agents did not attend to payoffs before acquisition, and held no prior expectations about the payoff. For agents that held two behaviors in repertoire, the behavior that was not chosen in a given timestep was updated with $\pi_k = 0$, allowing for information loss over time.

Using a softmax function, expected payoffs were transformed into values between 0 and 1, which represented the probability of producing a behavior in the absence of social information. α determined the risk-appetite of the agents. If $\alpha < 1$, agents were risk-averse, and would prefer to produce the behavior for which they held the highest expected payoff. If $\alpha > 1$, agents were risk-tolerant, and would engage in exploratory sampling of behavior, insensitive to expected payoffs. When $\alpha = 1$, agents were linearly sensitive to differences in expected payoffs. When agents knew only 1 behavior k, $I_{i,k}(t) = P_{i,k}(t) = 1$.

$$I_{i,k}(t) = \frac{exp(\alpha^{-1}E_{i,k}(t))}{\sum\limits_{k\in Z_i} exp(\alpha^{-1}E_{i,k}(t))}. \tag{5}$$

In cases where agents have observed neighbors' behaviors, these social observations are factored into the decision of an agent. For each behavior k in an agent's repertoire, the agent calculated the proportion of all observed behaviors from neighbors defined by $a_{i,j}$ that were of k over memory window m.

$$S_{i,k}(t) = \frac{\sum\limits_{j=1}^{N} a_{i,j} \sum\limits_{r=t-m}^{t} n_{k,j}(r)}{\sum\limits_{k\in Z_i}\left(\sum\limits_{j=1}^{N} a_{i,j} \sum\limits_{r=t-m}^{t} n_{k,j}(r)\right)}. \tag{6}$$

Lastly, both personally experienced payoffs $I_{i,k}(t)$ and socially observed information $S_{i,k}$ were placed in a convex combination to produce the final choice probability $P_{i,k}(t)$ for each behavior in repertoire.

$$P_{i,k}(t) = (1-\sigma)I_{i,k}(t) + \sigma S_{i,k}(t) \tag{7}$$

2.3 Measurements and conditions

We manipulated the magnitude of turnover T_m from 0% of the population to 50% of the population: $T_m \in \{0, 0.0625, .125, .1875, .25, .3125, 0.375, .4375, .5\}$. We also varied the tempo of turnover T_t: $T_t \in \{5, 10, 20, 40, 80, 160\}$. Turnover regimes with a magnitude of 0 were static populations. In total, we tested 49 different combinations of turnover magnitude and tempo (including the static condition).

We tested random regular networks with a size of N agents, each with fixed degree k. We chose random regular architecture because degree was important to standardize between agents, as it directly influenced the probabilities calculated in the sub-model of acquisition (Equation 2). We tested 3 populations sizes ($N \in \{16, 32, 64\}$ along with 3 levels of network density by changing the relative proportion of k against N ($k \in \{.125N, .25N, .5N\}$). For example, a network with $N = 32$ and $k = .25N$ yielded $k = 8$—a comparable density to a network where $N = 16$ and $k = .5N$, and $N = 64$ and $k = .125N$. This allowed us to compare network sizes while controlling for density, and vice-versa. We also varied the transmissibility of behaviors, or how easily an agent could socially acquire either the novel or established behavior ($s \in \{5, 10, 20\}$).

Finally, we tested the effects of turnover across several different types of decision-making rules, as defined by the sub-model of behavioral production. Our reference setting was parameterized such that recent and past personal experience were weighted equally ($\rho = 0.5$), agents were risk-neutral ($\alpha = 1$), and personal and social information were weighted equally ($\sigma = 0.5$). We tested 3 other parameterizations of decision making rules: 1) Agents were strongly biased towards past information ($\rho = 0.01$) and learned the expected payoffs of either behavior very slowly; 2) Agents ignored any social information in their decisions ($\sigma = 0$) and only considered personal experience; and 3) Agents were risk-averse ($\alpha = .5$) and strongly preferred the behavior with a higher expected payoff.

In order to understand the effect of turnover on cultural evolution, we conducted a sensitivity analysis in which we varied one parameter at a time, while holding all others at the reference setting. Our reference setting was

$$T_m = .25; T_t = 20; N = 32; K = .25N; s = 10; \rho = 0.5; \alpha = 1; \sigma = 0.5. \tag{8}$$

For each of the $10,584$ points in parameter space described above, we recorded 100 simulations, each of which ran for 5000 time-steps. At each time-step, we recorded behavioral frequencies, agents' repertoires, and agents' expected payoffs ($E_{ik}(t)$) about the behavior in their repertoires. Throughout the results, we assumed that distributions of values were not necessarily normal, and thus report the median and $Q1$, $Q3$ values.

3 Results

We first explored the simulation dynamics of static populations as the baseline for comparing all other turnover regimes against. In the static condition under the reference setting (Equation 8), the novel behavior diffused to all individuals in a population with a median [Q1,Q3] of $278\,[249,308]$ time-steps. During the final 1000 timesteps of the simulation, the novel behavior represented a median proportion of $.594\,[.531,.656]\%$ of all behaviors produced. This value was similar across all parameter constellations where the production parameters were not manipulated (range: $56.2 - 62.5\%$). Agents' median expected payoffs from behaviors a and b were $0.204\,[0.182,0.226]$ and $0.593\,[0.548,0.636]$, respectively. These were lower than the true payoffs due to information loss when one behavior was chosen over the other (Equation 4).

3.1 The effect of turnover magnitude and tempo

We then explored how altering turnover magnitude and tempo influenced simulation dynamics (detailed summary in Table S1 and Table S2). At the reference constellation, holding tempo at $T_t = 20$, we found that the average proportion of high payoff behavioral productions increased as magnitude increased, although this relationship was quadratic with a maximum at $T_m = .25$. At this maximum, the high payoff behavior represented a median of proportion of $0.95\,[0.862,1]\%$ of all behaviors produced within the final 1000 timesteps of simulation (Figure 1A). The next highest proportion was found at $T_m = 0.3125$ at 94%. Generally, for a given tempo, there were several magnitudes that resulted in similar behavioral proportions. At the reference level, all magnitude values yielded a larger percentage of the high payoff behavior on average compared to static (range: $.625 - .950\%$). While holding magnitude constant at $T_m = .25$, we observed a similar pattern of increasing proportion of high-payoff behaviors as tempo increased, with a maximum at $T_t = 20$ (Figure 1B). If tempo was slow enough, populations could experience higher magnitudes with no detrimental effect (see Figure 2, reference panel where $T_t = 160, 80$). However, this benefit quickly diminished as the tempo continued to increase. Agents were simply not present in the population for long enough to acquire either behavior, and cultural extinction frequently occurred.

To better understand the mechanisms that allowed for this relationship between turnover and group behavior, we explored the knowledge states of agents: their repertoire, and the expectations they held about behaviors in their repertoire. In static populations, 100% of agents were behaviorally polymorphic (knew both behaviors). As magnitude or tempo increased towards their optimal values, the proportion of high-payoff monomorphic agents (only knew behavior b) increased, with a maximum of $.594\,[0.469,0.719]$ at optimal values of magnitude and tempo (Figure 1C, D). By contrast, the median numbers polymorphic and of low-payoff monomorphic agents (only knew behavior a) remained low. There were 3.8 times as many high-payoff monomorphic agents as there were polymorphic agents, which was the largest difference across all other magnitudes and tempos. These changes to the composition of the population increased the probability of producing the high-payoff behavior at any given timestep, which in turn increased its probability of acquisition.

As turnover magnitude and tempo reached more extreme levels, the proportion of polymorphic agents and high-payoff monomorphic agents fell. Interestingly, the proportion of low-payoff monomorphic agents began to rise. This was caused by two reasons: 1) the rare independent innovation and subsequent diffusion of the

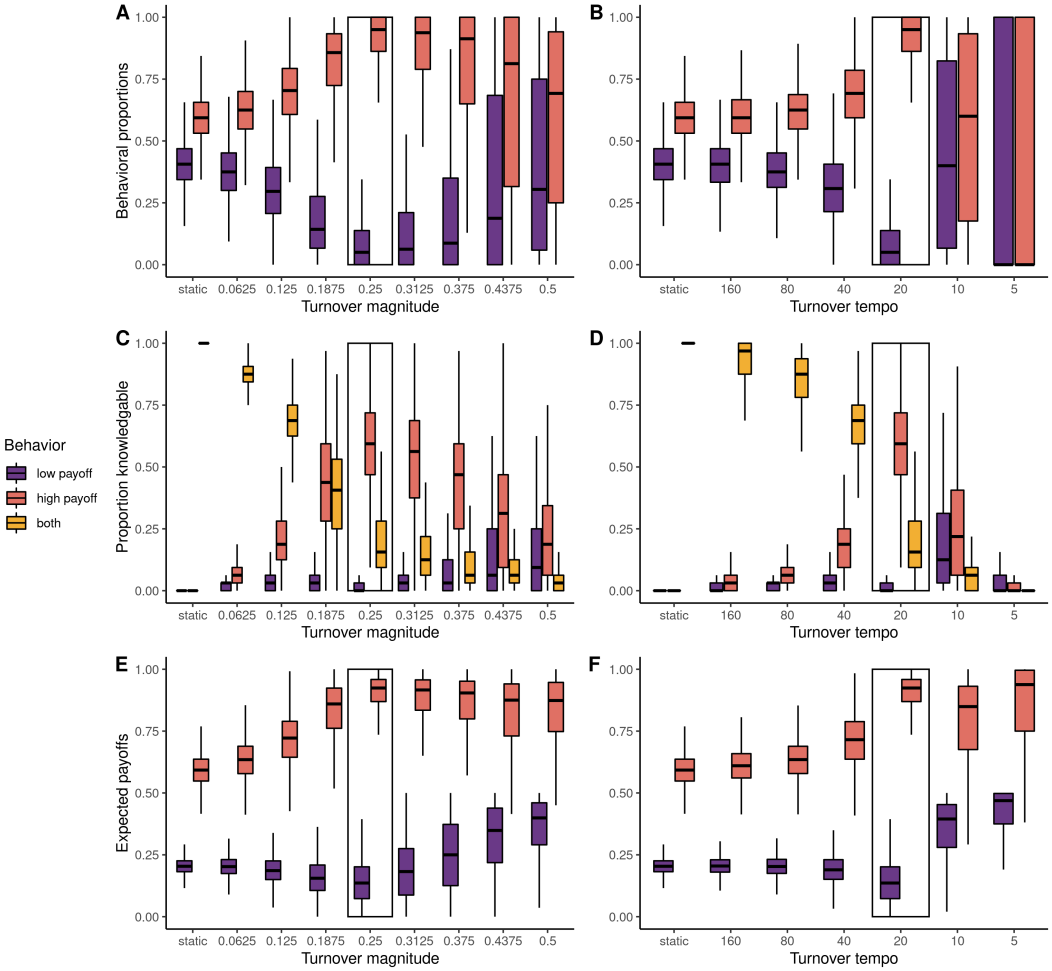

Figure 1: **Turnover acts on culture through information loss**. Comparison of distributions of 3 key metrics from the final 1000 timesteps: behavioral productions, percent of agents that were knowledgeable, and expected payoffs ($E_{ik}(t)$). Rectangles indicate optimal turnover regimes given the respective reference levels. **A, B)** Comparison of the distributions of behavioral productions of low-payoff a (purple) or high-payoff behavior b (salmon). Tempo is held at 20 timesteps, the optimal magnitude, as measured by the largest proportion of high-payoff behaviors produced is found at $.25 * N$, and vice-versa. **C, D)** Comparison of agents knowledgeable of a only (purple), b only (salmon), and both behaviors (yellow). As turnover magnitude and turnover tempo increased, the number of individuals which know both behaviors in any given time-step decreased. The peak spread between these two values was found at the optimal magnitude and tempo, with few individuals knowledgeable about a. **E, F)** Comparison of expected payoffs that knowledgeable agents held about either behavior. Turnover influenced the beliefs of knowledgeable agents. Highest expected payoffs of b and lowest expected payoffs of a were found at optimal regimes. This was driven by the high proportion of individuals who only knew b, and the social influence they exerted on those who knew both.

low-payoff behavior to completely naive agents, and 2) the properties of reinforcement learning over short time periods. Under strong turnover regimes, the two behaviors became more competitive against each other because knowledgeable agents spent less time in the population and had less experience with either behavior. They therefore weren't able to fully learn their expected payoffs.

We also measured the expected payoffs that knowledgeable agents attributed to either behavior (Figure 1E, F). At optimal magnitude and tempo, agents held elevated expectations about the high-payoff behavior ($E_b = 0.924\,[0.869, 0.959]$) and diminished expectations about the low-payoff behavior ($E_a = 0.136\,[0.073, 0.201]$), compared to static populations. We measured the expected payoffs of agents in each knowledge state (summarized in Table S3) to determine whether monomorphic agents or polymorphic agents were driving these exaggerated expectations. Interestingly, the expectations of polymorphic agents about behavior b were more exaggerated than high-payoff monomorphic agents. At optimal turnover levels, polymorphic agents held a median expected payoff $E_a = 0.023\,[0.007, 0.053]$ of the low-payoff behavior, and $E_b = .921\,[0.861, 0.958]$ of the high-payoff behavior. High-payoff monomorphic agents held relatively lower expectations of the high-payoff behavior $E_b = 0.714\,[0.616, 0.806]$. After acquiring b, they frequently transitioned to polymorphic repertoires before they could have learned the true expected payoff. Low-payoff monomorphic agents held lower expectations of the low-payoff behavior, compared to polymorphic agents ($E_a = 0\,[0, 0.09]$). The acquisition probability

of a was low given its infrequent production relative to b, and these agents were likely being replaced shortly after acquiring a, or transitioning to polymorphic. Thus, the effect of turnover on expectations was driven by the slow transmission of the low-payoff behavior relative to turnover tempo, as well as the transition of high-payoff monomorphic agents to polymorphic agents. High-payoff monomorphic agents' experience with b gave the novel behavior a competitive edge against the low-payoff behavior once agents had become polymorphic.

3.2 Optimal turnover regimes depended on network structure, transmissibility and production rules

We then looked across all of the combinations of magnitude and tempo to assess the relative efficiency of each regime compared to static populations. Of the 48 regimes tested at reference level, we found that 18 regimes obtained a higher relative efficiency than static populations, 10 regimes performed similarly to static, and 10 obtained a lower relative efficiency (Figure 2A). The general pattern was that regimes with slow tempos and low magnitudes resulted in equivalent relative efficiency to static populations. Relative efficiency of regimes increased as magnitude and tempo increased to a certain threshold, with faster tempos required when magnitude was small, and larger magnitudes when tempo was slow. Beyond this threshold, the relative efficiency began to drop to equivalent levels found in static populations. Regimes with large magnitudes and fast tempos resulted in very poor performance, especially when tempo was fastest.

The thresholds for the transitions between neutral, optimal and sub-optimal relative efficiency depended on three variables: network size, density and transmissiblity (Figure 2B, C, D). Fast tempos were most detrimental in small networks, sparse networks, and for behaviors which were difficult to socially learn. Large networks, dense networks and easily learnable behaviors all increased the number of turnover regimes that a population could undergo without negative performance compared to static populations. Additionally, the benefits of optimal regimes improved under these same conditions. However, with the exception of network size, these conditions also increased the tempos required to out-perform static populations.

There were two underlying reasons for these effects. Network size determined the amount of memory available within a population. Altering the size changed the probability of behavioral extinction, with a larger risk of extinction in smaller networks. When tempo was faster, agents were less likely to have innovated in their lifetime. Altering network density indirectly increased the transmissibility of behavior. The more associates any agent had, the more likely they were to observe either behavior, which increased the rate of social transmission. Of course, directly increasing the transmissibility of the behavior via the social learning rate also hastened acquisition by naive agents (NB: this parameter did not increase the probability of independent innovation). Regardless of the mechanism, if behaviors were more easily acquired, populations were more resilient against effects of extreme turnover regimes.

Finally, the flexibility of our production sub-model allowed us to test the effect of turnover on different types of learners. Populations composed of risk-averse agents obtained the largest number of optimal regimes (33/48), as regimes that obtained neutral effects on relative efficiency at reference level became beneficial (Figure S2B). Populations that were strongly biased towards past information ($\rho = 0.01$), and populations that ignored social information in production decisions ($\sigma = 0$) still saw benefit from turnover, although the levels of relative efficiency of optimal regimes were lower than reference (Figure S2C,D).

4 Discussion

In summary, our results demonstrated that turnover increased the rate of cultural evolution in populations with competing cultural variants. There were optimal regimes of turnover, given network size and density, and given the transmissibility of behavior. However, turnover was a double-edged sword, with strong turnover regimes also causing rapid repertoire loss. We identified two key mechanisms by which turnover influenced cultural evolution: loss of repertoire and of expectations. Under optimal regimes, naive agents were more likely to acquire the high-payoff behavior only. If they eventually acquired both behaviors, they would maintain a lower expected payoff for the low-payoff behavior. This would cause them to produce the low-payoff behavior less, further increasing the probability of naive agents acquiring the high-payoff behavior. Thus, a process of internal selection via reinforcement learning during maintenance [31], modulated by population turnover, led to cultural selection of the more efficient behavior. Under strong turnover regimes, by contrast, rapid repertoire loss was caused by a change in composition of the population from polymorphic, where a majority of individuals knew both behaviors, to monomorphic, where individuals only knew one behavior. This fragmentation of the population appeared similar to information gerrymandering [53], although resulted from the social process of replacement rather than assortativity, and resulted in a diminished carrying capacity for cultural traits.

Our findings provide theoretical support for the hypothesis that naive individuals can drive the cultural evolution of efficiency simply by being "better" samplers, overcoming the cultural inertia of knowledgeable individuals [28, 47, 30]. This is a generalizable prediction, as our model did not assume any particular social learning mechanism, and could represent anything from enhancement to imitation [54]. Importantly, this does not oppose the hypothesis that naive incomers introduce innovations[29], and both mechanisms might operate depending on the behavioral context. In our model, each simulation contained one knowledgeable seed agent to control for innovation timings, and the probability of asocial innovation was equally low for residents or immigrants. An alternative model would be where the probability of innovation decreased with time spent in the population. Such a case would increase the relative advantage of turnover populations against static populations, since if innovation did not occur quickly, it would become increasingly unlikely that static populations would ever innovate. Populations which underwent turnover would also be more likely to continue to innovate if there were more than two behaviors, and extirpation of the least rewarding behaviors would occur at a faster rate. Additionally, our hypothesis complements, rather than contrasts, the hypothesis that informational cognitive biases of naive learners, such as a bias for simplicity, shape the evolution of cultural

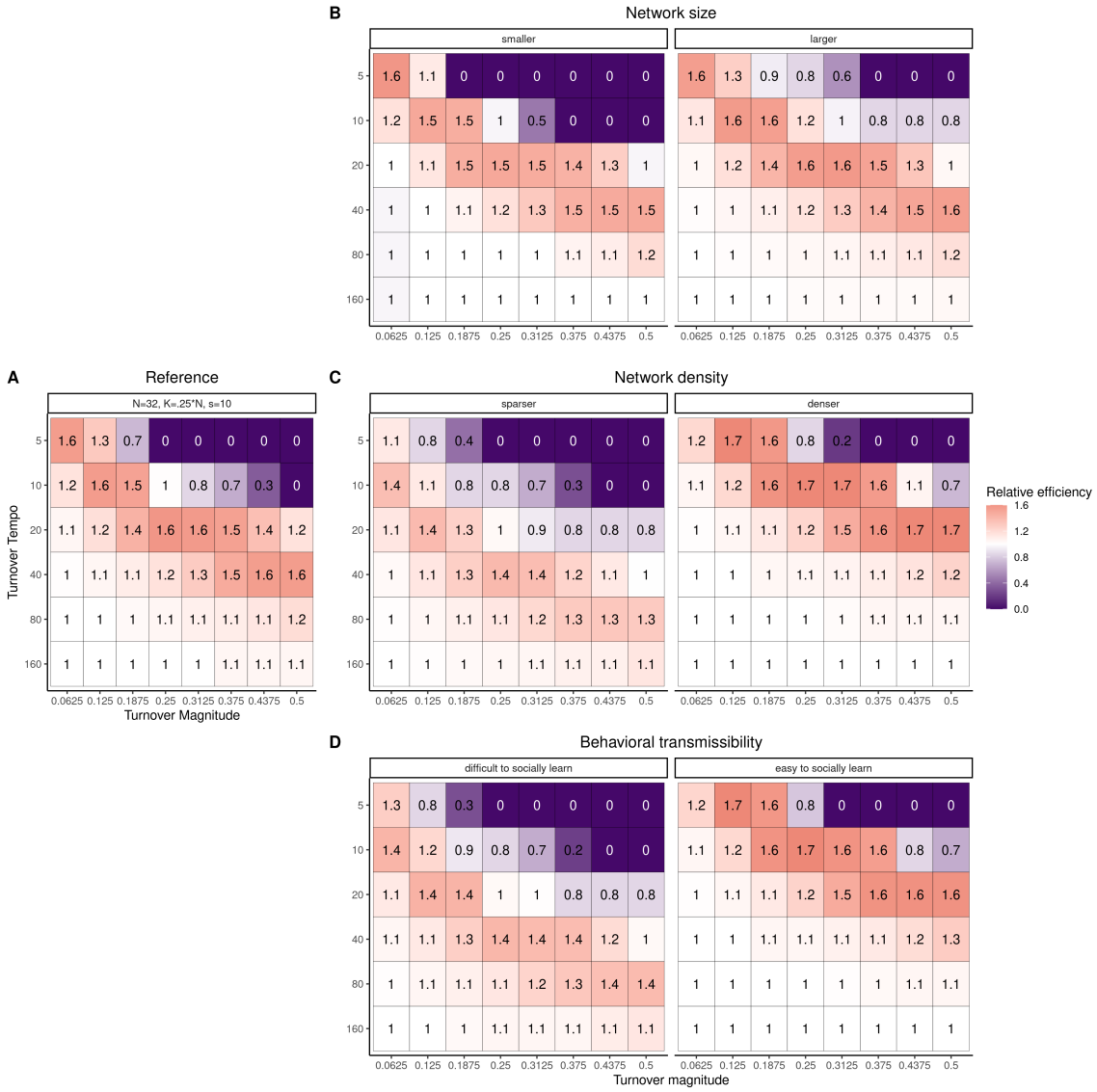

Figure 2: **Optimal turnover regimes depended on network size, density, and transmissibility of behavior.** Relative efficiency (fill, label) shown for each turnover regime: the combination of turnover magnitude (x-axis) and turnover tempo (y-axis). Relative efficiency was measured against the proportion of b produced by the static populations under a given condition, where the color white is equivalent performance, salmon is over-performance and purple is under-performance. Smaller, sparser networks, and cases where behaviors are not easily transmissible were less tolerant of turnover, yielded less benefit from optimal regimes and under-performed under a larger number of regimes. The opposite was true of larger, denser networks with more transmissible behaviors. A larger number of turnover regimes also yielded equivalent performance to static networks.

traits, studied in the context of language [55, 56, 57], music [58, 59, 60] the evolution of technology [61]. We did not implement any type of cognitive bias towards one behavior or the other, yet one could imagine that the expression of any latent informational bias would be amplified in the absence of preferences developed through reward or punishment.

Our agents did not inherit knowledge from replaced individuals, and fitness levels did not influence probabilities of replacement. We therefore suggest that our model's predictions be interpreted as applying to intra-generational time-scales of animals who exhibit fission-fusion social systems, such as passerine birds [62]. Not only can fission-fusion benefit the initial diffusion of a novel behavior [33, 63], but we have demonstrated how it can result in cultural selection. We did not consider migration between multiple populations in the current model (as in Somveille et al. 2018 [64]), yet it is predictable that the risk of cultural extinction might be mitigated by population mixing via fission-fusion. Movement between populations would distribute behavioral information over larger portions of the population, buffering against acute cultural extinction. This decentralization of repertoire merits further exploration.

However, our results do allow us to speculate on the effects of turnover at evolutionary time-scales. The capacity for horizontal cultural transmission is an adaptive strategy in environments that vary over larger time-scales relative to generation times (i.e. red noise environments)[65, 66]. Population turnover could therefore be most beneficial for cultural species in the relatively stable periods in-between large environmental changes. Interestingly, fission-fusion dynamics have also been predicted to evolve in such cases of "white noise" variability, when there is predictable temporal variation paired with intermediate levels of spatial variation [42]. The loss of polymorphic individuals under strong turnover regimes could lead to traps at longer time-scales, especially if behavior is costly to acquire (either socially or asocially) or if there is no long-term retention of information, e.g., via vertical transmission. In such a case, populations could be composed of monomorphic individuals who are best fit the previous environmental state. Despite this, drastic turnover can still improve fitness when the reinvention of behavior is cheap and obligatory, as illustrated by the example of naive blue-headed wrasse choosing more optimal spawning sites, overcoming cultural inertia [28, 47]. While we did not directly test the performance of populations in variable environments, this would be a fruitful future direction for the model.

Stable social groups and longer memories have been hypothesized to be more adaptive in variable environments, as they allow for the accumulation of rare but important knowledge, such as in matriarch elephants [67], and give ample opportunity for the social transmission of complex behaviors [17]. However, such species are also often characterized by behavioral conservatism [5, 68, 69, 70, 71], and may make maladaptive, conserved decisions, especially when innovation is costly [66, 72]. This conservatism may be detrimental to the diffusion of novel behavior [32], and even if some individuals possess a large repertoire of behavioral knowledge, the realized usage of such knowledge might be constrained by conservative decision-making rules [32]. Importantly, we have shown that in populations of risk-averse learners, even weak regimes of turnover can be as beneficial as stronger regimes in the short-term. This supports the hypothesis that population turnover is a key mechanism of cultural evolution in behaviorally conservative species [30].

Intra-generational turnover is commonly found in many species via fission-fusion dynamics [41], and the introduction of naive learners is a common occurrence in such a social system. The transmission of behavior to naive learners is an essential part of cultural evolution [40], yet population turnover has not often been the object of study itself. Our results suggest that turnover is an important mechanism of cultural evolution, as much so as the better studied social factors of population size [73] or network connectivity [74]. Optimal turnover regimes could lead to cultural selection without transmission biases or meta-cognition about the choice of demonstrators [26, 27, 20, 75]. However turnover can also constrain the carrying capacity for culture, and lead to extirpation. We demonstrated these beneficial and detrimental effects of turnover with the minimal assumptions that 1) agents could learn from reward, and that 2) the transmission of a behavior depended on the number of associates and the frequencies of their productions. Thus, we suggest the prediction that naive learners can drive cultural selection is broadly applicable across species that can socially learn novel behavior.

5 Data Availability

Code and data for statistical analyses and main text figures, as well as code to replicate the agent based model is available at `https://github.com/michaelchimento/turnover_abm`, to be made publicly available upon acceptance.

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7 Author Contributions

Conceptualisation, M.C., L.M.A.; Methodology, M.C.; Software, M.C.; Investigation, M.C.; Resources, M.C.; Writing - Original Draft, M.C.; Writing - Review & Editing, M.C., L.M.A.; Visualization, M.C.; Supervision, L.M.A.; Funding Acquisition, L.M.A.

8 Competing Interests

The authors declare no competing interests, financial or otherwise.

9 Materials & Correspondence

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