

1 **High-magnitude innovators as keystone individuals in the evolution of**
2 **culture**

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24 **Abstract**

25 Borrowing from the concept of keystone species in ecological food webs, a recent focus in
26 the field of animal behaviour has been keystone individuals: individuals whose impact on
27 population dynamics is disproportionately larger than their frequency in the population. In
28 populations evolving culture, such may be the role of high-magnitude innovators:
29 individuals whose innovations are a major departure from the population's existing
30 behavioural repertoire. Their effect on cultural evolution is twofold: they produce
31 innovations that constitute a 'cultural leap', and, once copied, their innovations may induce
32 further innovations by conspecifics (socially induced innovations), as they explore the new
33 behaviour themselves. I use computer simulations to study the co-evolution of independent
34 innovations, socially induced innovations, and innovation magnitude, and show that while
35 socially induced innovation is assumed here to be less costly than independent innovation,
36 it does not readily evolve. When it evolves, it may in some conditions select against
37 independent innovation and lower its frequency, despite it requiring independent
38 innovation in order to operate; at the same time, however, it leads to much faster cultural
39 evolution. These results confirm the role of high-magnitude innovators as keystones, and
40 suggest a novel explanation for low frequency of independent innovation.

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47 **Introduction**

48 The concept of keystone species, originally suggested by Robert Paine to describe species
49 whose impact on their ecosystem is much greater than their part in it [1–3], has been
50 recently adopted by animal behaviour researchers, to describe individuals whose impact
51 on the population they live in is much greater than their proportion in it, and whose
52 removal from the population would result in a profound and lasting effect on group
53 dynamics [4]. While the general concept is relatively new, effects of such individuals have
54 been noted and documented over decades and across social species, by more situation-
55 specific titles, such as dominants, tutors, or leaders (see detailed review in Modlmeier et al.
56 2014). Recent studies utilizing the keystone individuals concept have shown, for example,
57 that the presence of a few bold individuals in colonies of social spiders, and the quality of
58 the knowledge these individuals possess affects the colony's foraging behaviour and
59 success [5,6], and that an ant colony's nest site selection is faster and more accurate when
60 it includes highly exploratory individuals [7]. The keystone framework is also gaining some
61 traction in conservation biology: it has recently been proposed that identification of
62 keystone individuals and analysis of their effect on the population is valuable in
63 conservation and management of social species [8].

64

65 In the context of cultural evolution, we may consider innovators of behaviours that spread
66 in a population, and individuals who serve as a popular copying model, to be keystones [4].
67 Theoretical and experimental work assessing the role of innovation in cultural evolution
68 has focused on the conditions favouring social learning over innovation (or individual
69 learning) and vice versa (e.g. [9–17]), as well as on the diffusion of innovations [18–20].

70 Lately, a series of models turned the spotlight onto the way different types of innovations
71 may shape the evolution of culture [21–23]. The different nature that innovations may have
72 pertains to a longstanding dispute in the animal behaviour literature. While it is intuitively
73 clear that not all innovations are similar in their inception and impact, how can we define
74 the differences between them in general terms?

75

76 In a recent paper, we approached this issue by describing behavioural innovations as
77 measured by their magnitude [24]. Relying on a previous definition [25], we suggested that
78 any new behaviour, no matter how similar to behaviours already in the populations'
79 behavioural repertoire, should be considered an innovation; however, we argued that these
80 innovations may differ in how close to or far from the population's mean behaviour they
81 are. Innovations that are far from the mean are considered high-magnitude innovations,
82 while innovations that are close to the mean are considered of low-magnitude (see detailed
83 discussion in [24]). Offering a great increase in the population's fitness, high-magnitude
84 innovations that spread in the population may therefore be viewed as a cultural 'leap' [21].

85

86 High-magnitude innovations, by definition, differ significantly from familiar behaviours.

87 They may include the introduction of a new object to interact with [26], a new territory to
88 forage in [27], a new feeding method to utilize [28], or a new song to replicate [29].

89 Viewing others interact with an unfamiliar object may allow neophobic individuals to
90 overcome their fear, or simply draw attention to an object that copiers have not noticed
91 before [30,31]. Thus, high-magnitude innovations allow copiers of the innovation to

92 explore a new domain and perhaps modify it by innovating themselves. Models focusing on

93 the effect of different innovation types on human cultural evolution have utilized the latter
94 idea, suggesting to account for the punctuated evolutionary pattern found in the human
95 artifact archeological record [21–23]. High-magnitude innovators may therefore not only
96 serve as keystone individuals by generating cultural leaps, but also by facilitating socially
97 induced innovations, that further modify their own.

98

99 In this study, I expand upon our previous work on the magnitude of innovation in social
100 animals [24], to include cultural evolution. I investigate whether a trait allowing socially
101 induced innovation can evolve, examine the effect of such a trait on the evolution of
102 independent innovation and on the magnitude of innovation, and finally, analyze how all
103 these traits interact to shape the progression of culture.

104

105 **THE MODEL**

106 I simulated a population of individuals genetically varying in their (1) tendencies to
107 innovate and to copy others; (2) innovation magnitude, and (3) tendency to modify high-
108 magnitude innovations they have copied. A generation's life began with a series of $T = 10$
109 discrete learning steps, in each of them individuals acquire one new behaviour either by
110 innovating, or by copying the innovations that others produced during that specific
111 learning step t ($0 < t \leq T$). Individuals who copied high magnitude innovations in step t
112 could, based on their genetic tendency, be “inspired” to innovate in the next learning step
113 ($t+1$), to produce a modification of the copied innovation. This modified innovation could
114 be copied by others during that step ($t+1 \leq T$) as any innovation, and could serve as a basis
115 for further socially induced innovations in the next learning step ($t+2 \leq T$), in the same

116 manner. After the T steps of the learning phase, individuals applied the behaviours they
117 have acquired, with greater weight given to higher-paying behaviours. Individuals then
118 produced offspring in proportion to the relative payoff they have accumulated during their
119 lifetime, and died. The mean of the highest paying behaviours learned by parents was
120 defined as their generation's cultural contribution, and considered the new generation's
121 behavioural baseline for cultural evolution calculations.

122

123 *The population*

124 A population of $n = 100$ individuals is modeled, with each individual characterized by three
125 focal genes: L (Learning gene), I (Innovation magnitude gene), and C (socially induced
126 innovation gene). The learning gene, L , determined the probability the individual will, at
127 each learning step, produce an independent innovation, or copy a conspecific's innovation.
128 There were 11 possible alleles in this gene: 0, 0.1, 0.2 ... 1, where 0 coded for full-time
129 copying, or social learning, 1 for full-time independent innovation, and all other alleles for a
130 combination of the two (e.g. a carrier of the 0.3 allele spent 30% of the time, on average,
131 copying, complemented by an average of 70% independent innovation). The innovation
132 magnitude gene, I , affected how far from the population's norm an individual's innovations
133 will be when innovating. There were again 11 possible alleles in this gene: 0, 0.1, 0.2 ..., 1,
134 which represented standard deviations from the population's mean behaviour; this value
135 was used to draw a value from a normal distribution whose mean was the population's
136 mean behaviour, and standard deviation was the individual's I allele (see below). The
137 socially induced innovation gene, C , determined the probability that, after copying a high-
138 magnitude innovation, the copier will proceed to modify this innovation in its next learning

139 step. This gene included three alleles: C_0 – for zero probability, i.e. no effect; C_{sqrt} – the
140 square root of the individual’s probability to innovate as set by its L allele, i.e. an increase in
141 innovation probability that is proportional to genetic tendency for independent innovation;
142 and C_1 – for a probability of 1, i.e. the individual is certain to innovate. Just like independent
143 innovation, the magnitude of an individual’s socially induced innovation was determined
144 by its genotype in the I gene.

145

146 *Learning phase*

147 All individuals in the population had a limited number of learning steps $T = 10$. In each of
148 these steps they acquired one new behaviour, either by innovation or by copying an
149 innovation a conspecific has produced at that specific step (our previous model analyzing
150 the case of $T = 100$ found no significant differences between the two case, see Arbilly and
151 Laland 2017). At the beginning of each step, it was determined for each individual whether
152 it would innovate or copy, based on the probability dictated by its L genotype. Individuals
153 who were to innovate generated a new behaviour. The value of this innovative behaviour
154 (i.e. its payoff) was drawn from a normal distribution whose mean was the population’s
155 mean behaviour, and whose standard deviation was the innovator’s allele in the I gene; for
156 convenience, the population’s mean behaviour value was set to 0. Then, individuals who
157 were to copy in this learning step, copied the behaviours generated by innovators. All
158 innovations were ranked according to their value, and which innovations would be copied
159 depended on the selectivity of social learning in the population (which was kept constant
160 per population). The selectivity of social learning was controlled using the variable D ,
161 defined as $1 - [\text{the fraction of demonstrators copied}]$. When selectivity was high (high D)

162 only innovations with the highest value were copied (e.g. when $D = 0.9$ only the top 10% of
163 innovation were copied); as the selectivity of social learning became lower, copying
164 became more random (and was completely random at $D = 0$).

165

166 In cases where individuals copied a high-magnitude innovation, defined as an innovation
167 whose value was greater than 1 (putting it at a distance greater than one standard
168 deviation from the population's mean behaviour), it was determined whether they will
169 modify this innovation in the following learning step, $t+1$, based on their socially induced
170 innovation (C) allele. If they were to innovate, the magnitude of their innovation was set by
171 their I allele. These individuals produced an innovation at the beginning of step $t+1$ along
172 with independent innovators (described above). However, for these socially induced
173 innovators, the value of their innovation was added to the value of the high-magnitude
174 innovation they copied in their previous learning step (t), to yield a new innovation for step
175 $t+1$. This innovation was then ranked along with all innovations and copied by individuals
176 who, in step $t+1$, are copying others, as described above. The choice to have socially
177 induced innovation triggered only by the copying of high-magnitude innovations, rather
178 than the copying of any innovation, was made in order to set these innovations apart from
179 independent innovations (see Discussion).

180

181 *Application phase*

182 After acquiring the behaviours, individuals apply these behaviours and will tend to use
183 them with a frequency directly proportional to the payoff they offer. To calculate the
184 proportion of time allotted to each behaviour, and since payoffs can be negative as well as

185 positive, an exponential transformation of the form:

$$186 \quad p_x = \frac{e^{\sigma\beta_x}}{\sum_{i=1}^j e^{\sigma\beta_i}} \quad (1)$$

187 is used, where p_x is the proportion of time spent using behaviour x , β_x is the payoff of
188 behaviour x , $i = 1 \dots j$ are the behaviours the individual has acquired during its learning
189 phase ($j = T$), and σ is the application sensitivity: the degree to which agents can distinguish
190 between payoffs in choosing which behaviours to apply. This value is the same for all
191 agents. Following previous analysis [24], σ was set to its high value ($\sigma = 3.3$), such that
192 agents spend a higher proportion of their time applying the highest paying behaviour and
193 little to no time applying low value behaviours. Note that due to the stochastic process used
194 in the simulation to generate new behaviours, then unless there is no innovation in the
195 population, behaviours $1 \dots j$ will each be unique.

196

197 The payoff accumulated from applying the learned behaviours, W_A was then calculated by
198 summing up the multiplications of each behaviour's payoff and the proportion of time
199 spent applying it:

$$200 \quad W_A = \sum_{i=1}^j p_i \beta_i \quad (2)$$

201

202 *Selection and reproduction*

203 To calculate the total payoff to individuals in the population, W_T , the payoff obtained both
204 during the learning phase, W_L (which is the sum of all payoffs of behaviours learned), and

205 during the application phase, W_A , was summed using a weight factor $\alpha = 0.1$ to account for
206 the relative time allocated to the learning phase compared to the application phase:

$$207 \quad W_T = \alpha W_L + (1 - \alpha) W_A.$$

(3)

208 Payoff received for behaviours was included in the learning phase payoff calculation (in the
209 form of W_L) regardless of whether they were applied, as it is assumed that agents perform
210 behaviours when they are learning them, in order to experience their exact payoff.

211

212 Individuals then reproduced, producing a number of offspring proportional to their total
213 payoff relative to the payoff of all other individuals in the population. Since the total payoff
214 could be negative, we again use an exponential transformation of the form:

$$215 \quad r_y = \frac{e^{\lambda W_{T,y}}}{\sum_{k=1}^n e^{\lambda W_{T,k}}} \quad (4)$$

216 Where r_y is the probability of reproduction for individual y , and λ is the strength of
217 selection. Following previous analysis [24], λ was set to its high value ($\lambda = 3.3$), to generate
218 strong selection: individuals who obtained higher total payoff had much higher chances to
219 reproduce than individuals who obtained a lower payoff. Among the offspring, mutation
220 occurred at a rate of $\mu = 1/n$ in all genes. Mutation was random and the new variant was
221 drawn from each gene's pre-defined allele pool.

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224

225 *Cumulative culture*

226 After parents are selected, each parent's highest paying behaviour is recorded. The mean of
227 all these behaviours from the parental generation is then counted as that generation's
228 cultural contribution. This assumption accounts for a situation where a full repertoire of
229 behaviours are transferred to the new generation, and not just one. This mean was then
230 viewed as the new generation's mean behaviour. Since values of behaviour here are
231 arbitrary, the actual value of this mean does not matter for purposes of innovation in the
232 next generation, and furthermore, using it as the mean for the distribution from which the
233 next generation draws innovations inflates cultural evolution rates, this cultural
234 contribution was set aside and the actual mean used to draw innovations was zero for all
235 generations. These cultural contributions were then used cumulatively to calculate the
236 progress of cultural evolution. For example, if generation 1's contribution was 1.5, and
237 generation 2's contribution was 0.5, the final value of culture for generation 2 was
238 $1.5+0.5=2$, and so on for following generations. The choice to use the mean of parents'
239 highest paying behaviours is conservative: using only the single highest paying behaviour
240 for each generation would have resulted in higher cultural rates.

241

242 **RESULTS**

243 *Evolution of socially induced innovation*

244 The allele frequency in socially induced innovation gene, C , changed with social learning
245 selectivity, D (figure 1). The C_1 allele, setting the probability of socially induced innovation
246 to 1, had a clear advantage when the selectivity of social learning was low ($D \leq 0.1$). The
247 allele enhancing the probability of innovation, C_{sqr} , was also selected at $D = 0$, although at a

248 much lower frequency, with some advantage over C_0 (allele coding for no effect); this
249 advantage of C_{sqr} over C_0 disappeared when $D = 0.1$. When selectivity was higher, C_1 was
250 found at low frequencies, while C_{sqr} and C_0 appeared at similar frequencies (between 40%
251 and 50% each). It should be noted that in that range of social learning selectivity D ,
252 independent innovation rate, set by the L gene, was close to zero (figure 2a): in most
253 generations individuals had an independent innovation rate of zero, therefore the C_{sqr}
254 allele would have no effect on them, similar to C_0 .

255

256 *Rate of independent innovation in the presence of socially induced innovation*

257 A comparison of the genetic probability of independent innovation rate in the presence and
258 in the absence of the C gene shows an effect changing with the selectivity of social learning,
259 D (figure 2a). While in the absence of C the genetic probability represents the expected
260 probability of innovation in the population, in the presence of C , the actual rate of
261 independent innovation may be lower than the genetic probability, as individuals may use
262 some of their learning steps for socially induced innovation, instead of drawing between
263 innovation and social learning based on their L allele. When the selectivity of social
264 learning was at its lowest – where copying is completely random – socially induced
265 innovation significantly decreased the rate of independent innovation. When social
266 learning selectivity was poor while still eliminating the worst innovations ($D = 0.1$), the
267 rate of independent innovation was the same with and without C . When selectivity was
268 higher but still in the low range ($0.2 \leq D \leq 0.5$), the rate of independent innovation was
269 slightly higher in the presence of the C gene. As the effect is very small, and due to the
270 complicated frequency-dependent interaction between the three genes, it is difficult to

271 determine whether this is due to noise created by drift in the C gene, because socially
272 induced innovations increase the benefit of independent innovation by increasing the
273 competition, because carriers of the C_{sqr} allele benefit when also carrying an L allele with a
274 value that is higher than zero, or some combination of these. However, more selective
275 social learning resulted in similar, close to zero rates of independent innovation, with and
276 without socially induced innovation.

277

278 *Magnitude of innovation in the presence of socially induced innovation*

279 When the selectivity of social learning was at its lowest – where copying was completely
280 random – the magnitude of innovation was lower in the presence of socially induced
281 innovation, although still very high (0.91 compared to 0.99; figure 2b). In the medium
282 range of social learning selectivity, however, the magnitude of innovation was consistently
283 higher in the presence of socially induced innovation, and as in the absence of socially
284 induced innovation, decreased as selectivity in social learning increased.

285

286 *Cultural evolution*

287 Culture as measured by the accumulation of innovations, was higher when the selectivity in
288 social learning (D) was lower (figure 3). Socially induced innovation (the C gene) increased
289 the rate of cultural evolution; this effect was found even in the case of random copying ($D =$
290 0), where the rate of independent innovation was much lower in the presence of socially
291 induced innovation than in its absence (figure 2a).

292

293

294 **Discussion**

295 Socially induced innovations would seem to have a clear advantage: building on a known
296 high-magnitude innovation, they offer the possibility of generating an even better
297 innovation, with a lower risk compared to independent innovation. That is, even if the
298 socially induced innovation resulted in a lower value behaviour compared to the
299 independent innovation it was building upon, it is still less likely to be below the
300 population's mean value of behaviour, unlike independent innovations. Still, socially
301 induced innovations do not evolve when the selectivity of social learning is high: in that
302 situation, others are likely to copy a high-magnitude socially induced innovation, without
303 incurring the possible cost of producing a low-magnitude innovation. The cost for the
304 socially induced innovator here is not only in having a lower value behaviour in its
305 repertoire, but also in missing the chance of copying a better behaviour produced by
306 someone else at that time step. This opportunity cost stems from the assumptions of the
307 model, whereby individuals must perform the behaviour in order to learn it, know its exact
308 payoff, and be "inspired" to modify it further with their own innovation.

309
310 Most significant is the effect of socially induced innovation on the rate of independent
311 innovation when copying was random ($D = 0$). In that condition, in the absence of the C
312 gene, the rate of independent innovation is up to 0.64 ± 0.02 , but when incorporating the C
313 gene, the rate was down to 0.13 ± 0.01 . The magnitude of innovation was also somewhat
314 lower. The dominating allele in the C gene at that time was C_1 , guaranteeing a socially
315 induced innovation whenever a high-magnitude innovation was copied. This combination
316 of traits is, perhaps unsurprisingly, "safer" than a high rate of independent innovation

317 alone, for the reason discussed above. It should be noted that, while this result was found
318 when social learning selectivity is low, the selectivity in application of behaviour is high,
319 thus individuals do not blindly utilize behaviours; they are simply unable to judge the value
320 of a behaviour without performing it first themselves. Regardless of the specific condition,
321 it demonstrates how socially induced innovation may affect independent innovation, in a
322 situation where independent innovation would otherwise be highly favoured. While
323 lowering the rate of independent innovation, and the magnitude of all innovations, the *C*
324 gene also lead here to a much higher rate of cultural evolution: socially induced innovations
325 may be copied by others, who may subsequently use them as a basis for further socially-
326 induced innovations, resulting in a cascade of innovations. Altogether, socially induced
327 innovation, which can only act in the presence of high-magnitude independent innovation,
328 selects here against high-magnitude independent innovators, and by lowering their
329 frequency makes their role, as initiators of the innovation cascade, more crucial. In other
330 words, it makes them keystone individuals.

331
332 The definition of keystone individuals, as discussed by Modlmeier et al [4], asserts that
333 keystones cannot be “generic”: if removed, their niche cannot simply be filled by others. In
334 the model presented here, individuals may be genetically identical, but few may, by chance,
335 produce a high-magnitude independent innovation, while others may copy it and modify it.
336 Their role as keystones is determined based on the result of their actions. Their
337 independent innovations are a product of probability, and within a generation lifetime do
338 not depend on whether others may have or may not have produced high-magnitude
339 independent innovations of their own. Thus, the removal of a specific keystone individual

340 would indeed not result in another individual in the population producing a high-
341 magnitude innovation in its place.

342
343 The results of the model provide, through proof of concept, insight into the co-evolution of
344 independent and socially induced innovation. As human technology is undoubtedly made
345 of cascades of innovations [32], the finding that socially induced innovations may select
346 against independent innovation is highly relevant, and fits nicely with results of models
347 that combine these two types of innovations, to demonstrate how human culture may have
348 evolved in “bursts”, composed of initial ‘lucky leap’ innovations that are followed by further
349 innovations that are inspired by the leap [21–23]. Furthermore, the results presented here
350 demonstrate how socially induced innovation may help maintain independent innovations,
351 or lucky leaps, at a low frequency, when it is tough to gauge the payoff of a behaviour
352 without first-hand experience (see discussion of selectivity above).

353
354 While the model aims to be general, cumulative culture in nonhuman animals, to the extent
355 that it exists, is difficult to track. Some exceptions to this rule, however, are bird song [29],
356 and whale song [33], where populations have been documented evolving unique vocal
357 repertoires. Studies in bird song suggest possible costs to song innovation (e.g. the signal
358 not conveying the signaler’s intended information [29]), as well as benefits (adjusting song
359 to new ecological circumstances, e.g. songs that travel better in an urban environment [34–
360 36]). They also suggest that innovations often arise through copying errors [29]. This is
361 especially interesting in the context of socially induced innovation, as a novel song (i.e. an
362 innovation), only performed by a single individual, would seem more likely to be replicated

363 with errors by listeners (i.e. lead to socially induced innovation), compared to a song
364 performed by many in the population (i.e. the mean behaviour).

365

366 Is the concept of keystone individuals conducive to our understanding of the evolution of
367 culture? What if, for example, individuals were induced to innovate by copying any
368 innovation, regardless of its magnitude? In such a case, socially induced innovations would
369 have no benefit over independent innovations: if the original innovation they innovate
370 upon is not of high value, socially induced innovations are just as likely to result in below-
371 average behaviour as an independent innovation. Thus, cultural evolution rates with such
372 indiscriminate socially induced innovations is likely to be the same as in their absence.

373 Having the keystone concept in mind contributed much to the design of the model
374 presented in this paper, and in turn, to its insight into the possible evolutionary interaction
375 between independent innovation, socially induced innovation, and innovation magnitude,
376 and how this interaction can shape the evolution of culture.

377

378 **Supporting materials**

379 The Matlab code for the simulations used in this paper has been uploaded as part of the
380 electronic supplementary material.

381

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385

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479 **Figure 1:** Mean frequency of alleles in the socially induced innovation gene, C , as a function
480 of social learning selectivity, D . C_0 allele codes for no socially induced innovation; C_1 allele
481 codes for certain socially induced innovation; C_{sqrt} sets the probability of socially induced
482 innovation to the square root of the probability of independent innovation (L genotype).
483 Means and standard errors are calculated for generations 4001-5000, across 100 repeats of
484 each simulation.

485

486 **Figure 2:** Effect of the socially induced innovation gene, C , on the frequency and magnitude
487 of innovation. (a) Mean frequency of independent innovation, based on mean genotype in
488 the L gene; (b) Mean magnitude of innovation, among individuals with the genetic potential
489 of independent and/or socially induced innovation. Means and standard errors are
490 calculated for generations 4001-5000, across 100 repeats of each simulation.

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492 **Figure 3:** Effect of socially induced innovation gene, C , on cumulative culture. Means and
493 standard errors are calculated over 100 repeats of each simulation.

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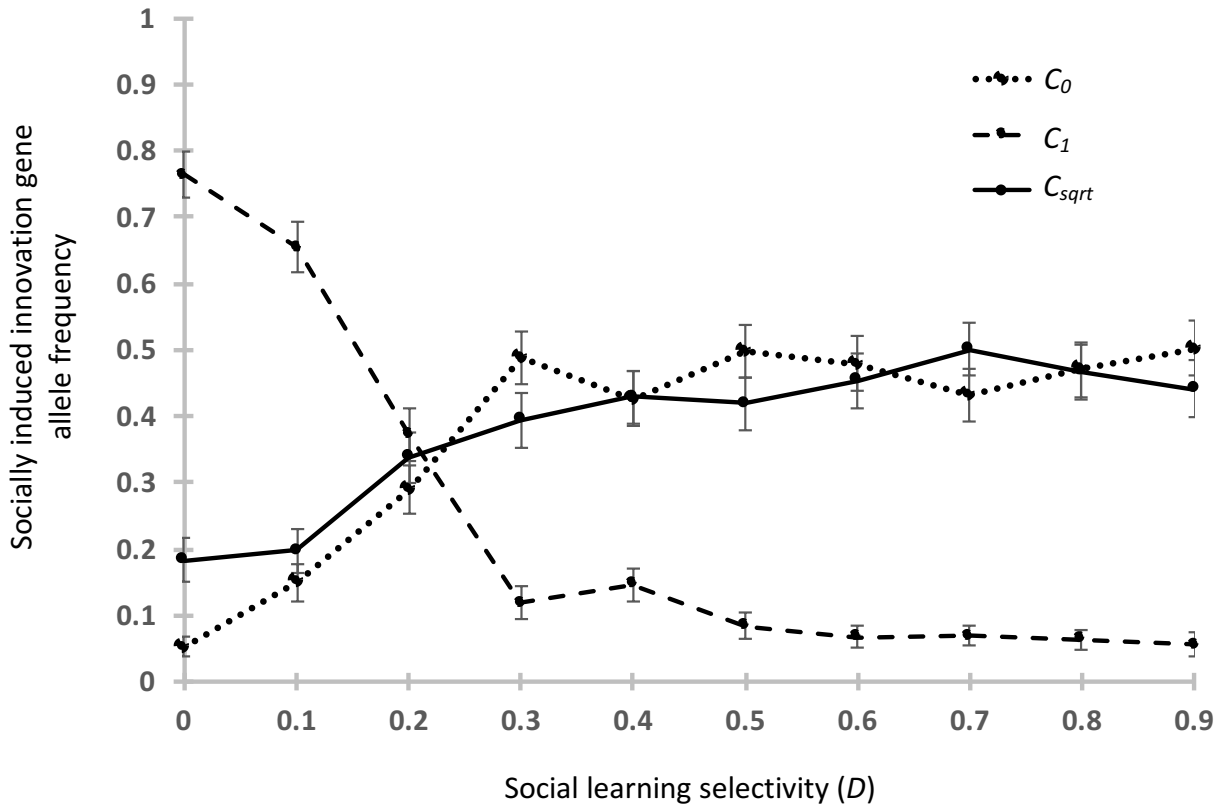


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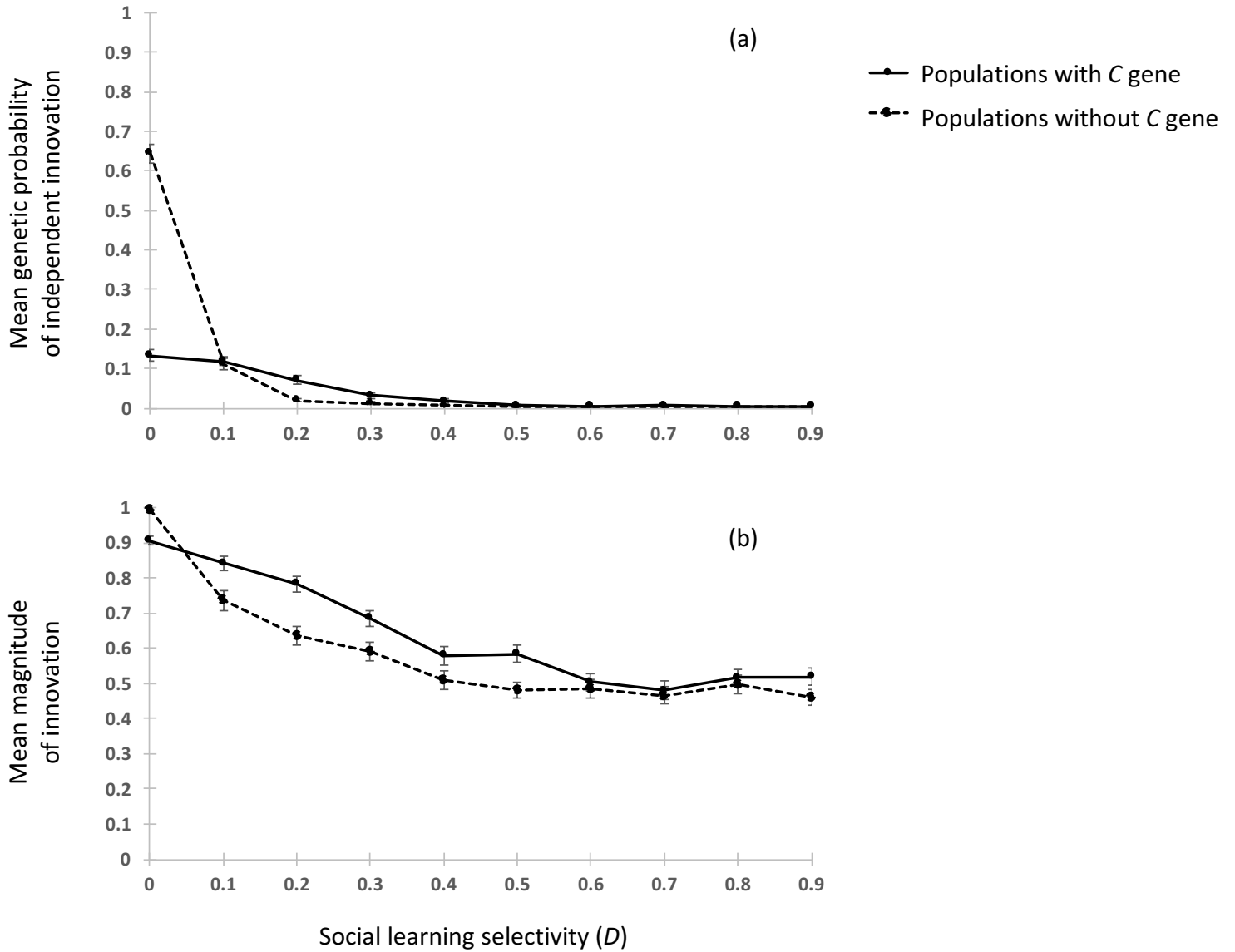


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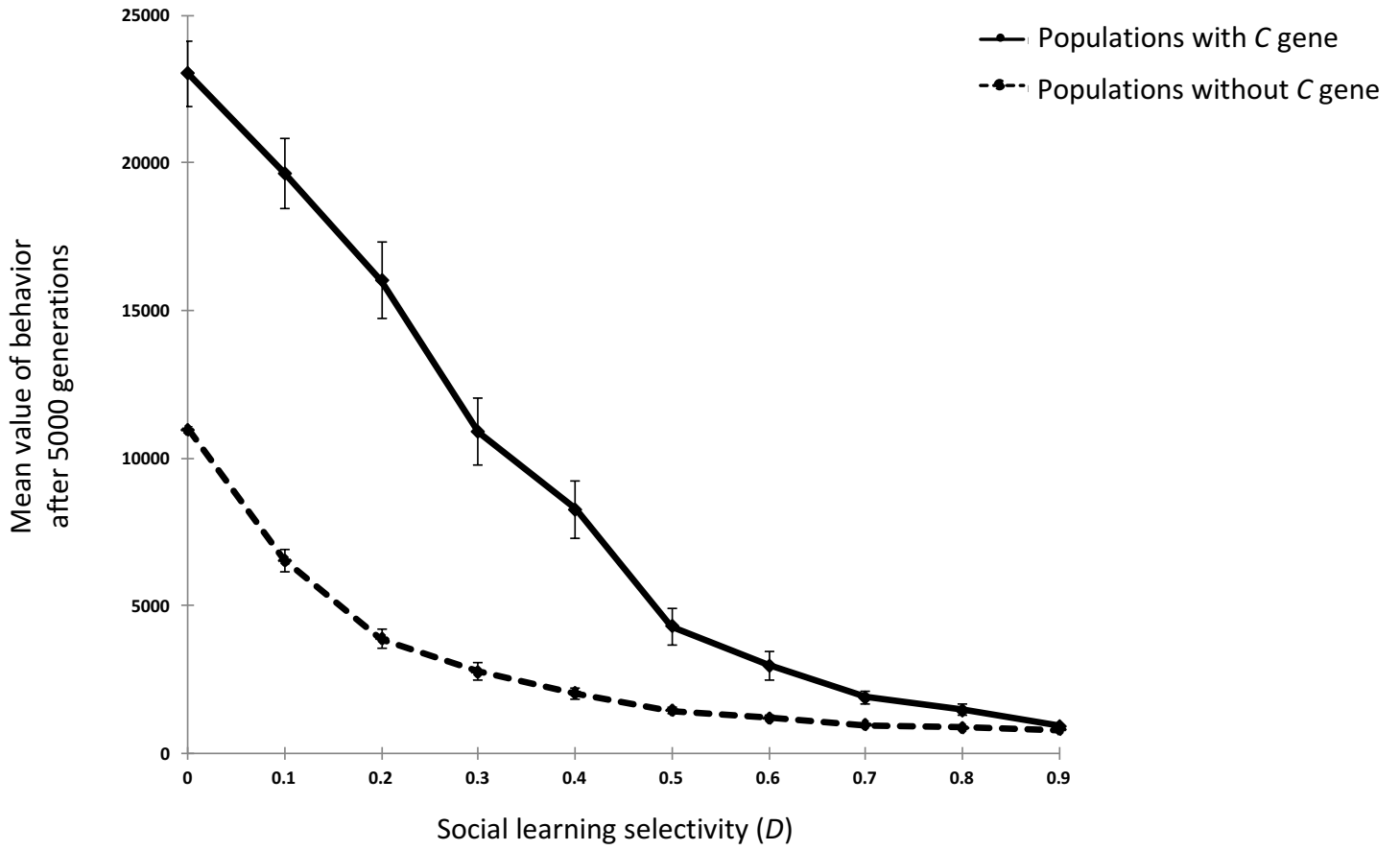


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