

1 **Zombie Ants VR: Using trial-and-error gameplay mechanics to intuitively teach players**
2 **about natural selection**

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11
12 **Abstract**

13 *Background*

14 Understanding the process of evolution is important for making informed decisions about the use
15 of antibiotics and vaccinations to combat pathogens. Unfortunately, discussing the intersection of
16 evolution and infectious diseases with the public can be difficult due to preexisting religious views
17 and/or political beliefs. However, an individual's acceptance of evolution is not as important as
18 their understanding of its underlying mechanisms when it comes to making public health choices.
19 Therefore, our interdisciplinary research team, consisting of microbiologists, game and media
20 technology experts, and teachers, sought to explore whether gamification techniques like trial-and-
21 error gameplay could be used to teach players about the process of evolution without explicitly
22 defining the theory.

25 *Results*

26 We created a freely available, open-access serious virtual reality game called *Zombie Ants VR*. In
27 this game, participants take on the role of the zombie fungus *Ophiocordyceps* with the goal of
28 infecting and behaviorally manipulating ants. Throughout their journey, players are faced with
29 several tasks and choices that reflect the life cycle of the parasite. Ultimately, the player's decisions
30 determine whether they succeed and reproduce or if they die and must try again as a new spore.
31 By emphasizing that each new attempt takes place with a new individual, the gameplay mechanic
32 teaches about natural selection and how it acts at the population level without using evolutionary
33 biology specific vocabulary. Comparisons between pre-game and post-game questionnaires
34 showed that playing *Zombie Ants VR* significantly increased players' understanding of the process
35 of natural selection, and that this effect was independent of the players' preexisting beliefs.

36
37 *Conclusions*

38 By using gameplay mechanics as the main educational tool, we were able to teach participants
39 about natural selection without the need for trigger words (e.g., evolution) that can elicit defensive
40 responses within certain demographics. Moreover, by using zombie-making parasites as an
41 example, which appeals to a diverse general audience, we were able to explain the fundamental
42 process of evolution within the context of infectious diseases. This demonstrates that gamification
43 techniques can be used to teach important biological topics in a way that does not conflict with
44 preexisting views.

45
46 **Keywords**

47 Evolution, Adaptation, Infectious Diseases, Gamification, Serious Games, Virtual Reality, Public
48 Engagement, Interdisciplinary.

49 **Introduction**

50 Teaching evolution remains a challenging aspect of biology education due to its conceived conflict
51 with certain religious and/or political beliefs often held by students (Barnes & Brownell, 2017),
52 particularly institutions with religious affiliations (Tolamn et al., 2022). This issue is further
53 reflected in the public sphere with over 1/3 of the US population outright rejecting evolutionary
54 principles (Miller et al., 2022), a problem made worse in recent years by online platforms and
55 algorithms that push controversial information containing misinformation (Park et al., 2023).
56 While the severity of this problem can differ between countries (Miller et al., 2006), it remains a
57 waxing global issue in part due to the resurgence of science skepticism (Rutjens & van der Lee,
58 2020) emboldened by nationalism and other anti-intellectual movements, e.g., Neo-Calvinism in
59 the Netherlands (Flipse, 2012). This is unfortunately occurring at a time when global warming is
60 contributing to the evolution of thermotolerant human pathogens (de Oliveira et al., 2023) and
61 multi-drug-resistant organisms are become increasingly problematic (Miller & Arias, 2024). The
62 COVID-19 pandemic, for example, was highly politicized and particularly fraught with
63 misinformation, which has made the discussion about infectious disease even more difficult
64 (Baxter-King et al., 2021; Hornik et al., 2020).

65 However, it is also important to recognize that a mere acceptance of evolutionary principles
66 does not necessarily translate to a clear understanding of the process, nor does it reflect an ability
67 to properly apply these principles to major life choices. Even in academic circles, educated
68 individuals often misunderstand evolution as a process that affects individuals, a misinterpretation
69 that is more in line with Lamarck's misconceptions on the process of evolution (Beckerson et al.
70 2024). This misattribution of selective pressures on individuals is just one of many fallacies that
71 makes teaching students about evolution a persistent challenge in biology education (Smith, 2022;
72 Sickel & Friedrich, 2013; Gregory, 2009). Even a fractional degree of ignorance regarding

73 evolutionary science can have major impacts when it comes to societal choices like vaccination
74 and herd immunity (Fine et al., 2011). It is therefore important that we as educators find new ways
75 to address evolution literacy so university students and the wider public can make educated
76 decisions related to climate change, personal and public health, and the emergence of antibiotic-
77 resistant pathogens.

78 The time-sensitive nature of these global issues can lead to a sense of urgency that can
79 move educators to push too aggressively against those with non-conforming views. This approach
80 has been overwhelmingly shown to elicit psychological reactance in those who feel their freedom
81 of choice is threatened, resulting in a “boomerang” or “backfire” effect where people become even
82 more entrenched in their beliefs (Courtright, 2025; Douglas et al., 2025; Jonason & Dane, 2014;
83 Lewandowsky et al., 2012). Therefore, science communicators may be going about things the
84 wrong way when trying to win an uphill battle against the personal anecdotes and misinformation
85 that fuels conspiracy theories and science denial by chastising ignorance and repeating scientific
86 facts. In the end, whether individuals acknowledge evolution as the driving force behind the
87 emergence of new pandemics is less important, with regards to the societal impact of their
88 decision-making. Instead, fostering a foundational level of understanding about the underlying
89 mechanisms of evolution, i.e., how selective pressures can result in small, stepwise changes to the
90 genomes of bacteria, fungi, and viruses and lead to new host ranges and various forms of
91 resistance, might provide a more effective strategy.

92 This can be accomplished by using other, natural examples of infection that tap into an
93 individual’s curiosity rather than emotion-laden relevant human diseases. For that reason, we
94 asked ourselves whether it is possible to teach about the process of evolution in the context of
95 other, more entertaining examples of infectious disease, e.g., zombie fungi, without using trigger

96 words that can elicit strong emotional responses that effectively halt the learning process before it
97 has even begun (Malyuga & Rimmer, 2021; Capraro & Vanzo, 2019; Brady et al., 2017).

98 Education-based games can help captivate public audiences beyond the traditional
99 classroom setting and facilitate learning through gameplay elements. This is particularly true for
100 games that use failure as an opportunity to elaborate on player choices and improve their gameplay.
101 This dynamic is based on conceptual change, also known as “productive failure” in psychology
102 (Loibl & Leuders, 2019). Error-full learning, followed by corrective feedback, has been associated
103 with greater learning outcomes than traditional error-avoidant instruction, particularly when
104 individuals have a strong confidence in the errors they are making (Metcalfe, 2016). We therefore
105 set out to develop an activity that could teach the process of evolution while being fun and
106 incorporating elements of trial-and-error gameplay.

107 We also emphasized the need to move beyond a traditional lecture-style conversation in
108 favor of an active learning exercise that incorporates higher-order thinking (Adams, 2015).
109 Towards this end, we decided to lean on our scientific work and expertise across the fields of
110 microbiology and neuroparasitology to make a game about zombie ants. Reminiscent of zombies
111 in movies, TV series, and video games, zombie ants are ants infected by the fungal parasite
112 *Ophiocordyceps* which changes their behavior in ways that benefit the parasite’s spread to new
113 hosts. As part of their life cycle, *Ophiocordyceps* first causes infected ants to abandon their social
114 roles in the nest to avoid defense behaviors of nestmates that might destroy the fungus (Trinh et
115 al., 2021). Next, it causes them to climb nearby vegetation to position the host at an elevated
116 position that promotes both the growth of the fungal reproductive structure (i.e., fruiting body) and
117 the effective spread of the infectious spores (Will et al., 2022). This is where the fungus causes the
118 ant to bite down irreversibly to prevent the host from falling after death, a behavior also known
119 as “the death grip” (Hughes et al., 2011). By causing the host to climb to a higher location and

120 attach itself to the substrate, the fungus is better able to spread the next generation of infectious
121 spores to more potential hosts using the wind. This is a common infection and disease transmission
122 strategy found amongst many behavior-manipulating parasites called “summit disease” (de Bekker
123 et al., 2021). Ultimately, these behaviors caused by the fungal parasites are the result of the
124 biomolecules made from their own genome to change the behavioral phenotypes of their hosts; a
125 phenomenon known as an “extended phenotype” (Dawkins 1990). These extended phenotypes
126 have evolved over millions of years of reciprocal selection called coevolution. As such, zombie
127 ants and other behavior-manipulating parasites are great tools for teaching students about natural
128 selection, symbioses, and disease transmission.

129 In addition to its suitability for teaching important biological concepts, zombie ants are
130 importantly an increasingly well-known pop science topic, thanks in large part to media like the
131 HBO series *The Last of Us* (Mazin & Druckmann, 2023) based on a video game series of the same
132 name (Naughty Dog, 2013-2025). This series is famously based on zombie ants, as stated by its
133 creative leads, and has been discussed in many science communication outlets including *The*
134 *Biology Behind The Last of Us* with WIRED https://youtu.be/GnEIwL_SgI0; *The Fungus Among*
135 *Us* with The Colin McEnroe Show <https://www.ctpublic.org/show/the-colin-mcenroe-show/2023-02-06/the-fungus-among-us>; and *True Facts: Fungi That Control The Insects They Eat* with Ze
136 Frank <https://youtu.be/NdaYRSW76Mg>). The topic’s popularity of the topic has benefited in part
137 from the morbid curiosity that “real-life-zombies” instills in the public eye. This makes the topic
138 of zombie ants is an incredibly useful tool for getting a foot-in-the-door to discuss biology with
139 the public. Furthermore, by focusing educational outcomes pertaining to natural selection and
140 disease transmission on ants instead of humans, we can help mitigate stimuli or social cues that
141 may invoke a defensive response with dissociation.

143 While games are typically designed with commercial goals in mind, we sought to create a
144 freely available “serious game” for the sole purpose of improving public education. Serious games
145 are characterized by their purpose-driven prerogative, leveraging the engaging and interactive
146 elements of games to teach the player. Examples of serious games include Duolingo (language
147 learning software), Minecraft: Education Edition (coding, math, and teamwork), and various flight
148 simulators (piloting). To gamify the topic of evolution, we elected to use the trial-and-error format
149 of memory games, but with one important change relating to the identity of the player. Instead of
150 allowing the player’s character to retry failed activities, we instead require the player to start over
151 as a new character. While this does not change any functionality of the game, we aimed to impress
152 upon the player the population-level dynamics of natural selection by adding this stipulation.
153 Applied to the topic of zombie-making fungi, each new attempt must be performed using a new
154 spore and involves infecting a new host. We hypothesized that structuring the game this way would
155 teach players about the process of evolution by natural selection without explicitly explaining the
156 theory.

157 As a medium for our game, we made use of virtual reality (VR) technology to allow the
158 player to view the world from the perspective of a zombie ant. VR provides an unparalleled sense
159 of immersive presence and a strong association with virtual objects that promotes learning (Lin et
160 al. 2024; Liu et al., 2023; Merchant et al., 2014). It also allows players to experience an
161 environment on limitless scales, like visualizing the universe on galactic scales, e.g., Galactic
162 Center VR (Russel 2020), or at the microscopic level, e.g., BloodBlast VR (Kalinka, 2020). By
163 designing the game from the perspective of a fungal spore and infected ant, we reasoned that we
164 could also use the game to teach the players about ants and their social structures as secondary
165 learning objectives. More importantly, by using an immersive virtual environment, we were able

166 to further our goal of dissociating the player from their personal perspectives and facilitate a more
167 open mindset for the educational experience.

168 Finally, to bring this project to life, we engaged in an interdisciplinary effort to create an
169 educational serious game, which we called *Zombie Ants VR*. This collaboration involved
170 microbiologists who study the zombie ant phenomenon in detail (Beckerson et al., 2025; de Bekker
171 et al., 2021), educators in biology, game design, and interactive media, and game developers across
172 various career stages, all of whom are listed in the acknowledgment section for their important
173 contributions to the creation of this game. Upon its completion, we tested whether the biological
174 zombie ant example, together with the trial-and-error gameplay mechanics in an immersive VR
175 setting, could improve understanding of evolutionary principles at its intersection with infectious
176 diseases.

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178 **Methods**

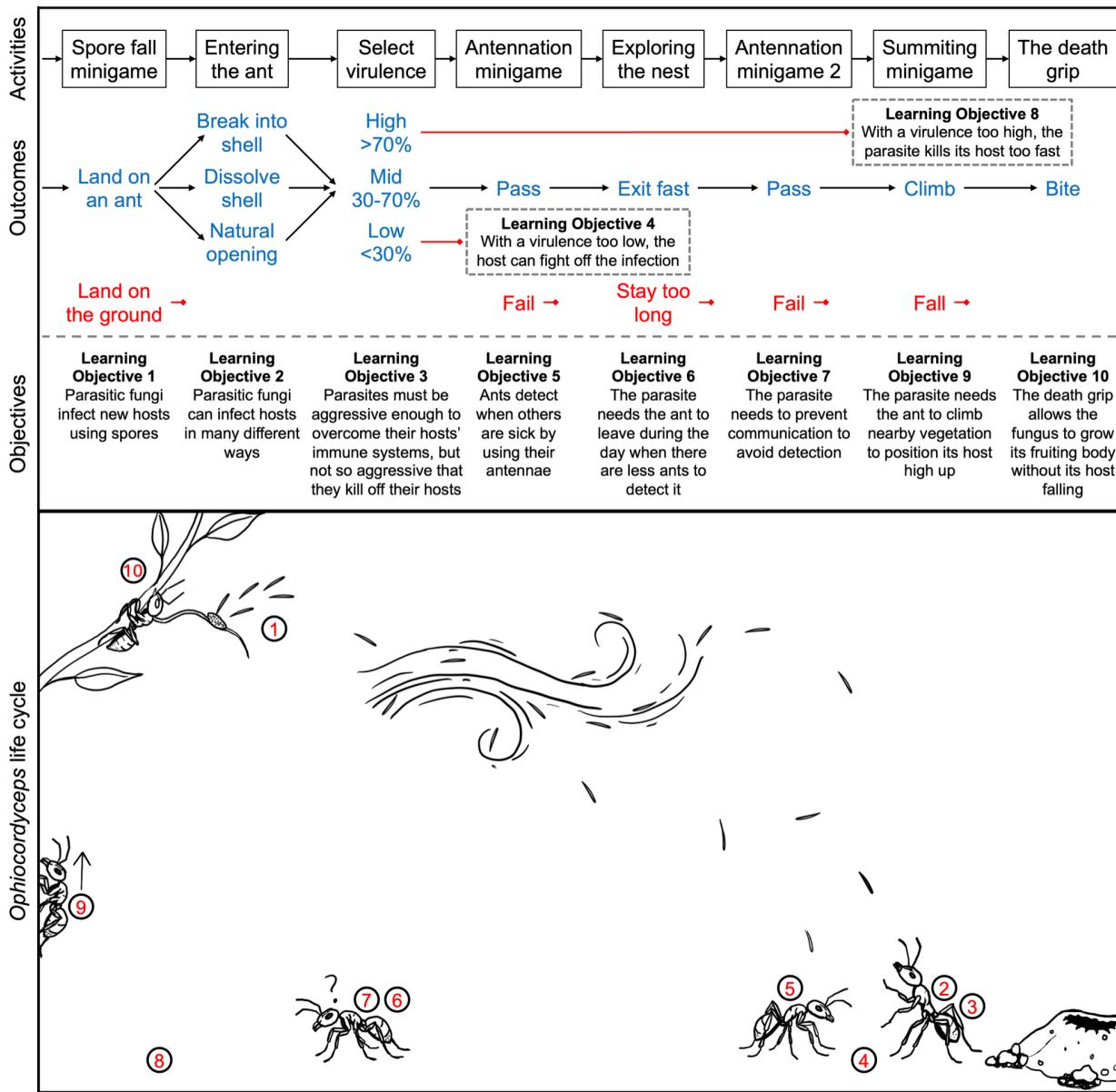
179 *Incorporation of educational components*

180 The game was designed with children and young adults in mind (ages 12-25), reflecting the
181 population most familiar with VR technology and keeping with the lower age limitation
182 suggestions of Meta Quest headsets (Meta Platforms, Inc.). Because parasites like *Ophiocordyceps*
183 and other disease-causing agents operate at a much smaller scale than is experienced by human
184 beings, VR was immediately attractive as a medium for this project. Using VR, we aimed to enrich
185 learning by creating an immersive environment that transports the player into a tiny world with a
186 perspective that is entirely new to them. We hypothesized that this element of escapism would
187 help remove players from preexisting beliefs that could hinder learning about evolution (Petersen
188 et al., 2022). Being as small as a fungal spore, and later an ant, players can explore and interact
189 with a “wilderness” of small plants, animals, and fungal organisms, as if a blade of grass were the

size of a tree. Similar approaches have been used with great success since the origin of three-dimensional video games (e.g., A Bugs Life by Traveller's Tales, 1998; Pikmin by Nintendo, 2001; and Grounded by Obsidian Entertainment, 2020).

While the immersive capabilities of VR tools have demonstrated success with improving learning when applied in various educational settings (Lin et al. 2024; Liu et al., 2023; Merchant et al., 2014), a recent systemic review has also shown that creators often focus too heavily on the application of VR itself and not enough on the underlying educational theory, resulting in poor learning outcomes (Radianti et al., 2020). We sought to avoid this common mistake by prioritizing gameplay mechanics associated with our evolution learning objectives. By letting players make their own choices in the game, most of which result in failure, we mirror the essence of natural selection and create a myriad of productive failure opportunities (Loibl & Leuders, 2019; Metcalfe, 2016). Allowing the players to make mistakes and incorporate adjustments through repetition induces positive reinforcement through a feeling of fulfillment from accomplishing something challenging. This leads to longer-lasting impact on memory, a strategy that is commonly used for memory-based studying (Karpicke & Blunt, 2011).

We also emphasized secondary learning goals relating to disease transmission, ant biology, and the life cycle of *Ophiocordyceps* fungi using a narrative-driven, choose-your-own-adventure format with several branching paths and multiple endings (Figure 1). In total, there are ten possible secondary learning objectives, nine of which are accessed through incorrect choices made along the adventure (Figure 1). While it is unlikely that every player will access all ten endings on a single playthrough, this design provides more targeted instruction in areas where misconceptions exist. In essence, if the player intuitively makes the correct choice, they will not access the learning objective for the corresponding incorrect choice. The game thus functions in a formative assessment manner comparable to test corrections in an academic setting.



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222 Originally, we included additional information, primarily pertaining to the life cycle of
223 ants, as in-game pop-up text boxes near points of interest for players to read at their leisure.
224 However, alpha testing of the game showed that many participants, particularly adolescents,
225 immediately skipped the text boxes as they appeared on screen so they could continue exploring
226 the virtual world. Therefore, to help facilitate these learning objectives whilst maintaining the
227 immersive feel of the game, we collaborated with acting students to record in-game voice overs.
228 The voice overs were split into two parts: a “naturalist” who took on the role of the narrator and a
229 fungal “hive mind” that took on the role of the player’s parasite mentor. By having two separate
230 voices, we were able to distribute the in-game information into fungus-related information and
231 ant-related information (Supplementary material 1). Other informational material that pertained to
232 gameplay elements, e.g., movement controls and mini-game instructions, were not narrated.

233

234 *Game Development*

235 The creation of this game presented an opportunity for mutual learning and career development at
236 different stages. This included the incorporation of students throughout the project. The prototype
237 for the game was created as part of an undergraduate Game Design course focusing on VR.
238 Students were first given a survey of published games and a set of tutorials on using Unity to
239 produce VR applications. Then, they formed groups to “pitch” sponsors for the opportunity to
240 work on their projects, which ensured student participation in the game’s construction was interest
241 driven. Those who elected to work on the prototype of *Zombie Ants VR* developed a proposal in
242 response to the research team’s Request for Proposals (RFP) and used it as a guide throughout
243 development. This RFP included the following objectives: 1) educate the players about behavior
244 manipulation of ants via fungal infection, 2) allow players to participate in these processes by
245 simulating an immersive experience, and 3) showcase the latest scientific research and our current

246 understanding of zombie ants. It was also made clear that players should be tasked with making a
247 series of decisions based on their scientific understanding of the disease dynamics and given
248 formative feedback during the experience. The concept of merging these choices with the structure
249 of a walking simulator was ultimately suggested to reinforce the narrative of the player enacting
250 the role of the fungus and its infected host. Students worked as a team and met regularly with the
251 sponsors, implemented the basic scene structure, and created some of the VR interaction
252 mechanics. The final course version of the game included a combination of custom gameplay
253 logic, student-created models and animation, and narrator dialogue that was reviewed by the
254 sponsor.

255 After completion of the course, bachelor's students in digital media and game design, and
256 a recent master's graduate in game and interactive media design, were hired to build on the
257 prototype to create an alpha model for game play testing. This testing would inform future work
258 on the definitive (beta) version of the game. They were tasked with further developing and
259 improving the game's graphics and overall gameplay dynamics. This was largely done using the
260 cross-platform game engine Unity (Unity Technologies) in combination with UtilitySO for
261 scripting objects. This tool provided unity events with easy access methods from other key game
262 scripts, simplifying them to fit into Unity events and allowing for event triggers to be used. These
263 event triggers were placed throughout the game to prompt text boxes, voice acting lines, and
264 minigames (Figure 2). The selectable choices and minigame dynamics were designed with action-
265 based outcomes that are tied to each of the ten secondary learning objectives.

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Figure 2. Virtual environment. The game can be broken down into three levels. The left-most panel in each row depicts the map of the virtual environment for each level. The panels to the right show screenshots of each in-game event. The top row shows level 1, in which the players learn about how fungal parasites infect new hosts. The middle row shows level 2, in which players explore the ant nest and learn how ants communicate, detect infections, and organize their colonies. The bottom row shows level 3, which can be accessed in either night mode or day mode depending on choices made in level 2. Here, players learn why *Ophiocordyceps* parasites manipulate daily rhythms in their hosts and that they induce summing and death grip behaviors in manipulated ants to improve the spread of new spores, at which point the whole cycle starts again.

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Game Modes

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For *Zombie Ants VR: Definitive Edition*, we created three different game modes to facilitate its use in different educational environments: In the original game mode, which is called “Survival” mode in the start menu, the game is played as intended. This version of the game most resembles natural selection, requiring all players to start over from the very beginning as a new

282 spore after each mistake. By having the players start from the beginning, the game reinforces
283 learning through active recall in the same manner as other common metacognition learning tools
284 and retrieval-based active learning strategies (e.g., flash cards, spaced repetition, or dual coding)
285 that are associated with greater learning outcomes (Karpicke & Blunt, 2011).

286 While Survival mode is hypothesized to result in the greatest degree of learning, public
287 engagement events often require fast-paced experiences with a higher turnover rate for
288 participants. For this reason, we created the “Exhibit” mode. This mode reduces the overall
289 gameplay time by allowing the players to continue from spots in which they fail and repeatedly
290 retry failed events. Importantly, this mode still maintains elements of the Survival mode that are
291 vital for teaching about evolution, primarily the use of “restart” and “continue” buttons that instead
292 say, “Spawn New Spore”. Since the players can correct their mistakes in this mode, it was
293 important to make clear that any second attempt is performed with a new spore that has made it
294 back to this stage of the game. Like in Survival mode, this reinforces elements of natural selection
295 that act on the level of populations. Failure to make this clear may otherwise misconstrue learning
296 outcomes towards a more individualistic, Lamarckian view of evolution.

297 Exhibit mode reduces the overall gameplay time to around 10-15 min depending on the
298 number of failed attempts and to the degree of active exploration by the player. This flexibility
299 preserves the immersive curiosity we aim to foster in the game; however, the remaining
300 unpredictability of playtime can make it challenging to implement in a classroom environment. To
301 address this concern, we also made an “Educational” mode that has a more linearized progression
302 design, sometimes referred to as “railroading”. To achieve this, we made two further changes to
303 the Exhibit mode: 1) we removed the player’s movement capabilities and replaced them with a
304 teleportation system, and 2) we changed the continue mechanic to respawn new spores on the other
305 side of failed choices or minigames as if they had succeeded. Importantly, the player is still

confronted with the death screen and its associated learning materials upon fail. Moreover, while Education mode does not allow the player to move their character, they are still able to look around at each teleportation junction, retaining some of the immersive elements of gameplay. Together, this makes the duration of the gameplay much more predictable in this game mode so it can be used along with a projector and a volunteer to provide lectures or other types of timed presentations about the zombie ant life cycle. Furthermore, in addition to its use for presentations, we found that this game mode is also more amenable for children under the age of 12 for whom the minigames are often a bit too difficult to play.

Accessibility

VR provides new opportunities for visual learners and those with physical disabilities (Chițu et al., 2023), helping to bridge inclusivity gaps in education. That being said, the use of VR hardware does come with potential risks for some users. This includes musculoskeletal risks such as neck, shoulder, or back strain from the weight of the headset. Users can also suffer from eye or vision strain, fatigue, or dryness resulting from vergence-accommodation conflict. Motion sickness from a disconnect between visual inputs and vestibular system inputs can also be experienced (Saredakis et al., 2020), as well as neurological or cognitive issues like “VR hangover” (Porter III & Robb, 2022), cognitive overload, or risk of seizure. Fortunately, many of these risks can be mitigated with supervised use of the hardware and through the incorporation of in-game accessibility features.

With these risks in mind, we assured our game did not include any flashing lights that could induce epileptic seizures (Hermes et al., 2018). We also included a motion sickness option in which the smooth video transitions are replaced with a blinking effect. This blinking effect darkens the screen to black during non-player-directed movements and returns only after

330 teleporting the player to the next instance. This dramatically improved the game's playability for
331 individuals with more severe forms of motion sickness.

332 In addition to health and safety concerns, we also aimed to improve accessibility by using
333 colorblind-friendly color palettes, incorporating stationary game controls for those with physical
334 disabilities, and text box popups in game for those with auditorial impairment. The game also has
335 two language options, English and Dutch, with the framework to easily add more in the future. To
336 make the game accessible to participants of all education levels and ages, the text and voice acting
337 lines for both English and Dutch were written at the standardized language level B2 according to
338 the Common European Framework of Reference for Languages (CEFR). This was verified with
339 the Dutch CEFR text analysis tool (Velleman & van der Geest, 2014). B2 level is characterized by
340 short sentences and common word use and represents an “upper intermediate” proficiency at which
341 individuals can interact fluently. Exceptions to this rule were made when scientific terms were
342 needed as part of learning objectives.

343

344 *Questionnaires to test educational outcomes*

345 To test whether playing *Zombie Ants VR: Definitive Edition* resulted in a better understanding of
346 disease evolution, we opted to compare participant responses through pre-game and post-game
347 questionnaires. We designed these questionnaires with careful consideration to avoid common
348 pitfalls outlined by Kishore et al. (2021). This included techniques to mitigate testing biases that
349 commonly lead to unreliable results in surveys. Both questionnaires were written in B2-level
350 language based on the same CEFR standards used for in-game text and audio lines and checked
351 using the Dutch CEFR text analysis tool (Velleman & van der Geest, 2014). The questions were
352 designed using a combination of four-answer multiple-choice questions and five-point Likert scale
353 responses. To deliver these questionnaires to study participants, we used the software Qualtrics

(Silver Lake and CPP Investments). Responses were anonymized using randomized three-letter codes that were entered at the top of each questionnaire. The order of all other questions was randomized to prevent test-taking effects (Stefkovics & Kmetty, 2022; Tourangeau, 2012). We also randomized the answers for each multiple-choice question, apart from questions that asked about age range and education level, which were arranged in a logical, incremental order from least to greatest age/experience (Supplementary Material 2 & 3). We also limited the number of questions on each questionnaire to avoid testing fatigue associated with rapid-guessing behavior and a decrease in satisfaction (Lindner et al. 2019).

One question on each questionnaire was related to the participants' understanding of evolution. These questions were designed to specifically test the players' pre-existing understanding of evolution and to see if their understanding improved after playing the game. Importantly, the game never uses the words evolution or natural selection, relying instead on gameplay mechanics to subtly impress upon the player the process of evolution as it occurs at the population level. We tested this effect using a multiple-choice format with four answers that reflect the correct definition of evolution and the three most common misconceptions about evolution. Of the three incorrect answers, one was designed to reflect an individual's acceptance of evolutionary theory but with an incorrect understanding of its mechanics. This response followed a more Lamarckian view of evolution, suggesting that natural selection acts at the level of an individual. By incorporating two scientific responses, we aimed to distinguish between mere acceptance and acceptance with understanding of evolutionary principles. This goes one step further than most research projects that focus merely on the acceptance of evolutionary theory as a metric for science literacy, but which fall short in addressing common difficulties with teaching the process of evolution, i.e., "organisms do not evolve; *populations* evolve" (Gregory, 2009).

377 The remaining two incorrect answers reflect common philosophical responses from
378 creationist and essentialist viewpoints, mainly that things are either “created” the way that they are
379 or simply “have always been” the way that they are. To further eliminate biases related to recall,
380 i.e., familiarity with the questions, we opted to reword the question about evolution on the post-
381 game questionnaire. While the question about evolution on the pre-game questionnaire asked,
382 “*Which of the following best describes how bacteria, fungi, and viruses change to infect new*
383 *hosts?*”, the post-game version asked, “*How does Ophiocordyceps infect new ants over time?*”. By
384 shifting the focus of the question from all pathogens to just *Ophiocordyceps* pathogens, we aimed
385 to prevent participants from simply answering the post-game question with the same answer used
386 in the pre-game question based on memory. This strategy was maintained across all possible
387 answers to the question as well (Table 1).

388

389 Table 1. Questionnaire response options for “*How do bacteria, fungi and viruses change to infect*
390 *new hosts?*” (pre-game) and “*How does Ophiocordyceps infect new ants over time?*” (post-game)

	Pre-game Answers	Post-game Answers
Darwinian	They change randomly with only the strongest infecting new hosts.	Each spore tries to infect new hosts, but only the successful ones survive
Lamarckian	They learn how to better infect new hosts through experience.	Each spore learns how to better infect new hosts over time
Creationist	They don't change; they are designed to infect new hosts.	Spores are designed to be able to infect new hosts
Essentialist	They don't change, the hosts become easier to infect.	The ants become easier to infect over time.

391

392 Since both the Darwinian (D) and Lamarckian (L) responses reflect an acceptance of evolution,
393 while the creationist (C) and essentialist (E) responses reflect a dismissal of these principles, we
394 were able to compare the ratio of DL responses to CE responses to gauge the general level of

395 scientific acceptance in our test population. We could then compare the ratio of D responses to
396 LCE responses to test the level of scientific literacy in our test population.

397 In addition to the question about evolution, we included another science-based question in
398 each questionnaire, which asked about disease transmission. However, because the in-game
399 activity for Learning Objective 2 does concern modes of infection, the game does not provide a
400 mechanism for reinforcing any particular learning outcome related to this topic. All three actions
401 provided are thus viewed as potentially correct and result in success (Figure 1). As such, the
402 answers on the post-game questionnaire for this question should closely match either the players'
403 pre-game answers or their selected choice in-game. This set of questions, therefore, acts as a
404 negative control for the evolution question.

405 The remaining questions on the pre-game questionnaire asked participants about their age,
406 experience with video games, education level, and their appreciation for biological topics (i.e.,
407 nature). The remaining questions on the post-game questionnaire asked participants about the
408 difficulty and perceived quality of the game, as well as their overall experience while playing the
409 game. These answers were used to screen for any sort of additional correlations that may contribute
410 to learning outcomes. All questions and possible answers for the pre-game and post-game
411 questionnaires can be found in Supplementary Materials 2 and 3, respectively.

412

413 *Exhibition and data acquisition for Zombie Ants VR: Definitive Edition*

414 *Zombie Ants VR: Definitive Edition* was debuted as a temporary exhibit at the University
415 Museum Utrecht in the Netherlands. The exhibit took place over four separate weekends with a
416 showcase from 10:00 – 16:00 every Saturday and Sunday. Museum attendees could view an
417 informational poster about zombie insects written for a young audience (De Bekker et al., 2023),
418 observe real-life samples of zombie ants under a stereomicroscope, and play the *Zombie Ants VR*:

419 *Definitive Edition* game. To ensure data protection for all players, the game was run directly from
420 a local laptop using a hardline to our Meta Quest 3 VR headset (Reality Labs).

421 Individuals interested in playing the VR game ages 12 and older were offered the
422 opportunity to participate in the study, which involved answering the pre-game questionnaire,
423 playing the game, and then answering the post-game questionnaire. Questionnaires were provided
424 on an iPad through links to Qualtrics surveys available in both English and Dutch. Participants
425 who wished to contribute to the study were told that the goal of the study was to test the educational
426 merit of the game and were further informed about the health and safety risks of VR hardware,
427 their data protection rights, and other frequently asked questions about the project. All adult
428 participants who agreed with the terms were asked to sign a consent form (Supplementary Material
429 4), while all participants under the age of 18 were asked to provide a verbal statement of
430 understanding regarding the experimental procedures and a verbal agreement to participate.
431 Furthermore, their legal guardians were asked to sign the consent form on their behalf, indicating
432 their agreement to allow their child to participate in the study. After signing, each participant was
433 provided a physical copy of the aforementioned information in addition to information regarding
434 project members and oversight personnel with contact information should they have further
435 questions or wish to withdraw from the study at a later date.

436 In total, the exhibit had 421 attendees, around 200 total players, and 30 participants who
437 agreed to partake in the study. Of these 30 participants, only one requested withdrawal of their
438 data from the study. From the remaining 29 participants, one individual did not answer the question
439 about evolution on the post-game questionnaire and another did not answer the control question
440 about disease transmission. This resulted in a total of 28 data points for which direct correlations
441 can be drawn between participants' pre-game knowledge and post-game learning outcomes
442 (Supplementary Material 5. Data).

443 The gameplay of each player was displayed from the headset to a large TV screen behind
444 them, allowing other museum attendees at the exhibit to watch their progress throughout the game.
445 This gameplay was recorded using an HDMI AVerMedia USB Live Gamer Portable 2 Plus AVT-
446 C878 Plus DV478 capture card (AVerMedia) and saved under file names using the same 3-letter
447 code as the questionnaires. We were careful not to include participants in the study who had
448 already seen the game. In the few cases where multiple people attended together and wanted to
449 participate in the study, the pre-game questionnaires were given to each participant before the first
450 player began their playthrough.

451

452 *Data analysis*

453 Gameplay footage of participants was scored manually using time stamps that started as soon as
454 the player exited the instruction panel and ended when the screen faded to black for the game
455 completion screen. The number of mistakes made throughout the game, and subsequent number
456 of times the player spawned new spores, was counted using each instance a failure screen appeared.
457 This information, together with the biographical information, perceived entertainment values, and
458 the difficulty level of the game was analyzed alongside the directionality of responses for the
459 question about evolution. In this way, we aimed to determine if the game significantly improved
460 understanding of evolution and whether these variables contributed to its success.

461 All statistical analyses were performed using R and R-studio Version 2023.06.0+421
462 (2023.06.0+421). To test if there was a significant increase in the number of correct answers about
463 evolution provided on post-game questionnaires compared to pre-game questionnaires, we used
464 the McNemar's statistical test designed for paired binary outcomes where the correct answer was
465 assigned the numerical value 1 and all other wrong answers were assigned the numerical value 0.
466 This was followed by a Fisher's exact test. To test if length of gameplay was correlated with

467 learning outcomes, we used a logistic regression for data involving continuous predictor, time, and
468 binary outcomes, i.e., correct or incorrect answers on the post-game questionnaire. We also used
469 a Wilcoxon rank-sum test to test whether an individual's duration of gameplay affected learning
470 outcomes. Finally, a paired odds ratio comparison was used to determine the degree of
471 improvement or decline of learning outcomes, and Spearman's rank correlations were used to
472 screen for other effects between learning outcomes and information about the player. The code
473 used to perform these tests was written with assistance from artificial intelligence (AI) and is
474 provided in Supplementary Material 6. For ethical and data privacy reasons, this was the only use
475 of AI in the project.

476

477 *Ethics Approval*

478 We received approval from the Utrecht University Science-Geosciences Ethics Review Board to
479 conduct this study at the University Museum Utrecht. The Science-Geosciences Ethics Review
480 Board provides professional and independent reviews of research proposals involving human
481 subjects and advises on ethical and privacy issues. They primarily review studies that do not fall
482 under the scope of the Dutch Medical Research involving Human Subjects Act (Wet medisch
483 wetenschappelijk onderzoek met mensen). The committee had no objections to the research
484 activities as described in our proposal titled 'Zombie Ants VR: Using virtual reality to engage the
485 public and improve science literacy', which was approved on April 18th, 2025. The resulting
486 research project was then carried out in the month of June 2025. By securing ethics approval, we
487 met the due diligence and required standards for participant safety, data handling, and scientific
488 integrity.

489

490

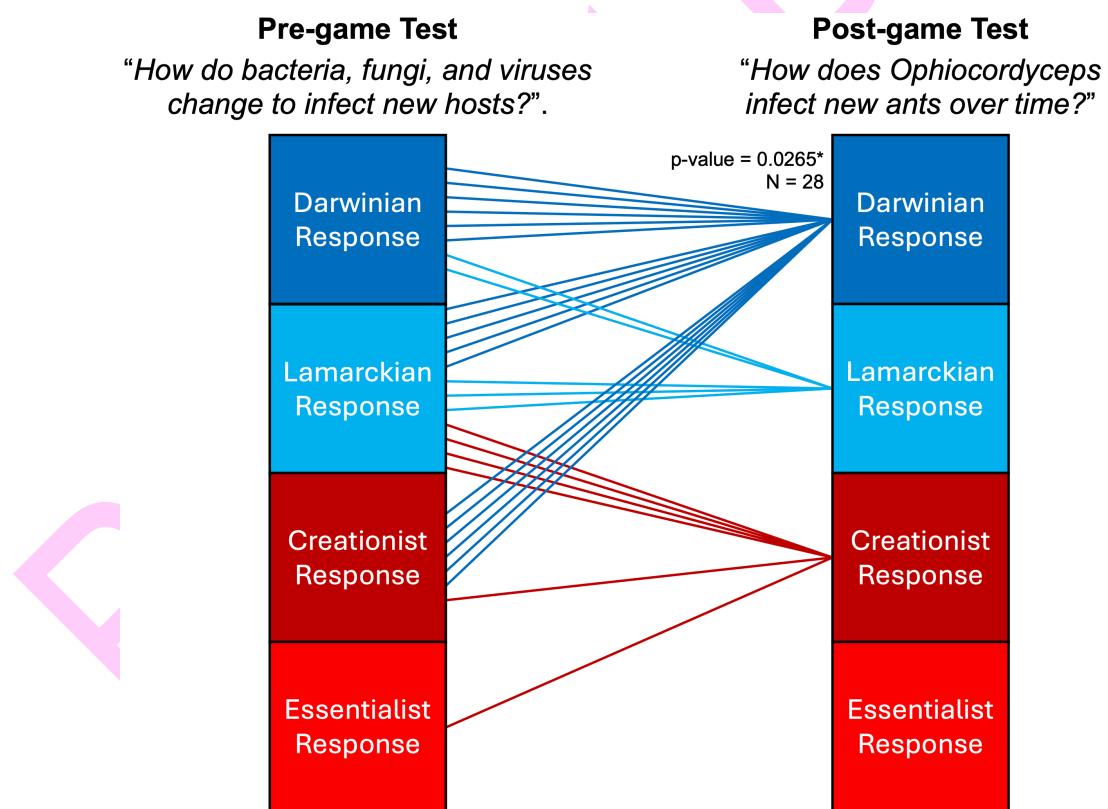
491

Results

492 *Does playing Zombie Ants VR: Definitive Edition improve evolution literacy?*

493 The number of correct answers on the pre-game test was eight (28.6%) which significantly
 494 improved to 17 on the post-game test (60.7%, McNemar's p-value of 0.0265*; Figure 3). A paired
 495 odds ratio test showed this result was correlated with participants going from an incorrect response
 496 to a correct one after playing the game, which occurred 5.5 times more often than the inverse (5%
 497 confidence interval between 1.219 and 24.814). We further compared these results to our negative
 498 control test questions about disease transmission, which did not show any significant increase in
 499 correct responses (McNemar's test p-value of 0.7237 NS).

500



501

502 **Figure 3. Learning outcomes for *Zombie Ants VR: Definitive Edition*.** Results showed that out
 503 of 28 responses, only eight individuals answered with the correct Darwinian response on the pre-
 504 game questionnaire; however, after playing *Zombie Ants VR: Definitive Edition*, the number of

505 correct responses improved to 17 (McNemar's p-value of 0.0265*). While two participants who
506 originally selected the correct response answered incorrectly on the post-game questionnaire, a
507 Paired Odds Ratio tests showed that overall participants were 5.5 time more likely to improve in
508 their understanding of evolution after playing the game (5% confidence interval between 1.219
509 and 24.814).

510

511 *Are preexisting views correlated with learning outcomes?*

512 To test if a participant's preexisting understanding or acceptance of evolution was predictive of
513 the choice they made after playing the game, we used a Chi-square test of independence
514 (Supplementary Materials 6). Because some of the groups contained fewer than five participants,
515 we used the Fisher's Exact Test variant. We were particularly interested to know if a player's
516 preexisting non-scientific views were correlated with a corresponding non-scientific answer after
517 playing the game. This was shown not to be the case with the Fisher's Exact Test for Count Data
518 determining a lack of significant correlation between pre- and post-game answer types ($p =$
519 0.1212). Of the 28 participants who answered the evolutionary question on both questionnaires,
520 20 individuals provided a science-based response (71.4%) while seven participants gave
521 creationist responses (25%) and one answered with an essentialist response (3.6%). Of those
522 providing a scientific response, only eight (38.1%) gave the correct Darwinian response while the
523 other 13 (61.9%) chose the Lamarckian response reflecting a misunderstanding of evolutionary
524 principles. This suggests that nearly 2/3 of our study participants who accept evolution
525 misunderstand how it works. After playing the game, 22 of the answers on the post-game
526 questionnaire reflected scientific responses, suggesting only a marked improvement in the overall
527 number of scientific answers (71.4% to 78.6%); However, as was noted in the previous test, the
528 number of correct Darwinian responses significantly increased. Six of these correct responses

529 came from the seven participants who had previously selected creationist responses on the pre-
530 game questionnaire, indicating that the game was successfully able to teach evolutionary principles
531 to 85.7% of those with creationist views.

532

533 *Does age or prior experience with video games affect learning outcomes?*

534 The group with the highest amount of video game experience in our study, with an average score
535 of 3.6 out of 5.0 on a Likert scale, was 12–15-year-olds. This was much higher than other groups
536 which all scored between 1.0 and 2.0. Despite this advantage, we saw an increase in the number
537 of correct responses after playing the game in every age bracket, regardless of video game
538 experience, with the exception of 22–30-year-olds for whom the number of correct answers
539 remained the same (Table 2).

540

541 Table 2. The relationship between learning outcomes and the age or average gaming experience
542 of participants.

Age	Number of participants	Average gaming experience	Correct answers Pre-game	Correct answers post-game
12 – 15	8	3.6	1	4*
16 – 18	1	1.0	0	1*
19 – 21	2	1.0	0	1*
22 – 30	7	2.0	5	5
31 – 40	5	1.6	1	3*
> 40	6	1.5	1	3*

543 * Indicates an increase in overall number of correct answers

544

545 *Does level of education affect learning outcomes?*

546 Our data showed that recent university graduates were the group with the highest ratio of initial
547 correct answers; however, a person's level of education did not appear to significantly affect
548 learning outcomes. Scores were improved across all groups, with the exception of 4-year university

549 graduates and those who had obtained doctoral degrees for whom the number remained the same
550 (Table 3).

551

552 Table 3. The relationship between learning outcomes and prior education of participants.

Education	Number of participants	Correct answers Pre-game	Correct answers post-game
Elementary School	2	0	1*
Middle School	4	1	2*
University Preparatory Education	5	1	3*
2 Years University	1	0	1*
4 Years University	6	2	2
Master's Degree	7	1	5*
Doctoral Degree	4	3	3

553 * Increase in overall number of correct answers

554

555 *Does appreciation for nature affect learning outcomes?*

556

557 There appeared to be a correlation between a participant's interest in nature and an increase in
558 correct responses on the post-game questionnaire; however, our sample size was much too small
559 to demonstrate a significant effect (Spearman's rank correlation, $p = 0.6853$, $\rho = 0.0786$).

560

561 Individuals who provided negative opinions on their appreciation for nature (1 or 2 on a 5-point
562 Likert scale) did not improve in their understanding of evolution after playing the game (Table 4).

563

564 Individuals with neutral responses (3 on a 5-point Likert scale) saw an increase in correct responses
from 33% to 66%, while individuals with positive views on appreciation for nature (4 or 5 on a 5-
point Likert scale) saw an increase in correct responses from 28.6% to 61.9%.

565 Table 4. The relationship between learning outcomes and the participants' level of appreciation
566 for nature.

Appreciation for Nature	Number of participants	Correct answers Pre-game	Correct answers post-game
1	1	0	0
2	1	0	0
3	6	2	4*
4	8	2	6*
5	13	4	7*

567 * Increase in overall number of correct answers

568

569 *Does entertainment value affect learning outcomes?*

570 Overall, participants enjoyed playing the game with an average score of 3.62/5.00 on a Likert
571 scale, reflecting a slightly positive view. While the one participant that provided a neutral answer
572 did not improve their understanding of evolution, all other groups showed an increase in number
573 of correct answers on the post-game questionnaire (Table 5). This included an increase in correct
574 answers from 30% to 65% among participants who viewed the game as enjoyable and an increase
575 from 25% to 50% for participants who viewed the game as unenjoyable.

576

577 Table 5. The relationship between learning outcomes and level of enjoyment experienced by
578 participants during the game.

Enjoyed the game	Number of participants	Correct answers Pre-game	Correct answers post-game
1	3	1	2*
2	5	1	2*
3	1	0	0
4	11	3	8*
5	9	3	5*

579 * Increase in overall number of correct answers

580

581

582 *Does performance affect learning outcomes?*

583 Analysis of the gameplay footage showed that the average completion time of the game was 12:58
584 min. To test if length of gameplay was correlated with learning outcomes, we used a logistic
585 regression and Wilcoxon rank-sum test. In both cases, we found that length of gameplay was not
586 a significant indicator of learning (Logistic regression p-value of 0.331 and a Wilcoxon rank-sum
587 p-value of 0.3938). While we hypothesized that a longer gameplay experience would result in
588 greater odds of positive outcomes, we found that the average amount of time played by individuals
589 who answered incorrectly on the post-game questionnaire was actually longer than those who
590 chose the proper Darwinian response by nearly 2 min (111.5 s; Supplementary Materials 5). This
591 finding was consistent even when only considering individuals who fully completed the game
592 (Logistic regression p-value of 0.597 and Wilcoxon rank-sum p-value of 0.7544). Furthermore,
593 we also found that the number of mistakes made during the game was not associated with learning
594 outcomes (4.59 on average with a median of 4 and a mode of 3; Logistic regression p-value of
595 0.600 and Wilcoxon rank-sum p-value of 0.3831 for full dataset, 0.964 and 0.7202 for data limited
596 to complete runs).

597

598 Discussion

599 By using gameplay mechanics rather than informational prompts to teach players about the
600 process of evolution, *Zombie Ants VR: Definitive Edition* significantly improved evolution literacy,
601 regardless of players' age, education level, (previous) gaming experience, and appreciation for
602 nature. This was true for both participants who answered with a scientific but incorrect answer on
603 the pre-game questionnaire and for those who provided non-scientific answers. In total, six out of
604 seven participants changed their response from a creationist stance to the correct Darwinian view
605 after playing the game, while five out of 11 changed their response from Lamarckian to Darwinian.

606 This suggests that the game is not only an effective public engagement tool but also useful for
607 addressing misconceptions about the theory common in more formal biology education
608 environments.

609 While none of the participants who answered with a Darwinian response in the pre-game
610 questionnaire changed their answer to a non-scientific choice, two did change their answers to the
611 Lamarckian response. This could be indicative of a counterproductive outcome of playing the
612 game. Though, this small number could also be explained guesswork, a common characteristic of
613 survey data (Ward & Meade, 2023). While ideally we do not want anyone to change their answer
614 from a correct understanding of evolution to an incorrect one, the 5.5 times higher rate of
615 improvement to the correct response indicates that our VR game has an overall positive
616 educational impact.

617 In addition to demonstrating the educational potential of gamification techniques and VR
618 technology, our study also helps illuminate other issues pertaining to the state of evolution literacy
619 in our community. While comparatively, the Netherlands has higher rates of scientific literacy and
620 acceptance of evolutionary principles than other countries like the United States (Miller et al.,
621 2006), our study shows that only about a third of participants understood these evolutionary
622 principles. When combined with the non-scientific responses, only about a quarter of participants
623 properly understand evolution to a degree required for educated decision making with regards to
624 public health. This provides further evidence that mere acceptance of evolution is not necessarily
625 correlated with an understanding of evolution and highlight a greater need for further public
626 outreach efforts, even in countries for which science is more generally accepted.

627 Our study also shows that, when used properly, gamification and VR can be used for
628 inclusive biology educational purposes. Our target audience was originally children and young
629 adults ages 12-22 to encourage fascination for the natural world and science in their teenage years

630 during which these interests tend to wane (Bonnette, 2019; Potvin & Hasni, 2014). However, we
631 found that the game had a positive educational impact on nearly all participants, regardless of age
632 or experience with video games. While we noticed a clear difference in how long it took younger
633 players to get used to the controls (fast) compared to older players (slower), those who kept with
634 it and completed large portions of the game benefited from the desired learning outcomes. These
635 findings provide additional support for educational systems around the world, at various levels of
636 education, who aim to incorporate virtual reality and its immersive potential to provide new
637 perspectives to students.

638 Furthermore, while our study did not provide any metrics for the comradery or group
639 learning offered by displaying participants' gameplay on the screen, the collaborative learning that
640 appeared to occur between families and friend groups who played the game together was notable.
641 Parent who were watching their children playing *Zombie Ants VR: Definitive Edition* would
642 frequently ask the present researchers questions about the biology portrayed in the game. Quite
643 often, just getting a foot in the door can be the hardest part about science outreach. Creating a tool
644 that is entertaining enough to permeate that barrier is, in itself, a valuable resource for science
645 communication.

646

647 **Limitations**

648 This study was conducted in the Netherlands with museum attendees at the University Museum
649 Utrecht (UMU). Because UMU largely caters to families as their target audience, our data set has
650 a bimodal distribution of participants skewing towards children (ages 12-15) and older adults. It is
651 also important to note that we intentionally did not collect data on sex, nationality, or residence
652 status of study participants to provide a greater feeling of inclusion and safety. We therefore cannot
653 draw any conclusions about demographics variables beyond age. We can however make inferences

about the nationality of participants based on their voluntary selection of Dutch as the primary language for gameplay. From this information, we infer that most participants in this study were Dutch. Our results thus largely reflect the current state of scientific literacy in the Netherlands. Other studies seeking to repeat our work should keep this in mind and reflect on the socio-political status in other nations as an attenuating factor.

Furthermore, because we conducted our study with museum attendees, it is likely that our data skews more towards scientifically inclined portion of the general population. This may have impacted the relative ratio of DL answers to CE answers on our pre-gameplay questionnaire and may not be an accurate representation of the general views of people from the Netherlands. The gallery style expectations of the museum environment, where museum attendees do not spend much time at each exhibit, also limited the learning objectives that we could test during this study. For this reason, our questionnaires were designed to be short and focused on testing one learning objective: the process of evolution. This study therefore does not include any test data for the secondary learning objectives of the game pertaining to the pathogenic life cycle of behavior-manipulating fungi and the social structure of ants.

Finally, the survey data collected in this study was analyzed under the assumption that participants fully understood the meaning of each possible response to the evolution questions. Language interpretation, particularly in multi-lingual studies, can be tricky. Without controls for ensuring the participants' understanding of the intended meaning for each possible answer, it is possible that some of the participants' answers were given with a different interpretation of the text. We did not incorporate these sorts of controls in our study because discussing, for example, information that may stem from a participant's religious background could have elicited the defensive responses that we sought to circumvent. Furthermore, the fast-paced museum format of the study also limited our ability to have players explain or express their understanding in a

678 longer, written response. We therefore cannot be certain that participant responses accurately
679 reflect conceptual knowledge or if they are skewed by one's ability to express that knowledge
680 correctly or discern written descriptions within the parameters of this study.

681

682 **Conclusions**

683 The results from our project demonstrate that gamification, particularly the use of trial-and-error
684 mechanics, can be used to teach the process of evolution within the context of infectious disease
685 in a way that does not conflict with people's preexisting political or religious views. This makes
686 gamification a powerful tool capable of improving science literacy, both in the classroom and in
687 the greater community. By understanding how evolution contributes to disease transmission
688 dynamic and the emergence of new thermotolerant and antimicrobial-resistant pathogens, we hope
689 that educated individuals will be able to make better public health decisions in the future.

690

691 **List of abbreviations**

- 692 • VR – Virtual Reality
- 693 • CEFR – Common European Framework of References for Learning
- 694 • RFP – Request for Proposal
- 695 • D - Darwinian
- 696 • L - Lamarckian
- 697 • C - Creationism
- 698 • E – Essentialism
- 699 • UMU – University Museum Utrecht
- 700 • AI – Artificial Intelligence

701

702

703 **Declarations**

704 *Availability of data and materials*

705 The data acquired and used for statistical analyses in this study is provided as supplemental
706 material 5.

707
708 *Competing interests*

709 Authors declare that they have no competing interests.

710
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719
720 *Authors' contributions (CRediT)*

- 721 1. Conceptualization: WCB, JM, CdB
- 722 2. Methodology: WCB, MG, CdB
- 723 3. Software: BJM, NSC
- 724 4. Validation: WCB, MG, CdB
- 725 5. Formal Analysis: WCB
- 726 6. Investigation: WCB, MG, BJM, CdB

- 727 7. Resources: WCB, CdB
- 728 8. Data Curation: WCB
- 729 9. Writing – Original Draft: WCB
- 730 10. Writing – Review & Editing: WCB, MG, BFM, NSC, JM, CdB
- 731 11. Visualization: WCB, BJM, NSC
- 732 12. Supervision: WCB, NSC, JM, CdB
- 733 13. Project Administration: WCB, NSC, JM, CdB
- 734 14. Funding Acquisition: WCB, CdB

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747

748 **Footnotes**

749 n/a

750

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751

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932 *Supplementary material/Web links*

933 Supplementary material 1. Voice acting lines.docx

934 Supplementary material 2. Pre-game questionnaire.docx

935 Supplementary material 3. Post-game questionnaire.docx

936 Supplementary material 4. Consent form.docx

937 Supplementary material 5. Data.xlsx

938 Supplementary material 6. R-code.R

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940 *Zombie Ants VR: Definitive Edition* download page on Steam:

941 https://store.steampowered.com/app/3765230/Zombie_Ants_VR_Definitive_Edition/