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Quantitative Genetics of Body Size Evolution in Islands: an individual-based simulation approach

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Ethics

Does your article include research that required ethical approval or permits?:

This article does not present research with ethical considerations

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CUST_IF_YES_ETHICS :No data available.

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It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:

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JAFD-F, P. R., J. H. and A. M. S. conceived the study and wrote the first draft. JAFD-F, L.J. and TFR wrote the main codes and L.J. conducted all simulations; JAFD-F, J. H., A.M.S. and PR discussed the results and interpretations, and P.H.H. and N.R.E. provided original environmental data for time series analyses. All authors contributed to writing of the final version of the manuscript.

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4 **Quantitative Genetics of Body Size Evolution in Islands: an**
5 **individual-based simulation approach**

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24 **ABSTRACT**

25 According to the Island Rule small-bodied vertebrates will tend to evolve larger body size
26 on island, whereas the opposite happens to large-bodied species. This controversial pattern
27 has been studied at the macroecological and biogeographical scales, but new developments
28 in quantitative evolutionary genetics now allow studying the Island Rule from a
29 mechanistic perspective. Here we develop a simulation approach based on an Individual-
30 Based Model (IBM) to model body size change on islands as a progressive adaptation to a
31 moving optimum, determined by density-dependent population dynamics. We applied the
32 model to evaluate body size differentiation in the pigmy extinct hominin *Homo floresiensis*,
33 showing that dwarfing may have occurred in only about 360 generations (95% CI ranging
34 from 150 to 675 generations). This result agrees with reports suggesting rapid dwarfing on
35 large mammals on islands, as well as with the recent discovery that small-sized hominins
36 lived in Flores as early as 700 kyr ago. Our simulations illustrate the power of analyzing
37 ecological and evolutionary patterns from an explicit quantitative genetics perspective.

38

39 **Keywords:** adaptation, body size, dwarfing, island rule, *Homo*

40

41

42 1. Introduction

43 The Island rule is amongst the most widely discussed body size patterns in Ecology, with a
44 long history of heated debates and controversies [1-5]. This biogeographical pattern states
45 that after colonizing an island, small-bodied vertebrates will tend to evolve towards larger
46 bodies (i.e. gigantism), whereas large-bodied species will reduce their body size (i.e.
47 dwarfing) [6,7], in a continuous linear grade [8]. Despite the enduring controversy and the
48 discussions around the ubiquity of the pattern and the ecological and evolutionary
49 mechanisms behind it [2, 5, 9], islands are legitimately renowned for some spectacular
50 examples of dwarfing in large artiodactyls, proboscideans and even hominids [see 10-14].

51 The Island rule was traditionally studied at the macroecological and biogeographical
52 scales, comparing several island species at once and trying to correlate their shift in body
53 size from their presumed ancestor [8] with i) the islands physical and environmental
54 characteristics or ii) with biotic characteristics that could be surrogates of competition or
55 predation [15-18]. At the macroevolutionary scale these patterns are better described by a
56 punctuated model in which body size shifts occur fast after speciation and are followed by a
57 stasis [19]. However, regardless of the macroevolutionary and macroecological
58 generalization of the Island rule, it is important to recognize that this pattern must derive
59 from population-level processes that are still little explored.

60 Body size changes in insular populations may occur over a relatively short time,
61 involving combined effects of genetic adaptations and phenotypic plasticity [16, 20-21].
62 Palovacs [20] proposed a general life-history framework to explain the evolutionary
63 trajectory of body size on islands (see also [22] for first insights on life-history patterns in
64 island species evolution). Both gigantism and dwarfing would thus be explained by a
65 complex interaction of adaptive responses involving the balance between reduction of
66 growth rates under resource depletion and reduced mortality on islands [23], or simply by
67 changes in life history traits related to reduction in the age of sexual maturity [24, 25].
68 Ecological processes involving phenotypic plasticity and life-history shifts may occur fast,
69 in the first few generations after the island colonization event, triggering or canalizing long-
70 term changes by natural selection due to intraspecific competition [16, 24].

71 Several theoretical models have been proposed to describe the evolutionary
72 dynamics of quantitative traits under different processes since first developments of
73 quantitative and population genetics in early 20th century [26]. In the context of insular
74 evolution, Diniz-Filho and Raia [27] used quantitative evolutionary genetics models to
75 evaluate brain and body size differentiation in *Homo floresiensis*, showing that adaptive
76 explanations for its dwarfing from an *H. erectus* ancestor are plausible. However,
77 incorporating complex evolutionary dynamics with more realistic population dynamics
78 under demographic and environmental stochasticity requires alternative approaches. Here
79 we expand upon our previous analysis [27] by using a simulation approach based on an
80 individual-based model (IBM) grounded on first principles of population and quantitative
81 genetics [26, 28]. Our main focus is to evaluate the plausibility of fast dwarfism in *H.*
82 *floresiensis* [29] incorporating several evolutionary processes and based on a new model in
83 which adaptation occurs under a moving optimum determined by density-dependent
84 population dynamics.

85

86 2. Methods

87 (a) *Modeling evolutionary processes within and between generations*

88 The details of the simulation model and the parametrization are available as Electronic
89 Supplementary Material (ESM). The simulation starts with a vector \mathbf{G} of genotypic values
90 for body size from N_0 individuals representing the initial deme colonizing the island,
91 sampled from a normal distribution with mean u_G and additive genetic variance v_A , for a
92 single quantitative trait (i.e., body size), thus assuming an infinitesimal model [30]. After
93 island colonization, the deme starts to grow in numbers following a logistic process up to
94 the island carrying capacity K . The process stops after t_G generations, when the mean
95 phenotypic value is close to the final adaptive peak defined for the island.

96 Phenotypic values of the population (\mathbf{P}) are obtained by adding to \mathbf{G} a vector with
97 randomly distributed environmental effects \mathbf{E} with mean zero and environmental variance
98 v_E (which is in turn determined assuming a known heritability h^2 for the trait), with
99 phenotypic plasticity incorporated as a linear reaction norm [31-34]. Fitness W_i for each
100 individual is defined according to a Gaussian approximation of stabilizing selection with an

101 optimum equal to O (the adaptive peak; see below for properties of this optimum). In our
102 model, natural selection acts through both differential survival (i.e., before reproduction)
103 and fecundity (i.e., number of offspring). Inbreeding is modeled by a Markovian
104 approximation tracking brother-sister breeding and reduces fitness by increasing mortality
105 in newborns [35, 36].

106 Variance in populations is restored by incorporating mutation and migration to our
107 model. Mutation is added as a mutation kernel [37], adding to \mathbf{G} values of the newborn a
108 vector with mean 0 and variance v_M/v_A (assumed to vary between 0.02-0.03 v_A for polygenic
109 traits such as body size [38]). We also added to the model the probability of island
110 colonization by new individuals, with genotypic values sampled from the original values of
111 \mathbf{G} at the beginning of the simulations (assuming that the continental population is large and
112 under demographic and genetic equilibrium).

113 Lastly, under a classical adaptive model for islands the optimum body size O would
114 be smaller than on the continent (so that the Gaussian adaptive landscape would converge
115 to a Gaussian, non-linear directional selection function if mean \mathbf{P} differs from O [39, 40]).
116 It is realistic that the intensity of dwarfing should be density-dependent and would thus be
117 small in the initial phases of colonization (i.e. when $N \ll K$). For instance, a reduction in
118 the age of sexual maturity due to abundant per-capita resources leading to small body size
119 would be initially attributed to plasticity [16, 23, 31] and followed by a second phase of
120 intraspecific competition and selection (this pattern also appears in Lister's [16] two-phase
121 model for dwarfing). Thus, it is expected that the initial adaptive peak (O_0) equals the mean
122 continental body size at the beginning, and natural selection would start favoring smaller
123 individuals as the population starts growing towards K .

124 At each step of the simulation individual body size will thus evolve and the time to
125 adaptation is defined as the time taken by mean \mathbf{P} to achieve the final optimum. As this is
126 an iterative process across generations, it is possible to record several parameters and
127 outcomes of the model at intermediate steps, including the mean and variance of \mathbf{G} ,
128 population density, inbreeding level, realized heritability h^2 , as well as statistics describing
129 the intensity of selection process (i.e., mean-standardized selection gradient, [41, 42]).

130

131 (b) *Evolution of body size in Homo floresiensis*

132 We parametrized and tested our simulation model using empirical data for *Homo*
133 *floresiensis*, a case previously investigated by two of us [27]. *H. floresiensis* was a small-
134 bodied fossil hominin of about 25-30 kg discovered on Flores Island, Indonesia, in 2004
135 [11, 43]. It most likely represents a dwarf form of *Homo erectus*, the first hominine species
136 to colonize South-East Asia almost 2 mya [43, 44].

137 We simulated dwarfing in *H. floresiensis* from a large-bodied ancestor in the range
138 of *H. erectus* (i.e., 45-55 kg), under 10,000 random combinations of parameters sampled
139 within the ranges defined in Table 1 (see also ESM and Diniz-Filho and Raia [27] for
140 details and references). Adaptation to the new final peak is considered “successful” if mean
141 \mathbf{G} is below 30 kg, given the uncertainty of around 5% around the 27 kg usually estimated
142 for *H. floresiensis* [11, 43-44]. Body mass values are used here as a general surrogate for
143 body size, in a comparative and interspecific sense [e.g., 45]. The main response variable in
144 our simulations is the time for adaptation, t_G . Finally, we analyzed how the simulation
145 parameters explain the realized mean-standardized selection gradient across simulations
146 (see also Fig. S2 in ESM).

147

148

149 3. Results

150 Under the realistic range of demographic and genetic parameters successful adaptations
151 happened in 97.3% of the simulations. In these simulations, the time to adaptation t_G is log-
152 normally distributed, with median time equal to 346 generations, and 95% non-parametric
153 confidence intervals ranging from 150 to 675 generations (Fig. 1). This median corresponds
154 to about 5190 years (95% CI ranging from 2250 and 10125 years), assuming some 15 years
155 as the mean age for sexual maturity and generation length (see also ESM for some
156 additional results fixing some of the most important parameters in the simulations).

157 We explained about 70% of the variation in log-transformed t_G across the
158 simulations by a multiple linear regression. Lower t_G are found for simulations with high
159 mutation rate, large initial population size and large size of the demes recolonizing the

160 island (even with maximum of 10 new individuals with a maximum low probability of
161 recolonizing equal to 0.1 per generation). Despite the high overall explanatory power of
162 this model and the high effect size of these three parameters, the individual ability of each
163 parameter to predict t_G is rather low (see ESM Fig. S4), suggesting that the response
164 emerge from a complex interaction of different parameters (which may actually explain
165 log-normally distribution of t_G)

166 Realized mean-standardized selection gradients in the simulation are left-skewed
167 (Fig. 2), with median equal to -0.29 (95% CI ranging from -0.167 to -0.562), with about
168 82% of its variance explained by simulation parameters. Higher selection strength is
169 necessary to drive adaptation in either shorter adaptive landscapes, when ancestral mean
170 body sizes are large, and/or when the amount of variation explained by phenotypic
171 plasticity is low (although these two last effects are smaller; see ESM Table 2).

172

173

174 4. Discussion

175 Our simulations support the hypothesis that *H. floresiensis* plausibly became dwarf over a
176 relatively short time. Gomez-Robles [29] recently raised the question of whether it would
177 be possible for the extreme reduction of the brain and body of *H. floresiensis* to have
178 occurred over a mere 300,000 years, given estimated ages of *H. floresiensis* fossil record
179 [43, 46-47]. Confirming the results from classical quantitative genetics models [27], we
180 showed here that dwarfism in *H. floresiensis* could have been much faster than this. In 97%
181 of the simulations, adaptation occurred with median time for dwarfism equal to some 5000
182 years, or ~350 generations. Indeed, it is documented that the effects of natural selection on
183 trait variations can be very fast on islands, covering a few tenths of generations at most [19,
184 48-50]. Moreover, recent analyses point out to larger effects of phenotypic plasticity,
185 especially in early phases of island colonization, as also proposed in Lister's [16] two-phase
186 model and by acceleration of life-history traits evolution due to biotic release [20, 24-25].

187 As expected, the mean-standardized selection gradient is higher than previously
188 found by using analytical solutions in ref. [27], at around -0.3, but even so this value is

189 quite close to common estimates in natural populations [51]. Moreover, these values
190 emerged from a realistic set of demographic and genetic parameters and widely accepted
191 processes. Although these coefficients are indisputably related to the adaptive landscape
192 adopted, we assumed relatively weak selection within generations (i.e., $w^2 < 100v_A$), and a
193 moving peak that allows population survival and quick expansion just after island
194 colonization.

195 Of course, our analyses do not make it possible to establish that *H. floresiensis* is a
196 dwarfed form of *H. erectus* [see 43, 52-54 for discussions], or to state that speciation
197 occurred as fast as 5,000 years, as many other complex morphological traits, in addition to
198 body size, differentiate *H. floresiensis* from *H. erectus* (and other related species; see [43,
199 52-54]). Rather, our analyses should be better viewed as a proof of concept that fast
200 dwarfing is plausible even in hominins.

201 The simulation model used here still uses a phenomenological approach to
202 quantitative genetics [55], in the sense that the adaptive landscape and peak are defined on
203 the target dwarfed species evolving from a large-bodied ancestor. Even so, we believe our
204 simulation illustrates the power of analyzing ecological and evolutionary patterns from an
205 explicit quantitative genetics perspective. We argue the IBM model developed here could
206 be viewed as a starting point for a quasi-experimental model, to better understand which
207 demographic and genetic parameters may really lead to rapid dwarfing in insular
208 vertebrates.

209

210

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219

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337

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341 P.H.H. and N.R.E. provided original environmental data for time series analyses. All
342 authors contributed to writing of the final version of the manuscript.

343 **Statement on Competing Interests** - We have no competing interests

344

345 **Ethics statement** - We declare all ethical procedures were followed during the current
346 study.

347 **Data accessibility statement** - All data necessary to reproduce the results in this paper can
348 be found in the electronic appendix

349

350

351 **Figure Captions:**

352

353 **Fig. 1.** Distribution of time for adaptation (in generations) obtained from the IBM
354 simulating dwarfing of *H. floresiensis* based on 10,000 random combinations of parameters
355 defined in Table 1. Median time is equal to 346 generations (CI 95% ranging from 150 and
356 675 generations).

357

358 **Fig. 2.** Distribution of mean-standardized selection gradients generated in the IBM
359 simulating dwarfing of *H. floresiensis* based on 10,000 random combinations of parameters
360 defined in Table 1. Median selection strength is equal to -0.29 (CI 95% ranging from -0.167
361 and -0.562).

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Table 1. Genetic and demographic parameters used in the Individual-Based Model for body size evolution in *Homo floresiensis*.

<i>Parameter</i>	<i>Symbol</i>	<i>range of values</i>
Initial adaptive peak (kg)	O_0	45 – 55
Final adaptive peak (kg)	O	27
Heritability	h^2	0.6 – 0.85
Phenotypic coefficient of variation	Cv	0.04 – 0.06
mutational variance	v_U / v_A	0.02 – 0.04
Length of adaptive landscape (x v_A)	w^2	100 – 150
Phenotypic plasticity	b	0.1 – 0.5
Inbreeding depression	I	0.7
Initial inbreeding coefficient	F	0.1
Initial Population	N_0	25 – 100
Carrying capacity	K	10,000 x NPP_t
Number of immigrants (per generation)	N_R	1 – 10
Probability of recolonization (per generation)	P_R	0.05 – 0.1
Fecundity	F	5.5 ± 1.5

Table 2. Effects of demographic and genetic parameters (standardized effect size, given by the regression slope by its error) on time for adaptation (t_G) and on the mean-standardized selection coefficient (β_u) (see also Figs. S4 and S5 in Supplementary Online Material).

parameters	t_G	β_u
h^2	-18.5	12.9
cv	-11.7	10.1
v_U	-92.9	-11.2
O_0	22.6	-47.9
N_0	-79.2	-5.5
N_R	-49.2	12.9
P_R	-16.7	5.2
w^2	-1.3	38.2
F	-14.8	13.1
b	-3.6	58.3

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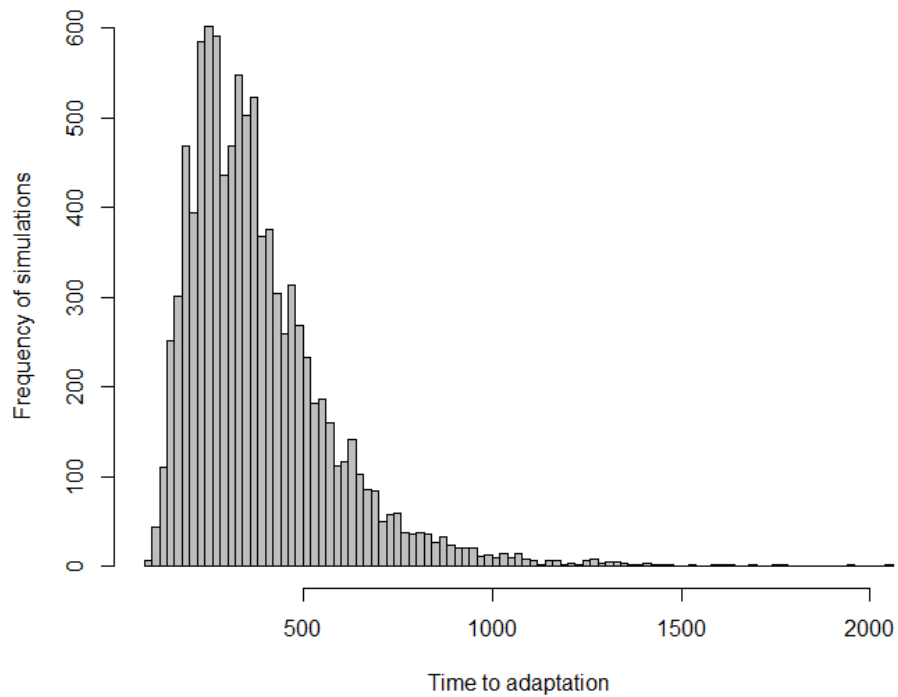


Fig. 1. Distribution of time for adaptation (in generations) obtained from the IBM simulating dwarfing of *H. floresiensis* based on 10,000 random combinations of parameters defined in Table 1. Median time is equal to 346 generations (CI 95% ranging from 150 and 675 generations).

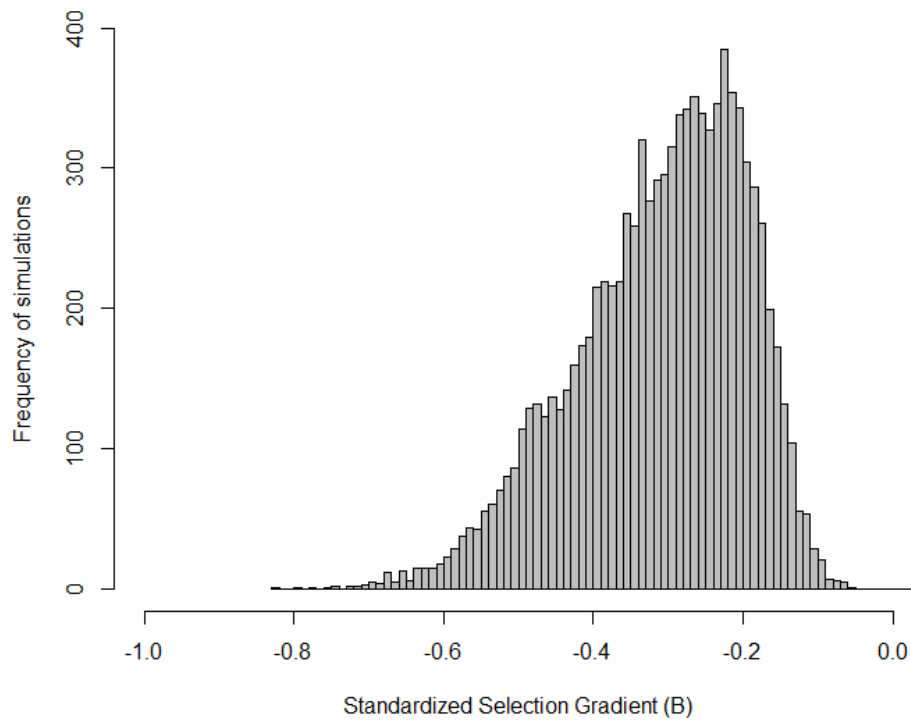


Fig. 2. Distribution of mean-standardized selection gradients generated in the IBM simulating dwarfing of *H. floresiensis* based on 10,000 random combinations of parameters defined in Table 1. Median selection strength is equal to -0.29 (CI 95% ranging from -0.167 and -0.562).