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# Quantitative genetics of body size evolution on islands: an individual-based simulation approach

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

## 1. Introduction

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

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

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

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

## 2. Methods

### (a) Modelling evolutionary processes within and between generations

The details of the simulation model and the parametrization are available as electronic supplementary material. The simulation starts with a vector **G** of genotypic values for body size from $N_0$ individuals representing the initial deme colonizing the island, sampled from a normal distribution with mean $u_G$ and additive genetic variance $v_A$, for a single quantitative trait (i.e. body size), thus assuming an infinitesimal model [30]. After island colonization, the deme starts to grow in numbers following a logistic process up to the island carrying capacity $K$. The process stops after $t_G$ generations, when the mean phenotypic value is close to the final adaptive peak defined for the island.

Phenotypic values of the population (**P**) are obtained by adding to **G** a vector with randomly distributed environmental effects **E** with mean zero and environmental variance $v_{\mathrm{E}}$ (which is, in turn, determined assuming a known heritability $h^2$ for the trait), with phenotypic plasticity incorporated as a linear reaction norm [31–34]. Fitness $W_i$ for each individual is defined according to a Gaussian approximation of stabilizing selection with an optimum equal to $O$ (the adaptive peak; see below for properties of this optimum). In our model, natural selection acts through both differential survival (i.e. before reproduction) and fecundity (i.e. number of offspring). Inbreeding is modelled by a Markovian approximation tracking brother–sister breeding and reduces fitness by increasing mortality in newborns [35,36].

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

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

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

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

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

We simulated dwarfing in *H. floresiensis* from a large-bodied ancestor in the range of *H. erectus* (i.e. 45–55 kg), under 10 000 random combinations of parameters sampled within the ranges defined in table 1 (see also electronic supplementary material and Diniz-Filho & Raia [27] for details and references). Adaptation to the new final peak is considered 'successful' if mean **G** is below 30 kg, given the uncertainty of around 5% around the 27 kg usually estimated for *H. floresiensis* [11,43,44]. Body mass values are used here as a general surrogate for body size, in a comparative and interspecific sense (e.g. [45]). The main response variable in our simulations is the time for adaptation, $t_G$. Finally, we analysed how the simulation parameters explain

**Table 1.** Genetic and demographic parameters used in the individual-based model for body size evolution in *Homo floresiensis*.

| parameter | symbol | range of values |
|---|---|---|
| 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 (× vA) | $w^2$ | 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× $NPP_t$ |
| 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 |

the realized mean-standardized selection gradient across simulations (see also electronic supplementary material figure S2).

## 3. Results

Under the realistic range of demographic and genetic parameters, successful adaptations happened in 97.3% of the simulations. In these simulations, the time to adaptation $t_G$ is lognormally distributed, with median time equal to 346 generations, and 95% non-parametric confidence intervals ranging from 150 to 675 generations (figure 1). This median corresponds to about 5190 years (95% CI ranging from 2250 and 10 125 years), assuming some 15 years as the mean age for sexual maturity and generation length (see also electronic supplementary material for some additional results fixing some of the most important parameters in the simulations).

We explained about 70% of the variation in log-transformed $t_G$ across the simulations by a multiple linear regression. Lower $t_G$ are found for simulations with high mutation rate, large initial population size and large size of the demes recolonizing the island (even with maximum of 10 new individuals with a maximum low probability of recolonizing equal to 0.1 per generation). Despite the high overall explanatory power of this model and the high effect size of these three parameters, the individual ability of each parameter to predict $t_G$ is rather low (see electronic supplementary material, figure S4), suggesting that the response emerges from a complex interaction of different parameters (which may actually explain the lognormal distribution of $t_G$) (table 2).

Realized mean-standardized selection gradients in the simulation are left-skewed (figure 2), with median equal to −0.29 (95% CI ranging from −0.167 to −0.562), with about 82% of its variance explained by simulation parameters. Higher selection strength is necessary to drive adaptation in either shorter adaptive landscapes, when ancestral mean body sizes are large, and/or when the amount of variation explained by phenotypic plasticity is low (although these two last effects are smaller; see electronic supplementary material, table S2).

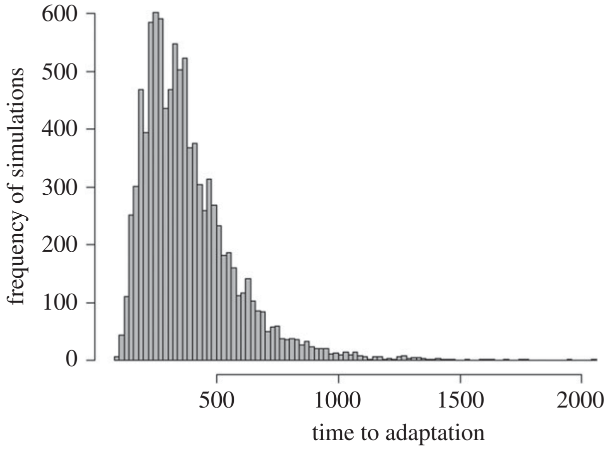

**Figure 1.** Distribution of time for adaptation (in generations) obtained from the IBM simulating dwarfing of *H. floresiensis* based on 10 000 random combinations of parameters defined in table 1. Median time is equal to 346 generations (CI 95% ranging from 150 to 675 generations).

**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 ($\beta_u$) (see also electronic supplementary material, figures S4 and S5).

| parameters | $t_G$ | $\beta_u$ |
|---|---|---|
| $h^2$ | −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 |

## 4. Discussion

Our simulations support the hypothesis that *H. floresiensis* became dwarfed over a relatively short time. Gomez-Robles [29] recently raised the question of whether it would be possible for the extreme reduction of the brain and body of *H. floresiensis* to have occurred over a mere 300 000 years, given estimated ages of *H. floresiensis* fossil record [43,46,47]. Confirming the results from classical quantitative genetics models [27], we showed here that dwarfism in *H. floresiensis* could have been much faster than this. In 97% of the simulations, adaptation occurred with median time for dwarfism equal to some 5000 years, or approximately 350 generations. Indeed, it is documented that the effects of natural selection on trait variations can be very fast on islands, covering a few tens of generations at most [19,48–50].

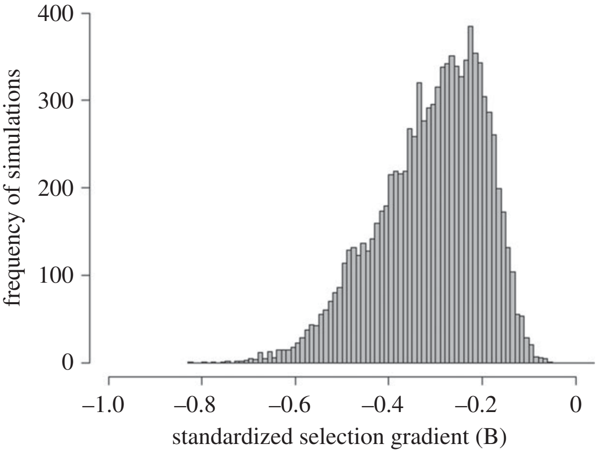

**Figure 2.** Distribution of mean-standardized selection gradients generated in the IBM simulating dwarfing of *H. floresiensis* based on 10 000 random combinations of parameters defined in table 1. Median selection strength is equal to −0.29 (CI 95% ranging from −0.167 to −0.562).

Moreover, recent analyses point to larger effects of phenotypic plasticity, especially in early phases of island colonization, as also proposed in Lister's [16] two-phase model and by the acceleration of life-history trait evolution due to biotic release [20,24–25].

As expected, the mean-standardized selection gradient is higher than previously found by using analytical solutions in [27], at around –0.3, but even so this value is quite close to common estimates in natural populations [51]. Moreover, these values emerged from a realistic set of demographic and genetic parameters and widely accepted processes. Although these coefficients are indisputably related to the adaptive landscape adopted, we assumed relatively weak selection within generations (i.e. $w^2 < 100v_A$), and a moving peak that allows population survival and quick expansion just after island colonization.

Of course, our analyses do not make it possible to establish that *H. floresiensis* is a dwarfed form of *H. erectus* (see [43,52–54] for discussions), or to state that speciation occurred as fast as 5000 years, as many other complex morphological traits, in addition to body size, differentiate *H. floresiensis* from *H. erectus* (and other related species; see [43,52–54]). Rather, our analyses should be better viewed as a proof of concept that fast dwarfing is plausible even in hominins.

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

Ethics. We declare all ethical procedures were followed during the current study.

Data accessibility. All data necessary to reproduce the results in this paper can be found in the electronic supplementary material.

Authors' contributions. J.A.F.D.-F., P.R., J.H. and A.M.C.S. conceived the study and wrote the first draft. J.A.F.D.-F., L.J. and T.F.R. wrote the main codes and L.J. conducted all simulations; J.A.F.D.-F., J.H., A.M.C.S. and P.R. discussed the results and interpretations, and P.B.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.

Competing interests. We have no competing interests.

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