Mito-nuclear selection induces a trade-off between species ecological dominance and evolutionary lifespan

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Mitochondrial and nuclear genomes must be co-adapted to ensure proper cellular respiration and energy production. Mito-nuclear incompatibility reduces individual fitness and induces hybrid infertility, which can drive reproductive barriers and speciation. Here, we develop a birth–death model for evolution in spatially extended populations under selection for mito-nuclear co-adaptation. Mating is constrained by physical and genetic proximity, and offspring inherit nuclear genomes from both parents, with recombination. The model predicts macroscopic patterns including a community's species diversity, species abundance distribution, speciation and extinction rates, as well as intraspecific and interspecific genetic variation. We explore how these long-term outcomes depend upon the parameters of reproduction: individual fitness governed by mito-nuclear compatibility, constraints on mating compatibility and ecological carrying capacity. We find that strong selection for mito-nuclear compatibility reduces the equilibrium number of species after a radiation, increasing species' abundances and simultaneously increasing both speciation and extinction rates. The negative correlation between species diversity and diversification rates in our model agrees with the broad empirical pattern of lower diversity and higher speciation/extinction rates in temperate regions, compared to the tropics. We conclude that these empirical patterns may be caused in part by latitudinal variation in metabolic demands and corresponding variation in selection for mito-nuclear function.

The origin, maintenance and extinction of species involve diverse ecological and evolutionary mechanisms, so that they are rarely explained by a single hypothesis. Mathematical models have still been helpful in understanding empirical patterns of biodiversity, such as species abundance distributions (SADs) and the species–area curve, which are well described by both neutral and niche-based theories of community assembly. However, models that explain species abundances or species–area curves in a community seldom make predictions for long-term evolutionary patterns, such as speciation rates and species lifetimes, nor do they provide a mechanistic description for the formation of species. Studies describing mechanisms of speciation, on the other hand, use both genetic and ecological drivers, rarely connect these processes to macro-evolutionary patterns, whereas macro-ecological models succeed in reproducing such patterns but may lack a detailed connection with organism and population properties to explain variation in diversification rates. In this context, linking micro-evolutionary processes to macro-evolutionary patterns is key to understanding what drives diversification, especially when...
similar evolutionary signatures can result from different population processes. Genetic interactions between the mitochondrial (mtDNA) and nuclear (nDNA) genomes are necessary for cellular respiration, which depends on biochemically compatible proteins. Incompatibilities between those genes can severely reduce individual fitness and fertility. Thus, mutations in the mitochondrial genome induce selection for compatible genes in the nuclear genome, driving molecular co-evolution and ultimately promoting compensatory changes. Mitochondrial co-evolution has been proposed as a driver of speciation possibly preceding the evolution of reproductive barriers, although the extent of its role remains uncertain. Since respiration efficiency is fundamental to energy production in eukaryotes, selection for mitochondrial co-adaptation has the potential to leave signatures across biological scales—from metabolism of an individual cell, to fitness of an individual, reproductive barriers within a population and even speciation in a community.

We develop an individual-based model to describe selection for mito-nuclear compatibility. We follow the process of radiation and eventual equilibrium towards a stationary number of species in a community. The model accounts for mitochondrial genetic material and its interactions with a portion of the nuclear genome in a phenomologically approach based on the lock-and-key principle for interactions between proteins coded by both genomes. Simulations of our model record all forms of diversification events—speciation, extinction and hybridization—and allow us to evaluate the impact of selection on the emergence and persistence of species. In addition, we can use the model to reconstruct the history of an extant community and analyse the dominance of species throughout their evolutionary lifetime. The model reveals how mito-nuclear selection can jointly influence species abundances and diversity within a community as well as long-term patterns of species lifetimes.

We use the results of our model to help explain longitudinal patterns in species diversity and speciation rates, related to a cline of environmental harshness. Selection for mito-nuclear compatibility is expected to be stronger in harsh, temperate environments that demand optimal metabolic function. Whereas tropical environments, where resources are abundant and energy efficiency is less important, present weaker selection for mito-nuclear compatibility and function. There are well-known patterns in diversity that vary from tropical to temperate regions, with the former displaying high biodiversity, old species and low speciation and extinction rates and the latter displaying fewer species and elevated recent speciation rates. We hypothesize that mito-nuclear selection might play a role in forming these patterns, as resource availability should correlate with selection for metabolic efficiency which, in turn, governs patterns of diversity and speciation rates in our model.

**Results**

**Model for selection on mito-nuclear compatibility**

We used a spatially explicit, agent-based model (Fig. 1: Methods) based on ref. 35, in which neutral processes driven by recombination and mutation change allele frequencies in a community. The environment is homogeneous and the community size is kept constant at the carrying capacity. Mating is restricted by both genetic similarity and spatial proximity, so that species emerge through isolation by distance. Here, we start from the same neutral assumptions as in ref. 35 and introduce mito-nuclear genetic compatibility as a component of individual fitness. Simulating communities that evolve under these micro-evolutionary dynamics, we catalogue the resulting macro-evolutionary patterns under weak and strong mito-nuclear selection.

Following ref. 35, each individual is described by a haploid, bi-allelic sequence of $B$ sites that represent its nDNA. To describe the mito-nuclear interaction we also consider a shorter string of $B_{\text{mut}}$ sites representing the individual’s mtDNA. Sexes are separated and sexual reproduction with non-overlapping generations occurs as follows: during the reproduction phase, all individuals have a probability to randomly choose a mating partner within a spatial range of radius $S$, called the mating neighbourhood. Genetic compatibility between individuals is determined by the Hamming distance between their nDNAs (the number of loci bearing different alleles) and must be below the threshold of $G$ sites for successful mating. The nuclear genome of the offspring is built from free recombination of the nuclear material of the parents, with a probability of mutation $\mu$ per site. The mtDNA is directly inherited from the mother, with mutation probability per site $\mu_{\text{mt}}$. Starting from identical individuals, species emerge as clusters of genetically compatible individuals, that is, as groups with ongoing gene flow among individuals, determined by the genetic mating restriction $G$ but no gene flow between different groups (Methods).

We model mito-nuclear compatibility in an individual as a locus-by-locus interaction between the mtDNA and the first $B_{\text{mut}}$ sites of the nuclear genome (the remaining $(B - B_{\text{mut}})$ nuclear genes do not participate in the interaction); the interacting pair of loci is compatible if they have the same allele value (Fig. 1b). The mito-nuclear distance $d$ is then the fraction of incompatible sites. Such a scheme is a phenomologically description of the biochemical and structural compatibility between proteins coded by both genomes necessary for the respiration process. In the absence of selection, all individuals have an equal probability of reproduction and nDNA and mtDNA evolve independently. When mito-nuclear compatibility is under selection, fitness $w$ is assigned to individuals according to their mito-nuclear distance, with strength expressed by a parameter $\sigma_0$, such that $w = e^{-d^2/2\sigma_0^2}$, that is, small $\sigma_0$ implies strong selection. Individuals with higher fitness, normalized within the mating range, have a higher probability of reproduction. We tracked all events during the dynamics, registering speciation, hybridization and extinctions, and recorded the ancestry of all species.

**Diversification rates and species richness**

We simulated the evolution of communities under various strengths of selection on mito-nuclear compatibility, $\sigma_0$. In the non-interacting scenario (NI), the mito-nuclear distance is not considered for reproduction (equivalent to $\sigma_0 \rightarrow \infty$). Selection was simulated with $\sigma_0$ ranging from 0.175 (weak selection) to 0.025 (strong selection). Results are shown for 50 independent realizations for each set of parameters. Starting from a population of identical individuals, all simulations are characterized by a period of rapid increase in species numbers (a radiation period), followed by relaxation to a steady-state species richness. During the dynamics, all diversification events were registered (Fig. 2a). The communities were simulated for time $T = 2,000$ generations, a time longer than necessary for the completion of a radiation and relaxation to an equilibrium number of species. The equilibrium, defined by the moment when the number of species reaches a plateau, occurred after about $T = 500$ generations in all cases (Fig. 2b). Because the community size is nearly constant, equilibrium results from a balance between speciation, extinctions and hybridization events (compatible with the hypothesis of ecological limits). Selection had the clear effect of reducing the number of species in equilibrium and introducing a delay in the radiation process.

We define a speciation event or branching, as the moment when a species splits into two or more reproductively isolated groups. The lifetime of the mother species is considered over at this point and the species disappears as two (or more) sister species are born, with a positive net balance in the number of species. A species also disappears by extinction, when its population becomes small (few individuals) and eventually does not produce descendants, due to random ecological drift and by the accumulation of mito-nuclear incompatibilities that lead to low fitness and low fecundity. A species may alternatively disappear by hybridization—when two or more species re-establish gene
Mutation of an individual is measured by the distance between its mtDNA and nDNA genomes described by binary sequences of B and B_m, respectively. Sexual reproduction occurs with non-overlapping generations. Individuals look for a mating partner within a spatial range of radius S and they must be genetically compatible (within nuclear distance G) to mate. Offspring are generated with recombination of the nDNA and mutation probability \( \mu \) per locus, with direct inheritance of maternal mtDNA with mutation probability \( \mu_{mt} \). Mito-nuclear compatibility of an individual is measured by the distance between its mtDNA and B_m.

Flow. When species hybridize, we consider that the more abundant species persists while the other one disappears as it merges. Linear regression of the number of events in equilibrium provided the rates of speciation, extinction and hybridization (Fig. 2c). In equilibrium, when the average number of species has stabilized, the rate at which species are born (speciation) is equal to the rate at which species die (extinction plus hybridization). In this regime, speciation, extinction and hybridization rates per species increase with the strength of selection for mito-nuclear compatibility (Supplementary Fig. 1). However, since the number of extant species decreases with selection, the nominal rates reach a maximum for intermediate values of \( \alpha_w \), as shown in Fig. 2c. The decrease in species richness, on the other hand, results from the radiation process because selection decreases the net diversification (speciation minus extinction and hybridization) during the transient (Supplementary Fig. 2).

Species abundance distributions and lifespans
Selection for mito-nuclear compatibility decreased the number of species in equilibrium and, because the community size is fixed, this led to an increase in the average species abundance and variance of the SADs (Fig. 3a). Since our simulations resulted in an average number of species no greater than 25, we accumulated data over several independent runs to obtain a clear signal for the expected distribution of abundances, for each value of \( \alpha_w \). This procedure is justified because the lattice is much larger than the mating range and species' range sizes are smaller than the available space (Supplementary Text 2).

We recorded species abundances in generation \( T = 1,000 \) and found an approximately lognormal-shaped distribution of species abundances, even in the presence of strong selection for mito-nuclear compatibility (Fig. 3a). Selection increased both the mean species abundance and the variance: the histograms became wider and right-shifted under strong selection (Supplementary Fig. 5). The SADs are asymmetric and, although they present a tail on the left side, low-abundant species were infrequent because speciation occurs in our model by fission of abundant species, producing relatively few rare species (similarly to a stick breaking speciation model in a community with finite resources\(^{17} \)). SADs were stable during equilibrium, such that distributions taken at any time step after \( T > 500 \) generations were very similar (Supplementary Fig. 4).

The time of birth and disappearance of all species were also recorded and species ages and remaining lifespans were known for all species present at time \( T = 1,000 \) (Supplementary Fig. 6). The distribution of species lifespans, for species binned by same abundance class (Fig. 3b), shows that selection tended to reduce species ages and lifetimes in all abundances classes. In all cases, species born with intermediary relative abundance had the highest longevity within their species.
communities. In the absence of selection (NI), species lifetimes were short for low-abundant species and they had similar distributions for species of intermediate versus large abundance. Some of those species even persisted until the end of the simulation ($T = 2,000$). By contrast, large species evolving under strong selection showed drastically reduced longevity, which may seem surprising. In the non-interacting case (no selection), the most-right filled bin (log abundance class 7) had a slight reduction of lifespan, indicating that there was also a small effect of species abundance but selection induces a much stronger reduction in lifespan for abundant species. There are similar patterns for species ages and for remaining lifespan at the time of sampling ($T = 1,000$): species of intermediate abundance are the oldest and have the longest remaining lifetimes, and species’ ages of any abundance class decrease with selection (Supplementary Fig. 6).

Species abundances at time $T = 1,000$ were also related to the distribution of subsequent diversification events (Fig. 4), that is, the mode of disappearance of each species (branching, extinction or hybridization) or whether it persisted through generation $T = 2,000$. Regardless of selection strength, most species had two possible endings: by branching, if it was dominant within the community; or by extinction, if it had low abundance. Remarkably, in the absence of mito-nuclear selection, a substantial portion of species persisted through to generation $T = 2,000$. Selection suppressed the persistence of species, even when weak ($\sigma_w = 0.175$). Selection also increased the rate of hybridization (note that hybridization events were counted only for low-abundant species due to our convention of considering the least-abundant species involved as dying during the fusion, whereas the more abundant species persists with increased abundance). Notably, species belonging to the same class of abundances had different fates, depending on whether they were under strong, weak or no selection. For instance, a species belonging to bin 6 in the non-interacting scenario (NI) could persist for 1,000 generations ahead, while a species of the same abundance was most likely to go extinct in any scenario with selection. Abundance class 7 was the largest one in simulations without selection, more likely to speciate; but it was not dominant and more likely to go extinct under strong selection.

Greater species abundances are expected when the number of species is smaller because we assume a constant community size; and so it is not clear if the macro-evolutionary patterns we observe are attributable to species abundances per se or to mito-nuclear selection.
To tease apart these mechanisms, we simulated communities in the absence of mito-nuclear selection, relaxing the genetic threshold for mating compatibility (from $G = 75$ to $G = 220$) so that they produced a similar number of species in steady-state as communities under strong mito-nuclear selection (Supplementary Text 8 and Supplementary Figs. 10–16). SADs were shifted towards higher abundances as expected but all diversification rates were reduced and species lifespans were substantially longer (hence turnover was not increased), even though radiation was delayed (Supplementary Fig. 10). Therefore, we conclude that the relationship between high speciation rate and low species diversity results directly from the selection for mito-nuclear compatibility.

Genetic diversity
The analysis of genetic patterns can help to elucidate the mechanism by which mito-nuclear selection promotes or hinders diversification. We evaluated genetic diversity within and between species by measuring the nuclear genetic distance between pairs of individuals at time $T = 2,000$. Mito-nuclear selection drastically reduced the genetic distances between individuals belonging to different species (Fig. 5a). In the absence of selection (NI), species were genetically well isolated from each other, with a prominent peak around 650 loci. Increasing the strength of selection (reducing $\sigma_w$) made species progressively more similar to each other genetically. However, the opposite effect holds for conspecific individuals (Fig. 5b): under strong selection we observed a slightly larger nuclear divergence within a species than in the absence of selection. Notably, for strong selection, several pairs of conspecific individuals even had distances exceeding the genetic threshold ($G = 75$) required for mating. In this case, species cohesion was maintained by ongoing gene flow across the landscape.

The patterns of diversity between different species were similar for the mtDNA content (Supplementary Fig. 7a) and are explained by the effect of the mito-nuclear selection on reducing both nuclear and mitochondrial substitutions. When reproduction can only occur in individuals with high fitness (low mito-nuclear distance), fixation of a mutation in any of the genomes is hampered because it must be followed by a mutation in the corresponding site of the interacting pair to maintain the mito-nuclear compatibility. As a result, interacting sites had lower substitution rates in both the mitochondrial and nuclear genomes (Supplementary Fig. 8). Within a species, the mean nDNA distance is
positively correlated to the species’ abundance (Fig. 5c), independent of the selection strength. As selection increased species abundances, the effect on populations was to increase the nDNA distances within each species. Therefore, mito-nuclear interaction promoted intraspecies genetic diversity but reduced global diversity in the community.

Although our model reproduces the broad empirical signatures of mito-nuclear co-evolution, it does not produce strong signatures of positive selection associated with compensatory evolution of nDNA in response to mutations in mtDNA. This is because we have simulated a radiation starting from perfectly coordinated mtDNA and nDNA, so that most selection for interacting mito-nuclear sites is purifying selection.

A chain of effects connects selection for mito-nuclear genetic compatibility within an individual to skewed SADs in a community, shorter species’ lifespans and elevated macro-evolutionary turnover rate, that is high speciation and high extinction rates (chart in Fig. 6). Strong selection promotes the conservation of nuclear genetic content in the community because mutations accumulate more slowly. Consequently, the disruption of gene flow is hindered and the number of species diminished. With a reduced number of species, they are naturally more abundant and support more intraspecific diversity, favouring evolutionary branching events. Therefore, the speciation rate increases and abundant species have reduced lifetimes. Low-abundant (non-dominant) species are also short-lived because they are more susceptible to fluctuations in abundance. The reduced genetic distances between different species also promotes hybridization, with sister species merging more easily after speciation. As a result, communities under strong mito-nuclear selection are characterized by a low number of species with larger abundances, short species lifespans and high rates of speciation, extinction and hybridization.

### Discussion

We have investigated how micro-evolutionary processes impact ecological and macro-evolutionary patterns in a model with selection for mito-nuclear compatibility. Speciation, hybridization and extinction are emergent phenomena in our model, byproducts of changes in allele frequencies in the populations, as well as spatial and genetic restrictions on mating. We have shown that strong mito-nuclear selection at the individual level triggers a succession of effects in species and communities, with low species richness in equilibrium, reduced species lifespans and a high rate of evolutionary turnover (Fig. 6). We investigated the mechanisms by which selection induces these effects and how they are correlated across scales.

The negative correlation between species diversity and speciation rates predicted by our model has been observed empirically—in particular, across latitudinal gradients. The number of species in a taxa typically increases towards the tropics while showing reduced speciation rates, compared to temperate zones, along with increasing ages of sister species. The properties of populations evolved under strong mito-nuclear selection in our model are thus broadly similar to empirical populations in temperate zones; whereas model predictions under weak or no mito-nuclear selection are similar to empirical patterns in the tropics (table in Fig. 6). However, these empirical patterns are probably the result of many different ecological, evolutionary and biogeographical processes, or even neutral processes. Indeed, there is no consensus about what causes the richness gradient across latitudes, or even whether such patterns are universal across geographic and time scales. Indeed, we have shown that selection for mitochondria-nuclear co-adaptation is one possible mechanism that connects environmental demands on metabolism, population genetics and species trajectories. In this way, our study helps to link macro-evolutionary patterns of diversification and species turnover with first principles of fitness and mating operating within individuals and populations.

Temperate zones are generally regarded as harsh environments with low resource availability, in which metabolic function is critical. This stands to reason that selection for mito-nuclear co-adaptation, to support efficient metabolic function, is stronger in such zones. The empirical correlation between environmental harshness and the differentiation within species suggests that speciation is frequent in those regions, which is supported by the observation of young species ages. Others scrutinized how harsh environments promote the recurrent fragmentation of species in space, which may sequentially develop reproductive barriers. Those incipient species evolve through local adaptation and ecological speciation and are therefore more prone to hybridization. Our model produces similar patterns in a process driven by stabilizing (purifying) selection, in contrast to the mechanism of ecological speciation (based on divergent selection)—which shows that the same macro-evolutionary pattern can result from distinct population processes.

The genetic patterns in our simulated communities reflect the primary causes of variation in diversification rates. A negative correlation between speciation rates and species richness based on a spatially explicit genetic model was also obtained in ref. 24, as a result of sexual reproduction (independent of selection strength). In our model, by contrast, strong mito-nuclear selection reduces the nuclear genetic
distance between species (Fig. 5a), as the maintenance of mito-nuclear compatibility slows the fixation of mutations for both nDNA and mtDNA (Supplementary Fig. 8). Substitutions occur more slowly, delaying and prolonging radiation and promoting the conservation of genetic content in the community. Since gene flow is higher, there are fewer species that are each more abundant and contain greater intraspecific genetic diversity (Fig. 5b, c). Those abundant species branch more frequently, shortening their lifetimes and resulting in a high speciation rate, despite the lower substitution rate of the nuclear alleles. Notably, the average rate of substitutions was not positively correlated with the speciation rate71, which has previously been proposed to be a driver of biodiversity (revised by ref. 64). The large intraspecies genetic diversity in communities with low richness in our model is similar to wider niches72,73 and consistent with predictions of the niche hypothesis (which proposes that ecological opportunity is greater where diversity is low, leading to faster evolution at high latitudes71).

In contrast to rare species that are more extinction-prone, abundant species are expected to be old and long-lived, so more robust to the ecological drift 4,11. However, we found that strong mito-nuclear selection reduced species’ lifespans even though they were abundant (Fig. 3). We conclude that, for abundant species, the intrinsic robustness to ecological drift was opposed by purifying selection against mito-nuclear incompatibilities that rapidly decreased individual fitness as mutations accumulated. Frequent speciation by species’ fission was responsible for the death of abundant species under strong selection, which explains the relationship between their short lifetime and the corresponding high speciation rate (also suggested by ref. 13).

Genetic divergence between species is generally greater in the tropics than in temperate regions, which is usually explained by the long age of tropical species54. Likewise, intraspecific divergences are generally higher in temperate zones, associated with recent speciation rates52,53,70,74,75. Our results suggest that the process of accumulating intraspecific genetic diversity may be the cause, rather than the consequence, of a species being older or younger.

**Methods**

**Model**

We use an individual-based model of reproduction and eventual speciation adapted from refs. 5,22, following the methodology of previous work40. We consider a spatially distributed population evolving in a
Fig. 6 | From selection at the individual level to ecological and macro-evolutionary patterns. The flow chart (left) summarizes the cascade of events connecting selection for mito-nuclear compatibility within individuals to its effects on populations, species and evolutionary turnover. Colours represent the scale of effects: genetic (purple), ecological (green) and evolutionary (orange). The table (right) compares the equilibrium eco-evolutionary patterns in communities under weak versus strong selection. These predictions are qualitatively similar to empirical ecological and evolutionary patterns in tropical (weak selection) versus temperate zones (strong selection).

homogeneous environment, in the absence of geographic barriers and under the influence of neutral micro-evolutionary processes—mutation and genetic drift. Resources are finite but readily available, so that the population is always close to the carrying capacity $M$ (ref. 57). Reproduction occurs through pairwise mating of parents.

Derrida and Peliti76 first demonstrated this simple model of sympatric speciation with infinite bi-allelic genomes in the absence of natural selection. For sexual reproduction, the only requirement for speciation to occur is genetic compatibility, a weak form of assortative mating requiring a threshold genetic distance $G$ between mating pairs$^{90,91}$. Implementation of finite genomes $^{92}$ requires also spatial proximity of mating individuals, which must be separated by a maximum spatial distance $S$, changing from a sympatric to a parapatric mode of speciation $^{93}$. We call the area of radius $S$ around an individual its mating neighbourhood. These are the minimal conditions that guarantee the evolution of reproductive isolation and they allow us to introduce selection for mito-nuclear compatibility into the model. Species emerge from the dynamics as groups of individuals connected by gene flow and separated from all others by the genetic mating restriction $G$. Not all individuals of a species need to be compatible since gene flow can be established through intermediary individuals. In other words, species correspond to the components of a network where individuals (nodes) are connected if their nuclear genetic distance is less than or equal to $G$. The model predicts patterns of biodiversity, such as SADs and species–area relationships, similar to previous neutral models $^{43,44}$.

To include mito-nuclear selection, individuals are described by an nDNA, which undergoes recombination and defines genetic compatibility for mating, and by an mtDNA, inherited from the mother. Both genomes are modelled as binary strings with sizes $B$ and $B_m$, respectively. Sexes are separated and individuals are randomly distributed over a square area of size $L \times L$ (Fig. 1a) with periodic boundary conditions (individuals can, by chance, occupy the same lattice site). Generations do not overlap and the population is fully replaced by the offspring. Each individual has a probability $p$ to reproduce and a probability $Q = 1 - p$ of dying without leaving offspring. For reproduction, a mating partner is randomly chosen among genetically compatible individuals in its mating neighbourhood. The nuclear genetic distance $D_n$ between individuals is defined as the Hamming distance between their nuclear genomes and compatibility requires $D_n \leq G$. If a genetically compatible mate is found within the mating neighbourhood of the focal individual, an offspring is produced with locus-by-locus recombination of the nuclear genomes, followed by mutation with probability $\mu$ per locus. The mtDNA is inherited from the mother, with mutations with probability $\mu_m$ (Fig. 1a). The offspring is placed at the site of the focal individual or, with diffusion probability $D$, in one of $S_n$ randomly chosen nearest-neighbour sites. Note that individuals can generate more than one offspring: when selected as mating partner by their neighbours or when playing the role of focal individual. If the focal individual cannot find a compatible mate in its mating neighbourhood, it expands its search area to radius $S + 1$ and then to $S + 2$. If no compatible mate is found in the extended area, or if the individual dies without reproducing (probability $Q$), another individual is randomly selected within its original mating neighbourhood to reproduce in its place, keeping the population size constant. On rare occasions, however, due to population fluctuations, the mating neighbourhood might be empty and no replacement can be found. In these cases, mating does not occur and the population size decreases by one. To restore the population to its carrying capacity $M$, we allow individuals to have two offspring in the next generation if their mating neighbours have densities <60% of the expected average value $M$ per $L^2$. This procedure introduces small fluctuations in community size.

We compare the neutral process, when mito-nuclear selection is absent, with the scenario where mito-nuclear compatibility promotes fitness differences in the population, testing different levels of selective pressure while keeping all other parameters fixed. The mito-nuclear distance $d$ measures the compatibility between the mtDNA and the corresponding loci of nDNA, assigned to each individual, ranging from 0 (fully compatible sequences) to 1 (totally incompatible sequences); for completely random sequences, the expected value of $d$ is 0.5. The individual’s fitness $u$ depends on $d$ according to a Gaussian function with width $\sigma_u$, which quantifies the selective strength of the mito-nuclear interaction (Fig. 1b). The parameter $\sigma_u$ is related to the population average $\langle d \rangle$ in equilibrium (Supplementary Fig. 9), such that the absence of selection leads to $\langle d \rangle = 0.5$ and increasing the
selection diminishes \( (d) \) towards 0. Selection over mito-nuclear compatibility changes the probability of an individual to reproduce, that is, it affects its fecundity. The focal individual has its chance for reproduction modified by its fitness as follows: first the fitness values of all individuals in the population are computed as \( w(i) = e^{-\mu d_{ij}/2} \), second, \( Q \) for individual \( i \) is modified to \( Q_{w}(i) = 2Q \frac{(w_{\max} - w(i))(w_{\max} - w_{\min})}{w_{\max} + w_{\min}} \), where \( w_{\max} \) and \( w_{\min} \) are the maximum and minimum fitness in the population, respectively. Individuals with \( w(i) - w_{\min} \) have \( Q_{w}(i) = 0 \) and probability of reproducing \( P_{w} = 1 - Q_{w} = 1 \). Those with \( w(i) - w_{\max} \) have \( Q_{w}(i) = 2Q \) and \( P_{w} = 1 - 2Q \). Therefore, individuals with low fitness still have a small chance of reproducing. If the individual dies without reproducing, another one is selected in its mating neighbourhood, also according to fitness, to reproduce in its place, keeping the total population constant. Finally, a mating partner is selected from the compatible individuals in the mating neighbourhood, with probability proportional to their fitness.

For the analysis, we considered a standard set of parameters following previous demonstrations of the model that explored the evolution of species under different conditions\(^{23,27} \). We choose a population size \( M \) and a nuclear genome length \( B \) that guarantee the onset of radiation and establishment of the equilibrium of the number of species after a few hundred generations. The chosen parameters values were: a population of \( M = 1,300 \) individuals randomly distributed in \((100 \times 100)\) lattice with reflecting boundary conditions; the nuclear genome length is \( B = 1,500 \), with mutation rate \( \mu = 0.00025 \), genetic similarity threshold \( G = 75 = 0.05B \) and mating range \( S = 5 \). Population density is 0.13, indicating many empty sites in the lattice; the average number of individuals in the mating neighbourhood is ten. The mitochondrial genome length is \( B_{\text{mt}} = 500 \), with mutation rate \( \mu_{\text{mt}} = 3\mu \). We start from an initial condition where all individuals are identical, thus emulating a radiation process. We also fixed \( D = 0.02 \) and \( S_{w} = 20 \). In this work, we simulate the evolutionary process for \( T = 2,000 \) generations. We fixed \( Q = 0.37 + e^{a} \) as the neutral probability of dying without leaving offspring (equal to the chance of not selecting one particular individual in \( M \) trials with replacement\(^{24} \)). The effects of these parameters on speciation have been studied in previous works. Increasing \( G \) or \( S \), for example, increases gene flow and hinders speciation\(^{25} \), whereas increasing \( B \) or \( \mu \) facilitates the formation of species and decreases the time to equilibration\(^{26,27} \). Increasing the carrying capacity leads to an increase in the number of species by the same factor without affecting the relative abundances distribution if \( L \gg S \) and the density of individuals is kept constant (Supplementary Text 2). We ran 50 independent realizations of each parameter set and we present the ensemble-averages or accumulated measurements.

**Processes of diversification**

Throughout the evolutionary dynamics, recombination and mutation change allele frequencies in the population and, combined with the genetic and spatial restrictions for mating, reproductively isolated species can emerge. New species are born from an abundant one that eventually divides into smaller clusters with disrupted gene flow. Due to the model’s stochasticity, species abundances and species richness fluctuate randomly (ecological drift). The number of individuals of a species can progressively diminish until no offspring is left to the next generation, due to lack of compatible partners in the mating neighbourhood, or by chance, and the species is extinct. Also, genetically close species can merge by the re-establishment of the gene flow due to mutations, hybridizing. Therefore, we identify three classes of events in which a species can disappear when registering the evolutionary history of the populations as follows. (1) Speciation or branching, when an abundant species breaks into two or more new species. The mother species is considered dead and new species are born, adding to the number of living species. (2) Extinction, when the number of individuals of the species progressively diminishes until it reaches a null abundance. (3) Hybridization, when the descendants of individuals from two or more different species at \( T \rightarrow 1 \) belong to the same species at the generation \( T \), re-establishing the gene flow. In this case, we adopted the protocol of maintaining the largest species and consider the smaller species dead, absorbed by the largest one.

Branching events increase species richness, while extinction and hybridization decrease the number of extant species, reducing biodiversity. Hybridization is an emergent event in our model and only causes loss of diversity. In nature, however, hybridization may increase species richness inducing the evolution of reproductive barriers\(^{79} \). Here, we emulated the loss of diversity due to hybridization from lineage fusion, speciation reversals\(^{80} \) and hybrid breakdown\(^{40} \). We included in this category events of failed speciation attempts (when two or more recent sister species merge back) and events of reticulate evolution (when there are two speciation events in a row and a species fuses with the one with the most distant ancestor).

**Species abundances distributions**

In our simulations, the number of species in equilibrium \( (T \geq 500) \) ranged from about 20 in the non-interacting case to about 5 for strong selection (Fig. 2b). To generate abundance distribution plots with statistical significance, we have run 50 independent simulations for each set of parameters and accumulated the results. This increased the number of species in the histograms to about 1,000 for the non-interacting case and 100 for the case of strong selection. Supplementary Text 2 justifies the validity of this procedure.

To generate the species’ abundances histograms, data were binned in abundances classes \((\log_{10}) \). There are several methods for choosing the boundaries of bins and we followed the method adopted by ref. \(^{91} \); bins were built by using the powers of two as the centre of bins. The boundaries then come as \( 2^{n} \) and \( 2^{n+1} \). Thus, \( b = 0 \) stores species with one individual, \( b = 1 \) counts species with two individuals, \( b = 2 \) species with three, four and five individuals and so on.

**Reporting summary**

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Data availability**

There are no empirical data associated with this study.

**Code availability**

All simulations were coded in Fortran. All code for simulations and Python scripts for data analysis are available in the GitHub repository at https://github.com/deborah/mito-nuclear-speciation.

**References**

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There are no empirical data associated with this study.

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