Recurrent speciation rates on islands decline with species number

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Abstract

In an archipelagic system, species diversity is maintained and determined by the balance among speciation, extinction, and migration. As the number of species increases, the average population size of each species decreases, and the extinction likelihood of any given species grows. In contrast, the role of reduced population size in geographic speciation has received comparatively less research attention. Here, to study the rate of recurrent speciation, we adopted a simple multi-species two-island model and considered symmetric interspecific competition on each island. As the number of species increases on an island, the competition intensifies, and the size of the resident population decreases. In contrast, the number of migrants is likely to exhibit a weaker than a proportional relationship with the size of the source population due to rare oceanic dispersal. If this is the case, as the number of species on the recipient island increases, the impact of migration strengthens and decelerates the occurrence of further speciation events. According to our analyses, the number of species can be stabilised at a finite level, even in the absence of extinction.

Keywords: intermediate-dispersal hypothesis (IDH), island biogeography, speciation, symmetric interspecific competition.

1. Introduction

Understanding how biodiversity is shaped and maintained is a central problem in ecology and evolutionary biology. The number of species is determined by the balance between the extinction and origination of species (*sensu* [1]). Extinction rates and the possibility of multiple species coexisting are major research topics in ecology, while the genetic, demographic, and ecological processes that lead to speciation are studied by evolutionary biologists. However, when biodiversity is discussed from the perspective of ecology, speciation is modelled in a simplified manner, just as a process that provides a new species in a community. In previous studies, the number of species was assumed to increase when migration occurred in a focal community from source populations that were located elsewhere (e.g. a nearby continent) [2], or when a new species arose from point-mutation-like speciation [1] or as random fission of a species [3] in a community. Since the work of MacArthur and Levins [4], the process that determines species richness in a community has been thought to be due to ecological processes that mediate the exclusion of species from the community. Elucidation of the connection between the theory of biodiversity with explicit speciation mechanisms remains underexplored and exploration can provide further insights into species diversity patterns.

One of the most controversial questions in linking speciation and biodiversity is whether species diversity promotes further increases in species diversity. Emerson and Kolm [5,6] showed that species diversity itself could be a driver of species diversification by analysing the proportion of endemics in archipelagic systems, providing an index of speciation rates (cf. [7]). Increasing species diversity may lead to greater community structural complexity, and this has been suggested as a possible evolutionary force for driving speciation. Nevertheless, as MacArthur and Wilson [2] considered in their study, a higher number of species increases the likelihood of extinction of any given species. The theory of limiting similarity predicts that the average population size decreases as species diversity increases [4]. Hence, speciation and extinction are indeed in balance, but they are not independent of each other. This argument raises important questions: how does the reduced population size of existing species affect the speciation process, and how will it ultimately affect the speciation rate in an island-model?

Mathematical models for speciation generally consider a certain genetic distance representing the degree of reproductive isolation [8]. The distance between two populations of a single species increases due to the accumulation of mutations and decreases due to gene flow. When their differences either reach a threshold distance or

satisfy a specific combination of alleles, reproductive isolation is achieved, and the two populations can be regarded as different species [9]. Recently, the threshold of genetic distance to speciation has been proposed as a detectable 'tipping point' in non-linear speciation dynamics [10,11], and the concept of the tipping point has been applied to genomic data to investigate species boundaries in natural populations [12].

These concepts are highlights of the current study, where we have explored the manner in which a simple threshold model for speciation that considers population dynamics and the number of species affects speciation rate. The point-mutation model for speciation that is often used in community ecology assumes a constant rate of the appearance of a new species within the focal community [1]. In contrast, if we focus on the genetic distance between populations as an index of their divergence, the change in population size and migration influences the dynamics of genetic differentiation. The population size is determined by the quality and size of the habitat that provides the appropriate conditions for individuals and populations [13,14], and it is also affected by the interactions between organisms.

In the present study, we focussed on the mechanisms by which increases in species numbers associated with recurrent speciation affect changes in population size and its feedback with long-term speciation rates. In particular, we construct a speciation model that does not consider the adaptation process or ecological niches. We argue that species diversity saturates at a certain level under when explicit local adaptation or niche evolution are not considered. We also discuss the hypothesis that intermediate dispersal leads to the most diverse clades (referred as the intermediate-dispersal hypothesis, IDH). The IDH is represented well by Price and Wagner [15], who stated that 'species-rich lineages may have moderate dispersibility that is effective enough to extend the geographic range of whole lineages, yet infrequent enough to depress levels of gene flow'. In ecology and evolution, the IDH only verbally builds on ideas by earlier authors [16]. Yamaguchi and Iwasa [17] were the first to mathematically model the IDH by formulating the waiting times of recurrent speciation and colonisation on the two-island system. Recently, empirical support for the IDH has accumulated in various archipelagic organisms [18,19,20]. Additionally, Ashby et al. [21] found that, using a stochastic metapopulation simulation, the pattern of IDH was extraordinarily robust with a wide range of parameters, including variation in niche breadth, the number of available niches, carrying capacities, the number of patches, and the relative speed of ecological dynamics. It is noteworthy that Ashby et al. [21] adopted single species existence in just one location as an initial condition of simulation, whereas our current model starts with an omnipresent single species. Although finding available niches was the reason to generate the IDH pattern in the study of Ashby et al.

[21], the current study assumes a more complex mechanism for the IDH; it shows the differences in the relative importance of gene flow depending on the size of recipient populations. The patterns generated by IDH are likely to be general across the models, and the hypothesis is an ideal starting point to explore recurrent speciation.

In this study, we excluded details (e.g. adaptation or genetic architecture) and illustrated the mechanisms by which sequential speciation—genetic divergence, colonisation, and the population size of each species—affected the dynamics of species accumulation. Similar to any evolutionary ecology model, our general model can be applied across many taxa to assess the effects of competition and migration on extant clade diversity.

2. The model

To explore the process of recurrent speciation, we used a simple two-island model (Fig. 1), formalised as the IDH [17,22]. We considered a diploid sexual species with non-overlapping generations that exists on a pair of islands. In the initial state, the populations on the two islands were genetically the same. At a very low rate, organisms from one population may disperse to other populations. In a successful migration event, several individuals from one island arrive at the other island. During the period between two successive events of a successful migration, the two populations accumulated mutations independently, resulting in divergence of their genetic content. Most migration attempts fail, and successful migration events occur infrequently but are important in shaping macroevolutionary patterns in archipelagic systems [23].

The immigrants reproduce with the resident population of the same species. Thus, migration events contribute to gene flow between populations of the same species. If the two populations exceeded a differentiation threshold, the migrants form a new population of the species with the same genetic content as the original population. Therefore, migration events play two different roles in the recurrent speciation process: to provide gene flow and slow down genetic differentiation and to colonise and make both islands occupied by the same species.

(a) Dynamics of the genetic differentiation of two populations

Here, we begin with a single species living on two islands (or island-like habitats). We assume that each of the two populations of the species has N individuals. Let l be the number of autosomal loci that control incompatibility. For a pair of individuals, we call the fraction of loci with different alleles their 'genetic distance',

which is denoted by z. Here, we adopt a threshold model [17], which assumes that the individuals can engage in sexual reproduction and produce fully viable offspring when their distance z is equal to or less than a threshold z_c, but cannot hybridise, and instead form a genetically and ecologically independent population, if $z > z_c$. The threshold value may vary among species [24]. This threshold model of speciation can represent the evolution of reproductive isolation with the balance between the accumulation of mutations and gene flow [11,25,26].

We posit that the mutation rate of the loci that control incompatibility is much lower than the inverse of the carrying capacity N ($u \ll 1/N$). This assumption renders island populations genetically monomorphic most of the time, except for brief periods of allelic replacement and migration events [27]. This allows us to discuss the genetic distance between populations as the distance between two individuals from different populations.

Since migration events are extremely rare, there is a long interval between successive migration events. During this period, the distance between the two populations increases as they accumulate different mutations. We adopted an infinite allele model [28]. We also assumed that these mutations are neutral in the process of accumulation as a one-step difference (an increment of genetic distance by a single mutation, $1/l$) does not cause any significant effect on incompatibility. We have considered that a single species exists on both islands, although they may differ in some of the loci that control incompatibility, but it is not adequately strong to cause reproductive isolation. The two populations experienced allele replacement at a rate of $2u$ per locus per generation. Allele replacement increases the genetic distance between populations if the locus has the same allele in the two populations before the replacement. Hence, the rate of increase in genetic distance attributable to replacement by novel mutations has a factor of $1-z$, indicating the fraction of loci common between populations. The increase in z over a time interval Δt is given by:

$$\Delta z = z(t+\Delta t) - z(t) = 2u(1-z)\Delta t \,. \qquad (1)$$

Note that the length of the interval Δt is much shorter than the interval between successful migration events, but it is much longer than the time required for the fixation of a neutral mutation.

Next, we consider migration events and the subsequent reduction of genetic differences between populations. The successful migration rate is m per generation, where m is very small, indicating that the interval between successful migrations is long. If immigrants and residents have different alleles in a fraction z of all l loci, and if z is larger than z_c, the immigrants and residents cannot mix sexually and should be treated as different species. In contrast, if z is smaller than the threshold z_c,

individuals from the two populations can freely exchange genomes via sexual reproduction. The population genetics theory of neutral mutations indicates that a population eventually becomes monomorphic when one allele is fixed, and the other becomes extinct. The probability of fixation of an allele is proportional to its initial frequency.

Immediately after a successful migration event, the recipient population becomes temporarily polymorphic in the *lz* loci. After a certain number of generations, alleles introduced by a migration event become fixed or lost. Since the recipient population size is also sufficiently small, polymorphisms that disappear within a short period can be ignored at a time scale we can handle. The expected fraction of loci carrying immigrant alleles (instead of resident alleles) is equal to the fraction of immigrants: $\varepsilon = N'/(N+N')$. For simplicity, we assumed that the immigrant population has the same size (i.e. N' is constant), and that the loci are unlinked. Thus, the decrease in $z(t)$ that occurs over a short time interval Δt is given by:

$$\Delta z = z(t+\Delta t) - z(t) = -2m\varepsilon z. \qquad (2)$$

Thus, whole deterministic dynamics is given by $\frac{dz}{dt} = 2u(1-z) - 2m\varepsilon z$ with a limit of $\Delta t \to 0$. It grows and converges smoothly to the asymptotic value $\hat{z} = u/(u+m\varepsilon)$, which is determined by the mutation-migration balance. For the mathematical background and analytical solutions of the model, please see [29].

(b) Population size decreases with the number of competing species

We considered a situation where the population size at equilibrium (N^*) on each island depends on the number of other species existing on the same island. Since we considered the process of recurrent speciation, even if we start from a single species, their descendants will face the situation of coexisting with multiple other species that are somewhat similar in ecology and resource use because they have originated from the same species.

Here, we considered a situation in which species living on the same island engage in competition with each other. Since they may develop some differentiation in niches, they can coexist, but their abundance should be reduced by the presence of their competitors. For simplicity, we assumed symmetric competition among species on the same island. Let N_i be the population size of the *i*th species on an island. We considered that they engaged in the classical Lotka–Volterra competition model [30,31], in which the carrying capacity K is the same as the case without competitors

on the same island. Let a be the interspecific competition coefficient (relative to intraspecific competition). Then, in equilibrium, the population size N_i^* is given as:

$$N_i^* = \frac{K}{1+a(s-1)}. \quad (3)$$

N_i^* depends on the total number of species s on the islands, the carrying capacity of the island K, and the coefficient of interspecific competition a. Here, we assumed that $0 \leq a < 1$, which implies that the interspecific competition is weaker than the intraspecific competition, allowing their stable coexistence. From Eq. (3), the equilibrium population size decreases as the number of species on the island increases. Note that if we set $a = 0$ (i.e. no interspecific competition), then the population size of each species is K and is independent of the number of species.

Here, we assumed that the number of migrants at the time of a successful migration event will increase with the abundance of the species on the source island, but its dependence is weaker than proportional. This assumption is plausible because migration events are caused by abiotic processes such as storms and drifts on the sea (e.g. see [32,33] for oceanic dispersal by rafting). Thus, migration rarely occurs, and migrants can arrive at the opposite side of the archipelago as a group when a successful migration occurs, even if the total population size in the recipient island becomes small. It means that migrants mature sexually during a successful migration, and the time required for their dispersal is more than that for population regulation. The small size of the recipient population would strengthen the impact of gene flow from each migration event. In the following analysis, for the sake of simplification, we first analysed the case in which the number of migrants in a successful migration was independent of their population size on the source island. We later discuss the results when alternative assumptions were adopted.

Specifically, let $\varepsilon_i = N' / \left(N_i^* + N'\right)$ be the impact of gene flow between two populations of an ith species. As the number of species on the recipient island increases, the size of the recipient population N_i^* decreases (see Eq. (3)), which increases the relative impact of migration and facilitates gene flow between populations. Thus, our current model included some ecological aspects (e.g. population dynamics and immigrant colonisation) in a simplified manner, in addition to the evolutionary process of genetic differentiation. We described the simulation scheme in detail in SI Appendix 1.

3. Results

We have analysed the model and explained it in detail in SI Appendices 2 and 3. Here, we report a summary of the behaviour of the model obtained from numerical analyses. We calculated 4000 generations for each simulation run unless otherwise stated.

(a) Genetic divergence and equilibrium

The genetic distance between the populations on the two islands $z(t)$ increased with time, and the rate of increase slowed down as the difference in the fraction of the loci between the two populations increased (see Eq. (1)). The dynamics of genetic distance $z(t)$ finally converged to an asymptotic value determined by the balance of mutation and migration. Speciation was assumed to have occurred if the threshold level z_c was smaller than the asymptotic value. However, as the number of species on an island increased, the asymptotic value decreased because the effect of gene flow was facilitated by the reduced size of the recipient population (Figure S1). Speciation occurred as long as the asymptotic value of $z(t)$ was higher than z_c. However, as the number of species increased, the asymptotic value of $z(t)$ became lower than z_c, and no new speciation event occurred. In the model, when the size of each population on the islands became sufficiently small, speciation ceased, and the system became stationary, even in the absence of species extinction.

(b) Maximum number of species originated and interspecific competition intensity

In our model, the number of species monotonically increased in each simulation run. Figure 2 represents the accumulation of the number of species over time, using a lineage-through-time (LTT) plot to visualise the overall pattern of diversification. If there was no competition among species ($a = 0$), the total number of species increased exponentially because the presence of other species has no effect on the population size of any of the local species. The aspect that limits speciation in our model is the effective strengthening of gene flow when recipient populations become small. If this mechanism loses functionality, then a limit on speciation no longer exists, thereby explaining the exponential growth in species numbers.

As the competition coefficient increased, the species number converged to a finite level. The LTT plot was an S-shaped curve: slow growth at first, followed by a period of faster growth, before levelling off to a saturated value. Here, we note that the equilibrium species number was realised from the speciation rate decreasing with the species number, rather than the extinction rate increasing with the species number (N.B., no extinction was considered in our model). Additionally, the population size of each species decreased as the strength of interspecific competition a increased.

Consequently, the equilibrium number of the species on the two islands decreased as the competition coefficient a increased (Figure S2).

The deterministic treatment of the dynamics of genetic distance predicted that speciation should cease when the number of species becomes sufficiently high (see Eq. (A2.4) in SI Appendix 2). However, we note an important caveat to accept this new finding: although the rate of species origination decreases with the number of species on the recipient island, it increases with the number of species on the source island. Let S_i be the number of species on the island i $(i = 1, 2)$. The rate of increase in S_2 decreases with S_2, but increases with S_1. In a similar manner, the rate of increase in S_1 decreases with S_1, but increases with S_2.

(c) Speciation-maximising migration rate and interspecific competition intensity

There exists an intermediate speciation-maximising migration rate between the two islands that achieves the maximum rate of species origination in the absence of interspecific competition [17,29]. If migration events occur very rarely, then the two populations on different islands diverge to become different species without gene flow preventing this. However, one of the newly formed species has to colonise the other island for subsequent new speciation events to occur, and this happens only infrequently if the migration rates are very low (Fig. 1). Taken together, this means that the overall rate of speciation remains rather low. On the other hand, if the migration rate is considerably high, then genetic divergence slows down, and it takes longer for the genetic distance to reach the speciation threshold. The rate of migration that maximised the chance of species origination was close to the migration rate, which minimised the sum of the mean time to speciation and the mean time to the next migration event ($1/m$) (Figure S3). The sum indicates the 'cycle time' and is depicted as a U-shaped function of the migration rate. The inverse of the cycle time was approximately equal to the speciation rate by this mechanism. In SI Appendix 3, we mathematically show that the cycle time is always a convex function of the migration rate, and there exists an intermediate speciation-maximising migration rate.

If interspecific competition exists, then our model still predicts that an intermediate migration rate maximises the rate of species origination. As shown in Figure 3, the speciation-maximising migration rate in the presence of competition is smaller than without interspecific competition. The speciation-maximising migration rate was around 0.005 under the existence of interspecific competition ($a = 0.2$, Figure 3), but it was higher when we assumed no competition ($a = 0$, Figure S3), with all the other parameters being the same. In the absence of competition, the cycle time remained

constant. However, in the presence of competition, the cycle time changed with time because the average waiting time to speciation increased as the number of species increased. In Figure 3 (where $a > 0$), the two cycle times corresponding to s=1 and s=10 are indicated by two curves as examples. In contrast, in Figure S3 (where $a = 0$), a single curve for the cycle time is shown. The speciation-maximising migration rate under competition might be obtained from the average of varying cycle times for different numbers of species. As the total number of species increased, the average waiting time until speciation became longer, and the sum of the mean waiting time until the next migration event was minimised with a slower migration rate (indicated by the solid arrow in Figure 3).

In Figure 4, we summarise a combination of the migration rate and a competition coefficient to maximise the number of species originating through the recurrent speciation process. As the competition intensified, both the total number of originated species produced in a period and the speciation-maximising migration rate became smaller. It is also worth noting that the total population size on each island increased as the number of species increased when the interspecific competition coefficient was lower than 1 ($a < 1$, Figure S4), which is needed for the stable coexistence of competing species. Furthermore, the results presented in Fig. 3 and 4 were obtained from halting the simulations at 4000 generations (i.e. species accumulation at an early stage). If the migration is quite low, the speciation rate will also be low due to the difficulty of colonisation events, but the equilibrium number of species should be large when we wait for a very long time. The speciation-maximising migration rate maximises not the equilibrium number of species but the rate of speciation.

4. Discussion

In this study, we have reported an attempt to shed light on an aspect that has not been explored previously. We explored the manner in which the rate of species origination changes with the existing number of species. Specifically, we built a mathematical model of recurrent speciation based on the independent mutation accumulation of incompatibility loci plus the rare but recurrent migration events (i.e. intermediate dispersal hypothesis: IDH) in a two-island system (Fig.1). This contrasts sharply with most of the previous ecological arguments on biodiversity, in which speciation is regarded as a point-mutation-like process that has a rate independent of the number of extant species.

The most striking finding of our theory is that the rate of species origination declined with the number of existing species on the recipient island. As the number of

species on an island increases, the population size per species on an island decreases on average. Then, the effect of gene flow on the population that receives accepting migrants becomes stronger. As a result, genetic differentiation between populations of species on different islands slows down. This elongation of the waiting time to speciation finally ceases species origination. What is especially notable is that there is a possibility of reaching a finite stationary number of species, even in the absence of species extinction (Fig. 2).

To repeat multiple speciation events in an archipelagic system, interspecific competition among newly diverged (and closely related) species is inevitable in secondary contact. In the words of MacArthur and Levins [4], 'environmental instability sets a limit to the degree of specialisation and, for a given degree of specialisation, competition may, but does not always, set a limit to the similarity of coexisting species.' In our study, we considered the case with 'diffuse competition' [34], in which there is no explicit niche structure. Thus, groups of species engage in interspecific competition in a symmetric manner. The coefficient of interspecific competition a, therefore, measures the magnitude of population growth rate suppression by resource competition relative to intraspecific competition [4,35]. The reduction in population size due to competition not only increases the extinction rate (as discussed in the literature), but also suppresses speciation rates through facilitated gene flow because small recipient populations tend to be more strongly affected by introgression than larger recipient populations.

(a) Character displacement and niche specialisation

There are several different processes to explain the manner in which the number of species in an archipelagic system is determined, including the one we proposed in this study. This is demonstrated by the contrast between two well-studied systems of birds on the Galapagos Islands; Darwin's finches exhibit spectacular adaptive radiation, but mockingbirds seem to show an incipient radiation arrested in its early stages [36]. Mockingbirds have dispersed to all the archipelago islands, but have failed to establish sympatry on any one of them. The most considerable difference in the diversity of these two groups of birds cannot be explained by the presence/absence of competitors and predators because those would apply to both mockingbirds and finches. Despite the fact that these two taxa arrived at the Galapagos archipelago at almost the same time, the consequences of their diversification are completely different (15 species for finches vs. 4 allospecies for mockingbirds). Their feeding behaviours and potential for character displacement might contribute to the differences observed in species diversity (see Appendix 4 for detailed discussions). In the context of our current model,

the coefficient of interspecific competition can be reduced via character displacement.

Recently, biotic interaction-limited speciation events or immigration rates have been investigated. A study conducted by Alroy [37] supports that global species richness is limited exactly when local interspecific competitive interactions are strong. Additionally, the results by Alroy [37] are also consistent with a theory that high-diversity communities are more resistant to invasion because the chance of successful invasion is a negative function of local species richness. The number of colonising species in a region correlates positively with the number of source species because species-rich regions may present the existence of more niches, both occupied and open. Thus, the successful colonisation component can be dynamic, and our recurrent speciation model suggests that the limited species origination can be mitigated through character displacement or niche specialisation.

Alternatively, considering phylogenetic relationships among all Himalayan songbirds, Price et al. [38] revealed that an ultimate limit on repetitive speciation is responsible for niche filling (that is, ecological competition for resources), rather than the rate of acquisition of reproductive isolation. As observed in the case of our proposed model, range expansions are a critical step in the speciation cycle in the study system. Both the appearance of new species and morphological diversification have substantially decelerated, and species distributions are well explained by the abundance of resources. It implies that the ultimate limit on diversification can be best explained, not by a slow rate of accumulation of reproductive isolation, but by the failure of species to expand ranges into new localities, which has been attributed to competitive interactions. As range expansions are essential for the occurrence of most ongoing speciation events, local interactions ultimately determine regional speciation rates, rather than regional speciation rates determining and establishing local diversity.

(b) Extinction

By combining the formula for the rate of species origination investigated in this study and the rate of species extinction, we should be able to calculate the equilibrium species number at the final state. The simplest possible model is the one used by MacArthur and Wilson [2,39]), in which the rate of species extinction is independent of the number of species on the same island. If there are S species on the island, the rate of extinction is simply equal to bS, proportional to the existing species, where b is a constant. If the species have the same resource requirements and are regulated by the common carrying capacity (the total number of individuals), the neutral model is applicable. Halley and Iwasa [40] found that the species extinction

rate per generation S^2/K is proportional to the square of the number of existing species and inversely proportional to the total number of individuals on the island.

However, these simple formulas are not applicable to the current situation. In the model proposed in this study, there was interspecific competition between species that was weaker than the intraspecific competition because $a < 1$. This assumption positively supports the coexistence of all species in the community rather than the cases of neutral extinction (cf. SI Appendix 5). We expect that the rate of species extinction should be much lower than the neutral cases, which supports the intuition of many ecologists who search for processes that favour niche differentiation among species. To include the rate of species extinction in the current model, a stochastic formulation of this non-neutral situation will be necessary.

(c) Future studies

In this study, we have made several simplifying assumptions that warrant further exploration in future studies. First, we assumed that dispersal ability and competition are constant over time and are independent of the source population size. Future theoretical studies could explore the interactions between dispersal evolution and resource competition [41]. For example, archipelagic ecosystems that lack predators may concurrently lead to the loss of flight in organisms that would use flight to flee [42]. Behavioural plasticity can also be associated with a higher probability of colonisation and lower extinction risk in migratory birds [43]. These extensions may qualitatively change the results of the IDH. For a situation in which the number of immigrants depends on the population size of a source species (i.e. migration caused by biotic processes), as another simple extension of the current model, refer to SI Appendix 6 and Figure S5. The number of originated species reached a finite stationary state even in the absence of extinction when the number of migrants N' is not assumed to be a constant, but is assumed to be a saturating function of the population size N. This enables us to discuss a potential consequence that differed from the main scenario. Furthermore, regarding resource competition, our model implicitly assumed that ecological differentiation (intra-inter competition inequality) was simultaneously established when speciation occurred. Comparison of the results of the proposed model with those of the models explicitly considering local adaptation or niche evolution is one of the desirable options.

Second, our results were derived from a deterministic model for speciation. As shown by Yamaguchi and Iwasa [17,29], recurrent speciation slows down but continues to take place even when the asymptotic value of the genetic distance $\hat{z}_i$ is smaller than the threshold z_c in the corresponding stochastic dynamics. In fact, this

process includes a large fluctuation caused by the occasional long interval of migration events and the stochasticity of the timing of mutation fixations, which may allow genetic distance between the two islands $z(t)$ to fluctuate around $\hat{z}_i$ and reach z_c within a finite number of generations. The low rate of speciation caused by the stochasticity can be balanced with the slow rate of species extinction.

Finally, the relative importance of the impact of reduced speciation rates based on population dynamics and the biodiversity of local communities remains to be explored. The framework of our model was chosen deliberately as the simplest and most basic framework for extensibility. If we set the coefficient of interspecific competition as a=1 and extend it to a lottery model by assuming a zero-sum finite population, then the current model would be consistent with the community model of the unified neutral theory by Hubbell [1]. Additionally, from the viewpoint of species abundance distribution, our model possesses a limitation, i.e. our model considers that the development of all species is equally common. By increasing the number of islands, we may have a model with a meta-community structure. It would be worth exploring the relative impacts of geographic isolation, migration, and changes in population size on extinction and speciation, as well as their contribution to the dynamic equilibrium of biodiversity.

5. Conclusion

The rate of species origination has not been investigated with sufficient depth in the context of species diversity patterns. Hence, our finding that the rate of speciation is a decreasing function of the number of existing species provides an important insight into this process. Under the existence of interspecific competition, there is a possibility that the number of species can be stabilised at a finite level even in the absence of extinction. If interspecific competition may be mitigated by character displacement, then speciation rates would increase again with the population size. It will become even more important to measure the extent and evolutionary potential of character displacement. The context in which character displacement is measured has often been to seek the causes of segregation between closely related species with overlapping niche [44,45]. In the future, the relationship among the degree of character displacement, gene flow and population size will garner more attention and will be extensively used to reveal the manner in which the diversity of extant species affects the rate of speciation and extinction, and ecological surveys will be conducted to connect speciation and biodiversity studies.

Data accessibility

All codes necessary to repeat the analysis described in this study have been made available. C++ source codes of our model for speciation dynamics and *Mathematica* (version 11.2.0.0) codes that we used to produce figures are hosted on Dryad Digital Repository [46].

Authors' contributions

RY, YI, and YT designed the study; RY developed the computer simulation code and conducted analyses in consultation with YT; RY, YI, and YT wrote the manuscript.

Competing interests

We declare we have no competing interests.

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Figures

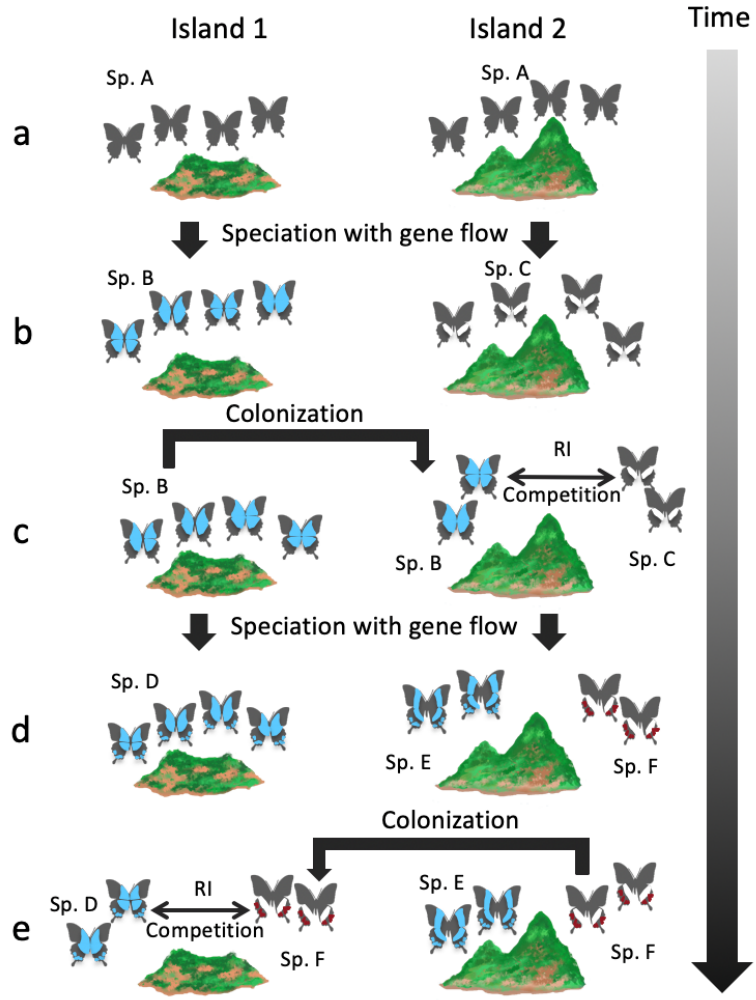

Figure 1. Schematic illustration of the recurrent parapatric speciation model. Here, focal diploid organisms are depicted as butterflies. (a) Initially, two populations of a single species (Sp. A) exist on two islands (Islands 1 and 2) that are geographically isolated. (b) After a period of divergence with slow gene flow, the populations become genetically different and do not exhibit the ability to hybridise. Then, they develop into different species (Sp. B and Sp. C). (c) Group of individuals from Sp. B on Island 1 migrate successfully to Island 2, which was occupied by Sp. C. On Island 2, the immigrants of Sp. B and residents of Sp. C compete with each other. If they can coexist with the reduced population sizes in both species, then two species are developed on Island 2. RI indicates reproductive isolation. (d) After many years, Sp. B on Island 1, Sp. B on Island 2, and Sp. C on Island 2 develop into Sp. D, Sp. E, and Sp. F, respectively. Thus, the total number of species on the two islands becomes three. (e) A group of individuals from Sp. F on Island 2 successfully invade Island 1. The immigrants of Sp. F and residents of Sp. D may compete with each other. If they

coexist in a similar manner, as explained in (c), the number of species would continue to increase, resulting in the occurrence of recurrent speciation events. As for the count of species number, one species in (a), two species in (b) and (c), and three species in (d) and (e) are observed.

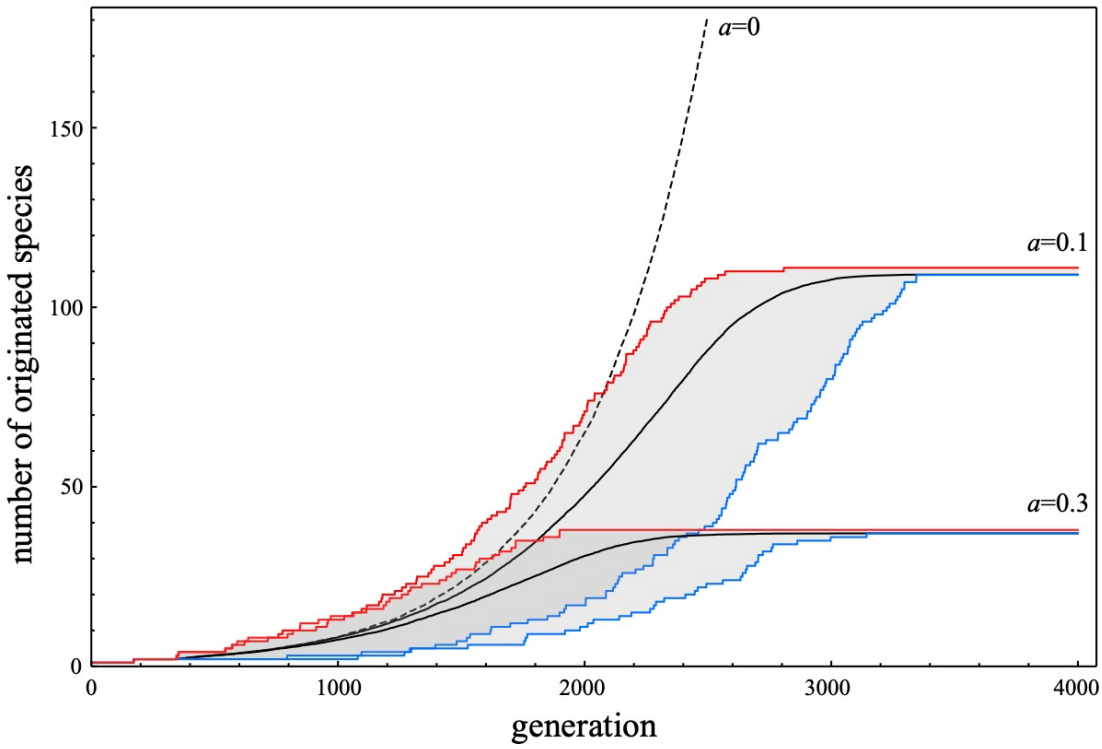

Figure 2. Lineage-through-time (LTT) plot generated to represent trajectories of the number of originated species. The horizontal axis indicates the time expressed in terms of the number of generations. The initial number of species considered is one. Cases with three different competition rates ($a = 0, 0.1$, and 0.3) are shown. 100 simulations were run for each parameter set, and the red, blue, and black curves represent the maximum, minimum, and mean, respectively, for $a = 0.1$ and $a = 0.3$. For $a = 0$, the expected value is depicted as a dashed line. Other parameters are: $u = 0.001$, $m = 0.005$, N'=10, $K = 100$, and $z_c = 0.27$.

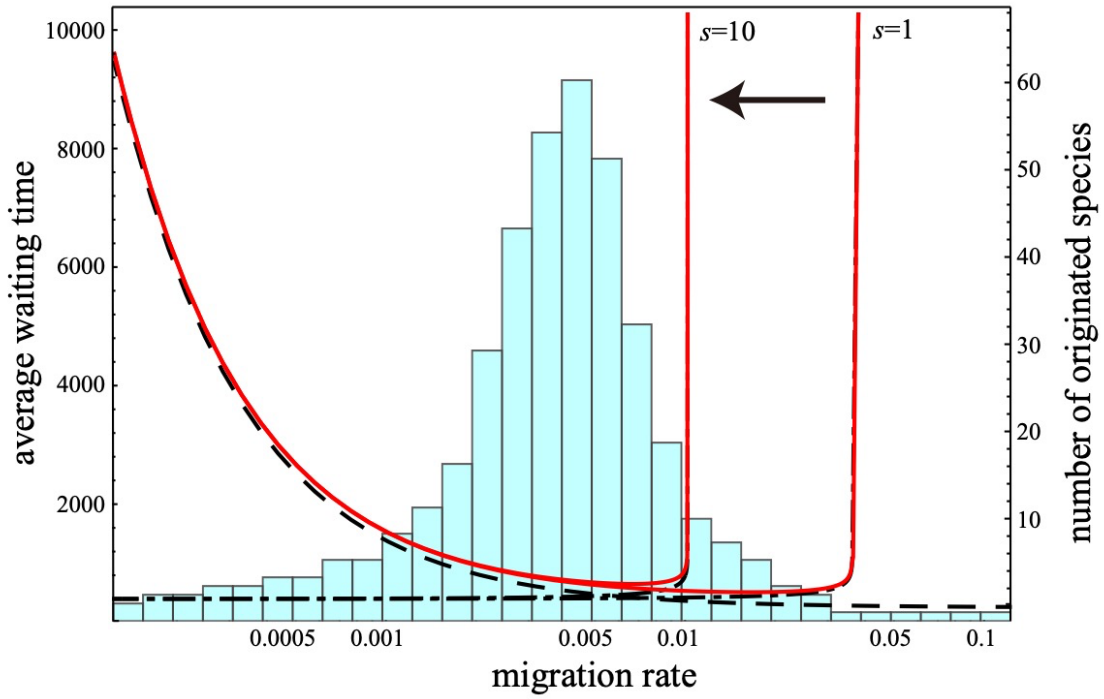

Figure 3. The speciation-maximising migration rate. The horizontal axis indicates the migration rate in the logarithmic scale m. The dashed lines indicate the mean time interval between migration events ($1/m$). The two dashed-and-dotted lines indicate the average waiting time until speciation for different number of species on two islands ($s = 1$ and $s = 10$). The solid red lines represent their sum (cycle time). All the lines are depicted by following the analytical solutions in Appendix 3. The solid arrow indicates that the cycle time changes with an increase in the species number. The blue bar chart indicates the average number of species that originated on the two islands. An average of 100 simulations were run for each migration rate. One species existed at time 0 in each simulation. The competition coefficient is $a = 0.1$. All other parameters are as those illustrated in Figure 2.

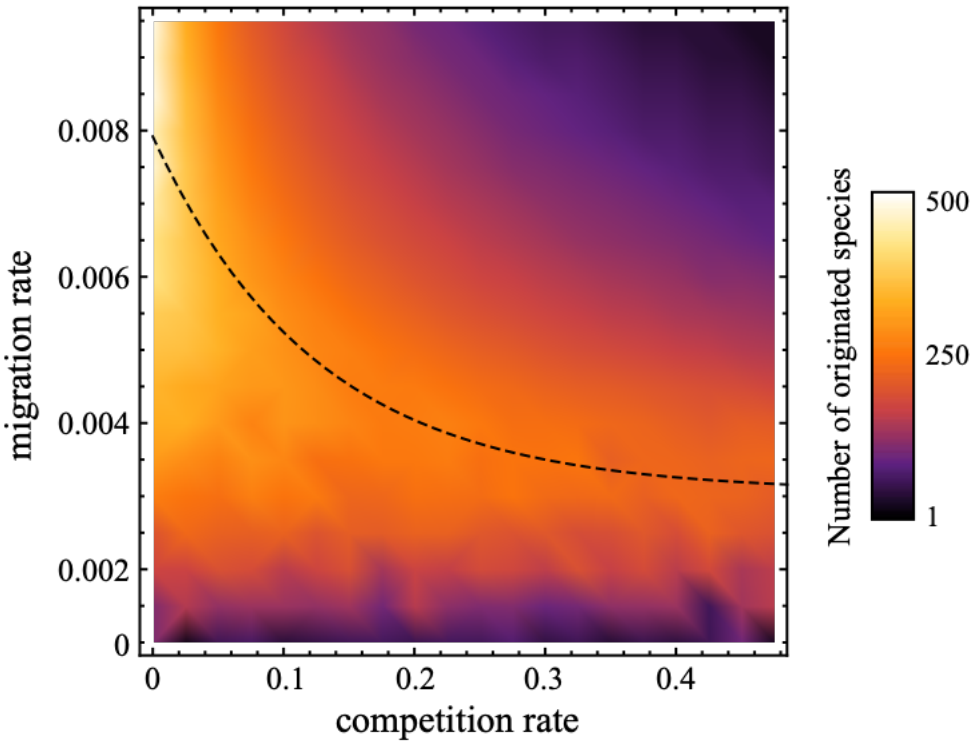

Figure 4. Dependence of the number of originated species on the competition rate and migration rate. Dark regions indicate a small number of species, while light-coloured regions indicate high species diversity from recurrent speciation processes. The speciation-maximising migration rate becomes lower when the competition rate is more intense (the dashed line). 360 combinations of parameter sets were used to illustrate this density plot, and for each parameter combination, 50 simulations were run to calculate the mean values. All other parameters are as those illustrated in Figure 2.