A generalized model of island biogeography

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MacArthur and Wilson's equilibrium theory is one of the most influential theories in ecology. Although evolution on islands is to be important to island biodiversity, speciation has not been well integrated into island biogeography models. By incorporating speciation and factors influencing it into the MacArthur-Wilson model, we propose a generalized model unifying ecological and evolutionary processes and island features. Intra-island speciation may play an important role in both island species richness and endemism, and the contribution of speciation to local species diversity may eventually be greater than that of immigration under certain conditions. Those conditions are related to the per species speciation rate, per species extinction rate, and island features, and they are independent of immigration rate. The model predicts that large islands will have a high, though not the highest, proportional endemism when other parameters are fixed. Based on the generalized model, changes in species richness and endemism on an oceanic island over time were predicted to be similar to empirical observations. Our model provides an ideal starting point for re-evaluating the role of speciation and re-analyzing available data on island species diversity, especially those biased by the MacArthur-Wilson model.

MacArthur and Wilson's equilibrium theory [1,2] is one of the most influential theories in biogeography, ecology and conservation biology [3,4]. As the paradigm of island biogeography, this dynamic equilibrium theory explains emergent patterns of species richness and endemism on an island based on two biogeographical processes (immigration and extinction) and on two physical features of the island (area and isolation) [1,2]. This theory has strongly influenced other fields of ecology and conservation biology for forty years and has stimulated many hundreds of studies on patterns of species richness in a great variety of ecosystems and biotas [5]. Evolution on islands is thought to be important on the evolutionary time scale [1,2], but it has not been well considered in the dynamic equilibrium model, even though evolution is commonly used to explain ex-

traordinarily high numbers of endemic species [6,7].

The role of speciation in the species diversity of oceanic islands has long been noted and frequently emphasized [6,8–13]. There have numerous attempts to link evolutionary and ecological dynamics building on the MacArthur-Wilson model [14,15]. However, the challenge of combining evolution, immigration, extinction and island features has not been well fulfilled, and there have been repeated calls for theoreticians to develop new models/theories [3,5,12,16].

Using a simple model of island biogeography theory, we previously predicted the relative contributions of speciation and immigration to island species diversity over time [17]. We also provided a theoretical explanation for the positive relationship between percentage endemism and species diversity on islands. In this paper, we extend the simple model to a more generalized one that includes the impacts of both biogeographical processes and island features.

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1 Materials and methods

As pointed out by MacArthur and Wilson [1], species richness on an island is ultimately determined by three biogeographical processes: immigration, which adds species to the island from the mainland or other islands; local speciation, which leads to divergence within some species; and extinction, which eliminates species from the island. Island features, such as area and isolation, may have an impact on these processes. Although many islands occur in archipelagos, to simplify the model, we treat an archipelago as an island, because migration among islands of an archipelago occurs at much higher rates than that between the archipelago and the mainland or other islands/archipelagos.

Without loss of generality, the numbers of new species added by immigration (I_t) and species eliminated by extinction (E_t) at time t can be expressed as [18,19]

$$I_t = I_0 D^{-\theta} A^{\mu} (S_M - S_{I(t)}),$$

$$E_t = E_0 D^{\xi} A^{-\nu} S_{I(t)},$$

where S_M is the species richness on the mainland; $S_{I(t)}$ is the species richness on the island at time t; I_0 and E_0 are per species immigration and extinction rates, or immigration and extinction coefficients, respectively [20]; D and A are distance to the mainland and island area, respectively; θ and ξ are positive constants scaling the impacts of distance on immigration and extinction, respectively; and μ and ν are positive constants scaling the impacts of area on immigration and extinction, respectively. The impact of island area on immigration, i.e., the target effect, and the impact of isolation/distance on extinction, i.e., the rescue effect [21], are also considered in the two equations. When all other parameters are fixed, larger islands have higher immigration rates, and nearer islands have lower extinction rates.

To incorporate the impact of evolution, we introduce the contribution of intra-island speciation into the model. Speciation adds new species and therefore increases species richness on the island. Larger islands generally have higher speciation rates [6,22–24], while isolation decreases gene flow among islands or between the island and the mainland, leading to increased differentiation and more speciation [24,25]. Thus, we take the following form to express the number of new species on an island added by speciation (λ_t) at time t:

$$\lambda_t = \lambda_0 D^{\tau} A^{\omega} S_{I(t)},$$

where λ_0 is the per species speciation rate, or speciation coefficient, i.e., the number of species added by speciation per unit time per species. To simplify the model, λ_0 is assumed constant. ω and τ are positive constants scaling the impacts of area and isolation on speciation, respectively. The smaller the value of ω or τ, the slighter the impact of island area or isolation on speciation.

Species diversity on the island at time $t+1$ is (see [1]) $S_{I(t+1)} = S_{I(t)} + I_t - E_t + \lambda_t$. Similar to our previous study [17], given $S_{I(0)} = 0$, we have the following equation:

$$S_{I(t)} = \frac{I_0 D^{-\theta} A^{\mu} S_M [1 - (1 - I_0 D^{-\theta} A^{\mu} - E_0 D^{\xi} A^{-\nu} + \lambda_0 D^{\tau} A^{\omega})^t]}{I_0 D^{-\theta} A^{\mu} + E_0 D^{\xi} A^{-\nu} - \lambda_0 D^{\tau} A^{\omega}}.$$

(1)

Given the very small values of I_0, E_0 and λ_0, as well as small values of the factors scaling the impacts of isolation and area, $I_0 D^{-\theta} A^{\mu} + E_0 D^{\xi} A^{-\nu} - \lambda_0 D^{\tau} A^{\omega}$ is much smaller than 1. Therefore, when $t \to \infty$, the number of species added by immigration and speciation equals that eliminated by extinction, and we get equilibrium richness on the island, i.e.,

$$S_I = \frac{I_0 D^{-\theta} A^{\mu} S_M}{I_0 D^{-\theta} A^{\mu} + E_0 D^{\xi} A^{-\nu} - \lambda_0 D^{\tau} A^{\omega}}.$$

(2)

Because our aim is to understand the effect of speciation on the species richness of islands, to simplify the model, we only consider speciation on islands and ignore speciation on the mainland. To meet the generality of lower richness on islands than on the mainland, this means that $E_0 D^{\xi} > \lambda_0 D^{\tau} A^{\omega+\nu}$. Nevertheless, our model has captured the main properties of the island biogeography equilibrium model [2,18]. For example, local species richness increases with increasing island area (Figure 1) and with decreasing isolation. Obviously, intra-island speciation increases island species diversity (Figure 1). Considering the impact of island area on speciation, there will be a positive relationship between
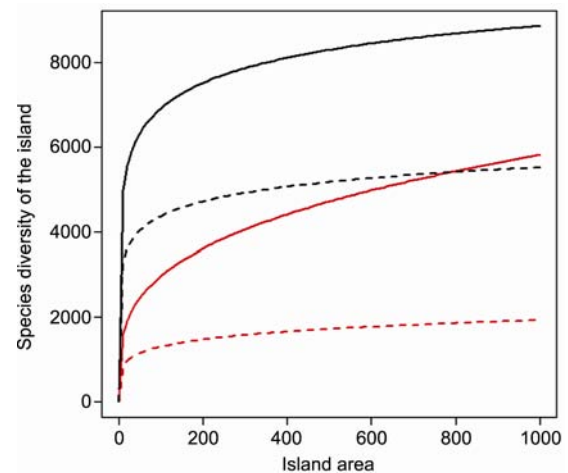

Figure 1 Effects of speciation, distance and area on island species richness when $S_M = 10000$, $I_0 = 0.8 \times 10^{-3}$, $E_0 = 0.5 \times 10^{-3}$, $\theta = 0.5$, $\mu = 0.1$, $\nu = 0.1$, and $\omega = \xi = 0.01$. Distances to the mainland are 25 (black lines) and 625 (red lines), respectively. Solid and dashed lines show the results when speciation is present ($\lambda_0 = 0.2 \times 10^{-3}$ and $\tau = 0.005$) and absent, respectively. Species richness of the island increases with island area and decreases with distance to the mainland. Speciation increases richness on the island.

species richness and ω and between species richness and island area, which has been frequently observed in island systems [26].

2 Results and discussion

2.1 Relative contribution of speciation and immigration to richness over time

Both ecological and evolutionary processes contribute to the species richness of an island. Generally, ecological processes are thought to be more important over the short-term, ecological time scale, while evolutionary processes are critical over the long-term, evolutionary time scale. More specifically, immigration plays an important role in the increase in species diversity in the early stages of an island, while speciation is critical in increasing species richness at later stages. Because the number of new species added by immigration decreases with increasing species diversity on the island, while the number added by speciation increases [3], can we expect that speciation will eventually add more species than immigration, and if so, when and under what conditions will this happen?

If we set speciation to add more new species per unit time than does immigration, i.e., $\lambda_t > I_t$, then $\lambda_0 D^\tau A^\omega S_{I(t)} > I_0 D^{-\theta} A^\mu (S_M - S_{I(t)})$. Therefore, we can easily obtain the

time: $t > \dfrac{\ln[(2\lambda_0 D^\tau A^\omega - E_0 D^\xi A^{-\nu})/(I_0 D^{-\theta} A^\mu + \lambda_0 D^\tau A^\omega)]}{\ln(1 - I_0 D^{-\theta} A^\mu - E_0 D^\xi A^{-\nu} + \lambda_0 D^\tau A^\omega)}$.

This relationship indicates that the critical time at which speciation adds more new species per unit time than does immigration is delayed by increasing extinction and occurs earlier with increasing immigration and speciation. This shift in relative importance of immigration and speciation to local diversity over time coincides with empirical observations. In the early stages, colonization plays a much more important role in species accumulation on newly-created or sterilized islands [27]. As time passes, the number of new species added by migration to the island decreases because the difference in species richness between the island and mainland decreases.

However, the shift described above is conditional. In addition to the condition above, the critical time should meet

$2\lambda_0 D^\tau A^\omega - E_0 D^\xi A^{-\nu} > 0$, or $\lambda_0 > \dfrac{1}{2} A^{-(\nu+\omega)} D^{\xi-\tau} E_0$, which

is independent of the immigration coefficient (Figure 2). When these conditions are met, the contribution of speciation to local species richness will eventually be larger than that of immigration. When all other parameters are fixed, the larger the island area, the smaller the per species speciation rate needed to effect the shift. For example, when $\nu + \omega = 0.25$, $A = 625$, $D=25$ and $\xi = \tau = 0.01$, and even if the per species speciation rate is as little as 10% of the per
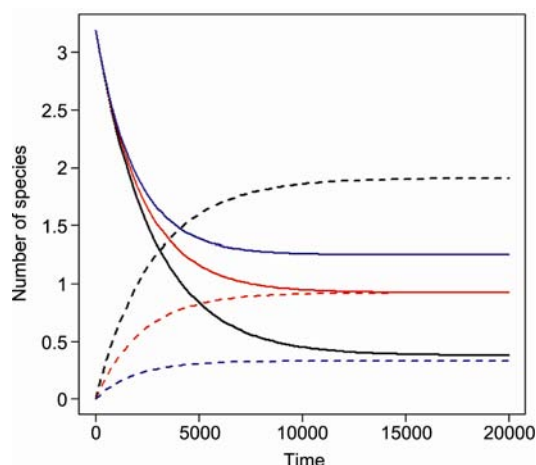

Figure 2 Number of species per unit time added by immigration (solid lines) and speciation (dashed lines), at λ_0=0.2×10^{-3} (black lines), 1.1966×10^{-4} (red lines), and 5×10^{-5} (blue lines), respectively, given S_M=10000, I_0=0.8× 10^{-3}, E_0=0.5×10^{-3}, D=25, q=0.5, μ=ν=0.15, ω=ξ=τ=0.01, and A=100. When $\lambda_0 > \dfrac{1}{2} A^{-(\nu+\omega)} D^{\xi-\tau} E_0$, speciation eventually adds more new species per unit time than immigration does (black lines). When $\lambda_0 = \dfrac{1}{2} A^{-(\nu+\omega)} D^{\xi-\tau} E_0$, the number of species added by speciation equals that by immigration (red lines). At $\lambda_0 < \dfrac{1}{2} A^{-(\nu+\omega)} D^{\xi-\tau} E_0$, speciation always adds fewer new species than immigration does (blue lines).

species extinction rate, speciation will eventually add more species than immigration per unit time. This indicates that, even at low rates, local speciation may play a crucial role in island species diversity, especially on large islands, and therefore speciation is much more important to island biodiversity than previously thought [15].

Although the occurrence of the shift is independent of the immigration coefficient, it is related to distance, because isolation impacts both speciation and extinction rates. When $\tau > \xi$, i.e., the increase in speciation rate is larger than that of the extinction rate, as isolation increases, speciation will add more species than immigration on islands with a distance of

$D > \left[\dfrac{E_0}{2\lambda_0 A^{\nu+\omega}}\right]^{\frac{1}{\tau-\xi}}$ from the mainland. MacArthur & Wil-

son [2] suggested that, near the outer limit of the dispersal range of a given taxon where it has a low immigration rate, the speciation rate can exceed the immigration rate. Their statement was correct, not because remote islands have very low immigration rates, but because the distance affects both speciation and extinction rates. However, if $\tau < \xi$ on an island with a distance to the mainland smaller than

$\left[\dfrac{2\lambda_0 A^{\nu+\omega}}{E_0}\right]^{\frac{1}{\xi-\tau}}$, speciation may also add more species than

immigration does after a certain time. This means that, when the impact of distance on the extinction rate is stronger than on the speciation rate, a distant island has too much extinction to accumulate species diversity, and the difference in species richness between the island and the mainland is very large, leading to high immigration pressure from the mainland. Thus, the contribution of immigration to local species richness is larger than that of speciation. However, on a near island, a high rate of immigration to the island decreases the difference in richness between the mainland and the island, and thus there are few immigrants per unit time after a certain time, while the speciation rate continues to rise as species numbers increase. Therefore, the contribution of speciation to local richness on the island is larger than that of immigration.

$$P_{E(t)} = \frac{S_{E(t)}}{S_{I(t)}}$$

$$= \frac{\lambda_0 D^\tau A^\omega - (1 - I_0 D^{-\theta} A^\mu - E_0 D^\xi A^{-\nu} + \lambda_0 D^\tau A^\omega)^t (I_0 D^{-\theta} A^\mu + E_0 D^\xi A^{-\nu})}{(I_0 D^{-\theta} A^\mu + E_0 D^\xi A^{-\nu})[1 - (1 - I_0 D^{-\theta} A^\mu - E_0 D^\xi A^{-\nu} + \lambda_0 D^\tau A^\omega)^t]}$$

$$+ \frac{(1 - I_0 D^{-\theta} A^\mu - E_0 D^\xi A^{-\nu})^t (I_0 D^{-\theta} A^\mu + E_0 D^\xi A^{-\nu} - \lambda_0 D^\tau A^\omega)}{(I_0 D^{-\theta} A^\mu + E_0 D^\xi A^{-\nu})[1 - (1 - I_0 D^{-\theta} A^\mu - E_0 D^\xi A^{-\nu} + \lambda_0 D^\tau A^\omega)^t]}.$$

We find that the proportion of endemic species increases with time (Figure 3), because more time allows for intra-island speciation to occur. This pattern agrees with observations that high proportions of endemics are often associated with ancient islands [29,30]. If time increases to infinity $(t \rightarrow \infty)$, we can obtain the proportional endemism of an island at equilibrium (P_E):

$$P_E = S_E / S_I = \frac{\lambda_0 D^\tau A^\omega}{I_0 D^{-\theta} A^\mu + E_0 D^\xi A^{-\nu}}. \tag{3}$$
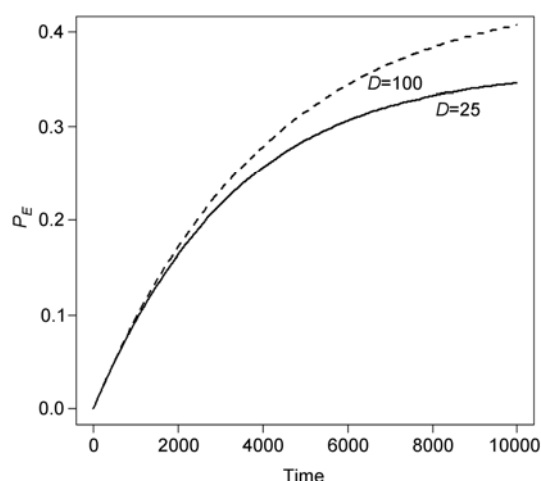
2.2 Island endemism

The presence of abundant endemic species is one of the most emergent properties of island biodiversity. We turn now to predicting proportional endemism (P_E) on the island. In this study, we only consider endemism caused by evolution [3,28], i.e., species resulting from speciation and ignore endemism caused by extinction on mainland and at other sites where evolution does not play a role. Because speciation adds endemic species to the island, extinction decreases the endemism, and migration also decreases the endemism by dispersing endemic species from the island to the mainland, we can obtain the number of endemics at time $t+1$: $S_{E(t+1)} = S_{E(t)} + \lambda_t - E_0 D^\xi A^{-\nu} S_{E(t)} - I_0 D^{-\theta} A^\mu S_{E(t)}$. Then, the proportional endemism at time t is

Eq. (3) shows that the proportional endemism of an island at equilibrium is determined by the rates of immigration, extinction and speciation per species, as well as by island physical features. The proportional endemism is positively correlated to speciation and negatively correlated to immigration and extinction [17]. Eq. (3) indicates that if $\xi \leq \tau$, i.e., the impact of distance on extinction is smaller than that of speciation at equilibrium, P_E increases with increasing isolation (Figure 4), a pattern observed in oceanic islands [25,31]. However, if $\xi > \tau$, proportional endemism increases with increasing distance and approaches a
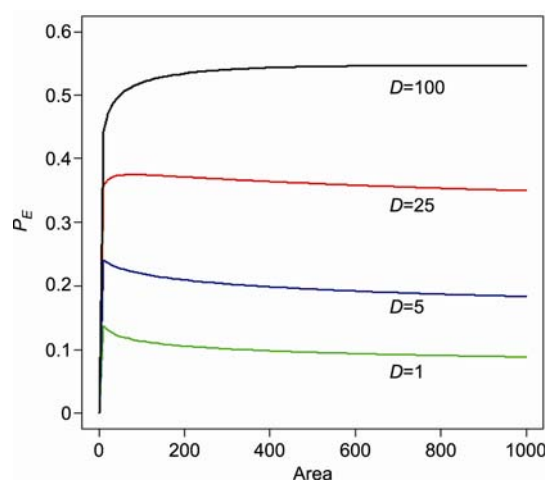

Figure 3 Proportional endemism of the island over time when S_M=10000, I_0=0.8×10^{-3}, E_0=0.5×10^{-3}, λ_0=0.2×10^{-3}, θ=0.5, μ=0.1, ν=0.1, ω=0.01, ξ=0.01, τ=0.01 and A=25.

Figure 4 Effects of isolation (*D*) and area (*A*) on the proportional endemism of the island when S_M=10000, I_0=0.8×10^{-3}, E_0=0.5×10^{-3}, λ_0=0.2×10^{-3}, θ=0.5, μ=ν=0.15, and ω=ξ=τ=0.01.

maximum at $D = \left[\dfrac{I_0 A^{\mu+\nu}(\tau+\theta)}{E_0(\xi-\tau)} \right]^{\frac{1}{\xi+\theta}}$. Eq. (3) shows no direct relationship between proportional endemism and island species richness. However, island species richness is also determined by migration, extinction, speciation, and island properties. Therefore, proportional endemism co-varies with island species richness, and a positive relationship can be observed between them [17].

Proportional endemism is also related to island area. If $\mu \leqslant \omega$, proportional endemism increases continuously with increased area. If $\mu > \omega$, proportional endemism increases with increasing area, approaches a maximum at $A=$

$\left[\dfrac{E_0 D^{\xi+\theta}(\nu+\omega)}{I_0(\mu-\omega)} \right]^{\frac{1}{\mu+\nu}}$, and then slowly but continuously

decreases. Because the effect of area on immigration is generally much larger than that on speciation, a maximum will be observed when area increases and other parameters are fixed. When area is small, extinction may lead to many species being lost, including endemic species produced by speciation; this effect decreases with increasing area. Meanwhile, immigration may result in a high proportion of new, non-endemic species, and this effect increases with increasing area. Therefore, it is reasonable to expect a critical area where P_E is highest. This result is different from MacArthur & Wilson's prediction that P_E might be highest on large islands located in circular zones close to the outermost dispersal ranges of the taxa [1]. Although an island with an area larger than this critical area will have a lowered proportional endemism, the decrease is not distinct (Figure 4). Therefore, a high proportion of endemism is generally expected on large islands [6,9].

2.3 Implications for species richness and endemism on islands across development

Many oceanic islands are volcanic in origin and experience a life cycle: a new volcanic island emerges from the sea, builds to a high cone-shaped form of maximal area and height, and then becomes increasing dissected and eroded [3,28,32]. To test our model, we predict the changes in immigration, extinction, speciation, and species richness on an island throughout its existence. For simplicity, we assume that area increases linearly over time and, after reaching its maximum, decreases linearly to zero (Figure 5A), similar to the assumption of Whittaker *et al.* [3]. As island area increases, the equilibrium diversity, or potential carrying capacity [3], of the island increases and becomes highest at maximal area. Realized species diversity also increases with increasing area, but maximum species diversity occurs after maximal area has been reached and passed (Figure 5A). This pattern is similar to the scenario described by Whittaker *et al.* [3,33]. In fact, the maximal value of realized
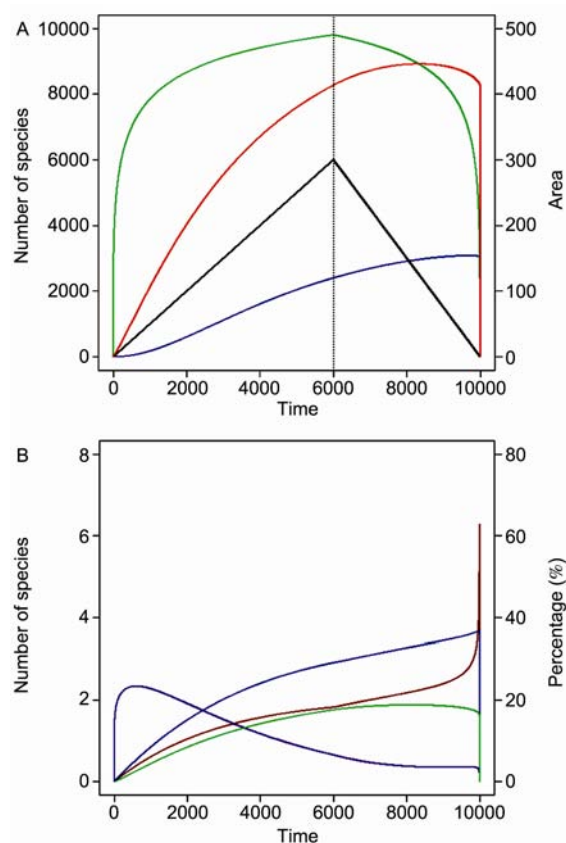

Figure 5 Key rates and properties during the life of an island predicted by the generalized island biogeography model when S_M, $I_0=0.8\times10^{-3}$, $E_0=0.5\times10^{-3}$, $\lambda_0=0.2\times10^{-3}$, $D=25$, $\theta=0.5$, $\mu=\nu=0.15$, and $\omega=\xi=\tau=0.01$. A, As in Whittaker *et al.* [3], we constructed a hypothetical island and simplified the island area (black line) to increase linearly over time ($A=0.05t$, $t\leqslant6000$); it approaches a maximum at $t=6000$ followed by a linear decrease over time until complete disappearance $\left(A = \dfrac{3000}{4} - \dfrac{3}{40}t,\ t > 6000 \right)$. The equilibrium diversity (green line) changes synchronously with island area. Realized species diversity (red line) increases with increasing area and approaches its maximum later than does area. Island endemism (blue line) increases with increasing area until the island has nearly disappeared. B, Changes in the impacts of immigration (purple line), extinction (brown line) and speciation (green line) on species diversity and proportional endemism (blue line) over time on the same hypothetical island.

species diversity occurs when it equals the equilibrium diversity and is followed by a slow decrease in diversity until the island is close to disappearing back into the sea (Figure 5A). Because our model has not considered interactions among species, inherently random extinction is the sole factor decreasing species diversity. Therefore, species diversity decreases slowly even when the realized species diversity is higher than equilibrium diversity. The final rapid decline is due to the island becoming too small to support high species richness.

During island development, extinction and speciation have similar trends, graphed by Whittaker *et al.* [3,28], except for a sharp increase in extinction and a sharp decrease in speciation when the island approaches disappearance

(Figure 5B). Such a deceleration of diversification over time, led by increasing extinction rates due to drastic area declines, was observed in the woodlouse-hunter spider genus *Dysdera* (Araneae, Dysderidae) on old volcanic islands [34]. Generally, the impact of immigration is also similar to that described by Whittaker *et al.* [3]. However, at the earliest stages of island development, the immigration rate is small, due to the very small area harboring low equilibrium diversity, and then increases rapidly to its maximum followed by a gradual decrease. Similar to the speciation rate, there is a sharp decrease in immigration rate when the island approaches disappearance (Figure 5B) due to very limited island size. During island development, the number of species eliminated by extinction becomes greater than that added by immigration and speciation at the time that realized species diversity becomes higher than the equilibrium diversity of the island (Figure 5A and B). The number and percentage of endemic species increases with time, even after the island approaches the maximal area and begins to erode, followed by a decrease when the island is eroded almost to disappearance (Figure 5A and B). Nevertheless, our model indicates that islands that are intermediate in age have the highest endemism. The pattern that old islands generally have higher endemism than younger ones has been frequently observed in archipelagos [29,30], but the oldest islands have a decreased endemism due to loss of area by erosion [3].

These results indicate that, based on the generalized model, the predicted patterns of species richness, endemism and relative contributions of immigration, speciation and extinction on an oceanic island across its development are similar to empirical observations [3,28].

3 Conclusion

The development of a theoretical model combining ecological and evolutionary processes as well as island features is of central importance to island biogeography. Based on MacArthur and Wilson's model, Lomolino [5] graphed a tripartite model of island biogeography as a general framework for understanding the relative roles of immigration, extinction and speciation in the maintenance of island species diversity and why islands have high endemism. Intra-island speciation plays an important role in both island species richness and endemism. The contribution of speciation to local species diversity may eventually exceed that of immigration under certain conditions, depending on the speciation and extinction rates per species and on island features. We predict that large islands have a high, but not the highest, proportional endemism. Furthermore, this model may predict changes in key rates, species diversity and endemism across the life of an island, providing explanations for the observed relationships between species richness or endemism and island features. However, we should

note that our model is based on a constant per species speciation rate on the island, although these rates are different on different islands. For example, a burst of speciation was found at the beginning of adaptive radiation and shortly thereafter [23]. Nevertheless, our model is an ideal starting point for re-evaluating the role of speciation and re-analyzing available data on island species diversity, especially those biased by the MacArthur-Wilson model.

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