

Temporal beta-diversity patterns are highly dependent on fundamental parameters of neutral dynamics

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Abstract

Temporal changes in community composition are a facet of biodiversity change and are referred to as temporal beta diversity. Macroecological patterns of temporal beta diversity have gained attention because of the recent biodiversity crisis. However, no one has seriously studied how temporal beta diversity differs from spatial beta diversity, and the most basic neutral dynamics and temporal beta-diversity patterns remain unknown. Therefore, the present study aimed to reveal the basic properties of temporal beta-diversity patterns under neutral dynamics and identify their differences from those of spatial beta-diversity patterns. A simulation of neutral dynamics was conducted to test the parameter dependency of temporal beta-diversity patterns. Specifically, four fundamental parameters of the neutral model—the fundamental biodiversity number, local community size, mortality rate, and immigration rate—were studied. To describe the form of the simulated temporal distance-decay patterns based on both the Bray–Curtis and Sørensen dissimilarity indices, a three-parameter negative exponential function was fitted for each simulated dissimilarity matrix. The negative exponential function was successfully fitted to all the simulated results and three estimated parameters and the intercepts of the function were plotted along the change in the four parameters of the neutral model. The simulated results demonstrated that upper limits exist in the temporal distance-decay patterns; thus, the temporal distance-decay curves saturate before reaching a completely dissimilar state. Additionally, the form of the curve strongly depends on the four parameters of the neutral model. These results suggest that the relationship between local communities and virtual species pools differs in temporal and spatial beta diversity. Specifically, they suggest that the species pool is spatially variable but temporally constant.

Introduction

Temporal changes in community composition are a facet of biodiversity change and are referred to as temporal beta diversity (Hatosy et al., 2013; Baselga, Bonthoux, & Balent, 2015; Legendre, 2019). Recently, the focus of temporal beta-diversity studies has expanded to multiple sites and a large spatial scale, that is, to macroecological contexts (Brice, Cazelles, Legendre, & Fortin, 2019; Gotelli et al., 2022). Macroecological patterns of temporal beta diversity have gained increasing attention during the ongoing biodiversity crisis resulting from various anthropogenic disturbances and climate change impacts (Dornelas et al., 2014; Brice et al., 2019; Magurran, Dornelas, Moyes, & Henderson, 2019). Although the use of beta-diversity indices in temporal beta-diversity studies is generally identical to that in spatial beta-diversity studies, no one has seriously studied how temporal beta diversity differs from spatial beta diversity. Therefore, so far, temporal beta-diversity studies have been conducted based on various uncertain assumptions dependent on spatial knowledge. This lack of basic knowledge about temporal beta diversity could lead to inaccurate assessments of biodiversity changes. Thus, revealing the basic properties of temporal beta-diversity patterns is an urgent issue.

The unified neutral theory proposed by Hubbell (2001) demonstrated that various types of common biodiversity patterns (e.g. species abundance distribution) are reproduced under both ecological neutrality and zero-sum assumptions (Rosindell, Hubbell, & Etienne, 2011; Shinohara, Nakadai, Suzuki, & Terui, 2023).

The neutral model would provide valuable base knowledge under the simplest conditions as a starting point (Rosindell et al. 2011; Rosindell, Hubbell, He, Harmon, & Etienne, 2012; Takeuchi, Ohtsuki, & Innan, 2022). The dynamics under a neutral model (i.e. neutral dynamics) would provide basic knowledge regarding temporal beta-diversity studies just as they have provided so far for other biodiversity patterns. Rosindell et al. (2011) argued that studying dynamics under a neutral model is a future challenge. Several previous studies (Dornelas et al., 2014; Sgardeli, Zografou, & Halley, 2016) related to temporal beta diversity have used predictions under neutral dynamics as a baseline to quantify targeted factors (i.e. climate change impacts). However, the effect of each parameter on the general temporal beta-diversity pattern under neutral dynamics remains unexplored. The present study aimed to reveal the basic properties of temporal beta-diversity patterns under neutral dynamics and identify their differences from those of spatial beta-diversity patterns. Specifically, the parameter dependency of four variables, viz., fundamental biodiversity number, local community size, mortality rate, and immigration rate, were examined.

Materials and methods

Simulation

To reveal the parameter dependency of temporal beta-diversity patterns under neutral dynamics, simulations were performed using the R package “ecolottery” (Munoz et al., 2018). This study focused on four fundamental parameters of the neutral model (Hubbell, 2001): fundamental biodiversity number (θ), local community size (J), mortality rate (d), and immigration rate (m) (Fig. 1a and b). Fundamental biodiversity number (θ) is a value associated with the properties of species pool diversity (Fig. 1a); specifically, species diversity in the species pool and their evenness increase as the fundamental biodiversity number increases, when the number of individuals included is the same (for the detailed derivation of fundamental biodiversity number, see Hubbell, 2001). In two extreme cases, the species pool includes only one species when the fundamental biodiversity number is zero ($\theta = 0$), and all species in the species pool have one individual when the fundamental biodiversity number is infinite ($\theta = [\infty]$). The local community size indicates the total number of individuals in a targeted local community. Under the zero-sum assumption, the number (J) is the same throughout the community dynamics for each simulation. Mortality rate (d) indicates the proportion of mortal individuals in the local community at each time step; thus, $J \times d$ is the actual number of mortal individuals (D) (Fig. 1b). The mortality rate (d) is identical to the turnover rate under the zero-sum assumption because the number of mortal individuals is identical to that of recruited (or birthed) individuals. The immigration rate (m) is the proportion of immigrated individuals in the number of recruited (or birthed) individuals at each time step; thus, $J \times d \times m$ is the number of immigrated individuals (M) and $J \times d \times (1 - m)$ is the number of locally recruited (or birthed) individuals ($D - M$) (Fig. 1b). The details of these parameters are summarised in Table 1.

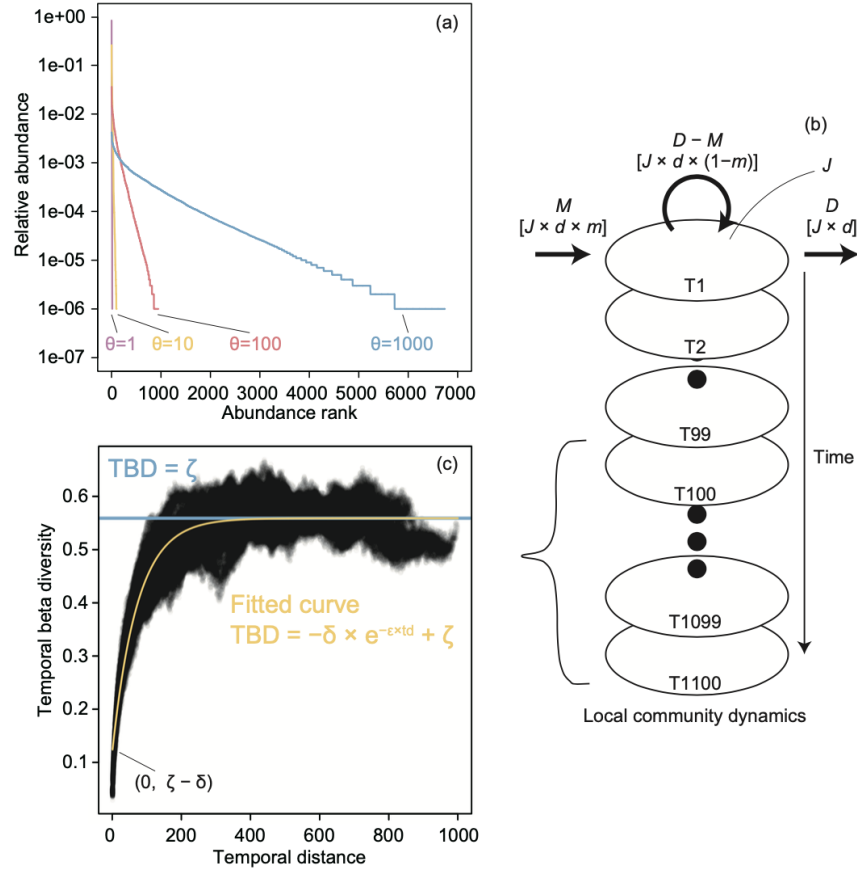


Figure 1 Schematic image of neutral dynamics simulation and temporal beta diversity patterns. The definitions of each parameter in the figure is summarized in Table 1.

Table 1 List of terms used in the main text

Term	Definition
ϑ	Fundamental biodiversity number
J	Total number of individuals in the local community
d	Mortality rate
D	Total number of mortal individuals [$J \times d$]
m	Immigration rate
M	Total number of immigrated individuals [$J \times d \times m$]
J_M	Total number of individuals in the species pool (i.e. metacommunity)
δ	a parameter of the negative exponential function that is related to the relative position of the intercept against the
ϵ	a parameter of the negative exponential function that is related to the curvature of the curve
ζ	a parameter of the negative exponential function that is related to the upper limit

The base parameter values were set as follows: species pool (i.e. metacommunity) size (J_M) = 1,000,000 individuals; fundamental biodiversity number (ϑ) = 100; local community size (J) = 1,000; mortality rate (d) = 0.1; immigration rate (m) = 0.1. Based on the base parameter values of this model, the parameter-dependency patterns were studied by changing the four targeted parameters (ϑ , J , d , and m). For the fundamental biodiversity number (ϑ), 100 numbers were randomly selected between 1 and 1,000, without

allowing duplicates. For the local community size (J), 25 numbers were randomly selected for each order of magnitude (10^2 – 10^5); thus, 100 numbers were selected in total. For both mortality rate (d) and immigration rate (m), 100 numbers were determined between 0.01–1.00, in 0.01 increments.

At the beginning of each simulation, local community members were chosen depending on the set number of local community size, and 1,100 time steps, including the initial state, were conducted for each simulation (Fig. 1b). After the simulation, the information of local community dynamics between time step 1 (T1) and time step 99 (T99) were excluded from the following analysis for testing parameter dependency because the randomness of the initial sampling could affect the community dynamics at the beginning phase. The dynamics from T100 to T1100 were targeted for the main analysis, and thus, a 1001 time-series dataset was used for each simulation (Fig. 1b). The Bray–Curtis dissimilarity index (Odum, 1950) and Sørensen dissimilarity index (Sørensen, 1948) were calculated for each simulation.

The preliminary analysis revealed that the temporal distance-decay curve rarely reached one (i.e. completely dissimilar); thus, upper limits exist at less than one in temporal beta diversity under neutral dynamics. Therefore, to describe the form of the simulated temporal distance-decay patterns of both the Bray–Curtis and Sørensen dissimilarity indices, a negative exponential curve was fitted for each dataset (Fig. 1c). The equation for the negative exponential function is as follows:

$$TBD = -\delta \times e^{-\varepsilon \times td} + \zeta,$$

where TBD is the temporal beta diversity value, e is Napier’s constant, td is the temporal distance between a pair of communities, and δ , ε , and ζ are the parameters of the negative exponential function (Table 1). The changes in the curve shape with parameter changes are summarised in Fig. 2. The parameter ζ determines the position of the upper limit of the curve; thus, a larger ζ indicates higher upper limits in the temporal distance-decay of temporal beta diversity (Fig. 2c). Parameter δ determines the relative position of the intercept against parameter ζ (i.e. the upper limit). The $\zeta - \delta$ value indicates the intercept of the curve; thus, a larger δ indicates a lower position of the intercept (Fig. 2a). Parameter ε determines the curvature of the curve; thus, a larger ε indicates a higher curvature of the curve (Fig. 2b). All estimated parameter values without errors were used in the analysis to check parameter dependency in the present study. Although Martín-Devasa, Martínez-Santalla, Gomez-Rodriguez, Crujeiras, & Baselga, (2022) recently developed a method to compare the fit of three different functions on distance-decay curves, judging the best-fitted function for a distance-decay curve was the main use of the method and ecologically interpreting the changes in parameter values was difficult based on their methods. Therefore, the three-parameter negative exponential function was used in this study owing to the differences in purpose.

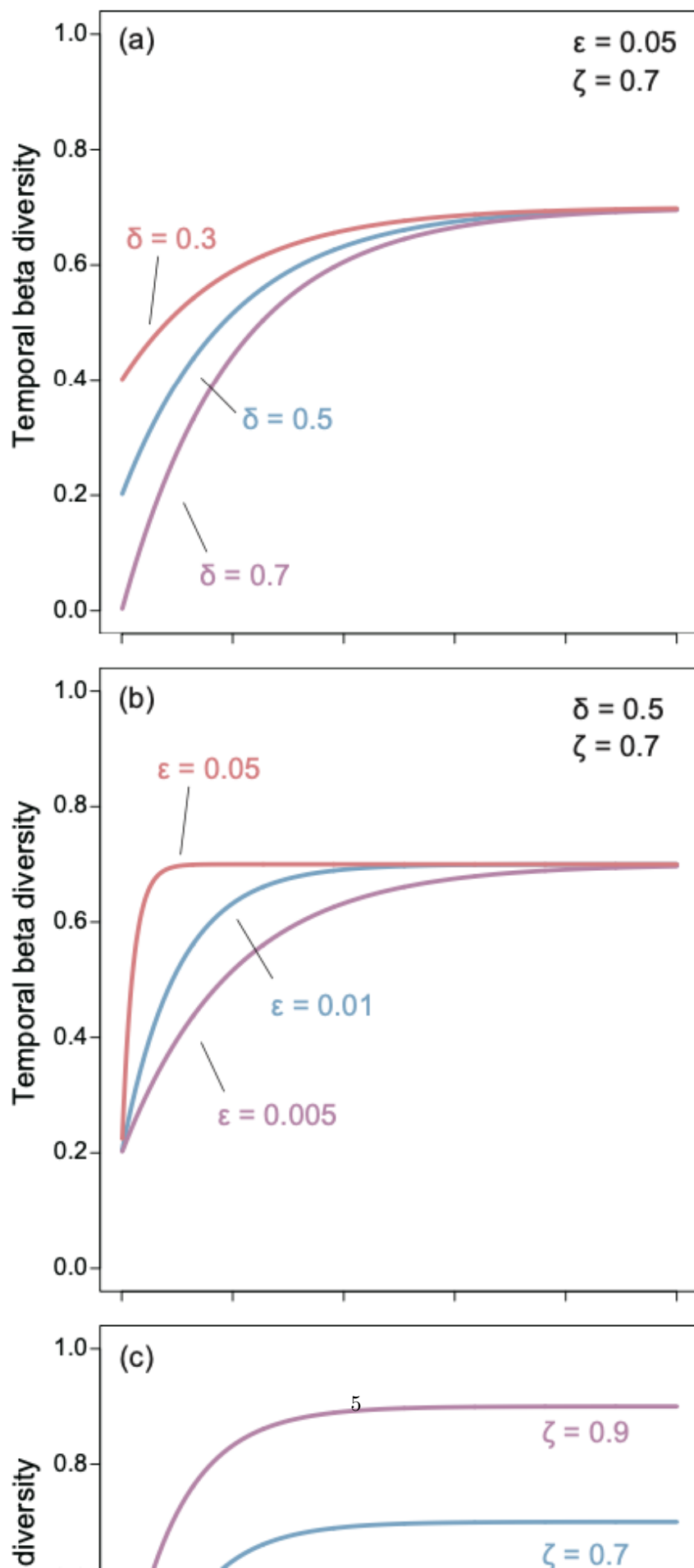


Figure 2 Representative examples showing parameter properties in the three-parameter negative exponential function.

Results

We successfully fitted the negative exponential function to all the simulated results and plotted the three estimated parameters (δ , ϵ , and ζ) and intercepts ($\zeta - \delta$) along with the change in the parameter values of the neutral model (ϑ , J , d , and m). The blue and orange circles indicate the results of the Bray–Curtis and Sørensen dissimilarity indices, respectively. First, as the fundamental biodiversity number (ϑ) increased, the parameters δ and ζ and the intercepts ($\zeta - \delta$) increased (Fig. 3a, i, m), but the parameter ϵ remained constant (Fig. 3e). Second, as the local community size (J) increased, the parameters δ and ζ and the intercepts ($\zeta - \delta$) decreased (Fig. 3b, j, n); however, the parameter ϵ increased and then remained constant when J was larger than approximately 10,000 (Fig. 3f). Third, as mortality rate (d) increased, the parameters δ and ζ and the intercepts ($\zeta - \delta$) decreased (Fig. 1c, k, o), but the parameter ϵ increased (Fig. 3g). Finally, as immigration rate (m) increased, the parameters δ and ζ and the intercepts ($\zeta - \delta$) decreased (Fig. 3d, l, p), but the parameter ϵ increases (Fig. 3h).

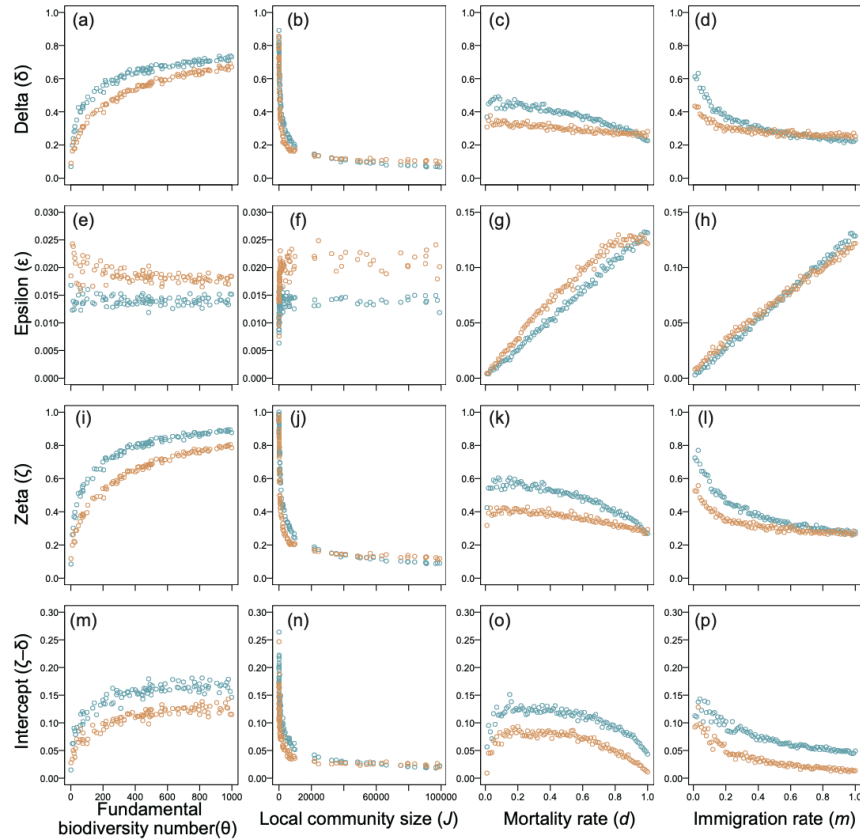


Figure 3 Relationships between parameters of the negative exponential function and those of the neutral model. The blue and the orange circles indicate the results of the Bray–Curtis and Sørensen dissimilarity indices, respectively.

Discussion

The simulated results under ecologically neutral dynamics demonstrated that the upper limits exist in temporal distance-decay patterns; thus, the temporal distance-decay curves saturate before reaching a completely

dissimilar state. In addition, the form of the curve strongly depends on four parameters of the neutral model: fundamental biodiversity number, local community size, mortality rate, and immigration rate. These results emphasise the importance of considering the basic information of the species pool and local communities as four parameters in the present study when temporal beta-diversity studies are expanded to macroecological contexts. No studies have seriously considered the differences between space and time; therefore, this study is the first to explore biodiversity changes from both basic and applied perspectives.

Macroecological interpretation of the targeted parameters in the neutral model

Previous studies have discussed four targeted parameters (ϑ , J , d , and m) of the neutral model in relation to geographical and climatic contexts (Turner, 2004). Here, for each parameter, the results of parameter dependency were interpreted from a macroecological perspective.

First, the fundamental biodiversity number (ϑ) was calculated as the product of species pool size (J_M) and speciation rate per individual in the species pool (v); however, the detailed equations differ among studies depending on the precision (Hubbell, 2001; He & Hu, 2005; Etienne & Alonso, 2007). Changes in speciation rates along geographical and climatic gradients are well reported (Mannion, Upchurch, Benson, & Goswami, 2014; Rabosky et al., 2018); thus, the fundamental biodiversity number should vary along geographical and climatic gradients. Fukaya, Kusumoto, Shiono, Fujinuma, & Kubota. (2020) recently estimated the fundamental biodiversity number of woody plant species at regional scales and found large variations among the four regions in Japan. In addition, speciation rates differ among taxonomic groups (Schluter & Pennell, 2017). In the simulated results, the upper limits (ζ) varied largely along the values of the fundamental biodiversity number (Fig. 3i). Therefore, even if the temporal beta-diversity values are identical, the meanings of the changes are different; for example, 0.4 is approximately the maximum value when the fundamental biodiversity number is 100, but that is half of the upper limit when the number is 600 (Fig. 3i). Therefore, when estimating the fundamental biodiversity number is difficult, considering the differences in species pool properties due to geography, climate, and taxonomy can be essential for future macroecological studies of temporal beta diversity.

Second, local community size is strongly associated with the relative influence of stochastic drift (Chave, 2004). The simulated results showed that both the upper limit of temporal beta diversity and the intercept increased as the size became smaller (Fig. 3j, n). These results suggest that the probability differences in individual turnover among the same species (i.e., apparent compositional equilibrium; Nakadai, 2020) affect the temporal beta-diversity patterns. Specifically, large local communities have more opportunities to obtain individuals that are of the same species as the dead individuals in the previous time step and cause less apparent compositional changes. In natural situations, local community sizes are directly related to habitat sizes, so small islands and conservation areas are likely to have more large compositional fluctuations over time.

Third, the mortality rates are identical to the turnover rates under the zero-sum assumption. If the contribution of individual turnover to compositional shift is constant, a larger amount of individual turnover causes more apparent compositional changes, and thus, larger temporal beta diversity (Nakadai, 2022). Simulation results support this fact, because the parameter ε , which is related to the curvature of the curve, linearly increases as mortality rates increase; thus, the curve becomes steeper (Fig. 3g). In contrast, the upper limits (ζ) decreased as the mortality rates increased (Fig. 3k). This result may be attributed to the fact that the increased mortality and turnover rates result in more individuals being randomly selected from the species pool, keeping the species composition of the local community close to that of the species pool. In nature, higher temperatures facilitate faster growth and shorter life span (Keil & de Magalhaes, 2015); therefore, mortality rates would be higher toward the tropics, resulting in less stable compositional dynamics.

Finally, immigration rates are the degree of habitat isolation from species sources, which is an influential factor in island ecosystems and both the protection and maintenance of conservation areas (MacArthur & Wilson, 1967; Prugh, Hodges, Sinclair, & Brashares, 2008; Fahrig, 2013). The parameter dependency of temporal beta-diversity patterns against immigration rates was similar to that against mortality rates (Fig.

3d, h, l, p). Specifically, the parameter ϵ increased linearly, and the upper limits (ζ) decreased as immigration rates increased (Fig. 3i, h). The interpretation of these results is the same as that of the mortality rate as discussed in the above paragraph; thus, larger immigration rates facilitate a similar community composition as that of the species pool. This process can reduce the temporal variability of species composition in the local community. Therefore, in nature, isolated island ecosystems and isolated conservation areas would be more temporally unstable.

Differences between space and time in biodiversity

The largest difference between spatial and temporal beta diversity was the property of the species pool. In the spatial context, if an observer moves sufficiently far from one location to a different region, the composition of the species pool will differ, and eventually, there will be no common species between the first and the second place; thus, the value of spatial beta diversity reaches 1. In contrast, in a temporal context, if it is not assumed that the composition of the species pool changes over time, it is rare to have a situation where common species are completely absent from the species composition at the outset. Surely, in evolutionary time scale, the species pool would gradually change, but at the ecological time scale (e.g. less than a hundred years), dramatic changes in the species pool should not be hypothesised as a normal condition. However, the influence of recent climate change and other anthropogenic disturbances will change the composition of the species pool through species distributional shifts (Dornelas et al., 2014; Koide, Yoshikawa, Ishihama, & Kadoya, 2022). Therefore, these influences would increase the upper limits of temporal beta diversity. The present study focused only on neutral dynamics to understand the fundamental properties of temporal beta diversity. However, in the future, more complex models should be studied to understand the influence of climate change and other anthropogenic disturbances.

Conclusions

The present study demonstrated the strong parameter dependency of temporal beta-diversity patterns on the four fundamental parameters of the neutral model. The results of the present study caution that macroecological studies of temporal beta diversity are challenging without considering these four parameters in any case. Neutral dynamics is a starting point for discussing the real drivers of temporal beta-diversity patterns. In simulation studies, relaxing the zero-sum and neutrality assumptions would provide more realistic patterns comparable to empirical patterns (Jabot, 2010; Jabot & Chave, 2011; Munoz & Huneman, 2016; Takeuchi et al., 2022). Moving forward, two future study directions of temporal beta diversity, more generally biodiversity changes, are recommended. One is toward the linking of biodiversity changes with the modern co-existence theory and other studies focusing on species co-existence, which would pave the way for a new field of study. For example, under variable climate conditions, different types of storage effects, which is a kind of mechanism facilitating species co-existence (Chesson & Warner, 1981; Chesson, 2000), would affect the apparent compositional changes; the persistence of long-lived individuals could contribute to decreasing the change in the short term, but the existence of buried seeds could contribute to less variability in community composition in the long term. The other is toward an explicit consideration of the spatial connections among the temporal beta-diversity patterns. Macroecological studies of temporal beta diversity often consider different sites as independent, but in reality, close distance sites are often connected. For example, animals move across sites and plants provide seeds to neighbouring sites (Howe & Smallwood, 1982; Bowler & Benton, 2005). For a deeper mechanistic understanding of temporal beta diversity, it is important to identify the direct effects through connections from simple synchronic responses to similar climate changes due to site closeness. Many future tasks remain to be accomplished in the study of temporal beta diversity, which is important in both basic and applied research.

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