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RESEARCH ARTICLE

Beta diversity dynamics in East Asian angiosperm woody plants: taxonomic turnover in relation to temperature gradients during the Cenozoic

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Abstract

Information on the paleo-beta diversity of fossil assemblages and its patterning in different geological time intervals helps us to better understand the community-level response of biodiversity patterns to current global warming. We focused on the impact of paleoclimate changes on large-scale taxonomic sorting related to geography; specifically, how cooler and warmer climatic conditions affect the distance-dependency of beta diversity. Using a dataset of Cenozoic fossil assemblages of angiosperm woody plants (7,468 data points; 310 genera in 95 families) in the Japanese portion of the East Asian archipelago (except Ryukyu islands), we modeled the distance-dependency of genus turnover (pairwise compositional dissimilarity) through the Oligocene, Miocene, Pliocene, Pleistocene, Last Glacial Period, Holocene, and present day. The genus turnover of angiosperm woody plants was significantly correlated with geographical and climatic distance only in the Last Glacial Period, Holocene, and present day. During the Oligocene to Pliocene, the warm periods, genus turnover was mostly independent of geographical distance. Spatial/climatic distance-dependent turnover under colder environments involved a climate-induced sorting process to spatially diversify woody-plant assemblages across the archipelago. Moreover, the predominance of distant-independent turnover suggested the effect of dispersal release under warmer, stable climates. Our findings suggest that future tropicalization in temperate habitats could promote geographical homogenization of biodiversity patterns.

Highlights

- We revealed the Cenozoic dynamics of woody-plant beta diversity by modeling the distance-dependency of taxonomic turnover.
- Warmer climates promoted geographical homogeneity of taxonomic composition, whereas cooler climates produced distance-dependent diversification.
- Dispersal release and/or climatic filter predominantly act to shape large-scale biodiversity patterns in relation to climate change.
- We noted the potential for increased community homogeneity in response to the current warming.

Keywords: angiosperm woody plants, climate change, distance-decay, East Asian islands, fossil assemblage, paleobiodiversity, taxonomic turnover, Tertiary relict flora

Introduction

Global warming is currently shifting the distribution ranges of particular species poleward (Sorte and Tompson 2007, Doney et al. 2012, VanDerWal et al. 2013) or to higher elevation (Konvicka et al. 2003, Kelly and Goulden 2008), and, moreover, causes local extinctions (Panetta et al. 2018, Román-Palacios and Wiens, 2020). Although a number of taxon-specific studies have been conducted, the response of paleocommunities to climate change remains little known, thus, understanding the impact of climate change on future biodiversity is a challenge in biogeography and macroecology (Williams et al. 2007). Paleontological information on fossil assemblages,

which reflect past warmer/cooler conditions, allows us to infer the dynamics of biodiversity patterns related to future climate changes (Willis and Birks 2006, Yasuhara et al. 2008, Yasuhara et al. 2009, Willis and Bhagwat 2010, Willis and MacDonald 2011). Previous studies of paleobiodiversity patterns have suggested that global-warming-specific processes have operated in the past: for example, the latitudinal diversity gradients that are observed today were not necessarily common in the past (e.g., Mannion et al. 2014). Climate-dependent environmental filtering and dispersal limitation on large-scale species sorting could be intensified or buffered, depending on geographical factors, and consequently should change biodiversity patterns.

Inter-regional differences in species composition (beta diversity) and spatially explicit analysis of beta diversity across geological time intervals provide important information to understand spatio-temporal changes in biodiversity (Nekola and White 1999, He et al. 2018): importantly, beta diversity can be partitioned into two components involving turnover and nestedness (Baselga 2010, Legendre 2014, Soininen et al. 2018). Notably, the distance-dependent pattern of taxonomic turnover and nestedness reveals the role of niche-based habitat filtering (Tuomisto et al. 2003, Leibold et al. 2004) and dispersal/extinction-driven processes (Garcillán and Ezcurra 2013) along environmental gradients and/or geographical isolation (Fitzpatrick et al. 2013, Warfe et al. 2013). For paleobiodiversity, however, there have been few studies on distance-dependent fluctuations of compositional similarity between local fossil assemblages (Na and Kiessling 2015): some studies found a relationship between species turnover and long-term climatic perturbations (Archibald et al. 2014, Fraser et al. 2014).

Here, we focus on the fossil (Cenozoic; Oligocene to Holocene) and living assemblages of angiosperm woody plants of the East Asian islands (specifically, the Japanese archipelago except Ryukyu islands), which currently harbor a relict flora including survivors that were distributed across a large part of the Northern Hemisphere during the Paleocene to Miocene (65 – 15 million years ago) (Milne and Abbott 2002). To clarify the impact of paleoclimate changes on taxonomic sorting and dispersal, we specifically investigate the distance-dependency of beta diversity, which especially represents taxonomic turnover along environmental gradients, in fossil assemblages and its patterning in different geological time intervals under different climate conditions. Previous studies revealed that, during times of warm climate, the East Asian archipelago functioned as a habitat for both tropical and temperate taxa (Kubota et al. 2017); i.e., past global warming eased climatic filtering along latitude (Shiono et al. 2018). Conversely, in colder intervals, climate barriers, which depend on taxon-specific temperature tolerance, enhanced abiotic filtering effects, especially at high latitudes (Shiono et al. 2018). Therefore, we made the following predictions about the Cenozoic spatial beta-diversity dynamics in angiosperm woody plants: (i) The distance-dependency of taxonomic turnover was mitigated during the Paleogene and Neogene because the climatic filter was weaker under warm, stable climates, however, (ii) distance-dependency became stronger under cold, unstable climates, especially beginning with the Quaternary ice ages. Reasoning from these predictions, we argue that the assemblage-level response of angiosperm woody plants (including tropical to boreal taxa) of the relict flora in the East Asian islands was regulated by habitat stability and dispersibility associated with region-specific paleoclimate and insularity during the Oligocene to Holocene.

Materials & Methods

Study area

We focused on angiosperm woody plant assemblage on continental islands of East Asia (specifically, the Japanese archipelago except Ryukyu islands), and studied fossil woody-plant angiosperm assemblages from the Oligocene to Holocene. We used this flora as a model for the following reasons. First, this region possesses diverse vegetation in boreal to subtropical zones stretched across a wide latitudinal zone, because the area has served as a refugium for vascular plants (Harrison et al. 2001, Kubota et al. 2015). Second, the flora has developed through geohistorical processes related to paleogeographic insularity and subsequent isolation. Insular systems can provide community-level entities with clear boundaries. In addition, although continental biomes sometimes suffered from intense cooling leading to massive species loss in glacial periods (Milne and Abbott 2002), the island biome experienced environmental gradients, and hence range shifts and local extinction (Shiono et al. 2018). For the above reasons involving a number of previous studies on paleofloras (e.g. Yabe 2016), angiosperm woody plant assemblage on the Japanese archipelago provides an ideal opportunity to study how global paleoclimatic events influenced spatial patterns of beta diversity, especially for testing environmental filtering/sorting processes in response to climate changes (Vázquez-Rivera and Currie 2015).

These islands are fundamentally divided into three biogeographical regions by straits, with the Tsugaru Strait lying between the northern and central regions and the Tokara Strait between the central and southern regions (Fig. 1; Millien-Parra and Jaeger 1999, Kubota et al. 2014). A strong warm current has continuously flowed eastward along the southern margin (i.e., the Pacific side) of the Japanese islands since the Paleogene (Saitoh et al. 2015). In the Japan Sea (East Sea) side of the archipelago, a cold current resembling the modern-day Liman Cold current and a warm current along Honshu and the southern Korean Peninsula had major effects on the formation of the relict flora (Pavlyutkin et al. 2016). Thus, even in the same latitudinal zone, there are considerable differences in the climatic and geohistorical settings. Therefore, our division into regions had to consider not only latitudinal zones, but also other factors resulting from the presence
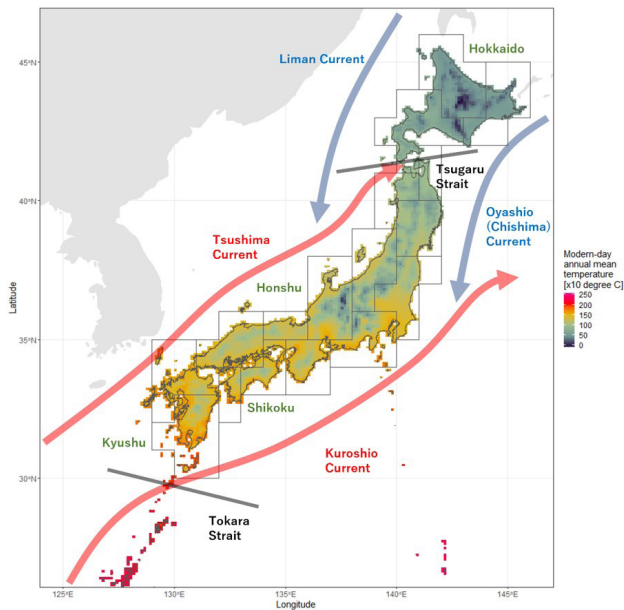
Figure 1. Sites classifications and geographical settings of the study area. Classification of grid cells into the 17 regions, and geographical/climatic settings around the study area. Division of study sites are illustrated in thin black lines. Warm and cold oceanic currents are shown in red and blue. Illustration of currents are based on Fig. 1 of Pavlyutkin et al (2016). Straits are in black. Names of islands are written in green characters. Annual mean temperature sources from Japanese Meteorological Agency (2002).

of mountains and adjacent ocean currents. Geographical settings (names of island, locations of oceanic currents and straits) and modern temperatures around the study sites are provided in Fig. 1.

Data analysis

We mainly used published datasets (Shiono et al. 2018) including fossil records observed from Oligocene to Pliocene, and modern flora. Additionally, we compiled a Quaternary dataset from several sources, including the Neotoma Paleoecology Database (https://www.neotomadb.org/), Data Publisher for Earth and Environmental Science (PANGAEA; https://www.pangaea.de/), Palynodata (https://paleobotany.ru/palynodata), and the Paleobiology Database (https://paleobiodb.org/) (see Appendix S1 for details). Finally, the compiled dataset included 4438 pollen fossils and 904 macrofossils (76 records are included as both forms) encompassing 191 woody angiosperm genera in 86 families. The whole data used in the analysis consisted of 322 genera in 105 families (see Appendix S2 and S3 for locations and detailed sample information by geological ages).

The age classification of individual fossil records followed the descriptions in the source literature that provided the names of geological age and/or numerical age. The boundary of geological ages was set as following GSSA (Cohen et al. 2015). In our analyses, we defined the Last Glacial Period as a period separate

from the Pleistocene, from the end of the Eemian Last Interglacial Period (0.115 Ma) to the end of the Younger Dryas stadial (0.0117 Ma) (Corella et al. 2022). Based on the information described in each literature, we applied the finest and most reliable classification age/interval for individual fossil records.

Fossil sites were classified into 17 sub-regions (assemblages) based on their geohistorical and biogeographical locations (Fig. 2 (a)): hierarchical clustering was applied to 1°-grid cells (n = 78; composed of cells containing land or recognizable coastlines of Hokkaido, Honshu, Shikoku, Kyushu, or islands with fossil occurrences), using longitude, latitude, coastal regions (Spalding et al 2007), and insularity of major islands (Hokkaido, Honshu, Shikoku, and Kyushu) to calculate beta diversity. The procedure used for classification of the study area is provided in Appendix S4.

Paleoclimate data

Paleoclimate data across the islands were obtained from the following sources: Frigola et al. (2018) for the Miocene; Paleoclim (http://paleoclim.org/) for the Pliocene, Pleistocene, and Last Glacial Period (LGP); and Japanese Meteorological Agency (2002) for the present day. Note that geographical position of Japanese archipelago has been stable since the early Miocene (Pavlyutkin et al. 2016) after the opening event of the Japan Sea (East Sea): the land of Japanese archipelago is located at the continental margin, and its latitudinal position has been preserved (Yabe et al. 2019). Therefore, the modern-day locations of the fossil sites were used to analyze spatial pattern in relation to paleoclimate along geography. In some cases, there are multiple prediction points for a single geological time interval: M2 (ca. 3.3 Ma) and the mid-Pliocene warm period for the Pliocene; and the Younger Dryas Stadial, Bølling–Allerød Interstadial, and Heinrich Stadial for the Last Glacial Period. In these cases, we averaged the data. Note that Oligocene climate data were not available, thus, we used Miocene temperature data to evaluate climatic effects on the beta-diversity pattern of the Oligocene. The Miocene and Oligocene climates in the Japanese archipelago were very similar (Yabe et al. 2019). We used modern climate data as Holocene temperature data. Then, we sampled the mean annual temperature using a 1° grid. Finally, we compiled the paleotemperature of each subdivision by averaging the temperature cells belonging to each subdivision. The paleotemperatures and their relationship to the spatial distance of each subdivision for each time interval are plotted in Fig. 2 (b).

Statistical analyses

A graphical explanation of the analysis is provided in Fig. 2 (b). Pairwise beta diversities were calculated for local assemblages pooled in 17 sub-regions across the East Asian islands (the results for smaller numbers of sub-regions are provided in Appendix S5 and S6). We applied the beta-diversity partitioning framework of Baselga (2010). This framework is based on Sørensen dissimilarity (β_{sor}), which can be partitioned into two
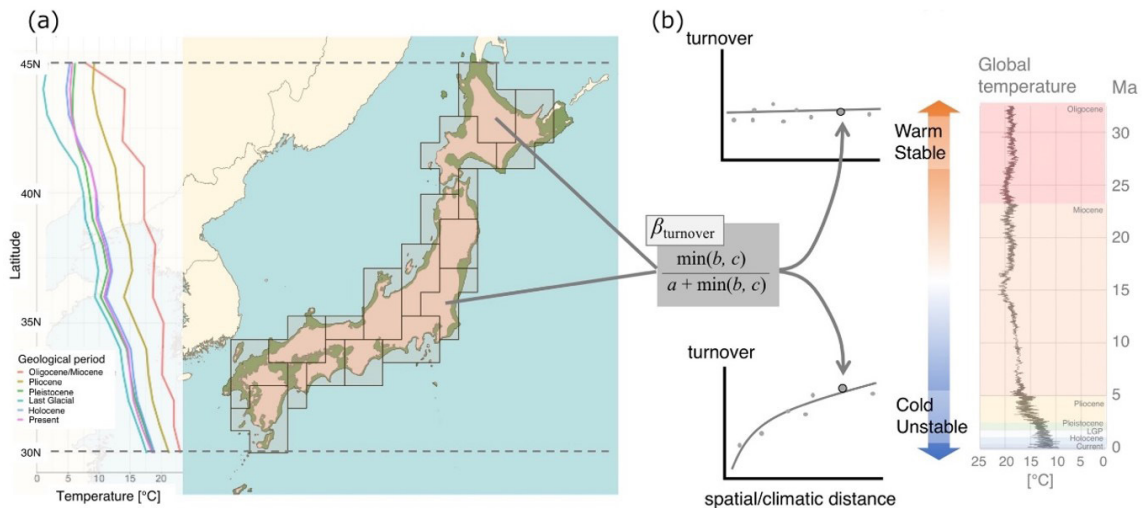
Figure 2. Geohistorical and paleoclimatic description of the study area and graphical explanation of the analysis. (a) Latitudinal temperature (annual mean) gradients in each geological time interval are shown in the left column; the red color denotes the current land area; the green area indicates the land area during the Last Glacial Period; and black frames represent the classification of local assemblages. (b) The analysis of pairwise beta diversities between local assemblages pooled in 17 sub-regions across the East Asian islands. The distance-dependency of taxonomic turnover is tested in relation to geography and climate. We predict that warmer climates promote geographical homogeneity of taxonomic composition, whereas cooler climate produces distance-dependent diversification. The temporal variations of global temperature are reproduced from Hansen et al. (2013).

components: turnover (β_{sim}) and nestedness (β_{sne}). In this study, we focused on the turnover component to evaluate the impact of paleoclimate change on taxonomic composition: notably, the turnover component is independent of nestedness, which is insensitive to the variance in sample coverage inherent in fossil data (Fraser et al. 2014). Then we tested the distance-dependency of genus-level turnover in individual geological time intervals. Note that we set three thresholds (N_{thre} = 5, 10, and 15 genera) for the number of genera found in local assemblages and illustrated the results for N_{thre} = 10; results for N_{thre} = 5 and 15 are provided in Appendix S7.

We modeled the relationship between genus turnover and inter-assemblage geographical/climatic distances in each geological time interval. In the regression analysis, we used negative exponential and power-law functions (Nekola and McGill 2014), fitted using generalized linear modeling with a Gaussian distribution and logistic regression (Kusumoto et al. 2021). We conducted model comparison with Akaike's Information Criterion that showed similar fits, and thus reported the results of the negative exponential model (see Appendix S8). The intercept and slope of the model correspond to the compositional variation among the closest local assemblages (initial dissimilarity) and the rate of distance-dependent turnover (along geographical/climatic distance) for a given geological time interval, respectively. All statistical analyses and graphical presentation were conducted using R 4.0.3 (R Core Team, 2020) and the related packages 'betaapart' (Baselga and Orme 2012) for pairwise beta diversity calculation and geosphere (Hijmans et al. 2017) for spatial distance.

Results

A positive correlation between genus turnover and geographical, climatic distance was found mostly after Pleistocene: Last Glacial Period, Holocene (ps < .05; Table 1 (a, b), Figs. 3 and 4), and present day (p < .001). Notably, there was little evidence on genus turnover related to geographical/climatic distance in the Paleogene and Neogene under warmer climates (ps > 0.1), despite the existence of a climate gradient (difference in temperature) in every geological interval (Appendix S2). Results with Sørensen dissimilarity (β_{sor}) and the nestedness component (β_{sne}) are provided in Supplementary materials (Appendix S9 and S10).

These patterns of genus turnover in relation to geographical and climatic distance were consistent across different thresholds (N_{thre}) with different numbers of sub-regions (Appendix S6), different numbers of genera per assemblage (Appendix S7), and irrespective of random removal of genera (Appendix S11); thus, sampling bias of the fossil record had little influence on the overall pattern.

Discussion

In this study, we clarified the long-term fluctuations in the taxonomic composition of angiosperm woody-plant assemblages on the East Asian islands under currently subtropical to subarctic climates. Interestingly, fossil assemblages of angiosperm woody plants showed varied beta-diversity patterns between geological intervals, supporting the hypothesis that the spatial turnover of genera was regulated by paleoclimate conditions. In general, our predictions

Table 1. Regression table of the negative exponential model. Minimum number of genera per region (N_{thre}) was set to 10.

Table 1 (a) Regression table of spatial distance-turnover relationship

	Oligocene	Miocene	Pliocene	Pleistocene	LastGlacial	Holocene	Present
Intercept	-0.933	-0.305	-0.412	-0.272	-0.117	-0.195	0.016
std.error	0.144	0.030	0.048	0.045	0.039	0.029	0.006
t-value	-6.486	-10.153	-8.522	-6.109	-3.018	-6.638	2.627
p-value	0.000	0.000	0.000	0.000	0.004	0.000	0.010
Spatial distance (x1000)	-0.051	0.015	-0.036	-0.055	0.147	0.104	0.156
std.error	0.150	0.039	0.062	0.052	0.058	0.046	0.008
t-value	0.338	-0.392	0.580	1.061	-2.524	-2.261	-19.947
p-value	0.737	0.696	0.564	0.292	0.015	0.027	0.000
Pseudo-R2	0.002	0.001	0.006	0.012	0.133	0.075	0.759
AIC	-17.775	-163.516	-70.722	-61.171	-68.940	-123.817	-537.418

**Table 1 (b)** Regression table of climatic distance-turnover relationship

	Oligocene	Miocene	Pliocene	Pleistocene	LastGlacial	Holocene	Present
Intercept	-0.909	-0.316	-0.373	-0.267	-0.140	-0.205	-0.008
std.error	0.116	0.023	0.039	0.040	0.033	0.024	0.006
t-value	-7.803	-13.839	-9.449	-6.674	-4.220	-8.484	-1.289
p-value	0.000	0.000	0.000	0.000	0.000	0.000	0.200
Climatic distance	-0.005	0.000	0.005	-0.008	0.015	0.014	0.021
std.error	0.024	0.006	0.010	0.008	0.006	0.006	0.001
t-value	0.187	0.064	-0.467	1.069	-2.323	-2.473	-15.146
p-value	0.853	0.949	0.642	0.288	0.025	0.016	0.000
Pseudo-R2	0.001	0.000	0.004	0.012	0.115	0.090	0.644
AIC	-17.698	-163.363	-70.604	-61.193	-68.039	-124.882	-484.617

on the patterns of genus turnover were supported: distance-dependency of taxonomic similarity was mostly absent in the past; moreover, genus turnover was not associated with either geographical or climatic distance across the East Asian islands through the Oligocene to Pliocene, times that were characterized by a warm, stable climate. Notably, a significant distance-dependent turnover was found only in glacial and post-glacial assemblages (i.e., in the Last Glacial Period, Holocene, and present day). These findings of distance-dependent changes in genus composition could be attributed to environmental factors and dispersal (Tuomisto et al. 2003, Soininen et al. 2007) and suggest that large-scale taxonomic sorting along geography and climate was determined (intensified or buffered) by climatic filter effects and dispersal limitation in response to paleoclimate dynamics, and consequent impacts on biodiversity patterns.

On the East Asian islands, the geographical pattern of woody-plant richness is fundamentally idiosyncratic and is related to paleoclimatic/geohistorical processes involving insularity and land-bridge formation (Kubota et al. 2018). Indeed, we found little evidence of a latitudinal diversity gradient of angiosperm woody-plant genera in this region in the Paleogene and Neogene (Appendix S12), which was consistent with previous findings (Harris et al. 2016, Shiono et al. 2018). In contrast, the unstable cold climate after the

Pliocene depressed generic richness at high latitudes: phylogenetically older genera selectively became extinct because of tropical niche conservatism without freezing tolerance, which is responsible for shaping the latitude-dependent diversity pattern during the Quaternary (Shiono et al. 2018, Appendix S12 and S13). Our findings suggest that the latitudinal gradient under these climate-related processes was underpinned by spatial dynamics of beta diversity.

Climate-driven local extinction that decreases distributions and dispersal to fill potential distributions might determine taxonomic turnover across the region (Na and Kiessling 2015). During the Paleogene and Neogene, when the Japanese archipelago contained tropical vegetation including mangroves (Pavlyutkin et al. 2016), distance-independent genus turnover was predominant: the stable warm climate might have mitigated dispersal limitation related to climatic/geographic distance between the regions. Angiosperm woody-plant genera had enough time to fill all the range of potential climate niches, which consequently blurred the pattern of genus turnover along geography and climate. In contrast, spatial/climatic distance-dependent genus turnover, which was found in modern post-glacial assemblages, resulted from environmental filtering processes, where tropical taxa became extinct in higher latitudes, and re-colonization lags were evident in range recovery from
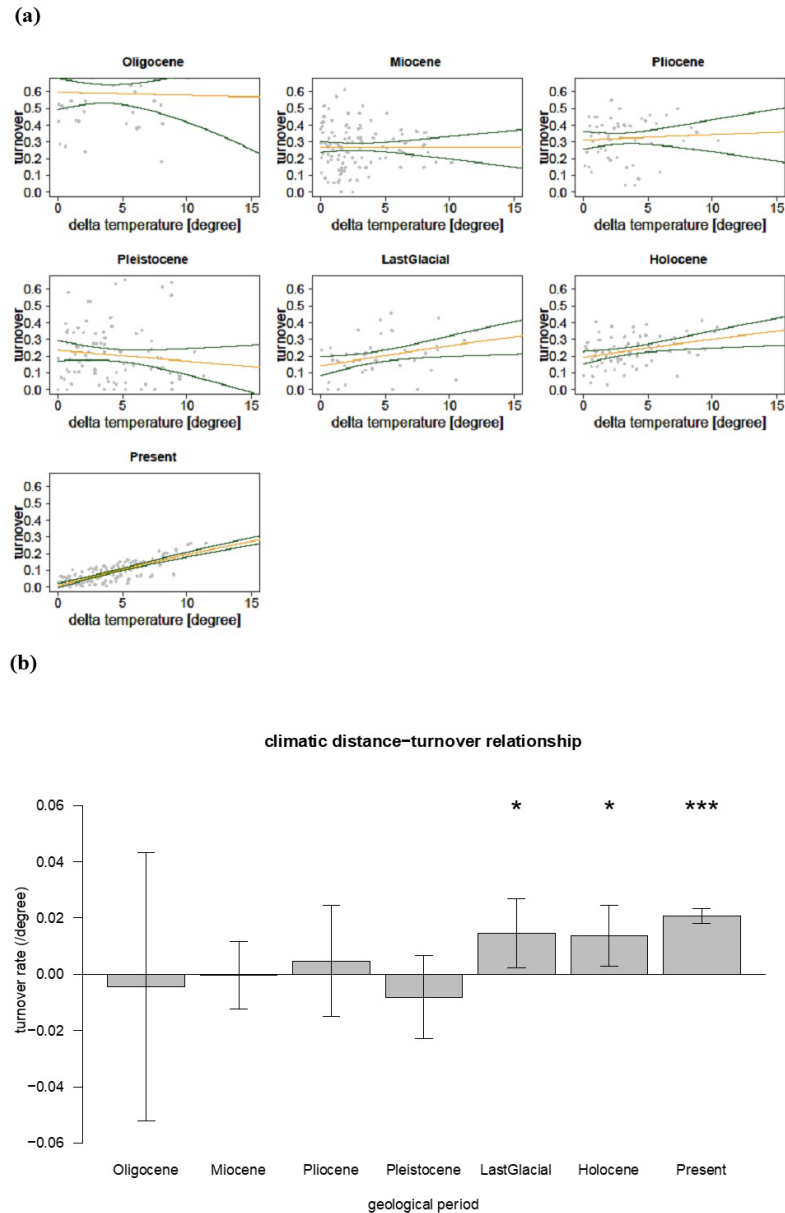
(a)

(b)
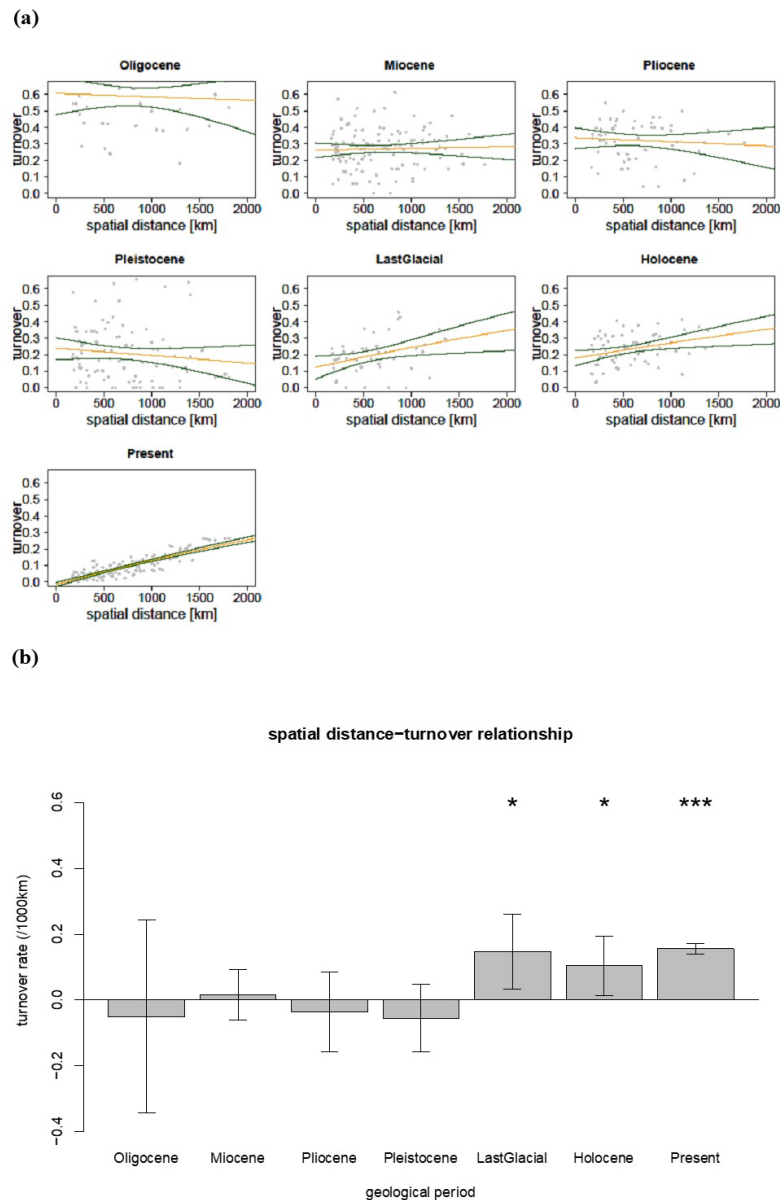
Figure 3. Taxonomic turnover in relation to geographical distance among local assemblages of angiosperm woody plants. (a) Relationships between geographical distance and genus turnover (β_{sim}) in different geological intervals. Yellow lines represent the predicted curves fitted by the negative exponential model. Green lines indicate 95% confidence intervals approximated using a first-order approximation of standard error. (b) Slope coefficient of the negative exponential model to explain the relationship between geographical distance and genus turnover. † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars represent 95% confidence intervals approximated using a first-order approximation of standard error.

refugia (Svenning and Skov 2004, Willner et al. 2009, Dullinger et al. 2012, Lobo 2011), especially in high latitudes. Indeed, we also found that the nestedness component correlated with spatial/climatic distance in Pleistocene (Appendix S10), suggesting that intense glaciation cycles (which repeated 22 times) may have caused local extinctions at high latitudes, although we note that the impact of extinction should be carefully investigated further because the nestedness resultant component is sensitive to the degree of data incompleteness (Baselga 2010). Furthermore, macroevolutionary processes, which generate new

taxa that occupy the novel cold habitats, may impact on the shaping of steep beta diversity gradients via taxon replacements related to spatial/climatic distance between sites, in addition to environmental filtering involving local extinction at high latitude (Kerkhoff et al. 2014, Shiono et al. 2018).

Our finding of distance-independent taxonomic turnover in the past warmer intervals has implications for biodiversity response to future climate changes: tropicalization in currently temperate habitats will promote spatial homogenization of species assembly patterns. This conclusion is also consistent with the

(a)

(b)

Figure 4. Taxonomic turnover in relation to climatic distance among local assemblages of angiosperm woody plants. (a) Relationships between temperature difference and genus turnover (β_{sim}) in different geological time intervals. Yellow lines represent the predicted curves fitted by the negative exponential model. Green lines indicate 95% confidence intervals approximated using a first-order approximation of standard error. (b) Slope coefficient of the negative exponential model to explain the relationship between climatic distance (Δtemperature) and genus turnover. † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars represent 95% confidence intervals approximated using a first-order approximation of standard error.

absence of spatial and climatic distance-turnover in the Pliocene, which was a transitional interval from warm to cold climate. Notably, in the Pleistocene, distance-dependent turnover was absent despite the emergence of latitudinal diversity patterns (Appendix S12 and S13), which requires further studies to better understand the interaction between beta diversity and the geographical diversity gradient. In this regard, a dataset with finer temporal resolution would make it possible to understand the variability over short time scales, which the current time-averaging method cannot

address (Darroch et al. 2014, He et al. 2018). Also, it is necessary to the consider possible effect of dominance of nestedness in the dataset on turnover component since both components are negatively correlated. Finally, the hypothesis on easing of environmental filtering and dispersal release under stable warm climates should be examined using other taxa with different dispersibilities, and by global-scale analyses, because of the different responses among taxa to climate change, and the fact that distance-turnover patterns are dependent on spatial extent (Soininen et al. 2018).

Acknowledgements

Data Accessibility

Referenced fossil occurrence data of the Oligocene, Miocene, and Pliocene and the modern-day presence-absence data are available in the electronic materials of Shiono et al. (2018). Quaternary fossil data and analysis codes are available at GitHub: https://github.com/anchor200/cenozoic_japan_wood

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Appendix S1. Procedure for the compilation of fossil data.
Appendix S2. Locations of fossil sites and temperature distribution by subdivisions and relationship between spatial and climatic distance of each geological age.
Appendix S3. Summary of fossil occurrence and coverage.
Appendix S4. Procedure for classification of the study area.
Appendix S5. Study area classified into the 12 regions.
Appendix S6. Regression tables with 12 sub-regions.
Appendix S7. Analysis with different number of minimum number of genera per assemblage.
Appendix S8. Model comparison of the regression analysis with negative exponential and power law models with 17 sub-regions. Minimum number of genera per region (Nthre) was set to 10.
Appendix S9. Regression analysis of beta diversity (Sørensen's pairwise dissimilarity) against spatial/climatic distance.
Appendix S10. Regression analysis of nestedness component of beta diversity against spatial/climatic distance.
Appendix S11. Effect of random removal of data.
Appendix S12. Latitudinal diversity gradients in the (a) fossil and (b) modern dataset.
Appendix S13. Geographic range of selected genera.

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