Degrees of compositional equilibrium in tree communities vary along a gradient of temperature change rates over one decade: Application of an individual-based temporal beta-diversity concept

Running title: Individual-based temporal beta diversity

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Author contribution

R.N. conceived the study, designed the methods described herein, conducted the analyses using empirical data, and wrote the manuscript.

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Data accessibility statement

All the data used in the present study were obtained from open sources. The forest monitoring data were extracted from the website of the Biodiversity Center of Japan (http://www.biodic.go.jp/moni1000/index.html, in Japanese: accessed on November 11, 2019) published in part by Ishihara *et al*. (2011). Climate data are from the Japanese Automated Meteorological Data Acquisition System (AMeDAS) database (http://www.jma.go.jp/jma/indexe.html, Japan Meteorological Agency accessed December 12, 2019). Taxonomic information was obtained from the Ylist (Yonekura & Kajita 2003: http://ylist.info/ylist_simple_sea rch.html, in Japanese: accessed December 8, 2019).

Abstract

Temporal patterns in communities have gained much attention recently. However, the persistence of identical individuals and turnover among other individuals within the same species over time have not been considered. To deal with this issue, I propose new index concepts for beta-diversity and the relative speed of community equilibrium in relation to individual turnover based on individual identity information within communities. I applied this new approach to individually tracked tree monitoring data in deciduous and evergreen broad-leaved forests across the Japanese archipelago. A new index explored the relative contributions of mortality and recruitment processes. Clear patterns emerged showing that an increase in the temperature change rate facilitated the relative contribution of mortality components. The relative speed of community equilibrium decreased with increasing temperature change rates in deciduous forests but increased in evergreen forests. The new concepts provide a way to identify novel and high-resolution temporal patterns in communities.

Introduction

All living organisms have finite life spans. Each individual tries to leave offspring before its death. The persistence of individuals and their reproduction in the past shape the current diversity patterns through temporal dynamics of populations, communities, and ecosystems. The effects of recent anthropogenically induced climate change on local and global biodiversity have received considerable attention (Permesan & Yohe 2003, Chen *et al*. 2011). Specifically, intensive efforts have focused on biodiversity loss (i.e., alpha- and gamma-diversity) and compositional shifts (i.e., beta-diversity) within the context of biodiversity conservation (e.g., Dornelas *et al*. 2014, Valtonen *et al*. 2016, Hillebrand *et al*. 2017). Ideally, long-term biodiversity monitoring programs that span multiple decades across replicated study sites using consistent methodologies and sampling efforts should be used to identify the effects of climate change. However, multi-decade monitoring programs are as yet very rare (Magurran *et al*. 2010; but see Valtonen *et al*. 2016).

Whittaker (1960, 1972) developed the concept of beta-diversity, which he defined as the variation in community composition among sites in a region. Since then, many new beta-diversity indices have been developed, and attempts have been made to relate the properties of beta-diversity and dissimilarity indices to background ecological processes (Harrison *et al*. 1992, Williams 1996, Lennon *et al*. 2001, Tuomisto & Ruokolainen 2006, Baselga 2010, Legendre 2010; reviewed by Koleff *et al*. 2003, Anderson *et al*. 2011, Jost *et al*. 2011, Legendre & De Cáceres 2013). More attention has been focused recently on temporal changes in community composition in either single sites or in a series of sites surveyed repeatedly over time (Magurran 2011, Matsuoka *et al*. 2016, Legendre & Condit 2019). Temporal changes in community composition are now termed “temporal beta-diversity” (Hatosy *et al*. 2013, Legendre & Gauthier 2014, Shimadzu *et al*. 2015). The patterns of decay in temporal distance, which involve increasing community dissimilarity from one time

point to the next in the same location, have been considered within the context of patterns of decay in geographical distance (Hatosy *et al*. 2013, Bahram *et al*. 2015, Matsuoka *et al*. 2016). Legendre (2019) elegantly partitioned temporal beta-diversity into loss and gain components of the compositional changes in each community, thereby facilitating mechanistic understanding of the temporal changes in community composition. Furthermore, recent studies have started to show that the temporal beta-diversity patterns differ among sites (Legendre & Condit 2019, Magurran *et al*. 2019). Environmental changes, including anthropogenically induced shifts, such as the present worldwide climate warming, are likely factors that drive spatial differences in temporal beta-diversity (Legendre 2019).

The persistence of individuals over time is an important component of the temporal beta-diversity concept, which has not been explicitly considered before. The persistence of individuals contributes to a static equilibrium in community composition. Nevertheless, there is turnover of different individuals belonging to the same species even when the community composition is stable over time, i.e., conventional temporal beta-diversity is zero when the community composition is at equilibrium, which contributes to a dynamic equilibrium in community composition. However, it is difficult to detect differences in turnover within the same species. Thus, the meaning of compositional changes in communities differs between sites with high and low individual turnover rates across time. Therefore, an appropriate evaluation of temporal changes in community composition could benefit from considering the fates of identifiable individuals in a community over time. Here, I propose new indices of temporal beta-diversity that take into account individual identity information. These new coefficients are individual-based in contrast to others that are incidence-based (e.g., the Sørensen index; Sørensen 1948), or abundance-based (e.g., the Bray–Curtis index; Bray & Curtis 1957). My new indices quantitatively evaluate the temporal changes in community composition by considering individual identity information

and reveal the relative contribution of different background processes to these temporal changes. I also propose a new index to quantify the relative speed of change away from compositional equilibrium in a community relative to the speed of individual turnover. I calculated the indices for 16 forest inventory datasets compiled across the Japanese archipelago. These datasets have individual identity information for two time periods. The indices identified the effects of climate changes on the composition of tree communities on a decadal time scale.

Materials and Methods

New indices of temporal beta-diversity and new statistics to evaluate the relative speed compositional equilibrium in relation to individual turnover

Two types of dissimilarity indices have been proposed in previous studies: incidence-based and abundance-based (Baselga *et al*. 2013) types. Specifically, the widely used Bray–Curtis dissimilarity index (Bray & Curtis 1957, which was proposed earlier as a proportional difference index by Odum 1950), is an abundance-based extension of the Sørensen index (Legendre & Legendre 1998, Baselga *et al*. 2013). I have excluded details of incidence-based indices that are tangential to the main topic in my study (see Anderson *et al*. 2011, Jost *et al*. 2011, Baselga *et al*. 2013). The conceptual basis for conventional beta-diversity indices and my new procedures relies on the fact that the intersection (A component) and the relative complement (B and C components) for species abundance can be formulated as follows:

$$A = \sum_i \min\left(x_{ij}, x_{ik}\right) \quad (1)$$

$$B = \sum_i x_{ij} - \min\left(x_{ij}, x_{ik}\right) \quad (2)$$

$$C = \sum_i x_{ik} - \min\left(x_{ij}, x_{ik}\right) \quad (3)$$

where x_{ij} is the abundance of species i at site j, and x_{ik} is the abundance of species i at site k. Therefore, A is the number of individuals of each species that occur at both sites j and k, while B and C are the numbers of individuals that are unique to sites j and k, respectively. This formulation of the Bray–Curtis (d_{BC}) index is expressed as follows:

$$d_{BC} = \frac{B + C}{2A + B + C} \quad . \tag{4}$$

In the temporal beta-diversity concept, the differences between data vectors correspond to observations made at time 1 (abbreviated T1) and time 2 (T2), which are referred to sites k and j in the spatial beta-diversity concept. The A, B, and C components are described as follows:

$$A_t = \sum_i \min(y_{i1}, y_{i2}) \tag{5}$$

$$B_t = \sum_i y_{i1} - \min(y_{i1}, y_{i2}) \tag{6}$$

$$C_t = \sum_i y_{i2} - \min(y_{i1}, y_{i2}) \tag{7}$$

where y_{i1} is the abundance of species i at time T1 at a site, and y_{i2} is the abundance of species i at time T2 at the site. Therefore, A_t is the number of individuals of each species that occur at both times T1 and T2, whereas B_t and C_t are the numbers of individuals that are unique to times T1 and T2, respectively. The temporal beta-diversity of the Bray–Curtis ($d_{t.BC}$) index is expressed as follows:

$$d_{t.BC} = \frac{B_t + C_t}{2A_t + B_t + C_t} \quad . \tag{8}$$

Using Equation 8, Legendre (2019) partitioned the temporal beta-diversity indices

into loss and gain components because a change through time is directional; species abundances would identify losses and/or gains between T1 and T2 as follows:

$$d_{t.BC} = \frac{B_t + C_t}{2A_t + B_t + C_t}$$
$$= \frac{B_t}{2A_t + B_t + C_t} + \frac{C_t}{2A_t + B_t + C_t} = d_{t.loss} + d_{t.gain} \ . \qquad (9)$$

Legendre and his collaborators applied the loss/gain partitioning procedure for temporal beta-diversity to many empirical datasets (e.g., Kuczynski *et al*. 2018, Brice *et al*. 2019), and constructed a new analytical trend in temporal beta-diversity.

In this study, I developed the concept of abundance-based temporal beta-diversity based on Bray–Curtis dissimilarity through extension of the individual-based temporal beta-diversity indices. The following P, M, and R components correspond to components A, B, and C, respectively. M refers to individuals occurring at T1, but dead before T2, thereby separately identifying the deaths of individuals during the time period between T1 and T2 (Fig. 1). R identifies individuals that were not alive at T1, but subsequently found at T2, thereby identifying the recruitment of individuals during the period between T1 and T2. Component P refers to the persistence of individuals from T1 to T2 (Fig. 1). The respective abundances were calculated as follows:

$$P = \sum_l \min(z_{l1}, z_{l2}) \qquad (10)$$
$$M = \sum_l z_{l1} - \min(z_{l1}, z_{l2}) \qquad (11)$$
$$R = \sum_l z_{l2} - \min(z_{l1}, z_{l2}) \qquad (12)$$

where z_{l1} is individual l at time T1, and z_{l2} is individual l at time T2. Both z_{l1} and z_{l2} take only 1 or 0, i.e., presence or absence. Therefore, *P* is the number of individuals present at both T1 and T2, whereas M and R are the numbers of individuals that are

unique to T1 or T2, respectively. Although P, M, and R refer to components A, B, and C, respectively, here I have used different characters to emphasize the meaning of the processes of each component. This formulation of the individual-based temporal beta-diversity index (d_{MR}) can be expressed as follows:

$$d_{MR} = \frac{M + R}{2P + M + R}. \tag{13}$$

Furthermore, this individual-based temporal beta-diversity can be partitioned into the relative contributions of mortality (d_M) and recruitment (d_R) processes using a similar procedure for the loss and gain component-partitioning of the temporal beta-diversity in Equation 9 (Legendre 2019) as follows:

$$\begin{aligned} d_{MR} &= \frac{M + R}{2P + M + R} \\ &= \frac{M}{2P + M + R} + \frac{R}{2P + M + R} = d_M + d_R. \end{aligned} \tag{14}$$

Traditionally, the equilibrium and non-equilibrium elements in community ecology indicate properties of the whole community that are directly related to species coexistence (Pickett 1980). However, some individuals replace others, and thus ecological communities are always dynamic and vary at least by some degree in space and time (Mori *et al*. 2018, Ryo *et al*. 2019). In addition, some individuals of long-lived species (e.g., trees and vertebrates) are persistent over the term, while individuals of short-lived species are replaced by conspecifics or different species. Therefore, it is possible to categorize the components of community dynamics into persistence (P), and components that change over time, i.e., mortality and recruitment part (M and R), as explained above. The elements of change are also separated into two component parts of compositional equilibrium (E) and shift (B_t and C_t). Specifically, component M can be partitioned into lost individuals that contribute to

compositional change in a community (B_t) and lost individuals that are replaced by conspecifics, contributing substantially to equilibrium in community composition (E_{loss}). Similarly, component R can be partitioned into gained individuals that contribute to compositional change in a community (C_t), and gained individuals replacing conspecifics, thereby contributing substantially to equilibrium in community composition (E_{gain}). By definition, the numbers of E_{loss} and E_{gain} individuals are identical; hence, I replaced both E_{loss} and E_{gain} with the coefficient E, the component that contributes to dynamic compositional equilibrium. The formulation is as follows:

$$
\begin{aligned}
d_{MR} &= \frac{M+R}{2P+M+R} \\
&= \frac{B_t + E_{loss} + C_t + E_{gain}}{2P+M+R} = \frac{B_t + C_t + 2E}{2P+M+R} \\
&= \frac{2E}{2P+M+R} + \frac{B_t + C_t}{2P+M+R} = d_E + d_S
\end{aligned}
\tag{15}
$$

where d_E and d_S indicate the contributions of equilibrium and shift to individual-based temporal beta-diversity.

Both M and R in equation 14 refer to total numbers of individuals, but original data for mortality and recruitment processes of individual species can also be analyzed in the same manner as community data (Fig. 1). Therefore, the calculation of Bray–Curtis dissimilarity between communities using mortality and recruitment is possible, as follows:

$$
\begin{aligned}
v_s &= \frac{B_t + C_t}{2E + B + C_t} \\
&= 1 - \frac{2E}{2E + B_t + C_t} = 1 - \frac{2E}{M+R} = 1 - v_e \,.
\end{aligned}
\tag{16}
$$

v_s indicates the speed of compositional shifts in a community relative to the total speed of individual turnover through mortality and recruitment processes. I used v_e

$= 2E/(M+R)$ for analyses of an empirical dataset because the meaning is intuitively clearer. If v_e is 1, the individual turnover would not contribute to compositional shifts in a community, i.e., the community composition of mortality and recruitment are identical and an equilibrium state exists. If v_e is 0, all individual turnovers contribute to compositional shifts, and the community composition of mortality and recruitment are completely different. In my main analyses, I focused only on an extension of Bray–Curtis dissimilarity. I also summarized explanations of individual-based beta-diversity using the Ružička dissimilarity index (Ružička 1958), which was identified by Podani *et al*. (2013) and Legendre (2014) as another appropriate index for beta-diversity studies. The Ružička dissimilarity index is also an abundance-based extension of the Jaccard dissimilarity index (Jaccard 1901).

Individual-tracked monitoring data for forests

I predicted the indices of individual-based beta-diversity and the relative speed of compositional equilibrium variation along degrees of climate change rate per year, i.e., average speed of local climate change. I tested the performance of the new indices using individual-tracked monitoring data for forests in Japan. Two types of temporal change in tree communities may result from climate change—the change due to changes in the obligate speed of individual turnover, e.g., climate warming facilitates the faster growth and shorter life span of each individual tree as a physiological process within individuals (Körner 2017, Munné-Bosch 2018), and the change due to the relative speed of compositional change, e.g., simple compositional shifts caused by climate change as an ecological process among individuals. Those can be referred to as d_{MR} and v_e, respectively.

The Japanese archipelago comprises a long chain of continental islands lying off the eastern coast of Asia; it is recognized as a hotspot of biodiversity (Mittermeier *et al*. 2011). The mean temperatures of the coldest months range from –18.4 to 22.3°C,

287 mean temperatures of the warmest months from 6.2 to 29.2°C, and the annual
288 precipitation ranges from 700.4 to 4477.2 mm (Japan Meteorological Agency,
289 1981–2010; http://www.jma.go.jp/jma/indexe.html). Typical forest biomes are
290 classified into four types: alpine meadow/creeping pine zone, subalpine coniferous
291 forest zone, deciduous broad-leaved forest zone, and evergreen broad-leaved forest
292 zone. The empirical tree census dataset used in this study was obtained from the
293 forest plots used in the Monitoring Sites 1000 Project; this project was launched by
294 the Ministry of the Environment, Japan (see Ishihara *et al*. 2011 for details). The
295 monitoring sites include five types of forest: deciduous broad-leaved, evergreen
296 broad-leaved, mixed broad-leaved and coniferous, evergreen coniferous, and artificial
297 forest (Ishihara *et al*., 2011, Suzuki *et al*. 2015). The full dataset is available on the
298 website of the Biodiversity Center of Japan
299 (http://www.biodic.go.jp/moni1000/index.html, in Japanese: accessed on November
300 11, 2019), and a subset of the data has been published as a data article (Ishihara *et al.*
301 2011).
302 To test the performance of the individual-based temporal beta-diversity approach, I
303 chose 16 forest plots: nine plots of deciduous broad-leaved forest and seven plots of
304 evergreen broad-leaved forest (Fig. 2, Table S1) using the following criteria: species
305 level identifications had been performed in each plot, the plots had been surveyed one
306 decade after a previous survey (in the period 2005–2008 to 2015–2018), individual
307 identity information was recorded throughout the two time periods, plot size was 1.0
308 ha square (100 × 100 m), and sufficient numbers of plots in various environments
309 within the forest types were available for use in analyses. In this analysis (which was
310 based on the contents of the original datasets) I chose tree individuals with stem
311 girths at breast height (GBH) ≥ 15.7 cm, which was approximately equivalent to a
312 diameter at breast height (DBH) ≥ 5 cm; these were considered target individuals in
313 the communities. I re-compiled the data at the level of individual trees before the

analyses; the original forest datasets had been compiled at the stem level. I used taxonomic information provided in the Ylist (Yonekura and Kajita 2003). The data I analyzed included 18,749 individuals belonging to 254 species found in the 16 plots (Fig. 2).

Climate variables

To obtain meteorological observation data and their changes over a decade, I searched for the meteorological station closest to each of the forest plots in the Japanese Automated Meteorological Data Acquisition System database (Japan Meteorological Agency; see details in Table S1, Fig. S1). Specifically, I extracted the monthly mean and total precipitation data (accessed December 12, 2019), and calculated the annual mean temperature (°C) and annual precipitation (mm) for each year and site. I estimated temperature differences from elevation differences between each of the forest plots and its nearest meteorological station using 0.55°C/100 m in elevation as the mean lapse rate; this relationship between temperature and elevation is commonly used by Japanese forestry researchers (e.g., Oshima *et al.* 1961, Fukushima *et al*. 2009). I used simple linear model in R software (R Development Core Team 2019) to calculate regression coefficients between years and annual climate (annual mean temperature and annual precipitation) for the targeted years (i.e., from the year of the first survey to the year of the second survey) for each plot. The correlation coefficients indicate the average temperature change per year in the targeted decade, and hence average change rate in annual mean temperature and annual precipitation in each plot. The average rates of change in annual mean temperature (°C) and annual precipitation (mm) were 0.004±0.047 (–0.105 to 0.063) and 5.714±32.795 (–37.082 to 77.791), respectively, in deciduous broad-leaved forests, and 0.003±0.043 (–0.040 to 0.059) and 20.860±18.737 (–0.176 to 47.261), respectively, in evergreen broad-leaved forests (mean ± SD [range]).

Macroecological patterns of indices describing individual-based temporal beta-diversity and the relative speed of compositional equilibrium

I focused mainly on the following indices: d_{MR}, d_M/d_R, d_E/d_S, and v_e. d_{MR} indicates total individual turnover between two time periods (i.e., individual-based temporal beta-diversity). Both d_M/d_R and d_E/d_S are indicators of the relative contribution to individual-based temporal beta-diversity (d_{MR}); they are rates of mortality to recruitment processes, and compositional equilibrium to shift, respectively. v_e is the relative speed of compositional equilibrium relative to total individual turnover. The relative contributions of compositional equilibrium and shift are formulated as follows:

$$d_E \div d_S = \frac{2E}{2P+M+R} \div \frac{B_t + C_t}{2P+M+R} = \frac{2E}{B_t + C_t} = \frac{2E}{M+R-2E} \quad (17)$$

Because "2*E*" in the denominator is simply the difference between v_e (equation 16) and d_E/d_S (equation 17), the two are strongly correlated (Table S6), but the two indices have different meaning.

First, I analyzed the relationships between these indices and the average rates of change in annual mean temperature and annual precipitation using both simple and polynomial regressions. Then I compared the Akaike's information criterion (AIC) values (Akaike 1976) among models, including the null model, and selected the best model for each. I did not use multiple regressions for further analyses because the number of data points available was insufficient.

To test the relationship between compositional equilibrium and structural change in communities over time, I also calculated the change in community evenness for each plot over a decade using Pielou's equation $J = H/Ln(S)$, where H is the Shannon diversity and S is total species richness in a community; the analyses were executed

368 with the "vegan" package in R software. I checked the trends of change in
369 community evenness using the procedures applied in the analyses of temporal trends
370 in indices d_{MR}, d_M/d_R, d_E/d_S, and v_e (described above). I examined the relationships
371 between compositional equilibrium (v_e) and structural change (J_{change}). All statistical
372 analyses were conducted in R.
373
374 **Results**
375 The values of d_{MR}, d_M/d_R, d_E/d_S, and v_e were 0.154±0.056 (0.084–0.242), 1.211±0.749
376 (0.415–2.460), 1.025±0.779 (0.134–2.909), and 0.455 ±0.167 (0.119–0.7449),
377 respectively, in deciduous broad-leaved forests, and 0.137±0.037 (0.102–0.198),
378 1.211±0.352 (0.541–1.733), 1.153±0.168 (0.978–1.412), and 0.533±0.036
379 (0.495–0.585), respectively, in evergreen broad-leaved forests.
380 I detected no trends in d_{MR} in relation to average rate of change in annual mean
381 temperature in either deciduous or evergreen broad-leaved forests (Fig. 3a, b, Table 1).
382 In analyses of d_M/d_R, the polynomial model was chosen by the AIC comparison as the
383 best model for deciduous broad-leaved forests; the simple model was the best for
384 evergreen broad-leaved forests. The increase in d_M/d_R was greatest at sites that
385 warmed most in the targeted decades. This was true for both types of forest. Thus, the
386 relative contribution of mortality process to individual based beta-diversity increased
387 with warming rate over time (Fig. 3c, d). The d_E/d_S index did not show any statistical
388 trends over time for deciduous forests (Fig. 3e); the simple regression model was
389 chosen by AIC comparison as the best for evergreen forests (Table 1). In evergreen
390 forests, d_E/d_S increased most over a decade in warming sites. Thus, the relative
391 contribution to individual based beta-diversity of individual turnover increased over
392 time in relation to the contribution with compositional shift (Fig. 3f). The polynomial
393 model of v_e was selected as the best for the deciduous forest type: v_e decreased with
394 larger temperature changes (Fig. 3g, Table 1). The simple model was selected for the

395 evergreen forest type: v_e increased linearly with increasing warming over time (Fig.
396 3h, Table 1).
397 The values of the J_{change} were –0.008±0.033 (–0.091 to 0.019) in deciduous
398 broad-leaved forests, and 0.010±0.022 (–0.025 to 0.041) in evergreen broad-leaved
399 forests. J_{change} decreased most at sites with larger temperature change rates in both
400 forest types (Fig. 3i, j). The statistical analyses of J_{change} changes in relation to the
401 average change rate in annual mean temperature are summarized in Table 1. I
402 detected a significant positive correlation for the relationship between these variables
403 in the deciduous forest type, (Fig. 4a), but not in the evergreen forest type (Fig. 4b).
404 The average rate of change in annual precipitation did not affect trends over time
405 for any of the calculated indices (Table S3).
406
407 **Discussion**
408 Quantitative analyses of biological community change over time are required to
409 expand our understanding of global climate change and its relationship to rapid losses
410 in biodiversity. The novel concepts and procedures that I have developed
411 quantitatively evaluated the relative speed of compositional equilibrium and the
412 relative contribution of mortality and recruitment processes in tree communities
413 along a gradient in temperature change rates across a decade. Compositional shifts in
414 tree communities are generally recognized as long-term phenomena in the absence of
415 disturbance. Therefore, 10 years is a relatively short-time period in which to analyze
416 compositional changes in tree communities comprising species with life spans
417 extending from decades to centuries (Loehle 1988). I found that community
418 responses to local climate change trends differed between forest types, but
419 nevertheless, there were real changes in community composition over only a decade.
420 The changes were caused by change in annual mean temperatures, and not by
421 changes in annual precipitation across the Japanese archipelago.

422 The effects of climate changes caused by human activity have been intensively
423 studied in many disciplines, e.g., analyses of species interactions, range shifts,
424 phenology, and ecosystem functioning (Thomas *et al*. 2004, Kordas *et al*. 2011,
425 Valtonen *et al*. 2014). However, studies of temporal changes in diversity and
426 composition in local communities have often produced mixed and/or different results
427 among sites and researchers (Vellend *et al*. 2013, Dornelas *et al*. 2014, Newbold *et al*.
428 2015, reviewed in Hisano *et al*. 2018). I used a novel index to evaluate compositional
429 changes, i.e., the relative speed of the compositional equilibrium in communities (v_e),
430 which clearly changed along the gradient of temperature change rates (Fig. 4, Table
431 1). Furthermore, the responses were different between deciduous and evergreen
432 broad-leaved forests. Specifically, the relative speed in evergreen forests was greater
433 at sites with most temperature warming. Furthermore, the range size of the values (v_e)
434 in deciduous forests was about 7-fold greater than the range size in evergreen forests.
435 Thus, deciduous forests are more affected by the differences in temperature change
436 rate. I did not detect statistically significant trends along a gradient of precipitation
437 change rate, although drought caused by climate change is a major factor in tree
438 mortality (Allen *et al*. 2010, Saiki *et al*. 2017). These contrasting results may be due
439 to the humid climate of the Japanese archipelago. To capture the effects of global
440 climate change accurately, a broad multi-site analysis across the globe using similar
441 methods will be required.
442 The association between the relative speed of compositional equilibrium and
443 structural changes in communities over time is an important ecological issue. I found
444 that in deciduous forests the relative speed was significantly and positively correlated
445 with changes in community evenness, but this was not the case for evergreen forests
446 (Fig. 4). Therefore, compositional changes were not always accompanied by
447 structural change (Fig. 4). I examined the patterns of community evenness in
448 mortality and recruitment communities (J_M and J_R respectively) to develop a

449 mechanistic interpretation of the temporal change in community evenness in
450 deciduous forests (Table S5). In detail, the evenness of the mortality communities
451 increased with an increasing rate of temperature change; thus, mortality processes
452 were a major contributor of the change in community evenness, but recruitment
453 communities did not track a significant trend (Table S4). Only d_R responded
454 positively to the warming rate, but no clear patterns were apparent for this index
455 (Table S4). The major response components differed between the changes in
456 composition and structures of communities. Although more supporting evidence is
457 needed, I therefore suggest that there might not be a direct relationship between
458 changes in community structure and composition over time.

459 Predicting community persistence from snapshot data on community structure is a
460 complicated issue for community ecologists. For example, Ulrich *et al*. (2018) argued
461 that it may be possible to evaluate species persistence and their relative proportions
462 from the patterns of species abundance distribution. If this were the case, the relative
463 speed of compositional equilibrium should provide a comparable estimate of
464 community persistence from both individual and species-based perspectives.
465 Specifically, using some time series datasets containing substantial annual individual
466 information, it should be technically possible to calculate the retention time for each
467 community, i.e., the lifespan durations of all individuals replaced in a focal
468 community. These calculations could be cross-compared to with snapshot community
469 structure data (e.g., species abundance patterns). In the present study, I used data for
470 only two time periods, so this cross-comparison was not possible. Nevertheless,
471 clarification of the relationship between changes in community structure and
472 composition should become possible in the near future. Underlying mechanisms
473 explaining the relationship may then be discernable.

474 One advantage of the methodology I have developed is that it dissects individual
475 turnover into mortality and recruitment components. For example, I detected no clear

476 patterns in the relationship between individual turnover (d_{MR}), which is the obligate
477 speed of temporal change in communities, and temperature change rate (Fig. 3).
478 However, by splitting the index into two components, I was able to identify relative
479 contributions to individual turnover (d_M/d_R). When this was done, clear patterns
480 emerged showing that an increase in the temperature change rate facilitated the
481 relative contribution of mortality components (Fig. 3, Table 1). Furthermore, by
482 checking the trend of each component separately, I was able to confirm that decreases
483 in recruitment components with increases in the temperature change rate drove the
484 pattern in deciduous forests, but I was not able to confirm this in evergreen forests
485 (Table S5).

486 The relative contribution of the index d_E/d_S to individual-based temporal
487 beta-diversity (d_{MR}) increased positively in evergreen forests as the warming rate
488 increased, although no trends in the individual components (d_E, d_S) were discerned.
489 Thus, the balance between the components changed in a consistent manner with
490 temperature change, although no patterns of variation in the individual components
491 were found. There were no clear trends in d_E/d_S in relation to temperature change
492 rates in deciduous forests. However, d_E was affected by the temperature change rate
493 in these forests: d_E decreased with increased warming rates; thus, there was a clear
494 contribution of compositional equilibrium decrease along these gradients (Table S5).

495 Compilation of long-term temporal datasets for macro species requires
496 considerable human effort and cost for monitoring and research surveys because large
497 organisms often have long life spans. Nevertheless, the new indices I developed
498 clearly enhanced the importance of the monitoring datasets assembled using
499 traditional detailed surveys (e.g., individual tracking in forest plots) in detecting the
500 temporal trends that occurred over short time periods. Therefore, I re-emphasize here
501 the significance of classical monitoring surveys to collect biodiversity information. I
502 also developed an approach that introduced the concept of individual-based

beta-diversity within the context of temporal changes in community composition. Theoretically, however, the procedure could be expanded to a spatial context for use in studies of animal behavioral ranges and movements, including long-distance migration, using monitoring and biologging datasets (Viana *et al*. 2016, Börger *et al*. 2020) that include multiple time series datasets collected from the same place within a shorter time frame than the life spans of the targeted organisms (e.g., bird ringing and classical mark–recapture procedures). Specifically, the approach could detect detailed spatial turnover for individuals within same species in communities.

Many ecology theories have been developed from the concept of species. The original concept of beta-diversity was proposed to reflect species turnover (Whittaker 1960). By contrast, much recent research has pointed out the problems of species-based studies and the importance of considering individuals in community ecology (Dupont *et al*. 2011, Nakazawa 2017, Tatsumi *et al*. 2019). Species are the consequences of ecological/evolutionary processes among individuals; to be accurate, the species themselves do not drive these processes, i.e., individuals do by competing with other individuals, and this does not involve the species directly. Although individuals were considered in the unified neutral theory (Hubbel 2001) and subsequent related studies (Hubert *et al*. 2015, Vanoverbeke *et al*. 2016, Tatsumi *et al*. 2019), the focus was restricted to the patterns of species richness, abundance, and related diversity indices. The effects of individual births and deaths on biodiversity patterns have not yet been considered sufficiently. Procedures for incorporating individual identity information into biodiversity evaluation, i.e., individual-based diversity indices, are required to facilitate further conceptual advances in ecology. New ecological concepts will emerge from combined considerations of species abundance and information relevant to individual identity in the future.

Conclusions

Previous studies have often detected temporal changes in local communities, likely as a result of human activities, but not at all times and places. In this study, I clearly showed the responses of tree communities to local and short-term climate change trends using datasets collected according to novel index concepts. Notably, the relative speed of compositional equilibrium in tree communities varied along a gradient of temperature change rates in this decade. This community level response resulted from individual sorting in mortality and recruitment processes. Therefore, accumulating more detailed information across the globe, specifically individual identity information at the local community level collected over time, is required for understanding both the actual changes due to global climate change in biodiversity and the background processes mechanistically. Mortality and recruitment rates are generally difficult to measure in empirical studies compared to loss and gain information based only on snapshot data, especially except in the case of plants or vertebrates. The individual-based approach may not be tractable for all taxonomic groups. However, information on individual organisms will help to bridge the disciplines of macroecology and study fields focusing on within-individual phenomena, for example, physiological ecology. The calculation of individual-based diversity indices from individual identity monitoring data will support efforts to quantitatively evaluate the impacts of climate change on future biodiversity. The further development of novel diversity index concepts that make use of individual-based biodiversity information to provide a more detailed and mechanistic understanding of biodiversity in general is needed.

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Legends

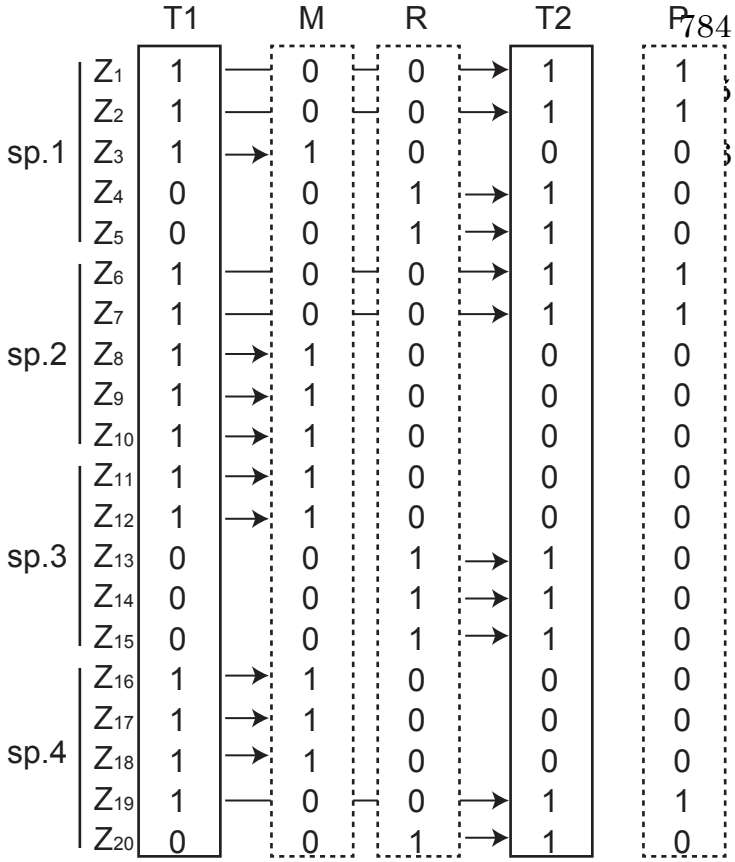
Figure 1 Schematic representation of individual-based temporal beta-diversity. T1 and T2 refer to the communities at times 1 (abbreviated T1) and 2 (T2), respectively. Both communities comprise four species (sp. 1, 2, 3, and 4) and all individuals are identified separately (*Zi*). M refers to individuals in existence at T1 but dead before T2, thereby separately identifying the deaths of individuals during the period between T1 and T2. R identifies individuals that were not alive at T1, but found at T2, thereby identifying the recruitment of individuals during the period between T1 and T2. P refers to individuals that persisted from T1 to T2, thus both T1 and T2 are 1. The arrows indicate the temporal trajectory for each individual; specifically, when they are present or absent in communities between T1 and T2.

Figure 2 Locations of the study sites within the Japanese archipelago. The crosses and asterisks indicate the locations of targeted plots in deciduous broad-leaved forest (DB) and evergreen broad-leaved forest (EB) included in the present study. The lettering adjacent to each symbol is the plot identification code (ID). Detailed plot information is listed in Table S2. The colors indicate four major vegetation types: purple, Alpine meadow or creeping pine zone; blue, subalpine coniferous forest zone; red, deciduous broad-leaved forest zone; green, evergreen broad-leaved forest zone. The information on vegetation type at a 1.0 km grid scale was obtained from the results of the fifth censuses (1992–1996) of the National Survey of the Natural Environment in Japan (http://www.biodic.go.jp/dload/mesh_vg.html; in Japanese, accessed December 12, 2019).

Figure 3 Trends in tree community indices across a gradient of temperature change rates over a decade. The left column of panels refers to trends in deciduous broad-leaved forests; the right column of panels refers to trends in evergreen broad-leaved forests. Panels (a) and (b) show the trends in individual-based temporal beta-diversity indices (d_{MR}). Panels (c) and (d) show trends in the d_M/d_R index, which

766 is an indicator of the relative contribution of mortality and recruitment processes to
767 individual-based temporal beta-diversity (d_{MR}). Panels (e) and (f) show trends in the
768 d_E/d_S index, which is an indicator of the relative contribution of equilibrium and shift
769 processes to individual-based temporal beta-diversity (d_{MR}). Panels (g) and (h) show
770 trends in the index v_e, which is an indicator of the relative speed of compositional
771 equilibrium. Panels (i) and (j) show trends in the index J_{change}, which is an indicator
772 of community evenness. The solid black lines indicate statistically significant ($P <$
773 0.05) trends. The dashed and the dot-dashed black lines indicate marginally
774 significant ($0.05 < P < 0.1$, $0.1 < P < 0.15$) trends respectively. The blue dashed lines
775 enclose the 95% confidence interval envelopes. Detailed results of statistical analyses
776 are presented in Table 1.
777 **Figure 4** Relationships between the change in community evenness (J_{change}) and the
778 relative speed of compositional equilibrium (v_e) in deciduous forests (a) (coefficients
779 = 3.190, $adj.R^2 = 0.314$, $P = 0.067$), and in evergreen forests (b) (coefficients = 0.716,
780 $adj.R^2 = 0.037$, $P = 0.318$).
781
782

783 **Figure 1**



784

Figure 2

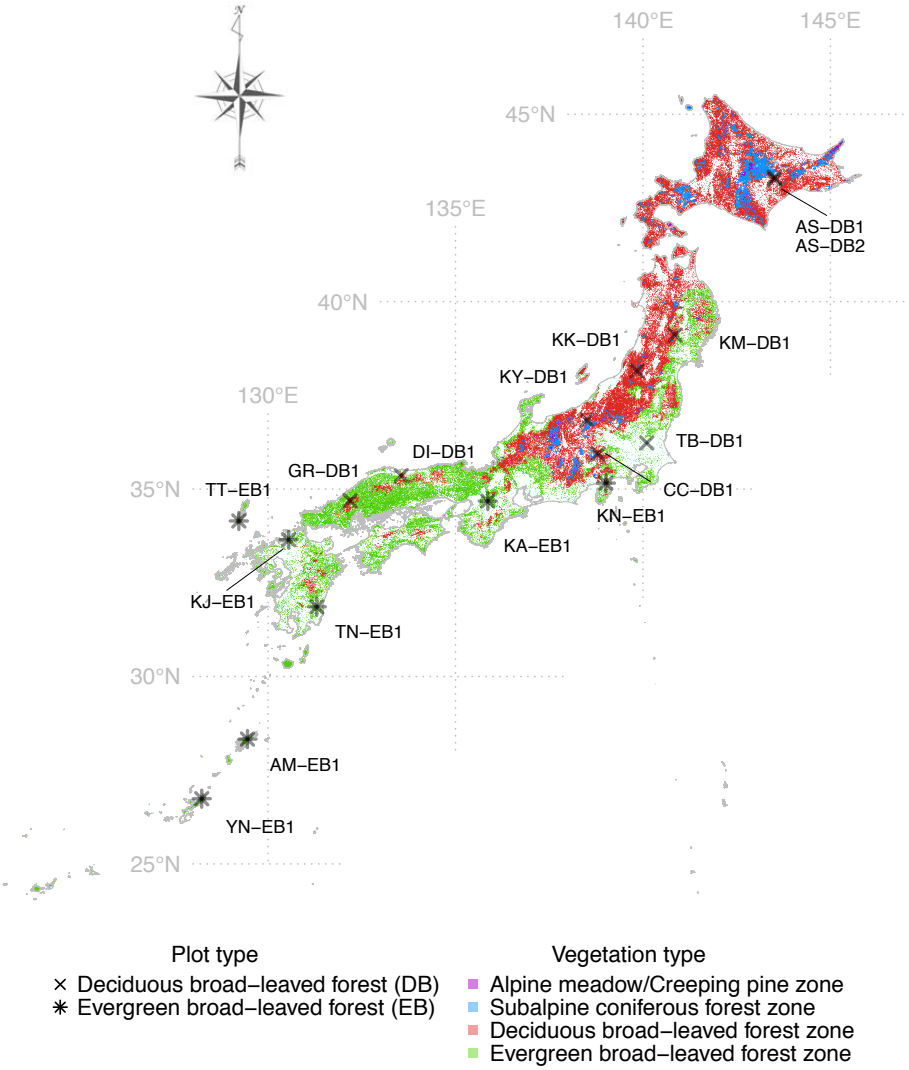

140°E
145°E
45°N
135°E
40°N
130°E
35°N
30°N
25°N
AS–DB1
AS–DB2
KK–DB1
KM–DB1
KY–DB1
TB–DB1
DI–DB1
GR–DB1
TT–EB1
CC–DB1
KN–EB1
KA–EB1
KJ–EB1
TN–EB1
AM–EB1
YN–EB1
Plot type
× Deciduous broad–leaved forest (DB)
✳ Evergreen broad–leaved forest (EB)
Vegetation type
Alpine meadow/Creeping pine zone
Subalpine coniferous forest zone
Deciduous broad–leaved forest zone
Evergreen broad–leaved forest zone

Figure 3

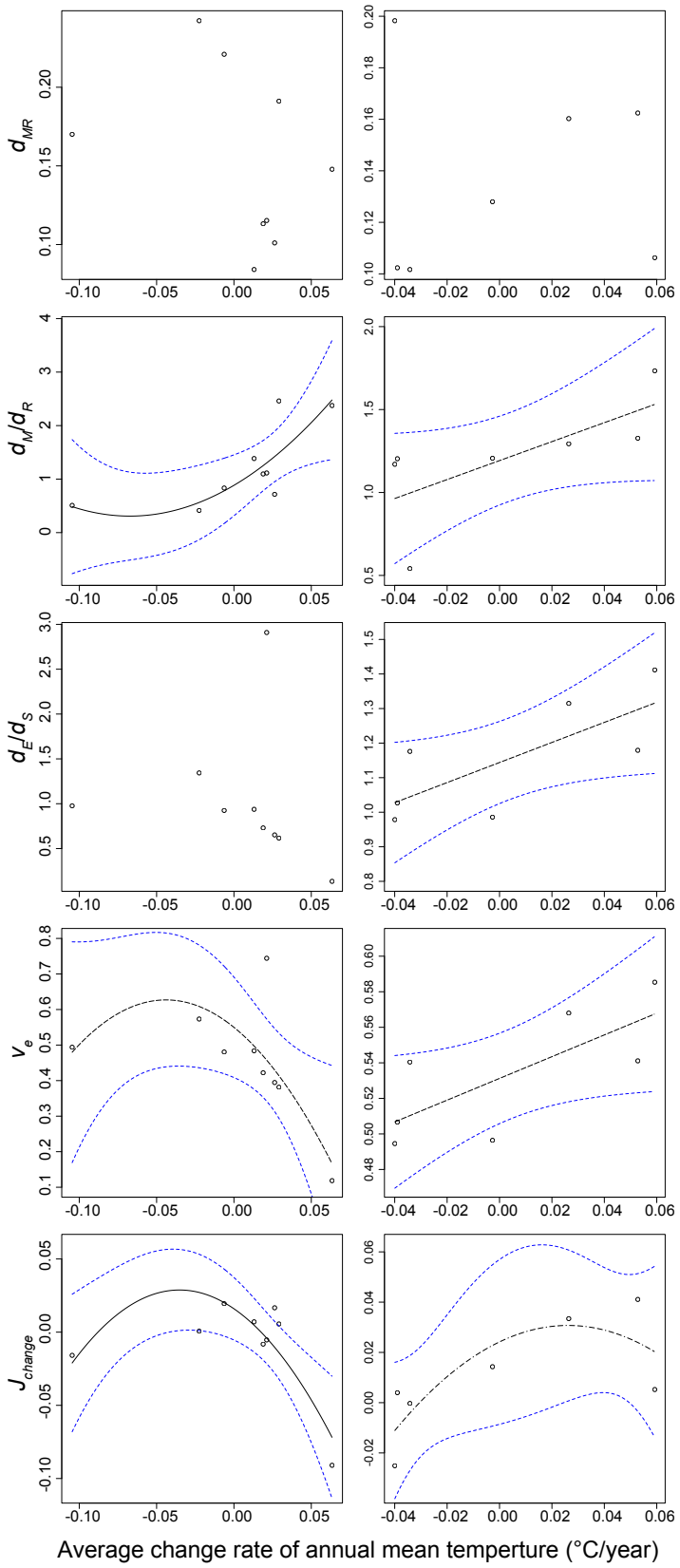

d_{MR}
d_M/d_R
d_E/d_S
v_e
J_{change}
Average change rate of annual mean temperture (°C/year)

Figure 4

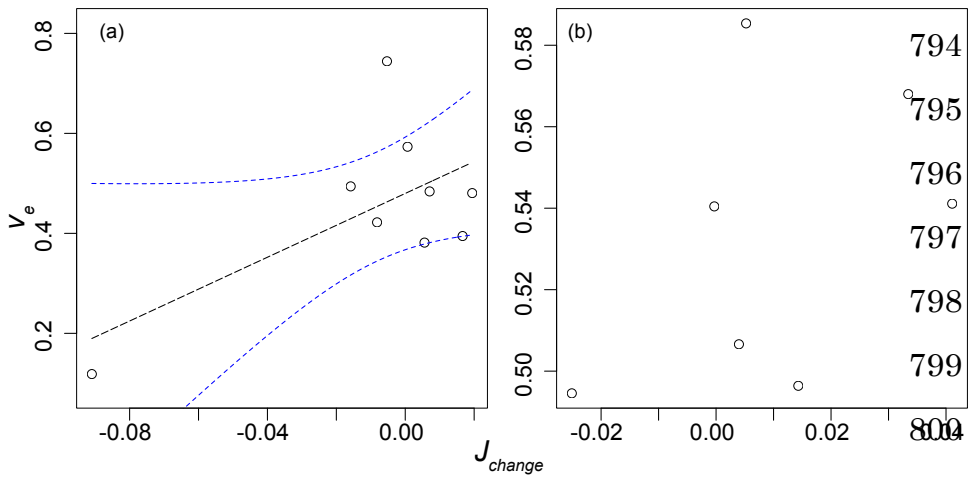

(a)
(b)
v_e
J_{change}
0.2
0.4
0.6
0.8
-0.08
-0.04
0.00
0.50
0.52
0.54
0.56
0.58
-0.02
0.00
0.02
0.04

Table 1 Statistical analyses of the relationships between the indices d_{MR}, d_M/d_R, d_E/d_S, v_e, and J_{change} and the temperature change rate across a decade for two different types of forest. The four indices are defined in the legend to Fig. 3. The analyses were performed using three models (null, simple regression, polynomial regression). *adj.* R^2, adjusted coefficient of determination. AIC, Akaike's information criterion. Fig. 3 presents plots of the trends analyzed in this table.

		Temperature change rate			Squared temperature change rate							
		Coefficient	*P*		Coefficient	*P*		*adj.* R^2	*P*		AIC	
(a) Deciduous broad-leaved forest												
d_{MR}	Null	–	–		–	–		–	–		–23.503	†
	Simple	–0.408	0.361		–	–		–0.006	0.361		–22.654	
	Polynomial	–0.620	0.344		–4.119	0.625		–0.124	0.598		–21.044	
d_M/d_R	Null	–	–		–	–		–	–		23.267	
	Simple	10.577	0.049	*	–	–		0.366	0.049	*	19.958	
	Polynomial	17.099	0.018	*	127.068	0.119		0.523	0.046	*	18.018	†
d_E/d_S	Null	–	–		–	–		–	–		23.990	†
	Simple	–2.601	0.685		–	–		–0.114	0.685		25.763	
	Polynomial	–8.456	0.351		–114.075	0.343		–0.105	0.570		26.302	

v_e	Null	–	–		–	–		–	–		–3.700	
	Simple	–1.461	0.270		–	–		0.052	0.270		–3.378	
	Polynomial	–3.513	0.036	*	–39.994	0.061	.	0.413	0.085	.	–7.083	†
J_{change}	Null	–	–		–	–		–	–		–32.832	
	Simple	–0.197	0.464		–	–		–0.053	0.464		–31.572	
	Polynomial	–0.729	0.010	*	–10.354	0.008	**	0.658	0.017	**	–41.082	†

(b) Evergreen broad–leaved forest

d_{MR}	Null	–	–		–	–		–	–		–23.200	†
	Simple	0.024	0.953		–	–		–0.199	0.953		–21.206	
	Polynomial	0.081	0.884		–3.666	0.855		–0.485	0.980		–19.272	
d_M/d_R	Null	–	–		–	–		–	–		8.171	
	Simple	5.717	0.079	.	–	–		0.391	0.079	.	5.419	†
	Polynomial	4.762	0.233		61.633	0.642		0.284	0.228		6.990	
d_E/d_S	Null	–	–		–	–		–	–		–2.211	

	Simple	2.902	0.053	.	–	–	0.472	0.053	.	–5.952	†
	Polynomial	2.529	0.171	.	24.065	0.683	0.370	0.177		–4.281	
v_e	Null	–	–		–	–	–	–		–23.911	
	Simple	0.612	0.056	.	–	–	0.462	0.056	.	–27.531	†
	Polynomial	0.536	0.175	.	4.918	0.697	0.356	0.184		–25.830	
J_{change}	Null	–	–		–	–	–	–		–30.588	
	Simple	0.352	0.087	.	–	–	0.369	0.087	.	–33.085	
	Polynomial	0.0500	0.050	.	–9.567	0.216	0.487	0.117		–34.104	†

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; '.,' $P < 0.1$

† The best of three models judged by the AIC

Appendices

Table S1 Data on the geography and climate of each plot and its nearest metrological station. See Fig. 2 for locations of plots in the Japanese archipelago.

Table S2 Indices calculated in this study

Table S3 Changes in the calculated individual-based temporal beta-diversity indices and the relative speed of compositional equilibrium in relation to temporal changes in annual precipitation.

Table S4 Results of simple linear regression analyses of the calculated indices on latitude, and the means and SDs of annual mean temperature and annual precipitation

Table S5 Results of simple linear regression analyses of other calculated indices, which were not included in the main analyses, on the change rates of annual mean temperature and annual precipitation

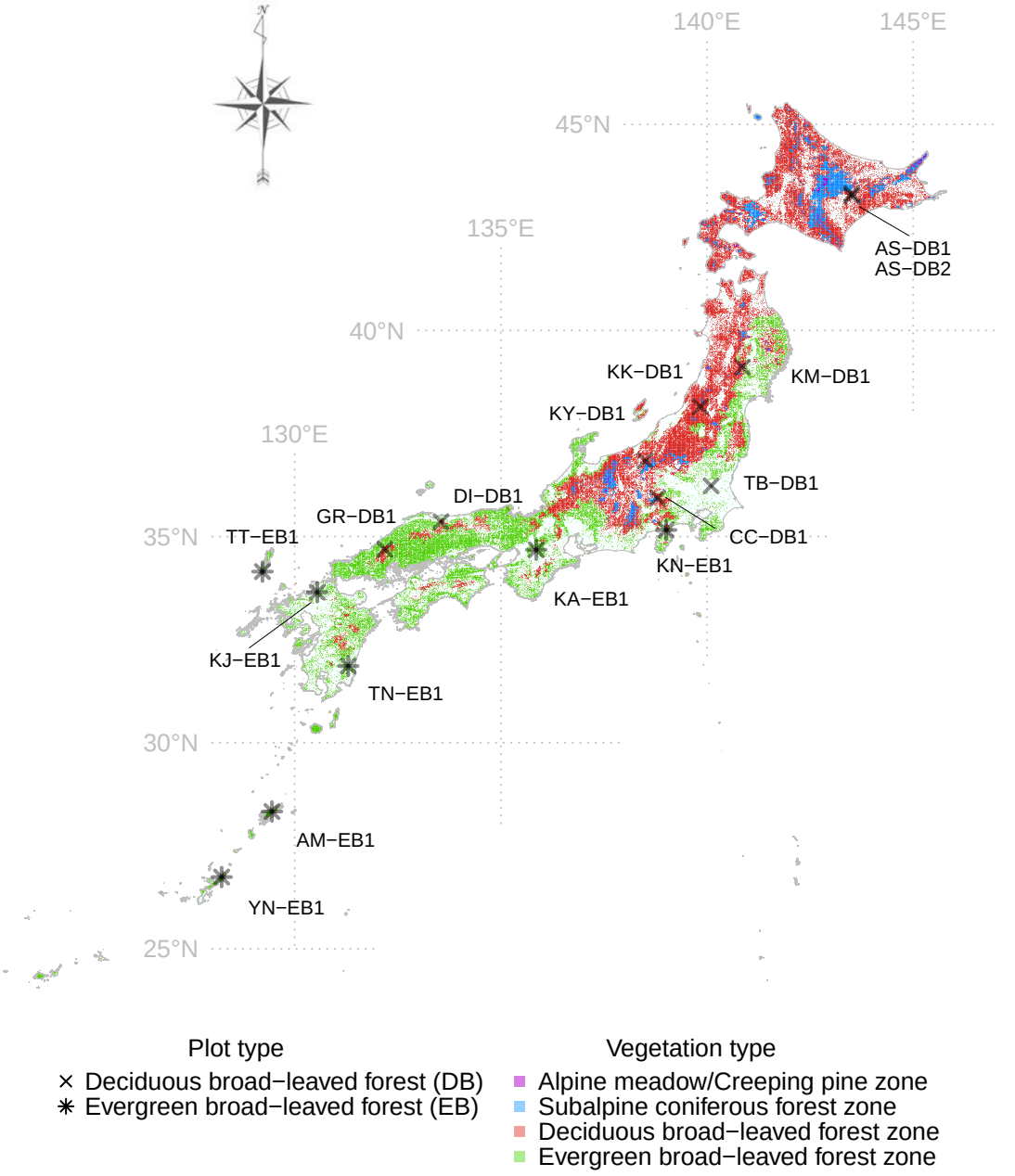
Table S6 Correlations among the geographical and environmental variables and their respective calculated indices.

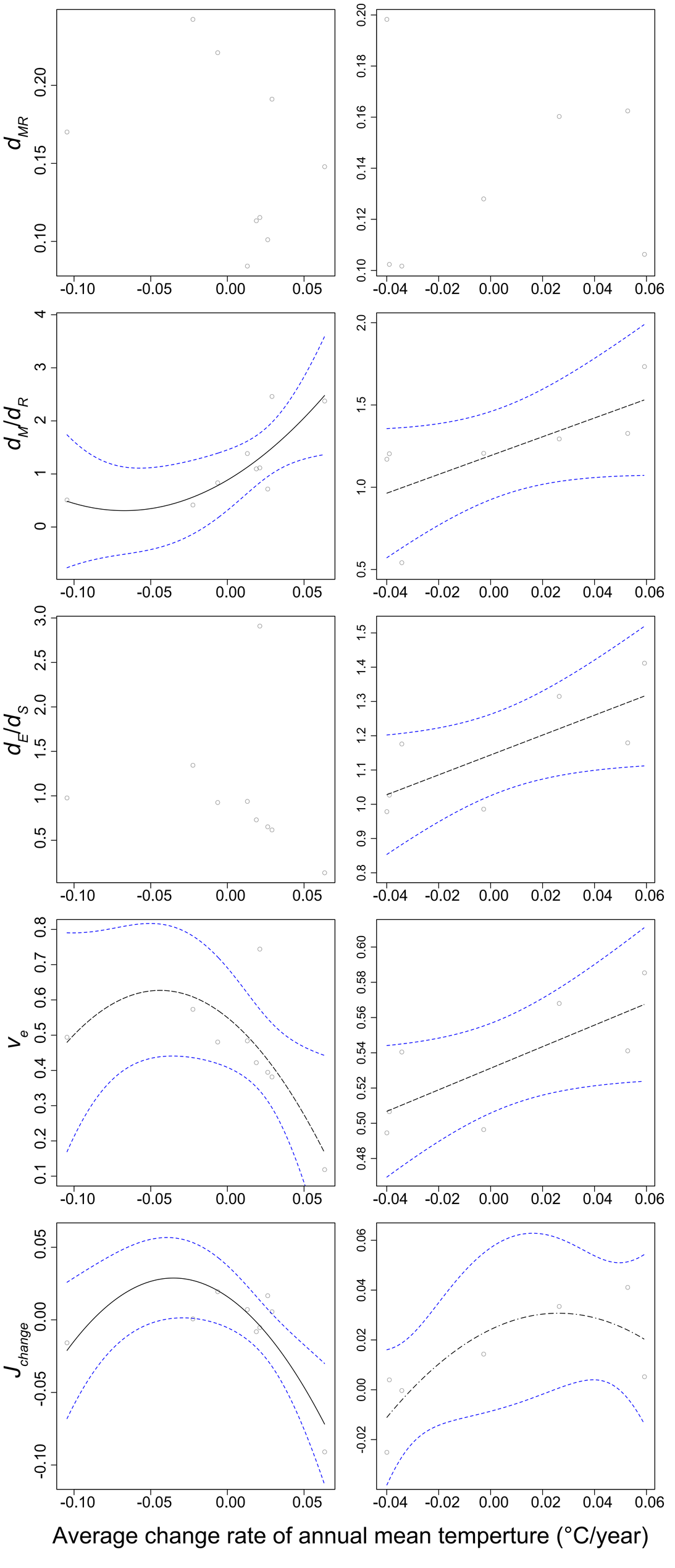
Figure S1 Annual mean temperature and annual precipitation in each year (2003–2018) at each site. The red circles and lines indicate the annual mean temperature; the blue bars indicate annual precipitation. The dashed line indicates the average annual mean temperature (1981–2010). The dot-dash line indicates the average of annual precipitation (1981–2010).

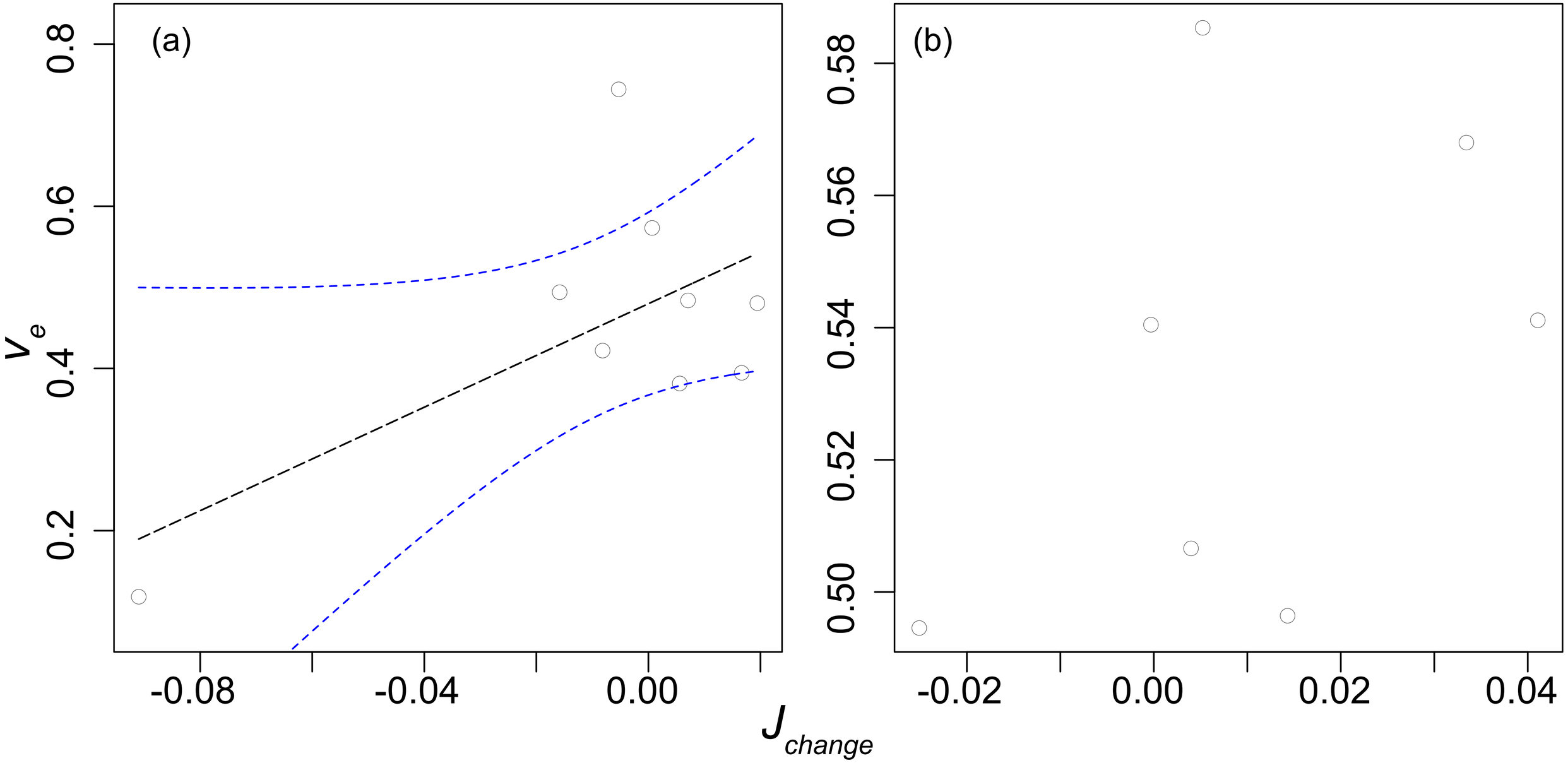
Supplementary text 1 Explanation of individual-based temporal beta-diversity in the Ružička dissimilarity index version

Supplementary file 1 R software script of individual-based temporal beta-diversity calculations using sample data

		T1	M	R	T2	P
sp.1	Z_1	1	0	0	1	1
	Z_2	1	0	0	1	1
	Z_3	1	1	0	0	0
	Z_4	0	0	1	1	0
	Z_5	0	0	1	1	0
sp.2	Z_6	1	0	0	1	1
	Z_7	1	0	0	1	1
	Z_8	1	1	0	0	0
	Z_9	1	1	0	0	0
	Z_{10}	1	1	0	0	0
sp.3	Z_{11}	1	1	0	0	0
	Z_{12}	1	1	0	0	0
	Z_{13}	0	0	1	1	0
	Z_{14}	0	0	1	1	0
	Z_{15}	0	0	1	1	0
sp.4	Z_{16}	1	1	0	0	0
	Z_{17}	1	1	0	0	0
	Z_{18}	1	1	0	0	0
	Z_{19}	1	0	0	1	1
	Z_{20}	0	0	1	1	0


140°E
145°E
45°N
135°E
40°N
130°E
35°N
30°N
25°N
AS−DB1
AS−DB2
KK−DB1
KM−DB1
KY−DB1
TB−DB1
DI−DB1
GR−DB1
TT−EB1
CC−DB1
KN−EB1
KA−EB1
KJ−EB1
TN−EB1
AM−EB1
YN−EB1
Plot type
× Deciduous broad−leaved forest (DB)
✳ Evergreen broad−leaved forest (EB)
Vegetation type
Alpine meadow/Creeping pine zone
Subalpine coniferous forest zone
Deciduous broad−leaved forest zone
Evergreen broad−leaved forest zone


d_{MR}
d_M/d_R
d_E/d_S
v_e
J_{change}
Average change rate of annual mean temperture (°C/year)


(a)
(b)
V_e
0.2
0.4
0.6
0.8
0.50
0.52
0.54
0.56
0.58
-0.08
-0.04
0.00
-0.02
0.00
0.02
0.04
J_{change}