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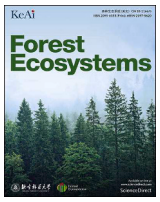

Original Article

Long-term monitoring reveals differential climate and disturbance responses in Japanese forest biome composition

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ABSTRACT

Tree community responses to climate change differ markedly among biomes, and multiple interacting drivers complicate interpretation. This study investigated structural and compositional changes across major forest biomes (boreal conifers, deciduous broadleaved trees, temperate conifers, and evergreen broadleaved trees) using extensive spatial and temporal forest community data. The analyzed dataset included 191 plots across Japan, spanning decades since the 1950s and encompassing old-growth and secondary forest age classes. For each plot, biome types were classified, and changes in tree communities were quantified. Forest structural shifts were evaluated using the total basal area of all trees, four tree functional types, and dominant species. Compositional shifts were assessed based on the relative dominance of each functional type. Associations between these changes and climatic conditions, climate change trends, and other potential forest disturbance drivers were analyzed. Results showed that forest structure and functional composition changed across all biomes, with structural change significantly linked to climatic trends. Distinct response patterns to climatic variables emerged depending on biome and forest age. In old-growth forests, structural change rates were positively associated with the mean annual temperature change and negatively associated with the annual precipitation change. Structural change declined notably in southwestern regions with increased annual precipitation, likely due to intensified typhoon disturbance. Boreal conifer functional types declined markedly in relative dominance in old-growth forests and were replaced by deciduous broadleaved trees. Additionally, evergreen broadleaved types increased in some deciduous broadleaved old-growth forests. Overall, these findings align with thermophilization and indicate a broader, ongoing biome shift.

1. Introduction

The impacts of global climate change are increasingly evident as measurable shifts in forest structure, composition, and function worldwide (Esquivel-Muelbert et al., 2019; Grimm et al., 2013; Johnstone et al., 2016; Seidl et al., 2017), driven by rising temperatures, altered precipitation patterns, and changing disturbance regimes. Identifying the drivers of these responses remains challenging, with prior studies highlighting intrinsic factors such as forest age, species composition, and diversity, along with environmental context, including ecoregions, climatic zones, and hydrological conditions (Chen and Luo, 2015; Chen et al., 2016; Coomes et al., 2014; Hellmann et al., 2016; Hisano et al., 2018; Sherriff et al., 2017).

Forest biomes are primarily defined by broad climatic conditions and ecosystem structure, reflecting large-scale vegetation patterns. Within biomes, ecosystem functional groups are hierarchically nested units that share ecological drivers and associated biotic traits (e.g., the IUCN Global Ecosystem Typology). In this framework, shifts in functional groups can indicate early climate responses, preceding biome-level changes via alterations in functional composition. Climate-driven changes in functional composition are widely documented, and substantial shifts in dominant functional types can alter forest ecosystem functioning at local and regional scales. At the local scale, such changes affect regeneration, productivity, and species interactions (Beckage et al., 2008; Evans and Brown, 2017; Searle and Chen, 2017). At the regional scale, their accumulation can drive transitions in forest biome distribution and structure (Beck et al., 2011; Grimm et al., 2013; Paquette and Messier, 2011; Reichstein et al., 2014).

Under global warming, functional composition is expected to shift toward warm-adapted types, increasing the dominance of species favoring higher temperatures, a process termed “thermophilization” (Duque et al., 2015). Although many studies have reported climate-driven changes in overall forest growth and functional composition (Beck et al., 2011; Hansen et al., 2001; McIntyre et al., 2015; Searle and Chen, 2017), most have focused on single biomes. Because the drivers of forest change vary widely among biomes and regions, cross-biome analyses of functional type responses and their interactions are required to develop a comprehensive understanding.

The Japanese archipelago, characterized by diverse forest biomes, provides an ideal setting to disentangle forest responses to climate and environmental drivers. Situated in monsoon Asia, it spans hemiboreal, cool-temperate, warm-temperate, and subtropical zones. Forest biomes, organized primarily along temperature gradients, are distinguished by dominant tree functional types (Aiba et al., 2016; Fukaya et al., 2020). Human disturbance has also created a mosaic of old-growth and secondary forests, with differing structures and climate sensitivities (Chen et al., 2016). Japan's climate shows long-term warming and declining snowfall, with no consistent annual precipitation trend (Japan Meteorological Agency, 2020). Concurrently, climate-related disturbances directly or indirectly affect forest communities (Aiba et al., 2016; Auffret and Thomas, 2019; Brice et al., 2019; Danneyrolles et al., 2019). For example, tropical typhoons strongly influence forest dynamics (Lin et al., 2020; Saito, 2002; Sato et al., 2017; Yoshida et al., 2011). Although total typhoon frequency may decline, intense events and associated rainfall are projected to increase with a warming climate (Seneviratne et al., 2021; Yamada et al., 2017). Indeed, typhoon-induced heavy rainfall has increased in recent decades in the southern coastal region of Japan (Utsumi and Kim, 2022). These interacting climatic and disturbance changes can substantially alter forest structure and composition.

Growing evidence indicates that forest structure and composition in Japan are changing, partly due to climate trends (Hiura et al., 2019; Koide et al., 2022; Nakashizuka et al., 2016; Shimazaki et al., 2011; Suzuki et al., 2015; Takahashi, 2018). For instance, Hiura et al. (2019) reported declines in evergreen conifer abundance and increased dominance of deciduous broadleaved trees in northern forests over the last four decades, consistent with patterns in other boreal and hemiboreal regions (Evans and Brown, 2017; Searle and Chen, 2017). Koide et al. (2022) identified nationwide shifts in functional types toward higher latitudes and elevations, with responses dependent on environmental and ecological contexts. Suzuki et al. (2015) analyzed data from 39 plots over 8 years and detected increases in evergreen species abundance and declines in deciduous species in moderately warm regions, as well as reductions in boreal tree abundance. These patterns suggest increasing dominance of warm-adapted species; however, prior studies remain limited in temporal, spatial, and functional coverage. Consequently, to establish a comprehensive understanding of forest community responses, an integrated approach is required, incorporating functional type classifications, cross-biome comparisons, long-term monitoring data, and disturbance factor analysis.

In this study, we investigated long-term changes in forest structure and composition across Japan and identified their drivers, focusing on functional types defining forest biomes. Using multidecadal forest plot data across Japan (Yoshikawa et al., 2024), we examined the associations of these changes with climatic conditions, temporal trends, and forest disturbance factors. We quantified temporal changes in total basal area, functional type basal area, and relative dominance, relating change rates to plot attributes and climate trends. We tested three

hypotheses for old-growth forests in Japan: (1) total basal area increases with rising temperature; (2) total basal area change rates are positively associated with increases in mean annual temperature and solar radiation owing to longer growing periods and greater light availability; (3) functional composition shifts toward warm-adapted types, consistent with thermophilization.

2. Materials and methods

2.1. Study region, biomes, tree functional types, and disturbance regimes

The Japanese archipelago spans latitudinal (20°25′ N to 45°33′ N) and elevational (0–3776 m a.s.l.) ranges, encompassing diverse climatic conditions and forest biomes (Fig. 1a). Forests cover 67% of Japan's land area, with natural forests comprising 27.5% (Ministry of Agriculture, Forestry and Fisheries). Forest biomes are primarily defined by dominant tree functional types (≥50% of abundance), namely boreal conifers (BC) in northern or alpine regions, deciduous broadleaved trees (DB) in cool-temperate areas, temperate conifers (TC) in temperate regions, and evergreen broadleaved trees (EB) in warm-temperate and subtropical regions (Kira, 1991; Numata et al., 1972; Ohsawa, 1996). Accordingly, all recorded tree species were classified into four functional types following Suzuki et al. (2015), namely bc, db, tc, and eb, with lowercase abbreviations used throughout. Representative species included *Abies mariesii*, *Abies sachalinensis*, and *Picea jezoensis* for bc; *Fagus crenata*, *Quercus crispula*, *Carpinus* spp., and *Acer* spp. for db; *Cryptomeria japonica*, *Chamaecyparis obtusa*, *Abies firma*, and *Pinus densiflora* for tc; and *Castanopsis sieboldii*, *Castanopsis cuspidata*, and *Quercus salicina* for eb. Although a few southern plots included tree-like bamboos and ferns, these were excluded owing to minimal abundance. Japanese nomenclature for the recorded species followed the BG plant database (Yonekura and Kajita, 2003).

Japanese forests experience multiple natural and anthropogenic disturbances. Tropical typhoons originating in the Pacific frequently damage forests during summer and autumn (Lin et al., 2011). Additionally, deer browsing and insect pest outbreaks have become major drivers of Japanese forest change (Nakajima and Ishida, 2014; Takatsuki, 2009). Although wildfire strongly affects forests in arid regions in Europe and North America, its impact in Japan is considered negligible.

2.2. Forest data collection

We collected repeated monitoring data on woody species (including lianas) from natural forests. Target data included (1) stem-level data representing girth at breast height (GBH) or diameter at breast height (DBH) for all stems above a fixed threshold, and (2) species-level data summarizing the basal area of all sufficiently large stems per species in each census year. Data were selected using the following criteria: plots located in natural or secondary forests without planted trees, monitored duration ≥ 5 years, plot area > 0.05 ha, and all stems with ≥ 5 cm DBH (≥15.70 cm GBH) measured. Exceptions included some BC plots near their southern range limit.

Much of the stem-level data were obtained from the Monitoring Site 1000 project (Ministry of the Environment, Japan; http://www.biodic.go.jp/moni1000/), a nationwide dataset (Yoshikawa et al., 2024), and additional local studies (Chubu Regional Forest Office, 2016; Enoki

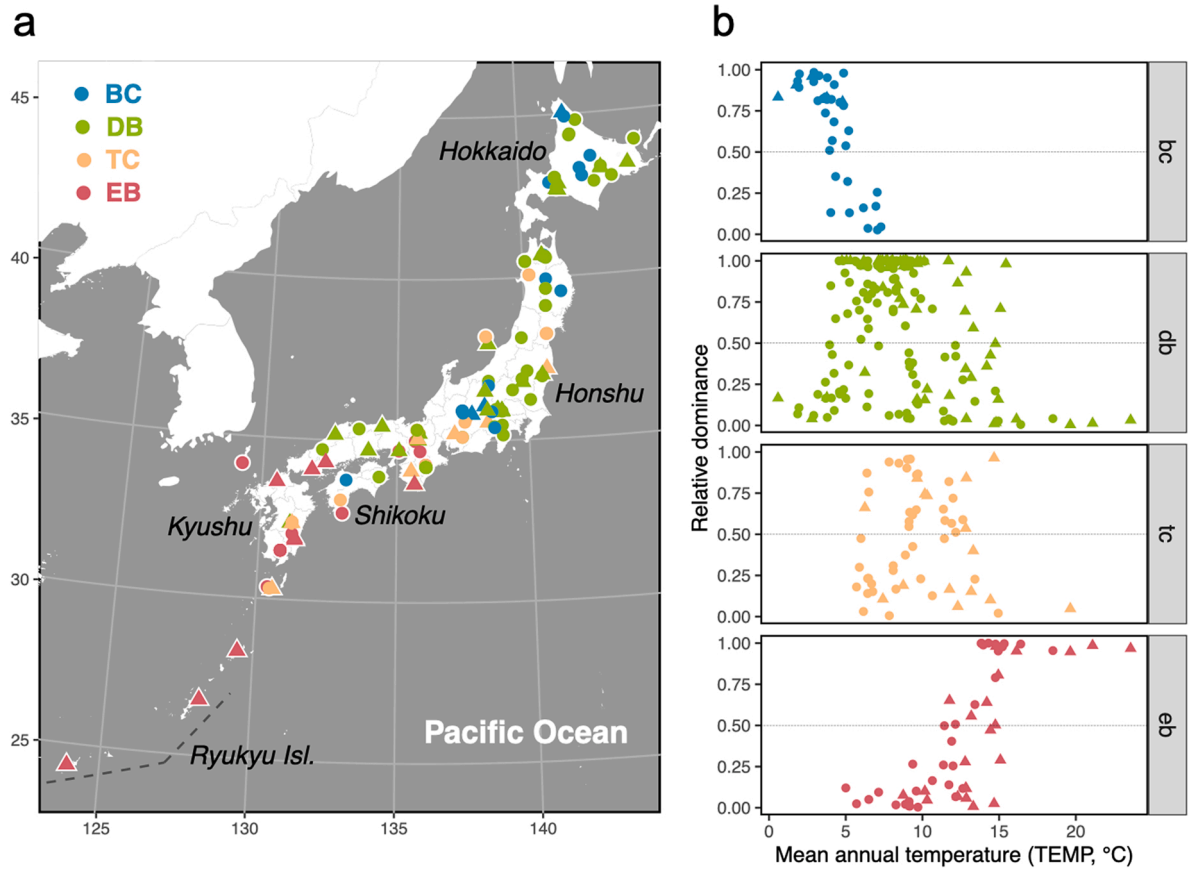

Fig. 1. **(a)** Spatial distribution of 191 forest plots across the Japanese archipelago. Plots were located on the four main islands (Hokkaido, Honshu, Shikoku, and Kyushu) and nearby islands, including the Ryukyus. Circles denote old-growth forests, and triangles denote secondary forests. Point colors indicate biome: blue, BC: boreal conifer; green, DB: deciduous broadleaved tree; orange, TC: temperate conifer; red, EB: evergreen broadleaved tree. **(b)** Relative dominance of the four functional types in each plot in relation to mean annual temperature. Functional types: bc: boreal conifer; db: deciduous broadleaved tree; tc: temperate conifer; eb: evergreen broadleaved tree. Dashed horizontal lines indicate 0.5 values of relative dominance.

et al., 2018; Igarashi et al., 2005, 2013; Itô, 2017; Nagamori et al., 1992; Ogawa et al., 2021; Saito et al., 2014; Takatoku et al., 2018; Teshio Experimental Forest, Hokkaido University, 2020a; Teshio Experimental Forest, Hokkaido University, 2020b). Some datasets included only stems with ≥ 10 cm DBH and were used exclusively for large-tree analyses. Species-level data were primarily extracted from published studies (Ando et al., 1998; Azuma et al., 2014; Enoki et al., 2017; Ishibashi et al., 2011; Iwaizumi et al., 2008; Kikuchi et al., 2009; Koganezawa et al., 2003; Kubota et al., 2007; Kyoto City, 2016; Matsumoto et al., 2012; Migita et al., 2012; Nagaike, 2017; Nagaike and Matsuzaki, 2010; Nakamori et al., 2009; Okano and Aragami, 1999; Sakaguchi et al., 2012; Sano et al., 2016; Sugita et al., 2008, 2010; Takahashi et al., 2003; Takyu et al., 2005; Teraoka et al., 1999; Wakamatsu et al., 2017; Yano et al., 2009), from which basal area values per species and census were extracted.

In total, data were compiled from 191 plots (Fig. 1a), ranging from 0.0325 to 6.25 ha (mean: 0.58 ha). Five plots (all in old-growth forests) included only trees with a DBH ≥ 10 cm and were analyzed solely for large-diameter trees. Dominant functional type per plot was defined by the greatest total basal area. Overall, 27, 108, 33, and 23 plots were dominated by BC, DB, TC, and EB, respectively, at their initial censuses. Mean monitoring duration was 16.8 years per plot (range: 5–50 years).

2.3. Plot attributes

We considered plot attributes related to forest age and disturbance history. Forest age is a key driver of forest dynamics and their response to environmental change. Forests were classified as old-growth (no major disturbances for ≥ 150 years before monitoring) or secondary (disturbed within the preceding 150 years, including clear-cutting, selective logging, or windthrow). Because these classes likely differ in climate responses, they were analyzed separately. Of the 191 plots, 126 were in old-growth forests, and 65 were in secondary forests.

Two natural disturbance types were evaluated as potential drivers of forest change: pest damage and deer browsing. For each plot, we recorded the presence or absence of tree damage or mortality caused by pine wilt disease and Japanese oak wilt disease, the major Japanese forest mortality drivers in recent decades (Fujihara, 1996; Nakajima and Ishida, 2014). Plots were also classified by deer impact based on evidence of browsing on understory vegetation, tree bark, or branches. Pest damage was recorded in 11 plots (pine wilt disease in 2 and Japanese oak wilt disease in 10), whereas deer damage was observed in 59 plots.

2.4. Compositional changes in functional type

First, we calculated the total basal areas for all trees and then the basal area for each functional type in each plot. We then calculated change rates between the first and last census as Eq. 1 following Condit et al. (1995):

$$\text{Total basal area change rate} = \frac{\ln \text{TBA}_{\text{all,last}} - \ln \text{TBA}_{\text{all,first}}}{t} \quad (1)$$

where $\text{TBA}_{\text{all, first}}$ and $\text{TBA}_{\text{all, last}}$ represent total basal areas at the initial and final censuses, respectively, and t is the time interval (years). We similarly calculated change rates for each functional type. To assess the patterns of change in large-diameter trees, we also calculated the annual change rate in total basal area for stems > 125.7 cm GBH (>40 cm DBH), using only plots with stem-level data.

Next, we calculated the relative dominance as the proportion of total basal area represented by each functional type at each census. The change rate in relative dominance for functional type "f1" ($\Delta\text{RD}_{\text{f1}}$) was calculated as Eq. 2 following Suzuki et al. (2015):

$$\text{Change rate in relative dominance of type f1} = \frac{\text{RD}_{\text{f1,last}} - \text{RD}_{\text{f1,first}}}{t} \quad (2)$$

where $\text{RD}_{\text{f1, first}}$ and $\text{RD}_{\text{f1, last}}$ denote relative dominance at the first and last censuses, respectively, and t is the interval in years. The analysis included plots where all stems with ≥ 15.7 cm GBH (5 cm DBH) were measured.

We also performed species-level analyses of basal area for dominant canopy species within each functional type. For each type, we selected up to two species with the greatest total basal area across plots and sufficient representation. Selected species included *A. sachalinensis* and *P. jezoensis* for bc, *F. crenata* and *Q. crispula* for db, and *C. japonica* and *A. firma* for tc. No suitable representative species were identified for eb; therefore, this type was excluded from analysis. Owing to the limited number of plots in secondary forests, species-level analysis was restricted to old-growth forests.

Before analysis, missing stem-level measurements were imputed conservatively. When both preceding and succeeding GBH values were available, missing values were estimated assuming constant growth. If only succeeding values existed, those values were used; if only preceding values existed, those values were retained. This approach minimized bias in estimating compositional change.

2.5. Climate and environmental variables

Climatic conditions for each plot were derived from the National Agriculture and Food Research Organization Agro-Meteorological Grid Square Data (Ohno et al., 2016), which provide daily data at a 1-km^2 resolution from 1980 onward. For a 1-km^2 grid cell containing a plot, we calculated 41-year means (1980–2020, fiscal-year based) for annual temperature (TEMP; °C), annual precipitation (PREC; mm), snow depth (SNOW; cm), and global solar radiation (RAD; MJ·m^{-2}). Mean annual temperature was adjusted for elevation differences between plot location and 1-km^2 grid center using a lapse rate of −0.6 °C per 100-m elevation.

We then calculated annual change rates for TEMP, PREC, SNOW, and RAD as regression slopes over time. Percentage change rates (%·year^{-1}) divided by 100 were used for PREC and RAD. Hereafter, these climatic trends are denoted υTEMP, υPREC, υSNOW, and υRAD for TEMP, PREC, SNOW, and RAD, respectively. Among the target 191 plots, the number of plots where monitoring started before 1980 is only 17 (8.8%). Although there was a temporal mismatch between forest monitoring periods and the period used to calculate climatic trends, its influence on the overall analysis was likely limited.

2.6. Statistical analysis

Annual change rates in total basal area, as well as in the basal area and relative dominance of each functional type, were analyzed separately for old-growth and secondary forests in relation to climatic and disturbance variables. To examine biome shift trajectories, dominance change rates were also compared among dominant functional types.

We used generalized least squares (GLS) models to evaluate drivers of annual change in total basal area and functional types, which enabled us to incorporate spatial autocorrelation among plots into the analysis. Explanatory variables included dominant functional type (treated as factors), initial total basal area (cm^2·ha^{-1}), 41-year climatic means (TEMP, PREC, SNOW, and RAD), their temporal trends (υTEMP, υPREC, υSNOW, and υRAD), and disturbance presence (deer- or pest-related damage; binary variables). Spatial autocorrelation among plots was modeled as an exponential decay function of geographic distance. Interactions among the explanatory variables were not incorporated into the models.

All possible model combinations were constructed, and the best models were selected using Akaike information criterion (AIC) via the MuMIn package in R. AIC is calculated as $-2\ln L + 2k$, where L denotes the maximum likelihood of the model and k number of free parameters. The model with the lowest AIC value was selected as the best model, and the models whose AIC values differed from that of the best model by less

than 2 (i.e., $\Delta AIC < 2$) were selected as second-best models. Prior to GLS analysis, correlations among explanatory variables were examined; although some pairs exceeded $r > 0.5$, selected models did not include strongly collinear variables. We assessed variance inflation factors (VIFs), which measure the severity of multicollinearity, and confirmed that all selected models had VIF < 10.

3. Results

3.1. Overview of plots and climatic conditions

Relative dominance of the four functional types varied with TEMP (Fig. 1b). The bc type dominated the coldest regions, db was widespread and dominant at intermediate temperatures, tc occurred under moderate temperature conditions, and eb was dominant in warmer areas. This trend was consistent across old-growth and secondary forests, although db showed higher relative dominance in warmer secondary forests than in old-growth forests.

Climatic conditions and their temporal trends varied widely among plots (Fig. S1). Over the 41-year period, the TEMP range was 0.6–23.6 °C, PREC was 825.9–4884.3 mm, SNOW was 0–152.0 cm, and RAD was 10.6–16.3 MJ·m^{-2}. Climatic trends over the 41 years also differed regionally (Fig. S1e–S1h). υTEMP was positive across all 191 plots (0.013–0.055 °C·year^{-1}) and generally higher in the archipelago's central regions (Fig. S1e). υPREC and υSNOW showed positive and negative values, ranging from −0.005 to 0.010 year^{-1} and from −0.52 to 0.68 cm·year^{-1}, respectively. PREC increased in some southern Pacific-facing areas but not on the Ryukyu Islands (Fig. S1b and S1f). υSNOW was greatest in northern Honshu, whereas RAD was generally higher in central Honshu and peaked near Mt. Fuji (the archipelago's highest mountain). υRAD was predominantly positive across the archipelago, except in parts of Hokkaido and near Mt. Fuji (Fig. S1h).

3.2. Annual change rate of total basal area

Annual change rates in total basal area ranged from −0.028 to 0.026 in old-growth forests and from −0.026 to 0.036 in secondary forests (Fig. S2). Mean change rate was significantly higher in secondary forests than in old-growth forests ($p < 0.01$). In the best GLS models, annual change rate in total basal area in old-growth forests was significantly positively associated with υTEMP (estimate: 0.526 ± 0.106; $p < 0.001$) and negatively associated with υPREC (estimate: -0.949 ± 0.244; $p < 0.001$; Fig. S3a and S3b and Table 1). In secondary forests, annual change rate was negatively associated with initial total basal area density (estimate: -0.0003 ± 0.00005; $p < 0.001$) and pine wilt disease (estimate: -0.035 ± 0.005; $p < 0.001$; Fig. S3c and Table 1), with both factors retained across selected models (Table S1).

No clear decline in the growth of large-diameter trees (DBH > 40 cm) was detected. Mean annual change in the basal area of these trees was significantly higher in secondary forests (0.038) than in old-growth forests (0.007; $p < 0.0001$), and both values were significantly greater than zero (*t*-test, $p < 0.0001$).

3.3. Change rates of basal area by functional type

In old-growth forests, annual change in basal area differed significantly among functional types (analysis of variance (ANOVA), $p = 0.032$; Fig. 2a). The bc type had the lowest mean value, significantly lower than that of tc (Bonferroni post-hoc test, $p = 0.019$). In secondary forests, annual change rate in basal area also differed significantly among functional types (ANOVA, $p = 0.007$; Fig. 2b), with tc and eb showing the lowest and highest mean values, respectively; significant differences were detected between db and tc, db and eb, and tc and eb (Bonferroni post-hoc test, all $p < 0.05$; Fig. 2b). However, these differences disappeared when pest-damaged plots were excluded ($p = 0.552$).

Best-fit models for basal area change rates in each functional type primarily included climate-trend variables, but model structure varied among functional types and forest ages (Table 2). Mean climate variables, initial total basal area, initial dominant functional type, and deer damage were not retained in the selected models for each forest class (Tables 2 and S2).

In old-growth forests, the bc change rate in basal area was best explained by υPREC, showing a significant negative association (estimate: -1.663 ± 0.761; $p < 0.05$; Table 2), consistent across other selected models (Table S2). Change rates of basal area for db and tc were positively associated with υTEMP (estimates: 0.435 ± 0.230 for db and 0.570 ± 0.369 for tc; Table 2). Change rates of basal area for eb were best modeled by significant positive associations with υTEMP (estimate: 1.160 ± 0.303) and υSNOW (estimate: 0.176 ± 0.063) as well as negative associations with υPREC (estimate: -0.768 ± 0.812) and υRAD (estimate: -0.513 ± 1.122; Table 2).

In secondary forests, change rates of basal areas for db, tc, and eb were all associated with υPREC or υRAD, although directions differed among functional types. The eb type showed a negative association with υPREC (estimate: -0.924 ± 1.241), whereas tc exhibited a positive association (estimate: 1.187 ± 1.216). Change rates of basal areas for db were negatively associated with υRAD (estimate: -0.331 ± 2.353), whereas those for tc and eb showed positive associations (estimate: 0.633 ± 2.719 and 6.718 ± 3.557, respectively). Pine wilt disease had a significant negative effect on the tc basal area change rate in secondary forests (estimate: -0.088 ± 0.005; Table 2).

3.4. Rates of change in the basal area for dominant species within each functional type

Species-level analyses in old-growth forests (Tables 3 and S3) showed patterns broadly consistent with those in functional type analyses (Table 2), particularly the dominant influence of climate-change-trend variables. However, these analyses also revealed notable interspecific differences in associated drivers. Among bc species, the annual change rate in basal area of *A. sachalinensis* was negatively associated with υPREC (estimate: -0.965 ± 2.393), consistent with functional type trends. It also showed a positive association with υTEMP (estimate: 1.081 ± 1.607) and a negative association with υRAD (estimate: -0.883 ± 3.485). In contrast, the bc species *P. jezoensis* exhibited positive associations between the annual change rate in basal area and both υPREC (estimate: 3.719 ± 3.002) and υRAD (estimate: 3.539 ± 3.568), as well as a negative association with υTEMP (estimate: -3.905 ± 1.901) in its best model.

For the annual change rate of total basal area, the two dominant db species, *F. crenata* and *Q. crispula*, both showed negative associations with υPREC (estimate: -0.842 ± 0.727 and -2.995 ± 3.167, respectively) in their best models. Similarly, negative associations with υPREC were detected in the best models of the tc species *C. japonica* and *A. firma*

Table 1
Results of generalized least squares (GLS) analyses of total basal area change in old-growth and secondary forests. The best model with the lowest AIC is presented.

	Constant	υTEMP	υPREC	υRAD	PWD	Initial total basal area density	AIC
Old-growth	-0.013 ± 0.004***	0.526 ± 0.106***	-0.949 ± 0.244***				−857.865
Secondary	0.019 ± 0.002***				-0.035 ± 0.005***	-0.0003 ± 0.00005***	−416.006

Note: υTEMP: annual temperature change rate; υPREC: annual precipitation change rate; υRAD: annual solar radiation change rate; PWD: pine wilt disease; AIC: Akaike information criterion. ***$p < 0.001$, *$0.001 \le p < 0.01$, and *$0.01 \le p < 0.05$.

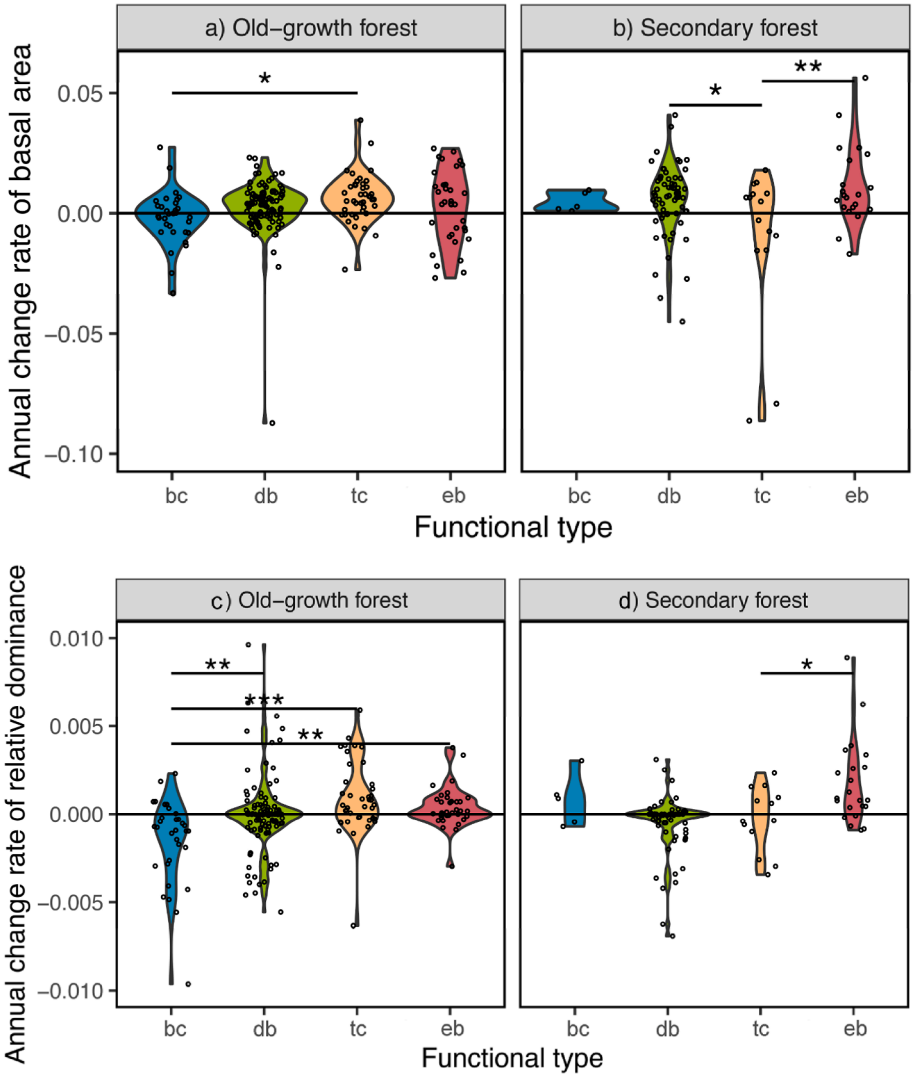

Fig. 2. Annual rate of change in basal area for four functional types in **(a, c)** old-growth and **(b, d)** secondary forests. Asterisks denote significant pairwise differences by pairwise *t*-test with Bonferroni correction: ***$p < 0.001$, *$0.001 \leq p < 0.01$, *$0.01 \leq p < 0.05$. Annual rate of change in relative dominance for the four functional types in old-growth forests and secondary forests. Asterisks indicate significant pairwise differences by pairwise *t*-test with Bonferroni correction: ***$p < 0.001$, *$0.001 \leq p < 0.01$, *$0.01 \leq p < 0.05$.

Table 2
Results of generalized least squares analyses of basal area change for each functional type in old-growth and secondary forests. The best model with the lowest AIC is presented.

Forest age	Functional type	Constant	υTEMP	υPREC	υSNOW	υRAD	Pine wilt disease	AIC
Old-growth	bc	−0.0001 ± 0.002		−1.663 ± 0.761*				−182.801
	db	−0.032 ± 2.841	0.435 ± 0.230					−668.008
	tc	−0.013 ± 0.013	0.570 ± 0.369					−243.104
	eb	−0.034 ± 0.012**	1.160 ± 0.303***	−0.768 ± 0.812	0.176 ± 0.063 **	−0.513 ± 1.122		−206.190
Secondary	db	0.004 ± 0.005				−0.331 ± 2.353		−348.073
	tc	−0.002 ± 0.006		1.187 ± 1.216		0.633 ± 2.719	−0.088 ± 0.005***	−72.703
	eb	0.002 ± 0.009		−0.924 ± 1.241		6.718 ± 3.557		−101.745

Note: Boreal conifer (bc) in secondary forests was excluded owing to small sample size. Asterisks indicate coefficient significance: ***$p < 0.001$, *$0.001 \leq p < 0.01$, and *$0.01 \leq p < 0.05$. υTEMP: annual temperature change rate; υPREC: annual precipitation change rate; υRAD: annual solar radiation change rate; AIC: Akaike information criterion.

(estimates: -3.924 ± 2.686 and -0.938 ± 0.857, respectively). Additionally, *A. firma* exhibited a significant positive association with υTEMP (estimate: 1.281 ± 0.501) and a significant negative association with υRAD (estimate: -9.856 ± 2.808) in the best-supported model.

3.5. Change rates in the relative dominance of each functional type

In both old-growth and secondary forests, mean dominance change rates differed significantly among the four functional types (one-way ANOVA, $p < 0.0001$; Fig. 2). In old-growth forests, bc showed the lowest mean change rate and was significantly below zero ($p < 0.002$), with significant differences relative to all other functional types (Bonferroni post-hoc test, all $p < 0.01$). In secondary forests, eb types exhibited the highest mean dominance change rate, significantly exceeding that of tc (Bonferroni post-hoc test, $p < 0.001$; Fig. 2d).

When stratified by biome and forest age, dominance change patterns varied markedly among the functional types (Fig. 3). In BC old-growth forests, bc declined sharply while db increased, with a significant difference detected (*t*-test, $p < 0.001$). In DB old-growth forests, no significant differences were detected among the functional types. In TC old-

Table 3
Results of generalized least squares analyses of annual basal area change rates for the dominant species of three functional types in old-growth forests. For each species, the best model with the lowest AIC is presented.

Functional type	Species	Constant	υTEMP	υPREC	υRAD	AIC
bc	*Abies sachalinensis*	−0.036 ± 0.056	1.081 ± 1.607	−0.965 ± 2.393	−0.883 ± 3.485	−60.776
	Picea jezoensis	0.116 ± 0.06	−3.905 ± 1.901*	3.719 ± 3.002	3.539 ± 3.568	−61.977
db	*Fagus crenata*	0.005 ± 0.002*		−0.842 ± 0.727		−227.881
	Quercus crispula	−0.011 ± 0.067	0.494 ± 1.928	−2.995 ± 3.167	−2.198 ± 3.157	−94.576
tc	*Cryptomeria japonica*	0.011 ± 0.012		−3.924 ± 2.686	5.027 ± 3.881	−71.457
	Abies firma	−0.023 ± 0.017	1.281 ± 0.501*	−0.938 ± 0.857	−9.856 ± 2.808***	−80.841

Note: Evergreen broadleaved (eb) species were excluded owing to limited data. Asterisks denote coefficient significance: ***$p < 0.001$, *$0.001 \leq p < 0.01$, *$0.01 \leq p < 0.05$. υTEMP: annual temperature change rate; υPREC: annual precipitation change rate; υRAD: annual solar radiation change rate; AIC: Akaike information criterion.

growth forests, dominance change rates differed significantly between db and tc ($p < 0.001$) and between tc and eb ($p = 0.024$). In DB and EB secondary forests, eb showed significantly higher dominance increases relative to db ($p = 0.003$ and $p = 0.008$, respectively).

Modeling of dominance change rates for functional types yielded null models for bc and tc in old-growth forests and db in secondary forests. Nevertheless, climate-change-trend variables were retained in several best models (Table 4). In old-growth forests, the db dominance change

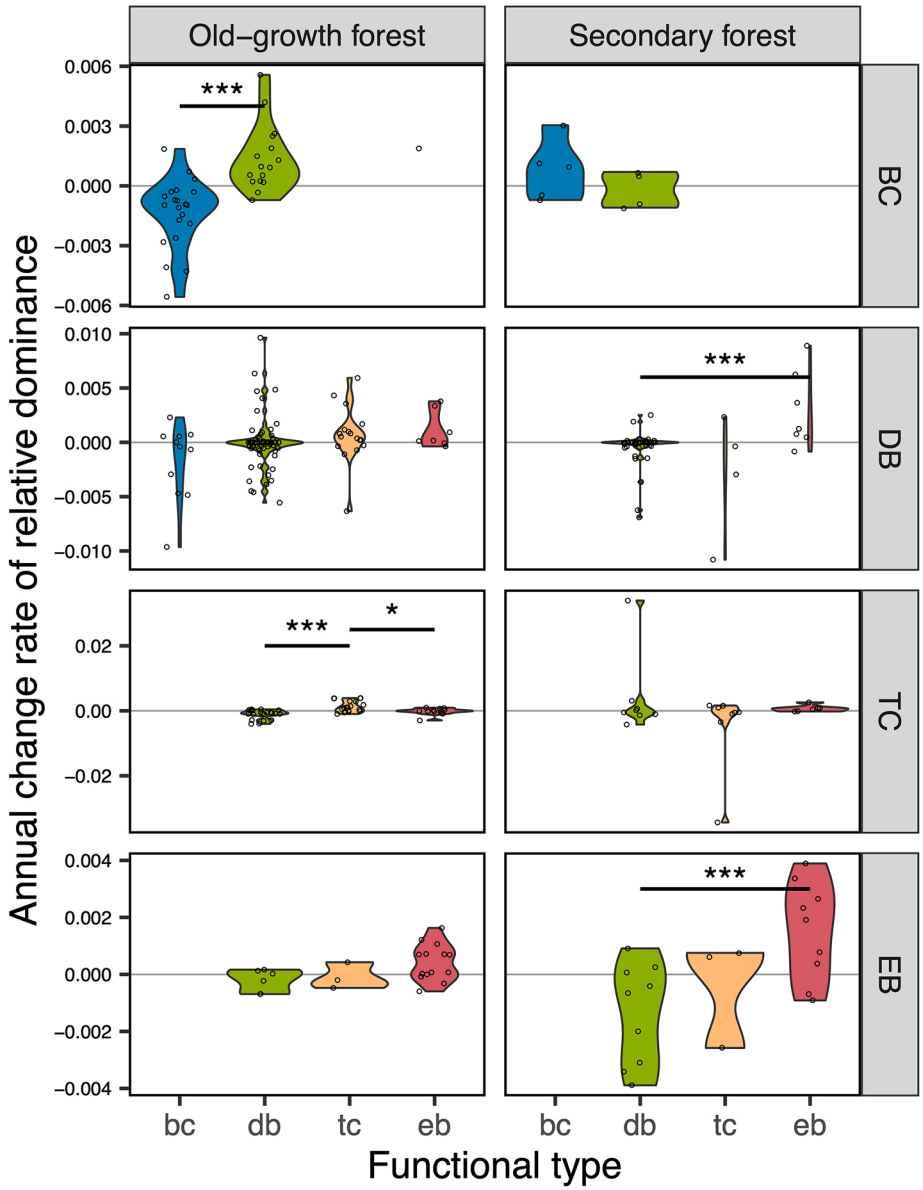

Fig. 3. Annual rate of change in relative dominance for four functional types, grouped by the dominant type in each plot. The left column shows old-growth forests, and the right column shows secondary forests. Rows correspond to plot biomes. Within each panel, differences among functional types are shown; asterisks indicate significant pairwise differences by pairwise *t*-test with Bonferroni correction: ***$p < 0.001$, *$0.001 \leq p < 0.01$, *$0.01 \leq p < 0.05$.

rate was significantly negatively associated with υPREC (estimate: -0.266 ± 0.090) and positively associated with υSNOW (estimate: 0.004 ± 0.001), and the eb dominance change rate was significantly negatively associated with υRAD (estimate: -0.267 ± 0.110). In secondary forests, the tc dominance change rate showed a significant negative association with pine wilt disease (estimate: -0.024 ± 0.004) and a positive association with υRAD (estimate: 1.636 ± 1.090), whereas the eb dominance change rate was significantly positively associated with υRAD (estimate: 1.066 ± 0.388; Table 4).

4. Discussion

4.1. Forest structural changes for all trees and each functional type

Our findings provide strong evidence of structural and compositional shifts in Japanese forests, particularly in old-growth forests, under climate change. These results corroborate and extend prior studies documenting tree community changes at both stand (Hiura et al., 2019; Nakashizuka et al., 2016; Shimazaki et al., 2011) and regional (Koide et al., 2022; Suzuki et al., 2015) scales, thereby providing a more integrated synthesis. Our first hypothesis, i.e., that total basal area would increase across the archipelago, was broadly supported in both old-growth and secondary forests. However, our second hypothesis, i.e., that annual change rates in total basal area would be positively associated with υTEMP and υRAD, was only partially supported. Instead, υPREC emerged as a key factor, showing a consistent negative association with the annual change rate in total basal area in old-growth forests.

In old-growth forests, total basal area increased across many plots during monitoring. Annual change rates were positively associated with υTEMP and negatively associated with υPREC in the best model (Table 1). The positive υTEMP relationship indicates enhanced tree growth driven by longer growing seasons, supporting our hypothesis. However, the negative υPREC association, not initially expected, is less straightforward. Declines in total basal area in old-growth forests were observed mainly in the southern Pacific regions (Shikoku and Kyushu; Fig. S1a), where υPREC was high (Fig. S1f). These areas coincide with frequent typhoon landfalls (Chi et al., 2015) and increasing heavy rainfall linked to typhoons (Utsumi and Kim, 2022). Utsumi and Kim (2022) evaluated recent increases of typhoon-induced heavy rainfall across Japan since 1961, and showed its remarkable increases in western and southern regions. This result supports the hypothesis that intensified typhoon disturbance in recent years, reflected in high υPREC, is responsible for the reduced basal area, at least in the western and southern regions. Supporting this interpretation, previous studies (Takyu et al., 2005) reported the negative impact of typhoon disturbance on forest growth during their monitoring periods. An alternative explanation is that increased precipitation reduced solar radiation and limited tree growth; however, this is unlikely, as υRAD was generally positive in regions with positive υPREC (Figs. S1f and S3h) and was not retained in the best GLS model (Table 1). Typhoons can damage forests both physically by wind and physiologically by heavy rainfall stresses (Lin et al., 2011). Future studies evaluating the effects of typhoon damage on forest communities need to disentangle complex mechanical processes of the damage.

In tropical and other forests, declines in the abundance of large-diameter trees and their carbon storage have been reported (Lindenmayer et al., 2012). Concern is particularly strong for old-growth forests, where declines are partly attributed to natural disturbances, such as drought and wildfires. However, in our target old-growth forests, clear declines in the growth of large-diameter trees with stems > 125.7 cm GBH were not detected (Fig. S1). Prior studies indicate that severe drought poses a major threat to large trees (Lindenmayer et al., 2012), but such stressors are currently uncommon on the Japanese archipelago, where precipitation levels are relatively high. Nevertheless, other disturbances, such as intensified typhoon damage or pest outbreaks, could still drive dieback of large-diameter trees. This possibility should be considered in future monitoring efforts.

At the level of functional type, the mean change rate in basal area did not differ from zero and, in old-growth forests, showed minimal variation among the four functional types (Fig. 2a). This indicates that many plots remained relatively stable overall. However, our GLS analysis revealed that climate change trends, including υPREC, υTEMP, and υRAD, were associated with the change rate in basal area for multiple functional types in old-growth and secondary forests (Table 2). Positive associations between the change rate in basal area and υTEMP were detected for db, tc, and eb in old-growth forests, suggesting increased growth due to longer growing seasons. Negative associations between the change rate in basal area and υPREC were identified for bc and eb in old-growth forests and for eb in secondary forests (Table 2). The trend for eb in old-growth forests may reflect typhoon impacts in southern Japan, whereas the negative association observed for bc may reflect complex mechanisms. One possible hypothesis is that elevated υPREC can be associated with changes in snow deposition, soil thermal regimes, and subsequent spring phenology, thereby resulting in bc decline in northern regions. Snow deposition and melt-timing are critical for maintaining hemiboreal conifers in Japan (Daimaru and Taoda, 2004; Hiura et al., 2019; Nakashizuka et al., 2016; Sugita, 1992). Some conifers are vulnerable to drought induced by early snowmelt (Hiura et al., 2019; Hu et al., 2010). Because these factors are complexly interlinked, and the number of plots is limited in this study, further detailed studies are needed to forecast future changes in bc tree communities.

The species-level analysis (Table 3 and S3) broadly supported the functional type analysis. Trends in the change rate in basal area for dominant species generally aligned with those of their respective functional types. Negative associations with υPREC were identified for five of the six primary species, further supporting the influence of typhoon disturbance on temperate species or altered snow dynamics on boreal species. Positive associations with υRAD were found for two species (*P. jezoensis*, bc; *C. japonica*, tc), whereas negative associations were detected for three species (*A. sachalinensis*, bc; *Q. crispula*, db; *A. firma*, tc). Positive associations with υRAD likely reflect enhanced growth under increased light availability. Negative associations with υRAD may

Table 4
Results of generalized least squares analyses of changes in relative dominance for each functional type in old-growth and secondary forests. For each functional type, the best model with the lowest AIC is presented.

Forest age	Functional type	Constant	υTEMP	υPREC	υSNOW	υRAD	Pine wilt disease	AIC
Old-growth	bc	-0.001 ± 0.0004**						−274.389
	db	0.0001 ± 0.0003		-0.266 ± 0.090**	0.004 ± 0.001***			−994.811
	tc	0.001 ± 0.0003**						−369.842
	eb	0.001 ± 0.0002**				-0.267 ± 0.110*		−355.606
Secondary	db	-0.0003 ± 0.001						−544.984
	tc	-0.003 ± 0.002				1.636 ± 1.090	-0.024 ± 0.004***	−90.091
	eb	-0.0005 ± 0.001				1.066 ± 0.388**		−188.084

Note: Boreal conifer (bc) in secondary forests was excluded owing to small sample size. Asterisks indicate coefficient significance: ***$p < 0.001$, *$0.001 \leq p < 0.01$, and *$0.01 \leq p < 0.05$. υTEMP: annual temperature change rate; υPREC: annual precipitation change rate; υRAD: annual solar radiation change; AIC: Akaike information criterion.

relate to changes in snow deposition or melt patterns, particularly for bc tree species, such as *A. sachalinensis*. Because the number of plots was limited in the species-level analysis, more detailed demographic studies are needed to clarify species-specific responses.

4.2. Compositional changes in old-growth forests

Our third hypothesis, i.e., that the relative dominance of warm-adapted functional types would increase within plots (the thermophilization scenario), was supported, particularly for bc and db in old-growth forests. Compositional shifts of tree species or types can be driven by climate change as well as by other processes, including succession and natural disturbance (Ruiz-Benito et al., 2017; Suzuki et al., 2015; Thom et al., 2017). In Japanese forests, pioneer trees include several db species and one tc species, whereas late-successional species occur across all functional types (Aiba et al., 2001; Kamijo et al., 2002; Ozaki and Ohsawa, 1995). Thus, in secondary forests, replacement of db or tc trees by evergreen types likely reflects succession. In contrast, in old-growth forests, where successional influence on composition is limited, observed compositional shifts can be more directly attributed to climate change.

In old-growth forests, we observed clear differences in dominance change among the four functional types (Fig. 2c) and detected pronounced compositional shifts, particularly in BC forests (Fig. 3). Functional type bc showed consistently negative dominance change in both BC and DB old-growth forests (Fig. 3). In BC forests, db exhibited substantially greater dominance increases relative to bc. Because bc is typically dominant in late-successional stages, these shifts cannot be explained by standard succession. This pattern provides strong evidence that cold-adapted functional types are declining and being replaced by warm-adapted types. Accordingly, our results demonstrate thermophilization (Bertrand et al., 2011; Fadrique et al., 2018) of forest communities in Japan at the tree functional type–level.

In old-growth forests, the mean change rate in basal area for bc did not differ significantly from zero (*t*-test, $p = 0.342$), suggesting no widespread dieback in this group. Instead, increased growth and recruitment of db trees likely contributed to the observed decline in bc dominance. These patterns of decreasing bc and increasing db dominance align with previous studies in northern Japan (Hiura et al., 2019; Shimazaki et al., 2011) and in boreal and hemiboreal regions of North America and Europe (Beckage et al., 2008; Searle and Chen, 2017). Although Suzuki et al. (2015) also reported declining bc dominance, their plot coverage was limited. Hiura et al. (2019) and Nakashizuka et al. (2016) suggested that altered snow deposition and melt patterns have driven bc declines in northern Japan. More broadly, rapid shifts at boreal–temperate ecotones raise concerns that ecoregional change could destabilize forest structure and ecosystem functioning (Evans and Brown, 2017).

In DB old-growth forests, eb increased in relative dominance in some plots (Fig. 3), consistent with greater abundance of warm-adapted types. In TC and EB old-growth forests, tc and eb, respectively, also increased in dominance within plots (Fig. 3). These patterns may partly reflect succession, as tc and eb include shade-tolerant, late-successional species (Kamijo et al., 2002). However, they may also indicate climate-driven responses, as warming has been linked to enhanced growth of the dominant tc and eb species in mixed old-growth forests (Takahashi and Okuhara, 2012). Regardless of mechanism, reinforcement of dominant functional types indicates the persistence of these biomes, at least in the near term.

4.3. Difference in forest changes between old-growth and secondary forests

This study showed that forest structural and compositional responses to climate change differ between old-growth and secondary forests (Tables 1 and 2), consistent with prior findings on forest age effects (Chen et al., 2016). Although secondary forests were at least 40 years old, their annual change rate in total basal area differed markedly from that of old-growth forests (Fig. S2). Our models did not detect significant climatic associations with annual changes in total basal area in secondary forests; instead, initial basal area and pest damage were key predictors (Table 1 and Fig. S3c). This likely reflects the stronger influence of growth dynamics and succession, which can obscure associations among forest structural changes and climate trends in secondary forests. Nevertheless, models for secondary forests identified some climatic associations with functional type changes. For instance, negative associations between υPREC and the change rate in basal area were found for eb, whereas tc showed a positive association (Table 2). The negative relationship may indicate increased damage from typhoon-related disturbances. The dominance change rates of tc and eb were also positively associated with υRAD (Table 4), potentially reflecting enhanced growth under increased light availability. Although causal mechanisms remain uncertain, these findings suggest that climate change can alter successional trajectories and thereby exert long-term effects on forest structure, composition, and function. Such interactions between climate change and succession remain poorly understood and warrant further investigation (Thom et al., 2017).

4.4. Impacts of disturbances related to climate change

The Japanese archipelago is among the regions most frequently affected by tropical cyclones (Lin et al., 2020). Typhoon-induced windthrow can produce both short- and long-term effects on tree mortality in subtropical Asia (Lin et al., 2011) and northeastern Asia (Miura et al., 2001; Sato et al., 2017; Yamada et al., 2011; Yoshida et al., 2011). Such disturbances strongly influence forest dynamics in Japan, especially in southwestern regions (Miura et al., 2001; Yamada et al., 2011). As discussed earlier, declines in total basal area (Fig. S2) and in some functional types in southwestern areas are likely attributable to increases in typhoon intensity. Although the observed declines may partly reflect short-term disturbance effects, similar reductions in total basal area are expected to persist and expand geographically, given projections of more intense typhoons in East Asia and poleward shifts in their storm tracks (Seneviratne et al., 2021). Typhoons affect forest dynamics not only through windthrow (Sato et al., 2017) but also via heavy rainfall and associated soil disturbance (Morimoto et al., 2021), both of which cause substantial damage. Moreover, the synergistic effects of typhoon disturbance and climate change may further intensify ecosystem impacts. Accordingly, understanding typhoon-driven disturbance and its consequences for forest structure and function should be a priority for future monitoring and management (Morimoto et al., 2021).

We also evaluated pest damage and deer browsing as additional disturbance drivers of forest structural and compositional change. Pest damage, particularly from pine wilt disease, exerted strong effects in several secondary forests. In these plots, total basal area and that of tc declined markedly, largely due to damage to Japanese red pine (*P. densiflora*). Although oak wilt disease effects were not detected in our analysis (Tables 1 and 2), its ongoing spread in eastern Honshu (Nakajima and Ishida, 2014) may cause future declines in *Quercus* spp., key db species in temperate forests. As such, pest-related damage is expected to intensify under climate change, and its role in accelerating forest change is a growing concern (Ikegami and Jenkins, 2018).

In contrast, we detected no clear negative effects of deer browsing on the annual change rate in total basal area or dominance changes in functional types. Deer browsing is widely recognized as a major threat to forest biodiversity in Japan, where deer populations are increasing (Takatsuki, 2009). One explanation for this apparent lack of effect is that deer primarily consume shrubs and juvenile trees, which were not included in the tree census data. Another possibility is that browsing occurred before monitoring began, leading to underestimation of its effects. Over longer timescales, deer browsing may still drive structural

changes, including biotic homogenization of plant communities, underscoring the need for continued monitoring in forest management.

4.5. Limitations of the analysis and prospects for future studies

To date, our analysis is the most comprehensive assessment of forest structural changes in the Japanese archipelago, but various limitations are present in it. First, there are some regions or biomes with a few representative plots in this study, such as boreal coniferous forests in northern or high-elevation regions and subtropical forests in southern Ryukyu Islands (Fig. 1). Results for these regions and biomes need to be interpreted carefully due to small sample sizes. Second, our analysis is not able to detect impacts of climatic extremes on forest dynamics. Future studies with forest and climatic data of high spatial and temporal resolutions need to be performed to evaluate the impacts of climate extremes. Similarly, incorporating complex interactions among various climate variables and disturbances into the analysis can be critical to forecast future forest dynamics. However, estimating such interactions remains a major challenge in forest ecology. Thirdly, plot size variation among the target plots may have affected the estimates of total basal area changes. Estimates from smaller plots may be more sensitive to local environmental conditions and demographic events, whereas estimates from larger plots may average over greater environmental heterogeneity. Although this plot size effect could be moderate because our target plots were not isolated forests, future studies based on more standardized monitoring are needed.

5. Conclusions

We demonstrated that forest structure and composition in Japan have changed over recent decades, with patterns differing among biomes, regions, and forest age classes, as revealed by a functional type-based approach. Some old-growth forests exhibited marked declines in total basal area, likely driven by intensified typhoon disturbance, especially in southwestern regions of the archipelago. We also showed ongoing compositional shifts in tree functional types, particularly in northern old-growth forests, where boreal conifers are being replaced by deciduous broadleaved trees. This transition reflects thermophilization, consistent with patterns reported in other boreal and hemiboreal regions (Evans and Brown, 2017; Searle and Chen, 2017). There is growing concern that climate change, altered disturbance regimes, and other anthropogenic pressures (e.g., land-use change) will interact to produce synergetic negative effects on forest ecosystems and their functioning (Johnstone et al., 2016). Additional disturbances, including pest outbreaks and deer overbrowsing, may further reduce forest resilience under these changing conditions (Jactel et al., 2019; Seidl et al., 2017). These challenges highlight the need for adaptive forest management strategies that consider multiple interacting drivers and enhance ecosystem resilience under ongoing environmental change.

CRediT authorship contribution statement

Tetsuro Yoshikawa: Writing – original draft, Visualization, Validation, Project administration, Formal analysis, Data curation, Conceptualization. **Yayoi Takeuchi:** Writing – review & editing, Data curation, Conceptualization, Funding acquisition, Project administration. **Taku Kadoya:** Writing – review & editing, Project administration, Funding acquisition, Data curation, Conceptualization. **Tsutomu Enoki:** Writing – review & editing, Investigation, Data curation. **Sakae Fujii:** Writing – review & editing, Investigation, Data curation. **Atsuko S. Fukamachi:** Writing – review & editing, Investigation, Data curation. **Mitsuru Hirota:** Writing – review & editing, Investigation, Data curation. **Kazuhiko Hoshizaki:** Writing – review & editing, Investigation, Data curation. **Naoki Iiyama:** Writing – review & editing, Investigation, Data curation. **Yukio Ishikawa:** Writing – review & editing, Investigation, Data curation. **Hiroki Itô:** Writing – review & editing, Investigation, Data curation. **Hajime Kobayashi:** Writing – review & editing, Investigation, Data curation. **Yasuo Konno:** Writing – review & editing, Investigation, Data curation. **Hiroko Kurokawa:** Writing – review & editing, Investigation, Data curation. **Akifumi Makita:** Writing – review & editing, Investigation, Data curation. **Akira S. Mori:** Writing – review & editing, Investigation, Data curation. **Dai Nagamatsu:** Writing – review & editing, Investigation, Data curation. **Tohru Nakashizuka:** Writing – review & editing, Investigation, Data curation. **Kanji Namikawa:** Writing – review & editing, Investigation, Data curation. **Mahoko Noguchi:** Writing – review & editing, Investigation, Data curation. **Michio Oguro:** Writing – review & editing, Investigation, Data curation. **Yoshinobu Ozaki:** Writing – review & editing, Investigation, Data curation. **Michinori Sakimoto:** Writing – review & editing, Investigation, Data curation. **Tamotsu Sato:** Writing – review & editing, Investigation, Data curation. **Hisashi Sugita:** Writing – review & editing, Investigation, Data curation. **Jun-Ichirou Suzuki:** Writing – review & editing, Investigation, Data curation. **Ryo O. Suzuki:** Writing – review & editing, Investigation, Data curation. **Satoshi N. Suzuki:** Writing – review & editing, Investigation, Data curation. **Koichi Takahashi:** Writing – review & editing, Investigation, Data curation. **Ryunosuke Tateno:** Writing – review & editing, Investigation, Data curation. **Ryuichi Watanabe:** Writing – review & editing, Investigation, Data curation. **Hiromi Yamagawa:** Writing – review & editing, Investigation, Data curation. **Tamon Yamashita:** Writing – review & editing, Investigation, Data curation. **Tomohiro Yoshida:** Writing – review & editing, Investigation, Data curation. **Masae I. Ishihara:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Tanaka Kenta:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Masahiro Nakamura:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Tsutom Hiura:** Writing – review & editing, Investigation, Data curation, Funding acquisition, Conceptualization.

Data availability

Data will be made available on request.

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Conflict of interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2026.100531.

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