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Stand development and soil C and N accumulation along a chronosequence of Japanese oak (*Quercus crispula*) plantations in eastern Hokkaido, Japan

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Introduction: *Quercus crispula* is a valuable and widely utilized tree species in Japan, yet standardized management practices for its plantations remain undeveloped, and no comprehensive study has examined the entire process from planting to harvesting. Although monoculture plantations may contribute to carbon sequestration, soil carbon dynamics under such systems are poorly understood. To address these gaps, we investigated stand development and soil properties using a chronosequence approach in the Ashoro Research Forest, Kyushu University, where *Q. crispula* has been planted annually for 50 years.

Methods: Seven stands aged 8 to 48 years (established in 2014, 2003, 1996, 1991, 1987, 1980, and 1974) were sampled, with one plot per stand. We assessed stand structure through the relationship between mean stem diameter and stem density, and measured soil carbon and nitrogen contents. To evaluate the validity of chronosequence sampling, we compared current data with a regression model derived from 38 sites sampled 12 years earlier and a subset of six sites from that dataset.

Results: Aboveground biomass increased linearly with stand age and exceeded the predicted values. However, structural development appeared slower than expected when assessed by stem diameter–density relationships, likely due to the absence of thinning. Soil carbon and nitrogen concentrations showed little variation with stand age. However, leaf carbon and nitrogen concentrations and fine soil content differed from earlier measurements and model predictions.

Discussion: These findings indicate that chronosequence studies, when combined with repeated sampling, can provide valid predictions of aboveground biomass and structural development in *Q. crispula* plantations. However, discrepancy between predictions derived from chronosequence approaches and the observed changes in leaf traits and soil properties suggests that environmental changes during the observation period can obscure age-related trends inferred from chronosequences.

KEYWORDS

carbon sequestration, chronosequential test, nitrogen, thinning, tree biomass, understory

1 Introduction

Interactions between carbon and nitrogen cycles in terrestrial ecosystems are fundamental to regulating global climate change (Zaehule, 2013). Understanding these dynamics during forest stand development is essential for quantifying the role of secondary forests in the terrestrial carbon cycle and for elucidating long-term carbon–nitrogen interactions (Yang et al., 2011). These interactions significantly influence the persistence of terrestrial carbon sinks, such as secondary forests and plantations (Luo et al., 2006; Reich et al., 2006), with nitrogen dynamics acting as key regulators of long-term carbon sequestration (Johnson, 2006; Rastetter et al., 1997).

Although vegetation is widely recognized as a carbon sink during stand development (Silver et al., 2000; Yang et al., 2011), the dynamics of soil carbon in secondary forests remain poorly understood (Yanai et al., 2003). Soils are the largest terrestrial reservoirs of organic carbon and nitrogen (Dixon et al., 1994; Yang et al., 2007), playing a central role in global carbon cycling (Lal, 2004) and influencing ecosystem productivity through carbon–nitrogen interactions (Reich et al., 2006). The carbon-to-nitrogen (C/N) ratio is a sensitive indicator of soil quality and biogeochemical processes (Zhang et al., 2016), and both soil carbon and nitrogen are widely used to assess forest ecosystem functions (Dong et al., 2021; Gong et al., 2022).

Oak species are dominant components of temperate, subtropical, and Mediterranean forests, exhibiting ecological diversity and adaptability (Johnson et al., 2009; Nixon, 2006). Their drought tolerance (Hu et al., 2013; Du et al., 2024; Zhang et al., 2021) and nitrogen-use efficiency (Maeda et al., 2018; Tang et al., 2023) support their resilience across diverse environments. However, natural regeneration of oaks is often constrained by biotic and abiotic factors (Modrow et al., 2020) including competition from understory vegetation (Barrio-Anta and Álvarez-González, 2005; Dobrowolska, 2008).

In Japan, *Quercus crispula* (Japanese oak) is a representative species in cool-temperate forests. Despite its high economic value, regeneration is often hindered by dwarf bamboo (Noguchi and Yoshida, 2004). Regeneration typically occurs following severe disturbances, with small canopy opening facilitating oak regeneration, whereas large openings tended to promote the dominance of dwarf bamboo (Altman et al., 2016). Soil scarification has been applied in Hokkaido, northern Japan, to improve regeneration success (Yoshida et al., 2005), although this silvicultural technique remains under refinement, with particular attention given to preventing the dominance of fast-growing species (Aoyama et al., 2011; Asada et al., 2017; Haratani and Yoshida, 2024). To date, no comprehensive study has investigated the entire process from planting to harvesting in *Q. crispula* afforestation.

The chronosequence approach is a useful method for revealing forest dynamics over time (Genet et al., 2009). In the Ashoro Research Forest of Kyushu University, located in eastern Hokkaido, *Q. crispula* has been planted annually since 1972 to establish a normal forest composed of stands ranging from 1 to 150 years old (Imada, 1996). This study provides a unique opportunity to evaluate long-term stand development and soil properties. Previous research described temporal patterns of stand development and soil carbon and nitrogen accumulation in plantations (Ohtsu et al., 2015), and although monoculture plantations may enhance overall carbon sequestration (Domke et al., 2020), the underlying soil carbon dynamics—such as accumulation, stabilization, and turnover—remain unclear and may vary with site conditions and management practices (Bruckman et al., 2011; Marín-Spiotta and Sharma, 2013; Paul et al., 2002; Turner et al., 2005; Yang

et al., 2011). Chronosequence studies often face limitations due to the assumption that different sites share identical environmental conditions (Yanai et al., 2003; Chazdon, 2008; Preston et al., 2020). Research on age-related changes in forest aboveground structure and soil carbon and nitrogen accumulation often involves repeated measurements at chronosequence sites at regular intervals following initial surveys. This approach generates dynamic data, overcoming the limitations of static observations that arise from temporal variability, topographic effects (Preston et al., 2020), soil characteristics (Bárcena et al., 2014; Bartuska and Frouz, 2015), and forest management practices (Nash et al., 2024). However, it remains challenging to determine whether observed changes reflect intrinsic stand development or are driven by other factors, and in some cases, such distinctions cannot be made with confidence (Yanai et al., 2000). Furthermore, to date, no studies have investigated the developmental processes of aboveground forest structure and associated changes in soil properties across forest age using both chronological and repeated sampling approaches.

This study aims to evaluate the development of *Q. crispula* plantations over a 50-year period using chronosequence and repeated sampling approaches. Specifically, we compared observed stand trajectories with predictive models based on natural forest growth data (Imada, 1976), assessed stand structure through tree size–density relationships, and examined soil carbon and nitrogen dynamics. To address the limited availability of comprehensive studies on *Q. crispula* afforestation and to mitigate limitations inherent in chronosequence approaches, we minimized environmental variability among the chronosequence sites and conducted resampling designed to exclude the effects of disturbances that occurred during the repeated sampling period. In this study, we propose the following hypotheses:

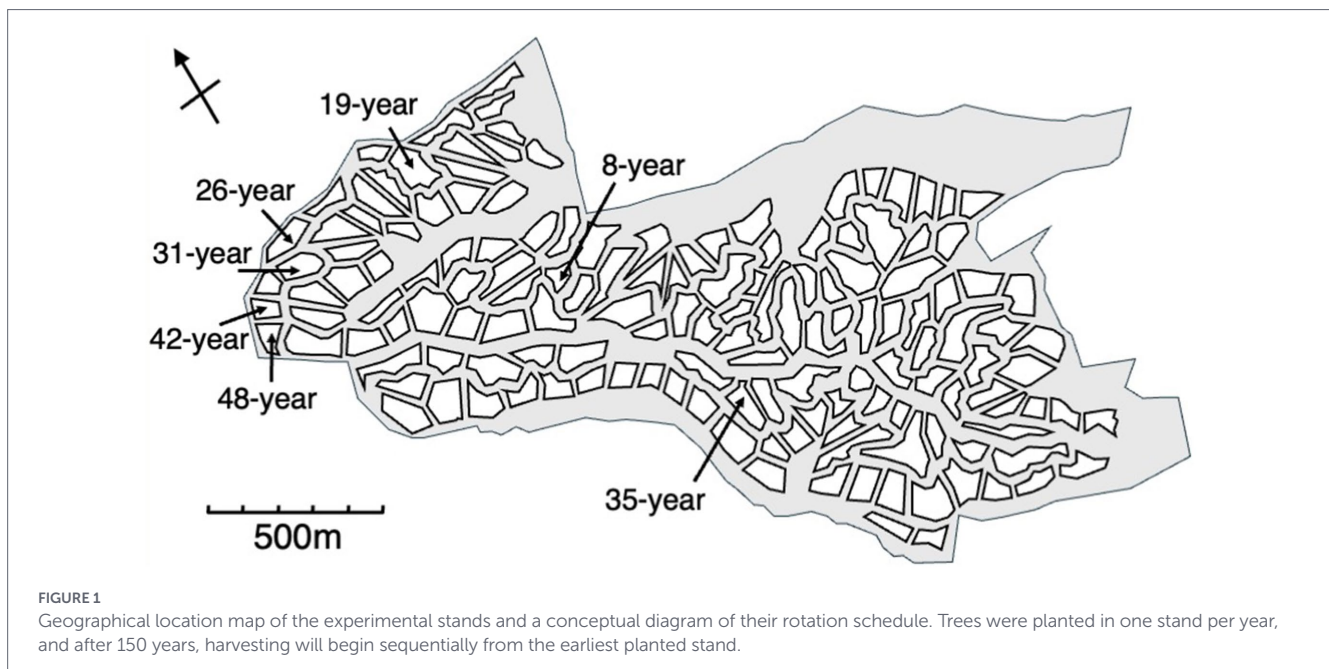
- (1) Stand development in *Q. crispula* plantations follows similar patterns of height–diameter relationships and biomass accumulation as those observed in natural forests.
- (2) Soil carbon and nitrogen accumulate during stand development.
- (3) Combining the chronosequence approach with repeated sampling provides reliable estimates of temporal changes in stand structure and soil properties.

2 Methods

2.1 Study site

The study was conducted in the Ashoro Research Forest (ARF; ca. 3,700 ha) of Kyushu University, located in eastern Hokkaido, Japan (43°15′N, 143°33′E). The ARF experiences an inland climate characterized by low precipitation, cool temperatures, and seasonal soil freezing during winter, with snow cover typically lasting from late December to mid-April (Hishi et al., 2014). The mean annual precipitation and temperature from 2017 to 2021 were 796.8 mm and 6.88 °C, respectively (Japan Meteorological Agency, 2025). The natural forests in this region are dominated by *Q. crispula*, *Acer pictum* subsp. *mono*, *Tilia japonica* and *Ulmus davidiana* var. *japonica* (Okano, 1994).

The study was conducted on *Q. crispula* plantations ranging from 0 to 50 years in age (Figure 1, Supplementary Figure 1). The elevation of the study area (ca. 200 ha) ranged from 350 to 400 m, with slopes between 2.9° and 22.7° (average 11.6° ± 5.1°) (Ohtsu et al., 2015).



Each plantation stand was located on a small ridge (Imada, 1996). The soils were classified as Cambisols, derived from volcanic ash, with a black surface soil layer. The understory was predominantly covered by *Sasa nipponica*.

Plantations in this area have been established annually since 1972 using a clear-cutting system in tongue-shaped blocks surrounded by shelterbelts, with a planned rotation period of 150 years (Imada, 1973). The reforestation process involved several steps. Prior to seed dispersal in early September, all non-seeded trees and understory vegetation were removed from the designated cutting areas. Line scarification of the forest floor was then performed using a cultivator on gentle slopes or manually with a hoe on steeper terrain. After seed dispersal in mid-October, seeds that fell onto non-regeneration strips (1 m wide) were relocated to designated regeneration strips (0.5 m wide). Immediately after relocation, the seeds were covered with soil, using the same methods employed during site preparation. A detailed description of these regeneration procedures is provided in Imada (1996).

2.2 Stand sampling design

This study utilized a chronosequence of seven *Q. crispula* stands, established in 2014 (8 years old), 2003 (19 years old), 1996 (26 years old), 1991 (31 years old), 1987 (35 years old), 1980 (42 years old), and 1974 (48 years old). In August 2022, we selected these seven sites for sampling in 2022 because many of the 38 sites of Ohtsu et al. (2015) were severely affected by disturbances, which made it difficult to assess differences with stand age, and additional logistical constraints also arose. One sample plot was established in each stand. Owing to the higher tree density observed in the youngest stand, a plot size of 5 m × 5 m was used for the 8-year-old stand, whereas a larger plot size of 10 m × 10 m was applied to the remaining six stands.

2.3 Estimation of the aboveground biomass

In August 2022, a vegetation survey was conducted in each plot to estimate the aboveground biomass using allometric models. Girth at

breast height (GBH) was measured at 1.3 m above ground level for all individual trees taller than 2 m. For trees shorter than 2 m, species identity and tree height were recorded.

Aboveground biomass was estimated for canopy species, including *Q. crispula*, *Betula platyphylla*, *Cerasus sargentii*, *Acer pictum* subsp. *mono*, *Cerasus maximowiczii*, *Betula maximowicziana*, and *Kalopanax septemlobus*. Biomass estimation was based on the following allometric equations, parameterized for *Betula ermanii*, *Q. crispula*, and *Abies sachalinensis* in Hokkaido (Ohtsu et al., 2015; Takagi et al., 2010):

$$\ln W = 2.8325 \ln(H) - 1.1843 \quad (r^2 = 0.79) \quad (1)$$

$$\ln W = 2.428 \ln(DBH) - 2.282 \quad (r^2 = 0.99) \quad (2)$$

where W is the aboveground biomass (kg), H is the tree height (m), and DBH is the diameter at breast height (cm). Equation 1 (Ohtsu et al., 2015) was used for trees under 2 m in height, and Equation 2 (Takagi et al., 2010) was used for trees with 2 m and taller.

To estimate understory biomass, vegetation was harvested in August 2022 from a 1 m × 1 m quadrat placed in an undisturbed area of the forest floor within each plot. The harvested material was separated into three categories: *S. nipponica* leaves and culms, and other understory components (including herbaceous plants, grasses, shrubs, etc.). Each category was placed in brown paper bags, oven-dried at 70 °C for 48 h, and then weighed.

2.4 Estimation of leaf biomass

To evaluate canopy development, overstory leaf biomass was estimated using the Leaf Area Index (LAI) and Leaf Mass per unit Area (LMA). During the vegetation survey in August 2022, hemispherical images were taken near the center of each plot at a height of 100 cm above the forest floor using a RICOH Theta-V 360 spherical camera connected to a smartphone under overcast

conditions. The camera settings were ISO 100, focal length 1.31 mm, aperture 2, and shutter speed 1/1600. The LAI was calculated from these images using a Gap Light Analyzer (version 2.0, Simon Fraser University, Canada; Institute of Ecosystem Studies, USA). Since the measurements were taken only once during the leaf emergence period, the obtained values likely represent plant area index (PAI) rather than true leaf area index (LAI) (Chen et al., 1991).

To determine the LMA, unshaded fresh leaves from the uppermost canopy of *Q. crispula* were collected using a pole pruner. In each plot, leaves were sampled from five trees, with one branch per tree and three leaves per branch, totaling 15 leaves per plot. The collected leaves were scanned using a flatbed scanner (EPSON GT-X 980), and leaf area was measured using ImageJ software (National Institutes of Health, USA). The LMA (g/m^2) was calculated based on the scanned leaf area and dry mass. All leaves were oven-dried at 70 °C for 48 h and then weighed. The dried leaf material was then ground into a fine powder using a mill for carbon and nitrogen analyses. Overstory leaf biomass (Mg/ha) was estimated as the product of the LAI and LMA. As the overstory in the study area consisted of deciduous species, the estimated leaf biomass was considered equivalent to the annual litter input from the canopy.

2.5 Soil sampling and collection of the fine roots

In October 2022, soil samples were collected from three layers: the organic layer (O-layer) and mineral soil at depths of 0–5 cm and 5–10 cm. Sampling was limited to 10 cm because fine roots of *Q. crispula* are concentrated in the surface layer. Previous measurements down to 30 cm in a *Q. crispula* forest in the ARF (Maeda et al., 2018) indicated that the amount of roots obtained within the top 10 cm was comparable to that collected from the entire 30 cm depth, suggesting that sampling to 10 cm was sufficient. Sampling was conducted at the four corners of each study plot. Plot sizes were either 10 × 10 m or 5 × 5 m. For both plot sizes, we assumed no spatial dependence in soil property variability. In total, four samples were taken per plot (one at each corner), resulting in 28 samples across seven plots. At each sampling point, a quadrat (20 cm × 20 cm internal dimensions) was placed on a section of the forest floor with minimal signs of recent human disturbance. The organic layers within the quadrats were carefully cut and collected using a sharp knife. After removing the O-layer, mineral soil samples were collected using a 100 mL stainless steel sampling tube equipped with a supplemental soil sampler. The first mineral soil layer was sampled from a depth of 0–5 cm, and the second layer was collected from a depth of 5–10 cm in an adjacent area. Organic layer samples from the four corners of each plot were homogenized, randomly subsampled, and ground using a mill prior to chemical analysis. Mineral soil samples were also homogenized, manually crushed, and sieved through a 2 mm mesh to separate fine soil (<2 mm) and coarse components (≥ 2 mm). From the coarse fraction, fine roots (<2 mm in diameter), coarse roots (≥ 2 mm), litter, and gravel (≥ 2 mm) were extracted by wet-sieving and manually separated using forceps. All collected components were thoroughly washed to remove adhering soil particles, oven-dried at 70 °C for 48 h, and subsequently weighed. To estimate the fine root biomass, dried fine roots were categorized into two groups: *S. nipponica* and non-*S. nipponica* (primarily *Q. crispula*), based on the following morphological characteristics: fine roots of

S. nipponica are yellowish white, have shorter and narrower tips, and exhibit a wider branching angle near the root tip compared to those of woody species.

2.6 Carbon and nitrogen contents

Carbon and nitrogen concentrations (%) in the O-layer, fine soil fractions from two mineral soil depths (0–5 cm and 5–10 cm), and fresh leaf samples were determined using a CN analyzer (J-Science, JM-1000CN, Kyoto, Japan). Carbon and nitrogen contents were calculated by multiplying the concentration values by the dry weight of the organic layer and by the fine soil mass for the mineral soil samples. These values were then converted to a per-hectare basis to facilitate comparisons across plots.

2.7 Statistical analysis

In 2010, Ohtsu et al. (2015) conducted a survey in the present study area to evaluate the effects of changes in stand structure—including understory vegetation (*S. nipponica*)—on soil carbon and nitrogen accumulation in *Q. crispula* plantations ranging from 0 to 38 years of age. Their analysis employed a model comparison technique to assess the fit between observed and predicted values. The logistic model (Equation 3), the linear model (Equation 4), the exponential model (Equation 5), and the null model (Equation 6) were used (Supplementary Figure 2):

$$y = \frac{a}{1 + \exp(b - ct)} \quad (3)$$

$$y = at + b \quad (4)$$

$$y = at \times \exp(bt) + c \quad (5)$$

$$y = a \quad (6)$$

where y is the measurements described in Table 1, t is the stand age, and a , b , and c are the regression coefficients. Model selection was based on the Akaike Information Criterion (AIC), with the model yielding the lowest AIC value considered optimal (Ohtsu model; Ohtsu et al., 2015). To assess model fit, the root mean squared error (RMSE) was calculated. Regression models were constructed using data collected in 2010 from 38 sites, each representing a distinct stand age ranging from 1 to 38 years (Ohtsu et al., 2015). These models were applied to canopy tree leaf biomass, understory biomass, and fine root biomass, in addition to stand structure and soil carbon and nitrogen accumulation. First, to assess how representative the selected seven sites were compared to the original 38 sites, we calculated the RMSE as the deviation between the model derived from the 38 sites in Ohtsu et al. (2015) (hereafter referred to as the Ohtsu model) and the data from the selected six sites (one of seven sites was a 8-year-old site that did not exist in 2010). We then compared this deviation with the RMSE between the Ohtsu model and the data collected from the seven sites in 2022. In addition, we compared the observed changes in measured values between 2010 and 2022 with the 12-year changes predicted by the Ohtsu model using Wilcoxon test. All statistical analyses were performed using the R statistical software version 4.2.3 (R Core Team, 2023).

TABLE 1 General characteristics of the experimental stands.

Year planted	Stand age (years)	No. of <i>Q. crispula</i> (no./ha)	Aboveground biomass of <i>Q. crispula</i> (Mg/ha)	Mean DBH of <i>Q. crispula</i> (cm)	Mean height of <i>Q. crispula</i> (m)	Slope aspect
2014	8	20,000	7.98	1.2 (0.8)	4.2 (1.0)	NE
2003	19	7,100	23.08	3.8 (2.1)	7.9 (2.0)	E
1996	26	3,100	60.00	7.8 (3.3)	11.7 (2.3)	SE
1991	31	2,900	73.79	8.9 (3.3)	11.7 (1.7)	SE
1987	35	6,600	87.34	6.7 (2.7)	12.5 (2.1)	SW
1980	42	2,500	116.27	11.2 (4.7)	17.9 (3.5)	S
1974	48	1,600	127.58	14.2 (5.4)	17.8 (3.8)	SE

The values in parentheses indicate standard deviations. Stand age (years): age of the stands as of August 2022.

3 Results

3.1 Stand development

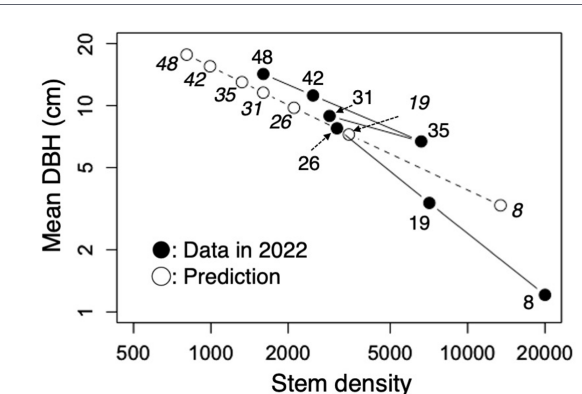
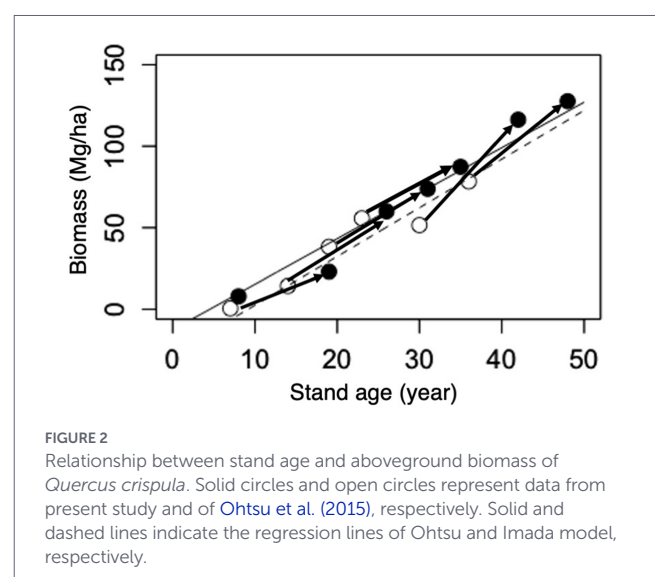
The biomass of *Q. crispula* increased linearly with stand age and closely followed the predictions of the Ohtsu model based on data from 38 chronosequence sites surveyed in 2010 (Figure 2). These biomass values were higher than those predicted by the Imada model, which was developed using data from natural forests of various ages in the ARF. The mean diameter at breast height (DBH) of *Q. crispula* increased with stand age, whereas stem density generally decreased, except at the 35-year-old site (Figure 3). Although the relationship between DBH and stem density resembled that predicted by the Imada model, overall stand development was slower than projected.

3.2 Soil carbon and nitrogen

Carbon mass in the O-layer did not vary substantially with stand age, and the observed values closely matched those predicted by the Ohtsu model (Figure 4). In the mineral soil at depths of 0–5 cm, carbon mass was lower in the 8-year-old stand, whereas no significant differences were observed among the other stands. Overall, carbon mass in the 0–5 cm mineral soil layer was higher than the values recorded in 2010. A similar pattern was observed in the 5–10 cm layer, with lower carbon mass in the youngest stand and relatively stable values across the older stands. Nitrogen mass in all layers showed no significant variation with stand age (Figure 5). However, nitrogen mass in both layers of the mineral soil was greater than the values recorded in 2010.

3.3 Comparison between observed data and model predictions over a 12-year interval

The root mean square errors (RMSEs) of the Ohtsu model (based on 38 stands in 2010) and those of a subset of six sites extracted from the original dataset did not differ substantially for any of the measured variables (Table 2, Supplementary Figures 3, 4). Similarly, most RMSEs from the seven sites sampled in 2022 were comparable to those of the Ohtsu model. However, the RMSEs for carbon and nitrogen concentrations in the fresh leaves of *Q. crispula* as well as for fine soil contents in 2022, were relatively higher than those of the Ohtsu model.



Overstory leaf biomass generally followed the prediction of the Ohtsu model (Supplementary Figure 3). However, carbon and nitrogen concentrations of the overstory leaves were relatively higher than

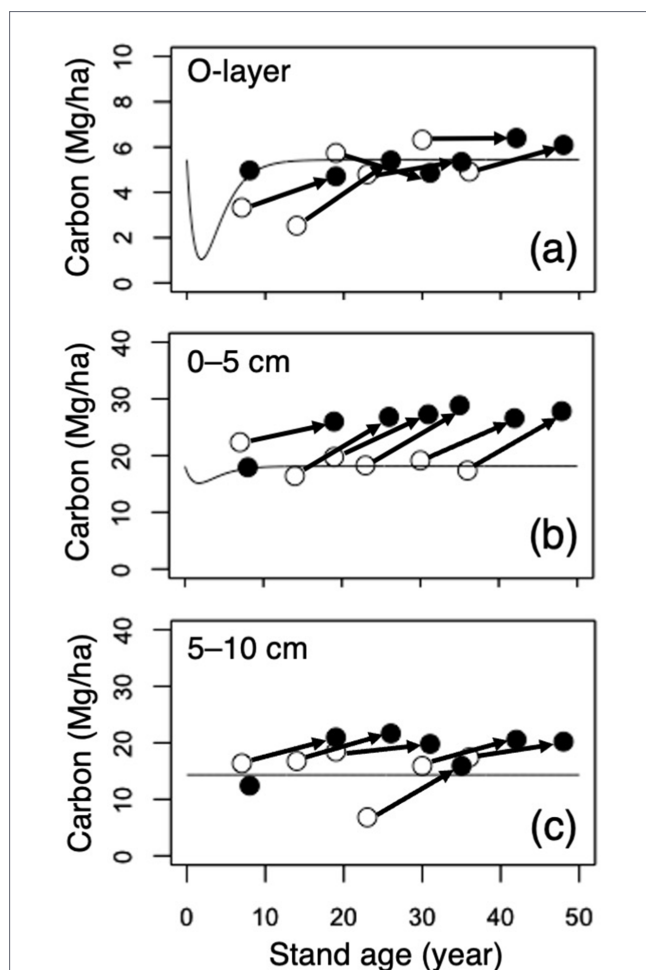


FIGURE 4
Relationship between stand age and carbon mass in (a) O-layer, (b) mineral soil at depths of 0–5 cm, and (c) at depth of 5–10 cm. The solid circles represent the observed values in 2022, and the open circles represent the observed values in 2010. Regression lines represent the models using data obtained at 38 sites in 2010.

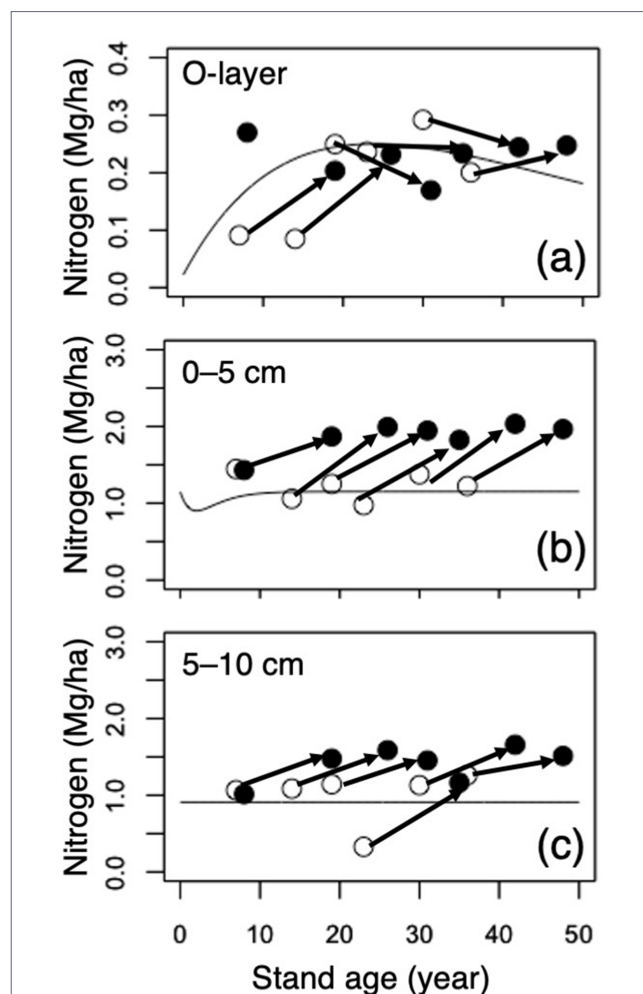


FIGURE 5
Relationship between stand age and nitrogen mass in (a) O-layer, (b) mineral soil at depths of 0–5 cm, and (c) at depth of 5–10 cm. The solid circles represent the observed values in 2022, and the open circles represent the observed values in 2010. Regression lines represent the models using data obtained at 38 sites in 2010.

those predicted, whereas the C/N ratio was relatively lower. Understory biomass was generally close to the regression line of the Ohtsu model but showed a decreasing trend over the 12-year period.

All fine root biomass values were relatively lower than those predicted by the Ohtsu model, with no apparent change over the 12 years. The fine root biomass of *S. nipponica* was also relatively lower than predicted and showed a decreasing trend. Other fine root biomass values varied widely and did not exhibit a clear pattern with respect to stand age or temporal change over the 12-year period.

O-layer mass was generally consistent with that of the Ohtsu model (Supplementary Figure 4). The carbon concentration in the O-layer was relatively higher than predicted, whereas the nitrogen concentration was generally consistent with the Ohtsu model. The C/N ratio of the O-layer showed variability. Fine soil content at depths of 0–5 cm and 5–10 cm was relatively higher than predicted. Carbon and nitrogen concentrations at depths of 0–5 cm did not differ significantly from those predicted by the model, although the C/N ratio was slightly relatively lower than predicted.

The observed change in measured values between 2010 and 2022 differed from the 12-year changes predicted by the Ohtsu model for the following variables: carbon and nitrogen concentrations of overstory leaves; fine root mass of trees, *S. nipponica* and

their combined total; carbon concentration of the O-layer; fine soil content, carbon and nitrogen mass and the C/N ratio of soil at depth of 0–5 cm; fine soil content, carbon and nitrogen concentration and mass and the C/N ratio soil at depth of 5–10 cm ($p < 0.05$; Wicoxon test, Table 2, Figures 6–8, Supplementary Figures 5, 6).

4 Discussion

The biomass of *Q. crispula* increased linearly with stand age, consistent with the Imada prediction model (1996), which was developed using data from natural forests in the ARE. However, stand development—as indicated by the increase in mean DBH and the decrease in tree density—progressed more slowly than predicted. One possible reason for this delay is the absence of the thinning operations originally planned in the management scheme. When a simulation was conducted to model the thinning of small-diameter trees, with tree density adjusted to match the stand age and the resulting values for mean DBH and tree density closely aligned with the Imada model (Supplementary Figure 7).

TABLE 2 Results of RMSE from the observed values and predicted model values of the initial survey (2010) and the present study (2022) and the present study (2022), and results of Wilcoxon tests comparing the difference between the 12-year change in observed values and the 12-year change predicted by the model (p-value).

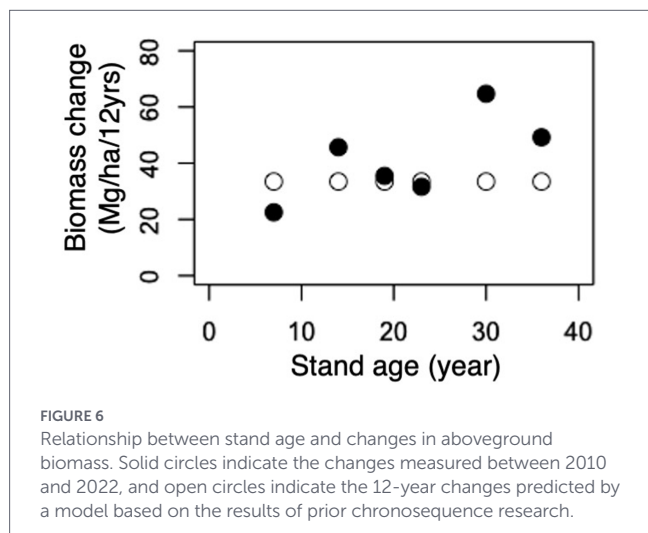
Measurements	Regression model	RMSE			p-value
		2022	2010	2010	
		7 sites	6 sites	All sites	
Overstory biomass (Mg/ha)	Li: $y = -12.54 + 2.79 t$	8.318	11.89	12.68	0.347
Understory biomass (Mg/ha)	Exp: $y = 1.49 t * e^{-0.18t} + 1.47$	0.918	1.140	1.224	0.937
Leaf biomass of the overstory (Mg/ha)	Lg: $y = 2.67 / (1 + e^{(6.82 - 0.58t)})$	0.486	0.645	0.642	0.818
Fresh leaf: C concentration (%)	Li: $y = 44.84$	1.536	0.749	1.033	0.049
Fresh leaf: N concentration (%)	Li: $y = 2.14 - 0.0051 t$	0.440	0.192	0.182	0.003
Fresh leaf: C:N ratio (fresh leaf)	Li: $y = 20.9 + 0.065 t$	3.763	2.019	1.931	0.003
Fine root mass (Total, Mg/ha)	N: $y = 287$	107.4	187.2	169.8	0.347
Fine root mass (<i>Sasa nipponica</i> , Mg/ha)	Exp: $y = 48.0 t * e^{-0.16t} + 73.4$	84.88	116.1	122.9	0.015
Fine root mass (Other spp., Mg/ha)	Li: $y = 82.85 + 1.52 t$	85.55	128.3	150.9	0.049
Organic layer: mass (Mg/ha)	Exp: $y = -9.07 t * e^{-0.40t} + 14.5$	2.142	3.497	4.602	0.699
Organic layer: C concentration (%)	Lg: $y = 38.39 / (1 + e^{(1.40 - 1.02t)})$	3.886	3.822	4.018	0.002
Organic layer: N concentration (%)	Exp: $y = 0.064 t * e^{-0.030t} + 0.98$	0.326	0.295	0.291	0.818
Organic layer: C mass (Mg/ha)	Exp: $y = -6.46 t * e^{-0.54t} + 5.44$	0.567	1.385	1.362	0.132
Organic layer: N mass (Mg/ha)	Exp: $y = 0.026 t * e^{-0.042t} + 0.022$	0.056	0.069	0.072	0.699
Organic layer: CN ratio	Exp: $y = 3.23 t * e^{-0.15t} + 21.32$	5.229	4.804	5.088	0.394
0–5 cm: fine soil content (kg/m ³)	Li: $y = 419.39 - 1.28 t$	66.42	45.33	51.38	0.003
0–5 cm: C concentration (%)	Exp: $y = -2.55 t * e^{-0.41t} + 9.95$	1.429	3.608	3.847	0.394
0–5 cm: N concentration (%)	Exp: $y = -0.17 t * e^{-0.38t} + 0.63$	0.098	0.247	0.253	0.999
0–5 cm: C mass (Mg/ha)	Exp: $y = -4.53 t * e^{-0.56t} + 18.11$	8.479	2.064	2.118	0.002
0–5 cm: N mass (Mg/ha)	Exp: $y = -0.33 t * e^{-0.49t} + 1.15$	0.744	0.181	0.179	0.002
0–5 cm: CN ratio	N: $y = 16.06$	2.409	3.375	3.755	0.003
5–10 cm: fine soil content (kg/m ³)	N: $y = 492.92$	75.23	54.33	57.04	0.003
5–10 cm: C concentration (%)	N: $y = 6.14$	1.464	2.558	2.662	0.049
5–10 cm: N concentration (%)	N: $y = 0.39$	5.554	6.151	7.356	0.049

(Continued)

TABLE 2 (Continued)

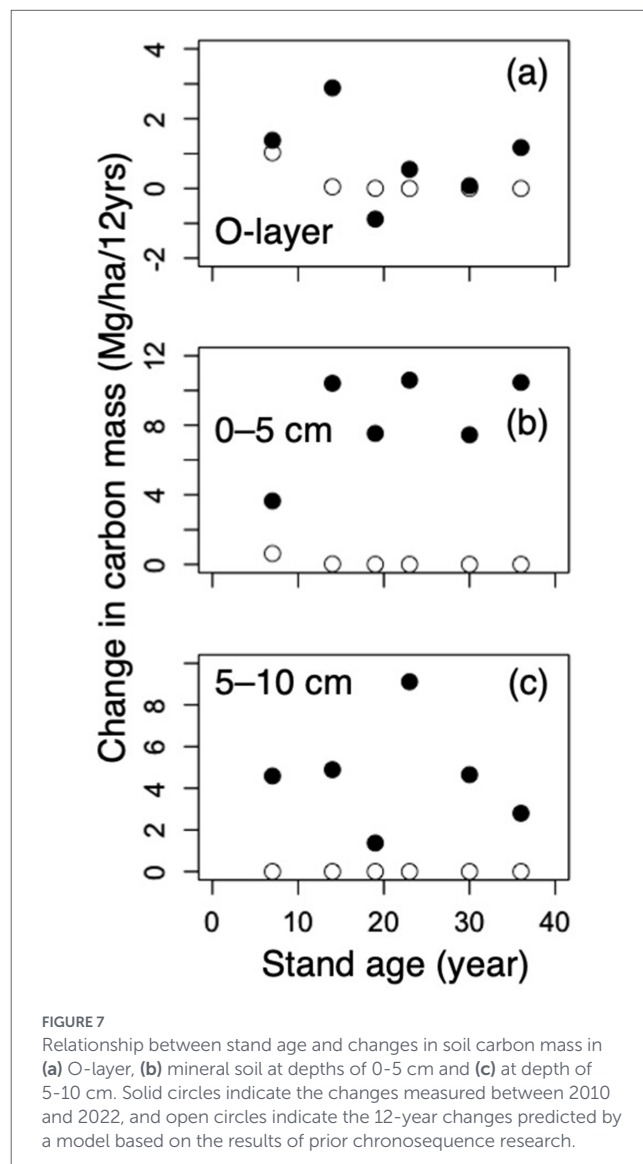
Measurements	Regression model	RMSE			p-value
		2022	2010	2010	
		7 sites	6 sites	All sites	
5–10 cm: C mass (Mg/ha)	N: $y = 14.32$	5.443	3.218	3.361	0.003
5–10 cm: N mass (Mg/ha)	N: $y = 0.91$	0.544	0.272	0.279	0.003
5–10 cm: CN ratio	N: $y = 16.08$	15.64	15.59	15.60	0.049

Exp: exponential model, Lg: logistic model, Li: linear model, N: null model, y: response variable, t: stand age.



The greater observed biomass compared to the predicted model suggests that small-diameter trees, which were originally intended to be removed through thinning, still remain in the stands. The finding that excluding smaller individuals resulted in an average DBH nearly identical to that predicted by the Imada model indicates that the growth of dominant trees was comparable to that assumed in the model. This, in turn, implies that thinning would have little effect on the growth of dominant individuals. In other words, the stand appears to have already undergone differentiation between dominant and suppressed trees, implying that further thinning may no longer be necessary. The mean DBH values of *Q. crispula* in the present study and in the Imada model were smaller than those shown in the stem density control chart developed by Kikuzawa (1979), which was based on data from other *Q. crispula* forests in Hokkaido, Japan. This suggests that the relationship between DBH and stem density in *Q. crispula* stands varies depending on site conditions including soil characteristics and climatic factors. To support effective management of *Q. crispula* plantations, further data from diverse environments, different genetic lineages, and thinning experiments are required.

The observed carbon and nitrogen mass in the O-layer in 2010 and 2022 also showed little change, consistent with the predictions of the Ohtsu model. In *Quercus petraea* forests, soil carbon mass was similarly unaffected by forest development, regardless of the management type (high forest or coppice with standards, Bruckman et al., 2011). A global synthesis of previous studies also showed that the carbon and nitrogen mass from the surface to the mineral soil layers did not change significantly in most cases (Yang et al., 2011). At the present study site, O-layer mass stabilized relatively early



during stand development (Ohtsu et al., 2015), although previous studies have reported that organic layer mass initially decreased, then gradually increased, and stabilized with stand age (Kawaguchi and Yoda, 1986). Carbon mass recovery occurred more rapidly than canopy litter supply, taking approximately 5 years after plantation establishment in this study area. This suggests that carbon and nitrogen mass in the O-layer reached a stable state relatively quickly due to the rapid expansion of understory vegetation (*S. nipponica*)

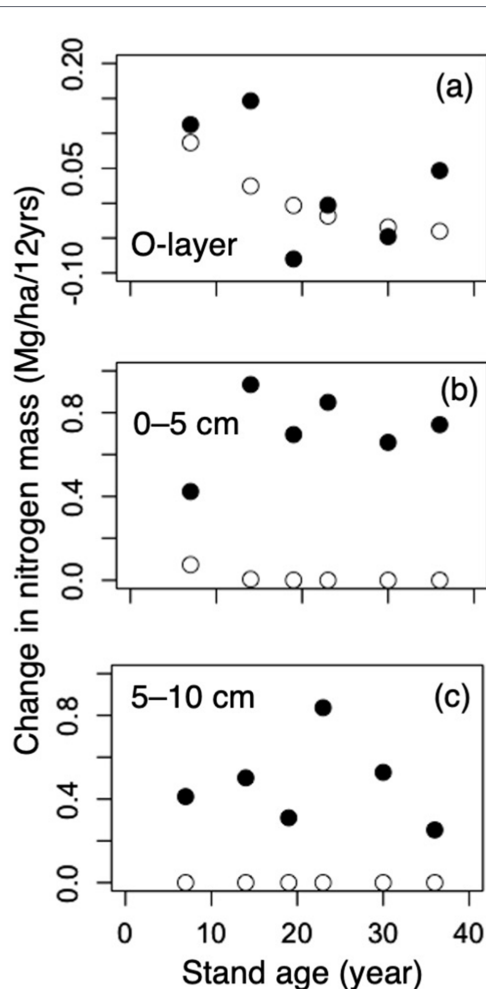


FIGURE 8
Relationship between stand age and changes in soil nitrogen mass in (a) O-layer, (b) mineral soil at depths of 0–5 cm and (c) at depth of 5–10 cm. Solid circles indicate the changes measured between 2010 and 2022, and open circles indicate the 12-year changes predicted by a model based on the results of prior chronosequence research.

and the recovery of litter input following clear-cutting in this study area (Ohtsu et al., 2015).

Previous studies have shown that a decline in the C/N ratio in the O-layer during early stand development reflects enhanced nitrogen mineralization (Olsson et al., 1996). In the present study, the C/N ratio peaked shortly after afforestation and then gradually declined, suggesting differences in carbon and nitrogen accumulation rates. Unlike Japanese cedar plantations, where litter C/N ratios remain elevated for decades after canopy closure (Fukushima et al., 2011; Tateno et al., 2009), the early peak observed here was attributed to shifts in litter composition from understory to overstory vegetation rather than long-term nitrogen limitation (Ohtsu et al., 2015). Prior to afforestation, the natural vegetation in this area was a secondary forest of *Q. crispula*, the same species as the plantation. Clear-cutting was conducted when the soil was frozen (Ohtsu et al., 2015), which may have reduced the impact of afforestation and disturbance on species composition. The absence of species conversion may be one of the reasons for the minimal impact on soil properties.

On the other hand, the observed carbon and nitrogen mass in the mineral soil layers increased over the 12-year period, although no

apparent changes with stand age were predicted by the Ohtsu model. These increases were largely due to an increase in fine soil content rather than to increase in soil carbon and nitrogen concentrations. The increase in fine soil content in the mineral soil was observed between 2010 and 2022, despite the absence of significant stand-age-related changes in soil carbon and nitrogen mass. Although the cause of the increase in fine soil content remains unclear, the increase was observed in most plots, suggesting that it reflects environmental changes occurring across the entire study area during the study period. The discrepancy between predictions derived from chronosequence approaches and the actual observed changes in aboveground biomass indicates that environmental changes during the observation period can override age-related trends inferred from chronosequences. Such effects have been well documented for aboveground biomass growth including enhanced growth associated with increase in temperature and CO₂ concentration (McMahon et al., 2010), and reduced growth caused by drought stress (Suzuki, 2021). Similarly, in the present study, environmental changes may have influenced soil properties, as reflected by the observed increase in fine soil content. The increase in fine soil content might be related to the rise in sika deer populations and their impact on soil physical properties. Deer grazing has been shown to cause substantial changes in surface soil, including compaction, increased bulk density, and elevated fine soil content in breeding areas (Kumbasli et al., 2010). Although no significant feeding damage to *S. nipponica* leaves by deer was observed, a decrease in *S. nipponica* fine roots was noted. Instead, feeding damage by moth larvae (unidentified species) was observed approximately 1 year prior to the 2022 survey. This damage by moth larvae may have contributed to the reduction in *S. nipponica* fine roots, and consequently, to the changes in fine soil content.

For all measured variables, the RMSE of the model created using data from 38 sites did not differ apparently from that of the dataset from six sites, suggesting that data from the six sites can reasonably represent the temporal pattern of plantation development with stand age. The RMSE of the data collected from the same sites 12 years later was also largely consistent for most variables. However, noticeable deviations from the model were observed for soil properties and leaf carbon and nitrogen concentrations. In addition, the observed 12-year changes in these variables differed significantly from the model predictions. These changes are unlikely to be associated with stand development per se. The changes in soil properties may have been influenced by factors such as sika deer browsing and feeding damage by moth larvae as abovementioned. Temporal variability in canopy leaf carbon and nitrogen concentrations was likely influenced by environmental conditions, including interannual climatic variability. Grassi et al. (2005), for instance, documented annual changes in nitrogen concentrations in *Quercus robur* leaves under dry conditions.

Although the present study made considerable efforts to align environmental and stand conditions to clarify temporal patterns associated with stand development, the repeated measurements did not consistently match chronosequence-based expectations. This suggests that regression models derived from single-time chronosequence observations may not be reliable for variables with greater annual variability than stand age-related trends. Previous studies have examined factors such as topography (Preston et al., 2020), soil properties (Bárcena et al., 2014; Bartuska and Frouz, 2015) and forest management practices (Nash et al., 2024) in attempts to identify drivers other than time. However, distinguishing whether observed changes reflect

stand development or other influences has remained challenging, and in some cases may be difficult to determine with confidence (Yanai et al., 2000).

In the present study, we avoided sites with obvious disturbance and conducted repeated sampling. Nevertheless, stochastic factors such as deer browsing or insect outbreaks—similar to windthrow (Nash et al., 2024) in their unpredictable occurrence—cannot be fully controlled. Ideally, sites showing clear *post hoc* impacts would be excluded, but such impacts are often subtle or difficult to detect. Consequently, the underlying reasons for the 12-year changes observed here remain unresolved. On the other hand, the apparent lack of detectable effects on aboveground structure and leaf production, despite changes in soil and leaf traits, raises the possibility that *Q. crispula* may possess a substantial capacity for acclimation. Additional repeated measurements at the chronosequence sites will likely provide further insights into these mechanisms.

5 Conclusion

The aboveground biomass of *Q. crispula* in eastern Hokkaido, Japan increased linearly with stand age, consistent with model predictions based on data from surrounding natural forests. However, the rate of stand development, indicated by changes in mean diameter and stem density, was slightly slower than predicted. At the same time, the greater biomass relative to model prediction suggests that small-diameter trees remain in the stands, whereas the growth of dominant trees consistent with the model. This finding implies that additional thinning may have limited effects on promoting the growth of dominant individuals. Overall, these results indicate that the chronosequence approach was effective for assessing age-related changes in stand structure.

In contrast, soil carbon and nitrogen mass showed little change with stand age in the *Q. crispula* plantations, consistent with chronosequence model predictions. However, fine soil content in the surface layer increased over the 12-year measurement period, and carbon and nitrogen concentrations in *Q. crispula* leaves also varied during this time. The pronounced discrepancies between changes observed through repeated measurements and those predicted by the chronosequence model indicates that environmental changes during the observation period can obscure age-related trends derived from chronosequences. Continued implementation of the repeated measurements at the chronosequence site is expected to provide further insights.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

ZW: Writing – review & editing, Formal analysis, Writing – original draft, Data curation, Investigation. NT: Writing – review & editing,

Investigation, Methodology. TH: Data curation, Conceptualization, Methodology, Investigation, Writing – review & editing. TE: Writing – review & editing, Methodology, Supervision, Writing – original draft, Conceptualization, Formal analysis, Data curation, Visualization.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2026.1721988/full#supplementary-material>

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