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Research article

Human-mediated forest transition shapes long-term occurrence patterns of pine caterpillar (*Dendrolimus spectabilis*) in the Korean Peninsula

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ABSTRACT

Both intrinsic and exogenous factors affect the population dynamics of forest insects. Time series analysis based on long-term data provides insights into the ecological processes driving their oscillation or fluctuation. This study investigated the long-term occurrence patterns of the pine caterpillar (*Dendrolimus spectabilis*) based on both historical records and recent monitoring data. Historical records were obtained from books compiled by ancient governments (918–1903) on the Korean Peninsula, while recent monitoring data were collected from 22 monitoring sites in South Korea during 1968–2005. Forest growing stock and air temperature were used as indicators of forest change (deforestation and reforestation) and climate change, respectively, which are the major drivers of forest ecosystems. Convergent cross mapping (CCM) was applied to infer potential causal effects of growing stock and air temperature on the abundance of pine caterpillar based on the recent monitoring data. The occurrence patterns of pine caterpillar in both historical and recent monitoring data were characterized using spectral and wavelet analyses. The CCM analysis indicated that increased growing stock (reforestation) was a potential driver of the decline of pine caterpillar outbreaks in the 1970s, while no clear evidence supported a causal influence of temperature on its density. Both short- and long-term occurrence periodicities were observed in both historical and recent monitoring data, ranging from several years up to more than a hundred years. Interestingly, the periodicities were primarily detected when the frequency of outbreak or the abundance of pine caterpillars was high, suggesting that the high occurrence of pine caterpillars in both historical and recent monitoring data was considerably associated with deforestation of the pine forest caused by human activities. These data reveal a possible role of human-mediated habitat transition in driving the outbreaks and dynamics of the pine caterpillar.

1. Introduction

The long-term population dynamics of forest insects are influenced by both intrinsic and exogenous factors. Identifying the drivers of temporal outbreak patterns of organisms is an important topic in ecology because of their theoretical significance in population dynamics and their usefulness (Asaro and Chamberlin, 2015; Haynes et al., 2014, 2018; Li et al., 2015; Zhang et al., 2023). Recent increases in human-mediated disturbances, including deforestation and climate change, induce changes in population oscillations and fluctuations as exogenous drivers (Guégan et al., 2023; Johnson and Haynes, 2023).

Anthropogenic disturbances, including climate change induced by human activities, overexploitation for timber, and changes in land cover, alter cyclic population behavior (Ciesla, 2015). For instance, continuous periodic outbreaks of the larch budmoth (*Zeiraphera diniana*) in the European Alps during 1200 years ceased after 1981 because of the warm winter temperatures (Esper et al., 2007). Similarly, the outbreak cycle of *Dendrolimus pini* in Germany collapsed due to the high fall temperature and low winter precipitation (Haynes et al., 2014). Furthermore, the outbreak spatial extent of *Coloradia pandora* in Oregon, USA, decreased in the 1960s due to forest fragmentation caused by timber harvest and land-use changes (Speer et al., 2001).

Time series analysis based on long-term data provides insights into clarifying the major drivers that influence population dynamics (Choi

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and Park, 2019; Choi et al., 2011b; Turchin and Taylor, 1992). Various types of time series analysis techniques were applied in ecological studies to investigate the properties of population dynamics, such as autocorrelation (Choi et al., 2011b; Cooke, 2024; Fay et al., 2020), cross-correlation (Hanski, 1987; Tobin and Bjørnstad, 2003), spectral analysis (Munoz et al., 2007; Reuman et al., 2006), and wavelet analysis (Cazelles et al., 2008; Haynes et al., 2014). Nevertheless, these techniques have limitations in explaining the cause-and-effect between variables in multivariable time series data.

Detecting the causal relationships in complex systems is a fundamental yet extremely challenging goal of scientific research (Sugihara et al., 2012). The convergent cross mapping (CCM) (Sugihara et al., 2012), a nonparametric approach, has been proposed for detecting causal dependence between time series (Barraquand et al., 2021). CCM has been applied in diverse fields, including ecology, such as for detecting causality in complex ecosystems (Sugihara et al., 2012), detecting causal relationships between plant and environmental variables from short time series (Clark et al., 2015), inferring species interactions (Barraquand et al., 2021), and quantifying the effects of driving factors on temperature (Yu et al., 2022).

Deforestation is a major disturbance factor in forest ecosystems, and in Korean forests, due to the overexploitation of timber, it has been recorded with a long history since the Joseon Dynasty (1392–1910) (Chun, 2022). In the 17th century, the Little Ice Age and the introduction of a house heating system (Ondol in Korean) accelerated deforestation in the Korean Peninsula because of the high increase in the requirement of wooden material (Bae et al., 2020). In the pre-modern Korea, wood was the main building material, and the architecture from various periods reflects the availability of timber for construction. The Korean War in the early 1950s intensified deforestation, as wood was used extensively for fuel and slash-and-burn agriculture (Bae et al., 2010). The practice of slash-and-burn agriculture continued to expand until the early 1970s, when government policies prohibited it and promoted reforestation and the planting of young trees throughout South Korea. Consequently, these efforts led to the maturation of Korean forests through natural succession following successful reforestation initiatives (Bae et al., 2020).

The pine caterpillar (*Dendrolimus spectabilis*) is a spring-feeding species that overwinters as larvae. Adults emerge from July through August and lay their egg masses in August, the first instar larvae emerge in late August or early September, and most larvae overwinter as fifth instars (Shin et al., 2008). Neonate larvae are susceptible to mortality from heavy rain, and variation in this mortality is the key factor influencing population changes (Maeto, 1991; Park and Hyun, 1982). In addition to precipitation, lower winter temperatures are considered another factor reducing the moth population (Korea Forest Research Institute, 2011). Due to the severe damage of pine trees caused by the pine caterpillar in the Korean Peninsula, its outbreak management activities have been well recorded in Korean historical records such as the History of the Goryeo Dynasty (Goryeosa) (918–1392) and the Annals of the Joseon Dynasty (AJD) (1392–1903) (Kang, 2012; Lim and Shim, 2002; Paik and Paik, 1977). Due to its historical value, the AJD was listed by the UNESCO as an item of cultural importance in 2001 (http://www.heritage.go.kr).

In the 1960s and 1970s, the pine caterpillar was one of the most injurious defoliators of the Korean red pine (*Pinus densiflora*) and Japanese black pine (*P. thunbergii*) in Northeast Asia, especially in Korea and Japan (Choi et al., 2011a, 2019; Kamata, 2002). However, its outbreaks have gradually decreased since the mid-1970s, and it is now considered an occasional pest in inland Korea (Choi et al., 2011a). Choi et al. (2019) proposed that the decline in pine caterpillar outbreaks in Korea might be due to the increased outbreak periodicity over the past century, heightened activity of natural enemies, and a reduction in younger stands preferred by the larvae due to forest succession after reforestation. To understand the long-term population dynamics of the pine caterpillar, including its historical fluctuations and recent decline, it is important to investigate the influence of potential drivers. It is also necessary to clarify the spatiotemporal characteristics of population behavior, such as periodicity and spatial synchrony, based on long-term population census data of the moth.

Therefore, we conducted this study to investigate the occurrence patterns of pine caterpillar in historical records and recent monitoring data using time series analysis approaches. Specifically, our aims were to explore the following aspects: (1) whether an increase in growing stock and air temperature affects the occurrence or outbreak of the pine caterpillar in recent data, (2) the occurrence periodicity of the pine caterpillar in both historical records and recent monitoring data, (3) the spatial synchrony of its occurrence at a decadal scale using recent monitoring data, and (4) the potential factors that might impact pine caterpillar outbreaks, based on findings from historical records and recent monitoring data in the Korean Peninsula. This study would improve our understanding of the long-term population dynamics of the pine caterpillar and the cause of its outbreaks related to anthropogenic disturbances.

2. Materials and methods

2.1. Historical and monitoring records of pine caterpillar

We used two different types of occurrence data for the pine caterpillar, viz., historical records in the Goryeosa and AJD from 918 to 1903 and recent monitoring data in South Korea from 1968 to 2005. The Goryeosa and AJD are available in an online database (Korea History Database, http://db.history.go.kr). The occurrence data of pine caterpillar were searched from the database using the keyword “pine caterpillar (송충, 松蟲).” We assumed that the entries for the pine caterpillar in the historical books reflected severe defoliation of pine trees or government responses to such an event. Although various defoliators have been reported in Korea, the pine caterpillar is the only species known to cause large-scale defoliation (Shin et al., 2008). Moths of the genus *Dendrolimus* are distributed across Asia and Europe, with *D. spectabilis* being the primary species in Korea (Kononov et al., 2016). Therefore, these historical records illustrate the occurrence pattern of the pine caterpillar, *D. spectabilis,* outbreaks in the Korean Peninsula over an approximately 1000-year period (918–1903), with the majority of records concentrated near the capitals of the Goryeo and Joseon dynasties.

Although spatial patterns could not be discerned from the historical data and were therefore excluded from spatial analysis, we assumed that the records reliably captured long-term outbreak history despite their spatial limitations and temporal inconsistencies, including gaps caused by war and natural disasters such as the Great Famine.

The Korea Forest Research Institute conducted a monitoring program for the occurrence of major forest insect pests on a nationwide scale in South Korea from 1968 to 2005 (Fig. 1). The monitoring was conducted at 22 monitoring sites two times in May and October each year. Two branches were collected from the upper and lower canopies of pine trees, with a 5-m distance between the sampled trees. The number of pine caterpillar larvae was counted from 20 pine trees at each site, and the length and diameter of the tree branches were measured. The density of pine caterpillar was recorded on the basis of the number of larvae per branch of 100 cm^2. The last occurrence of the pine caterpillar at the monitoring sites was observed in 2000. In our study, the seasonal mean densities from 22 monitoring sites were used in the time series analysis to identify multidecadal occurrence patterns. Density data from 22 monitoring sites were pooled separately for spring and autumn, as annual changes in pine caterpillar density among these 22 sites were similar, depicting high-density in 1970 and 1975, followed by a fluctuation at low density after the 1980s. These data were also used to evaluate the spatial synchrony of pine caterpillar outbreaks across South Korea.

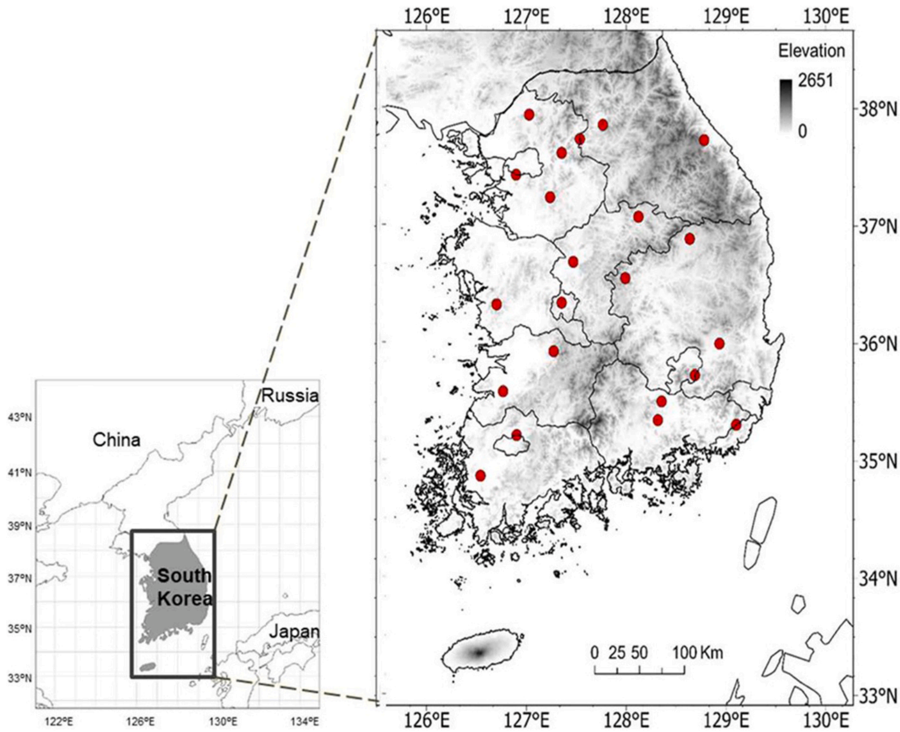

Fig. 1. Monitoring sites for pine caterpillar in South Korea from 1968 to 2005.

2.2. Environmental data

As an indicator of forest change (deforestation and reforestation), data on growing stocks (m^3) in forests were acquired from the literature covering the 1400s–1900s (Bae et al., 2020; Chun, 2022) and 1970s–2010s (Choi et al., 2019). Annually consecutive growing stock information was available from the 1970s–2010s, whereas only estimated growing stock data were available from the 1400s–1900s. The average air temperature data across South Korea, provided by the Korea Meteorological Administration (https://www.weather.go.kr), was utilized as a climate driver.

2.3. Time series analysis

CCM, a statistical test for a cause-and-effect relationship between time series (Sugihara et al., 2012; Sugihara and May 1990), was used to assess the influence of two environmental factors, growing stocks and temperature, on the density of pine caterpillar. CCM addresses the common issue that correlation does not imply causation by detecting whether changes in one variable can reliably predict changes in another, thereby providing evidence of causality (Sugihara et al., 2012). The core concept of CCM is to reconstruct system states from two time series variables and measure their relationship by applying nearest neighbor forecasting (Sugihara and May 1990; Ye et al., 2015).

In the CCM analysis, we used the density of pine caterpillar observed in spring and autumn from 1968 to 2000 (33 time points), and the density was log-transformed as ln $(x + 0.5)$ to stabilize the variance and normalize the data (Kawatsu et al., 2020). To reconstruct the dynamic systems of the time series in the caterpillar density, the optimal embedding dimension (E), representing the number of lagged time steps required to reconstruct the system, was estimated by searching up to E $= 15$, and the optimal E values for both spring and autumn densities were determined based on the simplex prediction skill of each time series (Sugihara et al., 2012). The optimal embedding dimension was estimated using a *EmbedDimension* function in the *rEDM* package (Park et al., 2024) in R (R Core Team, 2024). Then, the causal relationships between the densities of pine caterpillars in spring and autumn and the two variables of growing stocks and temperature were tested.

Cross-map skill (ρ) was computed across increasing library sizes using the optima E values identified separately for spring and autumn densities. At the maximum library size, ρ was compared with the absolute Pearson correlation coefficient between caterpillar density and each environmental variable. A one-sample *t*-test was performed using the *stats* package (R Core Team, 2024) in R (R Core Team, 2024) to assess whether the ρ significantly exceeded the linear correlation, indicating nonlinear predictive capacity. To assess whether the observed ρ could arise by chance, 1000 surrogate time series were generated for each driver using a *SurrogateData* function in the *rEDM* package (Park et al., 2024) in R (R Core Team, 2024). These surrogates retained the statistical properties of the original data while disrupting potential dynamic coupling. The pine caterpillar time series were then analyzed against these surrogates at the maximum library size (Kawatsu et al., 2020). Causal influence was deemed significant when the ρ computed from the original data exceeded the null distribution derived from the surrogates ($p < 0.05$).

To determine the periodic occurrence patterns of pine caterpillar, spectral analysis (Turner et al., 1991) and continuous wavelet transformation (Torrence and Compo, 1998) were applied to both the centurial historical records and decadal monitoring data. Spectral analysis identifies scales of repeated patterns in a contiguous sequence (Turner et al., 1991) and is suitable for analyzing complex information sets, as it is not affected by errors related to the location of the starting point in the data due to its use of sine and cosine transformations (Ripley, 1978). In the case of historical data, periodicity was measured based on presence (outbreak) only data, whereas in recent monitoring data the density of pine caterpillar was used to evaluate the periodicity of pine caterpillar. The spectral analyses were conducted using the statistical software STATISTICA (StatSoft Inc, 2004).

Continuous wavelet transformation is a technique used to extract the dominant features of nonstationary time series by decomposing them into a time-frequency space (Grinsted et al., 2004; Torrence and Compo, 1998). For the historical data, binary data indicating presence (occurrence) or absence (no occurrence) were utilized, while recent monitoring data employed densities recorded in spring and autumn. In analyzing the historical data, periodicities exceeding 200 years were excluded to align with the temporal scope of the dataset. The densities in spring and autumn were determined by using a spline curve with a frequency response of 0.50 and a wavelength corresponding to 0.67 times the series length. For the continuous wavelet transformation, time series were convolved with a base function (Morlet wavelet in this study) to calculate wavelet coefficients each time and frequency. The wavelet power spectrum was then computed by square the wavelet coefficients to examine the signal power for time-frequency space (Torrence and Compo, 1998). The significance of the observed wavelet power spectrum was evaluated using a Monte Carlo method with the background power spectrum (Grinsted et al., 2004). Background power spectrum represents the null hypothesis that given time series is generated by a stationary process. Since pine caterpillar data were temporally auto-correlated, the first-order autoregressive model was used to calculate background power spectrum in this study (Gilman et al., 1963). The χ^2 test was employed to compare differences between the observed wavelet spectrum and background power spectrum (Torrence and Compo, 1998). However, the opposite ends of the continuous wavelet transformation were influenced by the lack of data; hence, the region where the edge effects are statistically significant at the 95 % confidence level was drawn in the wavelet power spectrum (Torrence and Compo, 1998). Continuous wavelet transformation was conducted using a *biwavelet* package (Gouhier et al., 2021) in R (R Core Team, 2024).

2.4. Spatial synchrony analysis

To evaluate the spatial synchrony of pine caterpillar population dynamics in the recent monitoring data, Mantel correlograms (Gouhier and Guichard, 2014) were estimated for caterpillar densities in spring and autumn. The correlograms describe how the spatial correlation of the various sets of time series data depends on the spatial distance separating the monitoring areas and how the spatial correlation at short distances compares with the regional synchrony within the study area (Choi et al., 2011b; Økland and Bjørnstad, 2003). This analysis was conducted using a *synchrony* package (Gouhier and Guichard, 2014) in R (R Core Team, 2024).

3. Results

3.1. Influence of deforestation and temperature

The occurrence frequency of the pine caterpillar from 1100 to 1903 increased in the historical data (Fig. 2A), and its density rapidly decreased after the outbreak in the 1970s in the recent monitoring data (Fig. 2B). The forest growing stock was 100 m^3/ha in the 1400s and gradually decreased to 17 m^3/ha in 1927 (Fig. 2C), after which it remained at $<$ 20 m^3/ha until the 1970s (Fig. 2D). Since the 1970s, the forest growing stock gradually has increased up to 125 m^3/ha in the 2010s, whereas the proportion of coniferous trees has decreased, despite the increase in the growing stock (Fig. 2D). Deforested areas comprised 67.7 % of the total forest in 1910, with pine forests accounting for 53.0 % of this deforested area (Bae et al., 2020). In South Korea, after the Korean War in the 1950s, the growing stock in forests continuously decreased until the 1970s due to the increased demand for wood as the primary fuel source and for construction, driven by the increase in human population.

The optimal embedding dimensions for the recent monitoring data were determined to be three for spring density and one for autumn density. In the CCM plots, the ρ values for growing stock demonstrated convergence as the library size increased, whereas temperature exhibited inconsistent patterns (Fig. 3). Notably, no convergence was observed in the CCM curves for autumn density and temperature. At the maximum library size, ρ values varied across variables and seasons. For the growing stock, ρ values in both spring and autumn were significantly higher than the absolute values of Pearson correlation coefficients. Conversely, for temperature, ρ surpassed the linear correlation only in spring, and was substantially lower in autumn (growing stock → spring density: $t = 69.92$, $df = 99$, $p < 0.001$; spring density → growing stock: $t = -31.70$, $df = 99$, $p = 1.00$; temperature → spring density: $t = 65.57$, $df = 99$, $p < 0.001$; spring density → temperature: $t = -197.72$, $df = 99$, $p = 1.00$; growing stock → autumn density: $t = 129.23$, $df = 99$, $p < 0.001$; autumn density → growing stock: $t = 21.47$, $df = 99$, $p < 0.001$; temperature → autumn density: $t = -99.60$, $df = 99$, $p = 1.00$; autumn density → temperature: $t = -74.84$, $df = 99$, $p = 1.00$). Moreover, ρ values derived from the original growing stock series were significantly higher than those from surrogate series in both spring ($p = 0.001$) and autumn ($p = 0.004$), whereas the temperature series showed no significant difference from the surrogate-based null distribution (spring: $p =$

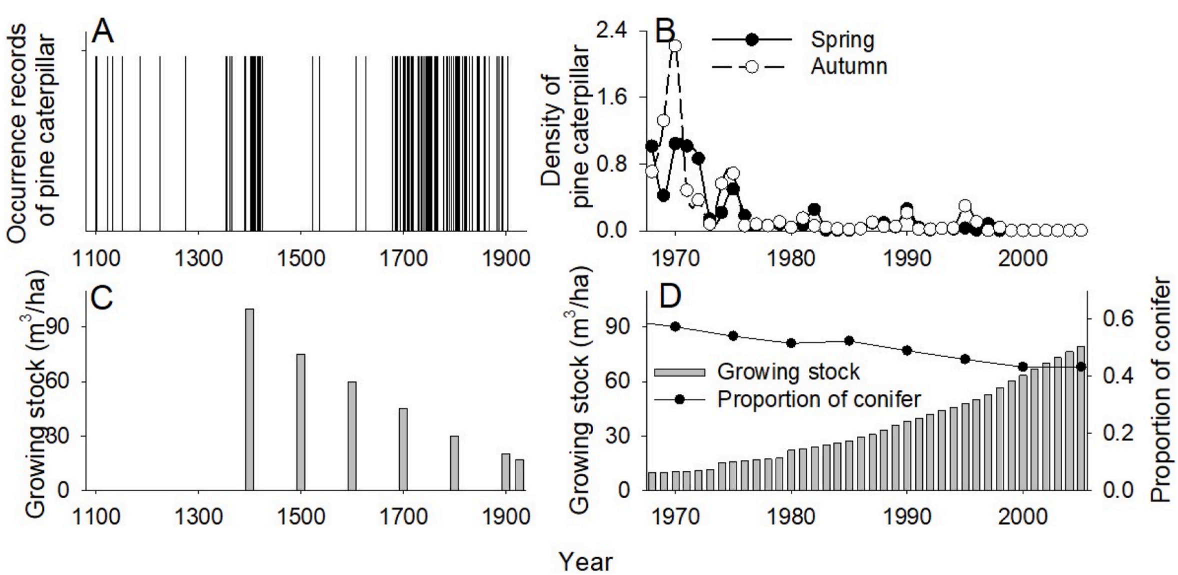

Fig. 2. (A) Occurrence records of pine caterpillar from the History of the Goryeo Dynasty (1100–1392) and the Annals of the Joseon Dynasty (1392–1903) in ancient Korea, (B) annual density changes of pine caterpillar larvae in South Korea in spring and autumn from 1968 to 2015, (C) changes in growing stock (m^3/ha) in the Joseon Dynasty (Bae et al., 2020; Chun, 2022), (D) changes in the growing stock and proportion of coniferous forests in South Korea (Choi et al., 2019).

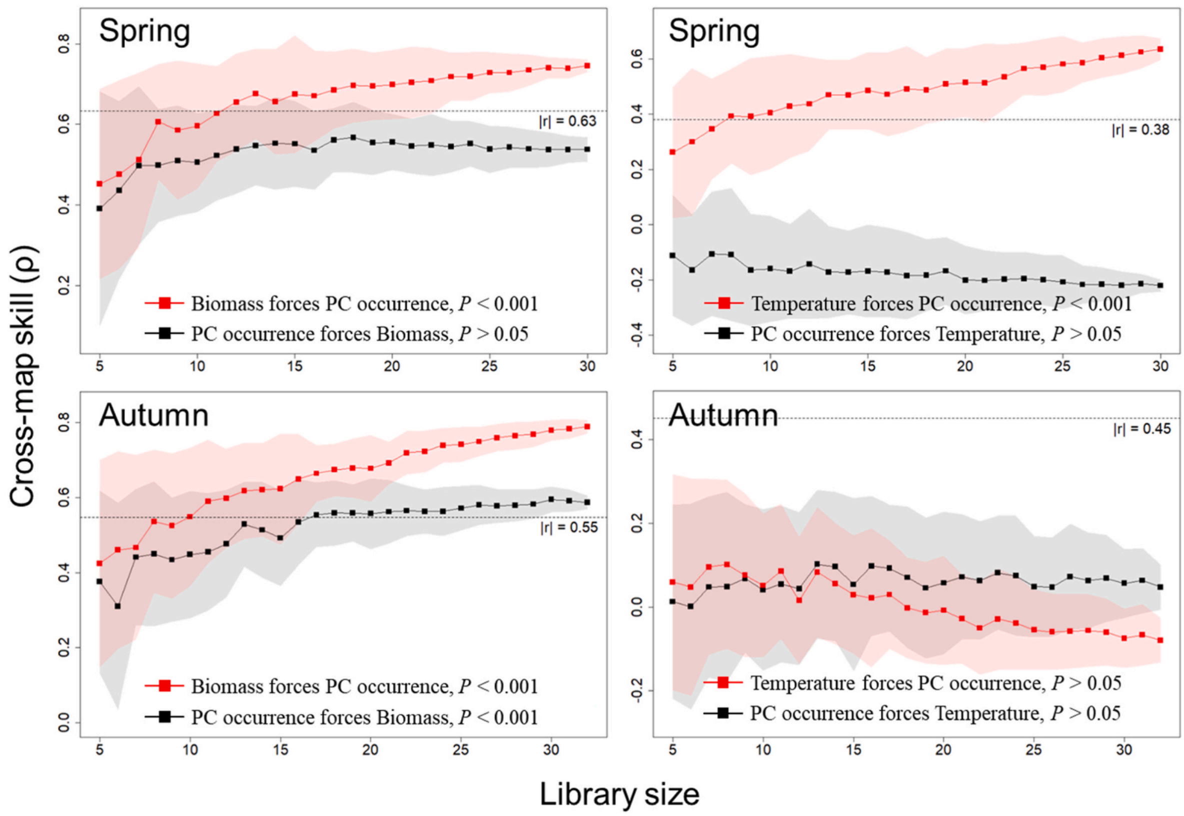

Fig. 3. Convergent cross mapping (CCM) results for the bidirectional relationships between pine caterpillar (PC) and two candidate drivers (Biomass and temperature) across spring and autumn seasons. Curves represent the mean cross-map skill (ρ) ± standard deviation based on 100 bootstrapped samples.

0.772; autumn: $p = 0.360$).

3.2. *Periodicity and spatial synchrony in recent monitoring data*

Recent monitoring data indicated a pine caterpillar outbreak in the 1960s, followed by a significant decline in its outbreaks after the early 1970s (Fig. 2B). The average density of pine caterpillars across the 22 monitoring sites decreased from 2.2 individuals/100 cm^2 in 1970 to 0.7 individuals/100 cm^2 in autumn 1975. Subsequently, the density stabilized to <0.5 individuals/100 cm^2. The spectral analysis estimated periodicities of 3.8 and 5.4 years for the spring and autumn populations, respectively (Fig. 4). Continuous wavelet transformation analysis revealed periodicities of <4 years for the spring population and <7 years for the autumn population (Fig. 5).

The spatial synchrony of the spring and autumn populations exhibited similar trends (Fig. 6). The spatial synchrony of the spring populations was 0.38 ($p < 0.05$) at a lag distance of 21.6 km and −0.24 ($p < 0.05$) at 101.4 km. The spatial synchrony of the autumn population was 0.50, 0.25, and −0.22 at lag distances of 21.6, 44.0, and 101.4 km ($p < 0.05$), respectively (Fig. 6A). Despite the similar trends in the relationships between the Mantel correlation and lag distance for the spring and autumn populations, a damped sine function was only fitted for the autumn population ($r^2 = 0.92$; $df = 3, 6$; $F = 23.06$; $p < 0.05$). The relationship among the spring populations was not fitted to the damped sine function because of asynchrony over a 200-km lag distance ($r^2 = 0.63$; $df = 3, 6$; $F = 3.45$; $p = 0.09$) (Fig. 6B).

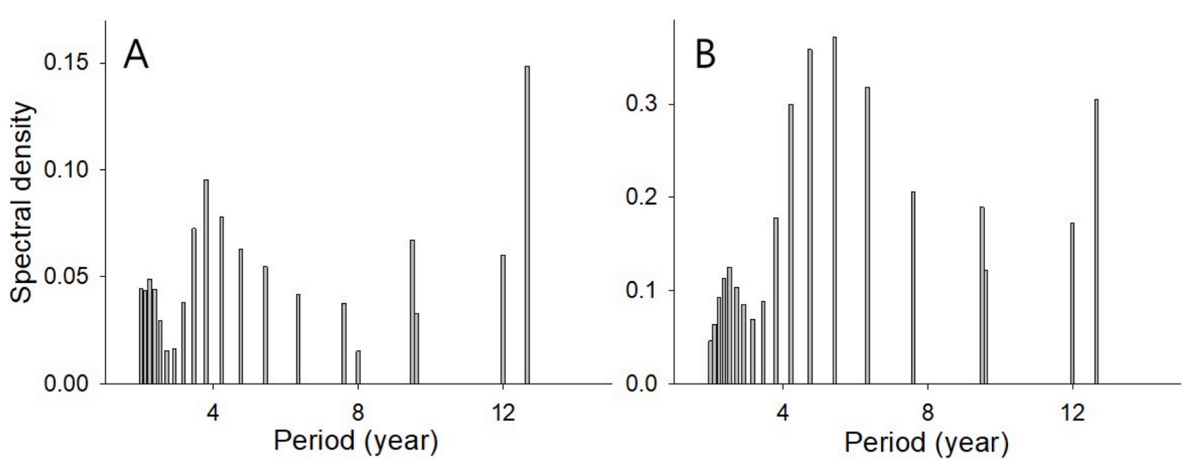

Fig. 4. Spectral density plots for the pine caterpillar in spring (A) and autumn (B) populations from 1968 to 2005.

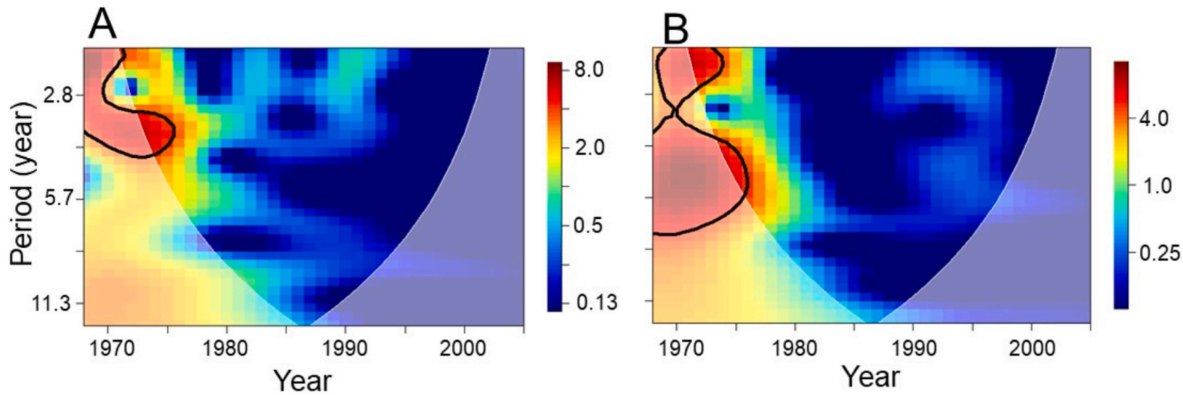

Fig. 5. Continuous wavelet power spectrum of pine caterpillar occurrence in spring (A) and autumn (B) populations from 1968 to 2005. Areas above the white convex line (influence cone) and the surrounded thick contour (in red and yellow color) indicate significant periodicities ($p < 0.05$).

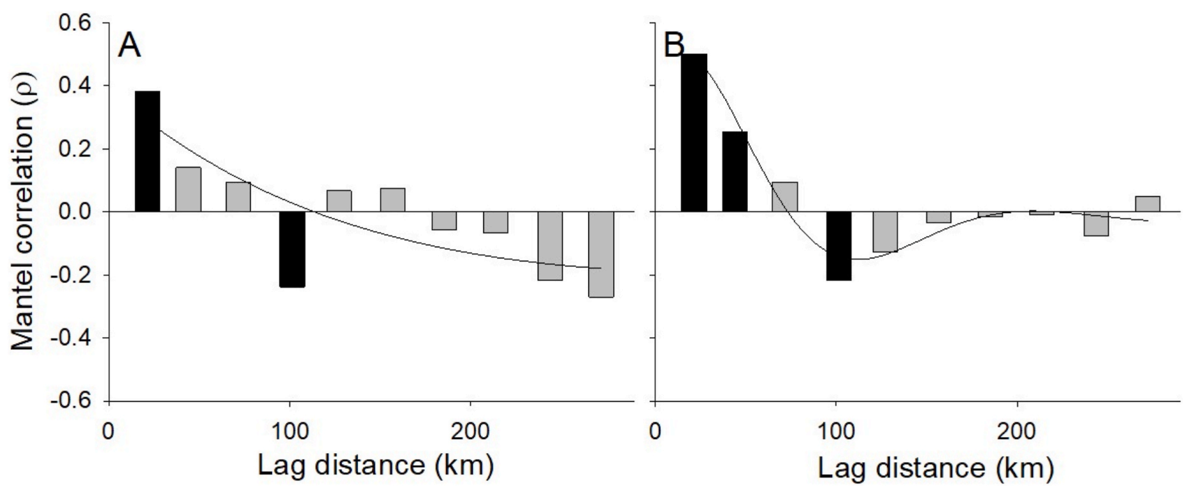

Fig. 6. Spatial synchrony of the pine caterpillar population in spring (A) and autumn (B) from 1970 to 1990. Black bars represent statistically significant levels of synchrony ($p < 0.05$).

3.3. Periodicity of occurrences in historical data

After the first outbreak record of the pine caterpillar in 1101, 110 subsequent occurrences (probably similar to outbreaks) were recorded for 800 years from 1101 to 1903 (Fig. 2A). The frequency of the occurrence varied according to periods as follows: 0.06 times/year with 18 occurrence records for 291 years from 1101 to 1391, 0.50 times/year with 17 occurrence records for only 34 years in the late 1300s and early 1400s, 0.019 times/year with only 5 occurrence records for 254 years between 1426 and 1677, and 0.31 times/year with 70 occurrence records for 224 years from 1678 to the end of these records in 1903 (Fig. 2A).

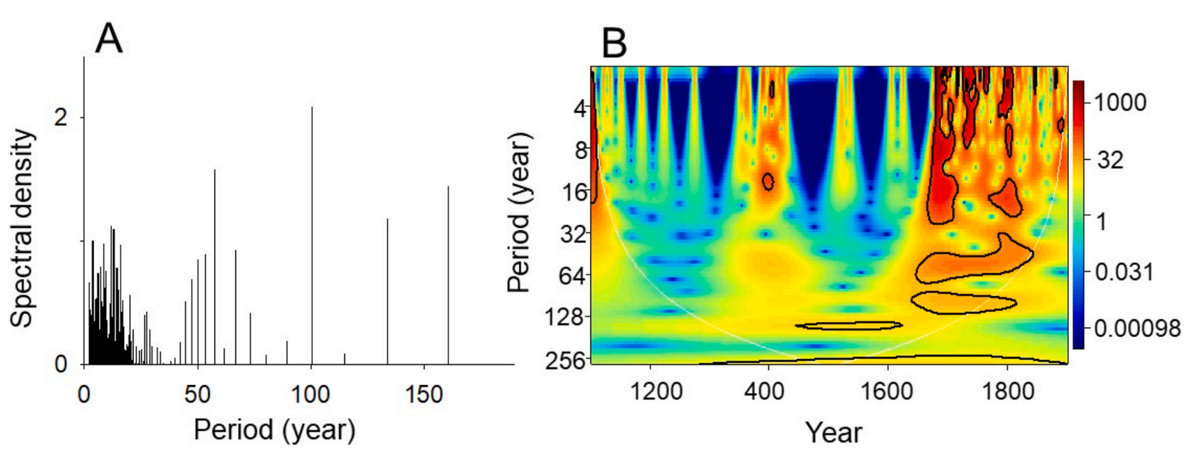

Fig. 7. Spectral density plots (A) and continuous wavelet power spectrum (B) of pine caterpillar occurrences collected from the History of the Goryeo Dynasty (1392–1903) and the Annals of the Joseon Dynasty (1100–1903). Areas above the white convex line (influence cone) and the surrounded thick contour (in red and yellow color) indicate significant periodicities ($p < 0.05$).

Spectral analysis estimated the major occurrence periodicity of the pine caterpillar as every 100.5 years in the historical data (Fig. 7A), followed by 57.4 and 160.8 years of the second and third periodicities, respectively, with several short-term periodicities (Fig. 7A). A long-term periodicity exceeding 100 years and a short-term periodicity of <10 years were identified using continuous wavelet transformation (Fig. 7B). The wavelet plot revealed prominent periodicities, particularly in the 1400s and from 1700 to 1903, consistent with periods when the occurrences of the pine caterpillar were most concentrated.

4. Discussion

4.1. Factors affecting long-term occurrence patterns of pine caterpillars

Deforestation and reforestation might have been significant drivers influencing the long-term outbreak periodicity of the pine caterpillar. Our analysis suggested that these outbreaks were concentrated during the early and mid-1400s, 1700s, 1800s, and early and mid-1900s. The Joseon Dynasty, established in 1392, experienced a renaissance in the 1700s following the Japanese invasion from 1592 to 1598 (http://sillok.history.go.kr). During these periods, it is inferred that forests were intensively exploited for construction and restoration after the war, as well as for fuel sources for home heating during the Little Ice Age. Park and Lee (2007) reported that the Korean red pine was the dominant material used for construction throughout the Joseon Dynasty from 1392 to 1897. The prevalence of pine in wooden materials, reflecting its dominance in vegetation, increased from 73 % in the early Joseon Dynasty (1392–1724) to 88 % by the late Joseon Dynasty (1725–1910). This trend was attributed to human-driven deforestation, followed by the regrowth of pines, which are pioneer species. Overexploitation in the 1700s created favorable conditions for pine forests with younger stands. Furthermore, the Little Ice Age from 1571 provided a more suitable environment for pine trees than for oak species (Yoon et al., 2014). Consequently, the abundance of pine trees, coupled with the pine caterpillar's preference for young trees, likely triggered the outbreaks of pine caterpillar (Kamata, 2002). These outbreaks may have further accelerated deforestation due to foliage loss and tree mortality.

In the contemporary period, from the 1950s to the early 1970s, the Korean red pine was extensively used for home heating, resulting in the consumption of 10 million m^3 of wood annually, including pine wood (Bae and Lee, 2006). The practice of slash-and-burn lumbering expanded until 1967 (Lee and Bae, 2007). Consequently, the heavy harvesting of pine trees led to a stagnation in average annual forest growing stock South Korea until 1972 (Bae, 2009). These disturbances had several impacts on the forest ecosystem: there was an increase in the dominance of young pine trees, a loss of forest area due to intense exploitation and slash-and-burn practices, and a decrease in biodiversity, including natural enemies (Bae et al., 2010; Jactel et al., 2005). During this period, outbreaks of pine caterpillar were frequently reported, with the average density of the pine caterpillar being significantly higher compared to the 1980s and 1990s (Fig. 2A). This forest-use history indicates that human activities altered the long-term periodicity or outbreak frequency of the pine caterpillar (Fig. 8).

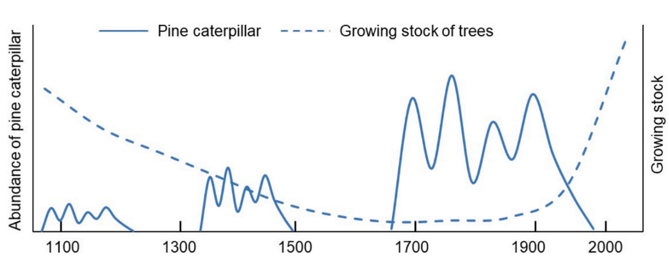

Fig. 8. Schematic of changes in outbreak frequency and growing stock in Korea from 1100 to 2010.

Forest transition influences the frequency and severity of pine caterpillar outbreaks more through indirect effects than direct ones. Deforestation impacts forest structure, biodiversity, and micro-climate within the stand by increasing the dominance of younger trees, causing fragmentation, and reducing biodiversity in both plant and animal, as well as creating drier conditions (Atkins et al., 2023; Chen et al., 1999; Lawrence and Vandecar, 2015). Conversely, increased tree diversity enhances ecosystem resilience against pest damage, as a diverse composition of plants provides physical or chemical barriers (Jactel et al., 2005; Jactel and Brockerhoff, 2007).

Natural enemies play a role in the decline of pine caterpillar population [37], and forest cover influences in shaping the activity of the natural enemies. Greater forest cover correlates with increased abundance and predation activity of natural enemies. For instance, predatory wasps exhibit enhanced activity in areas with more extensive surrounding forest cover [62]. Microclimatic changes associated with deforestation can diminish the effectiveness of natural enemies. This reduction in effectiveness may create conditions more favorable for forest insect outbreaks, with these effects potentially being further amplified by ongoing climate change.

Climate change, particularly the increase in temperature, is a significant driver influencing the population dynamics of forest insects (Pureswaran et al., 2018). The occurrence patterns of the pine caterpillar have likely been influenced by climatic changes, as the pine caterpillar has experienced various climatic periods, including the Medieval Warm Period, the Little Ice Age, and the current warm period (Mann et al., 2009; Matthews and Briffa, 2005; Moberg et al., 2005). The population dynamics of the pine caterpillar are significantly affected by drought conditions in spring and summer, as well as by winter temperatures (Korea Forest Research Institute, 2011; Maeto, 1991; Park and Hyun, 1982), which can lead to periodic variations in outbreak patterns. Climate change has led to an increase in voltinism of the pine caterpillar from univoltine to bivoltine, accompanied by a host switch from the Korean red pine to pitch pine (*Pinus rigida* Mill) in Korea (Choi et al., 2011a). This shift is unfavorable for caterpillar outbreaks, as the fitness of the second generation decreases, likely due to summer heat stress and feeding challenges posed by the hardened needles. In Germany, drought was a major factor driving the outbreaks of *D. pini*, but these outbreaks have likely ceased due to climate change (Haynes et al., 2014). Similarly, while drought was the primary driver of *Dendrolimus* spp. outbreaks, their frequency may decline under future climate change scenarios (RCP 8.5) beyond 2046 (Bao et al., 2020).

The CCM results for pine caterpillar densities indicated a potential causal relationship with growing stocks, whereas temperature was not identified as a significant driver. The ρ values from the original time series of growing stock were significantly higher than those from the null series, suggesting potential causal link between growing stock and pine caterpillar density. The superior performance of ρ values compared to simple linear correlations strengthens the likelihood of a causal link from environmental variables to caterpillar density. However, these findings cannot entirely rule out the possibility that the observed coupling may be due to coincidental co-variation or the influence of unmeasured confounding factors affecting both growing stock and caterpillar dynamics simultaneously. This concern is particularly relevant given the relatively short duration of the time series (33 years), which might limit the statistical power necessary to distinguish true causality from spurious correlations. Consequently, the hypotheses supported by this study require further validation through extended monitoring and experimental approaches to ensure robust conclusions.

4.2. Periodicity in population dynamics of pine caterpillar

The pine caterpillar exhibited occurrence periodicity over both short- and long-term scales. Periodicity in the population dynamics of Lepidoptera has been observed for at least 15 species in North America, Europe, and Asia (Li et al., 2015). For instance, periodicity of the pine processionary moth (*Thaumetopoea pityocampa*) varied from 4 to 11 years among the surveyed areas, and that of *C. pandora* ranged from 9 to 156 years depending on forest stands (Speer et al., 2001). Similarly, the pine caterpillar has a clear periodicity, with shorter periodicity over shorter time scales. Variation in periodicity could be attributed to species and regions as well as the influence of abiotic factors. Myers and Cory (2016) proposed the following three factors required for cyclic population dynamics: 1) high fecundity to allow rapid population growth, 2) density-dependent mortality factors to initiate decline in population at peak density, and 3) delayed-density-dependent mechanisms that prolong population decline. In the context of these three factors, the pine caterpillar appears to have these biological requirements as follows.

(1) *High fertility*: Female pine caterpillars lay approximately 500 eggs (Shin et al., 2008).
(2) *Pathogens*: Pine caterpillar outbreaks are generally terminated by insect pathogens that operate in a density-dependent manner on high-density populations (Kamata, 2002). The termination of local pine caterpillar outbreaks by insect pathogens has been observed in Korea (personal observation).
(3) *Sources of delayed-density-dependent mortality*: Starvation might also play a role in a delayed-density-dependent manner because pine caterpillar outbreaks often completely consume all available pine foliage and then disperse. This requires more time for the dispersing caterpillars to locate and establish new populations after the collapse of high-density populations. This process probably functions as a delayed-density-dependent mechanism affecting mortality.

4.3. Spatial synchrony of the pine caterpillar

Positive spatial synchrony in pine caterpillar occurrences was evident only at inter-site distances of <50 km (Fig. 6). This phenomenon has been observed over a range of 1–1000 km depending on the species involved (Liebhold et al., 2004). Spatial synchrony is believed to arise from any of the following mechanisms: dispersal between populations, Moran (environmental) effects, and trophic interactions (Walter et al., 2017). For instance, the spatial synchrony of *Thecodiplosis japonensis* in South Korea occurred over several hundred kilometers, with Moran effects such as maximum temperature and precipitation being the primary drivers of this synchrony (Choi et al., 2011b).

The dispersal capacity of the pine caterpillar was not well understood, but it was estimated to be approximately 15–50 km based on the dispersal capacity of *D. sibiricus*, a species similar in size to the pine caterpillar (EFSA PLH Panel et al., 2018). Among environmental factors, precipitation was the major mortality factor of the pine caterpillar. In South Korea, August precipitation significantly influenced pine caterpillar population density by increasing mortality among younger larvae (Park and Hyun, 1982). In Japan, precipitation caused 70 %–80 % mortality in the first two instars of the pine caterpillar (Kokubo, 1965). The local-scale synchrony of pine caterpillars in South Korea is likely due to the localized nature of August precipitation, which does not occur over widespread areas. During the early 1970s, the role of natural enemies in controlling pine caterpillar populations was limited, and therefore, their influence on spatial synchrony appeared to be minimal.

4.4. Limitation of the study

Although our results showed long-term occurrence trends of the pine caterpillar in accordance with forest transition, uncertainty existed due to limitations in data and assumption of analytical methods. The historical records might be influenced and biased by the social and political conditions in the recording time. The inconsistency of historical data might influence the periodicity of pine caterpillar outbreaks to some extent. The occurrences of the pine caterpillar were concentrated in the 1400s and from the 1700s–1900s. It is possible that during or after the Mongolian invasion (1231–1270) in the Goryeo Dynasty and the Japanese invasion (1592–1598) in the Joeseon Dynasty, pine caterpillar outbreaks had received less attention. Moreover, the policy of the Joseon Dynasty to protect pine forests after their establishment could contribute to the suppression of extensive pine caterpillar outbreaks. However, the historical records of the pine caterpillar remain useful to our understanding of the long-term occurrence history of the moth in Korea.

Temporal concentration in data frequency affected stationary of spectral analysis. In contemporary, density of the pine caterpillar dramatically stabilized after early 1970s, and this trend might affect our results although the data was detrended. Moreover, time series length was limited because the pine caterpillars were rarely detected after the early 1980s in the monitoring plots. Moreover, the periodicity of contemporary was only observed in the early 1970s. Due to the relatively short time series length, the ability of CCM to reliably detect causality is constrained. Probably the reason of bidirectional causality of growing stock on autumn density of the caterpillar was attributed to limited length of time series.

Climate change significantly influences population dynamics. However, in our study, air temperature was not the primary factor driving pine caterpillar outbreaks, even though there was some correlation between temperature changes and caterpillar populations. This discrepancy might stem from the nature of the temperature data, which was sourced from weather stations near, but not at, the monitoring sites. Consequently, further research is needed to gain a more comprehensive understanding of the relationship between climate and caterpillar outbreaks, utilizing more detailed biological and meteorological data.

5. Conclusions

Our analysis of both historical and recent monitoring data has provided significant insights into the occurrence patterns of the pine caterpillar. These caterpillar population exhibits periodicities on both short- and long-term scales, with short-term cycles of less than 10 years and long-term cycles exceeding 100 years. These patterns were especially evident during periods of heightened occurrence frequency or density. Notably, the short-term cycles were most pronounced in the early 1970s, while the long-term cycles were primarily observed from the late 1600s to the 1800s, a period characterized by severe deforestation. The positive spatial synchrony of caterpillar occurrences was limited to areas within 50 km, highlighting the localized nature of these impacts. Additionally, an inverse relationship was observed between long-term trends in growing stock and pine caterpillar outbreaks. Our study highlights that high outbreak frequencies and caterpillar density were closely linked to extensive deforestation, primarily driven by human activities. Conversely, reforestation (increased growing stock) has played a crucial role in mitigating these outbreaks, underscoring the significant impact of human-induced habitat changes on the dynamics of pine caterpillar populations. Forest recovery fosters conditions that are less conducive to caterpillar proliferation, thereby enhancing the resilience of forest ecosystems. Consequently, afforestation emerges as a vital strategy for stabilizing pine caterpillar populations and reducing outbreak occurrences. Furthermore, this research emphasizes the importance of ongoing studies into the effects of climate on pine caterpillar population dynamics. Understanding these intricate patterns is essential for developing effective forest management strategies aimed at mitigating the future impacts of these outbreaks.

CRediT authorship contribution statement

Won Il Choi: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Jong Bin Jung:** Writing – review & editing, Writing – original draft, Formal analysis. **Min-Jung Kim:** Writing – review & editing, Formal analysis, Data curation. **Tae-Sung Kwon:** Writing – review & editing, Data curation. **Young-Seuk Park:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Availability of data

Data are provided in the paper.

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