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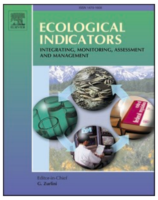

Biotic interactions outweigh direct climate effects in shaping subarctic mountain birch ecosystem: Insights from four decades of integrated monitoring

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ABSTRACT

High-latitude ecosystems are undergoing rapid climate warming, yet long-term ecological response remain poorly understood due to the scarcity of sustained monitoring records. We analyse a unique 40-year dataset from a subarctic mountain birch (*Betula pubescens* ssp. *czerepanovii*) ecosystem in northern Fennoscandia, integrating climate, plant reproduction, insect herbivory, phenology, and large herbivore performance. Mean annual temperature increased by 0.6 °C per decade since 1981. Despite strong warming signal, ecosystem dynamics were dominated by cyclic biotic interactions rather than linear effects of climate warming. Birch reproductive indicators (pollen accumulation rate and catkin production) and reindeer calving success exhibited 2–4-year cycles, while geometrid moth populations showed recurrent ~10-year outbreak dynamics. While warming weakly correlates with birch reproduction, it is strongly associated with increased moth abundance, establishment of the previously temperature-limited winter moth, and reindeer calving success. Moth outbreaks, combined with reindeer grazing pressure, led to birch defoliation and delayed post-outbreak recovery lasting 6–8 years. Potential positive effect of climate warming on mountain birch reproduction in subarctic ecosystem is, therefore, largely counterbalanced by increased herbivory pressure. Birch flowering and moth larval emergence phenology remained tightly synchronized, with no detectable phenological mismatch under warming. This indicates substantial phenological plasticity, likely reflecting adaptation to historically high interannual climate variability. Our results demonstrate that climate impacts in subarctic ecosystems are best captured by multi-trophic biotic indicators reflecting trophic interactions, disturbance regimes, and species redistribution. We highlight the critical role of long-term monitoring for adaptive ecosystem management planning under continued climate change.

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1. Introduction

Recent climate change affects ecosystems through changes in both mean conditions and variability (Malhi et al., 2020). High-latitude regions are warming faster than the global average (Rantanen et al., 2022), with cascading effects on species-poor ecosystems where key taxa disproportionately influence ecosystem structure (Manna et al., 2022). Furthermore, the structure and function of subarctic ecosystems is mediated by a complex interaction among several abiotic and biotic variables and the effects of climatic warming can be buffered by factors like moisture availability, species interactions, successional traits, and phenology (Lu et al., 2025).

In Fennoscandia, the mountain birch (*Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti, or var. *pumila* (L.) Govaerts, *formerly* ssp. *tortuosa* (Ledeb.) Nyman) forms the subarctic tree line, interacting critically with herbivores: geometrid moths and semi-domesticated reindeer (*Rangifer tarandus* (Linnaeus)). While warming may facilitate birch expansion upward in mountains and northward, its southern limits face pressure from boreal conifers (*Pinus sylvestris* (L.) and *Picea abies* (L.) H. Karst.) and silver birch (*Betula pendula* Roth) (Saikkonen et al., 2025; Tømmervik et al., 2009). Strong connection between increasing temperatures, pollen production, investment into reproduction (the number of flowers, pollen and seed production) and pollination season duration has been observed at high northern latitudes (Zhang et al., 2014; Ziska et al., 2019). Ongoing aerobiological pollen monitoring provides critical multi-decadal records of these reproductive responses (Myszkowska, 2020), complementing ground observations.

Birch biomass may be expected to increase as a direct consequence of climate warming (Rundqvist et al., 2011), but its growth may be constrained by need for intensified defence allocation against herbivory (Meyer et al., 2021) resulting in nonlinear responses to warming (Post et al., 2019; Severova and Volkova, 2017; Skre et al., 2005; Yli-Panula et al., 2009; Zhang and Steiner, 2022). Changes in herbivore dynamics, intensifying moth outbreaks and fluctuating reindeer grazing, could amplify or offset these climate-driven shifts necessitating long-term data to disentangle interactions.

The autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*) cause large-scale birch defoliations (Blackburn et al., 2020; Jepsen et al., 2008, 2009). Likewise, reindeer exert continuous grazing pressure that can either constrain or facilitate birch regeneration depending on density and management practices (Kumpula et al., 2011; Sisenis et al., 2016). How these biotic interactions collectively mediate birch reproductive processes and ecosystem responses to rapid warming remains a major open question in subarctic ecology.

To address this gap, we utilize a unique 40-year dataset from the Kevo Subarctic Research Station encompassing climate, phenological, and population data for birch, geometrid moths, and reindeer. This unprecedented temporal coverage enables detection of feedbacks and delayed responses that shorter datasets overlook.

We hypothesize that warming climate modifies the dynamics of the mountain birch ecosystem primarily through altered herbivore pressures rather than direct physiological responses to temperature. Accordingly, we ask:

1. How does climate warming influence subarctic ecosystem components and phenology?
2. Is the effect of climate warming on mountain birch mediated by biotic interactions?
3. Are any cyclic or lagged relationships linking birch, moths, and reindeer over time?

2. Material and methods

2.1. Study area

The Kevo Research Station of the University of Turku is situated at the edge of the Kevo Strict Nature Reserve, northern Lapland, Finland (69°45′N, 27°01′E). The region is characterized by a moderately hilly landscape (Fig. 1). The station is situated in the subarctic mountain birch forest zone, about 60 km north of the continuous Scots pine (*Pinus sylvestris* L.) forest line. The main distribution area of downy birch (*B. pubescens* Ehrh.) lies about 100 km south of Kevo, and that of pendulate birch (*B. pendula*) about 60 km south. The mountain birch is cold tolerant, and forms open woodlands (Fig. 1c), with sparse tree cover around Kevo. In favourable microclimatic conditions scattered stands of Scots pine and downy birch occur. The vegetation composition of the area is influenced by elevation, with mountain birch forests at lower elevations (up to about 200 m a.s.l) and shrub-tundra communities including dwarf birch prevailing at higher elevations (above about 300 m a.s.l). Here we explore long-term monitoring datasets (Fig. 1, Table 1, Table S1) from northern Lapland collected between 1981 and 2020.

2.2. *Mountain birch*

Birch pollen accumulation was monitored using three methods: a Burkard trap, a Tauber trap, and a sediment core from Lake Kevojärvi (Table 1, Fig. 1d, Table S1, S2). These monitoring series cover different time periods (Table S1). In Tauber trap, birch pollen was identified as three types: dwarf birch (*Betula nana* L), mountain birch, and tree-form birch (*B. pubescens* Ehrh. and *B. pendula*). While pollen from the Burkard sampler and sediment core was identified only at the genus level (*Betula* spp.) the results are highly correlated ($R = 0.74$, $p < 0.0001$) with mountain birch recorded in Tauber trap suggesting that most of recorded birch pollen is originated from the locally dominant mountain birch. However, it should be kept in mind that the dataset may also contain some pollen from dwarf birch and, less frequently, from tree-form birch common south of Kevo. To ensure consistency, we use the term pollen accumulation rate (PAR) for all datasets, though methods differ: the Burkard sampler measures airborne pollen grains per m^3 of air, while the Tauber trap and sediment core record annual deposition per cm^2.

Mountain birch flower (catkin) production was not recorded. However, male catkin counts for downy birch, the parent species of mountain birch, have been monitored annually since 1979 at six sites in northern Lapland (Table 1, Fig. 1a, Table S1, S2). At each site, about 50 mature trees are surveyed in autumn after leaf fall, with catkins counted visually using binoculars. Given the strong synchrony in birch flowering across species in Finland (Gallego Zamorano et al., 2016; Ranta et al., 2008), we use the average catkin count from these sites as a proxy for mountain birch catkin abundance in northern Lapland.

Henceforth these datasets are referred as follows: PAR_{Burk} (birch pollen data collected using Burkard sampler), PAR_{Taub} (birch pollen data collected using Tauber trap), PAR_{Sed} (birch pollen data collected from sediment core); CATKIN (number of catkins).

2.3. Geometrid moths

Both monitored geometrid moth species at Kevo, the autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*) are univoltine. Adult moth abundance was monitored since 1971 close to the Kevo Research Station (Table 1, Fig. 1d) using Jalas-type light traps (Jalas, 1960). One to four traps (Aitarysä, Suorysä, Saunarysä, Rantarysä; Fig. 1d) operated from late May to late September or early October. From 1971 to 2011, traps used 500 W mercury-vapor lamps placed 50–70 cm above ground; in 2012 (Aitarysä) and 2013 (Suorysä), lamps were changed to 250 W. Traps were emptied weekly, and all moths were identified and counted. Moth abundance was characterized by the annual mean count across traps. Autumnal moth catches included

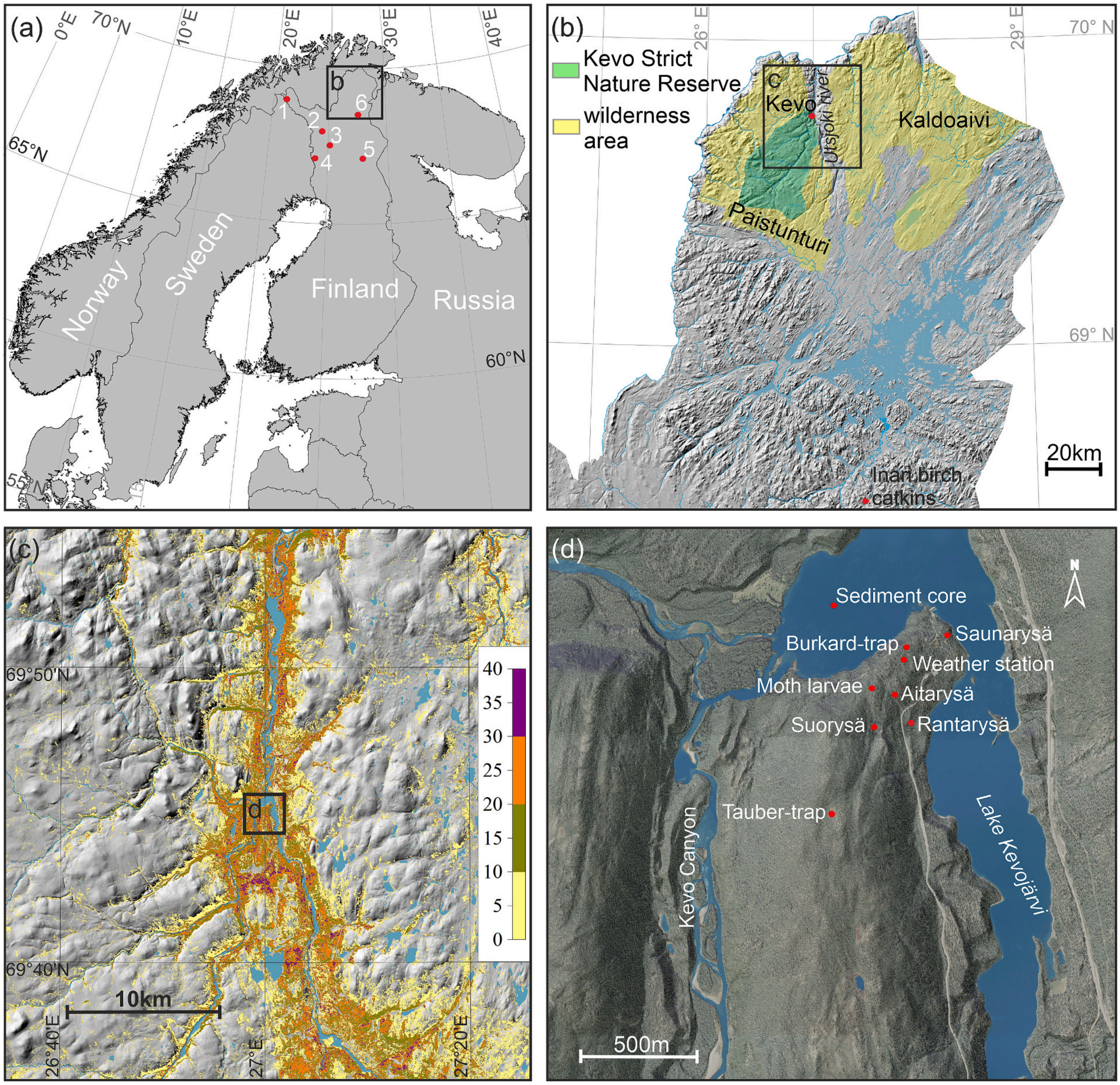


Fig. 1. Overview map (a) and shaded relief map of northern Lapland, Finland (b). Mountain birch volume in m^3 per hectare (Natural Resources Institute Finland, 2022) around the Kevo Research Station (c). Detailed map of the study area at the Kevo Research Station (d), monitoring sites are marked with red points. Maps and orthophotos are derived from the National Land Survey of Finland Topographic Database 04/2022. Downy birch catkin monitoring sites (a): 1 Enontekiö, 2 Kittilä I, 3 Kittilä II, 4 Kolari, 5 Pelkosenniemi, 6 Inari. Geometrid moth adult light traps (d): Aitarysä, Suorysä, Saunarysä and Rantarysä. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

both sexes; winter moth catches included only males, as females are wingless. Since 1987, autumnal moth larval abundance has also been recorded by counting larvae found in 10 min within an approximately 1 ha mountain birch plot (Ruohomäki, 1992). Larval counts reflect local densities, while adult catches represent a broader area.

Henceforth these datasets are referred as follows: OB_{adults} (number of adult winter moths), EA_{adults} (number of adult autumnal moths), and EA_{larvae} (number of autumnal moth larvae).

2.4. Reindeer

The size, gender and age composition of semi-domesticated reindeer (*Rangifer tarandus*) herds of the Kaldoaivi and Paistunturi herding co-operatives are monitored annually in the Kaldoaivi and Paistunturi wilderness areas (Table 1, Fig. 1b). The number of overwintering reindeer in each reindeer herding cooperative is regulated by the state, with the permitted maximum renegotiated every ten years. Since the 1990s, the maximum allowed has been 5300 overwintering reindeer in Kaldoaivi and 6300 in Paistunturi (Finlex, 2020)). To assess changes in reindeer well-being independent of state-imposed herd size limits, we used calving percentage (calves per 100 female) (Vuojala-Magga and Turunen, 2015). Data for 1981–2020 were obtained from the official statistics of the Reindeer Herders' Association (https://paliskunnat.fi/reindeer-herders-association/). Henceforth, the calving percentage will be referred to as CALV%.

2.5. Meteorological data

The Finnish Meteorological Institute (FMI) Kevo weather station (Table 1, Fig. 1d), established in 1962, records key climate parameters such as temperature, precipitation, radiation, and wind speed. Daily maximum (TD_{max}) and minimum (TD_{min}) temperatures, as well as monthly temperature data for 1980–2020, were obtained from FMI website (en.ilmatieteenlaitos.fi/weather/utsjoki/kevo). Mean annual

Table 1
List of the used monitoring datasets.

Monitoring dataset		Geographical coordinates	Elevation (m asl)	Observation time span	Principal investigator	–
Birch pollen accumulation rate (PAR)*(Betula* spp.: *B. pubescens* ssp. *czerepanoviiB . nana, B. pendulaB. pubescens)*	Burkard-trap	69°45′24″ 27°00′24”	102	1974 - ongoing	Annika Saarto	
	Tauber-trap	69°45′00″ 26°59′53”	184	1981 - ongoing	Anneli Poska Sheila Hicks	
	Sediment core	69°45′30″ 26°59′54”	75	1984–2011	Olga Lisitsyna Saija Saarni Timo Saarinen	
Leaf budburst ‘LEAF$_{budburst}$’**; and flowering onset** ‘FLOWER$_{onset}$’ **of mountain birch** *(B. pubescens* ssp. *czerepanovii)*		69°45′ 27°01′	93–115	1977 - ongoing	Elina Vainio	
No. of downy birch (*B. pubescens*) **catkins** ‘CATKIN’	Inari	68°29′50″ 27°28′02”	206	1979 - ongoing	Pekka Helenius	
	Enontekiö	69°01′08″ 20°53′18”	522	1979 - ongoing	Pekka Helenius	
	Kittilä I	67°44′11″ 24°57′19”	207	1979 - ongoing	Pekka Helenius	
	Kittilä II	68°00′14″ 24°16′59”	304	1979 - ongoing	Pekka Helenius	
	Kolari	67°09′59″ 23°43′37”	178	1999 - ongoing	Pekka Helenius	
	Pelkosenniemi	67°05′37″ 28°05′27”	246	1994 - ongoing	Pekka Helenius	
No of autumnal moth (*Epirrita autumnata*) **and winter moth** (*Operophtera brumata*)	Autumnal moth adults ‘EA$_{adults}$’	69°45′18″ 27°00′09”	113	1972 -ongoing	Tommi Andersson	
	Winter moth adults ‘OB$_{adults}$’				Seppo Kopponen	
	Autumnal moth larvae ‘EA$_{larvae}$’	69°45′18″ 27°00′09”	113	1987 - ongoing	Kai Ruohomäki	
Proportion of female reindeer (*Rangifer tarandus*) **with calves at wilderness areas Kaldoaivi and Paistunturi** CALV%			30–500	1981–2020	Reindeer Herders' Association	
Meteorological data	**Mean annual temperature** ‘MAT’ **Degree days > 5 °C** ‘DD5’ **Days below −36 °C** ‘FREEZ$_{<-36°C}$’	69°45′22″ 27°00′22”	107	1962 - ongoing	University of Turku Finnish Meteorological Institute	

temperature (MAT) was calculated from monthly averages and is used to represent overall climate change. Annual heat accumulation, expressed as the annual sum of degree days above 5 °C (DD5), was calculated as (TD_{max} + TD_{min})/2–5. DD5 is linked to phenological events, such as geometrid moth hatching (Fält-Nardmann et al., 2016), plant productivity (Chmura et al., 2019; Ercan et al., 2020) and, pollen production (Hicks, 2001). Days with winter temperatures below −36 °C, which are lethal for overwintering geometrid moth eggs (Tenow and Nilssen, 1990), were counted using daily temperature records.

Henceforth these datasets are referred as follows: MAT (mean annual temperature in °C), DD5 (annual sum of degree days above 5 °C), and FREEZ$_{<-36°C}$ (number of days with temperature below −36 °C).

2.6. Phenological data

Mountain birch leaf budburst (since 1980) and flowering onset (since 1977) dates were recorded near the Kevo Research Station (Table 1, Table S1, S2). Leaf budburst was observed at the stand level and, since 1997, by monitoring 1–15 trees at least twice a week. Flowering onset was determined similarly. Fält-Nardmann et al. (2016) showed a strong connection between spring accumulation of DD5 and the hatching of autumnal (DD5 = 54.5) and winter (DD5 = 117.0) moth larvae in northern Finland. To test for climate-driven phenological shifts, we calculated probable hatching dates based on DD5 requirements for both moth species. Furthermore, the offset between expected moth hatching and observed birch budburst dates was calculated to assess potential phenological mismatches. All phenological dates were converted to days since the start of the year for statistical analysis.

Henceforth, the variables above are referred to as: EA$_{hatch}$ (number of days to autumnal moth hatching); OB$_{hatch}$ (number of days to winter moth hatching); LEAF$_{budburst}$ (number of days to mountain birch leaf budburst) and FLOWER$_{onset}$; (number of days to flowering onset of mountain birch); LEAF$_{budburst}$–EA$_{hatch}$ (number of days between leaf budburst of mountain birch and autumnal moth hatching) and LEAF$_{budburst}$–OB$_{hatch}$ (number of days between leaf budburst of mountain birch and winter moth hatching).

2.7. Numerical analyses

All numerical analyses were performed in R version 4.3.1 (The R Core team, 2023). To characterize the major trends in annually highly variable data, the datasets were divided into four decades (1981–1990, 1991–2000, 2001–2010, and 2011–2020) and the mean, minimum, and maximum were calculated for each decade. To visualise and analyse temporal trends in monitoring series we used generalized additive models (GAMs). These models were fitted using the default settings of the ‘gam’ function from the ‘mgcv’ package in R (Wood, 2011).

To detect inherent periodic patterns (e.g., alternating resting and masting years) or those potentially induced by unmeasured factors (such as parasite pressure on moth populations), we analyzed uninterrupted biotic time series (PAR$_{Burk}$, CATKIN, EA$_{adults}$, OB$_{adults}$, and CALV%) with wavelet analysis using the R package ‘WaveletComp’ (Roesch and

Schmidbauer, 2018). Prior to analysis, linear trends were removed by detrending with the package's default LOESS method (span = 0.75). We used the Morlet wavelet to compute the cross-wavelet power spectrum. To assess possible time-lagged associations between biotic variables, we applied the cross-correlation function ‘ccf’ in R to the same detrended datasets used for wavelet analysis.

To examine biotic responses to recent climate warming, we calculated Pearson's pairwise correlations for both within-year and one-year-lagged climatic relationships for all phenological and biotic variables. Right-skewed variables were log10-transformed to approximate normality. Biotic datasets containing zeros were transformed as log (value +1). Additionally, biotic variables were detrended for periodicity identified by the wavelet analysis using the ‘ts’ function in R.

To test for combinatory effects, we used forward stepwise regression (R function ‘lm’) to identify the combination of variables with the greatest explanatory power for each biotic factor. Models were run separately for each biotic variable, using the dataset detrended for cyclicity as in the correlation analysis. All relevant climatic and biotic variables, along with the taxon-specific phenological variables, were considered as explanatory variables in each model.

3. Results

Decadal averages reveal a clear warming trend (Table 2). Between the first (1981–1990) and last (2011−2020) observed decades, the MAT increased by 1.7 °C, while the DD5 rose by 23%. In contrast, PAR_{Burk} and CATKIN were higher during the first two decades (1981–2000) compared to the last two decades (2001−2020).

Generalized additive models (GAMs) indicated significant linear increases in both MAT and DD5 over time (Fig. 2). The EA_{adults} showed three distinct outbreak peaks during the 40-year study period, while OB_{adults} were nearly absent until the late 1990s but have increased sharply since then. The CALV% also rose significantly, reaching its highest values in the most recent decades.

Analysis of periodic patterns using wavelet analysis on detrended data revealed that both PAR_{Burk} and CATKIN exhibited significant two-year cycles, although this periodicity was disrupted during 2000–2010 (Fig. 3). The CALV% showed also a significant two-year periodicity. While EA_{adults} displayed a highly significant 10-year cycle, no significant cycles were observed for OB_{adults}.

The results cross-correlation analysis showed that increases in PAR_{Burk} lagged peaks in EA_{adults} by six years and behind OB_{adults} by eight years (Fig. 4a). Population peaks of EA_{adults} were followed by increases in OB_{adults} after a two-year lag. The significant decrease in CALV% is preceded by 8-years by rise in PAR_{Burk} and has 6-year lag to EA_{adults}.

Within-year correlations (Fig. 4b) demonstrated strong positive relationships between PAR_{Burk}, PAR_{Tauber}, and CATKIN. PAR_{Burk} was weakly but significantly negatively correlated with MAT, while birch PAR sources were positively correlated with the $FREEZ_{<-36^{\circ}C}$. The timing of birch $LEAF_{budburst}$ and $FLOWER_{onset}$ were strongly positively correlated with each other and negatively correlated with both DD5 and MAT. The EA_{adults} and EA_{larvae} were highly correlated (Fig. 4). The abundances of both investigated moth species were positively correlated with DD5 and MAT, while their hatching times were positively correlated with the timing of birch $LEAF_{budburst}$ and $FLOWER_{onset}$. There was no significant correlation between the $FREEZ_{<-36^{\circ}C}$ and geometrid moth abundance. CALV% was positively correlated with DD5, MAT, and the abundances of both moth species.

Analysis of one-year lagged correlations (Fig. 4) revealed that PAR_{Burk} was positively associated with DD5 from the previous year. The abundances of both moth species were significantly correlated with DD5 and MAT from the previous year, while CALV% was negatively correlated with these climate variables from the preceding year.

Finally, stepwise regression analysis identified DD5 (or previous-year DD5) as a key explanatory variable in all models (Table 3). Other predictors included MAT for PAR_{Burk}; the $LEAF_{budburst} – EA_{hatch}$, as well as MAT, for EA_{adults}; $LEAF_{budburst} – OB_{hatch}$ together with CALV%, for OB_{adults}; and OB_{adults} abundance for CALV%.

4. Discussion

The unique four-decade dataset from the subarctic mountain birch ecosystem of northern Fennoscandia provides critical insights into how biotic interactions outweigh direct climate effects in shaping ecosystem dynamics. Accelerated climate warming has been observed at high latitudes (Post et al., 2019; Rantanen et al., 2022), and at Kevo the warming is nearly 0.6 °C per decade, triple the global average. A mean air temperature increase of similar magnitude (0.3–0.5 °C per decade) has been recorded elsewhere in northern Finland (Marshall et al., 2018; Merkouriadi et al., 2017) and attributed to changes in atmospheric circulation patterns with enhanced westerly airflow from the North Atlantic due to changes in the Arctic Oscillation and North Atlantic Oscillation (Irannezhad et al., 2015), which have remained tightly synchronized under warming.

Table 2

Decadal averages of selected biotic and climate parameters and the full range (min…max) of observed values. *Phenology values refer to days since 1st of January.

Variables	1981–1990	1991–2000	2001–2010	2010–2020
Biotic				
PAR_{Burk}	3683 (652...12004)	3715 (572...18139)	1642 (326...6055)	1872 (430...6955)
CATKIN	324 (66...1245)	198 (25...774)	133 (12...245)	149 (22...399)
OB_{adults}	4 (0—24)	2 (0...13)	333 (0...3114)	670 (0...2721)
EA_{adults}	377 (22...1368)	3992 (39...29895)	7380 (88...44644)	3273 (575...11219)
EA_{larvae}	0 (0...0)	1 (0...6)	5 (0...28)	1 (0...2)
CALV%	52 (36...64)	57 (42...71)	76 (69...80)	74 (70...80)
Phenology*				
$LEAF_{budburst}$	160 (143...175)	160 (152...169)	155 (147...169)	152 (144...166)
$FLOWER_{onset}$	162 (142…179)	163 (154…176)	158 (145…170)	157 (148…169)
EA_{hatch}	160 (144…172)	161 (150…170)	153 (145…166)	151 (143…167)
$LEAF_{budb.}–EA_{hatch}$	0 (−4...7)	-1 (−6...2)	2 (−2...7)	0 (−2...3)
OB_{hatch}	173 (156…184)	176 (163…185)	169 (159…178)	166 (153…183)
$LEAF_{budb.}–OA_{hatch}$	−14 (−21…−9)	−16 (−21…-11)	−13 (−20…−9)	−14 (−17…−9)
Climate				
MAT (°C)	−1.9 (−3.7...0.2)	−1.3 (−3.3...0.0)	−0.7 (−2.3...0.2)	−0.2 (−1.5...0.5)
DD5	645 (471...806)	661 (553...781)	758 (544...857)	798 (617...1079)
$FREEZ_{< -36^{\circ}C}$	5 (0...12)	3 (0...11)	2 (0...5)	2 (0...4)

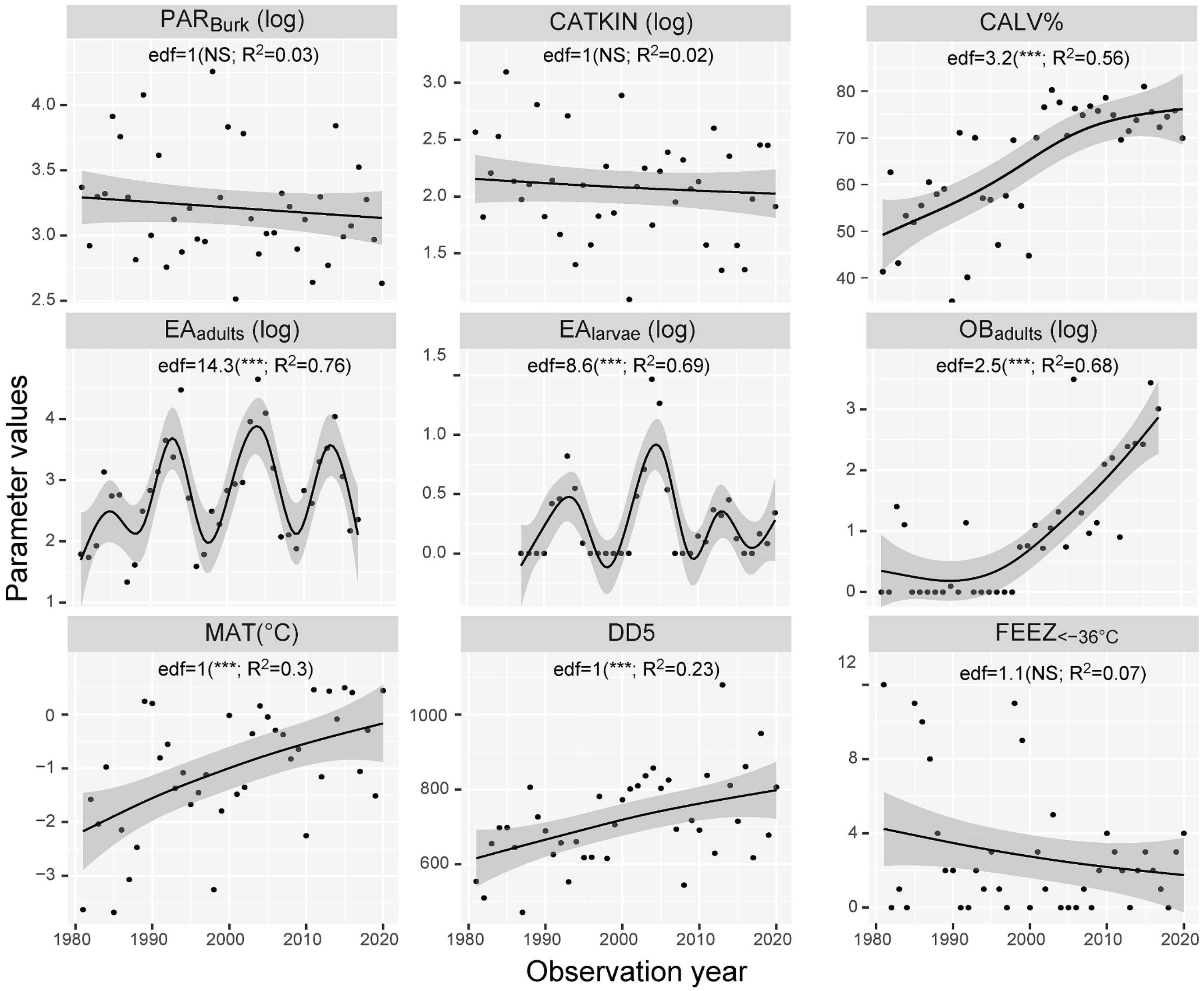


Fig. 2. Changes of biotic and climate variables in time. The black line shows generalized additive model (GAM) fit and the grey area represents the standard error of the GAM. The estimated degrees of freedom (edf) and R^2 value of the GAM fit are shown.

We hypothesized that climate warming alters mountain birch ecosystem dynamics chiefly by changing herbivore pressure, rather than via direct physiological responses to temperature.

Indeed, despite the rapid warming the response of mountain birch reproduction to the warming is relatively weak. The repeated ~10-year moth outbreaks cause severe defoliation and 6–8-year delays in birch flowering recovery. Reindeer calving success increased during first observed decades and stabilized since 2000's at high levels, apparently strongly associated with warmer conditions and adaptive herding practices, even as overall herd size declined. The biotic cycles in birch reproduction, moth outbreaks, and reindeer performance together show that ecosystem dynamics are governed by interacting trophic processes and management, rather than by climate acting directly on birch physiology.

4.1. Climate as a driver of mountain birch population

Recent warming is expected to boost birch biomass and reproduction in the subarctic. In our analyses, the variables related to birch flowering were only weakly linked to climate (Fig. 4) and we did not find expected increase in birch PAR and number of catkins (Fig. 2). However, the importance of climate was highlighted by regression model (Table 3), where previous year's DD5 and flowering years MAT were most significant explanatory variables (Fig. 4 and Table 3). Furthermore, PAR_{Burk} was positively correlated with the previous year's DD5, supporting the idea that summer heat accumulation during flower bud formation influences reproductive output (Hicks, 2001). Overall, weak climate – birch reproduction correlations may reflect offsetting effects of generally increased herbivory, major geometrid outbreaks, and plant competition, which may counteract productivity gains from warming (Callaghan et al., 2013). In Fennoscandia semi-domesticated reindeer grazing keeps landscapes open and controls the deciduous tree line overriding climatic effects (Cairns and Moen, 2004; Forbes et al., 2019; Tenow et al., 2005). A comparable pattern has also been reported from the Himalayas, where early-successional birch (*Betula utilis*) is being progressively displaced by late-successional fir (*Abies spectabilis*), despite expectations of enhanced birch performance (Sigdel et al., 2024). Similarly at Kevo, our personal observations suggest that while shifts in the range of mountain birch are not unambiguously detectable, the recruitment success of Scots pine has increased markedly. Scots pine is less affected by herbivore pressure which can be assumed to give it competitive advantage over the mountain birch.

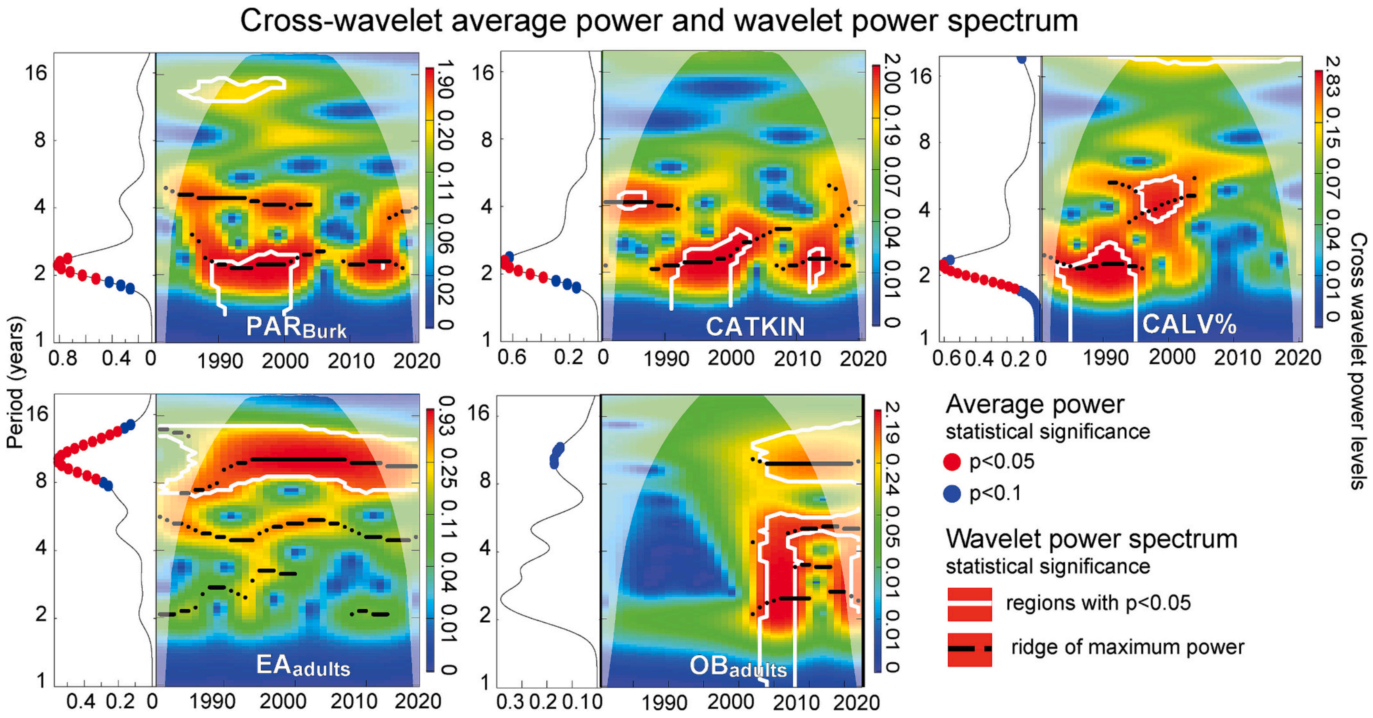


Fig. 3. The timing and signal strength of the periodic changes in selected records detected by Wavelet analysis.

4.2. *Climate as a driver of geometrid moth abundance*

Geometrid moth abundance showed strong positive correlations with temperature variables, particularly DD5 (Fig. 4), likely due to enhanced reproduction and activity in warmer conditions, consistent with studies from northern Sweden (Silfver et al., 2020; Young et al., 2014). While ongoing warming may further increase moth populations, intensifying pressure on birch forests, the rising temperatures could also facilitate the establishment of natural enemies (e.g. parasitoids) of geometrid moth, potentially mirroring southern non-mountainous Fennoscandia where autumnal moths do not reach outbreak levels (Tenow, 1972; Vindstad et al., 2022).

The temperatures below −36 °C, which are lethal to geometrid moth eggs (Tenow and Nilssen, 1990) showed no association with the observed moth abundance (Fig. 4). A probable explanation is that the here tested total number of days below −36 °C is not primarily important as these temperatures are lethal already at first occurrence (Tenow and Nilssen, 1990) making correlations with total number less relevant.

The winter moth, which is more cold-sensitive than the autumnal moth, was historically temperature-restricted at Kevo (Jepsen et al., 2008). Sporadic occurrences of the winter moth began in the 1980s, with consistent records from 1999 and onward, suggesting local establishment of the species. Its abundance is positively correlated with DD5 and MAT, likely reflecting the species' response to climate warming, and this aligns well with its documented expansion into northern birch forests and shrub tundra (Vindstad et al., 2022).

Strong correlations are visible between DD5, MAT, and birch/moth phenology. Moth hatching closely tracks birch budburst and flowering (Fig. 4), driven by similar heat thresholds (Fält-Nardmann et al., 2016). Therefore, despite climate change, phenological plasticity has allowed synchronized responses in birch and moths, with no increase in temporal mismatch.

However, climate warming can lead to further expansion of formerly temperature-restricted generalist consumers (and their predators and parasitoids) (Vindstad et al., 2022) and may enable boreal species, like the scarce umber (*Agriopis aurantiaria* (Hübner)), to colonize subarctic ecosystems. A recent Kevo catch of this species highlights this risk, linked to rising spring temperatures and reduced phenological gaps (Jepsen et al., 2011). With continued warming, such expansions are likely to accelerate, potentially altering ecological balance in the coming decades.

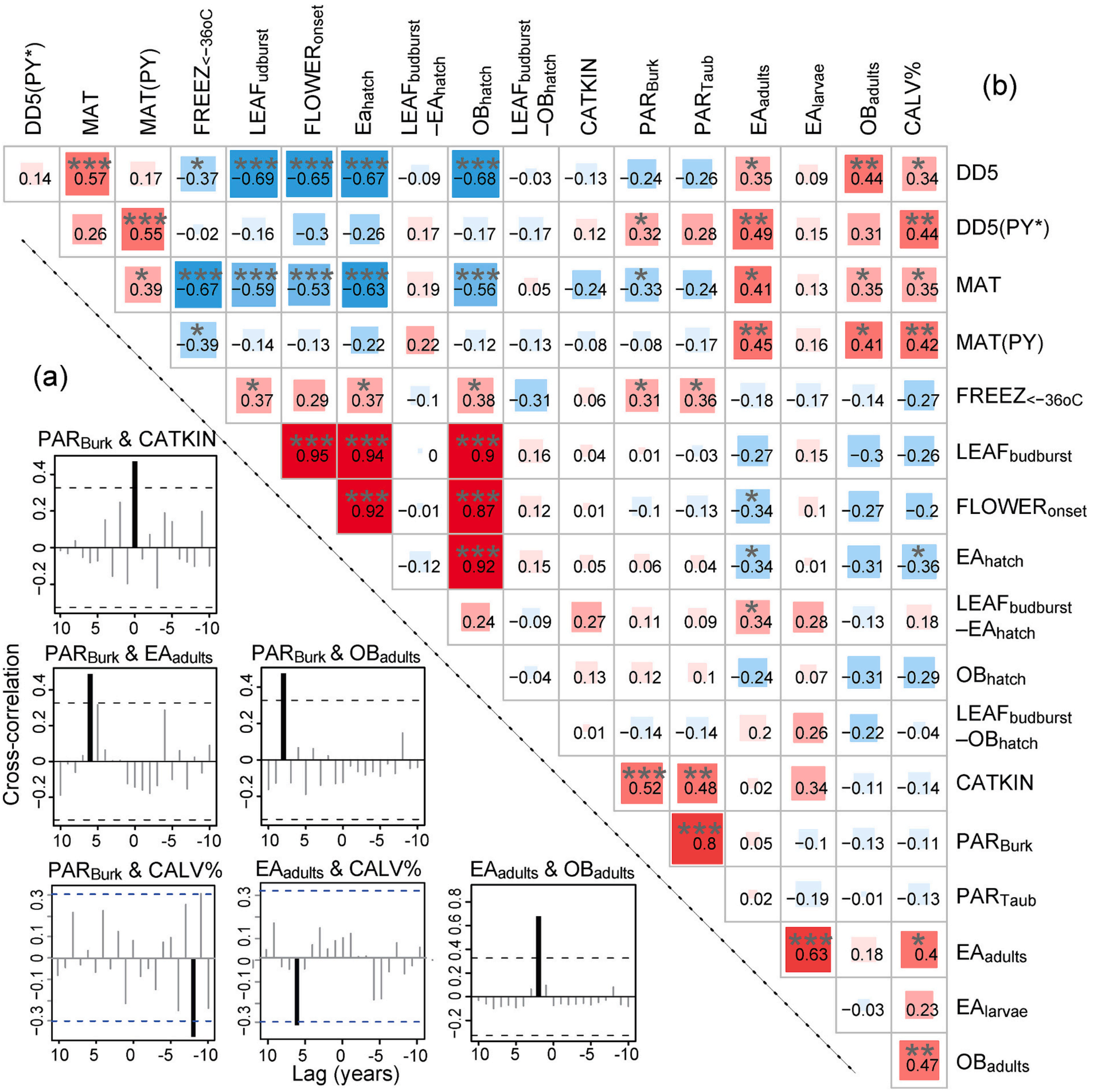
4.3. *Climate as a driver of reindeer well-being*

We used the proportion of females with calves (CALV%) as an indicator of reindeer population well-being under changing climate conditions. Although the overall herd size in the area has declined significantly since its peak in the 1980s, calving percentage has shown a clear positive trend (Vuojala-Magga and Turunen, 2015). Our results confirm a statistically significant increase in CALV% from 1980 to 2010, followed by stabilization during 2010–2020 (Fig. 2, Table 3).

Persistent and significant positive correlations between CALV% and steadily warming climate (MAT, DD5), especially reflecting conditions of the previous year (Fig. 4), suggest a strong association between a warming climate and reindeer populations in the Kevo area. Associations could reflect a general increase in herd well-being resulting from a combination of reduced grazing pressure due to (human-induced) smaller herd sizes and warming-related increase in plant (Kumpula et al., 2014) productivity during the growing season. The early snowmelt due to spring warming, as snow-free vegetation patches in spring have been shown to be important for reindeer calf survival (Helle and Kojola, 2008). However, reindeer responses to climate warming vary across northern Fennoscandia, (Degteva et al., 2024; Mallory and Boyce, 2018; Pape and Löffler, 2012; Rasmus et al., 2020), and satellite-based observations suggest that vegetation density has decreased despite continuing warming in northern Fennoscandia in recent decades (Kumpula et al., 2014).

4.4. *Biotic cycles and their impacts on the mountain birch ecosystem*

Many trees show cyclic reproduction, with prolific flowering years alternating with weaker ones over 2–12-year intervals (Kelly and Sork, 2002; Silvertown, 1980). In our data, 2-year cycles in birch pollen (PAR_{Burk}) and catkin production likely reflect inherent reproductive



	DD5(PY*)	MAT	MAT(PY)	FREEZ<−36oC	LEAFudburst	FLOWERonset	Eahatch	LEAFbudburst −EAhatch	OBhatch	LEAFbudburst −OBhatch	CATKIN	PARBurk	PARTaub	EAadults	EAlarvae	OBadults	CALV%
DD5	0.14	*** 0.57	0.17	* −0.37	*** −0.69	*** −0.65	*** −0.67	−0.09	*** −0.68	−0.03	−0.13	−0.24	−0.26	* 0.35	0.09	** 0.44	* 0.34
DD5(PY*)		0.26	*** 0.55	−0.02	−0.16	−0.3	−0.26	0.17	−0.17	−0.17	0.12	* 0.32	0.28	** 0.49	0.15	0.31	** 0.44
MAT			* 0.39	*** −0.67	*** −0.59	*** −0.53	*** −0.63	0.19	*** −0.56	0.05	−0.24	* −0.33	−0.24	* 0.41	0.13	* 0.35	* 0.35
MAT(PY)				* −0.39	−0.14	−0.13	−0.22	0.22	−0.12	−0.13	−0.08	−0.08	−0.17	** 0.45	0.16	* 0.41	** 0.42
FREEZ<−36oC					* 0.37	0.29	* 0.37	−0.1	* 0.38	−0.31	0.06	* 0.31	* 0.36	−0.18	−0.17	−0.14	−0.27
LEAFbudburst						*** 0.95	*** 0.94	0	*** 0.9	0.16	0.04	0.01	−0.03	−0.27	0.15	−0.3	−0.26
FLOWERonset							*** 0.92	−0.01	*** 0.87	0.12	0.01	−0.1	−0.13	* −0.34	0.1	−0.27	−0.2
EAhatch								−0.12	*** 0.92	0.15	0.05	0.06	0.04	* −0.34	0.01	−0.31	* −0.36
LEAFbudburst −EAhatch									0.24	−0.09	0.27	0.11	0.09	* 0.34	0.28	−0.13	0.18
OBhatch										−0.04	0.13	0.12	0.1	−0.24	0.07	−0.31	−0.29
LEAFbudburst −OBhatch											0.01	−0.14	−0.14	0.2	0.26	−0.22	−0.04
CATKIN												*** 0.52	** 0.48	0.02	0.34	−0.11	−0.14
PARBurk													*** 0.8	0.05	−0.1	−0.13	−0.11
PARTaub														0.02	−0.19	−0.01	−0.13
EAadults															*** 0.63	0.18	* 0.4
EAlarvae																−0.03	0.23
OBadults																	** 0.47

Fig. 4. Cross correlation analysis results: (a) Time dependent cross-correlations between the biotic datasets. The dashed lines mark the limits of statistically significant ($p \leq 0.05$) cross-correlations. The associations exceeding the significance threshold are marked with black columns. (b) Pearson's pairwise correlations for all variables. The red colours mark positive and blue colours negative correlations, the strength of correlation is indicated by intensity of colour. The statistical significance is marked with ***($p < 0.001$), **($p < 0.01$), *($p < 0.05$); (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

strategies, with superimposed 4-year “super-cycles” indicating prolonged recovery after mast years. This pattern was disrupted during 2000–2010, coinciding with consecutive autumnal and winter moth outbreaks, when severe defoliation appears to have overridden the cyclic flowering regime (Hawkes and Sullivan, 2001).

Autumnal moth outbreaks with ~10-year periodicity are well documented across Fennoscandia and are largely regulated by parasitoids (N. Klemola et al., 2010; Klemola et al., 2003). The recent emergence of winter moth populations with similar dynamics suggests shared control, likely parasitoid-mediated, though lagged responses may reflect niche partitioning or differences in parasitoid efficacy (Klemola et al., 2009; Tenow et al., 2007). Comparable 7–11-year cycles have been reported for winter moth in Central Europe (Hittenbeck et al., 2019). Climate warming has probably facilitated the expansion of previously temperature-limited winter moth into continental Lapland, adding another defoliator to this relatively species-poor ecosystem.

Successive autumnal (2002–2004) and winter moth (2006–2009) outbreaks defoliated ~20,000 ha of birch in Utsjoki (Pääkkö et al., 2019), coinciding with sharp declines in birch PAR at Kevo in 2001–2010 and only partial recovery thereafter. Although moth impacts on defoliation and vegetative regeneration are well known (Jepsen et al., 2023; Vindstad et al., 2019a), their effects on sexual reproduction are less studied. Larvae preferentially feed on male catkins (T. Klemola et al., 2010), and links to mast seeding have been proposed (Selås et al., 2001), yet our data, in line with Klemola et al. (2003), do not support a direct relationship. Instead, time-lagged correlations between PAR_{Burk} and autumnal (6-year lag) and winter moth (8-year lag) abundance indicate that flowering recovery takes roughly 6–8 years. While birch can withstand moderate damage (Tenow et al., 2004), severe outbreaks may leave stands treeless for decades, and combined pressure from

Table 3
Forward stepwise selection modelling results. Values mark components of best model, in bold are given statistically significant ones. Significance codes: ‘***’ $p < 0.001$; ‘**’$p < 0.01$; ‘*’ $p < 0.05$; “$p < 0.1$.

Variables	PAR_{Burk}	EA_{adults}	OB_{adults}	CALV%
	$R^2 = 0.25/p = 0.002$	$R^2 = 0.33/p = 0.002$	$R^2 = 0.28/p = 0.001$	$R^2 = 0.30/p = 0.001$
DD5	+	0.27	**0.33***	+
DD5 (PY)	**0.43****	**0.35***	+	**0.35***
MAT	**−0.45****	0.09	+	+
MAT (PY)	+	+	+	+
$FREEZ_{<-36^\circ C}$	+	+	+	+
$LEAF_{budburst}$	+			
$FLOWERING_{onset}$	+			
$LEAF_{budburst} - EA_{hatch}$		**0.30***		
$LEAF_{budburst} - OB_{hatch}$			−0.24	
EA_{hatch}		+		
OB_{hatch}			+	
PAR_{Burk}	~	+	+	+
EA_{adults}	+	~	+	+
OB_{adults}	+	+	~	**0.37***
CALV%	+	+	**0.37***	~

autumnal moth, winter moth, scarce umber, and other herbivores could trigger unforeseen, potentially compound disturbance effects (Vindstad et al., 2019a).

Reindeer is another major herbivore in the system. Decades-long cyclic variation in herd size is known in Fennoscandia (Reinert and Oskal, 2024), but the biannual periodicity in calving success evident in our 40-year record has not been described previously. The 2-year cycles in calving rates before 2000, followed by stable, high success (~75%) thereafter, likely reflect a combined effect of warming and management. Warmer summers (higher DD5/MAT) can improve forage availability and female condition (Paoli et al., 2018), while winter and spring herding with supplementary feeding buffers winter stress (Lee et al., 2000; Vuojala-Magga and Turunen, 2015). Because reindeer in Kevo do not rely primarily on birch foliage but on a broader summer diet and winter lichens, birch PAR and catkin production showed no direct linear correlation with reindeer abundance, even though lichen biomass has declined (Kumpula et al., 2009, 2014). At the same time, rising importance of fodder supplementation (Muuttoranta and Mäki-Tanila, 2012; Tonkopeeva et al., 2024) suggest that current herd numbers exceed the carrying capacity of natural pastures and that grazing pressure is not ecologically sustainable, despite a weak direct linkage to birch reproductive metrics.

4.5. *Notions on data quality*

The exceptional length of our monitoring series enabled the analysis of time-lagged associations in this multi-cyclic biotic system. Although autumnal moth outbreaks follow an approximately 10-year cycle, catastrophic regional outbreaks that devastate mountain birch forests occur only once or twice per century (e.g., 1960s and 2000s in northern Fennoscandia) (Sandén et al., 2020), necessitating even longer monitoring series than available in this study.

The differences between temporal coverage between datasets has limited some analyses (Table S1). We estimate that the change in light trap power (from 500 W to 250 W in 2012/2013) reduced total geometrid moth catches by approximately 1.3-fold in later years, leading to underestimation of moth abundances.

It is important to note that the spatial scales of the datasets vary: while birch pollen and adult moths can theoretically originate from hundreds of kilometres away (Hjelmroos, 1991; Tobin and Blackburn, 2008; Vindstad et al., 2019b), local sources tend to dominate due to exponential decay of dispersal with distance (Poska and Pidek, 2010). Therefore, birch PAR, catkin counts, CALV%, and adult moths reflect conditions in wider northern Lapland, while counts of larvae, phenology, and meteorological data focus on narrower Kevo Research Station area (Fig. 1).

We used pollen accumulation rate (PAR) as birch population proxy, thereby avoiding limitations associated with remote sensing and field-based biomass estimation methods (Li et al., 2020). PAR is an effective proxy of tree biomass when other data are unavailable (Knight et al., 2022; Matthias and Giesecke, 2014; Mazier et al., 2012). Strong correlations between PAR_{Burk} (airborne) and PAR_{Taub} (depositional) (Table 2, Fig. 4) confirm synchronous birch flowering across region (Ranta et al., 2008), with mountain birch as the primary pollen source. The poor correlation between Lake Kevojärvi sediment PAR and trap data can be attributed to several factors like local hydrological condition of sampling site, the continuity and length of the data series and nature of these proxy (Lisitsyna et al., 2012). First, the sediment samples contain a mixture of pollen that arrived both through the air, via water transport and with melting water. Second, strong inflows and the potential for sediment redeposition within the lake can further blur the relationship between yearly local pollen production and what is ultimately recorded in the sediments. Finally, uncertainties in determining the exact timing of sediment deposition introduce additional error, complicating direct comparisons with trap-based records. This aligns with broader European and American studies showing good comparability between different pollen trapping methods (Levetin et al., 2000; Volkova and Severova, 2017), while highlighting sediment-specific methodological challenges (Lisitsyna et al., 2012).

5. Conclusions

This study revealed new multi-trophic interactions that, while expressing plasticity to climate warming, overshadow the effect of climate change on individual species. In subarctic and other harsh environments, trophic interactions might be lower in number but show stronger dependencies due to fewer co-existing species. Understanding these dependencies and interactions is crucial in the evaluation of long-term changes in the composition of subarctic ecosystems. Long-term ecological indicators from the subarctic mountain birch ecosystem at Kevo show that, despite rapid climate warming (~0.6 °C per decade since 1981), ecosystem dynamics are driven mainly by cyclic biotic interactions rather than direct climatic forcing. Temperature indicators (MAT, DD5) associated with moth abundance and the establishment of the previously temperature limited winter moth, while birch reproduction responds weakly to temperature and is strongly influenced by moth herbivory and 6–8 year postoutbreak recovery. The fact that birch and insect phenology have maintained synchrony under warming suggests substantial phenological plasticity in both. The 40-year record reveals distinct but recurring dynamics: birch reproductive output and reindeer calving success follow 2–4 year cycles, whereas geometrid moth populations exhibit ~10 year outbreak periodicity. Reindeer calving success has increased with warmer winters and adaptive management, but widespread winter fodder supplementation implies that current herd sizes exceed the carrying capacity of natural pastures. Overall, the effects of climate warming in subarctic systems are best tracked using multiple biotic indicators that capture trophic interactions, recurrent cycles and disturbance regimes, rather than plant productivity alone.

CRediT authorship contribution statement

Anneli Poska: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Annika Saarto:** Writing – review & editing, Writing – original draft, Resources, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Triin Reitalu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Investigation, Formal analysis. **Jüri Vassiljev:** Writing – review &

editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Olga Lisitsyna:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Tommi Andersson:** Writing – review & editing, Writing – original draft, Validation, Data curation. **Pekka Helenius:** Writing – review & editing, Writing – original draft, Validation, Data curation. **Kai Ruohomäki:** Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Saija Saarni:** Writing – review & editing, Writing – original draft, Resources, Funding acquisition, Data curation. **Timo Saarinen:** Writing – review & editing, Writing – original draft, Funding acquisition, Data curation. **Otso Suominen:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Funding acquisition, Formal analysis, Data curation. **Ilkka Syvänperä:** Writing – review & editing, Writing – original draft, Validation, Data curation. **Elina Vainio:** Writing – review & editing, Writing – original draft, Validation, Data curation. **Sheila Hicks:** Writing – review & editing, Writing – original draft, Methodology, Data curation, Conceptualization.

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.

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Appendix A. Supplementary data

Supplementary data Table S1 (Temporal coverage of monitoring datasets) and Table S2 (Birch related monitoring results) to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.114806.

Data availability

Birch and phenological data is included; Geometrid data is available from authors; Reindeer data is available from Reindeer Herders' Association; Meteorological data is available from the FMI

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