



Winners and losers in subarctic moth communities in a changing climate: Marine regime shifts as predictors for terrestrial insect biomass

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Abstract

1. Understanding the role of climate change in the globally reported declines of insect populations is difficult due to complex interactions between climate and other drivers, such as agricultural practices and changes in land use practices.
2. We focused on subarctic moth communities in northernmost Finland, a region with significant climatic changes and minimal human impact. We use moth species abundance data from 45 years of light-trap monitoring at the Kevo Subarctic Research Institute.
3. TRIM analyses showed a significant positive trend in total moth biomass between 1972 and 2017.
4. There were large differences in biomass trends between different groups based on life-history traits.
5. Seven trait-based groups had significant positive population trends: species pupating early in the season, overwintering as eggs, feeding as larvae on live vascular plants, feeding on both herbaceous and woody plants, species with larvae chewing freely on leaves and those with leaf-rolling larvae, as well as generalists feeding on at least three plant genera.
6. Moths overwintering as larvae, species feeding only on herbaceous plants and specialists feeding on only one plant genus had negative trends.
7. Five groups had no significant trends.
8. Linear mixed models revealed significant correlations between regime shifts in the Baltic Sea and biomass in five moth groups. Temperature and degree-day variables

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were also important. A negative relation between a positive NAO (North Atlantic Oscillation) index in spring and moth biomass was implied.

9. Our results suggest that large-scale oceanic climate patterns, such as regime shifts and the NAO, can be useful proxies for predicting the effects of complex climatic phenomena on terrestrial ecosystems.

KEYWORDS

biomass, climate change, functional groups, long-term monitoring, moths, North Atlantic oscillation, northern Fennoscandia, population trends, regime shifts

INTRODUCTION

Assessing the magnitude and causes of worldwide insect declines is a prominent research focus (e.g., van Klink et al., 2020). A direct, negative human impact on insect populations through changes in land-use practice and agriculture is significant (Outhwaite et al., 2022; Uhler et al., 2021). However, ectotherm invertebrates are also strongly tied to climatic conditions, and anthropogenic climate change affects them in different ways around the globe (e.g., Deutsch et al., 2008; Müller et al., 2023; van Klink et al., 2020). Distinguishing the influence of climate change on insect populations from other anthropogenic factors, such as changes in land-use practice or intensive agriculture (e.g., Fox et al., 2014) and discerning among the effects of different climatic components, remains difficult.

By concentrating on biomass and the level of ecological guilds and functional groups rather than just taxonomic groups or species composition and abundance, the results can be related to the energy flow between trophic levels and ecosystem functions. Grouping species by phenological traits and their resource use helps identify when caterpillars are active and which plants affect their life cycles. It also helps clarify differences in reactions to environmental parameters that may not be seen at a species level (Coulthard et al., 2019; Kozlov et al., 2010). We classified the moths according to six traits, each of which could be affected differently by environmental parameters such as climate change.

First, the life stage in which a moth overwinters may predict how it reacts to climate change (Bale & Hayward, 2010). The feeding caterpillars and the flying adults have different environmental optima, and while, for example, rising temperatures in a certain season may benefit some life stages, they might be detrimental for others. The overwintering stage affects the risk of mismatch with caterpillars and budburst of their host plants at the onset of feeding (Bale & Hayward, 2010; Renner & Zohner, 2018). If spring proceeds very fast, host plants may quickly become unpalatable and nutritionally less valuable for spring-hatching caterpillars as well as species overwintering as larvae and resuming feeding in early spring (Renner & Zohner, 2018). Winter survival may also depend on the overwintering stage. While eggs—usually laid above ground—are relatively insensitive to winter temperatures, cycles of thawing and freezing during a warm winter may be fatal for larvae or pupae in the soil (Lamb et al., 1985; Mattila et al., 2008). A thick snow layer, in contrast, may help isolate these species from extreme winter colds (Lamb et al., 1985; Virtanen &

Neuvonen, 1999). Likewise, as a second classification criterion, species pupating early and late in the season may have different environmental preferences.

Third, the effect of weather parameters may also be conveyed to moths through the type of host plant that their caterpillars feed on (Altermatt, 2010). Temperature parameters during the feeding season may be of great relevance for species that are feeding on rapidly growing leaves of vascular plants to avoid mismatches between caterpillar and host (Renner & Zohner, 2018). Meanwhile, species feeding on mosses, lichens or fungi may not be as sensitive to temperature. Precipitation is also known to affect lepidopteran populations and ranges together with temperature (e.g., Hawkins & Porter, 2003; Hordley et al., 2023; Mills et al., 2017). As a fourth classification, we used the larval feeding guild, as exposed larvae chewing on leaves may experience changes in the environment differently than larvae feeding on rolled leaves, mining the leaves, or feeding on the roots or the shoot of the plant.

The variety of the diet also plays a role. Our fifth classification criterion is the host plant life form, as herbaceous and woody plants may react differently to climate change (Altermatt, 2010). The final classification concerns the degree of specialization. Worldwide and across taxa, specialist animal species are on the decline, while generalists tend to fare better (Börschig et al., 2013; Clavel et al., 2011; Gough et al., 2015; Mattila et al., 2008). We wanted to test whether this pattern is also discernible in subarctic moths, and whether the trends of these different groups are tied to certain climatic factors.

Yazdani et al. (2023) recently found no evidence of population declines in different functional groups of Finnish macrolepidoptera between 1993 and 2019. Instead, there was an increase in the biomasses of species using coniferous trees, lichens, or mushrooms as hosts and multivoltine species and monophagous and oligophagous species that feed on trees. Other groups remained stable over time. Our study spans a longer time period from 1972 to 2017, but concentrates on the geographically most remote northern area of the country, further highlighting the effects of climate change.

Exploring the local effects of large-scale climate patterns

While climate change may have different effects on aquatic and terrestrial invertebrates (Pilotto et al., 2020; van Klink et al., 2020), major

climate patterns over the oceans also would affect insect communities on land (Mysterud et al., 2003). Using large-scale atmospheric climate indices as predictors for animal populations remains controversial (van de Pol et al., 2013), and in recent years, the focus has shifted to local weather data. In our research, we combined both kinds of parameters. Although moths in Northern Lapland are unlikely to be directly dependent on changes in the Atlantic Ocean or the Baltic Sea, we wanted to evaluate the usefulness of marine climate patterns as proxies for complex underlying phenomena that affect ecosystems both in the sea and on land. Instead of trying to assess and model parameters, such as average and extreme temperatures, precipitation, snow cover, evaporation, atmospheric pressure and cloud cover, regional parameters can be used to define the variation and the interactions among different components of climate (Hurrell, 1995).

The North Atlantic Oscillation (NAO) index describes the fluctuating differences in air pressure between the low-pressure centre over Iceland and the high-pressure centre over the Azores. As these pressure differences determine the strength of the westerly winds that reach the European continent from the Atlantic Ocean and the amount of rainfall brought by these winds, this weather phenomenon has an enormous effect on the climate of Europe. Positive NAO values indicate a strong Icelandic Low, which leads to mild, rainy winters in Western and Northern Europe, while negative values predict cold and dry winters (Hurrell, 1995). The NAO index is commonly used in describing and explaining biological phenomena in aquatic environments (Ottersen et al., 2001; Stenseth et al., 2002). The differences in air pressure over the Atlantic affect, for instance, zooplankton in the Baltic Sea through a chain of effects on freshwater runoff and saltwater inflow (Hänninen et al., 2003; Rousi et al., 2024; Vuorinen et al., 2003). On land, the effects of the NAO are mediated mostly through temperature and rain or snowfall. In terrestrial invertebrate research, the NAO index is less common (Mysterud et al., 2003), but there are examples of its association with insect populations (e.g., Aluja et al., 2012; Camarero et al., 2022; Hóðar et al., 2011; Klemola et al., 2003; Saldaña et al., 2007; Wan et al., 2022).

Since 1990, the NAO index has remained in a predominantly positive phase, especially during the winter season. This change in winter temperatures between 1989 and 1990 is the second of two recent climate-induced Regime shifts in the Baltic Sea, with the first one taking place after the last major Baltic inflow from the North Sea in the winter 1975–1976. Regime shifts mark large-scale atmospheric circulation changes that cause abrupt, long-lasting changes in the physical properties of a marine environment; shifts from one stable state to another. They can affect sea currents, salinity, temperature and inflow patterns, and, consequently, the marine ecological system (Beaugrand et al., 2015; Dippner et al., 2014). Simultaneously with the Baltic Regime shifts, similar shifts have been recorded in other marine basins in the northern hemisphere, which underlines the interconnectivity of these different regions and their dependence on the same climatic drivers (Beaugrand et al., 2015). While Regime shifts affect marine animals (Dippner et al., 2014; Möllmann et al., 2009; Österblom et al., 2007), the impact of these major changes on terrestrial life remains unclear (Kotta et al., 2018; Scheffer & Carpenter, 2003). We

present new findings linking Regime shifts in the Baltic Sea with terrestrial insect communities.

On the local scale, as a comparison to the regional climate patterns, we used weather data on seasonal daily temperature minima and maxima, degree days, precipitation and snow depth. These directly affect the physiology and phenology of moths. Temperature is often the single most important factor limiting the range of ectotherm insects, affecting their mobility and metabolism (e.g., Danks, 2004; Keret et al., 2020). It is linked to the length of the growing season, which also limits how large insects can grow and how many generations occur during 1 year (e.g., Keret et al., 2020). Precipitation patterns not only determine vegetation but are of particular importance in winter through the insulating effect of snow cover in the Subarctic, which is essential for the survival of many species (Bale & Hayward, 2010; Sinclair et al., 2003). In the study of Yazdani et al. (2023), the length and temperature of the growing season and winter conditions were the most important climatic factors associated with the biomass of various macrolepidopteran functional groups.

Here, subarctic moth communities, using species abundance data from 45 years of light-trap monitoring in a nature reserve in northernmost Finland, were studied. The remote location has experienced minimal direct human intervention, with no notable settlements, road networks or agriculture nearby, but has undergone clear climatic changes. The aims of our study were to determine the changes in the biomass of subarctic moths during the last decades; to investigate the differences in biomass trends between life-history traits; to report the climatic factors influencing the biomass of the moth groups; and to assess the accuracy of two climate indicators commonly used in marine research, being the NAO index and Regime shifts, to explain biomass trends in a terrestrial invertebrate taxon. The ecological effects of these large-scale climatic phenomena are unlikely to be limited to aquatic environments, as the wind and precipitation patterns connected to them are also apparent on land. Here, as in the sea, these patterns could be proxy factors offering a single index for assessing climate rather than dealing with multiple factors separately, such as precipitation, temperature averages and extremes (Hurrell, 1995).

MATERIALS AND METHODS

Study area and environmental parameters

The study was conducted at the Kevo Subarctic Research Institute in Finnish Lapland (WGS84: 69.757° N; 27.008° E; Figure 1). The institute is situated in the subarctic vegetation zone close to the border with the northern boreal zone. The characteristic vegetation types are forests dominated by mountain birch, *Betula pubescens* subsp. *czerepanovii* (Orlova) Hämet-Ahti; or Scots pine, *Pinus sylvestris* L., in river valleys and extensive mires (Kozlov et al., 2010). Light traps (see Section 2.2) were placed within an area of approximately 400 × 150 m surrounding the station and were in common habitats of mixed pine-birch forest, birch shrub, willow shrub, dwarf birch and sedge mire

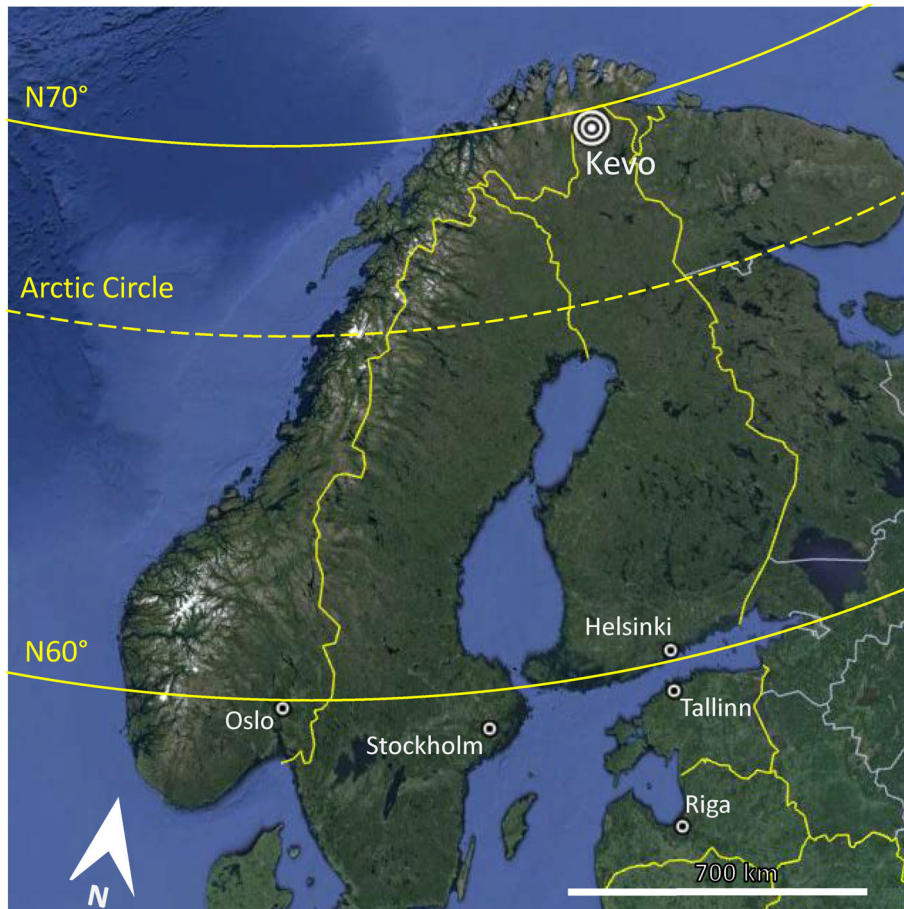


FIGURE 1 Map displaying the location of Kevo Subarctic Research Institute. Google Earth Pro (2024); all labels and the north arrow are the author's own additions.

and at a lake shore with birches (Linnaluoto & Koponen, 1980). The elevation of trapping sites varied between 80 and 120 m a.s.l. Although frequent in the study area, barren fells and birch woodlands were not sampled.

The Kevo research institute is surrounded by a restricted nature reserve, and the direct influence of human activities in the area is minimal. The effects of anthropogenic climate change, on the other hand, are clearly discernible at high latitudes (Figures A3 and A4, Rantanen et al., 2022). The Finnish Meteorological Institute provided us with datasets on local daily temperatures, rainfall and snow depth from a long-running weather station ('Utsjoki Kevo') at the research institute. In addition, data on NAO indices were obtained from the NOAA (<https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml>, last accessed 2024-04-26). In a pilot study, we found out that at Kevo, years with higher NAO index values tend to be warmer but not rainier than years with a lower NAO index (see details in Section 3.1 and Table A3).

Based on Hunter et al. (2014), we used a division of a year into four subarctic seasons, with spring lasting from 16th of March to 15th of May, summer from 16th of May to 15th of July, autumn from 16th of July to 15th of October and winter from 16th of October until the 15th of March in the following year. This division fits best the climatic and plant phenological conditions in the Kevo area, defining summer

as the time of leaf expansion. Of note, despite the rapidly lengthening days in spring, the ground on Kevo is still mostly under a snow cover during this season. At the end of the year, a lasting snow cover falls towards the end of autumn or the beginning of winter.

The conventional time span definitions for winter, created for the different phenological seasons of lower latitudes and milder climates, could not be used in this subarctic study. Therefore, it is important to note that after adjusting for the winter season in a high-latitude location, the time frame for winter deviates from other research that uses the winter NAO (Hurrell, 1995).

Climatic variables included in the study were average daily maximum and minimum temperatures, average daily precipitation and average NAO indices for each season, as well as the minimum temperature of the previous winter and average annual snow depth. Based on daily average temperatures, we also calculated degree days (dd) for the entire year and for periods from January to the 15th of June, the 1st of July and the 15th of July using +5°C and +3°C as accumulation thresholds. To account for a one-generation lag in climate variable effects on moths, we also included the same parameters for the previous year (the parent generation) for all seasons except winter, as well as all the degree days. In addition, we included climate-induced regime shifts as known from the Baltic Sea as its own parameter with

the classes 0 (years 1972–1975), 1 (1976–1989) and 2 (1990–2017) (Dippner et al., 2012).

Moth sampling

Since 1972, regular nocturnal moth monitoring with light traps has been conducted at Kevo with a preceding pilot study in 1971. For most years, four traps with 500-W blended-light lamps, two of which were changed for 250 W lamps in 2012 to 2013, were used throughout the growing season. A detailed overview of the trapping regime can be found in Table A1. The placement of the traps reflects the different vegetation types commonly found around the research station. The sampling and species determination methods are explained in detail by Kozlov et al. (2010). For our analyses, we used sampling data from the years 1972 to 2017. However, during the years 2004, 2005 and 2009, only macrolepidopterans were determined.

For common species, average dry weights for individual moths were obtained by weighing moth samples with precision scales. In 2021, microlepidoptera for weighing were sampled from light-trap catches from the Värriö Subarctic Research Station (WGS84: 67.445° N; 29.363° E), counted (1–49 individuals per species) and dried at +40°C until their weight no longer changed. Macrolepidoptera were obtained from Kevo light-trap catches. For rarer species, a sample of 3–84 individuals from 2021 was used and treated the same way as described for microlepidoptera above. For the 11 most common species, a sample of 50–900 individuals from light-trap catches from the years 1990–2017 was used and weighed with no extra prior drying. However, the catches had been stored in dry conditions for years before weighing (Marjamäki, 2022). The sex of the sampled individuals was not considered, as in many cases, the number of males was considerably larger than the number of females. Although there are differences in weight between male and female moths (Marjamäki, 2022) and the weight of females changes during the flight period as they lay their eggs, we presume that the weighed random samples or weighing the entire available batch of a species reflect the sex and weight ratio of each species in the trap catches. Although the method varied between species as described, we consider the results comparable. Likewise, we presume that there is no considerable difference in individual weight between moths of the same species from the two subarctic locations, Kevo and Värriö. In 2021, for fewer microlepidopteran species, we calculated an average individual weight of 1.64 mg based on all trapped individuals from Kevo. For this, we used the same method for drying and weighing as for the species-specific microlepidoptera weights. Within the macrolepidopterans, however, the size variation between species is considerable that the same approach was considered too imprecise, and we had to omit less frequently caught species from the analyses (Table 1).

Defining species groups

To achieve comparability between years where different numbers of traps had been active for different lengths of time, we used the moth

TABLE 1 Relative sizes of the taxonomic and trait-based groups of Lepidoptera.

	Number of species	Average number of individuals per trap per day, including/ omitting <i>E. autumnata</i>
Total	330 ^a	30.70/6.63
Macrolepidoptera	85 ^a	27.06/2.99
Microlepidoptera	245 ^a	3.64
Species with known average weight	263 ^a	30.54/6.48
Macrolepidoptera	18	26.90/2.84
Microlepidoptera	245 ^a	3.64
Timing of pupation		
Early in the season ^b	129	29.07/5.00
Late in the season ^b	53	1.20
Overwintering stage		
Egg	29	26.23/2.17
Larva	86	2.79
Pupa	55	1.12
Imago	9	0.05
Larval food		
Live vascular plants	162	29.59/5.53
Other	24	0.50
Larval feeding type		
Chewer	57	28.46/4.40
Leaf miner	41	0.21
Leaf roller	58	1.20
Shoot/root borer	15	0.14
Host-plant life form		
Herbaceous	38	0.21
Woody plants	111	3.69
Both forms	15	25.94/1.87
Larval specialization		
Feeding on 1 plant genus	105	1.73
Feeding on 2 plant genera	24	0.53
Feeding on 3 or more plant genera	37	27.61/3.54

Note: The division of species by life-history traits follows that reported in Kozlov et al. (2010). Only species with a known average individual weight are included in the groups. As *Epirrita autumnata* is the most common species by multiple orders of magnitude, it was analysed separately from the other species in its respective groups. During the years 2004, 2005 and 2009, microlepidopterans were not determined to species. Nevertheless, these years are included in the average counts below with zero microlepidopterans marked for each of the 3 years, and their effect on the averages was minimal. In the analyses, the missing years were accounted for through imputation (see Section 2.4.2).

^a1 macrolepidopteran and 11 microlepidopteran entries were only determined to the family level.

^bSpecies completing larval development by early July are considered pupating early (Kozlov et al., 2010).

dry weight (mg) per trap per day as our base unit for annual moth biomass.

We used the same classification of life-history traits as Kozlov et al. (2010) to sort moth species into different groups (Table 1). Some groups are *trait-based*, dividing the species by resource use or phenology. Other groups are purely *taxonomic* and reflect the historical categorization into macro- and microlepidoptera. Even though the division is not phylogenetically rigid, it adds to the comparability with other studies, as the two groups are still commonly used in recent and related literature (e.g., Hunter et al., 2014). Of all the moths observed in the trapping programme, the families Drepanidae, Erebidae, Geometridae, Lasiocampidae and Noctuidae were counted into macrolepidoptera with the rest into microlepidoptera. The groups are overlapping, that is, a species can belong to multiple groups. Where only the term *group* is mentioned, we define this as both taxonomic and trait-based groups together.

As some life history traits are more common than others and as not all life history traits are known for all species, the groups were of varying sizes. In Table 1, an overview of our final trait database structure can be seen. The species of 935 individuals could not be determined, and in the data, they are limited to the genus level. In cases where all the species of the genus in question belong to the same trait-based group, these individuals were included in that group; otherwise, they were omitted from the analyses. In total, 263 species amounting to 676,558 moth individuals were included in the analyses (Table A1).

Epirrita autumnata (Borkhausen, 1794), the autumnal moth (Geometridae), was separated from the other moths and the groups that it would belong to and analysed as a taxonomic entity of its own. This species is the most significant defoliator moth in northern Fennoscandia (e.g., Bylund, 1999; Tenow, 1972) and outweighs by far any other species in the number of trapped individuals. In its peak outbreak year in 2004, individuals of this cyclically occurring generalist made up almost 99.5% of the total moth biomass in our study, and, even 3 years later, when the population had crashed and its biomass percentage declined to 19.06%, it remained considerably more abundant than any other species.

Statistical analysis

All data used in the analyses, as well as the codes used, are publicly available in the Dryad data repository (Fält-Nardmann et al., 2026).

The effect of NAO on climate parameters

We wanted to explore whether there was a connection between seasonal NAO indices and local weather parameters in the Kevo region, Northern Lapland. To achieve this, the NAO in a season was used to predict local climatic data. All possible combinations of seasonal NAO indices and included weather parameters were compared. To conduct the comparisons, generalized linear mixed models (GLIMMIX of SAS®

9.4) were applied. The effect of seasonal NAO (spring, summer, autumn, winter) on seasonal average daily maximum and minimum temperatures, degree day variables, average annual snow depth and seasonal average daily precipitation was analysed (SAS Institute Inc., 2013).

GLIMMIX was chosen, as it can deal with non-normal data distributions, interdependencies between variables, interdependencies between observations, or autocorrelation and non-constant variability, typical in environmental datasets (McCulloch et al., 2008). In addition, besides the usual fixed-effects analyses, random effects can also be included in the linear predictor in GLIMMIX (Breslow & Clayton, 1993). In the models, fixed effects included a seasonal NAO variable (e.g., spring NAO) and a local climatic variable (e.g., average daily maximum temperature). In addition, the year was included as a random variable. Before GLIMMIX, SAS Enterprise Guide® 8.3. software (SAS Institute Inc., 2020) was applied to examine the distributions and covariance structures of each variable to ensure using of the correct link function and covariance matrix. Depending on the outcome, we were able to apply a negative binomial, log-normal, Gaussian, or t-distribution as a link function in the analyses (Table A3). The covariance matrix had a first-order autoregressive structure AR(1). Satterthwaite approximation was used to define degrees of freedom (SAS Institute Inc., 2013). To estimate the model's fitting, we compared the changes of values of the -2 Res Log Likelihood, AIC and Generalized χ^2/DF to reach the best parsimony of the model. Models, which had a Generalized χ^2/DF value >0 and <2 , -2 Res Log Likelihood $<$ Generalized χ^2 and whose AIC value was the least in comparison with the alternative models, were regarded as trustworthy (SAS Institute Inc., 2013).

TRIM analyses: Trends in moth group biomasses

The TRIM model (Pannekoek & van Strien, 2005) is widely used for analysis of changes in animal populations. In this study, the trends in the yearly biomass of moth groups were studied using TRIM models. The actual analyses were carried out using R software and its *rtrim* package (Pannekoek et al., 2018).

TRIM typically assumes Poisson-distributed data. The observed moth biomass y_{ij} in a trap site i at year j can be seen as a weighted observed count of individual moth species, where the weight depends on the moth species: $y_{ij} = \sum wkn_{ijk}$ where wk is the specimen weight and n_{ijk} is the number of specimens for the species k . As shown in Chapter 2.3 of Pannekoek & van Strien, 2005, TRIM can also be applied to weighted observed counts, which is the case for our biomass response.

Our TRIM model $\ln(\mu_{ij}) = \alpha_i + \beta(j-1) + \omega u_{ij}$ exponential growth or decline over time, where μ_{ij} is the expected moth group biomass observed at trap site i at year j . Here, u_{ij} is a 1/0 indicator for using a 250 W lamp at trap i at year j . The lamp-type correction parameter ω was estimated first separately using log-linear generalized linear models (GLM) $\ln(\mu_{ij}) = \alpha_i + \beta_j + \omega u_{ij}$ and then used as a correction factor in the TRIM model. In our data, the occurrence of overdispersion

seemed apparent and was expected due to the sensitivity of insect populations to weather conditions and parasitism. Thus, our model includes an overdispersion parameter, θ , that is related to variance via $\text{VAR}(y_{ij}) = \theta \mu_{ij}$ (Pannekoek et al., 2018). Most northern moth populations show heavy cyclic variations, and thus the model assumed a serial correlation between adjacent years, $\text{cov}(y_{ij}, y_{ij-1}) = \rho$. The serial correlation parameter ρ was estimated with the other model parameters.

The standard imputation practice within the TRIM framework is model-based imputation derived from the fitted log-linear imputation model $\ln(\mu_{ij}) = \alpha_i + \beta_j$ (Pannekoek & van Strien, 2005). The imputation model is estimated based on all non-missing data. Then a missing trap-year values are replaced by their predictions $\hat{\mu}_{ij}$ from the imputation model. However, this approach cannot be applied when data are missing from all traps within a given year, because the corresponding year effect β_j becomes non-estimable. For the 3 years with complete absence of microlepidoptera biomass determinations (2004, 2005 and 2009), we therefore first applied an exponentially weighted moving average (EWMA) separately for each trap. The EWMA weighting scheme was chosen to reflect the geometrically decaying serial dependence corresponding to the AR(1) structure employed in the TRIM model. After EWMA-imputation of missing microlepidoptera years, the standard TRIM imputation was applied to the rest of the missing trap-years. The imputation approach applied makes the information of temporal dependence of microlepidoptera to enable utilization of macrolepidoptera biomass determinations also for years 2004, 2005 and 2009 in the hypothesis testing of each functional group.

Modelling the effect of climate parameters on moth groups with linear mixed models

Linear mixed models offer a flexible framework suited for modelling animal population data with repeated measurements and hierarchical structures. In this study, the effect of climate on the yearly biomass of moth groups was modelled using the model $\ln(\mu_{ij}) = a_i + b_j + X_j' \beta + \omega u_{ij}$, where a_i is a random effect related to trap i , b_j is a random effect related to year j , X_j is a vector of NAO and weather variables at year j . Again, u_{ij} is a binary indicator for using a 250 W lamp. The parameter ω is for the difference between 250 W and 500 W lamps and was estimated among the fixed effects. The error terms ε_{ij} were assumed to be Gaussian distributed, independent between trap sites and temporally correlated with a short-memory ARMA(p,q)-structure. Trap-related and year-related random effects a_i and b_j were assumed to be zero-mean Gaussian. The ARMA parameters p and q were selected separately for each moth group to minimize AIC.

The reasoning for using a random effect for the year variable is that northern moth populations typically show year-to-year variation common to large geographic regions. Those variations are not completely caused by weather but are largely accounted for by interactions with parasitoids and probably also by other unknown random factors. In this way, the concurrent dynamics of biomass between the

trap sites are incorporated into the model, which is necessary to get realistic p-values for weather covariates.

The analysis was carried out using the R package nlme (Pinheiro & Bates, 2000). The weather variables included in X_j were selected separately for each moth group to minimize AIC using the forward stepwise approach of the R package MASS (Venables & Ripley, 2002). The model resulting from the forward stagewise variable selection typically included about 2–6 covariates and was used as a base model, and then testing the significance of other covariates. The four seasonal NAO indices and NAO regime classification variable were included in the base model before starting the forward selection of weather variables. The parameter estimates, confidence intervals and p-values presented in Tables A5–A8 were calculated by adding the NAO/weather covariate being analysed into this base model, one covariate at a time.

Missing values were imputed using the procedure explained earlier for the TRIM analyses.

RESULTS

The relationship between NAO and climate parameters in northern Lapland

A higher NAO index value was associated with significantly higher average daily minimum and maximum temperatures in winter, spring and summer but not in autumn (Table A3). High summer NAO index values also contributed to significantly higher degree days (+3 as well as +5°C as accumulation thresholds) both over the entire year and for all three parameter periods except for January to the 15th of June when using +3°C as a threshold. We found no significant relationship between NAO and precipitation variables or the winter minimum temperature (Table A3).

Population trends in different moth groups

The overall moth biomass increased significantly (+ 421%; $p = 0.027$, Figure 2a) at Kevo between 1972 and 2017. Also after excluding the cyclically outbreaking *E. autumnata*, the increase remains significant though less steep (+ 93%; $p = 0.010$, Figure 2b). *E. autumnata* itself has a significant positive trend (+508%; $p = 0.036$). The same pattern was discernible in macrolepidoptera (+453%; $p = 0.027$ with *E. autumnata* and + 150%; $p = 0.002$ without *E. autumnata*), whereas microlepidoptera biomass had no significant trend (Table 2).

Seven trait-based groups being pupating early, overwintering as eggs, larvae feeding on live vascular plants, chewers, leaf rollers, larvae feeding on both herbaceous and woody plants and generalists feeding on at least three plant genera had a significant positive trend (Figures 2e,g and 3a,c,e-g). Three trait-based groups, being overwintering as larvae, larvae feeding only on herbaceous plant and specialists feeding on only one plant genera showed a significant negative trend (Figures 2h and Figure 3b,d), and five trait-based groups had no

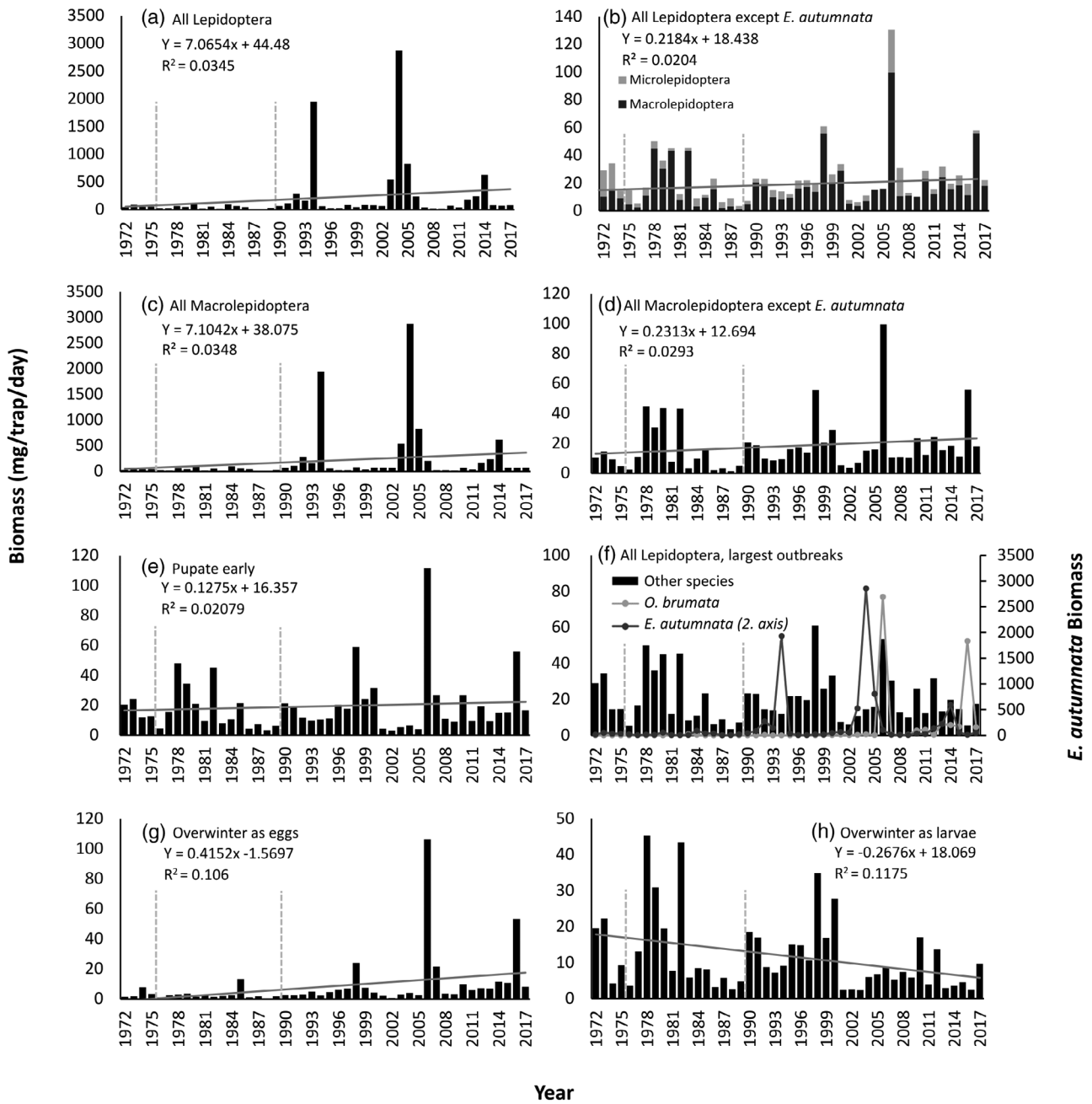


FIGURE 2 Moth biomasses from 1972 to 2017: Groups based on taxonomy and phenology. Only the trait-based groups with a significant TRIM trend are displayed. The y-axis scale (mass) varies as the groups differ in the number of species and individuals, as well as the micro-macrolepidoptera ratio. Dashed vertical lines indicate the occasions of confirmed marine regime shifts in the Baltic Sea.

significant trend (Table 2). Three trait-based groups being overwintering as imagines, larval food other than vascular plants and shoot/root borers were considered sparsely represented either by the number of species or individuals or too dominated by a single species for their results to be considered representative of an entire group (Table 1). Nevertheless, all three groups displayed a highly significant trend being positive for species overwintering as imagines and negative for the other two groups (Table 1). Species with clear outbreak dynamics made up a considerable part of total moth biomass in their peak years (Figures 2f and 4).

During the study period, around 30 of the species included in the study could be recorded as new and later established arrivals (Table A1). These arrivals are equally divided between the three decades from 1980 to 2010. At the same time, six species can be considered to have disappeared during the 1990s or 2000s. No particular trait-based groups are overrepresented in either category.

The effect of environmental parameters on different moth groups.

Our linear mixed models revealed regime shifts in the Baltic Sea as the environmental parameter that is significant for three of the

TABLE 2 Biomass trends of all moth groups obtained by TRIM analysis.

	Trend	<i>p</i>	CI
All moths	421%	0.027	[+ 23%, + 2001%]
All moths, except <i>E. autumnata</i>	93%	0.010	[+ 19%, + 212%]
<i>E. autumnata</i>	508%	0.036	[+ 14%, + 2946%]
Macrolepidoptera	453%	0.027	[+ 25%, + 2241%]
Macrolepidoptera except <i>E. autumnata</i>	150%	0.002	[+ 44%, + 331%]
Microlepidoptera	-17%	0.640	[-61%, + 78%]
Timing of pupation			
Early in the season ^{a,b}	100%	0.014	[+ 17%, + 237%]
Late in the season ^b	72%	0.150	[-17%, + 252%]
Overwintering stage			
Egg ^a	2131%	<0.001	[+ 722%, + 5825%]
Larva	-60%	<0.001	[-75%, -34%]
Pupa	-19%	0.450	[-52%, + 37%]
Imago	1431%	0.008^c	[+ 118%, + 9830%]
Larval food			
Live vascular plants ^a	104%	0.009	[+ 22%, + 240%]
Other	-67%	<0.001^c	[-78%, -51%]
Larval feeding guild			
Chewer ^a	118%	0.009	[+ 24%, + 279%]
Leaf miner	-34%	0.240	[-67%, + 29%]
Leaf roller	45%	0.030	[+ 5%, + 102%]
Shoot/root borer	-84%	<0.001^c	[-94%, -63%]
Host-plant life form			
Herbaceous	-76%	<0.001	[-86%, -57%]
Woody plants	-17%	0.460	[-48%, + 34%]
Both forms ^a	941%	<0.001	[+ 373%, + 2158%]
Larval specialization			
Feeding on 1 plant genus	-44%	0.005	[-62%, -17%]
Feeding on 2 plant genera	-17%	0.270	[-40%, + 15%]
Feeding on 3 or more plant genera ^a	175%	0.004	[+ 42%, + 430%]

Note: Statistically significant trends ($p < 0.05$) are marked in bold font. The sample size (n) of all models is 184.

^a*Epirrita autumnata* would belong to these groups but has been omitted from the analyses.

^bSpecies completing larval development by early July are considered pupating early (Kozlov et al., 2010).

^cAs this group contains very few species or is dominated by one species, the results cannot be regarded as representative of the entire group.

15 trait-based groups, as well as for total moth biomass and macrolepidopteran biomass with and without *E. autumnata* (Figure A1, Table 3). For all moths and macrolepidopteran totals as well as for moths overwintering as eggs and generalists feeding on at least three plant genera, the current regime, where the NAO has turned predominantly positive (years 1990–2017), was associated with higher biomass than the two previous regimes. For moths only feeding on herbaceous plants, the first regime, ending with the last major Baltic inflow from the North Sea and the related change in wind patterns from easterly to westerly during the winter of 1975 to 1976, was associated with higher biomass than the two later regimes (Figure 3b).

Of the temperature parameters, average daily maximum and minimum temperatures of the previous summer (i.e., parent generation) were significant for three groups, each with higher temperatures associated with higher moth biomass (Table 3). Average daily maximum autumn temperatures were associated with higher moth biomass in two groups. The remaining temperature and precipitation parameters were significant in one or none of the 22 models (Table 3).

Annual degree days of the previous year of greater than +3°C and +5°C, as well as degree days of greater than +5°C accumulated until the 15th of July in the previous year, were positively associated with 3 moth groups each. Degree day parameters

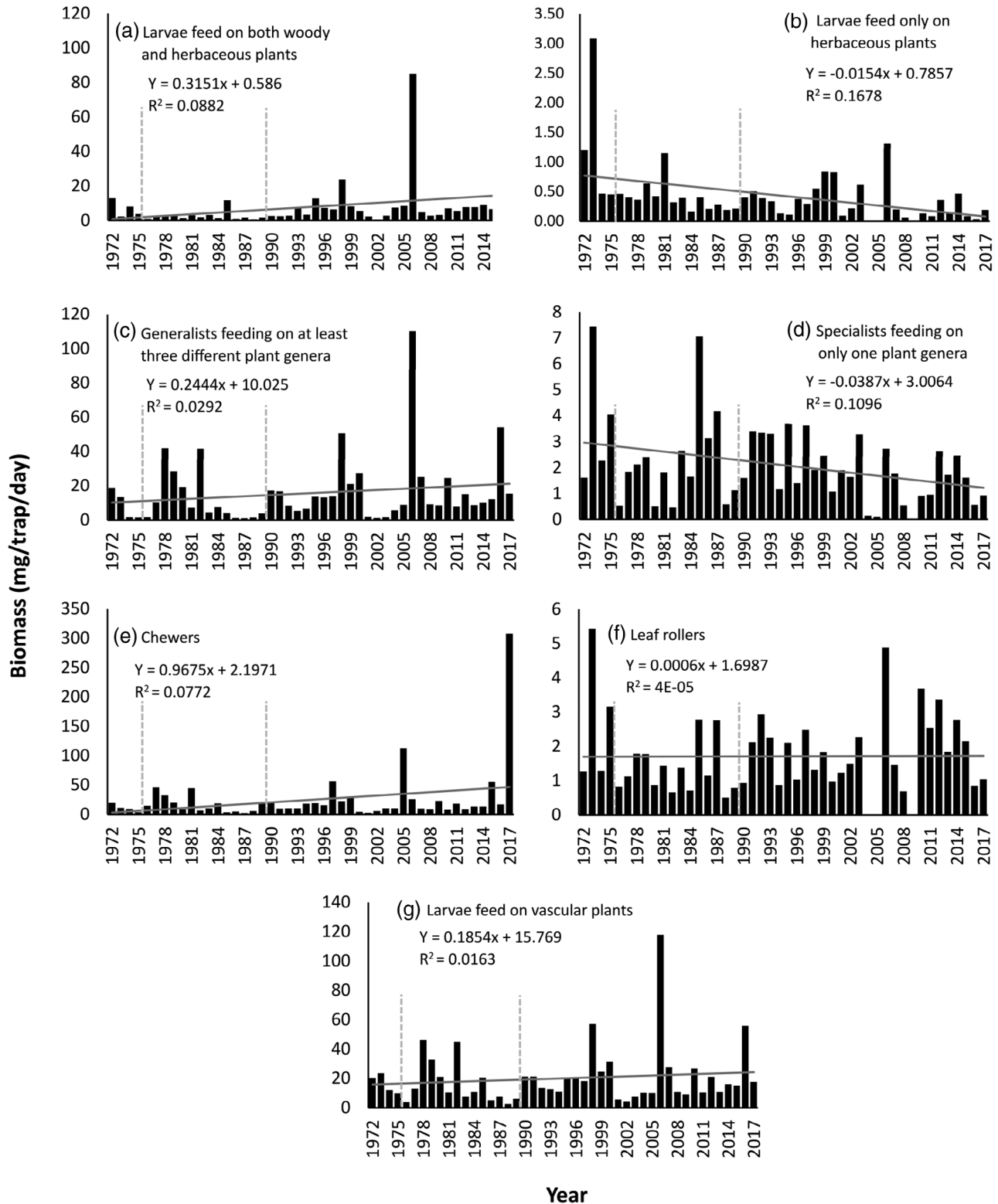


FIGURE 3 Moth biomasses from 1972 to 2017: Groups based on resource use. Only the trait-based groups with a significant TRIM trend are displayed. The y-axis scale (mass) varies as the groups differ in the number of species and individuals, as well as the micro-macrolepidoptera ratio. Dashed vertical lines indicate the occasions of confirmed marine Regime shifts in the Baltic Sea.

accumulated until the 15th of June were significant in single models and always negatively associated with moth biomass (Table 3).

Of the seasonal NAO indices, only spring and autumn were negatively associated with moth biomass in one model each (Table 3). However, a negative effect of positive spring NAO on moth biomass

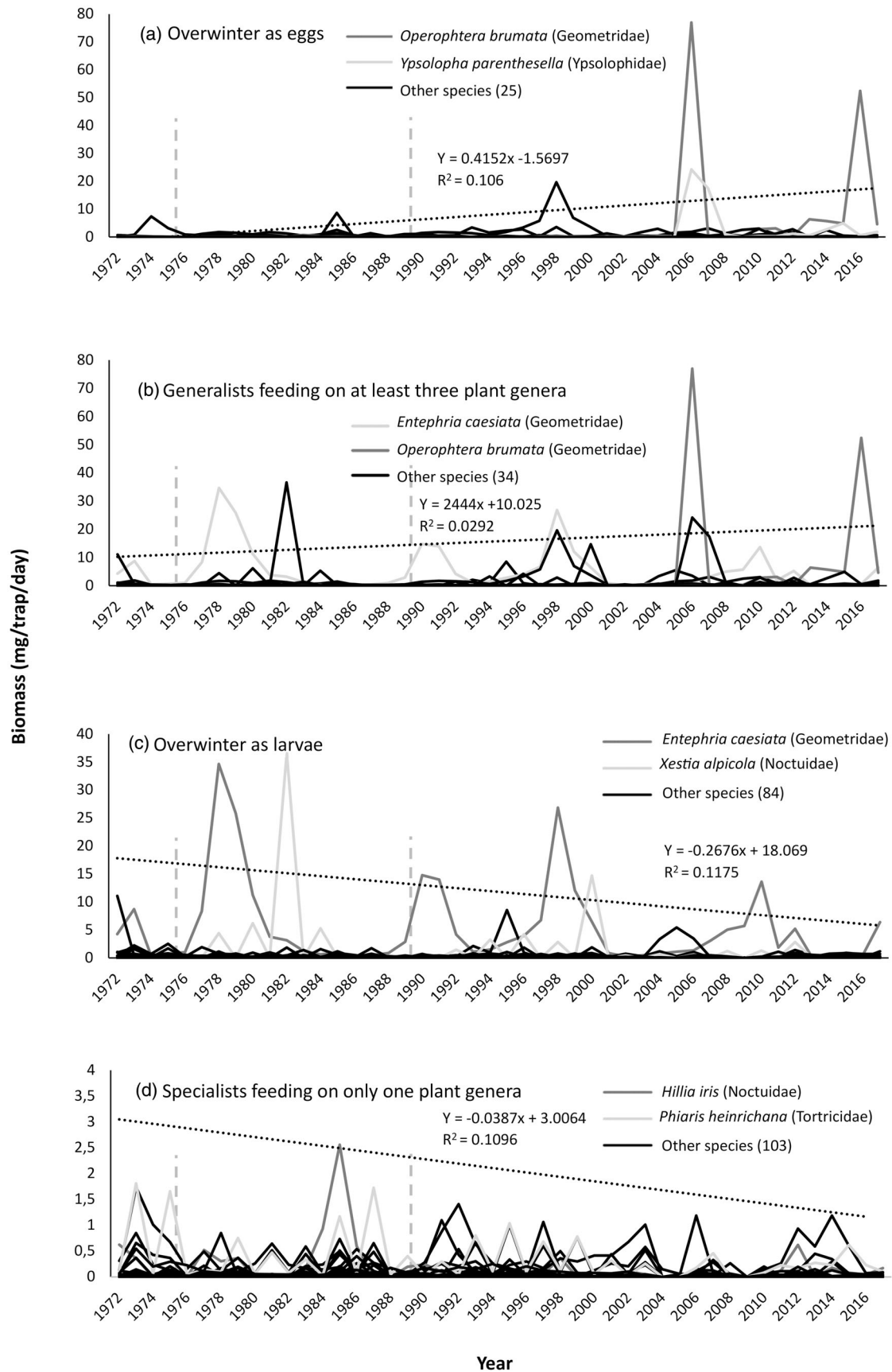


FIGURE 4 Species structure of four different trait-based groups with significant population trends (dotted line). Dashed vertical lines indicate the occasions of confirmed marine regime shifts in the Baltic Sea. The y-axis scale (mass) varies as the groups differ in the number of species and individuals, as well as the micro-macrolepidoptera ratio. Two prominent species have been highlighted as examples in each of the subfigures.

was implied in four further groups, though the associations were not statistically significant ($p = 0.070$ to 0.099) (Table A8).

DISCUSSION

We showed significant differences between subarctic moth groups in biomass trends and their response to environmental conditions, with some groups following and others contradicting larger global patterns (van Klink et al., 2020). These differences remain unseen if we only consider the broader taxonomic level of the order Lepidoptera. This can cause different interpretations of the significance of, for instance, climate change on insect communities. In many cases, differences between groups are driven by their most abundant representative species that frequently display outbreak dynamics. In addition, we uncovered connections between subarctic moth biomass and regime shifts in the Baltic Sea.

Differences among moth groups

Our results support the worldwide trend of a decline in specialist species and an increase in generalists (Figure 2h, Table 2; Börschig et al., 2013; Clavel et al., 2011; Gough et al., 2015; Mattila et al., 2008). This trend may be caused by climate change, changes in land use, or other anthropogenic factors, but as direct human influence is minimal at our research site (although there may be an indirect effect of reindeer husbandry, s. below), our results are likely due to changes in the natural environment, most prominently, a rapidly changing climate. The biomass of generalist species, whose larvae feed on three or more plant genera, is positively associated with a regime shift. Specialists feeding on only one plant genus are positively associated with snow depth, which has been declining at Kevo (Figure A2). However, specialist biomass is also positively associated with daily average maximum and minimum temperatures from the previous summer. Interestingly, while these temperatures have slightly increased over the research period, the temperatures have risen less in summer than in other seasons (Figure A3; Box, 2021). In general, specialists may be more vulnerable to changes in the availability or the phenology of their single host plant, which, in turn, may be affected by, for example, snow depth or summer temperatures. Generalists, however, may be able to shift between differently available food sources.

A similar pattern occurs between the declining biomass of species whose larvae only feed on herbaceous plants (Figure 3b) and the biomass increase of potentially more versatile species feeding on both herbaceous and woody plants (Figure 3a). However, species that only feed on woody plants do not show a significant trend (Table 2). In a similar study on population trends of common and widely spread lepidoptera in the United Kingdom by Coulthard et al. (2019), especially species feeding on woody plants were declining, though no direct association between larval specialism and population trends was found.

Although *E. autumnata* was excluded from the trait-based groups, the generalists, as well as the group feeding on both herbaceous and woody plants, still include the successful outbreaking geometrid *Operophtera brumata* (Linnaeus, 1758). Though the magnitude of the outbreaks of *O. brumata* is much lower than that of *E. autumnata* (Figure 2f), the species clearly dominates these two groups in its outbreak years (Figure 4b).

The study site is located within the Finnish reindeer husbandry area and is frequently visited by grazing semi-domesticated reindeer. Reindeer grazing is known to affect especially lichen growth (Bernes et al., 2015), and enclosure experiments have shown that reindeer grazing may influence populations of insect herbivores such as leaf beetles and sawflies (den Herder et al., 2004). Thus, it cannot be excluded that the indirect human influence of reindeer husbandry would affect especially moth species specialized on lichens (in our study included in the small group feeding on other than live vascular plants) and potentially also the declining specialists on herbaceous plants.

The largest differences in population trends are found between trait-based groups overwintering at different stages. As predicted by Virtanen & Neuvonen et al. (1999), the biomass of species overwintering as eggs has increased massively, as has that of species overwintering as imagines, a small group highly dominated by the tortricid *Acleris maccana*. Meanwhile, the biomass of species overwintering as larvae has decreased significantly (Figures 2h and 4).

These changes in biomass can be explained by changing temperatures at critical life stages. Species overwintering as eggs are positively associated with daily maximum temperatures in autumn, annual degree days (+ 3°C) of the previous year, and the current Regime. Increased temperatures are beneficial for laying eggs during summer and autumn, which could explain the recent success of these species. Moths overwintering as eggs may also benefit from warmer and shorter winters (e.g., Ammunét et al., 2012; Bale & Hayward, 2010; Jepsen et al., 2008; Neuvonen et al., 1999), though they were not associated with winter temperatures or snow in this study. Eggs of the major outbreaking species *E. autumnata* and *O. brumata* die at temperatures around -35°C (MacPhee, 1967; Tenow & Nilssen, 1990), which have become progressively rarer in the past decades (Figure A4). For most species, the thermal minimum thresholds are, however, unknown.

On the other hand, *A. maccana* and the group overwintering as imagines are associated positively with higher daily maximum temperatures in spring, which might mean an early start into the season, possibly to escape predators such as migratory birds arriving later (Renner & Zohner, 2018). Larval overwintering is negatively associated with degree days accumulated by early summer in both the current and the previous year, and the decline of this group is thus tightly bound to the rising temperatures in the north. One possible reason for this negative association is a phenological mismatch between larvae and host plants in case the hosts develop prematurely to a stage where their leaves are hardened and of worse nutritional quality for the emerging larvae (Renner & Zohner, 2018).

TABLE 3 Significant ($p < 0.05$) environmental parameters in the linear mixed models of the different moth groups.

	Aver. Daily max. T			Aver. Daily min. T			Aver. Daily prec.			Dd > 3°C			Dd > 5°C			NAO index					
	Spring			Summer			Autumn			Winter			Snow			Annual			Regime		
	Summer ^a	Autumn ^a	Winter	Spring ^a	Summer ^a	Autumn ^a	Winter	Spring ^a	Summer ^a	Autumn ^a	Winter	Spring ^a	Summer ^a	Autumn ^a	Winter	Spring ^a	Summer ^a	Autumn ^a	Winter		
All moths																					
All moths except <i>E. autumnata</i>																					
<i>E. autumnata</i>																					
Macrolepidoptera																					
Macrolepidoptera, except <i>E. autumnata</i>																					
Microlepidoptera																					
Timing of pupation																					
Early in the season ^{b,c}																					
Late in the season ^c																					
Overwintering stage																					
Egg ^b																					
Larva																					
Pupa																					
Imago ^d																					
Larval food																					
Live vascular plants ^b																					
Other ^d																					
Larval feeding guild																					
Chewer ^b																					
Leaf miner																					
Leaf roller																					
Shoot/root borer ^d																					
Host-plant life form																					
Herbaceous																					
Woody plants																					
Both forms ^b																					
Larval specialization																					
Feeding on one plant genus																					
Feeding on 2 plant genera																					
Feeding on at least 3 plant genera																					

Note: Grey boxes indicate that the parameter was significant with a one-year lag (effect through the parental generation), and black boxes indicate an effect on the population of the same year. Lag was not applied to winter-season parameters, regime or NAO indices. A '+' indicates a positive effect estimate and a '-' a negative one. The model parameters and key statistics for each model are shown in Tables A5–A8.

^aThe parameter was also included with a 1-year lag.

^b*Epirrita autumnata* would belong to these groups but has been omitted from the analyses.

^cSpecies completing larval development by early July are considered pupating early.

^dAs the group contains very few species or is dominated by one species, the results cannot be regarded as representative of the entire group.

Differences in the survival through the harsh, yet rapidly warming winter season could explain differences between the overwintering groups. Eggs, often attached to trees or other vegetation, may be less susceptible to the lack of snow cover and repeating cycles of soil freezing and thawing than larvae mainly overwintering on the ground (Mattila et al., 2008). However, we found no connection between any overwintering type and winter temperatures or snow depth, though these are commonly acknowledged as important survival factors on a species level (e.g., Ammunét et al., 2012; Bale & Hayward, 2010; Jepsen et al., 2008; Neuvonen et al., 1999).

As in the above comparison of groups with different host preferences, the group of species overwintering as eggs include *O. brumata* and other species with outbreak dynamics such as the microlepidopteran *Ypsolopha parenthesesella* (Linnaeus, 1761). Here in this study, the groups often overlap. For instance, many of the species that feed on both herbaceous and woody plants also overwinter as eggs (Figure 2 d–f, Table A1). Thus, especially in the smaller groups skewed towards a few major species or groups containing major outbreaking species, the found effects may not be associated with the group denominator but with other traits shared by the group members (Mattila et al., 2008). However, no two groups shared the same set of significant environmental factors, implying that there are true differences between these different assemblages of species. As is common practice in moth studies in Fennoscandia, we separated *E. autumnata* as its own entity, as its population peaks are about two orders of magnitude larger than those of all other species, but decided to include the other outbreaking species in their respective trait-based groups (Dallas et al., 2020; Yazdanian et al., 2023). They remain, functionally and phenologically, members of their trait-based groups and make up a significant portion of the biomass and thus the ecological effect of these groups. This means, for example, that in its outbreak years, *O. brumata* is the most abundantly available food source for birds looking for spring-hatching caterpillars and is the most significant generalist defoliator in the region.

Species pupating by early July show a significant positive trend (Figure 2 e), but are not associated with any particular climate parameters. The same is true for species feeding on vascular plants (Figure 3 g). Species feeding on something else, such as fungi or lichens, have a significant negative trend, though this group is represented by a few individuals and two dominant species.

When dividing moths into trait-based groups by larval feeding guild, chewers and leaf rollers both have positive trends (Figure 3 e, f), with chewers lacking any significant associations with climate parameters and leaf rollers having a positive association with average daily maximum temperatures of the previous summer. The shoot and root borers are another small group displaying a significant negative trend, but dominated by just two species.

Our results differ from those of Yazdanian et al. (2023), who found no significant biomass declines in any functional groups of macrolepidoptera and, for instance, found all functional groups based on the overwintering stage to be stable. These results need not be contradictory with ours, as their data cover multiple sampling sites and are projected over a much larger, climatically, environmentally,

and botanically diverse area—the entire country of Finland— while ours are collected in one extremely remote northern location. As the authors also point out, insect abundance trend studies are sensitive to time series length, and our dataset starts 21 years earlier but ends 2 years before theirs.

Population trends and outbreaks

Outbreaks of a few moth species surpass much of the variation in less frequent and sparsely numbered species. For higher trophic levels, such as insectivorous birds, this means a significant variation in food availability between years. Similarly, host plants of a certain moth group or species may be defoliated entirely during some years while experiencing hardly any herbivory in others (e.g., Tenow et al., 2007).

Outbreaks of *E. autumnata* contribute greatly to the rising trend between 1972 and 2017 in the total biomass of moths trapped at the Kevo subarctic research institute. After *E. autumnata* is excluded from the analysis, outbreaks of other species, such as *O. brumata* or *Y. parenthesesella*, that are present become visible (Figure 4). Rising trends depend on a few species, the outbreaks of which have been getting larger (Figure 4 a–b) and negative trends by diminishing outbreaks or the lack of outbreaking species (Figure 4 c–d).

Dominant and outbreaking species mask some of the variation in less prominent species in our data. If the species with the highest biomass are removed from the data, some trends change; for instance, the decrease in microlepidoptera is significant if *Y. parenthesesella* is removed from the data, and the positive trend of generalists feeding on three or more plant genera is no longer significant if *Entephria caesiata* (Denis & Schiffermüller, 1775) and *O. brumata* are omitted (Table A2). On the other hand, as these species make up the very largest part of the biomass of their respective groups (25.9% and 54.5% respectively in the above example, Table A2), they have the greatest impact in their communities. The exact moth species, or whether a newcomer or a well-established local species, is usually of secondary importance for other members of the same trophic network. Insectivorous birds nimbly switch between prey species to maximize nutritional gain for their chicks (Eeva et al., 2000). Equally, for the sparse subarctic vegetation undergoing severe defoliation, the total amount of moths and their caterpillars is more important. Nevertheless, it is important to remember that species-level population trends may starkly differ from group and biomass trends; even in groups with an overall positive trend, there may be more declining than increasing species (Antão et al., 2022; Yazdanian et al., 2023).

This report's data range ends in 2017. Since the spectrum of outbreaking species has changed rapidly, as at least two new geometrid species, *Hypomecis atomaria* (Linnaeus, 1758) and *Macaria fusca* (Thunberg, 1792), have reached outbreak densities in Lapland (Andersson, 2024; Koistinen & Andersson, 2024). While there are records of *H. atomaria* outbreaks in the 2010s in Kamchatka and Sakha (Burnasheva, 2011; Lobkova, 2020), outbreaks of *M. fusca*, though they may have contributed to defoliation in 1974 in Skállovárri near Kevo (T.A. pers. comm.), are undocumented. Both species are

generalists feeding on both woody and herbaceous vascular plants and resemble the largest geometrid outbreak species (Koistinen & Andersson, 2024).

Regime, the NAO and climate

Regime shifts, as defined and recorded for the Baltic Sea (Dippner et al., 2012), were more often than any other environmental parameter a significant explanatory factor of the biomass of different moth groups. Especially the shift in 1989/90 to a regime of a predominantly positive NAO also affected our remote terrestrial community of moths. These results imply that regime shifts and NAO indices are useful proxies for summarizing various climate phenomena and can be effectively used in parallel to local climate data. Further exploration of this topic would be possible, as we have not found any other publications linking Baltic Regime shifts with terrestrial invertebrate populations. Clearly, however, the same large-scale climate patterns and the regime shifts that mark radical changes in these patterns affect both marine and terrestrial ecosystems.

Here, we also explored the relationship between the NAO index and temperature as well as precipitation parameters at Kevo. Higher NAO index values are generally associated with warm westerly wind directions associated with elevated precipitation in Western and Northern Europe, including the Baltic Sea. Our comparison shows that, while a positive NAO indicates warmer winters, springs and summers also at Kevo, it does not affect precipitation at this location. Most likely, the increased rains will remain on the western slopes of the Scandinavian Mountains in Norway. This highlights the usefulness of the NAO as a climate parameter indicating change, although the specific effects may be different in different geographical and topographical locations.

Changes in the NAO cannot be simplified as a change in temperature, as they contain many different weather factors. On the other hand, in the current climate change, changes in the NAO do not cover all the fluctuations in temperature. While we know the links between NAO and at least some aquatic invertebrate populations (Hänninen et al., 2003), the exact chain of effects between NAO and moth populations remains unknown and would be a topic for future research. Likely, at least some of the observed effects, especially on resource-based moth groups, are mediated by changes in vegetation (Mod & Luoto, 2016). While no systematic vegetation monitoring data exist for the research area, recent shrubification (Mekonnen et al., 2021) can be observed in some parts of it. This may, for instance, have an effect on specialists feeding on herbaceous plants if their host plants are superseded by woody shrubs.

Methodology

The light-trap monitoring time series from the Kevo Subarctic Research Institute is a unique dataset, as it spans over 40 years and is obtained from a natural environment without direct human

interference. The northern location of the research station beyond the Arctic Circle also gives insight into the ongoing climate change that can clearly be observed at high latitudes (Rantanen, 2024; Rantanen et al., 2022).

As in most monitoring programmes running this long, there have been some adjustments in methodology over time. The number and exact location of traps have varied, lamps have been exchanged, and the trapping period has varied in length (Table A3). To account for the latter, we used the moth dry weight per trap per day as a unit for biomass in order to take into account the varying length of the trapping period. Including lamp efficiency as a covariate in our study considerably strengthened the significance of the obtained results, although no significant differences were found in catch-efficiency between the different lamp types used on Kevo in a 30-year Finland-wide monitoring of nocturnal moths (Huikkonen et al., 2024).

Light-trap data from high latitudes, where the nights around midsummer are bright, and the traps are thus considerably less conspicuous than in spring and autumn, should always be considered as 'seasonally weighted'. Here, in our data, some trait-based groups that mostly fly during the midsummer weeks are likely underrepresented. However, this error is systematic and the same every year.

In years where the traps were active exceptionally late in the autumn, these may have lower average biomasses per trap than years where the trapping season was shorter, as fewer species are still flying late in the year. Similarly, there is a risk that some early flying species were not fully recorded in years when trapping started late. However, the long duration of the light-trap monitoring programme, 45 years by 2017, makes the data robust against single exceptionally short or long monitoring years and sufficient for revealing long-term trends of moth populations. Trapping efficiency can also depend on weather conditions indirectly. In light-trap studies in Southern and Central Finland, species that are usually common during the warmest part of summer are caught in greater amounts during cooler years than in warm-weather ones (I. J., personal communication). The reason for this is that in cold years, their peak flight occurs later in the season when the nights are darker and light traps are more attractive. However, while we cannot fully control all variations between years, the beginning and end of trapping periods were determined yearly by on-site scientific personnel based on the local weather conditions to cover the full flight season of subarctic moths.

Potential increasing or decreasing trends in the size and biomass of individual moths were not accounted for in this study. For the analyses, we used average weights based on dry moth samples (see 2.2) and the number of individuals. It is therefore possible that the actual biomass of the captured moths differs from our calculated biomass, and the discrepancy may have a systematic trend if individuals of certain species have increased or decreased in size in the past decades (Bowden et al. 2015). Bergmann's rule and the temperature-size rule both suggest that animals may grow smaller in warmer than in colder conditions (Bowden et al., 2015); however, far from all invertebrates follow this pattern (Shelomi, 2012). If subarctic moths have indeed decreased in size over the past decades, the biomass increases that we found may be overestimated, while decreases may be underestimated.

Conclusions and outlook

In this novel study, we studied the relationship between marine regime shifts of the Baltic Sea and a terrestrial insect community and found that this proxy parameter for climatic and environmental change affected more moth groups than any other climate parameter. Although the total biomass of moths between the years 1972 and 2017 at the Kevo Subarctic Research Institute had a positive trend, different trait-based groups had different responses to the changing climate, with the clear difference between thriving generalist species and a decline in specialist biomass. Likewise, species overwintering as eggs had a positive trend, whereas species overwintering as larvae had a negative trend. These trends can be related to changes in climate affecting the trophic relationships between moths and their host plants and antagonists. Species with mass outbreaks influence moth fauna, with single species such as *E. autumnata*, *O. brumata* and *Y. parthenesella* comprising a significant part of the biomass of different groups and having a considerable effect on their biomass trends.

In the future, comparing the results from Kevo, located less than 100 km from the Arctic Ocean, with those from a more continental location to see whether the regime shifts and the NAO index are equally useful as indicators further inland. The division into trait-based groups could also be expanded, as climate could affect, for example, moths that pupate or lay their eggs on high branches differently than species diapausing on the ground and under the snow. In addition to the level of ecological guilds and functional groups, our study showed that single key species and their trends are also clearly visible in the subarctic moth community and could be further studied in relation to changes in their environment.

Changes in moth fauna can have a significant effect on other trophic levels, such as the host plants of the moth larvae or insectivorous birds. In a future study, we intend to include these. We want to contribute to a greater understanding of the impact of global climatic developments on different terrestrial and aquatic ecosystems, beginning with a comparison of these subarctic moths and their aquatic counterparts, the mesozooplankton in the Baltic Sea (Rousi et al., 2024).

AUTHOR CONTRIBUTIONS

Julia J. J. Fält-Nardmann: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; project administration; data curation; resources. **Heta E. J. Rousi:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; writing – review and editing; formal analysis; project administration. **Ilmari Juutilainen:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis. **Tommi Andersson:** Investigation; methodology; writing – review and editing; data curation; resources. **Betty Marjamäki:** Investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; data curation; resources. **Juhani Itämies:** Conceptualization; investigation; writing – review and editing; data curation; resources. **Pekka Niemelä:** Conceptualization; investigation; funding acquisition;

writing – original draft; methodology; writing – review and editing; project administration; supervision; resources. **Jari Hänninen:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; project administration; formal analysis; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are available from the Dryad Digital repository: <https://doi.org/10.5061/dryad.g79cnp640> (Fält-Nardmann et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure A1. The effect of Regime shifts in the Baltic Sea system on moths in GLIMMIX models, where regime was included as a significant environmental parameter. Regime 0: 1972–1975, Regime 1: 1976–1989, Regime 2: 1990–2017. The key statistics for each model are shown in Table A6.

Figure A2. Average daily snow depth per year at Kevo Subarctic Research Station, 1972–2017. A linear trendline is marked with a black dotted line. Dashed vertical lines indicate the occasions of confirmed marine Regime shifts in the Baltic Sea.

Figure A3. Average daily maximum (light grey) and average daily minimum (dark grey) temperatures per year measured at Kevo Subarctic

Research Station 1972–2017 and seasonal NAO-indices (black, secondary y-axis). Linear trendlines are marked with black dotted lines. Dashed vertical lines indicate the occasions of confirmed marine Regime shifts in the Baltic Sea.

Figure A4. Number of days with average or minimum temperatures $\leq -35^{\circ}\text{C}$ measured at Kevo Subarctic Research Station 1972–2017.

Table A1. Moth division into ecological guilds and occurrence data from 1972 to 2017. Filled cells indicate years when the species was recorded in a light trap on Kevo. Blue cells indicate the year when the species was first recorded in a light trap on Kevo. Red cells indicate the last record of the species.

Table A2. Biomass trends of all moth groups obtained by TRIM analysis with all species included and the 1–2 largest species removed. Statistically significant trends ($p < 0.05$) are marked in bold font. The sample size (n) of all models is 184.

Table A3. Active traps in 1972–2017. A ‘1’ represents a day when a trap was active. Each colour represents one of five trap locations around the Kevo Subarctic Research Station. Darker shades indicate days when the traps were emptied. The trap days -count refers to the sum of the number of days each trap was active during the year. Occasional gaps that can be found in the trapping regime have occurred due to maintenance, storm damage and a Midsummer holiday in 1977.

Table A4. GLIMMIX model fixed effect results and estimates for the climate variables used in the study. Seasonal NAO indices were used as explanatory variables in the models. Satterthwaite degrees of freedom are used. Significant parameters are highlighted with bold font.

Table A5. All temperature parameters in the linear mixed models of the different moth groups. Previous year parameters imply an effect through the parental generation; for the winter season parameters, these were not included in the models. Significant parameters are highlighted in bold font.

Table A6. All precipitation parameters in the linear mixed models of the different moth groups. Previous year parameters imply an effect through the parental generation; for the winter season parameters, these were not included in the models. Significant parameters are highlighted in bold font.

Table A7. All degree day parameters in the linear mixed models of the different moth groups. Previous year parameters imply an effect through the parental generation. Significant parameters are highlighted in bold font.

Table A8. Regime and NAO-index parameters in the linear mixed models of the different moth groups. Significant parameters are highlighted in bold font.

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