



HAL
open science

Evaluation of moth community changes and northward shifts in response to climate warming in Korea using both local and global occurrences

Tae-Sung Kwon, Sung-Soo Kim, Elie Gaget, Won Il Choi, Dae-Seong Lee, Young-Seuk Park

► To cite this version:

Tae-Sung Kwon, Sung-Soo Kim, Elie Gaget, Won Il Choi, Dae-Seong Lee, et al.. Evaluation of moth community changes and northward shifts in response to climate warming in Korea using both local and global occurrences. *Global Ecology and Conservation*, 2024, 49, pp.e02763. 10.1016/j.gecco.2023.e02763 . hal-04697148

HAL Id: hal-04697148

<https://hal.science/hal-04697148v1>

Submitted on 13 Sep 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Evaluation of moth community changes and northward shifts in response to climate warming in Korea using both local and global occurrences

Tae-Sung Kwon^a, Sung-Soo Kim^b, Elie Gaget^c, Won IL Choi^d, Dae-Seong Lee^e, Young-Seuk Park^{e,*}

^a Alpha Insect Diversity Lab, Nowon, Seoul 01746, South Korea

^b Research Institute for East Asian Environment and Biology, Gangdong, Seoul 05236, South Korea

^c Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, Le Sambuc, Arles 13200, France

^d Division of Forest Ecology, National Institute of Forest Science, Dongdaemun, Seoul 02445, South Korea

^e Department of Biology, Kyung Hee University, Dongdaemun, Seoul 02447, South Korea

ARTICLE INFO

Keywords:

Climate warming
Climate change
Range shift
Community temperature index
Cold-adapted species
Warm-adapted species

ABSTRACT

Although climate warming arguably induces changes in species distribution, thereby causing poleward shifts in various taxa, comprehensive research on the response of moths to climate warming is lacking. This study compared the distribution of macro-moths between historical (1978–2002) and recent (2011–2016) periods in South Korea using the macro-moth data collected at 18 survey sites to elucidate the changes in community composition. We used the community temperature index (CTI) to quantify the effect of temperature change on moth community changes. The CTI represents the average value of the species temperature index (STI; mid-value of thermal range) calculated using our local observations and global occurrences reported in the online database of the Global Biodiversity Information Facility. Our analysis revealed no significant difference in species richness between historical and recent surveys. However, some taxa, such as Uraniidae, Nolidae, Sphingidae, and Lasiocampidae, exhibited high turnover rates, while the number of sphingid moths with large body sizes greatly decreased. The temperature changes at the survey sites became pronounced with an increase in the survey interval (year) between historical and recent surveys (temperature increase = 0.0465 °C /year), while the CTI change exhibited a weak signal for northward shift of moth species. The CTI using the local data indicated 0.09 km/year of northward shift of moths, which is considerably slower than the northward shift (9.6 km/year) of the isothermal bands. However, the CTI using global occurrence data, expected to improve the estimation of species thermal niches, did not show any sign of northward shift. When observed, the northward shifts of moths were primarily identified in the cold-adapted species with low STI values, suggesting that cold-adapted species are more sensitive and vulnerable to climate warming than warm-adapted species. These results indicate that the current distribution changes of species were uneven, and the species adapted to cold regions are the ones primarily responding to the temperature increase by migrating northward and to high elevations.

* Corresponding author.

E-mail addresses: insectcom@naver.com (T.-S. Kwon), nabifri@chol.com (S.-S. Kim), gaget@tourduvalat.org (E. Gaget), dleotjd520@naver.com (D.-S. Lee), parkys@khu.ac.kr (Y.-S. Park).

<https://doi.org/10.1016/j.gecco.2023.e02763>

Received 15 June 2023; Received in revised form 6 November 2023; Accepted 6 December 2023

Available online 7 December 2023

2351-9894/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Various taxa have experienced northward shifts owing to climate warming in the Northern Hemisphere (Parmesan and Yohe, 2003), with butterflies being the most frequently reported insects (Fourcade et al., 2017; Parmesan et al., 1999; Warren et al., 2001). However, studies on the changes in the distribution of moths, which constitute a majority of Lepidoptera, are limited. Butterflies are active during the day and are popular among people because of their beautiful shapes and colors, which prompted many professional and amateur researchers to collect a substantial amount of data on them (Dennis et al., 2017). Although the climate warming-induced changes in butterfly distribution have been investigated and revealed, the understanding about the distribution and distribution changes in response to climate warming of night-time-active moths remains limited.

Moths, alongside beetles, bees, and flies, form the dominant insects with the highest biodiversity, thereby playing a vital role in maintaining biodiversity by fertilizing flowers, feeding on plants, and representing a major food source for birds and bats (Wagner et al., 2021). However, moth diversity has been decreasing at a global scale (Dar and Jamal, 2021; Wagner, 2012; Wagner et al., 2021), and distribution changes in response to climate warming are being observed at local scales, mostly in Europe and North America. For example, long-term surveys in the UK and Finland demonstrated an increase in abundance of warm-adapted species (Itäimies et al., 2011; Sparks et al., 2007) and distribution changes toward high latitudes (Itäimies et al., 2011). Based on the comparison of results from historical and recent surveys conducted in alpine regions of the tropics, moths appeared to be moving to high elevations (Chen et al., 2009; Cheng et al., 2019), showing the influence of climate warming on the changes in moth distribution. Despite evidence of the impact of climate warming on moth distribution, such results remain limited to specific geographic regions (Forsman et al., 2016; Itäimies et al., 2011; Lindström et al., 2012). However, moth observations collected by taxonomy experts and citizen science programs could be used to expand our knowledge on changes in moth distribution (Wagner et al., 2021).

Assessing distribution changes using an inventory that relies on a limited number of survey sites is challenging. Identifying changes occurring at range margins, particularly in the northernmost and southernmost distribution areas, is common; however, obtaining large-scale distribution data with high reliability is necessary, which requires substantial sampling efforts. Obtaining such data might be challenging owing to various reasons. For example, in the Korean Peninsula, it is impossible to conduct investigations north of the demilitarized zone (DMZ) because of political constraints. If such data are missing, distribution change can be quantified using the community temperature index (CTI) (Devictor et al., 2008). The CTI is a community weighted mean index that relies on a species thermal niche to estimate community responses to climate warming. Although it was initially developed for bird communities (Devictor et al., 2008), it is being used on a diverse number of taxa in various ecosystems (Bowler and Böhning-Gaese, 2017; Burrows et al., 2019; Devictor et al., 2012; Kwon et al., 2021; Lee et al., 2021a). The CTI is the average value of the species temperature index of all species present in a community (STI; mid-value of the thermal range). As the distribution changes with an increase in temperature, the number of cold-adapted species with low STI values can decrease and the number of warm-adapted species with high STI values can increase, thereby inducing a CTI increase. Considering this, CTI has been developed to quantify the thermal aspect of community changes and infer distributional changes in response to climate warming (Devictor et al., 2008).

In temperate regions of the Northern Hemisphere, the CTI of the community and the temperature exhibit a linear pattern by decreasing with increasing latitude (Kwon, 2017). The regression equation describing this pattern can be used to estimate the distance (km) of the average distribution shift of the species in response to climate warming (Devictor et al., 2008). Consequently, using a subset of sampling sites with temporal surveys, we can estimate community response to climate warming and infer species distribution change over time.

In this study, we investigated the responses of moth to climate warming in South Korea. The annual mean temperature in South Korea has increased at a rate of 0.18 °C per decade during the last century (1912–2017) (National Institute of Meteorological Research, 2018), exceeding the global average increase of 0.08 °C per decade (1880–2021) (NOAA National Centers for Environmental Information, 2022). Previous studies have compared the past and recent distribution limits of butterflies in South Korea and revealed a northward shift of the northern margin of warm-adapted species (Kwon et al., 2013; Kwon et al., 2010). Owing to the increase in warm-adapted species (Forsman et al., 2016; Keret et al., 2020; Kuchlein and Ellis, 1997; Lindström et al., 2012; Sparks et al., 2007), a northward shift of moths in Korea is plausible. However, when evaluating the distribution change of Korean butterflies using CTI, the distribution remained stable over the 60-year period under investigation (Kwon et al., 2021). Hence, the distribution changes observed in butterflies may not have occurred in a similar manner in moths, and such expectation prompts further evaluation of these discrepancies.

We used the CTI approach to compare the occurrence of macro-moths between historical (1978–2002) and recent (2011–2016) periods using moth data collected from 18 sites in South Korea. We hypothesized that the moths moved northward in response to the increase in temperature, and that the CTI values of the recent survey would be higher than those of the historical survey because of a community turnover driven by climate warming. Thus, the larger the survey interval (years) or temperature increase of each survey site, the greater the increase in CTI. To address these concerns and because Eastern-Asian moth distribution is mostly unassessed, we used two different means of calculating the CTI. They were based on species temperature index (STI) assessed from local occurrence data and global occurrence data. We expected that the two types of CTI would show similar temporal changes if thermal niches were estimated in a similar manner from local and global data, showing similar responses by moths as a result of climate warming.

2. Materials and methods

2.1. Sites and sampling

Moth occurrence data were obtained from historical studies from 1978 to 2002 and recent surveys from 2011 to 2016. Based on historical surveys, recent field surveys were conducted for six years from 2011 to 2016 at the same (or nearby) 18 locations and in the same season (month), as in the literature data (Fig. 1, Table 1). Of the 18 survey sites, five were located on islands, and 13 in inland, from the northernmost to the southernmost areas of South Korea. The interval between the historical and recent surveys was 24 years on average (12–37 years). A description of the nature (same or changed) of the survey sites between the historical and recent years is provided in Table 1. Because the locations of survey sites slightly varied between historical and recent surveys, our results focusing on community temporal changes might also reflect changes related to survey site re-location (see discussion). For five historical sites, moth surveying was impossible owing to land cover changes, including urbanization. The field surveys were conducted in open green habitats (mostly grassland with shrubs and scattered trees) adjacent to forests.

The landscape of the survey sites primarily comprised forests with agricultural areas and grasslands, followed by urban, barren, and wetland areas in recent years (Appendix A Table S1). South Korea is located in the temperate broad-leaved forest zone, with 37% of the forest being broad-leaved, primarily comprising oak, with the remaining 33% being coniferous forests, such as pine and cypress (National Geographic Information Institute, 2020). The mean annual temperature (MAT) in South Korea is 12.79 °C, annual precipitation is 1305.4 mm (Korea Meteorological Administration, 2021), and total forest cover of the country is 42% of the total country area (National Geographic Information Institute, 2020). In South Korea, the MAT has increased by 1.8 °C over the last century owing to climate warming (National Institute of Meteorological Research, 2018).

Macro-moths in the recent surveys were collected on a monthly basis between 21:00 and 24:00 on survey days from May to October using light traps. Macro-moths were defined as per Korean moth taxonomists. In the recent surveys, moths were also collected using a light lamp (black light, 12 Voltage DC power source, BioQuip Co. USA) installed on a screen. Light trap types in the historical surveys were diverse, ranging from a gasoline lamp at survey site 14; incandescent lamp at sites 10, 11, and 17; black light at sites 15 and 16; fluorescent lamp at sites 1, 3, 5, 7, and 8; and mercury lamp at site 18 or were not recorded. Recent survey data matching that of historical surveys (same month) among six surveys were used for analysis (Table 1). Rarefaction curves (observed species richness) were performed for comparison of species richness between historical dataset and recent dataset using a vegan package (Oksanen et al., 2019) in R (R Core Team, 2020).

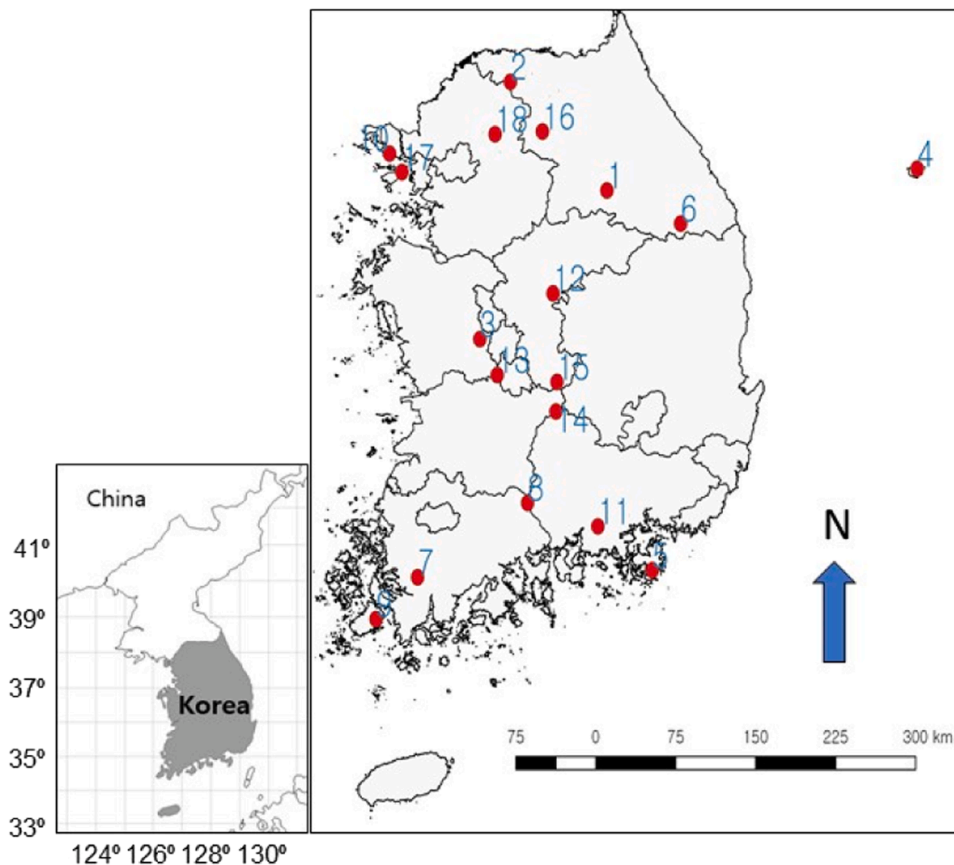


Fig. 1. Map of moth survey sites in South Korea. Additional details are provided in Table 1.

Table 1

Moth survey sites and years in South Korea. The identity indicates the difference in sampling sites between the historical and recent studies. 1: Both historical and recent surveys were conducted at the same sites, 2: Recent survey was conducted at several sites of historical surveys, and 3: Recent survey sites are not the same as historical sites; however, both sites are similar in elevation and landscape in the same region. Coordinates in parentheses represent those of historical survey sites, where sampling sites were changed.

Site			Location		Elevation (m)	Historical survey year	Recent survey year	Interval (year)	Month of survey	Reference for historical survey
No	Name	Identity	Latitude	Longitude						
1	Baekdeoksan	1	37.37275	128.25772	438	1981	2011	30	5, 7, 8, 9	(Shin, 1984)
2	Gwangdeoksan	1	38.1101	127.44358	647	1991	2011	20	5, 6, 7	(Shin, 1991)
3	Gaeryongsan	1	36.36439	127.18629	173	1980	2011	31	5, 6, 8, 9	(Shin, 1981)
4	Uleungdo	2	37.51998	130.87111	390	1998	2012	14	5, 7, 8	(Kim, 1999)
5	Geojaedo	3	34.79627 (34.801003)	128.63954 (128.619538)	125	1991	2012	21	4, 5, 6, 7, 8, 9	(Shin and Cheong, 1992)
6	Taebaeksan	3	37.14791 (37.112183)	128.87892 (128.924026)	841	1987	2012	25	5, 6, 7	(Shin et al., 1990)
7	Weolchulsan	2	34.74858	126.66203	133	1988	2013	25	5, 7, 8	(Shin et al., 1989)
8	Jirisan	1	35.25331	127.58898	294	1982	2013	31	5, 7, 8	(Shin, 1983)
9	Jindo	2	34.46505	126.31184	131	1989	2013	24	5, 6, 7, 8	(Shin and Joo, 1991)
10	Ganghwado	1	37.62323	126.42613	141	1997	2014	17	6, 9	(Paek et al., 1997)
11	Jinju	3	35.0939 (35.198881)	128.18147 (128.079942)	98	1984	2014	30	5, 6, 7, 8, 9	(Park and O, 1988)
12	Soklisan	2	36.67476	127.80328	153	2002	2014	12	5, 6, 7, 9	(Sohn et al., 2003)
13	Daedunsan	1	36.12027	127.33339	276	1992	2015	23	5	(Byun et al., 1993)
14	Deokyusan	3	35.87306 (35.881128)	127.82822 (127.770976)	787	1978	2015	37	6, 7, 8	(Jun and Shin, 1980)
15	Minjujisan	1	36.0731	127.83681	717	1992	2015	23	5, 6, 7, 8, 9	(Nam, 1993)
16	Samaksan	3	37.77293 (37.836649)	127.7146 (127.65647)	248	1990	2016	26	5, 6	(Park and Ju, 1990)
17	Yeongjongdo	1	37.49742	126.5303	60	1995	2016	21	5, 6, 7, 9	(Bae et al., 1996)
18	Chukryungsan	1	37.75461	127.31487	380	1998	2016	18	6, 7, 8, 9	(Sohn et al., 1998)

2.2. Temperature data

Given the absence of weather stations in the study sites, the MAT data of the survey sites were obtained using interpolated temperature maps. The annual temperature maps were produced at the nationwide scale from 2009 to 2016 via the inverse distance weighting method using the mean temperature measured at the weather stations of the Korea Meteorological Administration. By 2020, the Korea Meteorological Administration had been operating 629 national weather stations with automatic weather systems (526 stations) and automated synoptic observing systems (103 stations). Subsequently, we extracted the MAT of each survey site from the maps based on the coordinates of the study sites. The historical MATs of the survey sites were estimated using the temperature change recorded at the nearest meteorological station during the survey interval and the recent MAT of each survey site. These fine scaled temperature data were used for local STIs.

2.3. Landscape data

The landscape data of the survey sites were obtained based on the open land coverage map of South Korea. The Ministry of Environment in South Korea provides a land coverage map comprising seven classes (urban, agriculture, forest, grassland, wetland, barren, and water areas) through the Environmental Geographic Information Service (<https://egis.me.go.kr>). Using the land coverage map from different periods (late 1980 s, late 1990 s, late 2000 s, and late 2010 s), landscape data for all survey sites were obtained from the time of the survey. All land coverage maps have a spatial resolution of 30 m and use the EPSG:5186 coordinate system. Land cover within a radius of 2 km from the survey sites was used as the landscape data and was converted into percentages.

2.4. CTI calculation and analyses

We used the CTI approach to assess moth responses to climate warming (Devictor et al., 2008). The CTI relies on the STI of species, which is the mean temperature of the species distribution range. Such STI values are typically calculated from species atlases (Devictor et al., 2008). However, in the case of Korean moths, information on species distribution range is limited. To address this limitation, we used two ways to calculate STI: first by estimating STI from the local survey sites and second from global occurrences collected from the online database of the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>). Using different spatial references to assess STI values might result in different CTI values. However, as observed by Devictor et al. (2012), the CTI temporal trend that is used to assess community response to climate warming is robust to different STI calculations if they preserve relative differences between species.

First, we assessed STI values from the surveyed sites (hereafter “local STI”). The local STI was estimated using the occurrence data from both the historical and recent surveys. Both historical and recent STIs were obtained based on the MAT of the surveys. Pooled STIs of co-occurred species that occurred in both historical and recent surveys were obtained using an average of two STIs. Regression models of co-occurring species between historical STIs and pooled STIs and between recent STIs and pooled STIs were used to estimate pooled STIs of restricted moth species, which occurred only in either the historical or recent survey.

Second, we assessed STI values using the GBIF data (hereafter “global STI”). The global STI was estimated using the global occurrence data from GBIF (GBIF.org, 2023) and global climate data from WorldClim (<https://www.worldclim.org/>, spatial resolution of 2.5°). Species with no data on GBIF or fewer than 20 records on GBIF were not used for CTI estimation. Of the 1074 species, 863 species were used for CTI estimation (Appendix A Table S2). The R script for this process is shown in the electronic supplementary data (Appendix A).

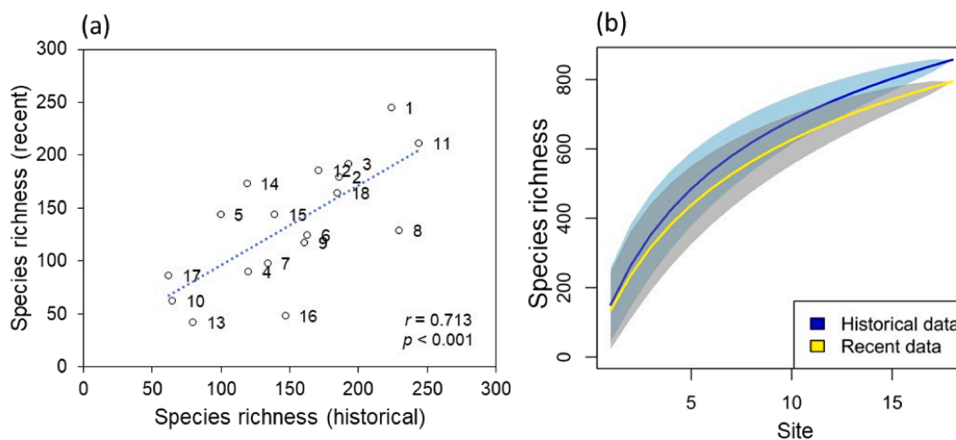


Fig. 2. (a) Pearson correlation coefficient between historical species richness and recent species richness across 18 sampling sites, (b) rarefaction curves showing observed species richness in both historical and recent datasets. Numbers in (a) indicate sampling sites, and gray scales in (b) present the confidence interval of each species richness.

Fundamentally, CTI is the average of the STI values of the collected species at a site. Generally, abundance is weighted in the calculation of the CTI (Burrows et al., 2019). However, we did not weigh the abundance in the CTI calculation because not all individuals of abundant species were collected. In particular, Devictor et al. (2008) had revealed a minor difference between the abundance-weighted and unweighted CTIs, which was supported by Kwon (2017). Thus, we calculated CTI values at historical and recent times as an average value of the species observed at these times.

If moths were to move northward, recent CTI would be higher than historical CTI at each survey site. Therefore, the mean changed CTI (=recent CTI - historical CTI) would be greater than zero. Therefore, to assess this relationship, we conducted a one-sample *t*-test. The increased CTI value was utilized to evaluate the northward shifts of moths (Devictor et al., 2008) using the slope of the regression model that linked CTI (response variable) with latitude and elevation (explaining variables). In this estimation, we considered the difference in years between the average historical survey year and the average recent survey year as the survey interval. The same method was applied to estimate the northward shift of the isotherm.

Two key variables (temperature change and interval between historical and recent surveys) for testing the influence of climate warming were significantly correlated (Fig. 2). Therefore, they were separately used for analyzing the influence of climate warming through a simple regression model. Meanwhile, a generalized linear model was used to evaluate the multiple influences of selected covariates such as latitude, elevation, site identity, location (island or inland), and forest (%) on the CTI change along with temperature change or survey interval. Forest (%) was selected because it is the main habitat for most of the moth species (Emmet, 1991) and the primary land type at the survey sites, having a high correlation with land cover change (Appendix A Tables S1). Land cover change is the percentage of all changed land cover types within a specific area. A generalized linear model was conducted from a full (five explaining variables) model to one variable model, leading to a step-by-step removal of the least significant variable with the highest statistical significance. The model with the lowest Akaike information criterion (AIC) was selected for the optimum model.

Finally, we investigated the absolute temporal turnover per moth family between historical and recent surveys to assess community change. The CTI changes reflect thermal affinity turnover in the communities in response to temperature changes; however, communities can also change depending on other environmental changes. The turnover rate of families was calculated as follows: turnover rate (TR) = ((SR in historical survey only) + (SR in recent survey only)) / (SR in both surveys), where SR is species richness.

All statistical analyses were performed using the stat package in R (R Core Team, 2020). The data used for analysis are shown in Appendix A Tables S2 and S3.

3. Results

In the historical data, 857 species were recorded showing the highest species richness at site 11 with 244 species, whereas the recent data comprised 794 recorded species displaying the highest species richness at site 1 with 211 species (Fig. 2a, Appendix A Table S2). This marked a strong positive correlation between the historical and recent data ($r = 0.713$, $p < 0.001$). Species richness in both historical and recent datasets were not saturated in rarefaction curves as the number of sampling sites increased because of the large moth diversity (Fig. 2b).

The temperature changes at the survey sites increased as the survey interval (years) between historical and recent surveys increased (Fig. 3). The slope of the regression equation was estimated to be 0.0465, reflecting an increase of 0.0465 ± 0.0192 °C (mean \pm SE) per year ($p < 0.03$). The areas around the survey sites primarily comprised forested areas ($88.1 \pm 13.8\%$, mean \pm SD, Appendix A Table S1) followed by agricultural areas ($8.1 \pm 8.7\%$), grassland ($1.5 \pm 1.4\%$), and built-up areas ($1.1 \pm 1.9\%$). Compared to that during the historical survey years, $3.8 \pm 3.1\%$ of the total area changed to another land type, with the conserved forest ($0.3 \pm 3.2\%$) showing properly conserved moth habitats. The rate of land cover change was significantly different according to site characteristics (same sites $2.9 \pm 4.5\%$, $n = 13$, changed sites $12.6 \pm 4.5\%$, $n = 5$; $F_{1,16} = 5.34$, $p = 0.034$) (Appendix A Table S3). The percentage of

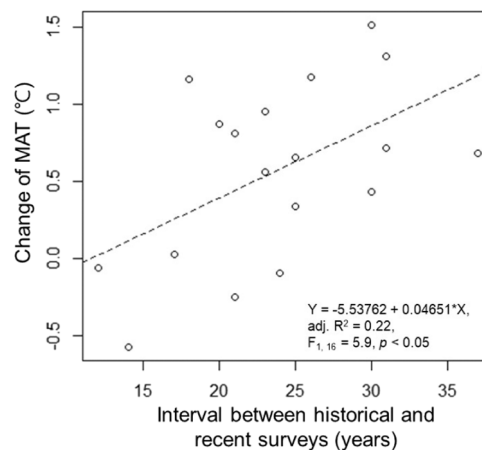


Fig. 3. Changes in mean annual temperature (MAT) at the 18 moth survey sites. The dotted line represents regression model. The data of MAT change were obtained from the weather stations nearest to the sites.

forest is a key variable for the conservation of land because it is significantly correlated with land cover change ($r = -0.7, p = 0.001$) (Appendix A Table S4).

In the dataset, 857 and 794 species were recorded in historical and recent surveys, respectively, resulting in 1074 species in total (Table 2). Geometridae was the most diverse, with 344 species, followed by Erebiidae (270 species), and Noctuidae (258 species). These three dominant taxa accounted for 81% of the total species richness in the analyzed data. Of the total species, 497 species that occurred only once in the historical or recent surveys accounted for 46% of the total species richness. The TR between the historical and recent survey data was 0.46, with Uraniidae exhibiting the highest TR (0.6), followed by Nolidae (0.56), Sphingidae (0.55), and Lasiocampidae (0.54); all of them exhibited low species richness of 5–38 species. In Sphingidae, the number of species in the recent survey (18 species) was only half that in the historical survey (37 species), showing a significant decrease in species richness.

The local STI values were significantly correlated with the global STI values with a low determinant coefficient (adj. $R^2 = 0.109, p < 0.001$, Fig. 4a). In addition, global STI values had a larger range distribution (2–25 °C) than local STI values (7–15 °C), suggesting that global STIs were more representative of species thermal niches than local STIs. Despite a low correlation between global and local STI values, the CTI values using local STIs (local CTIs, hereafter) were highly correlated (adj. $R^2 = 0.675, p < 0.001$) with those using global STIs (global CTIs, hereafter, Fig. 4b).

The significant positive relationships between CTIs and MATs were found in both local and global CTIs ($R^2 = 0.898, p < 0.001; R^2 = 0.332, p < 0.01$, respectively), implying that moth thermal community composition was correlated with site temperature (Fig. 5a). However, the relationship between local CTIs and MATs was considerably stronger than that between global CTIs and MATs (Fig. 5a). Neither local nor global CTIs temporal changes had significant relationships with survey interval (years) ($p = 0.054$ and 0.123 , respectively) (Fig. 5b) or with temperature change ($p = 0.22$ and 0.27 , respectively) (Fig. 5c). The average of the local CTI changes of the 18 sites was significantly higher than zero ($t = 2.55, df = 17, p = 0.02, 0.1 \pm 0.17, \text{mean} \pm \text{SD}$), whereas that of global CTI was not different from zero ($t = 0.198, df = 17, p = 0.85, 0.018 \pm 0.38$). Therefore, the local CTI exhibited a northward shift trend; however, the global CTI did not show the same pattern.

Northward shifts can be estimated using the increased value of the local CTI. When the effect of elevation was accounted for, the CTI decreased by 0.1886988 per latitude degree ($Z = 18.5217531 - 0.1886988 \times X - 0.0012092 \times Y$, adj. $R^2 = 0.69, F_{2, 15} = 19.87, p < 0.0001, X = \text{latitude}, Y = \text{altitude}$). Thus, the increased CTI value (0.1) was equivalent to a latitude change of 0.0189° , corresponding to a northward shift of 2.1 km over a period of 23.8 years ($1^\circ \text{latitude} = 111 \text{ km}$ in South Korea). When the effect of elevation was considered, the temperature decreased by 0.536°C per degree increase in latitude ($Z = 32.09333 - 0.536008 \times X - 0.002835 \times Y$, adj. $R^2 = 0.42, F_{2, 15} = 7.25, p < 0.01$). Furthermore, a latitude difference of 1.866° (207 km) in Korea corresponded to a 1°C temperature change. Therefore, an annual increase of 0.0465°C (Fig. 3) implied a northward shift of the isotherm by 9.6 km, equivalent to 228 km of northward shift over a period of 23.8 years. Thus, the northward shift (2.1 km) of moths based on the local CTI was considerably slower than the isothermal shift (228 km). In contrast, the global CTI did not display a northward shift trend. Lastly, species with low local STI values exhibited pronounced northward or upward shifts (Fig. 6a, c). The global STI displayed an increased northward shift in species with low STI values but did not show an upward shift (Fig. 6b, d). Neither of the STIs showed a relationship with changes in occurrence (Fig. 6 e, f).

Of five covariates, elevation and forest (%) were significant variables influencing the CTI changes in the generalized linear models; however, site identity (Id), location (island or inland), and latitude did not play significant role (Table 3). Elevation had a negative coefficient ($-0.0003 \pm 0.0002 \text{ SE}$) in the regression model, whereas forest (%) had a positive coefficient (0.005 ± 0.003). For the global CTI change, only the survey interval was a significant variable in the model. Of the four optimum models, although only the model of the survey interval on local CTI change was significant ($p = 0.04$), and other models were not significant ($p = 0.12\text{--}0.17$), all the slope values of survey interval or temperature change were positive.

Table 2

Number of moth species observed at the 18 survey sites in South Korea. Common: occurred in both of historical and recent studies. TR (Turnover rate) = ((Historical survey only) + (Recent survey only))/Pooled.

Family	Historical	Recent	Common	Historical survey only	Recent survey only	Pooled	TR
Bombycidae	2	3	2	0	1	3	0.33
Brahmaeidae	2	2	2	0	0	2	0.00
Drepanidae	28	27	23	5	4	32	0.28
Endomidae	1	0	0	1	0	1	1.00
Epicopeiidae	1	0	0	1	0	1	1.00
Erebiidae	215	218	163	52	55	270	0.40
Euteliidae	2	3	2	0	1	3	0.33
Geometridae	259	277	192	67	85	344	0.44
Lasiocampidae	13	6	6	7	0	13	0.54
Limacodidae	1	0	0	1	0	1	1.00
Noctuidae	202	168	112	90	56	258	0.57
Nolidae	18	18	11	7	7	25	0.56
Notodontidae	67	45	41	26	4	71	0.42
Saturniidae	6	5	4	2	1	7	0.43
Sphingidae	37	18	17	20	1	38	0.55
Uraniidae	3	4	2	1	2	5	0.60
Total	857	794	577	280	217	1074	0.46

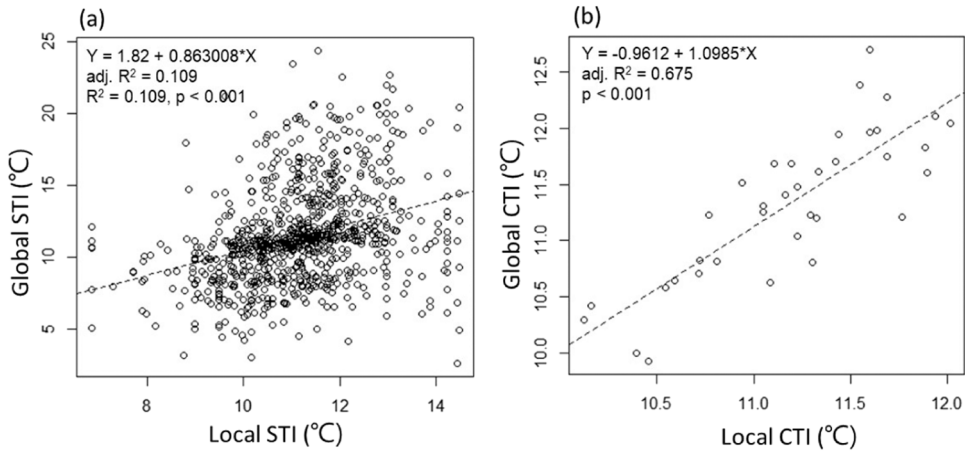


Fig. 4. Relationships (a) between local and global species temperature index (STIs) of 864 moth species used for the estimation of CTI and (b) between local and global community temperature index (CTIs) of 36 sites (18 historical and 18 recent). The dotted lines represent the regression models.

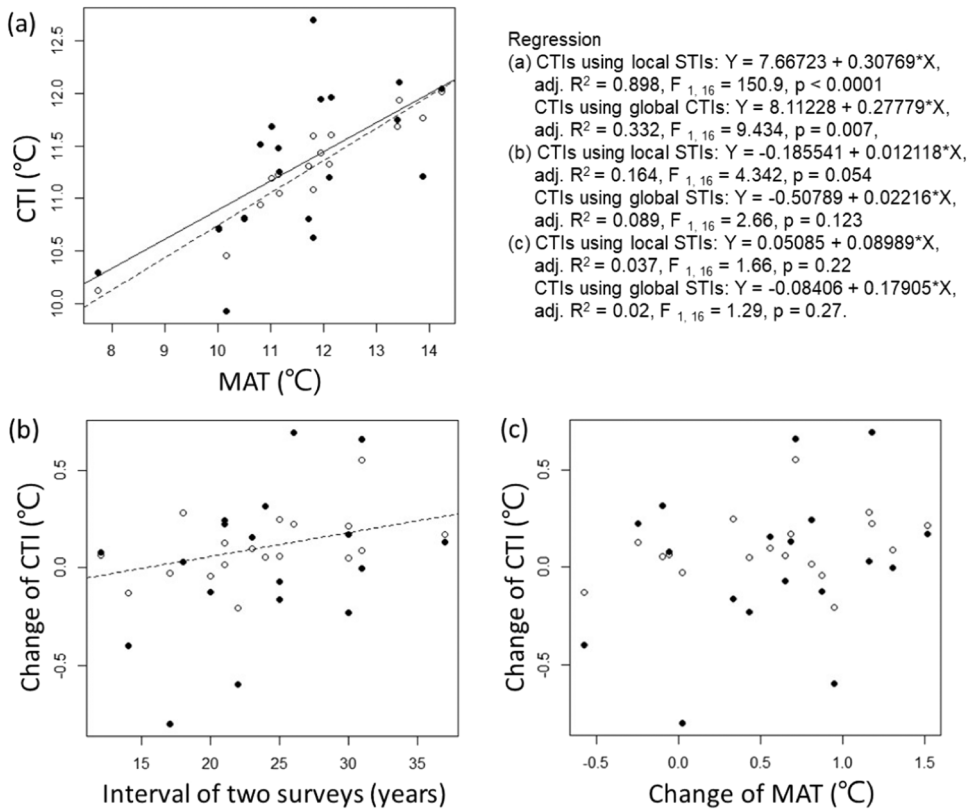
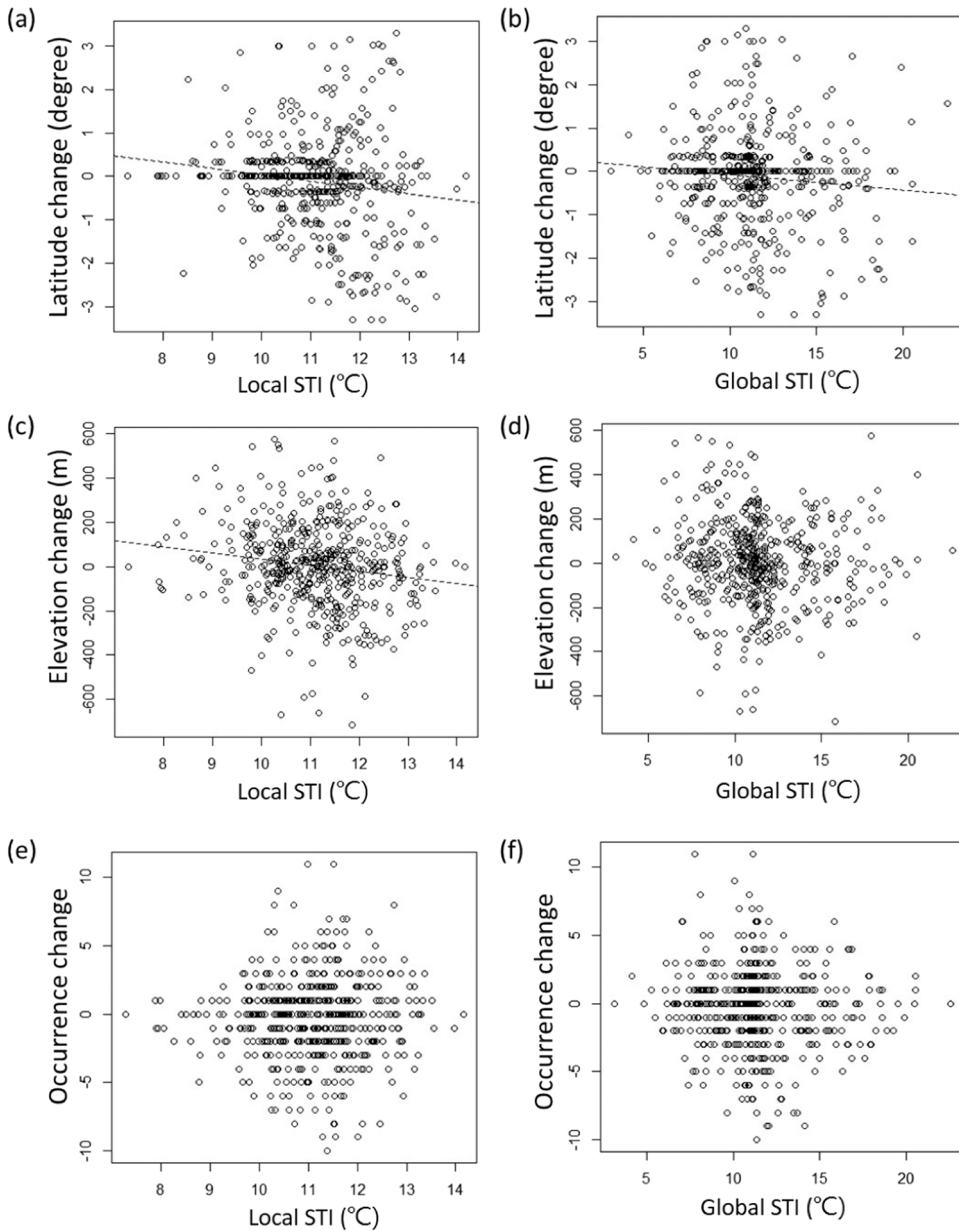


Fig. 5. Relationships (a) between community temperature index (CTIs) and mean annual temperatures (MAT) of 18 moth assemblages, (b) between changes in CTIs and interval of two (historical and recent) surveys, and (c) between changes in CTIs and changes in MAT. Open circles represent CTIs using local STIs, and closed circles represent CTIs using global STIs. The dotted line represents a regression model of CTIs using local STIs, whereas the solid line is that using global STIs.



Regression

(a) $Y = 1.82606 - 0.16729 \cdot X$, adj. $R^2 = 0.031$, $F_{1,512} = 17.65$, $p = 0.00003$

(b) $Y = 0.40906 - 0.03882 \cdot X$, adj. $R^2 = 0.011$, $F_{1,512} = 6.676$, $p = 0.01$

(c) $Y = 310.811 - 27.643 \cdot X$, adj. $R^2 = 0.022$, $F_{1,512} = 12.65$, $p = 0.0004$

(d) $Y = 42.343 - 3.381 \cdot X$, adj. $R^2 = 0.0006$, $F_{1,512} = 1.328$, $p = 0.25$

(e) $Y = -1.23757 + 0.08278 \cdot X$, adj. $R^2 = -0.001$, $F_{1,512} = 0.45$, $p = 0.5$

(f) $Y = 0.27241 - 0.05228 \cdot X$, adj. $R^2 = 0.0006$, $F_{1,512} = 1.293$, $p = 0.26$.

Fig. 6. Relationships (a and b) between changes in latitude, (c and d) elevation, and (e and f) occurrence of local and global species temperature indices (STIs). The latitude change represents the changes in latitude means, and occurrence change represents the difference between number of sites where a species occurred in recent survey and the number of sites where it occurred in historical survey (i.e., recent value – historical value). The dotted lines indicate regression models.

Table 3

Influence of survey interval (SI, years) or temperature change (TC) on CTI change (local or global) with other covariates in generalized linear model. Local CTI and global CTI use local STI and global STI, respectively. Other covariates are as follows: site identity (Id), location of site (island or inland) (Loc), latitude (Lat), elevation (Ele), and forest (%) in total land (Forest). Bold values are optimum models with lowest Akaike information criterion (AIC) values. Values in SI and TC columns represent their coefficients in each generalized linear model. Other covariate variables are presented with statistically significant status without their coefficients.

CTI change (Dependent variable)	Survey interval (SI) (independent variable)									Temperature change (TC) (independent variable)								
	SI	Id	Loc	Lat	Ele	Forest	<i>p</i>	Adj. R ²	AIC	TC	Id	Loc	Lat	Ele	Forest	<i>p</i>	Adj. R ²	AIC
Local	0.017.	ns	ns	ns	*	ns	0.17	0.24	-10.70	0.150 ns	ns	ns	ns	ns	ns	0.36	0.08	-7.13
	0.017 *		ns	ns	*	ns	0.09	0.30	-12.60	0.172 *	ns		ns	ns	ns	0.23	0.15	-9.01
	0.019 *			ns	*	*	0.051	0.34	-14.00	0.167 *	ns		*	.	.	0.15	0.19	-10.50
	0.015 *				*	.	0.04	0.31	-14.00	0.132.			.	ns	ns	0.14	0.17	-11.00
	0.014 *				ns		0.07	0.198	-12.00	0.116 ns				ns		0.24	0.06	-9.22
	0.012.						0.054	0.16	-12.10	0.089 ns						0.22	0.04	-9.57
Global	0.036.	ns	ns	ns	.	ns	0.45	0.012	23.12	0.517.	ns	ns	ns	ns	ns	0.37	0.07	22.04
	0.036.	ns		ns	.	ns	0.30	0.095	21.12	0.507.	.	ns	.	ns	ns	0.24	0.14	20.11
	0.035.			ns	ns	ns	0.27	0.097	20.53	0.383 *	.		.	ns	ns	0.17	0.17	18.90
	0.027.				ns	ns	0.22	0.11	19.64	0.343.	ns			ns		0.18	0.13	19.14
	0.026.				ns		0.16	0.11	18.85	0.259 ns	ns					0.26	0.05	19.94
	0.022 ns						0.12	0.09	18.40	0.179						0.27	0.02	19.80

ns: $p > 0.1$,.: $p < 0.1$, and * : $p < 0.05$.

4. Discussion

The analysis of CTI changes between historical and recent survey data in South Korea showed an absence or a weak indication of a relationship between climate warming and thermal community change in moths. Local CTI showed a weak northward shift but global CTI did not. The northward shift from the local CTI increased value was also considerably slower (2 km for 24 years) than isothermal shifts (228 km for 24 years). However, the global CTI did not show any significant signs, such as an increase in the average of changed values and annual increase for the northward shift. A time lag of the northward shift, compared to the isothermal shift, can be deemed as a climatic debt (Devictor et al., 2008). Based on CTI, such time lags have been previously reported in European birds and butterflies, where the northward shifts of birds and butterflies were 2.8 km/year and 6.3 km/year, respectively (Devictor et al., 2012), thereby being slower than the isothermal northward speeds with 11.8 km/year and 7.5 km/year, respectively. In Sweden, moths moved northward at a rate at 1.3 km/year for 41 years (1973–2014) (Forsman et al., 2016), while butterflies in Korea exhibited a northward shift of the northern limit at 1.5 km/year for 60 years (Kwon et al., 2014). Notably, even the latter is considerably faster than that of the moths (0.09 km/year) in this study. However, the northward shift of the butterfly distribution was not identified in CTI analysis (Kwon et al., 2021), which was repeatedly observed in the global CTI of moths. Therefore, the northward shift of the moth analyzed in this study was too slow or non-existent. Thus, a remarkably large variation was observed in the speed of the species northward shift depending on the survey area, taxon, and analysis method. The changes in the distribution limit line directly indicate the distribution changes; however, the CTI method only indirectly reflects the distribution changes based on the changes in the community structure. To interpret species distribution change from positive CTI trends, further analyses would be required, such as calculating species contribution to the CTI trend (Gaget et al., 2018) and colonization-extinction patterns from the standard deviation of the CTI (Gaget et al., 2021). In Europe, CTI has been previously used to efficiently reveal the northward or upward shifts of butterflies, birds, and plants (Devictor et al., 2008; Devictor et al., 2012; Roth et al., 2014; Zografou et al., 2014). Therefore, to evaluate the quantitative relationship between the CTI and species distribution changes, more theoretical studies based on numerical simulations are required alongside comprehensive field investigations.

The responses of moths to climate change exhibit notable variability, dependent upon their environmental conditions and geographical regions. In tropical regions with lower latitudes, such as Hong Kong, only one out of the 123 species examined demonstrated an increased probability of occurrence across various elevations. Conversely, all other species showed no significant change in occupancy despite the observation of significant increases in maximum temperatures and the occurrence of extreme weather events (Cheng et al., 2019). In British fixed monitoring sites within high-latitude regions, moth biomass fluctuated over a 50-year period, with both increases and decreases documented (Macgregor et al., 2019). The extent and nature of these changes varied among taxa and land use types. While two-thirds of individual moth species experienced declines, others exhibited increases (Conrad et al., 2006; Fox et al., 2014). On the other hand, positive shifts in species richness and moth abundance over five decades were observed in a mixed forest with relatively species-poor moth communities in the high-latitude area of Central Sweden (Franzén et al., 2023). This outcome differed from many previous studies (Franzén and Johannesson, 2007; Sánchez-Bayo and Wyckhuys, 2019). Moths with narrow thermal niches across their European distribution showed more pronounced shifts toward the north (Hällfors et al., 2023). These findings collectively suggest that the majority of studied species tend to either adapt to their current locations through shifts in phenology or migrate to different ranges (Hällfors et al., 2023). Species with broader tolerance to climatic conditions may adapt in situ and remain in their current habitats, while those less adaptable face strong pressure to relocate.

Climate change also influence the distribution of vegetation. Therefore, it is interesting to compare the moth shift with vegetation changes because the distribution of moths depends on the distribution of their host plants. In this study, the CTI, using local data, indicated a northward shift of moths at a rate of 0.09 km/year, which is considerably slower than the northward shift of the isothermal bands (9.6 km/year). The northward shift of moths was also slower than the vegetation changes. Heo et al. (2006) reported northward shifts of bamboos and garlic with an average of 0.8 km/year and 0.4 km/year, respectively, in South Korea. Similar results were observed in mountain regions, indicating that the average hemispheric shift rate (0.354 m/year) was merely half of what would be anticipated from climate warming alone (Lu et al., 2021). Consequently, the shift rate is most pronounced in response to climate warming, followed by vegetation changes, and then moths. Climate changes prompt alterations in vegetation composition and distribution, subsequently influencing shifts in insect community composition and their distribution (Hoffmann et al., 2019; Moon et al., 2018; Płóciennik et al., 2023).

In this study, the expected distribution changes from the historical survey and the recent survey (the northward and upward shift) were primarily identified among the species with low STIs; however, the species with high STIs did not show any significant responses (Fig. 6). These findings indicate that the current distribution changes in species were rather uneven, while the species that are adapted to cold regions primarily migrate to the north and high elevations in response to the temperature increase. As the distribution change based on CTI reflects the average trend of all species, the distribution change of cold-adapted species with low STI can exceed the estimated value. However, previous studies (Devictor et al., 2008; Devictor et al., 2012; Forsman et al., 2016) using CTI did not provide insights into different distribution changes based on the thermal optimum (STI) of the species. However, previous studies focused on the northward shift of the range margin indicated that the northern margins moved northward, whereas the southern margin did not (Parmesan et al., 1999). In South Korea, while the southern margins of cold-adapted butterfly species whose southern limit is located in Korea either remained unchanged or shifted southward, the northern limit line of the warm-adapted butterfly species with the northern margin of distribution moved northward (Kwon et al., 2014). These findings suggest that the warm-adapted species distributed in and near the northern margin are more sensitive to climate warming than the cold-adapted species distributed in and near the southern margin. However, this study used the median distribution (STI is in the middle of the thermal range) and found that the cold-adapted species were more sensitive to climate warming than warm-adapted species, thereby revealing the opposite

phenomenon. Moreover, we did not identify any pattern, which can be denoted as an “increase in the occurrence (or abundance) of warm-adapted species and decrease in the occurrence of cold-adapted species” (Kwon et al., 2013; Kwon et al., 2010; Wagner et al., 2021), which is expected owing to the northward shift of the distribution in temperate regions such as Korea (Fig. 6c, d).

Although the relationship between local and global STIs was not high, the resulting local and global CTIs were correlated. This result was expected because STI values are relative rather than absolute (Devictor et al., 2008). Owing to the high variations in global STIs, the global CTIs using them might fail to detect a weak signal in the response of moths to climate warming. However, even the global CTI showed a weak signal for the influence of climate warming despite no statistical significance (the positive relationship between CTI and survey interval or temperature change). Repeated weak signals with statistical non-significance must not be overlooked. This study showed that other covariates such as elevation and forest (%) influenced the increase in CTI. Elevation negatively influenced the increase in CTI; however, forest (%) had a positive influence. A negative correlation was observed between forest (%) and land cover change. The land cover change can negatively influence the increase in CTI (Gaget et al., 2020). Because of legal protection of forests in South Korea, a high proportion of forest means less change to the landscape. Such results suggest the complex influence of geography and landscape on the CTI changes in moth assemblages. In this study, moth surveys at five of the sites were not conducted at the historical survey sites, thereby weakening the statistical power of our results, as it reduces the sample size and potentially introduces biases. However, the site identity was not significant in any of the generalized linear models. The influence of site identity might be partially reflected by the forest (%). Notably, CTIs using local and global occurrence data are similar; however, the former is more sensitive to climate warming than the latter.

Furthermore, although we did not detect changes in species richness between historical and recent surveys, we observed high turnover rates (0.54 – 0.60) in Uraniidae, Nolidae, Sphingidae, and Lasiocampidae. This result is important because it suggests that other pressures, such as land cover change and light pollution might influence them (Dar and Jamal, 2021; Lee et al., 2021b; Truxa and Fiedler, 2012). In particular, the richness of Sphingidae, which generally have a large body size, significantly decreased in this study, and their diversity has decreased in other regions owing to habitat damage and light pollution (Wagner, 2012). Therefore, in South Korea, some vulnerable taxa might be rapidly decreasing because of habitat destruction and environmental degradation. As mentioned, unlike butterflies, moths rarely exhibit northward shifts, driven by climate warming. Moreover, most studies were conducted in northern Europe, where large-scale distribution data on moths have been accumulated over a long period (Forsman et al., 2016; Keret et al., 2020; Kuchlein and Ellis, 1997; Lindström et al., 2012; Sparks et al., 2007). Therefore, the northward shift of moths was tested in South Korea in our study, although the evidence for such northward shifts of moth distribution was weak. As the moth regional data are limited in South Korea, our results provide valuable insights into the distribution analysis of the moths in the region for the first time. To comprehensively elucidate the impact of climate warming on globally threatened moths various indices and statistical methods should be developed to capture the weak signal of distribution change from scanty and fragmented data. Notably, macro-moths were used in this study, and many studies support the decrease in macro-moth diversity owing to climate warming (Burner et al., 2021; Fox, 2013). However, the response of micro-moths to climate warming may differ and that should be analyzed in future studies.

In this study, CTIs based on moth occurrence data were compared between historical and recent survey sites with an interval of about 24 years (12–37 years) to test the northward shifts of Korean macro-moths owing to climate warming. The evidence for the northward shifts of Korean macro-moths was weak. We did not have sufficient data to test the northward shifts because CTI change was obtained from 18 sites rather than from continuous long-term monitoring data from many sites covering the whole region. Hence, more studies are needed to test the distribution shifts of moths in South Korea. The northward and upward shifts were primarily limited to cold-adapted species with low STIs, indicating that cold-adapted species are more sensitive to temperature increase than warm-adapted species. Hence, under a future climate warming it would be likely to see further decrease in cold-adapted moth species in South Korea. CTI using local occurrence data was similar to that using global occurrence data, and it responded more finely to climate warming than the latter. Lastly, the species richness was not significantly different between historical and recent surveys, despite some taxa (Uraniidae, Nolidae, Sphingidae, and Lasiocampidae) exhibiting high turnover rates, and sphingid moths with large body sizes exhibiting a great decrease.

Funding sources

This study was supported by the National Institute of Forest Science (Republic of Korea), the National Research Foundation of Korea (NRF) funded by the Korean government (grant number NRF-2019R1A2C1087099), and the R&D Program for Forest Science Technology (Project No. 2017042B10–2223-CA01) provided by Korea Forest Service (Korea Forestry Promotion Institute).

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.

Data availability

Data are provided in Appendix.

Acknowledgements

We would like to acknowledge the Korea Meteorological Agency for providing climate data.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02763](https://doi.org/10.1016/j.gecco.2023.e02763).

References

- Bowler, D., Böhning-Gaese, K., 2017. Improving the community-temperature index as a climate change indicator. *PLoS One* 12, e0184275.
- Burner, R.C., Selås, V., Kobro, S., Jacobsen, R.M., Sverdrup-Thygeson, A., 2021. Moth species richness and diversity decline in a 30-year time series in Norway, irrespective of species' latitudinal range extent and habitat. *J. Insect Conserv.* 25, 887–896.
- Burrows, M.T., Bates, A.E., Costello, M.J., Edwards, M., Edgar, G.J., Fox, C.J., Halpern, B.S., Hiddink, J.G., Pinsky, M.L., Batt, R.D., García Molinos, J., Payne, B.L., Schoeman, D.S., Stuart-Smith, R.D., Poloczanska, E.S., 2019. Ocean community warming responses explained by thermal affinities and temperature gradients. *Nat. Clim. Change* 9, 959–963.
- Chen, I.-C., Shiu, H.-J., Benedick, S., Holloway, J.D., Chey, V.K., Barlow, H.S., Hill, J.K., Thomas, C.D., 2009. Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. Natl. Acad. Sci.* 106, 1479–1483.
- Cheng, W., Kendrick, R.C., Guo, F., Xing, S., Tingley, M.W., Bonebrake, T.C., 2019. Complex elevational shifts in a tropical lowland moth community following a decade of climate change. *Divers. Distrib.* 25, 514–523.
- Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* 132, 279–291.
- Dar, A., Jamal, K., 2021. The decline of moths globally: a review of possible causes. *Munis Entomol. Zool. Journal* 16, 310–319.
- Dennis, E.B., Morgan, B.J.T., Brereton, T.M., Roy, D.B., Fox, R., 2017. Using citizen science butterfly counts to predict species population trends. *Conserv. Biol.: J. Soc. Conserv. Biol.* 31, 1350–1361.
- Devictor, V., Julliard, R., Couvet, D., Jiguet, F., 2008. Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B: Biol. Sci.* 275, 2743–2748.
- Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Wynhoff, I., Jiguet, F., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* 2, 121–124.
- Emmet, A.M., 1991. Life history and habitats of the British Lepidoptera. In: Emmet, A.A., Heath, J. (Eds.), *The Moths and Butterflies of Great Britain and Ireland*, vol. 7. Part 2. Harley Books, Cochester, pp. 61–203.
- Forsman, A., Betzholtz, P.-E., Franzén, M., 2016. Faster poleward range shifts in moths with more variable colour patterns. *Sci. Rep.* 6, 36265.
- Fourcade, Y., Ranius, T., Öckinger, E., 2017. Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configuration: Implications for climate-driven range shift in a butterfly. *J. Anim. Ecol.* 86, 1339–1351.
- Fox, R., 2013. The decline of moths in Great Britain: a review of possible causes. *Insect Conserv. Divers.* 6, 5–19.
- Fox, R., Oliver, T.H., Harrower, C., Parsons, M.S., Thomas, C.D., Roy, D.B., 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. *J. Appl. Ecol.* 51, 949–957.
- Franzén, M., Johannesson, M., 2007. Predicting extinction risk of butterflies and moths (Macrolepidoptera) from distribution patterns and species characteristics. *J. Insect Conserv.* 11, 367–390.
- Franzén, M., Francioli, Y., Sjöberg, G., Forsman, A., 2023. Positive shifts in species richness and abundance of moths over five decades coincide with community-wide phenotypic trait homogenisation. *J. Insect Conserv.* 27, 323–333.
- Gaget, E., Galewski, T., Jiguet, F., Le Viol, I., 2018. Waterbird communities adjust to climate warming according to conservation policy and species protection status. *Biol. Conserv.* 227, 205–212.
- Gaget, E., Galewski, T., Jiguet, F., Guelmami, A., Perennou, C., Beltrame, C., Le Viol, I., 2020. Antagonistic effect of natural habitat conversion on community adjustment to climate warming in nonbreeding waterbirds. *Conserv. Biol.* 34, 966–976.
- Gaget, E., Pavón-Jordán, D., Johnston, A., Lehikoinen, A., Hochachka, W.M., Sandercock, B.K., Soutan, A., Azafza, H., Bendjedda, N., Bino, T., Božić, L., Clausen, P., Dakki, M., Devos, K., Domsa, C., Encarnação, V., Erciyas-Yavuz, K., Faragó, S., Frost, T., Gaudard, C., Gosztonyi, L., Haas, F., Hornman, M., Langendoen, T., Ieronymidou, C., Kostyushin, V.A., Lewis, L.J., Lorentsen, S.-H., Luigujõe, L., Meissner, W., Mikuska, T., Molina, B., Musilová, Z., Natykanets, V., Paquet, J.-Y., Petkov, N., Portolou, D., Ridzoň, J., Sayoud, S., Šćiban, M., Sniauksta, L., Stipniec, A., Strebel, N., Teufelbauer, N., Topić, G., Uzunova, D., Vizi, A., Wahl, J., Zenatello, M., Brommer, J.E., 2021. Benefits of protected areas for nonbreeding waterbirds adjusting their distributions under climate warming. *Conserv. Biol.* 35, 834–845.
- GBIF.org, 2023. GBIF Occurrence Download <https://doi.org/10.15468/dl.7b568y> Accessed from R via [rgbif \(https://github.com/ropensci/rgbif\)](https://github.com/ropensci/rgbif) on 2023-05-26.
- Hällfors, M.H., Heikkinen, R.K., Kuussaari, M., Lehikoinen, A., Luoto, M., Pöyry, J., Virkkala, R., Saastamoinen, M., Kujala, H., 2023. Recent range shifts of moths, butterflies, and birds are driven by the breadth of their climatic niche. *Evol. Lett.*
- Heo, I., Kwon, W.-T., Chun, Y., Lee, S., 2006. The impact of temperature rising on the distribution of plant - in case of bamboos and garlics. *J. Environ. Impact Assess.* 15, 67–78.
- Hoffmann, A.A., Rymer, P.D., Byrne, M., Ruthrof, K.X., Whinam, J., McGeoch, M., Bergstrom, D.M., Guerin, G.R., Sparrow, B., Joseph, L., Hill, S.J., Andrew, N.R., Camac, J., Bell, N., Riegler, M., Gardner, J.L., Williams, S.E., 2019. Impacts of recent climate change on terrestrial flora and fauna: Some emerging Australian examples. *Austral Ecol.* 44, 3–27.
- Itäimes, J.H., Leinonen, R., Meyer-Rochow, V.B., 2011. Climate change and shifts in the distribution of moth species in Finland, with a focus on the Province of Kainuu. In: Blanco, J., Kheradmand, H. (Eds.), *Climate Change - Geophysical Foundations and Ecological Effects*. IntechOpen, London.
- Keret, N.M., Mutanen, M.J., Orell, M.I., Itäimes, J.H., Välimäki, P.M., 2020. Climate change-driven elevational changes among boreal nocturnal moths. *Oecologia* 192, 1085–1098.
- Korea Meteorological Administration, 2021. *Climatological normals of Korea (1991 - 2020)*.
- Kuchlein, J.H., Ellis, W.N., 1997. Climate-induced changes in the microlepidoptera fauna of the Netherlands and the implications for nature conservation. *J. Insect Conserv.* 1, 73–80.
- Kwon, T.-S., Kim, S.-S., Chun, J.H., Byun, B.K., Lim, J.H., Shin, J.H., 2010. Changes in butterfly abundance in response to global warming and reforestation. *Environ. Entomol.* 39, 337–345.
- Kwon, T.-S., 2017. Temperature and ant assemblages: Biased values of community temperature index. *J. Asia-Pac. Entomol.* 20, 1077–1086.
- Kwon, T.-S., Kim, S.-S., Lee, C.M., 2013. Local change of butterfly species in response to global warming and reforestation in Korea. *Zool. Stud.* 52, 47.
- Kwon, T.-S., Lee, C.M., Kim, S.-S., 2014. Northward range shifts in Korean butterflies. *Clim. Chang* 126.
- Kwon, T.-S., Lee, C.M., Kim, E.-S., Won, M., Kim, S.-S., Park, Y.-S., 2021. Habitat change has greater effects than climate change on butterfly occurrence in South Korea. *Glob. Ecol. Conserv.* 26, e01464.

- Lee, D.-Y., Lee, D.-S., Park, C., Yun, S.J., Lim, J.-H., Park, Y.-S., 2021a. Comparison of benthic macroinvertebrate communities at two headwater streams located with different temperature regions in South Korea. *Korean J. Ecol. Environ.* 54, 87–95.
- Lee, H., Cho, Y.-C., Jung, S.-W., Kim, Y.-H., Lee, S.-G., 2021b. Changes in nocturnal insect communities in forest-dominated landscape relevant to artificial light intensity. *J. Ecol. Environ.* 45, 218–227.
- Lindström, Å., Green, M., Paulson, G., Smith, H.G., Devictor, V., 2012. Rapid changes in bird community at multiple temporal and spatial scales in response to recent climate change. *Ecography* 35, 1–10.
- Lu, X., Liang, E., Wang, Y., Babst, F., Camarero, J.J., 2021. Mountain treelines climb slowly despite rapid climate warming. *Glob. Ecol. Biogeogr.* 30, 305–315.
- Macgregor, C.J., Williams, J.H., Bell, J.R., Thomas, C.D., 2019. Moth biomass has fluctuated over 50 years in Britain but lacks a clear trend. *Nat. Ecol. Evol.* 3, 1645–1649.
- Moon, M.Y., Kim, S.-S., Lee, D.-S., Yang, H., Park, C.-W., Kim, H., Park, Y.-S., 2018. Effects of forest management practices on moth communities in a Japanese larch (*Larix kaempferi* (Lamb.) Carrière) plantation. *Forests* 9, 574.
- National Geographic Information Institute, 2020. The National Atlas of Korea II 2020.
- National Institute of Meteorological Research, 2018. Climate Change for 100 Years on the Korean Peninsula.
- NOAA National Centers for Environmental Information, 2022. State of the Climate: Monthly Global Climate Report for Annual 2021, published online January 2022, retrieved on September 7, 2022 from <https://www.ncei.noaa.gov/access/monitoring/monthly-report/global/202113>.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package. R package version 2.5–6. <https://CRAN.R-project.org/package=vegan>.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Parmesan, C., Phyholm, N., tefanescus, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kalla, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A., Warren, M., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399, 579–583.
- Plóciennik, M., Pabis, K., Zima, A., Kucharski, L., Sobczyk, R., 2023. Plant–moth community relationships at the degraded urban peat-bog in Central Europe. *Ecol. Evol.* 13, e9808.
- R Core Team, 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Roth, T., Plattner, M., Amrhein, V., 2014. Plants, birds and butterflies: short-term responses of species communities to climate warming vary by taxon and with altitude. *PLoS One* 9, e82490–e82490.
- Sánchez-Bayo, F., Wyckhuys, K., 2019. Worldwide decline of the entomofauna: a review of its drivers. *Biol. Conserv.* 232, 8–27.
- Sparks, T., Dennis, R., Croxton, P., Cade, M., 2007. Increased migration of Lepidoptera linked to climate change. *Eur. J. Entomol.* 104, 139–143.
- Truxa, C., Fiedler, K., 2012. Attraction to light – from how far do moths (Lepidoptera) return to weak artificial sources of light? *Eur. J. Entomol.* 109, 8.
- Wagner, D.L., 2012. Moth decline in the Northeastern United States. *N. Lepidopterists' Soc.* 54, 52–56.
- Wagner, D.L., Fox, R., Salcido, D.M., Dyer, L.A., 2021. A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous. *Proc. Natl. Acad. Sci.* 118, e2002549117.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoste, S., Harding, P., Jeffcoate, G., Willis, S.G., Gretorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414, 65–69.
- Zografou, K., Kati, V., Grill, A., Wilson, R.J., Tzirkalli, E., Pamperis, L.N., Halley, J.M., 2014. Signals of climate change in butterfly communities in a Mediterranean protected area. *PLoS One* 9, e87245.