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RESEARCH ARTICLE

Mechanistic understanding of how temperature and its variability shape body size composition in moth assemblages

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Abstract

1. Understanding how climate affects trait composition within a biological assemblage is critical for assessing and eventually mitigating climate change impacts on the assemblage and its ecological functioning. While body size is a fundamental trait of animals as it affects many aspects of species' biology and ecology, it remains unclear through what mechanisms temperature and its variability influence within-assemblage body size variation.
2. This study aims to understand how temperature and its variability shape body size variations in animal assemblages and potentially affect assemblages' vulnerability to climate change. Using >5300 individuals of 680 macromoth species collected from 13 assemblages along a ca. 3000 m elevational gradient in Taiwan, we examined (1) the strength of environmental filtering and niche partitioning in determining the intra- and inter-specific size variations within an assemblage, and (2) the effects of mean temperature and the daily and seasonal temperature variabilities on the strength of the two processes.
3. We found that the body size composition was strongly affected by temperature and its seasonality via both processes. High temperature seasonality enhanced niche partitioning, causing within-population size convergence. In contrast, low mean temperature and low seasonality both enhanced environmental filtering, causing within-assemblage size convergence. However, while low temperature restricted the lower size limit within an assemblage, low seasonality restricted both lower and upper size limits.
4. This study indicates an overlooked but important role of temperature seasonality in shaping intra- and inter-specific size variations in moth assemblages through both environmental filtering and niche partitioning. With rising temperatures and

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Stephanie Chia and Shipher Wu contributed equally to this work.

amplifying seasonality around the globe, potentially weakened filtering forces may increase the size variation within assemblages, reinforcing the assemblage-level resilience. Nevertheless, enhanced niche partitioning may limit size variation within populations, which may increase the population-level vulnerability to environmental changes. This study improves the mechanistic understanding of the climatic effects on trait composition in animal assemblages and provides essential information for biodiversity conservation under climate change.

KEYWORDS
climate change, community assembly, environmental filtering, intraspecific trait variation, Lepidoptera, niche partitioning, temperature variability

1 | INTRODUCTION

Increasing temperature and changing temperature variability have been driving rapid changes in biological assemblages (IPCC, 2022). They have been found to not only alter species composition (Baranov et al., 2020; Parmesan, 2006) but also reshape trait structure in an assemblage (Deldicq et al., 2021; Esquivel-Muelbert et al., 2019). Changes in trait composition may alter how an assemblage responds to both abiotic and biotic environments (Lavorel & Garnier, 2002), how it contributes to ecosystem functions and services (Lavorel, 2013), and how vulnerable it is to environmental changes (Pacifici et al., 2015). Therefore, understanding and ultimately predicting the response of assemblage trait composition to changing temperature regimes is essential for maintaining ecosystem integrity, functions and services in the face of global changes.

According to the community assembly theory (Weiher et al., 2011), two main processes determine which species from a regional pool, composed of all the species able to arrive at a place, can actually form a local assemblage there. Specifically, the environment of a place may serve as a filter in selecting species that possess certain traits that allow them to successfully establish and maintain populations under the environmental conditions. This filtering process thus makes the species in an assemblage have similar traits, leading to trait convergence in the assemblage (Keddy, 1992). In contrast, for species to coexist, niche partitioning among species may be required in response to resource competition or habitat heterogeneity (Questad & Foster, 2008; Silvertown, 2004), resulting in trait divergence (Stubbs & Bastow Wilson, 2004). Therefore, the trait composition of an assemblage is dependent on the relative strength of the two processes driven by the abiotic and biotic environments with which the assemblage interacts (Violle et al., 2012; Figure 1a).

The trait composition of an assemblage may in turn affect the vulnerability of the assemblage to environmental changes (Mori et al., 2013). Previous studies have shown that species with larger intraspecific trait variation or populations with larger trait variation among individuals can better adapt to varying environments (Bolnick et al., 2011; Bürger, 1999). Similarly, an assemblage with larger trait variation among species has been found to have more stable species and trait compositions in the face of environmental changes (Vallina et al., 2017). Therefore, it is expected that strong environmental filtering and niche partitioning would increase the vulnerability of an assemblage under changing environments by reducing within-assemblage and within-population trait variations respectively (Figure 1b).

Previous studies on the effects of mean temperature or temperature variability on the trait composition of assemblages suggest that these effects may occur through both processes of environmental filtering and niche partitioning in a complex way. For example, low temperatures might filter out small-sized individuals or species that are less cold-tolerant than larger ones due to their high surface-to-volume ratio, and thus increase the mean body size of the assemblage (Hoiss et al., 2012; Mungee & Athreya, 2021). Limited food resources under low temperatures might intensify competition between species within an assemblage, thus enhancing niche partitioning (Srinivasan et al., 2018). Similarly, temperature variability has also been found to have a filtering effect on plant assemblages, where high variability was considered a harsh condition that restricted trait variation within assemblages (Swenson et al., 2012). However, a variable environment could also act as a buffer, reducing the strength of interspecific competition for resources (Chesson, 2000). Therefore, disentangling the effects of temperature and its variability through the two processes is necessary to accurately assess and predict assemblage trait responses to changing temperature patterns. Despite that, few studies have simultaneously examined the effects of both mean temperature and temperature variability on trait composition (Beerli et al., 2019) and even fewer have explored the role of the two assembly processes in these effects, especially for animal assemblages (Srinivasan et al., 2018).

Body size is one of the most important species traits (Chown & Gaston, 2010; Nee & Lawton, 1996). It determines an organism's heating and cooling efficiency (Zamora-Camacho et al., 2014), rate of heat loss (Watt et al., 2010) and starvation resistance (Cushman et al., 1993), and can directly or indirectly influence the organism's fitness under different temperature conditions (Kingsolver & Huey, 2008). An organism's body size also influences its functions in the ecosystem, such as the efficiency in pollination (Jauker et al., 2016) and detritus decomposition (Dossena et al., 2012). However, although a substantial amount of studies have explored

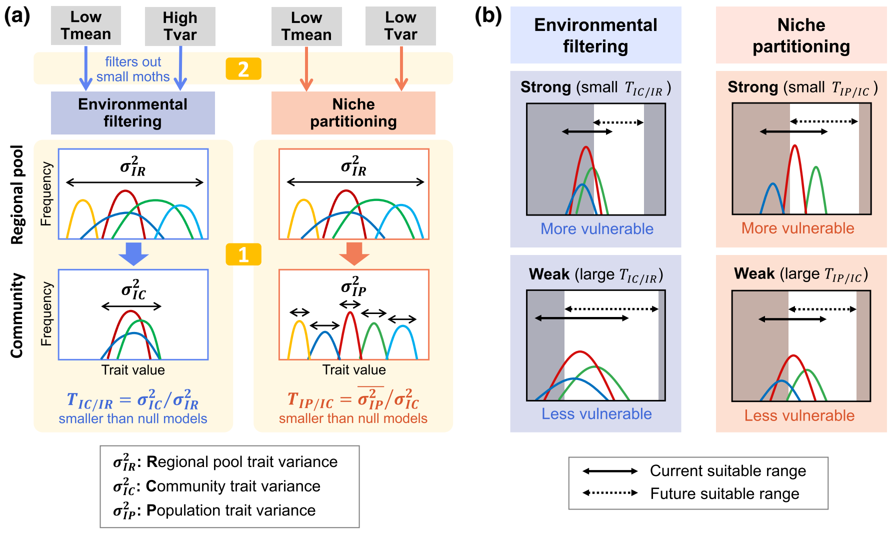

FIGURE 1 The conceptual frameworks laying out our expectations on how temperature variables influence trait composition within an assemblage through two community assembly processes (a) and how the strength of these processes determines the assemblage's vulnerability to environmental changes (b). Each curve represents the frequency distribution of trait values within species with different colours indicating different species. Environmental filtering affects the ratio ($T_{IC/IR}$) of within-assemblage trait variance (σ^2_{IC}) to variance in the regional pool (σ^2_{IR}), while niche partitioning affects the ratio ($T_{IP/IC}$) of mean within-population trait variances ($\overline{\sigma^2_{IP}}$) to within-assemblage variance (σ^2_{IC}). A lower ratio indicates a stronger process. Our research questions are annotated in numbered yellow blocks in panel (a). The first question examines the strengths of the two processes on assemblage composition. The second question explores how mean temperature (*T*mean) and temperature variabilities (*T*var) influence these processes, with our expectations specified in the figure. Since strong environmental filtering and niche partitioning reduce the within-assemblage trait variation and trait overlaps among species, respectively, both effects can increase the possibility of the trait values of a species falling out of the suitable range and thus increase the local extinction risk under environmental changes, as illustrated in (b).

the relationships between mean temperature and mean body sizes (Brehm et al., 2019; Chown & Gaston, 2010; Kivelä et al., 2011), there is currently a lack of knowledge on how daily and seasonal temperature variability affects the body size composition of animal assemblages.

To address the knowledge gap, the goal of this study was to understand how temperature and its variability can affect trait composition of an assemblage through the community assembly processes (Figure 1a) and discuss how the effects may potentially determine the assemblage's vulnerability to environmental changes (Figure 1b), using moth assemblages as an example. Moths constitute the second largest animal group, vary greatly in size and are distributed widely from the equator to subpolar regions (Kristensen et al., 2007; Wagner et al., 2021). They play vital roles in ecosystems, forming a major part of the diet of bats and birds, feeding on a wide variety of plants and serving as pollinators (Wagner et al., 2021). Because of their high mobility and close relationships with vegetation, moths are sensitive to environmental changes and useful as environmental indicators (Erhardt, 1985; Kitching et al., 2000). Therefore, moth assemblages serve as an ideal system for understanding the effects of temperature regimes and their changes on body size composition of an assemblage. Using the body size of over 5300 moth individuals in 13 assemblages along a ca. 3000 m elevational gradient as an example, we specifically (1) examined whether and how strongly the environmental filtering and niche partitioning shape the body size composition of the moth assemblages and (2) investigated how the mean temperature and daily and seasonal temperature variability influence the strength of the two processes and the direction of the filtering effect (i.e. filtering out small or large individuals). We expected stronger environmental filtering effects under harsh conditions such as low mean temperature and high temperature variability (Swenson et al., 2012), which would filter out smaller sized moths due to their limited tolerance to cold and starvation (Cushman et al., 1993; Watt et al., 2010). We also expected that low mean temperature would enhance competition for limited resources and lead to stronger niche partitioning, while high temperature variability would relax competition and thus weaken the niche partitioning effects (Chesson, 2000; Figure 1a). Mechanistic understanding of the associations between temperature regimes and trait composition of assemblages will provide essential information for developing conservation strategies in response to expected future climate change.

2 | MATERIALS AND METHODS

2.1 | Study area

Taiwan island is located off the southeast coast of the Eurasian continent at the western edge of the Pacific Ocean. It has a humid subtropical climate in the north transitioning to a tropical monsoon climate in the south. Two-thirds of the ca. 36,000 km^2 island consists of forest-covered mountains, with the highest peak reaching nearly

4000 m. This geography results in a wide range of climatic conditions and diverse types of natural vegetation ranging from tropical rainforest in the lowlands, through temperate forests, to alpine tundra at high elevations. The various natural habitats have nurtured a diverse fauna in Taiwan, including more than 4000 moth species from over 70 families (Shao & Chung, 2022). The east section of the Central Cross-Island Highway on the island rises from 60 to 3275 m above sea level, located in the Taroko National Park where anthropogenic disturbances are limited, providing an exceptional and ideal elevational gradient for this study (Figure 2). We divided the gradient into 13 elevational bands at 250 m intervals and set up a sampling site in a small open area near forests within each elevational band (Figure 2).

2.2 | Moth sampling

Moths were collected at each site on three nights during 20–24 July 2015, using modified Robinson traps (Taylor & French, 1974; Williams, 1948) with a 15 W fluorescent tube and a 5-L container with ethyl acetate inside, under a permission granted by Taroko National Park (No. 1040012350). The light tube was equipped with a light sensor, so the light was turned on automatically after sunset and kept on until sunrise based on the ambient illumination intensity. Moths attracted to the light traps were quickly killed by the ethyl acetate vapour in the container and collected in the following morning. We conducted the sampling during the season when adult moths tend to be relatively speciose and abundant in Taiwan (Taroko National Park Headquarters, 2007), and avoided collecting during a full moon phase to reduce the impact of moonlight on light trapping. Due to dense forests surrounding the sampling sites, the propagation distance of light should be limited, reducing the potential bias of capturing individuals from distant locations. Although we collected moths only in summer, due to the diverse life cycle patterns of different moth species, their larval stage may occur in different seasons of the year (Oregon Department of Agriculture, 2016). Since the adult body size is largely determined during the larval stage (Tammaru, 1998), we believe that our samples are representative to some extent of the year-round body size composition of the moth assemblages. We estimated the species richness of each site and the sample coverage of species richness using the asymptotic estimator Chao1 (Chao et al., 2009).

2.3 | Specimen measurement and identification

We dried and prepared each collected individual as a pinned specimen, and measured its forewing length from the wing–thorax junction to the wing apex as an index of body size (García-Barros, 2015; Wu et al., 2019). We identified the specimens based on original and subsequent references and type specimen examination, if available. For species groups that are difficult or impossible to identify by appearance (e.g. the geometrid genera *Abraxas* Leach, *Lomographa* Hübner, *Maxates* Moore, the noctuid genera *Mythimna* Ochsenheime, *Callopistria* Hübner, *Ctenoplusia* Dufay, the erebid *Miltochrista* Hübner, *Simplicia* Guenée etc.), additional morphological characters (e.g. antennal, leg, abdominal and genitalia characters) were carefully dissected for identification. The sex of specimens was determined through

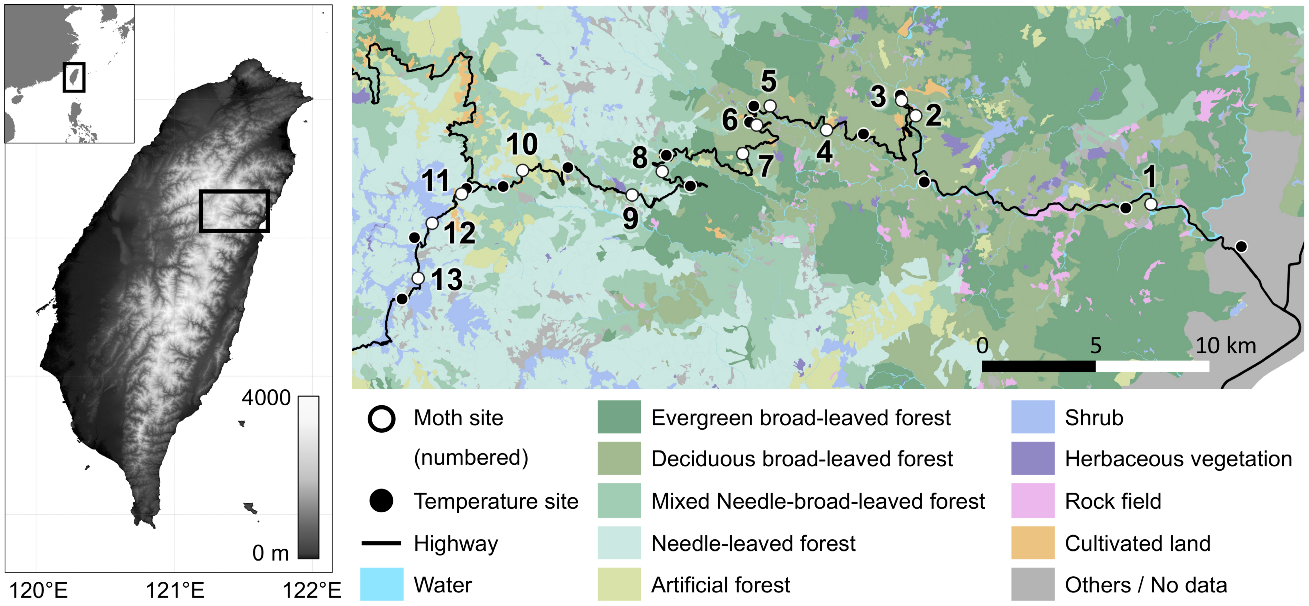

FIGURE 2 The locations, topography and surrounding vegetation of the moth sampling sites and temperature recording sites. The terrain information was obtained from the Ministry of the Interior, Taiwan (Retrieved from https://data.gov.tw/dataset/35430). The vegetation information was obtained from the Forestry and Nature Conservation Agency of Taiwan (Retrieved from https://data.gov.tw/en/datasets/9930). The code of each sampling site is shown on the map.

morphological features of antenna, legs, frenulum and genitalia. Individuals found to be damaged (e.g. incomplete wing apex or deficiency of important characteristics) and thus not possible for measurement or identification were excluded from the analyses. Since micromoths were easily damaged in the sampling process, resulting in a low proportion of identifiable individuals in our samples, we used only macromoths (the monophyletic taxon, Macroheterocera, in Lepidoptera) for the analyses. In addition, as sexual dimorphism is commonly found in many of the moth species (Allen et al., 2011), and we collected much more males than females (5341 males and 1581 females), we used only male samples for the analyses in this study.

2.4 | Temperature variables

We recorded air temperatures at 14 sites along the elevational gradient (Figure 2) using iButton data loggers (Maxim Integrated Products, Sunnyvale, CA, USA). The data loggers were hung at 1- to 1.5-m high under forest cover, which is a typical living environment for moths, recording the air temperature every 30 min from 1 January to 31 December 2015. We linearly interpolated the temperature measurements along the elevational gradient for the 13 moth sampling sites, and then calculated the annual mean temperature (*T*mean), seasonal temperature range (STR) and diurnal temperature range (DTR) for each site. The STR was calculated as the difference between the maximum and minimum monthly mean temperatures and the DTR as the annual mean difference between daily maximum and minimum temperatures. We performed pairwise Pearson's correlations among *T*mean, STR and DTR to examine the collinearity. The annual mean daily maximum and minimum temperatures were highly correlated with *T*mean (Pearson's correlation coefficients of 0.990 and 0.997, respectively) and were therefore excluded from the analysis.

As the assemblage composition may be affected by long-term climate conditions, and considering our limitation of having only 1 year of temperature data collected at the sampling sites, we conducted supplementary analyses using temperature variables derived from 60-year (1961–2020) temperature data (Taiwan Climate Change Projection Information and Adaptation Knowledge Platform, https://tccip.ncdr.nat.gov.tw/). Specifically, we used daily maximum, minimum and average temperatures at a 1-km resolution to compute annual values of *T*mean, STR and DTR at the sampling sites, and used the average values across the 60 years for the subsequent analysis. Since the gridded long-term data were interpolated from the records of weather stations, which are typically located in open areas, the data are expected to be less representative of the temperatures that the moths experienced in their habitats under forests than our field measurements. Therefore, we present the results associated with our self-measured temperature data in the main article and include those associated with the long-term data in the supplementary materials.

2.5 | Strength of environmental filtering and niche partitioning

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Community	Community	13

To quantify the strength of environmental filtering and niche partitioning in shaping each assemblage, we used two indices developed by Violle et al. (2012) based on trait variances at the population, assemblage and regional pool levels. The strength of environmental filtering was measured as the ratio of the within-assemblage variance to the variance within the regional pool:

$$T_{IC/IR} = \frac{\sigma^2_{IC}}{\sigma^2_{IR}},$$

where σ^2_{IC} is the variance of body size of moth individuals collected at a sampling site, and σ^2_{IR} is the variance of all individuals collected across the 13 sites. A lower value of $T_{IC/IR}$ indicates a more restricted variation in body size within the assemblage relative to the variation in the regional pool and thus a stronger environmental filtering effect. The strength of niche partitioning was measured as the ratio of the mean within-population variance over all populations in an assemblage to the within-assemblage variance:

$$T_{IP/IC} = \frac{\overline{\sigma^2_{IP}}}{\sigma^2_{IC}},$$

where σ^2_{IP} is the variance in the body size of all individuals of a species collected at a site, and $\overline{\sigma^2_{IP}}$ is the mean of σ^2_{IP} over all species at that site. A lower value of $T_{IP/IC}$ indicates a more restricted within-population body size variation relative to the within-assemblage variation, suggesting smaller overlaps of trait values between populations and thus a stronger niche partitioning effect. All body size values were log-transformed. Populations with only one individual were excluded from the calculation of the two indices. We performed resampling within each assemblage for different numbers of individuals to confirm that the sample size of each assemblage was sufficient to estimate σ^2_{IC} values (Figure S1). We also performed resampling within populations for different numbers of individuals to examine the effect of population size on the observed σ^2_{IP} (Figure S2). Because populations with a small number of individuals may result in underestimated σ^2_{IP} (Figure S2), we performed a sensitivity analysis with the minimum population size thresholds varying from 2 to 5 to confirm that the result is not sensitive to population size. In addition, the proportions of species having small population size were similar across assemblages, suggesting that the potential underestimation of variance is likely similar across assemblages (Table S1), which should have minimal impact on our regression analyses (see below).

To compare the $T_{IC/IR}$ and $T_{IP/IC}$ across sites, we calculated the standardized effect size (SES) of the two indices as $\left(I_{obs} - I_{null}\right) / \delta_{null}$, where I_{obs} is the observed index value for an assemblage, I_{null} is the expected value obtained from null models and δ_{null} is the standard deviation of the values among the null models. The null models were generated following the randomization processes described in Taudiere and Violle (2016). Specifically, for $T_{IC/IR}$, we permuted trait values among all individuals within the regional pool, while keeping the number of individuals in each assemblage unchanged. For $T_{IP/IC}$, we permuted trait values among individuals within each assemblage, while keeping the number of populations and the number of individuals within each population unchanged. For each index, we performed 999 times of random permutation and obtained the 95% confidence intervals of the index values derived from the randomization. We computed the SES values using the negative values of $T_{IC/IR}$ and $T_{IP/IC}$, so that a higher value of $SES_{IC/IR}$ and $SES_{IP/IC}$ indicates a stronger effect of environmental filtering and niche partitioning, respectively, on the community assembly.

2.6 | Climatic drivers of environmental filtering and niche partitioning

To identify the climatic drivers of environmental filtering and niche partitioning, we built multiple linear regression models for $SES_{IC/IR}$ and $SES_{IP/IC}$ separately to examine their relationships with the three temperature variables (i.e. *T*mean, STR and DTR). For each assembly process, we built regression models using all possible combinations of the three temperature variables and evaluated model performance using Akaike's information criterion corrected for small sample sizes (AIC_C). We retained all competing models with a ΔAIC_C value that was not greater than 2 relative to the best model (i.e. $\Delta AIC_C < 2$) because those models were considered to have similar performance (Richards, 2005). We then calculated the weighted average of the estimated coefficient for each independent variable included in any retained model based on the rescaled Akaike weights to derive the final model, following the natural averaging method (Burnham & Anderson, 2002). This model averaging approach can account for data-related uncertainties and enhance the stability of model inference (Burnham & Anderson, 2002). A temperature variable was considered significant if the 95% confidence interval of its averaged coefficient in the final model did not include zero. All temperature variables were standardized before being used for building the models.

2.7 | Climatic drivers of the upper and lower body size limits in an assemblage

Depending on the suitable trait range in an environment, the environmental filtering force may act on either large- or small-sized individuals in the assemblages, leading to a directional selection. Therefore, to further understand how the temperature variables influence body size composition within a moth assemblage via the environmental filtering, we built multiple linear regression models and used the model averaging approach mentioned above to examine the relationship between the temperature variables and the upper and lower size limits in an assemblage. We measured the upper and lower limits for each assemblage using the 95th and 5th percentiles, respectively, of the body size of all individuals in the assemblage. We conducted this analysis on the individual, but not species, level because the filtering effect is expected to be on individuals if the filtering is based on body size per se, rather than other factors related to species identity.

All the statistical analyses were performed in R 3.5.3 (R Core Team, 2020). We used the package *cati* (Taudiere & Violle, 2016) for analysing the strength of environmental filtering and niche partitioning, and used the package *MuMIn* (Bartoń, 2022) for model selection and averaging.

3 | RESULTS

We collected a total of 12,537 moths, including 8369 macromoths, from the sampling sites. We were able to identify the species and sex and measure the body size of 6922 well-preserved specimens of macromoths, among which 5341 are males and were included in the following analyses. Each sampling site had 411 ± 316 (mean ± SD) individuals belonging to 117 ± 72 species. Both the number of species and individuals peaked at mid elevations (Figure 3a; Table S2). An overview of the size distribution of the moth samples showed that the body sizes were roughly log-normally distributed both within assemblages (Figure S3a) and within the regional pool (all assemblages pooled together; Figure S3b). While the annual mean temperature (*T*mean) monotonically decreased from 21.3°C to 7.1°C as elevation increased, the seasonal temperature range (STR) was largest at mid elevations and the diurnal temperature range (DTR) showed a bimodal distribution along the elevation gradient (Figure 3b–d). *T*mean and DTR had no significant correlation with each other and had only a medium positive and negative correlation with STR respectively (Figure S4). *T*mean and STR derived from the weather station-based long-term temperature data showed similar trends along the elevational gradient, but DTR exhibited a different pattern and higher values in general, likely due to the difference between open-ground (weather stations) and understorey (self-measured) microclimates (Figure S5).

The observed $SES_{IC/IR}$ values were statistically significantly larger than the expected values at the six sites above 2000 m, but significantly lower at most sites below 1600 m (Figure 4a). This suggested that strong environmental filtering reduced the within-assemblage body size variation relative to the total variation in the regional pool at high elevations, but the effect was weak at low elevations. In contrast, the observed $SES_{IP/IC}$ values were significantly larger than the expected values at all 13 sampling sites (Figure 4b), suggesting that niche partitioning significantly reduced the within-population body size variation relative to the within-assemblage variation in all the moth assemblages. The strength of niche partitioning was particularly strong at mid-elevations from around 1000 to 2000 m (Figure 4b).

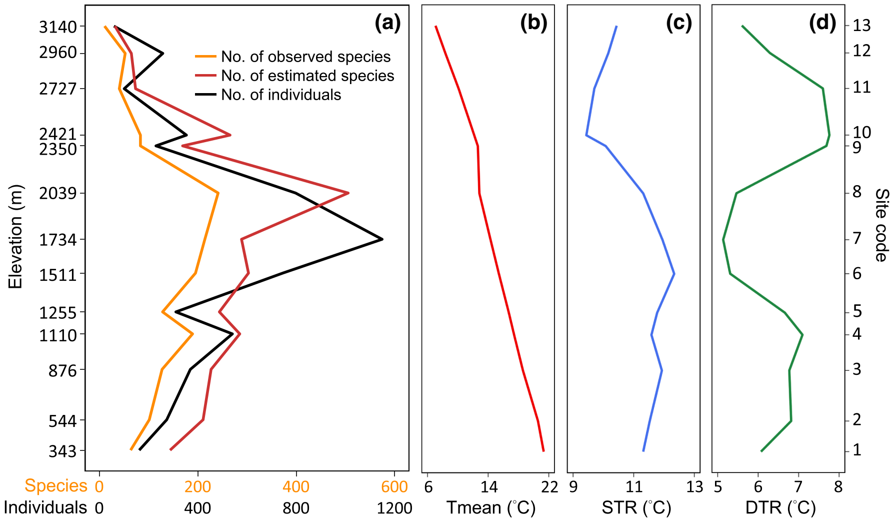

FIGURE 3 The number of individuals and the observed and estimated species of adult male macromoths (a), annual mean temperature (*T*mean; b), seasonal temperature range (STR; c) and diurnal temperature range (DTR; d) at the 13 sampling sites along the elevational gradient.

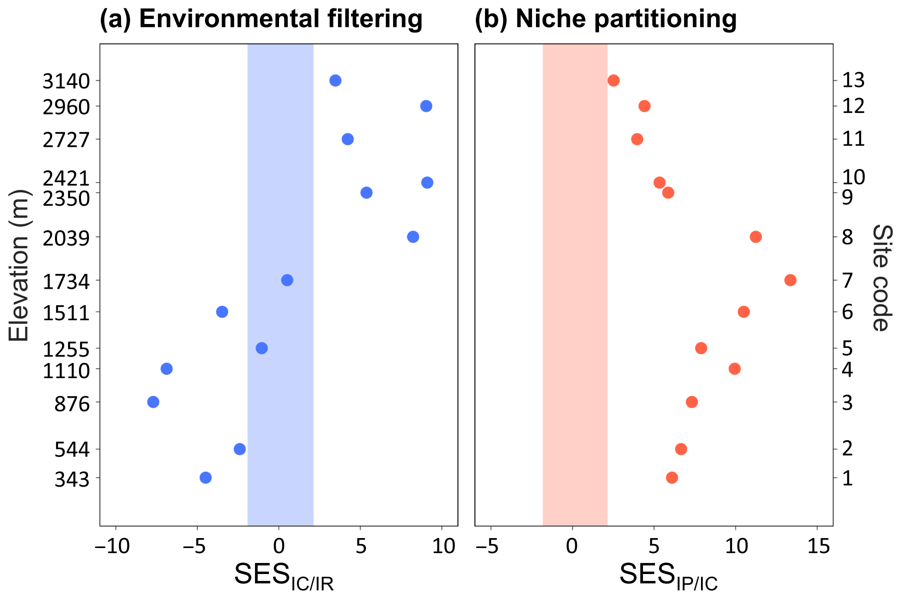

FIGURE 4 The strength of environmental filtering and niche partitioning in influencing the body size composition of the moth assemblages along the elevational gradient. The strength of environmental filtering (a) and niche partitioning (b) was measured as the standardized effect size $SES_{IC/IR}$ and $SES_{IP/IC}$, respectively, where higher values indicate a stronger process. The dots represent the observed values for individual assemblages, while the coloured boxes represent the 95% confidence intervals of expected values generated from the null models. The effect of a process is considered statistically significant on an assemblage if the observed value is higher than the confidence interval of expected values.

The final regression model for the strength of environmental filtering included all three temperature variables and showed that they were all negatively correlated with the $\mathrm{SES}_{IC/IR}$ values (Figure 5a; see all candidate models in Table 1a), indicating that the effect of environmental filtering on the body size composition was stronger when mean temperature, seasonal temperature variability or daily variability was lower. In contrast, the final model for the strength of niche partitioning only included STR (Figure 5b; see all candidate models in Table 1b). The significantly positive correlation between STR and $\mathrm{SES}_{IP/IC}$ values (Figure 5b) suggested that niche partitioning was stronger in the moth assemblages experiencing higher temperature seasonality. The results were generally consistent in all the alternative models built with different population size thresholds and temperature data, except that the effect of *T*mean and DTR could sometimes become insignificant or be excluded from the final model for the strength of environmental filtering (Figures S6 and S8), and STR became insignificant in the model built with weather station-based long-term temperature data (Figure S8b).

The final regression model for the upper body size limit included all three temperature variables, but only STR had a significantly positive correlation (Figure 6a; see all candidate models in Table 2a), indicating that moth assemblages experiencing small STR tended to lack large moth individuals. For the lower body size limit, *T*mean and STR were included in the final model and both showed a significantly negative correlation (Figure 6b; see all candidate models in Table 2b), indicating that moth assemblages experiencing low *T*mean or small STR tended to lack small individuals. Together, the results suggested that small STR may filter out both large and small moth individuals from an assemblage, while low mean temperature may filter out small individuals. The significant relationships between *T*mean or STR and the body size limits remained consistent in the models with alternative population size thresholds and temperature data (Figures S7 and S9).

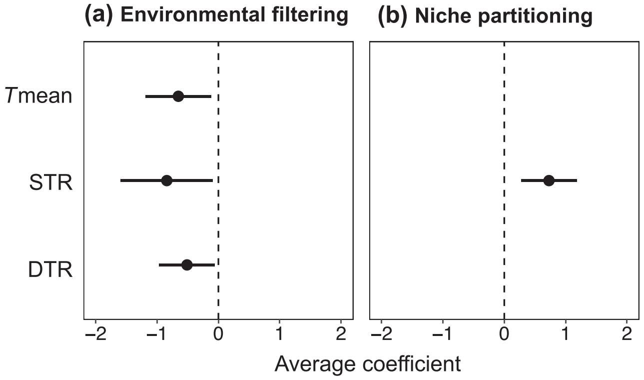

FIGURE 5 Effects of the annual mean temperature (*T*mean), seasonal temperature range (STR) and diurnal temperature range (DTR) on the strength of environmental filtering and niche partitioning in shaping the body size composition of the 13 moth assemblages. The dots and lines represent the model-averaged coefficients for the variables and their 95% confidence intervals, respectively, in the linear regression models for the strength of environmental filtering (a) and niche partitioning (b). The strength of the two processes was measured by $SES_{IC/IR}$ and $SES_{IP/IC}$ respectively. The values are shown only for the variables included in the final models.

4 | DISCUSSION

Using moth body size as a case study, we confirmed that mean temperature influences trait composition through environmental filtering. However, we further observed that temperature variability can shape trait composition in a community through both environmental filtering and niche partitioning processes. To the best of our knowledge, this is the first study revealing the potential assembly processes underlying the effect of temperature variability on body size composition in animal communities. Our results suggested that high seasonal temperature variability may drive body size partitioning

TABLE 1 Candidate models for the effects of temperature variables on the strength of (a) environmental filtering and (b) niche partitioning.

	Regression coefficients				
Model	*T*mean	STR	DTR	AICc	Δ
(a) Environmental filtering					
STR + DTR		**−1.05**	**−0.51**	**31.68**	**0.00**
***T*mean**	**−0.78**			**32.55**	**0.87**
***T*mean + STR**	**−0.50**	**−0.42**		**33.02**	**1.34**
STR		−0.75		33.74	2.07
*T*mean + DTR	−0.78		0.13	36.31	4.63
*T*mean + STR + DTR	−0.24	−0.81	−0.36	36.39	4.72
Null				41.05	9.38
DTR			0.11	44.35	12.67
(b) Niche partitioning					
STR		**0.73**		**34.68**	**0.00**
*T*mean + STR	−0.14	0.82		38.71	4.02
STR + DTR		0.68	−0.09	38.87	4.19
DTR			−0.49	40.95	6.27
Null				41.05	6.37
*T*mean + DTR	0.41		−0.50	42.03	7.35
*T*mean	0.40			42.26	7.58
*T*mean + STR + DTR	−0.14	0.82	0.00	44.28	9.60

Note: Regression models were built with all possible combinations of the three temperature variables. Presented are the parameter coefficients, corrected Akaike information criterion (AICc) and the difference of the AICc values from the lowest AICc value (Δ). Models with Δ < 2 (bolded text), if more than one, were used to perform model averaging for the final model output.

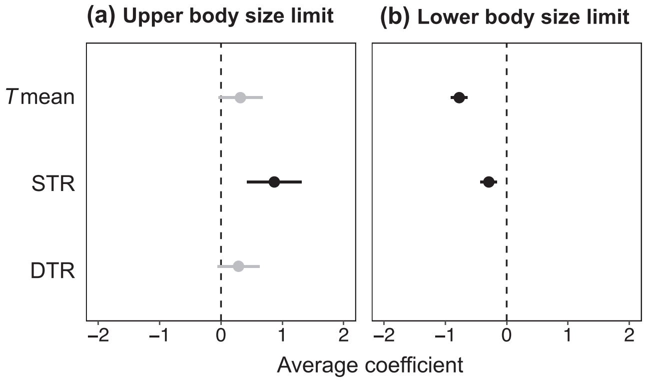

FIGURE 6 Effects of the annual mean temperature (*T*mean), seasonal temperature range (STR) and diurnal temperature range (DTR) on the upper and lower body size limits of a moth assemblage. The dots and lines represent the model-averaged coefficients for the variables and their 95% confidence intervals, respectively, in the linear regression models for the upper (a) and lower body size limits (b). The two limits were measured as the 95th and 5th percentiles, respectively, of the body size of moth individuals in an assemblage. The coefficients and confidence intervals are shown only for the variables included in the final models. They are shown in black if the confidence interval does not include zero, and in grey if the confidence interval includes zero.

among moth species. This leads to a reduced ratio between intraspecific and interspecific trait variability, implying intraspecific convergence and/or interspecific divergence in body size. In addition, both low temperature and low temperature variability may act as a filter restricting the body size variation within a moth assemblage, especially at high elevations. However, while low temperature tends to filter out small-sized moth individuals from an assemblage, low temperature seasonality tends to affect both small- and large-sized individuals. By identifying key climatic drivers and mechanisms that determine the within-assemblage composition of the important animal trait, this study provides new insights into the vulnerability of animal communities to environmental changes.

Several previous studies have indicated the importance of environmental filtering in shaping body size composition of animal assemblages, especially in harsh environments (Gomez et al., 2020; Liu et al., 2021; Mungee & Athreya, 2021; Zhang et al., 2020). As expected, our results showed that the strength of environmental filtering in shaping body size composition of moth assemblages increased as temperature decreased along the elevational gradient in Taiwan (Figures 4a and 5a). The filtering effect of low temperature acted mainly on small-sized moths in the assemblages (Figure 6b), meaning that it tended to filter out small moths. Although insects are

TABLE 2 Candidate models for the effects of temperature variables on the (a) upper and (b) lower body size limits.

	Regression coefficients				
Model	*T*mean	STR	DTR	AICc	Δ
(a) Upper body size limit					
STR		**0.89**		**24.04**	**0.00**
***T*mean + STR**	**0.32**	**0.68**		**24.20**	**0.16**
STR + DTR		**1.06**	**0.29**	**24.54**	**0.50**
*T*mean + STR + DTR	0.20	0.85	0.16	29.01	4.97
*T*mean + DTR	0.77		−0.36	32.57	8.52
*T*mean	0.76			33.10	9.06
Null				41.05	17.01
DTR			−0.34	42.88	18.84
(b) Lower body size limit					
***T*mean + STR**	**−0.77**	**−0.29**		**−1.01**	**0.00**
*T*mean + STR + DTR	−0.75	−0.33	−0.04	4.29	5.30
STR + DTR	−0.97		0.16	7.86	8.87
*T*mean	−0.96			9.91	10.92
STR + DTR		−1.10	−0.51	27.46	28.47
STR		−0.80		31.30	32.31
Null				41.05	42.06
DTR			0.14	44.25	45.26

Note: Regression models were built with all possible combinations of the three temperature variables ($n = 8$). Presented are the parameter coefficients, corrected Akaike information criterion (AICc) and the difference of the AICc values from the lowest AICc value (Δ). Models with $\Delta < 2$ (bolded text), if more than one, were used to perform model averaging for the final model output.

ectothermic, many of them exhibit some degree of thermoregulation, such as increasing and maintaining body temperatures prior to and during flight (May, 1979; McCrea & Heath, 1971). Low temperature may thus increase metabolic costs of flight activities (Heath & Adams, 1967). These cold-induced adversities are particularly severe for small-sized individuals because of their high surface-to-volume ratio that reduced the ability to maintain body temperatures (Watt et al., 2010), or the ability to resist starvation (Cushman et al., 1993) in low-productivity environments. Similar patterns were also found in the hawkmoths assemblages in eastern Himalayas (Mungee & Athreya, 2021).

In addition to the mean temperature, we found that temperature variability was another, perhaps even more significant, factor shaping the body size composition of the moth assemblages. Our results suggested that temperature seasonality may influence within-assemblage and within-population size variations through both environmental filtering and niche partitioning processes (Figure 5). However, contrary to our expectation of strong environmental filtering and/or weak niche partitioning under a variable environment (Chesson, 2000; Swenson et al., 2012), we found that the moth assemblages experiencing a larger seasonal temperature range tended to be shaped by stronger niche partitioning and weaker environmental filtering processes (Figure 5). We argued that the temporal fluctuations of climates could create additional and spatiotemporally dynamic habitat patches that enable the coexistence of diverse species (Astudillo et al., 2016; Terradas et al., 2009), leading to a weak environmental filtering effect. In particular, as the body size of moths can influence their resistance to starvation (Cushman et al., 1993), cold (Watt et al., 2010), predation (Remmel et al., 2011) and parasitism risks (Vogelweith et al., 2013), moths of different sizes may be able to employ different life-history strategies to thrive in dynamic environments, resulting in increased diversity of body sizes with expansion in both lower and upper size limits in the assemblage (Figure 6). The observed strong niche partitioning under a large seasonal temperature range could be due to niche specialization, in which temperature seasonality creates heterogeneous habitats in the environment (Tonkin et al., 2017) and species are sorted among different niches so that each species occupies the most suitable microhabitat (Leigh et al., 2004; Melbourne et al., 2007; Questad & Foster, 2008). Taking the two processes together, increased temporal dynamics and/or spatial heterogeneity of environments under large seasonal temperature ranges may relax the filtering effects on the within-assemblage trait composition and enhance species packing in the trait space, leading to an assemblage with high trait diversity (Pigot et al., 2016).

With rising temperatures and increasing seasonality in the current century (IPCC, 2022; Santer et al., 2018), the environmental filtering effect is expected to weaken, which would increase body size variability in moth assemblages and thus reinforce the resilience of these assemblages to environmental changes (Figure 1b). In addition, both the lower and upper body size limits of an assemblage would expand under increased temperatures and seasonality (Figure 6), which could potentially enrich the ecological function provided by moths serving as prey and pollinators in an ecosystem. Nevertheless, increasing temperature seasonality may also enhance niche partitioning and restrict within-population size variation, leading to high vulnerability of moth populations under unpredictable environmental changes (Figure 1b). The opposite effects of projected climate changes on the assemblage and population levels may lead to increased turnover of moth species in an assemblage in response to a changing environment. Therefore, to retain the local species and functional diversity of moth assemblages under climate change, efforts might be needed to ensure that the local establishment of populations due to the weakened filtering effect is no slower than the local extinction of densely packed populations under shifted climate conditions.

It is important to recognize that the body size composition of terrestrial insect communities can be influenced by a wide range of environmental and biotic factors beyond just temperature and its variability. Humidity can play a role in body size regulation to manage water loss (Kennington et al., 2003), while wind speed can affect body size by changing the thickness of the boundary layer on plant surfaces (Pincebourde et al., 2021). Additionally, factors such as nutrition quality, predators, host plants and voltinism (i.e. the number of broods per year) can all contribute to the determination of body size (Chown & Gaston, 2010; Horne et al., 2015; Kennington et al., 2003; Pincebourde et al., 2021). For the sake of model simplicity given the limitation of our sample size (13 sites), and considering that temperature often correlates and acts as a major driving force behind many of the aforementioned factors, we focused on the effect of temperature variables on body size. However, we acknowledge that these other factors could contribute significantly to body size variations in ways that are unrelated to temperature. To gain a more comprehensive understanding of the determinants of body size composition in insect communities, further investigations using alternative experimental designs are needed to explore the specific contributions of these factors.

This study is subject to certain other limitations. First, we analysed only the body size of males due to the uneven sample size between sexes. As female moths are often larger in size (Stillwell et al., 2014), we may have underestimated both the within-population and within-assemblage variances and the upper body size limit of the assemblages. While this should not critically affect the observed patterns among sampling sites if the sex ratio has no large variation among assemblages, it is worth exploring whether females actually respond to the temperature regimes similar to males in future studies. Second, the 1-year understorey temperature data we collected might not accurately reflect the long-term climate conditions, which could also play a significant role in determining the body size composition of moth assemblages. While the alternative long-term temperature data we used only led to minor discrepancies in the results, future studies could consider collecting temperature data and biological samples for multiple years to address this concern. Lastly, this study presented only the correlations between temperature regimes and the community assembly processes, which do not necessarily indicate causality. Nevertheless, the findings provide new insights that warrant future investigation through manipulative experiments to test our current propositions on the mechanisms of animal community assembly.

By examining the environmental filtering and niche partitioning processes, this study indicates a previously overlooked but important role of temperature seasonality in shaping the intra- and interspecific size variations in moth assemblages. Our results demonstrated significant effects of seasonal temperature variability on the community composition, and that through different assembly processes, it may have contrasting effects at different biological levels. This study not only improves the mechanistic understanding of the climatic determinants of trait composition in animal assemblages but also provides essential information for evaluating and prioritizing the conservation targets of biodiversity under climate change.

AUTHOR CONTRIBUTIONS

Stephanie Chia, Ya-Jung Lu, I-Ching Chen and Mao-Ning Tuanmu conceived the ideas and designed methodology; Shipher Wu, Yi-Shin Jang and Chien-Chen Huang collected the moth and climate data under the supervision of I-Ching Chen and Sheng-Feng Shen; Shipher Wu prepared the moth specimens and identified species; Stephanie Chia and Ya-Jung Lu analysed the data; Stephanie Chia and Mao-Ning Tuanmu led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code are available from Zenodo at https://doi.org/10.5281/zenodo.10029223 (Chia et al., 2023).

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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 S1: The effect of assemblage size on the variance of within-assemblage body sizes (σ^2_{IC}).

Figure S2: The effect of population size on the variance of within-population body sizes ($\boldsymbol{\sigma^2_{IP}}$).

Figure S3: Body size distribution of moth individuals within the 13 assemblages (a) and the regional pool (b).

Figure S4: Pairwise correlations among temperature variables.

Figure S5:. Annual mean temperature (*T*mean; a), seasonal temperature range (STR; b), and diurnal temperature range (DTR; c) at the 13 sampling sites along the elevational gradient, calculated from gridded 1-km historical climate data between 1961 and 2020 (Taiwan Climate Change Projection Information and Adaptation Knowledge Platform, https://tccip.ncdr.nat.gov.tw/).

Figure S6: Same with Figure 5, but only the populations with at least (a) three, (b) four, or (c) five individuals were included in the analysis.

Figure S7: Same with Figure 6, but only the populations with at least (a) three, (b) four, or (c) five individuals were included in the analysis.

Figure S8: Same as Figure 5, but with the temperature variables derived from long-term temperature data.

Figure S9: Same as Figure 6, but with the temperature variables derived from long-term temperature data.

Table S1: Species count and proportion across the population size thresholds of 2, 5, 10, and 20.

Table S2: Observed and estimated species richness of the moth assemblage samples.

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