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Functional traits of *Epirrita autumnata* (autumnal moth) across space and time: An entomological collection- based study

Master's thesis in Natural Resources Management

Supervisor: James D. M. Speed

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Abstract

Natural history collections represent an immense source of information relating individuals from different species to a point in space and time. This allows the study and analysis of how species traits change in relation to local environmental conditions. Here I investigate how wing length, area, color, and symmetry vary with climate. I focus on the well-known birch defoliator *Epirrita autumnata* (autumnal moth). The specimens used here were collected from Norway and curated within the natural history collections at the NTNU University Museum. I photograph the specimens and use image analyses to measure functional traits. GLS models are used to assess how the traits vary with climate conditions, where spring temperature has a negative effect on wing length, yet a positive effect on fluctuating asymmetry of wing area. Latitude and summer precipitation have a positive effect on wing length. Temperature is not significant in the change of traits such as wing color and fluctuating asymmetry of wing length. The patterns found may be of use to predict species response to climate change, while the method may be applied to other species of interest.

Keywords: Autumnal moth *Epirrita autumnata*; Natural History Collection; Lepidoptera; Functional traits; Wing morphology; Temperature; Norway

Sammendrag

Naturhistoriske samlinger representerer en enorm kilde til informasjon som knytter individer fra mange forskjellige arter til et punkt i rom og tid. Dette gjør det mulig å studere og analysere hvordan ulike artsegenskaper endres i forhold til lokale miljøforhold. Her undersøker jeg hvordan vingelengde, areal, farge og symmetri varierer med klima. Jeg fokuserer på den velkjente bjørkeavløveren *Epirrita autumnata* (høstmøll). Eksemplarene som er brukt her er samlet fra Norge og kuratert innenfor de naturhistoriske samlingene ved NTNU Universitetsmuseet. Jeg fotograferer individene og bruker bildeanalyser for å måle funksjonelle trekk. GLS-modeller brukes til å teste hvordan egenskapene varierer med klimaforhold, der vårtemperatur har negativ effekt på vingelengde, men likevel positiv effekt på svingende asymmetri i vingearreal. Desimalbreddegrad og sommernedbør har en positiv effekt på vingelengden. Temperaturen er ikke signifikant i endring av egenskaper som vingefarge og svingende asymmetri i vingelengden. Mønstrene som er funnet kan være nyttige for å forutsi arters respons på klimaendringer, mens metoden kan brukes på andre arter av interesse.

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1 INTRODUCTION

We live in a world in constant change, where species must adapt to changing conditions. Species react and show responses to environmental changes, and these responses carry implications to any given species' life history and ecology. Under the current climate change conditions, it is particularly relevant to study how species respond to changing climates. The expected effects of climate change on biodiversity are quite mixed, with some species benefitting while others are negatively affected, however the overall expected trend is negative (Bellard et al., 2012). One of the most expected effects of climate change on biodiversity is a change in distribution with movements towards higher latitudes and altitudes (Mikkola, 1997; Parmesan et al., 1999). Additionally, the development and phenology of many species will also be affected, with seasonal life stages occurring earlier in the year (Roy & Sparks, 2000; Sheridan et al., 2018). Furthermore, each species will react differently to environmental changes, which can also lead to widespread alterations and disruptions of interspecies interactions (Harrington et al., 1999; Parmesan, 2006).

To understand the implications of climate change on different species, as well as to make estimations about their future, it is important to study the way in which different climate variables affect species. A very effective way to study the effect of climate on traits of a given species relies on the use of natural history collections, taking advantage of the availability of samples representing long periods of time and diverse geographic locations (Fenberg et al., 2016; Sheridan et al., 2018; Wilson et al., 2019). Here, the response of *Epirrita autumnata* to different climatic conditions is assessed using specimens from natural history collections.

1.1 *Epirrita autumnata*

Commonly known as the autumnal moth, *Epirrita autumnata* is a geometrid moth, commonly found in northern Europe. This species is particularly known in Fennoscandia due to its association with birch (*Betula pubescens*) forests, in particular mountain birch (*B. pubescens ssp. czerepanovii*). *E. autumnata* is one of the main responsible species in the widespread defoliation outbreak events that affect birch forests mainly in northern Fennoscandia, a phenomenon that has been studied by multiple authors (Bylund, 1999; Hanhimaki et al., 1995; Jepsen et al., 2009; Tenow et al., 2007). These outbreaks have been documented as far back as the 1860s (Tenow et al., 2007), meaning that they are part of a longstanding relationship between vegetation and defoliators. Despite being mainly studied in northern Fennoscandia, it has been reported that these outbreaks present spatial synchrony and movement in waves, sometimes reaching southern Norway by moving south across the Scandes (Klemola et al., 2006; Tenow et al., 2007; Vindstad et al., 2019). It is important to note that even though they're mostly associated with mountain birch, the autumnal moth's range exceeds the range of mountain birch in the case for areas south of the range of mountain birch (Tenow, 1972, as cited in (Bylund, 1999).

The usual lifecycle of this univoltine species begins in autumn, when eggs are laid on the vegetation by the autumnal moth females (Klemola et al., 2006; Nilssen et al., 2007; Peterson & Nilssen, 1996). The eggs overwinter and then hatch in spring, usually but not exclusively around the time of budburst, resulting in larvae that feed on the vegetation until summer (late June - July). Then they move to the litter, where they enter pupal state

until late summer (late August - September), after which they emerge as adults and mate. After this, the cycle starts over again.

Even though the population dynamics of this species are influenced by various different factors, one key component that has a considerable effect on the ecology of *E. autumnata* is temperature (Bylund, 1999). Indeed, it has been reported that temperature can have diverse effects on *E. autumnata* depending on its development stage.

During the egg stage temperature has been reported as a key factor determining both egg survival and hatching timing (Kaitaniemi & Ruohomäki, 1999; Virtanen et al., 1998). Temperature is also a regulating factor in the developmental rate of both the larval and pupal state (Ayres & MacLean, 1987; Peterson & Nilssen, 1996). Furthermore, oviposition rate in females has also been found to be temperature mediated (Tammaru et al., 1996).

Considering the variety of ways in which temperature can affect the autumnal moth, it is particularly relevant to consider the implications that current climate change may have on *E. autumnata*. The expected effects of climate change on the autumnal moth are both positive and negative, including range expansions, altered phenology leading to possible mismatch with mountain birch, range overlap with natural enemies, and habitat change (Bylund, 1999; Kari & Neuvonen, 1998; Virtanen & Neuvonen, 1999). However, the effects of climate related variables on the morphology of *E. autumnata* have not been widely studied, thus resulting in a knowledge gap about climate effects at the individual trait level.

Increasing the knowledge about the effect of temperature on the morphology of the autumnal moth can be achieved with the use of entomological collections, which allow to measure different traits in individuals that have been sampled in different sites across time. Supplementing this information with climate datasets can make possible the study of the variability of the selected traits according to local temperatures.

1.2 Natural History Collections

It could be said that natural history collections represent the backbone for what has been the development of our understanding of the natural world. This is reflected in the long history of biological specimens being collected both for study and display in natural history collections. With the earliest records of collections dating hundreds of years back, as well as a considerable number of notorious institutions whose collections exist since more than a hundred years ago, these collections contain historical records of living organisms of all kinds (Ponder, 1999; Ponder et al., 2001; Pyke & Ehrlich, 2010; Winker, 2004). Furthermore, natural history collections have been an invaluable starting point for the development of disciplines such as taxonomy and systematics (Harvey, 1991; Pyke & Ehrlich, 2010; Renner & Ricklefs, 1994; Winker, 2004).

During the last few decades and up to the present time, there has been a significant increase in the use of natural history collections for research (Pyke & Ehrlich, 2010). Natural history collections can be considered as a window into the past, which allow us to see patterns and responses of different taxa to global change (Meineke & Daru, 2021; Pyke & Ehrlich, 2010). This is possible due to the variety of information that can be linked to collections, including geographic, climatic, and phylogenetic data. Additionally the wide temporal and spatial span that can be covered by collections enables a route for the study of patterns and changes in an evolutionary context, particularly those related to human impacts and activities (Meineke & Daru, 2021; Pyke & Ehrlich, 2010; Ricklefs, 1980;

Winker, 2004). As a result, natural history collections have become a subject of interest for the study of both ecological and environmental issues.

Despite the immense potential of natural history collections, some caution is needed when working with them. Natural history collections are naturally biased since they are the result of specific targets and judgements made by the collector (Meineke & Daru, 2021; Ponder et al., 2001; Pyke & Ehrlich, 2010). Different types of bias can be present, some of which are tied to the collector's interest, such as sampling of specific taxa and prioritizing certain traits when sampling, while excluding other potentially informative factors at the time and place of sampling (Daru et al., 2018; Engemann et al., 2015; Hromada et al., 2003; Meineke & Daru, 2021). Biases can also arise from sampling convenience, such as selection of easily accessible sites, and favorable times of the year for sampling, while sampling only lasts the timespan it takes to collect the samples needed for any given study (Daru et al., 2018; Engemann et al., 2015). As a result, natural history collections are uneven when it comes to geographic, temporal, taxonomic and trait coverage. Bias will always be present in any collection-based study; however, it is not different from bias inherent in other types of species occurrence data (Daru & Rodriguez, 2023; Speed et al., 2018). Furthermore, bias occur differentially across all collections, thus making their suitability dependent on both their inherent bias and the type of study to be carried out (Meineke & Daru, 2021; Pyke & Ehrlich, 2010).

These biases greatly affect studies on population dynamics, and species composition and richness at determined sites. Making natural history collections not an optimal choice for these types of study (David et al., 2007; Hansen & Richardson, 1999; Pyke & Ehrlich, 2010).

When complemented with observation records or field surveys, natural history collections have been successfully used in documenting changes in species distribution (Auderset Joye et al., 2002; Drost & Fellers, 1996; Lienert et al., 2002). Furthermore, when combined with environmental information, collections can be used to estimate the distribution of species and even forecast distribution changes according to environmental change scenarios (Anderson et al., 2004; Illoldi-Rangel et al., 2004; Peterson et al., 2002).

Perhaps the area where collection specimens have the most potential is in the study of individual attributes (Pyke & Ehrlich, 2010), this being particularly true for entomological collections, where well defined sampling protocols such as the use of insect catching traps, lead to a reduced effect of sampling bias.

The study of individual traits based on collections has given valuable insights into many different topics. Some of those subjects include spatial patterns of trait distribution, developmental studies, reproductive traits, variation patterns between individuals, disease dynamics, prevalence of abnormalities, environmental stress, symbiotic relationships, animal diet, among others (see examples in Pyke and Ehrlich (2010)).

1.3 Collection-Based Study of *Epirrita autumnata*

As has been discussed above, natural history collections are particularly suitable for studies involving specimen measurements, especially when it comes to insects as a study subject. Furthermore, different studies on Lepidoptera have been made using entomological collections (Fenberg et al., 2016; Wilson et al., 2019; Wilson et al., 2023). This, along with the known ecological relevance of *E. autumnata* makes a collection-based study focused on *E. autumnata* a viable and relevant possibility.

A very suitable collection for this is the one present at the NTNU University Museum, in Trondheim, Norway. This collection includes an ample section of land invertebrates, out of which the largest proportion (approximately 40%) corresponds to Lepidoptera (NTNU, n.d.). Furthermore, the collection has been digitized and its records for the specimens can be found in the Global Biodiversity Information Facility (GBIF). This collection is composed of specimens sampled all over Norway from 47 sites, covering a large latitudinal gradient (58.095°N – 69.815°N).

Measurements of functional traits in Lepidoptera can be easily done focusing on the wings, where measurements of length, area and color can be carried out with ease using entomological collections. Wing length is one of the most common traits measured on Lepidoptera. The measurement method for this trait is standardized, with measurements being made from the joint between the wing and the thorax to the wing apex (Correa-Carmona et al., 2022; Van Hook et al., 2012; Wilson et al., 2019). Furthermore, wing length has been used as a proxy for body size, making it a very useful and informative trait in the study of individual morphology (Correa-Carmona et al., 2022; Fenberg et al., 2016; Loder et al., 2008).

Although not as widespread as wing length measurements, wing area measurements are also used in studies focusing on Lepidoptera traits. It has been reported however, that wing area is strongly correlated with wing length (Fenberg et al., 2016). Measurements of wing area can be used for the measurement of wing loading, which is used as an indicator of flight and dispersal ability (Beck & Kitching, 2007; Correa-Carmona et al., 2022; Ruohomäki, 1992).

It is expected for these traits related to body size that they will follow Bergmann's rule, with larger individuals being found in colder environments (higher latitudes and altitudes) and smaller individuals in warmer environments. This is indeed what is often reported, with smaller body sizes being more prevalent considering current warming temperatures on the global scale (Coulthard et al., 2019; Hill et al., 2021). However, the effect of temperature on body size has been reported to be variable and dependent on different factors, including development stage and sex (Fenberg et al., 2016; Hill et al., 2021; Wilson et al., 2019). Furthermore, changes in body size-related traits are not exclusively determined by temperature driven selection, since they are also linked to dispersal and flight capability, for which larger wings are considered favorable (Beck & Kitching, 2007; Correa-Carmona et al., 2022; Ruohomäki, 1992).

When measurements for wing length and wing area are bilaterally available, it is possible to assess the degree of symmetry present between wings of individuals. This can be used to determine the fluctuating asymmetry of the measured trait, which can serve as an indicator of environmental stress, where increased levels of fluctuating asymmetry are prevalent under higher stress conditions (Beasley et al., 2013; Graham et al., 2010; Henriques & Cornelissen, 2019). It is worth noting that there are multiple factors, both biotic and abiotic as well as natural and anthropogenic, that can act as sources of stress, including temperature, nutrients, light, competition, predation, disease, pollution, among others (Beasley et al., 2013; Graham et al., 2010). Furthermore, these different factors may act simultaneously.

Measurements of color have been used to assess color variation or melanism in individuals. These measurements are usually utilized in the study of thermal adaptations to changing environmental conditions (Forsman et al., 2016; Hill et al., 2021; Scriber, 2020). Darker colors are seen as a favorable trait in areas where cold temperatures are prevalent, this

as a mechanism for thermoregulation (Hill et al., 2021; MacLean et al., 2016). It is therefore beneficial to have reduced melanism for species in places subject to warming temperatures (Zeuss et al., 2014).

This study aims to assess the effect of temperature on wing-measured (length, area, color, symmetry) traits of *E. autumnata*, using the specimens present at the entomological collection at the NTNU University Museum. For this purpose, the following hypotheses were formulated: 1. Higher temperatures lead to decreased wing length. 2. Lower temperatures lead to increased fluctuating asymmetry between wings. 3. Darker wings are more prevalent at lower temperatures.

2 METHODS

2.1 Moth Collection

The moth individuals used for this project were those found at NTNU's Natural History Museum for the autumn moth, which were also present in GBIF's database (GBIF.Org User, 2023, DOI: 10.15468/DL.AWZHXX), providing information related to date and place of collection.

The database includes a total of 1708 moth individuals which were sampled between 1879 and 2008 across all Norway in 47 locations (Figure 1).

2.2 Moth Photography

The main goal of the photography process was to capture the wing of the individuals, where the whole wing can be pictured in a single plane, thus allowing to make reliable measurements of different wing characteristics. As a result, 451 individuals had to be excluded from the study, due to damage to the wings or overall poor condition in which manipulation could result in damage to the individual.

The photography process was done using a 100mm macro lens on a Cannon EOS R camera, attached to a Kaiser RS2CP stand, set to a height of 36.7cm. Illumination was obtained from the Kaiser RB 218N HF integrated lights of the stand. The default camera settings were used, and the image output was set to the highest quality JPG file possible.

The placement of the moths for the photography process was done on a small foam tray, on which moths were pinned. The top of the foam surface was covered with one layer of black origami paper to provide a good contrast for the pictures. Since the main goal of the photography process was to capture the wing of the moths, different placements were used depending on the way the wings of the moth were set (folded, extended, intermediate point). As a result, moths with extended wings were placed vertically on the foam tray. Side photos were taken of moths with folded wings, for this a small foam wall was used to pin the moths horizontally, thus showing the wing surface towards the camera. Some specimens had neither completely extended nor folded wings, but rather an intermediate disposition, making necessary the use of a slanted pin direction, aiming to display the wing surface in a perpendicular plane to the camera lens (Figure 2).

Once all the photos were acquired, each photo file number was associated with the individual id in the database.

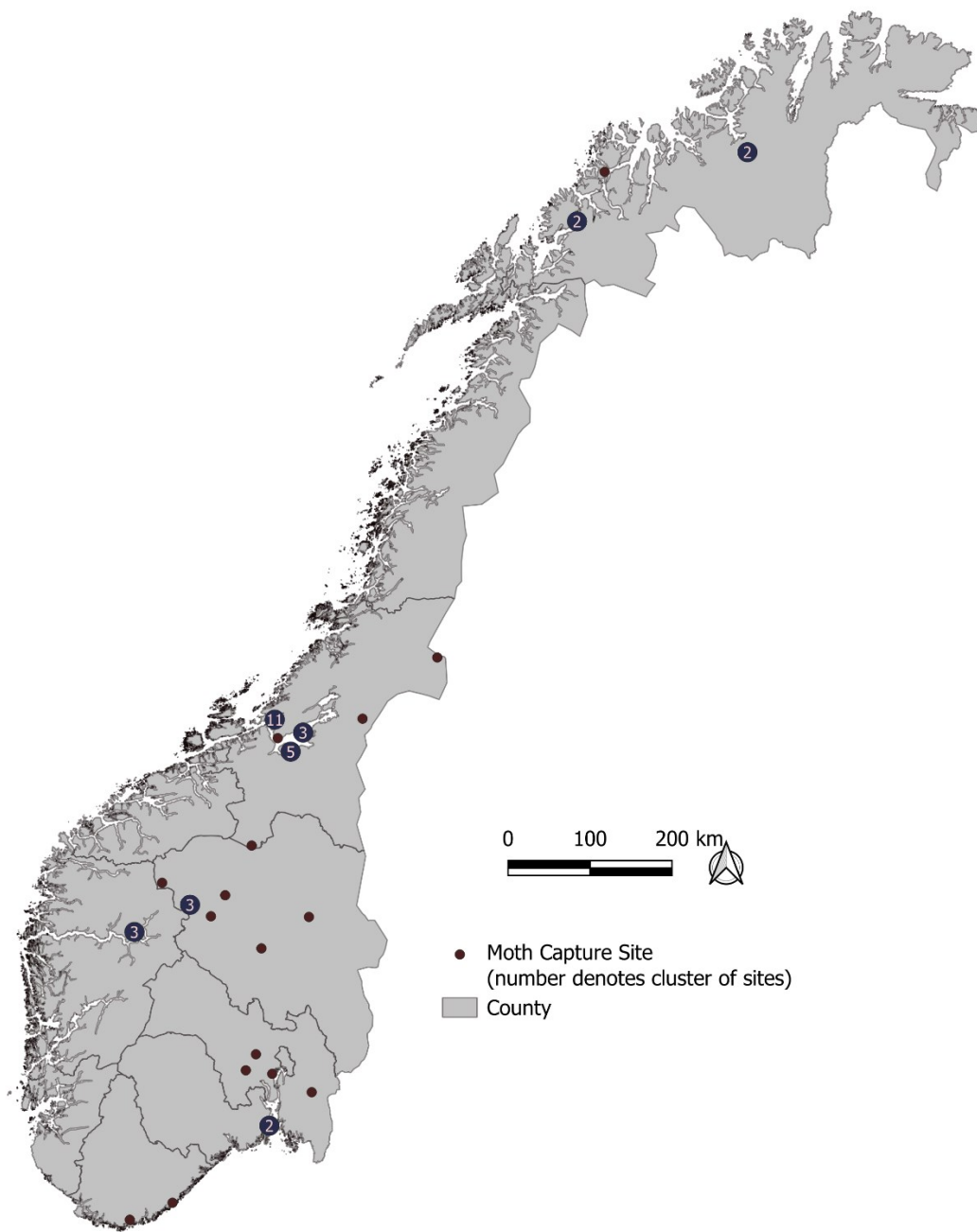


Figure 1 Sampling sites for *E. autumnata* individuals present in NTNU university museum collection. Each point represents a sampling site, while numbers denote clustered of sites in proximity to each other.



Figure 2 Top left: Extended wing setup; Top right: Upwards folded wing setup; Bottom left: Downwards folded wing moth setup; Bottom right Intermediate folded/extended wing setup.

2.3 Photo Measurements

Image J software was used to measure the photographs (Figure 3) and obtain measurements for wing length (mm), area (mm^2) and color intensity (8-bit scale, ranging from 0 = black to 255 = white). Only moths with wings in good condition that displayed the dorsal side of the forewing were measured, while individuals with damaged wings (137) and those displaying the ventral view of the wings (308) were excluded from measurement. Only individuals with extended wings showing both wings were considered for asymmetry tests.

The reliability and precision of the measurement was tested by selecting a subset of 20 individuals for which measurements were repeated. Then an Interclass Correlation Coefficient was carried out using the "irr" package in R for the measurement of each variable with values of 0.876 for length, 0.988 for area, and 0.987 for color (Gamer et al., 2019; R Core Team, 2023).

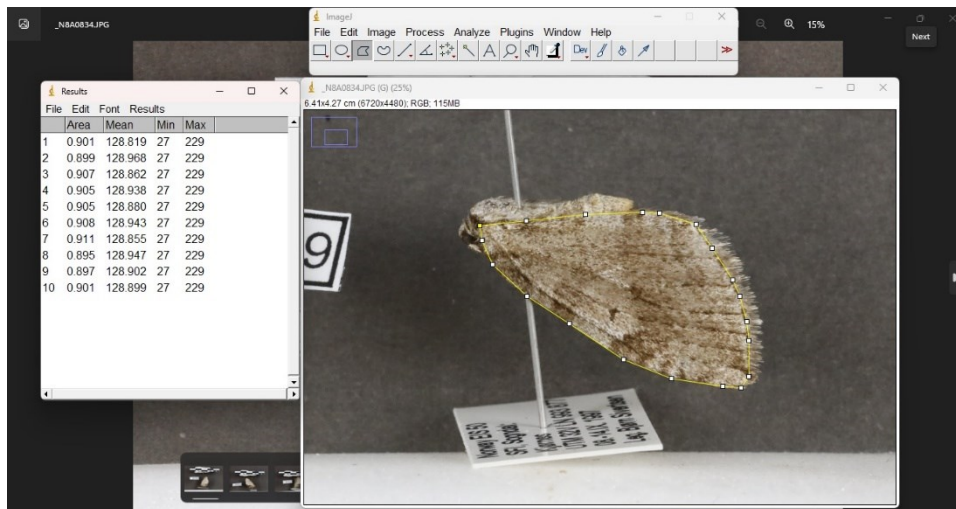


Figure 3 Example of measurement of wing area using ImageJ.

2.4 Climate Data

The climate dataset used was obtained from SeNorge, covering a time range from 1958 to 2008. Data corresponding to daily measurements temperature and precipitation was extracted for the different moth sampling sites using the "Sample (Spatial Analyst)" tool in ArcGIS. The R packages "dplyr" and "tidyr" were used to determine monthly and seasonal values for the climate variables of interest (temperature and precipitation) at each sampling site for the years where moths have been reported as well as the previous year to each moth sampling event (R Core Team, 2023; Wickham et al., 2023; Wickham et al., 2024). The seasons were defined as: Spring = months 3, 4 and 5; Summer = months 6, 7 and 8; Autumn = months 9, 10 and 11. Even though winter was calculated by default as the remaining months, it was not included in the study.

2.5 Asymmetry Measurement

For individuals mounted with extended wings, where both wings were in good condition and therefore measured, fluctuating asymmetry was calculated following the method described by Palmer and Strobeck (1986), this method accounts for the size of the individual when determining its fluctuating asymmetry value following the equation: $FA = \frac{Var\left(\frac{R_i - L_i}{(R_i + L_i)/2}\right)}$, where FA = fluctuating asymmetry, Var = sample variance, R_i = measured right wing trait, L_i = measured left wing trait. Furthermore, this method has been successfully used by Henriques and Cornelissen (2019) in studies involving Lepidoptera.

2.6 Working Dataset

Out of the total 1708 individuals in GBIF database, 1257 were in good shape to be photographed. 790 of the photographed individuals were measured, while the remaining 467 were excluded due to poor quality (137), unreliable data labeling (22) and showing hindwings over forewings (308). Only individuals for which climate variables were available were included in the analysis, resulting in 682 individuals meeting this condition. Out of these, 456 presented folded wings, while 226 had extended wings. Out of those with extended wings 124 met the criteria for asymmetry tests.

2.7 Moran Test for Spatial Autocorrelation

The package "spdep" was used in R to perform Moran's test for the measured wing traits (length, area, color) with the goal of determining the presence of spatial autocorrelation (Bivand, 2022; R Core Team, 2023). A distance-based approach with UTM zone 33N (EPSG 32633) was used to create the weight matrix. Spatial autocorrelation was found to be significant for wing length and area measurements ($p < 0.001$ in both cases). Meanwhile color did not present spatial autocorrelation.

2.8 Statistical Analysis

Pairwise correlation matrixes were created for both predictor and response variables (Appendix 1), to remove one of the elements in cases where high pairwise correlation (>0.5) was detected. Notable correlations found include wing length and area measurements among response variables (0.97), as a result only length was considered for the analysis. Among predictor variables all season temperature pairs were found to be correlated, it was decided to use spring temperature as the selected variable for all models, since all moths are sampled after spring, therefore making its value relevant for all individuals. Another notable high correlation occurred between spring temperature and year (0.829), which led to year being dropped from the models. Out of the considered covariates only current and previous year summer precipitation, along with previous year spring precipitation and decimal latitude were included in the models. All variables were included in the models as independent effects, additionally, an interaction term between average spring temperature and decimal latitude was included in the starting models.

Generalized least squares (GLS) models were chosen, with the goal of accounting for spatial autocorrelation in the model. To do this, the model was fitted using an exponential covariance structure, then the decimal coordinates of the sampling sites were transformed into UTM zone 33N (EPSG 32633) coordinates to be able to use meters as measurement unit. The models were carried out using the package "nlme" in R for measured traits (Pinheiro & Bates, 2023; R Core Team, 2023). Likelihood ratio tests were used for model selection (Appendix 2), removing the least significant ($p > 0.05$) term sequentially until all remaining terms were significant or the hypothesis variable (average spring temperature) set to be removed. Plots were generated using the R packages "ggplot2" and "ggeffects" (Lüdtke, 2018; R Core Team, 2023; Wickham, 2016).

3 RESULTS

GLS models were carried out using the measurements taken from the photographs. After fitting the models, spring temperature was significant ($P < 0.05$) for models of wing length and fluctuating asymmetry of wing area, meanwhile for models of wing color and fluctuating asymmetry of wing length, spring temperature was non-significant ($p > 0.05$)

3.1 Wing Length

The dataset utilized for the wing length model contained 682 individuals sampled in 33 locations. Even though the individuals present in the dataset are sampled between 1959 and 2008, the sampling is not evenly distributed across the entire period, varying from years without samples to years with considerable amounts of samples, particularly in 1997 (Figure 4). Similarly, the sampling is also not evenly distributed between the different counties, with counties such as Innlandet and Vestlandet being highly represented, while Vestfold og Telemark and Agder present low sampling numbers, additionally, Nordland presents no samples (Figure 4).

The resulting model for wing length was $\text{Wing Length} \sim \text{average Spring Temperature} + \text{Summer Precipitation} + \text{Decimal Latitude}$. An exponential spatial correlation structure was used for the model, however, spatial autocorrelation although present was very limited (range = 1.879 m). The likelihood ratio test statistic was determined ($p = 1$; $df = 7$), suggesting that there is no significant difference in the model fit between the starting model and the final model. This implies that the excluded variables did not contribute significantly to the model's ability to explain the studied relationship.

In the resulting model, spring temperature was found to have a negative effect on wing length (coefficient = -0.038; $se = 0.015$; $t = -2.614$ $p = 0.009$; Figure 5). The covariate of summer precipitation has a small yet positive effect on wing length (coefficient = 0.007; $se = 0.001$; $t = 6.754$; $p < 0.001$; Figure 5). Additionally, decimal latitude also has a positive effect on wing length (coefficient = 0.105; $se = 0.028$; $t = 3.691$; $p < 0.001$; Figure 5). Furthermore, the way in which spring temperature affects wing length can be effectively seen calculating marginal values, keeping fixed values for the other covariates in the model (Figure 6), here, the respective mean of each covariate is used as the intermediate fixed value, and a symmetric distance of one standard deviation above and below the mean for the other two fixed values.

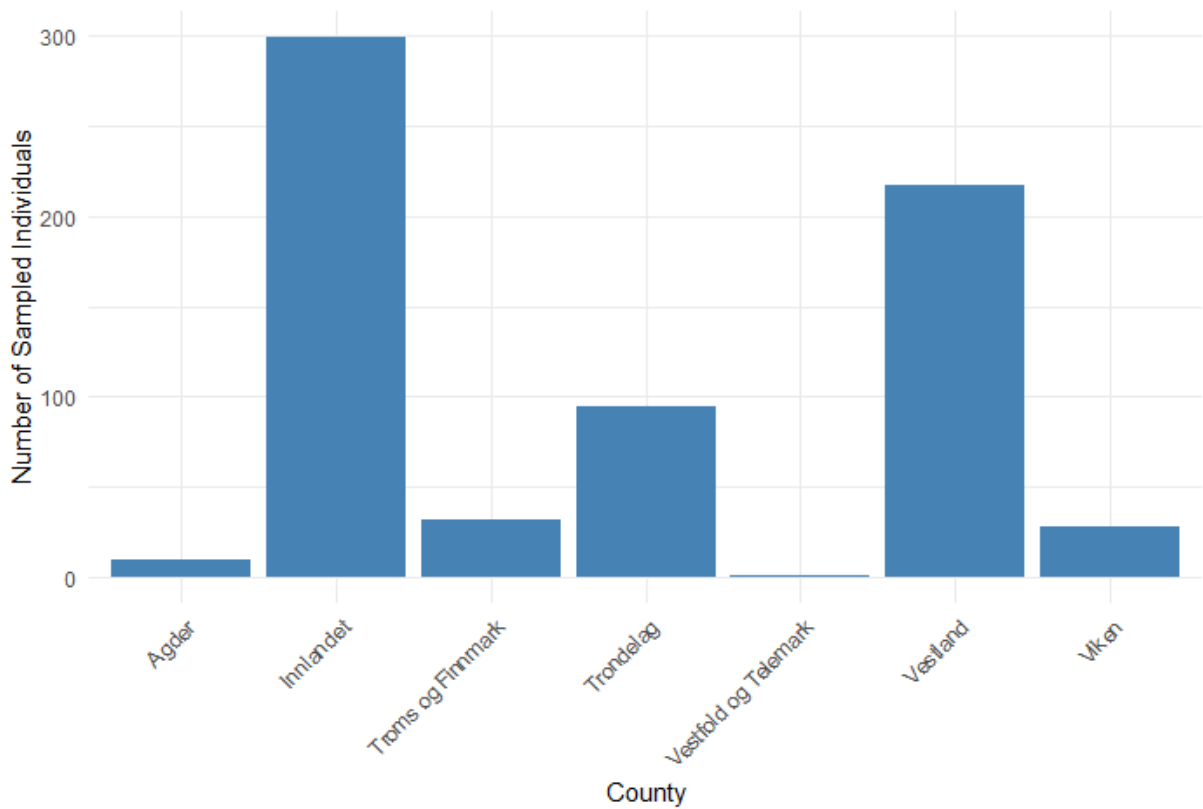
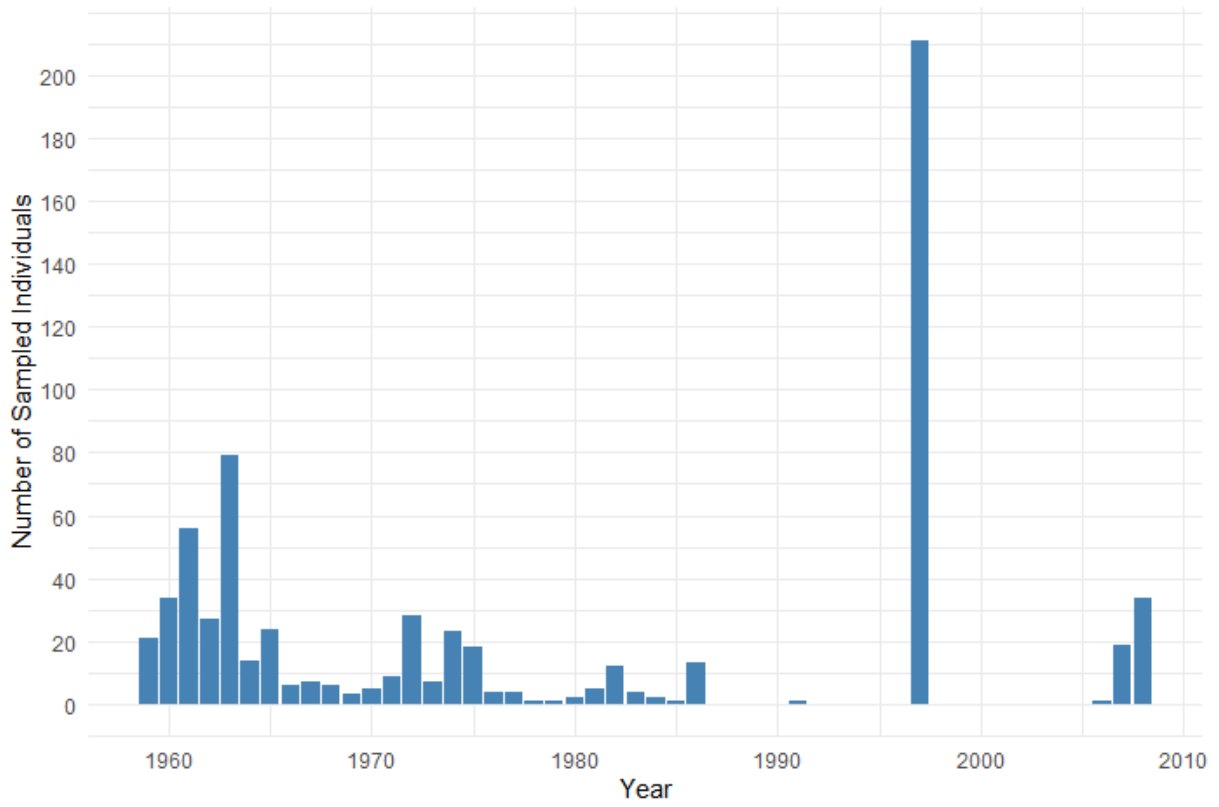


Figure 4 Number of samples included in the wing length model, both per year (top) and per county (bottom).

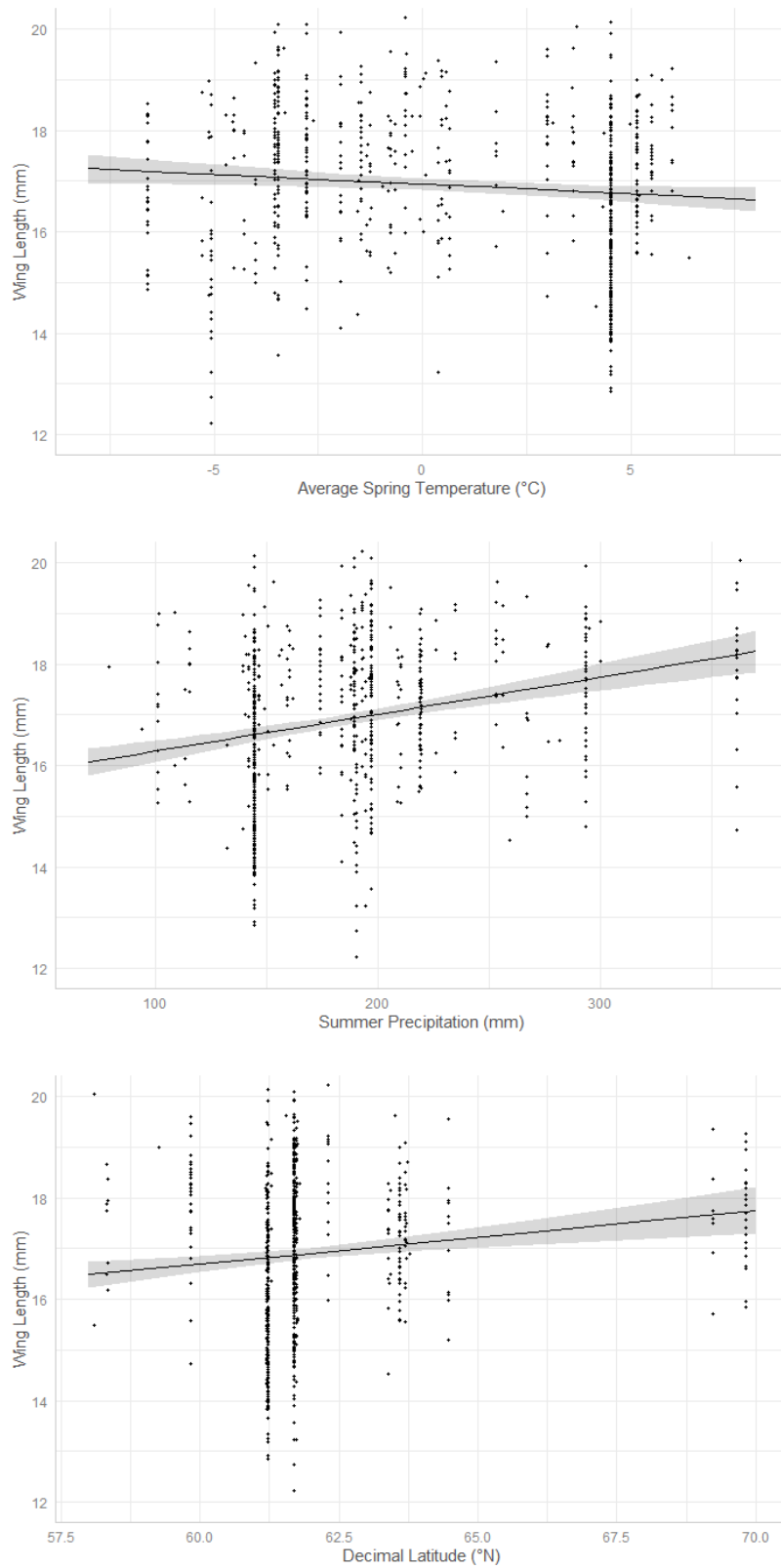


Figure 5 Relationship between wing length and average spring temperature (top), summer precipitation (middle), and decimal latitude (bottom) according to the wing length model.

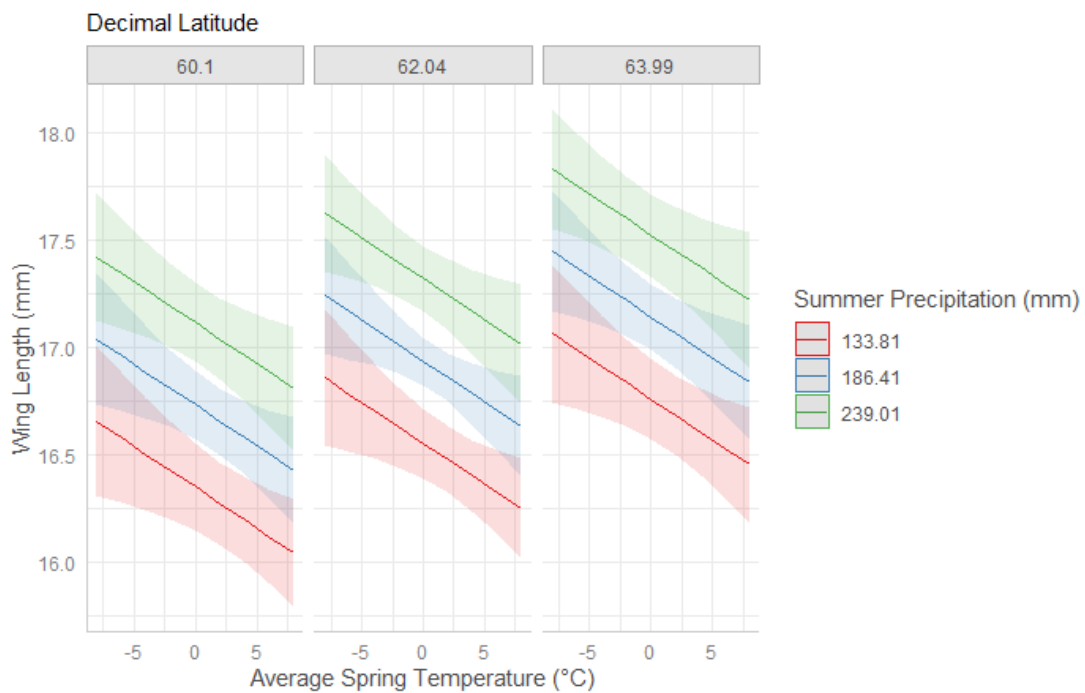


Figure 6 Effect of spring temperature on wing length at fixed levels of summer precipitation and latitude.

3.2 Fluctuating Asymmetry of Wing Area

The dataset used for the wing area fluctuating asymmetry model included 124 individuals, sampled in 13 different locations. The samples were unevenly distributed in space and time, with most being taken in the 1960's (Figure 7), and with the county of Inlandet being considerably overrepresented (Figure 7).

The resulting model for fluctuating asymmetry of wing area was Wing area fluctuating asymmetry \sim average Spring Temperature, where the effect of spring temperature on fluctuating asymmetry of wing area was positive and significant (coefficient = 1.004; se = 0.325; $t = 3.089$; $p = 0.002$; Figure 8). For this model the likelihood ratio test statistic ($p = 1$; $fa = 5$) indicates no significant difference in model fit between starting and final model, meaning that the excluded variables did not significantly contribute to the explanation of variation in fluctuating asymmetry of the wing area.

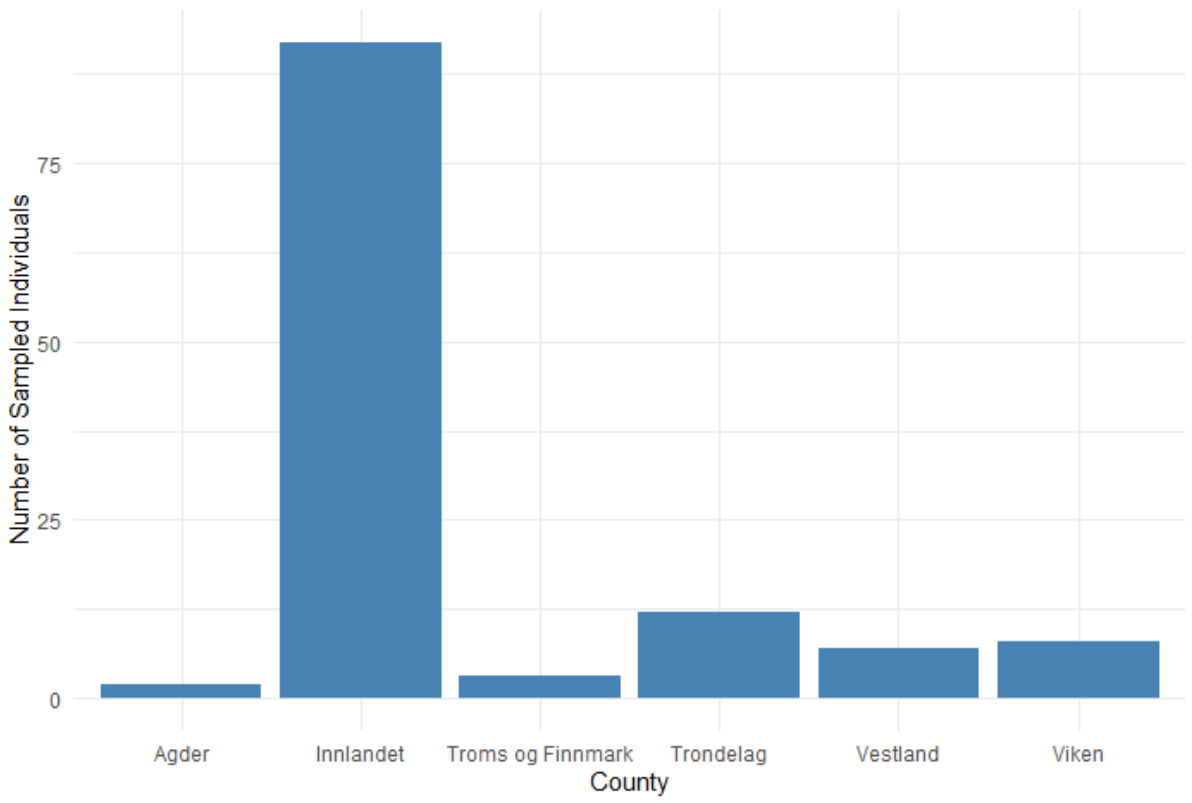
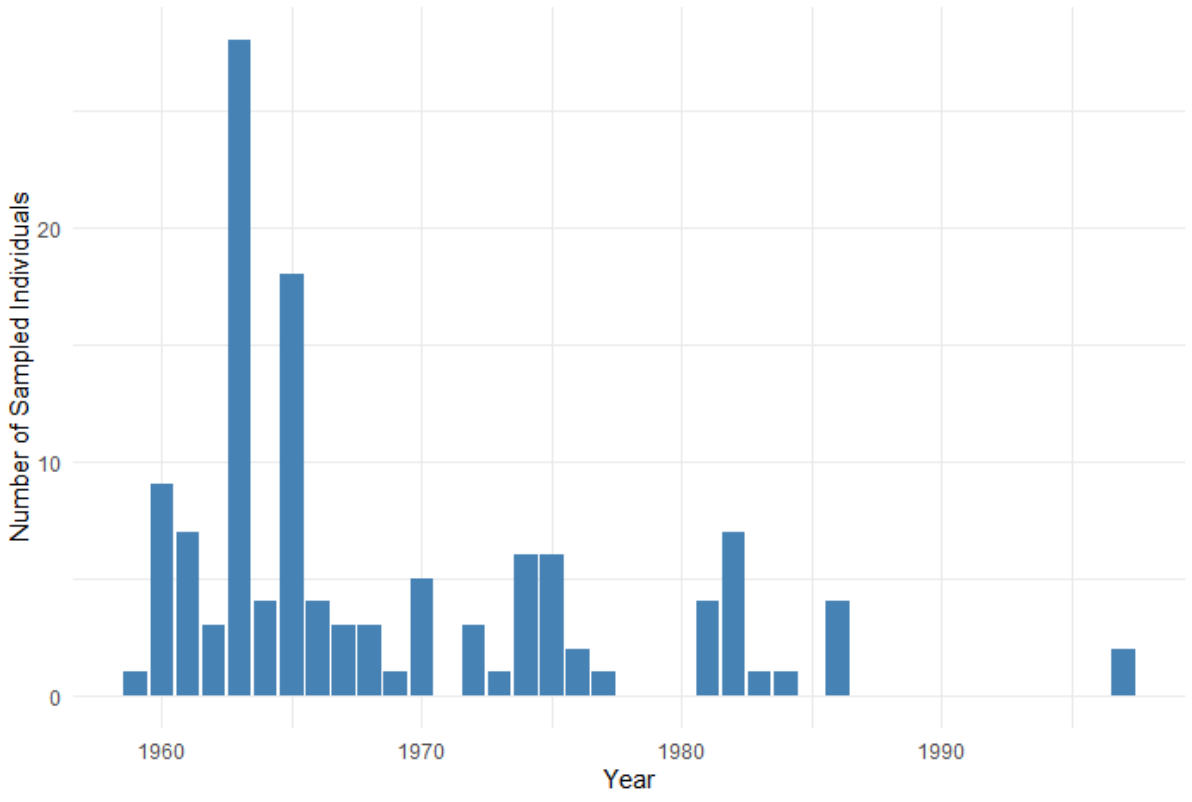


Figure 7 Number of samples included in the wing area fluctuating asymmetry model, both per year (top) and per county (bottom).

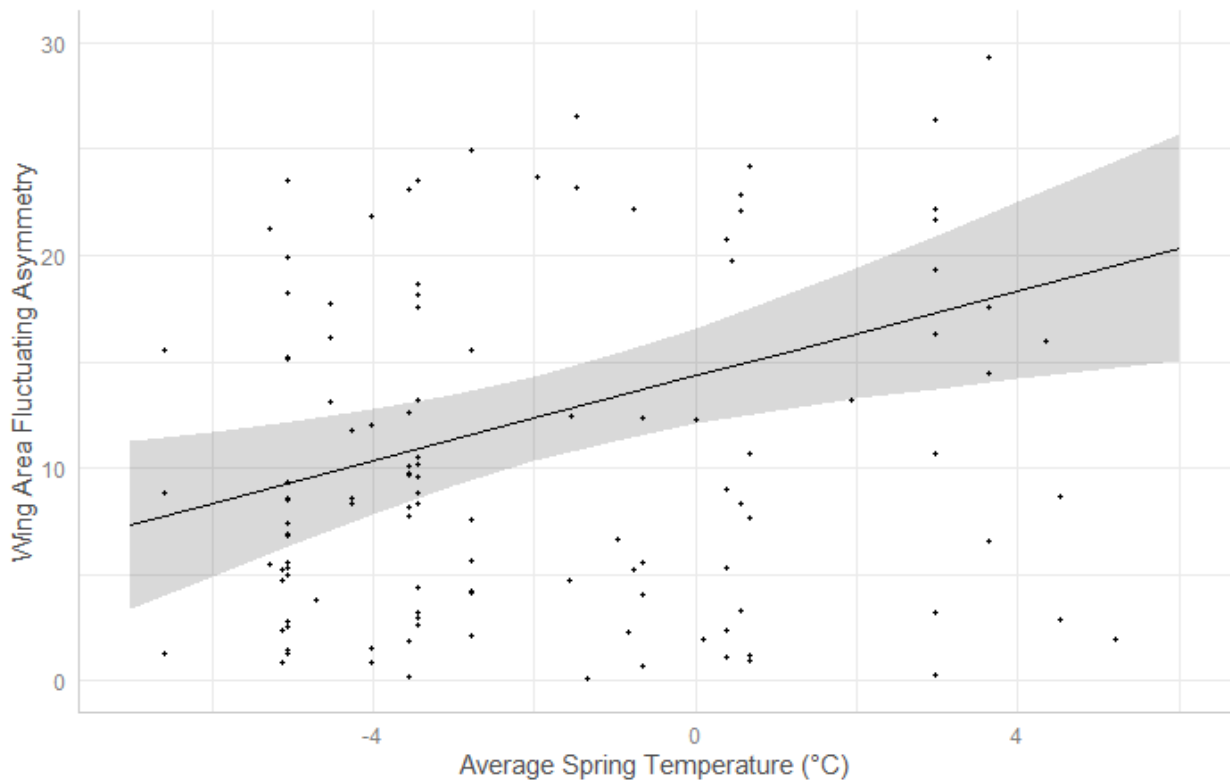


Figure 8 Relationship between wing length and fluctuating asymmetry of wing area.

3.3 Color and Fluctuating Asymmetry of Wing Length.

Spring temperature in the test of color and fluctuating asymmetry of wing length turned out to be not significant. The final color model was: wing color \sim spring temperature + previous year summer precipitation + summer precipitation + decimal latitude + Previous year spring precipitation + spring temperature:decimal latitude, where spring temperature had $p = 0.503$.

The final model for fluctuating asymmetry of wing length was: fluctuating asymmetry of wing length \sim spring temperature + summer precipitation + decimal latitude, where spring temperature had $p = 0.164$.

4 DISCUSSION

The results that were obtained show that spring temperature influences some of the measured wing traits of *E. autumnata*. These effects being significant in the case of the relationship between spring temperature and wing length (which was highly correlated to wing area), which is of negative character and leads to a reduction of 0.038 mm in length per each Celsius degree increase. Meanwhile, the relationship between spring temperature and fluctuating asymmetry of wing area showed a positive character. This is of particular interest, especially considering the current situation of climate change, thus giving an insight into how the Norwegian population of *E. autumnata* may change under a warming climate. Despite this, temperature alone is not enough to fully understand how changes in functional traits of this species are driven. There are several variables that interact and lead to a morphological response in *E. autumnata*, therefore other variables should also be considered to attain a better understanding of how climate drives changes in the autumnal moth and forecast changes according to climate change scenarios.

4.1 Wing Length

It was hypothesized that higher temperatures would have a negative effect on the forewing length of *E. autumnata* individuals, and indeed, following Bergmann's rule the results were consistent with the hypothesis. There are studies suggesting that negative relations between temperature and wing size can be found (Bowden et al., 2015; Brehm et al., 2019; Fischer & Fiedler, 2002), however, the response of this trait to temperature is variable and complex. Being highly dependent on other interacting factors such as sex, developmental stage of the organism, voltinism and the time scale at which temperature is calculated, furthermore, positive and negative responses have been found (Fenberg et al., 2016; Fischer & Fiedler, 2002; Wilson et al., 2019).

Given that the temperature variable used was average spring temperature, when put in the context of developmental stage, these temperature values are relevant for the final part of the egg stage and the earlier parts of the larval stage of *E. autumnata* (Bylund, 1999). Wilson et al. (2019) have studied the effect of temperature on wing length on different species of Lepidoptera, assessing the effect using monthly average temperatures, as well as considering certain development stages. The response of wing length to temperature can be strongly variable, with changes in the direction on the effect on consecutive spring months, as well as strong variability between and within species as well as between sexes and developmental stages (Wilson et al., 2019; Wilson et al., 2023).

The effect of precipitation on wing length is not that commonly studied; however, different studies have reported a positive effect of precipitation on wing size of different insects (Önder & Aksoy, 2022; Rosetti & Remis, 2018). This is consistent with the obtained model output where summer precipitation has a positive effect on wing length. However, its effect can also be negative (Bai et al., 2016), or vary depending on other variables, such as sex (Fiad et al., 2022; Önder & Aksoy, 2022). It is also highly likely that as with temperature, the effect of precipitation on wing size will differ according to the developmental stage of the study subject.

Just like with temperature, the effect of decimal latitude on wing length follows Bergmann's rule, with larger individuals at higher latitudes, which is also where colder temperatures are expected to be found. This result is consistent with literature reports (Huey et al., 2000; Land et al., 1999; Moya-Raygoza et al., 2005). However, opposite trends have also

been found in insects (Zheng et al., 2015), as well as nonlinear relationships where wing are longer at low and high latitudes, yet smaller at intermediate latitudes (Johansson, 2003). Furthermore, mixed effects have been found, where overall insect size and wing area increase with latitude while forewing length decreases (Vandewoestijne & Van Dyck, 2011). Additionally, landscape type has also been described as a variable interacting with latitude in their effect on wing size (Vandewoestijne & Van Dyck, 2011).

The negative relationship between wing length and temperature implies an important trade-off with the capability of the autumnal moth to potentially expand its range under current warming in its habitat, something that is strongly determined by temperature (Bylund, 1999). With increasing areas of birch forest becoming environmentally viable for the establishment of *E. autumnata*, morphological traits that favor dispersal become favorable, thus making larger wings a desirable trait (Hill et al., 2021; Ruohomäki, 1992). Despite this, the negative effect of temperature on wing length that was found suggests a negative outcome in dispersal ability. Indeed, it could be highly detrimental to the autumnal moth considering other possible effects of a warming climate, including range increases of natural enemies of *E. autumnata*, such as wood ants and different parasitoids. Additionally, competitor species could expand their range to a point where there is overlap with *E. autumnata*. Furthermore, an ecosystem shift towards a boreal mixed forest could occur, where the autumnal moth has no outbreak capability (Bylund, 1999; Kari & Neuvonen, 1998; Virtanen & Neuvonen, 1999).

However, along with warming temperatures, higher precipitation is also to be expected as part of climate change in Norway (Hanssen-Bauer et al., 2017). Here, the positive response of wing length to summer precipitation may counteract the negative effect that rising temperatures can have on wing length. It must be noted that although high temperatures and higher precipitation are expected to increase in Norway in a general level, these increases will vary depending on seasonality and geographic location, and similarly, morphology responses of the autumnal moth may be variable according to location.

4.2 Wing Asymmetry

It was hypothesized that the fluctuating asymmetry for the wing area would be driven by a negative relationship with temperature, however, the obtained model suggests the opposite, with increasing fluctuating asymmetry as temperatures increase. This finding goes against what has been reported by (Henriques & Cornelissen, 2019), where low temperatures are reported as one of the stress factors driving fluctuating asymmetry in Lepidoptera individuals.

Even though cold temperatures can be seen as a stress factor and a potential driver of fluctuating asymmetry, warming temperatures can have a similar effect. This is especially relevant in the face of current warming temperatures, where a more unstable climate with variation in temperature can be a factor positively influencing fluctuating asymmetry (Henriques & Cornelissen, 2019). Furthermore, warming temperatures may lead to accelerated development rates, resulting in developmental instability, which can be reflected as increased fluctuating asymmetry (Henriques & Cornelissen, 2019).

It is probable that the increase of fluctuating asymmetry with warming temperatures in the autumnal moth is driven by this accelerated development. However, it is important to keep in mind that temperature is rarely the sole stress factor acting at a given moment. Indeed, several biotic and abiotic factors may act as stressors simultaneously, thus stress

driven fluctuating asymmetry is also the result of a set of complex interactions between different variables (Beasley et al., 2013; Graham et al., 2010).

Meanwhile, in the model for fluctuating asymmetry of wing length, the hypothesis variable (average spring temperature) was deemed non-significant. However, just as with fluctuating asymmetry of wing area, fluctuating asymmetry for wing length is equally subject to a wide set of factors that compose a complex set of interaction that ultimately drives the asymmetrical development of the trait.

An important detail about the dataset used for the models on fluctuating asymmetry is that a very considerable proportion of the samples come from the county of Innlandet, representing a considerable geographical bias. In this sense, the inclusion of specimens from other collections may be desirable to even out spatial coverage, thus making any result more relevant for the Norwegian context.

4.3 Wing Color

The hypothesis variable (average spring temperature) for the wing color model resulted in being not significant. Meaning that spring temperatures do not have a significant effect on this trait. However, this by no means implies that no climate variables are acting on this trait, rather the involved variables are different from the ones used in the present study.

Color is another trait that can be dependent on a wide set of variables, both biotic and abiotic, thus making color the result of complex interactions between variables. The hypothesis that was formulated implied a negative change in melanism as temperatures increase, which is consistent with literature reporting this as a form of thermal adaptation (MacLean et al., 2016; Zeuss et al., 2014). However, another possible color response may be present. It has been reported for different Lepidoptera species in northern Scandinavia that range expansion considering current climate change is highly favored by presenting highly variable color patterns at the inter-individual level (Forsman et al., 2016). Where species showing the most color pattern variability are more proficient in expanding their range, by adapting more easily to changing environmental conditions. It is a possibility that wing color in *E. autumnata* responds in a similar way, where color patterns occur in a variable fashion, rather than fall in a trend of increased or decreased melanism.

4.4 Improvements and Future Possibilities

When considering possible improvements to the present study, the first question to be asked is about which other variables should be considered to best explain environmental effects on functional traits of *E. autumnata*. Some of the variables related to *E. autumnata* that should be included are sex and developmental stage of individuals, since these have been proven to present differential responses to environmental conditions in Lepidoptera studies, it is therefore important to account for them in further studies. Other environmental variables should also be considered, including elevation, snow related variables, UV light exposure, temperature minimums and maximums. Biotic variables should also be considered, such as the presence of competitor species, potential predators, and characteristics of surrounding vegetation, especially considering the close link between the autumnal moth and birch forest areas.

Temporal dimensions should also be considered, the present study utilized seasonal values for climatic variables, but smaller time scales may be better suited to study *E. autumnata*,

using a temporal dimension that allows to capture effects in relation to the phenology of *E. autumnata*. Indeed, an exciting possibility to further the study of *E. autumnata* in relation to climate is to focus this on the specific effects that can be present at each developmental stage of the autumnal moth. For example, with the current warming trends higher survival of eggs is expected, along with faster developmental rates (Ayres & MacLean, 1987; Peterson & Nilssen, 1996; Virtanen et al., 1998). Although, this is not necessarily positive since high temperatures can lead to earlier than usual egg hatching, which has been reported to result in a phenological mismatch of up to six weeks with budburst timing of mountain birch, thus causing larvae mortality (Kaitaniemi & Ruohomäki, 1999). Furthermore, high temperatures during the pupal stage may go over the ideal value and lead to decreased development and increased mortality (Peterson & Nilssen, 1996). Additionally, the expected size decrease on the autumnal moth that was shown in the models may have negative consequences to the species at least when considering traits such as flight and dispersal capability.

Another possible relevant subject is a trait study including both the autumnal moth and mountain birch, considering how closely linked these two species have been over time. This is important not only considering the possibility of the above-mentioned phenological mismatch, but also considering that climate induced change in traits of mountain birch can be reflected in *E. autumnata*. It has been shown that plant food quality is in part mediated by temperature and can influence larval survival and development rate in the autumnal moth (Hanhimäki et al., 1995; Virtanen & Neuvonen, 1999).

Different alternatives can be used to achieve this. It is possible to incorporate specimens from other collections, as well as mountain birch collection specimens, strengthening the dataset used while keeping the advantage of a wide temporal coverage, which is one of the biggest assets of the present study. Alternatively, carrying out field-based studies would be very beneficial, where it is possible to have much more control over the samples that are to be used, as well as the acquisition of environmental data of interest. This would help to avoid complications that are inherent to collection-based studies, especially those linked to temporal and geographic bias, as well as the loss of samples due to poor condition.

An important outcome of this study is not reflected in the results but is rather a product of the study design. This is the substantial increase of information related to the *E. autumnata* individuals of the collection at NTNU University Museum. Formerly these individuals appeared in the database of GBIF only as entries, but since this study implied the process of photographing and measuring a large proportion of the individuals in the collection, all this new information about the specimens is intended to be added to the database, thus strengthening its informative character substantially. Additionally, this project is a small token that highlights the value and potential that natural history collections represent in respect to the generation of new and relevant knowledge about how different species change across space and time. Additionally, the fact that the collection will remain in the museum, as well as having photographs and measurements available, represents a precedent from which it is possible to expand on by including different variables that may be of interest to the study of the ecology of this species.

Another exciting pathway that appears with projects of this kind is the potential use of technology to streamline the data extraction process, by using tools such as computer vision and machine learning to make the measurement process much more efficient, thus greatly reducing the number of human hours devoted to this highly time-consuming task. This has already been done successfully using Lepidoptera from entomological collections

(Wilson et al., 2023). This opens the possibility of extending this type of project to different taxa, and depending on each treated species extract information of different traits, thus aiming to make the most out of the potential offered by natural history collections.

5 CONCLUSION

This study showcases the potential of entomological collections in the study of variability of individual traits, especially regarding climatic variables. As hypothesized and following Bergmann's rule, temperature has a negative effect on wing size, in this case using wing length. Fluctuating asymmetry for wing area also increases with temperature, which despite being against what was hypothesized, may be a result of accelerated growth due to warmer temperatures. Although covariates such as precipitation and latitude also influenced the measured traits of *E. autumnata*, this is not enough to capture the entire complexity of interactions responsible for determining trait changes. Further studies should consider the incorporation of additional variables to attain a better understanding of the interactions taking place. Additionally, time should be assessed in relation to the known phenology of *E. autumnata* rather than just by season, considering that the effect of environmental variables can vary considerably according to developmental stage. This project also serves as a contribution to the natural history collection at the NTNU University Museum, by providing photographs and measurements of the specimens used, thus strengthening the informative character of the collection.

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Appendix 1: Pairwise Correlation Matrices

Response variables

Table 1. Pairwise correlation matrix for response variables

	Length	Area	Color	FA length	FA Area
Length	1	0.97	-0.051	-0.02	0.131
Area	0.97	1	-0.029	0.013	0.111
Color	-0.051	-0.029	1	-0.007	-0.021
FA Length	-0.02	0.013	-0.007	1	0.335
FA Area	0.131	0.111	-0.021	0.335	1

Predictor variables (next page)

Table 2. Pairwise correlation matrix for predictor variables

	Temperature				Precipitation				Previous Year Temperature				Previous Year Precipitation				Year	Decimal Latitude	Site
	Autumn	Spring	Summer	Winter	Autumn	Spring	Summer	Winter	Autumn	Spring	Summer	Winter	Autumn	Spring	Summer	Winter			
Temperature Autumn	1.000	0.970	0.915	0.877	0.698	0.776	-0.248	0.774	0.919	0.915	0.924	0.825	0.659	0.383	0.144	0.497	0.789	-0.142	-0.223
Temperature Spring	0.970	1.000	0.943	0.884	0.621	0.770	-0.247	0.757	0.907	0.914	0.941	0.819	0.597	0.357	0.062	0.480	0.829	-0.119	-0.198
Temperature Summer	0.915	0.943	1.000	0.825	0.462	0.800	-0.300	0.682	0.855	0.860	0.930	0.737	0.500	0.258	-0.066	0.340	0.817	-0.059	-0.197
Temperature Winter	0.877	0.884	0.825	1.000	0.527	0.744	-0.388	0.870	0.844	0.886	0.848	0.851	0.561	0.313	-0.124	0.438	0.825	-0.003	-0.135
Precipitation Autumn	0.698	0.621	0.462	0.527	1.000	0.294	0.134	0.504	0.715	0.624	0.582	0.684	0.764	0.592	0.351	0.794	0.429	-0.073	0.018
Precipitation Spring	0.776	0.770	0.800	0.744	0.294	1.000	-0.454	0.779	0.732	0.721	0.677	0.613	0.355	0.030	-0.077	0.197	0.756	-0.308	-0.449
Precipitation Summer	-0.248	-0.247	-0.300	-0.388	0.134	-0.454	1.000	-0.443	-0.147	-0.189	-0.216	-0.108	-0.020	0.341	0.369	0.162	-0.452	-0.054	0.050
Precipitation Winter	0.774	0.757	0.682	0.870	0.504	0.779	-0.443	1.000	0.798	0.796	0.683	0.748	0.554	0.234	-0.103	0.453	0.756	-0.111	-0.215
Prev Year Temperature Autumn	0.919	0.907	0.855	0.844	0.715	0.732	-0.147	0.798	1.000	0.907	0.874	0.863	0.699	0.463	0.019	0.605	0.772	-0.177	-0.214
Prev Year Temperature Spring	0.915	0.914	0.860	0.886	0.624	0.721	-0.189	0.796	0.907	1.000	0.929	0.846	0.649	0.396	0.128	0.443	0.807	-0.200	-0.268
Prev Year Temperature Summer	0.924	0.941	0.930	0.848	0.582	0.677	-0.216	0.683	0.874	0.929	1.000	0.739	0.556	0.364	0.031	0.384	0.815	-0.031	-0.103
Prev Year Temperature Winter	0.825	0.819	0.737	0.851	0.684	0.613	-0.108	0.748	0.863	0.846	0.739	1.000	0.639	0.411	0.013	0.668	0.697	-0.106	-0.166
Prev Year Precipitation Autumn	0.659	0.597	0.500	0.561	0.764	0.355	-0.020	0.554	0.699	0.649	0.556	0.639	1.000	0.646	0.223	0.724	0.566	-0.156	-0.082
Prev Year Precipitation Spring	0.383	0.357	0.258	0.313	0.592	0.030	0.341	0.234	0.463	0.396	0.364	0.411	0.646	1.000	0.210	0.540	0.347	0.137	0.221
Prev Year Precipitation Summer	0.144	0.062	-0.066	-0.124	0.351	-0.077	0.369	-0.103	0.019	0.128	0.031	0.013	0.223	0.210	1.000	0.036	-0.174	-0.340	-0.249
Prev Year Precipitation Winter	0.497	0.480	0.340	0.438	0.794	0.197	0.162	0.453	0.605	0.443	0.384	0.668	0.724	0.540	0.036	1.000	0.415	0.090	0.206
Year	0.789	0.829	0.817	0.825	0.429	0.756	-0.452	0.756	0.772	0.807	0.815	0.697	0.566	0.347	-0.174	0.415	1.000	0.005	-0.029
Decimal Latitude	-0.142	-0.119	-0.059	-0.003	-0.073	-0.308	-0.054	-0.111	-0.177	-0.200	-0.031	-0.106	-0.156	0.137	-0.340	0.090	0.005	1.000	0.921
Site	-0.223	-0.198	-0.197	-0.135	0.018	-0.449	0.050	-0.215	-0.214	-0.268	-0.103	-0.166	-0.082	0.221	-0.249	0.206	-0.029	0.921	1.000

Appendix 2: Model Selection

Likelihood ratio test, by progressive removal of the least significant (>0.05) variable (highlighted in red) until all remaining variables are significant (< 0.05) or the hypothesis variable (average spring temperature) is set to be removed.

Wing length

Starting model: Wing Length \sim Spring Temperature + Summer Precipitation + Previous Year Spring Precipitation + Previous Year Summer Precipitation + Latitude + Spring Temperature:Latitude

Final model: length \sim Spring Temperature + Summer Precipitation + Latitude

Table 3. Wing length model selection

	Variable	p-value
Starting model	Spring Temperature	< 0.001
	Summer Precipitation	< 0.001
	Previous Spring Precipitation	0.102
	Previous Summer Precipitation	0.775
	Latitude	< 0.001
	Spring Temperature:Latitude	0.356
First model simplification	Spring Temperature	< 0.001
	Summer Precipitation	< 0.001
	Previous Spring Precipitation	0.101
	Latitude	0.001
	Spring Temperature:Latitude	0.347
Second model simplification	Spring Temperature	< 0.001
	Summer Precipitation	< 0.001
	Previous Spring Precipitation	0.102
	Latitude	0.001
Final Model	Spring Temperature	< 0.001
	Summer Precipitation	< 0.001
	Latitude	< 0.001

Fluctuating Asymmetry of Wing Length

Starting model: Wing Length Fluctuating Asymmetry ~ Spring Temperature + Summer Precipitation + Previous Year Spring Precipitation + Previous Year Summer Precipitation + Latitude + Spring Temperature:Latitude

Final model: Wing Length Fluctuating Asymmetry ~ Spring Temperature + Summer Precipitation + Latitude

Table 4. Wing length fluctuating asymmetry model selection

	Variable	p-value
Starting model	Spring Temperature	0.170
	Summer Precipitation	0.048
	Previous Spring Precipitation	0.652
	Previous Summer Precipitation	0.946
	Latitude	0.003
	Spring Temperature:Latitude	0.220
First model simplification	Spring Temperature	0.171
	Summer Precipitation	0.048
	Previous Spring Precipitation	0.642
	Latitude	0.003
	Spring Temperature:Latitude	0.242
Second model simplification	Spring Temperature	0.167
	Summer Precipitation	0.046
	Latitude	0.003
	Spring Temperature:Latitude	0.233
Final model	Spring Temperature	0.164
	Summer Precipitation	0.046
	Latitude	0.003

Fluctuating Asymmetry of Wing Area

Starting model: Wing Area Fluctuating Asymmetry \sim Spring Temperature + Summer Precipitation + Previous Year Spring Precipitation + Previous Year Summer Precipitation + Latitude + Spring Temperature:Latitude

Final model: Wing Area Fluctuating Asymmetry \sim Spring Temperature

Table 5. Wing area fluctuating asymmetry model selection

	Variable	p-value
Starting model	Spring Temperature	0.002
	Summer Precipitation	0.802
	Previous Spring Precipitation	0.746
	Previous Summer Precipitation	0.968
	Latitude	0.113
	Spring Temperature:Latitude	0.102
	First model simplification	Spring Temperature
Summer Precipitation		0.783
Previous Spring Precipitation		0.754
Latitude		0.119
Spring Temperature:Latitude		0.109
Second model simplification	Spring Temperature	0.002
	Previous Spring Precipitation	0.884
	Latitude	0.117
	Spring Temperature:Latitude	0.098
Third model simplification	Spring Temperature	0.002
	Latitude	0.115
	Spring Temperature:Latitude	0.099
Fourth model simplification	Spring Temperature	0.002
	Spring Temperature:Latitude	0.082
Final model	Spring Temperature	0.002

Wing Color

Model: Wing Color \sim Spring Temperature + Summer Precipitation + Previous Year Spring Precipitation + Previous Year Summer Precipitation + Latitude + Spring Temperature:Latitude

Table 6. Wing color model selection

Variable	p-value
Spring Temperature	0.503
Summer Precipitation	0.229
Previous Spring Precipitation	0.184
Previous Summer Precipitation	0.001
Latitude	0.072
Spring Temperature:Latitude	0.029



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