Olive Fruit Fly Dynamics on Samos: A Spatiotemporal Analysis of Temperature and Altitude Dependence

By

Emily Orna Grünendieck

Submitted to the University of the Aegean

and

Central European University - Private University
Department of Environmental Sciences and Policy

In partial fulfilment of the requirements for the degree of Master of Environmental Sciences, Policy and Management.

Supervisor: Thanasis Kizos

Vienna, Austria
2025

MESPOM
Masters in Environmental Sciences, Policy and Management

This thesis is submitted in fulfillment of the Master of Science degree awarded as a result of successful completion of in Environmental Sciences, Policy and Management (MESPOM) jointly operated by the University of the Aegean, Central European University, Lund University and the University of Manchester.

Abstract

The olive fruit fly (*Bactrocera oleae*) remains the most significant pest affecting olive cultivation globally, with its population dynamics closely linked to climatic and environmental factors. This study analyses an eight-year dataset (2017–2024) collected from a network of climate data loggers and 399 McPhail traps across Samos Island in Greece. The research identifies distinct temporal population trends, revealing a seasonal bimodal distribution with a first peak in early July and a second, higher peak in late September. High temperature, measured by the hours with a temperature above 32°C, was a key factor influencing population dynamics, with higher heat stress leading to fewer olive fruit flies. Between July and September, significantly fewer flies were observed at low altitudes (0–200 m), while the highest population numbers progressively shifted from high (>400 m) to mid (200–400 m) and eventually low elevations in October, possibly suggesting a population movement across altitudes. Further analysis of four areas of the island (Marathokampos, Karlovasi, Agios Konstantinos/Kokkari, Pythagoreio) used Kriging interpolation to reveal regional differences in seasonal population dynamics, notably marked by a North-South divide of the island, likely related to regional temperature differences. Considering the impacts of climate change, the findings suggest that the population patterns will shift towards higher altitudes and the northern regions of Samos. By adopting a landscape-level approach, this study contributes to a better understanding of localised olive fruit fly dynamics, which can be a starting point for improving the monitoring system and informing more sustainable pest management strategies.

Author's Declaration

I, the undersigned, **Emily Orna Grünendieck**, candidate for the MSc degree in Environmental Sciences, Policy and Management, declare herewith that the present thesis titled "Olive Fruit Fly dynamics on Samos: A Spatiotemporal Analysis of Temperature and Altitude Influences" is exclusively my own work, based on my research and only such external information as properly credited in notes and bibliography. I declare that no unidentified and illegitimate use was made of the work of others, and no part of the thesis infringes on any person's or institution's copyright.

I also declare that no part of the thesis has been submitted in this form to any other institution of higher education for an academic degree, except as part of the co-tutelle agreement between Central European University Private University and the University of the Aegean.

Vienna, 31 May 2025

Emily Grünendieck

Acknowledgements

First and foremost, I would like to express my sincere gratitude to my supervisor, Thanasis, for his valuable input, guidance, and encouragement throughout this process. I am also thankful to Sofia for her unwavering technical support and motivation, and to Stratis for providing essential data for this work. This thesis would not have been possible without the contributions of many individuals to this ongoing research, including previous researchers and the trap-setters on Samos. A heartfelt thank you also to Judit for her incredibly supportive academic writing advice and unwavering encouragement.

To the MESPOM community, thank you for shaping my academic journey over the past two years. I'm especially grateful to Tunde and Anne-Sophie for their tireless organisational help, and to all professors, administrative staff, PhD students, researchers at CEU, at the University of the Aegean, and the IIIEE in Lund who contributed to my learning journey, and introduced me to many new exciting academic fields.

Thank you also to my MESPOM cohort. Even though I don't name each of you here, please know how deeply grateful I am to have shared this time with you, and how much you have helped me to grow personally and professionally.

I am also incredibly grateful to my family and Eigirdas for their constant love, support, and positive words: Thank you.

List of Figures

Figure 1: Map showing the four study areas on Samos with categorised elevation, trap placements, and olive grove locations: Marathokampos, Karlovasi, Agios Konstantinos/Kokkari and Pythagoreio....13

Figure 2: Map showing the locations of climate loggers, olive fruit fly traps, and olive groves on Samos....13

Figure 3: Minimum, maximum and average monthly temperatures for each year, along with the number of hours per month with temperatures above 32°C (Any32h and Avg32h)....17

Figure 4: Heatmap of average trap counts per sampling event by month and year....19

Figure 5: Total olive fruit fly (OFF) counts in 10-day intervals from June to October, 2017–2024. 20

Figure 6: Scatterplots with linear regression lines for the four population–temperature variable combinations, showing the relationship between average olive fruit fly counts and the number of hours exceeding 32°C (Any32h and Avg32h)....22

Figure 7: Scatterplot with linear regression line showing olive fruit fly counts per sampling event in July in relation to trap elevation....25

Figure 8: Average olive fruit fly counts for 10-day periods across all years, by elevation category: Low (0-200m), Medium (200-400m) and High (>400m)....25

Figure 9: Average olive fruit fly counts per 10-day period, grouped by elevation category (0–200 m, 200–400 m, >400 m) and year....27

Figure 10: Map series showing total olive fruit fly counts by month and year in the Marathokampos area, estimated using Kriging analysis....31

Figure 11: Map series showing total olive fruit fly counts by month and year in the Karlovasi area, estimated using Kriging analysis....32

Figure 12: Map series showing total olive fruit fly counts by month and year in the Agios Konstantinos / Kokkari area, estimated using Kriging analysis....34

Figure 13: Map series showing total olive fruit fly counts by month and year in the Pythagoreio area, estimated using Kriging analysis....35

Figure 14: Map series showing average monthly sums of olive fruit flies by year in the four study areas on Samos, estimated using Kriging analysis....36

Figure 15: Average seasonal trends of olive fruit fly counts per sampling event in ten-day periods (2017 - 2024) across the four study areas on Samos....37

List of Tables

Table 1: Pearson correlation coefficients and linear regression statistics for the relationship between average olive fruit fly counts (monthly (M) or 10-day period (10d)) and the number of hours exceeding 32 °C (Avg32h or Any32h). 23

Table 2: Pearson correlation coefficients and linear regression statistics for the relationship between olive fruit fly counts per sampling event and trap elevation. 24

Table 3: Summary statistics of olive fruit fly counts grouped by elevation category. 28

Table 4: Results of post-hoc Games-Howell tests between elevation categories for the entire monitoring period. 29

List of Abbreviations

10d	Based on 10-day interval values
Any32h	Number of hours in which at least one temperature sensor recorded temperatures above 32°C
Avg32h	Number of hours in which the average of all temperature sensors reached temperatures above 32°C
AW	Area-wide
AW-IPM	Area-wide Integrated Pest Management
B. olea	*Bactrocera oleae,* olive fruit fly
CI	Confidence Interval
df	Degrees of Freedom
IPM	Integrated Pest Management
M	Based on monthly values
OFF	Olive fruit fly
SRTM	Shuttle Radar Topography Mission
T	Temperature

Table of Contents

1. INTRODUCTION AND RELEVANCE **1**

1.1. RESEARCH AIM AND QUESTIONS 2

2. LITERATURE REVIEW **3**

2.1. THE CULTURAL AND ECONOMIC SIGNIFICANCE OF OLIVES AND OLIVE OIL 3
2.2. BIOLOGY OF THE OLIVE FLY 4
2.3. OLIVE FRUIT FLY MANAGEMENT 5
2.4. POPULATION DYNAMICS AND THEIR ENVIRONMENTAL AND GEOGRAPHIC DRIVERS 7
2.4.1. Population Dynamics 7
2.4.2. Temperature 7
2.4.3. Altitude and Spatial Patterns 9
2.4.4. Other Influencing Factors 10

3. MATERIALS AND METHODOLOGY **11**

3.1. SAMOS ISLAND 11
3.2. MANAGEMENT PROGRAM AND DATA COLLECTION 12
3.3. ANALYSIS APPROACHES 14
3.4. KRIGING 15
3.5. LIMITATIONS 15

4. RESULTS **17**

4.1. TEMPERATURE 17
4.2. TEMPORAL POPULATION TRENDS 19
4.3. INFLUENCE OF TEMPERATURE 21
4.4. ALTITUDE 24
4.4.1. Influence of Altitude 24
4.4.2. Altitude Categories 25
4.5. SPATIAL DISTRIBUTION 30

5. DISCUSSION **38**

5.1. TEMPORAL POPULATION TRENDS DISCUSSION 38
5.2. INFLUENCE OF TEMPERATURE DISCUSSION 40
5.3. ALTITUDE DISCUSSION 43
5.3.1. Linear Regression of Altitude Discussion 43
5.3.2. Altitude Categories Discussion 43
5.3.3. Altitude results in the context of literature 44

5.3.4. Implications of Altitude Dependence *46*
5.4. SPATIAL DISTRIBUTION DISCUSSION 48
6. CONCLUSION **51**
7. REFERENCES **54**
8. SUPPLEMENTARY MATERIALS **1**

1. Introduction and Relevance

Agriculture plays a vital role globally, providing food security, sustaining livelihoods, and contributing significantly to economic development. However, agricultural production is continually threatened by pests, necessitating intensive management efforts which often involve the use of pesticides. Sustainable pest management is a component of major European agricultural policies, such as the European Common Agricultural Policy (CAP), the European Green Deal and the EU Farm to Fork strategy, to promote economically, socially, and environmentally sustainable agriculture (EU Regulation 2021/2115; European Commission 2020).

In Greece, olive cultivation, particularly for olive oil production, is among the most important agricultural practices, both culturally and economically, producing 260.000t of olive oil annually (IOC 2023). A central threat to this sector is the Olive Fruit Fly (*Bactrocera oleae*), the most significant pest affecting olive trees. Known since ancient times, it remains a significant challenge in olive-producing regions today.

Despite the implementation of integrated pest management (IPM) systems, control of the Olive Fruit Fly still largely depends on pesticide application. This approach is not only labour-intensive and costly, but it also raises environmental concerns. Developing more effective and sustainable pest management strategies requires a deep understanding of the pest's ecology and distribution patterns

The Olive Fruit Fly is a globally significant agricultural pest, causing damage valued at approximately 1 billion dollars annually in the Mediterranean region (Asch et al. 2015). Extensive research has highlighted various environmental and ecological factors influencing its occurrence, including temperature, humidity, altitude, slope aspect, olive cultivar, and landscape composition. These numerous interacting variables underscore the complexity of the issue and suggest that localized monitoring and analysis are essential.

Understanding and predicting the spatial and temporal dynamics of *B. oleae* is key to refining pest control strategies (Nestel, Carvalho, and Nemny-Lavy 2004), especially considering the anticipated changes to agricultural systems and pest behaviour due to climate change. A spatially focused approach to monitoring could support more targeted interventions, reducing unnecessary pesticide use and enhancing the overall efficiency and sustainability of pest management efforts.

1.1. Research Aim and Questions

While previous studies on Olive Fruit Fly (*Bactrocera oleae*, OFF) populations on the island of Samos have been mainly descriptive in nature or based on limited datasets, this study expands both the scope and analytical depth of existing research. Notably, although Kriging has been applied in earlier work (see Kavroudakis et al. (2024); Katsikogiannis et al. (2023)), these studies were limited to just three years of monitoring data. In contrast, this study utilises a more comprehensive dataset spanning eight consecutive years, allowing for a more robust examination of spatial and temporal patterns.

By integrating geostatistical modelling (Kriging) and environmental variables, this research takes a landscape approach to understanding OFF dynamics, both at the scale of the entire island and within selected subregions. The primary aim is to generate a deeper insight into the seasonal and interannual variation in OFF populations and to explore how these patterns relate to factors such as altitude and temperature.

This study therefore followed these main goals:

1) to describe the temporal profiles of olive fruit fly populations on Samos;

2) to determine the degree to which elevation and temperature (hours with T>35°C) factors drive olive-fly population dynamics;

3) to describe the spatial patterns of olive fruit fly populations of four regions of Samos.

Ultimately, this research aims to provide a more localised understanding of the causes of olive fruit fly distribution patterns on Samos. This can serve as a starting point to improve the current monitoring system, asses possible climate change impacts, and inform more targeted pest management strategies, potentially leading to a reduction in pesticide use.

2. Literature Review

The following chapter provides the necessary background from previous research and context for this study. It begins with a general overview of the importance of olive cultivation and consumption to highlight the relevance of olive fruit fly research. Then, biological aspects of the olive fruit fly are discussed, followed by a review of current management and control strategies regarding the species. The chapter concludes with an overview of olive fruit fly population dynamics and its key influencing factors, including temperature, altitude and spatial variation.

2.1. The Cultural and Economic Significance of Olives and Olive Oil

The cultivation of olive trees and the use of its products has a long tradition, especially in the Mediterranean region. Olive oil in particular has been known for millennia to be used in food, medicine, and cosmetics. Even in ancient times, the Egyptians used it as a skin and hair care product (Gorini et al. 2019). The oil is considered very healthy, especially through its phenolic substances, and when ingested, it works as an anti-inflammatory and preventative against a range of diseases (Gorini et al. 2019). Apart from the health benefits, the oil is widely appreciated for its hedonic qualities, including smell and taste, and for being a key ingredient of the Mediterranean diet (Damijanić 2021).

Since the 20th century, olives and in particular olive oil have experienced a drastic increase in popularity, especially in non-traditional regions, such as central and Northern Europe, and North America. In consequence, new technologies and methods have been developed to intensify agriculture. These new methods are often more productive and price-efficient than the traditional farming systems. The Mediterranean region is still one of the largest producers in the world, but olive cultivation has also started in other parts of the world, such as California. Greece is a large producer of olives and olive products, supplying around 8% of the olive oil globally, with around 260.000t annually (IOC 2023).

While this increase in industrial olive agriculture can pose significant competition on the market for traditional farmers, the traditional methods have the potential to use intangible goods for their benefit, if they are open to change and can acquire the necessary new skills (Rodríguez-Cohard, Sánchez-Martínez, and Gallego-Simón 2019). As part of the local identity, olive oil and its surrounding history, traditions, and infrastructure, have also been identified as a high-potential source for sustainable tourism activities (Folgado-Fernández, Campón-Cerro, and Hernández-Mogollón 2019). The cultural importance of olives and olive oil goes so far that UNESCO proclaimed the 26th of November each year as World Olive Tree Day (UNESCO 2019).

It has been estimated that the olive fly causes 1 billion dollars in economic losses each year in the Mediterranean region (Asch et al. 2015). The presence of OFF eggs and larvae and the subsequent damage to the fruit have the potential to destroy olive harvests, for example, when infested fruits cannot be further processed and served as table olives. When processed to olive oil, a higher content of infested olives leads to stronger reductions in the quality and composition of the end product, which in turn leads to a lower value and lower economic revenue for the farmers, processors, and distributors (Malheiro et al. 2015).

2.2. Biology of the Olive Fly

The Olive Fruit Fly (OFF), *Bactrocera oleae,* from the Diptera Tephritidae, is a monophagous pest, feeding almost exclusively on olive, and it is widely distributed across nearly all regions where olive cultivation occurs (Daane and Johnson 2010). The species has been recognized as a significant agricultural pest for centuries, with various management strategies developed to mitigate its impact, most notably the application of insecticides (Daane and Johnson 2010).

The life cycle of *B. oleae* is influenced by environmental conditions such as climate and cultivation practices. Typically, the species undergoes multiple, overlapping generations per year (Kapatos and Fletcher 1984). In California, for instance, studies have documented up to four generations annually (Burrack et al. 2024), while other sources report as many as six to seven generations per year (Stavrianakis et al. 2025).

The life stages of the olive fruit fly are egg, larva, pupa, and adult, with the duration of each stage being temperature-dependent (Yokoyama 2012; Tsitsipis 1977). Female flies lay up to 12 eggs per day, generally one egg per fruit, with a lifetime fecundity of approximately 200–250 eggs per individual fly (Mavragani-Tsipidou 2002). After hatching, larvae consume the olive pulp and subsequently pupate for several weeks either inside the fruit or in the upper soil layers surrounding the tree, depending on the season (Kapatos and Fletcher 1984). An entire generation can be completed in as little as 30 to 35 days (Perović and Hrnčić 2013). A significant proportion of the population overwinters in the pupal stage, either within the soil or in fallen fruits, although flies in every development stage can generally also be observed in the winter (Kapatos and Fletcher 1984).

The rise of temperatures and change of precipitation patterns driven by climate change are expected to change agriculture and ecosystems, significantly challenging current pest control strategies (Calvin et al. 2023).The phenological changes of plants and animals that can be expected as a reaction to climate change may lead to changes in insect overwintering, migration, etc., bearing the risk of further decoupling plant-insect interactions (Gordo and Sanz 2005). The impact climate change will have on olive pests remains insufficiently understood (Caselli and Petacchi 2021). However, some research indicates that the geographic range of both the olive tree and the olive fruit fly is expected to expand to cooler regions (Gutierrez, Ponti, and Cossu 2009). As different insect species react differently to the changing climate, desynchronisation of the cycles of a pest and their natural enemy may occur (Forrest 2016). This can change plant-herbivore interactions through changes in phenology and distribution, potentially leading to ecological mismatches (Hamann et al. 2021). The changes in distribution caused by climate change can also lead to an increase in invasive species, and, as a consequence, increases in agricultural losses can occur, posing a risk of economic losses and food insecurity (Skendžić et al. 2021). Therefore, a comprehensive understanding of the spatiotemporal dynamics and their future changes is crucial for the sustainable management of olive cultivation (Castrignanò et al. 2012).

2.3. Olive Fruit Fly Management

While there are 255 types of organisms, including pests, mites and others, that can be harmful to the olive tree, the olive fruit fly remains the most significant pest of this crop (Caselli and Petacchi 2021; Haniotakis 2005). As the geographic scope of olive trees expanded globally, so too did the distribution of the olive fruit fly. Nowadays, its territory covers parts of Europe, particularly the Mediterranean region, as well as regions in North Africa, the Middle East, Asia, and the west coast of South America (Burrack et al. 2024). The species was first detected in North America in 1998 in California and has since spread throughout the region, including Mexico (Burrack et al. 2024). Australia remains the only major olive-cultivating region in the world without reports of olive fly infestations (Malheiro et al. 2015).

Given the olive fruit fly's highly destructive potential, various pest management strategies have been developed and implemented across affected regions. In many countries, including Greece, the dominant control method involves the application of chemical insecticides, delivered either as bait sprays or cover sprays (Kampouraki et al. 2018). Overusing or misusing insecticides can result in environmental degradation and the development of pesticide resistance, as observed in certain olive-growing regions by Kampouraki et al. (2018). However, the absence of pesticide spraying, such as in organic or abandoned groves, can lead to uncontrolled population growth of *B. oleae*, creating breeding grounds from which flies may spread into managed groves (Kavroudakis et al. 2024).

Alternative pest management strategies include using traps and the Sterile Insect Technique, although regulatory limitations, such as European Union restrictions on genetically modified organisms, limit the adoption of certain modern approaches (Kampouraki et al. 2018). Biological control agents, such as parasitoids, also reduce the pest population and are therefore increasingly considered as a part of pest management strategies (Daane and Johnson 2010).

Integrated Pest Management (IPM) has emerged as a more holistic framework that recognizes the harmful potential of pesticides and encompasses a combination of different control methods (Pretty and Bharucha 2015). Monitoring is a fundamental component of IPM, traditionally conducted using manual trap-based surveys. However, recent advancements in digital agriculture have led to the development of automated monitoring systems that enhance the efficiency and precision of pest detection (Lello et al. 2023). Additionally, certain farming practices, such as early harvesting, can be applied to support pest management (Topuz and Durmusoglu 2008). Area-wide (AW) pest management is an approach based on the principle that coordinated interventions across larger geographic regions are more effective than isolated efforts (Koul 2008). When integrated with IPM principles, this approach is called Area-Wide Integrated Pest Management (AW-IPM) (Vreysen et al. 2007).

The inclusion of reliable prediction models and web-based decision support systems can significantly contribute to more sustainable pest management practices and less pesticide use (Damos 2015). These systems can take the form of a Decision Support System as tested by Sciarretta et al. (2019), which allowed for a substantial reduction in pesticide application without increasing the numbers of olive fruit flies compared to conventional management. Another example of web-based applications for farmers is the FarmGeoBalance system tested on Lemnos Island in Greece, which assesses the impact of farming practices of individual farmers on multi-level biodiversity (Avanidou et al. 2023).

In Greece, including the island of Samos where this study is situated, governmental pest control programs operate at the administrative level to suppress *B. oleae* populations. These initiatives typically involve both systematic monitoring and the application of bait sprays. Several factors, including climatic conditions, the growth stage of the olive crop, and the density of the pest population, determine the frequency and quantity of treatments (Kavroudakis et al. 2024).

2.4. Population Dynamics and their Environmental and Geographic Drivers

2.4.1. Population Dynamics

Climatic conditions and their variability substantially influence the population dynamics of the olive fruit fly, offering potential explanations for spatial and temporal fluctuations observed across different regions (Ordano et al. 2015). Considering temporal trends, Topuz and Durmusoglu (2008) observed that population levels of the olive fruit fly were relatively low during July and August, while they reached their peak at the end of October. The olive fruit fly population development is also negatively related to the population density, with a synchronisation of different generations emphasising seasonal variation in population changes (Ordano et al. 2015). Although traps are widely used for monitoring and research, their results often show a high variability, even between neighbouring traps (Kounatidis et al. 2008; Castrignanò et al. 2012).

During early summer, a phenomenon known as summer reproductive diapause has been observed, characterized by a marked decline or absence of mature eggs in captured females. This condition is associated with high temperatures, arid conditions, and the unavailability of suitable olive fruits for oviposition (Burrack et al. 2024; Economopoulos et al. 1982). Alternatively, this phenomenon has been called reproductive dormancy (Ordano et al. 2015). Seasonal monitoring in regions such as California has revealed a bimodal population distribution of the olive fruit fly partially caused by this phenomenon, with population peaks occurring in spring and fall (Burrack et al. 2024).

2.4.2. Temperature

Laboratory studies have demonstrated that prolonged exposure to high temperatures (above 35 °C) can slow reproduction and decrease survival rates in B. oleae populations (Wang et al. 2009). Temperature is also a crucial influence on the development speed and survival of individual life stages. For example, temperatures in the range of 10–30 °C are generally favourable for egg hatching, with 27.5 °C identified as the optimal temperature for both rapid hatching and high hatching success, allowing for egg hatching within a single day (Tsitsipis 1977). In the pupal stage, survival rates have been shown to be significantly higher at temperatures between 14–21 °C compared to 26 °C, while adult longevity and survival are notably greater at 26 °C than at 36 °C, with humidity as a second influencing factor (Yokoyama 2012). The same study found that the life span of adult flies is similarly dependent on temperature and humidity, ranging from approximately two weeks to several months. Pappas et al. (2011) showed that heat stress, i.e., exposure to temperatures >34°C for two hours, reduced especially female longevity and the production of eggs.

At the landscape level, temperature fluctuations are one of the key variables in analysing population levels and dynamics of B. oleae. On the island of Samos, where the presented study is also located, a strong correlation was identified between trap capture counts and the number of hours with temperatures exceeding 32 °C, as well as relative humidity, particularly during the late season months of September and October (Kavroudakis et al. 2024). Similarly, Katsikogiannis et al. (2023) found that the number of hours above 32 °C provided a suitable metric to describe population trends as it shows more seasonal and annual variety than other climatic variables, such as the average temperature. Other temperature variables, such as night land surface temperatures, have also been found to be significant (Ordano et al. 2015). Furthermore, Ordano et al. (2015) attributed the absence of olive fruit fly activity in some Israeli groves during the summer to extreme temperatures, noting that activity was instead observed during the winter months. Another temperature variable that is commonly used in models to predict olive fruit fly attacks was Cumulative Degree Days (Marchi et al. 2016; Rondoni et al. 2024). It has also been shown that relating temperatures to olive fruit fly numbers with a temporal delay (e.g. of 7 days) can be successful and significant (Rondoni et al. 2024).

Minimum winter temperatures have been shown to correlate strongly with early-season infestation levels (Marchi et al. 2016). Rondoni et al. (2024) further observed that mild winters are associated with higher initial infestations, whereas elevated mean spring temperatures (March-May) are linked to reduced infestation numbers in July and August. Their findings also indicate that temperature patterns can shift the timing of olive fruit fly attacks, with warmer winter and spring conditions leading to earlier infestations compared to cooler years.

2.4.3. Altitude and Spatial Patterns

Altitude has frequently been used as a proxy for temperature in B. oleae population studies, either using exact altitude values (Kounatidis et al. 2008) or elevation categories (Katsikogiannis et al. 2023; Kavroudakis et al. 2024). It is especially useful when lacking fine-scale climate data (Castrignanò et al. 2012). Generally, higher-altitude regions exhibit earlier seasonal increases in olive fly populations, typically in the summer months (Kavroudakis et al. 2024). However, this pattern reverses later in the year, with lower-altitude areas becoming population hotspots during the autumn (Kounatidis et al. 2008). A similar seasonal shift in population density from higher to lower altitudes was also documented by Castrignanò et al. (2012), who found that the elevation influence during summer months, especially July, was larger than during October. Although linear analyses have not found a statistically significant relationship between monthly olive fly counts and altitude, a general trend of decreasing average trap captures with increasing elevation has been observed by Kavroudakis et al. (2024). However, the strength of this trend depends on the specific altitude range in consideration. The number of olive fruit flies and the timing of their attacks appear to be influenced by altitude, as Rondoni et al. (2024) observed a general delay in infestation events at higher elevations, along with lower fly numbers during the summer months of July and August.

Population movements of olive fruit flies and the drivers behind them are essential in understanding spatial dynamics. Several studies found that populations respond to climatic and environmental conditions by migrating to more favourable regions. For example, population patterns across altitudes and the north-south divide on Samos have been linked to the migration of olive fruit flies towards better climate conditions (Katsikogiannis et al. (2023; Kavroudakis et al. (2024)). In addition to temperature, fruit availability has been identified as a driver of movement, with Ragaglini, Tomassone, and Petacchi (2005) suggesting that flies relocate to regions offering more available and suitable olive fruits. Furthermore, Katsikogiannis et al. (2023) suggest that a movement between non-sprayed and sprayed areas is likely. Adult flies at the beginning of the season may migrate to abandoned olive groves that still contain fruit remains from the previous year, potentially skewing the population counts recorded in actively managed groves (Rondoni et al. 2024). The identification of hotspots can help to target areas from where the fruit flies may spread to surrounding regions (Kavroudakis et al. 2024).

2.4.4. Other Influencing Factors

Throughout different studies, various other variables have been identified as significant in shaping the distribution and population dynamics of B. olea. Due to the complexity of influences on olive fruit fly populations, several studies used multivariate models to analyse population trends (Rondoni et al. 2024; Castrignanò et al. 2012).

Adopting a landscape-scale perspective allows for a nuanced understanding of the complex interplay of environmental factors and plant-pest interactions affecting *B. oleae* populations (Tscharntke and Brandl 2024). Furthermore, geographic and climatic factors can influence the effect that temperature has on olive fruit fly populations, underscoring the need to analyse individual locations separately (Ordano et al. 2015). Landscape heterogeneity contributes to the formation of localised microclimates, which, in turn, influence pest dynamics. For example, humidity significantly impacts olive fruit fly populations. While a certain humidity level is necessary for adult survival, excessive rainfall, humidity fluctuations and levels below 33% can reduce reproductive success, egg viability, and survival rates (Stavrianakis et al. 2025; Broufas, Pappas, and Koveos 2009). Additional environmental variables identified as influential include solar radiation, wind speed (Rodríguez-Díaz et al. 2024), proximity to the sea and aspect (Petacchi et al. 2015). However, the impact of these factors can vary locally, as Kavroudakis et al. (2024) found no significant relationship between aspect and olive fruit fly density based on Kriging analysis.

The surrounding ecological context also influences olive fruit fly populations. For example, a higher biodiversity in the understory correlates with lower olive fruit fly populations (Stavrianakis et al. 2024). Similarly, structurally complex landscapes tend to support greater biodiversity and are associated with lower B. oleae abundance (Paredes et al. 2023). However, anthropogenic factors like infrastructure can impact this ecological complexity, for example, through habitat fragmentation (Tscharntke and Brandl 2024). Additionally, the olive cultivar significantly affects the tree's susceptibility to olive fruit fly infestations (Malheiro et al. 2015).

3. Materials and Methodology

3.1. Samos Island

Samos, a Greek island located in the Aegean Sea, spans an area of approximately 477.4 km^2 and is dominated by two mountain ranges that shape its topography. The island experiences a typical Mediterranean climate with hot and dry summers with many hours of sunshine, and mild and wet winters. Average temperatures throughout the year range from around 10 °C in February to 28.5 °C in July. February is generally the coldest month, with daily temperatures fluctuating between 6.5 °C and 13.2 °C, while July is the hottest, seeing averages from 22.2 °C to 32.5 °C. Annual precipitation varies between 700 and 900 mm, depending on the exact location, with the northern parts receiving slightly more rain. Nearly 60% of all rainfall occurs in winter, and July and August are typically very dry (Kavroudakis et al. 2024).

Wind patterns are predominantly towards the North, accounting for roughly 60% of the total annual wind direction. Land cover on the island is diverse, with shrublands making up the majority (54%), followed by agricultural areas (25%), within which olive groves dominate (53% of agricultural land), and vineyards contribute about 10% of agricultural land. The dominant olive cultivar is the local variety Throumpolia, with other notable varieties including Koroneiki, Manaki, and Kalamon (Katsikogiannis et al. 2023). Forests, mainly pine and oak, cover the remaining 21%. Some agricultural plots are no longer actively maintained, although exact figures on abandonment are not available. The fragmented terrain, together with a mixed topography of two mountain ranges and steep slopes, leads to the development of microclimates (Kavroudakis et al. 2024).

To further localise the results of this research, individual regions on Samos were selected for detailed analysis (see Figure 1). The two central mountain ranges of the island create a natural division between North and South. Additionally, land-use patterns lead to further division and possible development of different microecological zones. One region from each zone was selected, each having distinct geomorphological and climatic features. The selected regions are the following:

- **Marathokampos** (Southwest): Stretching along the southern coast, this long, narrow region can be characterized as a lowland area, mostly facing towards the South.

- **Karlovasi** (Northwest): Karlovasi lies between mountain ranges and is geographically separated from other regions by them. Its olive groves are situated at low to medium elevations.
- **Agios Konstantinos/ Kokkari** (Northeast): This region is typically considered cooler than others, due to its North-facing direction close to high altitudes.
- **Pythagoreio** (Southeast): Defined by low elevation and a generally south-facing orientation, Pythagoreio is considered one of the warmest regions on the island.

3.2. Management Program and Data Collection

The data utilized in this study were collected over eight years through a network of monitoring traps distributed across the island of Samos. Established in 2017, the system includes 399 McPhail traps, corresponding to approximately one trap per 2,000 olive trees. All trees that have traps attached to them are over one hundred years old and belong to the variety Throumpolia, which is the most common one on Samos (Kavroudakis et al. 2024). Trap monitoring occurs at five-day intervals, during which each trap is inspected, cleaned, and refilled with either a 2% ammonium sulfate solution or a protein-based food lure. Data collection is conducted annually from June to October, starting when the first olive flies are observed in a location, typically around the pit-hardening phase of olive development. Data from the traps is recorded manually by trained personnel, so-called "trap-setters", and reported to a central program coordinator, who stores the information in a central database.

In addition to the trap network, automated data loggers are installed across the island to record temperature and humidity levels (Katsikogiannis et al. 2023; Kavroudakis et al. 2024). This integrated system of traps and environmental sensors has served as the foundation for several previous studies on B. oleae population distribution and dynamics (see Katsikogiannis et al. 2023; Kavroudakis et al. 2024). The number of active climate data loggers has varied over the years, with a decreasing tendency. While 24 climate loggers were active in 2018, only seven recorded temperatures in 2024. Figure 2 illustrates the spatial distribution of olive groves, monitoring traps, and climate data loggers used in the experimental setup on Samos. The 10 climate data loggers depicted here are the ones that were active during most years.

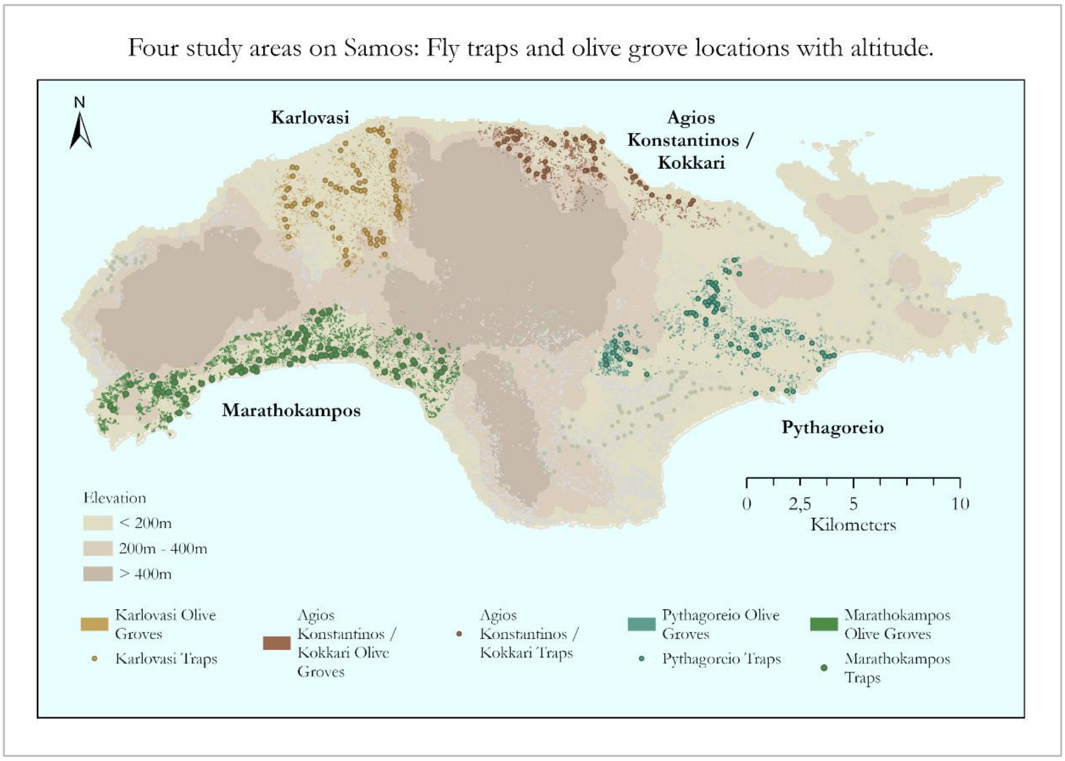

Figure 1: Map showing the four study areas on Samos with categorised elevation, trap placements, and olive grove locations: Marathokampos, Karlovasi, Agios Konstantinos/Kokkari and Pythagoreio.

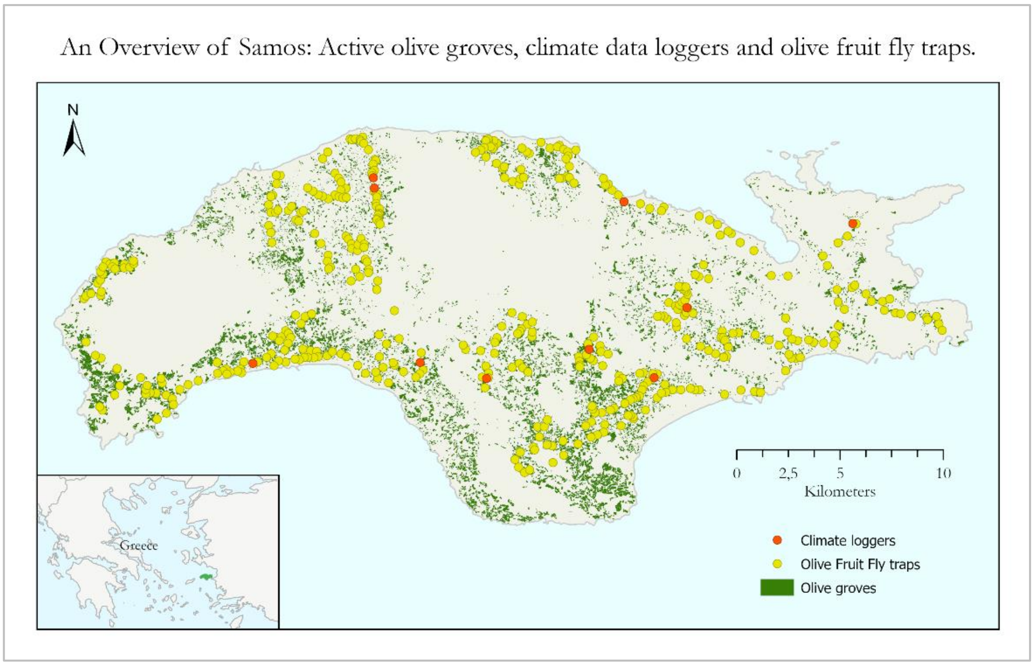

Figure 2: Map showing the locations of climate loggers, olive fruit fly traps, and olive groves on Samos.

3.3. Analysis Approaches

Although fruit fly population data were collected every five days, monthly and 10-day period averages were calculated for the analysis. This approach was chosen to homogenise the data across different years and take into account the variation of the sampling dates (see Kavroudakis et al. 2024). For the 10-day periods, this resulted in three such periods per month, except for June, which only included one, adding up to a total of 13 ten-day periods. This study focuses exclusively on the counts of female olive fruit flies, as these give a stronger indication of reproductive potential and population dynamics.

A few selected temperature metrics were calculated from the climate data loggers, including the monthly minimum, maximum, and average temperatures. The minimum and maximum temperatures were derived from hourly averages across all data loggers. Additionally, the number of hours exceeding 32°C was calculated, as they can be used to assess the impact of heat stress (Kavroudakis et al. (2024); Pappas et al. (2011)). This metric was calculated in two ways; first, as the number of hours during which at least one logger recorded a temperature above 32°C (*Any32h),* and second, as the number of hours in which the average temperature across all loggers surpassed 32°C (*Avg32h)*.

Elevation, here considered as the altitude above mean sea level, is one of the key variables analysed in this study. The terms elevation and altitude will be used synonymously in this study. Elevation data was taken from the Shuttle Radar Topography Mission (SRTM) dataset by NASA, with a spatial resolution of 28m x 28m per pixel. To test for general differences between elevation over distinct bands, the data were grouped into three elevation categories (0-200m, 200-400m, >400m), as shown in Figure 1, following the approach by Katsikogiannis et al. (2023). When testing for differences between these groups, Levene's test was applied first to assess the homogeneity of variances, which is an underlying assumption of ANOVA. If this condition was fulfilled, one-way ANOVA was used to test for overall differences between elevation categories. Where the ANOVA results indicated significance, Tukey's HSD test was conducted to identify those categories with statistically significant differences. If the condition of homogeneity of variances was not fulfilled, Welch's ANOVA test was applied, followed by a post-hoc Games-Howell test to identify the significantly different categories.

To test the relation between fruit fly numbers and continuous variables, such as elevation and temperature, Pearson correlation was employed to assess linear associations, using the correlation coefficient. Linear regression models were then used to evaluate the significance and strength of these relationships, using slope, p-values, and R^2 values as indicators of model fit.

A significance threshold of $p = 0.05$ was used in all statistical tests.

3.4. Kriging

Kriging is a method of geospatial interpolation that allows the estimation of values in places where no data is available. It also allows for the estimation of the uncertainty in the predictions. In the context of olive fruit flies, this method has been used in Samos ((Kavroudakis et al. 2024; Katsikogiannis et al. 2023)) and other regions (Petacchi et al. 2015; Castrignanò et al. 2012).

The analysis was conducted in RStudio using the gstat package in R. Ordinary Kriging was applied using monthly trap count data from June to October, for each year between 2017 and 2024. Before interpolation, data were filtered by year and month, and a spherical semivariogram model was fitted to the data. Kriging was performed on a regular grid, and all resulting outputs were assigned the WGS84 coordinate reference system and cropped to the study area extent, which consisted of one or all of the four selected regions on Samos. Final raster layers were saved as GeoTIFF files at a spatial resolution of 300 meters.

The resulting raster images were afterwards processed in ArcGIS Pro. Negative values were set to zero, as they do not carry any real ecological meaning in this context. The raster images were then clipped using a mask of the actively managed olive groves within the four selected study areas on Samos. The WGS84 coordinate system and raster resolution of 300 meters were continuously used throughout the analysis.

3.5. Limitations

Certain limitations in methodology or data should be considered when interpreting and discussing the results, and will be further discussed in the following.

This research was limited to temperature, elevation, and spatial distribution as the only analysed variables. Other variables, such as pesticide spraying, humidity, and aspect, have not been included, although they can potentially impact population numbers (see Section 2.4.4). Furthermore, all variables in this study were analysed in isolation, and no joint approach was taken.

There are also underlying biological assumptions that limit the scope of this study. For instance, only the number of female olive fruit flies was analysed, limiting comparability to other studies. Furthermore, all traps were placed on trees of the Throumpolia variety, the dominant cultivar on Samos. This indicates that the results, particularly the spatial ones, may not be reliable in areas with other cultivars. Additionally, trap counts do not necessarily translate proportionally into infestations in the olive fruit, although they exhibit similar overall trends (Kavroudakis et al. 2024).

The temperature data used in this study were derived from climate sensors with notable limitations. As mentioned in the Methodology (Section 3.2), the number of sensors varies over the years, changing the spatial coverage and affecting consistency. Furthermore, some sensors recorded extreme temperature readings of more than 60°C, possibly due to exposure to direct sunlight, which is unlikely to correspond to actual temperatures and potentially skews the overall temperature metrics.

The Kriging model applied in this study to predict fruit fly numbers in unsampled locations is a preliminary model. Cross-validation, comparison to other models, and analysis of uncertainties were not possible due to the time constraints of this research. However, these steps would likely increase the accuracy of the predictions. Furthermore, when the Kriging raster images were clipped to the olive grove shapefiles, the process resulted in a minor spatial misalignment, which depicts the raster images with a slight westward drift in the final maps, not affecting the accuracy of the underlying spatial patterns.

In conclusion, data-related and methodology limitations should be considered when analysing the results of this research. Nevertheless, the study can provide valid insights into the spatiotemporal dynamics of the olive fruit fly and the role of temperature and altitude in these dynamics.

4. Results

4.1. Temperature

As previously identified in the literature, temperature is one of the key parameters influencing the appearance and development of olive fly populations. Figure 3 presents a summary of key temperature indicators for each month from June to October over the period 2017 to 2024, based on the hourly measurements from the climate data loggers (see Figure 2).

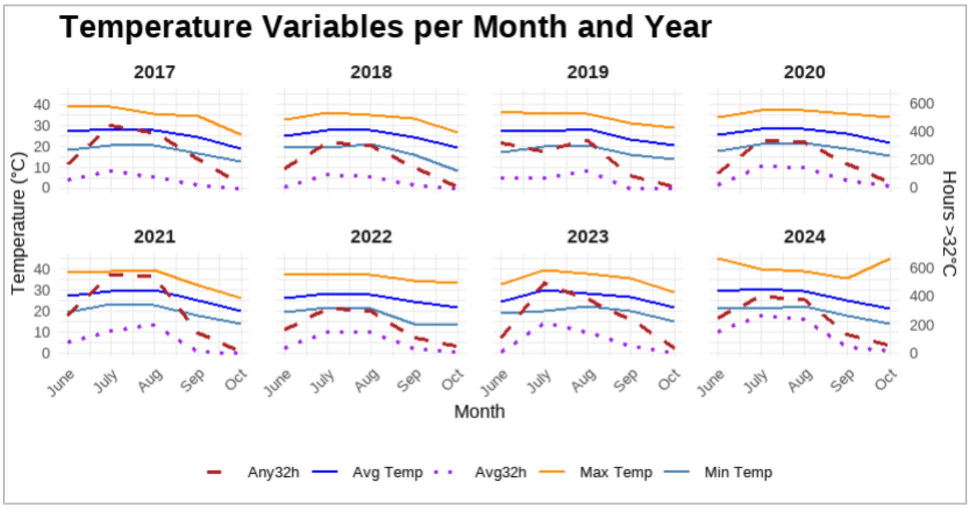

Figure 3: Minimum, maximum and average monthly temperatures for each year, along with the number of hours per month with temperatures above 32°C (Any32h and Avg32h).

Maximum temperatures ranged between 25°C and 40°C, typically peaking around August, with a slight increase before and a decline following this month. An exception was observed in 2024, when unusually high maximum temperatures of up to 45°C were recorded in both June and October, while mid-summer months showed comparatively lower values. Minimum temperatures across the dataset ranged from approximately 13°C to 23°C, with only one recorded instance of values falling below 10°C in October 2018. The seasonal development of minimum and maximum temperatures followed a similar, slightly curved pattern, with relatively flat peaks around August. Average temperatures fell between 20°C and 30°C, following the same trend. Across the eight-year monitoring period, these three metrics (minimum, maximum, and average temperatures) remained relatively stable, with only minor fluctuations. Due to this low seasonal variability, these temperature indicators are considered less effective for explaining or predicting trends in olive fruit fly populations.

In contrast, the number of hours exceeding 32°C displayed greater seasonal and interannual variability, with peaks typically occurring in July or August. The timing and duration of these peaks, however, differed across the years. Two variables of this indicator were determined (*Any32h* and *Avg32h),* and while both metrics followed similar temporal patterns, the average-based measure reached consistently lower values, since high temperatures are less frequent when averaged across the entire island compared to localized areas.

4.2. Temporal Population Trends

To begin analysing olive fruit fly population trends, it is essential to first examine how population levels fluctuate within a season and across different years. Figure 4 shows a heatmap of the average number of olive fruit flies captured per trap per month. The heatmap illustrates that, in general, average fly counts are relatively low in June and tend to increase in July. In August, population trends diverge, with some years showing continued increases and others decreases. September frequently marks a peak in population levels, though trends in October vary, with either further increases or decreases observed. Overall, the high degree of interannual and seasonal variability visible in the data makes it difficult to identify consistent patterns in population dynamics based on this overview.

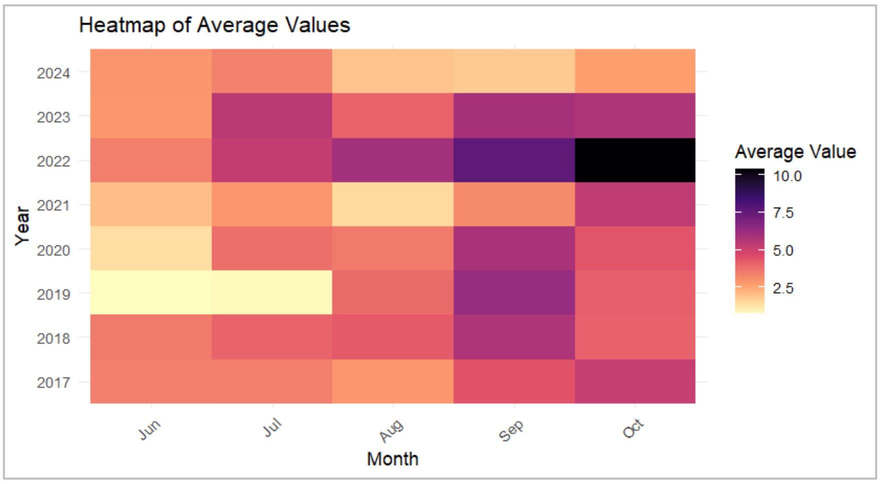

Figure 4: Heatmap of average trap counts per sampling event by month and year.

Compared to the monthly overview provided in Figure 4, Figure 5 offers a higher temporal resolution of population dynamics by depicting the total number of olive fruit flies captured during each 10-day interval. Some notable outliers, such as the exceptionally high counts at the end of the 2022 season and the unusually low early-season counts in 2019, are also evident in this representation. The graph further confirms that population developments vary substantially between years, making it difficult to identify consistent patterns at first glance.

To address this, an average trend line across all years was added. This line reveals a more coherent seasonal pattern: Olive fruit fly numbers generally rise throughout June, reaching an initial peak in early July. This is followed by a moderate decline until early August, after which numbers increase again, reaching a second, higher peak at the end of September. In October, a slight decline is observed, followed by a small increase during the final 10-day period. When comparing this average trend to the individual yearly developments, it becomes clear that no year perfectly follows the overall pattern. However, this kind of bimodal distribution (characterized by two distinct peaks) is observed in several years, notably 2017, 2018, 2020, 2021, and 2023, although the magnitude and timing of these peaks vary across years

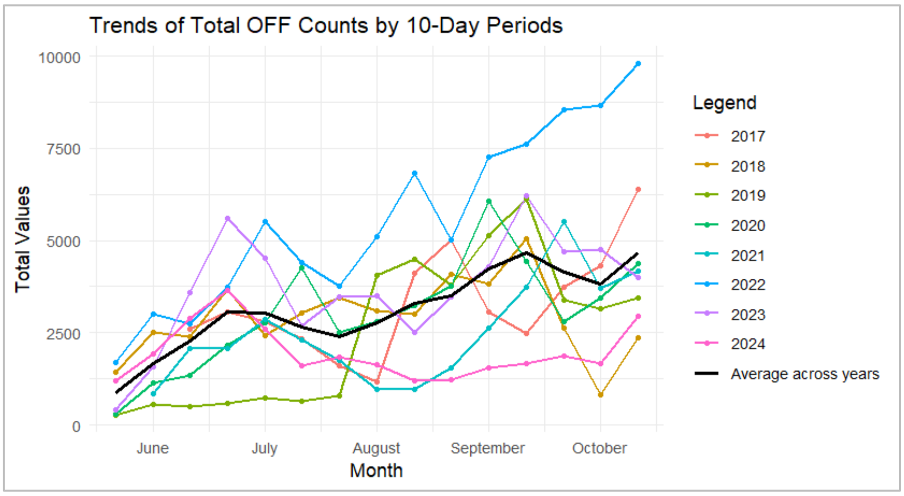

Figure 5: Total olive fruit fly (OFF) counts in 10-day intervals from June to October, 2017–2024.

Overall, the temporal dynamics of olive fruit fly populations across the summer seasons exhibit a bimodal distribution, peaking in July and September. However, the high degree of interannual variability often obscures the consistency of these patterns.

4.3. Influence of Temperature

To determine the influence of temperature on olive fruit fly populations, four combinations of temperature and population variables were tested for statistical significance. Two climatic variables were used:

a) The number of hours in which the average temperature across stations exceeded 32°C (*Avg32h*), and

b) The number of hours in which at least one station recorded temperatures above 32°C (*Any32h*).

Each of these was analysed using averages over both monthly averages (*M*) and 10-day intervals (*10d*), resulting in four distinct model combinations. The results of the Pearson correlation tests and the linear regressions are summarised in Figure 6 and

Table 1.

The overview shows a statistically significant relation between the number of hours above 32°C and the average olive fruit fly counts for three of the four model combinations. The only exception is the *Avg32h* model using monthly intervals, which did not reach significance. In general, as the number of hours above 32°C increases, OFF counts decrease. However, it can also be observed that the spread of average fruit fly counts is wide, with the strongest model accounting for less than 12% of the observed variation ($R^2 < 0.12$).

The comparison between the two temperature metrics highlights a consistent advantage of *Any32h* over *Avg32h*. The model using *Any32h*, which is more sensitive to local temperature extremes, shows stronger correlations, lower p-values, and higher R^2 values. Notably, *Any32h* records up to twice as many hours above 32°C compared to *Avg32h*. Additionally, the models using *Avg32h*, especially those based on 10-day intervals, show a concentration of data points at zero hours above 32°C.

Using 10-day intervals instead of months increases the number of data points to 117 instead of 40. This generally improved model performance, particularly through reduced p-values. However, not all metrics of the linear model improve when transitioning from monthly to 10-day period data. For example, in the *Any32h* model, the correlation was slightly stronger, and the R^2 value was higher with monthly data instead of 10-day period data. Considering model fit and significance, the *Any32h* 10-day model is the most suitable model.

Figure 6 presents the data points by year, revealing that the highest fruit fly counts were observed in 2022, while the most extreme temperatures, i.e., the highest number of hours above 32°C, were recorded in 2021. Interestingly, 2021 data points appear more frequently in the high-temperature range under the *Any32h* metric than *Avg32h*, suggesting that while extreme temperatures were common, they were often localised rather than widespread. It can also be seen that for higher numbers of hours above 32°C, there are fewer outliers with high values.

Overall, statistical analysis indicates a significant negative relationship between high temperatures and olive fruit fly counts, with the most robust results emerging from the 10-day model considering any localised temperature extremes (*Any32h*), though overall explanatory power remains limited.

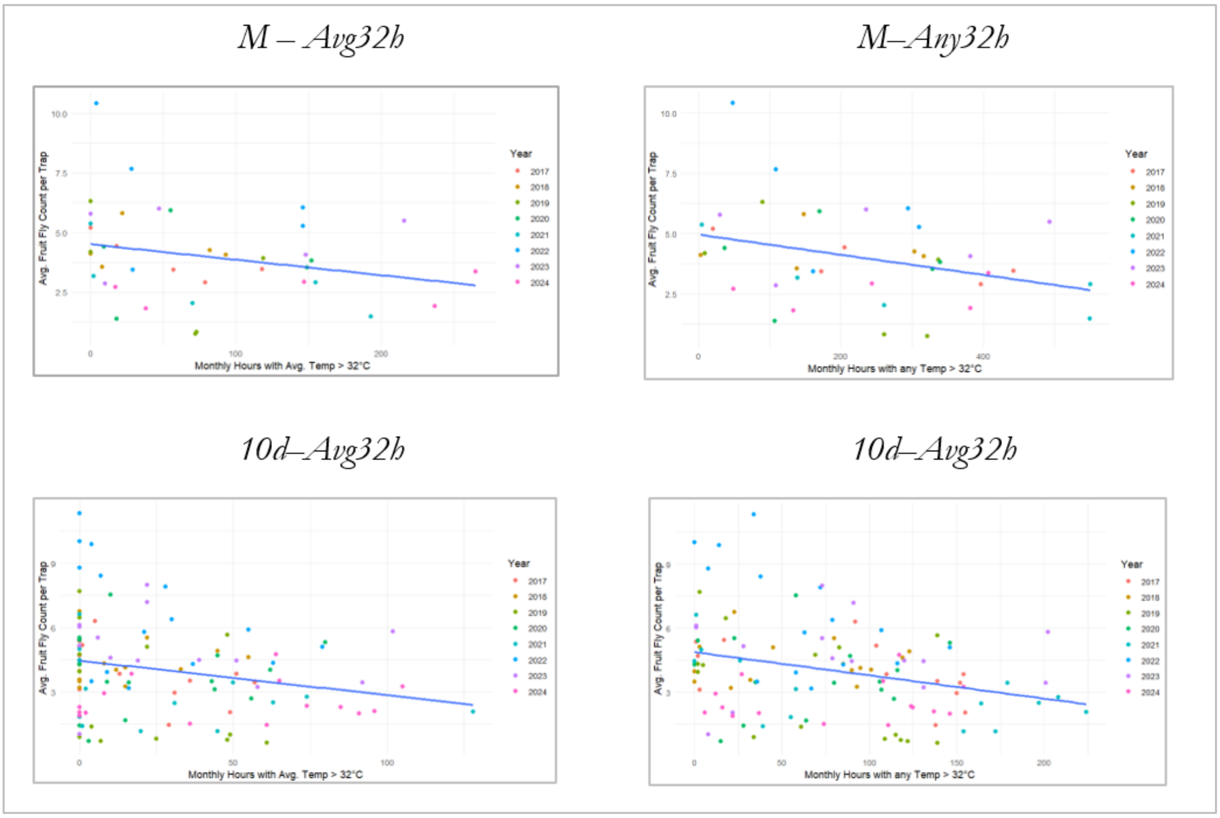

Figure 6: Scatterplots with linear regression lines for the four population–temperature variable combinations, showing the relationship between average olive fruit fly counts and the number of hours exceeding 32°C (Any32h and Avg32h).

Table 1: Pearson correlation coefficients and linear regression statistics for the relationship between average olive fruit fly counts (monthly (M) or 10-day period (10d)) and the number of hours exceeding 32 °C (Avg32h or Any32h).

Test	*M-Avg32h*	*M-Any32h*	*10d-Avg32h*	*10d-Any32h*
Correlation coefficient (Pearson)	-0.25	-0.34	-0.23	-0.30
Slope (linear regression)	-0.006	- 0.004	- 0.016	-0.010
R^2 (linear regression)	0.064	0.116	0.051	0.090
p (linear regression)	0,114	0.032	0.013	0.001
Significance ($p<0.05$)	No	Yes	Yes	Yes

4.4. Altitude

4.4.1. Influence of Altitude

To explore the relationship between trap elevation and the number of flies recorded per individual sampling event, a Pearson correlation analysis was performed. This was followed by a linear regression to further understand the strength and direction of the relation. Key statistical parameters from both analyses are summarised in Table 2.

Table 2: Pearson correlation coefficients and linear regression statistics for the relationship between olive fruit fly counts per sampling event and trap elevation.

Correlation coefficient (Pearson)	**p-value (linear regression)**	**Estimated slope**	**R^2**
0.035	$< 2 \times 10^{-16}$	0.002	0.0012

Table 2 indicates that while the relationship between trap elevation and olive fruit fly counts is statistically significant ($p < 0.05$), its practical relevance is negligible. The estimated slope suggests an increase of only 0.002 flies per sampling for each additional meter in elevation. Even across a 400-meter elevation difference, this equates to less than one additional fly. This effect is minimal compared to typical trap counts, which can exceed 150 flies.

This pattern is also observed when the analysis is repeated using data aggregated by month or 10-day intervals (see Supplementary Materials, Section 8). Although the p-values remain highly significant, the correlation coefficients and R^2 values consistently indicate a very low strength of this relation. This issue is further illustrated in Figure 7, which displays a scatterplot and regression line for July as an example, as other months show a very similar image. The wide variability in fly counts at similar elevations highlights the lack of a clear trend, and the regression line cannot capture the underlying dispersion in the data.

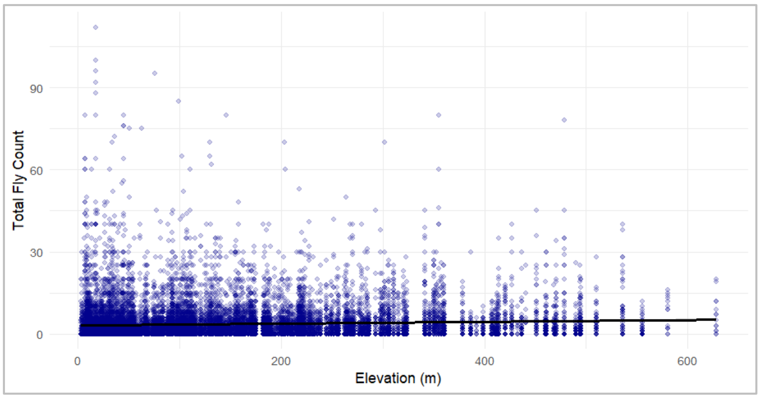

Figure 7: Scatterplot with linear regression line showing olive fruit fly counts per sampling event in July in relation to trap elevation.

4.4.2. Altitude Categories

Although elevation appears to be a significant factor, the correlation between individual trap elevation and olive fruit fly counts showed high variability and limited explanatory power. To further explore elevation-dependent patterns, the traps were divided into three elevation categories: 0m to 200m, 200m to 400m, and more than 400m. It should be noted that the distribution of traps across categories is uneven, with 293 (73,5%) being in the first one, 86 (21,5%) in the second one, and only 20 (5%) in the highest elevation category. Figure 8 shows the average fruit fly counts per sampling, across all years and by 10-day period and elevation.

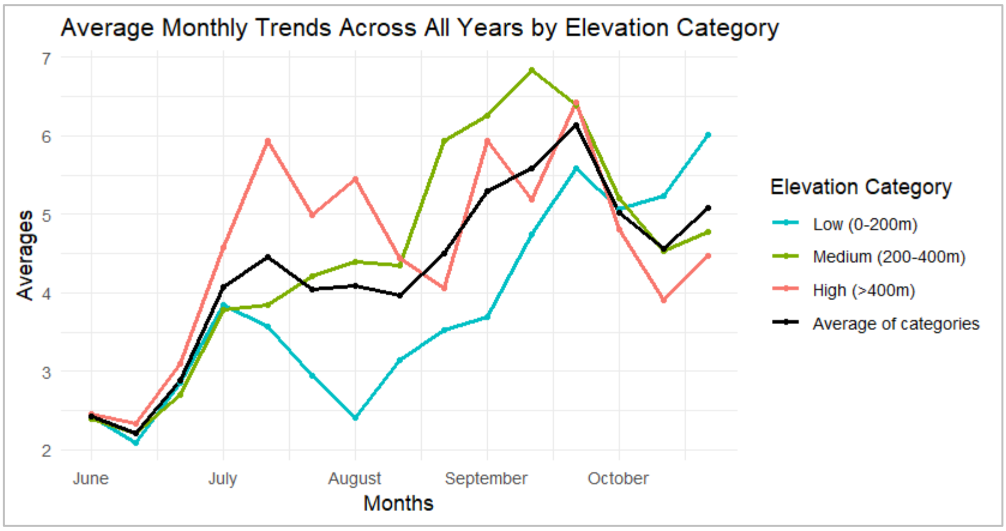

Figure 8: Average olive fruit fly counts for 10-day periods across all years, by elevation category: Low (0-200m), Medium (200-400m) and High (>400m).

The averages across all years show that there are typically two peaks each year, one around mid-July and the other in late September. This can also be observed for high and low elevations. The averages in medium elevations do not decrease after July, but instead follow a further but more shallow increase until the end of August, when the slope of the rise increases again. Another increase of numbers within the last 10-day period can be observed in all categories. The timing of the bimodal peaks varies slightly, with lower elevations reaching their first maximum one 10-day period before higher elevations have their maximum. The timing of the second peak later in the season is similar for all elevation categories.

The temporal dynamics of olive fruit fly populations vary noticeably across elevation categories, with the dominant elevation shifting over the course of the season. At the beginning of the season and through to August, high elevations exhibit the highest average population numbers per trap. This trend then shifts, with medium elevations showing the highest numbers between August and September, followed by a decline. By October, lower elevations surpass the others, showing the highest fly counts at the end of the season. At the point of the first seasonal peak, both low and medium elevations display lower average fruit fly numbers compared to high elevations. Additionally, the subsequent drop in fly numbers after the first peak is steeper and more pronounced at low elevations. Throughout most of the season, low elevations have the lowest observed fly count averages, with the exception of the final month. The shape and magnitude of the trendlines also differ significantly among elevation categories. At low elevations, fly numbers increase sharply over the season, with a second peak much higher than the first and even further growth toward the end. In contrast, high elevations show two peaks of similar magnitude, while medium elevations display a larger increase before their peak, followed by a significant drop in October.

While the average trends of all years presented in Figure 8 show a coherent picture, an overview of the development of average trends of individual years, shown in Figure 9, showcases a challenge to these explanations.

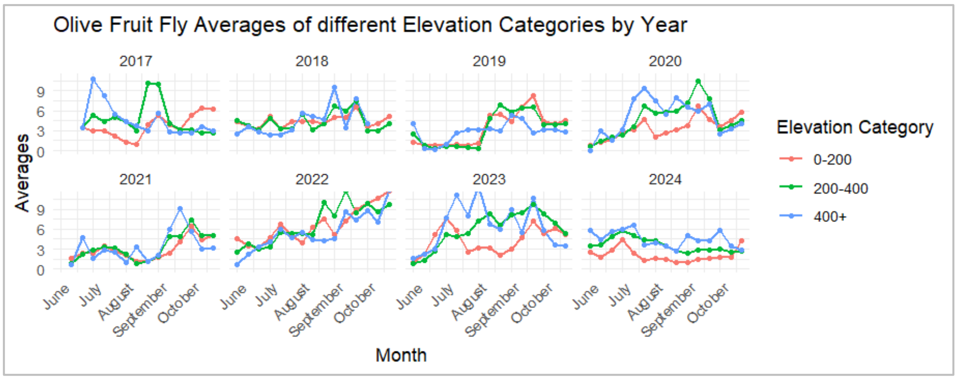

Figure 9: Average olive fruit fly counts per 10-day period, grouped by elevation category (0–200 m, 200–400 m, >400 m) and year.

The average fly counts strongly fluctuate within elevation categories and between years. The graphs also show that the average pattern previously described is not visible every year, and that population peaks can appear in different months. While in some years, like 2020 and 2023, the differences between the elevation categories appear strongly, in other years, like 2019 and 2021, there appears to be only a little difference between the categories. Overall, the use of elevation categories to visually analyse population trends is useful to detect overall trends and explain them, but it also becomes clear that interannual variations are so large that this use of elevation categories alone is insufficient to make reliable predictions.

To gain a statistical overview of the categories, Table 3 presents the total number of data points, mean values, ranges, and standard deviations for the three elevation groups. It is important to note that the number of data points reflects all measurements collected over the eight-year monitoring period. The lower elevation category contains substantially more data points than other categories, reflecting the higher number of traps deployed in these areas, and the medium elevation category contains more points than the high elevation category. Notably, the mean olive fruit fly count is considerably lower in the low-elevation group (3.91) compared to the medium and high elevation categories, which show similar averages (around 4.70), suggesting a potential elevation-related trend in population densities.

Table 3: Summary statistics of olive fruit fly counts grouped by elevation category.

Elevation Category (in m)	Number of data points	Mean	Maximum	Standard Deviation
0-200	66383	3.91	240	7.49
200-400	19499	4.70	196	7.54
400+	4549	4.70	193	7.23

To assess whether these differences are statistically significant, Levene's test was used to test for homogeneity of variances. The results (Supplementary Materials, Section 8) indicated that homogeneity of variances is not present throughout most of the season, except for June and early July. The tests on a 10-day basis also showed there is a period at the end of September when the condition is fulfilled. When compared to the trends in Figure 8, it seems that the condition of a homogeneity of variances is only fulfilled when all three elevation categories exhibit similar OFF averages.

Depending on whether the homogeneity of variances condition was fulfilled, ANOVA or Welsh's ANOVA tests were conducted for each month, each ten-day period, and all measurements overall (see Section 8). Overall, the results show statistically significant differences between the elevation categories. No statistical differences between categories were observed only in June and early July, as well as at the beginning of October.

To determine which elevation levels differed significantly, Tukey's HSD tests or post-hoc Games-Howell tests were conducted, depending again on the homogeneity of variances condition. As an example, the results for the entire monitoring period are presented in Table 4, while the remaining results can be found in the Supplementary Materials (Section 8).

Table 4: Results of post-hoc Games-Howell tests between elevation categories for the entire monitoring period.

Category 1	**Category 2**	**Mean Difference**	**95% CI**	**p-value**	**Significance ($p<0.05$)**
0–200	200–400	0.79	[0.65, 0.93]	<0.001	Yes
0–200	400+	0.79	[0.52, 1.05]	<0.001	Yes
200–400	400+	–0.005	[–0.29, 0.28]	0.999	No

The results indicate that low-elevation areas (0–200 m) differ significantly from both medium (200–400 m) and high (>400 m) elevation areas. In contrast, no significant difference was found between medium and high elevations. This is true for the entire monitoring season in summary and each month individually, except for June. On a 10-day basis, the results show a more dynamic pattern, generally following the observations in Figure 8. The trend persists whereby the low elevation category exhibits statistically significant differences from the other categories more frequently and more markedly than the differences observed between the medium and high elevation categories.

4.5. Spatial Distribution

This section discusses the spatial distribution of olive fruit flies in four distinct areas on Samos, presented as a monthly map series derived from Kriging analysis.

Marathokampos

Figure 10 shows a map series of the monthly spatial distribution of olive fruit fly counts in the Marathokampos region, modelled using Kriging analysis. A bimodal distribution can be observed across most years and in the average trend, with 2019 as the only exception. An increase in population from June to July is followed by a decline in August. September and October have significantly higher numbers than the previous month, and quite similar values to each other, but there is a slight increase towards October. 2020 stands out as a year with particularly high numbers towards the end of the season, while 2022 shows no exceptional behaviour, although this has been observed in the overall average (see Figure 5) as the year with the highest fruit fly numbers.

The shape of Marathokampos is a narrow, east–west stretch along the southern coast and appears to structure population dynamics into three sub-regions: East, Centre, and West. The first peak in July is more pronounced in the East and West, whereas the later peak in September and October is most evident in the central part of the region, which also lies more to the North than the side regions. In some maps, a North-South gradient is also observed, such as in August 2017.

It is also noteworthy that, in most years and in the average trend, zero counts are rare even at the beginning of the season, with few exceptions, including 2023. In contrast, some years, for instance, 2018 and 2024, show already elevated fruit fly activity across parts or all of the region as early as June.

Karlovasi

Figure 11 presents the map series for Karlovasi in the North-West of the island, including lower and medium elevations. The maps show that the olive fruit fly numbers in the region generally increase from June to September. Only from September to October, a decrease is observable in many years, leading to a distribution with only one peak, so not bimodal. Some exceptions can be seen in 2024, when September and October have the lowest fruit fly numbers of the season. Aligning with previous observations, 2022 stands out with the highest monthly numbers of fruit flies compared to other years.

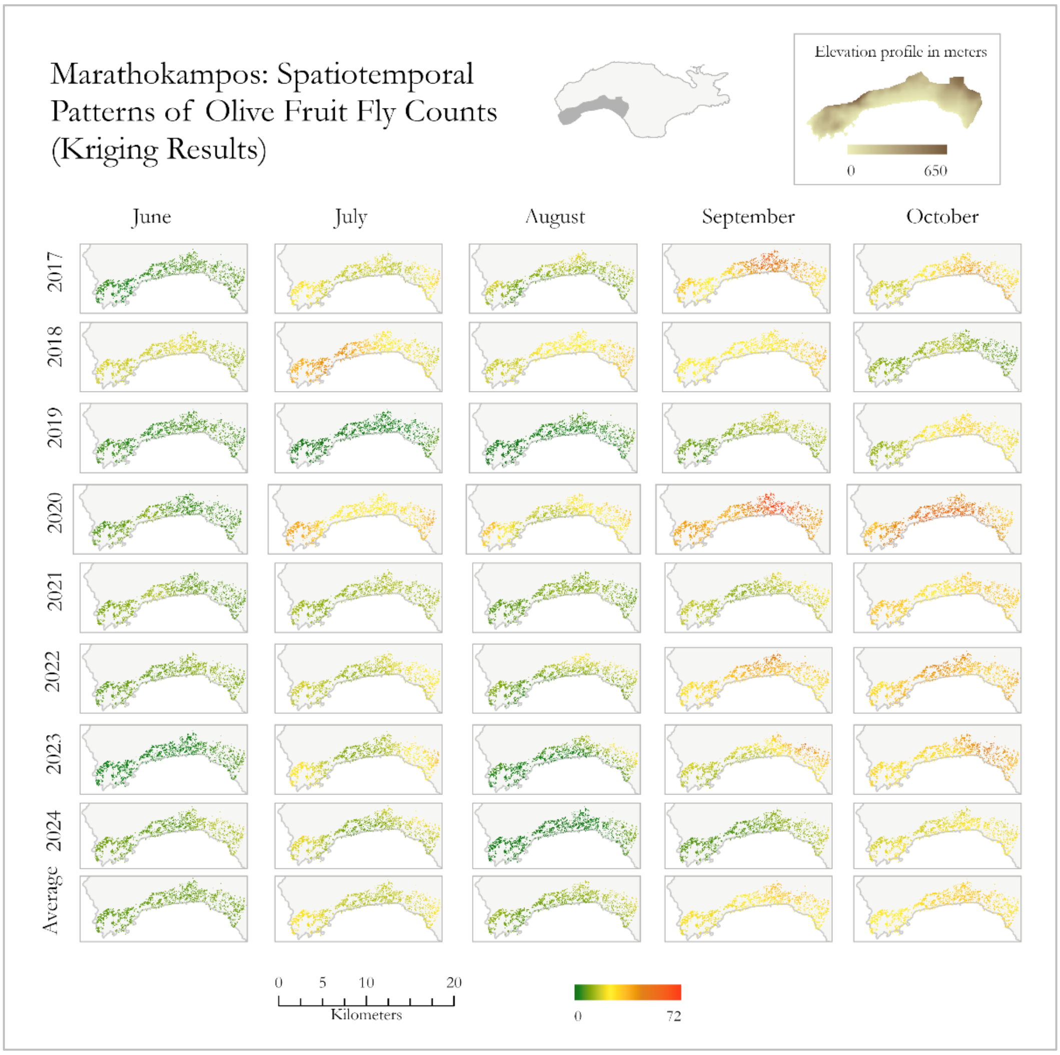

Figure 10: Map series showing total olive fruit fly counts by month and year in the Marathokampos area, estimated using Kriging analysis.

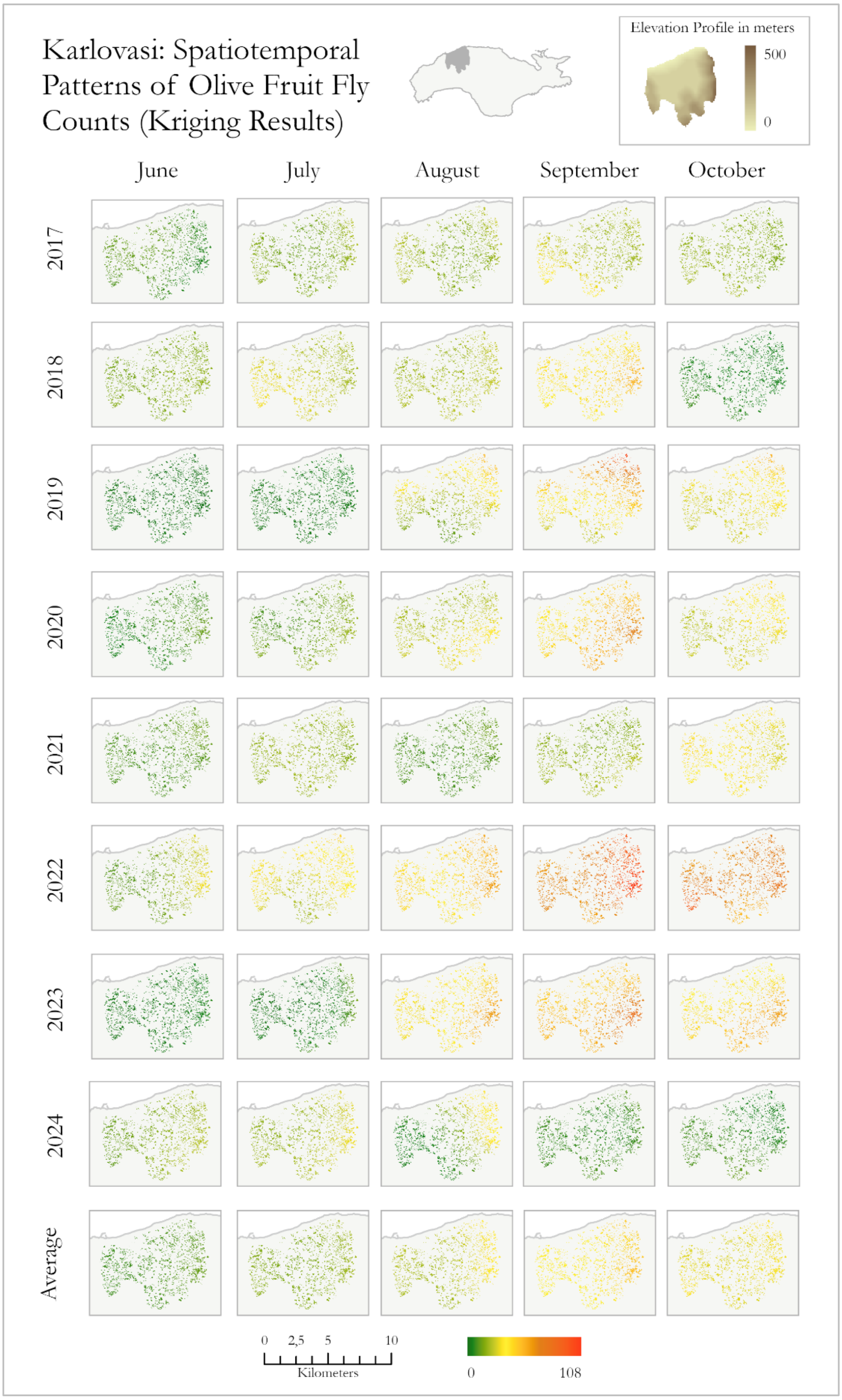

Figure 11: Map series showing total olive fruit fly counts by month and year in the Karlovasi area, estimated using Kriging analysis.

Spatially, population densities tend to be higher on the eastern side of Karlovasi, though the specific location of high densities varies between North-East and South-East. The East-West difference is particularly pronounced in August and September. In October, the long-term average suggests a slight decline in the east and a mild increase in the west, which balances the region overall.

Agios Konstantinos / Kokkari

The map series of spatial distribution for the region of Agios Konstantinos / Kokkari in the North-East of the island is shown in Figure 12. Lower population numbers are observed both at the start and at the end of the year, with typically one peak during August and September. However, some years, like 2018 and 2020, show a bimodal distribution. The annual maximum values vary in magnitude and timing, generally occurring between July and September.

The spatial distribution of olive flies within this area shows a distinction between the South-East and the North-West. In June, when overall numbers are still low, the South-Eastern region shows higher numbers in some years. This trend continues into July, except in 2017. From August onwards, this pattern shifts. Numbers in the North-West increase or remain steady, while those in the South-East often decline, and remain lower than in the North-West, except for 2022. In September, populations decrease slightly across both subregions, and by October, fly activity further diminishes, with relatively equal distributions of flies throughout the region or slightly higher counts in either North-East or South-West, depending on the year.

Pythagoreio

Figure 13 shows the map series for the Pythagoreio region in the South-East of Samos. Overall, the OFF numbers there show a bimodal distribution throughout the season, with a first peak in July and a substantial increase towards the second peak in October.

While this region does not show a sharp spatial divide, the olive fly distribution often shows a North-South gradient. From June to August, higher fly numbers are typically observed in the Northern part of the region, particularly in July when the first population peak occurs. However, this pattern shifts in September, and by October, populations rise in the Southern areas, often sharply, surpassing those in the North.

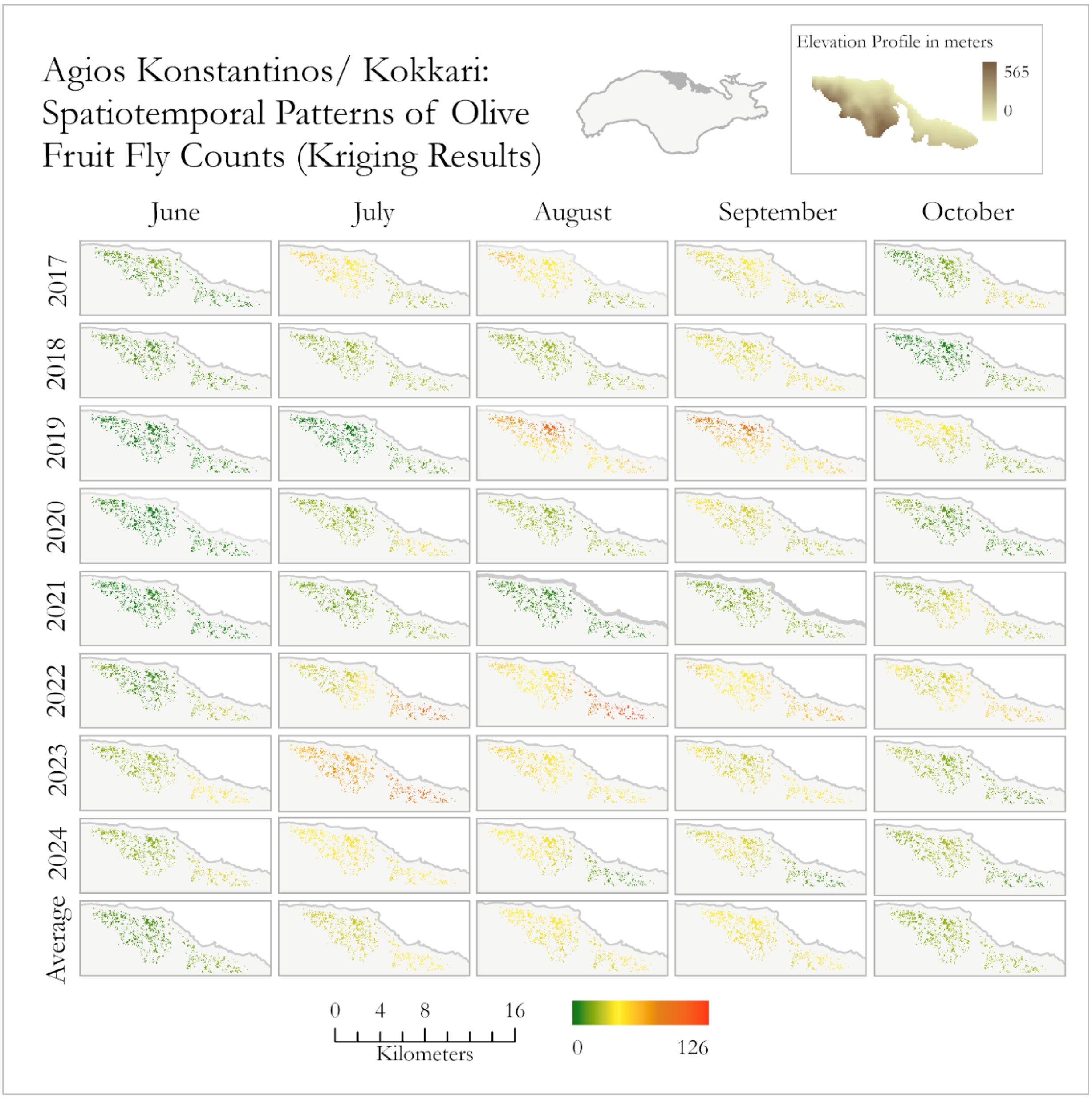

Figure 12: Map series showing total olive fruit fly counts by month and year in the Agios Konstantinos / Kokkari area, estimated using Kriging analysis.

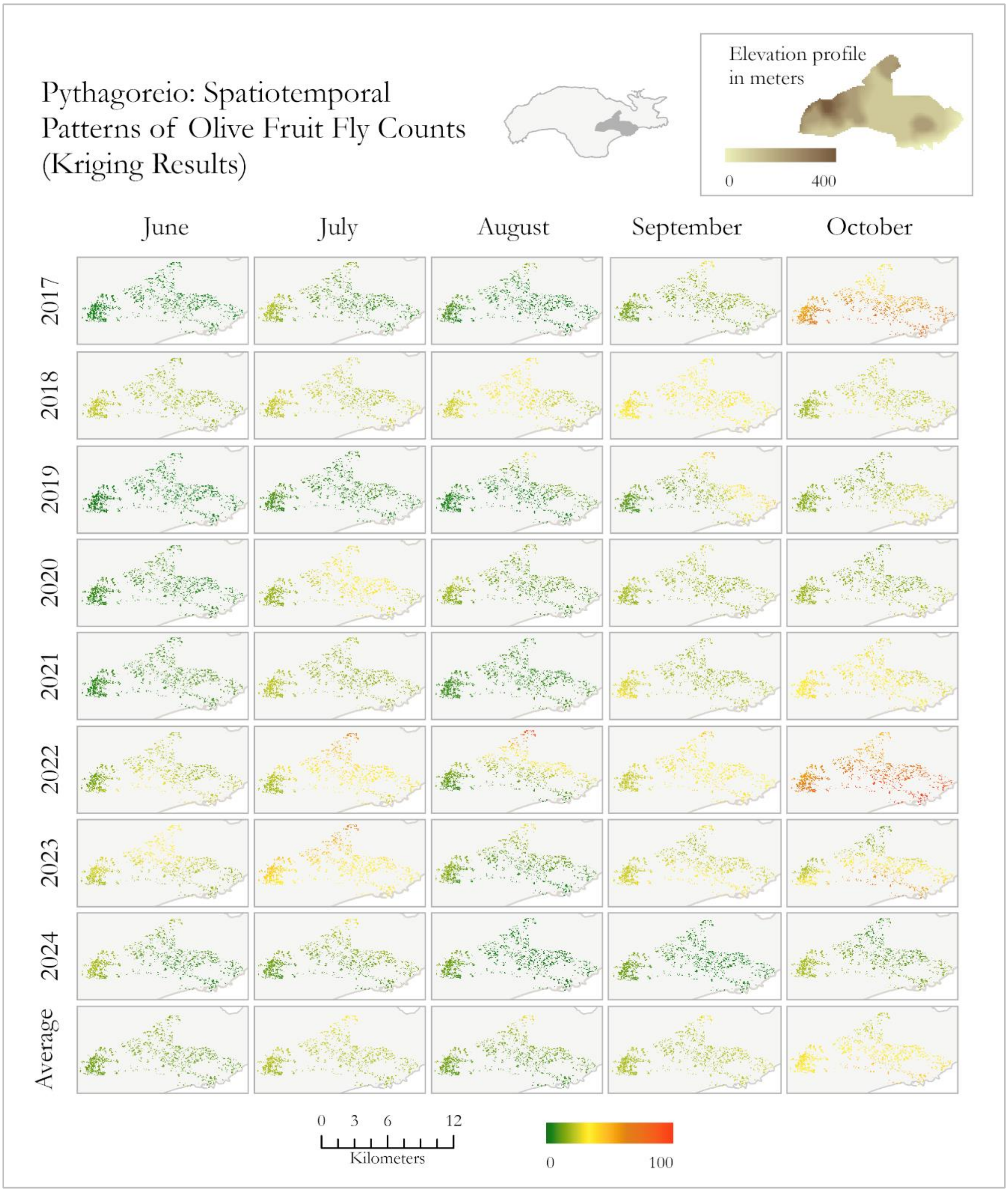

Figure 13: Map series showing total olive fruit fly counts by month and year in the Pythagoreio area, estimated using Kriging analysis.

Comparison of regions

Figure 14 presents a map series of the monthly totals of olive fruit flies, averaged across all years, for the four areas of interest. In all regions, fruit fly numbers increase from June to July. Between July to August, however, a North-South divide emerges. While populations continue to rise in the northern regions, they decline in the southern ones. In September, numbers increase again across all areas. The North-South pattern reverses in October when fruit fly numbers decline in the north but rise once more in the south. This seasonal dynamic suggests that a bimodal distribution is characteristic primarily of the southern regions, Marathokampos and Pythagoreio.

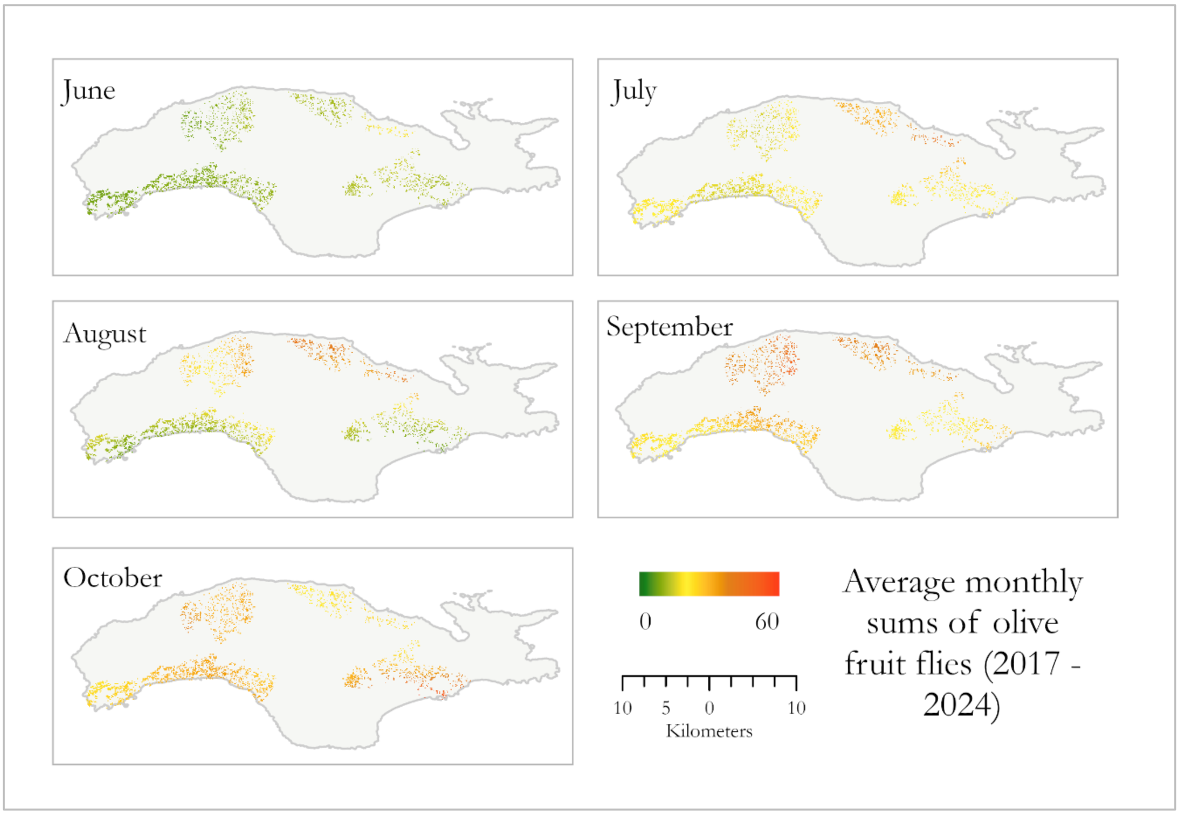

Figure 14: Map series showing average monthly sums of olive fruit flies by year in the four study areas on Samos, estimated using Kriging analysis.

Figure 15 shows the average annual development of olive fruit fly populations in 10-day intervals across the four regions. It generally confirms earlier observations about the seasonal patterns of individual regions, except for Agios Konstantinos / Kokkari, which displays a bimodal distribution. This differs from the map series in Figure 14, where this is not observed due to the lower temporal resolution.

Nevertheless, the North-South divide is also observable here, with Maraphokampos and Pythagoreio in the South showing a vaguely similar pattern and with numbers significantly under the higher numbers of Karlovasi and Agios Konstantinos / Kokkari in the North. However, this pattern emerges only in the second part of the season, from August onwards. Before, from early July to the end of August, Agios Konstantinos / Kokkari exhibits much higher numbers than the other regions, and its second peak also happens before the others. The other Northern region, Karlovasi, has its second population peak also two 10-day periods before the South regions. It is also notable that during the last ten-day period, fruit fly numbers increased in the western regions, while they declined in the eastern ones.

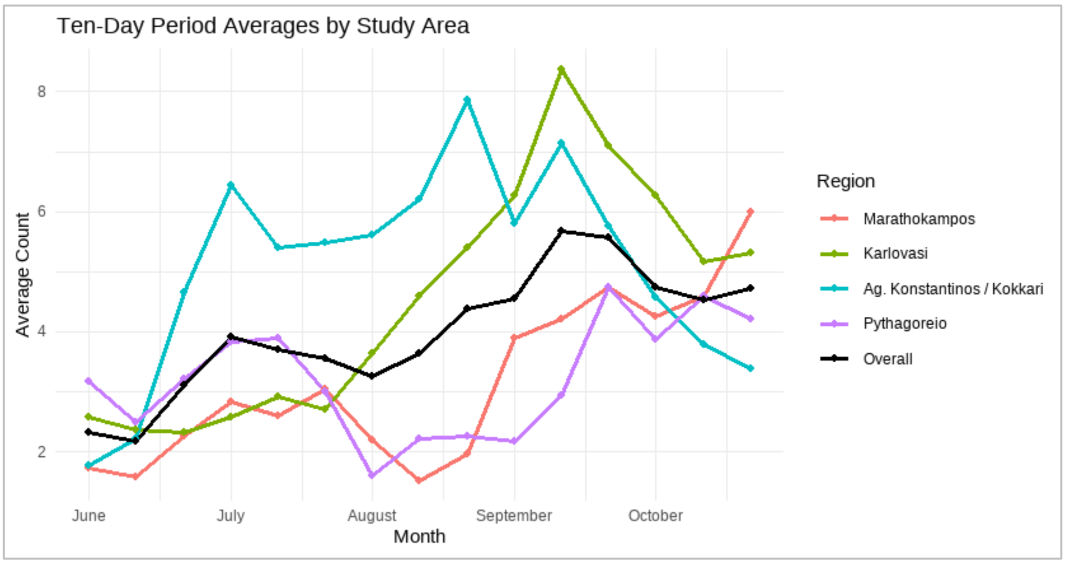

Figure 15: Average seasonal trends of olive fruit fly counts per sampling event in ten-day periods (2017 - 2024) across the four study areas on Samos.

5. Discussion

5.1. Temporal Population Trends Discussion

The temporal dynamics of olive fruit fly populations across the summer season showed two distinct peaks throughout the season, one in July and a higher second one in September. However, these patterns were observed in the average trends and showed very high variability and low consistency between years.

Two principal factors help to explain the observed temporal trends: Temperature (see Section 4.1) and the generational turnover of the olive fruit fly. Low counts in June and early July can be attributed to the emergence of the first generation of flies. As the season progresses, the overlap of the first and second generations in July contributes to a rise in numbers. However, rising temperatures in July likely account for the temporary decrease in population numbers observed in many years during August. Although August remains hot, it is often slightly cooler than July, facilitating a subsequent resurgence in fly numbers. During this time, the third and perhaps even the fourth generation of flies are expected, and the overlay of generations also contributes to the increased numbers observed in September, the month that typically records the highest fly counts. In October, population trends diverge, possibly depending on year-specific climatic conditions. The rise in average numbers observed in the last 10-day period of October can likely be explained by the increased availability of ripe olive fruits, which creates good conditions for fast reproduction and survival. This seasonal variability highlights the strong interaction between climatic factors and biological cycles in shaping olive fruit fly dynamics.

On a monthly scale, it should be kept in mind that the data from June is not directly comparable to the other months, as trap counting starts at different times depending on location and year. Due to the lower number of sampling events in June, the total number of OFF counts (Figure 5) is naturally lower than other months. Furthermore, the average values for the month (Figure 4) tends to reflect the numbers towards the end of the month when there were more sampling events, rather than the full monthly average. This temporal mismatch compared to other months further supports the use of 10-day intervals, as these make the averages more comparable throughout the season and offer a higher temporal resolution.

The seasonal patterns observed in this study are broadly consistent with previous findings. The bimodal population trend reported in other regions, like California (Burrack et al. 2024), is also reflected in the data from Samos. Similarly, like Topuz and Durmusoglu (2008), this study observed lower fly counts during the hottest summer months and the highest population peak later in the season. There is a slight difference in timing, e.g. the highest peak reported by Topuz and Durmusoglu (2008) is in October, while the one observed by this study is in late September. However, it can be assumed that this is due to regional differences like temperature patterns, but the overall trends are the same. The trends of this study also align with the concept of summer reproductive diapause or dormancy (Burrack et al. 2024; Economopoulos et al. 1982; Ordano et al. 2015), characterised by a temporary decline in reproduction, mainly due to high temperatures and arid conditions, which manifests here as the mid-season drop in fly numbers.

Currently, OFF monitoring begins at varying points in June and ends in late October, when harvesting is expected to start. However, a delayed harvest, due to heat, drought, or labour shortages, would indicate that relevant fruit fly activity may continue beyond this period. High end-of-season fly numbers and an increase in ripe olives suggest that monitoring should extend until the actual end of harvest. Additionally, a standardised start of monitoring in early June would show early population emergence and enable timely pest control, especially since previous monitoring already showed elevated early-season numbers in some years. Extending the monitoring season from early June to the end of harvest would improve understanding of fruit fly dynamics. However, it would also require logistical adjustments and a higher availability of personnel for trap maintenance.

Overall, while the observed seasonal trends in olive fruit fly populations are broadly consistent with established literature and can be explained through temperature effects and generational dynamics, the strong interannual variability makes it difficult to generalise these patterns across all years.

5.2. Influence of Temperature Discussion

The overall result of the test of temperature correlations indicated that many hours of heat stress negatively relate to olive fruit fly development. This aligns with previous studies, which found increased mortality under heat stress in laboratory conditions (Wang et al. 2009) and on a landscape level (Kavroudakis et al. 2024). Under the assumption that heat stress (hours above 32°C) also correlates with hotter temperatures in general, other factors, except heat-induced mortality, could influence the dynamics, particularly the development at individual life stages. Other reasons could include a delay in egg hatching, a shorter lifespan of adults or a delayed egg production (Tsitsipis 1977; Yokoyama 2012; Pappas et al. 2011).

The analysis does not address causality or temporal order. For example, in particularly hot years, fruit fly numbers may decline during summer heat and partially recover as temperatures cool, but remain lower than in colder years where summer conditions were more favourable for fruit fly development. For example, 2022 stands out among all years with the highest OFF averages. This pattern cannot be fully explained by temperature alone, because other years with similar numbers of hours above 32°C show much lower population levels. However, it is notable that in 2022, no period recorded more than 150 hours above 32°C, using *Any32h*. This suggests that fruit fly populations may remain high in years with fewer extreme heat events, even at lower numbers of hours above 32°C. Another example is 2021, which exhibited comparatively many hours exceeding 32°C, and fruit fly numbers remained comparatively low throughout the entire season. Even during periods with fewer heat hours, the population levels did not increase significantly, indicating a cumulative or delayed effect of prolonged heat exposure. This is supported by Kavroudakis et al. (2024), who found that the total number of hours above 32°C across the entire sampling period significantly correlated with the population developments at the end of the season, further indicating the presence of cumulative heat effects

At lower numbers of hours above 32°C, there is considerable variability in average fruit fly numbers, suggesting that additional factors, for example, ecological or environmental, strongly influence population levels in these conditions. This can explain the relatively low R^2 values observed in the models. As the number of heat hours increases, the range of fruit fly values narrows, and high outliers disappear. This pattern indicates that other drivers may be more influential under low or moderate temperature stress. In contrast, temperature becomes the limiting factor for OFF development under more extreme heat conditions.

Using *Any32h* as a temperature variable led to more accurate results than *Avg32h*. This is a valuable finding, as previous studies on a landscape level testing only the average of sensors (*Avg32h*) to calculate the number of hours with temperatures above 32°C (Kavroudakis et al. 2024). A likely explanation is that individual sensor readings can detect high temperatures more sensitively or earlier, since the threshold for registering a heat event is generally lower. This is why the x-axis is twice as long as in comparison, and fewer data points are clustered at the vertical line representing no hours above 32°C. While microclimates play an important role, all sensors are located on the same island and likely experience similar overall trends. An oncoming heat is more likely to be detected first by individual traps recording elevated temperatures, with the average rising later as more sensors register the heat.

This pattern suggests that a threshold for the average below 32°C could be more effective as a variable to describe fruit fly trends, as significant temperature conditions relevant to fruit fly development are already present by then, as shown by the results of this study. Previous studies have used different temperature thresholds, such as 34°C (Pappas et al. 2011), 35°C (Wang et al. 2009) or 36°C (Yokoyama 2012), and found similar overall trends. This indicates that different temperature thresholds for heat stress could be explored to identify the one that shows the highest correlation to the olive fruit fly numbers.

This analysis does not account for the underlying developments that lead to higher numbers of hours above 32°C. It remains unclear how influential microclimates are and, as a consequence, how significant the differences between individual temperature sensors are, and how this might influence the results. Additionally, thermal effects outside the selected threshold, both below and above 32°C, are not being considered here.

Climate change is expected to alter climate patterns and, thereby, the population dynamics of olive fruit flies. Based on the results of this study, hotter summers are likely to decrease olive fruit fly numbers, while milder spring and autumn conditions could become increasingly favourable. As a result, the two population peaks each year would become higher with steeper increases and declines, while the OFF numbers in the summer in between would be lower. Eventually, this shift may even lead to seasonal patterns observed in parts of Israel, where there is little to no OFF activity in summer, but instead throughout the winter (Ordano et al. 2015). Of course, this also depends on how the phenology of olive trees will react to the changing climate, possibly decoupling interactions between insect and plant, as highlighted by Gordo and Sanz (2005).

Future research could further explore the impact of temperatures on the population development of the olive fruit fly. This includes the analysis of population trends with a temporal lag, for example, using the aggregate temperature of the previous seven days, following the approach by Rondoni et al. (2024). Rather than assuming immediate effects, this would better reflect delayed biological responses, such as mortality and reproductive success. Furthermore, the influence of winter and spring temperatures on OFF emergence and development in spring could be analyzed, as demonstrated by Marchi et al. (2016).

The climate data logger system could be improved by increasing the number of active loggers and keeping the number and locations of traps consistent over time. Alternatively, high-resolution remote sensing could reduce potential biases associated with logger placement and variability.

In summary, this analysis shows that high temperatures, measured by hours exceeding 32°C, negatively correlate with olive fruit fly populations. However, the strength of this relationship is relatively weak, and not sufficient to predict exact fruit fly counts. Instead, temperature can be indicative of overall changes in population dynamics, keeping in mind the high variability between fruit fly counts. Models using individual sensor data (*Any32h*) perform better than those based on average temperatures (*Avg32h*), likely due to their greater sensitivity to localised heat events. While temperature is not the only driver of population changes, it becomes a significant limiting factor under extreme conditions, as seen in reduced population variability at high heat levels.

5.3. Altitude Discussion

Due to the length and depth of the altitude discussion, this chapter has been divided into several subsections. First, the linear regression results will be explained and examined, then those of the analysis of elevation categories. Afterwards, the results from both analyses will be contextualised within existing literature. At the end of the chapter, broader implications are discussed, including potential limitations, implications for population movements and climate change effects, and suggestions for future research directions.

5.3.1. Linear Regression of Altitude Discussion

An analysis of olive fruit fly counts in relation to the exact altitude of the respective traps revealed a statistically significant relationship across the full season, as well as in most monthly and some 10-day interval tests. However, the effect size was minimal and therefore practically negligible. This can be considered surprising, as other research previously found rather strong correlations between OFF counts and elevation (Castrignanò et al. 2012; Kounatidis et al. 2008; Rondoni et al. 2024).

One possible explanation is that the large number of data points, especially at lower elevations where most traps are located, inflates the statistical power and creates an appearance of a significant trend. This concern is further supported by the uneven distribution of traps across elevation gradients, with progressively fewer observations at higher altitudes, which may introduce bias and reduce the representativeness of results for those zones. Alternatively, the results may indeed show a true relationship between elevation and fruit fly numbers, although one that is very weak in terms of ecological significance. This would indicate that elevation has a minimal influence on fruit fly counts relative to other factors, possibly microclimate, host plant availability, or land management practices.

5.3.2. Altitude Categories Discussion

As the use of exact trap values showed statistically significant, but not very meaningful results, the next step involved grouping elevations into categories. This approach allowed for a simple visual inspection of the data in the categories and made it possible to identify relevant altitude-dependent population differences.

When altitude was analysed using elevation categories, the average trend shows a bimodal distribution, consistent with the general temporal patterns discussed in a previous chapter (Section 4.2), which are primarily explained by temperature changes and generation overlaps. This reasoning is further supported when the distinct seasonal patterns of low, middle, and high elevations are considered. Lower elevations, which experience earlier and stronger temperature increases in July, show an earlier population peak followed by a sharper decline. In contrast, higher elevations, with milder July conditions, maintain higher fly numbers later into the season, highlighting how temperature differences along elevation shape both the timing and intensity of population dynamics.

Statistical tests, including ANOVA and Welsh's ANOVA, confirmed that throughout large parts of the season, statistically significant differences between the elevation categories exist, and generally correspond to the trends observed in Figure 8. Notably, the lowest elevation category had significantly different olive fruit fly counts compared to the medium and high categories. That these differences were not observed in June can be explained by the slow emergence of OFF populations across all altitudes, or the inconsistencies of data collection in June, outlined in Chapter 385.1.

The seasonal shift in the elevation zone with the highest OFF densities suggests a moving window of optimal conditions for OFF development, primarily influenced by temperature. Early in the season, high elevations are more suitable because of cooler temperatures, as low and mid elevations experience heat. After July, as temperatures begin to decline, medium elevations become more favourable. This helps explain why the mid-elevation range (200–400 m) is the only category not displaying a bimodal distribution. In June and July, it follows a pattern similar to lower elevations but continues to show increasing fly numbers into August, even as low and high elevations see decreases. As the season continues towards October and temperatures drop further, low elevations become increasingly suitable, resulting in a late-season population rise. These shifting temperature conditions across elevations explain the distinct seasonal trends: Early steep increases at high elevations, continued growth at mid elevations, and a delayed increase at low elevations.

5.3.3. Altitude results in the context of literature

These trends show consistency with previous studies. Castrignano et al. (2012) and Kounatis et al. (2008) have also observed the trend that population numbers are higher and rise earlier in the summer in higher elevations, and towards autumn, the pattern reverses, and numbers rise more strongly in the South. Notably, both studies used distinct elevations of the traps rather than elevation categories. Rondoni et al. (2024) have also observed the different timings of the peaks. Their findings that fruit fly attacks are delayed at higher altitudes are also observed in this study during the first peak. However, during the second peak, Figure 8 shows that lower elevations have the peak later than other elevations, which would be expected as the temperature in these regions is longer suitable for olive fruit fly development.

The studies by Kavroudakis et al. (2024) and Katsikogiannis et al. (2023) offer relevant points of comparison, as they are based on the same monitoring system on Samos as this study. While the present results partly align with these previous findings, there are a few differences in the methodology, and the results are further discussed below.

Kavroudakis et al. (2024) found no practically relevant results in the linear regression analysis between trap elevations and OFF counts, similar to this study. While they used elevation categories to describe specific trends, like the average trap counts, they did not analyse those differences statistically. However, comparability with the present study is limited, as the classification of their elevation categories (0–100 m, 100–230 m, 230–602 m) differs from the one used here.

Katsikogiannis et al. (2023), who also used temperature trends to explain variations across altitudes, reported seasonal shifts in fruit fly activity that largely align with the findings of this study. Using the same elevation classification, they observed higher counts in high elevations in July, followed by higher counts in mid-elevations in August, and a shift to higher counts in low elevations in September and October. This generally mirrors the elevation-dependent seasonal progression described here, although the timing of trends may vary by a month. Another discrepancy lies in their June results, where they found elevated activity in low and mid elevations, whereas this study observed similar fly counts across all elevation levels for that month. Their statistical approach employed ANOVA to compare elevation categories on a monthly basis by year, rather than using multi-year averages as was done in this study. Due to the high interannual variability of olive fruit fly numbers within altitude categories (see Figure 9: Average olive fruit fly counts per 10-day period, grouped by elevation category (0–200 m, 200–400 m, >400 m) and year.Figure 9), this study's approach shows more consistent trends, particularly regarding the statistical differences observed at lower elevations compared to medium and higher ones.

A likely reason for these different results between Kavroudakis et al. (2024) and Katsikogiannis et al. (2023), and this study, is the observation period. With eight years of data rather than three, this study is better equipped to capture broader patterns and account for interannual variability, while short-term data may carry the risk of overinterpreting anomalies, which can skew the results, especially in a context where year-to-year fluctuations are as strong as in this one. Furthermore, the studies take into consideration all counted olive fruit flies, as opposed to this research, which focuses on the females. This also accounts for several of the differences in the results, for example, why Kavroudakis et al. (2024) find monthly averages that are around twice as high as the ones found in this study.

5.3.4. Implications of Altitude Dependence

Although average trends across elevation categories have been described and discussed, Figure 9, which presents seasonal population developments by elevation category and year, highlights the substantial interannual variability in olive fruit fly counts, even within the same elevation band. However, these findings align with the literature, which reports a high variability of fruit fly numbers, even in traps close to each other (Castrignanò et al. 2012; Kounatidis et al. 2008). While temperature has so far been considered the primary explanatory factor for population dynamics and elevation-based differences, the recorded temperature variables in Figure 3 do not fully account for the observed patterns. In particular, they fail to explain why some years show pronounced differences between elevation categories, while in other years these differences are minimal. This lack of explanatory power in the temperature data suggests that additional factors beyond temperature alone contribute to the interannual and elevation-based variability in fruit fly populations. Castrignanò et al. (2012) suggest farming practices like irrigation and cumulated pesticide effects as possible causes for the irregular distribution of the OFF numbers, under similar elevation and climate conditions.

Another consideration is the assumption that elevation is a reliable proxy for temperature or other environmental gradients. If this assumption is weak, the observed relationship between elevation and fly abundance may be misleading. To address this, further research could test the correlation between trap elevation and local temperature data from on-site sensors. Additionally, remote sensing data could be employed to detect spatial temperature variation across the island with higher resolution, and to lead to a better understanding of the suitability of altitude as a predictive variable.

It is also possible that the effects of other spatial variables, for example land cover, slope or aspect, reduce the explanatory power of elevation at the island scale. Those factors may individually or together overshadow the influence of altitude. Nevertheless, elevation might still play a more prominent role at smaller spatial scales, where local topography is more similar. As a next step, applying the same analysis at a localised level, focusing on the four identified areas of interest, may lead to stronger results regarding the impact of altitude on olive fruit fly populations.

While the overall patterns across altitudes found in this study could indicate local developments through population growth and higher reproductive success, they may also suggest OFF migration across altitudes, as proposed by Katsikogiannis et al. (2023) and Kavroudakis et al. (2024). This would imply that areas of decreasing fruit fly numbers do not necessarily become unsuitable, but that instead the flies relocate to altitudes with more favourable conditions at that time. While population movements across the landscape are supported by previous studies (see Rondoni et al. (2024); Ragaglini, Tomassone, and Petacchi (2005)), there is insufficient data on Samos to verify these suggestions with certainty.

The implications of climate change, already discussed in Section 5.2, suggest that rising temperatures will also change the spatial dynamics of olive fruit fly populations. Rising temperatures are expected to make higher elevations more suitable habitats due to cooler temperatures, shifting the balance of the OFF population along elevation gradients and influencing population movements. This aligns with the findings of Gutierrez, Ponti, and Cossu (2009), who suggested that the suitable range for OFF will expand towards cooler regions.

In summary, while a relationship between elevation and olive fruit fly populations was expected and confirmed to be statistically significant, it was not particularly strong or explanatory. The analysis of elevation categories showed significant differences throughout most of the monitoring season, particularly a substantial discrepancy between lower elevations (0-200m) and the medium (200-400m) and higher (>400m) ones. However, a high variability was observed across elevations and between years. The findings align with previous studies, suggesting that elevation influences population dynamics, possibly due to movement across altitudinal gradients. Overall, elevation plays an important role, but additional variables will be necessary to explain all observed trends and make reliable predictions.

5.4. Spatial Distribution Discussion

The overview of Kriging results by region (Figure 10 to Figure 14), along with the seasonal trends shown in Figure 15, show substantial variation in population dynamics across different parts of the island. While all areas share certain general patterns, such as the tendency toward bimodal population curves, distinct differences in timing and intensity highlight the impact of local environmental influences.

A distinct North–South divide in fruit fly activity stands out from both spatial and seasonal analyses. Northern regions exhibit higher populations and earlier, more pronounced peaks in September, followed by steeper declines. In contrast, the Southern areas generally show lower olive fruit fly numbers during the summer months and a steady increase towards September and October, when populations in the North are already decreasing. Due to the island's topography, there is a tendency for Northern areas to be generally North-facing and the Southern areas to be generally South-facing. Although this study did not focus on aspect as a variable, the observed patterns may suggest an influence on OFF populations, as observed by (Petacchi et al. 2015). Kavroudakis et al. (2024) found a significant but very minimal relationship between aspect and OFF densities in their Kriging analysis of Samos, but their results were based on only three years of data. With more years now available and given the high variability between years, a new analysis of aspect could be beneficial, as it likely contributes to local microclimates and temperature differences across the island: North-facing areas are cooler, allowing continued population growth during the summer, while hotter conditions in the South suppress fly activity. This argumentation again uses the range of optimal temperature conditions, which was also used to explain the differences between altitudes in Section 5.3. Katsikogiannis et al. (2023) and Kavroudakis et al. (2024) also observed this North-South divide of Samos, partly linking it to the movement of olive fruit flies towards better climate conditions.

Most regions show bimodal distribution patterns, although with varying intensity. This is expected as it aligns with general temporal trends over the season. However, Karlovasi stands out due to a very shallow first peak followed by a steep rise. One possible explanation is that Karlovasi, surrounded by mountains, experiences warm early-season temperatures similar to those in the South, which may initially suppress fly activity. Later, as temperatures drop, the area may become more suitable, leading to a rapid increase. The Agios Konstantinos/Kokkari region also shows unique behaviour during the second seasonal peak. A sharp drop in fruit fly counts is followed by a sudden increase within the next 10-day period. While this could suggest a trimodal distribution, it is more likely a short-term fluctuation within a generally bimodal pattern.

At the end of the season, during the final 10-day period, another regional divergence emerges. Eastern regions tend to continue declining, while the western regions show another increase in fruit fly numbers. As temperature patterns cannot fully account for this variation, possible explanations could involve the availability of ripe fruit or differences in local agricultural practices, such as harvest timing, although data would be needed to confirm this.

Climate change can be expected to change the distribution of olive fruit flies over the island. The Southern (South-facing) regions will become hotter, making the relatively cooler regions in the North (North-facing) more favourable. Also beyond the local context, these changing climate patterns could expand the geographic range of the olive fruit fly towards the North, while decreasing its numbers in Southern regions. This suggestion aligns with the findings of Gutierrez, Ponti, and Cossu (2009), who suggested that the geographic range for both olive cultivation and the OFF will expand towards Northern regions and higher altitudes.

In future research, a more detailed year-by-year comparison could help clarify these trends. For example, 2020 stands out with especially high fly counts in Marathokampos, while 2022 shows the highest values in Karlovasi and Pythagoreio, even though 2020 is less notable in those areas. This highlights the need to consider variability between years when analysing regional differences. Additionally, repeating the temperature and elevation analyses at the regional level could help isolate the effects of these factors locally, without being skewed by broader island-wide variation. While monthly maps provide a decent overview, data grouped by 10-day periods offers finer temporal resolution and is better suited to detect shifts in fly activity. It may therefore be valuable to develop a map series at this higher resolution. Statistical tests, such as ANOVA, could help assess the significance of observed regional differences. While the Kriging approach taken in this analysis produces reasonable results, a comparison of different Kriging models, including their estimated uncertainties, would improve confidence in the spatial predictions.

In conclusion, the Kriging analysis reveals notable regional variation in the seasonal trends of olive fruit fly dynamics across Samos Island, with a pronounced North–South divide. Regions in the North are cooler and exhibit higher fly populations and earlier peaks, while the regions in the South are warmer and show lower population numbers overall, but a rise towards the end of the season. These differences are likely driven by temperature trends. Most regions follow a bimodal pattern, although local deviations can be observed. Climate change is expected to shift the olive fruit fly populations further towards the cooler regions in the North, both locally and across the broader Mediterranean. Future research could capture and validate more spatial differences, for example by exploring regional population dynamics using year-by-year comparisons, by analysing regional temperature and elevation effects or using statistical testing for differences.

6. Conclusion

The olive fruit fly is the most economically damaging pest in olive cultivation worldwide. This study explored its population dynamics on the Greek island of Samos, with particular attention to the dependence on altitude, temperature, and location. Rather than aiming to provide definitive causal conclusions, its exploratory approach identifies key variables and spatial dynamics that can inform future research.

The analysis was based on data from an established monitoring program on Samos, including 399 monitoring traps and several climate data loggers across the island. Data was collected over eight years, covering the period from June to October. This research's data analysis methods included visual data inspection, statistical tests, including ANOVA, Welch's ANOVA, linear regression, and geospatial modelling using Kriging analysis in four study areas on Samos.

The research faced limitations, such as inconsistent climate sensor data and the limited testing of alternatives to the Kriging model. Despite these and a very high overall variability in population numbers across seasons, years, elevation, and similar climatic conditions, it was possible to identify recurring patterns and establish relationships between variables.

Seasonal population trends showed a generally bimodal distribution pattern, with peaks in July and late September, although with considerable interannual variability. This pattern corresponds with expected seasonal temperature dynamics, with warmer conditions typically reducing fly abundance and cooler ones increasing it. Out of different temperature-related statistical analyses, the linear regression between average OFF counts on a 10-day basis and the number of hours in which at least one trap exceeded 32°C showed the highest statistical significance. Increased heat hours were associated with lower OFF numbers, aligning with existing literature. Despite a high variability of olive fruit fly counts across temperature conditions, the number of heat hours seemed to be a limiting factor in suppressing high population outliers.

Altitude also played a significant role in population dynamics. While a linear regression between population counts and exact trap elevations showed statistical significance, the practical effect was minimal. Grouping traps into elevation categories (0-200m, 200-400m, 400+m) revealed a higher statistical significance and a better understanding of population dynamics. All elevation categories start with low fruit fly numbers in June. However, high altitudes quickly show higher numbers than the others in July, followed by medium elevations being dominant in late August and low elevations in October. Notably, low elevations significantly differed from the others throughout most of the season, especially through the low population numbers in the summer months. This shift suggests a moving window of optimal conditions, and potentially population movements across altitudes towards the most suitable conditions, although this cannot be confirmed with current data. As elevation can serve as a proxy for temperature, these differences are likely temperature-driven, with higher heat levels at lower altitudes contributing to reduced fly abundance.

Kriging analysis of the four study areas showed distinct patterns, suggesting a North-South divide of the island regarding olive fruit fly dynamics. While the Southern regions had significantly lower numbers from July to September, their numbers rose towards October. This corresponds to the differences between low and high altitudes, suggesting the same underlying causes of temperature and population movements.

Climate change is expected to impact the spatio-temporal trends of olive fruit fly populations. As this research indicated that high temperatures are linked to reduced fly numbers, summer populations may decline in the future. At the same time, spring and autumn conditions would become more favourable, resulting in higher seasonal peaks. Spatially, higher altitudes and northern regions are likely to become increasingly suitable, shifting the overall distribution pattern. Without monitoring and adapting appropriate pest management practices, these shifting OFF dynamics could lead to unexpected economic losses

The findings from this study suggest adjustments to the monitoring system, particularly extending the monitoring period from the beginning of June to the end of harvesting and improving the accuracy of temperature measurements. Furthermore, future research should also a) explore delayed temperature effects on population changes, b) compare and evaluate different Kriging models, c) repeat the analysis of altitude and temperature impacts per region, d) incorporate additional variables, such as humidity, aspect, and pesticide spraying, e) develop a multi-variable model for OFF population dynamics, f) map the landscape mosaic, with a focus on abandoned or unmanaged olive groves, and g) explore olive fruit fly movement patterns across the landscape. Taking these directions in future research could improve the reliability, consistency, and applicability of the results.

In conclusion, this study supports previous findings of bimodal population distributions over the season and a sensitivity to heat stress ($T>32°C$). Furthermore, low elevations and the Southern regions of the island experience lower numbers during the hotter summer months. The study used a landscape-level approach to provide spatio-temporal results on a small scale, which can serve as a starting point to adapt pest management and pesticide use to local needs instead of overall trends, thereby potentially reducing environmental impact.

7. References

Asch, Barbara van, Isabel Pereira-Castro, Fernando Trindade Rei, and Luís Teixeira da Costa. 2015. "Marked Genetic Differentiation between Western Iberian and Italic Populations of the Olive Fly: Southern France as an Intermediate Area." *PLOS ONE* 10 (5): e0126702. https://doi.org/10.1371/journal.pone.0126702.

Avanidou, Kalliopi, Thomas Alexandridis, Dimitris Kavroudakis, and Thanasis Kizos. 2023. "Development of a Multi Scale Interactive Web-GIS System to Monitor Farming Practices: A Case Study in Lemnos Island, Greece." *Smart Agricultural Technology* 5 (September):100313. https://doi.org/10.1016/j.atech.2023.100313.

Broufas, G D, M L Pappas, and D S Koveos. 2009. "Effect of Relative Humidity on Longevity, Ovarian Maturation, and Egg Production in the Olive Fruit Fly (Diptera: Tephritidae)." *Annals of the Entomological Society of America* 102 (1): 70–75. https://doi.org/10.1603/008.102.0107.

Burrack, Hannah J., Ray Bingham, Richard Price, and Joseph H. Connell. 2024. "Understanding the Seasonal and Reproductive Biology of Olive Fruit Fl y Is Critical to Its Management." *ResearchGate*, December. https://doi.org/10.3733/ca.v065n01p14.

Calvin, Katherine, Dipak Dasgupta, Gerhard Krinner, Aditi Mukherji, Peter W. Thorne, Christopher Trisos, José Romero, et al. 2023. "IPCC, 2023: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (Eds.)]. IPCC, Geneva, Switzerland." First. Intergovernmental Panel on Climate Change (IPCC). https://doi.org/10.59327/IPCC/AR6-9789291691647.

Caselli, Alice, and Ruggero Petacchi. 2021. "Climate Change and Major Pests of Mediterranean Olive Orchards: Are We Ready to Face the Global Heating?" *Insects* 12 (9): 802. https://doi.org/10.3390/insects12090802.

Castrignanò, A., L. Boccaccio, Y. Cohen, D. Nestel, I. Kounatidis, N. T. Papadopoulos, D. De Benedetto, and P. Mavragani-Tsipidou. 2012. "Spatio-Temporal Population Dynamics and Area-Wide Delineation of Bactrocera Oleae Monitoring Zones Using Multi-Variate Geostatistics." *Precision Agriculture* 13 (4): 421–41. https://doi.org/10.1007/s11119-012-9259-4.

Daane, Kent M., and Marshall W. Johnson. 2010. "Olive Fruit Fly: Managing an Ancient Pest in Modern Times." *Annual Review of Entomology* 55 (Volume 55, 2010): 151–69. https://doi.org/10.1146/annurev.ento.54.110807.090553.

Damijanić, Ana Težak. 2021. "Connections between Healthy Behaviour, Perception of Olive Oil Health Benefits, and Olive Oil Consumption Motives." *Sustainability* 13 (14). https://doi.org/10.3390/su13147630.

Damos, Petros. 2015. "Modular Structure of Web-Based Decision Support Systems for Integrated Pest Management. A Review." *Agronomy for Sustainable Development* 35 (4): 1347–72. https://doi.org/10.1007/s13593-015-0319-9.

Economopoulos, A. P., G. E. Haniotakis, S. Michelakis, G. J. Tsiropoulos, G. A. Zervas, J. A. Tsitsipis, A. G. Manoukas, A. Kiritsakis, and P. Kinigakis. 1982. "Population Studies on the Olive Fruit Fly, Dacus Oleae (Gmel.) (Dipt., Tephritidae) in Western Crete." *Zeitschrift Für Angewandte Entomologie* 93 (1–5): 463–76. https://doi.org/10.1111/j.1439-0418.1982.tb03621.x.

EU Regulation 2021/2115. 2021. *EU Regulation*. https://eur-lex.europa.eu/eli/reg/2021/2115/oj/eng.

European Commission. 2020. "A Farm to Fork Strategy for a Fair, Healthy and Environmentally-Friendly Food System." European Commission. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:52020DC0381.

Folgado-Fernández, José Antonio, Ana María Campón-Cerro, and José Manuel Hernández-Mogollón. 2019. "Potential of Olive Oil Tourism in Promoting Local Quality Food Products: A Case Study of the Region of Extremadura, Spain." *Heliyon* 5 (10): e02653. https://doi.org/10.1016/j.heliyon.2019.e02653.

Forrest, Jessica RK. 2016. "Complex Responses of Insect Phenology to Climate Change." *Current Opinion in Insect Science*, Global change biology * Molecular physiology, 17 (October):49–54. https://doi.org/10.1016/j.cois.2016.07.002.

Gordo, Oscar, and Juan José Sanz. 2005. "Phenology and Climate Change: A Long-Term Study in a Mediterranean Locality." *Oecologia* 146 (3): 484–95. https://doi.org/10.1007/s00442-005-0240-z.

Gorini, Ilaria, Silvia Iorio, Rosagemma Ciliberti, Marta Licata, and Giuseppe Armocida. 2019. "Olive Oil in Pharmacological and Cosmetic Traditions." *Journal of Cosmetic Dermatology* 18 (5): 1575–79. https://doi.org/10.1111/jocd.12838.

Gutierrez, Andrew Paul, Luigi Ponti, and Q. A. Cossu. 2009. "Effects of Climate Warming on Olive and Olive Fly (Bactrocera Oleae (Gmelin)) in California and Italy." *Climatic Change* 95 (1): 195–217. https://doi.org/10.1007/s10584-008-9528-4.

Hamann, Elena, Camille Blevins, Steven J. Franks, M. Inam Jameel, and Jill T. Anderson. 2021. "Climate Change Alters Plant–Herbivore Interactions." *New Phytologist* 229 (4): 1894–1910. https://doi.org/10.1111/nph.17036.

Haniotakis, E.G. 2005. "IOBC-WPRS Bulletin Vol. 28 (9), 2005." *International Organisation for Biological and Integrated Control West Palaearctic Regional Section* (blog). 2005. https://iobc-wprs.org/product/iobc-wprs-bulletin-vol-28-9-2005/.

IOC. 2023. "Olive Oil Dashboard." International Olive Council. 2023. https://www.internationaloliveoil.org/wp-content/uploads/2023/12/IOC-Olive-Oil-Dashboard.html#production-1.

Kampouraki, Anastasia, Marianna Stavrakaki, Aggeliki Karataraki, Georgios Katsikogiannis, Evanthia Pitika, Kiriaki Varikou, Antonia Vlachaki, et al. 2018. "Recent Evolution and Operational Impact of Insecticide Resistance in Olive Fruit Fly Bactrocera Oleae Populations from Greece." *Journal of Pest Science* 91 (4): 1429–39. https://doi.org/10.1007/s10340-018-1007-8.

Kapatos, E. T., and B. S. Fletcher. 1984. "The Phenology of the Olive Fly, Dacus Oleae (Gmel.) (Diptera, Tephritidae), in Corfu." *Zeitschrift Für Angewandte Entomologie* 97 (1–5): 360–70. https://doi.org/10.1111/j.1439-0418.1984.tb03760.x.

Katsikogiannis, Georgios, Thomas Tscheulin, Dimitris Kavroudakis, and Thanasis Kizos. 2023. "Population Dynamics of the Olive Fly, Bactrocera Oleae (Diptera: Tephritidae), Are Influenced by Different Climates, Seasons, and Pest Management." *Sustainability* 15 (October). https://doi.org/10.3390/su151914466.

Kavroudakis, Dimitris, Thanasis Kizos, Thomas Tscheulin, Georgios Katsikogiannis, Georgios Stavrianakis, and Labrini Tsalta. 2024. "Spatial Analysis of Olive Fly on Samos Island." *International Journal of Pest Management* 0 (0): 1–13. https://doi.org/10.1080/09670874.2024.2361369.

Koul, Opender. 2008. *Areawide Pest Management: Theory and Implementation*. https://doi.org/10.13140/2.1.2435.5521.

Kounatidis, I., N. T. Papadopoulos, P. Mavragani-Tsipidou, Y. Cohen, K. Tertivanidis, M. Nomikou, and D. Nestel. 2008. "Effect of Elevation on Spatio-Temporal Patterns of Olive Fly (Bactrocera Oleae) Populations in Northern Greece." *Journal of Applied Entomology* 132 (9–10): 722–33. https://doi.org/10.1111/j.1439-0418.2008.01349.x.

Lello, Florence, Mussa Dida, Mbazingwa Mkiramweni, Joseph Matiko, Roseline Akol, Mary Nsabagwa, and Andrew Katumba. 2023. "Fruit Fly Automatic Detection and Monitoring Techniques: A Review." *Smart Agricultural Technology* 5 (October):100294. https://doi.org/10.1016/j.atech.2023.100294.

Malheiro, Ricardo, Susana Casal, Paula Baptista, and José Alberto Pereira. 2015. "A Review of *Bactrocera Oleae* (Rossi) Impact in Olive Products: From the Tree to the Table." *Trends in Food Science & Technology* 44 (2): 226–42. https://doi.org/10.1016/j.tifs.2015.04.009.

Marchi, Susanna, Diego Guidotti, Massimo Ricciolini, and Ruggero Petacchi. 2016. "Towards Understanding Temporal and Spatial Dynamics of Bactrocera Oleae (Rossi) Infestations Using Decade-Long Agrometeorological Time Series." *International Journal of Biometeorology* 60 (11): 1681–94. https://doi.org/10.1007/s00484-016-1159-2.

Mavragani-Tsipidou, P. 2002. "Genetic and Cytogenetic Analysis of the Olive Fruit Fly Bactrocera Oleae(Diptera: Tephritidae)." *Genetica* 116 (1): 45–57. https://doi.org/10.1023/A:1020907624816.

Nestel, D., J. Carvalho, and E. Nemny-Lavy. 2004. "The Spatial Dimension in the Ecology of Insect Pests and Its Relevance to Pest Management." In *Insect Pest Management: Field and Protected Crops*, edited by A. Rami Horowitz and Isaac Ishaaya, 45–63. Berlin, Heidelberg: Springer. https://doi.org/10.1007/978-3-662-07913-3_3.

Ordano, Mariano, Izhar Engelhard, Polychronis Rempoulakis, Esther Nemny-Lavy, Moshe Blum, Sami Yasin, Itamar M. Lensky, Nikos T. Papadopoulos, and David Nestel. 2015. "Olive Fruit Fly (Bactrocera Oleae) Population Dynamics in the Eastern Mediterranean: Influence of Exogenous Uncertainty on a Monophagous Frugivorous Insect." *PLOS ONE* 10 (5): e0127798. https://doi.org/10.1371/journal.pone.0127798.

Pappas, M. L., G. D. Broufas, N. Koufali, P. Pieri, and D. S. Koveos. 2011. "Effect of Heat Stress on Survival and Reproduction of the Olive Fruit Fly Bactocera (Dacus) Oleae." *Journal of Applied Entomology* 135 (5): 359–66. https://doi.org/10.1111/j.1439-0418.2010.01579.x.

Paredes, Daniel, João Frederico Alves, Sara Mendes, José Miguel Costa, Joana Alves, António Alves da Silva, and José Paulo Sousa. 2023. "Landscape Simplification Increases Bactrocera Oleae Abundance in Olive Groves: Adult Population Dynamics in Different Land Uses." *Journal of Pest Science* 96 (1): 71–79. https://doi.org/10.1007/s10340-022-01489-1.

Perović, Tatjana, and Snježana Hrnčić. 2013. "Population Dynamics of Pre-Imaginal Stages of Olive Fruit Fly Bactrocera Oleae Gmel. (Diptera, Tephritidae) in the Region of Bar (Montenegro)." *Pesticidi i Fitomedicina* 28 (1): 23–29.

Petacchi, R., S. Marchi, S. Federici, and G. Ragaglini. 2015. "Large-Scale Simulation of Temperature-Dependent Phenology in Wintering Populations of Actrocera Oleae (Rossi)." *Journal of Applied Entomology* 139 (7): 496–509. https://doi.org/10.1111/jen.12189.

Pretty, Jules, and Zareen Pervez Bharucha. 2015. "Integrated Pest Management for Sustainable Intensification of Agriculture in Asia and Africa." *Insects* 6 (1): 152–82. https://doi.org/10.3390/insects6010152.

Ragaglini, G., Diego Tomassone, and Ruggero Petacchi. 2005. "Can Spring-Preventive Adulticide Treatments Be Assumed to Improve Bactrocera Oleae (Rossi) Management?" In .

Rodríguez-Cohard, Juan Carlos, José Domingo Sánchez-Martínez, and Vicente José Gallego-Simón. 2019. "Olive Crops and Rural Development: Capital, Knowledge and Tradition." *Regional Science Policy & Practice* 11 (6): 935–49. https://doi.org/10.1111/rsp3.12115.

Rodríguez-Díaz, F., A. M. Chacón-Maldonado, A. R. Troncoso-García, and G. Asencio-Cortés. 2024. "Explainable Olive Grove and Grapevine Pest Forecasting through Machine Learning-Based Classification and Regression." *Results in Engineering* 24 (December):103058. https://doi.org/10.1016/j.rineng.2024.103058.

Rondoni, Gabriele, Elisabetta Mattioli, Vito Antonio Giannuzzi, Elena Chierici, Andrea Betti, Gaetano Natale, Ruggero Petacchi, Franco Famiani, Antonio Natale, and Eric Conti. 2024. "Evaluation of the Effect of Agroclimatic Variables on the Probability and Timing of Olive Fruit Fly Attack." *Frontiers in Plant Science* 15 (July). https://doi.org/10.3389/fpls.2024.1401669.

Sciarretta, Andrea, Maria Rosaria Tabilio, Armando Amore, Marco Colacci, Miguel Á Miranda, David Nestel, Nikos T. Papadopoulos, and Pasquale Trematerra. 2019. "Defining and Evaluating a Decision Support System (DSS) for the Precise Pest Management of the Mediterranean Fruit Fly, Ceratitis Capitata, at the Farm Level." *Agronomy* 9 (10): 608. https://doi.org/10.3390/agronomy9100608.

Skendžić, Sandra, Monika Zovko, Ivana Pajač Živković, Vinko Lešić, and Darija Lemić. 2021. "Effect of Climate Change on Introduced and Native Agricultural Invasive Insect Pests in Europe." *Insects* 12 (11): 985. https://doi.org/10.3390/insects12110985.

Stavrianakis, Giorgos, Efstratios Sentas, Thomas Tscheulin, and Thanasis Kizos. 2024. "Does Biodiversity Affect Olive Fly Populations? Evidence from Different Understorey Treatments." *Discover Conservation* 1 (1): 3. https://doi.org/10.1007/s44353-024-00003-1.

Stavrianakis, Giorgos, Efstratios Sentas, Sofia Zafeirelli, Thomas Tscheulin, and Thanasis Kizos. 2025. "Utilizing Olive Fly Ecology Towards Sustainable Pest Management." *Biology* 14 (2): 125. https://doi.org/10.3390/biology14020125.

Topuz, H., and E. Durmusoglu. 2008. "The Effect of Early Harvest on Infestation Rate of Bactrocera Oleae (Gmelin) (Diptera: Tephritidae) as Well as Yield, Acidity and Fatty Acid Composition of Olive Oil." *Journal of Plant Diseases and Protection* 115 (4): 186–91. https://doi.org/10.1007/BF03356256.

Tscharntke, Teja, and Roland Brandl. 2024. "Plant-Insect Interactions in Fragmented Landscapes." *ResearchGate*, October. https://doi.org/10.1146/annurev.ento.49.061802.123339.

Tsitsipis, John. 1977. "Effect of Constant Temperatures on the Eggs of the Olive Fruit Fly, Dacus Oleae (Diptera, Tephritidae)." *Annales de Zoologie Ecologie Animale* 9 (1): 133–39.

UNESCO. 2019. "World Olive Tree Day: 26 November." https://unesdoc.unesco.org/ark:/48223/pf0000367371_eng.

Vreysen, M. J. B., A. S. Robinson, J. Hendrichs, and P. Kenmore. 2007. "Area-Wide Integrated Pest Management (AW-IPM): Principles, Practice and Prospects." In *Area-Wide Control of Insect Pests*, edited by M. J. B. Vreysen, A. S. Robinson, and J. Hendrichs, 3–33. Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-1-4020-6059-5_1.

Wang, Xin-Geng, Marshall W. Johnson, Kent M. Daane, and Hannah Nadel. 2009. "High Summer Temperatures Affect the Survival and Reproduction of Olive Fruit Fly (Diptera: Tephritidae)." *Environmental Entomology* 38 (5): 1496–1504. https://doi.org/10.1603/022.038.0518.

Yokoyama, Victoria Y. 2012. "Olive Fruit Fly (Diptera: Tephritidae) in California: Longevity, Oviposition, and Development in Canning Olives in the Laboratory and Greenhouse." *Journal of Economic Entomology* 105 (1): 186–95. https://doi.org/10.1603/EC11255.

8. Supplementary Materials

Table A. 1: Pearson correlation results between hours exceeding 32 °C (Avg32h or Any32h) and olive fruit fly population counts (Monthly (M) or 10-day period (10d)).

Metric	M–Avg32h	M–Any32h	10d–Avg32h	10d–Any32h
Correlation (r)	-0.254	-0.341	-0.228	-0.300
t-value	-1.618	-2.233	-2.509	-3.374
df	38	38	115	115
p-value	0.114	0.0315	0.0135	0.0010
95% CI (lower)	-0.524	-0.590	-0.393	-0.457
95% CI (upper)	0.063	-0.032	-0.048	-0.125
Significant (p < .05)	No	Yes	Yes	Yes

Table A. 2: Linear regression results between hours exceeding 32 °C (Avg32h or Any32h) and olive fruity fly population counts (Monthly (M) or 10-day period (10d)).

Metric	M–Avg32h	M–Any32h	10d–Avg32h	10d–Any32h
Slope	-0.0065	-0.0042	-0.0161	-0.0109
Std. Error	0.0040	0.0019	0.0064	0.0032
t-value	-1.618	-2.233	-2.509	-3.374
R^2	0.064	0.116	0.052	0.090
Adjusted R^2	0.040	0.093	0.044	0.082
Residual Std. Error	1.868	1.816	2.073	2.031
p-value	0.114	0.0315	0.0135	0.0010

Table A. 3: Pearson correlation results between population numbers in a given period (monthly and 10-day periods) and trap elevation.

Period	Correlation (r)	t-value	df	p-value	95% CI (lower)	95% CI (upper)
Overall	0.0349	10.5	90429	<2.2e-16	0.0284	0.0414
June	-0.0036	-0.426	13875	0.6704	-0.0202	0.0130
July	0.0603	8.371	19177	<2.2e-16	0.0462	0.0744

August	0.0967	13.488	19273	<2.2e-16	0.0827	0.1107
September	0.0694	9.655	19281	<2.2e-16	0.0553	0.0834
October	-0.0755	-10.389	18815	<2.2e-16	-0.0897	-0.0613
June-1	-0.037145	-1.7191	2139	0.085739	-0.079383	0.005226
June-2	0.008804	0.6439	5349	0.519654	-0.017995	0.035590
June-3	-0.002544	-0.2032	6383	0.838954	-0.027071	0.021987
July-1	0.004377	0.3497	6381	0.726603	-0.020158	0.028907
July-2	0.071443	5.7359	6413	1.01e-08	0.047053	0.095747
July-3	0.115979	9.3260	6379	1.48e-20	0.091703	0.140117
August-1	0.165994	13.4853	6418	6.85e-41	0.142109	0.189686
August-2	0.063566	5.1047	6423	3.41e-07	0.039174	0.087882
August-3	0.086041	6.9240	6428	4.82e-12	0.061727	0.110252
September-1	0.135620	10.9644	6416	9.97e-28	0.111524	0.159556
September-2	0.058179	4.6735	6431	3.02e-06	0.033789	0.082499
September-3	0.026933	2.1605	6430	0.030773	0.002495	0.051339
October-1	-0.016423	-1.3174	6433	0.187746	-0.040840	0.008014
October-2	-0.082781	-6.3723	5885	2.00e-10	-0.108098	-0.057356
October-3	-0.130359	-10.5946	6493	5.14e-26	-0.154191	-0.106376

Table A. 4: Linear regression results between population numbers in a given period (monthly and 10-day periods) and trap elevation.

Time	**Slope**	**Std. Error**	**t-value**	**R^2**	**Adj. R^2**	**p-value**
Overall	0.0021722	0.0002069	10.50	0.001218	0.001207	< 2e-16
June	-0.0001483	0.0003484	-0.426	1.305e-05	-5.902e-05	0.6704
July	0.003289	0.000393	8.371	0.00364	0.003588	< 2e-16
August	0.006502	0.000482	13.49	0.009351	0.0093	< 2e-16
September	0.004991	0.000517	9.655	0.004811	0.00476	< 2e-16
October	-0.004790	0.000461	-10.39	0.005703	0.00565	< 2e-16
June-1	-0.0014077	0.0008188	-1.719	0.00138	0.000913	0.0857
June-2	0.000293	0.000455	0.644	7.751e-05	-0.000109	0.5197
June-3	-0.0001203	0.0005921	-0.203	6.471e-06	-0.0001502	0.839
July-1	0.0002627	0.0007513	0.35	1.916e-05	-0.000138	0.7266
July-2	0.0037642	0.0006563	5.736	0.005104	0.004949	1.01e-08
July-3	0.0058337	0.0006255	9.326	0.01345	0.0133	< 2e-16
August-1	0.0083626	0.0006201	13.48	0.02755	0.0274	< 2e-16
August-2	0.0045298	0.0008874	5.105	0.004041	0.003886	3.41e-07

August-3	0.0066063	0.0009541	6.924	0.007403	0.007249	4.82e-12
September-1	0.008552	0.000780	10.96	0.01839	0.01824	< 2e-16
September-2	0.00437	0.000935	4.673	0.00339	0.00323	3.02e-06
September-3	0.00206	0.000953	2.160	0.00073	0.00057	0.0308
October-1	-0.00108	0.000819	-1.317	0.00027	0.00011	0.188
October-2	-0.00480	0.000754	-6.372	0.00685	0.00668	2.00e-10
October-3	-0.00856	0.000808	-10.60	0.01699	0.01684	<2e-16

Table A. 5: Levene's test for homogeneity of variances between the average fruit fly counts in different elevation categories (0-200m, 200-400m, >400m) for different time periods (M or 10d).

Period	**Df1 (Group)**	**Df2 (Residual)**	**F Value**	**p-value**	**Significance (p<0.05)**
Overall	2	90428	33.626	2.52e-15	**Yes**
Month 6	2	13874	1.042	0.3528	No
Month 7	2	19176	16.651	5.96e-08	**Yes**
Month 8	2	19272	50.882	<2.2e-16	**Yes**
Month 9	2	19280	36.269	<2.2e-16	**Yes**
Month 10	2	18814	17.980	1.58e-08	**Yes**
June-1	2	2138	0.9502	0.3868	No
June-2	2	5348	0.8492	0.4278	No
June-3	2	6382	1.2479	0.2872	No
July-1	2	6380	1.5262	0.2174	No
July-2	2	6412	10.238	3.64e-05	**Yes**
July-3	2	6378	25.476	9.55e-12	**Yes**
August-1	2	6417	52.603	<2.2e-16	**Yes**
August-2	2	6422	4.4431	0.0118	**Yes**
August-3	2	6427	22.265	2.31e-10	**Yes**
September-1	2	6415	37.641	<2.2e-16	**Yes**
September-2	2	6430	17.340	3.09e-08	**Yes**
September-3	2	6429	0.7419	0.4763	No
October-1	2	6432	1.1712	0.3101	No
October-2	2	5884	10.709	2.28e-05	**Yes**
October-3	2	6492	16.608	6.39e-08	**Yes**

Table A. 6: Results Comparing Olive Fruit Fly Counts Across Elevation Categories (0-200m, 200-400m, >400m) for different time periods (M or 10d).. Tests based on homogeneity of variances: standard ANOVA or Welch's ANOVA.

Time Period	Test	df1	df2	F value	p-value	Significance (p<0.05)
Overall	Welch's ANOVA	2	11613	98.287	< 2.2e-16	**Yes**
June	ANOVA	2	13,874	0.81	0.445	No
July	Welch's ANOVA	2	2424.5	33.030	7.031e-15	**Yes**
August	Welch's ANOVA	2	2639.2	96.156	< 2.2e-16	**Yes**
September	Welch's ANOVA	2	2458.2	72.112	< 2.2e-16	**Yes**
October	Welch's ANOVA	2	2455.6	16.768	5.847e-08	**Yes**
June-1	ANOVA	2	2138	0.622	0.537	No
June-2	ANOVA	2	5348	1.765	0.171	No
June-3	ANOVA	2	6382	0.812	0.444	No
July-1	ANOVA	2	6380	1.761	0.172	No
July-2	Welch's ANOVA	2	814.44	13.993	1.06e-06	**Yes**
July-3	Welch's ANOVA	2	772.13	32.476	2.87e-14	**Yes**
August-1	Welch's ANOVA	2	784.2	65.441	< 2.2e-16	**Yes**
August-2	Welch's ANOVA	2	925.3	15.535	2.311e-07	**Yes**
August-3	Welch's ANOVA	2	974.07	32.673	1.845e-14	**Yes**
September-1	Welch's ANOVA	2	798.64	55.206	< 2.2e-16	**Yes**
September-2	Welch's ANOVA	2	869.96	29.529	3.912e-13	**Yes**
September-3	ANOVA	2	6429	4.42	0.0121	**Yes**
October-1	ANOVA	2	6432	0.671	0.511	No
October-2	Welch's ANOVA	2	801.3	11.646	1.034e-05	**Yes**
October-3	Welch's ANOVA	2	775.5	19.825	4.007e-09	**Yes**

*Table A. 7: Results of post-hoc Games-Howell tests between elevation categories (Low (0-200m), Medium (200-400m), High (>400m)) for time periods (M or 10d) that showed significance in the (Welch's) ANOVA test. Periods marked with * were instead tested with a Tukey HSD test, as they fulfilled the condition of equal variances.*

Time Period	Category 1	Category 2	Mean Diff	95% CI	p-value	Significance (p<0.05)
Overall	0–200	200–400	0.79	[0.65, 0.93]	<0.001	**Yes**

Overall	0–200	400+	0.79	[0.52, 1.05]	<0.001	**Yes**
Overall	200–400	400+	–0.005	[–0.29, 0.28]	0.999	No
July	0-200	200-400	0.508	[0.249, 0.768]	1.31e-5	**Yes**
July	0-200	400+	1.72	[1.16, 2.28]	3.96e-12	**Yes**
July	200-400	400+	1.21	[0.62, 1.80]	4.76e-6	**Yes**
August	0-200	200-400	1.86	[1.52, 2.20]	3.54e-12	**Yes**
August	0-200	400+	1.58	[1.08, 2.09]	1.13e-12	**Yes**
August	200-400	400+	-0.278	[-0.845, 0.288]	0.482	No
September	0-200	200-400	1.83	[1.47, 2.20]	4.30e-12	**Yes**
September	0-200	400+	1.16	[0.405, 1.91]	9.26e-4	**Yes**
September	200-400	400+	-0.676	[-1.48, 0.124]	0.117	No
October	0-200	200-400	-0.518	[-0.839, -0.197]	0.000465	**Yes**
October	0-200	400+	-1.01	[-1.49, -0.525]	3.16e-6	**Yes**
October	200-400	400+	-0.488	[-1.03, 0.0483]	0.083	No
July-2	0-200	200-400	0.309	[-0.117, 0.735]	0.204	No
July-2	0-200	400+	2.33	[1.27, 3.39]	1.21e-6	**Yes**
July-2	200-400	400+	2.02	[0.92, 3.12]	5.87e-5	**Yes**
July-3	0-200	200-400	1.31	[0.835, 1.78]	4.23e-10	**Yes**
July-3	0-200	400+	2.05	[1.15, 2.94]	4.18e-7	**Yes**
July-3	200-400	400+	0.738	[-0.238, 1.71]	0.178	No
August-1	0-200	200-400	1.96	[1.47, 2.45]	2.76e-11	**Yes**
August-1	0-200	400+	3.00	[2.02, 3.99]	1.17e-11	**Yes**
August-1	200-400	400+	1.04	[-0.0276, 2.11]	0.058	No
August-2	0-200	200-400	1.19	[0.628, 1.76]	2.23e-6	**Yes**
August-2	0-200	400+	1.27	[0.414, 2.13]	0.002	**Yes**
August-2	200-400	400+	0.0823	[-0.847, 1.01]	0.976	No
August-3	0-200	200-400	2.42	[1.72, 3.12]	6.63e-11	**Yes**
August-3	0-200	400+	0.477	[-0.289, 1.24]	0.309	No
August-3	200-400	400+	-1.94	[-2.88, -1.01]	3.95e-6	**Yes**
September-1	0-200	200-400	2.53	[1.93, 3.14]	3.36e-11	**Yes**
September-1	0-200	400+	2.24	[1.11, 3.36]	1.20e-5	**Yes**
September-1	200-400	400+	-0.298	[-1.53, 0.932]	0.836	No
September-2	0-200	200-400	2.19	[1.52, 2.86]	5.98e-11	**Yes**
September-2	0-200	400+	0.466	[-0.554, 1.49]	0.531	No
September-2	200-400	400+	-1.72	[-2.86, -0.585]	0.001	**Yes**
September-3*	0–200	200–400	0.189	[-0.127, 0.505]	0.3395	No
September-3*	0–200	400+	0.353	[-0.235, 0.941]	0.3364	No
September-3*	200–400	400+	0.164	[-0.469, 0.797]	0.8163	No

October-2	0-200	200-400	-0.562	[-1.07, -0.0531]	0.026	**Yes**
October-2	0-200	400+	-1.38	[-2.11,-0.652]	3.15e-5	**Yes**
October-2	200-400	400+	-0.817	[-1.63, -0.00678]	0.048	**Yes**
October-3	0-200	200-400	-1.23	[-1.74, -0.719]	5.98e-8	**Yes**
October-3	0-200	400+	-1.47	[-2.43, -0.518]	0.000951	**Yes**
October-3	200-400	400+	-0.241	[-1.26, 0.774]	0.842	No