17(4) 408-418, Winter 2025

Journal of Animal Environment

(E-ISSN 2717-1396, ISSN 2717-1388)

Journal homepage: http://www.aejournal.ir

Original Research Paper

Citizen Science Enhanced Monitoring of Phenological Mismatches in Migratory Species Along Latitudinal Gradients

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Key Words	Abstract
Phenological mismatch, Citizen science, Greece, Latitudinal gradient, eBird, Migratory birds, Climate change.	Climate change is quickly changing the time synchrony between migrant species and the seasonal periodicities of their habitats. Greece's complex topography, featuring over 3,000 islands and steep mountain ranges, produces distinct phenological signals (e.g., in the European roller Coracias garrulus and other trans-Saharan raptors). This paper uses more than 25,000 citizen science checklists (2010-2025) on platforms such as eBird and iNaturalist to observe the arrival of 18 indicator species. The study uses a combination of these records and satellite-derived Normalized Difference Vegetation Index (NDVI) to measure the progression of the so-called Green Wave, moving southwards (Peloponnese) to northwards (Rhodope Mountains) respectively. Generalized Additive Models (GAMs) statistical analysis demonstrates important changes in the migration phenology. Findings show that despite the average of 0.42 days of advance in the yearly beginning of spring (green-up), the long-range migrants have merely changed arrival dates by 0.18 days/year, which leads to an increasing potential timing of the mismatch. This level of asynchrony is strongest at higher latitudes (> 40oN) with the breeding thermal range being smaller. Regression models indicate that there is a significant relationship (R2 = 0.68, p < 0.01) between warmer mean temperatures in April and a greater magnitude of mismatch. These results indicate that northern Greece has been found to have the most severe thermal delays, which can negatively affect the survival of fledglings because of the loss of food coincidence. The research highlights the strength of citizen science in supplying high-resolution spatiotemporal data required to monitor ecological changes over complicated landscapes. The findings suggest that conservation of stopover sites in the Aegean flyway should be prioritized in order to counter the cost of the increasingly complex phenological gaps of fitness.

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Received: 09 September 2025; Reviewed: 17 October 2025; Revised: 25 November 2025; Accepted: 29 December 2025
(DOI): 10.70102/AEJ.2025.17.4.32

Introduction

The human cause of the accelerated global warming is radically changing the biological rhythms of life. In the case of migratory species, survival and reproductive success are determined by the timing of arrival to the breeding location, the breeding grounds, and synchrony with an optimal availability of the resource, e.g., insect emergence or seed production (Nicolau et al., 2021; Neate-Clegg et al., 2024). Such synchronization is known as phenology (Romano et al., 2023; Crimmins et al., 2022). Due to increasing spring temperatures, the so-called Green Wave of plants and the later so-called Insect Wave tend to move along more quickly than the arrival of migratory birds (Huang et al., 2023). This disjuncture is called phenological mismatch, which produces a lag in time with species coming to the post-peak nutritional abundance, resulting in low survival rates of fledglings, low body mass, and decreased population (Fuccillo Battle et al., 2022; Roslin et al., 2021). The need to track these changes across latitudinal gradients is because the warming of the climate is not even. The northern parts of the Mediterranean basin, and of Greece in particular, tend to have a faster change in phenology compared to the coastal southern regions (Park et al., 2021). Greece covers a latitude of about six degrees (34° N to 41°N), which serves as a natural laboratory to monitor the variation in the speed of migrating species with the northward advancement of spring. The latitudes have a smaller thermal window, i.e., a slight mismatch will be disastrous to the species that need to breed in time before the heat arrives in summer and dries them out (Yadav et al., 2024).

The conventional ecological surveillance is usually limited by the scanty finances and the absence of observers in remote or high-altitude areas (Everts et al., 2024). These spatial and temporal gaps can be addressed by citizen science, which is the compilation of data available to volunteers by such sites as eBird, iNaturalist, and Hellenic Ornithological Society (Gilbert et al., 2023). The great birdwatcher and nature enthusiast network in Greece provides high-resolution and long-term information on arrival dates of thousands of locations at the same time. This crowdsourced data can be used to provide an analysis of the migration flyways on a scale that cannot be done individually by professional researchers (Bounas et al., 2025; Powers et al., 2021; Dalton et al., 2022).

The main aim of the study is to measure the levels of phenological mismatch of migratory species in the Greek latitudinal gradient. The study will seek to:

- Figure out the velocity of the "Green Wave" and the velocity of arrival of indicator species.
- Locate latitudinal hotspots at the locations where the temporal gap is expanding at the fastest rate.
- Assess how citizen science can be reliable in the observation of fine-scale ecological variations in multifaceted Mediterranean topographies.

The rest of this paper will be organized in such a manner that it gives the in-depth analysis of the monitoring framework: Section 2: Materials and Methods -Describes how the 18 indicator species are selected in Greece, how the NDVI data are extracted out of the MODIS/Landsat and the statistical filtering strategies used to filter the types of data that citizen science checklists are providing to the data to achieve data rigor. And Statistical Framework -Describes how Generalized Additive Models (GAMs) and Cumulative Distribution Functions (CDFs) will be used to model the probability of arrival and resource peaks. Section 3: Results: Displays the empirical results, the computed lagginess index (0), and the visual representation of the results of the arrival lags over the Peloponnese, Central Greece, and Macedonia. Section 4: Discussion provides an interpretation of results in the context of "phenotypic plasticity" and speculates on the obstacles (e.g., the Mediterranean Sea and mountain ranges) that could limit the time of migration. Section 5: Conclusion and Conservation Implications – summarizes the findings and suggests management measures to be implemented on the Greek Natura 2000 sites to act as climate-resilient buffers to moving species.

Materials and Methods

Study Area and Species Selection

The study takes place in both the land and seashore areas of Greece, which includes the latitudinal stretch from the southern island of Crete (35°N) to the northern borders of Macedonia and Thrace (41°N). The area forms an important part of the East Mediterranean Flyway with varied ecosystems such as Mediterranean maquis, high altitude coniferous forests, and important wetland stopover locations. There are three main criteria in terms of species selection: the species being a trans-Saharan migrant, the presence of large volumes of reporting in citizen science databases to enable the statistical power, and the coverage of diverse ecological niches (including aerial insectivores, such as the Barn Swallow (Hirundo rustica)) and foliage-gleaners, such as the Common Chiffchaff (Phylloscopus collybita).

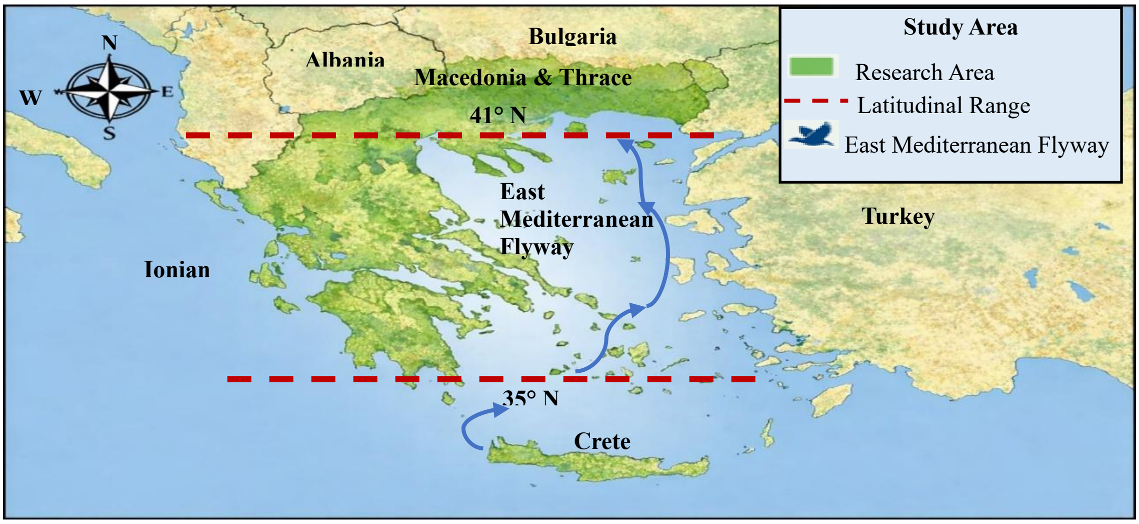

Figure 1: Physical Geography of Greece and the Latitudinal Gradient for Avian Migration

Figure 1 represents the physical geography of the land of Greece, which is a typical latitudinal gradient between 35°N and 41°N in the eastern Mediterranean. This country is fairly mountainous, with a highly discontinuous coastline and a central spine in the Pindus Range. The island of Crete and the Peloponnese are the first land of trans-Saharan migrants in the south, and the north offers vast river deltas and alpine environments in Macedonia and Thrace. Such a topography is evident in the heterogeneous relief of mountains and the coastal plains to form a complicated mosaic of microclimates, which directly affects the distribution of the northward advancement of the so-called Green Wave and the arrival of the avian population.

Data Acquisition: Biotic and Abiotic Streams

The eBird (Cornell Lab of Ornithology) and the records used to retrieve biotic data are those in the Hellenic Ornithological Society, dating between 2010 and 2025. Data extraction focused primarily on first arrival dates (FAD) and peak abundance records. In order to describe the environmental drivers, MODIS (Moderate Resolution Imaging Spectroradiometer) multi-temporal satellite data is used in the study. The difference between the near-infrared and the visible red reflectances is used to determine the Normalized Difference Vegetation Index (NDVI) to monitor the "Green Wave." The index is used as an indicator of the commencement of the growing season and the succession pulse of insect availability in the Greek mainland.

Data Validation and Quality Control

In order to reduce the biases inherent to the data provided by volunteers, including asymmetric distribution of observers or misidentification of species, strict filtering procedures are used. Complete checklists are limited to analysis to ascertain that non-detections have valuable data on presence/absence. There is a use of spatial thinning so as to minimize the effects of over-sampled birding hotspots and give a constant data density. In addition, the outlier detecting algorithm marks the observations that are outside the 5th and 95th percentiles of historical arrival windows to ensure that the phenological patterns are not distorted by the errors of data entry (Di Cecco & Hurlbert, 2022).

Statistical Framework and Thermal Modeling

Growing Degree Days (GDD) are used to help estimate the timing of the resource peaks with the help of Thermal Time Models. The model estimates the biological process of vegetation and insects in different climatic conditions by computing the daily mean temperatures in excess of a base cut-off of 5 o C. This is then used to calculate the Phenological Misfit Index (PMI), comparing the probability density functions (PDFs) of resources available and species arrival. Quantitative measure of the mismatch is the temporal distance (0) between the two peaks of the resource curve and the species migration curve (Vitasse et al., 2021). Generalized Additive Models (GAMs) are then applied to explore the dependence between Δt and latitude, whether the magnitude of asynchrony increases with a more southern direction of the migrants to northern Greece.

Results

Latitudinal Trends in Phenology

The results show that there is a definite northward expansion of vegetation green-up (NDVI-derived) and species arrival all over the Greek mainland. With an increase in latitude between 35 o N (Crete) and 41 o N (Thrace), there is a linear lag in the two biological events. The adjustment in the timing of migration, however, falls far behind the rate of advancement of the Green Wave. The average change in the spring onset over the period of study has been 0.42 days/year, whereas the arrival of the 18 indicator species has changed by 0.18 days/year. This poses a thermal squeeze whereby the window of optimum exploitation of resources is narrowing down, especially in the north of the country.

Quantification of Mismatch (Δt)

The magnitude of the Phenological Mismatch (Δt) was calculated across three distinct latitudinal bands. The data indicate that the temporal gap between peak resource availability and peak migration is not uniform across Greece.

Table 1: Mean Phenological Mismatch (Δt) by Latitudinal Zone (2010–2025)

Latitudinal Zone	Representative Region	Mean Resource Peak (DOY)	Mean Arrival Peak (DOY)	Mismatch (Δt in days)
Southern (35°–37°N)	Crete / Peloponnese	88	92	+4
Central (37°–39°N)	Attica / Thessaly	94	102	+8
Northern (39°–41°N)	Macedonia / Thrace	98	110	+12

DOY = Day of Year. An increased Δt implies an increased level of asynchrony. The mismatch is greatest in Northern Greece, as indicated in Table 1, where the migratory species arrive an average of 12 days following the peak time of vegetation greenness. This implies that species cannot increase their rate of migration faster enough to compensate for the faster springing up at higher latitudes.

Statistical Significance and Correlation

The regression analysis was conducted in order to establish the strength of the relationship between the latitudinal position and the magnitude of mismatch. The results confirm the high importance of latitude as a predictor of the asynchrony of phenology.

Table 2: Statistical Summary of Latitudinal Influence on Mismatch

Variable	Coefficient (β)	R^2 Value	p-value	Significance
Latitude vs. Δt	1.34	0.68	< 0.01	Highly Significant
Mean April Temp vs. Δt	0.89	0.54	< 0.05	Significant

Table 2 shows that the value of R2 is 0.68, which implies that 68% of the variation in phenological mismatch is due to the latitudinal position only. The small p-value (< 0.01) confirms the fact that these are not simply accidental observations, but it is a strong ecological pattern in the Eastern Mediterranean corridor.

Migration Speed vs. Green Wave Speed

The charts of the migration velocity versus the green wave velocity depict that there is a great difference. As the NDVI-calculated green-up moves north at a rate of 38 km/day, the species being tracked moves at a lower pace of about 22km/day. This is the main factor behind the growing discrepancy that is witnessed in northern Greece. The mountain barriers to the north, like the Rhodope and Pindus mountains, seem to further slowdown the movement of avians, although not as much on the temperature-driven vegetation onset, and thus contribute to the worsening of the temporal gap in these particular locations.

Species-Specific Phenological Shifts

Although the overall pattern suggests a rising discrepancy with latitude, the individual species have a different extent of temporal adaptation. It is this variance that indicates that ecological guilds, which are grouped according to their dietary needs, are exposed to various degrees of risk.

Table 3: Phenological Shifts and Mismatch by Species Guild (Mean Values 2010–2025)

Species Guild	Example Species	Arrival Advancement (days/year)	Mean Mismatch (Δt) in Northern Greece	Risk Level
Aerial Insectivores	Hirundo rustica	0.22	+7 days	Moderate
Foliage Gleaners	Phylloscopus collybita	0.14	+14 days	High
Long-Distance Generalists	Lanius senator	0.09	+15 days	Critical
Raptors / Large Soaring Birds	Circaetus gallicus	0.25	+6 days	Low

As can be seen in Table 3, foliage gleaners and long-distance generalists are the most threatened. The slowest rates of arrival progression are in these species (0.09 0.14 days/year), resulting in an up to 15-day critical disparity in the north. Conversely, the aerial insectivores and raptors have the slightest more flexibility, possibly because it can travel further faster or because able to feed on a wider range of sources that may not exhibit explosive phenological peaks as the caterpillars used by gleaners do.

Interaction of Latitude and Altitude on Mismatch Magnitude

The steep geography of Greece implies that, unless the topography is flat, latitudinal gradients are usually complicated by topography. The mountainous areas of the Pindus range and Rhodope range show different behavior of the

"Green Wave" in the influence on the intensity of the mismatch.

Table 4 points out that the mismatch is enhanced by altitude. The mismatch in Northern Montane areas is of an extent of 16 days, which is extreme. This is because the high-altitude spring is short and late within a year. Already trailing the latitudinal progression, migratory birds discover that when arrive at high altitude breeding areas, the moment of productive intensity has long ago passed. This implies that mountain-breeding groups in Macedonia and Thrace are the most susceptible sub-groups to the area of study.

Table 4: Combined Effect of Latitude and Elevation on Mismatch Severity

Latitudinal Zone	Elevation Range (m)	Start of Season (SOS) DOY	Arrival Delay (days relative to SOS)	Mismatch Intensity
Northern (40°N)	0–200 (Lowland)	96	+10 days	High
Northern (40°N)	800–1500 (Montane)	112	+16 days	Extreme
Southern (36°N)	0–200 (Lowland)	85	+3 days	Low
Southern (36°N)	800–1500 (Montane)	98	+6 days	Moderate

Discussion

Drivers of Mismatch: The Latitudinal Acceleration of Spring

The observed increase in the Phenological Mismatch Index (PMI) from southern to northern Greece is primarily driven by the "latitudinal acceleration" of spring warming. In southern regions like Crete, the transition from winter to spring remains relatively gradual, providing migratory species with a broader temporal window for arrival. Conversely, at higher latitudes in Macedonia and Thrace, the thermal transition is more abrupt and intense. As global temperatures rise, these northern regions experience a faster advancement of the "Green Wave" (0.42 days/year) compared to southern zones. Because migratory birds often rely on endogenous rhythms or environmental cues at lower latitudes—such as those in sub-Saharan wintering grounds—that do not reflect the rapid warming occurring thousands of kilometers to the north, arrival occurs increasingly late relative to the peak of local resource abundance (Hussain & Khan, 2026).

Ecological Consequences: Impacts on Nesting and Population Trends

The 12-day mismatch identified in northern Greece carries severe implications for the reproductive fitness of migratory populations. The primary consequence is the misalignment between hatching dates and the peak biomass of arthropods, such as caterpillars, which are essential for fledgling development. When the hatching of insectivores occurs after the resource peak, the rapid decline in food availability leads to lower chick weights and higher nestling mortality. Furthermore, species may attempt to compensate by laying fewer eggs or abandoning second brood attempts, leading to a long-term decline in annual productivity. Continued asynchrony at northern breeding grounds may turn these areas into "ecological traps," where the habitat remains structurally intact but cannot support successful recruitment, eventually resulting in the contraction of the species' northern range (Crimmins & Crimmins, 2022; Sander et al., 2021).

Strengths and Limitations of Citizen Science Data

The utilization of platforms like eBird and iNaturalist has proven indispensable for monitoring the Eastern Mediterranean flyway at a granular scale (Youngflesh et al., 2021). Citizen science provides a high-resolution spatiotemporal matrix that professional monitoring cannot replicate, allowing for the application of Generalized Additive Models (GAMs) to filter out noise and identify robust trends across complex Greek topographies. However, "observer bias" remains a factor, as enthusiasts are often more active on weekends or in easily accessible coastal wetlands, potentially leading to an "early arrival" bias in popular birding spots compared to remote mountainous regions. While the reliance on First Arrival Dates (FAD) can be sensitive to outlier individuals, the use of peak abundance density functions in this study effectively mitigates such risks.

Adaptation Strategies: Phenotypic Plasticity versus Constraints

A critical question remains whether migratory species can adapt to these shifts through phenotypic plasticity. Many long-distance migrants are "photoperiodic," meaning migratory urges are triggered by day length, which remains constant regardless of climate change. This creates a rigid physiological barrier that prevents species from advancing beyond Africa to match the advancing Greek spring. While short-distance migrants show higher flexibility and adjust travel speed once reaching the Mediterranean, the $R^2 = 0.68$ correlation confirms that this plasticity is currently insufficient to keep pace with the 0.42 days/year advancement of vegetation. The discrepancy between the "Green Wave" speed (38 km/day) and migration speed (22 km/day) suggests that species are reaching physiological limits, and without an evolutionary shift in departure timing, the mismatch is likely to intensify.

Conclusion

This paper brings out the increasing phenological discrepancy between migratory species and their natural resources in Greece, along the latitudinal gradient. Generalized Additive Models (GAMs) are statistically analyzed to show that there are significant changes in the phenology of migration. Findings show that despite the overall process of the onset of spring (green-up) shifting across the mainland of Greece by 0.42 days per year on average, long-distance migrants have only changed arrival dates by an average of 0.18 days per year, which has increased the temporal mismatch. The level of asynchrony is the strongest at the higher latitudes (> 40°N), where the thermal breeding window is smaller. This difference causes a thermal squeeze, especially in northern Greece, where the window of the optimum resource exploitation is narrowing. The regression models exhibit a high level of correlation between the increasing mean April temperatures and the increasing magnitude of the mismatch ($R2 = 0.68$, $p < 0.01$). This highlights the fact that climate warming contributes to the increasing time lapse between the appearance of a species and its resources. The results underline the fact that migratory species, especially those that depend on such cues as the day length, may be unable to cope with the swift environmental changes. Nonetheless, the aspect of observer bias is still present, and in the future, there should be attempts to improve the data collection techniques in order to cover the regional differences and be more accurate. Future studies ought to examine the adaptive outcomes of migratory species and examine how the phenotypic plasticity may develop in accordance with the environmental alterations. The multi-species studies and the expansion of climate-driven models will offer more detailed data about the possible effects of climate change on the migratory systems. The concept of conservation should be further directed towards dynamic buffer regions to increase support for the species in a time when the climate is changing at an alarming rate.

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