FROM DIVERSITY TO CONSERVATION: INSIGHTS FOR A NATIONAL GENETIC MONITORING PROGRAM FOR HONEY BEES IN THE FACE OF CLIMATE CHANGE

A THESIS SUBMITTED TO
THE GRADUATE SCHOOL OF NATURAL AND APPLIED SCIENCES
OF
MIDDLE EAST TECHNICAL UNIVERSITY

BY

MERT KÜKRER

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY
IN
BIOLOGY

MARCH 2024

Approval of the thesis:

FROM DIVERSITY TO CONSERVATION: INSIGHTS FOR A NATIONAL GENETIC MONITORING PROGRAM FOR HONEY BEES IN THE FACE OF CLIMATE CHANGE

submitted by **MERT KÜKRER** in partial fulfillment of the requirements for the degree of **Doctor of Philosophy** in **Biology, Middle East Technical University** by,

Prof. Dr. Naci Emre Altun
Dean, **Graduate School of Natural and Applied Sciences**

Prof. Dr. Mesut Muyan
Head of the Department, **Department of Biological Sciences**

Assist. Prof. Dr. C. Can Bilgin
Supervisor, **Department of Biological Sciences, METU**

Examining Committee Members:

Prof. Dr. Mehmet Somel
Department of Biological Sciences, METU

Prof. Dr. C. Can Bilgin
Department of Biological Sciences, METU

Prof. Dr. Tuğrul Giray
Department of Biology, University of Puerto Rico

Assoc. Prof. Dr. Hakan Gür
Department of Animal Production, Ahi Evran Unıversıty

Assist. Prof. Dr. Emrah Çoraman
Eurasia Institute of Earth Sciences, ITU

Date: 07.03.2024

I hereby declare that all information in this document has been obtained and presented in accordance with academic rules and ethical conduct. I also declare that, as required by these rules and conduct, I have fully cited and referenced all material and results that are not original to this work.

Name Last name : Mert Kükrer

Signature :

ABSTRACT

FROM DIVERSITY TO CONSERVATION: INSIGHTS FOR A NATIONAL GENETIC MONITORING PROGRAM FOR HONEY BEES IN THE FACE OF CLIMATE CHANGE

Kükrer, Mert
Doctor of Philosophy, Biology
Supervisor : Prof. Dr. C. Can Bilgin

March 2024, 155 pages

Understanding the population genetics and ecological dynamics of honey bees (*Apis mellifera*) is crucial for their conservation and sustainable management. In this study, we collected 460 honey bee samples from 392 localities across Anatolia and Thrace, representing five subspecies: *A. m. syriaca*, *A. m. caucasica*, *A. m. anatoliaca*, *A. m. meda*, and the C lineage ecotype from Thrace. Additionally, we acquired samples from other regions in Europe and the Caucasus, bringing the total number of samples to 691. We genotyped these samples at 30 microsatellite loci and used various statistical analyses to explore the genetic diversity and population structure of honey bees in the region. Our analyses revealed distinct genetic clusters corresponding to the subspecies' distribution and identified transition zones. We further investigated the environmental drivers of genetic variation using Gradient Forests and Generalized Dissimilarity Modeling. Our results indicate that climatic and geographic factors are essential in shaping honey bee population structure. Additionally, we analyzed temporal changes in genetic diversity under future climate scenarios, predicting potential shifts in the distribution of ancestral groups.

Moreover, we assessed protected area resemblance and proposed new conservation sites, considering representation and complementarity in ecological similarity. Overall, our study provides valuable insights into the population genetics and ecological patterns of honey bees, highlighting the importance of considering environmental factors for their conservation and management. These findings have implications for honey bee biodiversity conservation, management practices, and sustainable apiculture in the region and beyond.

Keywords: Honey Bee, Genetic Diversity, Population Structure, Climate Change, Conservation

ÖZ

ÇEŞİTLİLİKTEN KORUMAYA: İKLİM DEĞİŞİKLİĞİ KARŞISINDA BAL ARILARINA YÖNELİK BİR ULUSAL GENETİK İZLEME PROGRAMINA İLİŞKİN ÇIKARIMLAR

Kükrer, Mert
Doktora, Biyoloji
Tez Yöneticisi: Prof. Dr. C. Can Bilgin

Mart 2024, 155 sayfa

Bal arılarının (*Apis mellifera*) popülasyon genetiğini ve ekolojik dinamiklerini anlamak, koruma ve sürdürülebilir yönetim için önemlidir. Bu çalışmada Anadolu ve Trakya'daki 392 noktadan *A. m. syriaca, A. m. caucasica, A. m. anatoliaca, A. m. meda* alt türlerini ve C soy hattına ait bir ekotipi temsil eden 460 bal arısı örneği topladık. Ek olarak, Avrupa ve Kafkasya'nın diğer bölgelerinden örnekler alarak toplam örnek sayısını 691'e çıkardık. Bu örneklerde 30 mikrosatelit lokusunu genotipledik ve bölgedeki bal arılarının genetik çeşitliliğini ve popülasyon yapısını keşfetmek için çeşitli istatistiksel analizler kullandık. Analizlerimiz, alt türlerin dağılımına ve tanımlanan geçiş bölgelerine karşılık gelen farklı genetik kümeleri ortaya çıkardı. Gradyan Ormanı ve Genelleştirilmiş Benzeşmezlik Modellemesi kullanarak genetik çeşitliliğe dair çevresel itici güçleri tespit ettik. Sonuçlarımız, bal arısı popülasyon yapısını şekillendirmede iklimsel ve coğrafi etmenlerin önemini göstermektedir. Ek olarak, gelecekteki iklim senaryoları altında atasal grupların dağılımındaki olası değişiklikleri tahmin ettik. Ayrıca, korunan alanlara benzeşimi değerlendirdik ve temsil kabiliyeti ve tamamlayıcılığı göz önünde bulundurarak yeni koruma alanları önerdik. Genel olarak çalışmamız, bal arılarının popülasyon genetiği ve ekolojik örüntüleri hakkında değerli bilgiler sağlayarak, koruma ve yönetim için çevresel faktörlerin dikkate alınmasının önemini vurgulamaktadır. Bu bulguların, bölgede ve ötesinde bal arısı biyolojik çeşitliliğinin korunması, yönetimi ve sürdürülebilir arıcılık için çıkarımları vardır.

Anahtar Kelimeler: Bal Arısı, Genetik Çeşitlilik, Popülasyon Yapısı, İklim
Değişikliği, Koruma

I dedicate this thesis to the memory of “someone committed to rebel”—the socialist writer **Yaşar Kemal**, whose literary legacy continues to inspire and enrich our lives. On the occasion of his 100th birth year, I am grateful for the profound impact his words have had on my own journey. His dedication to social justice and his unapologetic stance on struggle against poverty and oppression will forever be remembered and cherished. May his timeless stories continue to captivate generations to come.

ACKNOWLEDGMENTS

I would like to express my heartfelt gratitude to the following individuals and organizations whose support and contributions have been instrumental in the completion of this thesis:

First and foremost, I extend my deepest appreciation to my supervisor, Dr. C. Can Bilgin, for his precious guidance, invaluable insights, and continuous encouragement throughout this research journey. His mentorship has been truly transformative.

I would like to pay tribute to the late Dr. Aykut Kence, my former supervisor, whose wisdom and expertise left a memorable mark on my academic pursuits. His legacy lives on through this work.

I would like to acknowledge the valuable contributions of Dr. Mesut Muyan, Dr. Mehmet Somel, Dr. Tuğrul Giray, and Dr. Hakan Gür, who provided their strong support and stood by me both in my thesis and personal endeavors.

My sincere appreciation goes to Dr. Emrah Çoraman for his friendly support and guidance. I extend my thanks to Dr. Ayşe Suzan Turak for her help and collaboration, which enhanced the quality of this study.

I am thankful to our beekeeping technician and my field companion Mustafa Nail Cırık for his dedicated assistance during the study. I thank Mert Elverici and my lab mates for the collaboration, and shared passion for research. I especially extend my gratitude to our students in the laboratory who actively participated in the fieldwork, beekeeper surveys, wet lab experiments, and data analyses. Their enthusiasm and hard work have been integral to the success of this project.

I am indebted to the beekeepers who generously provided the samples for this study, as well as the various beekeeper associations, ministry personnel, Şamil Tuncay Beştoy and the Society for Conservation of Environment and Honey Bees, and all

the individuals and entities in the field who supported and facilitated my research. Their cooperation and dedication are greatly appreciated.

Lastly, I am profoundly grateful to my dear partner, Özle Koyuncu Kükrer, and my dear sister Meriç Kükrer, and my family for their unwavering support, understanding, and patience throughout this challenging journey. Their belief in me has been my driving force.

This study was funded by Middle East Technical University Revolving Funds.

TABLE OF CONTENTS

CHAPTERS

APPENDICES

CHAPTER 1

BACKGROUND

Pollinators and ecosystems constitute a fundamental aspect of Earth's biodiversity, with the Western honey bee, *Apis mellifera*, standing as a central figure in the interplay between the two. Pollination of diverse flowering plants by honey bees underscores their crucial role in maintaining ecological balance and sustaining food security (Potts et al., 2010). However, the ongoing challenges associated with global change pose a threat to the persistence and resilience of these vital pollinators (IPBES, 2019).

1.1 Social structure and intracolony communication

A defining feature of *A. mellifera* is its highly organized social structure, characterized by complex caste differentiation and cooperative behaviors within colonies (Seeley, 2009). The colony comprises three castes: the queen, worker bees, and drones. The queen is the sole reproductive female, responsible for laying eggs, while worker bees engage in various tasks such as foraging, nursing, and hive maintenance. Drones, the male bees, are involved solely in mating with queens.

Their eusocial system contributes to the adaptation of honey bee colonies to their dynamic environment. The organization within colonies is orchestrated by sophisticated communication mechanisms, predominantly through pheromones and dance language (Winston, 1991). The waggle dance is particularly notable, with worker bees conveying information about the location of food sources to their hive mates (Seeley, 2009). This communication system enhances the efficiency of foraging activities and plays a crucial role in the overall functioning of the colony.

1.2 Foraging behavior and ecological significance

While foraging, honey bees serve as crucial pollinators for a multitude of crops and fruits crucial to global agriculture and wildflowers (Gallai et al., 2009). Thus, beyond their production of honey, the foraging behavior of *A. mellifera* is pivotal to its ecological significance and contributes to the biodiversity of terrestrial ecosystems and sustainability of natural habitats (Klein et al., 2007).

The global distribution of *A. mellifera* intersects with numerous biodiversity hotspots, where unique ecological conditions foster diverse assemblages of flora and fauna (Myers et al., 2000). In these regions, honey bees interact with an extraordinary array of plant species, forming intricate pollination networks. The co-evolutionary relationships between honey bees and local flora contribute to the overall biodiversity of these hotspots, making *A. mellifera* not just a beneficiary but also a key player in the ecological dynamics of these areas.

1.3 Evolutionary history and global distribution

The genus *Apis* encompasses 12 extant species grouped into three categories: giant honey bees, dwarf honey bees, and cavity-nesting honey bees (Arias and Sheppard, 2005). While the majority of *Apis* species are native to Asia, there is one notable exception, *A. mellifera*. Fossil evidence from the Oligocene period (34 to 23 million years ago) suggests that ancestral *Apis* originated in Europe, with subsequent migration occurring 23 to 5.5 million years ago during the Late Oligocene or the Miocene epoch (Ruttner, 1988; Kotthoff et al., 2013). Two primary hypotheses have been proposed to explain this migration: one proposes that ancestral *Apis* migrated from Europe to Asia, where it diversified into the three distinct categories; the other suggests that ancestral *Apis* remained widespread in Europe and Asia, with a later colonization of Africa via the Iberian Peninsula near the end of the Miocene, resulting in the emergence of *A. mellifera*, while other *Apis* species originated from Asian ancestors.

While it is widely agreed upon that the genus experienced significant diversification in Asia, uncertainties persist regarding the ancestral origins and adaptive radiation of contemporary Western honey bee lineages and subspecies (Lin et al., 2023). A comprehensive compilation based on morphological characteristics suggested four main lineages: the A lineage in Africa, the C lineage in eastern Europe, the M lineage in western and northern Europe, and the O lineage in western Asia (Ruttner, 1988). Recent molecular studies have largely corroborated these lineages and identified additional lineages, including the Y lineage for populations in the Arabian Peninsula, L in northeastern Africa, and U in Madagascar Island (Garnery et al., 1992; Franck et al., 2000; Franck et al., 2001; Whitfield et al., 2006; Meixner et al., 2013; Harpur et al., 2014; Wallberg et al., 2014; Cridland et al., 2017; Dogantzis et al., 2021).

Beekeeping has deep historical roots in Anatolia, dating back to 6600 BC during the reign of the Hittite civilization (Akkaya and Alkan, 2007). Türkiye hosts more than nine million hives distributed across the country, tripling those in the United States and equating to half the total hives in EU countries combined (FAO, 2022). Nearly one-fifth of recognized *A. mellifera* subspecies, including *A. m. meda*, *A. m. syriaca*, *A. m. caucasica*, and *A. m. anatoliaca* from the O-lineage, along with an ecotype from the C subspecies group, are found in Türkiye (Kandemir et al., 2005; Kükrer et al., 2021). Furthermore, genetic material from the A lineage has been identified in native bees along the Levantine coast of Türkiye, thereby amalgamating genetic elements from Africa, Europe, and Asia (Kandemir et al., 2006).

1.4 Local adaptation and global change

The relationship between humans and honey bees has played a significant role in expanding the geographic distribution of *A. mellifera*. Through anthropogenic translocation of colonies beyond their natural range, this species has become globally distributed and can be found on every inhabited continent, thriving in climates ranging from temperate regions to subtropical and tropical environments (De la Rúa et al., 2009). The geographic diversity of the Western honey bee is a testament to its historical ability to adapt and disperse across a wide array of ecosystems. Different subspecies of *A. mellifera* have developed specific adaptations to cope with varied temperature, precipitation, and seasonal patterns, showcasing an impressive capacity to thrive in climates ranging from subarctic to subtropical (Whitfield et al., 2006).

As the Earth's climate undergoes rapid transformations, honey bees find themselves grappling with a suite of challenges (Vanbergen et al., 2013). Alterations in temperature patterns, precipitation regimes, and the frequency of extreme weather events directly impact the foraging behavior, reproductive success, and overall health of honey bee colonies. The consequences of these changes extend beyond the individual level, affecting the intricate social dynamics within colonies and, consequently, the broader ecosystem. While the geographic diversity of *A. mellifera* has been a source of strength for the species, it also exposes populations to an array of threats. Habitat loss, pesticide exposure, and the spread of diseases pose challenges to honey bee populations worldwide (Goulson et al., 2015). Understanding how these threats interact with the diverse ecological contexts in which honey bees exist is crucial for developing effective conservation strategies.

REFERENCES

Akkaya, H., & Alkan, S. (2007). Beekeeping in Anatolia from the Hittites to the present day. Journal of apicultural research, 46(2), 120-124.

Arias, M. C., & Sheppard, W. S. (2005). Phylogenetic relationships of honey bees (Hymenoptera: Apinae: Apini) inferred from nuclear and mitochondrial DNA sequence data. Molecular Phylogenetics and Evolution, 37, 25–35.

Cridland, J. M., Tsutsui, N. D., & Ramírez, S. R. (2017). The complex demographic history and evolutionary origin of the western honey bee, Apis mellifera. Genome Biology and Evolution, 9, 457–472.

De la Rúa, P., Jaffé, R., Dall'Olio, R., Muñoz, I., & Serrano, J. (2009). Biodiversity, conservation and current threats to European honeybees. Apidologie, 40(3), 263-284.

Dogantzis, K. A., Tiwari, T., Conflitti, I. M., Dey, A., Patch, H. M., Muli, E. M., ... Zayed, A. (2021). Thrice out of Asia and the adaptive radiation of the western honey bee. Science Advances, 7, eabj2151.

Food and Agriculture Organization of the United Nations. (2022). FAOSTAT statistical database. [Rome] :FAO

Franck, P., Garnery, L., Loiseau, A., Oldroyd, B. P., Hepburn, H. R., Solignac, M., & Cornuet, J. M. (2001). Genetic diversity of the honeybee in Africa: Microsatellite and mitochondrial data. Heredity, 86, 420–430.

Franck, P., Garnery, L., Solignac, M., & Cornuet, J.-M. (2000). Molecular confirmation of a fourth lineage in honeybees from the Near East. Apidologie, 31, 167–180.

Gallai, N., Salles, J. M., Settele, J., & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological economics, 68(3), 810-821.

Garnery, L., Cornuet, J.-M., & Solignac, M. (1992). Evolutionary history of the honey bee Apis mellifera inferred from mitochondrial DNA analysis. Molecular Ecology, 1, 145–154.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science, 347(6229), 1255957.

Harpur, B. A., Kent, C. F., Molodtsova, D., Lebon, J. M. D., Alqarni, A. S., Owayss, A. A., & Zayed, A. (2014). Population genomics of the honey bee reveals strong signatures of positive selection on worker traits. Proceedings of the

National Academy of Sciences of the United States of America, 111, 2614–2619.

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services (summary for policy makers). IPBES Plenary at its seventh session (IPBES 7, Paris, 2019). Zenodo. https://doi.org/10.5281/zenodo.3553579

Kandemir, İ., Kence, M., & Kence, A. (2005). Morphometric and electrophoretic variation in different honeybee (Apis mellifera L.) populations. Turkish Journal of Veterinary & Animal Sciences, 29(3), 885-890.

Kandemir, I., Kence, M., Sheppard, W. S., & Kence, A. (2006). Mitochondrial DNA variation in honey bee (Apis mellifera L.) populations from Turkey. Journal of apicultural research, 45(1), 33-38.

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. Proceedings of the royal society B: biological sciences, 274(1608), 303-313.

Kotthoff, U., Wappler, T., & Engel, M. S. (2013). Greater past disparity and diversity hints at ancient migrations of European honey bee lineages into Africa and Asia. Journal of Biogeography, 40, 1832–1838.

Kükrer, M., Kence, M., & Kence, A. (2021). Honey bee diversity is swayed by migratory beekeeping and trade despite conservation practices: Genetic evidence for the impact of anthropogenic factors on population structure. Frontiers in Ecology and Evolution, 9, 556816.

Lin, Z., Zhu, Z., Zhuang, M., Wang, Z., Zhang, Y., Gao, F., Niu, Q., & Ji, T. (2023). Effects of local domestication warrant attention in honey bee population genetics. Science Advances. https://doi.org/ade7917

Meixner, M. D., Pinto, M. A., Bouga, M., Kryger, P., Ivanova, E., & Fuchs, S. (2013). Standard methods for characterising subspecies and ecotypes of Apis mellifera. Journal of Apicultural Research, 52, 1–28.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853-858.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. Trends in ecology & evolution, 25(6), 345-353.

Requier, F., Garnery, L., Kohl, P. L., Njovu, H. K., Pirk, C. W., Crewe, R. M., & Steffan-Dewenter, I. (2019). The conservation of native honey bees is crucial. Trends in ecology & evolution, 34(9), 789-798.

Ruttner, F. (1988). Biogeography and Taxonomy of Honeybees. Springer Berlin Heidelberg.

Seeley, T. D. (2009). The wisdom of the hive: the social physiology of honey bee colonies. Harvard University Press.

Vanbergen, A. J., & Initiative, T. I. P. (2013). Threats to an ecosystem service: pressures on pollinators. Frontiers in Ecology and the Environment, 11(5), 251-259.

Wallberg, A., Han, F., Wellhagen, G., Dahle, B., Kawata, M., Haddad, N., ... Webster, M. T. (2014). A worldwide survey of genome sequence variation provides insight into the evolutionary history of the honeybee Apis mellifera. Nature Genetics, 46, 1081–1088.

Whitfield, C. W., Behura, S. K., Berlocher, S. H., Clark, A. G., Johnston, J. S., Sheppard, W. S., ... Tsutsui, N. D. (2006). Thrice out of Africa: Ancient and recent expansions of the honey bee, Apis mellifera. Science, 314, 642–645.

Winston, M. L. (1991). The biology of the honey bee. Harvard University Press.

Zapata-Hernández, G., Gajardo-Rojas, M., Calderón-Seguel, M., Muñoz, A. A., Yáñez, K. P., Requier, F., ... & Arrieta, H. (2024). Advances and knowledge gaps on climate change impacts on honey bees and beekeeping: A systematic review. Global Change Biology, 30(3), e17219.

CHAPTER 2

PERSPECTIVE

(with Cemal Can Bilgin, published in *Bee Studies*).

2.1 Abstract

Quantitative studies concerning the impact of climate change on pollinators are generally lacking. Relationship between honey bee diversity, present local adaptations and adaptive capacity of subspecies and ecotypes in the face of climate change is an urgent but rather poorly studied topic worldwide. Actually, such an effort lies at the crossroads of various fields of inquiry. Those include conservation of local honey bee diversity, breeding various local stocks for desirable traits, and enabling resilient ecosystem services. With the ever-increasing availability of genomic tools, now it is more probable than ever to simultaneously fill such gaps. Current knowledge and growing awareness on honey bee diversity in Turkey let us progress into a more systematic utilization of this resource through development of climate-conscious models. Here we provide a framework that takes genomic diversity into account for assessing and monitoring various aspects of species' response to climate change which can potentially lead to drastic impacts.

2.2 Introduction

As the global environment alters with an increasing pace, ecosystem resilience becomes more reliant on the readjustment of species to emerging conditions. For this reason, it is important to evaluate, monitor and manage genetic diversity and related adaptation capacity based on scientific results. Given the possible angular effects of climate change in the upcoming decades, it is necessary to expose how ecosystems can benefit from genetic diversity. In addition, it is essential to develop and test best practice protocols to monitor genetic diversity that varies in space and time.

In terms of honey bee (*Apis mellifera*) biodiversity, the current direction of anthropogenic impact is in line with the loss of native races and the adaptations they have accumulated over thousands of years (de la Rúa et al., 2013; Jensen et al., 2005; Soland-Reckeweg et al., 2009). The factors that cause colony losses in honey bees are very diverse. Possible loss or decline of pollinators are thought to be due to a combined result of destruction and degradation of habitats, pollution and pesticide related toxicity, pathogen and parasite related diseases, and invasive species many of which also effect honey bees (De la Rúa et al., 2009; Goulson et al., 2015; et al., 2010; Van der Zee et al., 2015).

Increasing hybridization of honey bee subspecies due to human activities like migratory beekeeping and queen and colony trade also threaten honey bees by potentially leading to loss of gene combinations that provide local success (Kükrer et al., 2021). The absence of effective implementation of documentation and monitoring methods for uncovering the genetic basis of adaptive traits makes it difficult to understand and resist the trend of human induced loss of adaptive diversity. However, it is not possible to achieve success in long-term monitoring especially, without developing methods that are inexpensive and feasible but still able to provide meaningful data by deployment of technology-intensive procedures.

New risks and challenges are causing concern as global climate change potentially elevate temperatures and aridity in many parts of the world. We have very little information - not only in Turkey but in the world - about the overall impact of climate change on honey bees, even less on pollinators as a whole. However, most predictions suggest that climate change will worsen the situation by introducing new stressors (González-Varo et al., 2013; Le Conte and Navajas, 2008).

A reduction in adaptive genetic diversity will not only be loss of a historic natural heritage that is intrinsically valuable but also of various economic and ecological benefits for the society (Espregueira et al., 2020). Urgently focusing on the genomic analysis of the relationship of honey bees with their environment in the era of global climate change will be to the benefit of both the society and the nature. There is now a strong incentive to consider and investigate pronounced influences of environmental conditions on honey bees through a perspective of ecosystem resilience.

This article aims to emphasize the need for developing a framework that takes genomic diversity into account for monitoring the adaptive capacities of honey bee subspecies and ecotypes present in Turkey in response to climate change.

2.3 It is not known in what way the global climate change will affect honey bee populations

It is predicted that Turkey's climate will in general become hotter and more arid (Bilgin and Türkeş, 2008; Bilgin, 2013). However, the impact of this change on ecosystems and species still needs to be explored. It is of decisive importance whether the pollinators in general and honey bees in particular can adapt to a rapidly changing environment due to their role in nature and agricultural activities. However, our knowledge of the adaptation capacities in those species is limited. In addition to the identification of genes taking a role in adaption to hot and dry environments, documenting the existence and distribution of such genes in honey bee populations is important too.

Beyond single genes, the distribution of subspecies is determined under the influence of various climatic, geographical and biological factors. These complex factors can be combined to model the subspecies' ecological niches whose long-term characteristics will retain themselves under natural selection (Peterson, 2003). It is not always true that the combination of environmental conditions in which the species can survive is limited only by the current distribution of the species. Therefore, when it comes to modeling the distribution of a species, it is also necessary to refer to the basic niche, realized niche and potential niche concepts (Sillero, 2011).

Such models can be used not only to explain the current situation but also to model the distributions in the past - especially in the ice ages during which subspecies were drawn to refuges (Kozak et al., 2008). If a precise population genetic structure map can be generated based on genome surveys making use of high-density SNP data it might be possible to clarify how current distributions of the subspecies are affected by historical processes.

Similar models can be used to predict how species and sub-species would react under various climate change scenarios (Fordham et al., 2013). Findings to be obtained in this way are good candidates as contributions to conservation planning, since they provide hints about how ecologically and economically important gene resources may change in the future.

There is no doubt of the various difficulties in terms of distribution modeling in species that interact with humans. However, these difficulties do not create insurmountable obstacles. For example, in the case of honey bee subspecies, the fact that these can be transported by people from one region to another would even be useful, as it will facilitate understanding of the potential niche (Jimenez-Valverde et al., 2011).

Of course, the purpose of creating models related to climate change cannot be to make definitive judgments about distributions, especially for species that humans utilize. The main purpose should be to reveal the stress factors and selection pressures that will occur in future ranges. Ecological niche models assist in determining relative weights of a wide variety of climatic and geographical factors that will require adaptation or species' adaptive capacities.

There is already evidence that the current climate might be playing a role in the distribution of honey bee subspecies. Separate studies in the Carpathians and on Africanized bees in South America indicate that borders of the subspecies might be determined by their capacity to adapt to vital factors such as temperature and precipitation (Coroian et al., 2014; Nelson et al., 2017). This is in contrast to artificial selection efforts by humans which are not mainly related to climate and geography, but rather agricultural characteristics such as yield and disease resistance.

Considering that honey bees have an intense interaction with the environment, it is almost impossible to think that they would not be affected by climate change. Therefore, the detection of genes that may prove to be useful in adapting climate change and investigating the effects of this change on the distribution of subspecies and ecotypes would fill an important gap.

2.4 Unique adaptations of honey bees in Turkey are not studied at the genome level

Migratory beekeeping and bee trade are shown to act like a hybrid zone mobile in space and time, facilitating the partial amalgamation of subspecies in Turkey (Kükrer, 2013; Kükrer et al., 2021; Oskay et al., 2019). Despite that, high levels of geographically structured genetic diversity of honey bee subspecies in Turkey and the need to develop policies to maintain it, was also confirmed.

But how can the natural population genetic structure be preserved, when about 5 million of the 8 million hives in Turkey are taken from one region to another each year, and tens of thousands of queen bees change hands? Could environmental consequences play a certain role in the maintenance of distinct subspecies? In order to find answers, it should be examined whether there is a relationship between the distribution of various geographical and climatic factors such as temperature, humidity, altitude, precipitation regime, winter severity, insolation, flora, and the current distribution of subspecies. It can also be tested which particular genetic features obtained from whole genome sequencing change in a clinal fashion in line with environmental factors (Jones et al., 2013).

If honey bee populations are subject to natural selection due to their environment, then this selection force would emerge as a stabilizing factor for preserving locally adapted subspecies by acting against hybrids, and eventually restricting gene flow between populations (Feder and Nosil, 2010). In that case, natural selection would counterweigh the effect of gene flow between populations and random genetic drift. As a result, it is inevitable to observe different combinations of allele frequencies in various populations (Savolainen et al., 2013). Sudden changes are to be expected where selection is relatively strong while a smoother transition would be observed in regions where gene flow between populations is higher (Beekman et al., 2008).

Since random genetic drift increases the differentiation between populations isolated from each other, the effects of geographical barriers also become measurable. In cases where a certain climatic factor or selection is not causative, it should be considered that the significant genetic distance between populations depends on geographical isolation (Manel et al., 2003).

The functions of the DNA regions candidates for selection can be easily inferred since honey bee genome was sequenced at an early stage and is studied relatively well (The Honey Bee Genome Sequencing Consortium, 2006). Therefore, it is possible to investigate the relationship between selected genes and environmental factors. At this stage, the goal is to make biologically meaningful inferences about the functions of any candidate genes selected in relation to climatic and geographical variables.

In a recent study on the relationship between environmental conditions and genome-wide selection, it has been observed that altitude-related adaptations are preserved in two African subspecies where gene flow between them is so intense that it prevents observation of a genetic structure (Wallberg et al., 2017). It is normal to expect a similar process in Turkey where adaptations to environmental factors were preserved despite high levels of gene flow. In another study from Kenya, genes that could play an important role in adaptation to various climate types and geographies were investigated by comparing savanna, coastal, mountain and desert populations (Fuller et al., 2015). In research conducted on a newly identified subspecies in China, researchers focused on the genetic effects created by transition from tropics to the temperate zone (Chen et al., 2016). In the Iberian Peninsula where genome-wide selection signals based on bioclimatic variables were investigated (Henriques et al., 2018) the findings demonstrate that genes involved in regulation of the biological clock by biosynthesis of macromolecules are associated with local adaptations.

Concerning honey bee subspecies in Turkey, various studies making use of SNP markers in honey bees have been carried out in the past. Whitfield et al. (2006) included samples from Turkey in their research, but this work was essentially in the domain of phylogeography. Although 11 genes were identified as candidates for selection, that comparison was carried out on Italian, Western European and African bees but bees from Turkey were excluded from that part of the study. Wallberg et al. (2014) focused on local adaptations but samples obtained from Turkey were only evaluated for extraction of global population structure. Here, the main comparison was made between A-C, A-M and C-M lineages leaving aside O-lineage bees which also includes subspecies in Turkey. Cridland, Tsutsui, and Ramírez (2017), did not themselves gather samples from Turkey but made use of data generated by Wallberg et al. (2014). Uncertainties caused by a sequencing method that is no longer available due to high error rates were revealed and the need for analysis of high-quality genome data belonging to samples from Turkey and South West Asia was emphasized.

Although different aspects of genetic diversity of honey bee subspecies in Turkey were examined, the way they are adapted to the local conditions were not studied at the genome level. In addition, despite extensive research, the exact distributional ranges of the subspecies and the core areas where they are found in “pure” forms are still not clear. This also holds for regions where subspecies’ ranges overlap and they exchange genes with each other, as well as for critical regions where sudden changes in the subspecies composition occur.

It is possible that these deficiencies would be eliminated with a well-planned countrywide study which, in this way, would lead to a better understanding of genetic resources of native honey bee races and provide the most basic information that could be utilized in breeding efforts. Bearing in mind the global climate change, uncovering how climate and geography affect honey bees will be vital for the success of future breeding and conservation projects.

2.5 There is no model yet to monitor honey bee genetic diversity in Turkey

In Turkey, within the last decade, awareness about the potential value of the honey bee diversity has radically improved due to intensive efforts of scientists, beekeepers' associations and civil society organizations. In parallel, there has been an increase in conservation implementations and rehabilitation in the field of honey bee ecotypes (Gül, 2020). Currently, breeding herds are either being created or have already been established in Ankara, Ardahan, Artvin, Çanakkale, Çorum, Düzce, Hatay, İzmir, Kırklareli, Kırşehir and Muğla provinces. Since these activities are aimed at local ecotypes, important genetic material is thus put under protection. In concordance with these efforts, a number of subspecies and ecotypes are in the process of being registered by The Ministry of Agriculture and Forestry as native genetic resources of Turkey. This action, too, can be expected to contribute to conservation and breeding efforts in Turkey.

Monitoring programs are implemented in order to detect changes in genetic variability or in the frequencies and the distribution of adaptive variants (Flanagan et al., 2018). It is possible now, to further enhance the valuable steps taken till the moment and start monitoring of honey bee genetic diversity in Turkey and to consider making use of emerging technological tools in the field of genome sequencing as well as the decreasing costs.

However, till now, methods used for discrimination of subspecies in such efforts are mainly based on morphology, geometric morphometry and on mitochondrial as well as nuclear DNA markers like microsatellites. Resolution provided by such methods are far from precise discrimination of ecotypes, let alone allowing accurate reflection of diversity present in Turkey. Furthermore, and more importantly, they do not let us to take into account a conscious incorporation of genomic elements that play role in adaptation of ecotypes to their natural environment. Today conservation and breeding efforts should focus more on genetic variation specifically improving the subspecies’ capacity to adapt climate change. Constraints related to the adequate documentation of genetic diversity in Turkey do not enable yet, the development of functional and at the same time low-cost monitoring models.

An adaptive management context with an integrated monitoring step will enjoy the chances of both learning more about the local ecotypes and evaluating the effectiveness of management actions once they are initiated. After an initial genomic assessment by sequence capture methods or SNP arrays, it is possible to consistently genotype many individuals over time. This would certainly help to reach diverse objectives like diagnosing introgression and conservation efficacy, characterization of neutral and adaptive genetic variation especially related to climate change, as well as retrieving information about desirable traits (Aykanat et al., 2016).

2.6 A potent long-term ecological research perspective and scope

Basically, any research addressing the adaptive capacities of subspecies in Turkey against climate change should cover the following scope:

(i) Core regions in which 5 honey bee subspecies stay unmixed should be identified by an intense sampling effort across the country from stationary apiaries whose beekeepers reject to replace queens and colonies with non-native races. In order to achieve this, genome-wide data obtained with next generation sequencing techniques should be utilized.

(ii) Despite the anthropogenic impact in the form of migratory beekeeping and trade, subspecies are known to preserve their identities at certain places. Selection at the genomic level naturally relies on environmental conditions. Investigation of this phenomenon necessarily means comparing relative weights of natural selection, gene flow and genetic drift within populations.

(iii) Candidate genes located in genome regions under selection and playing a role in adaptation to local conditions should be identified. The functions of these genes and their relation with the environmental conditions should be examined. Genetic features that play a role in adaptation to elevated temperatures and aridity should be revealed through various comparisons between populations residing in such milieu. Existing conservation and breeding efforts like those supported and carried out by The Ministry of Agriculture and Forestry and Turkish Beekeepers' Association should better be reinforced by evolutionary knowledge. This will be achieved through purposeful introduction of locally adaptive genetic variants in addition to variants that provide adaptive potential under climate change within such stocks.

(iv) In order to preserve the genetic diversity and adaptation capacities documented in this way, a low-cost, feasible, but technology-intensive monitoring method should be developed. After an initial assessment, intensive sampling coupled with monitoring of conservation areas for these alleles by at least 5-year intervals should be guaranteed.

(v) Population structure obtained from genetic data should be used in models that will shed light on the evolutionary histories of subspecies and how their natural distribution would be affected under various global climate change scenarios.

2.7 Discussion

The most important needs of the actual period include the establishment of quantitative and regular implementations to appraise, monitor and manage the genetic resilience and adaptive capacity for species under human use or those not. This points to relevance for incorporation of genetic and evolutionary knowledge in policies concerning conservation planning and sustainability of ecosystem services, particularly under the severe impact of global climate change (COST Committee of Senior Officials, 2018).

The challenges faced in this area can be more easily overcome via piecing together of the following pursuit, akin but not limited to providing integration platforms in order to link together stakeholders and developing collaborations that combine experience in various areas of expertise to form the basis of a sustainable impact as well as integrating emerging technological tools into existing activities; explaining decision-makers how genetic diversity can benefit ecosystems; developing and testing best practice protocols for monitoring genetic diversity in space and time. As a key pollinator, honey bees (*Apis mellifera*) draw much attention among species aimed for determination and monitoring of the genetic adaptation capacities in response to climate change.

Although honey bees are intensively managed by humans, they cannot be regarded as fully domesticated. Apart from wild populations in the natural distribution range of the species or feral colonies that escaped from human hands, even colonies under human control act as part of wildlife due to nectar and pollen foraging activities. Their unique role in pollination makes bees a critical species for ecosystem resilience in addition to agricultural production and ecosystem services.

We need to put forward a monitoring model that can process honey bee diversity throughout the country. This also provides an opportunity to go beyond a general characterization of biodiversity. It can be aimed to monitor, in terms of presence and distribution, both specific alleles involved until now in local adaptation to native conditions and also genetic features that may contribute to adaptive potential under conditions of global climate change.

Long-term monitoring is a costly and labor-intensive process. This is also the most important reason for the fact that monitoring studies with a large spatial scale are not always possible. A technology-intensive monitoring model that combines the most cost-effective, feasible, state-of-the-art scientific methods developed and tested till now is likely to contribute to the goal of creating standard and routine tools.

Developing a model for monitoring and utilization of honey bee genomic diversity is not only useful for revealing the adaptive potential to climate change, but also with simple customizations, would provide new opportunities for implementation of marker assisted selection in breeding for disease resistance (varroosis, Nosema, foulbrood, etc.), obtaining desirable phenotypic characters (gentleness, wintering success, low swarming tendency, etc.) and increased yield (honey, royal jelly, pollen, propolis, bee venom and other bee products).

Genomic diversity and adaptive potentials are rapidly lost or undergoing serious changes under human influence. With such a model, decision-makers and field operators might have a chance to benefit from genomic and evolutionary information in the face of adverse human-induced effects.

This piece focuses on the limits of our knowledge on honey bee diversity in Turkey, its interaction with the environment, the consequences of this interaction for natural selection, and its implications for the future under global climate change. We recommend that further research in honey bee genetics would better seek previously unexplored phenomenon, structures and relationships. Such investigation would have the potential to innovatively apply to the situation the knowledge and techniques in the field of genomics and to contribute in the formation of an understanding that will be utilized in a way which may concern many stakeholders.

REFERENCES

Aykanat, T., Lindqvist, M., Pritchard, V. L., & Primmer, C. R. (2016). From population genomics to conservation and management: a workflow for targeted analysis of markers identified using genome-wide approaches in Atlantic salmon Salmo salar. Journal of Fish Biology, 89, 2658-2679. doi:10.1111/jfb.13149

Beekman, M., Allsopp, M. H., Wossler, T. C., & Oldroyd, B. P. (2008). Factors affecting the dynamics of the honey bee (Apis mellifera) hybrid zone of South Africa. Heredity, 100(1), 13–18. http://doi.org/10.1038/sj.hdy.6801058

Bilgin, C. C. & Türkeş, M. (2008). Turkey Country Report. In: R. Laušević, L. Jones-Walters, A. Nieto & A. Torre-Marín (Eds.), Climate change and biodiversity in South-East Europe: a concise summary of the scientific and policy context, issues and recommended actions (pp. 50-55). REC, Szentendre, Hungary; ECNC, Tilburg, the Netherlands

Bilgin, C. C. (2013). Türkiye'nin doğası iklim değişikliğinden nasıl etkilenecek? ODTÜ SEM Dönem Arası Seminerleri, 29-31 Ocak 2013, Ankara.

Chen, C., Liu, Z., Pan, Q., Chen, X., Wang, H., Guo, H., ... & Shi, W. (2016). Genomic analyses reveal demographic history and temperate adaptation of the newly discovered honey bee subspecies Apis mellifera sinisxinyuan n. ssp. Molecular Biology and Evolution, 33(5), 1337-1348.

Coroian, C. O., Muñoz, I., Schlüns, E. A., Paniti-Teleky, O. R., Erler, S., Furdui, E. M., ... & Moritz, R. F. (2014). Climate rather than geography separates two European honey bee subspecies. Molecular Ecology, 23(9), 2353-2361.

COST Committee of Senior Officials, (2018). Memorandum of Understanding for the implementation of the COST Action "Genomic Biodiversity Knowledge for Resilient Ecosystems" (G-BIKE) CA18134. https://e-services.cost.eu/files/domain_files/CA/Action_CA18134/mou/CA18134-e.pdf

Cridland, J. M., Tsutsui, N. D., & Ramírez, S. R. (2017). The Complex Demographic History and Evolutionary Origin of the Western Honey Bee, Apis mellifera. Genome Biology and Evolution, 9(2), 457-472.

De la Rua, P., Jaffé, R., Dall'Olio, R., Muñoz, I., & Serrano, J. (2009). Biodiversity, conservation and current threats to European honey bees. Apidologie, 40(3), 263-284.

De la Rúa, P., Jaffé, R., Muñoz, I., Serrano, J., Moritz, R. F. A., & Kraus, F. B. (2013). Conserving genetic diversity in the honeybee: Comments on Harpur et al. (2012). Molecular Ecology, 22, 3208-3210. doi:10.1111/mec.12333

Espregueira, G., Rey-Iglesia, A., Robles Tascón, L., Jensen, A. B., da Fonseca, R., & Campos, P. F. (2020). Declining genetic diversity of European honeybees along the twentieth century. Scientific Reports, 10, 10520. https://doi.org/10.1038/s41598-020-67370-2

Flanagan, S. P., Forester, B. R., Latch, E. K., Aitken, S. N., & Hoban, S. (2018). Guidelines for planning genomic assessment and monitoring of locally adaptive variation to inform species conservation. Evolutionary Applications, 11, 1035-1052. https://doi.org/10.1111/eva.12569

Feder, J. L., & Nosil, P. (2010). The efficacy of divergence hitchhiking in generating genomic islands during ecological speciation. Evolution, 64(6), 1729-1747.

Fordham, D. A., Akçakaya, H. R., Araújo, M. B., Keith, D. A., & Brook, B. W. (2013). Tools for integrating range change, extinction risk and climate change information into conservation management. Ecography, 36(9), 956–964. http://doi.org/10.1111/j.1600-0587.2013.00147.x

Fuller, Z. L., Niño, E. L., Patch, H. M., Bedoya-Reina, O. C., Baumgarten, T., Muli, E., ... & Masiga, D. (2015). Genome-wide analysis of signatures of selection in populations of African honey bees (Apis mellifera) using new web-based tools. BMC genomics, 16(1), 518.

González-Varo, J. P., Biesmeijer, J. C., Bommarco, R., Potts, S. G., Schweiger, O., Smith, H. G., ... & Vilà, M. (2013). Combined effects of global change pressures on animal-mediated pollination. Trends in Ecology & Evolution, 28(9), 524-530.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science, 347(6229).

Gül, A. (2020). Islah çalışmalarımız: “Türkiye’de Bulunan Bazı Arı (Apis mellifera L.) Irk ve Genotiplerini Temsil Eden Kolonilerin Orijinal Alanlarında Morfolojik ve Moleküler Karakterizasyonu ve Belirli Karakterler Yönünden İyileştirilmesi” projesi. TAB Arıcılık Dergisi, 3, 8-9.

Henriques, D., Wallberg, A., Chávez-Galarza, J., Johnston J., Webster M., & Pinto M. (2018). Whole genome SNP-associated signatures of local adaptation in honey bees of the Iberian Peninsula. Scientific Reports, 8(1), 11145. doi: 10.1038/s41598-018-29469-5.

Honey Bee Genome Sequencing Consortium (2006). Insights into social insects from the genome of the honey bee Apis mellifera. Nature, 443(7114), 931–949. https://doi.org/10.1038/nature05260

Jensen, A. B., Palmer, K. A., Boomsma, J. J., & Pedersen, B. V. (2005), Varying degrees of Apis mellifera ligustica introgression in protected populations of the black honeybee, Apis mellifera mellifera, in northwest Europe. Molecular Ecology, 14, 93-106. doi:10.1111/j.1365-294X.2004.02399.x

Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P., & Lobo, J. M. (2011). Use of niche models in invasive species risk assessments. Biological invasions, 13(12), 2785-2797.

Jones, M. R., Forester, B. R., Teufel, A. I., Adams, R. V., Anstett, D. N., Goodrich, B. A., … Manel, S. (2013). Integrating landscape genomics and spatially explicit approaches to detect loci under selection in clinal populations. Evolution, 67(12), 3455–3468. http://doi.org/10.1111/evo.12237

Kozak, K. H., Graham, C. H., & Wiens, J. J. (2008). Integrating GIS-based environmental data into evolutionary biology. Trends in Ecology and Evolution, 23(3), 141–148. http://doi.org/10.1016/j.tree.2008.02.001

Kükrer, M. (2013). Genetic diversity of honey bee populations in Turkey based on microsatellite markers: a comparison between migratory versus stationary apiaries and isolated regions versus regions open to migratory beekeeping (M.Sc. Thesis), METU, Ankara, Turkey.

Kükrer, M., Kence, M., & Kence, A. (2021). Honey bee diversity is swayed by migratory beekeeping and trade despite conservation practices: Genetic evidence for the impact of anthropogenic factors on population structure. Frontiers in Ecology and Evolution, 9, 556816.

Le Conte, Y., & Navajas, M. (2008). Climate change: impact on honey bee populations and diseases. Revue Scientifique et Technique-Office International des Epizooties, 27(2), 499-510.

Manel, S., Schwartz, M. K., Luikart, G., & Taberlet, P. (2003). Landscape genetics: Combining landscape ecology and population genetics. Trends in Ecology and Evolution, 18(4), 189–197. http://doi.org/10.1016/S0169-5347(03)00008-9

Nelson, R. M., Wallberg, A., Simões, Z. L. P., Lawson, D. J., & Webster, M. T. (2017). Genome-wide analysis of admixture and adaptation in the Africanized honey bee. Molecular Ecology, 26(14), 3603-3617.

Oskay, D., Kükrer, M., & Kence, A. (2019). Muğla Bal Arısında (Apis mellifera anatoliaca) Amerikan Yavru Çürüklüğü Hastalığına Karşı Direnç Geliştirilmesi. Arıcılık Araştırma Dergisi, 11(1), 8-20.

Peterson, A. T. (2003). Predicting the geography of species' invasions via ecological niche modeling. The quarterly review of biology, 78(4), 419-433.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution, 25(6), 345-353.

Savolainen, O., Lascoux, M., & Merilä, J. (2013). Ecological genomics of local adaptation. Nature Reviews. Genetics, 14(11), 807–820. http://doi.org/10.1038/nrg3522

Sillero, N. (2011). What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. Ecological Modelling, 222(8), 1343-1346.

Soland-Reckeweg, G., Heckel, G., Neumann, P., Fluri, P., & Excoffier L. (2009). Gene flow in admixed populations and implications for the conservation of the Western honeybee, Apis mellifera. Journal of Insect Conservation, 13, 317. https://doi.org/10.1007/s10841-008-9175-0

Van der Zee, R., Gray, A., Pisa, L., & de Rijk, T. (2015). An Observational Study of Honey Bee Colony Winter Losses and Their Association with Varroa destructor, Neonicotinoids and Other Risk Factors. PLoS ONE, 10(7), e0131611. https://doi.org/10.1371/journal.pone.0131611

Wallberg, A., Han, F., Wellhagen, G., Dahle, B., Kawata, M., Haddad, N., … Webster, M. T. (2014). A worldwide survey of genome sequence variation provides insight into the evolutionary history of the honey bee Apis mellifera. Nature Genetics, 46(August), 1081-1088. http://doi.org/10.1038/ng.3077

Wallberg, A., Schöning, C., Webster, M. T., & Hasselmann, M. (2017). Two extended haplotype blocks are associated with adaptation to high altitude habitats in East African honey bees. PLoS Genetics, 13(5), e1006792.

Whitfield, C. W., Behura, S. K., Berlocher, S. H., Clark, A. G., Johnston, J. S., Sheppard, W. S., … Tsutsui, N. D. (2006). Thrice out of Africa: ancient and recent expansions of the honey bee, Apis mellifera. Science (New York, N.Y.), 314(5799), 642–645. http://doi.org/10.1126/science.1132772

CHAPTER 3

INTRODUCTION

In the face of ongoing global change, biogeography has evolved into a dynamic field for understanding how species respond to environmental transformations (Parmesan, 2006). As habitats shift, ranges fluctuate, and ecosystems undergo rapid modifications, combining spatially explicit genetic data with information on species' adaptive traits enables the exploration of mechanisms shaping species distributions, including the role of selection (Joost et al., 2007; Gienapp et al., 2008; Eckert et al., 2008).

Divergent local geographic forms often result from spatially heterogeneous selection operating on complex alternative phenotypes influenced by the interplay between the external environment, genes, and their immediate genomic environment (Chevin and Hospital, 2008; Slatkin, 2009; Schwander et al., 2014). These traits are subjects of polygenic local adaptation and highly interconnected regulatory networks (Pritchard et al., 2010; Jones et al., 2012; Boyle et al., 2017). Correspondingly, selection acts upon multiple end phenotypes of whole organisms rather than single traits where harmoniously integrated gene complexes compromise between opposing selection pressures (Mayr, 1970).

When outbreeding is the disruptor of such coadapted gene complexes, locally adapted ecotypes can persist in parapatry despite gene flow (Lynch, 1991; Flaxman et al., 2013; Akerman and Bürger, 2014; Kulmuni and Westram, 2017). In that case, the observed geographic structure could be attributed to the interplay between the level of gene flow (migration) and selection pressure (local adaptation; Galindo et al., 2009; North et al., 2011; Kirk and Freeland, 2011). Interestingly, selective sweeps and background selection involved in local adaptation enhance the differentiation signal even at distant neutral loci (Charlesworth et al., 1997).

Moreover, a more pronounced differentiation at neutral loci in populations subject to local adaptation especially holds under high levels of inbreeding (Eckert et al., 2010), as is mostly the case with small populations isolated in refugia or confined to peripheries.

When selection acts on many loci, these boosted signals amplify further because it becomes more difficult for an allele to disentangle itself from non-neutral loci (Barton and Bengtsson, 1986). Thus, in the presence of local adaptation, the overall genetic structure *may act as a proxy* for the coupling between environment and organism, even if inferred from neutral markers. Although widely treated as a mere confounding element of adaptive marker identification (Yu et al., 2006), population structure may have adaptive significance and inform about dynamic responses to environmental change.

Identifying ecological patterns associated with genetic clines might be challenging (Jones et al., 2013). Nevertheless, approaches that account for non-linear interactions between environmental variables and ancestry compositions, such as Gradient Forests (GFs) and Generalized Dissimilarity Modeling (GDM), might be helpful (Ferrier et al., 2007; Ellis et al., 2012). GFs and GDM have been used in studying biodiversity at several layers, from ecosystems, communities, and species to populations, morphological traits, and genes (Bay et al., 2018; Mokany et al., 2019a, 2019b; Morgan et al., 2020; Gougherty et al., 2021; Fitzpatrick et al., 2021). Once biodiversity at any level is modeled as a function of multiple environmental gradients, the resulting models can be used to develop forecasts under global climate change scenarios (Fitzpatrick et al., 2011; Fitzpatrick & Keller, 2015).

The western honey bee (*Apis mellifera*) is a flagship species with a wide geographical range and ecological and economic significance (Ruttner, 1988; Franck et al., 2001; Meixner et al., 2010; Iwasaki and Hogendoorn, 2021). Due to their functional role as generalist, widespread, and efficient pollinators, honey bees may provide insights into ecosystems and respond to monitoring requirements about sustainability and diversity of communities (Quigley et al., 2019; Cunningham et al., 2022). Furthermore, spatio-temporal analyses on honey bee models can be implemented in various situations, biological questions, and species (Dearden et al., 2009).

Despite human-mediated gene flow, historical or current environmental features and genotype-environment interactions often continue to shape the spatially structured genomic diversity of distinct subspecies of honey bees (Büchler et al., 2014; Wallberg et al., 2014; Harpur et al., 2014; Cridland et al., 2017, 2018; Wragg et al., 2018; Parejo et al., 2020; Dogantzis et al., 2021; Gmel et al., 2023). Nevertheless, anthropogenic factors influence gene flow between honey bee populations. Queen/colony trade and migratory beekeeping practices create mobile hybrid zones in space and time (Kükrer et al., 2021). Although characterization of allelic divergence, selection candidates, and gene-environment associations across multiple honey bee species are well represented in the literature (Fuller et al., 2015; Chen et al., 2016, 2018; Wallberg et al., 2017; Henriques et al., 2018; Montero-Mendieta, 2019; Christmas et al., 2019; Ji et al., 2020; Cao et al., 2023; Everitt et al., 2023), the role of climate in compositional turnover among honey bee populations remains understudied.

Climate plays a crucial role in regulating various processes on Earth, for instance, ecosystem productivity and sustaining life, including humans (Howden et al., 2007; Willis and Bhagwat, 2009; Bellard et al., 2012). As climate change affects these processes, understanding the relationships involved is essential for mitigating negative impacts, particularly the expected profound changes in local extinctions, distribution ranges of species and ecosystems, community compositions, and ecosystem functioning by the end of the 21st century (Thuiller et al., 2019; Babcock et al., 2019; Román-Palacios & Wiens, 2020; Pörtner et al., 2022).

When climate vulnerability is high, economic damages become likely and may result in food insecurity, particularly in smallholder operations where environmental fluctuations magnify the challenges (Cohn et al., 2017; Coronese et al., 2019). Reducing economic damages and supporting food security may benefit from appreciation of locally adapted geographic forms, which may have higher yield, better colony development, greater performance and increased survival, infrequent occurrence or lower levels of pathogens, broader expression of desirable traits in swarming, defensiveness, or hygiene (Costa et al., 2012; Hatjina et al., 2014; Büchler et al., 2014; Meixner et al., 2014; Uzunov et al., 2014).

Quantitative studies regarding the various impacts of global change on honey bees and beekeeping are limited in comparison to the level of threats encountered (Gordo and Sanz, 2006; Kovac and Stabentheiner, 2011; Delgado et al., 2012; Howlett et al., 2013; Wang et al., 2016; Langowska et al., 2017; Flores et al., 2019; Nürnberger et al., 2019; Rowland et al., 2021; Keeler et al., 2021; Becsi et al., 2021; Gonzalez et al., 2022). This caveat is followed by the lack of forecasts about various impacts of environmental transformation on honey bees, such as spatio-temporal analyses of intra-specific turnover (Kükrer and Bilgin, 2020). The growing interest in ecological forecasting arises from the urgency to provide vital information on future population, community, and ecosystem states to enhance conservation, management, and adaptation strategies (Petchey et al., 2015).

A recent systematic review on climate change impacts on honey bees and beekeeping revealed significant negative impacts on various aspects of honey bee ecology and physiology, including food reserves, plant-pollinator networks, mortality rates, gene expression patterns, and metabolism (Zapata-Hernández et al., 2024). However, the assessment identified several key knowledge gaps in the existing literature. These include a limited number of predictive studies and a lack of comprehensive climate analysis, hindering our understanding of potential impacts on these vital pollinators. Moreover, studies have primarily focused on individual honey bee behavior rather than population dynamics, and have been conducted at relatively short spatial (<10 km) and temporal (<5 years) scales, limiting their applicability to larger-scale and mid-term assessments. Additionally, environmental analyses have predominantly relied on short-term weather data rather than long-term climate trends, further complicating efforts to forecast future impacts.

To assess honey bee diversity and habitats across temporal and spatial scales, we first characterize neutral genetic diversity and population structure across a historical refugium in and around Anatolia that poses a natural laboratory with diverse bee habitats and vast heterogeneity (Hewitt, 1999; Sönmez, 2022). Five native honey bee subspecies meet, exchange genes, and adapt to local conditions in Anatolia and Thrace, which comprise a unique experimental setting by bringing together genetic elements from Europe, Asia, and Africa (Kandemir et al., 2006; Kükrer et al., 2021). Deploying GFs, we identify drivers of intra-specific turnover by modeling genetic composition as a function of climate and geography. Then, we apply GDM to site-pair dissimilarities in GF-selected environmental variables to model ancestry estimates, which are treated as relative abundances and serve as the response variable. Finally, we carry out forecasts and spatio-temporal analyses to predict vulnerability and assess the persistence, resilience, and conservation efficacy of native populations to inform the management of honey bees.

CHAPTER 4

METHODS

4.1 Sampling and genotyping

We collected 460 honey bee samples from 392 localities in 75 provinces during fieldwork from May 2016 to November 2019. The localities cover the natural ranges of the five subspecies that occur in Türkiye: *A. m. syriaca*, *A. m. caucasica*, *A. m. anatoliaca*, and *A. m. meda* from the O lineage, as well as the ecotype from the C subspecies group that occurs in Thrace. We additionally acquired 45 *A. m. carnica* samples from Europe (Austria and Germany), 12 *A. m. caucasica* samples from the Caucasus (Georgia), and 174 samples from stationary beekeepers previously collected across Türkiye from March 2010 to August 2012 (Kükrer, 2013; Oskay et al., 2019). By doing so, the total number of samples gathered reached 691.

We grouped samples in and around Türkiye into 12 putative populations, as shown in **Figure 1**. Samples were grouped in those populations according to their proximity and similarities in climate, topography, and floral characteristics, alongside initial findings from prior research (Kandemir et al., 2006; Bodur et al., 2007; Tunca, 2009; Kükrer et al., 2021). Beekeepers in this study declared that they used honey bees from stocks native to their area and had not purchased non-native queens or colonies in the last ten years.

We isolated DNA from bee heads, grouped 30 microsatellite loci (Estoup et al., 1995; Solignac et al., 2003; Bodur et al., 2007; Shaibi et al., 2008; Tunca, 2009) into four sets (set 1: AP218, A113, AB024, AP249, A088, AP001, AP043; set 2: AP049, AP238, AC006, AP243, AP288, HBC1602, A107; set 3: A079, AC306, AP226, A007, HBC1601, AP068, A014, AP223; set 4: AP019, AB124, A043, A076, AP273, AP289, HBC1605, A028), amplified markers, determined fragment sizes, and binned the microsatellite alleles as specified in Kükrer et al. (2021). We excluded locus A076 since it did not consistently amplify across samples (see **Supplementary Table 1** for sample metadata, markers, and genotypes).

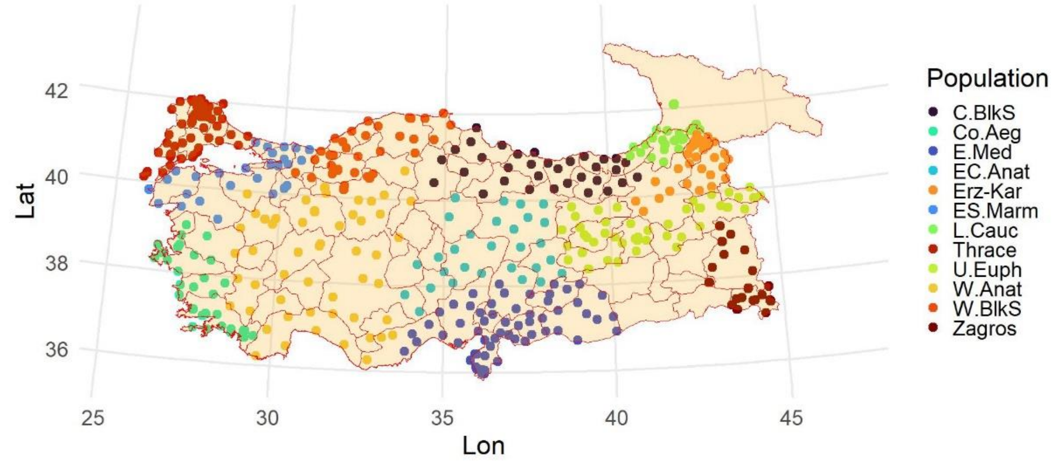


Figure 1. Sampling sites and populations.

Population abbreviations are as Eur: Europe, ES.Marm: East and South Marmara, Co.Aeg: Coastal Aegean, W.Anat: West Anatolia, W.BlkS: Western Black Sea, C.BlkS: Central Black Sea, L.Cauc: Lesser Caucasus, Erz-Kar: Erzurum-Kars Volcanic Plateau, U.Euph: Upper Euphrates, EC.Anat: East-Central Anatolia, E.Med: Eastern Mediterranean.

Since manual or automated genotyping of microsatellites may be prone to errors, we blindly double-genotyped 18,310 alleles in 290 individuals to estimate errors associated with the genotyping process. We took any mismatch between separate genotyping efforts as an error and corrected them by double-checking the raw electropherogram data. We removed eight samples genotyped at less than eight loci and a duplicated individual detected by the *R*-package *poppr* 2.9.4 (R Core Team 2022 version 4.2.2; Kamvar et al., 2014). To find full/half-sibs, we calculated relatedness by Colony 2.0 (Wang, 2012) and removed ten individuals assigned as siblings. This exclusion left 672 samples for downstream analyses.

4.2 Exploring genetic diversity and population structure

We estimated the frequency of null alleles by *popgenreport* 3.0.7 (Adamack and Gruber, 2014). We used the same package to calculate the total number of alleles per locus, observed and expected heterozygosity, deviations from Hardy-Weinberg equilibrium, linkage disequilibrium, the Shannon-Wiener diversity index, and the number of unique private alleles for each putative population. We estimated allelic richness and calculated the genetic fixation index (F_{st}), inbreeding coefficient (F_{is}), and allelic differentiation by *hierfstat* 0.5-11 (Goudet, 2005).

Before running a model-based clustering algorithm, we constructed phylogenies by UPGMA (Unweighted Pair Group Method with Arithmetic Mean) based on population genetic distances (Reynolds et al., 1983), visualized by the online tool Interactive Tree of Life v5 (Letunic and Bork, 2021). By AMOVA implemented in *poppr*, we tested whether genetic differences within and between populations differ from random expectations. We examined population structure by analyzing principal components through Discriminant Analysis of Principal Components (DAPC; Jombart et al., 2010), regular Principal Component Analysis (PCA), and a spatially explicit version of it: sPCA (Jombart et al., 2008). The sPCA method produces independent synthetic variables that maximize genetic variance and spatial autocorrelation (implemented in *adegenet* 2.1.10; Jombart, 2008).

We estimated individual membership coefficients (**Supplementary Table 1**) by Structure 2.3.4 (Pritchard et al., 2000), analyzed distinct K-values by Structure Harvester 0.6.94 (Earl and vonHoldt, 2012), permuted ancestry estimates by Clumpak (Kopelman et al., 2015), and visualized them with *dabestr* 0.3.0 (Ho et al., 2019). Based on population structure revealed through F_{st} values, phylogenetic tree, AMOVA results, and sPCA, we decided to carry out downstream analyses with five ancestral groups corresponding to five subspecies (*syriaca*, *caucasica*, *anatoliaca*, *meda*, and the C lineage ecotype from Thrace), in addition to the reference *carnica* population of C lineage.

However, the minimum K-value where all the subspecies became identifiable was seven rather than six, showcasing a spurious cluster that cannot be clearly traced to any particular geography but still staying within the distribution of *anatoliaca*. Hence, we summed membership coefficients from these two *anatoliaca* clusters for further analyses (see RESULTS section and **Figure 9**). Also, we combined residual *carnica* and Thracian clusters' membership coefficients to account for the total C lineage ancestry found in the samples. This summation across clusters left us with five ancestry estimates for each individual, i.e., Levantine (*syriaca*), Caucasian (*caucasica*), Anatolian (*anatoliaca*), Zagrosian (*meda*), and Thracian (C lineage) ancestral groups.

We identified spatial outliers for each of the five ancestral groups with *spdep* 1.2-8 (Bivand and Wong, 2018) by plotting ancestry estimates of each individual against their spatially lagged values within a mean radius of ~80 km. We manually checked those outliers and removed 80 samples with obvious mismatches to spatially expected ancestry. Elimination included unexpected cases such as unadmixed (i.e., with an estimated ancestry larger than 0.75) Caucasian individuals on the Aegean coast or unadmixed Thracian individuals in East Anatolia (see **Supplementary Figures 1, 2, 3, 4 and 5**). After this filtering according to admixture patterns (i.e., the particular composition of ancestry estimates at a specific site), there were 592 samples left for downstream analyses. Then, we interpolated ancestry estimates on geographic maps using a Kriging model where the covariance matrix of ancestry estimates exponentially decreases with distance (Jay et al., 2012).

4.3 Modeling intra-specific turnover and predicting ancestries

Besides the geographic distance, the kriging model leaves out any interaction between ancestry compositions and the environment. Nevertheless, the interplay between population structure and environment is usually more complex than isolation by distance alone. Hence, we modeled intra-specific turnover across the landscape to identify climatic and geographic drivers of variation in the admixture patterns. For that purpose, we fitted Gradient Forests (GFs) and Generalized Dissimilarity Models (GDMs) to ancestry estimates of 554 individuals in and around Anatolia (i.e., from Türkiye and Georgia), leaving out the 38 reference *carnica* samples from Austria and Germany to limit the study area.

While fitting the models, we used 19 bioclimatic variables from WorldClim 2.1 in 2.5-minute spatial resolution (Fick and Hijmans, 2017). This dataset describes annual and seasonal temperature and precipitation trends and extreme or limiting climatic factors. Envirem is another dataset likely to have direct relevance for ecological or physiological processes determining species distributions (Title and Bemmels, 2018). We used 18 climatic and topographic variables from the Envirem dataset to expand and complement WorldClim at the exact resolution. With the help of *raster* 3.6-23 (Hijmans, 2022), we retrieved altitude data based on remotely sensed digital elevation models obtained by The Shuttle Radar Topography Mission (SRTM) at 90-meter resolution (Jarvis et al., 2008). We used a buffer distance of 3 km for each variable, corresponding to an efficient foraging radius of a worker bee communicated by error-prone waggle dance (Haldane and Spurway, 1954; Visscher and Seeley, 1982). Complete variable names, abbreviations, and units used in the downstream analyses are summarized in **Table 1**.

GF is a machine learning approach that can model compositional turnover by fitting an ensemble of regression trees to construct cumulative importance functions of predictor variables. Implemented in *extendedForest* 1.6.1 and *gradientForest* 0.1-32 as an extension of the random forest method (Ellis et al., 2012), GFs determine how well arbitrary split values along a gradient explain biological variation across the two sides of that split. To identify where changes are rapid and which environmental gradients have greater overall importance than others, we fitted GFs to logit transformed values of ancestry estimates. GFs cannot directly incorporate geographic distances. Thus, we included the effects of spatial and latent processes by incorporating the first two Moran's Eigenvector Maps (MEMs) with cumulative adjusted R^2 values 0.9, calculated from the geographic coordinates of the sampling locations by *adespatial* 0.3-21 (Dray et al., 2023).

Table 1. Summary of environmental variables used in the study.

Abbreviation	Variable	Unit
TUR_alt	Altitude	m
meanT	bio1: annual mean temperature	°C
diurnalTrange	bio2: mean diurnal range	°C
isothermality	bio3: isothermality	-
Tseasonality	bio4: temperature seasonality	°C
maxTwarm	bio5: maximum temperature of warmest month	°C
minTcold	bio6: minimum temperature of coldest month	°C
annualTrange	bio7: temperature annual range	°C
Twettest	bio8: mean temperature of wettest quarter	°C
Tdriest	bio9: mean temperature of driest quarter	°C
Twarmest	bio10: mean temperature of warmest quarter	°C
Tcoldest	bio11: mean temperature of coldest quarter	°C
annualP	bio12: annual precipitation	mm
Pwet	bio13: precipitation of wettest month	mm
Pdry	bio14: precipitation of driest month	mm
Pseasonality	bio15: precipitation seasonality	-
Pwettest	bio16: precipitation of wettest quarter	mm
Pdriest	bio17: precipitation of driest quarter	mm
Pwarmest	bio18: precipitation of warmest quarter	mm
Pcoldest	bio19: precipitation of coldest quarter	mm
gdd5	sum of mean monthly temperature for months with mean temperature greater than 5°C multiplied by number of days	°C days
gdd0	sum of mean monthly temperature for months with mean temperature greater than 0°C multiplied by number of days	°C days
count10	count of the number of months with mean temperature greater than 10°C	months
thermicity	compensated thermicity index	°C
embergerQ	Emberger's pluviothermic quotient	-
annualPET	annual potential evapotranspiration	mm / year

Table 1 (continued).

Abbreviation	Variable	Unit
PETseasonality	monthly variability in potential evapotranspiration	mm / month
PETdriest	mean monthly potential evapotranspiration of driest quarter	mm / month
PETwettest	mean monthly potential evapotranspiration of wettest quarter	mm / month
PETwarmest	mean monthly potential evapotranspiration of warmest quarter	mm / month
PETcoldest	mean monthly potential evapotranspiration of coldest quarter	mm / month
aridity	Thornthwaite aridity index	-
moisture	a metric of relative wetness and aridity	-
maxTcold	maximum temperature of coldest month	℃
minTwarm	minimum temperature of warmest month	℃
continentality	mean temperature of warmest month - mean temperature of coldest month	℃
roughness	terrain roughness index	-
topoWet	topographic wetness index	-

We hypothesized that if local adaptation were to play a major role in genetic differentiation, then the cumulative R^2 of environmental predictors in explaining ancestry composition responses could potentially surpass that of MEM variables. We expect Levantine ancestry to respond to temperature-related environmental predictors aligning with their adaptation to Mediterranean climates characterized by hot summers. Meanwhile, we expect Caucasian ancestry to respond to moisture-related environmental predictors reflecting their adaptation to consistently moist environments during the flowering season. Since the relative importance of various environmental factors may differ between subspecies transition zones, we also constructed regional GF models containing a subset of samples and only fitted to ancestry compositions relevant to those transition zones. We considered variables with weighted R^2 values larger than 0.01 in this basal gradient forest analysis important contributors and incorporated them in the following GDM processes as potential predictors.

GDMs attempt to explain biological variation as a function of climate and geography. They can be used to identify environmental gradients associated with compositional turnover and where this turnover is rapid along each gradient (Ferrier et al., 2007). By applying generalized dissimilarity modeling, any biological distance can be related to how much sampling sites differ in their environmental conditions or how physically isolated they are. We used *gdm* 1.5.0-9.1 (Fitzpatrick et al., 2022) to fit GDMs and infer admixture patterns across the study area. As in the case of GFs, we fitted GDMs within more limited boundaries corresponding to transition zones between ancestral group pairs. We applied an elimination procedure based on the variance inflation factor (VIF) implemented in *usdm* 2.1-6 (Naimi et al., 2014) to account for multicollinearity between environmental variables. We set the correlation threshold to 0.75 and the VIF threshold to 5 to select independent variables we would incorporate into our models.

We constructed GDMs to transform those selected environmental variables into their relative importance for intra-specific turnover. We hypothesized that if local adaptation were to play a major role in genetic differentiation, the variance in compositional turnover explained by environmental predictors might exceed the variance explained by geographic distances alone. Such models derived from GDMs can be projected spatially across a sparsely sampled landscape, and we used this feature as a surrogate of ancestry compositions across the whole landscape. To visualize the rasters derived from transformed environmental variables, we reduced the outputs into synthetic variables using PCA, where the first three PCs represented a red-green-blue color palette. We cross-validated our global model ten times by training the data with 90% of the site pairs and testing it in the remaining 10%. We grouped predictors as temperature, precipitation, or their interaction (tXp) related variables and evaluated variance partitioning.

4.4 Spatio-temporal analysis of biodiversity patterns and conservation implications

Once there is a space-wide model based on transformed variables, it can be used to predict ecological similarity between any sites of interest, whether under current conditions or in future climates. Using our dissimilarity model, we analyzed spatio-temporal variation of ecological distances to answer several questions related to within species diversity patterns of honey bees. Ecological similarity computations are derived and slightly modified from those described in Mokany et al. (2022).

4.4.1 Survey gaps, uniqueness, and turnover speed

First, we assessed potential survey gaps within our study area. For each cell in the raster grid, we recorded the pairwise ecological similarity between that cell and the sampling site most similar to it, with lower scores indicating higher potential survey gaps. We evaluated the uniqueness of each cell as its mean ecological similarity to a set of random reference cells that correspond to 5% of the study area. We hypothesized that core regions where subspecies are found in unadmixed forms would be identified with high levels of uniqueness, whereas transitional zones would reflect more moderate values.

As uniqueness patterns might interact with turnover speed, we calculated the turnover speed at each site as the mean ecological similarity of the corresponding cell to its neighbors within a radius of 0.5 degrees. We predict that geographic or ecological barriers to gene flow would be characterized by fast turnover sites, indicative of isolation by barriers (IBB) or environment (IBE). Specifically, regions such as the Taurus Mountain Range, Sea of Marmara, Anatolian Diagonal, and East Anatolian Plateau might demonstrate heightened turnover rates. Conversely, sites exhibiting low turnover speed are anticipated to align with an isolation by distance (IBD) pattern.

4.4.2 Ancestral group similarity and hierarchical classification

We used the unadmixed sampling sites with an ancestry estimate exceeding 0.85 in one of the five ancestral groups to assess how ecological similarities to each ancestral group changed across the study space. For each ancestral group and each cell, we calculated the mean ecological similarities to those unadmixed reference cells and constructed affinity maps.

We followed a supervised approach to classify the study area into five clusters corresponding to five subspecies. First, we calculated pairwise ecological similarities between every unadmixed reference cell and fed the arising distances into hierarchical clustering. Then, we classified every cell into the cluster of the most similar unadmixed reference according to the previous hierarchy. In addition, we reiterated this classification method with six and seven clusters to gain insights about ancestry compositions arising in distinct ecological conditions—potential ecotypes below the subspecies level. To investigate the effectiveness of our supervised classification method, we repeated the same procedure with the random reference cells rather than the unadmixed references. We derived a hit rate for the accuracies of both approaches in predicting the dominant ancestral group at every sampling site with an ancestry estimate exceeding 0.625 (representing an F1 crossed to an F2 at a putative hybrid zone).

4.4.3 Protected area resemblance and conservation complementarity

Currently, there are eight protected areas in Türkiye where migratory beekeeping and queen/colony sales are restricted—established in Adıyaman, Ardahan, Artvin, Düzce, Hatay, İzmir, Kırklareli, and Muğla. Furthermore, located within these protected areas are breeding and conservation apiaries collected from a representative sample of native colonies from the corresponding province. To evaluate representation within the protected areas, we calculated the ecological similarities of each cell across the study grid to cells falling inside the conservatories. We recorded the maximum value as the resemblance index.

We further iterated this procedure three times by adding new hypothetical conservation sites (Hakkari, Çankırı, and Muş) considering complementarity in terms of ancestral clusters revealed by population structure analyses and spatial patterns observed in ecological similarities. In addition, we compared the resemblance indices of every cell under different conservation scenarios by a paired t-test and visualized stepwise resemblance gains by *dabestr*. For each conservation scenario, we compared the total surface area protected directly in conservation sites and indirectly through a resemblance index larger than a threshold of 0.7. Finally, we assessed the differential impact of additional conservation sites on the resemblance values within the study area classified to each ancestral cluster with analysis of variance (ANOVA) followed by a Tukey's test.

4.4.4 Temporal analyses

In the temporal analysis, we considered six Coupled Model Intercomparison Project Phase 6 (CMIP6) climate projections that exhibited favorable accuracy performance in the short term, along with varying long-term equilibrium climate sensitivity: CNRM-ESM2-1, INM-CM4-8, MPI-ESM1-2-HR, MIROC6, EC-Earth3-Veg, UKESM1-0-LL (Tokarska et al., 2020; Meehl et al., 2020). The data consisted of composite means of bioclimatic variables downloaded by *geodata* 0.5-3 (Hijmans et al., 2023) from WorldClim for Shared Socioeconomic Pathways (SSPs): 126, 245, 370, 585, and for mid-years: 2030, 2050, 2070, 2090. Using the projections above, we calculated the Envirem variables by *envirem* 2.3 (Title and Bemmels, 2018) from monthly average minimum/maximum temperatures and total precipitation.

We made predictions for the 16 SSP-time period combinations across the study area with the previously constructed dissimilarity model. Then, we assessed temporal changes for survey gaps, uniqueness, turnover speed, ancestral group similarities, and classification outcomes. Cell-level comparisons employed a paired t-test, and we visualized such changes using *dabestr*. We considered sites as under-sampled if their gap values were lower than 0.45, as unique if their uniqueness was lower than the 10th percentile, as fast turnover if they appeared before the 10th percentile of turnover speed values, as with high correspondence if their ecological similarity to any ancestral group exceeded 0.4.

We hypothesized that climate change-induced drastic impacts across the landscape would result in distinct manifestations. Firstly, we anticipate an increase in survey gaps as a consequence of increased mismatch between the characteristics of the sampling sites and the broader study area due to inadequate coverage of ecological gradients. Secondly, we predict that lowlands in cooler climates will experience invasions by populations preadapted to hotter and more arid conditions. With facilitated migration of such populations to new areas, we expect to observe increased homogenization leading to decreased uniqueness within affected areas, alongside dramatic shifts in ancestral group similarities and classification outcomes. Additionally, such shifts might lead to an increase in fast turnover sites due to increased interface between ancestral groups that occupy varying altitudes.

4.4.5 Persistence, resilience, disappearance, and emergence

To further evaluate the potential impact of climate change on honey bee diversity, we employed four additional indices: persistence (inverse offset), resilience (refugia value), disappearance (loss—forward offset), and emergence (novelty—reverse offset). For the persistence index, we began by calculating the ecological similarity of each cell to itself in the future to derive offset values. Then, to avoid any divisions to zero, we added 1 to the summed offset values before averaging across scenarios as a measure of consistent durability in ancestry compositions across SSPs and time periods. Since offsets are inversely related to persistence, we took the inverse of the final value.

For the disappearance index, we calculated the ecological similarity of each cell in the current conditions to all other future cells in the random reference set, recorded the maximum value for each scenario, and, in the end, averaged across the designs to derive a measure of continuous loss of ancestry compositions across SSPs and periods. In contrast, for the emergence index, we calculated the ecological similarity of each future cell to the current random set, recorded the maximum value for each scenario, and averaged across the designs as a measure of consistent novelty in ancestry compositions.

Finally, for the resilience index, we calculated the ratio of the mean ecological similarity of each cell in the future to their 0.5-degree radius neighbors under current or future conditions. So, a future cell of such a ratio higher than 1 exhibits higher ecological similarity to its neighbors' current conditions than their future conditions, thus having a high value as a potential refugium. We took the arithmetic mean of the rates across SSP-year combinations to get a measure of continuous refugia for ancestry compositions—hence, the resilience index.

We defined sites with high resilience if the refugia value was greater than 1, with low persistence if their average offset values were in the 4th quartile, and with high disappearance or emergence if their maximum similarity to reference cells was smaller than 0.6. A decline in persistence and resilience indices coupled with an uptick in disappearance and emergence indices over time would bolster the assertion that climate change constitutes a considerable threat to existing honey bee biodiversity.

Climate change could affect various ancestral groups disparately and exhibit varying impacts across spatial scales or protection statuses. For instance, a disproportionate impact observed within protected areas or sites characterized by high uniqueness may point to shortfalls in preservation efforts, carrying significant conservation implications. Thus, we also analyzed how our five indices of persistence, resilience, disappearance, emergence, and resemblance varied with other spatial patterns. For that purpose, we checked if index values differed significantly between sites:

densely/sparsely surveyed, unique/generic, fast/slow turnover, protected/unprotected, and with high/low ecological similarity to any ancestral group or classified to any of the clusters. To draw inferences from the interactions between indices and other spatial patterns, we carried out a Bonferroni corrected t-test for each index. In the case of classification outcomes, we applied an ANOVA followed by Tukey's test.

Detailed information regarding the R packages and the session information can be found in **Supplementary Table 2**.

CHAPTER 5

RESULTS

5.1 Rich tapestry of genetic variation reveals a multitude of population profiles and differentiation

Double-genotyping efforts revealed a low overall error rate of 2.7%. We found 499 mismatches out of 18310 microsatellite alleles genotyped and estimated initial per locus genotyping error rates between 0 and 0.07 (**Supplementary Table 3**). Since we rechecked the raw electropherograms of all the mismatches, the remaining genotyping error would be even lower.

The number of alleles per locus ranged from 4 to 53, and the total number of alleles was 574, of which 140 were private alleles. The estimated frequency of null alleles was in the range of -0.01 and 0.12 with a mean of 0.05 (**Supplementary Table 3**). Four loci pairs showed significant linkage disequilibrium in three populations (**Supplementary Table 4**), and there were 46 population-loci pairs out of 377 with significant deviations from Hardy-Weinberg equilibrium (**Supplementary Figure 6**). No loci showed widespread linkage disequilibrium, deviation from Hardy-Weinberg equilibrium, and high null allele frequencies simultaneously, so we kept all the loci for the rest of the analysis. We calculated several diversity indices and present them in **Supplementary Table 3**. The rest of these loci-based statistics include: expected and observed heterozygosity levels, F_{is}, F_{it}, and F_{st} estimations, evenness, G'_{st}, G_{st}, and Jost's D estimations.

At the population level, mean allelic richness per loci corrected for sample sizes ranged between 1.42 and 1.63, with a mean of 1.56, Thrace having the highest allelic richness observed. Eur, Thrace, and E.Med had the highest number of private alleles: 28, 25, and 23. E.Med and Thrace also showed the highest richness values of 4.38 and 4.34 in a Shannon-Wiener diversity index (**Supplementary Table 5**). Erz-Kar and L.Cauc populations had the highest inbreeding levels with F_{is} estimations of 0.15 and 0.11, where overall F_{is} was 0.04. We summarize expected and observed heterozygosity levels and F_{st} values for each population in **Supplementary Table 5**.

5.2 Population structure points to distinct ancestral groups but also widespread admixture across the landscape

Pairwise G'_{st}, G_{st}, Jost's D, and F_{st} estimations were highest among Eur and other populations (**Supplementary Table 6**). Notably, Thrace and ES.Marm populations displayed a more pronounced level of differentiation compared to the remaining populations in Anatolia, where the overall differentiation trend was comparatively weaker. Likewise, Eur population and samples from around Anatolia formed poles at opposite ends of the PCA, whereas Thrace samples stayed in between (**Fig. 2**)—a pattern repeated in the phylogeny. In the UPGMA tree, the Eur population was again the first to diverge, followed by Thrace and ES.Marm (**Fig. 3**). On the other hand, in a spatially explicit sPCA with samples excluding the Eur, each of the Thracian, Levantine, Caucasian, Anatolian, and Zagrosian ancestral groups formed distinct groups (**Fig. 4, 5, and 6**). Nevertheless, the transition between ancestral groups across the space was gradual—even demonstrating further substructure within Anatolian samples centered on Co.Aeg and W.BlkS populations (**Fig. 7 and 8**).

Given the distinct clusters in the UPGMA tree and sPCA plots, where Thrace, E.Med, L.Cauc, Zagros, and Co.Aeg populations form the cores, we conducted an AMOVA with only these five populations. The results of the AMOVA proved significant differentiation between these potentially unadmixed populations, highlighting their genetic distinctiveness ($p = 0.01$). (**Supplementary Table 7** and **Supplementary Figures 7, 8, 9, 10, and 11**). Thrace and Co.Aeg populations ($p = 0.01$) differed significantly from each other, just like Zagros differed from each of the E.Med ($p = 0.03$), L.Cauc ($p = 0.04$), and Co.Aeg ($p = 0.01$) populations. A DAPC plot also confirmed the presence of five genetic groups in honey bee populations (**Supplementary Figures 12 and 13)**.

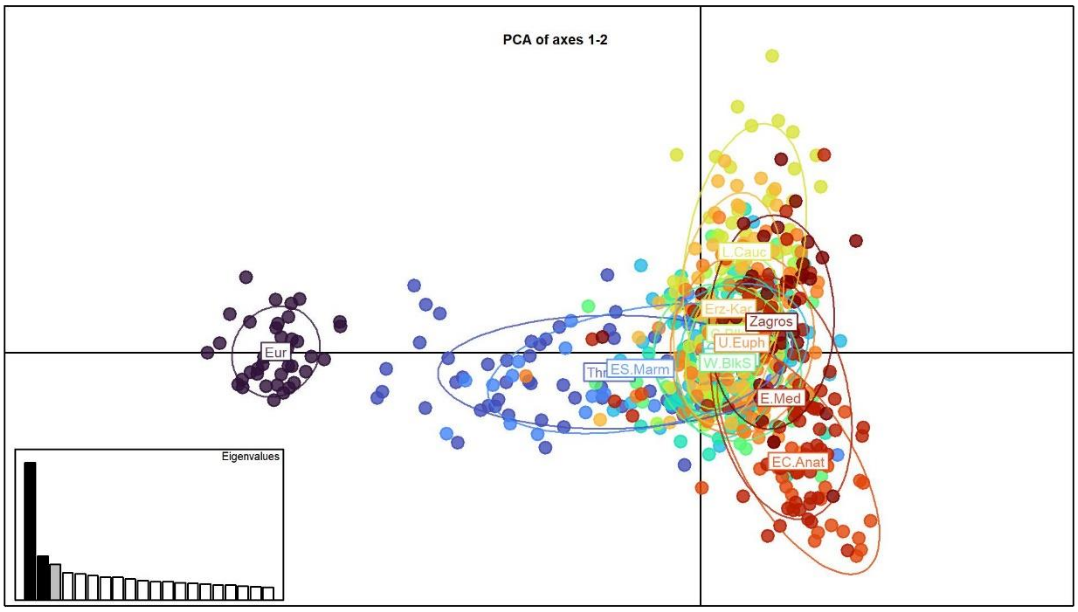


Figure 2. PCA plot revealing spatial distribution patterns. Eur and Asia Minor samples occupy opposite poles, while Thrace samples appear in an intermediary position. Inertia ellipse coefficients are 1.5. The horizontal axis explains 12.4% of the variance, and the vertical axis 4.0%.

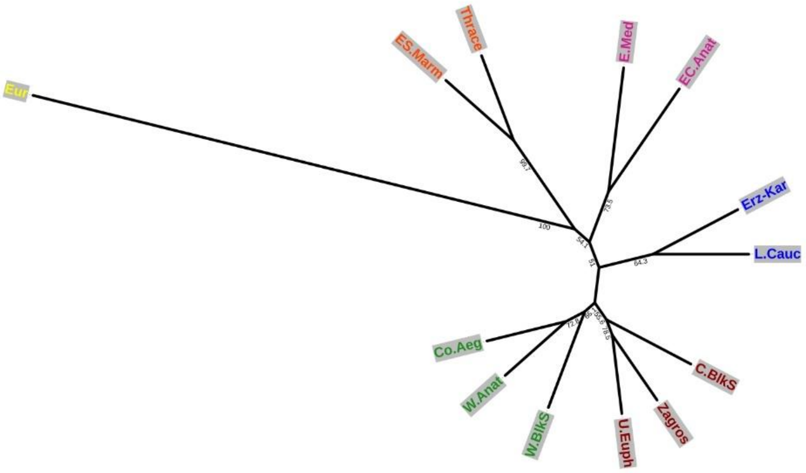


Figure 3. UPGMA tree showing genetic relationships among honey bee populations. The Eur population diverges first, followed by Thrace and ES.Marm populations.

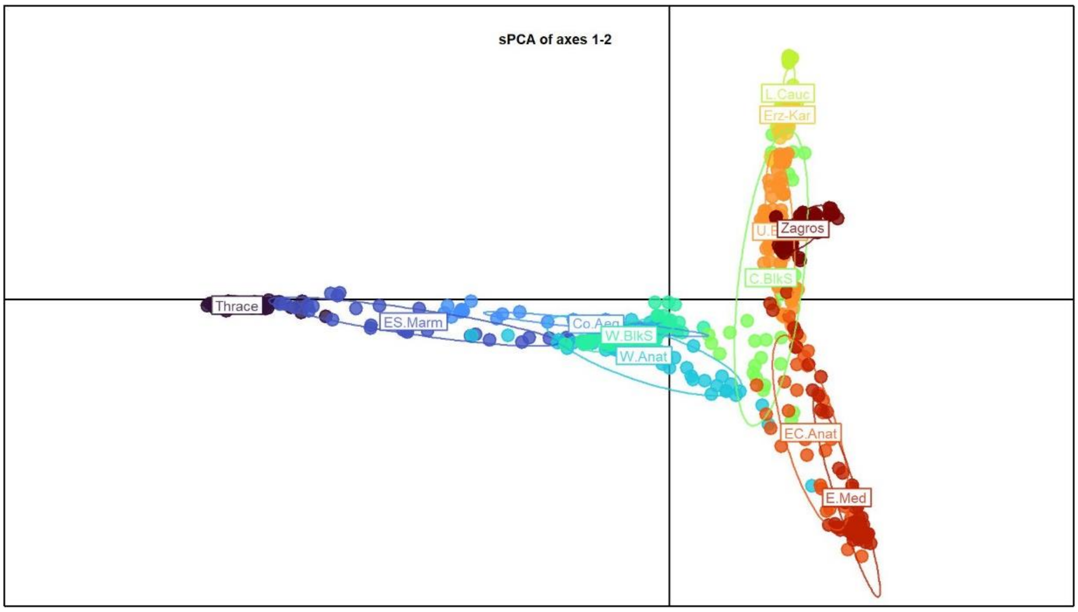


Figure 4. sPCA axes 1 and 2, displaying Thrace, L.Cauc, and E.Med populations at three poles. Inertia ellipse coefficients are 1.5. The first axis explains 52.3% of the variance, the second axis 21.6%.

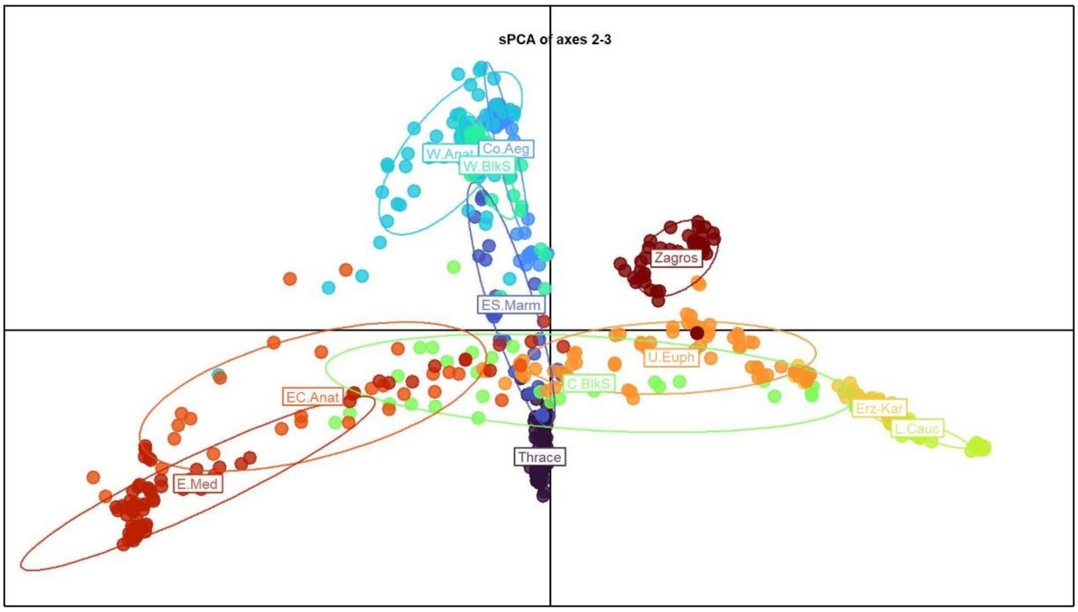


Figure 5. sPCA axes 2 and 3 highlight additional genetic structure; populations in western Anatolia form a pole against L.Cauc and E.Med populations. Inertia ellipse coefficients are 1.5. The second axis explains 21.6% of the variance, the third axis 7.8%.

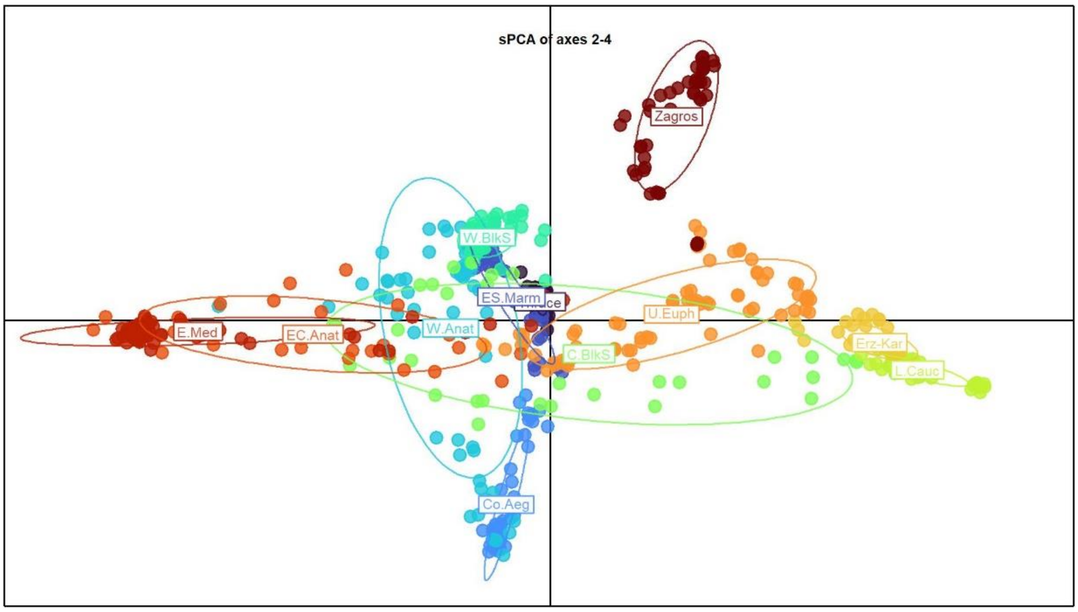


Figure 6. sPCA axes 2 and 4 differentiate the Zagros population from others. Inertia ellipse coefficients are 1.5. The second axis explains 21.6% of the variance, the fourth axis 4.0%.

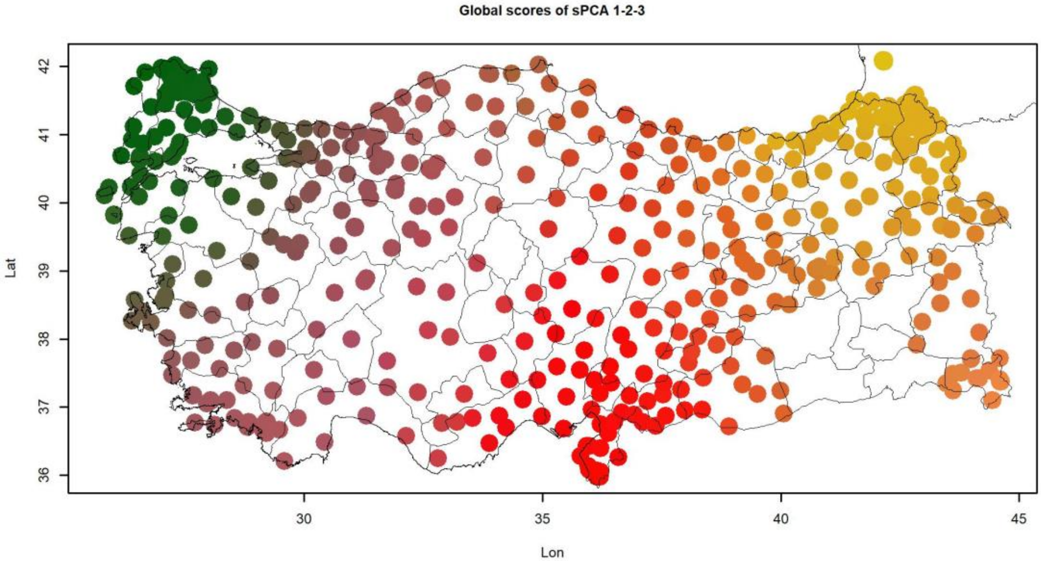


Figure 7. sPCA axes 1, 2, and 3 are plotted on a red-green-blue color scale proportional to the sPC scores, illustrating gradual transitions between populations.

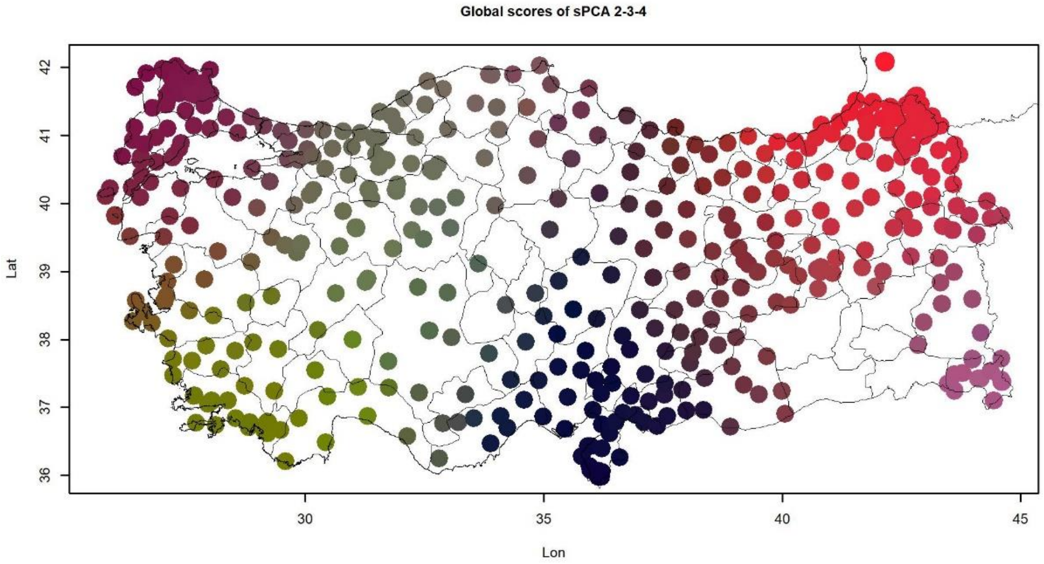


Figure 8. sPCA axes 2, 3, and 4 plotted on a red-green-blue color scale proportional to the sPC scores, showcasing genetic substructure in western Anatolia.

Clustering analysis unveiled main ancestral groups: Thracian, Anatolian, Caucasian, Levantine, and Zagrosian. When estimated at K = 2, individual membership coefficients differentiated samples from Europe and Asia (**Fig. 9a)**. Thracian samples emerged as a mixture of the two gene pools at that level and formed their cluster at K = 5. At K = 7, it was possible to observe all the subspecies plus a spurious cluster within the distribution range of *anatoliaca* (**Fig. 9b and 9c)**.

The structure model assumes a hypothetical ancestral population by allowing each population to drift away from that ancestral population at a different rate and considers that allele frequencies tend to be similar in various populations (Falush et al., 2003). Correspondingly, the model allows the existence of multiple populations with closely matched allele frequencies to capture subtle genetic structure. However, this broad definition of what constitutes a population may lead to the inference of spurious populations not stemming from genetic discontinuity, especially for those that exhibit wide geographical distribution under a stepping-stone migration model (Falush et al., 2003; Guillot et al., 2005). Such populations might erroneously persist due to the failure of the MCMC algorithm to eliminate them effectively, indicating a potential convergence issue (Guillot et al., 2005).

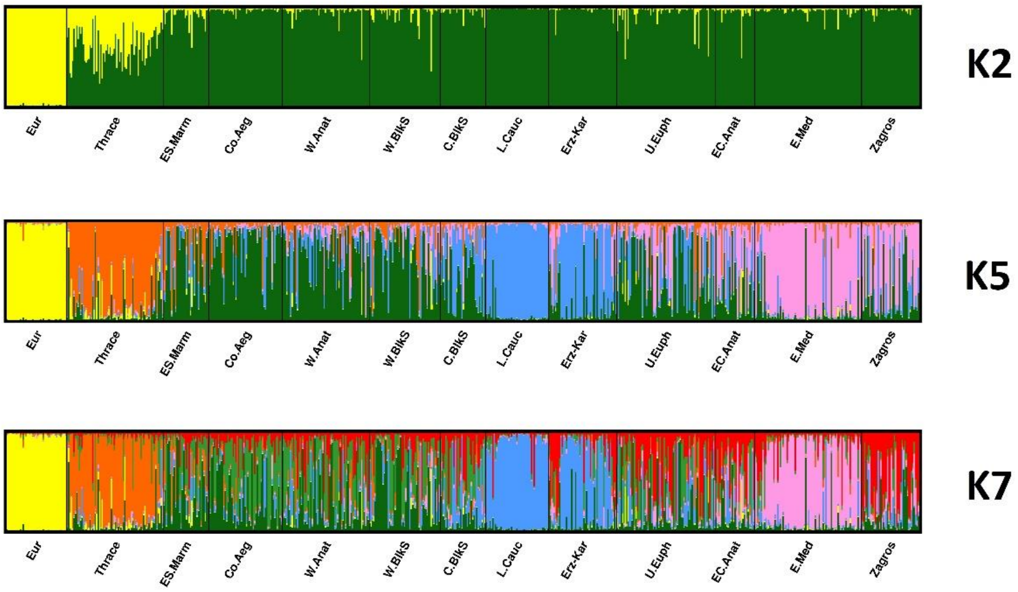


Figure 9. Ancestry estimates at different K values using STRUCTURE software.

The wide distribution of *anatoliaca* subspecies is quite heterogeneous regarding environmental conditions and involves transitions to multiple other subspecies. These transition patterns become evident when ancestry estimates of individuals within populations are plotted separately for each ancestral group (**Fig. 10, 11, 12, 13, and 14**). Populations mainly composed of individuals with high Anatolian ancestry (Co.Aeg, ES.Marm, W.Anat, W.BlkS) manifest in the country's western portion. Nevertheless, ES.Marm population neighboring Thrace, C.BlkS population neighboring Caucasus, EC.Anat population neighboring the Levant, and U.Euph population neighboring Zagros regions show high ancestry estimates, especially in the dominant ancestral groups at these neighboring sites (**Fig. 15**).

In fact, interpolation of ancestry estimates depicts a more detailed scenery of the gradual admixture patterns. In addition to providing a solid first glimpse of core regions where subspecies are found in unadmixed forms and transition zones where subspecies gradually transform into each other, the kriging outcome revealed areas where changes might be relatively rapid (**Fig. 16**). One exciting pattern showcased by interpolation has been the disturbance of graduality in transition between Anatolian and Zagrosian ancestral groups at East Anatolia. Whereas the dominant Zagrosian ancestry followed the northern route exacting the riverbed of the Araxes, the predominant Anatolian ancestry followed the routes exacting those of the Murat and the Karasu—the two main tributes of the Euphrates.

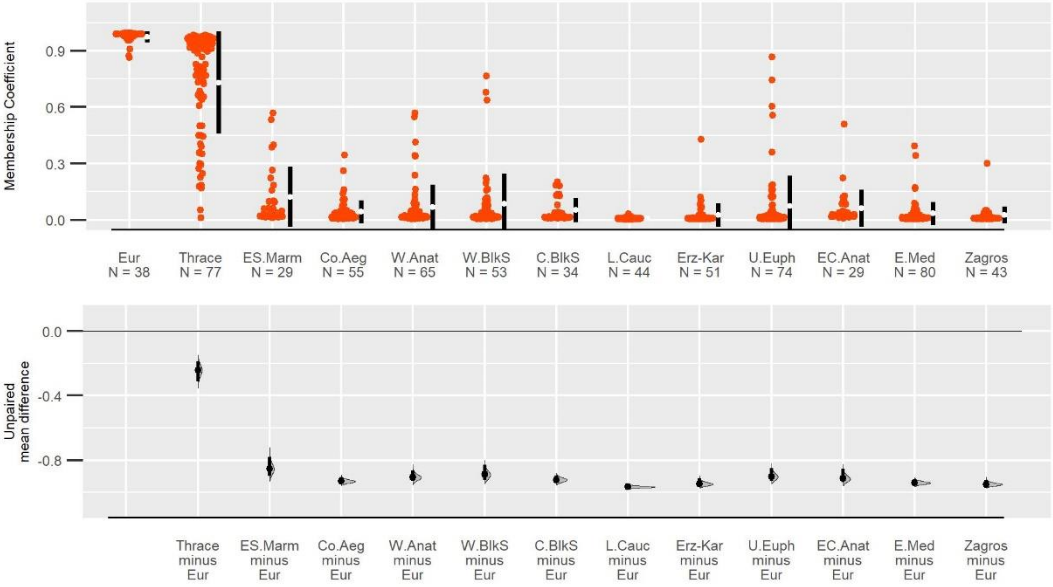
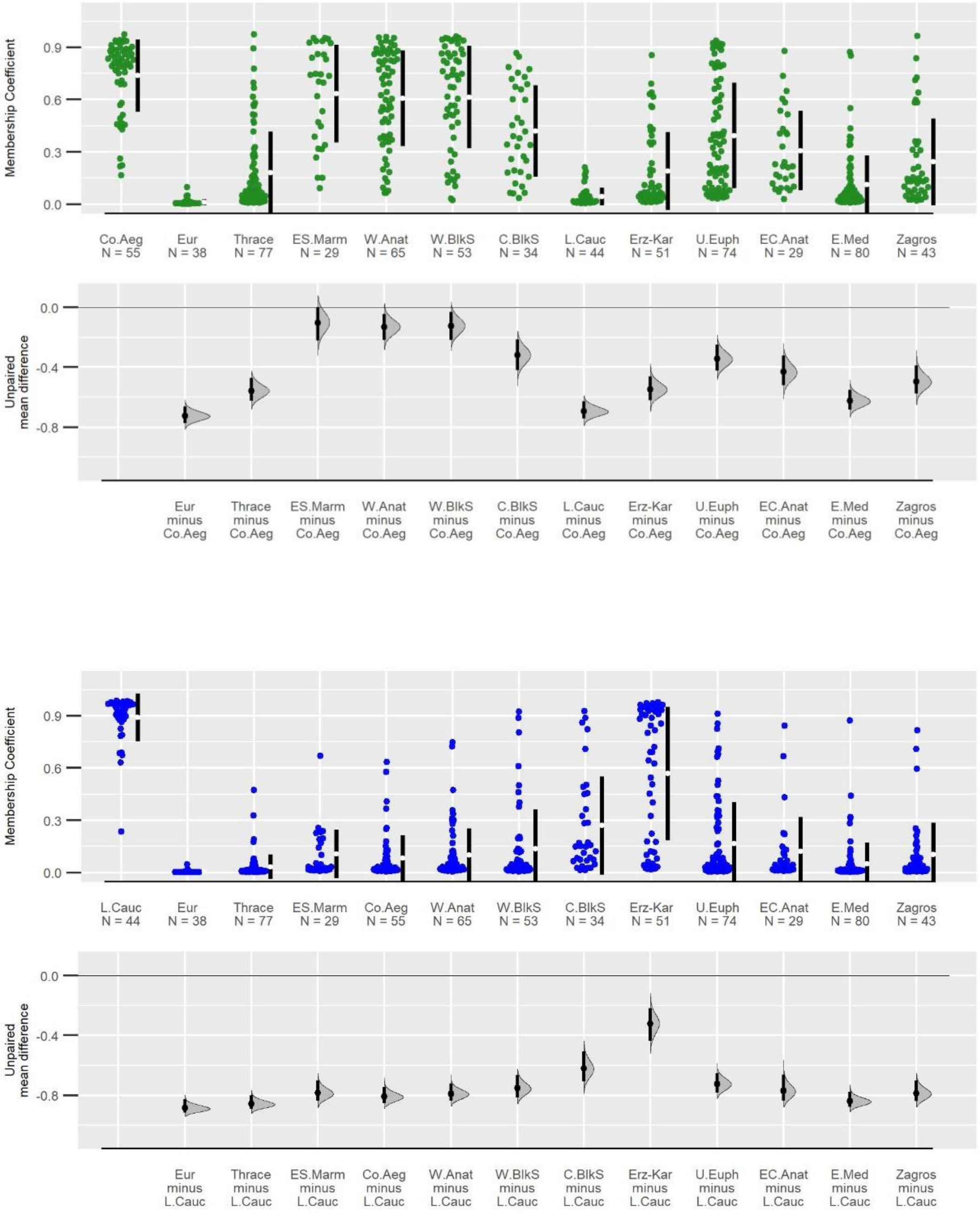
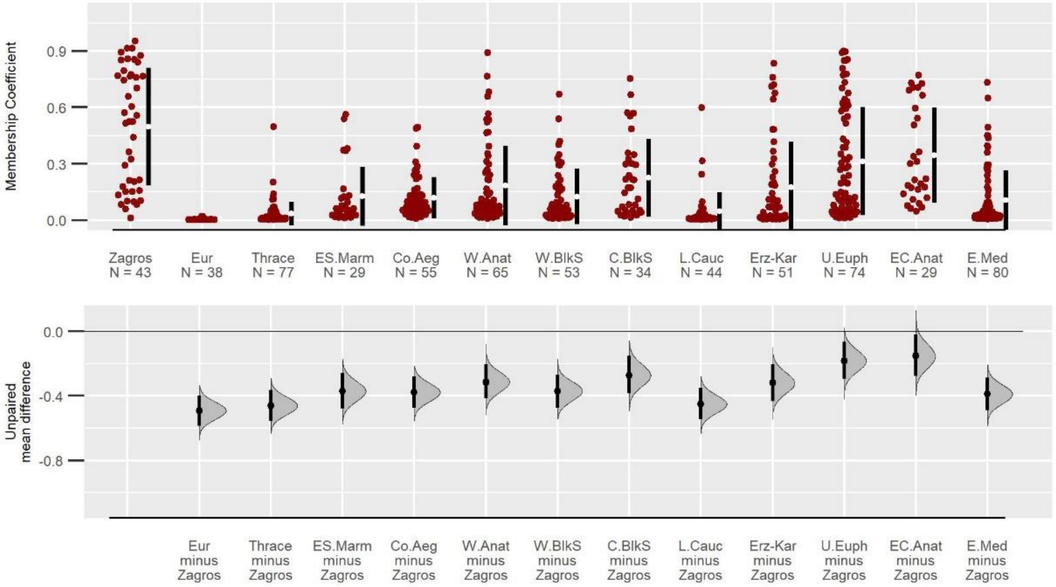


Figure 10. Scatter plot based on ancestry estimates contrasted against Eur population representative of Thracian ancestral group. The dots show Euclidean distances from means of representative populations with a 95% confidence interval bar around. The distribution of the estimation statistic accounts for the precision. Bars right to the data points refer to the 25 and 75% quartiles; the gap between them is the median value.



Figures 11 and 12. Scatter plot based on ancestry estimates contrasted against Co.Aeg and L.Cauc populations representative of Anatolian (green) and Caucasian (blue) ancestral groups. The dots show Euclidean distances from means of representative populations with a 95% confidence interval bar around. The distribution of the estimation statistic accounts for the precision. Bars right to the data points refer to the 25 and 75% quartiles; the gap between them is the median value.



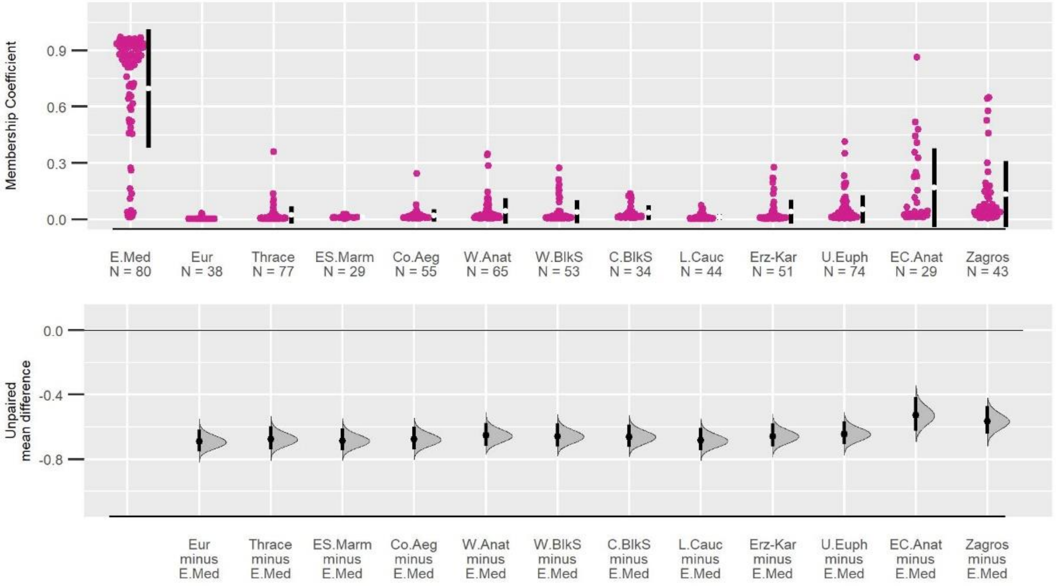


Figure 13 and 14. Scatter plot based on ancestry estimates contrasted against Zagros and E.Med populations representative of Zagrosian (red) and Levantine (violet) ancestral groups. The dots show Euclidean distances from means of representative populations with a 95% confidence interval bar around. The distribution of the estimation statistic accounts for the precision. Bars right to the data points refer to the 25 and 75% quartiles; the gap between them is the median value.

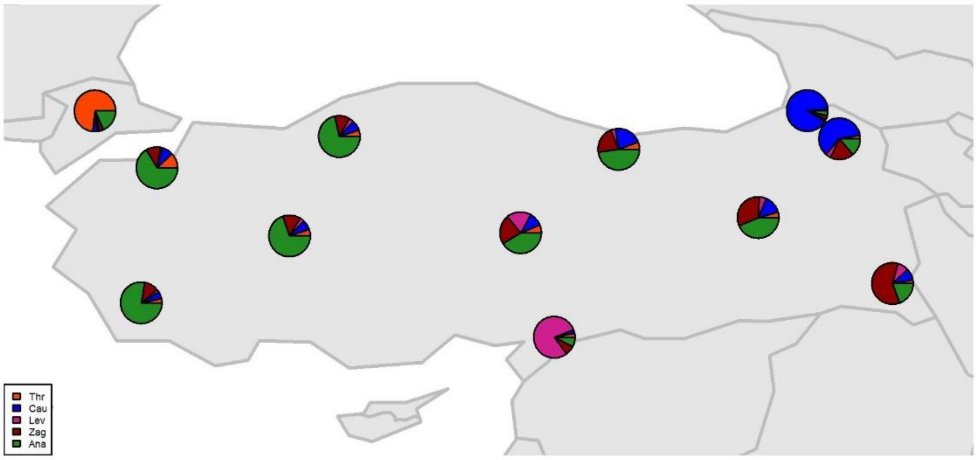


Figure 15. Geographic representation of ancestry compositions for each population, highlighting the proportions of ancestral group contributions. Thr: Thracian, Ana: Anatolian, Cau: Caucasian, Zag: Zagrosian, Lev: Levantine.

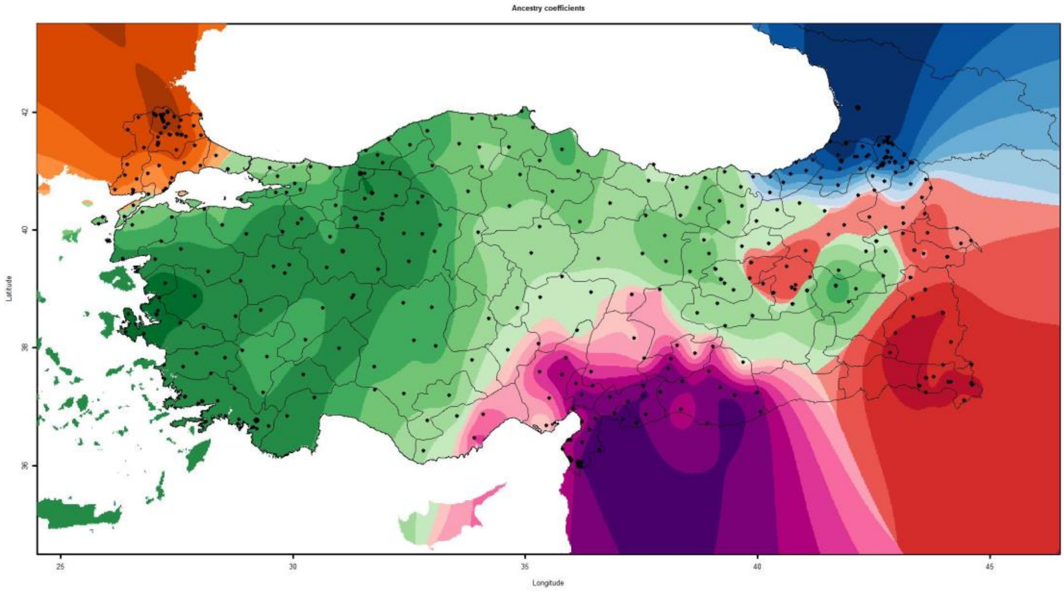


Figure 16. Kriging interpolation of ancestry estimates illustrates the nuanced landscape of gradual admixture patterns between ancestral groups. Note the interpenetration between Anatolian and Zagrosian ancestral groups along the riverbeds of the Euphrates and the Araxes.

5.3 GF models shed light on global and localized drivers of intra-specific turnover across environmental gradients

Model performances for distinct ancestral groups in the global GF model averaged 0.64, ranging from 0.41 for the Zagrosian cluster to 0.74 for the Levantine cluster (**Supplementary Table 8**). The model identified the first two MEMs capturing the spatial processes as the most important predictors of intra-specific turnover in ancestry compositions (**Fig. 17 and Supplementary Table 9**). The relatively vital role of MEM1 and MEM2 (R^2 values of 0.12 and 0.18, respectively) on the turnover would indicate the importance of spatial location or some other unmeasured environmental predictors. Although spatial MEMs had the highest relative contribution, climatic variables still constituted 53% of the captured R^2 after summing variable importance's (0.34 over 0.64). When limited to selected variables with R^2 over 0.01, the relative contribution of climatic factors comprised 40% of such variables in the global model (0.20 over 0.50).

PETwettest, Pwarmest, Tdriest, and isothermality followed the MEMS with the highest R^2-weighted importance. Other variables with weighted importance value larger than 0.01 and associated with excess turnover were aridity, Tseasonality, TUR_alt, continentality, Pdriest, Pwettest, minTwarm, PETdriest, and Pcoldest. Thracian ancestry responded strongly to PETwettest (especially < 30mm/month), TUR_alt (especially < 500m), and Pcoldest. In contrast, Caucasian ancestry showed the highest sensitivity to Pwarmest (especially > 150mm), Tdriest, aridity, Pwettest, and PETdriest (**Fig. 18**). On the other hand, Zagrosian, Levantine, and Anatolian ancestral groups responded similarly to most of the predictors except isothermality and Tseasonality for Zagrosian cluster and minTwarm for Levantine cluster (especially > 20 ^{o}C).

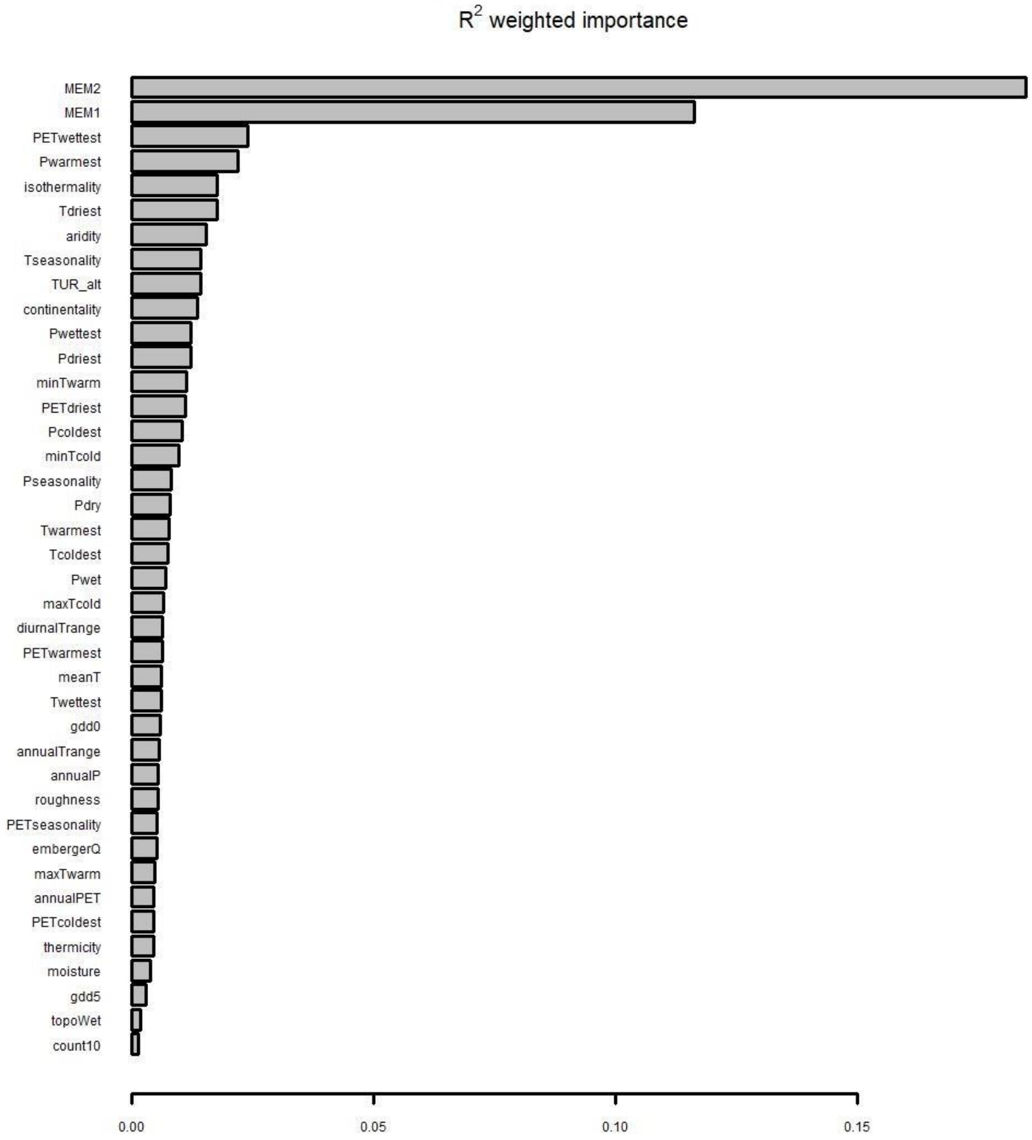


Figure 17. Variable importance scores (R^2 values) for the global GF model, highlighting the significance of spatial processes and key environmental variables driving intra-specific turnover in ancestry compositions.

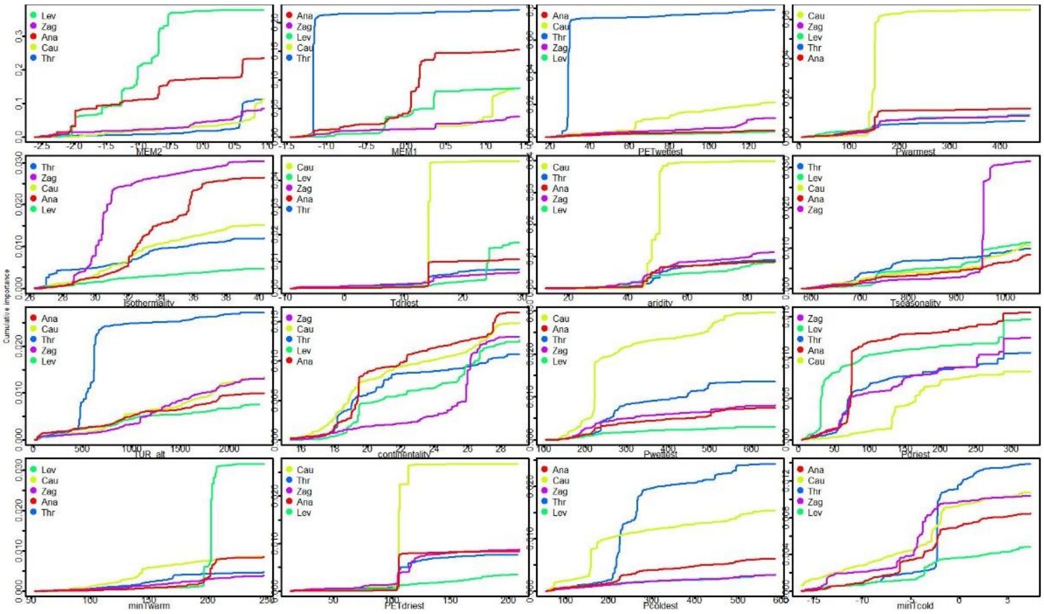


Figure 18. Ancestral group response curves illustrate sensitivity to specific environmental variables in the GF model. Vertical axes depict the relative cumulative importance of the variable to ancestral groups, identifying critical thresholds and regions along the environmental gradients. Thr: Thracian, Ana: Anatolian, Cau: Caucasian, Zag: Zagrosian, Lev: Levantine.

The ratio of captured R^2 by the climatic variables showed substantial differences when analyzed within subregions. Thracian to Anatolian transition had the lowest figure (36%), while Caucasian to Anatolian transition doubles this with the highest value observed (72%; **Supplementary Table 8**). In contrast to global patterns, regional GF models each time selected a lesser number of variables with $R^2 > 0.01$ at the transition zones between subspecies pairs (**Supplementary Table 9**). Still, the regional models highlighted specific environmental predictors that made minor contributions to the global model but played a significant role in driving local genetic differentiation, for instance, Pdriest at Thracian-Anatolian (**Supplementary Figures 14 and 15**), altitude and minTwarm at Anatolian-Levantine-Zagrosian (**Supplementary Figures 16 and 17**), or Pwettest at both Anatolian-Caucasian and Caucasian-Zagrosian transitions (**Supplementary Figures 18, 19, 20, and 21**).

5.4 GDMs disclose distinct patterns in environment-ancestry composition relationships

The global GDM included geographic distance and seven environmental variables as predictors after controlling for multicollinearity (Pdriest, minTwarm, Pwettest, PETdriest, continentality, PETwettest, and isothermality). All the explored variables, geographic or environmental, influenced predicted dissimilarities with summed coefficient values between 0.1 and 1.1. The mean dissimilarity between site pairs when they had identical predictor values (called the intercept), was 0.17. Predictor variables including geographic distance, explained 27.0% of the deviance with a mean absolute error of 0.19 in a ten times cross-validation. The seven climatic variables combined accounted for 15.6% of the deviance. In contrast, this figure was 5.5% for temperature (isothermality, minTwarm, and continentality), 6.8% for precipitation (Pwettest and Pdriest), and 8.6% for tXp (PETdriest and PETwettest) related variables.

Turnover was most sensitive in response to geographic distance and Pdriest, closely followed by minTwarm, Pwettest, and PETdriest (**Fig. 19**). The least influential environmental variables of continentality, PETwettest, and isothermality are more readily associated with transitions from Thracian to Anatolian or Anatolian to Zagrosian ancestral groups (**Fig. 20**). Those two transitions are somewhat more gradual than transitions to Caucasian or Levantine ancestral groups (**Fig. 21**).

As with such GF models, regional GDMs provided a more nuanced understanding of fine-scale patterns of turnover in ancestry compositions at a local level (**Supplementary Figures 22, 23, 24, and 25**). Indeed, geographic distance was the most important variable in the global model; in the regional models, it dropped to either second or third positions. Such as, at the Anatolian-Levantine-Zagrosian transition zone, minTwarm over-dominated the geographic distance (**Supplementary Figure 26**), just like isothermality at Thracian-Anatolian and Caucasian-Zagrosian (**Supplementary Figures 27 and 28**), or PETdriest at both

Anatolian-Caucasian and Caucasian-Zagrosian transitions (**Supplementary Figures 28 and 29**).

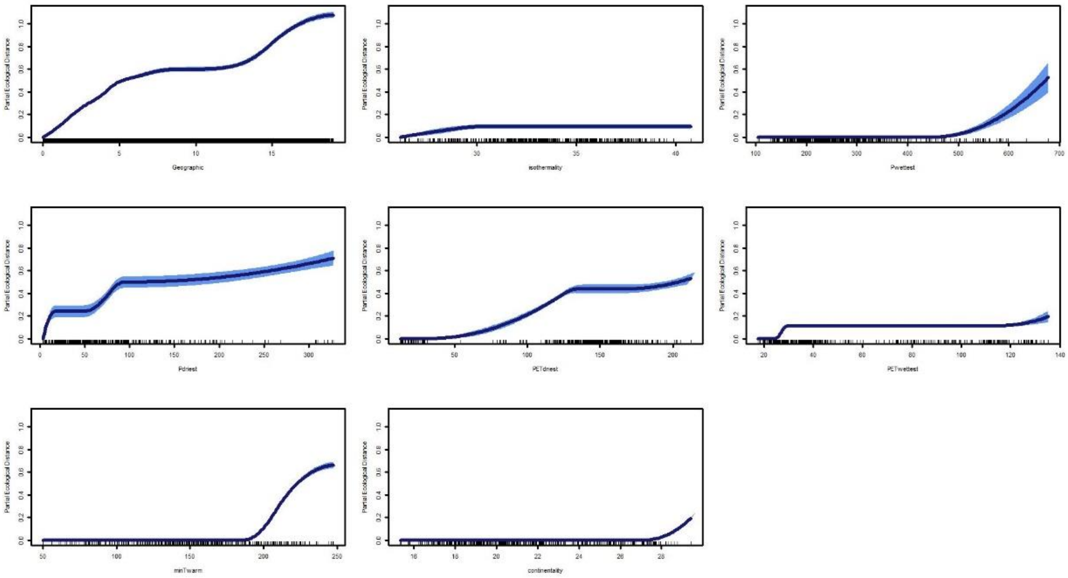


Figure 19. Variable I-splines, demonstrating the sensitivity of turnover in ancestry compositions to environmental predictors in GDM with error bands (+/- one standard deviation). While holding all other variables constant, the maximum height indicates the total amount of ecological distance associated with the gradient of the predictor, and the slope indicates the rate and variation along the gradient.

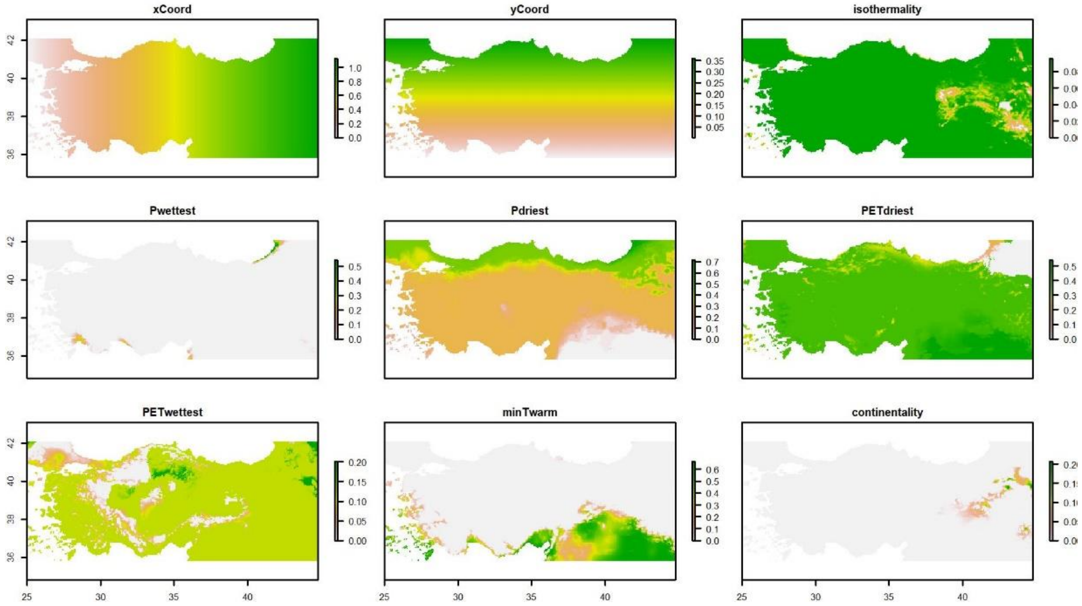


Figure 20. Influence of GDM transformed variables across the study space.

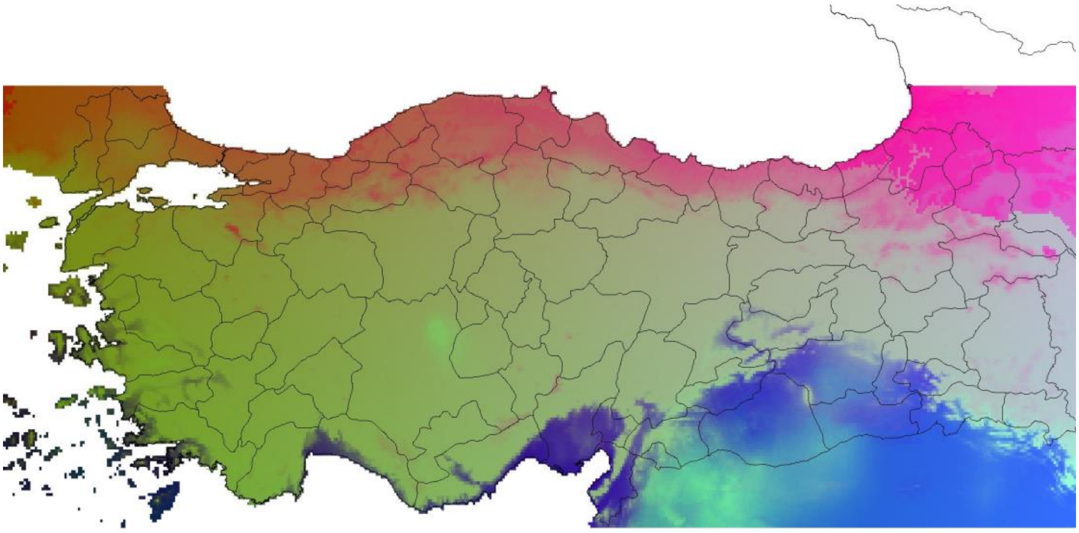


Figure 21. The GDM prediction map displays spatial patterns of predicted dissimilarity based on geographic distance and climatic variables. Colors represent gradients in genetic turnover in a red-green-blue scale according to the first three PC scores of transformed environmental variables.

5.5 Spatial analyses unveil ecological patterns and turnover dynamics

A great majority of the research area demonstrated considerable ecological coherence with the sampling sites (mean maximum similarity 0.78, SD = 0.07), allowing a robust analysis of interplay between ancestry compositions and environmental conditions (**Fig. 22**). Sites that deviated from the broader ecological context, thus identified as highly unique, corresponded primarily to the core zones where subspecies were found in an unadmixed form (**Fig. 23**), suggesting the presence of localized ecological conditions driving distinct adaptations. Furthermore, the spatial analysis revealed two regions with exceptionally high turnover speeds: the Taurus Mountains and the East Anatolian Plateau. The former exhibits a physical barrier to extensive gene flow. In contrast, the latter presents rapid ecological transitions indicative of dynamic environmental gradients or ecological boundaries (**Fig. 24**). These findings highlight the spatial heterogeneity of ecological similarities, as well as the eminence of core zones and various turnover dynamics within the study area.

In addition to the anticipated strong association of the five ancestral groups with their respective bastions that they are named after, survey sites displayed distinct patterns of ecological similarity to the sites unadmixed in certain ancestral groups (**Fig. 25, 26, 27, 28, and 29**). Specifically, while the western portion of Anatolia exhibited higher ecological similarity to the Thracian group, the strip of land along the eastern Black Sea coast showed a greater affinity in the Caucasian group, and the high similarity regions to the Levantine group extended towards East-Central Anatolia.

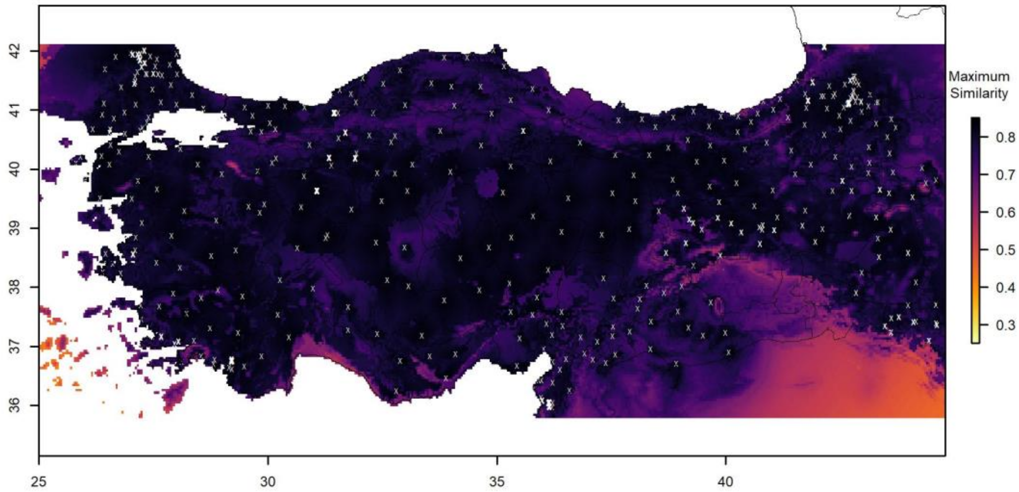


Figure 22. Scarcity of survey gaps enables robust analysis of the interplay between ancestry compositions and environmental conditions. White crosses depict sample locations.

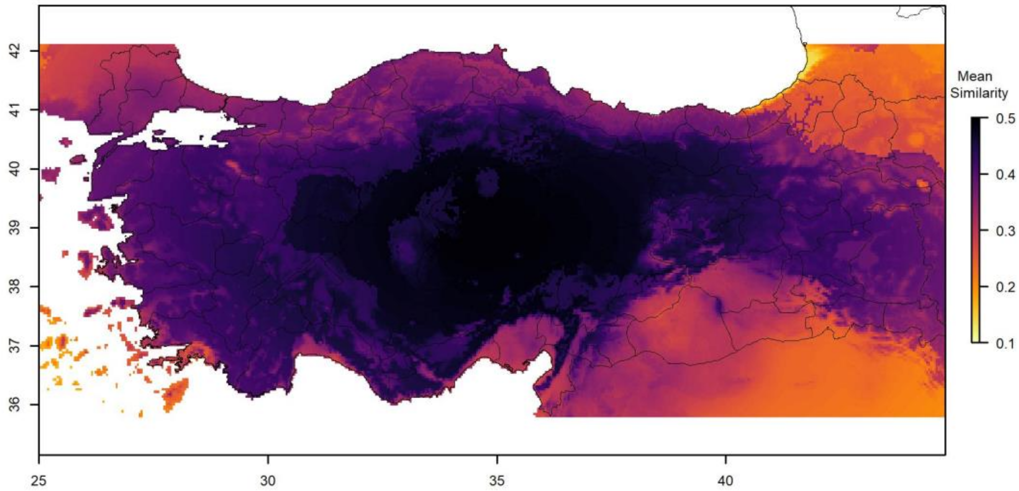


Figure 23. The uniqueness of sites—deviation from the broader ecological context—indicates localized ecological conditions driving distinct adaptations.

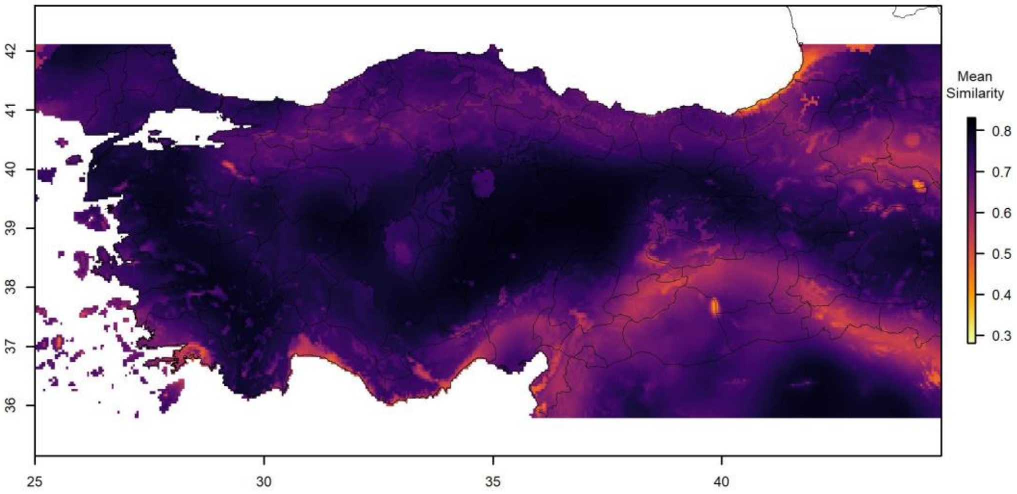


Figure 24. Spatial representation of turnover speeds, highlighting regions with exceptional turnover dynamics: the East Anatolian Plateau and the Taurus Mountains, respectively exemplifying isolation by environment and physical barriers.

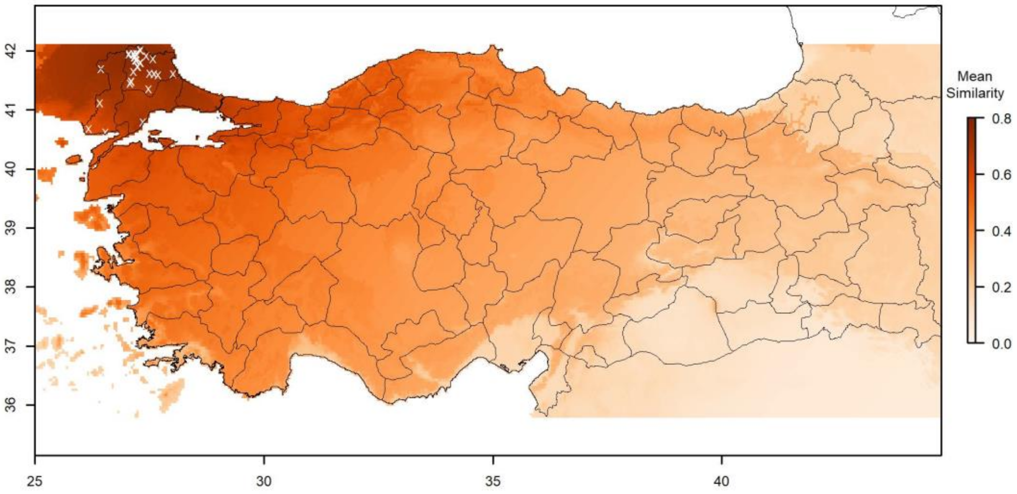


Figure 25. Patterns of ecological similarity across the study space to unadmixed reference sample locations (white crosses) reveal specific ecological affinities to Thracian ancestral group.

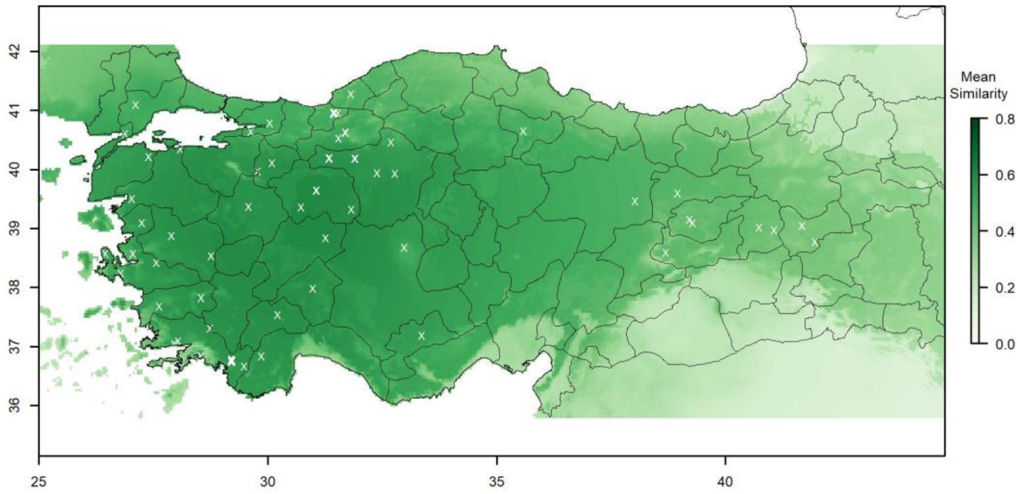


Figure 26. Patterns of ecological similarity across the study space to unadmixed reference sample locations (white crosses) reveal specific ecological affinities to Anatolian ancestral group.

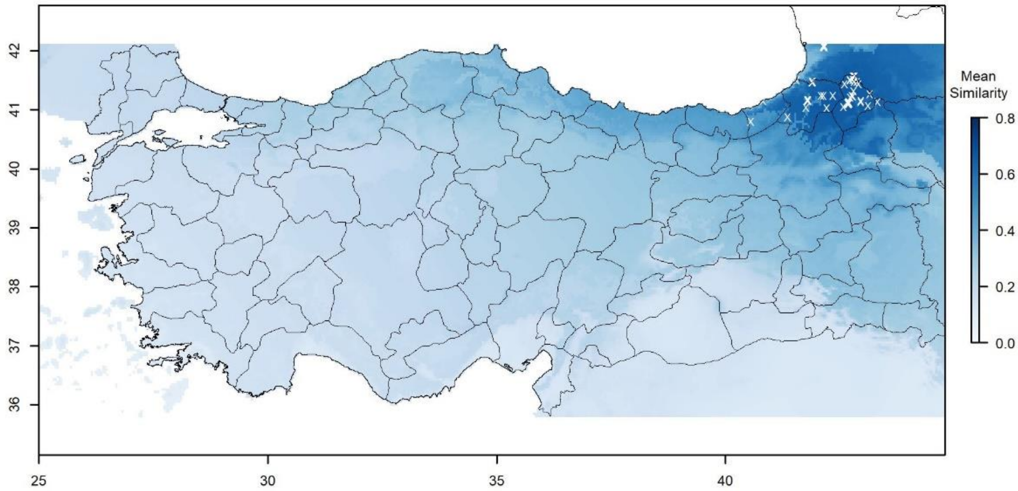


Figure 27. Patterns of ecological similarity across the study space to unadmixed reference sample locations (white crosses) reveal specific ecological affinities to Caucasian ancestral group.

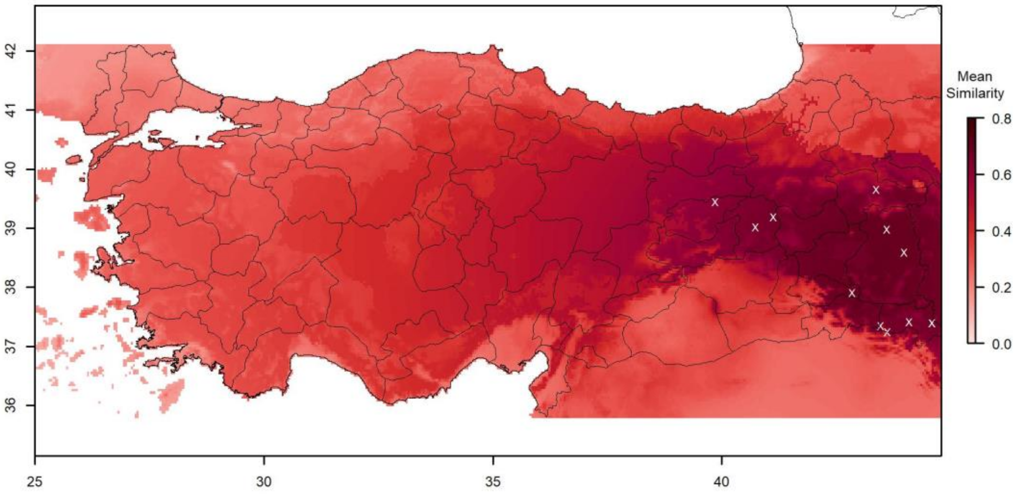


Figure 28. Patterns of ecological similarity across the study space to unadmixed reference sample locations (white crosses) reveal specific ecological affinities to Zagrosian ancestral group.

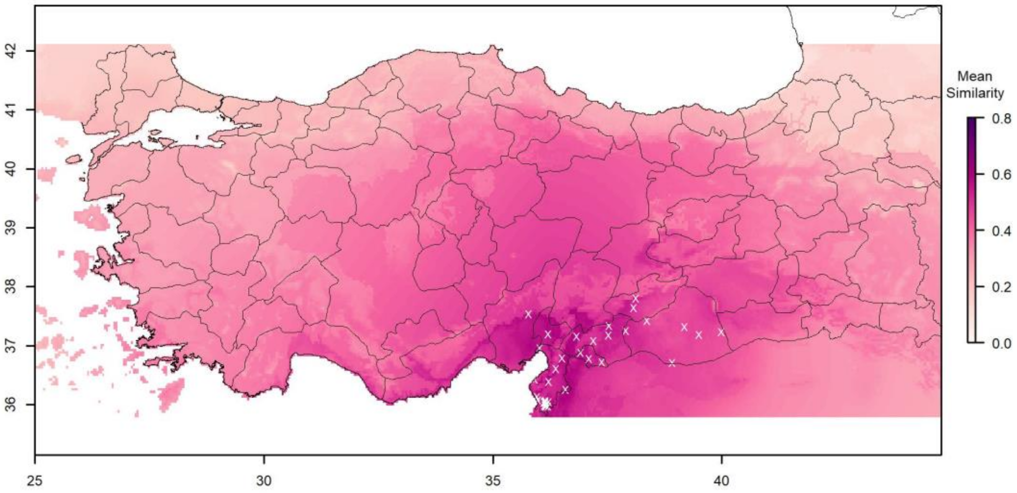


Figure 29. Patterns of ecological similarity across the study space to unadmixed reference sample locations (white crosses) reveal specific ecological affinities to Levantine ancestral group.

Based on our GDM, we classified the study area via hierarchical clustering supervised by unadmixed reference cells and identified five primary bioregions representing ancestral groups within the study area (**Fig. 30**). Increasing the number of clusters to six and seven provided insights into the potential ecotypes existing below the subspecies level, as influenced by distinct ecological conditions (**Fig. 31 and 32**). The two newly added clusters represented the coastal and inland populations of *anatoliaca* and *caucasica* bees with well-known and extensively studied distinct morphological and life-history traits. Our supervised classification approach proved accurate with a hit rate of 86% (n = 389) compared to the 59% of the approach based on random reference cells.

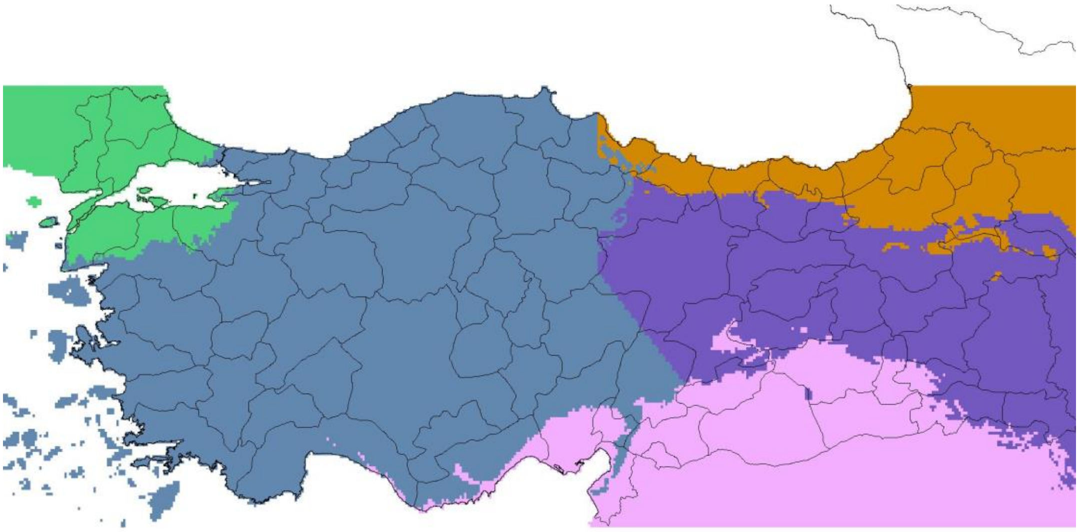


Figure 30. Hierarchical clustering of the study area supervised by unadmixed reference cells identifies five primary bioregions representing predicted ancestral group distributions.

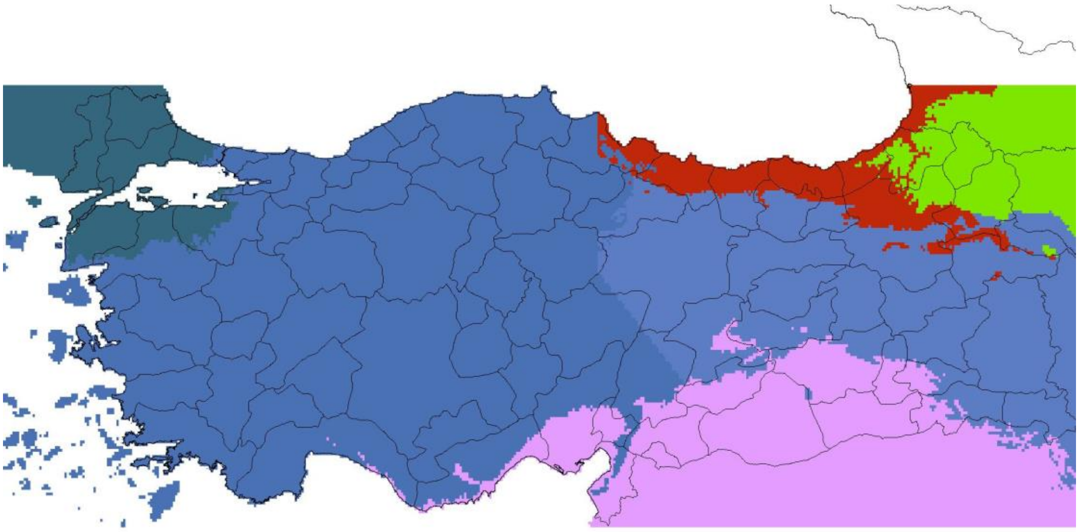


Figure 31. Classification of the study area into distinct ecotypes using 6 hierarchical clusters and supervised classification.

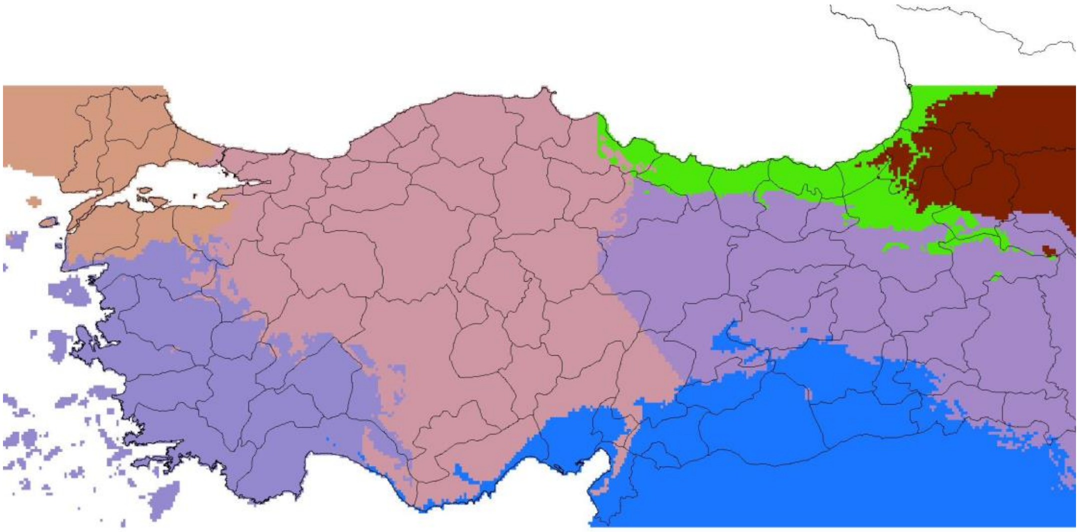


Figure 32. Classification of the study area into distinct ecotypes using 7 hierarchical clusters and supervised classification.

5.6 Assessment of protected area resemblance prompts recognition of new conservation sites

Established protected areas spanned and represented all ancestral groups except Zagrosian (**Fig. 33**). The protected area resemblance across the landscape notably increased when Hakkari was added to conservation sites to include the only unrepresented subspecies, *meda*, and subsequently, Çankırı and Muş to enhance complementarity and representativeness (**Fig. 34, 35, and 36**). In terms of the area protected directly, the current coverage of 59,711 km^2 increases to 81,949 km^2 when additional conservation sites are considered (**Fig. 37**). However, the indirectly protected area, as determined by a resemblance index greater than a threshold of 0.7, expands from 499,719 km^2 to 754,809 km^2—almost equaling the complete surface area of Türkiye (**Supplementary Table 10**). The mean gain per cell in resemblance was 0.023 when Hakkari was added, an additional 0.018 after Çankırı, and a further 0.007 after Muş (all $p < 0.001$). The total gains almost reach up to 0.05 (**Fig. 38**).

Initial differences between ancestral groups' resemblance were significant in a Tukey’s test (all $p < 0.001$). Currently, the Thracian and Caucasian groups are those best represented in the protected areas, followed by the Anatolian (with mean resemblance differences of 0.06 and 0.04). The Zagrosian group is the least represented, with a mean difference of 0.12 and 0.11 compared to these most well-protected groups. However, after including Hakkari, these figures dropped to 0.05 and 0.04 (still both $p < 0.001$). Following the inclusion of Çankırı in the conservatories, the mean difference in resemblance between Thracian and Anatolian groups reduced to 0.02 ($p < 0.001$). Meanwhile, the Caucasian and Anatolian groups had equal levels of representation. After including Muş, the resemblance of the Zagrosian, Anatolian, and Caucasian groups became equalized, while each stayed 0.02 below the Thracian group ($p < 0.001$). Considering all the scenarios, there was very little or no improvement in the resemblance of the Levantine ancestral group (**Supplementary Table 11**).

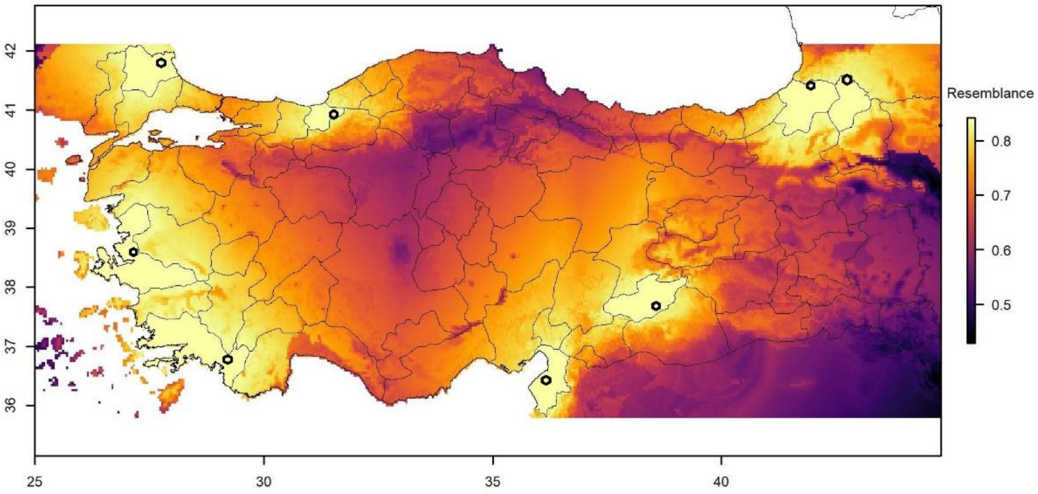


Figure 33. Protected area resemblance of sites and distribution of established protected areas (black hexagons) within the study area, representing ancestral groups except Zagrosian.

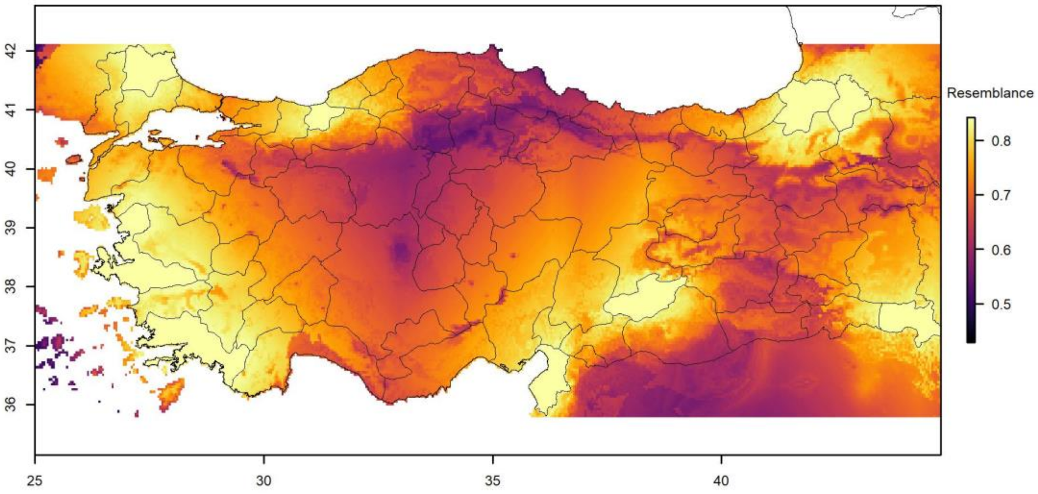


Figure 34. Spatial change in PA resemblance after adding Hakkari for representation of *meda* subspecies.

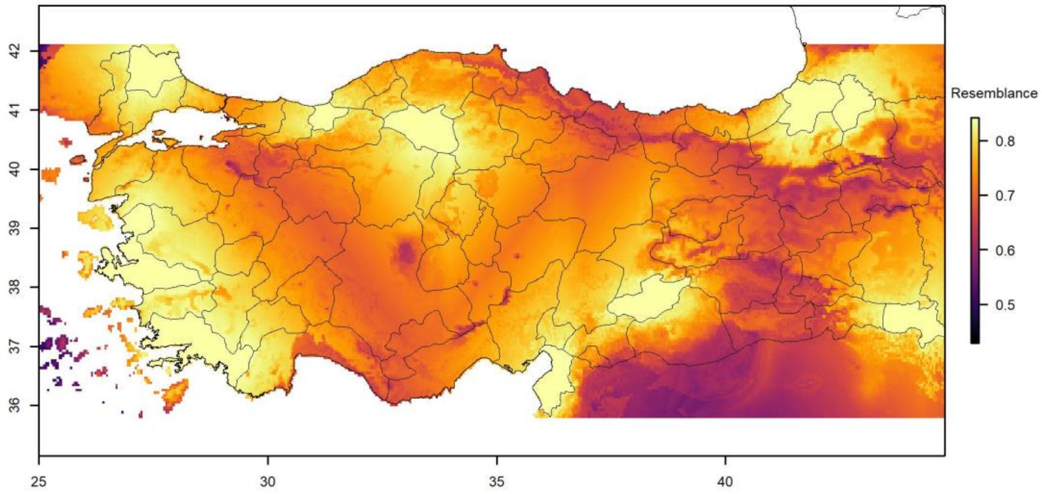


Figure 35. Resemblance increases further following the inclusion of Çankırı to complement existing conservation sites.

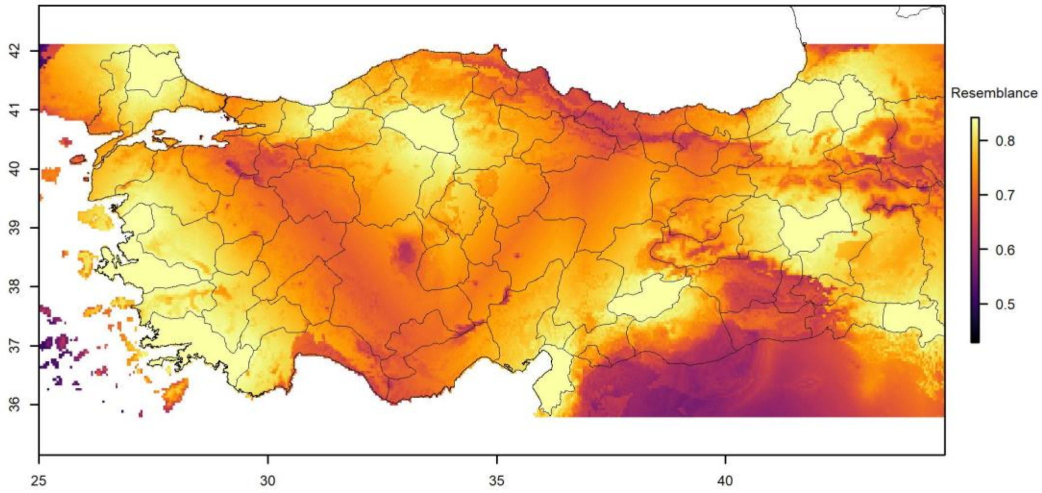


Figure 36. Continued improvement in resemblance with the addition of Muş for enhanced representativeness.

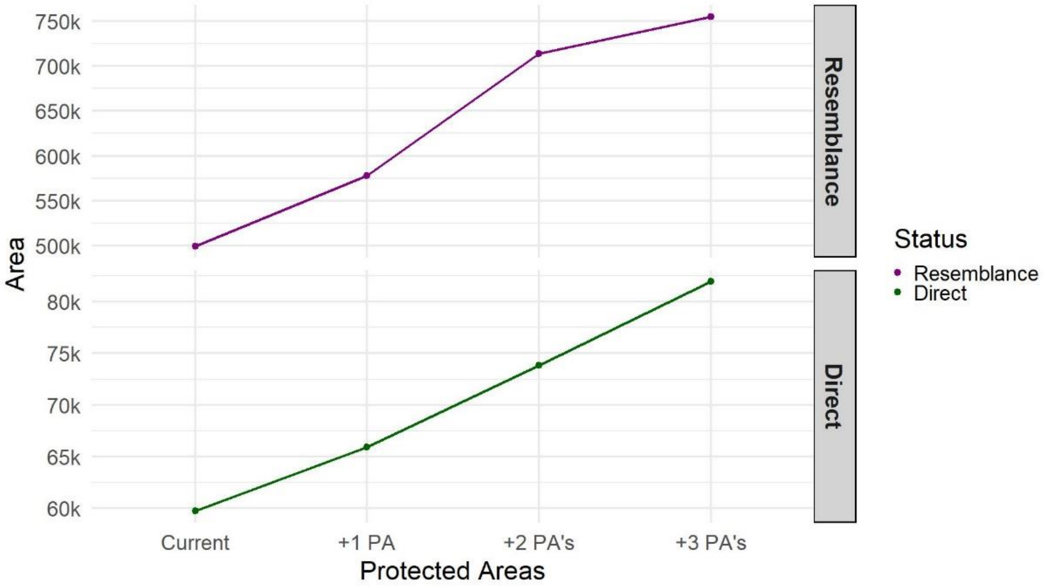


Figure 37. Comparison of areal gains in protection status with successive additions of Hakkari, Çankırı, and Muş, either directly within PAs or indirectly through PA resemblance higher than 0.7.

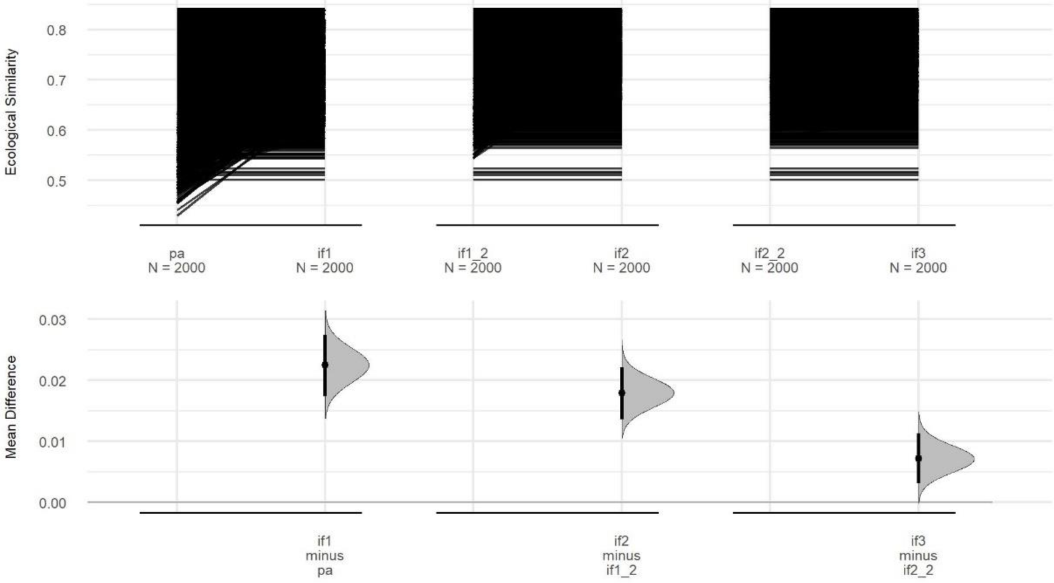


Figure 38. Mean gains in resemblance per cell through successive additions of Hakkari (if1 minus pa), Çankırı (if2 minus if1_2), and Muş (if3 minus if2_2) in 2000 randomly selected sites. Note the impact on the resemblance of least protected sites by including Hakkari.

5.7 Temporal analyses point to shifts in turnover patterns and the vulnerability of ancestral groups

Throughout the first half of the century, the general picture of ecological regions remained relatively stable; however, divergence emerged among the models in the latter half, particularly under the more pessimistic SSP scenarios (**Fig. 39**). Importantly, the impacts of climate change were not uniform across the study area. Thrace experienced substantial changes at an early phase, followed by a disruption in coherence in the Caucasus. Later, a divergence between highlands and lowlands intensified within Anatolia. Across the study area, coastal regions appeared more vulnerable initially, but in later years and under intense SSP scenarios, inland areas were affected similarly. Notably, the increases in minTwarm were a primary driver of these changes, alongside considerable impacts from changes in the PETdriest (**Supplementary Figure 30**).

An examination of the ecological similarities to each ancestral group revealed that cells particularly similar to any of the groups showed a consistent decline (**Fig. 40**). An exception was with the Levantine group, which initially declined but had gains later. At the end of the projection period, the number of cells that displayed high ecological similarity to unadmixed Thracian or Caucasian samples halved. Although the region with high similarity to the Zagrosian group showed a decline, the Anatolian counterpart experienced the most drastic case regarding the total surface area.

Nevertheless, these changes had other implications for classification results (**Fig. 41**). Despite the massive decline of high ecological similarity to unadmixed Anatolian samples, the Anatolian ancestral group still maintained its classified area until the late stages of the projection period (**Fig. 42**). Meanwhile, the Thracian group steadily decreased from over 50,000 km^2 to 25,000 km^2, the Caucasian group from circa 100,000 km^2 to 75,000 km^2, and the Zagrosian group from circa 200,000 km^2 to 150,000 km^2. Conversely, the Levantine group continued to gain ground, almost doubling its size from circa 175,000 km^2 to 300,000 km^2 by the end of the projection period. Classification changes across the study area reached 150,000 km^2 in total.

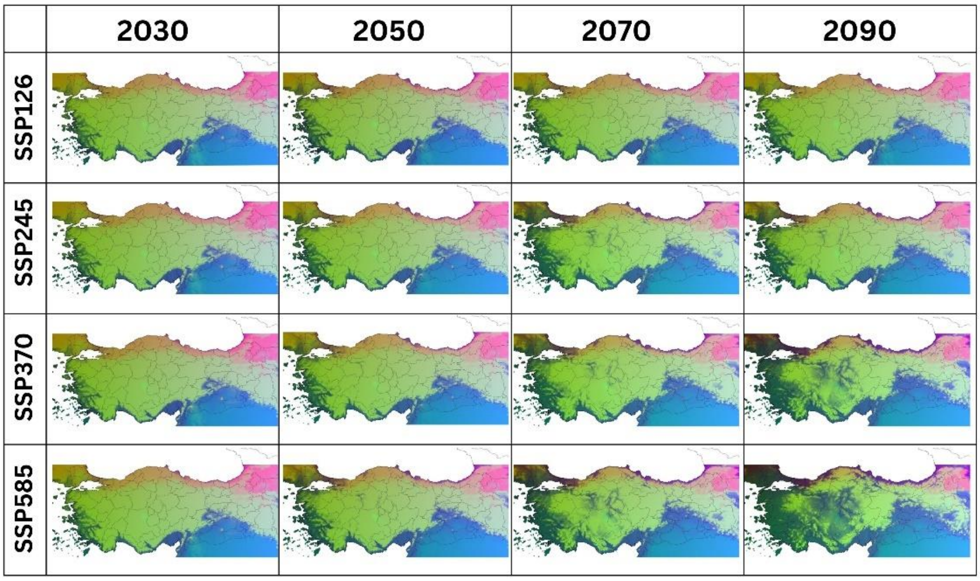


Figure 39. Climate change impact on turnover patterns. Temporal analyses point to shifts in intra-specific turnover patterns under different SSP scenarios at midyears of two-decade periods. The first half of the century shows relative stability, while divergence emerges in the latter half, particularly under more pessimistic SSP scenarios. Colors represent gradients in genetic turnover in a red-green-blue scale according to the first three PC scores of transformed environmental variables.

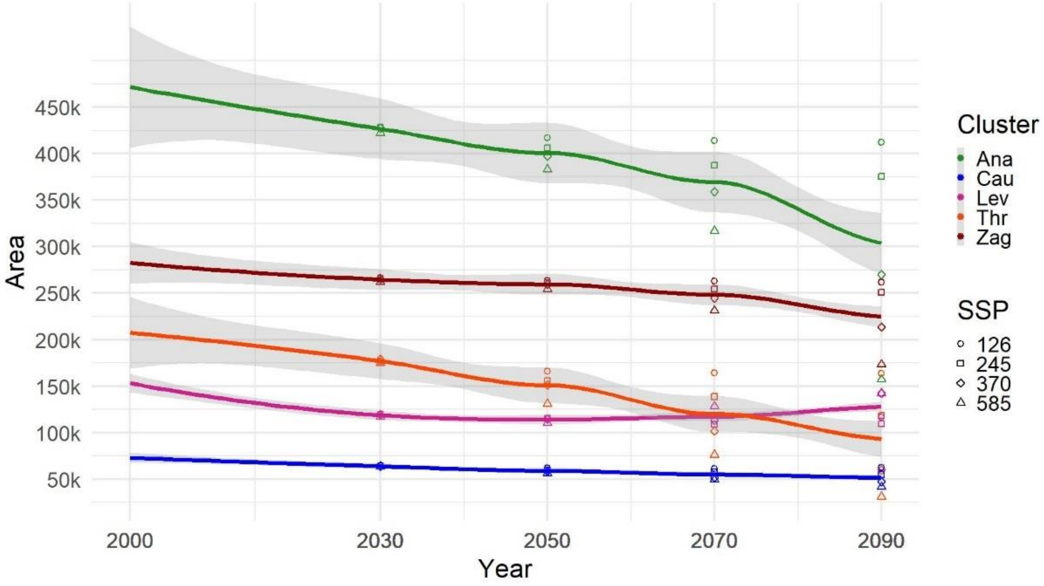


Figure 40. Study area showing high ecological similarity (greater than 0.4) to ancestral groups.

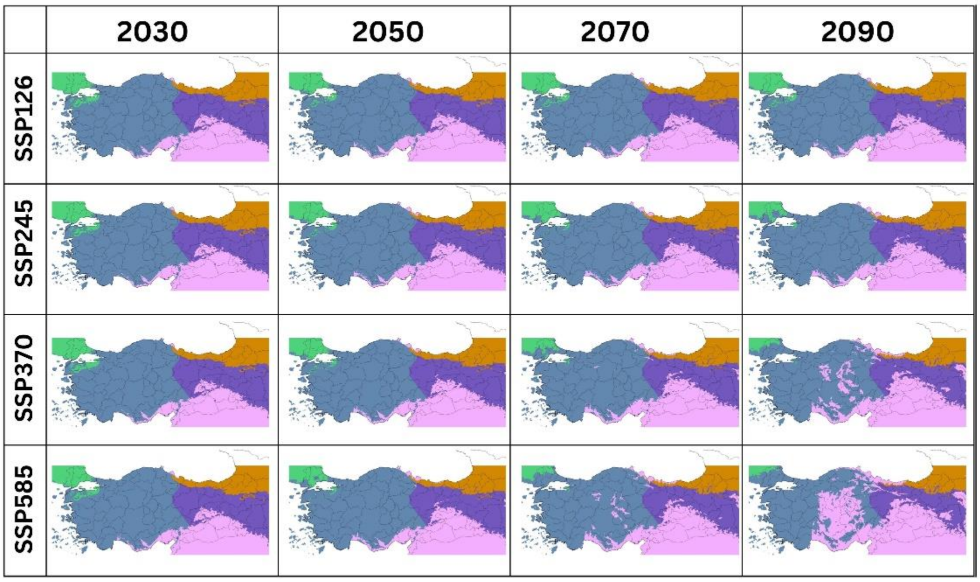


Figure 41. Alterations in five primary bioregions representing predicted ancestral group distributions under different SSP scenarios at midyears of two-decade periods.

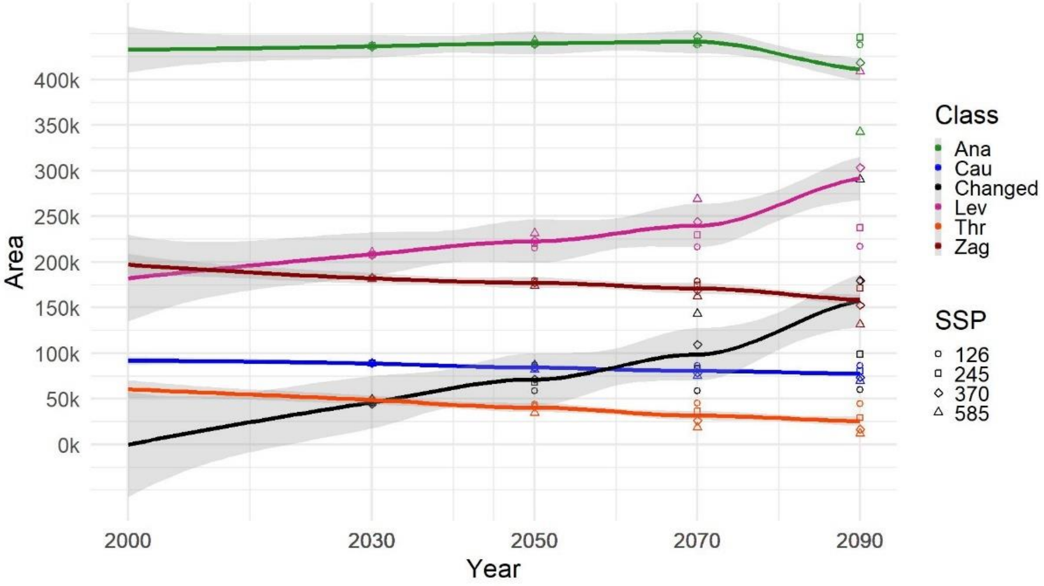


Figure 42. The study area is classified into each ancestral group, highlighting shifts and losses. The black line indicates the total area with a changed classification outcome.

The SSP-year combinations presented variation in probable scenarios, with the Thracian group shrinking drastically in some of them, nearly disappearing within the borders of Türkiye (**Fig. 43**). Relatively high losses of ecological similarity were apparent in rasters associated with the Caucasian group, indicating retreat and fragmentation, particularly at lower altitudes (**Fig. 44**). This pattern manifesting in the lowlands was observed in the Anatolian and Zagrosian rasters, albeit to a lesser degree (**Fig. 45 and 46**). In the extreme case of late SSP585 scenario, the Levantine group gained excessive ground in central Anatolia and even the central Black Sea (**Fig. 47**).

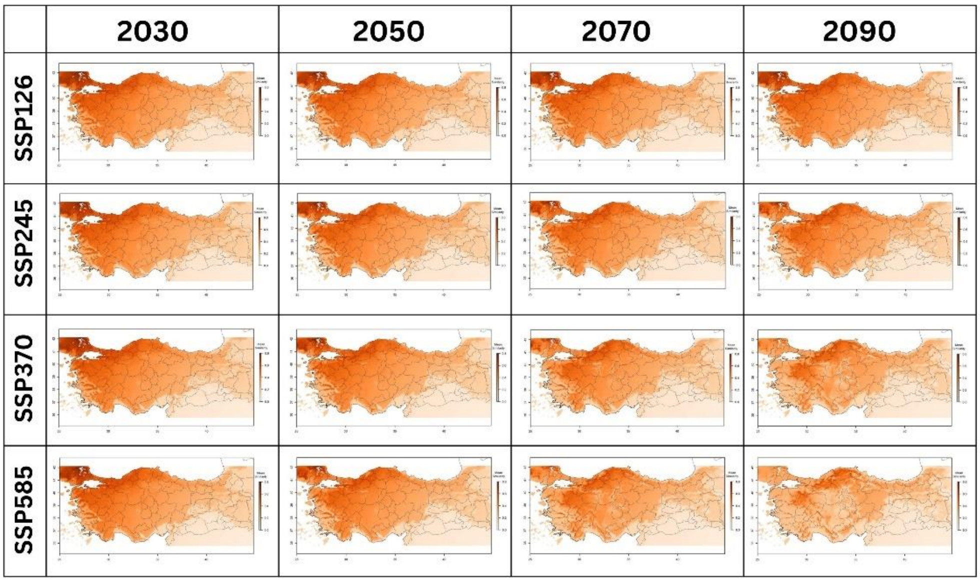


Figure 43. Projected changes in ecological similarity to unadmixed Thracian sampling locations in response to climate change.

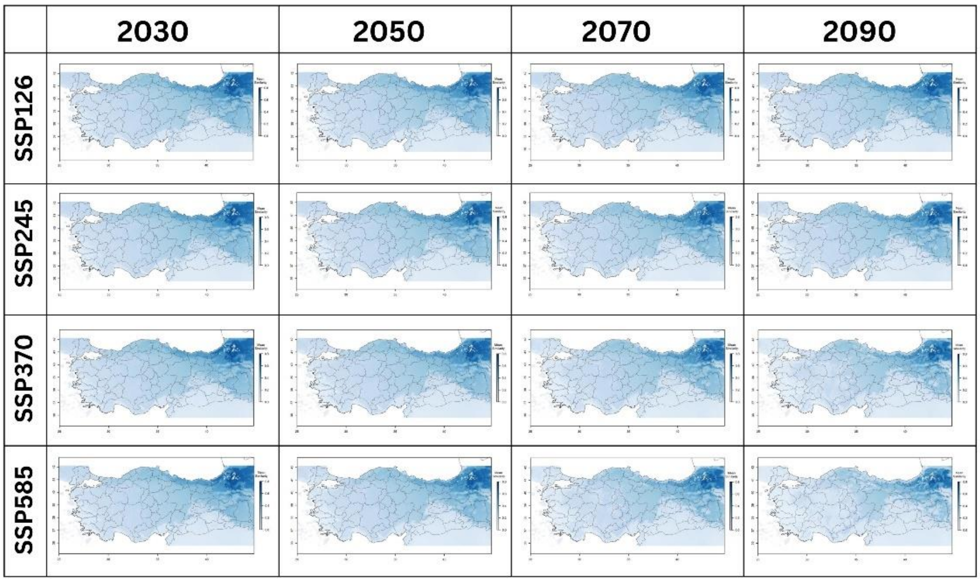


Figure 44. Projected changes in ecological similarity to unadmixed Caucasian sampling locations in response to climate change.

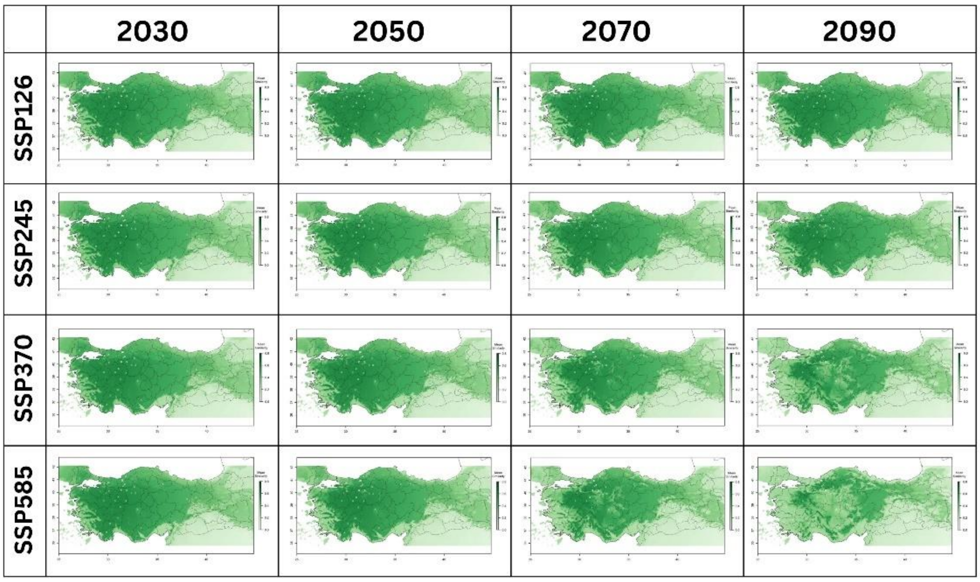


Figure 45. Projected changes in ecological similarity to unadmixed Anatolian sampling locations in response to climate change.

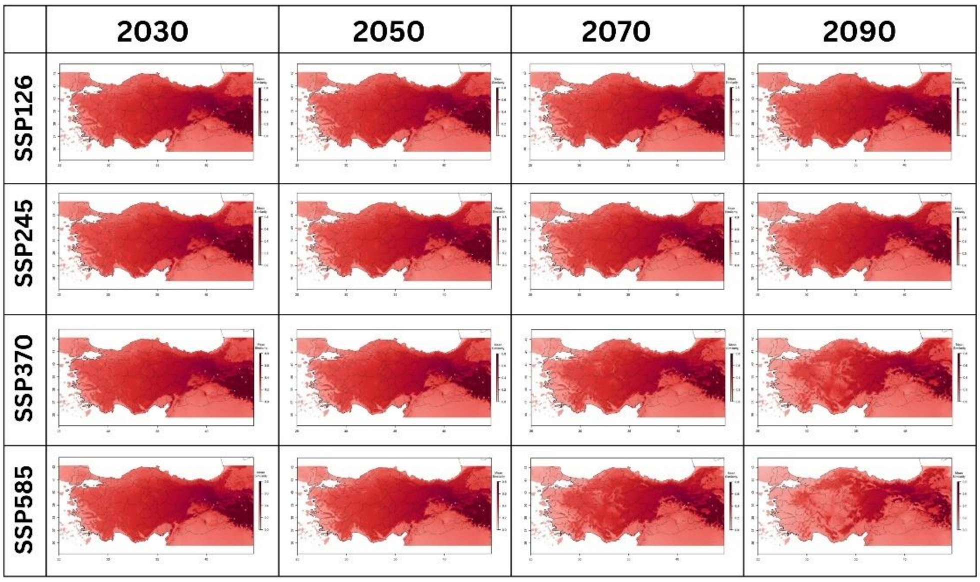


Figure 46. Projected changes in ecological similarity to unadmixed Zagrosian sampling locations in response to climate change.

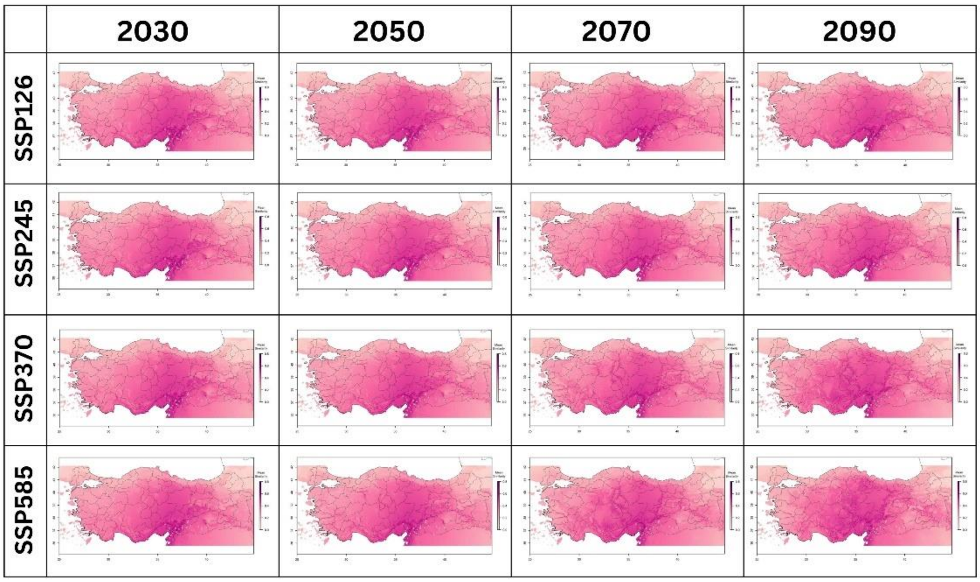


Figure 47. Projected changes in ecological similarity to unadmixed Levantine sampling locations in response to climate change.

Analyzing survey gaps, we observed a notable increase in that figure, especially in areas of higher climate impact (**Fig. 48**). There was a significant decrease in maximum ecological similarity to sampling sites, with a magnitude of similarity loss averaging around 0.06 at the cell level ($p < 0.001$; **Fig. 49**). The proportion of the study area with survey gap values exceeding the threshold increased continuously under each scenario throughout the years, ranging from nearly none to 50,000 km^2 by the end of the century (**Fig. 50**). Additionally, the uniqueness at the cell level increased, albeit to a lesser degree than survey gaps, averaging around 0.03 ($p < 0.001$). While each cell became more uncommon, the total area classified as highly unique consistently decreased from circa 100,000 km^2 to 75,000 km^2. The uniqueness of the sites at Levant and Thrace appeared to decline consistently across the SSP-year combinations, just as the coherence of the highly unique locations at the Caucasus was disrupted (**Fig. 51)**.

At the cell level, turnover speed did not exhibit substantial changes. However, across the study area, the proportion of sites with fast turnover had an observable increase, their surface area rising from circa 100,000 km^2 to 150,000 km^2. Furthermore, notable changes in turnover patterns were observed, including a shift of the geographical barrier at the mid-portion of the Southeast Taurus range to the Mercan Mountains in East Anatolia (**Fig. 52)**. The Aegean mountainous areas also displayed increased turnover speeds due to rising temperatures, as did the coastal regions along the Eastern Black Sea. Comparison of SSP scenarios across the time periods for the survey gaps, uniqueness, and turnover speed can be tracked from **Supplementary Figures 31, 32, and 33**.

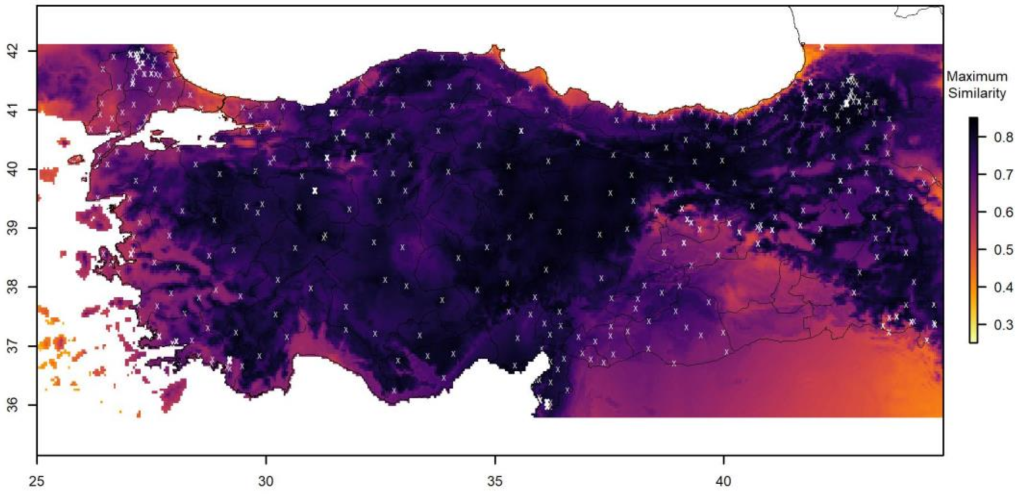
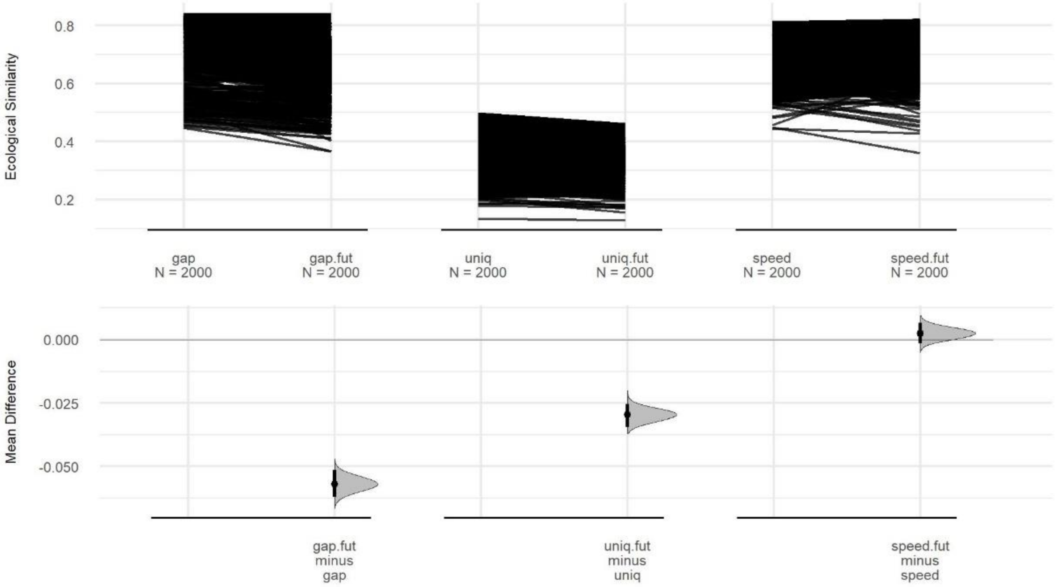
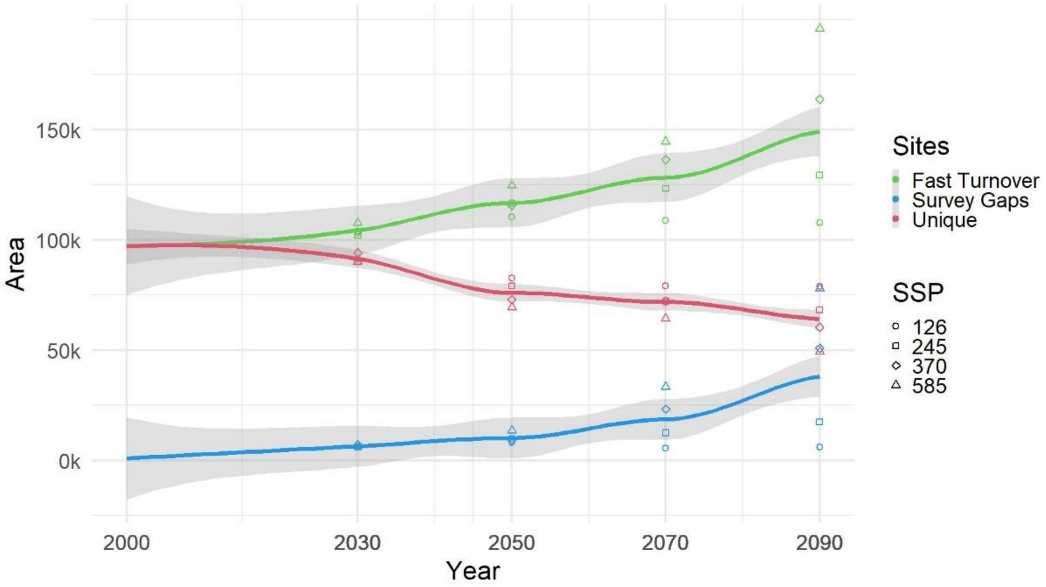


Figure 48. Mean survey gap values across the study space and climate change scenarios. White crosses show sample locations.





Figures 49 and 50. (a) Mean difference in maximum ecological similarity to sampling sites (i.e., survey gaps; gap.fut minus gap), uniqueness (uniq.fut minus uniq), and turnover speed (speed.fut minus speed) in 2000 randomly selected sites. (b) Study area with survey gap values, uniqueness, and turnover speed surpassing thresholds (0.45, 10th quantile, and 10th quantile, respectively) under different SSP scenarios throughout the years. Predictive curves and shadows represent the Locally Weighted Scatterplot Smoothing regression and confidence intervals of +/- one standard deviation.

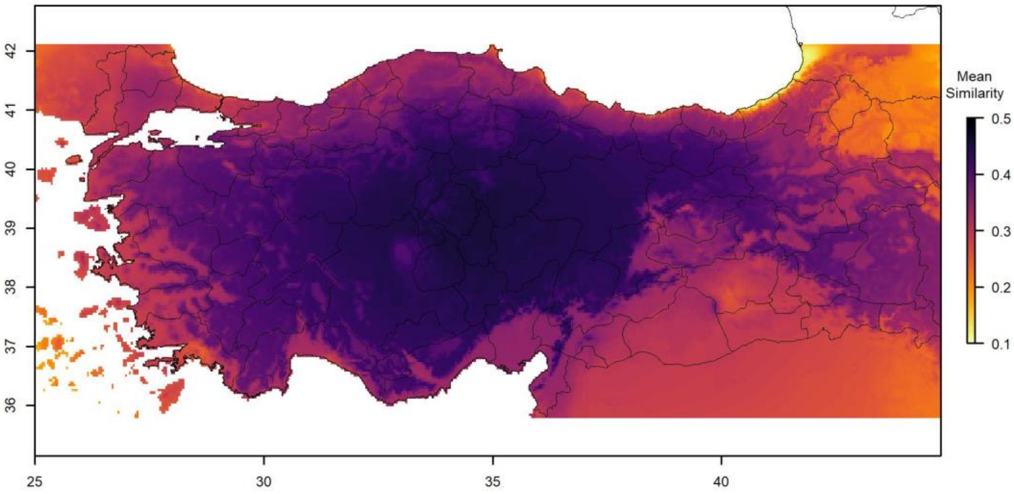


Figure 51. Mean uniqueness across the study space and climate change scenarios.

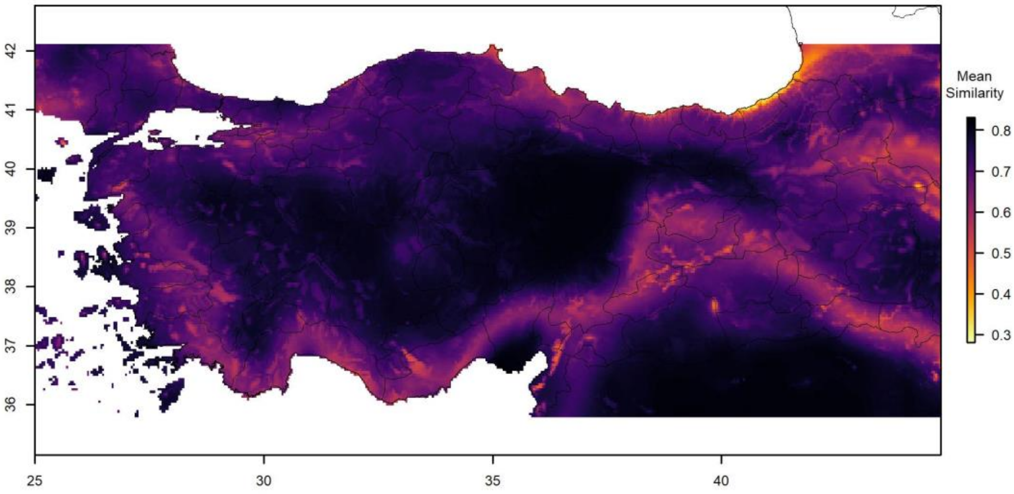


Figure 52. Mean turnover speeds across the study space and climate change scenarios.

5.8 Spatio-temporal complexity in climate change impact threatens persistence and resilience

Highly persistent sites exhibited a decline over time and across scenarios, along with sites displaying high resilience (**Fig. 53**). Conversely, sites with exceptionally high disappearance or emergence indices increased. The emergence of novel ancestry compositions unfolded later due to intensifying environmental changes. Regarding persistence, sites that remained high on that index decreased from around 800,000 km^2 to 575,000 km^2, affecting nearly one-fourth of the study area. Spatially, low persistence was heterogeneous (**Fig. 54**), with the Thrace, Upper Euphrates, and Levantine regions experiencing the highest declines, along with coastal areas of the Aegean, central Black Sea, and those neighboring the Caucasus (Colchis). In contrast, East-Central Anatolia showed the most extreme persistence, followed by the highlands of West and East Anatolia.

Spatial differences between persistence levels were reflected in significant mean differences in a Tukey's test between sites classified to various ancestral groups (all $p < 0.001$), with the Thracian group displaying the lowest scores (**Supplementary Table 12**). On the other hand, sites with high ecological similarity to either the Anatolian or Zagrosian groups showed significantly greater persistence (both $p < 0.001$; **Supplementary Table 13**). The persistence was significantly lower in regions with fast turnover rates and high resemblance to protected areas, meanwhile highly unique regions had high persistence (all $p < 0.001$ with mean differences 0.70, 0.21, and 0.35). Under SSP126, the loss of persistence was limited over the years, while SSP585 showed almost homogeneous low persistence across the study space, except for some restricted sites (**Fig. 55**).

The area that can potentially serve as refugia declined from 300,000 km^2 to 250,000 km^2. Refugium sites tended to concentrate around mountainous areas, especially those surrounded by lowlands or adjacent to low-persistence sites (**Fig. 56**). Regions classified to Thracian and Levantine ancestral groups suffered from an absence of such places in excess, therefore, significantly lacked efficient refugia (all $p < 0.001$).

In contrast, resilience was slightly higher in sites highly similar to the Zagrosian group, as in sites with slow turnover (both $p < 0.001$ with mean differences 0.08 and 0.07). Furthermore, there were considerable differences across SSPs. In extreme cases, newly established refugia were sometimes overridden, such as in Thrace and Aegean, or even in the central Anatolian plateau and the mid-portion of the Southeast Taurus range at later stages of the projection period (**Fig. 57**).

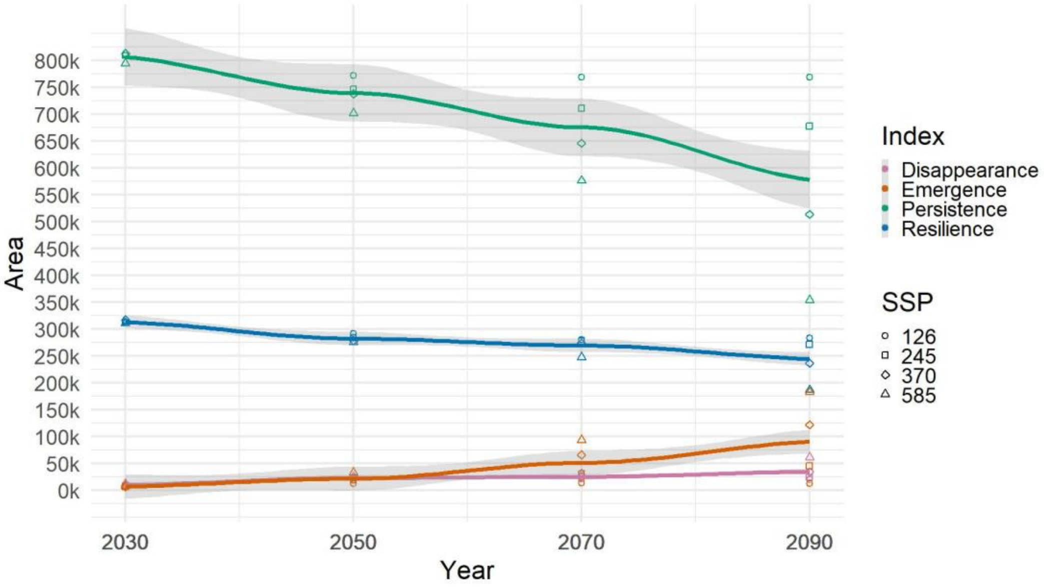


Figure 53. Study area with persistence, resilience, disappearance, and emergence indices surpassing thresholds (75th quantile, 1, 0.6, and 0.6, respectively) under different SSP scenarios throughout the years. Predictive curves and shadows represent the Locally Weighted Scatterplot Smoothing regression and confidence intervals of +/- one standard deviation.

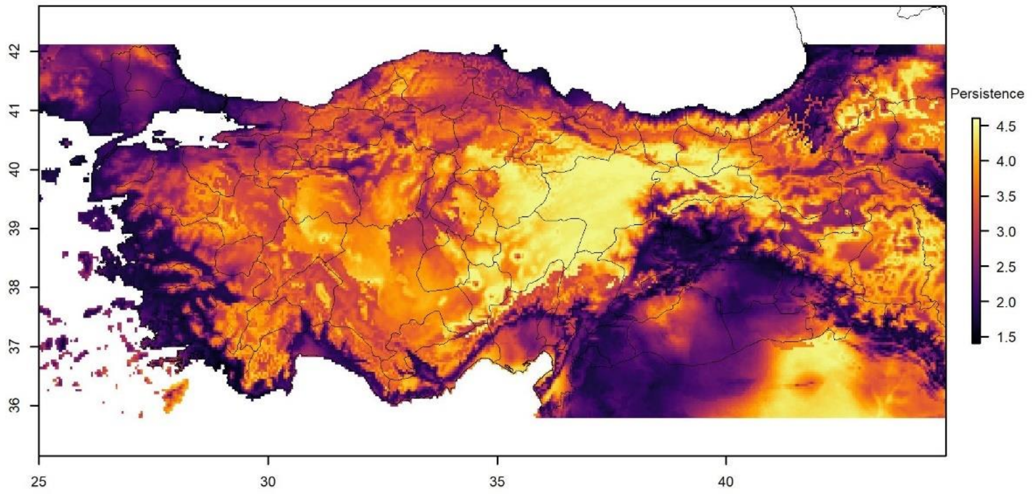


Figure 54. The spatial distribution of persistence levels measuring consistent durability in local ancestry compositions across the study space and climate change scenarios.

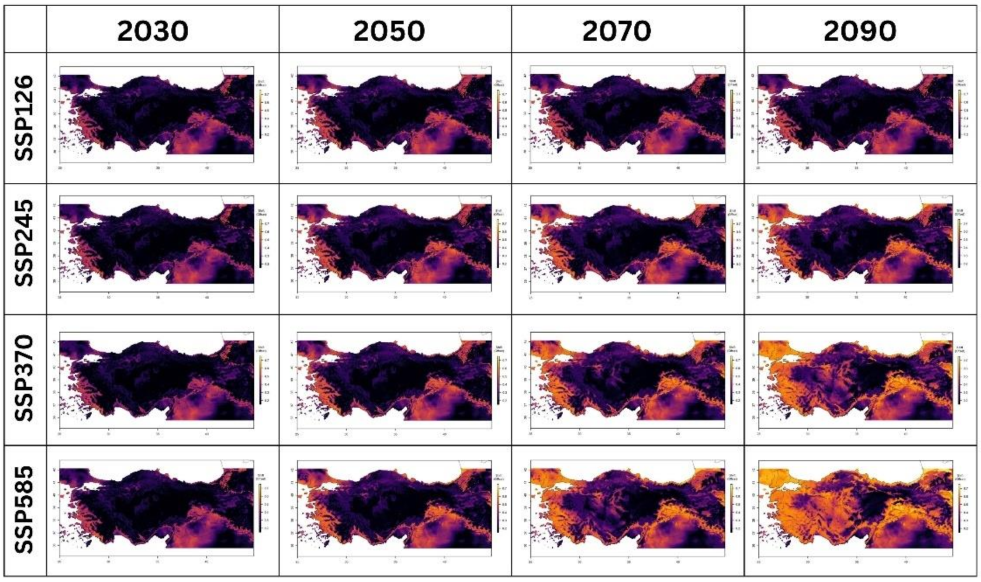


Figure 55. Impact of climate change on the persistence of ancestry compositions.

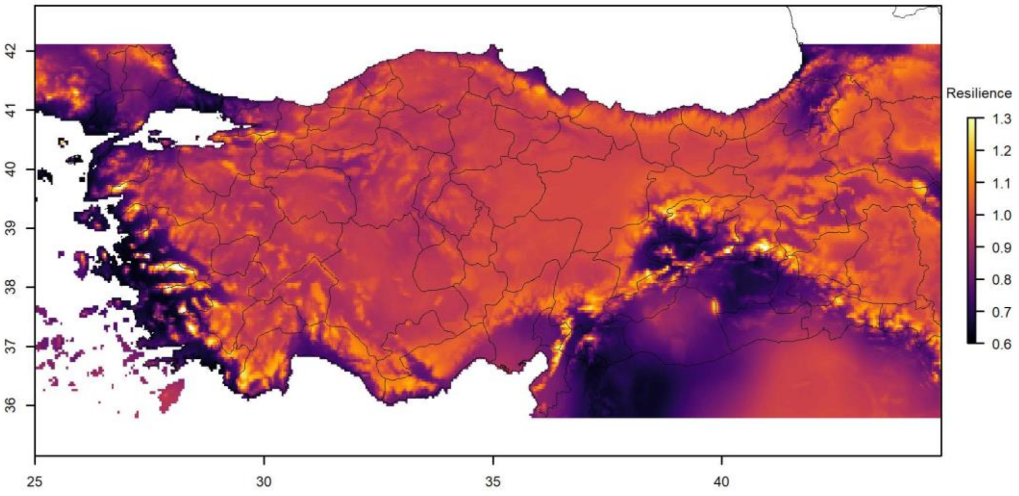


Figure 56. The spatial distribution of the resilience index measuring continuous refugium potential for local ancestry compositions across the study space and climate change scenarios.

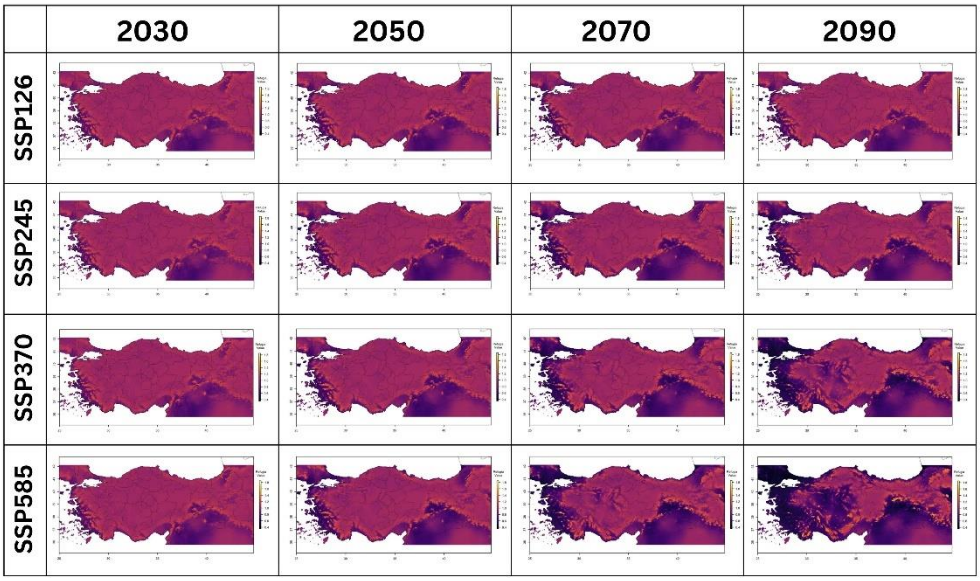


Figure 57. Impact of climate change on resilience of ancestry compositions.

Low persistence may result in the replacement of distinct local ancestry compositions with those from neighboring sites, but at other times may end up in ancestry compositions previously unknown. The disappearance of current ancestry compositions occurred relatively quickly and stabilized around 25,000 km^2. In contrast, the emergence of new ancestry compositions became more pronounced in the second half of the century, affecting an area of up to 100,000 km^2. Sites suffering the most from disappearance included the Colchis, a relatively restricted zone in South Aegean, Mount Uludağ in Marmara, and northern Syria, and likely the southern lowlands of the mid-portion of Southeast Taurus range (**Fig. 58**). Conversely, areas of emergence were prevalent in Colchis, around the Bosporus, the central Black Sea coast, and the Araxes River valley north of Mount Ararat in the easternmost part of Anatolia (**Fig. 59**).

In the late stage of pessimistic SSP scenarios, high disappearance was predicted throughout Thrace, entirely replaced by novel ancestry compositions, which extended to the western Black Sea region (**Fig. 60 and 61**). Significant mean differences register the consequences in disappearance and emergence indices between sites classified to the Thracian group or others (both $p < 0.001$). The two indices were slightly larger in regions with fast turnover (both $p < 0.001$ with mean differences of 0.08).

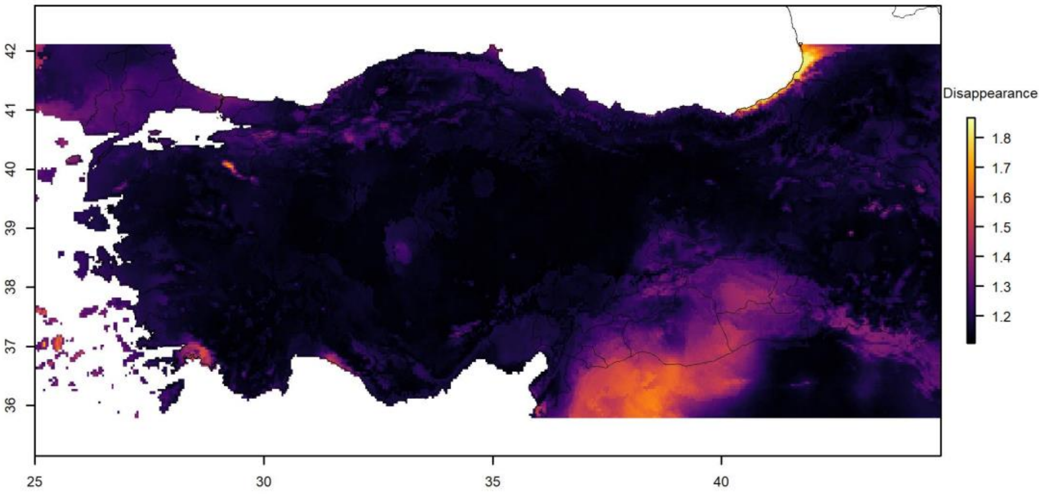


Figure 58. The spatial distribution of the disappearance index measuring the continuous loss in local ancestry compositions across the study space and climate change scenarios.

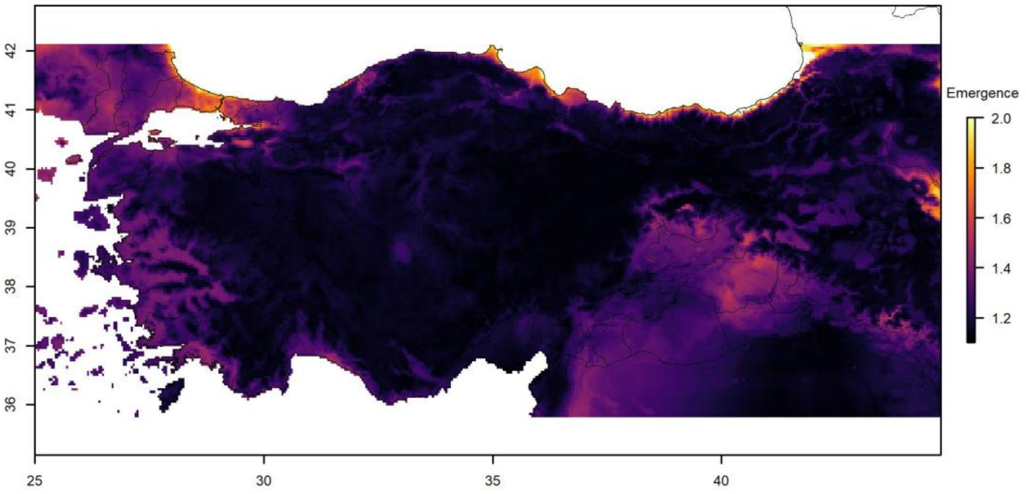


Figure 59. The spatial distribution of the emergence index measuring consistent novelty in local ancestry compositions across the study space and climate change scenarios.

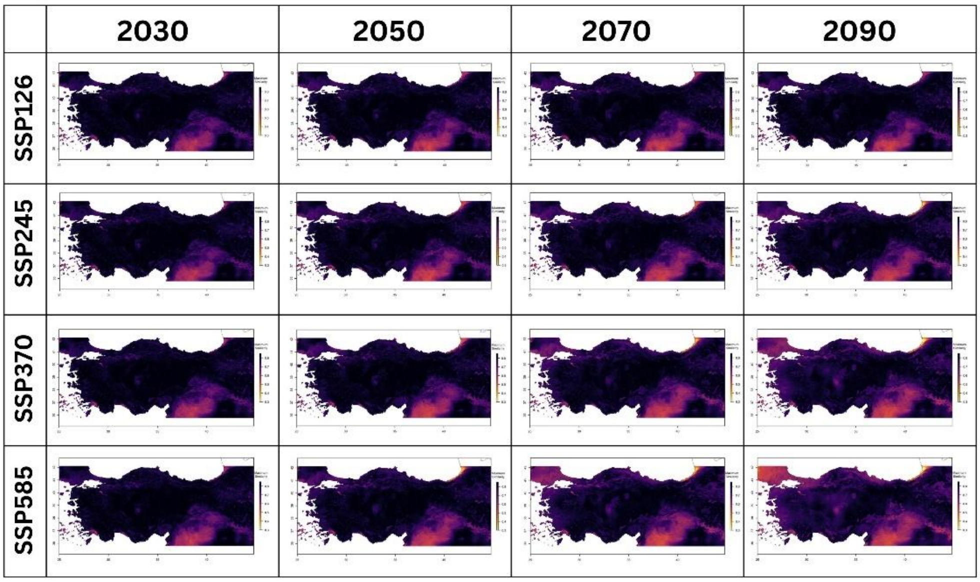


Figure 60. Impact of climate change on the disappearance of ancestry compositions.

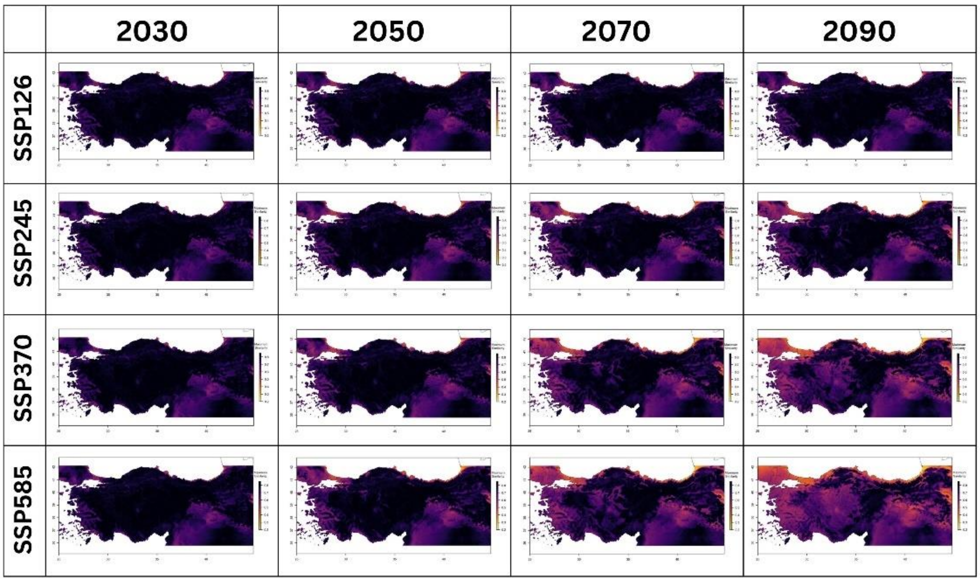


Figure 61. Impact of climate change on the emergence of ancestry compositions.

CHAPTER 6

DISCUSSION

The results presented in this study provide insights into the drivers of intra-specific turnover in ancestry compositions across honey bee populations and shed light on the complex dynamics of honey bee population structure in response to environmental gradients. The findings highlight the importance of both global and local factors in shaping genetic differentiation among honey bee subspecies and emphasize the significance of considering specific climatic variables beyond geographic distance in understanding the patterns of ancestry turnover. Furthermore, the spatio-temporal analyses of climate change impact raise concerns about the vulnerability of distinct ancestral groups and underscore the need to identify and incorporate new conservation sites to enhance the representation and resilience of honey bee populations.

6.1 Global and local drivers of intra-specific turnover

One of the key findings of this study was the identification of global and regional drivers of intra-specific turnover. The impact of localized climatic factors on the complexity of genetic differentiation highlights the importance of considering regional contexts and fine-scale ecological patterns (Kim et al., 2023). The global dissimilarity model heavily relied on precipitation amount and levels of potential evapotranspiration of the wettest and driest periods. These two metrics combined provide information on potential soil moisture gradients across seasons and landscapes—an essential predictor of plant phenology and community structure (Zhu et al., 2016; Liu et al., 2022; Dudenhöffer et al., 2022). Alterations in phenology and composition may significantly affect periodic resource availability and diversity, requiring life-history adaptations (Alstad et al., 2016; Grünzweig et al., 2022), which can drive dramatic shifts in insect phenology involving complex genomic architecture with polygenic effects, such as diapause timing in various species (Kinzner et al., 2019; Shah et al., 2020). Moisture-related variables had the highest predictive power for the Caucasian ancestry as anticipated.

Among the temperature-associated variables, the minimum temperature of the warmest period assumed a significant role in the global and local models. Maximum temperature extremes often define physiological limits to heat tolerance or interfere with sperm viability and queen failure (Sinervo et al., 2010; McAfee et al., 2020). Meanwhile, epigenetic, physiological, or behavioral adaptations in coordinated thermoregulatory activities to avoid overheating might depend on minimum temperature levels at the warmest period as a response threshold (Stabentheiner et al., 2022; Zhang et al., 2022; Alghamdi and Alattal, 2023; Alattal and Alghamdi, 2023). Aligning with their thermal tolerance limits, bees adapted to hotter environments exhibit longer foraging durations and extended foraging ranges in their natural habitats than exotic subspecies (Alattal and Alghamdi, 2015). As expected, Levantine ancestry responded strongly to minTwarm.

A. m. syriaca bees exhibit specific adaptations to elevated temperatures, including smaller size, lighter coloration, and shorter hair (Ruttner, 1988). In contrast, *A. m. caucasica* bees are large, dark, and hairy, with a tendency to hoard propolis (Kekeçoğlu et al., 2020). The two subspecies display extremely divergent behavior sets, which may be adaptive at their native distributions. Levantine bees produce a large number of swarms with multiple queens, are highly defensive, display high levels of hygienic and grooming behavior associated with the expression of genes with potential neurodevelopmental and behavioral effects, and sustain low levels of mite infestation (Kence et al., 2013; Yıldız and Karabağ, 2022). Caucasian bees enjoy sequential resource availability throughout the flowering season and are known for low levels of defensiveness, swarming tendency, and flower fidelity (Brillet et al., 2002; Çakmak et al., 2010). In contrast, *syriaca* foragers lack flexibility in learning, but the resulting flower constancy minimizes search time which may be beneficial in a Mediterranean climate with long summer draughts and high predator densities. Meanwhile, plasticity is significant when maximizing honey stores for long winters, which is an issue for *caucasica* bees (Claudio et al., 2018).

Differential neural, hormonal, and developmental responses across local populations may play a crucial role in shaping the range of physiological and behavioral plasticity displayed by individuals or colonies in response to daily and yearly thermal fluctuations (Willmer and Stone, 2004; Grodzicki and Caputa, 2014; Abram et al., 2017; González-Tokman, 2020). Along their clines, continentality and isothermality exert distinct effects on honey bee populations. Up-regulated stress responses during cooling or heating affect survival (Fahrenholz et al., 1989; Torson et al., 2015; Mucci et al., 2021; Kaya-Zeeb et al., 2022). For instance, the rate of temperature increases over time influenced critical thermal minima and maxima of *scutellata*-hybrids derived from African bees (Gonzalez et al., 2022). In this study, the Zagrosian ancestry in the native distribution of *A. m. meda* was most sensitive to predictors related to temperature oscillations.

Besides their direct impacts at the individual and colony levels, thermal fluctuations are associated with plant productivity and pollen richness (Reitalu et al., 2019). Whereas, higher minimum temperatures alter plant respiration and slow carbon accumulation for tree growth (Anderegg et al., 2015). Both factors influence land cover and nutrition (Niemczyk et al., 2021), hence may affect foraging and colony health.

Although climatic variables contributed a good share of the captured variance, spatial processes captured by MEMs in GFs, like the geographic distance in global GDM, appeared as the most critical predictors of intra-specific turnover. These results suggest that geographic distance and possible unmeasured environmental factors which are not captured by the other explicitly modeled predictors have shaped genetic differentiation among honey bee populations, as in some other species (Vanhove et al., 2021; Lima-Rezende et al., 2022).

In addition to geographic distance, multiple isolation patterns manifested across the study space, including isolation by environment and physical barriers. Despite the relatively small ecological distances and extant gene flow between subspecies on both sides of the Bosporus and the Dardanelles straits, the Sea of Marmara emerged as a primary demarcation line between western Anatolia and Thrace. Likewise, although accompanied by a more pronounced environmental signal, the transition from *syriaca* to *meda* and *anatoliaca* primarily aligned with the Taurus Mountains.

Consistent with findings in various other species, patterns of isolation by environment were evident along ecological boundaries and environmental gradients, attributable to well-known biogeographical breaks at suture zones and rapid ecological changes occurring at the East Anatolian Plateau and the Anatolian Diagonal (Bilgin, 2011; Gür, 2016; Nielsen et al., 2021). The transition from *anatoliaca* to *caucasica* was much quicker. In contrast, interpenetrated with the river beds of the Euphrates and the Araxes, the transformation to *meda* occurred at a relatively slower pace.

6.2 Climate vulnerability in the form of declining persistence and resilience

Our temporal analyses of climate change impact raise concerns about the persistence and resilience of honey bee diversity. Persistence is not uniform across the study area, and the findings suggest that honey bee populations may face shifts in turnover patterns and are vulnerable to climate change, as in other species (Nielsen et al., 2021). Shrinking regions of exceptional uniqueness, dramatic declines in the proportion of sites with high similarity to any of the ancestral groups, and physical shifts at sites of fast turnover and along transition zones all point to wider admixture across the landscape. Climate change-induced hybridization in insect populations can lead to various evolutionary outcomes apart from introgression, including species fusions, local extinctions, genetic swamping, and shifts in hybrid zone boundaries (Arce-Valdés and Sánchez-Guillén, 2022).

The area occupied by local subspecies except *syriaca* consistently shrinks under each forecast, particularly threatening the Thracian ancestral group. On the other hand, bees with Levantine ancestry bearing particular adaptations to elevated temperatures seem to gain an advantage in time. Intriguingly, those bees are not the subspecies of choice by beekeepers due to their high defensiveness, tendency to swarm, and low honey yields (Kence et al., 2013). When ecological barriers to gene flow are in place, only a limited number of alleles beneficial at both sides of the barrier may introgress (Akerman and Bürger, 2014). Without obstacles and selection pressure, populations widely admix and homogenize. However, it should be noted that physical barriers such as the Sea of Marmara and the Taurus Mountains may buffer the spread of Levantine ancestry to Anatolia and Anatolian ancestry to Thrace.

Our predictions about rapid shifts in intra-specific turnover are realistic and align well with ecological forecasts of other insect species with a mix of winners and losers (Neupane et al., 2024). Given their ectothermic nature, insect physiology and trophic or community-level interactions are highly dependent on ambient temperatures, rendering insect distributions vulnerable to impacts from warming or temperature extremes (Chen et al., 2011; Harvey et al., 2020). Furthermore, populations exhibiting enhanced survival responses in the face of predicted increase in drought frequency and intensity possess an evolutionary advantage (Exposito-Alonso et al., 2018). Morphometric analyses of honey bee samples from the Jordan Valley dating back 3000 years suggested a different geographical distribution of subspecies in the near past and indicated probable rapid shifts in the historical record by rejecting local *syriaca* ancestry in favor of *anatoliaca* (Bloch et al., 2010).

Under competitive advantage, *scutellata*-European hybrids derived from non-native African bees introduced to Brazil colonized the New World in less than 50 years (Calfee et al., 2020). Still, the invasion was halted at replicated hybrid zones in California and Argentina. Besides, a notable decrease in *scutellata* ancestry existed in the highland populations compared to lowlands (Everitt et al., 2023). More interestingly, genome-wide ancestry compositions were correlated between populations in similar habitats in Argentina and Colombia despite large geographical separation. While Calfee et al. (2020) confirmed the genomic cohesion and polygenic basis of the rapid expansion of *scutellata* ancestry and related fitness costs in cooler climates, it faced challenges deciphering the precise environmental variables driving the relationship between intra-specific turnover and latitude.

Common garden experiments point to a similar competitive advantage of locally adapted subspecies in honey bees (Costa et al., 2012; Hatjina et al., 2014; Büchler et al., 2014; Meixner et al., 2014; Uzunov et al., 2014). Space-for-time substitution is supported by common garden experiments and fossil pollen data in other species when spatial and temporal models capture comparable climate dissimilarities (Blois et al., 2013; Lovell et al., 2023), making it a widely employed method across eco-evolutionary subfields such as population phenotypes, genotypes, species' distributions, and ecological communities (Thomas et al., 2004; Wilczek et al., 2014; Alexander et al., 2015; Gougherty et al., 2021). Comparative studies conducted across various sites and gradients provide essential evidence regarding the environmental factors influencing variations in insect abundance and diversity (Blüthgen et al., 2022).

Potential refugia for the current ancestry compositions show a continuous decline across years and SSPs, accompanied by increasing disappearance and emergence indices. These putative refugia tend to concentrate around mountainous areas surrounded by lowlands and adjacent to low-persistence sites. Regions inhabited by Thracian and Levantine ancestral groups suffer from a lack of such refugia, impairing their resilience. In the face of rapid anthropogenic change, insect populations exhibit diverse resilience through shifts and adaptations (Lancaster et al., 2016; Dudaniec et al., 2018; Halsch et al., 2021; McCulloch and Waters, 2023). Geographically restricted alpine species with limited dispersal options face increased extinction risks, while surviving upland insect lineages may experience rapid adaptive changes (Kinzner et al., 2019; Shah et al., 2020).

Notably, newly established mountainous refugia were sometimes overridden in our study area at later stages of pessimistic climate scenarios. Moreover, in these instances, the ecological similarity between study sites and sampling sites exhibited a gradual decline, characterized by relatively low persistence and resilience values in these areas. This decline underscores the importance of intensifying monitoring and further sampling at such sites. Monitoring intraspecific genetic diversity is crucial for species' adaptation to changing environments and mitigating the risks particularly in regions vulnerable to climate-induced stresses (Pearman et al., 2024).

Climate responses can be asymmetric, often showing sharp declines beyond certain upper climate thresholds (DeMarche et al., 2019). Projected climate risks are significantly amplified under the SSP585 scenario compared to the SSP126 scenario, underscoring the urgency for implementing stringent emission controls (Kim et al., 2023). Considering the higher equilibrium climate sensitivity in the CMIP6 models, these more pessimistic scenarios where warming exceeds 4 °C might not be unrealistic (Meehl et al., 2020; Lee et al., 2023). Thus, our results incorporating all four SSPs might be considered more as a baseline regarding the climate vulnerability of honey bee populations.

Although we focused on Anatolia and Thrace for our model system, our approach holds significant importance for monitoring and conservation of managed and wild honey bee populations across neighboring countries of Iran, Iraq, Syria, Cyprus, Greece, Bulgaria, Georgia, and Armenia in Europe and Asia. This vulnerability and novel form of human-mediated gene flow associated with climate change could threaten populations, alongside ongoing anthropogenic impact stemming from migratory beekeeping and trade (Kükrer et al., 2021). Despite our study is based on managed honey bees, feral populations and wild pollinators might suffer from the same environmental changes (Jaffe et al., 2010; Requier et al., 2019). Furthermore, our modeling approach could benefit not only other insects but also domestic and wild animal or plant species, particularly around the Mediterranean, where similar pressures may apply.

6.3 Assessing and enhancing conservation strategies through resemblance analyses

Our findings have important implications for breeding and conservation management. Breeding programs often rely on locally adapted geographic forms, but our study shows that even these populations might be maladapted to future conditions (Hoffmann, 2010; Breed et al., 2013; Henry, 2016; Marsh et al., 2021). Sites with low persistence have an alarming overlap with established protected areas. Thrace, the Aegean coast, and parts of the Caucasus range, all harboring conservatories, suffer from low persistence. Moreover, sites with a high resemblance to protected areas display significantly reduced persistence.

Incorporating environmental variation in conservation decision-making is feasible. Hanson et al. (2017) confirmed that environmental and geographic variation could predict adaptive and neutral genetic variation and be used as surrogates in 27 plant species collected over the European Alps. Pairwise ecological similarities we used to compute resemblance indices incorporate climatic variation within the study space and consider the distribution of ancestry compositions across the landscape.

Our assessment of protected area resemblance highlights the critical need to identify and incorporate new conservation sites to enhance the representation of ancestral groups and increase protected area coverage (Rodrigues and Brooks, 2007; Kukkala and Moilanen, 2013). By adding specific unprotected areas to the conservation sites, the indirectly protected area through resemblance could expand significantly, covering a substantial portion of the study area.

According to our analysis, *A. m. meda* is currently unprotected, making it an urgent conservation priority. Meanwhile, adding Muş to the conservation sites could be beneficial, as it appears to be the epicenter of Anatolian ancestry in the east, where *meda* and *anatoliaca* populations interpenetrate each other along distinct river beds of the Euphrates and the Araxes. Moreover, due to the ecological similarity of Muş to the sites harboring high Zagrosian ancestry, such a conservation measure would also benefit that group.

While our conservation proposals could not increase the protected area resemblance in the Levantine ancestral group, an observational examination of the resemblance layers suggests that adding Mardin to the conservatories could benefit conservation through increased representativeness. However, we lack samples from this area or its immediate neighbors to assess the genetic makeup of the region directly, so we refrain this time from suggesting the province among the proposed protected areas.

Another spatial approach concerning complementarity and representation can be a backward assessment of current protected areas. Removing protected areas sequentially and monitoring changes in resemblance values can identify potential overlaps and inform more efficient future resource allocations.

Our results emphasize the potential benefits of incorporating localized conservation strategies to promote conservation complementarity and protect the unique genetic diversity of honey bee populations (Sarkar, 2006). However, it should be noted that climate change may significantly impact protected areas (Geldmann et al., 2019). Our analyses show that freely evolving conservation sites may shift in ancestry compositions in response to environmental change. When deciding on new protected areas, choosing sites with high persistence and resilience indices might be adaptive in the face of climate change. Pushing forward, it is possible to assess the climate efficacy of current protected areas by computing resemblance indices for future rasters.

An even more interesting option involves considering freely evolving protected areas and identifying current sites with lowered resemblance to future protected areas, thus with eroding conservation statuses. Alternatively, computing the resemblance between future sites and future protected areas can identify potential overlaps and reveal places that would be indirectly protected at a later stage—or those with low ecological similarity to protected areas, thus would stay uncovered. In that case, controlled mating, including artificial insemination, can benefit conservation herds.

Mating control can effectively maintain or enhance protected area resemblance in the face of climate change. Additionally, it can be strategically utilized to bolster adaptive capacity within protected areas, mainly by assisted gene flow of identified adaptive markers (Gaitán-Espitia and Hobday, 2021).

This study provides essential first steps in national genetic monitoring and conservation planning of honey bee populations in Türkiye. It brings together specimen and genetic data across the country, identifies conservation goals, evaluates existing protected areas, and designs expansions as in the original description of systematic conservation planning (Kukkala and Moilanen, 2013). This first assessment of honey bee conservation sites in Türkiye integrates genetic and environmental factors to evaluate complementarity and representativeness.

In the future, our results can be incorporated into more sophisticated decision-making and advanced systematic conservation planning tools. These tools can include spatial, genetic, and ecological data to optimize conservation decision-making and identify priority conservation areas for honey bee populations (Zurell et al., 2022; Nielsen et al., 2022; Andrello et al., 2022). Integrating insights from resemblance analyses with these sophisticated conservation decision tools will provide better implementations for safeguarding honey bee genetic diversity and adaptive capacity.

6.4 Methodological limitations and contributions

Both fitness and climate are multidimensional, and locally adapted lineages are expected to display a wide range of responses across various vital rates and environmental drivers (DeMarche et al., 2019). We assume past trends have been stable and current states reflect an optimally balanced situation. This complexity and difficulty in specifying ecological niches constitute a challenge in predicting novel system states in response to change. The unpredictability is further exacerbated by computational irreducibility, wherein evolution may be considered a chaotic process.

As a result, ecological systems exhibit low intrinsic predictability (Coreau et al., 2009; Doebeli and Ispolatov, 2010; Beckage et al., 2011). To address challenges associated with climate unpredictability, we employed six general circulation models as future climate rasters for four shared socioeconomic pathways (SSPs) and periods. Additionally, we implemented a rigorous variable selection procedure, which involved considering the variance inflation factors and GF outcomes before modeling dissimilarities.

Despite the robustness of our models, forecasting ancestry estimates is still challenging due to widely unknown and potentially differential physiological limits, the intragroup genetic diversity that can determine adaptive capacities, developmental and other kinds of plasticity, and specific plant-pollinator interactions of populations under consideration (Franks et al., 2014; Quigley et al., 2019; Kükrer and Bilgin 2020; Keeler et al., 2021; Cunningham et al., 2022). Still, our turnover predictions can be considered an assessment of ongoing pressures and climatic stress on local populations that must cope with environmental transformations. The increased mismatch between existing gene combinations and the environment can undermine resilience through hindered colony development, reduced performance and survival, and higher levels and occurrence of pathogens (Hatjina et al., 2014; Büchler et al., 2014; Meixner et al., 2014).

In six tree species, randomly selected SNPs outperformed candidate loci in predicting the performance in common garden experiments (Fitzpatrick et al., 2021; Capblancq and Forester, 2021; Lachmuth et al., 2023; Lind et al., 2023). In *Arabidopsis thaliana*, while heritability levels were notably high, no individual SNP showed significant association with drought survival, instead, it was linked to genetic group membership (Exposito-Alonso et al., 2018). Similarly, Nielsen et al. (2021) found that both neutral and outlier loci followed biogeographical breaks in the Cape urchin, common shore crab, and granular limpet. These outcomes suggested that allele frequencies across the genome were generally aligned with the same environmental gradients crucial for local adaptation. Thus, the influence of environmental gradients on both adaptive and neutral genomic backgrounds was parallel or proportional.

Based on these insights, we utilized a novel approach by employing GDM to model ancestry estimates and forecast intra-specific turnover in ancestry compositions—the first time to our knowledge. Previous research has mainly used genetic distances or differentiation indices (F_{st}) to understand local adaptation to climate, but these methods may underestimate the true magnitude of local adaptation (DeMarche et al., 2019). In this study, we employed ancestry compositions inferred from putatively neutral microsatellite markers as a multidimensional proxy to represent the processes operating at the local scale, instead of reducing population differentiation to a single metric as in F_{st}. Forecasting with multi-dimensional ancestry compositions is a viable approach, given that neighboring populations with similar environmental constraints to future site conditions may already exhibit preadaptation (Davis and Shaw, 2001).

Elevated habitat suitability correlates positively with gene flow across landscapes, supported by both theoretical frameworks and empirical evidence from phylogeographical and landscape genetic studies (Auffret et al., 2017; Knowles and Massatti, 2017; Massatti and Winkler, 2022). Jay et al. (2015) utilized a model-based approach that integrates genetic and geographic data and employs Bayesian methods to infer admixture coefficients based on correlations with environmental variables and make forecasts. However, our specific interest lies in modeling pairwise dissimilarities between sites based on ecological gradients, for which GDM proves highly advantageous (Mokany et al., 2022). GDM effectively accounts for nonlinearities in the dissimilarity measures, including when pairs of assemblages are entirely different. Moreover, GDM allows for including a wide range of environmental covariates, enabling the identification of influential factors driving diversity. This flexibility allows us to explore various combinations of environmental variables and their effects on dissimilarity.

SNP markers are highly informative and can provide candidate markers involved in local adaptation. However, they often lack experimental validation of their fitness consequences under various environmental conditions and genetic backgrounds (Barghi et al., 2020). Besides, collating georeferenced SNP data with uniform and comparable methods across the entire range of *Apis mellifera* poses challenges. Instead, we focused on a historical refugium with significant environmental heterogeneity spanning almost 1 million square kilometers, utilizing microsatellite markers. Our sampling is highly dense to capture any relationships between ancestry compositions and the environment within our study area (Anderson et al., 2010; Landguth and Schwartz, 2014). Including proximate sites with both high and low environmental similarity characterize lower dissimilarity values more accurately (Mokany et al., 2022).

Our method to compute the forward and reverse offset calculations, simplified and slightly modified from Mokany et al. (2022), is faster and less computationally demanding while providing valuable insights. It allows us to determine (i) current ancestry compositions that may no longer be available in the future and (ii) novel ancestry compositions that are distinct from currently observed. By employing our approach, computation time is significantly reduced. A single run on a quad-core 2.40 GHz laptop with 12 GB of RAM, using a set of random reference cells representing 5% of the study space, took only 10 hours. The analyses would take approximately ten days if all pairwise comparisons were used. While its broader efficacy requires further testing and may not capture sites extremely rare, our method remains informative because it considers minimum ecological distances between study sites and the random set rather than relying solely on mean similarities. It offers a suitable tool for assessing the impact of climate change, especially in the developing world, where computational resources might be limited.

Our streamlined approach and the provided code (**Supplementary Code**) are valuable for assessing vulnerability and enabling straightforward interpretation. The four vulnerability indices (persistence, resilience, disappearance, and emergence) offer specific averages across outcomes of scenario-period combinations for understanding the consistent and continuous impacts. Additionally, we introduce a supervised classification approach with high sensitivity based on type sites (in our case, sites with highly unadmixed samples) to predict expected cluster distributions from genetic and environmental variables jointly. This approach is applicable across different taxonomic levels, ecosystems, and communities while classifying biodiversity.

Overall, the results presented in this study provide valuable insights into the complex interplay between environmental factors and genetic differentiation in honey bee populations. The findings highlight the importance of considering global and regional aspects and specific climatic variables in understanding the patterns of ancestry turnover. Additionally, the spatio-temporal analyses of climate change impact raise essential conservation implications and underscore the urgency of implementing targeted conservation strategies to protect honey bee populations' genetic diversity and ensure their long-term persistence and resilience in the face of global change.

CHAPTER 7

CONCLUSION

Our research sheds light on the drivers of intra-specific turnover in ancestry compositions across honey bee populations. It reveals the complex interplay between global and localized factors in shaping genetic differentiation. Integrating spatial analyses, GF models, and GDM approaches provides comprehensive insights into honey bee populations' diversity patterns and turnover dynamics. Our findings underscore the significance of spatial processes and specific climatic variables influential in genetic differentiation. Furthermore, assessing climate change impacts reveals the vulnerability of honey bee populations with declining persistence and resilience levels. These results highlight the urgent need to identify and incorporate new conservation sites to enhance the representation and resilience of ancestral groups. Overall, this study contributes crucial knowledge to honey bee biogeography, facilitating informed conservation strategies for safeguarding their unique diversity and persistence in the face of global change.

REFERENCES

Abram, P. K., Boivin, G., Moiroux, J., & Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biological Reviews, 92(4), 1859-1876.

Adamack, A. T., & Gruber, B. (2014). PopGenReport: simplifying basic population genetic analyses in R. Methods in Ecology and Evolution, 5(4), 384-387.

Akerman, A., & Bürger, R. (2014). The consequences of gene flow for local adaptation and differentiation: a two-locus two-deme model. Journal of mathematical biology, 68(5), 1135-1198.

Alattal, Y. Z., & Alghamdi, A. A. (2023). Linking histone methylation states and hsp transcriptional regulation in thermo-tolerant and thermo-susceptible A. mellifera L. subspecies in response to heat stress. Insects, 14(3), 225.

Alattal, Y., & AlGhamdi, A. (2015). Impact of temperature extremes on survival of indigenous and exotic honey bee subspecies, Apis mellifera, under desert and semiarid climates. Bulletin of Insectology, 68(2), 219-222.

Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. Nature, 525(7570), 515-518.

Alghamdi, A. A., & Alattal, Y. Z. (2023). Expression levels of heat-shock proteins in Apis mellifera jemenetica and Apis mellifera carnica foragers in the desert climate of Saudi Arabia. Insects, 14(5), 432.

Alstad, A. O., Damschen, E. I., Givnish, T. J., Harrington, J. A., Leach, M. K., Rogers, D. A., & Waller, D. M. (2016). The pace of plant community change is accelerating in remnant prairies. Science Advances, 2(2), e1500975.

Anderegg, W. R., Ballantyne, A. P., Smith, W. K., Majkut, J., Rabin, S., Beaulieu, C., ... & Pacala, S. W. (2015). Tropical nighttime warming as a dominant driver of variability in the terrestrial carbon sink. Proceedings of the National Academy of Sciences, 112(51), 15591-15596.

Anderson, C. D., Epperson, B. K., Fortin, M. J., Holderegger, R., James, P. M., Rosenberg, M. S., ... & Spear, S. (2010). Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular ecology, 19(17), 3565-3575.

Andrello, M., D'aloia, C., Dalongeville, A., Escalante, M. A., Guerrero, J., Perrier, C., ... & Manel, S. (2022). Evolving spatial conservation prioritization with intraspecific genetic data. Trends in Ecology & Evolution, 37(6), 553-564.

Arce-Valdés, L. R., & Sánchez-Guillén, R. A. (2022). The evolutionary outcomes of climate-change-induced hybridization in insect populations. Current Opinion in Insect Science, 54, 100966.

Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A., Pakeman, R. J., Soons, M. B., ... & Cousins, S. A. (2017). Plant functional connectivity–integrating landscape structure and effective dispersal. Journal of Ecology, 105(6), 1648-1656.

Babcock, R. C., Bustamante, R. H., Fulton, E. A., Fulton, D. J., Haywood, M. D., Hobday, A. J., ... & Vanderklift, M. A. (2019). Severe continental-scale impacts of climate change are happening now: Extreme climate events impact marine habitat forming communities along 45% of Australia's coast. Frontiers in Marine Science, 411.

Barghi, N., Hermisson, J., & Schlötterer, C. (2020). Polygenic adaptation: a unifying framework to understand positive selection. Nature Reviews Genetics, 21(12), 769-781.

Barton, N., & Bengtsson, B. O. (1986). The barrier to genetic exchange between hybridising populations. Heredity, 57(3), 357-376.

Bay, R. A., Harrigan, R. J., Underwood, V. L., Gibbs, H. L., Smith, T. B., & Ruegg, K. (2018). Genomic signals of selection predict climate-driven population declines in a migratory bird. Science, 359(6371), 83-86.

Beckage, B., Gross, L. J., & Kauffman, S. (2011). The limits to prediction in ecological systems. Ecosphere, 2(11), 1-12.

Becsi, B., Formayer, H., & Brodschneider, R. (2021). A biophysical approach to assess weather impacts on honey bee colony winter mortality. Royal Society open science, 8(9), 210618.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. Ecology letters, 15(4), 365-377.

Bilgin, R. (2011). Back to the suture: the distribution of intraspecific genetic diversity in and around Anatolia. International Journal of Molecular Sciences, 12(6), 4080-4103.

Bivand, R. S., & Wong, D. W. (2018). Comparing implementations of global and local indicators of spatial association. Test, 27(3), 716-748.

Bloch, G., Francoy, T. M., Wachtel, I., Panitz-Cohen, N., Fuchs, S., & Mazar, A. (2010). Industrial apiculture in the Jordan valley during Biblical times with Anatolian honeybees. Proceedings of the National Academy of Sciences, 107(25), 11240-11244.

Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. Proceedings of the national academy of sciences, 110(23), 9374-9379.

Blüthgen, N., Staab, M., Achury, R., & Weisser, W. W. (2022). Unravelling insect declines: can space replace time?. Biology Letters, 18(4), 20210666.

Bodur, Ç., Kence, M., & Kence, A. (2007). Genetic structure of honeybee, Apis mellifera L.(Hymenoptera: Apidae) populations of Turkey inferred from microsatellite analysis. Journal of Apicultural Research, 46(1), 50-56.

Boyle, E. A., Li, Y. I., & Pritchard, J. K. (2017). An expanded view of complex traits: from polygenic to omnigenic. Cell, 169(7), 1177-1186.

Breed, M. F., Stead, M. G., Ottewell, K. M., Gardner, M. G., & Lowe, A. J. (2013). Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. Conservation Genetics, 14, 1-10.

Brillet, C., Robinson, G. E., Bues, R., & Le Conte, Y. (2002). Racial differences in division of labor in colonies of the honey bee (Apis mellifera). Ethology, 108(2), 115-126.

Büchler, R., Costa, C., Hatjina, F., Andonov, S., Meixner, M. D., Conte, Y. L., ... & Wilde, J. (2014). The influence of genetic origin and its interaction with environmental effects on the survival of Apis mellifera L. colonies in Europe. Journal of Apicultural Research, 53(2), 205-214.

Calfee, E., Agra, M. N., Palacio, M. A., Ramírez, S. R., & Coop, G. (2020). Selection and hybridization shaped the rapid spread of African honey bee ancestry in the Americas. PLoS genetics, 16(10), e1009038.

Cao, L., Dai, Z., Tan, H., Zheng, H., Wang, Y., Chen, J., ... & Zhang, Z. (2023). Population Structure, Demographic History, and Adaptation of Giant Honeybees in China Revealed by Population Genomic Data. Genome Biology and Evolution, 15(3), evad025.

Capblancq, T., & Forester, B. R. (2021). Redundancy analysis: A Swiss Army Knife for landscape genomics. Methods in Ecology and Evolution, 12(12), 2298-2309.

Charlesworth, B., Nordborg, M., & Charlesworth, D. (1997). The effects of local selection, balanced polymorphism and background selection on equilibrium patterns of genetic diversity in subdivided populations. Genetics Research, 70(2), 155-174.

Chen, C., Liu, Z., Pan, Q., Chen, X., Wang, H., Guo, H., ... & Shi, W. (2016). Genomic analyses reveal demographic history and temperate adaptation of the newly discovered honey bee subspecies Apis mellifera sinisxinyuan n. ssp. Molecular biology and evolution, 33(5), 1337-1348.

Chen, C., Wang, H., Liu, Z., Chen, X., Tang, J., Meng, F., & Shi, W. (2018). Population genomics provide insights into the evolution and adaptation of the eastern honey bee (Apis cerana). Molecular Biology and Evolution, 35(9), 2260-2271.

Chen, I. C., Hill, J. K., Shiu, H. J., Holloway, J. D., Benedick, S., Chey, V. K., ... & Thomas, C. D. (2011). Asymmetric boundary shifts of tropical montane Lepidoptera over four decades of climate warming. Global Ecology and Biogeography, 20(1), 34-45.

Chevin, L. M., & Hospital, F. (2008). Selective sweep at a quantitative trait locus in the presence of background genetic variation. Genetics, 180(3), 1645-1660.

Christmas, M. J., Wallberg, A., Bunikis, I., Olsson, A., Wallerman, O., & Webster, M. T. (2019). Chromosomal inversions associated with environmental adaptation in honeybees. Molecular ecology, 28(6), 1358-1374.

Claudio, E. P., Rodriguez-Cruz, Y., Arslan, O. C., Giray, T., Rivera, J. L. A., Kence, M., ... & Abramson, C. I. (2018). Appetitive reversal learning differences of two honey bee subspecies with different foraging behaviors. PeerJ, 6, e5918.

Cohn, A. S., Newton, P., Gil, J. D., Kuhl, L., Samberg, L., Ricciardi, V., ... & Northrop, S. (2017). Smallholder agriculture and climate change. Annual Review of Environment and Resources, 42, 347-375.

Coreau, A., Pinay, G., Thompson, J. D., Cheptou, P. O., & Mermet, L. (2009). The rise of research on futures in ecology: rebalancing scenarios and predictions. Ecology letters, 12(12), 1277-1286.

Coronese, M., Lamperti, F., Keller, K., Chiaromonte, F., & Roventini, A. (2019). Evidence for sharp increase in the economic damages of extreme natural disasters. Proceedings of the National Academy of Sciences, 116(43), 21450-21455.

Costa, C., Lodesani, M., & Bienefeld, K. (2012). Differences in colony phenotypes across different origins and locations: evidence for genotype by environment interactions in the Italian honeybee (Apis mellifera ligustica)?. Apidologie, 43(6), 634-642.

Cridland, J. M., Ramirez, S. R., Dean, C. A., Sciligo, A., & Tsutsui, N. D. (2018). Genome sequencing of museum specimens reveals rapid changes in the genetic composition of honey bees in California. Genome biology and evolution, 10(2), 458-472.

Cridland, J. M., Tsutsui, N. D., & Ramírez, S. R. (2017). The complex demographic history and evolutionary origin of the western honey bee, Apis mellifera. Genome Biology and Evolution, 9(2), 457-472.

Cunningham, M. M., Tran, L., McKee, C. G., Polo, R. O., Newman, T., Lansing, L., ... & Guarna, M. M. (2022). Honey bees as biomonitors of environmental contaminants, pathogens, and climate change. Ecological Indicators, 134, 108457.

Çakmak, I., Song, D. S., Mixson, T. A., Serrano, E., Clement, M. L., Savitski, A., ... & Wells, H. (2010). Foraging response of Turkish honey bee subspecies to flower color choices and reward consistency. Journal of insect behavior, 23, 100-116.

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. Science, 292(5517), 673-679.

Dearden, P. K., Duncan, E. J., & Wilson, M. J. (2009). The honeybee Apis mellifera. Cold Spring Harbor Protocols, 2009(6), pdb-emo123.

Delgado, D. L., Pérez, M. E., Galindo-Cardona, A., Giray, T., & Restrepo, C. (2012). Forecasting the influence of climate change on agroecosystem services: potential impacts on honey yields in a small-island developing state. Psyche: A Journal of Entomology, 2012, 1-10.

DeMarche, M. L., Doak, D. F., & Morris, W. F. (2019). Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. Global Change Biology, 25(3), 775-793.

Doebeli, M., & Ispolatov, I. (2010). Complexity and diversity. Science, 328(5977), 494-497.

Dogantzis, Kathleen A., Tanushree Tiwari, Ida M. Conflitti, Alivia Dey, Harland M. Patch, Elliud M. Muli, Lionel Garnery et al. "Thrice out of Asia and the adaptive radiation of the western honey bee." Science advances 7, no. 49 (2021): eabj2151.

Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guénard G, Jombart T, Larocque G, Legendre P, Madi N, Wagner HH (2023). adespatial: Multivariate Multiscale Spatial Analysis. R package version 0.3-23, https://CRAN.R-project.org/package=adespatial.

Dudaniec, R. Y., Yong, C. J., Lancaster, L. T., Svensson, E. I., & Hansson, B. (2018). Signatures of local adaptation along environmental gradients in a range-expanding damselfly (Ischnura elegans). Molecular Ecology, 27(11), 2576-2593.

Dudenhöffer, J. H., Luecke, N. C., & Crawford, K. M. (2022). Changes in precipitation patterns can destabilize plant species coexistence via changes in plant–soil feedback. Nature Ecology & Evolution, 6(5), 546-554.

Earl, D. A., & VonHoldt, B. M. (2012). STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation genetics resources, 4, 359-361.

Eckert, A. J., Van Heerwaarden, J., Wegrzyn, J. L., Nelson, C. D., Ross-Ibarra, J., González-Martínez, S. C., & Neale, D. B. (2010). Patterns of population structure and environmental associations to aridity across the range of loblolly pine (Pinus taeda L., Pinaceae). Genetics, 185(3), 969-982.

Eckert, C. G., Samis, K. E., & Lougheed, S. C. (2008). Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. Molecular ecology, 17(5), 1170-1188.

Ellis, N., Smith, S. J., & Pitcher, C. R. (2012). Gradient forests: calculating importance gradients on physical predictors. Ecology, 93(1), 156-168.

Estoup, A., Garnery, L., Solignac, M., & Cornuet, J. M. (1995). Microsatellite variation in honey bee (Apis mellifera L.) populations: hierarchical genetic structure and test of the infinite allele and stepwise mutation models. Genetics, 140(2), 679-695.

Everitt, T., Wallberg, A., Christmas, M. J., Olsson, A., Hoffmann, W., Neumann, P., & Webster, M. T. (2023). The genomic basis of adaptation to high elevations in Africanized honey bees. Genome biology and evolution, 15(9), evad157.

Exposito-Alonso, M., Vasseur, F., Ding, W., Wang, G., Burbano, H. A., & Weigel, D. (2018). Genomic basis and evolutionary potential for extreme drought adaptation in Arabidopsis thaliana. Nature ecology & evolution, 2(2), 352-358.

Fahrenholz, L., Lamprecht, I., & Schricker, B. (1989). Thermal investigations of a honey bee colony: thermoregulation of the hive during summer and winter and heat production of members of different bee castes. Journal of Comparative Physiology B, 159, 551-560.

Falush, D., Stephens, M., & Pritchard, J. K. (2003). Inference of population structure using multilocus genotype data: linked loci and correlated allele frequencies. Genetics, 164(4), 1567-1587.

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. Diversity and distributions, 13(3), 252-264.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International journal of climatology, 37(12), 4302-4315.

Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modelling of biodiversity: Mapping the genomic landscape of current and future environmental adaptation. Ecology letters, 18(1), 1-16.

Fitzpatrick, M. C., Chhatre, V. E., Soolanayakanahally, R. Y., & Keller, S. R. (2021). Experimental support for genomic prediction of climate maladaptation using the machine learning approach Gradient Forests. Molecular Ecology Resources, 21(8), 2749-2765.

Fitzpatrick, M. C., Sanders, N. J., Ferrier, S., Longino, J. T., Weiser, M. D., & Dunn, R. (2011). Forecasting the future of biodiversity: a test of single-and multi-species models for ants in North America. Ecography, 34(5), 836-847.

Fitzpatrick, M., Mokany, K., Manion, G., Nieto-Lugilde, D., Ferrier, S., Lisk, M., ... & Fitzpatrick, M. M. (2022). Package 'gdm'.

Flaxman, S. M., Feder, J. L., & Nosil, P. (2013). Genetic hitchhiking and the dynamic buildup of genomic divergence during speciation with gene flow. Evolution, 67(9), 2577-2591.

Flores, J. M., Gil-Lebrero, S., Gámiz, V., Rodríguez, M. I., Ortiz, M. A., & Quiles, F. J. (2019). Effect of the climate change on honey bee colonies in a temperate Mediterranean zone assessed through remote hive weight monitoring system in conjunction with exhaustive colonies assessment. Science of the Total Environment, 653, 1111-1119.

Franck, P., Garnery, L., Loiseau, A., Oldroyd, B. P., Hepburn, H. R., Solignac, M., & Cornuet, J. M. (2001). Genetic diversity of the honeybee in Africa: microsatellite and mitochondrial data. Heredity, 86(4), 420-430.

Franks, S. J., Weber, J. J., & Aitken, S. N. (2014). Evolutionary and plastic responses to climate change in terrestrial plant populations. Evolutionary applications, 7(1), 123-139.

Fuller, Z. L., Niño, E. L., Patch, H. M., Bedoya-Reina, O. C., Baumgarten, T., Muli, E., ... & Miller, W. (2015). Genome-wide analysis of signatures of selection in populations of African honey bees (Apis mellifera) using new web-based tools. BMC genomics, 16(1), 1-18.

Gaitán-Espitia, J. D., & Hobday, A. J. (2021). Evolutionary principles and genetic considerations for guiding conservation interventions under climate change. Global Change Biology, 27(3), 475-488.

Galindo, J., Morán, P., & Rolán-Alvarez, E. (2009). Comparing geographical genetic differentiation between candidate and noncandidate loci for adaptation strengthens support for parallel ecological divergence in the marine snail Littorina saxatilis. Molecular Ecology, 18(5), 919-930.

Geldmann, J., Manica, A., Burgess, N. D., Coad, L., & Balmford, A. (2019). A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. Proceedings of the National Academy of Sciences, 116(46), 23209-23215.

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. (2008). Climate change and evolution: Disentangling environmental and genetic responses. Molecular Ecology, 17(1), 167-178.

Gmel, A. I., Guichard, M., Dainat, B., Williams, G. R., Eynard, S., Vignal, A., ... & Neuditschko, M. (2023). Identification of runs of homozygosity in Western honey bees (Apis mellifera) using whole-genome sequencing data. Ecology and Evolution, 13(1), e9723.

Gonzalez, V. H., Oyen, K., Ávila, O., & Ospina, R. (2022). Thermal limits of Africanized honey bees are influenced by temperature ramping rate but not by other experimental conditions. Journal of Thermal Biology, 110, 103369.

González-Tokman, D., Córdoba-Aguilar, A., Dáttilo, W., Lira-Noriega, A., Sánchez-Guillén, R. A., & Villalobos, F. (2020). Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. Biological Reviews, 95(3), 802-821.

Gordo, O., & Sanz, J. J. (2006). Temporal trends in phenology of the honey bee Apis mellifera (L.) and the small white Pieris rapae (L.) in the Iberian Peninsula (1952–2004). Ecological Entomology, 31(3), 261-268.

Goudet, J. (2005). Hierfstat, a package for R to compute and test hierarchical F-statistics. Molecular ecology notes, 5(1), 184-186.

Gougherty, A. V., Keller, S. R., & Fitzpatrick, M. C. (2021). Maladaptation, migration and extirpation fuel climate change risk in a forest tree species. Nature Climate Change, 11(2), 166-171.

Grodzicki, P., & Caputa, M. (2014). Diurnal and seasonal changes in thermal preference of single, isolated bees and small groups of bees (Apis mellifera L.). Journal of insect behavior, 27, 701-711.

Grünzweig, J. M., De Boeck, H. J., Rey, A., Santos, M. J., Adam, O., Bahn, M., ... & Yakir, D. (2022). Dryland mechanisms could widely control ecosystem functioning in a drier and warmer world. Nature ecology & evolution, 6(8), 1064-1076.

Guillot, G., Estoup, A., Mortier, F., & Cosson, J. F. (2005). A spatial statistical model for landscape genetics. Genetics, 170(3), 1261-1280.

Gür, H. (2016). The Anatolian diagonal revisited: Testing the ecological basis of a biogeographic boundary. Zoology in the Middle East, 62(3), 189-199.

Haldane, J. B., & Spurway, H. (1954). A statistical analysis of communication in "Apis mellifera" and a comparison with communication in other animals. Insectes sociaux, 1, 247-283.

Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. Proceedings of the national academy of sciences, 118(2), e2002543117.

Hanson, J. O., Rhodes, J. R., Riginos, C., & Fuller, R. A. (2017). Environmental and geographic variables are effective surrogates for genetic variation in conservation planning. Proceedings of the National Academy of Sciences, 114(48), 12755-12760.

Harpur, B. A., Kent, C. F., Molodtsova, D., Lebon, J. M., Alqarni, A. S., Owayss, A. A., & Zayed, A. (2014). Population genomics of the honey bee reveals strong signatures of positive selection on worker traits. Proceedings of the National Academy of Sciences, 111(7), 2614-2619.

Harvey, J. A., Heinen, R., Gols, R., & Thakur, M. P. (2020). Climate change-mediated temperature extremes and insects: From outbreaks to breakdowns. Global change biology, 26(12), 6685-6701.

Hatjina, F., Costa, C., Büchler, R., Uzunov, A., Drazic, M., Filipi, J., ... & Kezic, N. (2014). Population dynamics of European honey bee genotypes under different environmental conditions. Journal of Apicultural Research, 53(2), 233-247.

Henriques, D., Wallberg, A., Chávez-Galarza, J., Johnston, J. S., Webster, M. T., & Pinto, M. A. (2018). Whole genome SNP-associated signatures of local adaptation in honeybees of the Iberian Peninsula. Scientific Reports, 8(1), 11145.

Henry, R. J. (2016). Genomics strategies for germplasm characterization and the development of climate resilient crops. In Crop Breeding (pp. 25-34). Apple Academic Press.

Hewitt, G. M. (1999). Post-glacial re-colonization of European biota. Biological journal of the Linnean Society, 68(1-2), 87-112.

Hijmans R (2022). raster: Geographic Data Analysis and Modeling. R package version 3.6-23, https://rspatial.org/raster.

Hijmans, Robert J., Marcia Barbosa, Aniruddha Ghosh, and Alex Mandel. (2023). Geodata: Download Geographic Data.

Ho, J., Tumkaya, T., Aryal, S., Choi, H., & Claridge-Chang, A. (2019). Moving beyond P values: data analysis with estimation graphics. Nature methods, 16(7), 565-566.

Hoffmann, I. (2010). Climate change and the characterization, breeding and conservation of animal genetic resources. Animal genetics, 41, 32-46.

Howden, S. M., Soussana, J. F., Tubiello, F. N., Chhetri, N., Dunlop, M., & Meinke, H. (2007). Adapting agriculture to climate change. Proceedings of the national academy of sciences, 104(50), 19691-19696.

Howlett, B. G., Butler, R. C., Nelson, W., & Donovan, B. J. (2013). Impact of climate change on crop pollinator in New Zealand. Wellington: Ministry for Primary Industries.

Iwasaki, J. M., & Hogendoorn, K. (2021). How protection of honey bees can help and hinder bee conservation. Current Opinion in Insect Science, 46, 112-118.

Jaffe, R., Dietemann, V., Allsopp, M. H., Costa, C., Crewe, R. M., Dall'Olio, R., ... & Moritz, R. F. (2010). Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses. Conservation biology, 24(2), 583-593.

Jarvis A., H.I. Reuter, A. Nelson, E. Guevara, 2008, Hole-filled seamless SRTM data V4, International Centre for Tropical Agriculture (CIAT), available from https://srtm.csi.cgiar.org.

Jay, F., François, O., Durand, E. Y., & Blum, M. G. (2015). POPS: A software for prediction of population genetic structure using latent regression models. Journal of Statistical Software, 68, 1-19.

Jay, F., Manel, S., Alvarez, N., Durand, E. Y., Thuiller, W., Holderegger, R., ... & François, O. (2012). Forecasting changes in population genetic structure of alpine plants in response to global warming. Molecular ecology, 21(10), 2354-2368.

Ji, Y., Li, X., Ji, T., Tang, J., Qiu, L., Hu, J., ... & Zhou, X. (2020). Gene reuse facilitates rapid radiation and independent adaptation to diverse habitats in the Asian honeybee. Science Advances, 6(51), eabd3590.

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics, 24(11), 1403-1405.

Jombart, T., Devillard, S., & Balloux, F. (2010). Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC genetics, 11, 1-15.

Jombart, T., Devillard, S., Dufour, A. B., & Pontier, D. (2008). Revealing cryptic spatial patterns in genetic variability by a new multivariate method. Heredity, 101(1), 92-103.

Jones, F. C., Grabherr, M. G., Chan, Y. F., Russell, P., Mauceli, E., Johnson, J., ... & Kingsley, D. M. (2012). The genomic basis of adaptive evolution in threespine sticklebacks. Nature, 484(7392), 55-61.

Jones, M. R., Forester, B. R., Teufel, A. I., Adams, R. V., Anstett, D. N., Goodrich, B. A., ... & Manel, S. (2013). Integrating landscape genomics and spatially explicit approaches to detect loci under selection in clinal populations. Evolution, 67(12), 3455-3468.

Joost, S., Bonin, A., Bruford, M. W., Després, L., Conord, C., Erhardt, G., ... & Taberlet, P. (2007). A spatial analysis method (SAM) to detect candidate loci for selection: Towards a landscape genomics approach to adaptation. Molecular Ecology, 16(18), 3955-3969.

Kamvar, Z. N., Tabima, J. F., & Grünwald, N. J. (2014). Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. PeerJ, 2, e281.

Kandemir, I., Kence, M., Sheppard, W. S., & Kence, A. (2006). Mitochondrial DNA variation in honey bee (Apis mellifera L.) populations from Turkey. Journal of apicultural research, 45(1), 33-38.

Kaya-Zeeb, S., Delac, S., Wolf, L., Marante, A. L., Scherf-Clavel, O., & Thamm, M. (2022). Robustness of the honeybee neuro-muscular octopaminergic system in the face of cold stress. Frontiers in physiology, 1979.

Keeler, A. M., Rose-Person, A., & Rafferty, N. E. (2021). From the ground up: Building predictions for how climate change will affect belowground mutualisms, floral traits, and bee behavior. Climate Change Ecology, 1, 100013.

Kekeçoğlu, M., Eroğlu, N., Kambur, M., & Münir, U. Ç. A. K. (2020). The relationships between propolis collecting capability and morphometric features of some honey bee races and ecotypes in Anatolia. Journal of Agricultural Sciences, 26(1), 71-77.

Kence, M., Oskay, D., Giray, T., & Kence, A. (2013). Honey bee colonies from different races show variation in defenses against the varroa mite in a ‘common garden’. Entomologia Experimentalis et Applicata, 149(1), 36-43.

Kim, S. W., Sommer, B., Beger, M., & Pandolfi, J. M. (2023). Regional and global climate risks for reef corals: Incorporating species-specific vulnerability and exposure to climate hazards. Global Change Biology.

Kinzner, M. C., Gamisch, A., Hoffmann, A. A., Seifert, B., Haider, M., Arthofer, W., ... & Steiner, F. M. (2019). Major range loss predicted from lack of heat adaptability in an alpine Drosophila species. Science of the Total Environment, 695, 133753.

Kirk, H., & Freeland, J. R. (2011). Applications and implications of neutral versus non-neutral markers in molecular ecology. International journal of molecular sciences, 12(6), 3966-3988.

Knowles, L. L., & Massatti, R. (2017). Distributional shifts–not geographic isolation–as a probable driver of montane species divergence. Ecography, 40(12), 1475-1485.

Kopelman, N. M., Mayzel, J., Jakobsson, M., Rosenberg, N. A., & Mayrose, I. (2015). Clumpak: a program for identifying clustering modes and packaging population structure inferences across K. Molecular ecology resources, 15(5), 1179-1191.

Kovac, H., & Stabentheiner, A. (2011). Thermoregulation of foraging honeybees on flowering plants: seasonal variability and influence of radiative heat gain. Ecological entomology, 36(6), 686-699.

Kukkala, A. S., & Moilanen, A. (2013). Core concepts of spatial prioritisation in systematic conservation planning. Biological Reviews, 88(2), 443-464.

Kulmuni, J., & Westram, A. M. (2017). Intrinsic incompatibilities evolving as a by-product of divergent ecological selection: Considering them in empirical studies on divergence with gene flow.

Kükrer, M. (2013). Genetic diversity of honey bee populations in Turkey based on microsatellite markers: A comparison between migratory versus stationary apiaries and isolated regions versus regions open to migratory beekeeping (Master's thesis, Middle East Technical University).

Kükrer, M., & Bilgin, C. C. (2020). Climate change prompts monitoring and systematic utilization of honey bee diversity in Turkey. Bee Studies, 12(1), 19-25.

Kükrer, M., Kence, M., & Kence, A. (2021). Honey bee diversity is swayed by migratory beekeeping and trade despite conservation practices: Genetic evidence for the impact of anthropogenic factors on population structure. Frontiers in Ecology and Evolution, 9, 556816.

Lachmuth, S., Capblancq, T., Keller, S. R., & Fitzpatrick, M. C. (2023). Assessing uncertainty in genomic offset forecasts from landscape genomic models (and implications for restoration and assisted migration). Frontiers in Ecology and Evolution, 11, 1155783.

Lancaster, L. T. (2016). Widespread range expansions shape latitudinal variation in insect thermal limits. Nature climate change, 6(6), 618-621.

Landguth, E. L., & Schwartz, M. K. (2014). Evaluating sample allocation and effort in detecting population differentiation for discrete and continuously distributed individuals. Conservation Genetics, 15, 981-992.

Langowska, A., Zawilak, M., Sparks, T. H., Glazaczow, A., Tomkins, P. W., & Tryjanowski, P. (2017). Long-term effect of temperature on honey yield and honeybee phenology. International journal of biometeorology, 61, 1125-1132.

Lee, H., Calvin, K., Dasgupta, D., Krinner, G., Mukherji, A., Thorne, P., ... & Park, Y. (2023). IPCC, 2023: Climate Change 2023: Synthesis Report, Summary for Policymakers. 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.

Letunic, I., & Bork, P. (2021). Interactive Tree Of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. Nucleic acids research, 49(W1), W293-W296.

Lima-Rezende, C. A., Cabanne, G. S., Rocha, A. V., Carboni, M., Zink, R. M., & Caparroz, R. (2022). A comparative phylogenomic analysis of birds reveals heterogeneous differentiation processes among Neotropical savannas. Molecular Ecology, 31(12), 3451-3467.

Lind, B. M., Candido-Ribeiro, R., Singh, P., Lu, M., Obreht Vidakovic, D., Booker, T. R., ... & Aitken, S. N. (2024). How useful are genomic data for predicting maladaptation to future climate?. Global Change Biology, 30(4), e17227.

Liu, Z., Fu, Y. H., Shi, X., Lock, T. R., Kallenbach, R. L., & Yuan, Z. (2022). Soil moisture determines the effects of climate warming on spring phenology in grasslands. Agricultural and Forest Meteorology, 323, 109039.

Lovell, R. S., Collins, S., Martin, S. H., Pigot, A. L., & Phillimore, A. B. (2023). Space-for-time substitutions in climate change ecology and evolution. Biological Reviews, 98(6), 2243-2270.

Lynch, M. 1991. The genetic interpretation of inbreed- ing depression and outbreeding depression. Evolution 45:622-629.

Marsh, J. I., Hu, H., Gill, M., Batley, J., & Edwards, D. (2021). Crop breeding for a changing climate: Integrating phenomics and genomics with bioinformatics. Theoretical and Applied Genetics, 134, 1677-1690.

Massatti, R., & Winkler, D. E. (2022). Spatially explicit management of genetic diversity using ancestry probability surfaces. Methods in Ecology and Evolution, 13(12), 2668-2681.

Mayr, E. 1970. Populations, species, and evolution. Harvard University Press, Cambridge, Massachusetts

McAfee, A., Chapman, A., Higo, H., Underwood, R., Milone, J., Foster, L. J., ... & Pettis, J. S. (2020). Vulnerability of honey bee queens to heat-induced loss of fertility. Nature Sustainability, 3(5), 367-376.

McCulloch, G. A., & Waters, J. M. (2023). Rapid adaptation in a fast-changing world: Emerging insights from insect genomics. Global Change Biology, 29(4), 943-954.

Meehl, G. A., Senior, C. A., Eyring, V., Flato, G., Lamarque, J. F., Stouffer, R. J., ... & Schlund, M. (2020). Context for interpreting equilibrium climate sensitivity and transient climate response from the CMIP6 Earth system models. Science Advances, 6(26), eaba1981.

Meixner, M. D., Costa, C., Kryger, P., Hatjina, F., Bouga, M., Ivanova, E., & Büchler, R. (2010). Conserving diversity and vitality for honey bee breeding. Journal of Apicultural Research, 49(1), 85-92.

Meixner, M. D., Francis, R. M., Gajda, A., Kryger, P., Andonov, S., Uzunov, A., ... & Wilde, J. (2014). Occurrence of parasites and pathogens in honey bee colonies used in a European genotype-environment interactions experiment. Journal of Apicultural Research, 53(2), 215-229.

Mokany, K., Bush, A., & Ferrier, S. (2019b). Community assembly processes restrict the capacity for genetic adaptation under climate change. Ecography, 42(6), 1164-1174.

Mokany, K., Harwood, T. D., Halse, S. A., & Ferrier, S. (2019a). Riddles in the dark: Assessing diversity patterns for cryptic subterranean fauna of the Pilbara. Diversity and Distributions, 25(2), 240-254.

Mokany, K., Ware, C., Woolley, S. N., Ferrier, S., & Fitzpatrick, M. C. (2022). A working guide to harnessing generalized dissimilarity modelling for biodiversity analysis and conservation assessment. Global Ecology and Biogeography, 31(4), 802-821.

Montero-Mendieta, S., Tan, K., Christmas, M. J., Olsson, A., Vilà, C., Wallberg, A., & Webster, M. T. (2019). The genomic basis of adaptation to high-altitude habitats in the eastern honey bee (Apis cerana). Molecular Ecology, 28(4), 746-760.

Morgan, K., Mboumba, J. F., Ntie, S., Mickala, P., Miller, C. A., Zhen, Y., ... & Anthony, N. M. (2020). Precipitation and vegetation shape patterns of genomic and craniometric variation in the central African rodent Praomys misonnei. Proceedings of the Royal Society B, 287(1930), 20200449.

Mucci, C. A., Ramirez, L., Giffoni, R. S., & Lamattina, L. (2021). Cold stress induces specific antioxidant responses in honey bee brood. Apidologie, 52, 596-607.

Naimi, B., Hamm, N. A., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling?. Ecography, 37(2), 191-203.

Neupane, N., Larsen, E. A., & Ries, L. (2024). Ecological forecasts of insect range dynamics: a broad range of taxa include winners and losers under future climate. Current Opinion in Insect Science, 101159.

Nielsen, E. S., Hanson, J. O., Carvalho, S. B., Beger, M., Henriques, R., Kershaw, F., & Von der Heyden, S. (2022). Molecular ecology meets systematic conservation planning. Trends in Ecology & Evolution.

Nielsen, E. S., Henriques, R., Beger, M., & von der Heyden, S. (2021). Distinct interspecific and intraspecific vulnerability of coastal species to global change. Global Change Biology, 27(15), 3415-3431.

Niemczyk, M., Chmura, D. J., Socha, J., Wojda, T., Mroczek, P., Gil, W., & Thomas, B. R. (2021). How geographic and climatic factors affect the adaptation of Douglas-fir provenances to the temperate continental climate zone in Europe. European Journal of Forest Research, 140(6), 1341-1361.

North, A., Pennanen, J., Ovaskainen, O., & Laine, A. L. (2011). Local adaptation in a changing world: The roles of gene-flow, mutation, and sexual reproduction. Evolution, 65(1), 79-89.

Nürnberger, F., Härtel, S., & Steffan-Dewenter, I. (2019). Seasonal timing in honey bee colonies: phenology shifts affect honey stores and varroa infestation levels. Oecologia, 189, 1121-1131.

Oskay, D., Kükrer, M., & Kence, A. (2019). Muğla bal arısında (Apis mellifera anatoliaca) Amerikan yavru çürüklüğü hastalığına karşı direnç geliştirilmesi. Arıcılık Araştırma Dergisi, 11(1), 8-20.

Parejo, M., Wragg, D., Henriques, D., Charriere, J. D., & Estonba, A. (2020). Digging into the genomic past of Swiss honey bees by whole-genome sequencing museum specimens. Genome biology and evolution, 12(12), 2535-2551.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics, 37, 637-669.

Pearman, P. B., Zachos, F. E., & Paz-Vinas, I. (2024). European monitoring of genetic diversity must expand to detect impacts of climate change. NATURE ECOLOGY & EVOLUTION.

Petchey, O. L., Pontarp, M., Massie, T. M., Kéfi, S., Ozgul, A., Weilenmann, M., ... & Pearse, I. S. (2015). The ecological forecast horizon, and examples of its uses and determinants. Ecology letters, 18(7), 597-611.

Pörtner, H. O., Roberts, D. C., Poloczanska, E. S., Mintenbeck, K., Tignor, M., Alegría, A., ... & Okem, A. (2022). IPCC, 2022: Summary for policymakers.

Pritchard, J. K., Pickrell, J. K., & Coop, G. (2010). The genetics of human adaptation: hard sweeps, soft sweeps, and polygenic adaptation. Current Biology, 20(4), R208-R215.

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multilocus genotype data. Genetics, 155(2), 945-959.

Quigley, T. P., Amdam, G. V., & Harwood, G. H. (2019). Honey bees as bioindicators of changing global agricultural landscapes. Current opinion in insect science, 35, 132-137.

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reitalu, T., Bjune, A. E., Blaus, A., Giesecke, T., Helm, A., Matthias, I., ... & Birks, H. J. B. (2019). Patterns of modern pollen and plant richness across northern Europe. Journal of Ecology, 107(4), 1662-1677.

Requier, F., Garnery, L., Kohl, P. L., Njovu, H. K., Pirk, C. W., Crewe, R. M., & Steffan-Dewenter, I. (2019). The conservation of native honey bees is crucial. Trends in ecology & evolution, 34(9), 789-798.

Reynolds, J., Weir, B. S., & Cockerham, C. C. (1983). Estimation of the coancestry coefficient: basis for a short-term genetic distance. Genetics, 105(3), 767-779.

Rodrigues, A. S., & Brooks, T. M. (2007). Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. Annu. Rev. Ecol. Evol. Syst., 38, 713-737.

Román-Palacios, C., & Wiens, J. J. (2020). Recent responses to climate change reveal the drivers of species extinction and survival. Proceedings of the National Academy of Sciences, 117(8), 4211-4217.

Rowland, B. W., Rushton, S. P., Shirley, M. D., Brown, M. A., & Budge, G. E. (2021). Identifying the climatic drivers of honey bee disease in England and Wales. Scientific reports, 11(1), 21953.

Ruttner, F. (1988). Biogeography and Taxonomy of Honeybees. Springer-Verlag, Berlin Heidelberg.

Sarkar, S. (2006). Ecological diversity and biodiversity as concepts for conservation planning: comments on Ricotta. Acta Biotheoretica, 54, 133-140.

Schwander, T., Libbrecht, R., & Keller, L. (2014). Supergenes and complex phenotypes. Current Biology, 24(7), R288-R294.

Shah, A. A., Dillon, M. E., Hotaling, S., & Woods, H. A. (2020). High elevation insect communities face shifting ecological and evolutionary landscapes. Current Opinion in Insect Science, 41, 1-6.

Shaibi, T., Lattorff, H. M. G., & Moritz, R. F. A. (2008). A microsatellite DNA toolkit for studying population structure in Apis mellifera. Molecular Ecology Resources, 8(5), 1034-1036.

Sinervo, B., Mendez-De-La-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., ... & Sites Jr, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. Science, 328(5980), 894-899.

Slatkin, M. (2009). Epigenetic inheritance and the missing heritability problem. Genetics, 182(3), 845-850.

Solignac, M., Vautrin, D., Loiseau, A., Mougel, F., Baudry, E., Estoup, A., ... & Cornuet, J. M. (2003). Five hundred and fifty microsatellite markers for the study of the honeybee (Apis mellifera L.) genome. Molecular ecology notes, 3(2), 307-311.

Sönmez, S. (2022). Assessing the potential of Anatolia as a climate refugium (Master's thesis, Istanbul Technical University).

Stabentheiner, A., Nagy, J. M., Kovac, H., Käfer, H., Petrocelli, I., & Turillazzi, S. (2022). Effect of climate on strategies of nest and body temperature regulation in paper wasps, Polistes biglumis and Polistes gallicus. Scientific reports, 12(1), 3372.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... & Williams, S. E. (2004). Extinction risk from climate change. Nature, 427(6970), 145-148.

Thuiller, W., Guéguen, M., Renaud, J., Karger, D. N., & Zimmermann, N. E. (2019). Uncertainty in ensembles of global biodiversity scenarios. Nature Communications, 10(1), 1446.

Title, P. O., & Bemmels, J. B. (2018). ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. Ecography, 41(2), 291-307.

Tokarska, K. B., Stolpe, M. B., Sippel, S., Fischer, E. M., Smith, C. J., Lehner, F., & Knutti, R. (2020). Past warming trend constrains future warming in CMIP6 models. Science advances, 6(12), eaaz9549.

Torson, A. S., Yocum, G. D., Rinehart, J. P., Kemp, W. P., & Bowsher, J. H. (2015). Transcriptional responses to fluctuating thermal regimes underpinning differences in survival in the solitary bee Megachile rotundata. The Journal of Experimental Biology, 218(7), 1060-1068.

Tunca, R. I. (2009). Determination and comparison of genetic variation in honey bee (Apis mellifera L.) populations of Turkey by Random Amplified Polymorphic DNA and microsatellite analyses. METU. Unpublished) Ph. D. Thesis, Middle East Technical University, Ankara, Turkey.

Uzunov, A., Costa, C., Panasiuk, B., Meixner, M., Kryger, P., Hatjina, F., ... & Büchler, R. (2014). Swarming, defensive and hygienic behaviour in honey bee colonies of different genetic origin in a pan-European experiment. Journal of Apicultural Research, 53(2), 248-260.

Vanhove, M., Pina-Martins, F., Coelho, A. C., Branquinho, C., Costa, A., Batista, D., ... & Paulo, O. S. (2021). Using gradient Forest to predict climate response and adaptation in Cork oak. Journal of Evolutionary Biology, 34(6), 910-923.

Visscher, P. K., & Seeley, T. D. (1982). Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology, 63(6), 1790-1801.

Wallberg, A., Han, F., Wellhagen, G., Dahle, B., Kawata, M., Haddad, N., ... & Webster, M. T. (2014). A worldwide survey of genome sequence variation provides insight into the evolutionary history of the honeybee Apis mellifera. Nature Genetics, 46(10), 1081-1088.

Wallberg, A., Schoening, C., Webster, M. T., & Hasselmann, M. (2017). Two extended haplotype blocks are associated with adaptation to high altitude habitats in East African honey bees. PLoS Genetics, 13(5), e1006792.

Wang, J. (2012). Computationally efficient sibship and parentage assignment from multilocus marker data. Genetics, 191(1), 183-194.

Wang, Q., Xu, X., Zhu, X., Chen, L., Zhou, S., Huang, Z. Y., & Zhou, B. (2016). Low-temperature stress during capped brood stage increases pupal mortality, misorientation and adult mortality in honey bees. PloS one, 11(5), e0154547.

Wilczek, A. M., Cooper, M. D., Korves, T. M., & Schmitt, J. (2014). Lagging adaptation to warming climate in Arabidopsis thaliana. Proceedings of the National Academy of Sciences, 111(22), 7906-7913.

Willis, K. J., & Bhagwat, S. A. (2009). Biodiversity and climate change. Science, 326(5954), 806-807.

Willmer, P. G., & Stone, G. N. (2004). Behavioral, ecological, and physiological determinants of the activity patterns of bees. Advances in the Study of Behavior, 34(34), 347-466.

Wragg, D., Techer, M. A., Canale-Tabet, K., Basso, B., Bidanel, J. P., Labarthe, E., ... & Vignal, A. (2018). Autosomal and mitochondrial adaptation following admixture: a case study on the honeybees of Reunion Island. Genome Biology and Evolution, 10(1), 220-238.

Yıldız, B. I., & Karabağ, K. (2022). Quantitation of neuroxin-1, ataxin-3 and atlastin genes related to grooming behavior in five races of honey bee, Apis mellifera L., 1758 (Hymenoptera: Apidae), in Turkey. Turkish Journal of Entomology, 46(1), 3-11.

Yu, J., Pressoir, G., Briggs, W. H., Vroh Bi, I., Yamasaki, M., Doebley, J. F., ... & Buckler, E. S. (2006). A unified mixed-model method for association mapping that accounts for multiple levels of relatedness. Nature genetics, 38(2), 203-208.

Zapata-Hernández, G., Gajardo-Rojas, M., Calderón-Seguel, M., Muñoz, A. A., Yáñez, K. P., Requier, F., ... & Arrieta, H. (2024). Advances and knowledge gaps on climate change impacts on honey bees and beekeeping: A systematic review. Global Change Biology, 30(3), e17219.

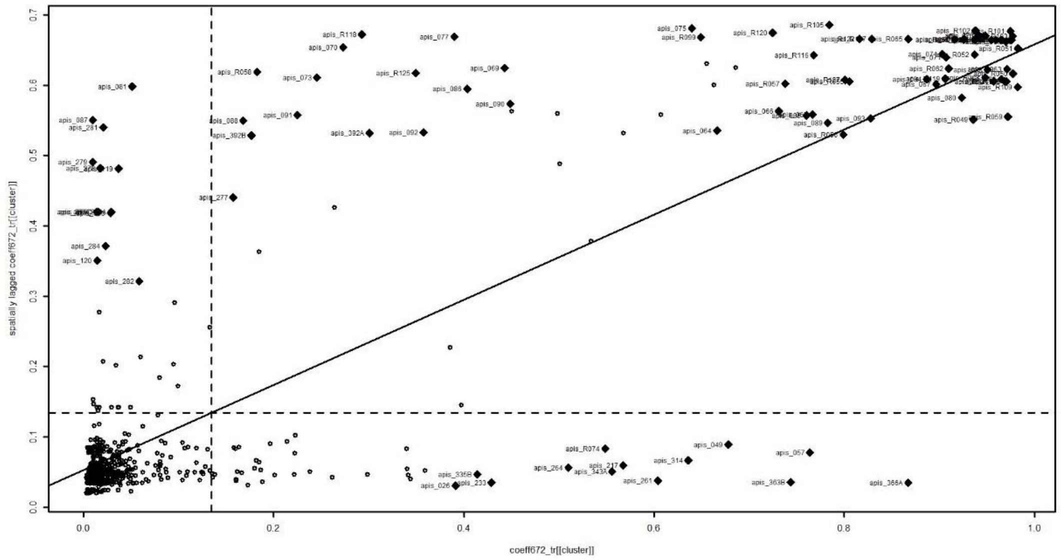
Zhang, M., Keenan, T. F., Luo, X., Serra-Diaz, J. M., Li, W., King, T., ... & Gong, P. (2022). Elevated CO2 moderates the impact of climate change on future bamboo distribution in Madagascar. Science of The Total Environment, 810, 152235.

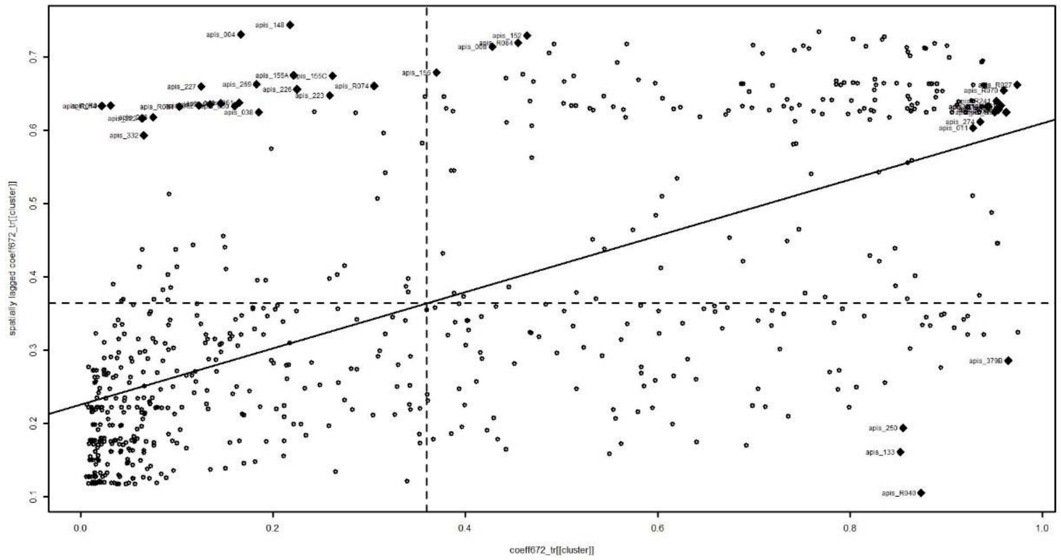
Zhu, J., Zhang, Y., & Wang, W. (2016). Interactions between warming and soil moisture increase overlap in reproductive phenology among species in an alpine meadow. Biology Letters, 12(7), 20150749.

Zurell, D., König, C., Malchow, A. K., Kapitza, S., Bocedi, G., Travis, J., & Fandos, G. (2022). Spatially explicit models for decision-making in animal conservation and restoration. Ecography, 2022(4).

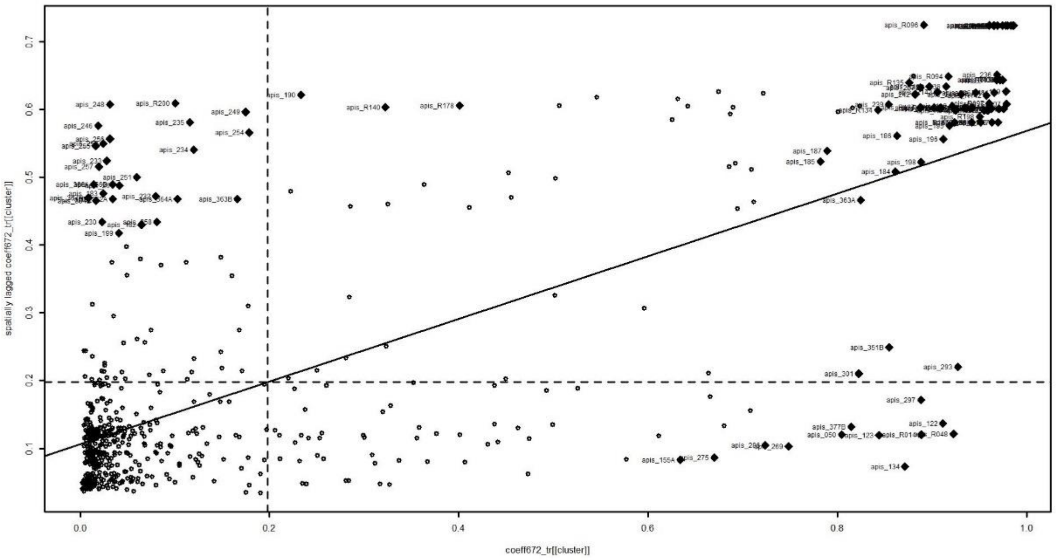
APPENDICES

A. Supplementary Figures

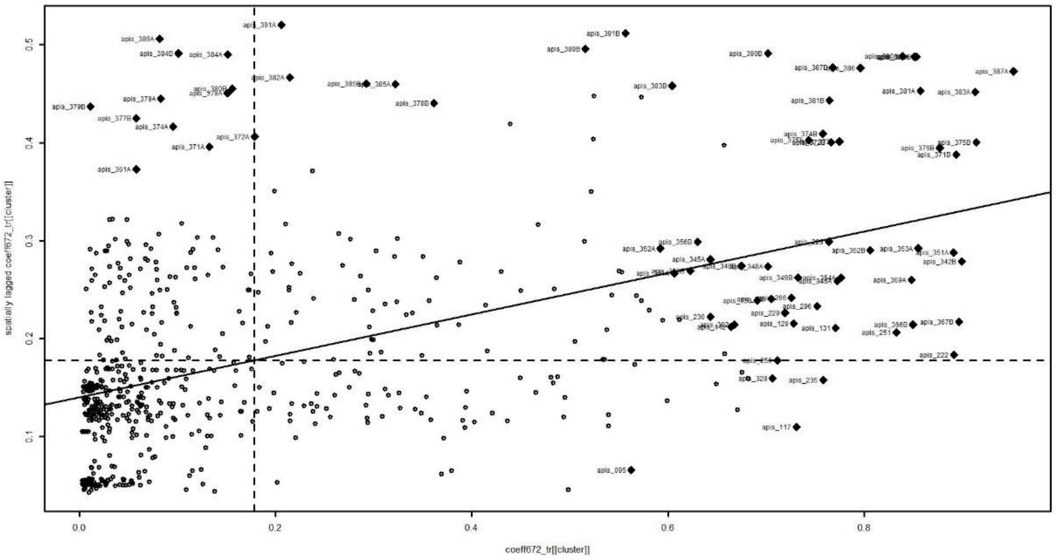




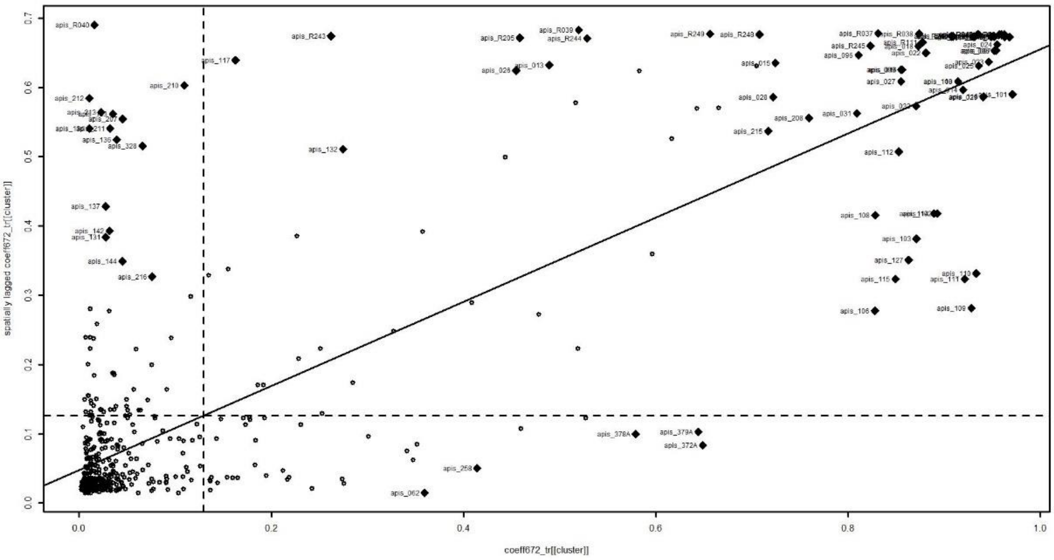
Supplementary Figures 1 and 2. Moran plots identifying spatial outliers for (a) Thracian, (b) Anatolian ancestral groups.



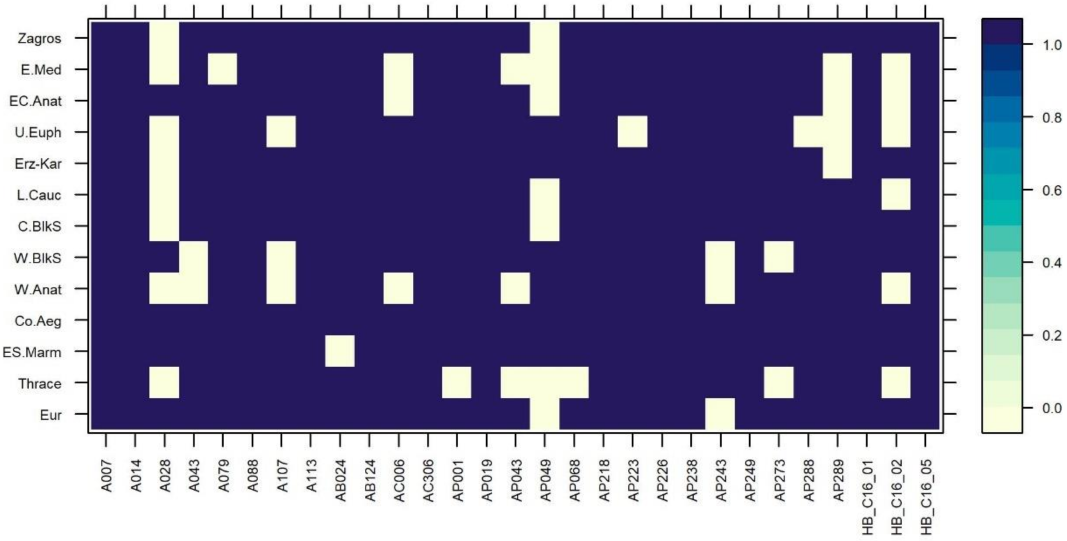
Supplementary Figure 3. Moran plot identifying spatial outliers for Caucasian ancestral group.



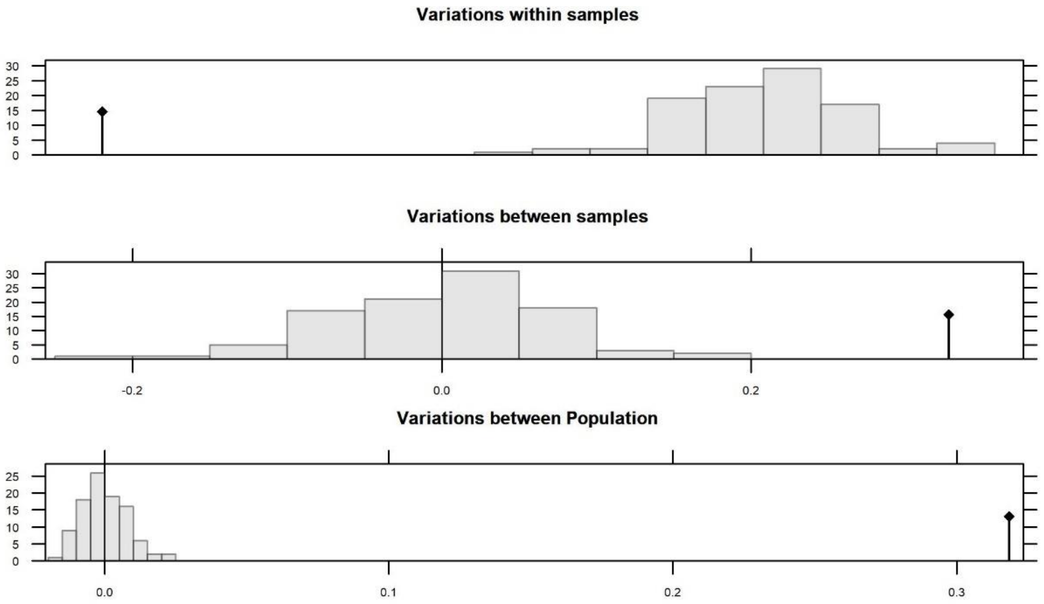
Supplementary Figure 4. Moran plot identifying spatial outliers for Zagrosian ancestral group.



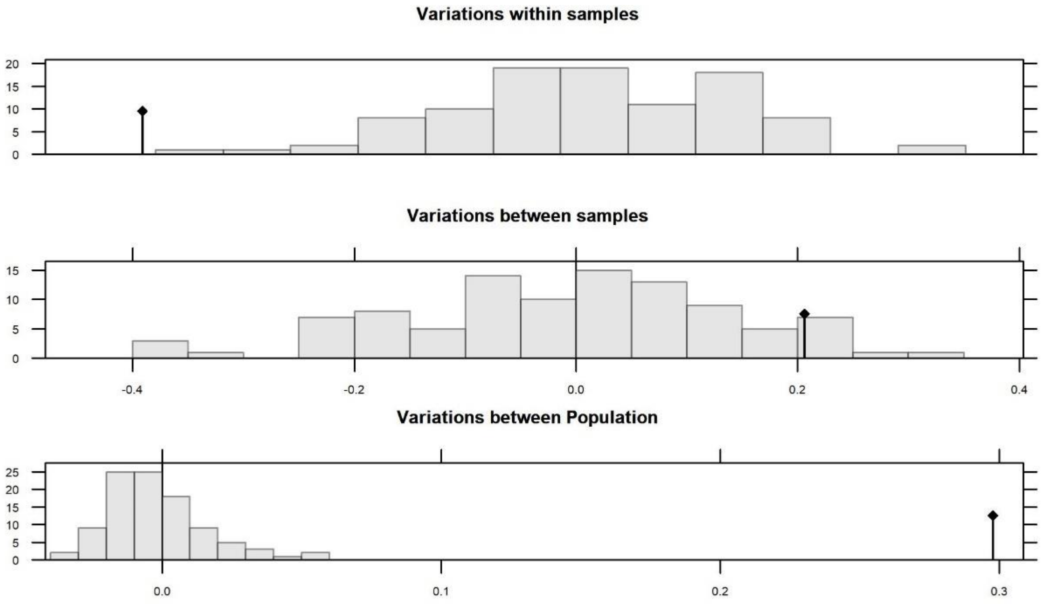
Supplementary Figure 5. Moran plot identifying spatial outliers for Levantine ancestral group.



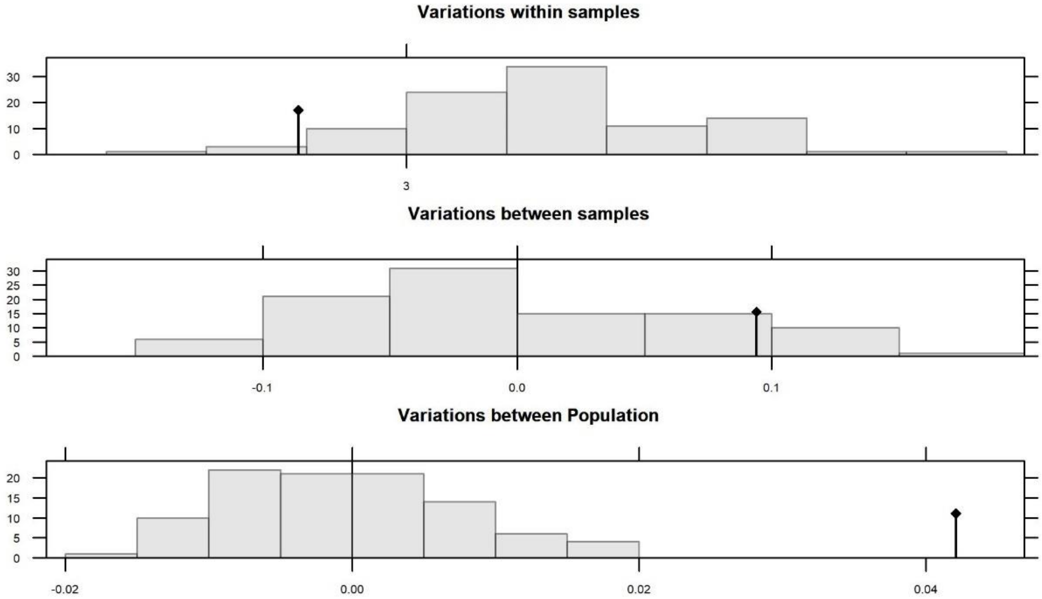
Supplementary Figure 6. Deviations from Hardy-Weinberg equilibrium across loci-population pairs.



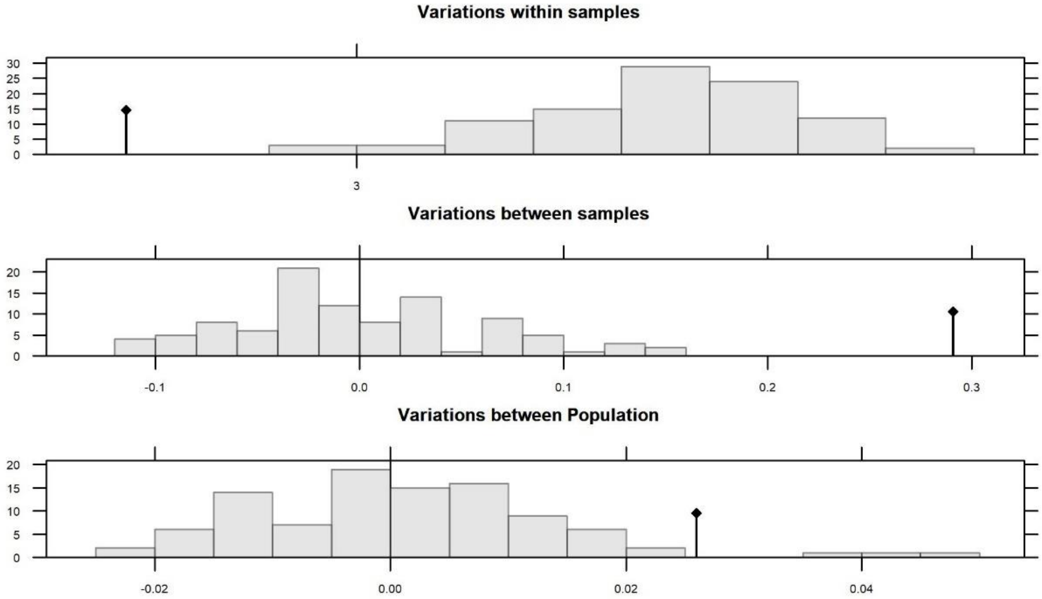
Supplementary Figure 7. AMOVA randomization test outcomes of all five representative populations: Thrace, Co.Aeg, L.Cauc, Zagros, and E.Med.



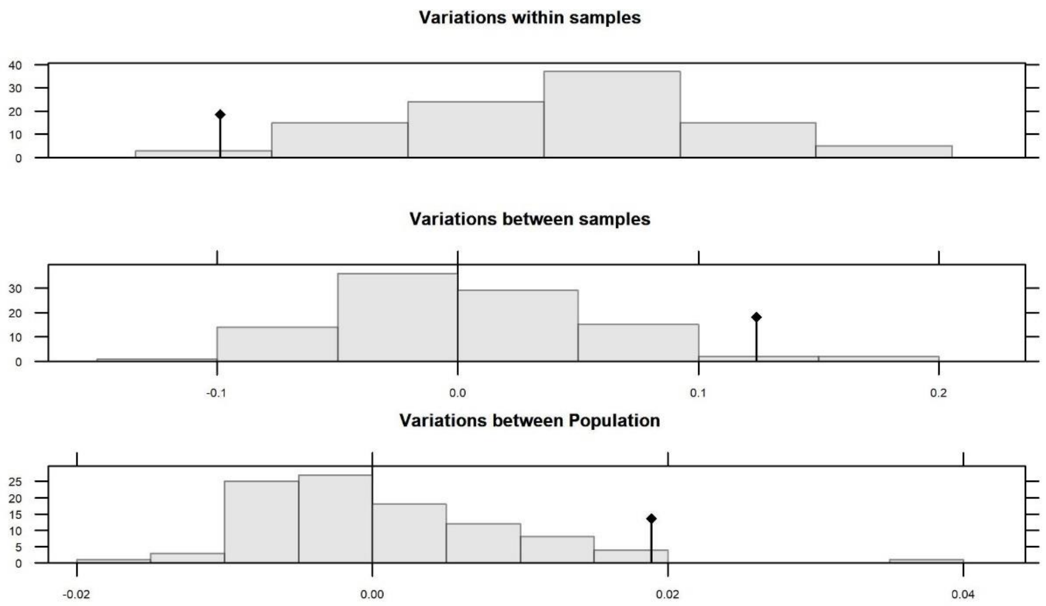
Supplementary Figure 8. AMOVA randomization test outcomes of Thrace and Co.Aeg populations.



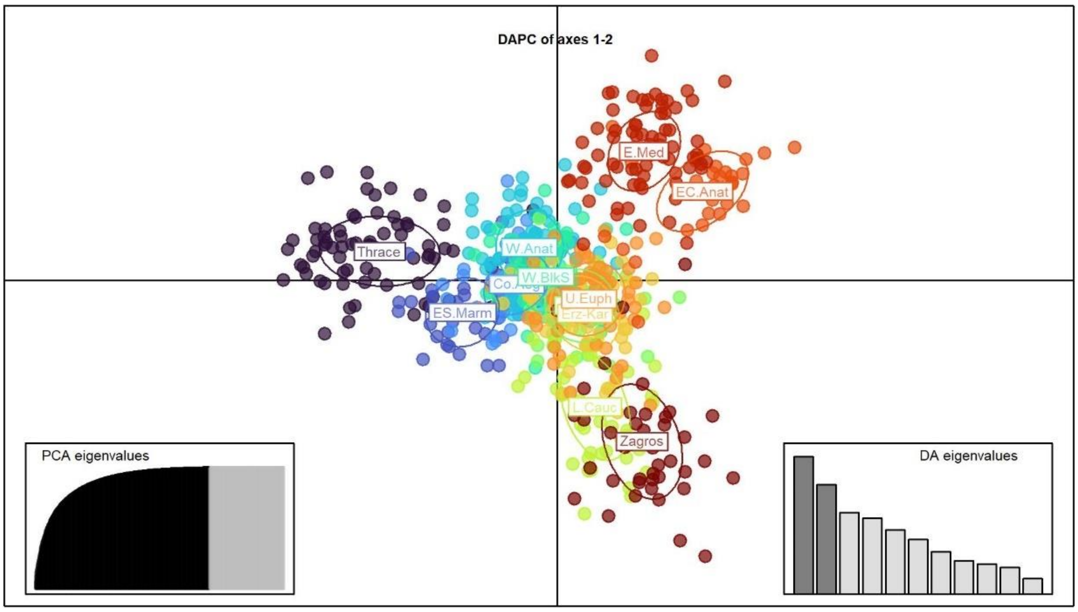
Supplementary Figure 9. AMOVA randomization test outcomes of Zagros and Co.Aeg populations.



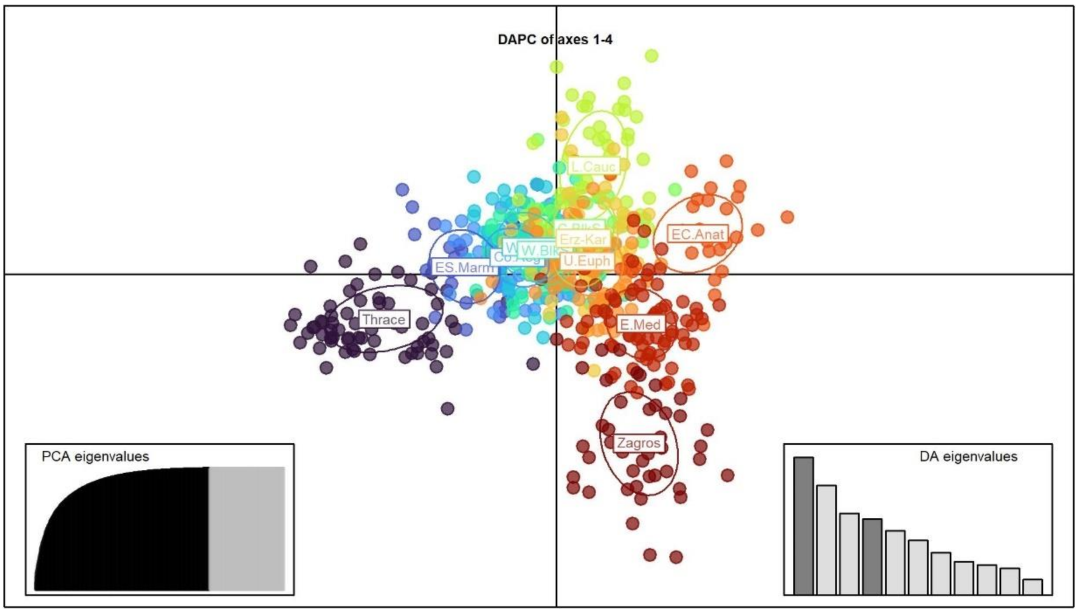
Supplementary Figure 10. AMOVA randomization test outcomes of Zagros and L.Cauc populations.



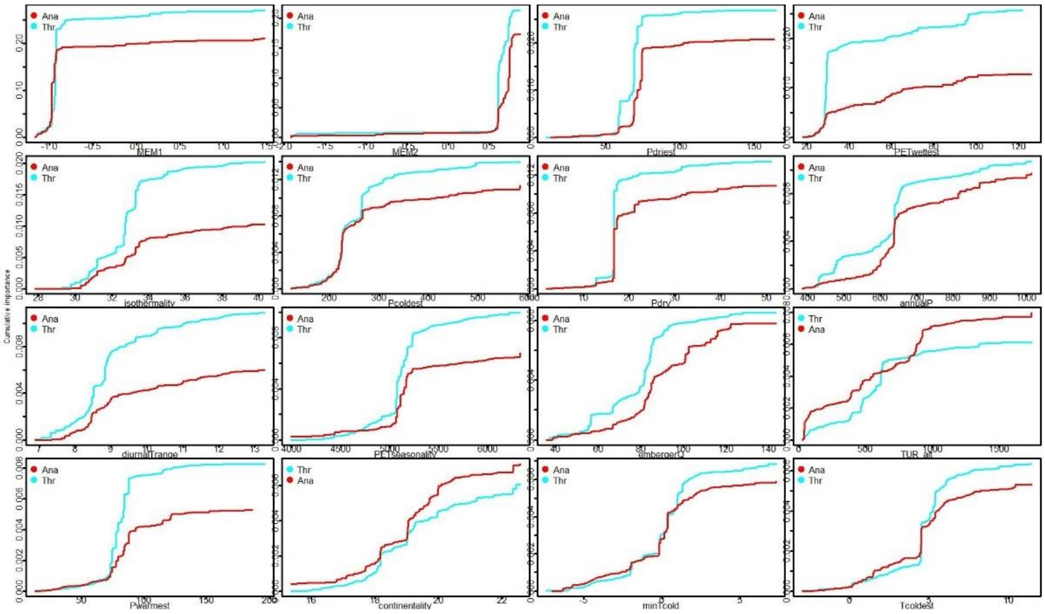
Supplementary Figure 11. AMOVA randomization test outcomes of Zagros and E.Med populations.



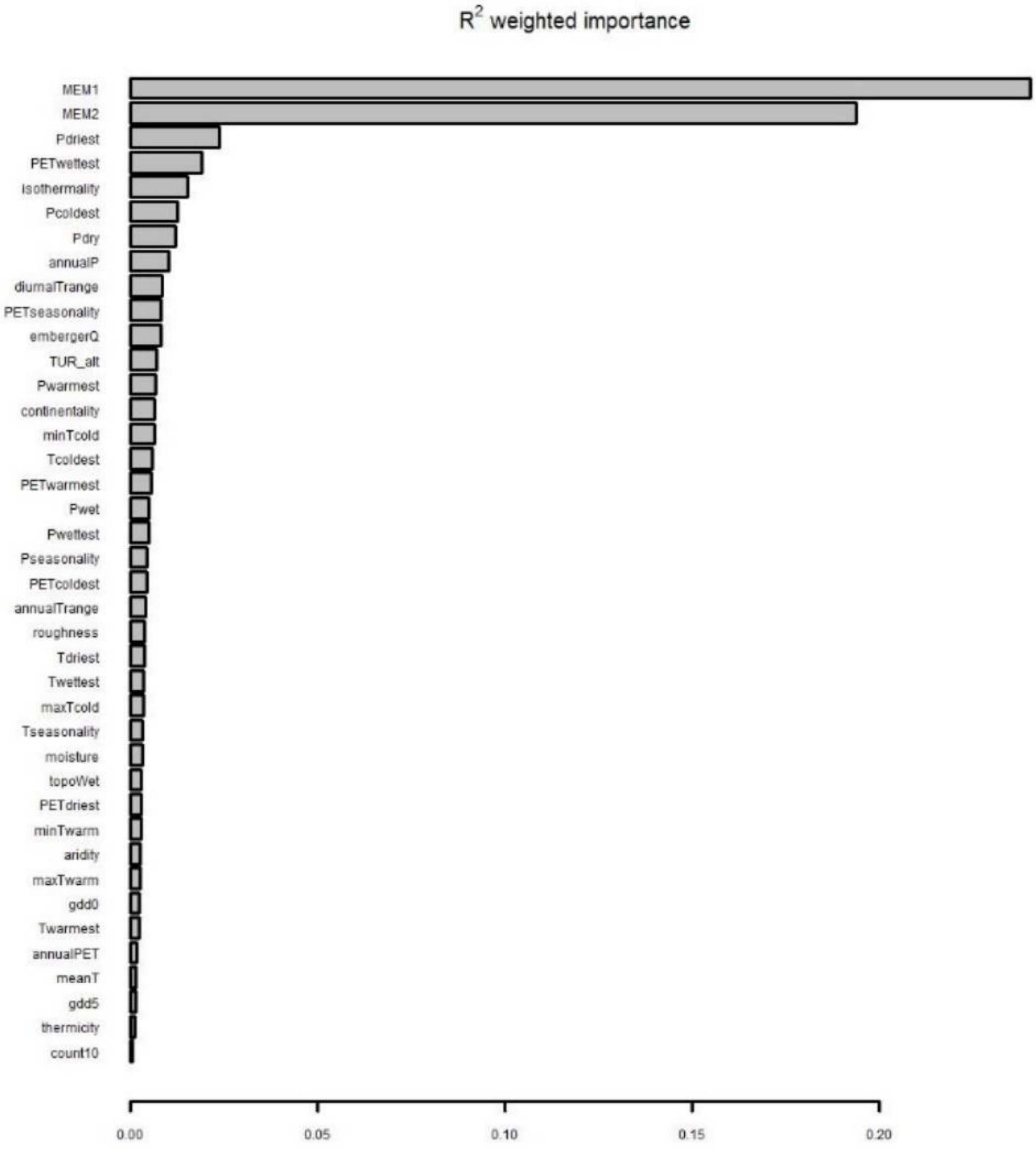
Supplementary Figure 12. DAPC plot of axes 1 and 2.



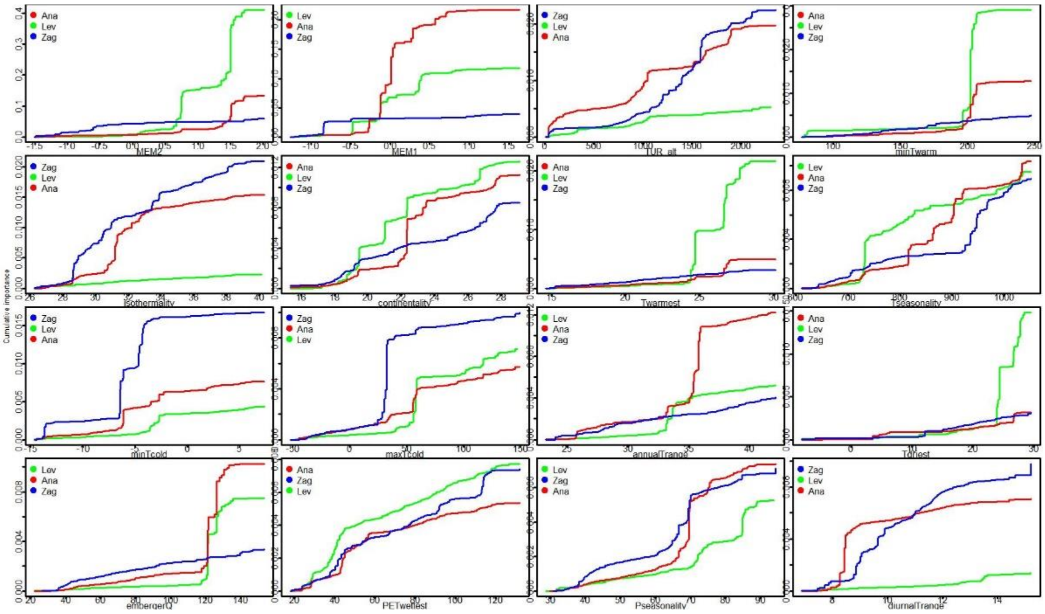
Supplementary Figure 13. DAPC plot of axes 1 and 4.



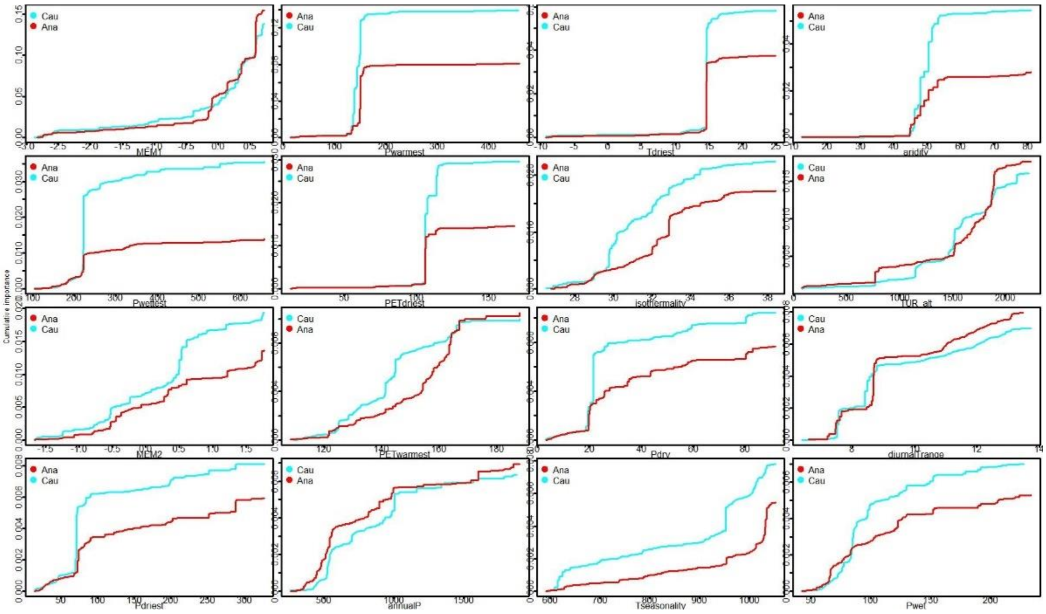
Supplementary Figure 14. Ancestral group response curves in the regional GF model at the transition zone between Thracian and Anatolian ancestral group pair. Thr: Thracian, Ana: Anatolian.



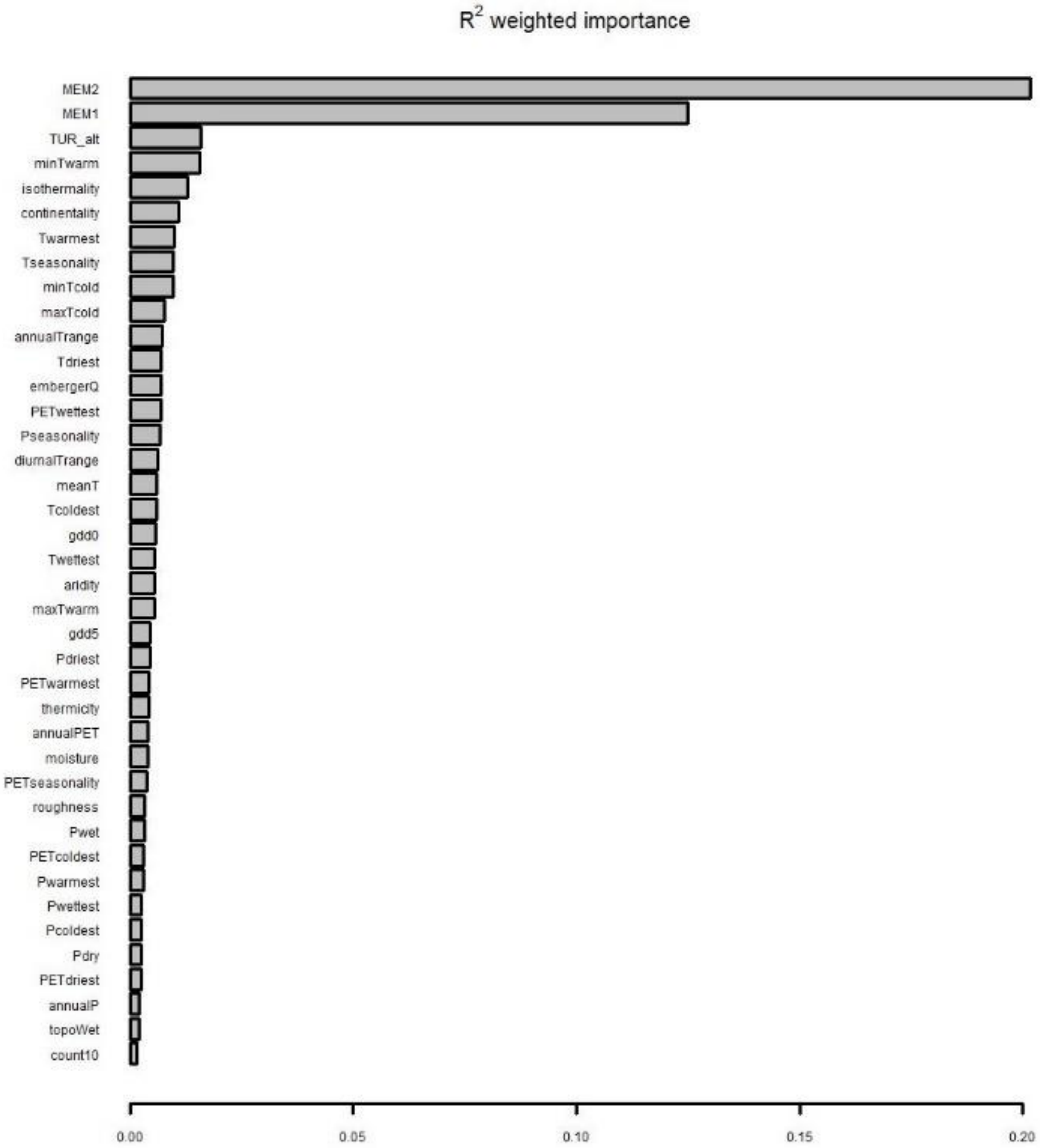
Supplementary Figure 15. Variable importance scores (R^2 values) for the regional GF model, highlighting the significance of spatial processes and key environmental variables driving intra-specific turnover in ancestry compositions at the transition zone between Thracian and Anatolian ancestral group pair.



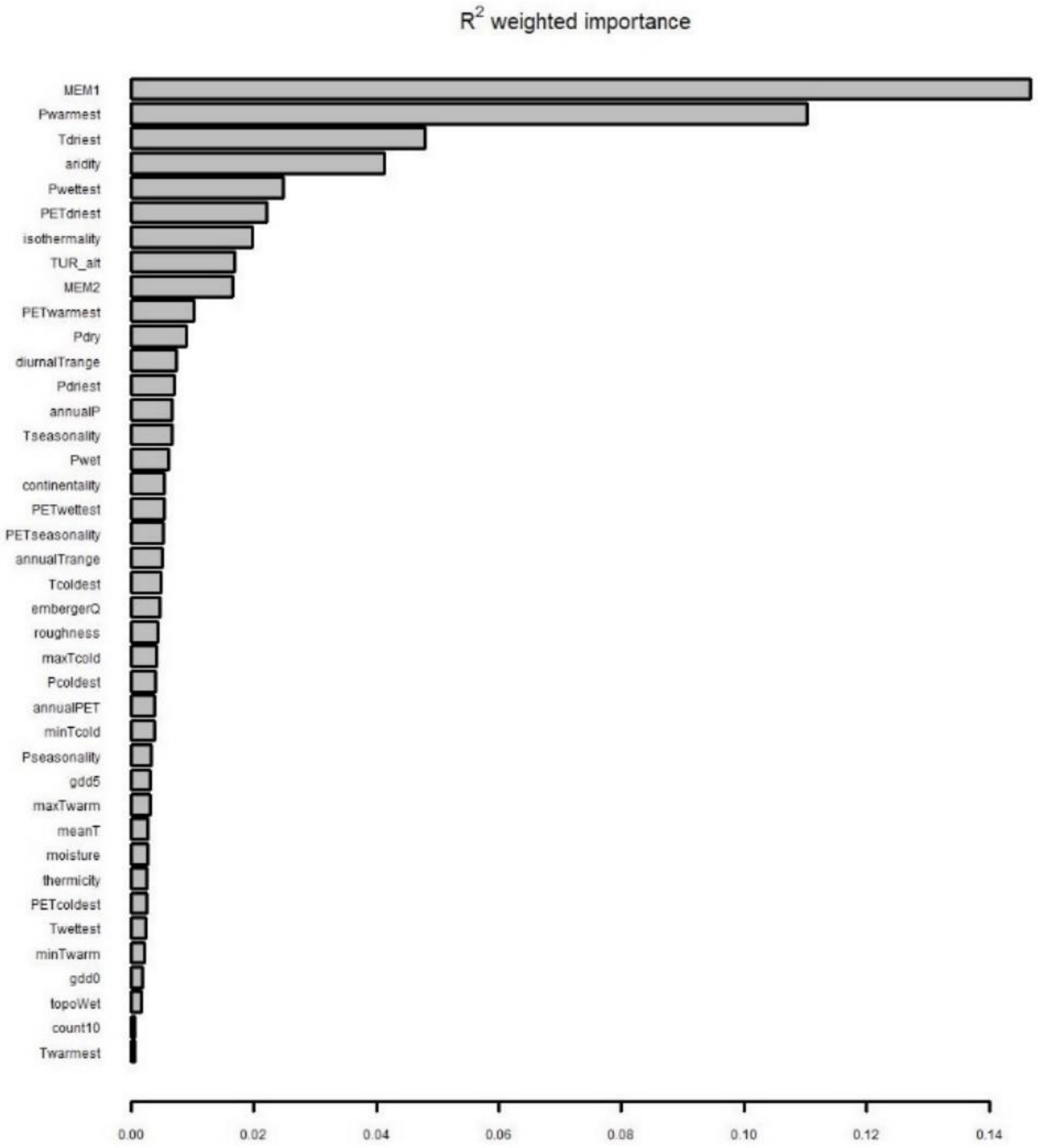
Supplementary Figure 16. Ancestral group response curves in the regional GF model at the transition zones between Anatolian, Levantine, and Zagrosian ancestral group pairs. Ana: Anatolian, Zag: Zagrosian, Lev: Levantine.



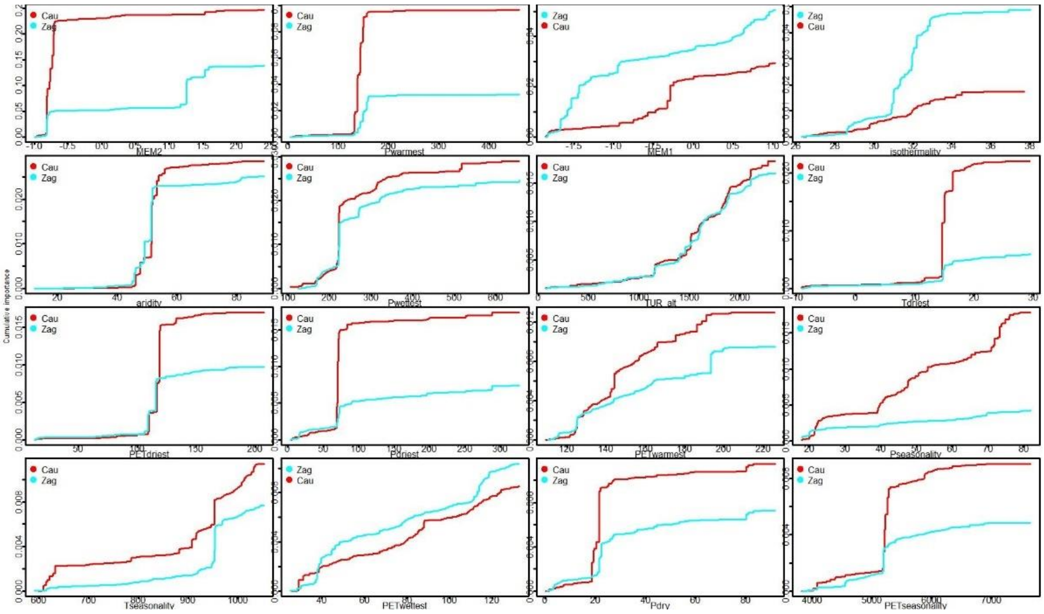
Supplementary Figure 18. Ancestral group response curves in the regional GF model at the transition zone between Anatolian and Caucasian ancestral group pair. Ana: Anatolian, Cau: Caucasian.



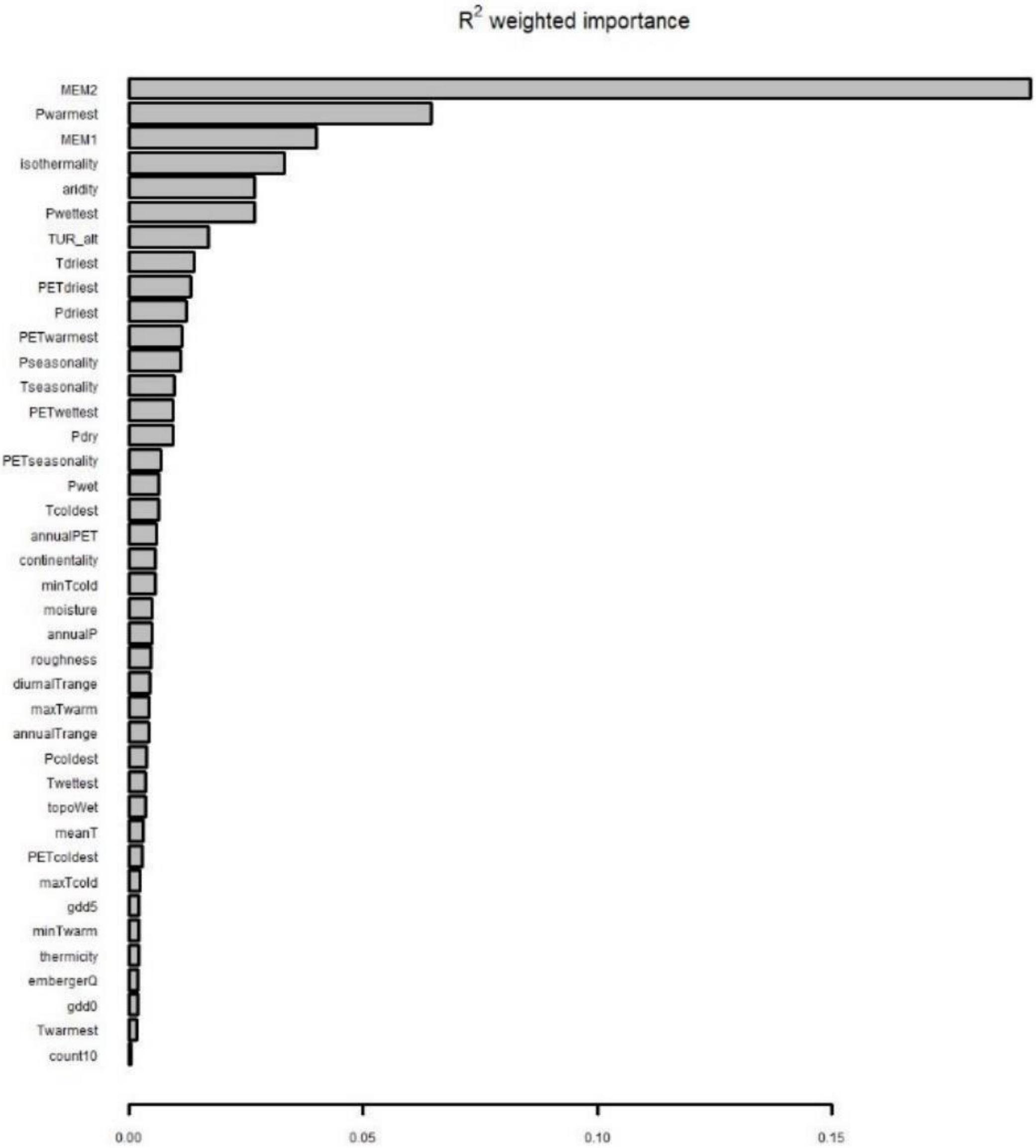
Supplementary Figure 17. Variable importance scores (R^2 values) for the regional GF model, highlighting the significance of spatial processes and key environmental variables driving intra-specific turnover in ancestry compositions at the transition zones between Anatolian, Levantine, and Zagrosian ancestral group pairs.



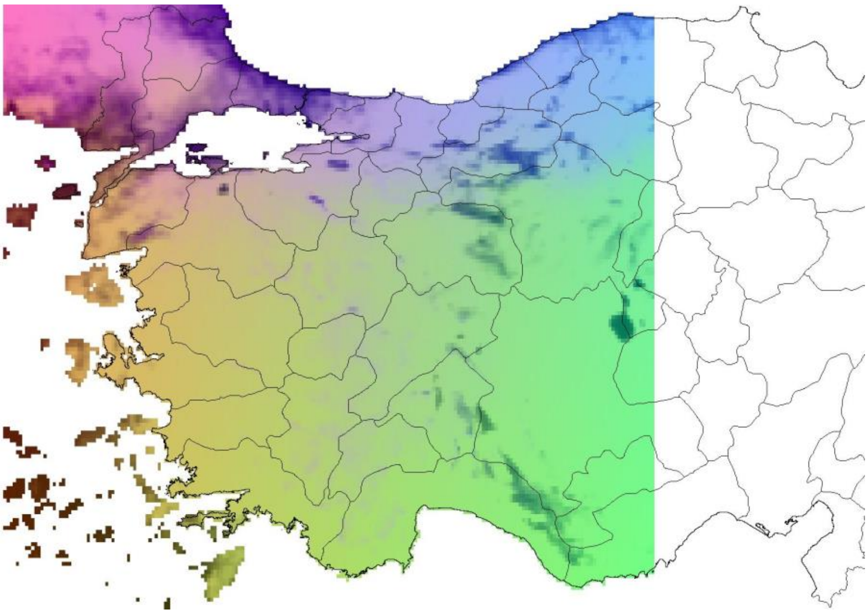
Supplementary Figure 19. Variable importance scores (R^2 values) for the regional GF model, highlighting the significance of spatial processes and key environmental variables driving intra-specific turnover in ancestry compositions at the transition zone between Anatolian and Caucasian ancestral group pair.



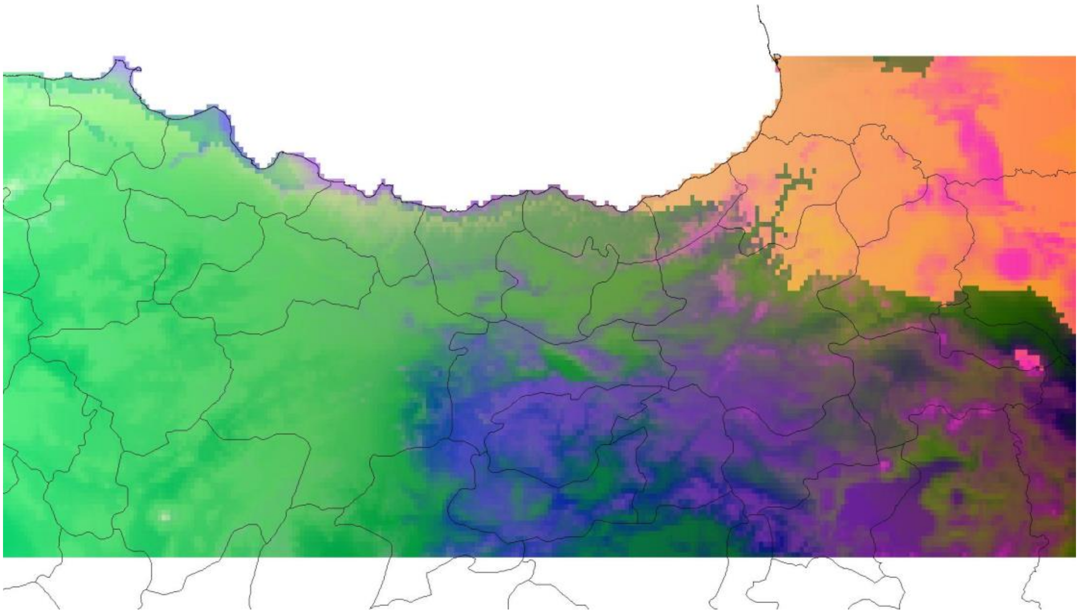
Supplementary Figure 20. Ancestral group response curves in the regional GF model at the transition zone between Caucasian and Zagrosian ancestral group pair. Zag: Zagrosian, Cau: Caucasian.



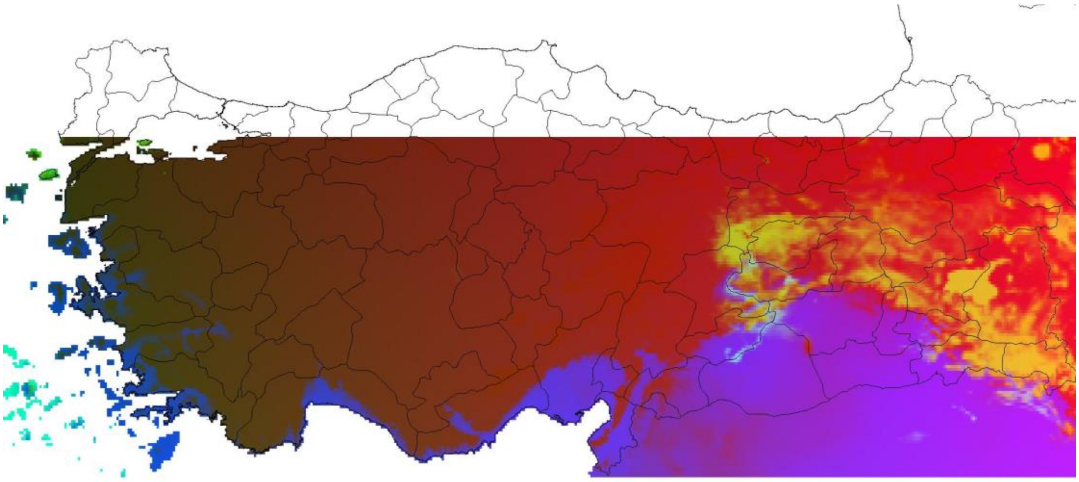
Supplementary Figure 21. Variable importance scores (R^2 values) for the regional GF model, highlighting the significance of spatial processes and key environmental variables driving intra-specific turnover in ancestry compositions at the transition zone between Caucasian and Zagrosian ancestral group pair.



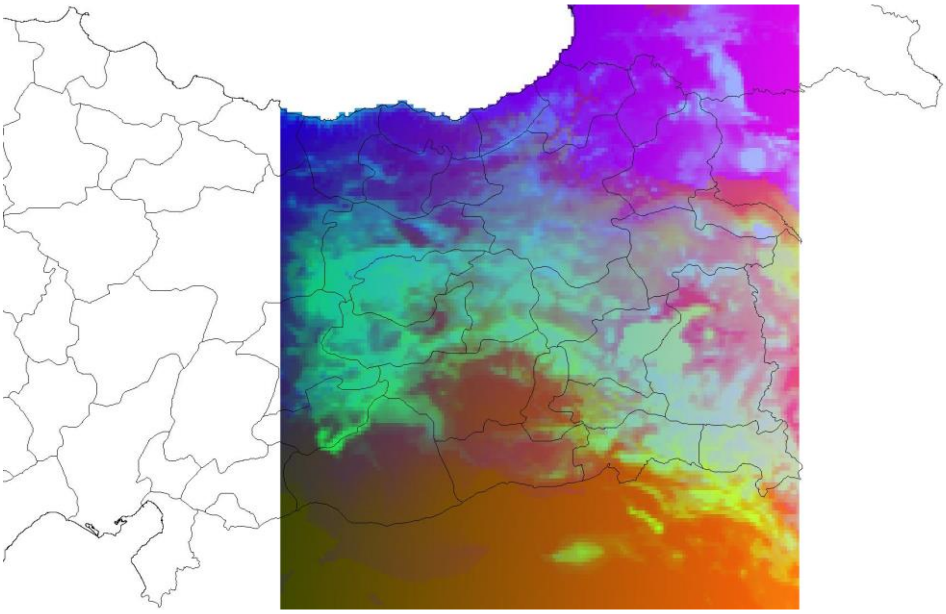
Supplementary Figure 22. Fine-scale turnover patterns in ancestry compositions in regional GDMs at the transition zone between Thracian and Anatolian ancestral group pair.



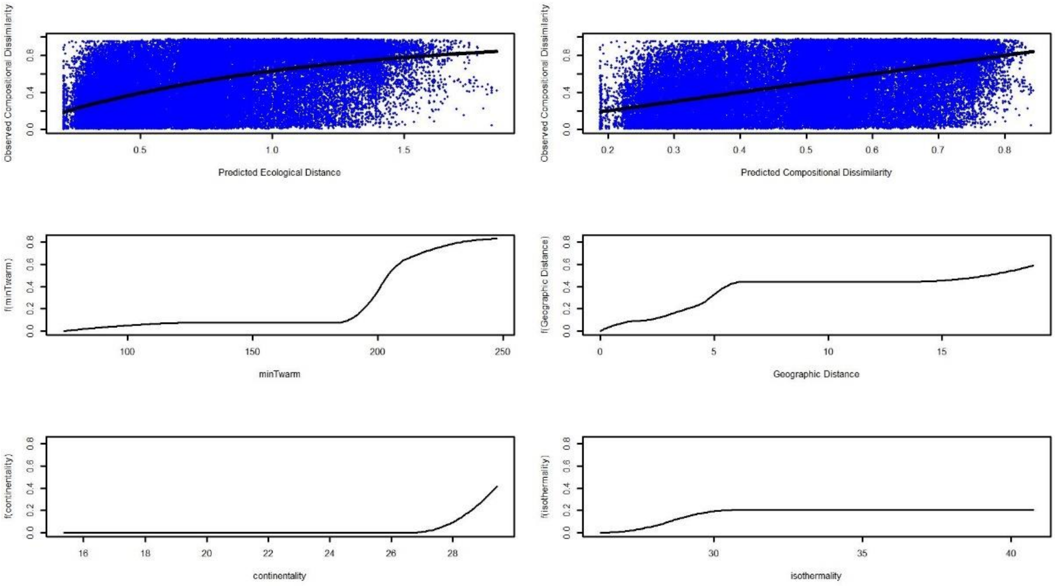
Supplementary Figure 23. Fine-scale turnover patterns in ancestry compositions in regional GDMs at the transition zone between Anatolian and Caucasian ancestral group pair.



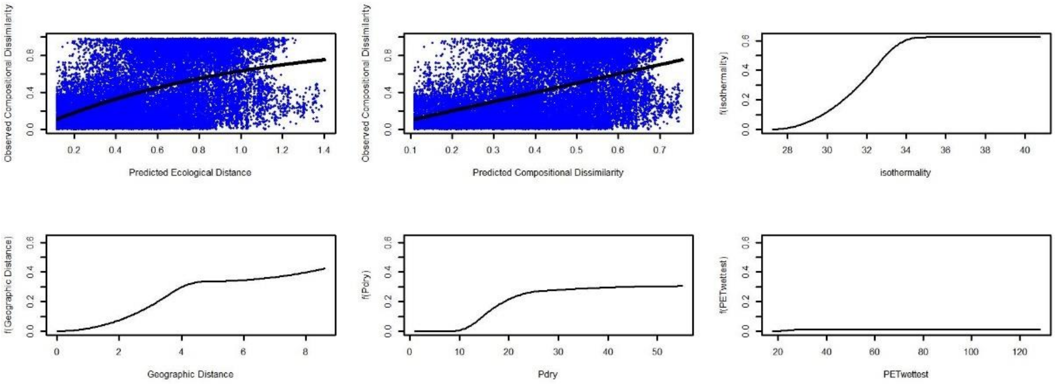
Supplementary Figure 24. Fine-scale turnover patterns in ancestry compositions in regional GDMs at the transition zones between Anatolian, Levantine, and Zagrosian ancestral group pairs.



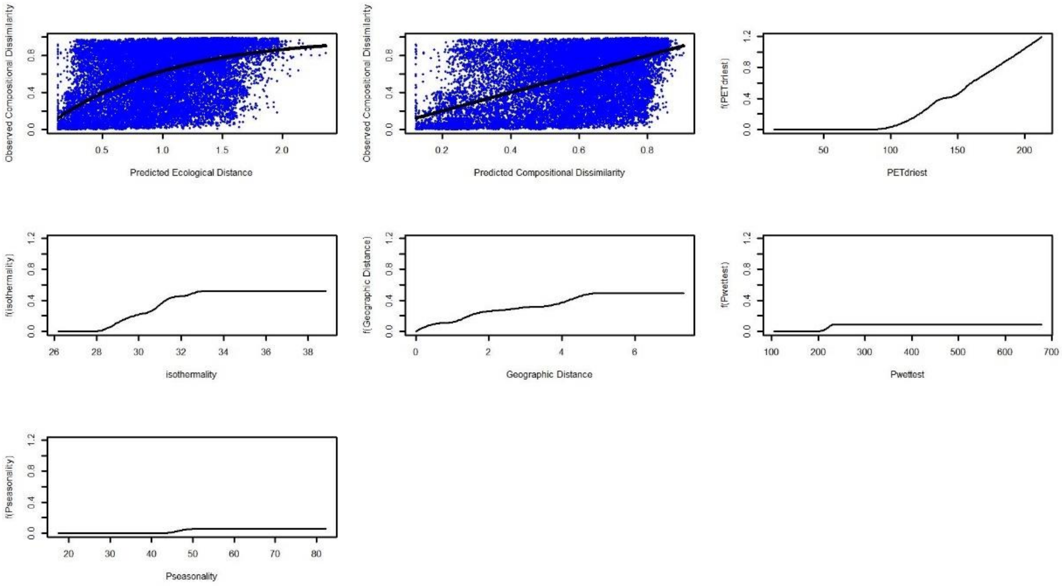
Supplementary Figure 25. Fine-scale turnover patterns in ancestry compositions in regional GDMs at the transition zone between Caucasian and Zagrosian ancestral group pair.



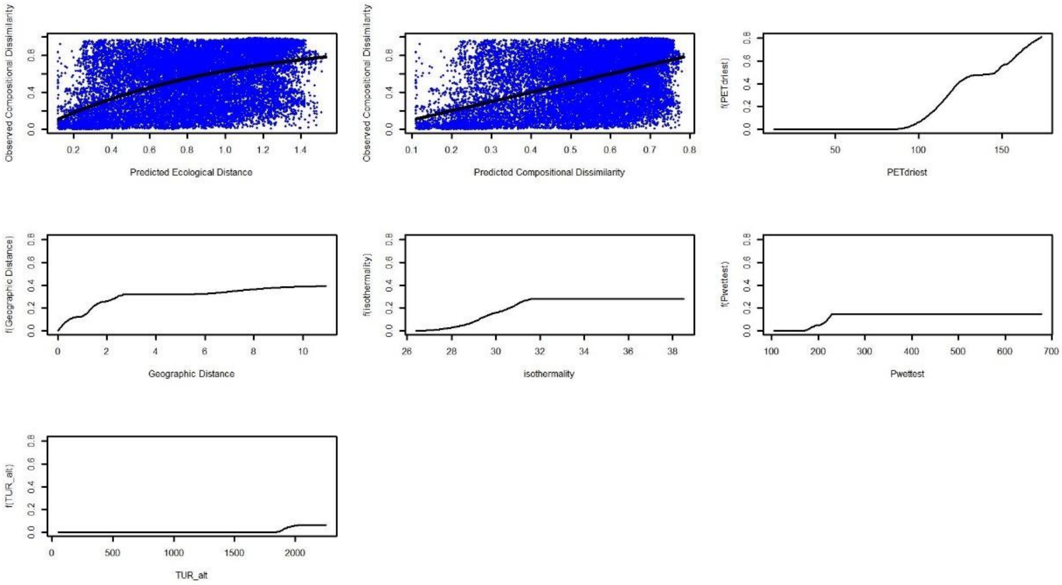
Supplementary Figure 26. Importance of specific environmental predictors at the transition zone between Thracian and Anatolian ancestral group pair.



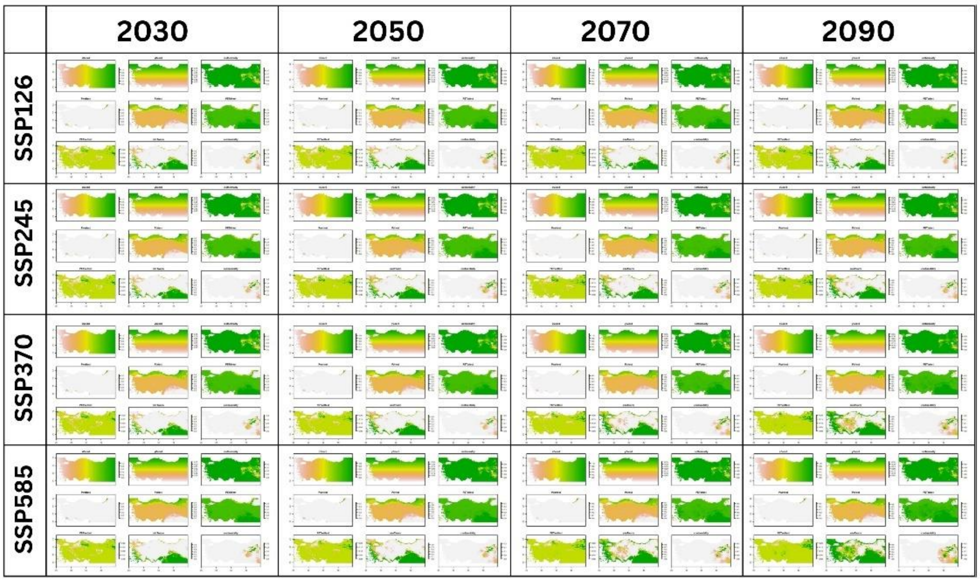
Supplementary Figure 27. Importance of specific environmental predictors at the transition zones between Anatolian, Levantine, and Zagrosian ancestral group pairs.



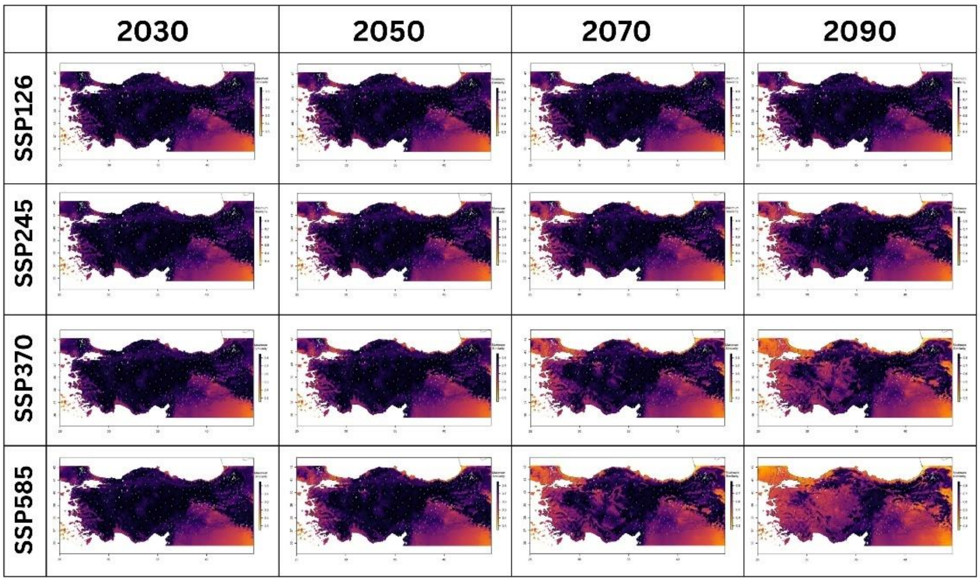
Supplementary Figure 28. Importance of specific environmental predictors at the transition zone between Caucasian and Zagrosian ancestral group pair.



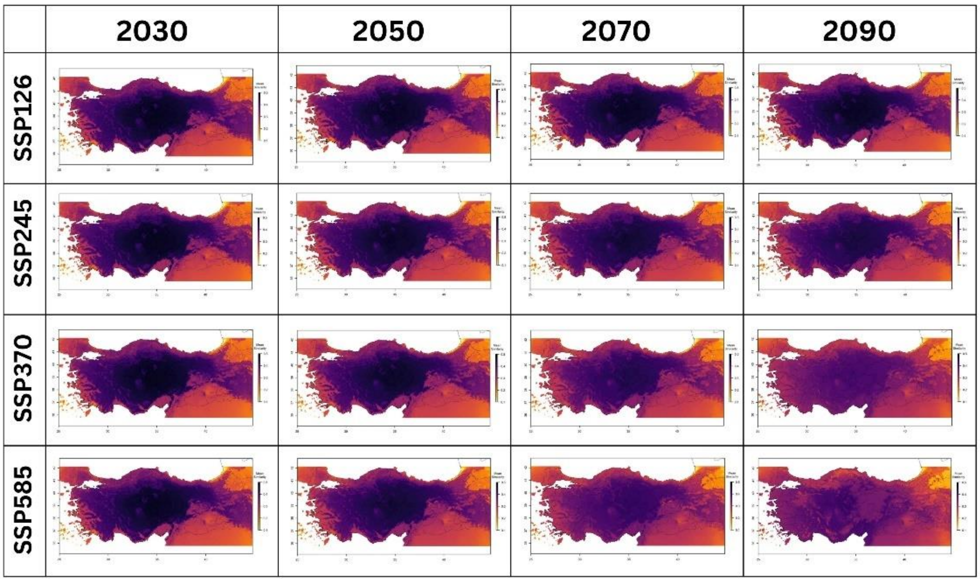
Supplementary Figure 29. Importance of specific environmental predictors at the transition zone between Anatolian and Caucasian ancestral group pair.



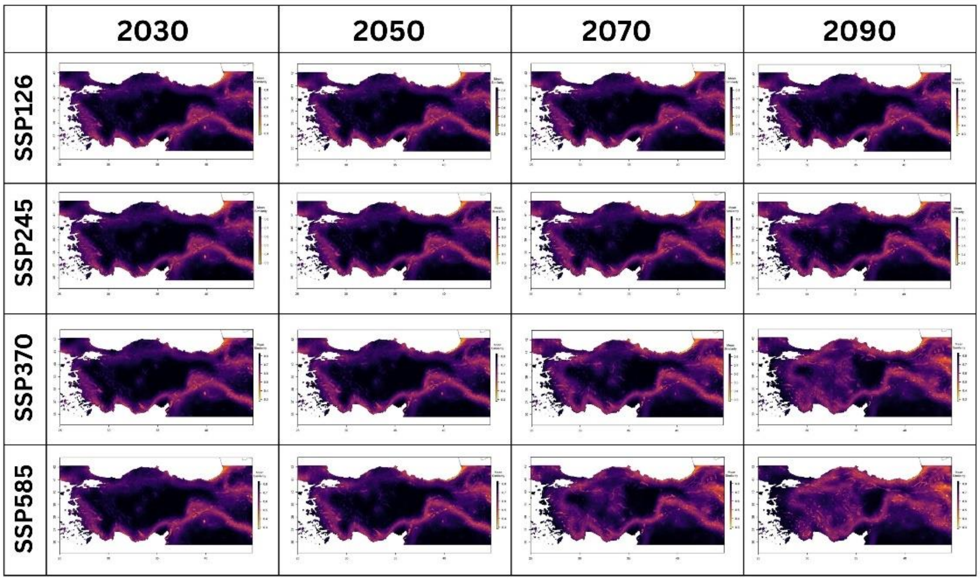
Supplementary Figure 30. Influence of GDM transformed variables under different SSP scenarios at midyears of two-decade periods.



Supplementary Figure 31. Survey gaps across different SSP scenarios and periods.



Supplementary Figure 32. Uniqueness across different SSP scenarios and periods.



Supplementary Figure 33. Turnover speed across different SSP scenarios and periods.

B. Supplementary Tables

Supplementary Table 1. Metadata and genotyping information for the honey bee samples, including locality, ancestry estimates, genotyping markers, and allelic information.

ID	Thr	Cau	Lev	Zag	Ana	Region	Population	Lon	Lat	A007	A014	A028	A043
apis_UGB4	0,97	0,00	0,00	0,01	0,02	1	Eur	6,12	51,05	120_120	217_217	137_137	140_142
apis_UGB5	0,99	0,00	0,00	0,00	0,00	1	Eur	6,12	51,06	120_120	217_217	131_137	140_140
apis_UGA5	0,99	0,00	0,00	0,00	0,00	1	Eur	6,15	51,06	113_113	217_234	131_137	125_140
apis_UGA1	0,99	0,00	0,00	0,00	0,01	1	Eur	7,46	53,42	113_120	217_234	137_137	125_140
apis_UGA2	0,99	0,00	0,00	0,00	0,00	1	Eur	7,46	53,43	113_120	217_217	131_137	125_125
apis_UGA3	0,99	0,00	0,00	0,00	0,00	1	Eur	7,47	53,42	113_113	217_234	127_131	140_142
apis_UGB1	0,98	0,00	0,00	0,00	0,01	1	Eur	9,68	52,17	113_120	217_234	NA	140_140
apis_UGB2	0,99	0,00	0,00	0,00	0,00	1	Eur	9,68	52,18	113_118	217_234	137_137	140_142
apis_PaxC1	0,96	0,00	0,01	0,01	0,02	1	Eur	11,92	51,49	126_164	217_223	131_137	127_140
apis_PaxC2	0,99	0,00	0,00	0,00	0,00	1	Eur	11,92	51,50	113_126	217_217	131_137	140_140
apis_PaxC3	0,87	0,00	0,01	0,02	0,10	1	Eur	11,92	51,51	113_126	217_217	137_137	140_140
apis_PaxC4	0,99	0,00	0,00	0,00	0,01	1	Eur	11,92	51,52	118_126	217_217	131_131	140_140
apis_PaxC5	0,98	0,00	0,01	0,01	0,01	1	Eur	11,92	51,53	120_124	217_217	131_131	127_140
apis_PaxB1	0,99	0,00	0,00	0,00	0,01	1	Eur	11,93	51,49	113_118	217_217	131_131	127_140
apis_PaxB2	1,00	0,00	0,00	0,00	0,00	1	Eur	11,93	51,50	118_118	217_217	131_131	127_127
apis_PaxB3	0,99	0,00	0,00	0,00	0,00	1	Eur	11,93	51,51	113_113	217_217	131_137	127_140
apis_PaxB4	0,99	0,00	0,00	0,00	0,00	1	Eur	11,93	51,52	113_118	217_217	137_137	125_140
apis_PaxB5	0,97	0,01	0,00	0,01	0,01	1	Eur	11,93	51,53	113_118	217_223	131_137	127_140
apis_PaxA2	0,98	0,00	0,00	0,00	0,01	1	Eur	11,94	51,49	113_118	217_217	137_137	139_142
apis_PaxA3	0,98	0,00	0,00	0,00	0,01	1	Eur	11,94	51,50	113_118	217_217	137_137	140_140
apis_PaxA4	0,96	0,00	0,03	0,00	0,01	1	Eur	11,94	51,52	118_118	217_217	137_137	125_140
apis_PaxA5	0,97	0,00	0,00	0,01	0,01	1	Eur	11,94	51,53	118_120	217_217	132_132	125_142
apis_PaxA1	0,99	0,00	0,00	0,00	0,00	1	Eur	11,94	51,51	113_120	217_217	137_137	140_142
apis_PaxD3	0,91	0,00	0,02	0,02	0,05	1	Eur	11,95	51,49	118_126	217_217	131_137	127_140
apis_PaxD4	0,99	0,00	0,00	0,00	0,00	1	Eur	11,95	51,52	120_126	217_217	137_137	127_140
apis_PaxD5	0,98	0,00	0,00	0,00	0,01	1	Eur	11,95	51,53	118_126	217_217	131_137	127_142
apis_PaxE2	0,96	0,02	0,00	0,01	0,02	1	Eur	11,96	51,50	118_120	217_217	137_137	125_142
apis_PaxE4	0,98	0,00	0,01	0,01	0,01	1	Eur	11,96	51,52	118_118	223_234	137_137	125_140
apis_PaxE5	0,98	0,00	0,01	0,00	0,01	1	Eur	11,96	51,53	118_120	217_217	131_137	127_140
apis_PaxF1	0,99	0,00	0,00	0,00	0,00	1	Eur	11,97	51,49	113_118	217_224	137_137	142_142
apis_PaxF3	0,87	0,05	0,03	0,01	0,05	1	Eur	11,97	51,51	118_118	217_217	137_137	142_142
apis_PaxF4	0,99	0,00	0,00	0,00	0,01	1	Eur	11,97	51,52	118_118	217_217	137_137	142_142
apis_PaxF5	0,97	0,01	0,00	0,01	0,01	1	Eur	11,97	51,53	118_118	217_217	137_137	140_142
apis_UAA1	0,96	0,00	0,00	0,01	0,02	1	Eur	14,75	47,16	113_118	217_234	133_137	140_142
apis_UAA2	0,98	0,00	0,00	0,00	0,01	1	Eur	14,75	47,17	115_115	217_234	137_137	125_140
apis_UAA3	0,99	0,00	0,00	0,00	0,00	1	Eur	14,76	47,16	115_118	217_217	132_137	125_140

Supplementary Table 2. Information about the R packages used in the study and session details.

```
R version 4.2.2 (2022-10-31 ucrt)
Platform: x86_64-w64-mingw32/x64 (64-bit)
Running under: Windows 10 x64 (build 19045)

Matrix products: default

locale:
[1] LC_COLLATE=Turkish_Turkey.utf8  LC_CTYPE=Turkish_Turkey.utf8    LC_MONETARY=Turkish_Turkey.utf8 LC_NUMERIC=C                    LC_TIME=Turkish_Turkey.utf8

attached base packages:
[1] parallel  stats     graphics  grDevices utils     datasets  methods   base

other attached packages:
 [1] gradientForest_0.1-32 extendedForest_1.6.1  tidyr_1.3.0           envirem_2.3           palinsol_0.93         gsl_2.1-8             gdm_1.5.0-9.1
 [8] lattice_0.21-8        maps_3.4.1            moments_0.14.1        cluster_2.1.4         rworldmap_1.3-6       RColorBrewer_1.1-3    fields_14.1
[15] spam_2.9-1            gtools_3.9.4          raster_3.6-23         ggplot2_3.4.2         viridis_0.6.3         viridisLite_0.4.1     dabestr_0.3.0
[22] splancs_2.01-43       sp_1.6-0              adespatial_0.3-21     hierfstat_0.5-11      PopGenReport_3.0.7    knitr_1.42            spdep_1.2-8
[29] sf_1.0-10             spData_2.2.2          pegas_1.2             ape_5.7-1             magrittr_2.0.3        poppr_2.9.4           adegenet_2.1.10
[36] ade4_1.7-22           dplyr_1.1.2           pkgbuild_1.4.2        pak_0.4.0             usdm_2.1-6            terra_1.7-39

loaded via a namespace (and not attached):
  [1] uuid_1.1-0          plyr_1.8.8          igraph_1.4.1        splines_4.2.2       gstat_2.1-1         rncl_0.8.7          gap.datasets_0.0.5  digest_0.6.31
  [9] foreach_1.5.2       htmltools_0.5.4     gdata_2.18.0.1      fansi_1.0.4         doParallel_1.0.17   R.utils_2.12.2      xts_0.13.0          prettyunits_1.1.1
 [17] jpeg_0.1-10         colorspace_2.1-0    mmod_1.3.3          xfun_0.37           rgdal_1.6-6         callr_3.7.3         crayon_1.5.2        phylobase_0.8.10
 [25] zoo_1.8-11          iterators_1.0.14    glue_1.6.2          gtable_0.3.1        seqinr_4.2-23       polysat_1.7-7       adegraphics_1.0-18  scales_1.2.1
 [33] mvtnorm_1.1-3       DBI_1.1.3           GGally_2.1.2        shapefiles_0.7.2    Rcpp_1.0.10         xtable_1.8-4        progress_1.2.2      units_0.8-1
 [41] foreign_0.8-83      proxy_0.4-27        dotCall64_1.0-2     intervals_0.15.3    dismo_1.3-9         httr_1.4.5          FNN_1.1.3.2         genetics_1.3.8.1.3
 [49] calibrate_1.7.7     wk_0.7.1            ellipsis_0.3.2      pkgconfig_2.0.3     reshape_0.8.9       XML_3.99-0.13       R.methodsS3_1.8.2   deldir_1.0-6
 [57] utf8_1.2.3          tidyselect_1.2.0    rlang_1.1.0         reshape2_1.4.4      later_1.3.0         munsell_0.5.0       adephylo_1.1-13     tools_4.2.2
 [65] cli_3.6.0           generics_0.1.3      evaluate_0.20       stringr_1.5.0       fastmap_1.1.1       yaml_2.3.7          processx_3.8.0      purrr_1.0.1
 [73] s2_1.1.2            RgoogleMaps_1.4.5.3 pbapply_1.7-0       nlme_3.1-160        mime_0.12           R.oo_1.25.0         xml2_1.3.3          gap_1.5-1
 [81] compiler_4.2.2      beeswarm_0.4.0      png_0.1-8           e1071_1.7-13        RSAGA_1.4.0         spacetime_1.3-0     tibble_3.2.0        RNeXML_2.4.11
 [89] stringi_1.7.12      gdistance_1.6       ps_1.7.2            Matrix_1.5-1        classInt_0.4-9      vegan_2.6-4         permute_0.9-7       vctrs_0.6.1
 [97] pillar_1.9.0        lifecycle_1.0.3     combinat_0.0-8      maptools_1.1-6      cowplot_1.1.1       httpuv_1.6.9        R6_2.5.1            latticeExtra_0.6-30
[105] promises_1.2.0.1    KernSmooth_2.23-20  gridExtra_2.3       vipor_0.4.5         codetools_0.2-18    boot_1.3-28         MASS_7.3-58.1       withr_2.5.0
[113] mgcv_1.8-41         hms_1.1.2           grid_4.2.2          class_7.3-20        rmarkdown_2.20      shiny_1.7.4         ggbeeswarm_0.7.1    interp_1.1-3
```

Supplementary Table 3. Loci-based genetic diversity measures.

Locus	Alleles	Private alleles	Genotyping error	Null alleles	Expected H	Observed H	Fis	Fit	Fst	Evenness	G'st	Gst	Jost's D
A007	53	15	1,79	0,03	0,95	0,89	0,03	0,07	0,04	0,68	0,43	0,03	0,41
A014	10	2	2,68	0,10	0,65	0,48	0,08	0,27	0,21	0,70	0,31	0,13	0,20
A028	15	4	6,26	0,08	0,39	0,28	0,25	0,29	0,06	0,43	0,10	0,06	0,04
A043	16	3	3,06	0,05	0,54	0,46	0,10	0,15	0,06	0,52	0,12	0,05	0,07
A079	14	5	0,89	0,03	0,78	0,73	0,01	0,07	0,07	0,76	0,33	0,09	0,26
A088	14	5	0,49	0,07	0,68	0,57	0,04	0,17	0,14	0,73	0,28	0,11	0,19
A107	44	6	4,00	0,01	0,94	0,93	0,00	0,02	0,02	0,68	0,27	0,02	0,25
A113	18	2	0,97	0,05	0,89	0,79	0,01	0,13	0,12	0,82	0,48	0,08	0,43
AB024	8	2	0,97	0,04	0,60	0,54	0,09	0,10	0,02	0,73	0,16	0,06	0,10
AB124	19	5	3,28	0,03	0,80	0,74	0,03	0,08	0,06	0,62	0,28	0,06	0,23
AC006	11	3	1,69	0,06	0,25	0,18	0,04	0,30	0,27	0,43	0,38	0,29	0,11
AC306	12	3	1,39	0,05	0,75	0,67	0,00	0,12	0,12	0,78	0,19	0,05	0,14
AP001	34	9	3,88	0,06	0,78	0,67	0,04	0,15	0,12	0,48	0,25	0,06	0,20
AP019	11	2	2,12	0,00	0,33	0,33	-0,01	0,02	0,03	0,45	0,04	0,03	0,01
AP043	36	9	5,83	0,05	0,87	0,77	0,08	0,12	0,05	0,54	0,29	0,06	0,24
AP049	18	7	3,07	0,08	0,43	0,31	0,13	0,30	0,19	0,46	0,35	0,21	0,16
AP068	12	2	4,02	-0,01	0,65	0,66	-0,03	-0,02	0,01	0,56	0,01	0,00	0,01
AP218	4	1	0,00	0,01	0,26	0,25	-0,03	0,05	0,08	0,55	0,06	0,04	0,02
AP223	9	3	2,68	0,04	0,67	0,60	0,03	0,12	0,09	0,80	0,23	0,08	0,16
AP226	8	3	1,34	0,10	0,35	0,21	0,08	0,43	0,38	0,49	0,40	0,29	0,12
AP238	5	1	0,27	0,04	0,45	0,39	0,01	0,14	0,14	0,77	0,26	0,15	0,12
AP243	12	6	0,98	0,01	0,16	0,15	0,06	0,07	0,01	0,38	0,02	0,01	0,00
AP249	11	1	3,40	0,09	0,75	0,59	0,07	0,22	0,16	0,68	0,56	0,21	0,44
AP273	7	2	1,32	0,01	0,46	0,44	-0,02	0,05	0,07	0,76	0,13	0,07	0,06
AP288	11	5	1,79	0,06	0,42	0,34	0,03	0,21	0,19	0,52	0,35	0,22	0,15
AP289	49	11	4,42	0,12	0,91	0,68	0,21	0,26	0,05	0,54	0,45	0,06	0,42
HB_C16_01	48	8	1,35	0,02	0,94	0,91	0,00	0,04	0,04	0,63	0,47	0,04	0,45
HB_C16_02	47	3	6,61	0,08	0,85	0,71	0,14	0,17	0,03	0,40	0,22	0,04	0,19
HB_C16_05	18	12	1,34	0,04	0,66	0,60	0,03	0,09	0,06	0,78	0,20	0,07	0,13

Supplementary Table 4. Significant linkage disequilibrium between loci pairs.

	Eur	Co.Aeg	EC.Anat
A107:AC306			0,0001
AB124:AP288		0,0001	
AC006:HB_C16_02	0,0001		
HB_C16_01:HB_C16_02	0,0001		

Supplementary Table 5. Population-based genetic diversity measures.

Population	N	Private alleles	Mean richness	Total richness	H	Hexp	Hobs	Fis	Fst
C.BlkS	34	1	1,42	41,17	3,53	0,51	0,50	0,05	0,15
Co.Aeg	55	8	1,59	46,16	4,01	0,60	0,58	-0,03	0,11
E.Med	80	23	1,54	44,55	4,38	0,54	0,50	0,05	0,08
EC.Anat	29	6	1,46	42,36	3,37	0,47	0,43	0,06	0,20
Erz-Kar	51	6	1,60	46,34	3,93	0,66	0,61	0,15	0,10
ES.Marm	29	6	1,63	47,23	3,37	0,64	0,62	0,00	-0,05
Eur	38	28	1,54	44,80	3,64	0,55	0,54	0,02	0,03
L.Cauc	44	8	1,58	45,76	3,78	0,58	0,54	0,11	0,05
Thrace	77	25	1,63	47,38	4,34	0,64	0,62	0,03	-0,05
U.Euph	74	11	1,58	45,87	4,30	0,59	0,55	0,02	0,11
W.Anat	65	6	1,57	45,49	4,17	0,57	0,56	0,00	0,09
W.BlkS	53	5	1,58	45,72	3,97	0,58	0,53	0,06	0,10
Zagros	43	7	1,57	45,64	3,76	0,58	0,53	0,05	0,04

Supplementary Table 7. AMOVA results.

Subset	Test	Obs	Std Obs	Expectation	Variance	Alter	Pvalue
all	Variations within samples	5,13	-8,19	5,70	0,07	less	0,0100
all	Variations between samples	0,33	4,82	0,00	0,07	greater	0,0100
all	Variations between Population	0,32	40,01	0,00	0,01	greater	0,0100
t-a	Variations within samples	7,29	-3,21	7,62	0,10	less	0,0100
t-a	Variations between samples	0,21	1,47	-0,01	0,15	greater	0,1000
t-a	Variations between Population	0,30	17,05	0,00	0,02	greater	0,0100
z-a	Variations within samples	2,95	-1,75	3,07	0,07	less	0,0300
z-a	Variations between samples	0,09	1,39	0,00	0,07	greater	0,1300
z-a	Variations between Population	0,04	5,33	0,00	0,01	greater	0,0100
z-l	Variations within samples	2,68	-2,24	2,81	0,06	less	0,0300
z-l	Variations between samples	0,12	2,25	0,00	0,05	greater	0,0400
z-l	Variations between Population	0,02	2,26	0,00	0,01	greater	0,0300
z-c	Variations within samples	2,87	-4,21	3,18	0,07	less	0,0100
z-c	Variations between samples	0,29	4,73	0,00	0,06	greater	0,0100
z-c	Variations between Population	0,03	2,00	0,00	0,01	greater	0,0400

Supplementary Table 6. Pairwise genetic differentiation estimates among populations.

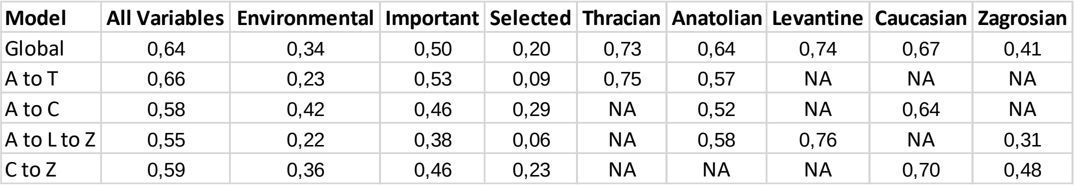
G'st	**Eur**	**Thrace**	**ES.Marm**	**Co.Aeg**	**W.Anat**	**W.BlkS**	**C.BlkS**	**L.Cauc**	**Erz-Kar**	**U.Euph**	**EC.Anat**	**E.Med**	**Zagros**
Eur	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Thrace	0,39	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ES.Marm	0,46	0,00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Co.Aeg	0,65	0,11	0,06	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.Anat	0,66	0,13	0,08	0,02	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.BlkS	0,67	0,15	0,09	0,02	0,02	NA	NA	NA	NA	NA	NA	NA	NA
C.BlkS	0,75	0,24	0,18	0,08	0,14	0,09	NA	NA	NA	NA	NA	NA	NA
L.Cauc	0,70	0,27	0,22	0,13	0,16	0,15	0,06	NA	NA	NA	NA	NA	NA
Erz-Kar	0,64	0,11	0,06	-0,01	0,02	0,03	-0,02	-0,02	NA	NA	NA	NA	NA
U.Euph	0,66	0,14	0,09	0,02	0,02	0,02	0,05	0,10	-0,03	NA	NA	NA	NA
EC.Anat	0,74	0,28	0,24	0,16	0,14	0,13	0,20	0,28	0,19	0,14	NA	NA	NA
E.Med	0,69	0,18	0,13	0,05	0,05	0,04	0,09	0,15	0,04	0,03	0,06	NA	NA
Zagros	0,69	0,19	0,13	0,05	0,04	0,03	0,08	0,08	0,00	0,01	0,14	0,04	NA

Gst	**Eur**	**Thrace**	**ES.Marm**	**Co.Aeg**	**W.Anat**	**W.BlkS**	**C.BlkS**	**L.Cauc**	**Erz-Kar**	**U.Euph**	**EC.Anat**	**E.Med**	**Zagros**
Eur	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Thrace	0,09	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ES.Marm	0,10	0,00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Co.Aeg	0,16	0,02	0,01	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.Anat	0,17	0,03	0,02	0,00	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.BlkS	0,17	0,03	0,02	0,00	0,00	NA	NA	NA	NA	NA	NA	NA	NA
C.BlkS	0,21	0,05	0,04	0,02	0,03	0,02	NA	NA	NA	NA	NA	NA	NA
L.Cauc	0,18	0,05	0,04	0,03	0,03	0,03	0,01	NA	NA	NA	NA	NA	NA
Erz-Kar	0,15	0,02	0,01	0,00	0,00	0,01	0,00	0,00	NA	NA	NA	NA	NA
U.Euph	0,17	0,03	0,02	0,00	0,01	0,00	0,01	0,02	-0,01	NA	NA	NA	NA
EC.Anat	0,22	0,07	0,06	0,04	0,04	0,03	0,05	0,07	0,05	0,03	NA	NA	NA
E.Med	0,19	0,04	0,03	0,01	0,01	0,01	0,02	0,03	0,01	0,01	0,02	NA	NA
Zagros	0,18	0,04	0,03	0,01	0,01	0,01	0,02	0,02	0,00	0,00	0,03	0,01	NA

D	**Eur**	**Thrace**	**ES.Marm**	**Co.Aeg**	**W.Anat**	**W.BlkS**	**C.BlkS**	**L.Cauc**	**Erz-Kar**	**U.Euph**	**EC.Anat**	**E.Med**	**Zagros**
Eur	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Thrace	0,28	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ES.Marm	0,33	0,00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Co.Aeg	0,52	0,07	0,04	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.Anat	0,52	0,08	0,05	0,01	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.BlkS	0,54	0,09	0,05	0,01	0,01	NA	NA	NA	NA	NA	NA	NA	NA
C.BlkS	0,61	0,16	0,11	0,05	0,08	0,05	NA	NA	NA	NA	NA	NA	NA
L.Cauc	0,57	0,18	0,15	0,08	0,10	0,09	0,03	NA	NA	NA	NA	NA	NA
Erz-Kar	0,51	0,07	0,04	-0,01	0,01	0,02	-0,01	-0,01	NA	NA	NA	NA	NA
U.Euph	0,52	0,09	0,06	0,01	0,01	0,01	0,03	0,06	-0,02	NA	NA	NA	NA
EC.Anat	0,59	0,18	0,15	0,09	0,08	0,07	0,11	0,17	0,12	0,08	NA	NA	NA
E.Med	0,55	0,11	0,08	0,03	0,03	0,02	0,05	0,09	0,02	0,02	0,03	NA	NA
Zagros	0,56	0,12	0,09	0,03	0,03	0,02	0,05	0,05	0,00	0,01	0,08	0,02	NA

Fst	**Eur**	**Thrace**	**ES.Marm**	**Co.Aeg**	**W.Anat**	**W.BlkS**	**C.BlkS**	**L.Cauc**	**Erz-Kar**	**U.Euph**	**EC.Anat**	**E.Med**	**Zagros**
Eur	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Thrace	0,16	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
ES.Marm	0,19	0,00	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Co.Aeg	0,28	0,04	0,02	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.Anat	0,29	0,05	0,03	0,01	NA	NA	NA	NA	NA	NA	NA	NA	NA
W.BlkS	0,29	0,06	0,03	0,01	0,01	NA	NA	NA	NA	NA	NA	NA	NA
C.BlkS	0,35	0,09	0,06	0,02	0,05	0,01	NA	NA	NA	NA	NA	NA	NA
L.Cauc	0,30	0,10	0,09	0,05	0,07	0,06	0,01	NA	NA	NA	NA	NA	NA
Erz-Kar	0,26	0,04	0,02	-0,01	0,01	0,00	-0,06	-0,01	NA	NA	NA	NA	NA
U.Euph	0,28	0,05	0,04	0,01	0,01	0,01	0,01	0,04	-0,01	NA	NA	NA	NA
EC.Anat	0,36	0,12	0,11	0,07	0,07	0,06	0,10	0,13	0,09	0,07	NA	NA	NA
E.Med	0,31	0,07	0,05	0,02	0,02	0,02	0,02	0,07	0,01	0,01	0,03	NA	NA
Zagros	0,30	0,07	0,05	0,02	0,02	0,01	0,02	0,03	0,00	0,01	0,07	0,02	NA

Supplementary Table 8. Model performance for ancestral groups in global and regional GFs and relative contributions of environmental variables.



Model	All Variables	Environmental	Important	Selected	Thracian	Anatolian	Levantine	Caucasian	Zagrosian
Global	0,64	0,34	0,50	0,20	0,73	0,64	0,74	0,67	0,41
A to T	0,66	0,23	0,53	0,09	0,75	0,57	NA	NA	NA
A to C	0,58	0,42	0,46	0,29	NA	0,52	NA	0,64	NA
A to L to Z	0,55	0,22	0,38	0,06	NA	0,58	0,76	NA	0,31
C to Z	0,59	0,36	0,46	0,23	NA	NA	NA	0,70	0,48

Supplementary Table 10. Areal gains in protection status, directly within PAs or indirectly through PA resemblance under different scenarios.

Status	Class	Area
Direct	Current	59711
Direct	+1 PA	65898
Direct	+2 PA's	73819
Direct	+3 PA's	81949
Resemblance	Current	499719
Resemblance	+1 PA	577674
Resemblance	+2 PA's	713422
Resemblance	+3 PA's	754809

Supplementary Table 9. Weighted importance of environmental variables in predicting intra-specific turnover in the global and regional GFs.

Var	Global	A to T	A to C	A to L to Z	C to Z
MEM2	0,1849	0,1937	0,0165	0,2017	0,1925
MEM1	0,1164	0,2404	0,1468	0,1249	0,0401
PETwettest	0,0240	0,0193	0,0053	0,0068	0,0095
Pwarmest	0,0220	0,0068	0,1102	0,0029	0,0647
isothermality	0,0177	0,0153	0,0199	0,0129	0,0331
Tdriest	0,0176	0,0039	0,0479	0,0071	0,0140
aridity	0,0153	0,0027	0,0413	0,0055	0,0268
Tseasonality	0,0143	0,0034	0,0066	0,0096	0,0096
TUR_alt	0,0143	0,0071	0,0169	0,0159	0,0171
continentality	0,0135	0,0067	0,0054	0,0108	0,0056
Pwettest	0,0123	0,0049	0,0248	0,0025	0,0268
Pdriest	0,0123	0,0238	0,0070	0,0044	0,0124
minTwarm	0,0114	0,0030	0,0021	0,0157	0,0021
PETdriest	0,0110	0,0030	0,0221	0,0024	0,0133
Pcoldest	0,0105	0,0127	0,0040	0,0025	0,0038
minTcold	0,0097	0,0064	0,0038	0,0096	0,0056
Pseasonality	0,0082	0,0046	0,0032	0,0066	0,0111
Pdry	0,0079	0,0122	0,0090	0,0025	0,0094
Twarmest	0,0076	0,0024	0,0005	0,0099	0,0018
Tcoldest	0,0076	0,0058	0,0048	0,0059	0,0064
Pwet	0,0070	0,0051	0,0062	0,0031	0,0065
maxTcold	0,0067	0,0036	0,0041	0,0076	0,0023
diurnalTrange	0,0064	0,0085	0,0075	0,0061	0,0044
PETwarmest	0,0063	0,0057	0,0102	0,0042	0,0112
meanT	0,0061	0,0016	0,0027	0,0060	0,0030
Twettest	0,0061	0,0037	0,0024	0,0055	0,0036
gdd0	0,0058	0,0025	0,0019	0,0057	0,0020
annualTrange	0,0058	0,0040	0,0050	0,0072	0,0043
annualP	0,0056	0,0102	0,0067	0,0020	0,0049
roughness	0,0054	0,0039	0,0044	0,0032	0,0047
PETseasonality	0,0052	0,0084	0,0052	0,0038	0,0070
embergerQ	0,0052	0,0082	0,0047	0,0070	0,0020
maxTwarm	0,0049	0,0026	0,0030	0,0054	0,0043
annualPET	0,0046	0,0017	0,0038	0,0041	0,0059
PETcoldest	0,0045	0,0043	0,0025	0,0030	0,0030
thermicity	0,0045	0,0013	0,0026	0,0041	0,0021
moisture	0,0038	0,0031	0,0027	0,0040	0,0049
gdd5	0,0030	0,0014	0,0030	0,0044	0,0022
topoWet	0,0018	0,0030	0,0016	0,0019	0,0035
count10	0,0013	0,0006	0,0006	0,0016	0,0004

Supplementary Table 11. Mean differences between ancestral groups' PA resemblance under different scenarios.

Comparison	PAs	Difference	p_adj
Cau-Ana	pa	0,04	0,0000
Lev-Ana	pa	-0,07	0,0000
Thr-Ana	pa	0,06	0,0000
Zag-Ana	pa	-0,06	0,0000
Lev-Cau	pa	-0,11	0,0000
Thr-Cau	pa	0,02	0,0000
Zag-Cau	pa	-0,1	0,0000
Thr-Lev	pa	0,13	0,0000
Zag-Lev	pa	0,01	0,0000
Zag-Thr	pa	-0,12	0,0000
Cau-Ana	if1	0,04	0,0000
Lev-Ana	if1	-0,03	0,0000
Thr-Ana	if1	0,06	0,0000
Zag-Ana	if1	0,01	0,0000
Lev-Cau	if1	-0,07	0,0000
Thr-Cau	if1	0,02	0,0000
Zag-Cau	if1	-0,04	0,0000
Thr-Lev	if1	0,08	0,0000
Zag-Lev	if1	0,03	0,0000
Zag-Thr	if1	-0,05	0,0000
Cau-Ana	if2	0	0,0000
Lev-Ana	if2	-0,07	0,0000
Thr-Ana	if2	0,02	0,0000
Zag-Ana	if2	-0,03	0,0000
Lev-Cau	if2	-0,07	0,0000
Thr-Cau	if2	0,02	0,0000
Zag-Cau	if2	-0,04	0,0000
Thr-Lev	if2	0,08	0,0000
Zag-Lev	if2	0,03	0,0000
Zag-Thr	if2	-0,05	0,0000
Cau-Ana	if3	0	0,0000
Lev-Ana	if3	-0,07	0,0000
Thr-Ana	if3	0,02	0,0000
Zag-Ana	if3	0	0,0100
Lev-Cau	if3	-0,07	0,0000
Thr-Cau	if3	0,02	0,0000
Zag-Cau	if3	0	0,1500
Thr-Lev	if3	0,08	0,0000
Zag-Lev	if3	0,07	0,0000
Zag-Thr	if3	-0,02	0,0000

Supplementary Table 12. Mean differences between persistence, resilience, disappearance, and emergence indices of ancestral groups.

Comparison	Index	Difference	p_adj
Cau-Ana	persistence	-0,17	0,0000
Lev-Ana	persistence	-0,42	0,0000
Thr-Ana	persistence	-0,93	0,0000
Zag-Ana	persistence	0,17	0,0000
Lev-Cau	persistence	-0,25	0,0000
Thr-Cau	persistence	-0,75	0,0000
Zag-Cau	persistence	0,34	0,0000
Thr-Lev	persistence	-0,51	0,0000
Zag-Lev	persistence	0,59	0,0000
Zag-Thr	persistence	1,1	0,0000
Cau-Ana	resilience	0,02	0,0000
Lev-Ana	resilience	-0,13	0,0000
Thr-Ana	resilience	-0,11	0,0000
Zag-Ana	resilience	0,03	0,0000
Lev-Cau	resilience	-0,15	0,0000
Thr-Cau	resilience	-0,14	0,0000
Zag-Cau	resilience	0,01	0,0001
Thr-Lev	resilience	0,01	0,0000
Zag-Lev	resilience	0,16	0,0000
Zag-Thr	resilience	0,15	0,0000
Cau-Ana	disappearance	0,03	0,0000
Lev-Ana	disappearance	0,13	0,0000
Thr-Ana	disappearance	0,07	0,0000
Zag-Ana	disappearance	0	0,0100
Lev-Cau	disappearance	0,1	0,0000
Thr-Cau	disappearance	0,04	0,0000
Zag-Cau	disappearance	-0,03	0,0000
Thr-Lev	disappearance	-0,06	0,0000
Zag-Lev	disappearance	-0,13	0,0000
Zag-Thr	disappearance	-0,07	0,0000
Cau-Ana	emergence	0,05	0,0000
Lev-Ana	emergence	0,05	0,0000
Thr-Ana	emergence	0,17	0,0000
Zag-Ana	emergence	0,01	0,0000
Lev-Cau	emergence	0	0,2750
Thr-Cau	emergence	0,12	0,0000
Zag-Cau	emergence	-0,04	0,0000
Thr-Lev	emergence	0,13	0,0000
Zag-Lev	emergence	-0,04	0,0000
Zag-Thr	emergence	-0,16	0,0000
Cau-Ana	resemblance	0,04	0,0000
Lev-Ana	resemblance	-0,07	0,0000
Thr-Ana	resemblance	0,06	0,0000
Zag-Ana	resemblance	-0,06	0,0000
Lev-Cau	resemblance	-0,11	0,0000
Thr-Cau	resemblance	0,02	0,0000
Zag-Cau	resemblance	-0,1	0,0000
Thr-Lev	resemblance	0,13	0,0000
Zag-Lev	resemblance	0,01	0,0000
Zag-Thr	resemblance	-0,12	0,0000

Supplementary Table 13. Interactions of persistence, resilience, disappearance, emergence, and resemblance indices with other spatial patterns.

Index	First Mean	Mean1	Mean2	p	p_adj
Persistence	**sparse**	2,88	3,13	0,0000	0,0000
Persistence	**unique**	3,45	3,1	0,0000	0,0000
Persistence	**fast**	2,5	3,2	0,0000	0,0000
Persistence	**unprot**	3,24	3,03	0,0000	0,0000
Persistence	**Tlow**	3,23	2,92	0,0000	0,0000
Persistence	**Clow**	3,13	3,12	0,3842	0,3842
Persistence	**Alow**	2,97	3,25	0,0000	0,0000
Persistence	**Llow**	3,12	3,17	0,0000	0,0000
Persistence	**Zlow**	2,9	3,49	0,0000	0,0000
Resilience	**sparse**	0,86	0,93	0,0000	0,0000
Resilience	**unique**	0,94	0,92	0,0000	0,0000
Resilience	**fast**	0,86	0,93	0,0000	0,0000
Resilience	**unprot**	0,93	0,92	0,0000	0,0000
Resilience	**Tlow**	0,93	0,92	0,0000	0,0000
Resilience	**Clow**	0,92	0,98	0,0000	0,0000
Resilience	**Alow**	0,9	0,95	0,0000	0,0000
Resilience	**Llow**	0,94	0,89	0,0000	0,0000
Resilience	**Zlow**	0,89	0,97	0,0000	0,0000
Disappearance	**sparse**	1,29	1,19	0,0000	0,0000
Disappearance	**unique**	1,19	1,19	0,2703	0,2703
Disappearance	**fast**	1,26	1,18	0,0000	0,0000
Disappearance	**unprot**	1,2	1,18	0,0000	0,0000
Disappearance	**Tlow**	1,19	1,17	0,0000	0,0000
Disappearance	**Clow**	1,19	1,18	0,0000	0,0000
Disappearance	**Alow**	1,23	1,16	0,0000	0,0000
Disappearance	**Llow**	1,17	1,22	0,0000	0,0000
Disappearance	**Zlow**	1,21	1,15	0,0000	0,0000
Emergence	**sparse**	1,28	1,21	0,0000	0,0000
Emergence	**unique**	1,21	1,22	0,0001	0,0001
Emergence	**fast**	1,29	1,21	0,0000	0,0000
Emergence	**unprot**	1,2	1,22	0,0000	0,0000
Emergence	**Tlow**	1,2	1,23	0,0000	0,0000
Emergence	**Clow**	1,21	1,22	0,3473	0,3473
Emergence	**Alow**	1,24	1,2	0,0000	0,0000
Emergence	**Llow**	1,22	1,2	0,0000	0,0000
Emergence	**Zlow**	1,24	1,18	0,0000	0,0000
Resemblance	**sparse**	0,51	0,7	0,0000	0,0000
Resemblance	**unique**	0,64	0,71	0,0000	0,0000
Resemblance	**fast**	0,69	0,7	0,0000	0,0000
Resemblance	**Tlow**	0,68	0,74	0,0000	0,0000
Resemblance	**Clow**	0,69	0,76	0,0000	0,0000
Resemblance	**Alow**	0,66	0,73	0,0000	0,0000
Resemblance	**Llow**	0,7	0,71	0,0000	0,0000
Resemblance	**Zlow**	0,71	0,68	0,0000	0,0000

CURRICULUM VITAE

Surname, Name: Kükrer, Mert

EDUCATION

Degree	Institution	Year of Graduation
MS	METU Biology	2013
BS	METU Molecular Biology and Genetics	2009
High School	60th Year Anatolian High School, İzmir	2004

PUBLICATIONS

1. Kükrer, M., Kence, M., & Kence, A. (2021). Honey bee diversity is swayed by migratory beekeeping and trade despite conservation practices: Genetic evidence for the impact of anthropogenic factors on population structure. *Frontiers in Ecology and Evolution*, *9*, 556816.

2. Kükrer, M., & Bilgin, C. C. (2020). Climate change prompts monitoring and systematic utilization of honey bee diversity in Turkey. *Bee Studies*, *12*(1), 19-25.

3. Oskay, D., Kükrer, M., & Kence, A. (2019). Muğla bal arısında (*Apis mellifera anatoliaca*) Amerikan yavru çürüklüğü hastalığına karşı direnç geliştirilmesi. *Arıcılık Araştırma Dergisi*, *11*(1), 8-20.

4. Donthu R., Marcelino J., Giordano R., Tao Y., et al. (*in press*). HBeeID: A Molecular Tool That Identifies Honey Bee Subspecies from Different Geographic Populations.