

Article

Impact of Transhumant Livestock Grazing Abandonment on Pseudo-Alpine Grasslands in Greece in the Context of Climatic Change

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Abstract: Pseudo-alpine grassland ecosystems have started to decline during the past few decades. According to many studies, climate change and abandonment of traditional anthropogenic activities are directly linked to this phenomenon. However, the interaction of these two factors with pseudo-alpine grasslands has not been studied in Greece. The aim of this study was to assess the impact of climatic change and abandonment of transhumant livestock grazing on pseudo-alpine grassland ecosystems structure and stability in Mt Vermio and Mt Zireia. Geographic Information System data on land use/land cover from 1945 and 2020, as well as climatological and livestock data, have been examined and presented. Landscape metrics were also used to quantify landscape structure changes. Although both mountains' pseudo-alpine grasslands have reduced in size, Mt Zireia has experienced an upward treeline shift, which seems to be the result of climate change, while in Mt Vermio, the more severe transhumance abandonment caused horizontal tree expansion. There are strong indications that a rise in temperature is the main driver for the upward increase in treeline.

Keywords: Mt Zireia; Mt Vermio; landscape metrics; treeline shift; temperature; grazing; GIS; land use/land cover change



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1. Introduction

Alpine and pseudo-alpine grasslands are uncultivated areas with natural vegetation, mainly herbaceous plants, managed with ecological principles [1,2] and characterized by harsh climatic conditions that limit the plant growth period to a few months [3]. In Greece, forest boundaries are between 1700 and 2000 m [4], however, grasslands over 1200 m are ecologically connected to the pseudo-alpine zone and are therefore considered as pseudo-alpine [5]. They are among the European regions where conservation is of the utmost importance (Council Directive 92/43/EEC of 21 May 1992) [6] and they make up most of Greece's Special Protection Zones for Mountainous Areas [7].

Alpine and pseudo-alpine grasslands are hotspots for biodiversity and have significant cultural heritage values [8], supporting numerous rare and/or endangered animals and plants species. They provide many ecosystem services, such as nitrogen (N) and carbon (C) storage [6,9], water purification and retention [6,10], valuable genetic material storage [2], provision of pharmaceuticals [11], soil conservation [9,11], nutrient recycling, pollination and climate regulation [11], forage for animals [11], and can generate substantial economic value through the production of meat and milk [6]. They represent areas for recreation, tourism, and cultural heritage [6,9,11] and create a sustainable framework that ensures the future of rural areas [2].

Species diversity, ecosystem function and landscape structure in pseudo-alpine grasslands, like most terrestrial ecosystems, are concurrently affected by global climate change and anthropogenic activities such as livestock grazing, agriculture, urbanization, etc. [12–18]. Changes in vegetation pattern and floristic composition are the main effects of livestock grazing on the landscape. The nature and extent of these changes depend on livestock species [19], grazing period, pressure, and history [20–22], as well as on abiotic variables such as soil type, temperature, and precipitation [15,23].

Pseudo-alpine grasslands are often referred to as summer grasslands because they are grazed in the summer. For this reason, they were mostly associated with transhumance [24]. In the past, these grasslands were the hub of summer grazing activities with animals and herders, along with their families, living there for more than five months each year [25]. The animals arrived at the end of spring and left at the end of the summer, grazing the abundant annual growth of forage species. The herders made efficient use of natural resources and created unique natural landscapes [26,27], while also enhancing the genetic diversity by rearing autochthonous breeds and providing ecosystem services [28,29]. In addition, transhumance protected rural livelihoods, reducing the depopulation of marginal and remote areas, and effectively mitigated climate change effects (e.g., soil carbon stock in rangelands) [26].

Transhumance during the centuries has had a major impact on landscape structure, vegetation composition, and ecosystem services in the mountainous areas [30–32] not only in many Mediterranean mountains [33], but also in high mountains such as the Himalayas [34]. This kind of animal husbandry has helped conserve the rangelands and open forests—two important types of landscape. The decline in the transhumant livestock system over the last few decades has impacted the structure and composition of grassland ecosystems [30,35] and has reduced their multi-functionality, particularly in regions where grazing was prohibited for an extended period of time [35]. In addition to livestock grazing, strong evidence suggests that global warming is leading to dramatic shifts in structure, species diversity, and functioning in alpine vegetation communities [3,15,36,37]. Although climate change is affecting the entire globe, alpine regions are particularly vulnerable to its consequences [38–40]. The increase in air temperature may change the type of vegetation from grasslands to shrublands and finally to forests [41]. Most of the uses involving woody species tend to integrate rapidly, now forming a more homogeneous mosaic landscape [42].

Despite significant regional variations, the majority of Europe has seen temperature rises of roughly 0.8 °C on average this century [43]. The impact of climate change varies with latitude [44–46], with southern, drier regions being more affected than northern ones [43,47]. Treeline shifts due to climate change and the cessation of transhumance have significant implications for pseudo-alpine grassland spatial distribution [48]. In the Central Austrian Alps, for example, treelines that have been impacted by pastoral use for centuries respond to climate change differently than treelines that have not been altered [49].

Numerous studies demonstrate that grazing increases spatial heterogeneity, mostly because of differences between grazed and ungrazed patches as well as other grazing-related effects such as manuring and trampling [50]. A shift in treeline results in changes in the edge habitat, which could lead to either landscape fragmentation or homogenization, loss of diversity [20,51], and poses a major threat to the conservation value of grasslands [11]. Landscape spatial structure changes can be better described and quantified using landscape metrics [52–55].

While there have been numerous studies on how climate change affects treeline, there are no studies, as far as we are aware, about alpine grasslands. The changes in both climate and land use pose a threat to the long-term survival of the existing plant mosaic in the pseudo-alpine grasslands [8]. This study aimed to investigate the impact of climatic change and abandonment of transhumant livestock grazing system on the pseudo-alpine grassland ecosystem structure and stability of two mountains in Greece. We set out to answer the following question: Does the climate and the abandonment of transhumance affect land use changes in the pseudo-alpine zone, and how?

2. Materials and Methods

2.1. Study Area

The research was conducted on Mt Vermio and Zireia, in the pseudo-alpine zone over 1200 m (Figure 1).

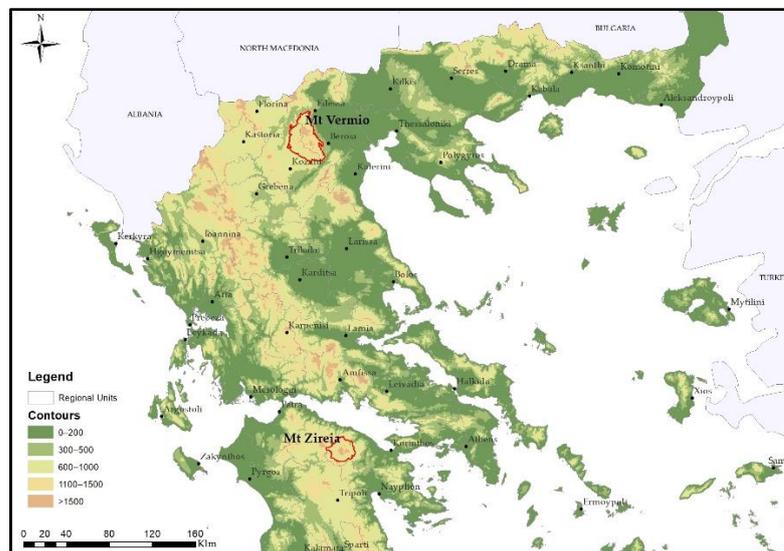


Figure 1. The study areas (red outline) in Mt Vermio (North Greece) and Mt Zireia (South Greece).

Mt Vermio is located in central-western Macedonia and administratively belongs to Imathia, Kozani, and Pella Regional Units. It has a north-south orientation with its tallest peak at 2052 m [25]. The climate is sub-Mediterranean in the uplands and meso-Mediterranean in the lowlands. The driest months are July and August, but due to the vicinity of archipelagos, the atmosphere is never completely dry [56]. The climate under the Köppen and Geiger [57] classification system ranges from Mediterranean-influenced warm-summer humid continental (Dsb) to warm-summer humid continental (Dfb). According to the classification approach of Mavromatis [58], Mt Vermio belongs to the bioclimatic zone wet with severe winter and to two different bioclimatic character categories: axeric temperate and sub-Mediterranean. Most of Mt Vermio is part of the network of the Natura 2000 protected areas [59]. Forests and shrublands are found mainly on the eastern part of the mountain.

Vermio is a mountain where transhumant livestock animals used to have a very strong presence in the past. According to Chatzimichali [60], it accommodated 66% of Macedonia's goats and sheep. It covered the needs for forage production for almost the whole of Thessaly (Central Greece) and beyond [25,61] because it was easily accessible and had plenty of grasslands with an abundance of forage production during summer [62]. The entire region served as summer grazing land for flocks owned by an ethnic group known as the "Sarakatsanaioi". The "Tseligkata" social structure that the Sarakatsanaioi established allowed many small-scale transhumant families to collaborate and work together [63].

According to Katsaros [62], in the 1950s there were about 150,000–170,000 sheep and goats grazing in the area, but over the past few decades the number of animals and therefore the grazing pressure has significantly decreased. As in most of Greece, the Tseligkato system today has become almost extinct in Mt Vermio [64]. Sidiropoulou and co-authors [25] estimate that there were only 27,532 sheep and goats grazing freely in Mt Vermio in 2011. This declining trend in transhumance has caused changes in the size and distribution of grasslands and forests [20,65,66].

Mt Zireia (Kyllini) is southeast of the Corinth Regional Unit in Peloponnese. It is the second highest mountain of the Peloponnese peninsula, with the highest peak at 2374 m. The climate under the Köppen and Geiger [57] classification system ranges from Mediterranean-influenced warm-summer humid continental (Dsb) to warm-summer

Mediterranean (Csb). According to the classification approach of Mavromatis [58], Mt Zireia belongs to the bioclimatic zone wet with severe winter and to three different bioclimatic character categories: sub-axeric cold with a sub-dry period, sub-Mediterranean and mild meso-mediterranean. The majority of Mt Zireia is protected by the Natura 2000 network [67,68]. The study area's flora is rich and contains several significant endemic species for the Peloponnese and Greece as a whole [67,69]. Above 800 m there are forests and in the higher elevation zone there are mainly grasslands with thorny shrubs and grasses, many of which are unique and rare endemic and rocky areas [67]. In Mt Zireia there were about 38,000 transhumant sheep and goats in 1960 [70]. Families and flocks were moved on foot from different areas of the Peloponnese peninsula or West Attica [60]. However, in recent years, there was remarkable decrease of transhumant animals. According to Karatassiou and coauthors [70] in 2020 there were 13,717 transhumant sheep and goats in Mt Zireia.

2.2. Methods

Long-term (1990–2019) time series analysis of annual precipitation, mean annual air temperature, and maximum annual air temperature were based on the TerraClimate dataset [71], a high-spatial resolution ($1/24^\circ$, ~4 km) dataset of monthly climate and climatic water balance for global terrestrial surfaces from 1958 until now. The aridity index of De Martonne (I_{dM}) [72] was calculated for the same period using the following Formula (1):

$$I_{dM} = P / (T + 10) \quad (1)$$

where P is the average annual precipitation (mm) and T the average mean annual air temperature ($^\circ\text{C}$). The aridity index (I_{dM}) is a key environmental component influencing the development of natural vegetation and categorizes climate types in proportion to water availability [15] because of its efficiency and relevance in relation to the arid/humid climate classification [73,74].

Livestock data were collected from Chatzimichali [60], Katsaros [62] and the Payment and Control Agency for Guidance and Guarantee Community [75]. Grazing pressure by transhumant sheep and goats in the pseudo-alpine zone was the quotient of transhumant animals/pseudo-alpine grazing areas (grasslands, shrublands, silvopastoral systems).

Land Use/Land Cover (LULC) data for Mt Vermio and Mt Zireia were obtained for 1945 and 2020, to analyze temporal land use changes in the two study areas:

- Aerial orthophotographs (spatial resolution of 1 m) of 1945 provided by the National Cadastre and Mapping Agency S.A. [76] were used to digitize past LULC (scale 1:5000);
- Google Earth satellites images were used to digitize current (2020) LULC types.

The LULC data for 1945 and 2020, for Mt Vermio and Mt Zireia, were classified according to Ref. [25] into the following six categories: pseudo-alpine grasslands, shrublands, silvopastoral systems, forests, agricultural land, and other land uses (mainly built-up areas and a few water surfaces).

Data was processed within ArcGIS v10.8.1 software [77], and the minimum cartographic unit was set to 1 ha. The selected classification method detected various components on aerial orthophotos and Google Earth images using basic photographic keys (tone, texture, pattern, shadow, shape, and size) and feature association [47,78]. Visual photointerpretation was supported by extensive field sampling verifications from a group of scientists, with more than 20-years of research experience in the specific areas. The pseudo-alpine zone was isolated using the "clip" command and a few peaks that were not part of the main mountain core were excluded. The transition matrix method was used to represent all possible landscape changes between 1945 and 2020 for both study areas.

To examine the slopes and elevation zones of the two mountains, a Digital Elevation Model (ASTER Global DEM) [79] with a resolution of 30 m (pixel size) was processed.

To assess the extent of forest invasion on grasslands, the temporal variations in all-time forest distribution were analyzed by merging the elevation zones (100 m altitudinal difference) and forest cover with the “union” command in ArcGIS v10.8.1.

Patch Analyst/Grid Extension for ArcGIS [80] was used to compute four quantitative metrics for analyzing landscape structure [81,82]. Based on previous multi-temporal landscape studies [25,55] the chosen metrics were Number of patches (NumP), Mean patch size (MPS), Edge density (ED), and Interspersion Juxtaposition index (JI) (Table 1).

Table 1. List and description of the landscape metrics used in the study.

Landscape Metrics	Abbreviation	Description	Unit
Number of Patches	NumP	Total number of patches	-
Mean Patch Size	MPS	Average patch size	ha
Edge Density	ED	Amount of edge relative to the landscape	m/ha
Interspersion Juxtaposition Index	IJI	Spatial intermixing of different patch types	%

Metrics were calculated for all LULC types at the landscape level and exclusively for grasslands at the class level. Classes corresponded to the different LULC types, and each class consisted of numerous polygons (patches). The cell size for grid analysis was set to 10 m.

3. Results

The average values of mean annual air temperature for both Mt Zireia and Mt Vermio over the last 30 years are shown on Figure 2. Mt Vermio is substantially cooler compared to Mt Zireia by 1–2 °C and differences were rather consistent throughout the last 30 years.

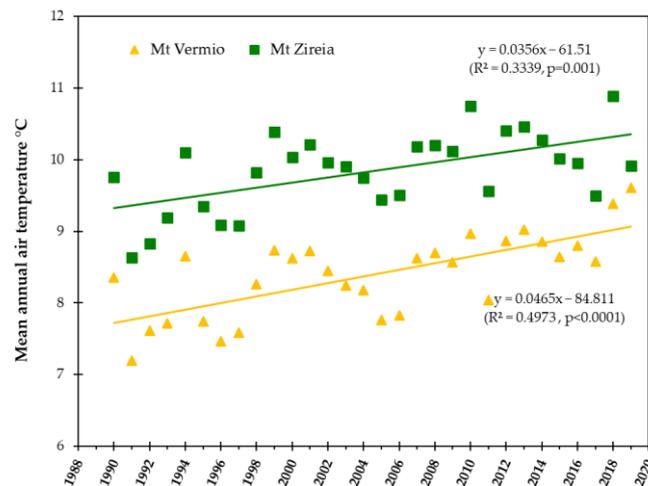


Figure 2. Mean annual air temperature between 1990 and 2019 for Mt Vermio and Mt Zireia.

The mean annual temperature between 1990 and 2019 was 8.3 °C and 9.8 °C for Mt Vermio and Mt Zireia, respectively, and the max annual temperature for the same period was 13.3 °C and 14.9 °C, respectively (Table 2).

Table 2. Climatological parameters for the study areas between 1990 and 2019. Values present means \pm SD (n = 29).

Climatological Parameters	Mt Vermio	Mt Zireia
Mean Annual Temperature (°C)	8.3 \pm 0.58	9.8 \pm 0.54
Max Annual Temperature (°C)	13.3 \pm 0.65	14.9 \pm 0.55
Annual Precipitation (mm)	666.8 \pm 121.54	917.3 \pm 170.48
De Martonne Aridity Index	36.3	46.2

The annual precipitation between 1990 and 2019 was 666.8 mm for Mt Vermio and 917.3 mm for Mt Zireia (Table 2). Similar to temperature, annual precipitation for both Mt Zireia and Mt Vermio during the past 30 years showed considerable year-to-year variation (Figure 3).

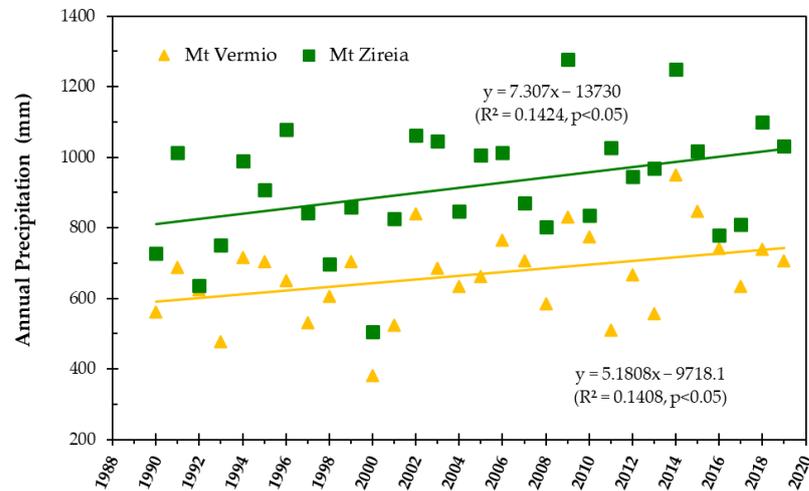


Figure 3. Annual precipitation between 1990 and 2019 for Mt Vermio and Mt Zireia.

The aridity index (I_{dM}) for the same period was 36.3 for Mt Vermio and 46.2 for Mt Zireia (Table 2) and the two study areas were classified as moderately humid and humid [74].

Transhumance was once prevalent on Mt Vermio, which could hold nearly 170,000 transhumant sheep and goats (Table 3). Currently, there are 22,308 transhumant animals, a dramatic decrease of approximately 86.1%. On the contrary, on Mt Zireia, the number of transhumant animals in the past was much smaller (38,230). However, just like on Mt Vermio, transhumance has declined. Today on Mt Zireia there are only 13,717 transhumant animals, a decrease of 64.1% (Table 3).

Table 3. Number of transhumant animals (sheep, goat) in the entire mountainous zone.

Mountain	1950–1960	2020
Vermio	150,000–170,000	22,308
Zireia	38,230	13,717

Today, there are fewer than 22,000 transhumant animals in both mountains, however grazing pressure (transhumant animals/pseudo-alpine grazing areas) in the pseudo-alpine zone of Mt Vermio is only 0.69, compared to 0.94 in Mt Zireia (Table 4).

Table 4. Grazing pressure in the pseudo-alpine zone of the study areas.

	Mt Vermio	Mt Zireia
Transhumant animals	16,841	7124
Pseudo-alpine area (ha)	24,585.2	7611.4
Grazing pressure	0.69	0.94

The spatial distribution of LULC on Mt Vermio between 1945 and 2020 is presented in Figure 4.

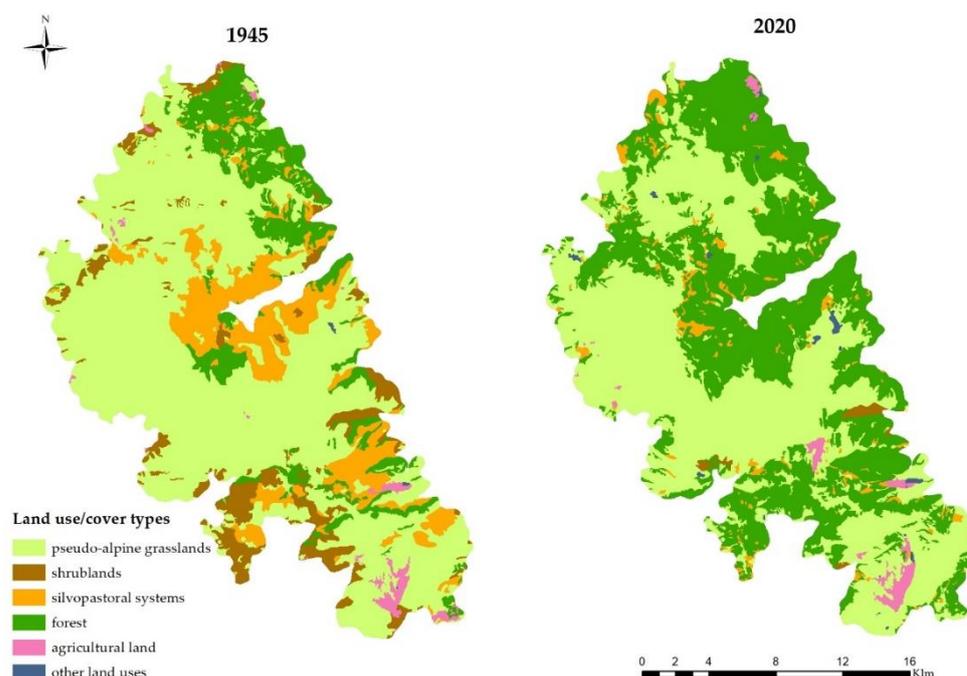


Figure 4. Spatial distribution of Land Use/Land Cover types of Mt Vermio for 1945 and 2020.

In 1945, pseudo-alpine grasslands on Mt Vermio occupied most of the area (28,581.2 ha), followed by silvopastoral systems (6308.5 ha), forests (5568 ha), and shrublands (3623.9 ha) (Table 5). In 2020 there was a significant increase (245.7%) in forest size, while pseudo-alpine grasslands, silvopastoral systems, and shrublands have substantially decreased by -19.8% , -77.9% , and -92.8% , respectively.

Table 5. Temporal evolution of Land Use/Land Cover (LULC) types of Mt Vermio for 1945 and 2020.

LULC	1945 (ha)	2020 (ha)	2020–1945 (%)
Silvopastoral systems	6308.5	1397.1	-77.9
Agricultural land	585.7	659.6	12.6
Forests	5568.0	19,247.0	245.7
Shrublands	3623.9	261.7	-92.8
Pseudo-alpine grasslands	28,581.2	22,926.3	-19.8
Other land uses	23.0	198.5	764.5
Total	44,690.3	44,690.3	

The spatial distribution of LULC types on Mt Zireia for 1945 and 2020 is presented in Figure 5.

In 1945, most areas of Mt. Zireia were covered by pseudo-alpine grasslands (4712.3 ha), followed by forests (3130.5 ha), shrublands (2504.3 ha), and silvopastoral systems (2300.2 ha) (Table 6). In 2020 there was an increase (54.4%) in forests and shrublands (8.7%), while pseudo-alpine grasslands and silvopastoral systems decreased by -19.8% and -51.7% , respectively.

According to Tables 7 and 8, between 1945–2020 almost 37% the total landscape area of Mt Vermio and 28% of Mt Zireia changed land use. The most important changes in terms of gain for both mountains were forest expansion and in terms of loss, pseudo-alpine grassland and silvopastoral systems reduction. On Mt Zireia a slight increase was also recorded for shrublands, silvopastoral areas, and pseudo-alpine grasslands (Table 8, gain values). Further analysis of the transition data showed that on Mt Vermio, the dominant expansion of forests occurred equally at the expense of silvopastoral systems and pseudo-alpine grasslands, and to a lesser extent at the expense of shrublands. On Mt Zireia however, the growth of forests was mainly done at the expense of silvopastoral systems.

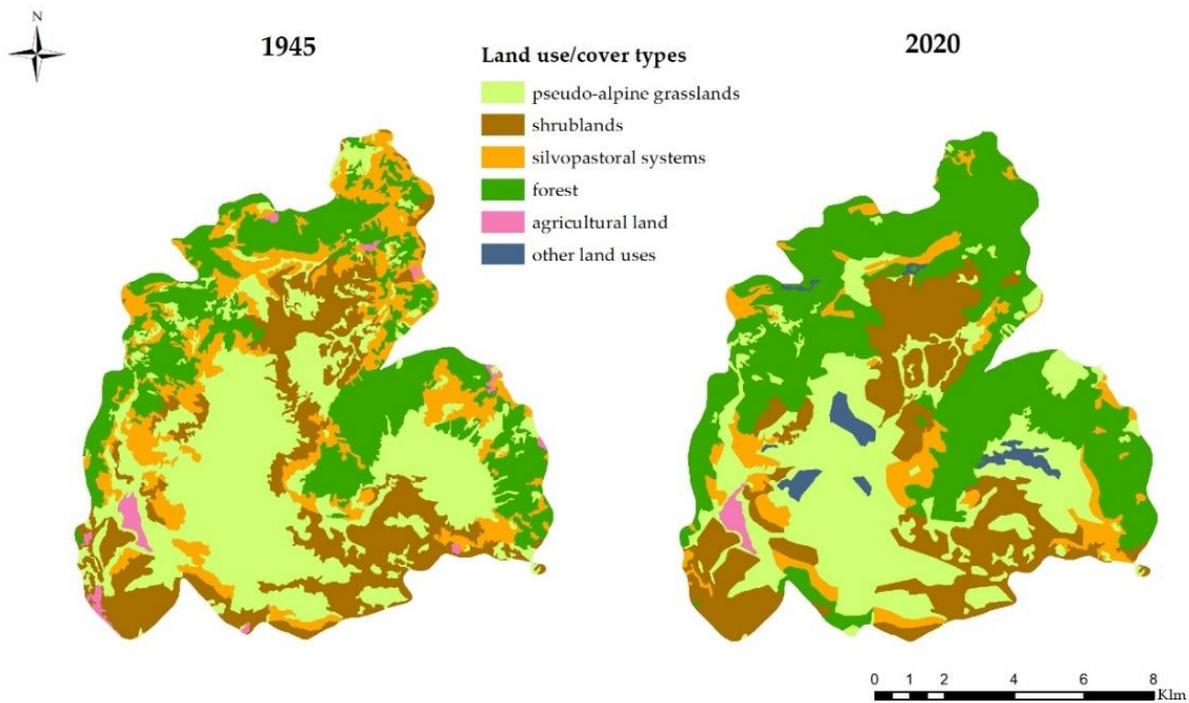


Figure 5. Spatial distribution of Land Use/Land Cover (LULC) types of Mt Zireia for 1945 and 2020.

Table 6. Temporal evolution of Land Use/Land Cover (LULC) types of Mt Zireia for 1945 and 2020.

LULC	1945 (ha)	2020 (ha)	2020–1945 (%)
Silvopastoral systems	2300.2	1111.6	−51.7
Agricultural land	156.4	75.5	−51.7
Forests	3130.5	4833.8	54.4
Shrublands	2504.3	2721.3	8.7
Pseudo-alpine grasslands	4712.3	3778.5	−19.8
Other land uses	0.0	283.1	
Total	12,803.8	12,803.8	

Table 7. Transition matrix for Land Use/Land Cover (LULC) types on Mt Vermio between 1945 and 2020 (% from total area).

		LULC 2020						Total 1945	Loss
		For	Sil	Shr	Psa	Agr	Oth		
LULC 1945	For *	12.27	0.06	0.00	0.12	0.01	0.00	12.46	0.19
	Sil	12.26	0.95	0.00	0.85	0.04	0.01	14.11	13.16
	Shr	6.10	0.31	0.37	1.33	0.01	0.00	8.12	7.75
	Psa	12.26	1.79	0.21	48.67	0.66	0.36	63.95	15.28
	Agr	0.19	0.01	0.00	0.32	0.76	0.03	1.31	0.55
	Oth	0.00	0.00	0.00	0.00	0.00	0.05	0.05	0.00
Total 2020		43.08	3.12	0.58	51.29	1.48	0.45	100	0
Gain		30.81	2.17	0.21	2.62	0.72	0.40	0	36.93

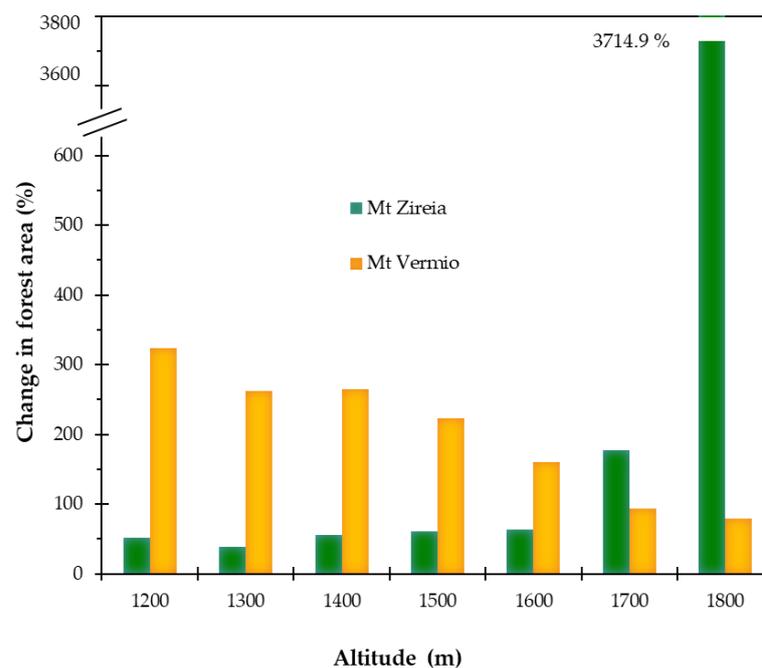
* For: Forest; Sil: Silvopastoral systems; Shr: Shrublands; Psa: Pseudo-alpine grasslands; Agr: Agricultural land; Oth: Other land uses. Cells filled with a gray background display the percentage of each land use that remained unchanged.

Table 8. Transition matrix for Land Use/Land Cover (LULC) types on Mt Zireia between 1945 and 2020 (% from total area).

		LULC 2020					Total 1945	Loss
		For	Sil	Shr	Psa	Agr		
LULC 1945	For *	23.31	0.79	0.02	0.90	0.00	25.02	1.71
	Sil	10.75	5.49	1.07	1.06	0.00	18.37	12.88
	Shr	1.72	0.38	16.34	1.56	0.00	20.00	3.66
	Psa	2.66	2.22	4.07	26.33	0.10	35.38	9.05
	Agr	0.17	0.00	0.23	0.33	0.50	1.23	0.73
	Total 2020	38.61	8.88	21.73	30.18	0.60	100	0
Gain		15.30	3.39	5.39	3.85	0.10	0	28.03

* For: Forest; Sil: Silvopastoral systems; Shr: Shrublands; Psa: Pseudo-alpine grasslands; Agr: Agricultural land. Cells filled with a gray background display the percentage of each land use that remained unchanged.

According to the analysis of the Digital Elevation Model, Mt Vermio had primarily moderate slopes (16–30%), whereas Mt Zireia had primarily very steep slopes (>46%). As per the analysis of changes in forest cover (%) per altitudinal zone between 2020 and 1945 for the two mountains, Mt Zireia had an increase in forest cover in higher altitudes, indicating an upward shift in treeline, whereas Mt Vermio showed the opposite trend (Figure 6). On Mt Vermio, forest expansion was higher at 1200 m while in Mt Zireia it was at 1700 m.

**Figure 6.** Change (%) in forest area per altitudinal zone between 1945 and 2020 for Mt Zireia and Mt Vermio.

On Mt Vermio, although the spread of the forest was intense and dynamic, it happened horizontally rather than vertically, as the treeline did not shift upwards (Figure 7).

Between 1945 and 2020, the forest area on Mt. Zireia had expanded upward, primarily on the mountain's northeast side where the slopes were gentle (Figure 8).

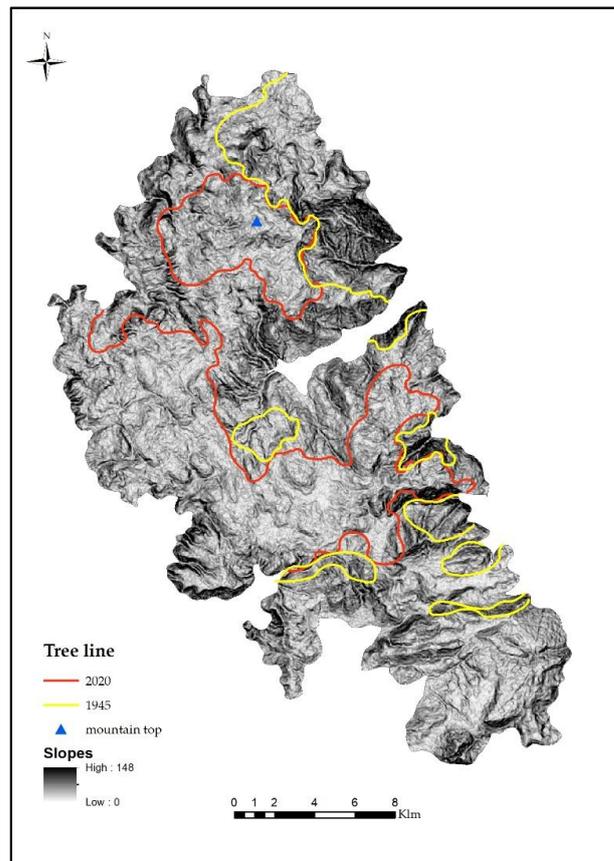


Figure 7. Treeline shifts between 1945 and 2020 in relation to the slopes on Mt Vermio.

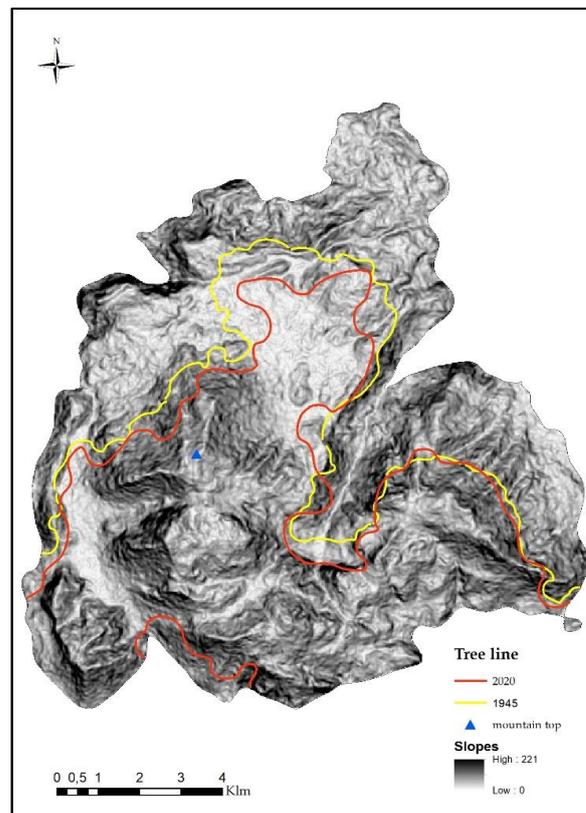


Figure 8. Treeline shifts between 1945 and 2020 in relation to the slopes on Mt Zireia.

The values of the landscape metrics, which constitute the most effective technique to measure and analyze changes in land uses, for Mt Vermio and Mt Zireia from 1945 to 2020, are presented in Table 9.

Table 9. The landscape level metric values for Mt Vermio and Mt Zireia for 1945 and 2020.

	Mt Vermio			Mt Zireia		
	1945	2020	2020–1945%	1945	2020	2020–1945%
NumP *	363.0	480.0	32.2	196.0	115.0	−41.3
MPS (ha)	123.1	93.1	−24.4	65.3	111.3	70.4
ED (m/ha)	40.0	44.5	11.1	90.1	56.9	−36.8
IJI (%)	69.1	44.9	−35.0	75.4	70.5	−6.5

* NumP: Number of Patches, MPS: Mean Patch Size, ED: Edge Density, IJI: Interspersion Juxtaposition Index.

The NumP increased (32.2%) over the study period on Mt Vermio suggesting that larger vegetation areas had been divided up into smaller pieces. The MPS, which has reduced from 123.1 hectares in 1945 to 93.1 ha in 2020, also serves as a proxy for the degree of vegetation fragmentation. The decrease in IJI by 35% suggests that landscape patches have clumped, and they are interspersed disproportionately.

On Mt Zireia on the contrary, the NumP has substantially decreased (41.3%), while MPS dramatically increased from 65.3 ha in 1945 to 111.3 ha in 2020. This indicates that the landscape is less subdivided and fragmented.

For 1945 and 2020, a class level analysis focused on the grasslands of Mt Vermio and Mt Zireia revealed similar tendencies (Table 10).

Table 10. Class level metric values for the pseudo-alpine grasslands of Mt Vermio and Mt Zireia for 1945 and 2020.

	Mt Vermio			Mt Zireia		
	1945	2020	2020–1945%	1945	2020	2020–1945%
NumP *	90.0	136.0	51.1	84.0	49.0	−41.7
MPS (ha)	317.6	168.6	−46.9	56.1	77.1	37.4
ED (m/ha)	15.0	17.2	14.7	26.7	18.3	−31.5
CA	28581.2	22926.3	−19.8	4712.3	3778.5	−19.8
IJI (%)	81.4	44.3	−45.6	81.8	82.2	0.5

* NumP: Number of Patches, MPS: Mean Patch Size, ED: Edge Density, IJI: Interspersion Juxtaposition Index.

On Mt Vermio, during the period 1945–2020, NumP increased significantly (51.1%) while MPS decreased from 317.6 ha in 1945 to 168.6 ha in 2020. The 45.6% decline in IJI values suggests that grasslands are less equally adjacent to each other.

On Mt Zireia, during the period from 1945 to 2020, NumP decreased by 41.7% while MPS increased from 56.1 ha in 1945 to 77.1 ha in 2020. Grasslands appear less fragmented and more united. In addition, grassland edges (ED) showed a reduction (−31.5%), indicating a negative impact of the changes to landscape patches to the ecotones and therefore in biodiversity.

4. Discussion

Our findings suggest that the climate and the abandonment of transhumance may have had a substantial impact on land use changes in the pseudo-alpine zone of the two mountains in the current study. Forests expanded at the expense of other land uses, mainly pseudo-alpine grasslands, shrublands, and silvopastoral systems. In the meantime, higher mean annual air temperature led to an upward shift in treeline and a subsequent retreat of pseudo-alpine grasslands.

In the past, grazing pressure of transhumant animals and the harvest of timber and firewood, maintained an open, mosaic-like landscape, and created openings and corridors

in forests [25]. This way, not only the expansion of invasive or colonizing grass species [50], but also of trees, was prevented. Today, transhumance has declined in Greece, following a pattern that has been observed across Europe [83]. The reasons are agricultural reform, World War II, rural depopulation, and the restriction on grazing in mountainous areas [25,61,84]. On Mt Vermio and Mt Zireia, this trend led to the abandonment or under-utilization of pseudo-alpine grasslands [85]. On Mt Vermio the number of transhumant animals decreased dramatically (Table 3), and the entire mountain was abandoned. The changes in landscape structure are depicted in the values of landscape metrics. Trees started to penetrate former unified, large grassland patches, creating a more fragmented landscape (NumP, MPS, IJI) (Table 9). This fragmentation reduced the habitat area and increased the spatial discontinuity [51] leading to a reduction in species richness and biodiversity, impeding the possibilities of dispersion and an increase of vulnerability that is associated with risk of extinction [11].

On Mt Zireia, grazing pressure was higher (0.94 animals/ha) than Mt Vermio (0.69 animals/ha) and it was constant in lower altitudes, thus preventing the expansion of forest over 1700 m. The abandonment of transhumance on higher altitudes seems to have affected mainly the small grassland patches inside the forest that began to disappear. This phenomenon led to a more cohesive and homogenized landscape (NumP, MPS, ED).

Overall, Mt. Vermio appears to be at an advanced stage of abandonment, where the trees have invaded the grasslands and broken their coherence, whereas Mt. Zireia is in an earlier stage of abandonment where the grassland gaps in the forest started to close. This result is consistent with the claims of many researchers [86–89] who suggest that variation in grazing pressure could be the driver of land use changes in the pseudo-alpine zone.

Similar to the rest of Europe, Mt. Vermio and Mt. Zireia's temperature and precipitation have risen during the past 30 years [71,90]. However, Mt Zireia had higher mean annual air temperature and annual precipitation (Table 2) and therefore different water balance [91], plant growth period [92], and annual above-ground productivity [93]. The differences in climatic conditions were expected due to the influence of orography and spatial climate variability [94], but mainly due to the geographical location of the two mountains.

The higher mean annual air temperature in Mt Zireia could have led to the upward shift in treeline (Figure 7) since most researchers agree that it is the main driver of upward expansion of the treeline [8,95–101]. Particularly young trees respond to environmental change by closing the forest gaps [100,102]. Furthermore, the increase in annual precipitation over the past 30 years in Mt. Zireia (Figure 3) facilitated treeline upward elevation.

On the island of Crete's Samaria National Park, Beloiu and colleagues [103] noted that despite a drop in precipitation over the previous 70 years, there had been no treeline change. A combination of meteorological and topographic conditions, such as decreased precipitation with rising warmth and the absence of a sheltering effect because of high topographic wind exposure, are the main causes of the absence of treeline shift in Crete. Even though changes in temperature and precipitation may intensify shifts in treeline, temperature increases and precipitation drop may interact unpredictable as far as an effect on the treeline is regarded. Precipitation restricts the growth of trees, especially in semi-arid regions with little water storage, where it raises evapotranspiration and aggravates moisture stress [104]. On the other hand, topographic factors, such as the lack of shelter due to high topographic wind exposure may interact with temperature and precipitation and regulate the trends in treeline shifts in Crete [105]. However, Zindros and coauthors [101] concluded that treeline shift results from the significant temperature increase during the growing season in National Park of Mt Olympus, Greece.

Today, on Mt Zireia, forests have replaced pseudo-alpine grasslands primarily in the northeast region, where the conditions were more favorable for forests to intrude (lower inclination) (Figure 7). Lundbäck and coauthors [105] estimate that 82% of the world's forests grow on slopes $<15^\circ$. The amount of solar radiation in mountainous or hilly environments is impacted by the slope aspect, which has an immediate impact on species distribution and tree growth [106]. At mid-latitudes in the Northern Hemisphere, south-

facing slopes receive significantly more direct solar radiation than comparable northern slopes [107]. Thus, it is anticipated that treeline elevation will be higher on south-facing, warmer slopes than on their north-facing, cooler equivalents. However, in the Mediterranean region, south-facing slopes can be more vulnerable to dryness than north-facing slopes [107,108]. As a result, the elevation of the treeline can be significantly lowered. With a few exceptions, seasonal root temperatures globally coincide with treeline height [109]. Given that they are found in regions with warmer temperatures than indicated by the global distribution pattern, Mediterranean treelines serve as an example of one of these outliers. This has been explained by the absence of cold-resistant treeline taxa or by the prevalence of treelines that have been affected by anthropogenic use in the past [110]. Most mountainous regions of the world anticipate considerable increases in air temperatures in the future decades, but it is unclear how local characteristics (such as elevation, aspect, and soil) will affect how trees near treelines react to the warming. Because different bio-geographical patterns of tree development respond to temperature differently, a warmer climate may have distinct effects on treeline dynamics [111].

In our case study, we found the following trends considering forest expansion. Trees either moved up the mountain to a higher elevation (upward/vertical shift = elevational expansion) or expanded horizontally (latitudinal expansion). On Mt Vermio, the spread of the forest was intense and dynamic (245% increase) but happened horizontally rather than vertically (Figure 8). This is in accordance with a review study related to treelines in the world [112], where the majority of treeline sites (92%) addressed elevational treeline advances while 8% addressed the latitudinal advances. Hansson and coauthors [112], suggest that this is likely due to easier horizontal dispersal of trees across landscapes, because the elevational gradient acts as a barrier for seedling dispersal and the temperature remains consistent within the same altitudinal zone.

According to the values of gains and losses of forests and pseudo-alpine grasslands for the two mountains (Table 7), the “forest increase vs. pseudo-alpine grasslands reduction” trend was less extensive on Mt Zireia. The expansion of forests over grasslands was less than 3% of the total landscape and was limited on the northeast side. This may be explained by the “mountain effect”, which states that higher mountains face less abandonment than medium ones [113]. Simultaneously on Mt Zireia, there was an upward shift of treeline. As mentioned earlier, most researchers agree that treeline position is limited by the average temperatures, however, according to Piper and coauthors [108], in the Mediterranean region, the absence of an elevational trend in tree growth shows the presence of other abiotic factors than temperature, including drought, which towards the end of the growing season may overwhelm the temperature-driven elevational increase. Increased temperatures may have an impact on tree development, although Hansson and colleagues [112] report that it also depends on the topography and water availability of the area.

5. Conclusions

Pseudo-alpine grasslands on both mountains have reduced. The abandonment of the transhumant livestock grazing system on Mt Vermio has resulted in the horizontal expansion of the forest. However, this is not enough to cause a corresponding upward increase in treeline. The main driver for the latter seems to be climate change, specifically a rise in temperature, as in the case of Mt Zireia.

Pseudo-alpine grasslands have been significantly impacted by both climate change and transhumance abandonment. Given the importance of these areas, more field-based research is required. Long-term monitoring of landscape spatial patterns and climatic conditions could help prevent drastic changes in high-mountain ecosystems such as Mt Vermio and Mt Zireia.

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