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Abandonment of Silvopastoral Practices Affects the Use of Habitats by the European Hare (*Lepus europaeus*)

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Abstract: Silvopasture, a traditional agroforestry practice, combines the presence of trees, shrubs, herbage, and livestock in time and space to provide multiple ecosystem services that contribute to human well-being. However, the abandonment of traditional agroforestry practices across Europe has led to substantial changes in vegetation characteristics, mainly due to woody plant expansion and, as a consequence, changes in wildlife that rely on open habitats. This study examines the effects of a 20-year abandonment of silvopastoral practices (i.e., livestock grazing and fuelwood harvesting) in a typical agroforestry Mediterranean landscape (kermes oak shrubland, natural grassland, and olive groves) on European hare (*Lepus europaeus*) habitat use. We estimated tree, shrub, and herb cover using a densitometer and hare habitat use using pellet counts within 2004-m^2 rectangular plots in 2002, 2011, and 2021. Hare pellet density in olive groves was significantly lower in 2021 compared to 2002, while the opposite trend was found in grassland for the same period. Woody plant cover expanded from 2002 to 2021. We suggest that the woody plant encroachment that followed the abandonment of traditional silvopastoral practices in the area is the main driver behind the reported decline in hare use of the habitat, as it became less open and therefore less favorable for the species. Maintaining a mosaic of open and closed habitats at the landscape level, which was once provided by silvopastures, is vital for the conservation of this species.

Keywords: livestock–wildlife interactions; herbivory; animal behavior; rangeland management; wildlife management

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1. Introduction

Silvopasture is among the oldest traditional agroforestry practices; it combines the presence of trees, shrubs, herbage and livestock in the same time and space [1,2]. It has been practiced since the Neolithic times [3], creating landscapes with high habitat heterogeneity including wooded, open, partially open, and shrubland areas [2,4]. These silvopastoral systems, under appropriate management, can lead to more effective and sustainable land use in relation to other single land use systems [5], providing multiple ecosystem services, such as erosion control, fire prevention, biodiversity enhancement, and carbon storage, that contribute to human well-being [6,7]. As a result, appropriate design and implementation of silvopastoral systems can maximize both environmental benefits and livestock productivity, and silvopasture should therefore be recognized as an efficient use of agricultural land.

Despite their recognized value in terms of environmental and human well-being, silvopasture and other agroforestry systems have been gradually abandoned across Europe over the last decades due to a series of environmental and socio-economic factors [4,8]. Although the reasons behind these landscape level changes are complex, agricultural land abandonment in some areas and agricultural intensification in others have been identified as the major drivers [9–12]. Agroforestry abandonment has been recorded during the last decades throughout Europe [4,11], resulting in more homogenized landscapes and changes in their floral and faunal communities [12]. One species that has been negatively affected by

the observed landscape homogenization in once agroforestry landscapes is the European hare (*Lepus europaeus* Pallas—hereafter hare), the populations of which typically thrive in habitats with high heterogeneity [13,14].

The European hare has a wide range across Eurasia and has been successfully introduced into other countries around the globe [15,16]. However, declines in its population size have been reported in many areas since the 1960s [16,17]. These have been associated mainly with the intensification of agricultural practices, land cover changes, diseases, and pollutants [16,18,19]. The hare prefers grazed and partially disturbed habitats, such as grasslands, scrublands, clearings in scrub and forest stands, and farmland [20,21], and this is why habitat heterogeneity plays a key role in its population dynamics [13,14,16,17,22]. Although its diet consists of a wide range of herb species, grasses and graminoids usually constitute the bulk of its diet composition [23,24].

Livestock grazing, as well as other anthropogenic activities such as tree and shrub growing for fruits, firewood, fodder for animals, etc., affect the composition, structure and the secondary succession of vegetation, which is often beneficial for wild herbivores predominating in areas at early vegetation succession stages [18,19]. Grazing regimes in silvopastoral areas, along with the other human activities associated with tree and shrub exploitation, can influence plant communities in ways that usually promote habitat heterogeneity [25,26]. For example, hares use moderately grazed pastures (about 40% of the annual production grazed) with a sparse herb layer more intensively than lightly grazed pastures (about 20%), and avoid ungrazed patches [27]. Furthermore, grazing reduces vegetation height, which is thought to be advantageous for small- and medium-sized herbivores such as the hare, as they can visually better detect predators [27–29]. Similar effects of livestock grazing on vegetation and wildlife by retarding vegetation succession and maintaining a low vegetation height have also been reported on the northwestern European coast [30,31]. Therefore, silvopastoral practices can be a valuable 'tool' for managers aiming to improve small- and medium-sized herbivore habitats [27,32]. Despite its importance, little is known about the long-term impact on wildlife's use of abandoned silvopastures.

The aim of this study was to investigate the effects of silvopastoralism abandonment in a typical Mediterranean system on habitat use by the hare. Although agroforestry systems (including silvopastoral ones) have been reported as rich in biodiversity, the majority of relevant studies focus on birds, plants, fungi, and insect assemblages [33]. To our knowledge, this is the first study reporting on hare habitat use changes over a 20-year period since silvopastoralism abandonment. Our null hypothesis was that there would be no significant difference in the use of olive farms, kermes oak shrubland, and permanent grassland by the European hare after silvopastoral abandonment in a typical Mediterranean landscape. Given that the hare is known to avoid ungrazed sites [27] and uses microhabitats covered by short and sparse herb layer [34], we predicted that the null hypothesis would be rejected by our results.

2. Material and Methods

2.1. Study Area Description

The study was conducted in a 190 ha area (38°43′27.9″–38°42′31.2″ N, 22°33′22.2″–22°34′23.7″ E, elevation 520–900 m) located in central Greece (Figure 1). This area consists of a mosaic of kermes oak (*Quercus coccifera* L.) shrubland (approximately 55%), permanent grassland (about 35%), and olive groves (about 10%). We considered these three habitat categories (i.e., kermes oak shrubland, grassland, olive groves) as treatments. The soil is shallow, of low productivity, and partially degraded. The climate is semiarid with cold winters and hot dry summers. Mean annual temperature was 15.7 ± 0.43 °C and mean annual precipitation 966.3 ± 240.75 mm during the period 2006–2021. Meteorological data were derived from the nearest meteorological station (7.5 km south of the study area, elevation 440 m).

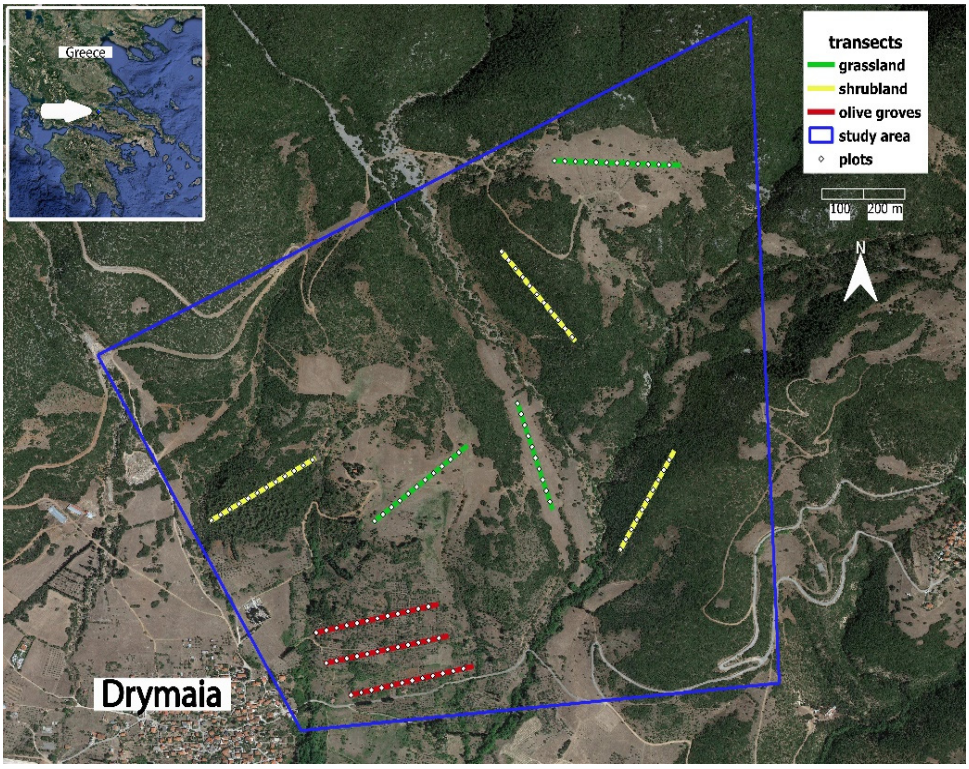

Figure 1. Study area (blue line). Available from Google earth (14 August 2019).

Kermes oak shrubland occupies the largest part of the study area. Livestock grazing was the primary land use in the area and the shrubland has also been exploited for firewood for many years. The shrub layer, in addition to the dominant kermes oak, also includes prickly juniper (*Juniperus oxycedrus* L.), Jerusalem thorn (*Paliurus spina-cristi* Mill.), hawthorn (*Crataegus monogyna* Jacq.), mastic tree (*Pistacia lentiscus* L.), *Rosa* spp., Mediterranean buckthorn (*Rhamnus alaternus* L.), and almond-leaved pear (*Pyrus spinosa* Forssk.). Phryganic plants also occur in this shrubland, with the main species being *Thymus* spp., thorny burnet (*Sarcopoterium spinosum* Spach.), asparagus (*Asparagus acutifolius* L.), and *Cistus* spp., whereas the most important herb species are goatgrass (*Aegilops triuncialis* L.), cocksfoot (*Dactylis glomerata* L.), and squarrose brome (*Bromus squarosus* L.).

Grasslands are dominated by goatgrass, cocksfoot, squarrose brome, drooping brome (*Bromus tectorum* L.), mosquito grass (*Dasypyrum vilosum* L.), cocksfoot, *Lathyrus* spp., *Vicia* spp., *Trifolium* spp., and *Ranunculus* spp. Sparse trees, shrubs, and phryganic plants also occur such as almond-leaved pear, kermes oak, Jerusalem thorn, and asparagus.

Olive groves are cultivated in the study area primarily for olive oil production and secondarily for table olives. The layer of trees (overstory) is dominated by olive trees and the layer of herbs (understory) by goatgrass, cocksfoot, squarrose brome, drooping brome, species of the Asteraceae family, etc. The shrub layer is practically absent, with only few individuals of kermes oak, Jerusalem thorn, and *Rubus* spp. usually growing solitarily near the trunks of the olive trees.

The entire study area was grazed by mixed sheep and goat herds (approximate ratio 4:1) for several decades, following a traditional continuous grazing system. However, the number of livestock grazing in the study area gradually reduced from 350 to 100 animals from 1985 to 2000, and since 2002, no livestock grazing has occurred, as people moved to urban centers and pastoral life was abandoned. At that time (2002), about 80–90 residents were living in the nearest village (Drymaia) with about 90% of them aged over 65. The same trend of pastoralism has been observed for the other silvopastoral practices in the area, such as olive cultivation and firewood collection.

2.2. Plant Cover

In each treatment (kermes oak shrubland, grassland, olive groves), three transects (200 m each) were established at the end of spring 2002 (Figure 1), ensuring that transects did not cross vegetation (treatment) boundaries and that they were spaced at least 80 m apart. We took note of both starting coordinates and directions for all transects. Relative cover of the tree, shrub, and herb layers in each treatment was estimated using a densitometer (GRS™) and the line-point transect method. Measurements were taken every 2 m (100 points per transect) and the measurements were repeated in 2011 and 2020 at the end of spring. The starting point of each transect was located using a handheld global positioning system. Overstory and understory vegetation coverage was recorded by turning the densitometer's front towards the canopy or to the ground, respectively, while always keeping the densitometer's body parallel to the ground.

2.3. Pellet Counts

The use of the study area by hares was based on pellet counts, which is to considered to be an appropriate method for estimating the abundance and feeding intensity of hare in an area [35]. We counted hare pellets within ten circular plots with 0.5 m radius per transect (spaced 20 m apart) at the same time and during the same years as the plant cover measurements. The first plot was established at the start of each transect. In total, 30 plots were counted per habitat each year. Special attention was given during plot establishment so as to avoid edge effects. During the experiment, we excluded plots covered with fallen branches, rolling rocks, and other objects to avoid distorting our data. Only fresh pellets (moist, not crumbly, and brown to dark colored) were counted.

2.4. Statistical Analysis

Pellet-count data were subjected to a two-way factorial ANOVA using the SPSS statistical software (version 20.0 Inc., Chicago, IL, USA). Treatments and years were considered as fixed factors. Levene's test was performed prior to the analysis in order to check the homogeneity of variances. Mean differences were evaluated with Tukey's honestly significant difference (HSD) test. In order to identify treatments used more often by hares each year, we used a main-effects analysis using SPSS Syntax. Differences were considered significant at $p < 0.05$.

3. Results

3.1. Plant Cover per Treatment

Tree and shrub coverage increased in all treatments during the 20-year study period. Specifically, tree coverage increased by approximately 6%, 2%, and 10% in shrubland, grassland, and olive groves, respectively, from 2002 to 2021 (Figure 2). A similar increasing trend was observed for shrub coverage, with an 8%, 9%, and 9% increment in shrubland, grassland, and olive groves, respectively. On the contrary, herb coverage was reduced by about 9%, 6%, and 11% in shrubland, grassland, and olive groves, respectively (Figure 2).

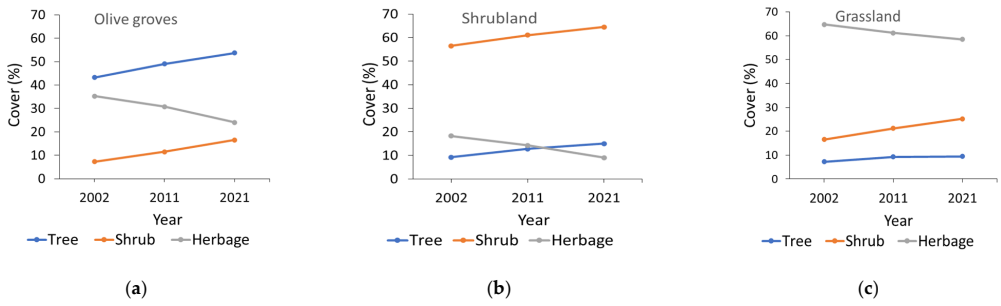

Figure 2. Mean change in tree (**a**), shrub (**b**), and herbage (**c**) coverage in olive groves, shrubland, and grassland transects from 2002 to 2021.

3.2. Habitat Use by Hare

Two-way factorial analysis revealed a significant effect of habitat type on the mean number of hare pellets (Table 1), whereas year did not have a significant effect. However, there was a statistically significant interaction (F = 2.683, df = 4, $p = 0.032$) between habitat and year on the mean number of hare pellets. Simple main effects analysis (pairwise comparisons) showed that the mean number of hare pellets in olive groves was significantly higher ($p = 0.031$) in 2002 compared to 2021 (Figure 3). In contrast, the mean number of hare pellets in grassland was significantly higher ($p = 0.024$) in 2021 compared to 2002. No significant differences were found in the mean number of hare pellets in shrubland across years, with it remaining the lowest (ranging from 1.07 pellets/m^2 in 2002 to 0.60 pellets/m^2 in 2021) throughout the study period. The mean number of hare pellets in the entire study area remained more or less stable ($p = 0.915$) during the 20-year study period, i.e., 1.99, 2.01 and 2.12 pellets/m^2 in 2002, 2011, and 2021, respectively.

Table 1. Two-way factorial analysis output with year (three levels: 2002, 2011, 2021) and habitats (three levels: olive groves, shrubland, grassland) as fixed factors and number of hare pellets as the dependent variable.

Source	Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	360.92	8	45.12	8.777	<0.001
Intercept	1124.45	1	1124.45	218.749	<0.001
Year	0.92	2	0.46	0.089	0.915
Habitats	304.83	2	152.42	29.651	<0.001
Year * Habitats	55.17	4	13.79	2.683	0.032
Error	1341.63	261	5.14		

*: interaction between year and habitats, df: degrees of freedom, F: Fisher statistic, Sig.: significance.

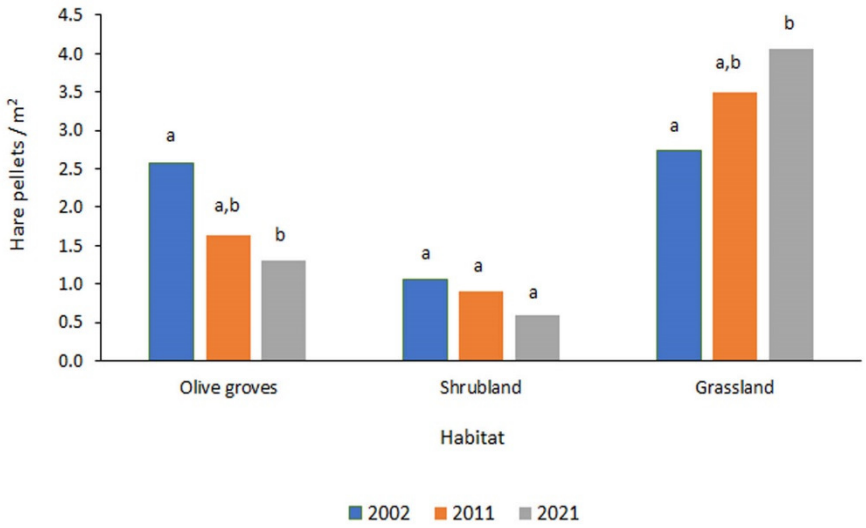

Figure 3. Mean number of hare pellets deposited in olive groves, shrubland and grassland in 2002, 2011, and 2021. Different letters between columns within the same habitat indicate significant differences ($p < 0.05$).

4. Discussion

The silvopastoral abandonment in our study area, which commenced in 2002, has initiated secondary succession processes with the encroachment of woody species (trees and shrubs) at the expense of herbs. This can be attributed to the cessation of both livestock grazing and practices associated with silvopastoralism, such as pruning of olive trees and collection of kermes oak for firewood that took place historically in the area. The observed vegetation changes were anticipated and have been documented in abandoned

agroforestry systems throughout Europe, especially in the Mediterranean zone [36,37]. The depopulation of rural areas and agricultural intensification during the second half of the 20th century, along with the associated vegetation changes, are expected to negatively affect wildlife species that prefer habitats in earlier stages of succession, such as the hare [16,27].

This was corroborated by the observed higher pellet counts in olive groves in 2002 compared to 2021, whereas grassland use by the hare went in the opposite direction; i.e., grassland use was significantly higher in 2021 than in 2002. It is well known that herbivory and other silvopastoral practices have a prominent role in determining the structure of plant communities [38–42]. It seems that the hare more often uses areas covered by short and sparse vegetation [34]; a behavior thought to be linked to increased hare ability to visually detect approaching predators in such habitats [27–29]. However, this behavior may change, at least temporarily, in the case of elevated predation risk [43]. Of course, changes in habitat use could reflect changes in the overall population size of a species [44]. However, in this study, the non-significant differences in the mean number of hare pellets in the entire study area indicates a stability of hare population size during the study period; i.e., the 20-year abandonment of silvopastoral practices seemingly did not negatively affect the hare's population dynamics. We can therefore reasonably assume that the observed shift in habitat use by hares is probably due to the vegetation changes caused by the abandonment of traditional silvopastoral practices and not by marked changes of its population size. Theoretically, if the observed encroachment of woody species continues during the next decades, then a reduction of the total grassland area is expected to take place and hares may be forced to move out of the study area to look for more preferred feeding areas.

The observed higher use of grasslands by hares in relation to shrublands have been reported in other studies as well [27,28]. However, the low use of kermes oak stands does not mean that this kind of habitat is invalid for hares. It is well documented that such stands, as well as forested areas, provide shelter for adult hares and their offspring against predators [28,45]. In essence, kermes oak stands may be of trivial importance as feeding places for hares, but they may be of prime importance for their survival ability and reproduction success.

Our findings show the hare's ability to adapt to vegetation cover changes in an area by shifting habitat use. Such behavioral plasticity in the face of environmental changes has been previously reported for the species [45,46]. Although the study design (monitoring of three years spaced along a 20-year interval) was not able to capture nuanced changes and interannual variation in habitat structure, we believe that it is adequate for the aim of this study, i.e., to investigate the long-term effects of silvopastoralism abandonment on the use of olive farms, kermes oak shrubland, and permanent grassland by the hare in a typical Mediterranean system. However, along with the changes of coverage of main plant forms (tree, shrub, herbage) investigated in this study, other vegetation characteristics have also been reported to influence the use of space by hares. For example, sparse and low-height vegetation communities in grasslands are used more intensively by hares in relation to dense and tall herbage communities [27]. In addition, the movement behavior of hares can be influenced by the presence of specific plant species [46,47]. For vulnerable species such as the hare, the availabilities of both forage and cover (shelter against predators) have been reported as critical factors affecting the use of space [28,48]. From this perspective, the presence of the specific plant species that constitute the bulk of the diet of the hare and/or provide shelter against predators could influence the spatial distribution of the hare in this study. Future research should focus on further understanding the effect of traditional silvopastoral practices on modifying vegetation structure and composition in relation to hare population dynamics and behavior.

5. Conclusions

In our study area, Silvopastoral abandonment since 2002 (cessation of livestock grazing, olive cultivation, firewood collection) initiated secondary succession processes that provided the opportunity for the encroachment of woody species (trees and shrubs) at

the expense of herbs. These vegetative changes had cascading effects on hare habitat use patterns, as this species prefers habitats in earlier stages of vegetation succession. The lower use of olive groves by the hare, which was accompanied by increased use of grasslands, shows the species' aversion to the vegetation structure changes that occurred following silvopasture abandonment. The habitat use plasticity of the hare to landscape level vegetation changes suggests that silvopastoralism, under appropriate management, can be used as a "tool" for the conservation of hare populations.

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