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Review

Is the Impact of the European Mouflon on Vegetation Influenced by the Allochthonous Nature of the Species?

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Abstract: The mouflon (*Ovis gmelini musimon*) is an introduced ungulate in continental Europe. It has adapted well to its occupied habitats over the last 150 years. Its growing population has drawn increasing attention to its impact on autochthonous species, especially in endangered ecosystems. Its allochthonous character, habitat selection, and feeding led scientists to question the raison d'etre of mouflons. The mouflon's space use and foraging strategies highlighted some pressure elements it exerts on those habitats. Mouflon trampling damage may be behind the degradation of rare, endangered grasslands. We review studies to discuss the results and the limitations of exclusion experiments to evaluate the extent of mouflon-caused damage in the context of population density. We review the forest damage attributed to mouflons considering interspecies competition with other large herbivores such as red deer (*Cervus elaphus*) and chamois (*Rupicapra rupicapra*). Climate change makes the mouflon use its space differently when seeking shelter in southern habitats; consequently, the increased trampling and foraging pressures suggest new challenges in managing its impact. We review research results on these direct impacts of the species; however, the long-term effects on herbaceous plant communities, such as rock grasslands, are still unclear. This is true for the mouflon's influence under changing population dynamics. Our results intend to set directions for future research on long-term experiments with density impact, coexistence with red deer or chamois, and warming-climate-driven behavior change.

Keywords: mouflon; invasive species; rock grassland; trampling; grazing damage

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1. Introduction

The taxonomic classification and scientific designation of mouflons have caused much debate among scientists [1]. There is a consensus that the mouflon of the Mediterranean islands of Cyprus, Corsica, and Sardinia descended from the Asian mouflon (*Ovis gmelini*) living from Turkey and Armenia to Iran [2]. They appeared in the Mediterranean basin about 8500 years Before the Common Era (BCE) at the beginning of the first waves of human-mediated animal population dispersal in the Mediterranean [3,4]. Asian mouflons were introduced to the Mediterranean islands by Neolithic humans, probably following a pre-domestication phase between 4500 and 8500 years (BCE), as shown by evidence from Neolithic archaeological sites [3,5–7]. The domestication process is assumed to have been limited, without morphological selection, but with preference for better survival success against predatory pressure [3,8]. Therefore, contrary to previous opinions that have taxonomically described the mouflon introduced to the Mediterranean islands as domestic sheep (*Ovis aries musimon/ophion*) due to pre-domestication [9]—that were later abandoned and became feral—we consider the mouflon present in Corsica and Sardinia and later introduced into continental Europe as a subspecies of the Asian mouflon (*Ovis gmelini musimon*), following the lead of several authors [1,10–15].

The first recorded introduction to continental Europe was by Prince Eugen of Savoy, who introduced mouflons to the Belvedere Game Park near Vienna in Austria in 1729–1731 [16]. To our knowledge, the first successful introduction of mouflon into the wild was in the territory of the Austro-Hungarian Monarchy, in Ghymes, Nyitra County, where 80–100 mouflons, previously introduced into a hunting reserve in 1868–69, were released in 1883 on the estate of Count Károly Forgách to increase the variety of species for hunting purposes [17]. These mouflons came from Corsica and Sardinia via the Frankfurt am Main and Brussels zoos [18].

Although introductions to the European continent began in the 18th century, the population grew rapidly just after World War II. Haltenorth and Trense [19] estimated the European population at 14,000 individuals in 1955; Uloth [20] at 22,000 in 1968; Lochman [21] at 53,000 in 1978; Tomiczek and Türcke [22] at 84,000 in 1992; Weller [23] at 111–117,000 in 2001; and Apollonio et al. [24] at around 140,000 individuals in 2005, of which at least 23,000 are annually harvested. It is now a widespread species on the European continent, present in 24 countries from the Mediterranean to Scandinavia and from Spain to Ukraine [1,23].

There is a debate about whether the mouflon of Mediterranean islands can be called an autochthonous subspecies. In the case of the Cypriot mouflon, it cannot be excluded that wild mouflons arrived in Cyprus on their own during the last ice age when the Mediterranean Sea was 125 m below the current sea level [25], in which case it could be considered an autochthonous subspecies. Considering the presence of the mouflon in the Mediterranean islands for thousands of years, Satta et al. [26] declared the Sardinian population to be autochthonous. However, in our view, following Ferretti and Lovari [27], we consider those species or subspecies as an "alien" (allochthonous, non-native, non-indigenous, exotic) taxon that occurs outside its natural range (past or present) and dispersal potential (i.e., outside the range it occupies naturally), as a result of intentional or accidental introduction by man [28,29]. According to this definition, the Sardinian (and Corsican) mouflons cannot be considered autochthonous, and this is also true for the mouflons introduced from these islands to continental Europe [30–34]. However, as the mouflon population has been expanding and increasing in density over the decades raising conservation concerns due to the damage mouflons cause by trampling and grazing on rocky grasslands, in Hungary, they have been listed as an allochthonous species and an invasive subspecies as well [32].

The EU uses the term invasive alien species (IAS) to classify species whose introduction or spread threatens or negatively impacts biodiversity and ecosystem services [35]. Although only a small percentage of introduced species become invasive, their negative impacts may become substantial over time [36]. The invasive alien character definition has three criteria: the spatial scale, the temporal scale, and the threat to biodiversity [37,38]. By displacing native plants and animals, invasive species change the former ecological conditions and transform the human environment, causing unpredictable harm [39]. Studies [40] and survey results [41] about invasive species identified habitat loss and fragmentation as the top risk in Europe, while invasive species ranked second. Unlike the regulations of some EU member states such as Hungary—e.g., [42,43]—the EU IAS regulations [35,44] or the updated EU list [45] does not list mouflon as a concern of the Union. However, in Hungary, the survey [41] posited a contrary result by placing invasive species at the top of the threat-to-biodiversity list, ranking the mouflon as the fourth most harmful invader of ecosystems.

Scientific studies consider the mouflon invasive and claim a negative impact on ecosystems [46,47] due to its (1) trampling and degradation of grasslands [47,48], (2) invasiveness by displacing native species [40,41,47,49], and (3) foraging strategies. Therefore, our review included the mouflons' morphophysiology, habitat selection, and food preference with their impacts, against the backdrop of the ecological and legislative debate on invasiveness and its European regulation.

At the same time, Ricciardi and Cohen [50] quantified the rate of spread and impact of invaders on native species. Their results showed that the correlation is weak or does not exist between the mechanisms of invasion and its impact. Invasiveness is purely a potential of a species to spread fast on a new territory. In their view "*the term "invasive" should not be used to connote negative environmental impact*" [50] (p. 309). They argue that introduced species reaching high densities can quickly attain higher establishment success levels and dominate native communities. A widely spread introduced species will likely affect multiple native species *"over large fractions of their respective ranges and drive"* [50] (p.310). However, success of invasion and ecological impacts highly depend on dispersal opportunity and anthropogenic factors. Their argumentation emphasizes a link between invasiveness and impact, if exists any, is significantly determined by human activity [50].

To investigate whether this is the case for the mouflon, we review experiments aimed to define the actual trampling in parts of habitats and the foraging damage the mouflon causes within the context of interspecific diet competition and population density. We identify potential positive impacts of the species and propose a balanced evaluation of all its effects. Finally, we also highlight recent findings linked to climate change that are relevant to the impact the mouflon exerts as an invasive species.

2. Habitat Use, Diet, and Feeding Strategy of Mouflons

Rock grasslands and meadows are the preferred habitat types [51] for the mouflon in its home range because they resemble the south-exposed, warm, and dry surfaces found in its original Mediterranean habitats. Cransac and Hewison [52] argue that the mouflon spends 80% of its time in non-forested ranges regardless of the season. Náhlik and Dremmel [53] defined the mouflon's habitat use, with most occurring in range parts covered by oak, beech, broadleaved woods, or meadows and clear-cut fields. The habitat preference analysis found positive responses for younger beech, 50+-year-old oak woods, meadows, and clear-cut areas. The findings suggest that mouflon habitat use may cause browsing damage [53], primarily to forest regeneration seedlings [51,54,55] and in open habitats created by human activity [48].

Large-herbivore-induced ecosystem or economic damage is often associated with large groups [56–58]. Concerning the degradation risk, mouflon herds are a factor because they maintain the large social group form throughout the year. The mouflon group size depends on habitat coverage, population density, disturbance level (including predation and hunting), and forage concentration [59–62].

According to their foraging strategies, ruminants are classified into three categories: grazers, browsers, and intermediate feeders [63–65]. Each type leads to differing resource exploitation and vegetation impact. Gordon [65] argued that the difference between ruminants is behavioral rather than morphological, while the food supply determines the difference between grazers and browsers. Ecological studies on foraging focus on the immediate intake rate and diet selection, while animal scientists evaluate diet selection as per nutritional value. The relationship between morphology and physiology still requires more understanding because browsers and grazers have distinct perspectives on resource distribution. This perception drives their distribution and shifts around the resources [65].

Marchand [66] promoted ruminant classification by considering the digestive system morphology and diet composition. Rumen morphophysiology is very diverse per the ability to graze or browse [66,67]. It constrains the animal's diet selection, thus can influence the species' impact on vegetation. To highlight the morphophysiological differences of the rumen, Clauss et al. [67] proposed the distinction of ruminants as either moose type or cattle type, arguing that Hofmann's [63] triad classification should be used for diet composition only. Clauss et al.'s [67] principle defines ranges of >75% or >90% grass consumption for grazers. Placing species on the scale shows that there are fewer obligate grazers than browsers. Variation analysis of the diet composition is forward-looking when assessing new threats on vegetation and land use arising from climate-warming-led changes that alter large herbivore foraging.

Both diet composition and morphophysiology place the mouflon into the grazer category [54,68–71]. Accordingly, in mountainous habitats and Central European forests, the mouflon's summer diet comprises a high proportion of grass and grass-like species.

In the autumn and winter, the mouflon shifts to seeds, fruits, and woody components (also due to snow cover) [54,72,73]. The seasonal variation was found to be smaller in Mediterranean ranges, i.e., environmental seasonality has a great influence on the mouflon's diet composition [66].

The mouflon's rumen structure is an important morphological element in our review. The mouflon's rumen is less viscous and more stratified [67], ensuring a longer retention time, and it can digest low-quality food well. Marchand's [66] data showed a higher proportion of shrubs and trees in the diet composition; thus, the grazers' grass proportion threshold of 75%–90% was not reached. Therefore, they consider the mouflon as a variable grazer (consuming a low but significant portion of dicots) and not an obligate grazer. Mouflons can occupy habitats where grass is scarce, which draws into question the extent to which cattle-type species can include forage other than grass in their diet [66]. The mouflons' ability to live and still maintain their population where grass is scarce makes specific locations attractive because they limit competition from native herbivores [74]. Marchand's [66] study stated that mouflons can show unusual feeding strategies even with 73% up to 83% forbs and below 20% graminoid intake. Despite Bertolino et al. [74] and Dremmel [72] describing the mouflon's diet variation as the most stable throughout the year compared to red deer and chamois, the mouflon adapts to changing environmental conditions and food availability by changing its diet habits. Seasonal availability of feeding species also causes a shift [54,72–74] in its diet, leading to a plant taxon proportion change. This confirms the mouflon's opportunistic foraging strategy; therefore, analyzing the mouflon's diet composition helps to understand its impact on those ecosystems and its competition with native ungulates [66,72].

Based on different mouflon diet composition analyses, habitat preference is of greater significance than food preference [51]. The species commits to its habitats even if they deteriorate, thereby narrowing its diet or forcing it to intake a higher proportion of fibrous forage. However, as Derioz et al. [75] found in France, significant habitat change can force the mouflon to alter home ranges. The data did not prove severe grazing damage to the ecosystems because the rare or protected plants were in similar abundance to other plant species. Instead, seasonal weather conditions caused high diversity [51]. With the seasonal variety noted above, rumen content examinations in Central European areas showed high levels of graminoid species, forest mushrooms, some dicots or fruits, and nuts. These results support the hypothesis that herbivore foraging is much more diversified than that of domesticated or bred-in-captivity wild species [76].

Baráth et al. [48] referred to earlier micro-histopathological examinations of mouflon feces. Their results determined an 80% proportion of monocotyledons, while woody plants accounted for only up to 7.8%. Rumen content analyses in the Czech Republic also showed the dominance of herbaceous plants over the whole year, with woody species being included during wintertime. Studying an overlap of three ungulate species' (wild goat (*Capra aegagrus*), roe deer (*Capreolus capreolus*), and mouflon) foraging strategies, Heroldová's [73] results stated that the mouflon is a typical grazer, combining its diet composition with shoots and seeds in colder periods. She found a high similarity between goat and mouflon diets and the least overlap between the diets of roe deer and mouflons. In winter months, the three species showed high competition for broadleaved sprouts, which caused high levels of vegetation damage. Within this context, the mouflon should still display an advantage compared to other large herbivores because it is a non-selective, generalist feeder that can consume lower-quality food that other species do not because of its ability to digest fibrous forage. A higher proportion of grass in its diet predicts lower forest damage, but with overlapping diet niches in wintertime, it is comparable to the diet of red deer [73,75]. Slovak and Hungarian studies also confirmed woody plants in the mouflon's winter diets, comprising up to 35% and 32%, respectively [72,77,78].

When studying the crop damage extent of the mouflons, the Czech research compared the proportion and quality of agricultural crops versus natural forest species and showed red deer, roe deer, and mouflons ingesting all agricultural plants grown next to a forest.

However, the proportions of agricultural food consumed varied with the seasons for all these three herbivores. The comparison proved that agricultural plants were of lesser importance despite the lower nutritional value of the natural forage [79].

A diet niche comparison study for red deer, roe deer, chamois, and mouflons conducted in an Alpine environment confirmed similar results. The mouflons demonstrated the lowest diet variability with very high graminoid consumption [74]. The obligate grazer level of over 75% grass-like species' ingestion was not reached in these habitats either [67]. Dicot species consumption reached its highest level in summer, comprising 22% of the annual diet.

Groups of these species were stable in Alpine environments, and the mouflon did not switch to woody species and conifers despite the findings of Heroldová et al. [77] and Homolka [54], who demonstrated that the species did switch in Central European low-, mid-, and highlands. Redjadj et al. [80] also emphasized the diet overlap between chamois and mouflons, classifying chamois' grass ingestion as obligate grazing, while other studies [74] found the grass intake ratio to be in the lower range with seasonal differences. In contrast, mouflons—and sheep [81]—showed a stable grass consumption proportion with no seasonality. Loison et al. [82] discussed interspecific competition among ibex, chamois, and mouflon. Referring to the impact of body size difference between red deer and mouflons [83–85], with red deer displacing mouflons, the same impact is described in relation to mouflons and chamois. Habitat partition occurs as the chamois moves to safer, higher places because of the presence of mouflons [31]. The same displacement behavior was reported in the Pyrenees [74]. Habitat selection and home range use preference are crucial to understanding species interactions and resource sharing. Individuals can exploit abundant resources, but when resources are constrained, the high diet niche overlap leads to competition [74]. Homolka's [54] and Heroldová's [73] high diet overlap analysis result between red deer and mouflons in Central Europe was confirmed by Dremmel [72] in Hungary and by Bertolino et al. [74] in Alpine regions as well. They proved that these two herbivores share similar resources and, at the same time, also confirmed the low diet overlap with roe deer. These results also prove the limitations of exclusion experiments, which underscores the necessity for a complex view of mouflon-caused trampling and browsing damages when it shares ranges with red deer. It also draws the invasive character of the mouflon into question.

The results of the stable diet composition study with fewer species by Bertolino et al. [74] confirm the data collected earlier in French Caroux Massif [71]. Grasses were reported in a relatively constant manner over seasons as primary food, with shrubs and trees being of little significance. The diet composition difference between original habitats in Corsica and the Alpine regions (low variety and less dicot species) and lower lands in Central Europe (high species variety, more shrubs and woody species) proves the mouflon's ability to adapt to different environments via its opportunistic foraging strategy. A study presenting the diet composition change in France also proves this statement: with shrinking meadows and an advanced succession process [75], the mouflon consumed grass and shrubs in equal proportion [52].

Climate warming poses new problems in terms of the effects of habitat selection, use, and consequently feeding. As climate change accelerates, experiment results gained in France's Caroux Massif provide forward-looking insights into mouflon population management and the conservation of temperate, protected areas. Mammal thermoregulation is either behavioral or autonomic (involuntary, e.g., sweating). Behavioral thermoregulation lasts longer at a lower cost versus autonomic reactions [64] and stands as a primary response to thermal conditions crossing the critical threshold. Past this limit, large herbivores adapt by changing their thermogenic foraging strategies and their habitat preference for higher thermal coverage, i.e., moving to the woods from moorland [64]. Marchand et al. [64] measured a sex- and scale-dependent response to hot periods. Females selected better foraging opportunities over thermal cover for lambing and avoided unsafe plateaus. Older males preferred selected forests on the plateau with thermal cover. On the hottest days, both sexes preferred forests, and rams leveraged the moorlands' food and thermal cover until twilight, while females exchanged food and cover for shelter. Within seasonal and diurnal shifts, thermal conditions play an increasingly vital role in habitat use and preference in winter (snow coverage) and summer. Nature conservationists and wildlife managers should consider this.

3. Impact on the Ecosystem and Its Assessment

3.1. Negative Impacts on Vegetation

Some studies in Central Europe highlight the negative impact of mouflons on native ecosystems—mainly rare rock grasslands [30,34,41]. Such papers argue that trampling and grazing change the composition of phytocenosis or endanger the existence of certain plant species: while monocotyledon species and poisonous dicotyledons proliferate, sensitive species, such as holoendemic species, are critically endangered by the treading and grazing [86,87] of overpopulated ungulates [87]. The degradation of southern, rocky hillsides endangers the survival of other rare species too, e.g., the Pannonian copper skink (*Ablepharus kitaibelii fitzingeri*) [88]. Orosz [89] also argues that mouflon forest damage is insignificant compared to that caused by other large herbivores and wild boar (*Sus scrofa*). Instead, the mouflon's foraging habits and trampling specifically endanger protected plants in rock grasslands. Either way, this view posits that the mouflon damages ecosystems by decreasing the rich diversity of herbaceous plants and preventing forest renewal, which red deer also harm with their browsing.

3.2. Positive Impacts on Vegetation

Other scientists are permissive when balancing arguments. In such views, the habitat selection and preference of ungulate species impact the ecosystem by creating a dynamic heathland–scrub web complex on their ranges. Together with climate change influence, these impacts allow the high-value mountain gramineous species to appear and survive in open areas [90]. Mountainous grassland management practices in Hungary rely on scrub clearing, mowing, and pasturage. However, it is unknown to what extent large herbivore grazing, browsing, and trampling slow the succession process contributing to the survival of these areas or to rare rocky land patches [91].

Domestic grazers are limited in their movements, do not migrate, and cannot change their habitat of their own accord. Therefore, such free-ranging herbivore activity can affect the ecosystem positively [92]. Some studies argue that natural grazing declined in Europe with the disappearance of large herbivores, which has contributed significantly to maintaining open fields. For example, before the introduction of mouflons into France, Caroux Massif had already existed as an abandoned agricultural landscape for a long time [75]. The open grasslands represented 61% of the area, which decreased to 31% by 1992, with 55% forest extensions and reforestation. The mouflon reacted to this change with broader distribution in a much larger area. The succession process led to feeding area fragmentation, with the population modifying its social organization into smaller groups. The mouflon was forced to change its habitat use and forage beyond its usual home range, resulting in significant forest damage. An additional phenotype change became evident in decreasing individual weight as the mouflon changed its diet composition. Grass proportion decreases in favor of a woody diet negatively impacted ram horn quality, leading to economic losses in recreational hunting income [75].

High-natural-value mountainous grasslands are critically endangered by transformation via the succession process and reforestation. Shrub clearance and pasturage by long-term, high-density ungulate populations can maintain open grasslands, and the ecological impact naturally delays shrubs and forest succession [92,93]. Studies by Treitler et al. [92], Katona et al. [93], and Pápay [94] have already promoted the positive role of large herbivores in slowing the succession process in grass–shrub webs. Although trampling endangers vital rare species patches, complete game exclusion would accelerate cover growth and shrub succession [93]. Ungulate populations have likely attained their highest abundance in Europe in modern history, and they profoundly affect the ecological dynamics of natural and human-modified ecosystems [95]. The same happened in Central European countries with a high mouflon and red deer abundance [96–98]. Both mouflon and red deer populations increased, not only in Hungary. Burbaité and Csányi [99] analyzed red deer population changes in Europe using game management statistics and found that the population, density, and harvest increased in all of Europe except for the south-eastern part of the continent. Millner et al. [100] arrived at similar results by comparing harvesting data from 12 European countries. Considering the above, the question arises: if natural-like extensive grazing contributes to healthy ecosystem sustainability, why is mouflon grazing not judged more positively?

While intensive browsing and trampling on weak flora will degrade the field irreversibly, limited browsing can contribute to interspecies competition by increasing biodiversity as the arrival of alien species to a new habitat often increases local biodiversity [101]. The irreversibility of the change is one of the arguments against allochthonous and invasive species. Nature conservationists aim to restore the original status of the ecosystem, presumably by selecting a point in time preceding the impact of human activity on natural ecosystems. However, no objective criteria require a species to be resident before being considered native. It is also uncertain how long the timeframe needs to be extended to qualify a species as "formerly native" [102]. The spatial scale of the alienness definition also displays uncertainties when defining the geographical territory in which a species should be considered native. Human activity already harms our ecosystems [103]; therefore, what should be restored is unclear. Furthermore, ecosystems comprise humans primarily, not animals [102,103].

3.3. Limitations of Exclusion Experiments

Game exclusion and phytocenosis experiments have been conducted to understand the mouflon's real trampling impact and to support nature conservation actions. These trials aimed to exclude the mouflon from certain habitat types [51] and observe the natural regeneration of rock grasslands and forests. The concept provides a frame of vegetation and a foundational web formed by dominant gramineous species and sedges [104] to create a matrix that ensures the stability of the plant population. The diversity of species combination is a sensitive indicator of an ecosystem, and exclusion experiments study the changes in these biodiversity indicators [105]. The trials hypothesized that the exclusion of mouflons and other autochthonous large game from meadows and moorlands improves the natural status. It was expected that the data would prove whether the presence of mouflons on grasslands causes degradation. The trial results showed that the plant diversity and composition changed on game-excluded control fields, with a higher diversity index than the starting point. The habitat selection of mouflons [51,52] and Tsaparis et al.'s [105] data—namely that mouflon mainly uses the higher-inclined, steeper hillsides—indicate that southern-exposed rocky dolomite meadows degrade not only because of the mouflon's grazing but also because of its trampling pressure, which also caused advancing soil erosion [48,106]. The asymmetric, sharp trotter adapted to rocky habitats is a key feature of mouflon morphology. The pressure of mouflon hooves per unit area is higher than, e.g., that of fallow deer. Consequently, mouflon trampling exerts a greater impact [107]; however, the opposite is true in comparison with red red deer.

Similar experiments on red deer also showed that the exclusion of large ungulates favors the plant ecosystem [108]. The red deer is an intermediate feeder [63] and primarily consumes concentrated food items, mainly browsing trees and shrubs. In mixed deciduous forests, grasses and sedges comprise a big part of the mouflon's diet [109]. Mouflons are mainly grazers in the same habitat, yet they also consume woody plants, which increase in proportion in winter when snow covers the herbaceous vegetation [72,73]. The second morphological characteristic of the mouflon is the forked upper lip that enables the animal to move each part independently and to graze very close to the ground near plant roots [110].

According to Dremmel [72], the results of exclusion studies can be misleading because they cannot be used to clearly identify the species causing problems or the exact impact of a species. Knowledge of feeding habits cannot be of definitive help here either as supply, and environmental factors significantly affect food intake. In addition, exclusions create conditions without browsing. They merely illustrate the recovery on the control field, but the effects of browsing history are not eliminated in the evaluation. Other factors also influence recovery and change [111], for instance, the seed banks of the soil [112]. Most importantly, browsing should be viewed as a "continuous variable" instead of a binary correlation. Exclusion experiments must, therefore, be combined with the ungulate density's impact on various elements of diversity [113].

In the definition of invasive alien character, the indirect threat to biodiversity refers to the effects of habitat changes caused by the invasive species, such as indirect competition and native food chain modification [37,38]. Menge [113] emphasized the importance of ungulates' indirect effects on ecosystems, which may be of significant magnitude in community structures and compositions. In his study, Menge [113] assumed equal importance between direct and indirect effects. Exclusion research considers the indirect ungulate effects through food web and habitat modifications but overlooks the indirect effects on structural ecological changes [112]. Game exclusion trials' results are doubtful [93] because only smaller control patches from the whole range are examined, and the complete exclusion of large herbivores does not correspond to the natural situation. Under such conditions, the natural development of phytocenosis is not representative; consequently, neither are the conclusions.

3.4. Species Densities and Coexistence

Greater gradient angles increase the presence of mouflons and simultaneously decrease the density of other large ungulates [105]. However, the mouflon is a social species and lives in herds apart from the old rams. The red deer and the mouflon tolerate each other's company and are observed together from time to time [114]. It is unclear whether mouflon introduction is exclusively to blame for the impoverishment of hillside flora or whether other factors also contribute to some extent [72]. It is worth noting that the red deer population density in Hungary has increased in parallel with the mouflon population [96].

Both species occupy the same habitats, including rock grassland and moorlands, but red deer cause more forest damage. Because of its social behavior, the mouflon's distribution is unequal in its range because it lives in herds in some selected range parts [60,115]. Red deer have a larger body size, and larger deer densities can also damage grasslands [85]. However, there is no doubt that large groups forming in high-density mouflon populations can cause immense damage to flora. Nogales et al. [40] also argued that invasive (and allochthonous) species inflict the biggest biodiversity loss. To distinguish between invaders with minor or profound impact, they refer to the progress of identification and measure non-native species' impact on ecosystems.

By comparing browsing on protected and unprotected plots, Anderson et al. [116] demonstrated that the diversity of prairie forbs was maximized at an intermediate level of deer browsing, supporting the intermediate disturbance hypothesis, which posits that diversity is maximized at intermediate levels of disturbance. They could not detect changes in community quality because the complement of species on their site did not change over time. However, changes in the relative abundances of species did occur. However, Augustine and deCalesta [117] argued that overabundance should be defined as a condition in which deer cause the local extinction of native plant species.

Rooney et al. [112] stated that plant densities can have two stable statuses in response to browsing pressure. Sensitive species with a low initial density are likely to be extirpated, even if the herbivore population is low. With high ungulate density, some plant species can also face extirpation regardless of their initial densities. Instead of identifying winner or loser species case by case, they proposed to create plant guilds or functional groups according to shared characteristics to anticipate the densities at which ungulates threaten diversity in ecosystems.

The impact of large herbivores on the ecosystem dynamics and landscape management also must be managed in integration with mountain grasslands. Mouflon and chamois (*Rupicapra rupicapra*) occupy ranges in Alpine regions where grasslands are not the most abundant vegetation. Therefore, their foraging shows plasticity. None of these species are migratory; their seasonal range shifts happen altitudinally, or they reduce their range sizes [82], leading to density growth and potential overpopulation with the increased risk of vegetation damage. Pasturage and firewood collection have harmed Alpine ecosystems for centuries. Since the 1960s—the period of mouflon introduction and spread—alpine farms declined, with stable livestock levels leading to grazing pressure concentration in certain areas, while shrubs and tall grass species invaded other meadows. Wild ungulates species can maintain such grasslands by substituting for domestic grazers despite their differences in feeding selectivity and seasonality. Thus, the presence of large herbivores in these grasslands is positive, even if they cause some damage to economically important woody vegetation [106].

4. Conclusions

Mouflon is an introduced, allochthonous species in its "original" habitat on Mediterranean islands and in recently occupied mountainous and temperate forest ranges in continental Europe. However, its place in our environment is ambiguous from ecological and legislative standpoints. The EU does not list mouflon as an IAS [35,45], yet some member states do [43]. We argue that the alien character in continental Europe frequently has a negative connotation, and in some cases, the species is simply considered to be invasive.

The mouflon's morphology—with asymmetric sharps hooves and forked upper lips—and its social behavior of living in groups throughout year can cause trampling and browsing damage in rock grasslands and in forests in winter. However, the exclusion experiments did not conclusively prove that rare rock grasslands' ecological damages and their biodiversity loss are linked exclusively to the mouflon's presence; its non-native character does not mean it would cause greater harm than a native species (red deer).

Our review promotes the understanding that the mouflon is not studied enough to quantify the ecological damages caused. Studies have not fully revealed the core damage causes and impacts. An elucidation of the indirect impacts and the balance of the mouflon's positive effects on biodiversity and the conservation of rare ecosystems is also missing. Studies also lack the integrated approach of considering the mouflon's diet composition with its seasonal changes within the context of diet niche overlap and interspecies competition with red deer in lower lands [72] and with chamois in higher lands. The ecological damages and the risk of biodiversity loss should be examined by considering the mouflon density within the context of red deer density. Such analyses need to weigh the degradation stage of the field and, consequently, rare plant species density and the weather conditions over extended periods.

Experimental research in Hungary suggests that mouflons may support the maintenance of abandoned grasslands by delaying the succession process. The mouflon adapts well by utilizing habitat choice and foraging strategy change in response to climate challenges. Climate has an increasing impact on species' behavior, and as is evident in Southern Europe, longer and hotter periods change the space use of mouflons [64]. Future studies are required to assess the changes in trampling and foraging damages by altering space use, particularly in habitats with ongoing climate change, such as those in Central Europe.

With the literature review of both the ecological and social aspects of the species, we argue that the mouflon's allochthonous character itself does not influence its impact on the vegetation. From an ecological perspective, using Wonham's [37] invasive alien species triad definition, we also propose that the mouflon cannot be considered an invasive species [53] and does not represent a higher risk to biodiversity than a native species such as red deer. Instead, we agree with Warren's classification [102] after Usher [118] to consider the mouflon as naturalized or being of a "post-invasive" character, Kopij [33].

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