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Ecological Impacts of Introduced European Rabbits (*Oryctolagus cuniculus*) on Island Ecosystems in the Mediterranean

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Abstract: The Cyclades Islands (Aegean Sea, Greece) are part of the Mediterranean Basin biodiversity hotspot and harbor a plethora of endemic species. Plant communities on the smaller islands in this region have largely evolved in the absence of herbivory and frequently lack antiherbivore defenses. This study evaluates the short- and long-term effects of the European rabbit (*Oryctolagus cuniculus*), an herbivore that has been released on numerous islands in the region, by comparing islands that 1. have historically been rabbit-free (ungrazed); 2. are currently grazed by rabbits, and 3. have previously been grazed, but are now rabbit-free. Ecological impacts of rabbits on the Aegean Islands were investigated by assessing the abundance, composition, and diversity of plant and arthropod communities as well as soil characteristics. Our results indicate that ungrazed islands have more arthropod species, more specialized or endemic plant species, and less exposed soil than currently grazed islands. While ungrazed islands did not necessarily possess higher total plant species richness, they did harbor significantly more small-island endemic taxa relative to presently grazed islands. This study indicates that native plant communities on Mediterranean islets are not adapted to the presence of this introduced species and that the practice of intentionally releasing rabbits on islands has significant and lasting negative ecological impacts, especially on small islands. While a complete recovery of post-rabbit was not evident over the time span of our research, both arthropod and plant data indicate that partial recovery is possible once rabbits have been removed.

Keywords: plant–animal interactions; invasive herbivores; soil erosion; endangered plants; island endemic species; lagomorphs; Cyclades; Greece; island communities

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1. Introduction

Islands are critically important ecosystems for many of the world's endemic and specialist species. While islands account for only 6.67% of the world's emergent land [1], they harbor more than 20% of Earth's biodiversity [2]. Islands have been identified as global centers of endemism for both plants and vertebrates [3]. The Mediterranean Basin, specifically, is one of the world's most diverse regions in terms of faunal and botanical richness [4]. Indeed, with over 13,000 endemic plant species native to this region, the Mediterranean Basin is a global biodiversity hotspot and a prime target for large-scale conservation [5].

Islands also harbor numerous species of conservation concern: approximately 50% of all species recognized as threatened by the International Union for Conservation of Nature (IUCN) occur in island ecosystems. Island biodiversity is disproportionately imperiled by a variety of anthropogenic causes, including hunting, habitat loss, and the introduction of invasive species [2]. Invasive taxa are recognized today as perhaps the primary cause of island species decline and extinction, and their removal from island systems has emerged as a critically important conservation tool [6].

The Aegean Islands (Greece), located in the NE Mediterranean Basin, are a key part of the Mediterranean biodiversity hotspot and harbor thousands of endemic taxa [7]. The Cyclades island cluster, containing 250+ primarily land-bridge islands, is situated in the central Aegean Sea (Greece) and provides an ideal setting to understand how humans affect native species communities. Humans have continuously inhabited islands in the Cyclades since Paleolithic times [8] and, over that period, have used the landscape extensively for agriculture and livestock grazing. As a result of the pervasive presence of sheep and goats, most of the Cyclades plant communities are shaped by herbivory, with many of the species that are shared with mainland and mainland islands having well-developed defenses such as thorns and various allelochemicals. However, in contrast to the larger islands, many of the smaller Cyclades islets have been too arid to sustain human populations and consequently have escaped the impacts of introduced livestock. Consequently, many of the endemic plant species lacking herbivore defenses have survived to this day on such small islands. As these species have evolved without the risk of herbivory, they lack the ability to defend themselves against introduced herbivores [9], such as the European rabbit (*Oryctolagus cuniculus*), which is native to the Western Mediterranean Basin. Indeed, Bergmeier and Dimopoulos [10] have shown that introduced herbivores can severely affect the competitive balance of species on the islands. The combination of limited range size and vulnerability to herbivory makes small island specialists highly susceptible to extinction following the introduction of invasive herbivores.

The European rabbit, *Oryctolagus cuniculus*, is native to the Iberian Peninsula in SW Europe, but now it has a worldwide distribution, being found on all continents except Antarctica [11]. These rabbits are considered to be a generalist species, as they can flexibly adapt their dietary strategies depending on the environment and the availability of various vegetation types [11]. As a result, rabbits have become one of the most widespread invasive mammals worldwide, having a variety of serious effects in newly colonized habitats [11]. Previous studies have documented the devastating impacts that rabbits have on ecosystems through excessive herbivory [12,13]. For instance, on Laysan Island in the Hawaiian archipelago, rabbits were responsible for the extinction of 26 native species between 1903 and 1923 [12]. On Tenerife in the Canary Islands, previous research has demonstrated that endemic plant species were more palatable to the introduced European rabbit than non-endemic species [14].

Beyond the impacts on plants they feed on, introduced rabbits have also been the cause of significant population declines in various other native species around the world, including reptiles and birds [12,13]. For example, previous studies have shown that rabbit competition with native species for food and resources, as well as the destruction of habitat from burrowing and digging, have led to long-term losses of native taxa of oceanic islands [12]. On islands in Western Mexico, rabbits alone were responsible for the near extinction of *Dudleya linearis*, an endemic succulent that only showed signs of recovery after the removal of rabbits from the islands [15]. Studies from a diversity of islands worldwide have supported these findings, showing that the ecosystem-wide impacts of rabbits on isolated islands can be severe, damaging whole island food webs [16–18]. Interestingly, while considered an invasive exotic in areas where they have been introduced, these rabbits are becoming endangered in their native range, creating a conservation paradox [19].

The European rabbit has a wide distribution on both large and small islands of the Aegean Sea. Being a Western Mediterranean Basin endemic, this species is well adapted to the locally prevailing, semi-arid conditions. While populations on large islands are more stable and have been introduced for at least 300 years [20], their presence on the Cyclades islands was first studied by Dr. Theodor Erhard in 1858 [21] (see also Table A2 in Appendix A). Only relatively recently, rabbits have been released on small, otherwise uninhabited islets by both Aegean farmers and hunters as an additional source of hunted protein. Based on informal conversations, such introductions are perceived by locals as a way to 'give life' to the islands. While this practice is probably older, it became more widespread in the later half of the 20th century as motorboats made travel to smaller islands safer and access more dependable: lack of reliable motorboat transportation to islands and a dearth of rabbit stock likely made this impractical before the 1900s.

The impacts of rabbits on Aegean Sea island ecosystems are not well understood. Because the rabbits' native habitat is near the study region, it is possible that local species have adapted to their presence, and it is hence reasonable to assume that the impact of introduced rabbits on islands would remain moderate. However, a recent study on Lemnos, a large island in the Northeastern Aegean Sea, showed that European rabbits could readily adapt to seasonal changes in food quality and availability and become quite abundant [22]. As a matter of fact, rabbit populations have grown so rapidly there that the species is now considered to be an agricultural pest [23]. Similarly, on smaller islands with important seabird nesting colonies, rabbit herbivory alone can reduce densities of nesting seabirds by approximately 54%, and the simultaneous presence of both rabbits and goats will reduce gull colony density by 71% [24]. While introduced goats have also been shown to have an impact on small islands [24], the impacts of goats cannot be readily extrapolated to rabbits. This is because the two species differ in key herbivory characteristics, including foraging height and trampling impacts. Consequently, little information exists on the impacts of rabbits on Mediterranean island ecosystems, especially in regard to the native plant communities. At the same time, climate change is expected to increase rabbit populations on island ecosystems due to a positive correlation between temperature and rabbit abundance [25], creating a pressing need for relevant information to guide management policies.

Anthropogenically induced climate change is also threatening endemic island plant communities, as it leads to regionally higher wind speeds, which, in turn, drive the aridification of the islands [26]. Thus, the drier and hotter conditions that the region is now facing are also likely to exacerbate the effects of any herbivory [27–29]. For example, the effects of herbivory on soil erosion are likely to be worsened by an expected increase in wind, as well as decreased vegetation cover on the islands [26,30]. Ultimately, this will likely decrease the already limited habitat available for the endemic flora and fauna, resulting in higher extinction rates, especially for climate-sensitive species.

The aim of this study is both to quantify the effects of European rabbit populations on Aegean island ecosystems and also to provide insights into the potential for restoration following rabbit removal from such islands. As herbivory leads to a decrease in vegetation cover, primary consumers, such as arthropods, may also be impacted by the loss of essential resources [31]. By comparing islands without rabbits, islands with rabbits, and islands with eradicated rabbit populations, we tested the short- and long-term impacts that rabbit grazing is having on the abundance, composition, and diversity of the vegetation and arthropods, as well as soil loss on small islands. Consequently, rabbit-free islands served as control sites to assess the impacts of current rabbit grazing on island floras, while islands previously—but not anymore—inhabited by rabbits were used to assess the potential for islands to recover after grazing.

2. Materials and Methods

2.1. Study Area

This study was conducted on a subset of the islands within the Cyclades islands located in the Central Aegean Sea (Greece, NE Mediterranean Basin). Previous surveys of the archipelago documented the presence of rabbits across both large and small islands of the region [32], setting the stage for our own regional background surveys. One of the authors [JF] conducted extensive surveys of the archipelago, visiting about 200 islands between 2004 and 2024. During these surveys, a combination of interviews with locals and extensive on-foot habitat searches were used to look for the presence of rabbits. Because of logistical difficulties, isolation, and weather-restricted travel, however, no rabbit densities were obtained.

Beyond this regional survey, during the May–July 2022 field season, we collected detailed comparative ecological data on 11 islands: 4 islands currently grazed by rabbits

(Panterionisi, Lower Fira, Filitzi, and Glarombi); 3 islands without any introduced herbivores (Agia Kali, Tourlos, and Grambonisi); and 4 islands with previously eradicated rabbit populations within the last ~20 years (Upper Fira, Galiatsos, Gramvousa, and Tigani) (Figure 1).

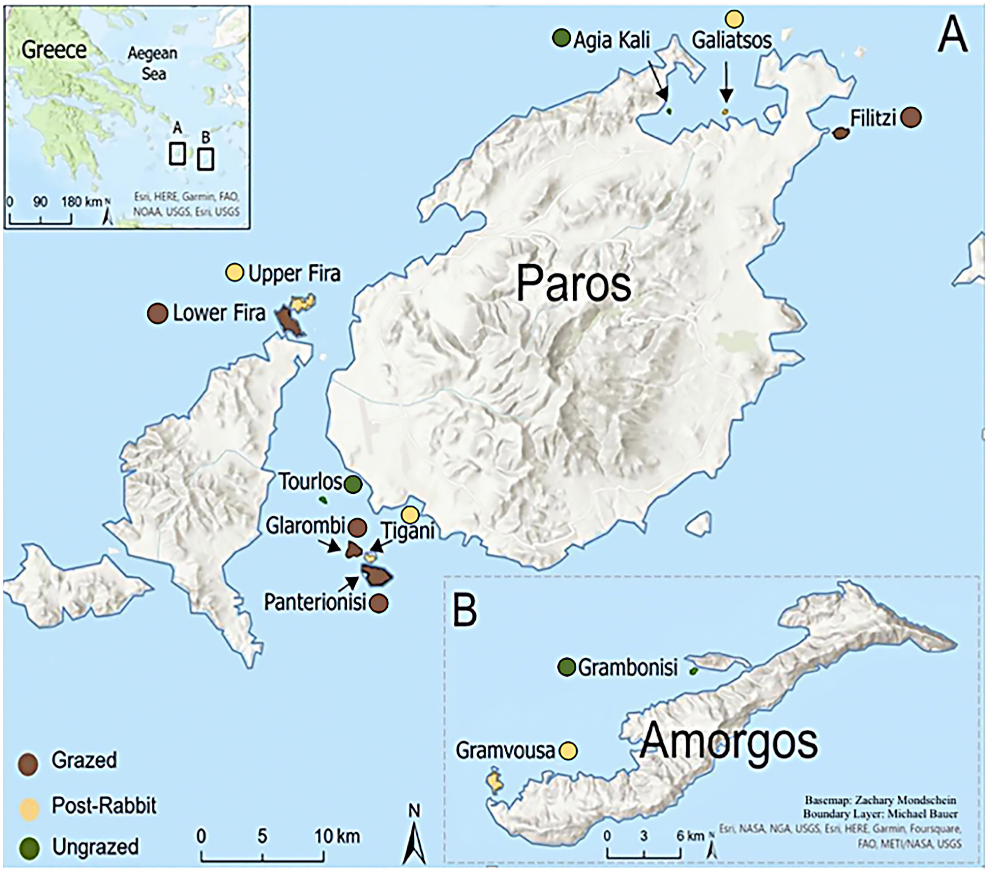

Figure 1. Map of study sites, with brown indicating islands that are currently being grazed by rabbits, green indicating islands that have never been grazed, and yellow representing islands with eradicated rabbit populations.

Islands were selected for general ecological similarity so as to not confound the effect of rabbit grazing with other island characteristics. Beyond being situated in the same region and experiencing the same environmental conditions, all islands were under 1 km^2 in area (the largest being 0.79 km^2, and the smallest being 0.01 km^2) and less than 2.5 km from the closest large island (i.e., Paros, Antiparos, or Amorgos). Additionally, the islands consisted predominantly of limestone, and the vegetation was predominantly halophytic coastal heath and phrygana, which are adapted to withstand long periods of dryness and heat [33]. The status of rabbit populations was determined by a combination of direct and indirect evidence, including extensive in-person field surveys for rabbit presence or recent signs of rabbits such as pellets, burrows, and signs of digging. Past status was determined either from our own past field surveys and/or conversations with local fishermen or hunters who are typically well aware of the history of the presence of the rabbits on the islands, often going back almost a century. Rabbits are considered by locals to be a desirable source of protein, and residents have traditionally raised them in small numbers.

2.2. Grazing Intensity

To determine the intensity of grazing on islands inhabited by rabbits and quantify the amount of biomass consumed, we collected rabbit fecal matter on grazed islands along two

50 m long and 60 cm wide transects. The pellets collected were then dried in the sun until no more weight loss was detected, and then mass (in g) was recorded (see Gizicki et al.) [24].

2.3. Vegetation Assessment

For each of the study islands, we assessed plant structural characteristics, including the percentage of vegetation cover, vegetation biomass, average plant height, distribution and abundance of endemic and specialist species within the quadrats, and total number of plant taxa. This was performed using a combination of line transects and study quadrats [24]. Four transects of 30 m were established on each island, one in each of the four cardinal directions from the same starting point. To calculate the percentage of vegetation cover, the percent of bare ground cover was quantified by categorizing the type of cover into four categories: rock; soil; bush (woody scrub); and herbaceous (non-woody plants). At intervals of 1 m along each transect, the cover type was recorded by dropping a pin from the meter mark and recording whatever vegetation existed where the pin landed. If vegetation was present, we measured its height. Vegetation height measurements (cm) were averaged for each transect (4 per island) to determine the variations across grazing categories. Percentages of each substrate type were then calculated for each of the four transects per island [24]. Additionally, five quadrats (60 cm × 60 cm squares) were placed on each island (sites were chosen by placing the quadrat where a marker landed on the island), and the vegetation in each quadrat was identified to species [34,35]. To determine the standing biomass on each island, all aboveground biomass from each quadrat was clipped to ground level, and the clipped material was collected, sun-dried, and weighed until the weight remained constant for a minimum of two days [24]. All identified plants were assigned to one of three categories [34–37] (native generalist, islet endemic or specialist, and weedy/invasive species), depending on their distribution pattern on the islands, habitat types, and ecological requirements.

2.4. Arthropod Community Assessment

Arthropod abundance and characteristics were quantified using sticky traps and pitfall traps on the study islands, 5 on each island. Traps were deployed on each island and left for an average of 61.79 ± 19.37 h. The sticky traps consisted of a bright yellow plastic card (7.62 cm × 12.7 cm) covered with a sticky, non-drying film and affixed to metal wire holders approximately ~20 cm above the ground. The pitfall traps (~7 cm in diameter and ~11 cm deep) were constructed from plastic cups that were sunk into the ground, ensuring that the rim of the cup was flush and level with the soil surface. To prevent extraneous materials from falling into the trap, all cups were covered by a flat rock raised 3–4 cm over the ground and resting on three smaller stones. The cups were partially filled with ethylene glycol [38]. After ~2.5 days, pitfall traps were collected, and the species were cleaned, identified, counted, and then dried and weighed. Arthropod abundance data for both pitfall and sticky traps were standardized by both the area and time deployed, as well as the number of successful traps. All specimens were eventually preserved in isopropyl alcohol and sent to the Natural History Museum at the University of Crete to be incorporated into their collections.

2.5. Soil Characteristics

To determine whether European rabbits are contributing to soil loss, we assessed the soil depth on the islands. Islands with active agriculture were excluded from the following analyses because plowing and cultivation are practices that promote soil loss and can confound data interpretation. Soil depth measurements were collected in the summer of 2022 for all islands, excluding Gramvousa and Grambonisi, where data were collected in the summer of 2023. Measurements for Tourlos were collected in both 2022 and 2023. Soil depth measurements were taken on each island at haphazardly chosen locations by hammering an iron rod into the soil and measuring the depth of penetration before bedrock was encountered. If a selected location had exposed bedrock, a depth of 0 cm was recorded.

In addition, in order to determine any effects of rabbits on soil chemistry, 4–5 soil samples were collected per island at haphazardly selected locations. Soil samples were collected, placed in plastic containers, and shipped to the laboratory of one of the authors (P.A.) at the University of Patras, where they were sorted, cleaned, dried, and homogenized by the lab staff who conducted all of the analyses.

Both total organic carbon (TOC) and total nitrogen (TN) measurements were carried out using a Shimadzu TOC analyzer (TOC-VCSH) coupled to a chemiluminescence detector (TNM-1 TN unit), creating a simultaneous analysis system [39–41]. A digital hand-held soil calcimeter (FOGGII/Version 2/2014; BD INVENTIONS, Thessaloniki, Greece) was used to determine the carbonate content ($CaCO_3$).

2.6. Statistical Analyses

All statistical analyses were run in RStudio [42], and SpadeR was used for all species diversity estimates [43]. Variables were compared across the three grazing classifications—ungrazed, grazed, and post-rabbit. Linear Mixed Models were used to analyze the differences among islands for the variables with multiple samples per island, with island included as a fixed effect; one-way ANOVAs were used for variables with a single sample per island (plant and arthropod species richness (both estimated and observed) and arthropod biomass). Pearson Product–Moment correlations were used to determine the relationships between variables.

To analyze species evenness for plants, a bias-corrected Chao 1 nonparametric asymptotic estimator was used to approximate the number of plant species on the island using the SpadeR program version 0.1.1 [43,44] (see Appendix A). This uses the formula

$$\hat{S}_{Chao1} = D + f_1(f_1 - 1)/[2(f_2 + 1)],$$

where $\hat{S}_{Chao1}$ is the estimated number of species on the island; D is the distinct number of species observed; f_j is the number of species represented $_j$ times in a sample, with j = 0, 1, 2 . . . n [43]. To account for any possible underlying confounding effects of island area on resident species number because of the species–area relationship [45], the estimated species per island (for both plants and arthropods) was divided by each island's area to determine if there was a difference in species richness across the three types of grazing classifications.

3. Results

3.1. Survey

Our regional surveys revealed the widespread introduction of rabbits on numerous Cycladic islands beyond the already known presence on the major inhabited islands (Figure 2). Thus, we detected for the first time the species on almost 50 islands in the archipelago, demonstrating the widespread occurrence of this species in the region (Figure 2).

3.2. Grazing Intensity

Fecal pellets were only collected on four currently grazed islands; Lower Fira had the most fecal pellet weight (total of 717 g), followed by Filitzi (527 g), then Panterionisi (138 g), and then Glarombi (123 g). No significant relationship existed between aboveground biomass and fecal pellet weight (R = 0.78, p-value = 0.22, Pearson).

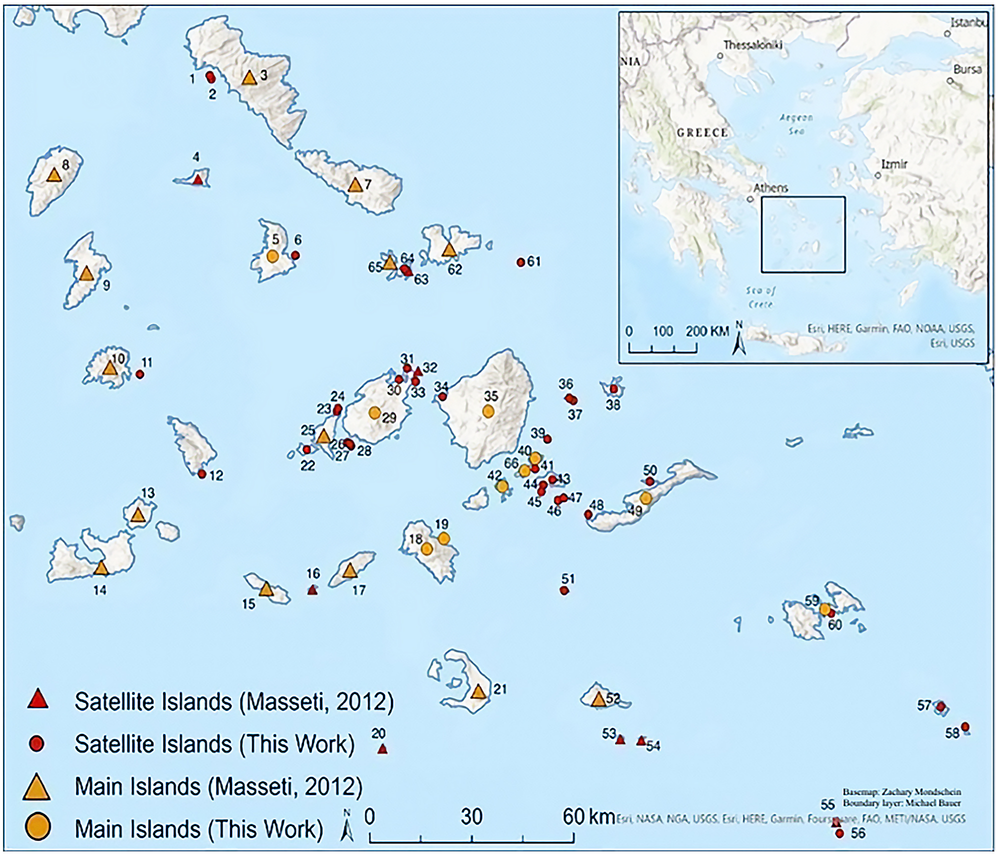

Figure 2. Rabbit introductions have been an increasingly widespread phenomenon on Aegean Sea islands [32]. The above map shows the islands in the Cyclades with documented introduced European rabbit populations. Satellite islands (denoted in red) are likely to harbor floras with small island specialists and, therefore, more likely to be impacted by rabbits. Larger islands (denoted in orange) are inhabited by humans and livestock and have plant species communities largely adapted to herbivory. Islands are listed in Table A2 in the Appendix A.

3.3. Vegetation

3.3.1. Ground Cover

Bush and herbaceous cover were combined to determine the total percentage of vegetation cover, while rock and soil cover were combined to determine the total percentage of the bare area on each island. Each cover type—rock, soil, bush, and herbaceous—was also analyzed individually to look at the specific differences in the cover types (Figure 3). The extent of bare soil on grazed islands (40.75%) doubled that from ungrazed islands (20.20%) (T = −2.63, N = 44, p-value = 0.03, LMM). There was also a non-significant trend indicating the reduction of 7.42% in herbaceous vegetation cover between ungrazed and grazed islands (1.67% (grazed) vs. 9.09% (ungrazed); T = 2.08; N = 44; p-value = 0.07, LMM). The percentage of vegetation (combination of herbaceous and bush cover) showed a non-significant trend where vegetation cover was higher on ungrazed islands compared to grazed islands (43.75% (grazed) vs. 62.63% (ungrazed); T = 2.05; N = 44; p-value = 0.08 LMM), with ungrazed islands having an average of 18.88% more vegetation coverage per island. There were no significant differences between post-rabbit islands and the other rabbit presence categories.

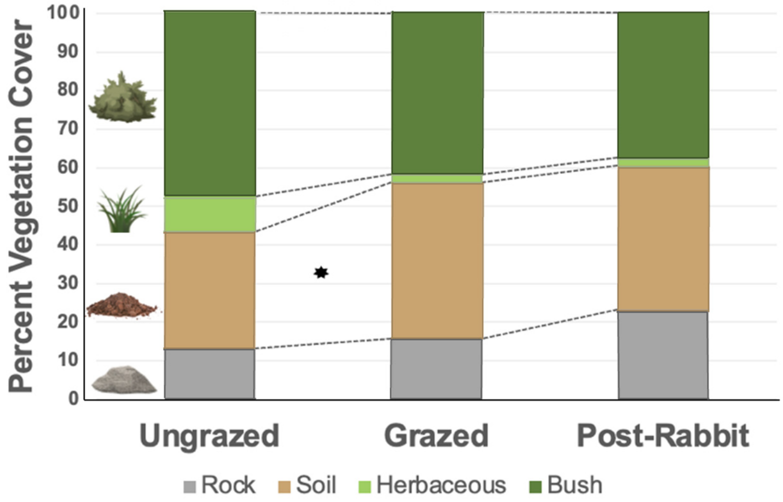

Figure 3. Changes in the percent of bush, herbaceous vegetation, bare soil, and exposed rock cover across the three types of grazing categories. Dark green represents bush cover; light green represents herbaceous cover; brown represents soil cover, and gray represents rock cover. Significant differences ($p < 0.05$) are denoted by *.

3.3.2. Vegetation Height

Vegetation height was not statistically different between the three classifications of islands (F = 2.00; N = 44; *p*-value = 0.20, LMM) (see Appendix A). However, vegetation height was significantly positively correlated with vegetation cover (R = 0.49; *p*-value = 0.0007, Pearson), indicating that areas with higher vegetation cover also harbored taller vegetation (Figure 4). This may be because exposure to very strong winds most of the year suppresses vegetation height unless a large amount of vegetation cover resists and deflects wind, allowing for the plants to grow higher.

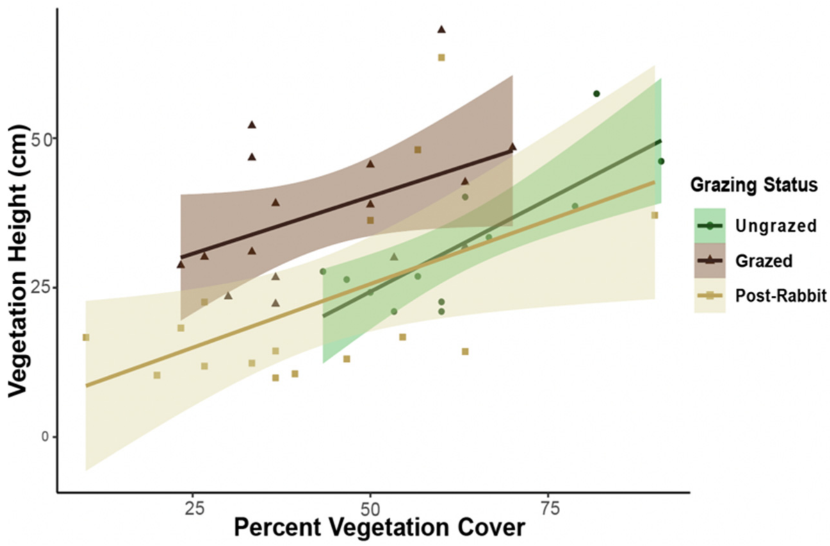

Figure 4. Relationship between vegetation height (cm) and percent vegetation cover on the study islands, shown separately for each category of rabbit grazing status.

3.3.3. Vegetation Biomass

There was a non-significant trend toward reduction in aboveground plant biomass on grazed islands relative to ungrazed ones (T = 1.81, N = 55, *p*-value = 0.08, LMM). Ungrazed islands had an average of 169.5 g (See Table A1 in Appendix A) more standing biomass (94.82% greater than grazed islands). There was no significant difference between post-rabbit and either ungrazed or post-rabbit and grazed islands; however, post-rabbit islands had an average of 17.05 g more aboveground biomass than grazed islands. Aboveground biomass was not significantly correlated with vegetation height (R = 0.12; p-value = 0.43, Pearson's R).

3.3.4. Vegetation Species Richness

A total of 67 species were identified across the 11 islands and categorized as weedy, generalist, and specialist/endemic species based on distribution patterns and habitat/survival requirements. There were no significant differences between ungrazed, grazed, and post-rabbit sites in the observed total number of species (F = 1.01; N = 11; p-value = 0.41, ANOVA), nor the estimated (Chao 1 estimator standardized by island area) number of species per island (F = 0.65; N = 11; p-value = 0.55, ANOVA). Of the identified species, the number of endemic and specialist species was quantified per island and compared across grazing treatments. Ungrazed islands had a statistically significant greater number of specialist and endemic taxa (F = 6.50; N = 11; p-value = 0.02, ANOVA) compared to grazed islands. While post-rabbit islands did not differ significantly from either (Figure 5), they did have more than grazed islands (but less than ungrazed islands). Island types did not differ significantly in the number of weedy species (F = 0.1; N = 11; p-value = 0.91, ANOVA).

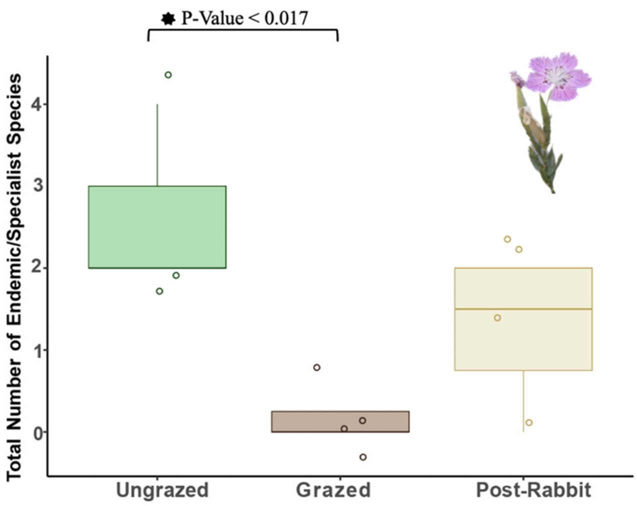

Figure 5. Total number of specialist/endemic plant species across the three different grazing statuses. Islands with rabbits had significantly fewer such plant species relative to ungrazed islands.

3.4. *Arthropods*

Arthropod abundance, richness, and diversity were quantified using data from both the pitfall and sticky traps on the 11 study islands. A total of 3194 individuals were collected from the pitfall and sticky traps. The most common taxa collected were Hymenoptera, Coleoptera, and Arachnids. On Galiatsos, Filitzi, and Grambonisi, some of the traps were damaged and had to be removed from subsequent analyses. The amount of time each trap was deployed was not significantly correlated with the arthropod abundance in pitfall traps (R = 0.43; N = 11; p-value = 0.19, Pearson), sticky traps (R = 0.17; N = 11; p-value = 0.61, Pearson's R), nor in species diversity of the pitfall (R = 0.26; N = 11; p-value = 0.45, Pearson) or sticky traps (R = −0.31; N = 11; p-value = 0.37, Pearson). However, to remain consistent with standard practice, we still standardized for the time in the following analyses.

The biomass of arthropods collected from the pitfall traps per day was not significantly different between ungrazed, grazed, and post-rabbit islands (F = 0.15; N = 11; p-value = 0.86, ANOVA). There was, however, a significant difference in the abundance of arthropods caught per pitfall trap (corrected for area), with ungrazed islands having significantly higher abundance per day than grazed and post-rabbit islands (F = 9.92; N = 48; p-value = 0.0003, LMM; Figure 6). There were significantly more species per trap found in pitfalls (corrected for area) on ungrazed islands compared to grazed islands (F = 4.87;

N = 10; *p*-value = 0.05, ANOVA), with no differences found between the other classifications. There were no significant differences between the abundance of arthropods caught in the sticky traps per day (corrected for area) between island classifications (F = 0.72; N = 55; *p*-value = 0.52, LMM).

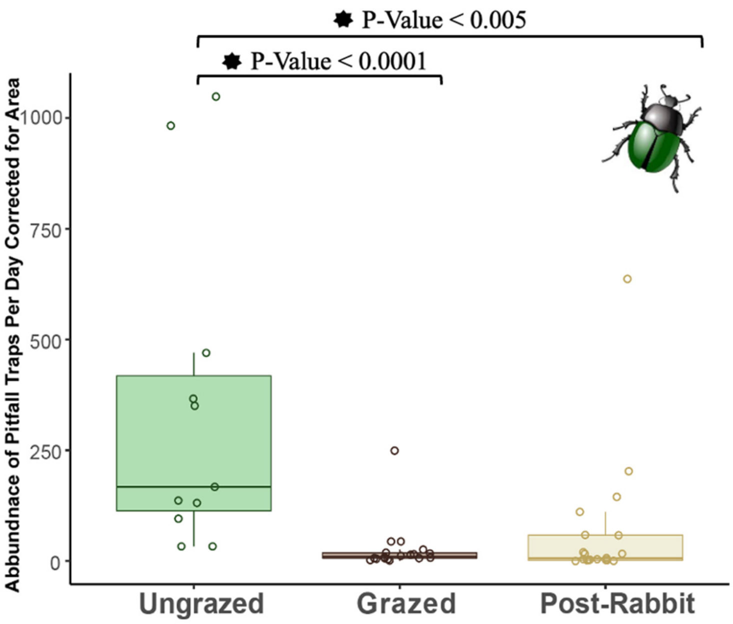

Figure 6. Differences in abundance of arthropods per pitfall trap on the study islands (corrected for island area).

3.5. Soil

Average soil depth declined from ungrazed to post-rabbit islands (F = 3.90; N = 67; *p*-value = 0.03, LMM; Figure 7). No significant differences were recorded between other treatments.

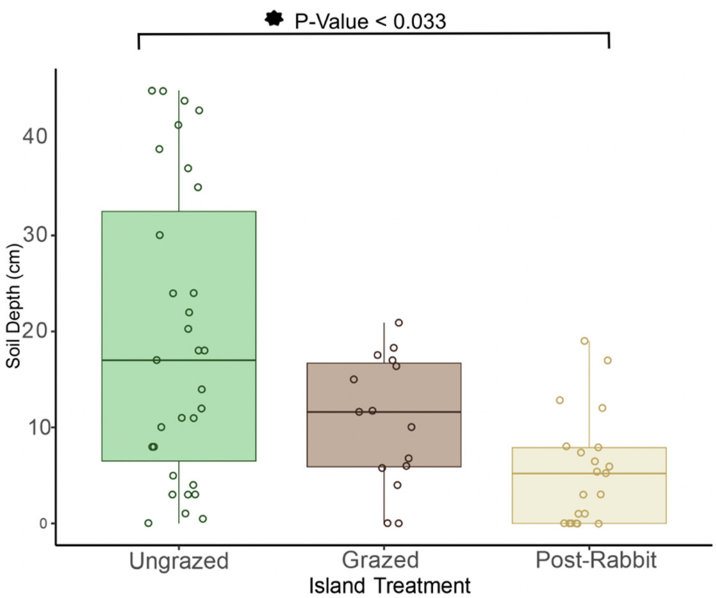

Figure 7. Boxplot of soil depth with individual data points overlaid across the three island categories.

Analysis of the chemical composition of soil samples showed no differences in % $CaCO_3$ (F = 1.19; N = 39; *p*-value = 0.37), total N (F = 0.18; N = 39; *p*-value = 0.84, LMM), and total organic C (F = 1.74; N = 39; *p*-value = 0.25, LMM) across island categories.

4. Discussion

Here, we determine for the first time in a quantitatively rigorous manner the impacts of the European rabbit (*Oryctolagus cuniculus*), an introduced herbivore, on small island ecosystems in the Aegean Sea and demonstrate that rabbit presence and herbivory have far-reaching effects on island ecosystems in the region.

One of the most notable effects of rabbit grazing is the removal of vegetation in ways that affect its long-term potential for preventing soil erosion. Specifically, we found that the extent of bare ground (i.e., areas of vegetation-free soil) was significantly higher on grazed islands, showing how severely rabbit herbivory can impact island plant communities. We also documented a non-significant but distinct trend toward less herbaceous vegetation cover on grazed islands, indicating that rabbits have a disproportionate preference for herbaceous over woody plants. Indeed, on rabbit islands, perennial vegetation such as the bushes *Pistacea lentiscus* and *Juniperus turbinata*—which tend to be structurally and chemically defended—were still relatively common, while endemic and specialist herbs were significantly less abundant. For example, *Brassica cretica* is mostly undefended and can be heavily impacted by herbivores (Figure 8). While we document the impacts of rabbits predominantly on herbaceous plants, it is likely that select perennial taxa were also affected, often indirectly, via root exposure and erosion. Nonetheless, we did not detect great differences in total vegetation biomass, as the weight of the severely impacted smaller herbaceous plants found on ungrazed islands was relatively minor in comparison to the larger bushes that persisted on rabbit islands.

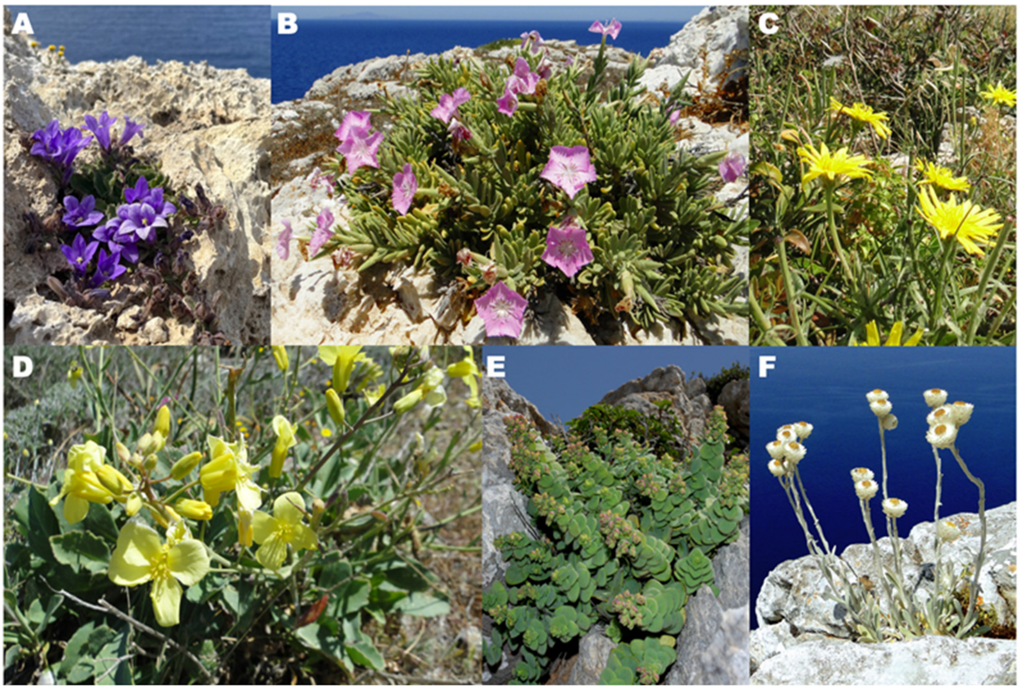

Figure 8. Endemic plant taxa found on Aegean Islets that are vulnerable to impacts from grazing. (**A**) *Campanula heterophylla* (JF). (**B**) *Dianthus fruticosus* (JF). (**C**) *Scorzonera araneosa* (JF). (**D**) *Brassica cretica* (JF). (**E**) *Origanum calcaratum* (*G. Gavalas*). (**F**) *Helichrysum amorginum* (JF).

Rabbits increase the vulnerability of islands to soil erosion processes. In addition to more bare ground on grazed islands, we found a significant reduction in soil depth from ungrazed to post-rabbit islands. The Cyclades have a relatively arid and windy climate, leading to significant aeolian erosion. The impacts of such wind erosion are likely to be further intensified in the future by expected increases in wind (as a result of climate change) [26,30]. Beyond vegetation removal, rabbits further accelerate soil erosion as a result of digging and burrowing [12], activities that loosen the friable soil that is then more easily blown away. Ultimately, the impacts of rabbit activity on island communities are likely to become further exacerbated in the future by the increasingly drier and hotter conditions that the region is now facing as a result of climate change [28,29].

Across its non-native distribution, the release of these lagomorphs poses consequential ecological concerns [46]. Reduced plant cover, diminished aboveground biomass, and shallower soil depth all contribute to shifts of plant assemblages on the rabbit islands. At first review, there is no difference in the total number of estimated plant species per island between the three island classifications, most likely because when transported to the islands, lagomorphs facilitate plant dispersal by carrying disseminules in their fur [47]. However, we did document important shifts in plant community composition.

Greece harbors one of the richest and most diverse floras in Europe [48], and many of the endemic plant species are located on the Aegean Sea islands. However, these island floras are also quite vulnerable, with populations of endemic species frequently in decline or facing extinction [49] (Figure 8). Insular ecosystems are subject to disproportionately higher rates of extinction due to a combination of geographically narrow ranges as well as exotic species impacts. Endemic island plants have frequently evolved in the absence of mammalian herbivory and, therefore, often lack the necessary antiherbivore defenses such as thorns or allelopathic chemicals [9,50]. This study documents that the island specialist and endemic plants are significantly less frequent on grazed islands, suggesting that rabbits are shifting island species' community compositions in ways that are disproportionately unfavorable to endemic vegetation. These findings also mirror the results of previous studies in other island ecosystems that show how rabbit herbivory can disproportionately damage endemic species communities [16–18]. On our study islands, soil chemical characteristics did not appear to be altered by the presence of rabbit herbivory. However, previous studies suggest that in addition to altering the species dominance patterns in the areas where they are introduced, grazing from rabbits can also alter the soil chemistry, decreasing soil N and negatively impacting the growth of endemic species [51]. In this system, the main limiting factor for vegetation growth appears to be the combination of soil and water availability.

A significantly greater number of arthropod species and individuals were observed on ungrazed islands, indicating that arthropods are also vulnerable to impacts from grazing [52]. These changes may be either the direct consequence of diminished plant resources or the result of indirect effects on soil erosion and island desertification. However, in general, morphospecies identifications may not be precise enough to determine changes in arthropod communities, and future researchers are encouraged to further study the implications of grazing on arthropod communities on the Aegean Islands.

Both arthropod and plant data from this study suggest a partial recovery of species after the removal of the European rabbits from the islands (Figure 9). The total number of endemic/specialist species was the highest on ungrazed islands; however, the intermediate value of post-rabbit island indicated a partial recovery of endemic/specialist species richness. A complete recovery was not evident in this study, potentially because of the limited time elapsed since eradication (less than 20 years), and more time may be needed for species to recover, especially in a low-productivity system. However, some key species may have gone completely extinct from these islands, inhibiting a full recovery even after the removal of rabbits.

Unfortunately, geological evidence suggests that soil formation is such a slow process that it will likely take thousands of years to recover [53]. These findings are corroborated by a study conducted on Macquarie Island, an island in the Pacific Ocean, that demonstrated that partial recovery in vegetation after rabbit control programs were implemented was possible [54]. Similar trends in island recovery were observed in 2015 from grazing by goat populations on the Aegean Islands [24].

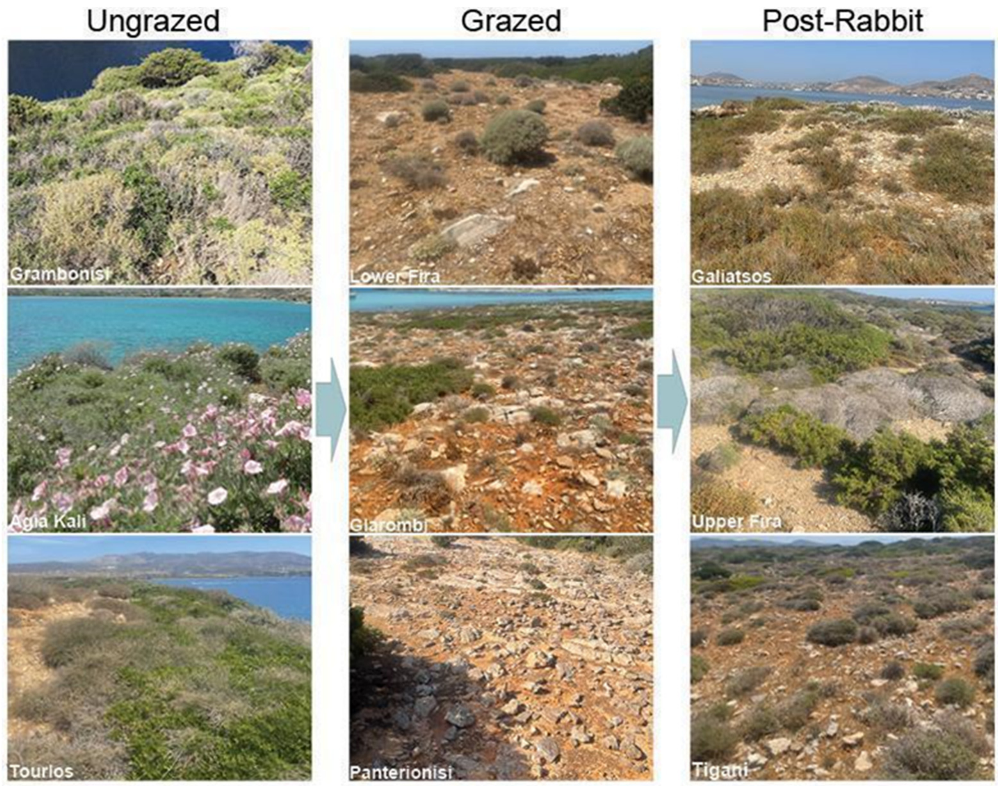

Figure 9. Photographs of some of our study islands across the three rabbit presence categories. Images show how rabbits mainly target low, herbaceous vegetation and less woody perennial species (e.g., *Pistacea lentiscus*) that often remain unaffected by rabbits due to their chemical and physical defenses or height. Post-rabbit islands are characterized primarily by the re-colonization of areas between these scrubby perennials by low annuals. However, any such recovery never attains the original, ungrazed levels of vegetation cover, at least not without additional restoration steps. Images from Angelina Kossoff, 2022, and Agia Kali from Johannes Foufopoulos, 2022.

Despite a potential lack of full recovery, this work provides evidence that eradication of rabbits from Cyclades islands will still deliver clear conservation benefits for local ecosystems. While past eradication efforts in other parts of the world have been, at times, logistically complex (such as the eradication of rabbits on Macquarie Island [54]), several factors suggest that this will not be as challenging on the Aegean Sea islands. First, because the focal islands are relatively small and often have fairly smooth terrain, all parts can typically be accessed by conservation managers without difficulty. Furthermore, because the islands lack structurally complex vegetation and typically even a sufficiently deep soil layer, rabbits often are not able to dig warrens, making them much easier to identify and find. As a matter of fact, because of the arid conditions and general dearth of food, the long-term survival of rabbit populations appears to be precarious, and local hunters report that rabbit populations are often wiped out, requiring repeat releases. This suggests that well-planned eradication efforts will be relatively easy to accomplish if local communities become involved. The potential misperception of rabbits 'giving life' to the islands could be a barrier to this ban, which is why it is particularly important to achieve buy-in from local residents and especially hunter associations, as ultimate removal success will only be accomplished if all future reintroductions cease.

Removal of exotic species from islands is sometimes accompanied by unintended ecological effects. For example, the removal of invasive herbivores in some locations resulted in an increase in exotic plant populations [55]. Might there be such unintended ecological consequences from rabbit removal from the Aegean Islands? Our investigation of islands that used to have rabbits and are now rabbit-free does not provide such evidence. Removal of rabbits did not result in the takeover of any exotic plant species released from rabbit herbivory. However, a potentially negative effect that may occur stems from the fact that small island rabbit populations sometimes appear to provide prey for resident Bonelli's eagles (*Hieraetus fasciatus*). Eradication of such rabbit populations may likely force resident eagles to switch their diet towards alternative prey taxa such as chukar partridges (*Alectoris chuckar*) or rock doves (*Columba livia*).

The results of this study indicate that measures should be taken to prevent the introduction of rabbits on Mediterranean islands. As at least partial recovery appears possible for islands where rabbit populations have been removed, these islands may benefit from additional recovery programs, including restoration of endemic species and restoration of nesting seabirds. We suggest thorough communication with locals and residents as to the best management program for the European rabbit, as well as policies that prevent the release of non-native species onto these ecologically important satellite islands. We also encourage future research to test the robustness of these findings by increasing sample sizes. Additionally, we suggest installing exclusion fences on currently grazed islands to quantify the impacts of rabbit herbivory on seedlings.

5. Conclusions

This study highlights the impacts of European rabbits (*Oryctolagus cuniculus*) on Mediterranean island ecosystems and demonstrates the need for proper management of the species in the region. We demonstrate that this introduced species affects disproportionately low, herbaceous plant species while impacting woody perennial bushes mostly in the long term. While rabbit presence is not necessarily associated with a decline in overall plant species richness, this conceals a shift in the species community away from the grazing-sensitive island endemics toward generalist taxa with widespread distributions. Arthropods also showed a significant decline in both the abundance and diversity on grazed islands. Additionally, the presence of rabbits increases soil erosion, both because removal of vegetation cover bares the soil to the effects of wind and also because the animals dig and tunnel, loosening the friable soil and, therefore, facilitating aeolian transportation. Further negative effects probably stem from the fact that rabbits have been shown to reduce the number of nesting seabirds, therefore undermining the supply of critical nutrients that are necessary for the proper functioning of these Mediterranean island ecosystems. This study indicates that although they originated in the Mediterranean Basin, European rabbits still act as severely disruptive agents to island species communities, and small islands are especially vulnerable but also feasible restoration sites.

This study demonstrated that at least partial vegetation recovery is possible after the removal of rabbits, thus adding urgency to such eradication efforts. However, island food webs do not recover fully to pre-rabbit levels, most likely due to long-term soil loss. Both this and the previous studies [24] demonstrate that ecological naivete, and restricted distributions render endemic taxa disproportionately vulnerable to grazing from introduced herbivores [14,50]. These data indicate that desertification is a result of grazing, as the percentage of soil cover was significantly higher on grazed islands. This study also explores how grazing from European rabbits has the potential to leave the island communities more susceptible to anthropogenic climate change via reduced vegetation cover and exposed soil. Ultimately, this underscores the significance of careful management of these islands and the need for further exploration of restoration techniques for endemic and vulnerable island species.

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Appendix A

Table A1. Ecological characteristics collected across the study islands (reported means ± S.D.).

	Agia Kali	Grambonisi	Tourlos	Glarombi	Lower Fira	Panterionisi	Filitzi	Galiastos	Tigani	Gramvousa	Upper Fira
Grazing Status	Ungrazed	Ungrazed	Ungrazed	Grazed	Grazed	Grazed	Grazed	Post-rabbit	Post-rabbit	Post-rabbit	Post-rabbit
Area (km^2)	0.01	0.15	0.03	0.21	0.46	0.48	0.04	0.01	0.08	0.79	0.26
Vegetation Height (cm)	15.26 ± 4.22	35.5 ± 5.21	13.35 ± 1.62	12.81 ± 3.40	29.72 ± 5.66	13.46 ± 5.28	13.74 ± 4.88	3.74 ± 2.85	6.02 ± 1.05	9.40 ± 5.28	24.12 ± 9.84
Observed Plant Species	12.00	15.00	8.00	9.00	8.00	11.00	9.00	8.00	10.00	17.00	8.00
Chao1 Bias-Corrected Estimate (plant)	14.55	16.99	9.76	9.00	6.00	17.50	14.75	14.82	13.62	75.14	7.47
Average Aboveground Biomass (g)	183.2 ± 98.24	417.99 ± 226.35	443.60 ± 112.45	63.06 ± 29.39	216.20 ± 145.96	120.80 ± 57.7	314.98 ± 151.52	111.6 ± 50.64	175.38 ± 106.22	278.89 ± 188.08	218 ± 44.56
Average Soil Depth (cm)	31.98	25.64	10.03	8.40	N/A	13.12	10.68	9.24	4.78	4.09	N/A
Observed Pitfall Trap Species	9.00	4.00	11.00	8.00	11.00	10.00	7.00	3.00	5.00	7.00	6.00
Average Arthropod Biomass per day (g)	0.036	0.244	0.085	0.020	0.024	0.199	0.008	0.022	0.040	0.159	0.003
Arthropod Abundance per day (pitfall)	24.79	20.50	46.97	4.75	37.33	21.00	13.14	10.81	14.40	7.33	11.20
Arthropod Abundance per day (sticky)	14.14 ± 2.28	39.1 ± 11.90	11.51 ± 3.32	6.75 ± 3.93	11.84 ± 2.36	26.9 ± 4.70	6.63 ± 1.88	23.73 ± 3.70	6.7 ± 0.93	30.53 ± 6.45	37.01 ± 14.35
Percent Vegetation Cover	53.33% ± 3.6	79.57% ± 5.01	55% ± 3.97	41.67% ± 7.39	56.67% ± 8.05	35% ± 5.53	41.67% ± 6.16	24.17% ± 1.6	45.83% ± 6.29	44.27% ± 4.85	54.17% ± 16.52

Table A2. Coordinates and names of islands featured in Figure 2 (map of rabbit distribution in the Cyclades). Highlighted islands were used in this study.

Number	Island	Documented By	Latitude	Longitude
1	Akamatis	JF	37.856210	24.746671
2	Megalo	JF	37.848055	24.750482
3	Andros	Masseti	37.854974	24.851252
4	Giaros	Masseti	37.611585	24.715466
5	Syros	JF	37.424795	24.912170
6	Dydimi	JF	37.426787	24.973094
7	Tinos	Masseti	37.599734	25.130841
8	Kea	Masseti	37.623806	24.336106
9	Kithnos	Masseti	37.387624	24.421376
10	Serifos	Masseti	37.162023	24.483325
11	Vous	JF	37.142318	24.561666
12	Kitriani	JF	36.904085	24.726438
13	Kimolos	Masseti	36.809761	24.557400
14	Milos	Masseti	36.683792	24.460690
15	Folegandros	Masseti	36.633207	24.896052
16	Kardiotisa	Masseti	36.629623	25.017722
17	Sikinos	Masseti	36.676971	25.116797
18	Ios	JF	36.724885	25.319705
19	Psathonisi	JF	36.749432	25.364105
20	Cristiana	Masseti	36.249606	25.202587
21	Santorini	Masseti	36.387112	25.455643
22	Despotiko	JF	36.962468	25.002743
23	**Lower Fira**	**JF**	**37.054512**	**25.082179**
24	**Upper Fira**	**JF**	**37.061153**	**25.085618**
25	Antiparos	Masseti	36.998277	25.047446
26	**Glarombi**	**JF**	**36.979221**	**25.109781**
27	**Tigani**	**JF**	**36.976707**	**25.116035**
28	**Panterionisi**	**JF**	**36.971061**	**25.119186**
29	**Paros**	**JF**	**37.050244**	**25.181891**
30	**Galiatsos**	**JF**	**37.130813**	**25.245973**
31	Gaidouronisi	JF	37.157282	25.268061
32	Ovriokastro	Masseti	37.152427	25.296432
33	**Filitzi**	**JF**	**37.124964**	**25.289978**
34	Mando	JF	37.089253	25.361565
35	Naxos	JF	37.054048	25.482152
36	Macheres	JF	37.085339	25.695641
37	Agia Paraskevi	JF	37.079723	25.70582
38	Donousa	JF	37.107447	25.812942
39	Prasoura	JF	36.986712	25.638222
40	Ano Koufonisi	JF	36.941124	25.606195
41	Glaronisi	JF	36.916409	25.605192
42	Schoinoussa	JF	36.873949	25.519387
43	Keros	JF	36.890691	25.651398

Table A2. *Cont.*

Number	Island	Documented By	Latitude	Longitude
44	Megali Plaka	JF	36.877677	25.626787
45	Andreas	JF	36.861629	25.621933
46	Kato Antikeri	JF	36.841104	25.665571
47	Pano Antikeri	JF	36.846570	25.680731
48	**Gramvousa**	**JF**	**36.807258**	**25.745579**
49	Amorgos	JF	36.846272	25.898340
50	Nikouria	JF	36.886292	25.908540
51	Anydros	JF	36.625212	25.682358
52	Anafi	Masseti	36.368622	25.773609
53	Pachia	Masseti	36.271722	25.830563
54	Makria	Masseti	36.269564	25.886052
55	Megalo Sofrano	JF	36.075218	26.400744
56	Mikro Sofrano	JF	36.046704	26.409475
57	Syrna	JF	36.347422	26.676584
58	Mesonisi	JF	36.299744	26.740516
59	Astypalea	JF	36.580607	26.370291
60	Diapori	JF	36.570960	26.387153
61	Chtapodia	JF	37.410302	25.567967
62	Mykonos	Masseti	37.444814	25.379182
63	Delos	Masseti	37.391613	25.271329
64	Megalos Revmatiaris	JF	37.394672	25.260716
65	Rhinia	Masseti	37.413464	25.222172
66	Kato Koufonisi	JF	36.912094	25.577397

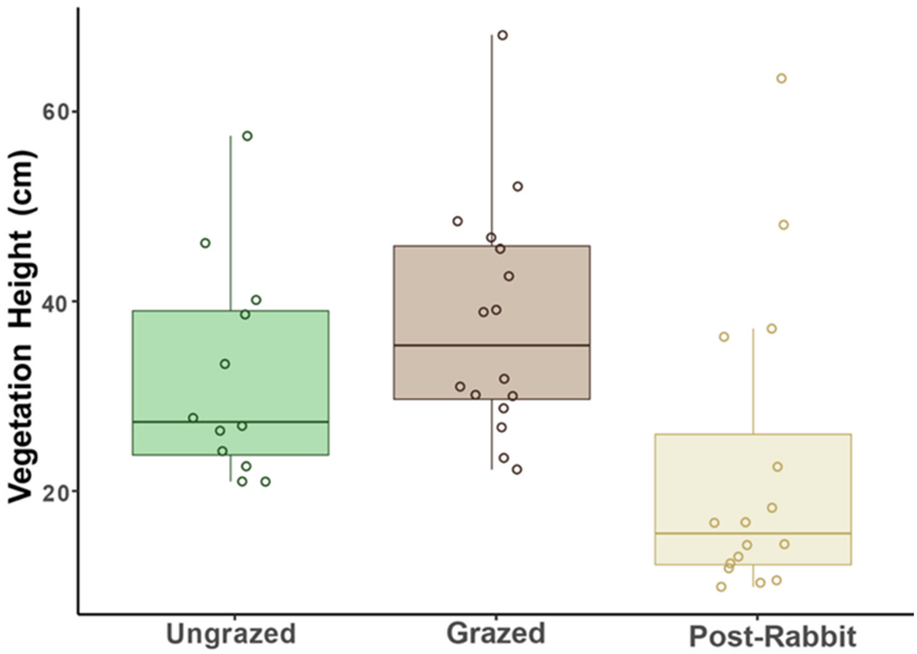

Figure A1. Box plot displaying the variation in vegetation height (cm) across the three island classifications. Individual data points are overlaid across the boxplots.

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