Management and Assessment of introduced European Rabbits (*Oryctolagus cuniculus*) in Island Ecosystems in the Mediterranean

By

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Abstract

The Cycladic Islands (in the Aegean Sea, Greece) are part of the Mediterranean Basin biodiversity hotspot and harbor many 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 impacts of the European rabbit (*Oryctolagus cuniculus*), an herbivore that has been released on numerous small 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 Aegean Islands were investigated by assessing the abundance, composition, and diversity of plant and arthropod communities. Our results indicate that ungrazed islands have more arthropod species, more specialized or endemic plant species, and less exposed soil. While ungrazed islands did not possess higher plant species richness, they did harbor significantly more small-island endemic taxa relative to presently grazed islands. A non-significant trend in variables collected from post-rabbit islands in comparison to either currently grazed or ungrazed islands suggested that these islands only partially recover after the pressure of grazing is removed. This study indicates that native plant communities in the Mediterranean are not adapted to the presence of this near-native species and that the practice of intentionally releasing rabbits has significant and lasting negative ecological impacts, especially on island endemic plants. We therefore recommend the practice be explicitly banned by government agencies and that rabbit removal projects are initiated to restore critically important small island habitats and protect them from the compounding effects of vegetation loss and climate change.

Keywords: *Oryctolagus cuniculus*, island communities, endemic species, introduced herbivores, rabbits, Mediterranean, Aegean Islands

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Contents

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 (Sayre et al., 2018) they harbor more 20% of Earth's biodiversity (Fernández-Palacios et al., 2021). Islands have been identified as global centers of endemism for both plants and vertebrates (Kier et al., 2009). The Mediterranean Basin specifically, is one of the world's most diverse regions in terms of faunal and botanical richness (Vié et al., 2009). 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 (Myers et al., 2000). More specifically, the Aegean Islands (Greece), located in the NE Mediterranean Basin, are a key part of this Mediterranean biodiversity hotspot and harbor thousands of endemic taxa (Cuttelod et al., 2009).

Approximately 50% of all species recognized as threatened by the International Union for Conservation of Nature (IUCN), occur in island ecosystems (Fernández-Palacios et al., 2021). Island biodiversity is disproportionately imperiled by a variety of anthropogenic causes, including hunting, habitat loss, and introduction of invasive species. For example, island endemic species face increasingly serious conservation challenges because of invasive organisms, accidentally or intentionally introduced by humans. 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 (Leclerc et al., 2018).

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 (Gratsia, 2010) and during that time have used the landscape extensively for agriculture and livestock grazing. As a result of the pervasive presence of sheep and goats, most of the Cycladic plant communities are shaped by herbivory, with many mainland island species having well-developed defenses such as thorns and various allelochemicals. However, in contrast to the larger islands, many of the smaller Cycladic islets have been too arid to sustain human populations, and consequently have escaped the impacts of introduced livestock. As a result, 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 (Salladay and Ramirez, 2018), such as the European rabbit (*Oryctolagus cuniculus*) that is native in the western Mediterranean. Bergmeier & Dimopoulos (2003) have shown that introduced herbivores can decrease the proportion of islet specialist plant taxa by modifying the competitive balance of species on the island. The combination of limited range size and vulnerability to herbivory makes such small island specialists highly susceptible to extinction with the introduction of invasive herbivores.

The European rabbit *Oryctolagus cuniculus* is native to the Iberian Peninsula in SW Europe, but now has a worldwide distribution, being found on all continents except Antarctica (Marín-Garcia and Llobat, 2021). These rabbits are considered to be a generalist species, as they can flexibly adapt their dietary strategies based on their environment and the availability of various vegetation types (Marín-Garcia and Llobat, 2021). As a result, rabbits are considered one of the most wide-spread invasive mammals worldwide, with a variety of serious effects in newly-colonized habitats (Marín-Garcia and Llobat, 2021). Previous studies have documented the devastating impacts that rabbits have on other ecosystems through excessive herbivory (Courchamp *et al.,* 1999, Carlberg et al., 2022). For example, on Laysan Island in the Hawaiian archipelago, rabbits were responsible for the extinction of 26 native species between the years of 1903 and 1923 (Courchamp et al., 1999).

Beyond the impacts on plants they feed on, introduced rabbits have also been the cause of significant population declines of various other native species around the world, including reptiles and birds (Courchamp et al., 1999, Carlberg et al., 2022). For example, previous studies have shown competition with native species for food and resources, as well as destruction of habitat from burrowing and digging, has led to long-term losses of the native taxa of oceanic islands (Courchamp et al., 1999). On islands in Western Mexico, rabbits alone were responsible for the near extinction of *Dudleyi linearis*, an endemic succulent that only showed signs of recovery after the removal of rabbits from the islands (Aguirre-Muñoz, 2008). 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 (Marchant et al., 2011, North et al., 1994, Eldridge and Myers, 2001). 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 (Lees and Bell, 2008).

The European rabbit has a wide distribution on both large and small islands of the Aegean Sea. Being a Western Mediterranean Basin endemic, the species is quasi-native, and well adapted to the locally prevailing, arid conditions. While large island populations are more stable and have been introduced for at least 300 years (Tournefort 1741), their presence on the Cycladic islands was first studied by Theodor Erhard (von Heldreich, 1878, Erhard, 1858; see also Table 2 in Appendix). Only relatively recently have rabbits been released on small, otherwise uninhabited islets by both Aegean locals and hunters as a secondary source of hunted protein and based on informal conversations 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 made this impractical before the 1900s.

The impacts of rabbits on Aegean Sea island ecosystems are not well understood. Because rabbits are semi-native to the region, it is possible that species have adapted to their presence, and it is reasonable to assume that European rabbit establishment and impact on islands would remain moderate. However, a recent study on Lemnos, a large island in the northeastern Aegean Sea, showed that European rabbits can readily adapt to seasonal changes in food quality and availability and become quite abundant (Kontsiotis et al., 2015). As a matter of fact, rabbit populations there have grown so rapidly, that the species is now considered to be an agricultural pest (Kontsiotis et al., 2019). Similarly, on smaller islands with seabird nesting colonies, rabbit herbivory alone can reduce densities of seabird colonies by approximately 54%, and the simultaneous presence of both rabbits and goats reduces gull colony density by 71% (Carlberg et al., 2022). While goats as herbivores also have impacts on small islands (Gicizki et al., 2018), the impact of goats cannot be readily extrapolated to rabbits. The reason 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 (Bello-Rodríguez et al., 2021), creating a pressing need for relevant information to guide management policies.

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. By comparing islands without rabbits, islands with rabbits, and islands with eradicated rabbit populations, we tested the short and long term impacts rabbit grazing is having on the abundance, composition, and diversity of the vegetation and arthropods of small islands, as well as whether vegetation removal is furthering soil erosion. Islands without rabbits served as control sites to assess current impacts on islands with rabbits, while islands previously inhabited by rabbits were used to assess the potential for islands to recover after grazing.

Methods

Study Area

Previous surveys of the Cycladic islands in the Aegean Sea (Greece, NE Mediterranean Basin) documented the presence of rabbits across many of the islands (Fig. 1). This included the work of Masseti [2012] and Johannes Foufopoulos [2010 - 2022]. Rabbits have a wide distribution on both larger and smaller islands in the Cyclades. Based on a combination of previously published information (Masseti, 2012) and our own data, it is clear that rabbits exist in all major inhabited islands in the region with a possible exception of Siphnos (see Figure 1). The species has also been detected on 42 smaller satellite islands in the region (see Figure 1).

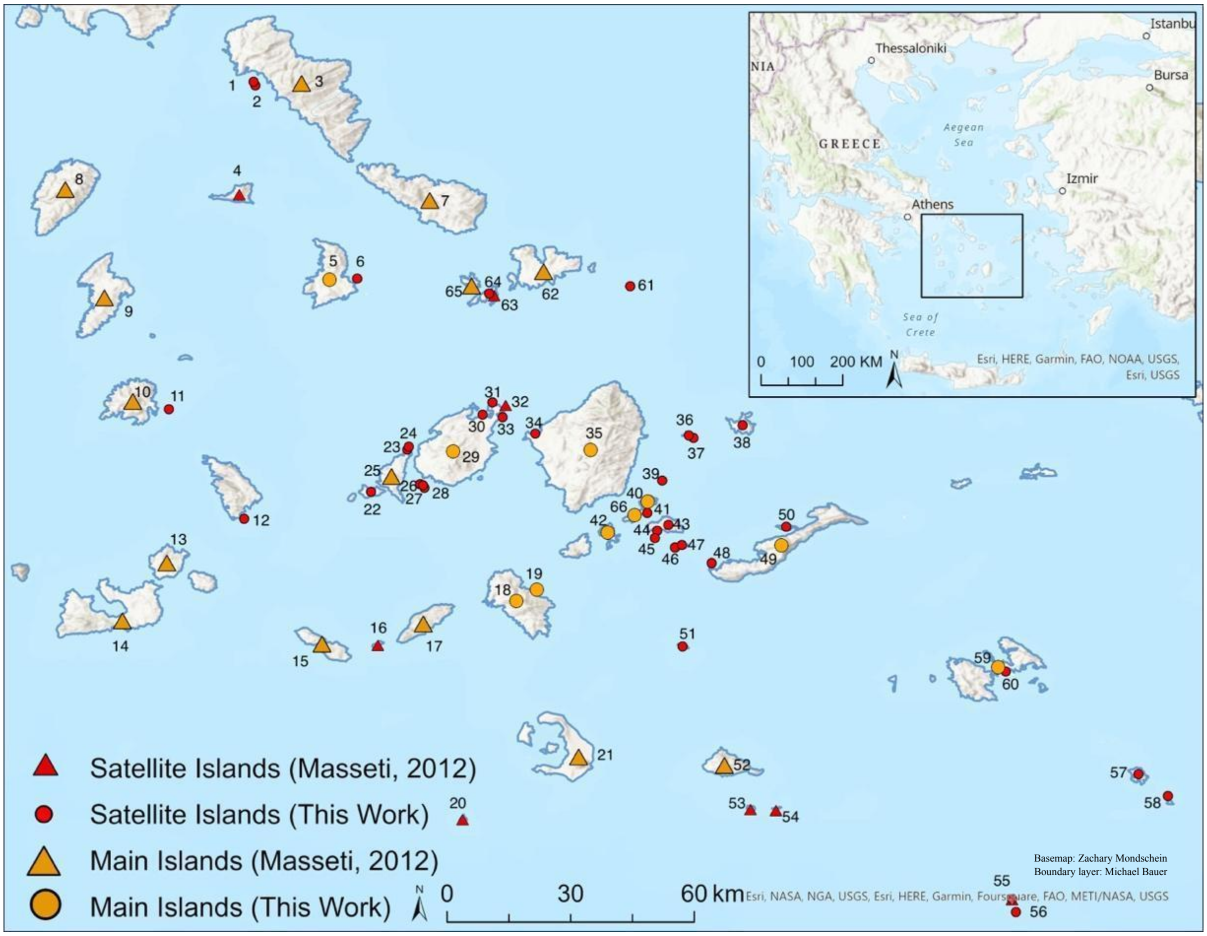

Figure 1: Rabbit introductions have been an increasingly widespread phenomenon on Aegean Sea islands. The above map is of the islands in the Cyclades with documented introduced European rabbit populations. Satellite islands (denoted in red) are likely to harbor floras with small island specialists and 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 2 in the Appendix.

During the May – July 2022 field season, we collected detailed comparative ecological data for a subset of the surveyed islands. Data were collected 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 2).

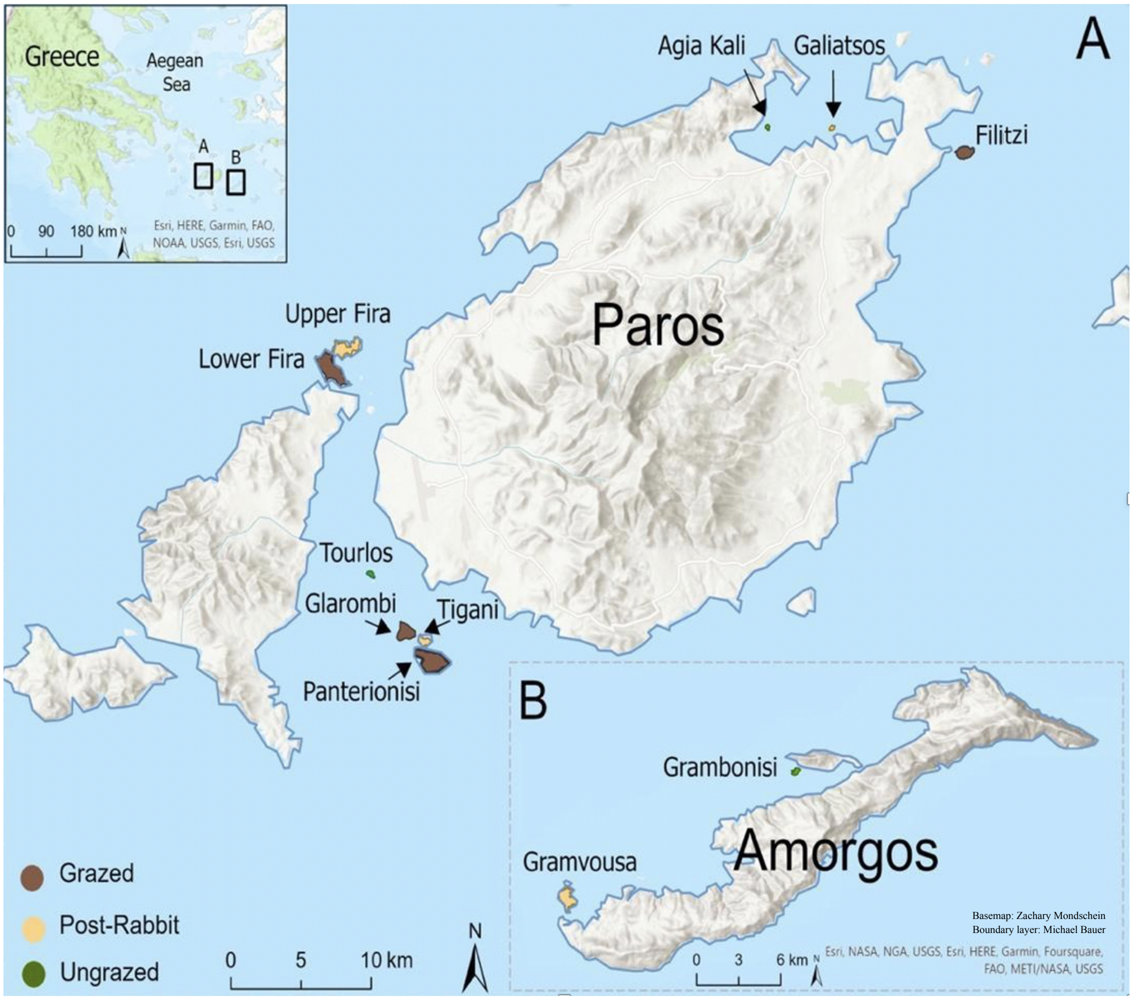

Figure 2: Map of study sites, with brown indicating islands that are currently grazed by rabbits, green indicating islands that have never been grazed, and orange representing islands with eradicated rabbit populations.

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 and less than 2.5 km from the closest large island (Paros, Antiparos, or Amorgos). There were no significant differences in island size between the three island categories (F = 0.862, N =11, P-value = 0.458, ANOVA). Additionally, 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 (Médail, 2022). 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. 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 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.

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 of endemic and specialist species, and total number of plant taxa. This was done using a combination of line transects and study quadrats (as in Gizicki et al., 2018). Four transects of 30 meters were established on each island, one in each of the four cardinal directions at a haphazard 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 meter along each transect, 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 (in cm). Vegetation height measurements (cm) were averaged for each transect (4 per island) to determine the variations across grazing categories. Percentage of each substrate type, as well as average vegetation height values were then calculated for each transect (Gizicki et al., 2018). Additionally, five quadrats (60cm x 60cm squares) were haphazardly placed on each island and the vegetation in each quadrat was identified to species (Lafranchis & Sfikas, 2009, Fielding and Turland, 2005). To determine the standing biomass on each island, all above-ground biomass from each quadrat was clipped, and the clipped material collected, sun-dried and weighed until the weight remained constant for a minimum of two days (Gizicki et al., 2018). All identified plants were assigned to one of three categories (generalist, endemic or specialist, and weedy species) dependent on their distribution pattern on the islands, habitat types, and ecological requirements.

Arthropod Community Assessment

Arthropod abundance and characteristics were quantified using sticky traps and pitfall traps on the study islands. The sticky traps consisted of a bright yellow plastic card (7.62cm x 12.7cm) covered with a sticky, non-drying film and affixed to metal wire holders approximately ~10 inches above the ground. The pitfall traps (~7cm in diameter and ~11cm deep), were constructed from plastic cups that were sunk into the ground, ensuring 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 (Schmidt et al., 2006). After ~2.5 days, pitfall traps were collected, and the species were identified, cleaned, counted, and then dried and weighed. Arthropod abundance data for both pitfall and sticky traps were standardized by both area and time deployed, as well as number of successful traps. All specimens were preserved in isopropyl alcohol and sent to the Natural History Museum at the University of Crete for long-term storage.

Grazing Intensity

In order to determine the intensity of grazing on islands inhabited by rabbits and quantify the amount of biomass consumed, we collected rabbit fecal matter along two, 50m long and 60cm wide, transect lines. The pellets collected were then dried in the sun until no more weight loss was detectable, and then mass (in g) was recorded.

Soil Characteristics

To determine whether European rabbits are contributing to soil loss, we assessed soil depth measured on all except two of the study islands (Grambonisi and Gramvousa, due to data collection limitations). Soil depth measurements were taken on each island at five 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 0cm was recorded. If the soil depth was greater than the iron rod, the measurement was recorded as the full length of the rod (40cm). In addition, in order to determine any effects of rabbits on soil chemistry, 4-5 soil samples were collected per island at haphazardly chosen locations and sent to a collaborating research group at the University of Patras (Greece).

Statistical Analyses

All statistical analyses were run in RStudio (Rstudio Team, 2023), and SpadeR was used for all species diversity estimates (Chao et al., 2015). Variables were compared across the three grazing classifications – ungrazed, grazed, and post-rabbit. To account for any possible underlying confounding effects of island area on resident species number because of the species-area relationship (MacArthur and Wilson, 1967), area was included when comparing species diversity (both plants and arthropods) across ungrazed, grazed, and post-rabbit islands. Linear Mixed Models were used to analyze for 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's Product-Moment correlations were used to determine the relationships between variables.

To analyze for species evenness for plants, a bias-corrected Chao1 nonparametric asymptotic estimator was used to approximate the number of plant species on the island using the SpadeR program (Chao et al., 2009, Chao et al., 2015) (see Appendix).

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

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 (Chao et al., 2015). The estimated species per island was then divided by area to determine if there was a difference across the three types of grazing classifications.

Results

Vegetation

Four types of vegetation characteristics were assessed, including the percentage of vegetation cover, aboveground biomass weight, vegetation height, and the diversity of plant species. A total of 67 species were identified across the 11 islands and categorized as weedy, generalist, and specialist or endemic species based on distribution patterns and habitat/survival requirements.

Ground Cover

Rock and soil cover were combined to determine the total percentage of bare cover on each island, and bush and herbaceous cover were combined to determine total percentage of vegetation cover. Each cover type - rock, soil, bush, and herbaceous - were also analyzed individually to look at the specific differences in the cover types (Figure 3). The extent of bare soil was 20.42% higher on grazed islands compared to ungrazed islands (40.75%

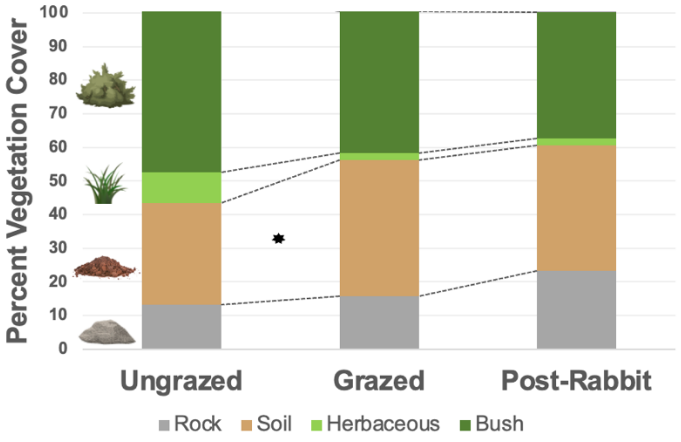

Figure 3: Changes in the percent of bush, herbaceous vegetation, bare soil, and exposed rock cover across the three types of grazing categories. Significant differences are denoted by *.

(grazed) vs. 20.20% (ungrazed); T = -2.626, N = 44, P-value = 0.030, LMM). There was also a near-significant reduction of 7.42% (1.67% (grazed) vs. 9.09% (ungrazed); T = 2.084, N = 44, P-value = 0.071, LMM) in herbaceous vegetation cover between ungrazed and grazed islands. The percentage of vegetation (combination of herbaceous and bush cover) showed a near-significant trend where vegetation cover was higher on ungrazed islands compared to grazed islands (43.75% (grazed) vs. 62.63% (ungrazed); T = 2.045, N = 44, P-value = 0.075 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.

Vegetation Height

Vegetation height was not statistically different between the three classifications of islands (F = 1.996, N = 44, P-value = 0.198, LMM) (see Appendix). However, vegetation height was significantly positively correlated with vegetation cover (R = 0.491, P-value = 0.0007, Pearson's R) indicating that

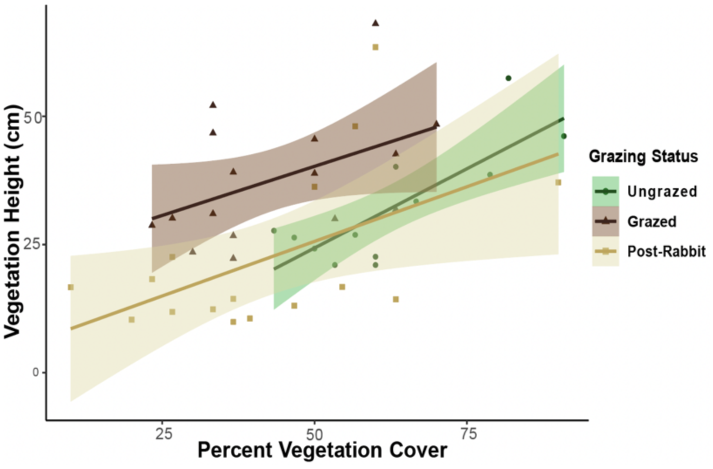

Figure 4: Correlation plot displaying the relationship between vegetation height (cm) and percent vegetation cover.

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 plants to grow higher.

Vegetation Biomass

There was a near-significant reduction in aboveground plant biomass on grazed islands relative to ungrazed ones (T = 1.806, N = 55, P-value = 0.077, LMM). Ungrazed islands had an average of 169.5g more standing biomass (94.82% greater than grazed islands). There was no documented difference between post-rabbit and ungrazed or post-rabbit and grazed islands, however, post-rabbit islands had an average of 17.05g more aboveground biomass than grazed islands. Aboveground biomass was not significantly correlated with vegetation height (R = 0.121, P-value = 0.432, Pearson's R).

Vegetation Species Richness

The estimated plant species richness per island (Chao1 estimator) was divided by area to determine if there was a difference in the estimated number of plant species between ungrazed, grazed, and post-rabbit sites. When considering the total number of plant species from each island, there were no significant differences between the three island categories in the observed number of species (F = 1.011, N = 11, P-value = 0.406, ANOVA), nor the estimated number of species per island (F = 0.646, 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 = 6.496, N = 11, P-value = 0.017, ANOVA) compared to grazed islands, while post-rabbit islands did not differ significantly from either (Figure 5). Island types did not differ significantly in the number of weedy species (F = 0.099, n = 11, P-value = 0.907, ANOVA).

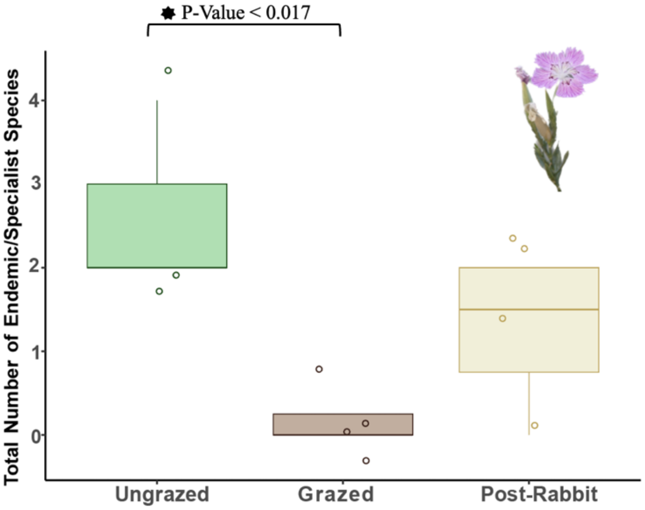

Figure 5: Total number of specialist or endemic plant species across the three different grazing statuses. Islands with rabbits had significantly fewer such plant species relative to ungrazed islands.

Grazing intensity

Fecal pellets were only collected on grazed islands; Lower Fira had the most fecal pellet weight (total of 717g), followed by Filitzi (527g), then Panterionisi (138g), and then Glarombi (123g). There was not a significant relationship between aboveground biomass and fecal pellet weight (R = 0.783, P-value = 0.218, Pearson's R).

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 3,194 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. Five pitfall and five sticky traps were deployed on each island and left for an average of 61.79 hours ± 19.37 hours without human interference. The amount of time each trap was deployed was not significantly correlated with the arthropod abundance in pitfall traps (R = .427, N = 11, P-value = 0.19, Pearson’s R), nor in sticky traps (R = 0.174, N = 11, P-value = 0.61, Pearson’s R) or species diversity of the pitfall (R = 0.256, N = 11, P-value = 0.446, Pearson’s R) or sticky traps (R = -0.305, N = 11, P-value = 0.367, Pearson’s R). However, to remain consistent with standard practice, we still standardized for time in the following analyses.

The daily biomass of arthropods collected per day was not significantly different between ungrazed, grazed, and post-rabbit islands (F = 0.153, 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 = 9.9204, 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 = 4.8668, N =

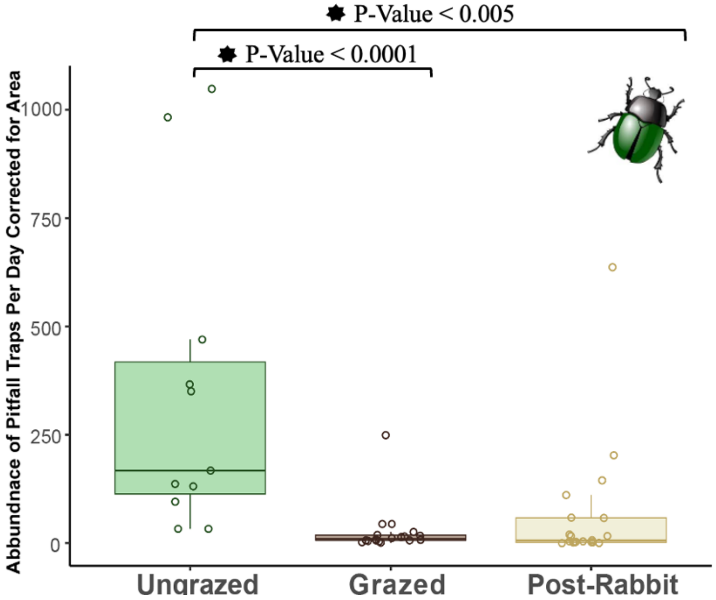

Figure 6: The graph displays the data for the abundance of arthropods per pitfall traps (divided by area)

10, P-value = 0.0473, 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 = 0.721, N = 55, P-value = 0.516, LMM).

Soil

We found no significant difference in soil depth between three island classifications (F = 0.23, N = 45, P = 0.801, LMM). There was a near-significant positive relationship between soil depth and the percentage of vegetation cover (R = 0.296, P-value = 0.08, Pearson's R).

Discussion

In this study, we determine for the first time in a quantitatively rigorous manner the presence and impacts of the near-native herbivore, the European rabbit (*Oryctolagus cuniculus)*, on island ecosystems in the Aegean Sea and indicate that herbivory from this species has far-reaching effects on island ecosystems in the Cyclades island cluster.

We found that the extent of bare ground (i.e. areas of vegetation-free soil) was higher on grazed islands, indicating that rabbits impacted the amount of island vegetation cover. We also document a non-significant but distinct trend toward less herbaceous vegetation cover on grazed islands, indicating that rabbits had a disproportionate preference for herbaceous plants over woody plants. Indeed, we found that on rabbit islands, perennial vegetation such as the bushes *Pistacea lentiscus* and *Juniperus phoenicea* - which tend to be structurally and chemically defended- were still relatively common, while endemic and specialist herbs were significantly less abundant. This most likely also contributed to the lack of strong differences in 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.

Additionally, grazed islands had significantly more bare ground than ungrazed islands. The effects of soil erosion are likely to be intensified by an expected increase in wind (as a result of climate change) as well as decreased vegetation cover on the islands (Bloom et al. 2008; Moemken et al. 2018). Rabbits also accelerate soil erosion as a result of digging and burrowing on the island (Courchamp et al., 1999), loosening the friable soil that is then more easily blown away. The effects of rabbit herbivory are likely to be further exacerbated in the future by the increasingly drier and hotter conditions that the region is now facing as the result of climate change (Haarsma et al. 2009; Ulbrich et al. 2006).

Across its non-native distribution, the release of these lagomorphs pose consequential ecological concerns (Rocha et al., 2017). Less plant cover, less aboveground biomass, and shallower soil depth contribute to the shifting of plant assemblages on the islands. We did not observe a difference in the 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 (Agnew and Flux, 1970).

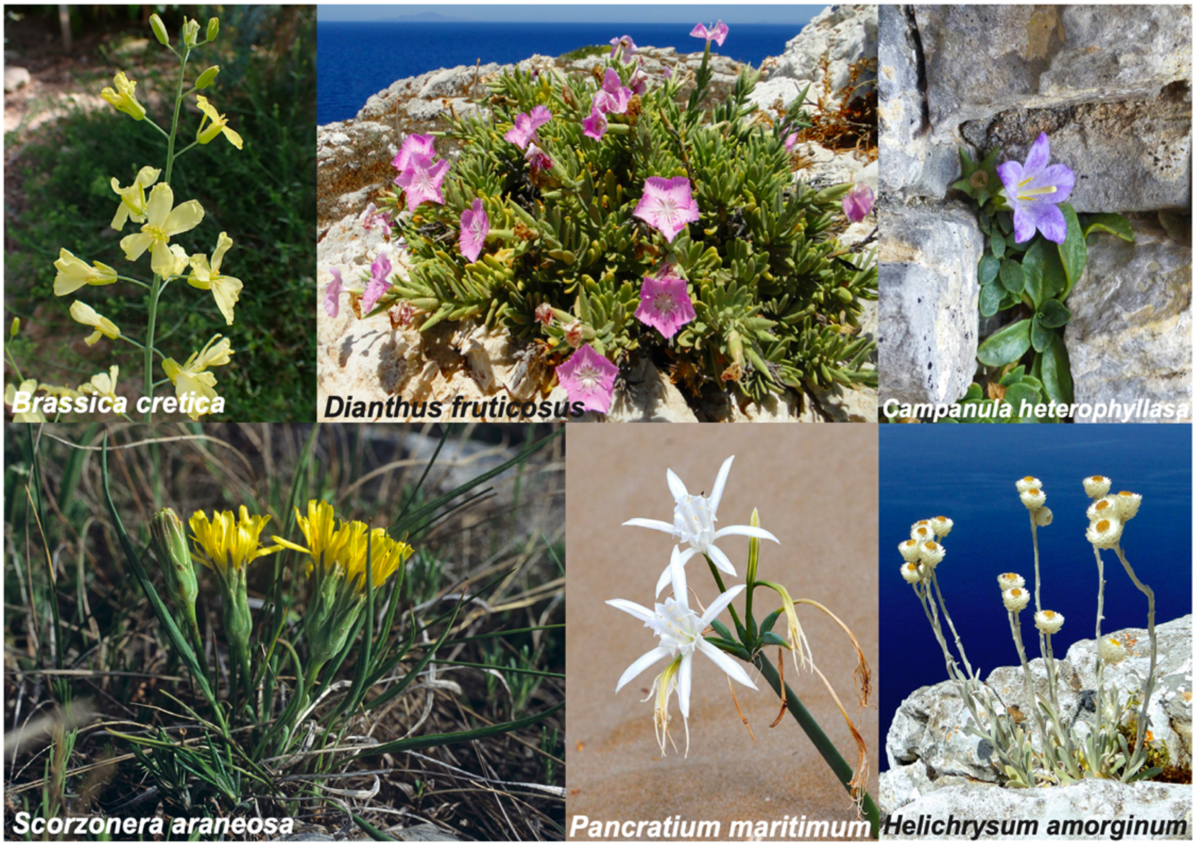

Figure 7: Endemic species found on the Aegean Islands - vulnerable to impacts from grazing. *Brassica cretica* (Kenraiz, 2022), *Dianthus fruticosus* (Foufopoulos, 2022), *Campanula heterophylla* (Ampithoe, 2017), *Scorzonera araneosa* (Eckstein, 2002), *Pancratium maritimum* (Cebeci, 2013), *Helichrysum amorginum* (I. Gavalas, 2014).

Greece harbors one of the richest and most diverse floras in Europe (Tzanoudakis and Panitsa, 1995), and much of the endemic plant species are located on the Aegean Islands. However, these island floras are also quite vulnerable, with populations of endemic species frequently in decline or facing extinction (Greuter, 1995) (Figure 7). Insular ecosystems are subject to disproportionately higher rates of extinction due to a combination of geographical 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 defenses such as thorns or toxic chemicals (Salladay and Ramirez, 2018). This study demonstrates that island specialist and endemic plants are significantly less frequent on grazed islands, suggesting that rabbits are shifting island species community compositions and disproportionally threatening endemic vegetation. These findings also mirror results of previous studies in other island ecosystems that show how rabbit herbivory can damage endemic species communities (Marchant et al., 2011, North et al., 1994, Eldridge and Myers, 2001). 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 nitrogen and negatively impacting the growth of endemic species (Cubas et al., 2018).

A significantly greater number of arthropod species and individuals were observed on ungrazed islands, suggesting that arthropods are also vulnerable to impacts from grazing. 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, morphospecies identifications may not be precise enough to determine changes in arthropod communities, and future research is encouraged to further study the implications of grazing on arthropod communities on the Aegean Islands. Finally, presence of lizards on some islands may also be a confounding variable when assessing herbivory impacts on arthropod assemblages, as some islands (Gramvousa, Grambonisi, Galiatsos, Upper Fira, and Lower Fira) harbored *Podarcis erhardii* (Aegean Wall Lizards) while others were lizard-free.

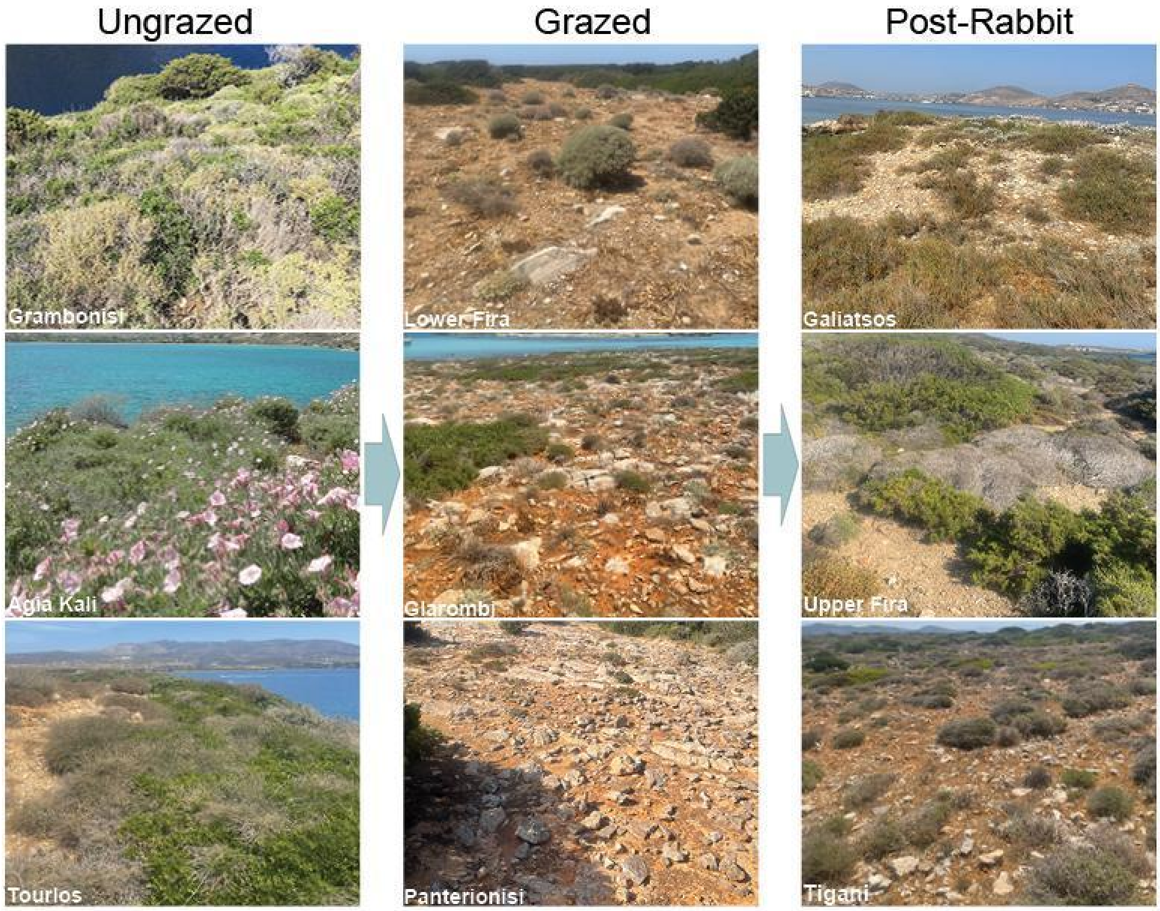

Figure 8: Photographs of some of our study islands across the three rabbit categories. Images reveal how rabbits mainly target low, herbaceous vegetation and less woody perennial species (e.g. *Pistacea lentiscus*) that often remain unaffected by rabbits due to their chemical and physical defenses or height. Post-rabbit islands are characterized primarily by the re-colonization of areas between these scrubby perrenials by low, annuals (R). However, any such recovery never attains the original, ungrazed levels of vegetation cover. Images from: Angelina Kossoff, 2022 and Agia Kali from Johannes Foufopoulos, 2022.

Both arthropod and plant data from this study suggest a partial recovery of species after the removal of the European rabbit on islands. A complete recovery was not shown in this study (Figure 8), potentially because 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. There was a trend showing that vegetation cover was correlated with deeper soil, so the decrease in vegetation cover suggests that until soil recovers, there will not be a full ecosystem recovery. Unfortunately, geological evidence suggests that soil formation is such a slow process that it will likely take thousands of years to recover (Van Breemen and Buurman, 2002).

These findings are corroborated by a study conducted on Macquarie Island, an island in the Pacific Ocean, that demonstrated partial recovery in vegetation after rabbit control programs were implemented was possible (Cospon and Whinam, 1998). Similar trends in island recovery were observed in 2015 from grazing by goat populations on the Aegean Islands (Gizicki et al., 2018).

Despite a potential lack of full recovery, this work provides evidence that eradication of rabbits from Cycladic islands will still deliver clear conservation benefits for the 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, Copson and Whinam, 2001), several factors suggest that this will not be as challenging on Aegean Sea islands. First, because the focal islands are relatively small, and often with 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 do not 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, 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 because 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 (Zavaleta et al., 2001). Might there be such unintended ecological consequences from rabbit removal from Aegean islands? Our investigation from islands that used to have rabbits and are now rabbit-free, does not provide such evidence. Removal of rabbits did not result in the take-over of any exotic plant species released from rabbit herbivory. The only 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*).

One limitation of this study includes lack of knowledge of the actual time elapsed since rabbit eradication on post-rabbit islands, as well as unknown time since rabbit introduction on grazed islands. However, in informal conversations local hunters indicated that most rabbit introductions occurred after WWII. Furthermore, they also suggested that past rabbit extirpations occurred in the last 20 years as the result of hunting, starvation, or diseases. We recommend that future research include obtaining a larger sample size to perform a path analysis while controlling for time since eradication and introduction.

Additionally, the inclusion of grazing intensity as a variable in the analyses could contribute to further understanding of impacts from the rabbit herbivory.

The results of this study indicate that measures should be taken to prevent the introduction of non-native species to insular ecosystems, even if their original habitat range is of similar ecological composition. 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 removal of invasives. 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.

Conclusion

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 show that this near-native species affects disproportionally 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 towards the generalist taxa with widespread distributions. Arthropods also showed a significant decline in both 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 numbers of nesting seabirds, therefore undermining the supply of critical nutrients that are necessary for proper functioning of these Mediterranean island ecosystems. This study indicates that although they originated in the Mediterranean Basin, European rabbits still act as disruptive agents to island species communities.

The study islands demonstrated that at least partial vegetation recovery is possible after the removal of rabbits 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 a previous study (Gizicki et al. 2018), demonstrate that ecological naivete and restricted distributions render endemic taxa disproportionately vulnerable to grazing from introduced herbivores. These data indicate that desertification is a result of grazing, as percent 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 through the reduced vegetation cover and exposed soil. Ultimately, this demonstrates the significance for careful management of these islands and the need for further exploration of restoration techniques for endemic and vulnerable island species.

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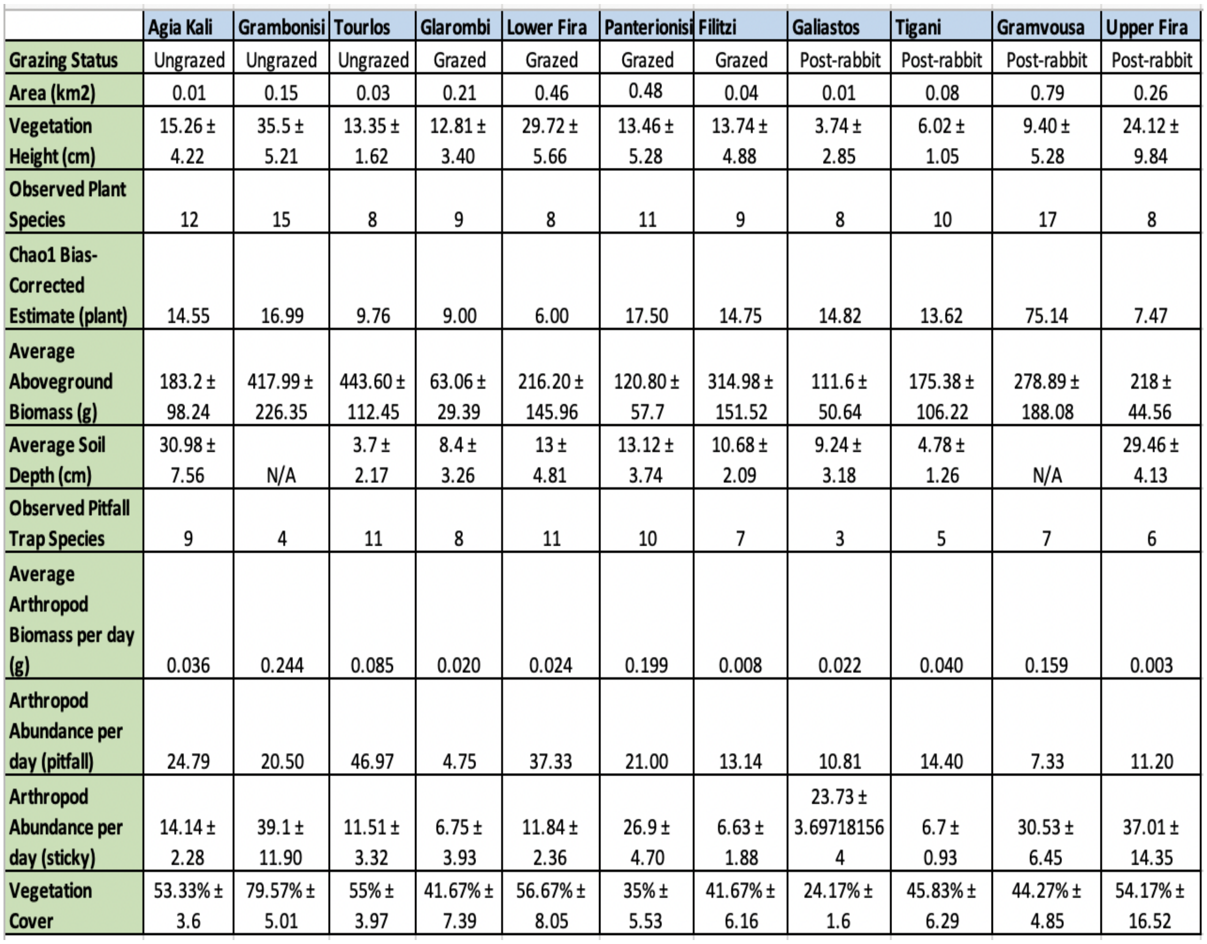
Appendix



	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 (km2)	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	15	8	9	8	11	9	8	10	17	8
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)	30.98 ± 7.56	N/A	3.7 ± 2.17	8.4 ± 3.26	13 ± 4.81	13.12 ± 3.74	10.68 ± 2.09	9.24 ± 3.18	4.78 ± 1.26	N/A	29.46 ± 4.13
Observed Pitfall Trap Species	9	4	11	8	11	10	7	3	5	7	6
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 ± 3.697181564	6.7 ± 0.93	30.53 ± 6.45	37.01 ± 14.35
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 1: Variables collected across study islands.

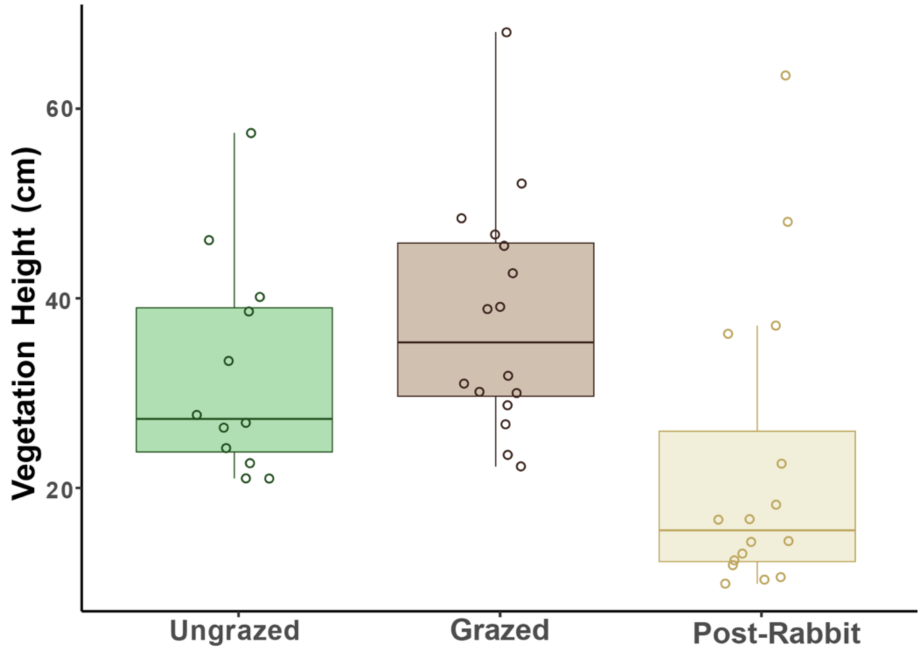


Figure 9: Box plot displaying the variation in vegetation height (cm) across the three island classifications. Individual data points are overlaid across the boxplots.

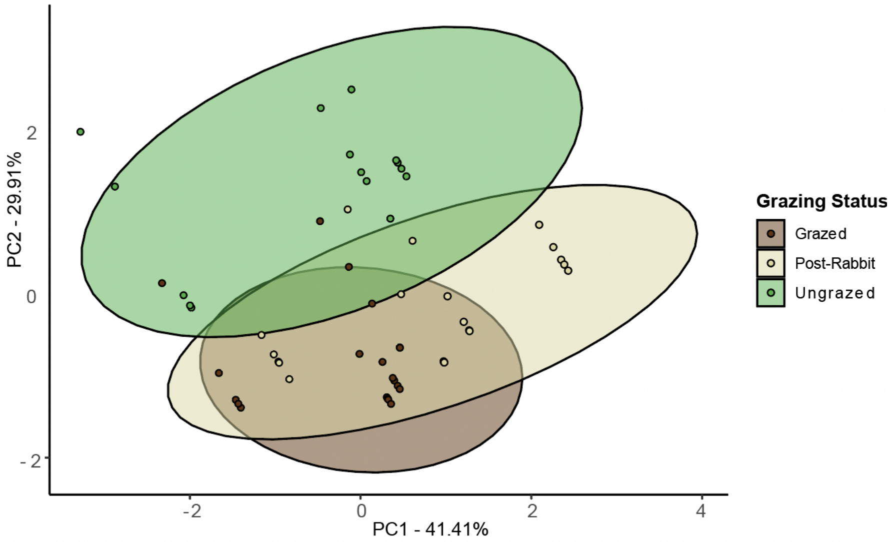


Figure 10: Principal components analysis including vegetation height, percent vegetation cover, arthropod abundance per day (corrected for area), and vegetation biomass. The figure visually represents the slight separation of ungrazed sites compared to post-rabbit and grazed islands.

Figure 11. Early historic map displaying European rabbit (*O. cuniculus*) presence on main islands in the Cyclades in the 1800s and demonstrating the complementary distributions between rabbits (red islands) and European hares (*Lepus lepus*) (blue islands) (T. Erhard, 1858).

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	Didimi	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	Kardiotissa	Masseti	36.629623	25.017722
17	Sikinos	Masseti	36.676971	25.116797
18	Ios	JF	36.724885	25.319705
19	Psathonissi	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	Gaidournosi	JF	37.157282	25.268061
32	Evreokastron	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 Pavaskevi	JF	37.079723	25.70582
38	Donousa	JF	37.107447	25.812942
39	Prasoura	JF	36.986712	25.638222
40	Ano Koufonissi	JF	36.941124	25.606195
41	Glarronissi	JF	36.916409	25.605192
42	Schoinoussa	JF	36.873949	25.519387
43	Keros	JF	36.890691	25.651398
44	Megali Plaka	JF	36.877677	25.626787
45	Coumboodians	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	Meronisi	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 Renatiatis	JF	37.394672	25.260716
65	Rhinia	Masseti	37.413464	25.222172
66	Kato Koufonissi	JF	36.912094	25.577397

Table 2: Coordinates and names of islands featured in Figure 1 (map of rabbit distribution in the Cyclades).