Effects of Invasive Goats (*Capra hircus*) on Mediterranean Island Communities

by

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Abstract

Although islands exhibit great biodiversity, a high rate of endemism and simplified food webs make them highly susceptible to disturbances such as invasive species. Introduced feral goats (*Capra hircus*), a generalist herbivore, are among the most important invasive species on islands. Many endemic island plants have evolved without intense grazing pressure and have developed few to no defenses against herbivory. Concern about the effects of goats on island communities has led to increasing numbers of goat eradication programs. Unintended consequences may follow eradications because goat grazing can have complex, community-wide effects on island food webs. We evaluated the long-term effects of goat herbivory and goat removal in a system of 16 islands in the Aegean Sea (Greece) located within the globally important Mediterranean biodiversity hotspot. In this region, goats have always been an integral part of rural economies. The seasonal introduction of goats onto small Aegean islands is of special conservation concern because these islands are inhabited by particular plant communities that have evolved in the absence of herbivory. Our data suggest that goats change plant community assemblages: they significantly decreased the height, percent cover, and biomass of vegetation on an island. Additionally, goats significantly contribute to the desertification of islands by initiating a long-term erosion cycle that delays recovery even once goats have been removed. In contrast, arthropods, important primary consumers, do not appear to be affected by goat removal as any advantages obtained in absence of goats appear to benefit higher trophic levels. This study also reaffirms the role of seabirds in providing valuable N and P marine subsidies to terrestrial food webs of Mediterranean islets. These findings demonstrate that goats have serious, long-lasting effects on small island ecosystems and that additional remediation steps are needed following goat removal.

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Contents

Introduction

One of the greatest threats to biodiversity is the worldwide spread of invasive species (Hooper et al. 2012). Both intentional and accidental introductions of exotic species have increased exponentially over the years and have radically reshaped native communities (Kolar & Lodge 2001). Myers et al. (2000) argue that at least 9 of the 25 proposed biodiversity hotspots consist entirely or principally of islands, highlighting their importance for global biodiversity. Islands host over 20% of the world's biodiversity despite only being roughly 5% of the global terrestrial area (Kier et al. 2009). Exotic species introductions have the most profound effects on isolated islands, especially those supporting unique biotic communities rich in endemic taxa (Mueller-Dombois 1981). Island ecosystems are highly susceptible to disturbances because they tend to have simplified trophic webs and high rates of endemism (Courchamp et al. 2003). Insular populations are more susceptible to extinction than mainland species (MacArthur & Wilson 1967; Foufopoulos et al. 2011). Reflecting their susceptibility, 90% of the 30 reported reptile and amphibian extinctions (Honegger 1981), 93% of the 176 documented avian extinctions (King 1985), and 81% of the 65 observed mammalian extinctions worldwide have occurred on islands (Ceballos & Brown 1995). Half of the documented extinctions of Mediterranean island endemic species have occurred on small islands (Greuter 1995). Many of the most detrimental island invasives are human associates, such as invasive rats (*Rattus spp.*), feral cats (*Felis catus*), rabbits (*Oryctolagus cuniculus*), and escaped livestock (Jones et al. 2008; Nogales et al. 2004; Bowen & Van Vuren 1997). More specifically, introduced feral livestock, such as pigs (*Sus scrofa*), sheep (*Ovis aries*), and goats (*Capra hircus*), tend to overgraze and damage island landscapes, causing soil erosion, devastating the native plant communities, and removing primary producers from island food webs (Coblentz 1978).

A key factor in the proliferation of introduced mammalian herbivores on islands is the vegetation's lack of defenses. Most plants have some sort of defense against herbivory (Marquis 1991) the extent of which is often proportional to the risk of browsing (Rhoades 1979). Until the arrival of humans, mammalian herbivores were absent from most small island ecosystems (Atkinson 1989). Due to the energetic costs of resistance in plants, species that have evolved on islands in the absence of grazing pressure often lack defenses against herbivory such as chemical deterrents, physical weapons, or a tolerance to grazing (Carlquist 1974; Coblentz 1978; Vitousek 1988). The lack of resistance traits can lead to strong shifts in the diet preferences of herbivores towards the less defended endemic flora, giving more heavily defended invasive plants a competitive advantage (Loope & Scowcroft 1985; Van Vuren & Coblentz 1987; Merlin & Juvik 1992). On New Zealand, Atkinson (2001) discovered that some of the native plants did have defenses against herbivory believed to be caused by associations with the extinct moa, a large flightless ratite. However, these defenses were only partially effective against introduced mammalian herbivores (Atkinson & Greenwood 1989). In the Mediterranean, plant species vary greatly in their levels of phenols; preferential grazing occurred on species with the lowest phenolic levels (Massei et al. 2000).

Today, goats are recognized as the sixth leading threat to vertebrate species worldwide (Bellard et al. 2016). In the early 20th century, Sir Alfred Russell Wallace noticed that, "goats are the greatest of all foes to trees" (Wallace 1911). Domesticated in the dry highlands of western Iran 10,000 years ago (Zeder & Hesse 2000), goats are able to utilize many arid habitats unsuitable for other herbivores. This adaptability arises from the combination of their slow metabolism, efficient digestive system, low water requirements, high reproduction rates, and a generalist diet (Silanikove 2000). Goats also have the ability to consume tougher, chemically-defended food, making more vegetation available to them (Devendra & McLeroy 1982).

Relatively few studies have been conducted to confirm quantitatively the effects of goat grazing on vegetation cover and species richness. Mueller-Dombois & Spatz (1972) found in Hawaii that areas where goats were excluded showed an increase in vegetation cover. Further, outside the goat exclosures, there were fewer endemic species, more exotic species, and much more barren soil and rock. Spatz & Mueller-Dombois (1973) found that the regeneration of the Hawaiian endemic koa tree (*Acacia koa*), was interrupted in areas of grazing but abundant in goat exclosures. In the Galápagos, goats have reduced or eliminated 77% of all plant species on the islands (Eckhardt 1972), and compete with the native herbivore, the Galápagos tortoise (MacFarland et al. 1974). Consequently, the decline of primary producers on islands with goat grazing constitutes a severe problem and requires better understanding and management.

Invasive goat numbers have been found in some studies to be negatively correlated with seabird populations (e.g., Pafilis et al. 2013). Islands constitute relatively closed terrestrial systems where local seabird populations provide critically important allochthonous marine nutrient subsidies to the simple local food webs (Sánchez-Piñero & Polis 2000). Seabirds leave guano, food scraps, and carrion on roosting and nesting sites. All of these serve as fertilizers for plants, which in turn can boost arthropod and other primary consumer populations (Sánchez-Piñero & Polis 2000). Indeed, nesting seabirds have been found to increase the limiting soil nutrients nitrogen (N) and phosphorus (P) (Wait et al. 2005), which in turn support dense insular primary producer populations (Kolb et al. 2010). Thus, one aim of this study was to investigate whether presence of goats is associated with decreased nesting seabird populations. Given the importance of seabirds for nutrient cycling in island systems, any factor that reduces their numbers can have impacts that go well beyond any immediate effects.

Driven by the perceived negative influences of feral goats on island ecosystems, conservation organizations have attempted to eradicate goats from numerous island sites worldwide – but with highly variable success. Failures can often be traced to a lack of quality demographic data on goat population size and ecology. To date, there have been over 120 eradications worldwide that succeeded thanks to advances in technology and improved field techniques. In recent years, eradication campaigns have been successful on increasingly larger islands. In part, success is due to new approaches: Global Positioning Systems (GPS), aerial hunting, as well as Judas goat methods (which take advantage of the gregarious lifestyles of goats to lure out all individuals; Campbell & Donlan 2005). Results of these eradications can be difficult to predict – the ecosystem may recover on its own, require some restoration or reintroduction, or become even more damaged due to ecological destabilization (Courchamp et al. 2003). Very few studies have implemented monitoring programs to evaluate the recovery of these systems after eradication. Of the few eradication studies completed, vegetation responses have varied based on region, habitat, and vegetation type, suggesting island-specific responses (Schweizer et al. 2016). Therefore, predicting the success of eradication attempts can be difficult.

Successful goat eradications can create surprising and unintended conservation problems. Adequate assessments of the consequences of eradication are hindered because ecological relationships among island organisms are often poorly understood prior to eradication (Zavaleta et al. 2001). For example, goat eradications on the Galápagos Islands led to a decline, rather than a recovery, of the endangered Galápagos Hawk (*Buteo galapagoensis*), because the species had come to depend on goat-altered habitats (Rivera-Parra et al. 2012). With declining Galápagos tortoise (*Geochelone elephantopus*) populations and goat eradications, the lack of herbivores on Pinta Island actually led to a decline in vegetation diversity through homogenization of the landscape (Hamann 1993). Similarly, on the Bonin Islands, unbeknownst to conservation managers, goat grazing kept newly arrived invasive plants under control. Once the goats were eradicated, these exotic plants overran the landscape, devastating the native plant communities (Mack & Lonsdale 2002). Roxburgh et al. (2004) discuss the "intermediate disturbance" hypothesis: the highest levels of biodiversity are attained with intermediate levels of disturbance e.g., fire, natural disasters, and grazing. Up to a point, grazing could allow less competitive, early successional species to coexist in the presence of stronger competitors (Hobbs & Huenneke 1992). In the Mediterranean, foraging by goats has been an important source of landscape heterogeneity, which allows for a mosaic of diverse habitats (San Miguel-Ayanz et al. 2010; Gabay et al. 2008). The ecological role of grazing has been so extensive, that many habitats are maintained by extensive livestock management systems (San Miguel-Ayanz et al. 2010). As a result, it has become obvious to the conservation community that in order to prevent unintended consequences of eradications, it is critical to understand the effects and life history traits of invasive goats before any eradication efforts are contemplated (Zavaleta et al. 2001).

In the Mediterranean, goat meat, milk, and cheese have always been an integral part of island economies (Hadjigeorgiou et al. 2002); most inhabited islands are grazed year-round by roving herds of goats. With the increased availability of boat motors and the reliability of access, shepherds have expanded their grazing area to relatively small but ecologically important islets. Typically, Mediterranean shepherds will release herds of goats onto such islands after the onset of the growing season, coming back to collect them after they feed on the spring vegetation flush. Such free-ranging goat herds will typically graze with limited, if any, supplemental feeding (Pafilis et al. 2013). Because islands are generally overstocked, even seasonal presence can have severe impacts on local plant communities.

However, in the last 20 years, because of policy changes and a shift away from traditional livestock husbandry, seasonal goat releases have been discontinued on several islands. This sets the stage for an investigation of the potential recovery of local ecosystems after goats have been removed.

In contrast to most studies that focus on exclosure plots, we test for effects on an island-wide scale (Greuter 1995). Islands represent spatially discrete entities making them reliable study systems. We examine effects on multiple trophic levels and their interactions. In particular, we quantify soil characteristics, vegetation characteristics, arthropod characteristics, and seabird populations on each island and combine these variables to elucidate the community-wide effects of grazing by goats.

Materials & Methods

Study Area

All fieldwork occurred in May-July 2015 on the Cycladic islands (central Aegean Sea, Greece). The climate is typical of the Mediterranean region with warm, dry summers and mild, wet winters (Gikas & Tchobanoglous 2009). Less than 14% of the precipitation in the Aegean Islands percolates into the ground, whereas 55% of the precipitation evaporates, and 33% runs off into the sea (Gikas & Tchobanoglous 2009). The islands are mainly composed of limestone and flysch substrates with shallow to no soil profiles. Located within the Mediterranean biodiversity hotspot, they represent a hyperdiverse landscape of many endemic, mainly semiarid phrygana and maquis vegetation types (Médail & Quézel 1999; Vogiatzakis & Griffiths 2008).

The vegetation is mainly arid-adapted, sclerophyllous scrub. "Islet specialist" plant species – taxa found only on small islands – play a major role in the ecosystems of the very small islands of the Aegean (Bergmeier & Dimopoulos 2003). All of the study islets have relatively simple food webs in which the top predators are lizards (*Podarcis erhardii*, *Hemidactylus turcicus*, and *Mediodactylus kotschyi*). Snakes (*Eryx jaculus*) are present only on the two largest islands in this study (Drionissi and Gramvoussa). All of our study islands are uninhabited and fall into one of three categories: islands currently being grazed by goats (Aspronissi, Fidussa, Agrilou, and Venetiko); islands which have never been grazed by goats (Turlos, Preza, Agia Kali, Drionissi, Grambonissi, North Varvaronissi, and South Varvaronissi); and those with recent goat removals (Mikros Ambelas, Petalidi, Kisiri, Psalida, and Gramvoussa) (Figure 1). Goats are kept on the islands on a seasonal basis (February-late May) coincident with the spring vegetation flush; they are removed before the onset of the long, dry summer season when the islands do not provide enough resources to support larger herbivores. We considered an island to be grazed if goats had been brought onto the island for more than one spring season. Because islands are relatively small, and the habitat open, we were able to census goats visually. From interviews with local shepherds, we determined that all islands considered eradicated have been devoid of goats for at least 10 years.

Soil Analysis

Five roughly 1kg soil samples were collected from each island. Samples were gathered from the four cardinal directions to minimize the effects of aspect on soil characteristics. Samples were kept in a freezer and transported to D. Hatzinikolaou at the University of Athens and P. Avramidis at the University of Patras, for analysis of chemical content and texture. Grain size distribution was made using a Malvern Mastersizer 2000. Moment measures were calculated using GRADISTAT V.4 software (Blott & Pye 2001) and based on Folk (1974) nomenclature. For total carbon (C) and total N, we used a Carlo Erba EA1108 CHNS-O Elemental analyzer. Total organic C content was estimated using the titration method according to Gaudette & Flight (1974). We divided the total C by total N to determine a C:N ratio. The ratio of C to N is a crucial measurement for decomposition (Parnas 1975). In addition, organic matter is an important aspect of erosion susceptibility because it acts as a glue to hold soil particles together. Since organic matter is roughly 58% C, the average percent of organic C was multiplied by 1.72 (Nelson & Sommers 1982). We calculated total P based on a persulfate digestion method according to APHA 4500-P (2005). $CaCO_3$ was measured using a digital hand-held soil calcimeter (FOGII/Version 2/2014; BD INVENTIONS). More specifically, CaCO3 (%) calculation was based on the measurement of emitted CO_2, a method modified from Müller & Gastner (1971). To determine the degree of erosion, soil depth measurements were taken from 30 random locations on each island using a graded metal bar that was sunk into the ground until it encountered bedrock; values were averaged to obtain an island wide value of soil depth.

Quantification of Vegetation Condition

To asses vegetation characteristics we established four 50m transects, one in each cardinal direction, on most study islands. On the smallest islands (Kisiri, Mikros Ambelas, and North Varvaronissi) that could not accommodate this design, fewer transects were used. We continuously measured each area of vegetation along the entire length of each transect and averaged the values. The average percent vegetation cover for each island was recorded. We also applied this method to assess percent bedrock and bare soil. To determine vegetation height, we measured the height of plants every 2m along each transect and averaged the values for each island. We sampled vegetation biomass in five randomly placed 80cm x 80cm quadrat squares around the island. In these samples, all vegetation was clipped to ground level; all plant matter within the quadrat was collected and sun-dried until no further weight losses were observed, and then weighed. For each island, all aboveground biomass data were averaged and expressed as a single g/m^2 value. Plant species communities were determined from ten 80cm x 80cm quadrat squares that were placed every 5m along each established transect; in each quadrat we recorded the identity of all plants (Lafranchis & Sfikas 2009). Utilizing the program EstimateS (Colwell 2013), we generated a sample-based incidence rarefaction curve (Gotelli & Colwell 2001; Colwell et al. 2004). A bias-corrected form of the Chao2 asymptotic estimator was used to estimate the actual number of plant species on the island (Chao 1987; Colwell & Coddington 1994, Gotelli & Colwell 2011):

$$S_{Chao2} = S_{obs} + \left(\frac{m-1}{m}\right)\frac{q_1(q_1-1)}{2(q_2+1)}$$

where S_{Chao2} = the estimated number of species, S_{obs} = the observed number of species, m = the total number of samples, q_1 = the number of unique species, and q_2 = the number of duplicate species (for examples of rarefaction curves see Appendix 2).

It is necessary to correct for area effects when making inter-island comparisons because the number of species increases with island size (MacArthur & Wilson 1967). This species-area relationship can be defined by the power law $S = CA^z$, where C and z are coefficients and A is the area. To estimate species density C (an area-independent metric of species richness given by the equation $C = S/A^z$), we obtained a data-based estimate of the coefficient z by plotting the species-area relationship for our study system and extracting the exponent of the fitted curve (Rosenzweig et al. 2011). To quantify species diversity, we used a Shannon-Wiener Diversity

Index that was developed to take into account both species richness and evenness (Maurer & McGill 2011). Evenness metrics examine how abundance is apportioned among species.

$$D_{Shannon} = -\sum p_i \ln(p_i)$$

where p_i is the proportion of abundance for species i.

Quantification of Arthropod Characteristics

Five pitfall traps, used to sample epigeal arthropods, were installed on each island at randomly chosen locations near each directional transect. The traps were constructed by sinking plastic cups (7cm in diameter and 11cm deep), filled 2/3 with ethylene glycol, flush into the ground. The ethylene glycol was used because of its dual properties as a preservative and its high evaporation point (Schmidt et al. 2006). Traps were placed under a large, elevated flat stone in a fashion that protected them from livestock trampling but would still allow free access to invertebrates. After approximately 2 weeks (on average 17.19 ± 4.59 days), the samples were collected, identified to morphospecies, counted, dried, and weighed.

Abundance of each species and total number of observed species were recorded for each island. The program EstimateS (Colwell 2013) was used to construct a sample-based abundance rarefaction curve for each island (Gotelli & Colwell 2001; Colwell et al. 2004). A bias-corrected form of the Chao1 asymptotic estimator was used to estimate the total number of arthropod species on the island (Chao 1987; Colwell & Coddington 1994, Gotelli & Colwell 2011):

$$S_{Chao1} = S_{obs} + \frac{f_1(f_1 - 1)}{2(f_2 + 1)}$$

where S_{Chao1} = the number of estimated species, S_{obs} = the observed number of species, f_1 = the number of singleton species, and f_2 = the number of doubleton species (for examples of rarefaction curves see Appendix 3). Since the number of species is intrinsically linked to the size of an island (MacArthur & Wilson 1967), area was accounted for using the coefficient C of the species-area relationship, where $C = S/A^z$ (Rosenzweig et al. 2011) in order to get a comparable measurement. We used a Shannon-Wiener Diversity Index to take into account both species richness and evenness (Maurer & McGill 2011).

$$D_{Shannon} = -\sum p_i \ln(p_i)$$

where p_i is the proportion of abundance for species i. The number of arthropod individuals was counted for each trap and then averaged for each island and divided by the number of days left out for collection. Each sample was dried under a heat lamp until no further weight reductions were observed and then the weight was recorded. Arthropod biomass was averaged for each island and divided by the number of days collected.

Quantification of Seabird Populations

Populations of nesting seabirds were determined over the course of several visits to each island during the bird nesting season. Animals were counted using binoculars by two independent observers and repeated until within 10% of each other. The values were then averaged and divided by island area to calculate seabird density (birds/km^2).

Statistical Analysis

We utilized Shapiro-Wilkes tests to test for normality; variables that failed to meet the normality assumption were either natural log transformed (arthropod biomass, number of arthropods, C:N), square root transformed (seabird density), or arcsine-square root transformed (% $CaCO_3$, % N, % Arachnida, and % Diptera). We compared all observed variables across the three island types – no goats, goats, and goats removed. We ran one-way ANOVA tests followed by post-hoc Tukey tests to examine if there were significant differences between the means for each variable. If normality criteria could not be met, we used Kruskal-Wallis tests instead. We also compared the observed variables using linear regressions to test for correlations. If normality assumptions could not be met, generalized linear models were used instead. All analyses were run in RStudio (RStudio Team 2015).

Results

Effects of Goats

Herbivory by goats has strong and significant effects on island plant communities. We identified 119 unique plant species from the 16 study islands (Appendices 1, 5). Grazing status of an island significantly affects the estimated plant species density (p=0.00676, F=7.521, n=16, ANOVA). Islands with removed goats have significantly fewer species relative to both grazed and ungrazed islands; they have lost 46.4% of their estimated taxa numbers compared to ungrazed islands (Figure 2). The Shannon-Wiener Diversity Index for plants (p=0.00412, F=8.628, n=16, ANOVA) follows a similar pattern: islands with removed goats have significantly lower SWDI values relative to ungrazed islands. Percent vegetation cover declines significantly (p=0.004, F=8.438, n=16, ANOVA) in both grazed (25.96%) and goat-removed (38.56%) islands relative to the ungrazed sample. Plant biomass also declines significantly (p=0.00267, F=9.679, n=16, ANOVA), with grazed islands experiencing an average of 66.4% loss in average vegetation biomass (Figure 3). Mean plant height (p=0.013, F=6.174, n=16, ANOVA) is on average 63.64% shorter on grazed islands and 64.85% shorter on goat-removed islands relative to ungrazed islands.

Grazing also is significantly associated with erosion as evidenced by an average increase of 82.45% in the amount of exposed bedrock (p=0.0158, F=5.804, n=16, ANOVA) and an average decrease of 44.41% of average soil depth (p=0.000983, F=12.36, n=16, ANOVA) (Figure 4) on grazed relative to ungrazed islands. More importantly, this process of soil loss continued even after goats had been removed, resulting in a 146.07% increase in average percent rock and a 68.31% decrease in average soil depth on islands with removed goats as compared to ungrazed islands (see Figure 5).

While grazing by goats was associated with declining amounts of soil, we found little evidence for effects on soil structure or chemistry. Grazing status does not significantly affect average % bare ground (p=0.525, F=0.678, n=16, ANOVA), average % organic matter (p=0.591, F=0.549, n=16, ANOVA), average % $CaCO_3$ (p=0.548, F=0.63, n=16, ANOVA), average % N (p=0.686, F=0.388, n=16, ANOVA), average % P (p=0.954, X^2=0.0947, n=16, Kruskal-Wallis), C:N ratio (p=0.836, F=0.182, n=16, ANOVA), average % sand (p=0.757, F=0.285, n=16, ANOVA), average % silt (p=0.762, X^2=0.545, n=16, Kruskal-Wallis), or average % clay (p=0.464, F=0.814, n=16, ANOVA).

We do document a marginally significant effect of goats on the arthropod Shannon-Wiener Diversity Index (p=0.064, F=3.417, n=16, ANOVA). Grazing status does not significantly affect estimated arthropod species density (p=0.489, F=0.757, n=16, ANOVA), average arthropod biomass/trap/day (p=0.611, F=0.511, n=16, ANOVA), or average number of arthropods/trap/day (p=0.561, F=0.604, n=16, ANOVA). Within separate arthropod taxa, only % dipterans is significantly affected by grazing (p=0.049, F=3.98, n=16, ANOVA) where we see a

109.25% increase in areas with goats compared to ungrazed islands. Grazing has a marginally significant effect on % hymenopterans ($p=0.063$, $F=3.442$, $n=16$, ANOVA) where goats result in a 53.2% decrease relative to ungrazed islands. The percentage of arachnids ($p=0.557$, $F=0.613$, $n=16$, ANOVA), coleopterans ($p=0.146$, $F=2.235$, $n=16$, ANOVA), isopods ($p=0.281$, $X^2=2.541$, $n=16$, Kruskal-Wallis), and hemipterans ($p=0.92$, $X^2=0.167$, $n=16$, Kruskal-Wallis) are not affected by grazing. Grazing also does not seem to affect seabird densities on islands ($p=0.154$, $F=2.168$, $n=16$, ANOVA). See Appendix 4 for more graphs.

Impacts of Soil Erosion

The erosion caused by goats has significant implications for vegetation characteristics. With the increased exposed rock that comes with goat grazing, there is on average significantly less plant biomass ($p=0.033$, $t=-2.373$, $n=16$, linear regression), less average percent vegetation cover ($p<0.00001$, $t=-8.157$, $n=16$, linear regression), and shorter average plant height ($p=0.00059$, $t=-4.416$, $n=16$, linear regression). Unexpectedly, we document a significant positive relationship between amounts of exposed bedrock and the Shannon-Wiener Diversity Index for arthropods ($p=0.033$, $t=2.361$, $n=16$, linear regression).

Similarly, soil depth is positively associated with vegetation cover ($p=0.0034$, $t=3.524$, $n=16$, linear regression) and average vegetation height ($p=0.01$, $t=2.975$, $n=16$, linear regression). Higher soil P and lower C:N ratios are positively correlated with the estimated arthropod species density ($p=0.013$, $t=2.826$, $n=16$, generalized linear model & $p=0.046$, $t=-2.190$, $n=16$, linear regression, respectively). Lastly, we document a marginally significant relationship between N content and average plant heights ($p=0.056$, $t=2.107$, $n=16$, linear regression) as well as P content and plant Shannon-Wiener Diversity Index ($p=0.086$, $t=-1.844$, $n=16$, generalized linear model).

Vegetation Effects on Arthropods

We collected a total of 7,054 individuals from 118 arthropod taxa. Hymenoptera (particularly ants), Isopoda, Coleoptera, and Arachnida were the most abundant taxa collectively comprising 84.2% of the collected arthropods (Hymenoptera 29.2%; Isopoda 24.3%; Coleoptera 22.7%; Arachnida 8%). A significant inverse relationship was found between arthropod Shannon-Wiener Diversity Index and average % vegetation cover ($p=0.049$, $t=-2.145$, $n=16$, linear regression). Marginally significant relationships were found between increasing average arthropod biomass/trap/day and increasing estimated plant species density ($p=0.076$, $t=1.917$, $n=16$, linear regression), as well as negatively between arthropod Shannon-Wiener Diversity Index and both average plant height ($p=0.061$, $t=-2.04$, $n=16$, linear regression) and average vegetation biomass ($p=0.089$, $t=-1.826$, $n=16$, linear regression).

Seabird Effects

The main seabird species on the study sites were the yellow-legged gull (*Larus michahellis*) and European shag (*Phalacrocorax aristotelis*), which nest on the islands. The density of these seabirds is associated with significantly increased levels of N ($p=0.0035$, $t=3.502$, $n=16$, linear regression) and P ($p=0.00155$, $t=3.915$, $n=16$, generalized linear model) in the soil presumably representing marine subsidies (Figures 6 & 7). A marginally-significant negative relationship was found between seabird densities and the vegetation Shannon-Wiener Diversity Index ($p=0.0617$, $t=-2.031$, $n=16$, linear regression). No significant relationships were detected between seabird densities and estimated plant species density ($p= 0.754$, $t=-0.32$, $n=16$, linear regression), average % vegetation cover ($p=0.494$, $t=0.702$, $n=16$, linear regression), average vegetation biomass ($p=0.264$, $t=1.164$, $n=16$, linear regression), average plant height ($p=0.2125$, $t=1.306$, $n=16$, linear regression), average soil depth ($p=0.345$, $t=0.977$, $n=16$, linear regression), average % organic matter (p=0.248, t=1.206, n=16, linear regression), average % $CaCO_3$ (p=0.184, t=-1.396, n=16, linear regression), C:N ratio (p=0.183, t=-1.4, n=16, linear regression), estimated arthropod species density (p=0.335, t=0.999, n=16, linear regression), arthropod Shannon-Wiener Diversity Index (p=0.937, t=0.081, n=16, linear regression), average arthropod biomass/trap/day (p=0.696, t=-0.398, n=16, linear regression), or average number of arthropods/trap/day (p=0.56, t=0.596, n=16, linear regression).

Discussion

Effects on Vegetation

The presence of goats on an island has a significant effect on that island's vegetation, and has implications for conservation programs. Our results indicate that goat grazing regimes set in motion a positive feedback loop of desertification on islands. Trampling of the soil and removal of vegetation dislodges and triggers soil movement which continues even after goats have been removed. The loss of soil combined with goat grazing lead to reduced plant cover, less plant biomass, and overall shorter plants. Once goats are removed from islands, some of the plant biomass returns to the island but remains restricted to the small pockets of soil persisting in rock depressions.

Bayne et al. (2004) saw a similar trend in Australia analyzing sediment fluxes in areas with varying grazing intensities and found that there was less vegetation in areas with more goats, which rendered the soil more susceptible to erosion and subsequently increased the risk of further plant loss. Overgrazing in tandem with trampling and compaction of soil and loss of vegetation, has the ability to even change the hydrology of ecosystems and increase stream flows through reduced infiltration and increased surface runoff (Van Vuren et al. 2001).

Despite these reductions in plant presence, we did not document a significant change in the estimated plant species density and the Shannon-Wiener Diversity Index between islands with and without goat grazing. Nonetheless, there were important differences in plant community composition. While plant assemblages on islands without goats are characterized by native, undefended species such as *Medicago arborea*, *Matthiola sinuata*, and *Atriplex halimus*, islands with goats are characterized by more generalist, low-lying plant species, usually with sticky seeds such as *Plantago coronopus*, *Tordylium apulum*, and *Phleum arenarium*. Panitsa et al. (2006) suggested that the increase in plant species associated with goat grazing can be traced to the introduction of seeds in the fur or feces of an animal. Snogerup & Snogerup (2004) classified roughly 100 taxa that were probably transported by grazing animals. Disturbances can be associated with higher levels of alpha diversity due to introductions of invasive species (Hobbs & Huenneke 1992). High grazing pressure can actually increase plant species richness in nutrient-rich ecosystems, such as islands where seabirds nest (Proulx & Mazumder 1998). Our observations suggest that once goats are removed from an island, the island begins to lose some of these weedier species, while the native species do not return, resulting in an overall decline in alpha diversity. Depending on the goals of conservation, the identities of the plant community may be more important than the actual biodiversity of an island.

Soil Effects

In this system, soil chemical characteristics do not seem to be influenced by grazing nor do they appear to affect the vegetation. Our results suggest that it is only the amount but not the chemical properties of soil that matter in this system. While N and P are normally limiting nutrients, it appears that they are not in our study. Rapid and pronounced losses of what are already shallow, erosion-prone soils result in sparse vegetation cover, short plants, and reduced vegetation biomass. We did detect a significant relationship between soil P and estimated arthropod species density. Kaspari et al. (2008) observed that P often tends to be the main limiting nutrient for decomposition in most ecosystems and fertilization experiments have shown that P addition stimulates cellulose-decomposing microbes resulting in greater arthropod biomass.

Effects on Arthropods

We did not observe an effect of island grazing status on the characteristics of arthropod communities. This could be because our morphospecies distinction was not specific enough to see changes in family-level assemblages. Gardner et al. (1997) found that grazing creates a shift in species communities from Carabid species associated with shady, vegetated areas to Carabid species associated with more open areas. Woodcock et al. (2005) found that individual beetle guilds were differentially influenced by plant diversity and percent cover of grasses. General arthropod characteristics also appear unaffected by seabird densities, agreeing with research conducted by Orgeas et al. (2003) who determined that while neither arthropod species richness nor biomass were affected by yellow-legged gulls, instead, species composition itself was affected, including increases in Tenebrionid species. We also found that in the face of an increase in vegetation, arthropods remained at low levels, probably because all the benefits procured were passed on to the trophic level above them, lizards. When we divide arthropods into separate taxa, only a significant grazing effect was found for Dipterans where grazing increased the proportion found in the samples. Dipterans and all other flying insects are found at disproportionately low rates due to the nature of our pitfall traps and the windy conditions of the Aegean which could confound results (Woodcock 2005).

Our observations of increasing estimated arthropod species density being associated with elevated soil P levels agree with parallel observations in the tropics (Sayer et al. 2010). We do not see grazing effects on arthropods because lizards are presumably continuously eating them and keeping them at constant levels.

Effects of Seabirds

Seabirds drive these islet communities through bottom-up trophic interactions. Seabirds are thought to prefer nesting on smaller islands (Vidal et al. 2001), an observation that was confirmed in this study. Previous studies in the region (Pafilis et al. 2013) have detected a significant inverse correlation between seabird density and grazing. While we noticed a similar pattern in our study region, this relationship did not quite rise to significance. We also detected a significant increase in soil N and P levels with higher seabird densities. Allochthonous nutrient inputs from marine subsidies are critically important for these isolated terrestrial islands (Sánchez-Piñero & Polis 2000). These nutrients may support higher plant biomass and more nitrophilous plant species (Polis et al. 2002). However, these nutrients were only found to stimulate primary productivity during wet periods (Polis et al. 2002), which may explain why – given the generally arid conditions in the study region – we do not see an effect of soil nutrients on vegetation characteristics in our study.

Seabirds can also reduce plant biomass by trampling and burrowing activities or by creating locally toxic conditions through extremely high nutrient levels (Hata et al. 2014). These negative effects may cancel out the positive effects in our study. Vidal et al. (1998) studied a Mediterranean archipelago near France and found that – especially on small islands – increasing yellow-legged gull densities allowed for proliferation of more non-native vegetation species. Seabirds can affect island arthropods in at least 2 ways – providing animal tissue including carcasses and food scraps for scavengers such as Tenebrionidae or Dermestidae beetles (Polis & Hurd 1996), or enhancing herbivorous or detritivorous arthropods through increased primary productivity (Anderson & Polis 1999). These bottom-up effects may then reverberate through the food web leading to increases in predatory spiders & lizards (Polis et al. 2002). Lastly, gulls can also act as important seed dispersers among islands, as large *Pistacia lentiscus* seeds were often found among the investigated guano.

Conclusion

This study demonstrates that goat herbivory has severe and long-term effects on some, but not on other aspects of island ecosystems. Goats set in motion a positive feedback loop of desertification, which continues even after removal. The grazing and the erosion contribute to changing plant communities, lower plant biomass, less vegetation cover, and shorter plants. There is also a broad negative trend in the relationship between seabirds, an important source of N and P in our system, and presence of goats, although this relationship is only marginally significant. Subsequent studies may benefit from including grazing intensity in the analyses. Restoration of small island ecosystems and their original communities will require a long time given the very long periods needed for soil regeneration. This study suggests that goat removal programs should be accompanied by restoration of the native vegetation before there is extensive loss of soils.

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Figures

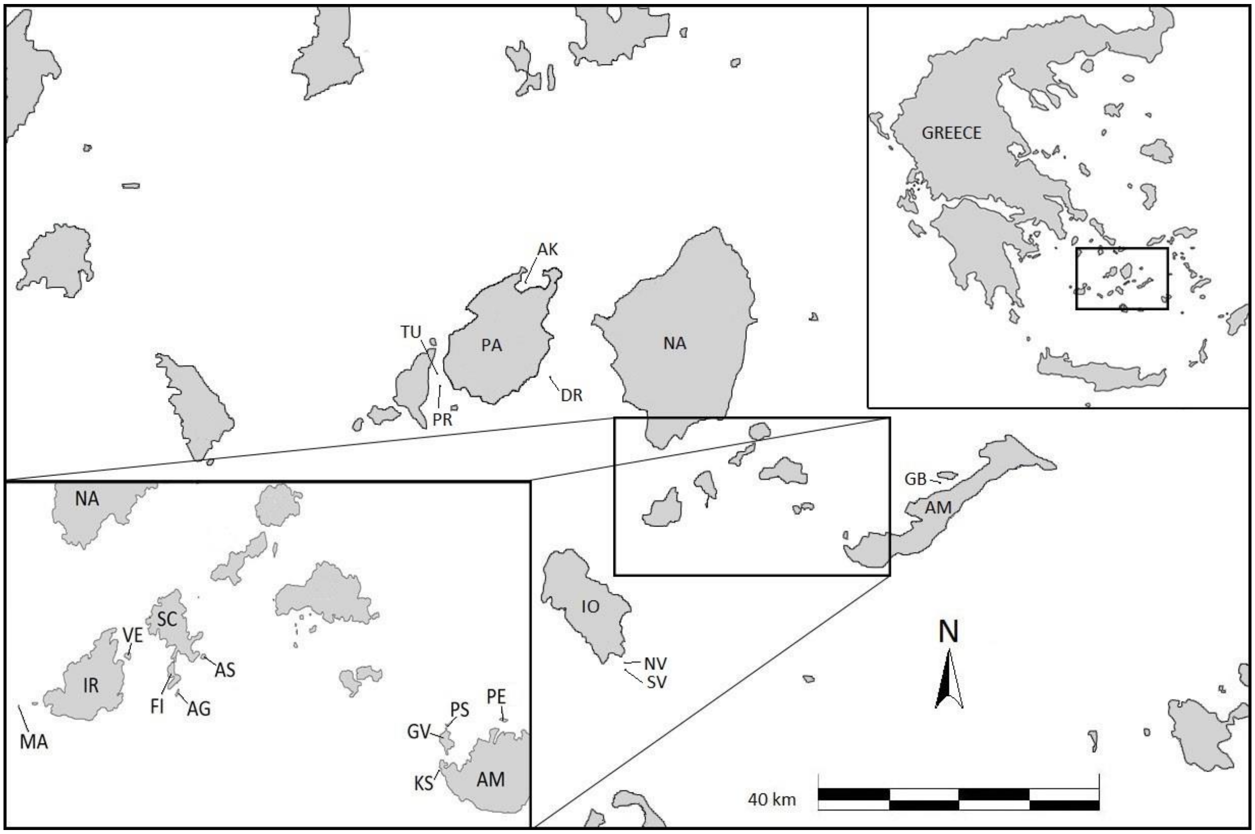


Figure 1. Map of Greece and Cycladic study areas in the Aegean. Study islands: Agia Kali (AK), Agrilou (AG), Aspronissi (AS), Drionissi (DR), Fidussa (FI), Grambonissi (GB), Gramvoussa (GV), Kisiri (KS), Mikros Ambelas (MA), North Varvaronissi (NV), Petalidi (PE), Preza (PR), Psalida (PS), South Varvaronissi (SV), Turlos (TU), and Venetiko (VE), all located within six island clusters: Amorgos (AM), Ios (IO), Irakleia (IR), Naxos (NA), Paros (PA), and Schinoussa (SC).

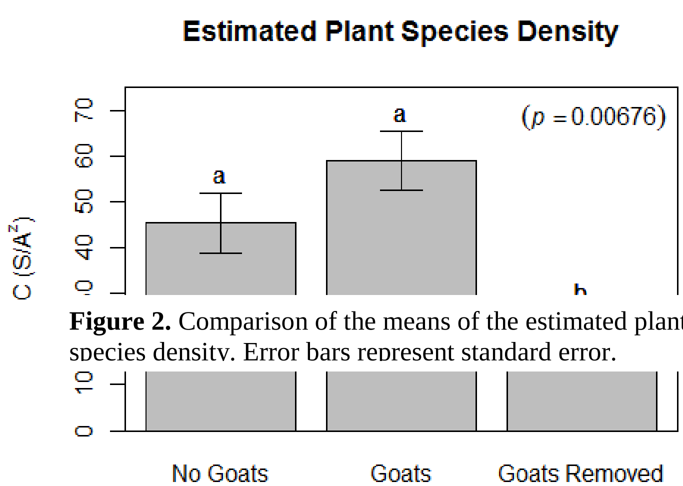


Figure 2. Comparison of the means of the estimated plant species density. Error bars represent standard error.

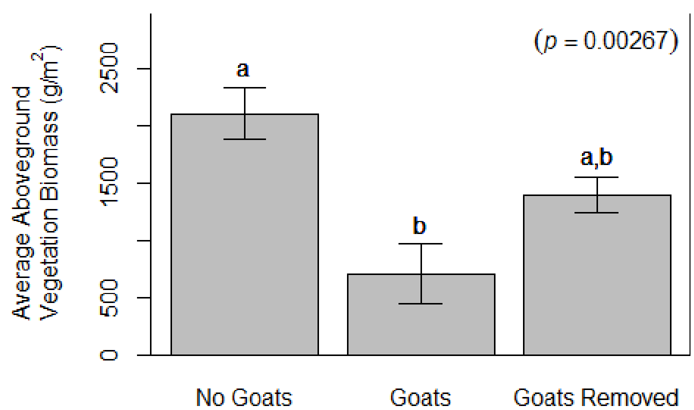


Figure 3. Comparison of the means of the average aboveground dry vegetation biomass (g/m^2). Error bars represent standard error.

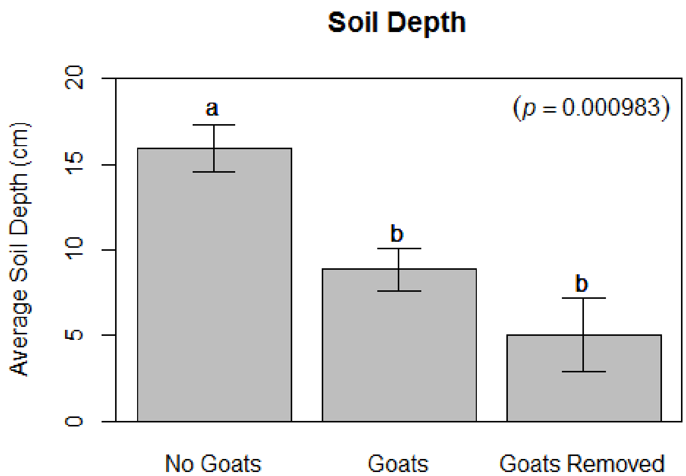


Figure 4) Grazing effects on average soil depth (cm). Error bars represent standard error.

Figure 5. Changes in typical vegetation cover from an island without goats, with goats, and removed goats.

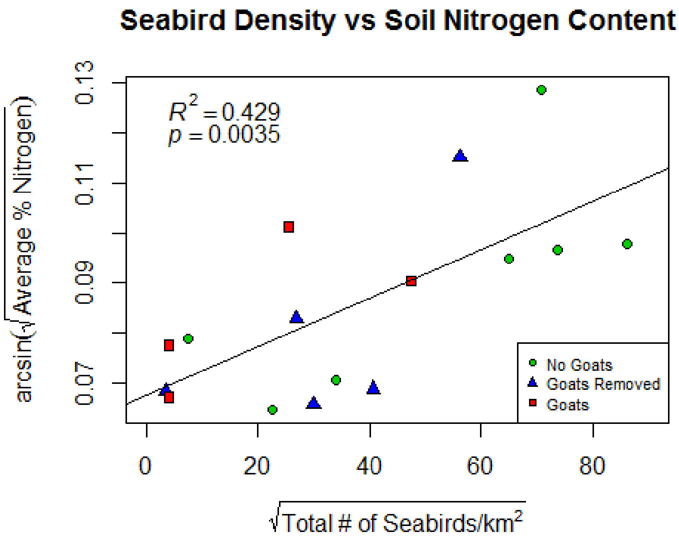


Figure 6. Linear regression showing the correlation between soil nitrogen content and seabird density. Note the axes.

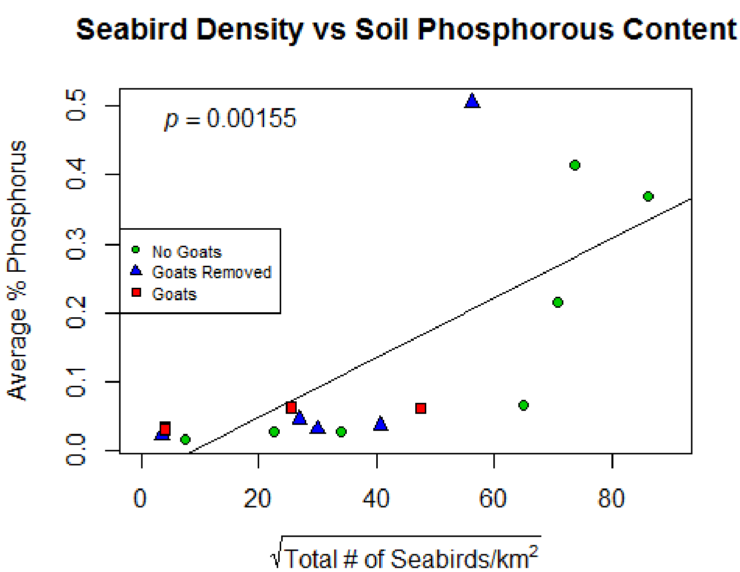


Figure 7. Generalized linear model showing the correlation between soil nitrogen content and seabird density. Note the axes.

Appendix 1 – Plant Species

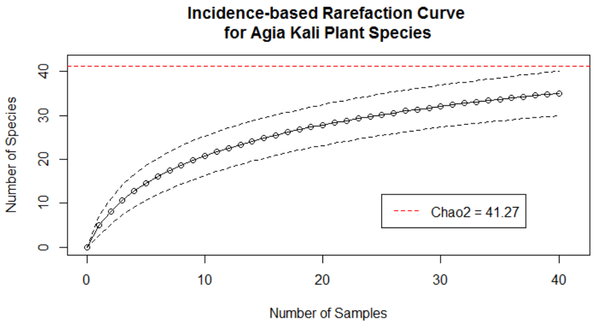
List of species found on Agia Kali (AK), Agrilou (AG), Aspronissi (AS), Drionissi (DR), Fidussa (FI), Grambonissi (GB), Gramvoussa (GV), Kisiri (KS), Mikros Ambelas (MA), North Varvaronissi (NV), Petalidi (PE), Preza (PR), Psalida (PS), South Varvaronissi (SV), Turlos (TU), and Venetiko (VE). Number indicates percent presence in quadrats.

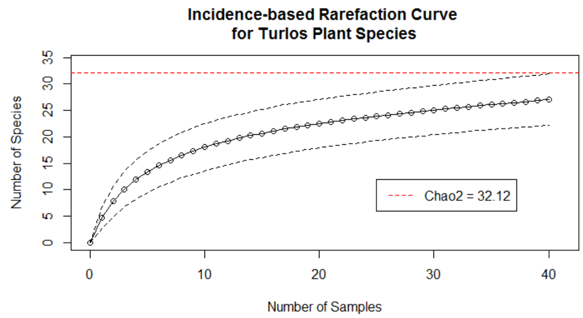
Species	AK	AG	AS	DR	FI	GB	GV	KS	MA	NV	PE	PR	PS	SV	TU	VE
Allium ampeloprasum	-	-	-	-	-	-	-	-	10	-	-	55	-	-	30	-
Allium sp.	-	7.5	10	-	-	-	-	23.3	-	-	12.5	-	-	-	12.5	2.5
Anacamptis pyramidalis	12.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anagallis arvensis	-	7.5	-	12.5	-	-	7.5	-	-	-	-	-	-	-	-	10
Anthemis cretica	-	-	-	-	-	-	-	-	33.3	-	-	-	-	-	-	-
Anthyllis hermanniae	-	-	-	77.5	-	-	30	-	-	-	-	-	-	-	-	-
Asparagus acutifolius	5	-	2.5	-	-	5	-	-	-	-	-	-	-	-	-	-
Asparagus aphyllus	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asparagus horridus	-	-	7.5	-	-	-	-	-	10	25	-	-	5	2.5	-	-
Asteriscus aquaticus	-	-	-	17.5	-	-	-	-	-	-	-	-	-	-	-	-
Astragalus tragacantha	-	-	-	-	-	-	7.5	-	-	-	-	-	-	-	-	-
Atriplex halimus	-	-	10	-	-	-	-	-	-	30	-	2.5	-	37.5	2.5	-
Atriplex portulacoides	-	-	-	-	-	-	-	-	-	-	-	22.5	-	-	-	-
Avena sterilis	-	32.5	20	-	-	-	-	-	-	-	-	2.5	-	7.5	-	5
Bituminaria bituminosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20
Bupleurum gracile	-	-	-	-	22.5	10	-	-	-	-	-	-	-	-	-	52.5
Bupleurum semicompositum	2.5	-	2.5	-	-	-	25	-	-	-	-	-	-	-	-	-
Calicotome villosa	-	-	-	-	-	7.5	-	-	-	-	-	-	-	-	-	-
Capparis spinosa	-	2.5	-	-	-	-	-	-	-	-	-	2.5	-	-	2.5	-
Carex sp.	20	-	-	17.5	5	-	-	-	-	-	-	-	-	-	-	10
Carlina corymbosa	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-
Catapodium marinum	-	52.5	2.5	-	2.5	-	-	-	-	-	-	-	-	-	-	17.5
Centaurium tenuiflorum	12.5	-	-	5	2.5	12.5	10	-	-	-	-	-	-	-	5	10
Chenopodium murale	-	-	5	-	-	-	-	-	-	5	-	15	-	-	-	-
Chrysanthemum coronarium	5	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirsium creticum	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-
Cistus creticus	-	2.5	-	17.5	-	5	27.5	-	-	-	-	-	-	-	-	-
Cistus parviflorus	-	-	-	60	2.5	-	-	-	-	-	-	-	-	-	-	-
Cistus salviifolius	-	-	-	12.5	-	-	-	-	-	-	-	-	-	-	-	-
Convulvulus dorycnium	95	55	-	-	-	12.5	2.5	-	10	5	22.5	65	-	42.5	67.5	52.5
Crepis capillaris	-	20	-	-	-	-	-	-	13.3	15	-	-	-	40	-	-
Crepis sp.	7.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crithmum maritimum	-	-	-	-	-	-	-	6.67	-	-	-	-	7.5	-	-	-
Cuscuta palaestina	2.5	-	-	-	2.5	-	2.5	-	-	-	-	-	-	-	-	-
Dactylis glomerata	27.5	5	-	10	-	15	15	-	-	-	2.5	-	-	-	20	17.5
Species	AK	AG	AS	DR	FI	GB	GV	KS	MA	NV	PE	PR	PS	SV	TU	VE

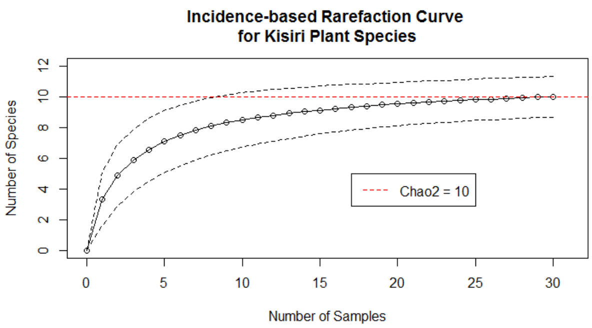
Species	AK	AG	AS	DR	FI	GB	GV	KS	MA	NV	PE	PR	PS	SV	TU	VE
Daucus carota	7.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Delphinium peregrinum	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-
Echium angustifolium	2.5	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-
Echium sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5
Elymus farctus	-	-	-	-	-	-	-	20	-	-	22.5	-	-	-	-	-
Ephedra foemina	-	-	-	-	-	-	-	-	-	25	-	5	-	-	-	-
Erica manipuliflora	-	2.5	-	35	10	52.5	10	-	-	-	-	-	-	-	-	-
Erodium malacoides	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbia acanthothamnos	-	-	-	-	-	-	7.5	-	-	-	-	-	-	-	-	-
Ferula communis	-	-	-	-	-	-	-	-	-	30	-	7.5	-	30	-	-
Frankenia hirsuta	-	-	-	-	-	-	20	86.6	-	-	60	-	80	-	-	-
Fumana thymifolia	-	-	-	-	37.5	35	15	-	-	-	-	-	-	-	-	-
Genista acanthoclada	-	-	-	-	-	40	-	-	-	-	-	-	-	-	-	-
Hedysarum spinosissimum	-	-	-	7.5	-	-	2.5	-	-	-	-	-	-	-	-	-
Helianthemum salicifolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-
Helichrysum stoechas	5	-	-	-	-	12.5	7.5	-	-	-	-	-	-	-	10	25
Hordeum murinum	-	22.5	37.5	20	52.5	35	2.5	-	-	-	-	-	-	12.5	-	52.5
Hymenocarpus circinnatus	2.5	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-
Hyparrhenia hirta	-	-	-	-	15	-	-	-	-	5	-	-	-	5	-	-
Juniperus phoenicea	-	-	-	-	27.5	17.5	2.5	-	-	-	-	-	-	-	-	7.5
Lactuca acanthifolia	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-
Lactuca tuberosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-
Lactuca sp.	-	30	2.5	-	12.5	-	-	-	-	-	-	-	-	-	-	27.5
Lagurus ovatus	7.5	40	7.5	-	-	-	-	-	-	-	-	-	-	10	-	5
Lavatera arborea	-	-	5	-	-	-	-	-	93.3	-	-	30	-	-	-	-
Limonium graecum	-	12.5	5	-	-	-	25	73.3	-	-	65	-	45	5	-	2.5
Limonium sinuatum	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Limonium sp.	2.5	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
Linum narbonense	-	-	-	-	-	-	-	-	-	-	-	-	-	-	22.5	-
Linum strictum	40	-	-	15	-	7.5	-	-	-	-	-	-	-	-	12.5	-
Lophochloa cristata	15	40	22.5	-	22.5	-	-	-	-	-	-	-	2.5	7.5	27.5	30
Lotus angustissimus	15	-	-	-	-	-	-	-	-	-	-	-	5	-	-	-
Lotus cytisoides	-	-	-	-	-	-	-	3.3	-	-	-	-	-	-	-	-
Lotus edulis	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lotus peregrinus	-	-	5	-	-	-	-	-	10	-	20	-	5	-	-	-
Lycium schweinfurthii	-	-	-	-	-	-	-	-	-	15	-	-	-	5	-	-
Malcolmia chia	-	17.5	37.5	-	-	2.5	-	26.6	-	-	42.5	45	15	2.5	-	-
Mandragora officinarum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5	-
Matthiola sinuata	-	-	-	-	-	-	-	-	10	5	-	-	-	7.5	12.5	-
Medicago arborea	-	-	-	-	-	-	-	-	-	70	-	-	-	5	-	-
Medicago truncatula	22.5	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Melica minuta	-	-	-	-	-	27.5	-	-	-	-	-	-	-	-	-	-
Mercurialis annua	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Mesembryanthemum nodiflorum	-	-	5	-	-	-	-	-	6.67	10	2.5	-	17.5	12.5	-	-
Muscari sp.	32.5	-	2.5	-	2.5	10	-	-	-	-	-	2.5	-	2.5	50	5
Species	AK	AG	AS	DR	FI	GB	GV	KS	MA	NV	PE	PR	PS	SV	TU	VE

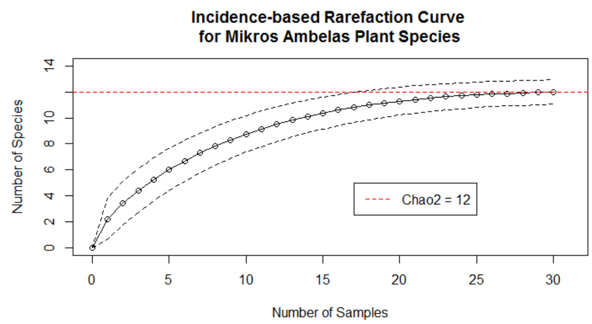
Species	AK	AG	AS	DR	FI	GB	GV	KS	MA	NV	PE	PR	PS	SV	TU	VE
Olea europaea subsp. oleaster	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-
Ononis pubescens	22.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ornithogalum narbonense	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-
Orobanche sp.	-	2.5	-	-	2.5	-	2.5	-	-	-	-	7.5	-	-	-	-
Pallenis spinosa	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	12.5
Pancratium maritimum	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-
Parietaria cretica	-	-	-	-	-	-	-	-	16.6	-	-	5	2.5	5	-	-
Paronychia macrosepala	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-	-	2.5
Phagnalon graecum	47.5	2.5	-	20	20	5	-	-	-	-	-	-	-	-	-	47.5
Phagnalon saxatile	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-
Phagnalon sp.	2.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phleum arenarium	-	20	2.5	-	2.5	-	-	-	3.3	-	-	-	-	-	-	-
Pistacia lentiscus	2.5	27.5	2.5	47.	27.5	57.5	32.5	-	-	15	-	-	-	-	47.5	35
Plantago afra	-	-	-	-	-	-	-	-	-	-	-	-	-	30	-	5
Plantago coronopus	-	5	20	-	-	-	-	-	-	-	-	-	-	-	-	10
Plantago lagopus	-	75	75	-	30	-	-	-	-	-	-	5	-	30	25.5	35
Prasium majus	-	-	-	5	7.5	-	5	-	-	-	-	-	-	-	5	2.5
Quercus coccifera	-	-	-	-	-	12.5	-	-	-	-	-	-	-	-	-	-
Reichardia picroides	-	47.5	30	-	45	-	-	-	-	-	-	-	5	-	-	10
Rhamnus lycioides	-	-	-	-	2.5	15	-	-	-	-	-	-	-	-	-	2.5
Salsola?	-	-	-	-	-	-	-	-	-	-	25	-	-	-	-	-
Sarcocornia fruticosa	-	-	-	-	-	-	-	36.6	6.67	15	2.5	5	17.5	25	-	-
Sarcopoterium spinosum	-	52.5	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5
Scorzonera sp.	-	-	-	-	-	-	-	46.6	-	-	70	-	2.5	-	-	-
Sedum litoreum	-	17.5	17.5	-	-	-	-	-	-	-	2.5	-	-	-	-	-
Senecio rupestris	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-
Silene sedoides	-	2.5	-	-	-	-	-	10	-	-	32.5	-	12.5	-	-	2.5
Sisymbrium officinale	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-
Sonchus arvenisis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	25	-
Sonchus oleraceus	-	-	-	-	2.5	-	-	-	-	-	-	2.5	-	-	7.5	-
Sorghum halepense	17.5	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-
Suaeda vera	2.5	-	50	-	20	-	-	-	-	-	-	-	-	-	2.5	-
Tamarix hampeana	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Teucrium brevifolium	-	2.5	-	-	5	77.5	30	-	-	-	-	-	-	-	47.5	22.5
Teucrium divericatum	-	2.5	-	25	-	17.5	-	-	-	-	-	-	-	-	15	17.5
Teucrium polium subsp. capitatum	-	15	-	17.5	27.5	15	20	-	-	-	-	-	-	-	17.5	-
Thymelea hirsuta	7.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Tordylium apulum	-	25	-	-	20	-	-	-	-	-	-	-	-	-	-	7.5
Trifolium campestre	32.5	10	-	-	5	-	-	-	-	-	-	-	-	-	-	20
Trifolium stellatum	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trigonella balansae	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-
Unknown Species 117	-	-	7.5	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown Species 118	-	2.5	-	-	12.5	-	-	-	-	-	-	-	-	-	-	5
Species	AK	AG	AS	DR	FI	GB	GV	KS	MA	NV	PE	PR	PS	SV	TU	VE

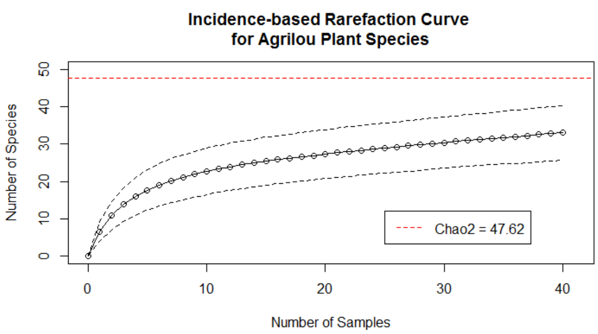
Appendix 2 – Select vegetation sample-based incidence rarefaction curves

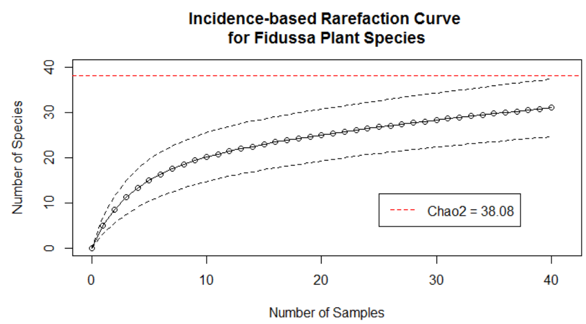




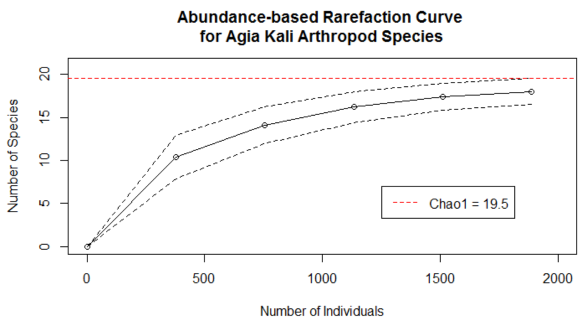


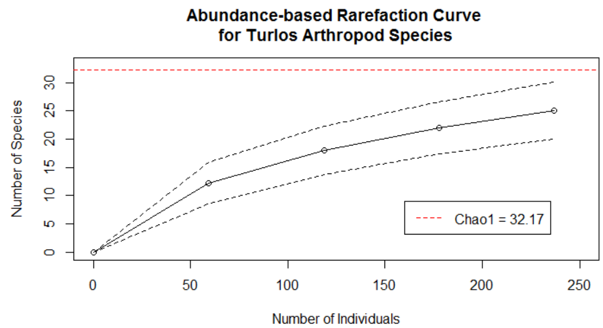


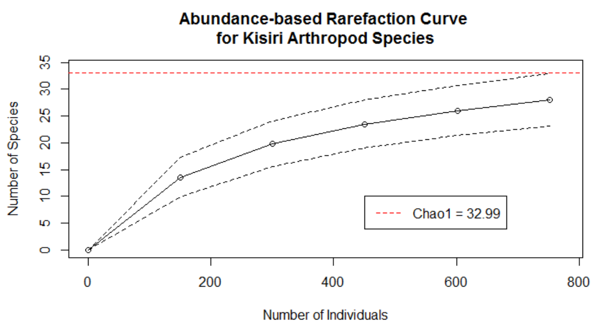


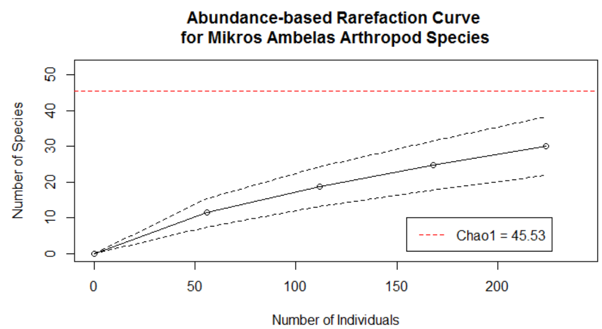


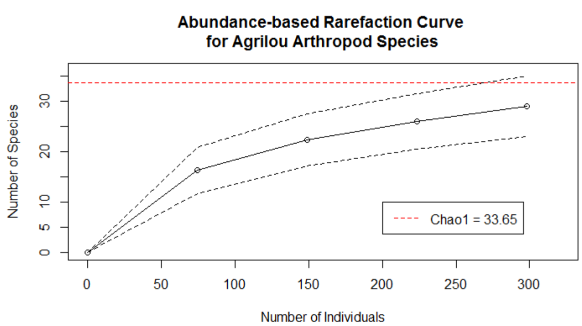
Appendix 3 – Select arthropod sample-based abundance rarefaction curves

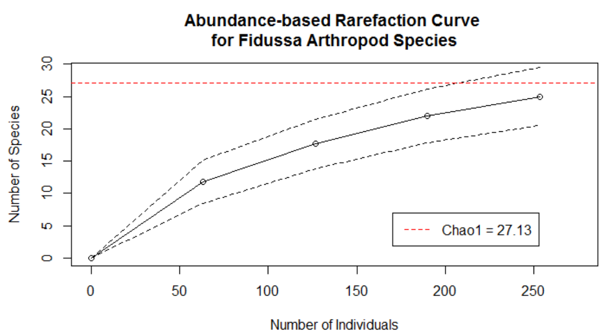




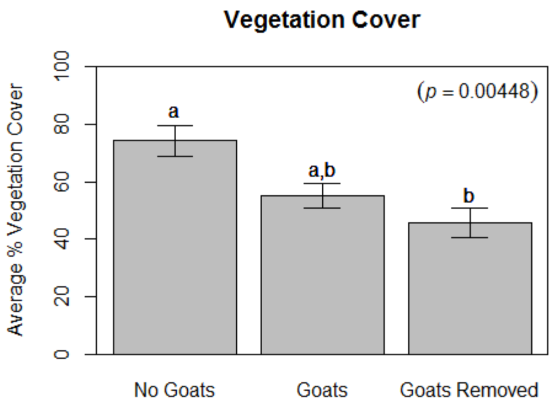


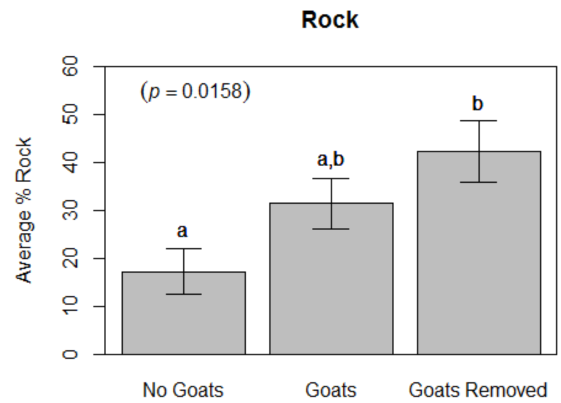


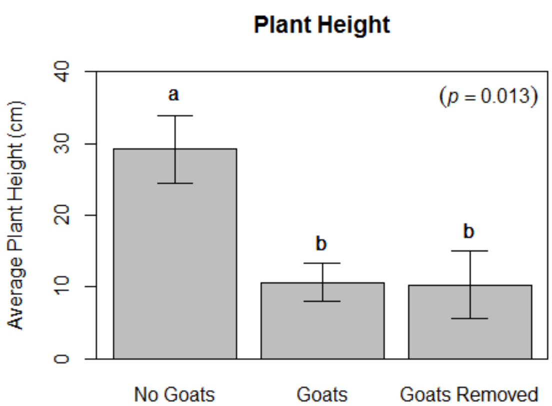


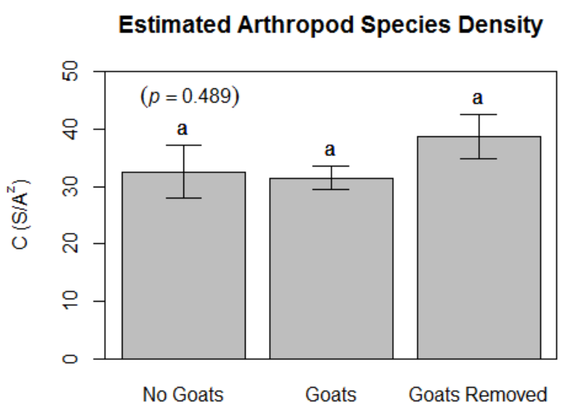


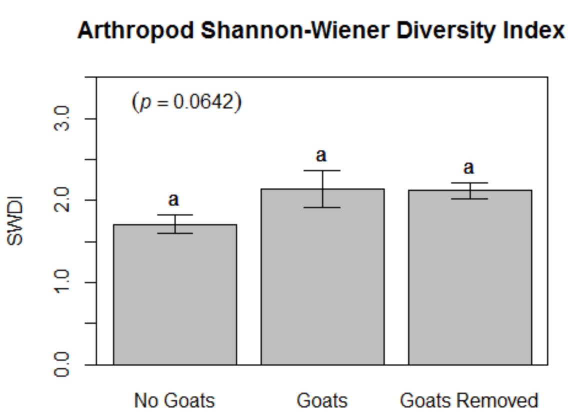
Appendix 4 – Other Relationships

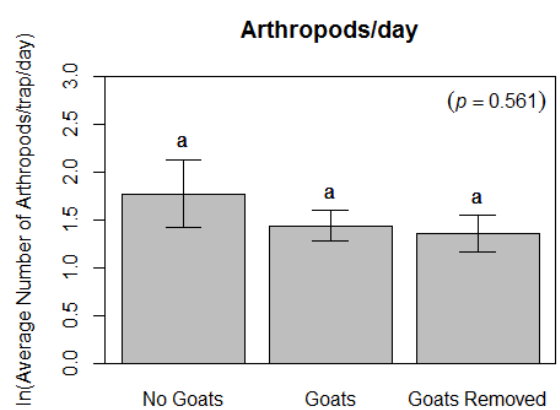


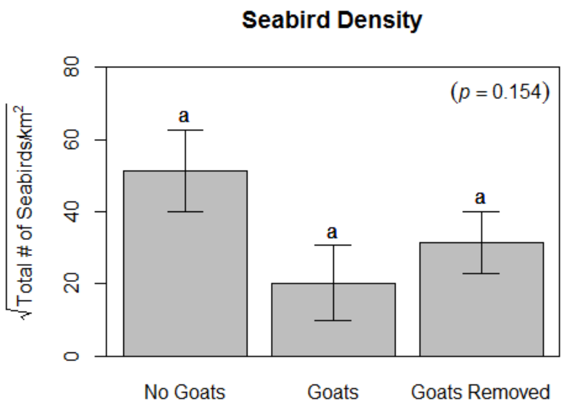


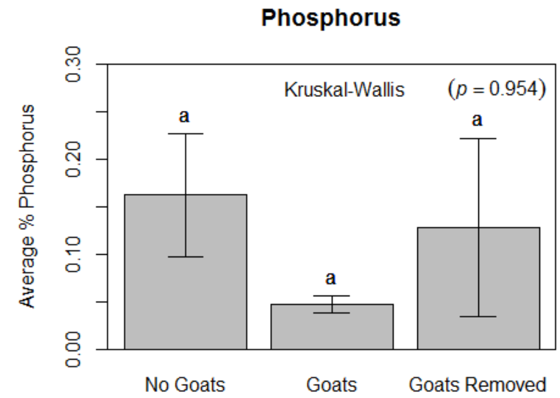


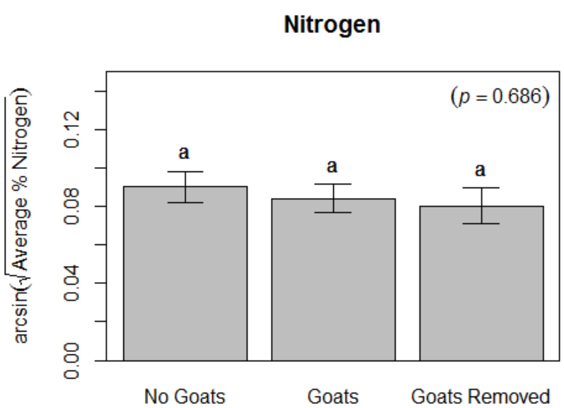


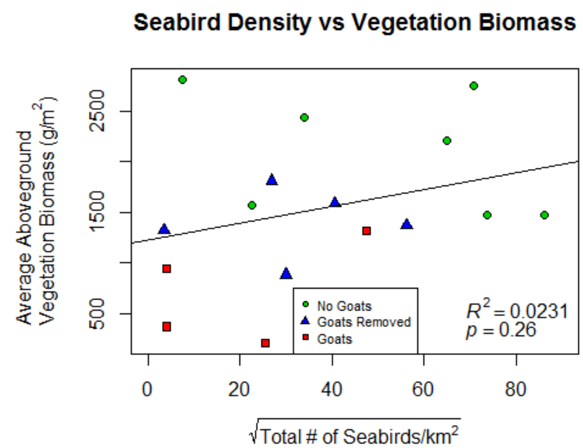


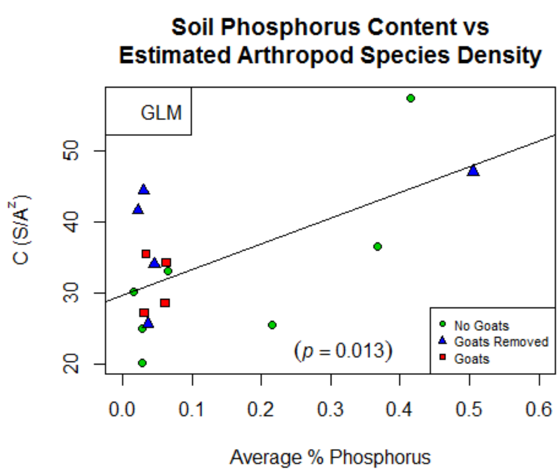


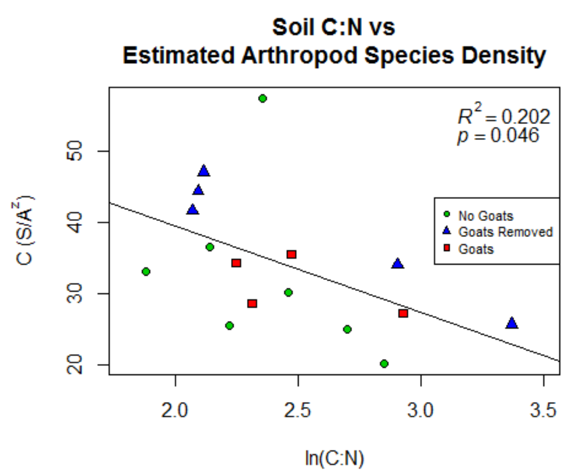

Seabird Density
(p = 0.154)
√Total # of Seabirds/km²
0
20
40
60
80
a
a
a
No Goats
Goats
Goats Removed

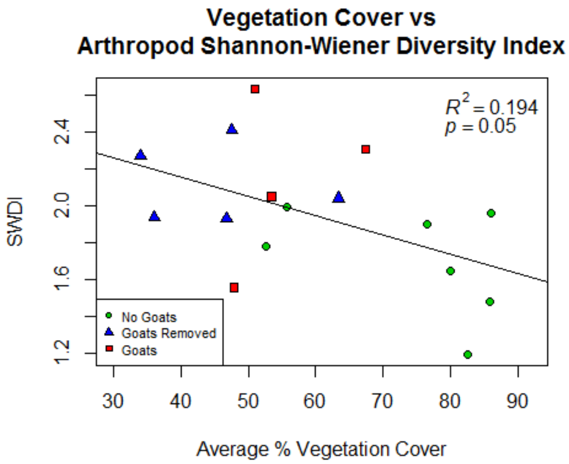

Phosphorus
Kruskal-Wallis
(p = 0.954)
Average % Phosphorus
0.00
0.10
0.20
0.30
a
a
a
No Goats
Goats
Goats Removed

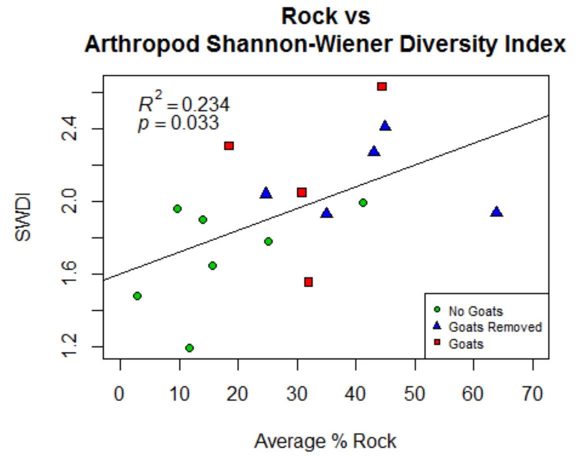

Nitrogen
(p = 0.686)
arcsin(√Average % Nitrogen)
0.00
0.04
0.08
0.12
a
a
a
No Goats
Goats
Goats Removed

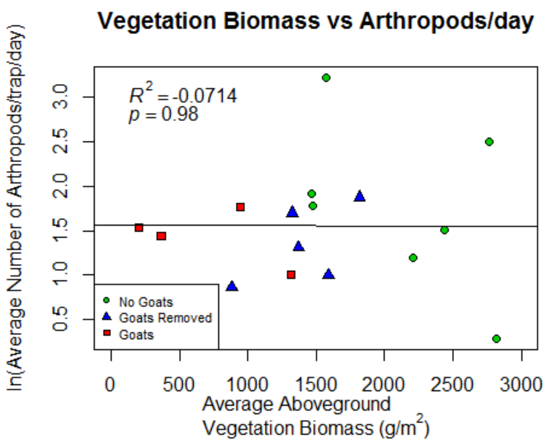

Seabird Density vs Vegetation Biomass
Average Aboveground
Vegetation Biomass (g/m²)
500
1500
2500
No Goats
Goats Removed
Goats
R² = 0.0231
p = 0.26
0
20
40
60
80
√Total # of Seabirds/km²

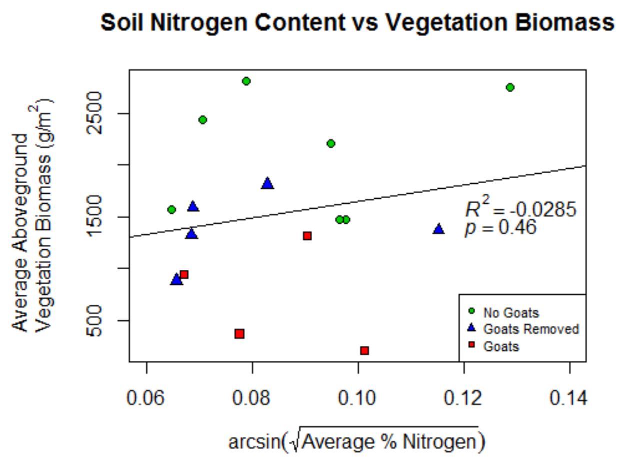

Soil Phosphorus Content vs
Estimated Arthropod Species Density
GLM
C (S/A^z)
20
30
40
50
(p = 0.013)
No Goats
Goats Removed
Goats
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Average % Phosphorus

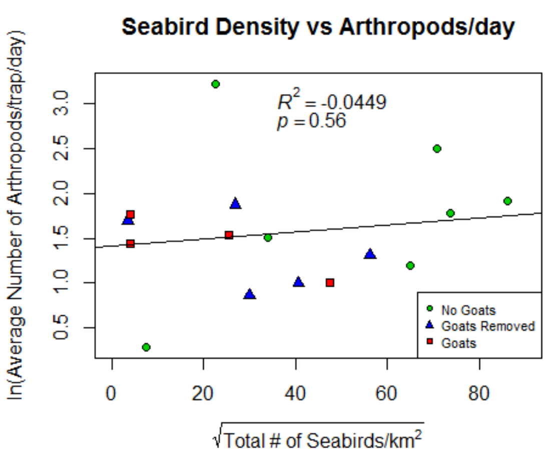

Soil C:N vs
Estimated Arthropod Species Density
R² = 0.202
p = 0.046
C (S/A^z)
20
30
40
50
No Goats
Goats Removed
Goats
2.0
2.5
3.0
3.5
ln(C:N)

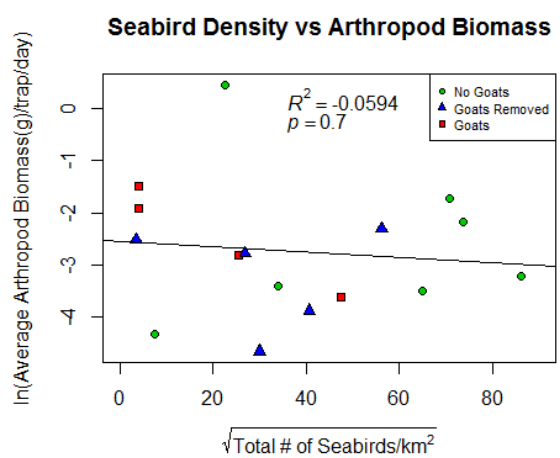

Vegetation Cover vs
Arthropod Shannon-Wiener Diversity Index
$R^2 = 0.194$
$p = 0.05$
No Goats
Goats Removed
Goats
SWDI
1.2
1.6
2.0
2.4
30
40
50
60
70
80
90
Average % Vegetation Cover


Rock vs
Arthropod Shannon-Wiener Diversity Index
$R^2 = 0.234$
$p = 0.033$
No Goats
Goats Removed
Goats
SWDI
1.2
1.6
2.0
2.4
0
10
20
30
40
50
60
70
Average % Rock


Vegetation Biomass vs Arthropods/day
$R^2 = -0.0714$
$p = 0.98$
No Goats
Goats Removed
Goats
ln(Average Number of Arthropods/trap/day)
0.5
1.0
1.5
2.0
2.5
3.0
0
500
1000
1500
2000
2500
3000
Average Aboveground
Vegetation Biomass (g/m^2)


Soil Nitrogen Content vs Vegetation Biomass
$R^2 = -0.0285$
$p = 0.46$
No Goats
Goats Removed
Goats
Average Aboveground
Vegetation Biomass (g/m^2)
500
1500
2500
0.06
0.08
0.10
0.12
0.14
arcsin($\sqrt{\text{Average \% Nitrogen}}$)


Seabird Density vs Arthropods/day
$R^2 = -0.0449$
$p = 0.56$
No Goats
Goats Removed
Goats
ln(Average Number of Arthropods/trap/day)
0.5
1.0
1.5
2.0
2.5
3.0
0
20
40
60
80
$\sqrt{\text{Total \# of Seabirds/km}^2}$


Seabird Density vs Arthropod Biomass
$R^2 = -0.0594$
$p = 0.7$
No Goats
Goats Removed
Goats
ln(Average Arthropod Biomass(g)/trap/day)
0
-1
-2
-3
-4
0
20
40
60
80
$\sqrt{\text{Total \# of Seabirds/km}^2}$

Appendix 5 – Summary of Data

Vegetation Data – N = No Goats. E = Eradicated. G = Goats. Averages show mean ± standard deviation.

Island	Status	Area (km^2)	Observed Plant Species	Estimated Plant Species	Estimated Plant Species Density	Plant SWDI	Average % Vegetation Cover	Average Plant Biomass (g/m^2)	Average Plant Height (cm)
Agia Kali	N	0.0137	34	41.27	80.215	3	82.545± 7.066	1572.188± 1027.247	39.71± 9.262
Agrilou	G	0.08445	33	47.62	69.833	3.07	50.94± 10.667	204.688± 120.196	5.86± 1.124
Aspronissi	G	0.04227	32	40.43	65.998	2.88	67.415± 7.537	1317.188± 530.951	14.96± 6.544
Drionissi	N	0.3763	23	25.17	29.284	2.74	76.55± 12.905	2436.25± 1634.541	17.73± 3.842
Fidussa	G	0.6304	32	38.08	40.901	3.03	53.48± 15.041	366.25± 275.081	15.37± 7.671
Grambonissi	N	0.1501	28	28.16	37.776	2.95	85.945± 5.659	2817.5± 1125.617	33.621± 6.317
Gramvoussa	E	0.7925	26	28.46	29.504	2.91	47.59± 25.821	1322.5± 1602.06	12.29± 7.779
Kisiri	E	0.01663	10	10	18.862	1.98	36.093± 5.546	1815.625± 1044.399	3.64± 0.655
Mikros Ambelas	E	0.01486	12	12	23.032	1.97	63.46± 11.856	1373.047± 604.461	28.04± 4.292
North Varvaronissi	N	0.007966	14	16.85	35.62	2.33	86.08± 6.59	2760.938± 1692.858	50.58± 7.948
Petalidi	E	0.0504	14	15.12	24.018	2.26	46.75± 6.01	880.938± 218.832	4.23± 0.247
Preza	N	0.01707	18	21.44	40.277	2.32	52.675± 14.129	1470.625± 860.324	22.875± 11.947
Psalida	E	0.02599	15	16.17	28.461	2.03	34.05± 1.409	1591.406± 1036.111	3.16± 1.219
South Varvaronissi	N	0.02825	22	22.98	39.929	2.7	55.69± 19.105	1470.938± 735.567	18.59± 9.746
Turlos	N	0.03214	27	32.12	54.706	2.86	79.935± 12.582	2206.875± 1664.413	21.46± 10.409
Venetiko	G	0.1218	37	42.46	58.832	3.2	47.915± 5.95	944.063± 1486.451	6.31± 1.15

Seabird & Arthropod Data – Averages show mean ± standard deviation

Island	Seabird Density (per m^2)	Pitfall Traps Days Collected	Observed Arthropod Species	Estimated Arthropod Species	Estimated Arthropod Species Density	Arthropod SWDI	Average Arthropod Biomass (g)/trap/day	Average # Arthropods/trap/day
Agia Kali	510.949	15	18	19.5	20.19	1.195	1.575± 0.673	25.187± 19.304
Agrilou	651.273	16	29	33.65	34.33	2.633	0.06± 0.057	4.656± 2.457
Aspronissi	2247.457	16	21	27.96	28.686	2.304	0.027± 0.025	2.734± 1.443
Drionissi	1153.335	15	23	24.87	25.068	1.903	0.034± 0.023	4.517± 4.339
Fidussa	15.863	15	25	27.13	27.232	2.051	0.148± 0.124	4.217± 2.694
Grambonissi	53.298	23	22	29.8	30.261	1.481	0.013± 0.01	1.33± 1.232
Gramvoussa	11.357	22	36	41.59	41.668	2.41	0.081± 0.018	5.491± 3.53
Kisiri	721.587	23	28	32.99	34.103	1.939	0.063± 0.046	6.539± 4.833
Mikros Ambelas	3162.853	15	30	45.53	47.109	2.04	0.101± 0.033	3.733± 1.612
North Varvaronissi	5021.341	9	22	24.5	25.478	1.962	0.179± 0.245	12.267± 8.428
Petalidi	892.857	21	27	43.43	44.494	1.931	0.01± 0.012	2.381± 2.067
Preza	7439.953	19	33	35.33	36.514	1.779	0.04± 0.034	6.803± 5.682
Psalida	1654.483	24	23	24.99	25.74	2.268	0.021± 0.026	2.729± 1.104
South Varvaronissi	5415.929	9	20	55.86	57.497	1.993	0.113± 0.066	5.911± 2.793
Turlos	4200.373	18	25	32.17	33.078	1.644	0.03± 0.015	3.292± 1.142
Venetiko	16.42	15	26	34.97	35.571	1.556	0.228± 0.069	5.85± 2.329

Arthropod Taxa - % of sample represented by each taxa.

Island	% Arachnida	% Coleoptera	% Diptera	% Hemiptera	% Hymenoptera	% Isopoda	% Ticks/Mites
Agia Kali	0.741	8.682	4.023	0.265	28.587	57.332	0.212
Agrilou	8.054	28.188	13.758	0.671	14.765	0.671	27.181
Aspronissi	19.429	28.571	4.571	0.571	21.714	18.857	5.143
Drionissi	14.76	15.129	1.107	0	50.923	12.177	4.428
Fidussa	8.3	46.64	17.391	0	20.553	0.395	3.557
Grambonissi	7.843	14.379	1.961	0	67.974	0.654	1.961
Gramvoussa	36.921	22.517	4.139	0.497	20.861	3.974	7.45
Kisiri	3.723	9.707	1.33	0.133	9.973	61.835	8.91
Mikros Ambelas	10.714	39.286	4.464	2.232	37.054	1.339	1.786
North Varvaronissi	3.08	51.087	0.906	0.181	18.841	1.63	5.072
Petalidi	6.4	8.4	7.6	0.4	40.8	1.6	0.4
Preza	3.288	19.923	4.836	7.544	60.155	1.741	0.387
Psalida	7.252	17.176	9.16	0.763	26.718	4.198	0.763
South Varvaronissi	11.654	49.248	1.88	1.128	22.932	7.143	2.632
Turlos	10.549	13.08	0.422	1.688	54.43	6.751	5.907
Venetiko	4.843	61.254	1.709	0.57	24.217	0.285	3.704

Soil Data – Averages show mean ± standard deviation

Island	Average % Bare Ground	Average % Rock	Average Soil Depth (cm)	Average % Organic Matter	Average % N	Average % P	Average % $CaCO_3$	Average C:N
Agia Kali	5.61± 2.44	11.845± 5.454	20.533± 14.906	5.43± 3.887	0.417± 0.150	0.028± 0.011	28.26± 17.947	17.335
Agrilou	4.62± 2.982	44.44± 12.409	8.1± 7.165	9.68± 5.465	1.023± 0.197	0.062± 0.039	6.72± 14.525	9.462
Aspronissi	14.14± 12.019	18.445± 9.659	12.467± 6.49	8.6± 6.787	0.816± 0.578	0.061± 0.005	6.44± 8.847	10.108
Drionissi	9.435± 7.754	14.015± 6.508	20.033± 13.382	6.72± 7.382	0.498± 0.313	0.028± 0.008	7.48± 7.633	14.875
Fidussa	15.705± 11.589	30.815± 22.383	7.833± 8.793	3.83± 3.926	0.6± 0.367	0.031± 0.007	6.567± 11.089	18.692
Grambonissi	11.125± 4.361	2.93± 3.612	13.633± 10.321	5.57± 3.349	0.621± 0.257	0.016± 0.005	17.04± 19.174	11.711
Gramvoussa	7.38± 6.499	45.03± 31.358	12.133± 9.733	2.87± 1.219	0.467± 0.255	0.022± 0.007	7.64± 6.714	7.915
Kisiri	0±0	63.907± 5.546	1.567± 2.712	9.03± 4.653	0.686± 0.185	0.045± 0.019	42.6± 17.201	18.273
Mikros Ambelas	11.767± 9.756	24.773± 4.491	7.767± 7.417	10.46± 4.424	1.322± 0.650	0.505± 0.221	1.02± 1.47	8.294
North Varvaronissi	4.17± 0.014	9.75± 6.576	12.7± 10.942	11.28± 7.098	1.647± 0.886	0.215± 0.256	3.34± 4.047	9.219
Petalidi	18.21± 10.849	35.04± 10.796	2.8± 3.01	1.93± 2.635	0.431± 0.111	0.031± 0.008	4.36± 2.992	8.109
Preza	22.075± 9.716	25.25± 13.186	17.533± 11.518	5.4± 1.714	0.952± 0.772	0.368± 0.297	0.12± 0.217	8.51
Psalida	22.905± 16.431	43.045± 17.829	0.933± 2.243	1.34± 1.584	0.473± 0.602	0.036± 0.017	18.4± 23.326	29.157
South Varvaronissi	3.175± 5.325	41.135± 21.857	15.967± 10.447	6.99± 3.19	0.93± 0.280	0.414± 0.458	1.38± 1.375	10.539
Turlos	4.49± 2.851	15.575± 11.5468	10.933± 7.071	4.5± 1.693	0.895± 0.319	0.065± 0.056	12.7± 8.501	6.562
Venetiko	20.155± 12.757	31.93± 17.483	6.967± 5.654	6.59± 2.22	0.45± 0.129	0.034± 0.013	0.28± 0.572	11.859

Soil Texture Data – Averages show mean ± standard

Island	Average % Sand	Average % Silt	Average % Clay
Agia Kali	19.5±8.02	71.42±6.47	9.09±1.99
Agrilou	9.37±4.7	76.11±0.74	14.52±4.55
Aspronissi	26.94±18.36	64.74±13.33	8.27±5.24
Drionissi	15.8±22.21	70.76±18.88	13.43±4.27
Fidussa	22.48±27.78	61.44±23.15	16.08±6.19
Grambonissi	25.19±42.1	62±34.75	12.82±8.37
Gramvoussa	13.49±9.67	78.07±9.43	8.44±3.81
Kisiri	11.99±15.13	74±12.95	14.01±2.97
Mikros Ambelas	10.92±11.77	76.36±8.26	12.72±4
North Varvaronissi	19.23±7.74	69.94±6.12	10.83±1.86
Petalidi	24.5±16.99	62.8±12.84	12.7±6.07
Preza	4.67±3.81	77.11±1.89	18.22±3.52
Psalida	28.15±22.55	61.65±21.62	10.2±4.41
South Varvaronissi	13.03±2.35	72.86±2.33	14.1±4.09
Turlos	4.47±1.39	76.73±3.77	18.8±3.34
Venetiko	10.52±8.18	72.99±5.15	16.49±3.7