

EFFECTS OF LIVESTOCK GRAZING ON
INVERTEBRATE-PROVIDED ECOSYSTEM
SERVICES IN THE AEGEAN

By

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Abstract

Over one-quarter of the world's terrestrial surface is used for livestock grazing, more land than for any other single human land use. Improperly managed grazing can lead to widespread biodiversity loss and desertification, which can undermine the livelihoods of entire communities and have devastating consequences for local ecosystems. Overgrazing has been shown to impact the diversity and structure of vegetation communities, promote erosion, and have negative consequences for arthropod populations, and worldwide is increasing in intensity and expanding in scope. Yet it is unclear whether or not overgrazing negatively impacts communities of invertebrate predators and pollinators in mixed use agroecological-pastoral systems, and whether such impacts can lead to a reduction in invertebrate-provided ecosystem services like biological pest control and pollination. Preliminary data from previous researchers have suggested that overgrazing may negatively affect native insect populations, which in turn may undermine their ability to provide these essential ecosystem services. This research project attempts to quantify the impact of livestock grazing on biological control and pollination services and answer whether or not increasing grazing intensity results in a decline in invertebrate biodiversity and if such an outcome leads to a corresponding reduction in ecosystem services provided.

In a typical Mediterranean ecosystem (Naxos Isl, Aegean Sea, Greece), fourteen study sites were established along a gradient of grazing intensity. Grazing intensity was determined by measuring the stocking rate (livestock/1000 m²) and dung mass (g/m²) at each location. Pitfall traps were deployed at each site to sample the ground-dwelling invertebrate community. To evaluate the differences in pest suppression services between sites, a field experiment was run comparing the differences in growth rates of aphid populations that were either protected from predation by a fine mesh, or open to the local invertebrate predator community; this was repeated at sites experiencing different levels of grazing intensity. To evaluate and quantify pollination services across the gradient of grazing intensity, pollinator observations and pollen grain counts were obtained from conehead thyme flowers (*Coridothymus capitatus*), the most important nectar-producing plant in the region. Linear mixed-effects models and Pearson's correlations were run using R software to determine the effect of grazing intensity on pest suppression and pollen counts.

Pitfall trap contents revealed that the total available predators per site remained unchanged across the gradient of grazing intensity. However, the data suggest that grazing is associated with declining populations of certain types of invertebrate predators including spiders. Combined with a partial data available from the pest suppression experiment, few clear conclusions can be drawn from the biological control portion of this project. However, a strong positive relationship exists between grazing intensity and pollen count. Additionally, pollen count declines with thyme flower coverage. This effect can be explained by the influence of thyme, rather than the direct effect of grazing itself. Due to its unpalatability, thyme coverage peaks at moderate levels of grazing. However, at even higher livestock densities, nearly all living vegetation is consumed or destroyed. The pattern of decreasing pollen counts with increasing thyme flower coverage can be attributed to the fact that amount of pollen on thyme is negatively correlated with the amount of thyme flowers in an area. The influence of livestock grazing on thyme populations outweighs any potential concomitant deterioration of the pollinator community and results in augmented pollination services in the form of more conspecific pollen grains per stigma on the flowers that do persevere through higher levels of grazing.

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Table of Contents

1. Introduction	6
2. Methods	12
2.1 <i>Location</i>	12
2.2 <i>Study Site</i>	12
2.3 <i>Grazing Intensity</i>	13
2.4 <i>Biological Control</i>	13
2.4.1 <i>Pitfall Traps</i>	13
2.4.2 <i>Predator Exclusion Experiments</i>	14
2.5 <i>Pollination Services</i>	17
2.5.1 <i>Pollinator Observations</i>	17
2.5.2 <i>Pollen Counts</i>	18
3. Results	20
3.1 <i>Biological Control</i>	20
3.1.1 <i>Pitfall Traps</i>	20
3.1.2 <i>Predator Exclusion Experiments</i>	22
3.2 <i>Pollination Services</i>	22
3.2.1 <i>Pollinator Observations</i>	22
3.2.2 <i>Pollen Counts</i>	23
4. Discussion	25
4.1 <i>Biological Control</i>	25
4.2 <i>Pollination Services</i>	27
4.3 <i>Final Conclusions</i>	29
5. Bibliography	30
6. Figures	34
7. Tables	40

1. Introduction

Human communities have been altering natural ecosystems since the advent of agriculture. Prior to the industrial revolution, agriculture was by far the most profound way in which humans modified and affected their natural surroundings and it continues to be one of the largest single contributors to global anthropogenic landscape changes. However, beyond conventional agriculture, much larger areas of the planet are impacted by the grazing of livestock. Grazing, today as in the past, can take many forms. However, usually a herd of hooved animals is watched over by a shepherd or rancher, and allowed to roam within variably defined boundaries. Grazing livestock consume local vegetation, usually grasses, converting the energy from the grass into meat, milk, or fur to be collected and utilized by humans (Vera, 2000).

Pressure on Earth's agricultural systems continues to intensify as global population and income continue to grow and more people desire protein-rich diets. This increasing demand for meat has encouraged many pastoralists and ranchers to supplement their incomes by adding more animals to their herds and/or opening up new lands for grazing, in short, putting more pressures on range lands (Sjodin et al., 2008). Many governments or multi-national bodies have further incentivized pastoralists to increase the stocking densities of their grazing lands via financial subsidies. All of these factors combine to ensure that livestock grazing is increasing in scope and intensity, with little regard for the health of local ecosystems (Negro et al., 2011). And while this may be good news for some pastoralists who can increase their short term profits, grazing can have devastating consequences for local habitats.

Low density livestock grazing can be sustainable in Mediterranean ecosystems, depending on the structure of the ecosystem in which the grazing is taking place (Bugalho et al., 2011). But when livestock densities rise beyond a certain point, mediterranean habitats like maquis or chapparral can become severely degraded. Overgrazing can affect vegetation communities,

and induce changes in local nutrient cycles, plant species composition, and/or primary producer structure and productivity (Bugalho et al., 2011). Livestock can directly alter plant communities via trampling and/or consuming plants and compacting the soil (McLaughlin and Mineau, 1995). However, perhaps the most significant long-term environmental issue stemming from overgrazing in arid ecosystems is the risk of desertification. Soil degradation and changes in vegetation cover and composition brought about by overgrazing can be primary factors driving semi-arid or prairie ecosystems towards increasingly arid, desert-like landscapes (Schaldach et al., 2013). Once a dryland has undergone desertification, it is very difficult to restore the ecosystem to its original precipitation regime and vegetation condition (Geeson et al., 2002). Globally, lands used for grazing cover more than one-quarter of the planet's terrestrial surface, more area than any other single human land use (Bugalho et al., 2011). With so much land currently open to livestock grazing, a substantial amount of the planet's surface is susceptible to desertification, with potentially disastrous consequences for the people residing in those areas. The Mediterranean region is particularly vulnerable to desertification due to its partially semi-arid climate and tradition of livestock grazing (Schaldach et al., 2013). For example in Greece, 40% of the total land area is classified as "rough grazing" by the National Statistics Service (Hadjigeorgiou et al., 2005), leaving a significant portion of the country susceptible to the negative consequences of mismanaged livestock husbandry.

Ecosystem services are benefits that are provided to humans by natural species communities; they often have a very substantial, yet hard to quantify, economic value (Lundin et al., 2013). This economic value is often overlooked and not incorporated into the cost of engaging in specific activities. Common examples of ecosystem services include flood control, air purification, agricultural pest control, and pollination (Losey and Vaughan, 2006). Pollination and biological pest control are two of the most critical ecosystem services, especially with regard to agricultural production in less

developed nations. While some vertebrate species do serve as pest predators or pollinators, it is invertebrates, especially arthropods, which are the biggest contributors towards biological control and pollination ecosystem services (Abrol, 2012; Lundin et al., 2013).

Biological pest control, or “biocontrol,” refers to arthropod predators (also termed “natural enemies”) – such as spiders, lacewings, and coccinellid beetles – that prey upon agricultural pests. In this manner, such invertebrate bio-control agents provide a valuable service to farmers by naturally reducing crop pests. Native insect pests alone are responsible for an estimated \$7.32 billion worth of crop damage annually in the United States (Losey and Vaughan, 2006), so pest suppression techniques are certainly of significant interest to farmers worldwide. While many commonly used natural enemies are non-native species, the native suite of arthropod predators can still play a not insignificant part in natural bio-control. In the United States alone, native invertebrate predators contribute at least \$4.5 billion of value annually via the natural suppression of agricultural pests (Losey and Vaughan, 2006). The economic benefits derived from bio-control mainly stem from the reduced crop yield losses and savings from lowered pesticide use, since farmers do not have to use as much pesticides as they would have if there was no bio-control (Bianchi et al., 2006).

Pollination by invertebrates is extremely important for many high-value crops worldwide, and many flowering plant species rely on animal pollination. As much as 35% of global agricultural production is dependent on pollinating animals (Abrol, 2012). Habitat alterations, pesticides, and diseases all threaten to degrade pollination services worldwide by affecting invertebrate pollinators. Specifically, honeybee populations across much of the world have been experiencing dramatic population declines in recent years, a trend which is not yet fully understood and which could have devastating consequences for global food security (Decourtye et al., 2010).

It is widely accepted in the agroecological research community that modern agricultural techniques may be compromising the potential bio-

control and pollination services of our ecosystems by reducing the abundance and/or variety of natural enemies and potential pollinators (Cardinale et al., 2003). Livestock grazing and the accompanying landscape alterations (including clearing of vegetation, burning of forests, and habitat fragmentation) have been identified as a significant threat to ecosystem functioning and biodiversity (Kearney et al., 2012). While no species extinctions have yet been directly attributed to livestock grazing alone, many in the scientific community believe that grazing can lead both to species extinctions and to substantial declines in species richness (Diaz et al., 2007; Luig et al., 2005). There is increasing evidence that non-cropped habitats adjacent to agricultural fields may play a critical role in maintaining the abundance and diversity of bio-control agents and potential pollinators in agroecosystems (Caballero-Lopez et al., 2012). Fields of crops are often close to, or surrounded by lands subject to livestock grazing. If such lands are overgrazed, the potential predator and pollinator communities on the adjacent croplands could be negatively affected and thus natural pest suppression and pollination services could be lost. If a relationship does exist between the intensity of livestock grazing in an agroecosystem and the abundance, richness, and/or effectiveness of the local invertebrate communities, then agroecologists and farmers need to be mindful of how their pastureland management decisions could affect close-by crop yields.

Numerous academic studies have attempted to examine the impact of grazing on floral and faunal communities (Borschig et al., 2013; Bugalho et al., 2011; Diaz et al., 2007; O'Neill et al., 2010; Rook et al., 2003; Yoshihara et al., 2008). From such studies, it is clear that overgrazing can have a negative impact on invertebrates. Grazing mainly affects invertebrate communities via alterations to the plant communities in a system (Borschig et al., 2013; Bugalho et al., 2011; Rook et al., 2003). Grazing livestock modify – via defoliation, treading, pawing, trampling, and the excretion of dung and urine – the relative abundance and competitive capacities of various plant species and favor a few species that can tolerate such alterations, therefor

reducing botanical diversity (Vickery et al., 2001). Grazing also changes the diversity, structure, and growing habits of the resident plant communities. All of these alterations to the vegetation of an area undoubtedly can impact the associated invertebrate community (Black et al., 2011; Rook et al., 2003). Additionally, soil compaction (via the hooves of grazing livestock) can make the soil habitat unsuitable for many invertebrate species (McLaughlin and Mineau, 1995). Grazing also modifies vegetation structure, microclimate, and soil physical properties in ways that can be unfavorable to invertebrates (Borschig et al., 2013; O'Neill et al., 2010). Not only do these livestock-induced landscape modifications create less than ideal ecosystems for certain invertebrate species, but they can destroy nesting sites and remove potential insect foraging and/or sheltering habitats (Black et al., 2010). Not surprisingly, such ecosystem changes have indeed been shown to reduce arthropod abundance and diversity in at least some systems (Batary et al., 2012). Reduced vegetation complexity was found to reduce both spider diversity and aphid capture rates (Diehl et al. 2013). In the United Kingdom, invertebrate abundance was found to increase following decreases in grazing intensity (Eshen et al., 2012). In an experiment which compared grazed plots with grazing-excluded plots, grazing at lower intensities was thus found to increase habitat heterogeneity and invertebrate diversity (Bugalho et al., 2011).

Livestock grazing has been a significant component of life in the Mediterranean for thousands of years. In recent decades, grazing intensity has increased following European Union subsidies that encourage pastoralists to graze their lands at higher densities by offering annual cash bonus incentives to shepherds for each additional goat or sheep they add to their flock (Bugalho et al., 2011).

A study in a Mediterranean climate ecosystem by Mayer (2004) found that more intensely grazed sites have lower abundance and diversity of insects than ungrazed sites, and that “fruit set is compromised under heavy grazing pressure” (Mayer, 2004). Preliminary data from past research

projects by University of Michigan students suggest that overgrazing impacts the populations of native invertebrates, which in turn could undermine their ability to provide essential ecosystem services such as biological pest control and pollination (W-C. Cheng, 2015).

The purpose of this research is to attempt to quantify the impact of livestock grazing effects on pest suppression services and pollination services. I hope to answer the following questions: Do more intensely grazed landscapes exhibit reduced invertebrate diversity and/or abundance when compared with more natural landscapes? Does declining diversity in natural enemies have a measurable effect on the actual pest suppression services provided by the natural enemy community? Does declining pollinator diversity have implications for the actual effectiveness of pollination services? In other words, does declining invertebrate biodiversity caused by increased livestock grazing intensity lead to a reduction in ecosystem services provided?

2. Methods

2.1 Location

All data were collected between May 13 and July 21, 2014 on the island of Naxos, the largest (430 km²) island in the Cyclades island cluster in the Aegean Sea (Greece). Located roughly midway between the Greek and Turkish mainlands, Naxos represents a typical Mediterranean landscape, featuring small urban centers, traditional villages, and mixed agro-pastoral ecosystems. Situated at the center of a globally important biodiversity hotspot, Naxos has a tremendous amount of biodiversity, especially in terms of plant and invertebrate taxa (Vogiatzakis et al., 2008). The interior of Naxos is dominated by maquis and phrygana plant communities. Phrygana communities consist of low woody, spinose, aromatic shrubs, are very species-rich (Vogiatzakis et al., 2008), and are typically grazed by free-ranging mixed herds of sheep and goats. The Cycladic islands have been grazed for thousands of years, a fact even reflected in the etymology of the region: ‘Aegean’ comes from the Greek word *αίγα* (goat). In recent years, European Union subsidies have encouraged shepherds to enlarge their herd size resulting in larger livestock populations and by extension increased grazing pressure (Hadjigeorgiou, 2011).

2.2 Study Sites

We established 14 study plots on the island along a gradient of grazing intensity, from which stocking rate and dung mass data were obtained (**Figure 1**). The gradient ranged from areas that experienced low/no grazing to areas that were heavily grazed. Low grazing sites were characterized by the dense vegetation cover of tall phrygana bushes, while the most heavily grazed sites harbored only discontinuous plant cover, often with large areas of barren ground between sparse patches of grazing-resistant vegetation. To avoid confounding effects, all sites were selected to have the same elevation (<400 m asl), slope (<10%), and substrate (limestone).

2.3 Grazing Intensity

We quantified grazing intensity using two primary metrics: stocking rate and dung mass. The stocking rate was defined as the number of grazing animals (goats and sheep) stocked per 1000 m². Stocking rates on the study plots were quantified through field flock counts and confirmation of these numbers through interviews with local shepherds (Victor, 2014). Dung mass, measured in grams of dried dung, provided an estimate of the biomass consumed by livestock at each site. Dung mass at each site was determined by sampling along a 100-meter transect and collecting and weighing the dung present within 0.8 meters of the transect line. The stocking rate and dung mass measurements used in this study were collected during the summer of 2013 by student assistants. Conditions at the sites did not change between years.

2.4 Biological Control

2.4.1 Pitfall Traps

To sample the ground-dwelling arthropod community, pitfall traps were deployed at all 14 study plots in the period between May 13 and 20, 2014. At each study site, nine pitfall traps (approximately ten centimeters in diameter) were established along two perpendicularly intersecting 100 meter transect lines, with one trap in the middle of the site where the two transects met, and a trap along each transect every 25 meters. The pitfall traps themselves were small plastic cups dug into the ground so that the lip of the cup was flush with the surrounding substrate, allowing invertebrates traveling on the ground to fall into the trap. A small amount of ethylene glycol was placed in each trap to kill and preserve any specimens. Finally, a rock “shelter” was constructed above each pitfall trap, which served to keep out rainwater and prevent livestock from stepping into the traps. These shelters were constructed so that a flat rock resting upon three smaller rocks formed

an elevated cover over the opening of the trap, which allowed invertebrates to fall into the trap but prevented larger animals from falling into or damaging the traps. After a standardized number of days, the contents of each trap were collected and placed into jars for further analysis in the laboratory. Once in the laboratory, the invertebrates collected in the pitfall traps were dried, sorted, and identified to Family. The number of individuals in each family, the number of families, and the relative weight of the largest families (i.e. biomass in gram) per pitfall trap were recorded. Predatory invertebrates (those that could be considered potential natural enemies to crop pests e.g. Coccinellidae) were furthermore also recorded separately.

2.4.2 Predator Exclusion Experiments

The main component of the biological control aspect of the research was a series of predator exclusion experiments. These experiments were designed to produce a quantifiable measurement of pest suppression services in a given area, to be compared between areas under different grazing intensities. We tested the hypothesis that at lower grazing intensities, larger number of pest predators would be present, resulting in a “pest suppression effect”, and conversely this pest suppression ecosystem service would be weakened in areas of more intense livestock grazing.

This experiment was conducted on three of the 14 study plots, selected to represent three levels of grazing intensity: one site experiencing high levels of grazing, one experiencing moderate levels of grazing, and one site experiencing little to no grazing (henceforth referred to as “high grazing,” “moderate grazing,” and “low grazing”).

The experiment involved comparing aphid growth rates on plants that were either open to the entire invertebrate predator community or surrounded by a fine mesh designed to exclude natural enemies and allow the aphids to grow unaffected by predation.

The plants that were put into the field were designed to essentially serve as scaffolding and self-contained microhabitats for the aphids. Two

different varieties of common garden plants, celery (*Apium graveolens*) and black bell peppers (*Capsicum annuum*), were purchased at a local nursery. Multiple species of plants and aphids were used in a redundant design in case one plant species could not grow in the field and/or a certain aphid species could not colonize one of the plant species. In a laboratory setting, each experimental plant was potted in approximately 1.5 liters of topsoil in a large pot which allowed for sufficient room to grow over the course of the field season. A wire-framed cage was built over each plant, large enough to allow for foliage growth throughout the season. This metal frame was designed to support a mesh covering to keep predators from reaching the aphids, and to keep the aphids from escaping. Twenty adult aphids were transferred from a harvested pomegranate tree branch onto each individual celery and pepper plant using Q-tips. Black aphids (*Brachycaudis persicae*) were placed on the celery and peach potato aphids (*Myzus persicae*) were placed on the peppers because each of those species grew more reliably on these particular plant species. After each plant had 20 living aphids on it, their wire frames were enclosed in mesh in preparation for transfer to the field. The meshed plants were given time to sit undisturbed in the lab to allow the aphids to settle on the plants (**Figure 2**). In total, 96 experimental plants were seeded with aphids, 32 for each site, divided evenly between celery and peppers (16 of each species at each site).

At each of the sites, plants were sunk into the ground in parallel rows inside two separate rectangular sub-plots approximately 1.5 meters by 3 meters (two sub-plots per site to guard against site effects). Native vegetation in each sub-plot was cleared to make room for the experimental plants. The ground surrounding the experimental plants was then littered with natural vegetation fragments and detritus in order to recreate natural conditions as best as possible. The potted plants were buried in the local substrate so that the lip of the pot was level with the ground, allowing unrestricted access to the plants by ground-dwelling invertebrates. Celery and pepper plants were mixed and dispersed randomly between the two sub-plots. Once the plants

were successfully implanted into the soil, the mesh covering was removed from the control plants to allow invertebrate predators access to the aphids. While it is impossible to ensure that the aphids remained on their original plant, each was planted with enough space between them that they did not touch or overlap, thus preventing the aphids from moving between plants (Losey and Denno, 1998).

At the start of the aphid counts, each of the sites contained 32 plants; 16 celery and 16 peppers, with individuals of each plant species divided evenly between control (open) and treatment (meshed) conditions (eight control plants and eight treatment plants of each species per site).

Each of the experimental sub-plots were surrounded by 1.0-1.5 meter high metal fencing, secured with rebar poles and wire to ensure that the plants were not eaten or disturbed by livestock or any other large grazing animals. Every individual plant was frequently watered, each receiving about 1.5 liters of water every two days. To minimize desiccation of the ground inside the plots, water from a backpack sprayer was misted on the ground after the plants had been watered. The leaves of the experimental plants were not sprayed directly in order to avoid disturbing the aphids and magnifying sun damage to the leaves. To minimize the potential detrimental effects of wind on the aphids, each plot was either constructed adjacent to a stand of bushes or small trees to serve as a wind break, or a windbreak was constructed around the fencing using vegetation clippings. These efforts were intended to keep the environments inside each plot as consistent as possible, and as natural for aphids and their predators as possible.

Following transportation to the field, the experimental plants were left undisturbed for a few days to allow the aphids time to settle onto the plants after the stress of relocating from the lab to the field. After this settling period, aphid counts began. Every individual aphid on every experimental plant in each plot at each site was meticulously counted by the same individual (to ensure consistency) every ten days for six weeks, between June 4 and July 20. The order in which the plants were counted for aphids was

randomly varied to reduce bias. For the treatment plants, the meshing was carefully removed to ensure the aphid counts were as accurate as possible, then replaced immediately after counting to ensure that potential natural enemies did not have access to the plant.

Linear mixed-effects models were run using R software (version 0.98.501) to determine the effect of grazing intensity on the aphid counts.

2.5 Pollination Services

We conducted two investigations attempting to evaluate and quantify pollination services across the gradient of grazing intensity. Pollinator observations and pollen grain counts were conducted at 13 sites in July of 2014 (one site was excluded due to logistical challenges). Both studies were designed to look at the entire pollinator community, rather than focusing on a single species or subgroup of pollinators (i.e. non-native honeybees).

2.5.1 Pollinator Observations

To assess the effectiveness of the pollinator community at each site, pollinator observations were carried out during the second half of the field season. Because the main species of melliferous plant on the island of Naxos is a hardy native species of thyme (*Coridothymus capitatus*), observations were focused on this taxon. A 0.8 m x 0.8 m wooden quadrat was placed over a randomly selected bush of flowing thyme. From a 1-meter distance from the thyme bush, we conducted pollinator observations over a 6-minute period. During this period, every time a pollinator landed on, or touched a thyme flower, it was recorded as a single pollinator visit. For example, one honeybee touching 5 different flowers and 5 honeybees touching one flower each would both be recorded as “5 honeybee (*Apis*) visits.” Every invertebrate to land on a thyme flower was counted as a potential pollinator, and the number pollinator visits, as well as the morphospecies group of the pollinators were recorded. The number of thyme flowers inside the 0.8 x 0.8 meter quadrat was counted in order to obtain a measure of pollinator visits

per thyme flower. At each study plot, 10 six-minute observations were carried out on ten different thyme bushes, totaling one hour of pollinator observations at each site. Observations were carried out during the period of July 7 to 17. All observations were conducted during daylight hours, under moderate wind conditions and before the hottest part of the day (mid-late afternoon) to ensure good pollinator presence. The observation data was analyzed by the number of pollinator visits per flower per site.

2.5.2 Pollen Counts

The final aspect of the pollination services portion of this research project was to quantify differences in the number of pollen grains on thyme stigmas between the different sites. This metric was intended to provide a measure of the effectiveness of the local pollinator community. Because thyme was the only plant blooming during the pollination portion of this study, all pollen grains present on stigmas were considered to belong to this species (Brabant et al., 1980; Kearns and Inouye, 1993). It is generally thought that, the more pollen grains present on the stigmas of local flowers, the better the pollination services in that area (Abrol, 2012). We hypothesized prior to beginning the pollen counts that the sites with more intense grazing would have fewer pollen grains per stigma on average.

At every site, after all pollinator observation periods were concluded, between 10-15 live, blooming thyme flowers were randomly selected, harvested, and carefully secured in separate containers for transport to the lab. Within six hours of returning the laboratory (to prevent desiccation), stigmas from the harvested thyme flowers were carefully extracted using tweezers. Microscope slides were prepared by staining the stigmas with a methyl blue dye (Kearns and Inouye, 1993) and gently pressing them under a cover slip. The slides were then observed under a compound microscope at the 10x magnification power, and every visible pollen grain was counted. Between ten and twenty stigmas were counted per site, from which an average pollen grain count per site was determined.

Linear mixed-effects models were run using R software to determine the effect of grazing intensity on the pollen counts.

All correlations below are given using Pearson's r unless otherwise noted.

3. Results

3.1 *Biological Control*

3.1.1 *Pitfall Traps*

Pitfall trap contents revealed that the total population of potential predators per site (i.e. number of individual predators) remained essentially unchanged across the 14 study plots along the gradient of grazing intensity, as measured by both stocking rate and dung mass (stocking rate: $r = 0.074$, $p = 0.445$, $n = 108$; dung mass: $r = 0.077$, $p = 0.428$, $n = 108$). Predator species richness – the number of predator species present at each site – also remained statistically unchanged across the different grazing intensities (stocking rate: $r = 0.080$, $p = 0.786$, $n = 14$; dung mass: $r = -0.103$, $p = 0.726$, $n = 14$).

Vegetation characteristics across the study plots were also evaluated as razing intensity can affect important vegetation characteristics in an ecosystem: vegetation height and biomass decreased with increasing grazing intensity at the sites due to the effects of grazing livestock. Consequently the average gap size between vegetation at a site, both basal gap and canopy gap, increased with increasing grazing intensity because patches of living vegetation grew sparser and patches of barren ground grew more frequent as grazing intensity increased (Brenton, 2016). We also investigated the relationship between the predator community (total predators and species richness) and various vegetation characteristics. In general there was little relationship between many metrics of invertebrate predator communities and many vegetation characteristics. There was no significant relationship between total individual predators and vegetation height/biomass (vegetation height: $r = 0.125$, $p = 0.199$, $n = 108$; vegetation biomass: $r = 0.196$, $p = 0.042$, $n = 108$), and total individual predators and canopy/basal gap (canopy gap: $r = -0.123$, $p = 0.206$, $n = 108$; basal gap: $r = -0.109$, $p = 0.260$, $n = 108$). However, predator species richness increased with rising vegetation biomass ($r = 0.316$, $p = 0.001$, $n = 108$; **Figure 3**); it also declined significantly with

increasing basal gap, and almost significantly declined with increasing canopy gap (basal gap: $r = -0.239$, $p = 0.013$, $n = 108$; **Figure 4**; canopy gap: $r = -0.183$, $p = 0.058$, $n = 108$). Total individual predators also increased with increasing vegetation biomass ($r = 0.196$, $p = 0.042$, $n = 108$; **Figure 5**).

Predator data were further subdivided into the main categories of “Araneae,” “Coleoptera,” and “Other” predators as the majority of individual predators fell into one of these three groups, with Araneae and Coleoptera dominating.

The number of predatory Coleoptera per site increased non-significantly with grazing intensity (dung and stocking) (stocking rate: $r = 0.103$, $p = 0.288$, $n = 108$; dung mass: $r = 0.132$, $p = 0.173$, $n = 108$), while the opposite pattern was observed for total individual Araneae per site and grazing intensity (decreased non-significantly) (stocking rate: $r = -0.200$, $p = 0.494$, $n = 108$; dung mass: $r = -0.154$, $p = 0.599$, $n = 108$). However, because these relationships are not significant, there is little evidence for a relationship between grazing intensity and Coleoptera or Araneae. Populations of Other invertebrate predators (e.g. Reduviidae, Cimicidae, Dermoptera, etc.), appeared to increase significantly with grazing intensity although the strength of this relationship depends on the grazing metric used (stocking rate: $r = 0.559$, $p = 0.038$, $n = 108$; dung mass: $r = 0.473$, $p = 0.088$, $n = 108$).

No significant relationship existed between total Coleoptera per site and vegetation biomass/canopy gap/basal gap (vegetation biomass: $r = -0.066$, $p = 0.497$; canopy gap: $r = 0.026$, $p = 0.790$; basal gap: $r = 0.065$, $p = 0.504$). The one group of invertebrate predators that was strongly affected by vegetation structure were spiders (Araneae). Total individual Araneae per site increased significantly when correlated with vegetation height and vegetation biomass (vegetation height: $r = 0.235$, $p = 0.014$, $n = 108$; vegetation biomass: $r = 0.324$, $p = 0.001$, $n = 108$), indicating that spiders increased in abundance in areas of greater vegetation biomass. Total individual Araneae per site decreased nearly significantly with increasing canopy gap and basal

gap, indicating that spider abundance declined as grazing intensified (canopy gap: $r = -0.205$, $p = 0.034$, $n = 108$; basal gap: $r = -0.215$, $p = 0.025$, $n = 108$).

3.1.2 Predator Exclusion Experiments

Over the course of the field season, experimental plants at the “natural” (low-grazing) experimental site were gradually destroyed by an unidentified species of rodent. Despite continued and evolving efforts to keep grazing livestock and smaller mammals from the experimental sub-plots, most of pepper and celery plants were eaten, including those that were meshed. The rodents clawed or chewed through any predator-exclusion mesh and any additional covering put in place to protect the plants. All plants were destroyed and/or eaten after roughly the midpoint of the field season: too early to obtain any partial statistical data from the aphid counts, and too late to replant new experiment plants or select a new low-grazing site. Thus, the statistical power of the aphid counts was greatly reduced as the available data only compared one heavily-grazed site with one moderately-grazed site.

For both plant species, the aphid populations on both meshed and open plants grew much better at the moderately-grazed site. However, aphid growth rates varied considerably between different individual plants and between plant species. The only consistent trend was that under both grazing regimes and both plant species, the aphids populations grew and persisted far better under the predator exclusion mesh than they did on the plants exposed to the invertebrate predator guild.

3.2 Pollination Services

3.2.1 Pollinator Observations

Flower coverage (m^2) during the peak of the springtime flower bloom varied between sites, with more heavily grazed sites having fewer flowers at peak spring flower bloom than lower-grazing sites. Thyme flower coverage (m^2) peaked at moderate levels of grazing intensity, at approximately 4.0 livestock/hectare or around 7.0 g of dung per m^2 .

Based on our record of pollinator observations, we calculated the Shannon-Wiener diversity index for each study plot. Pollinator diversity across the study plots did not correlate significantly with grazing intensity (stocking rate: $r = 0.073$, $p = 0.812$, $n = 13$; dung mass: $r = 0.056$, $p = 0.856$, $n = 13$). Similarly, there was no significant pattern observed between the visitation rate and grazing regime across the study plots (stocking rate: $r = 0.042$, $p = 0.892$, $n = 13$; dung mass: $r = -0.095$, $p = 0.758$, $n = 13$). No relationship exists between vegetation biomass and pollinator visitation either (visitation: $r = -0.448$, $p = 0.125$, $n = 13$). There was no significant relationship between the area of thyme flower (the m^2 of thyme flower) at a site and the visitation rate ($r = 0.384$, $p = 0.196$, $n = 13$). The same pattern was observed with thyme bush area as well but less significantly ($r = 0.302$, $p = 0.317$, $n = 13$).

3.2.2 Pollen Counts

We found a strong positive statistical relationship between pollen count and grazing intensity, whether quantified by dung mass or stocking rate (stocking rate: $r = 0.357$, $p < 0.001$, $n = 227$; dung mass: $r = 0.320$, $p < 0.001$, $n = 227$; **Figures 6 & 7**). As grazing intensity increased, pollen per stigma increased as well.

Another statistically supported correlation is between pollen grains per stigma and thyme flower area at a site. The higher the thyme flower coverage at a site, the fewer pollen grains were detected per stigma at that site ($r = -0.307$, $p < 0.001$, $n = 227$; **Figure 8**). Thus the amount of pollen grains decreases with thyme flower coverage.

However, pollen count and visitation rate appeared to have no significant statistical relationship (total visitation: $r = -0.018$, $p = 0.782$, $n = 227$). This holds true whether looking at potential pollinators in aggregate, or separated into *Apis* and non-*Apis* groups and investigating each individual group's visitation rate. This would appear to indicate that although pollen count increases with grazing intensity, it is not because the sites with more

pollen per stigma are receiving a higher rate of pollinator visits (Non-*Apis* visitation: $r = 0.165$, $p = 0.013$, $n = 227$; *Apis* visitation: $r = -0.107$, $p = 0.107$, $n = 227$).

Average pollen per stigma per site and visitation rate per site when compared directly revealed no pattern ($r = 0.040$, $p = 0.896$, $n = 13$).

In a follow-up analysis utilizing a linear mixed-effects model for the effects of both stocking rate and dung mass separately, both predictors were found to have significant positive effects on pollen count (stocking rate: 0.836 , $p = 0.007$; dung mass: 0.447 , $p = 0.019$), with stocking rate being the better indicator of pollen count.

4. Discussion

4.1 Biological Control

The results obtained from the pitfall trap contents in this study indicate that the overall number of potential natural pest control agents did not change across a gradient of grazing intensity. This could be interpreted as evidence against our initial hypothesis which stated that increases in grazing intensity should result in more depauperate invertebrate predator communities. Thus, according to this initial hypothesis, one would expect fewer predators and hence attenuated pest suppression services at locations under higher grazing pressure. Predator species richness - the number of natural predator species present at each site - remained statistically unchanged across the different grazing intensities, and was therefore not found to be affected by livestock grazing (although the relative proportion of each species group may in fact change with grazing intensity). Predator species richness did however increase with increasing vegetation biomass, and almost significantly declined with increasing amounts of gaps in the vegetation canopy. This is likely because sites with dense, lush vegetation (as indicated by smaller gaps in vegetation and more vegetation biomass) are likely to support more complex and more diverse invertebrate communities. Vegetation more closely spaced together means greater potential for diverse trophic interactions, as well as more vertical niches which in turn can support more invertebrate taxa (Caballero-Lopez et al., 2012; Eschen et al., 2012). Total populations of invertebrate predators also increased with rising vegetation biomass, in line with the expectation that sites with denser vegetation will be better able to support higher densities of predator populations.

Total number of spiders (Araneae) decreased with declining vegetation. This indicates the Araneae are more prevalent at less-grazed i.e. more densely vegetated sites, which dovetails with the well-known need of spiders to use vegetative structure to support their webs (Diehl et al., 2013).

Furthermore, Araneae are also thought to be more susceptible to desiccation in open habitats (Kovacs-Hostyanszki et al, 2013), further explaining why they would be more prevalent in areas with denser vegetation.

Coleoptera are thought to be the most significant predator of aphids in natural ecosystems (Aquilino et al., 2005). Given the lack of relationship between predatory Coleoptera numbers and grazing intensity, one might conclude that there is no support for the hypothesis that quality of pest suppression services is affected by levels of livestock herbivory. However, such a conclusion is undercut by the fact that beetles are just one of several categories of invertebrate predators so that their numbers can give only a partial picture. Ultimately the data obtained from the pitfall traps are inconclusive and cannot provide certainty as to whether pest suppression services are degraded by higher grazing intensities.

The results of the predator exclusion experiments are also inconclusive. The primary outcome of our experiments was the observed difference in aphid growth rates between the meshed and open experimental plants, with aphid populations growing much more robustly under the predator exclusion mesh irrespective of the presence or absence of natural predators. If this is a correct interpretation, it would suggest that meshing a plant provided additional benefits beyond predator exclusion, perhaps in the form of reduced airflow and thus attenuated desiccation risks for the meshed aphids.

It is also possible that abiotic conditions varied between the two experimental sites. The moderately-grazed site had greater plant biomass, perhaps suggestive of greater local humidity and lower wind speeds, both factors that may have provided better growing conditions for aphid propagation (Diehl et al., 2013). While every effort was made to control for matched abiotic conditions within each experimental sub-plot, the high grazing site was also closer to the ocean, and thus subject to stronger winds.

Another factor that might have affected the results of aphid counts was the presence of ants on the experimental plots. Many species of ants will

develop symbiotic relationships with aphids, protecting them from predators and “milking” their secreted honeydew. Some ant species will go so far as to “farm” the aphids, carrying entire populations of aphids back-and-forth between their colonies and plants where the aphids feed (Losey and Denno, 1998). At one point or another, ants were observed on all study plants, and while they were never observed explicitly tending aphids, it would not be surprising if their presence affected aphid population growth at least in some instances.

Overall, because the predator exclusion portion of this research examined only one site at each of three grazing intensities (high, moderate, and low grazing) – and because of the loss of data from the ungrazed site due to rodent predation, we cannot draw any firm conclusions regarding the effects of grazing on pest suppression. While the fact that aphids grew better at the moderately grazed than at the heavily grazed site is suggestive of the effects of ecosystem services being dependent on grazing conditions, this pattern can also be attributed to a variety of alternative factors. Further research is needed to elucidate the relationship between levels of livestock herbivory and ecosystem services in Mediterranean ecosystems.

4.2 Pollination Services

Our initial hypothesis postulated that sites under more intense grazing pressure would have less-diverse pollinator communities due to poorer vegetative and floral resources. However, our pollinator observation data indicate that the intensity of grazing appears to not be correlated with either the diversity of the active pollinator community or the pollinator visitation rate. This lack of relationship may be best attributed to the substantial mobility of most invertebrate pollinators: because they can range across fairly large areas, local conditions may not matter to them much. Furthermore, any negative relationship between grazing intensity and pollinator presence may be obscured by the presence of thyme, the only substantial flower species in the area, and a species that does reasonably well even in moderately grazed

areas. In other words, because in grazed areas, thyme –which by virtue of its strong taste is both relatively grazing-resistant, but also a prolific nectar producing plant – is more common, there may be more flowers attracting pollinators.

A counter-intuitive result of this study was that areas with more thyme had less pollen on each stigma. This negative correlation can be best explained by the number of available thyme flowers and the nature of the pollination process per se. Thus, in areas where grazing is increasingly heavy, thyme populations, as well as the flowers they produce, start to decline. In such intensely grazed areas, relatively few flowers are present, and each of them is subject to a high degree of visitation by the remaining pollinators, resulting in high stigma pollen counts in the most heavily grazed areas. Thus, the negative impact of heavy grazing on thyme populations overrides the concomitant decline in pollinator populations and results in increased pollination services in the flowers that do persist. Additionally, the amount of pollen produced per flower may be higher at the more intensively grazed sites as each bush produces fewer flowers and more resources can be committed to each flower. There can be significant differences in the number of conspecific pollen grains produced between different sites (Vulliamy et al., 2006).

Although flowering patches of thyme were selected at random for the pollination portion of this study, even at high grazing sites, there may still have been a statistical bias in the pollinator observation and pollen count data. At high grazing sites, thyme flowers tended to be the only flowers available, so to specifically target and sample them introduced bias – only getting data from very robust flowers at the heavily grazed sites. If this study were to be re-done, perhaps randomly selecting points within each site for observations, and counting patches of barren ground as a “zero,” for zero floral resources (representing a hypothetical flower that was not present at the site possibly due to grazing), would improve the statistical power.

4.3 Final Conclusions

The aim of this study was to obtain a quantitative measure of the effects of overgrazing on pest suppression and pollination services. Because the results of the predator-exclusion experiments were essentially inconclusive largely due to matters beyond our control, we were not able to generate any meaningful metric for quantifying the effects of livestock grazing on pest suppression services. The invertebrate predator pitfall data were collected and analyzed as an additional way to complement the results that were observed from the predator-exclusion experiments. Because pest suppression service data are available for only two of the total sites, it is not possible to readily compare predator abundance or diversity with pest suppression services, and thus predator population data can only be used as an approximate guide to formulate further ideas about why the pest suppression experiments produced such unexpected results.

Regarding pollination, the data obtained from pollinator observations revealed little about the relationship between livestock grazing intensity and pollination services. Because the diversity of the pollinator community did not vary across the gradient of grazing intensity, and because visitation rate did not change either, few conclusions can be drawn from these observations. The pollen count per stigma data reveals by far the most interesting and statistically significant relationship of anything in our study: the fact that the relationship between grazing intensity and pollen per stigma appears to be driven by thyme flower coverage. It is clear that more research is needed to elucidate the relationships between grazing intensity and pest suppression and pollination services.

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6. Figures

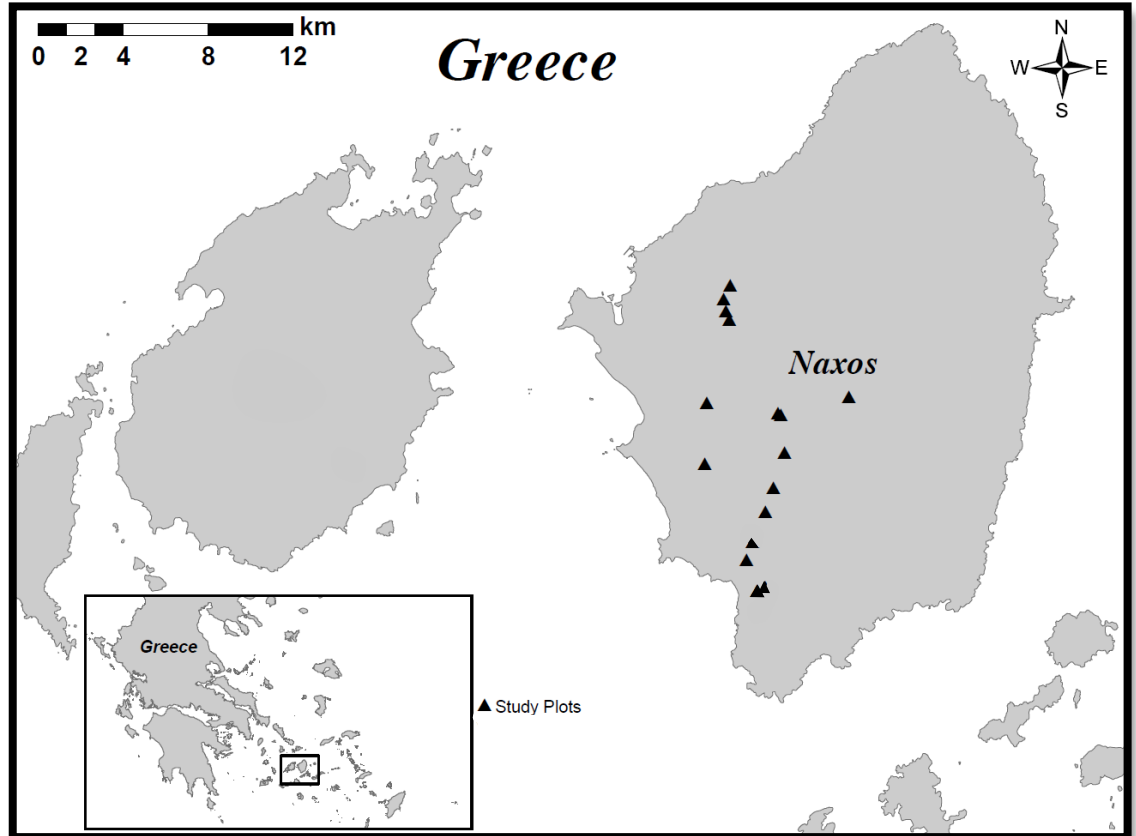


Figure 1: Location of study plots on Naxos, Greece.



Figure 2: Example of an experimental pepper plant covered in predator-exclusion mesh.

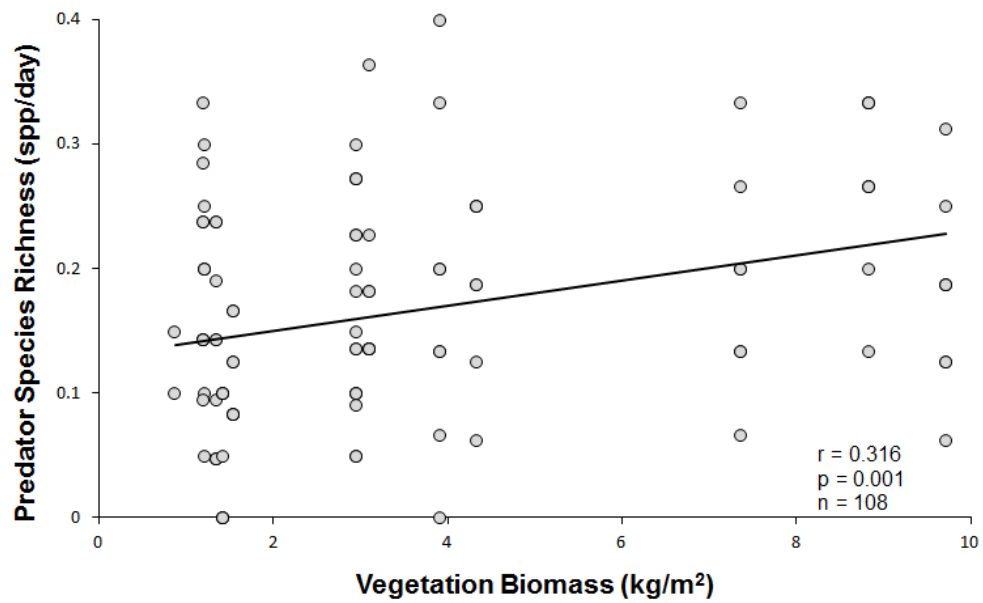


Figure 3: Scatterplot comparing vegetation biomass with predator species richness (Pearson's $r = 0.316$, $p = 0.001$, $n = 108$).

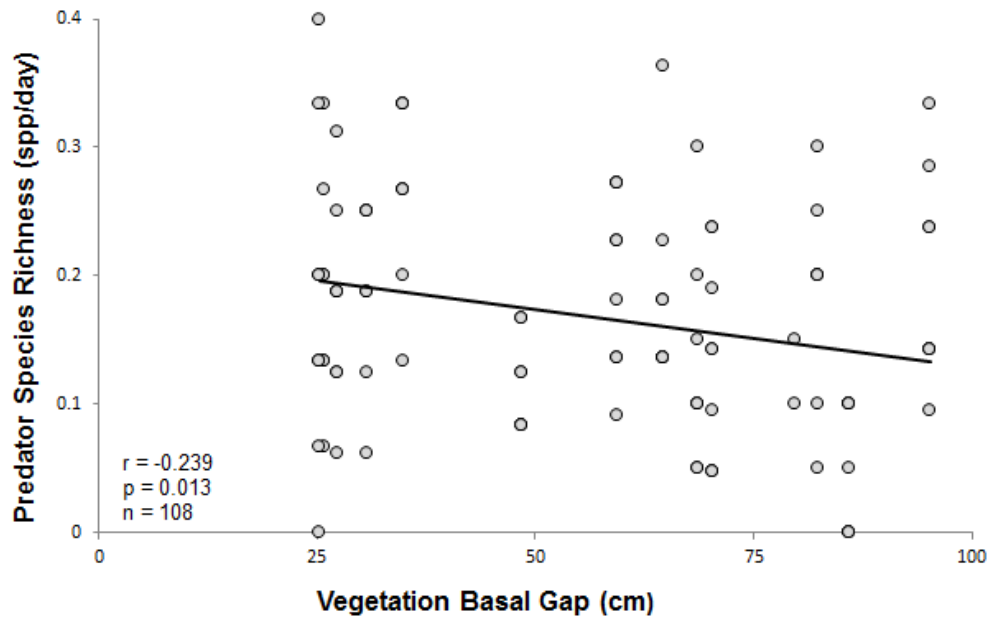


Figure 4: Scatterplot comparing vegetation basal gap with predator species richness (Pearson's $r = -0.239$, $p = 0.013$, $n = 108$).

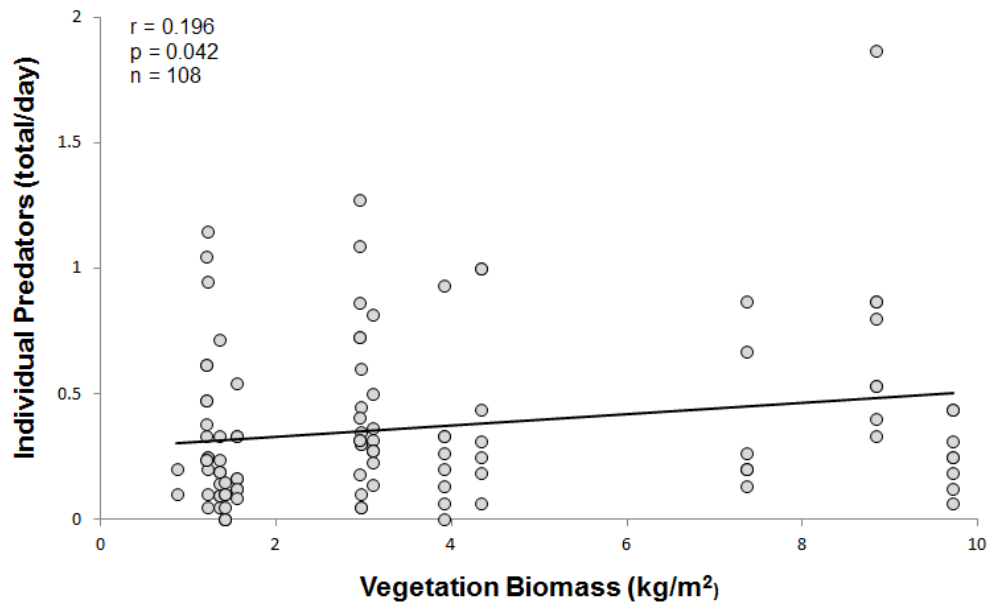


Figure 5: Scatterplot comparing vegetation biomass with total individual predators (Pearson's $r = 0.196$, $p = 0.042$, $n = 108$)

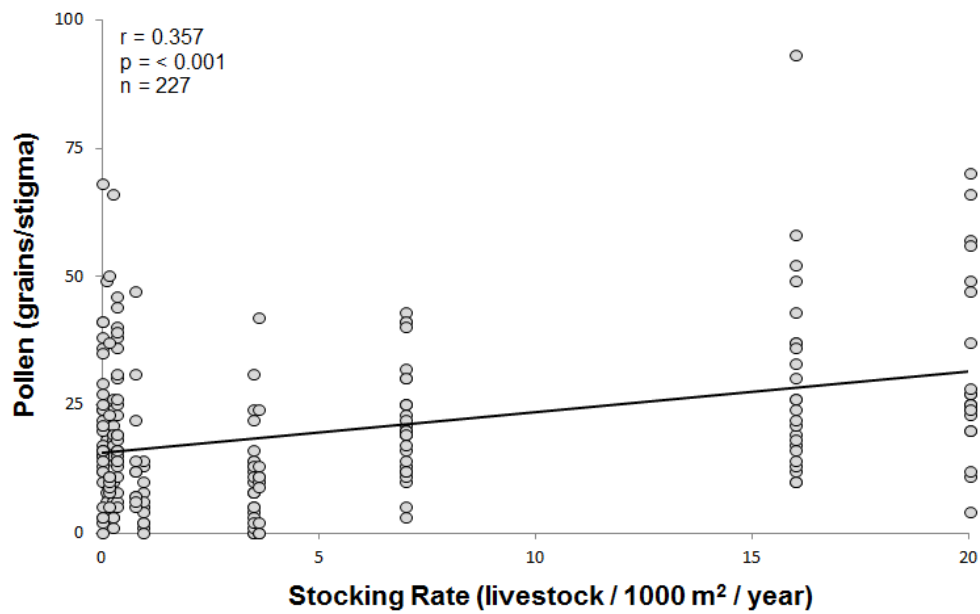


Figure 6: Scatterplot comparing pollen count with stocking rate (Pearson's $r = 0.357$, $p < 0.001$, $n = 227$).

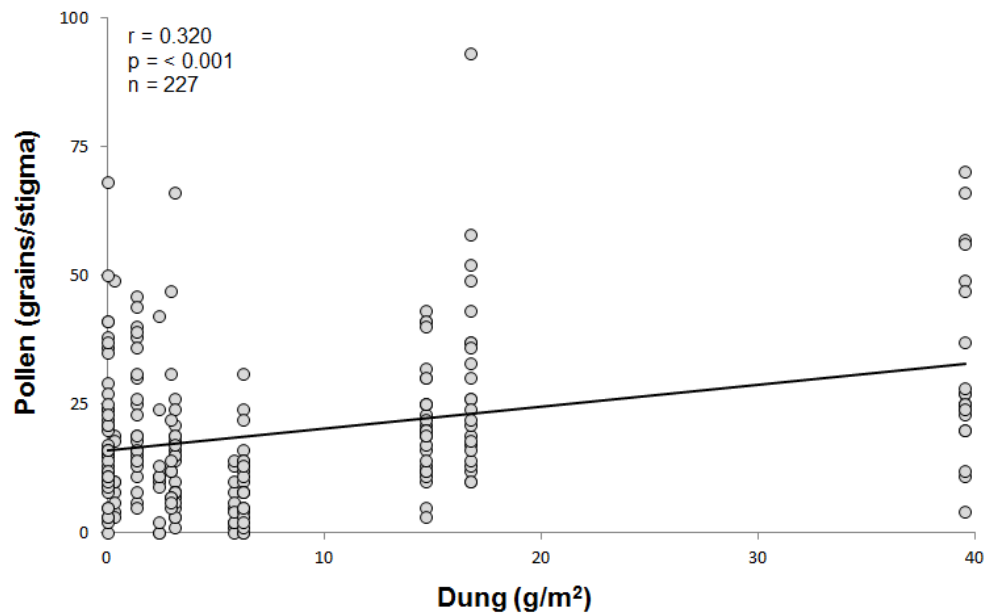


Figure 7: Scatterplot comparing pollen count with dung mass (Pearson's $r = 0.320$, $p < 0.001$, $n = 227$).

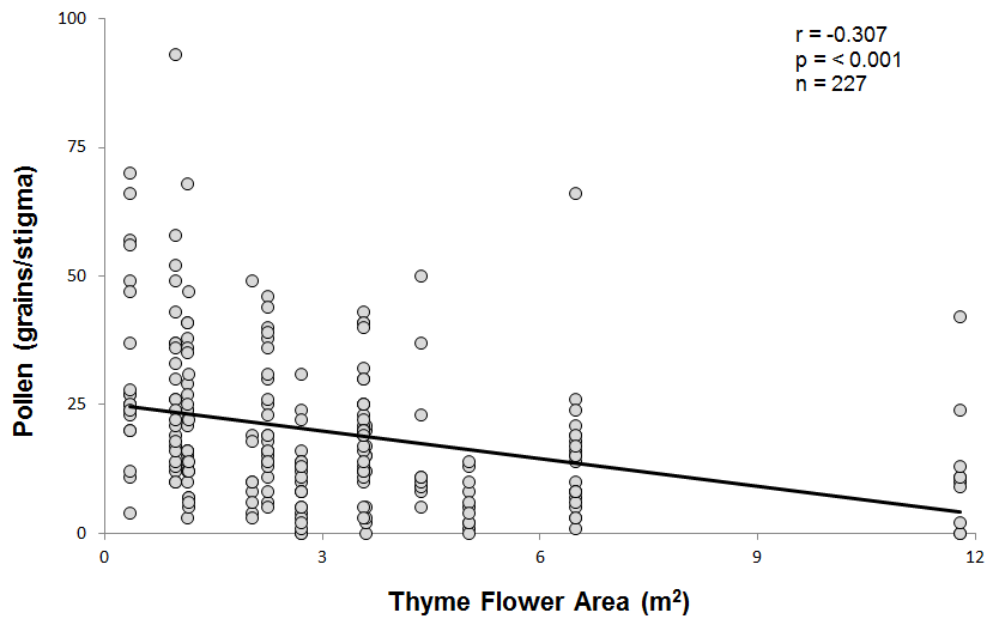


Figure 8: Scatterplot of pollen count against thyme flower coverage (Pearson's $r = -0.307$, $p < 0.001$, $n = 227$).

7. Tables

Table 1: Summary table comparing grazing intensity, vegetation condition, and pitfall trap results (predator species richness and total predators) between the fourteen study plots.

Site	Stocking Rate (animals/1000m ²)	Dung Mass (g/m ²)	Vegetation Biomass (kg/m ²)	Canopy Gap (cm)	Basal Gap (cm)	Predator Species Richness (Spp/trap/day)	Total Predators (pred/trap/day)
Agios Dimitrios Galanadou	0.0	0.0	8.84	9.0	34.7	0.083	0.775
Kokimas Galanadou	0.0	0.0	7.36	16.0	25.7	0.095	0.362
Agios Nikolaos Galanadou	0.15	0.0	4.34	5.1	30.7	0.107	0.464
Lofos Galanadou	0.10	0.33	3.92	16.2	25.3	0.092	0.283
Stavropigi Vivlou	0.36	1.0	9.71	18.4	27.3	0.076	0.257
Upper Bazeos tower	0.35	1.33	2.96	47.9	68.5	0.081	0.388
Platia Rachi	3.61	2.39	3.10	52.1	64.7	0.086	0.369
Koutsouria Filotiou	0.75	2.94	2.96	35.1	59.3	0.066	0.657
Upper Aghiassos	0.25	3.11	1.42	56.8	85.9	0.028	0.056
Gialous Agiassou	0.94	5.83	1.54	27.5	48.4	0.052	0.234
Lower Aghiassos	3.50	6.22	1.36	59.8	70.2	0.085	0.291
Lower Bazeos tower	7.0	14.67	1.22	58.9	82.4	0.100	0.500
Apaliros Castle	16.0	16.72	0.87	66.3	79.7	0.100	0.175
Hohlidia Agiassou	20.0	39.50	1.20	95.8	95.2	0.063	0.503

Table 2: Summary table comparing grazing intensity, spring flower coverage, thyme flower coverage, pollinator diversity, visitation rate, and pollen count between the thirteen study plots.

Site	Stocking Rate (animals/1000m ²)	Dung Mass (g/m ²)	Spring Flower Coverage (m ²)	Thyme Flower Area (m ²)	Pollinator Diversity (Shannon index, H)	Visitation Rate (pollinators/flower)	Pollen Count (grains/stigma)
Agios Dimitrios Galanadou	0.0	0.0	4.22	0.20	1.96	0.07	11.0
Kokimas Galanadou	0.0	0.0	7.01	1.20	1.52	0.03	24.8
Agios Nikolaos Galanadou	0.15	0.0	15.61	1.17	1.49	0.23	17.3
Lofos Galanadou	0.10	0.33	3.68	0.06	1.79	0.04	14.1
Upper Bazeos tower	0.35	1.33	5.00	0.00	1.72	0.24	22.7
Platia Rachi	3.61	2.39	6.30	0.66	1.42	0.50	12.2
Koutsouria Filotiou	0.75	2.94	7.55	1.26	1.07	0.33	16.3
Upper Aghiassos	0.25	3.11	1.63	0.09	1.89	0.63	14.7
Gialous Aghiassou	0.94	5.83	0.93	1.30	1.75	0.17	5.9
Lower Aghiassos	3.50	6.22	1.40	1.46	1.14	0.31	10.2
Lower Bazeos tower	7.0	14.67	6.39	1.21	1.51	0.40	21.3
Apaliros Castle	16.0	16.72	2.94	1.16	1.79	0.68	28.6
Hohlidia Aghiassou	20.0	39.50	1.57	0.18	1.66	0.03	32.2