IMPACT OF LIVESTOCK GRAZING ON ECOSYSTEMS SERVICES IN A MEDITERRANEAN ECOSYSTEM

by

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A thesis submitted
in partial fulfillment of the requirements
for the degree of
Master of Science
(Natural Resources and Environment)
at the University of Michigan
December 2015

Thesis Committee:

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Abstract

Livestock husbandry is one of the most important human activities in arid regions of the planet and is the predominant driver of environmental degradation in Mediterranean ecosystems. Nonetheless, despite the very long history of animal husbandry in this region, relatively little is known on the relationship between livestock grazing and the provisioning of ecosystem services in a Mediterranean setting.

Methods. This study focuses on mediterranean heathlands (‘*phrygana*’), a species-rich plant community that is widespread over large areas of the Mediterranean Basin, and a habitat subjected to goat and sheep grazing for almost 10,000 years. We evaluate multiple trophic levels of this community (including vegetation condition and structure, floral resources, as well as populations of primary and secondary consumers), across a spectrum of livestock grazing intensities in island ecosystems in the Aegean Sea (Greece). We also evaluated some of the important ecosystem services provided by phryganic habitats to local human communities, including vegetation productivity, erosion protection, pollination services, disease dilution, and maintenance of biodiversity.

Results. Results show that all measured aspects of vegetation condition and structure (vegetation biomass, canopy cover, basal cover, plant species richness and plant diversity) decline monotonically with rising levels of livestock grazing. Furthermore, while increasingly higher herbivore stocking rates result in diminished floral resources, the effects on pollinator populations and diversity are more equivocal. Secondary consumers (*Podarcis* wall lizards) appear to benefit the most from intermediate levels of grazing intensity. However, foraging rates by honey bees (*Apis mellifera*), an economically important species in the region, decline as livestock herbivory rates rise, suggesting that there are direct tradeoffs between livestock husbandry and apiculture in these landscapes.

Conclusions. Impacts of livestock husbandry on local ecosystems depend on stocking rates used. While at low stocking rates, grazing appears to have either equivocal or both positive and negative effects on different ecosystem services, at higher stocking rates these effects become mostly negative. While there is no specific stocking rate that is likely to minimize all impacts, our results suggest that intensive grazing has clear negative ecological consequences in terms of lost ecosystem services.

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Acknowledgement

First, I would like to express my gratitude to my Professor Foufopoulos for offering the great opportunity and the support of my Master thesis and field research in Greece. It is a long journey, but gratefully I completed the challenge under his guidance.

Besides my advisor, I would like to thank Professor Bilal Butt, Lecturer Sheila Schueller, and Lecturer David Costello for the insightful comments, technical support and spiritual encouragement during my research and thesis writing.

Thanks to my team members in Foufopoulos's lab, Kinsey Brock, Anat Belasen, Caitlin Weber, Clinton Bergmann, and Mary White, who share great experience with staying up late night, hard work, and all the fun in Greece.

Last but not the least, I would like to thank my family's support of both financially and spiritually to fulfill my dream for studying conversation ecology at University of Michigan.

1. Introduction

Livestock husbandry represents one of dominant economical land uses in arid and semiarid regions of the world, and is an activity of significant importance for environmental conservation (Bignal & McCracken, 2000; Clergue, 2009). Domestication of ungulates happened first at the eastern margins of the Mediterranean Basin, and livestock husbandry remains to this day the dominant human activity in the majority of this region (Driscoll et al. 2008). At the same time, the Mediterranean Basin constitutes an important biodiversity hotspot, harboring tens of thousands of endemic species, which in turn provide valuable ecosystem services to the resident human populations (Medail & Quezel, 1997; Médail & Quezél, 1999). Despite the importance of this issue and significant early work, many of the basic processes and long-term impacts of grazing in Mediterranean ecosystems are not well understood (Papanastis & Peters, 1998; Perevolotsky & Seligman, 1998). As an example, the mechanisms and the extent to which grazing affects ecosystem services remain vague, in part because they frequently depend on spatial and temporal covariates (Caballero et al., 2007; Papanikolaou et al. 2011).

Effects of herbivory on plant community traits, function, species diversity and ecosystem services

Herbivory by livestock can affect local species communities through a multitude of pathways. First, grazing may alter the physical structure of local vegetation communities (Huntly, 1991). Fleischner (1994) provides a number of examples where defoliation by grazing herbivores alters plant height and canopy cover, and has changed species composition to include structurally different types of plants. Beyond direct biomass consumption, trampling by hooves may further impact vegetation structure simply by breaking and beating down vegetation (Fleischner 1994). Second, driven by herbivore preferences for certain plants, grazing can dramatically select for, or against, specific plant species (Szaro, 1989). Third, grazing may either increase or decrease subsequent biomass production (Huntly 1991). On the one hand, light or moderate defoliation can actually promote shoot re-growth and enhance light levels, soil moisture and nutrient availability, as plants overcompensate to tissue loss (Frank et al., 1998). Overgrazing on the other hand, can significantly reduce biomass production when plants lack sufficient leaves and tissues to accomplish substantial photosynthesis. Finally, grazing can shape plant recruitment by positively or negatively affecting seed production, dispersal, and germination. Grazing animals may directly decrease flower and seed production by consuming reproductive structures, or indirectly by stressing the plant and reducing energy available to develop seeds. However, grazing animals can also facilitate seed dispersal by transporting seed in their coats, feet, or digestive tracts (Lacey, 1992; Olson & Lacey, 1995). Lastly, for some plant taxa, grazing ungulates have been shown to promote seed germination by trampling seed into the soil (Deregibus et al., 1994).

Livestock herbivory may have either positive or negative impacts on ecosystem services, dependent both on the intensity of grazing, as well as on the prevailing local circumstances (Belsky & Gelbard, 2000). Appropriate levels of grazing may facilitate carbon sequestration by stimulating the growth of plant biomass and can promote nutrient cycling throughout the food web (Belsky, 1987). Moderate populations of herbivores can enhance mineral availability to plants by increasing nutrient cycling within patches of their waste and enhancing nitrogen availability (Holland et al., 1992). Organic components of feces and urine from grazing animals can build soil organic matter reserves, resulting in soils having expanded water-holding capacity, increased water-infiltration rates, and improved structural stability. These changes in turn can help reduce soil loss by wind and water erosion (Hubbard et al., 2004). By contrast, overgrazing has also been shown to increase wind and water erosion by reducing vegetative cover and by disturbing soil surfaces (Belnap & Gillette, 1998). Trampling by excessive livestock numbers can also lead to compaction of soils, which damages plant roots (Watkins & Clements, 1978) and causes them to become concentrated near the soil surface (Dormaar & Willms, 1998).

As the result of all of these processes, grazing by livestock can have profound effects on rangeland species diversity and richness. On the one hand, overstocking with domestic ungulates is known to have devastating effects on local plant communities by promoting a shift to plant assemblages consisting of a few, unpalatable taxa or by facilitating incursion by invasive taxa (Belsky & Gelbard, 2000). On the other hand however, moderate herbivory may also enhance biodiversity because many plant species are dependent on specific microenvironments, which are maintained by grazing animals (Donihue et al. 2013). For example, decomposing carcasses of ungulates support important communities of decomposers and scavengers, which often constitute central nodes in local food webs (Dunne et al., 2002). In the absence of herbivory, dead vegetative biomass and litter tend to accumulate with resulting declines both in plant community diversity and even in its attractiveness to nesting birds. Thus, in North American tallgrass prairies, diversity and productivity are maintained by native herbivore grazing which stimulates growth of certain grasses, and which opens the pasture to early-succession plant species (Cotgreave & Forseth, 2002).

In many semi-arid regions some of the most important effects of herbivory stem from its interaction with fire regimes. Fire frequency, intensity, and behavior are dictated largely by condition and quantity of combustible vegetation (DiTomaso & Johnson, 2006). Grazing regimes alter fuel-load characteristics by changing plant biomass, community composition, and structure, which in turn can change fire-return cycles, fire temperature, and spread patterns. Such changes in fire regimes may lead to further changes in plant community composition e.g. as fire-tolerant populations replace fire-intolerant ones. Because grazing can be used to reduce fuel-loads in an area, it is considered an important management tool for reducing fire intensity ahead of prescribed burns (DiTomaso & Johnson, 2006), and has been used to protecting forests in S. Europe and California from devastating fires (Tsiouvaras et al. 1989, Leyton & Vicente 2012).

Livestock grazing in the Mediterranean Basin

Livestock grazing has been a critically important way of life for Mediterranean societies for millennia (Papanastis & Peter 1998). Reflecting the importance of this activity, rangelands occupy the majority of marginal landscapes in the Mediterranean Basin (Grove & Rackham 2001). Grazing lands cover of 44 % of the Greek land area (ca. 5.3 million ha) (Sarlis, 1998; Zervas, 1998). Sheep and goats raised for milk and meat production make up 75% of the livestock population in Greece (Hadjigeorgiou et al., 1998). Typically, mixed flocks of these species are shepherded across unfenced pastures during the day while returning to a protected pen during the night (Zervas, 1998; Tsiboukas, 1987). Traditionally, each flock of livestock is owned by an individual family and shepherded across public lands to which grazing rights have been inherited or acquired. On the mainland and to a lesser extend on the islands, transhumance has been practiced, although such nomadic traditions have been in decline in recent years (Gkoltsiou, 2011). Livestock numbers are subject to both national and European Union-wide policies; however despite extensification efforts by the central planning authorities, a process of livestock farming intensification has occurred in many –but not all- regions of the Mediterranean North over the course of the last two decades (Hadjigeorgiou, 2011, Hadjigeorgiou & Zervas, 2009). As a result, many regions of the Mediterranean are today facing ecological changes stemming from either land abandonment or overgrazing, which can lead to desertification (Arianoutsou-Fraggitaki 1985).

Important gaps exist in our understanding of the effects of grazing on the provision of valuable ecosystem services in the Mediterranean Basin bioregion, which harbors tens of thousands of endemic species (Mittermeier et al. 2005, Cuttelot et al. 2008). Such ecosystem services, provided free of charge to local human communities, include provisioning of natural products like honey and medicinal plants, but also fundamental ecological services such as crop pollination by wild pollinators. In the Mediterranean region, robust crop pollination services are provided predominately by wild arthropod pollinator communities which have been shown to be among the most diverse on the planet (Petanidou & Ellis 1993). Both pollinator abundance and biodiversity depend critically on available floral resources (Winfree, et al. 2011). Such resources have also been shown to be important in supporting domesticated bee populations which in the Mediterranean produce a highly valued honey (Bagella et al. 2013). Floral resources in turn are apt to be shaped by levels and patterns of herbivory (Mayer, 2007; Sjödin, 2007). Recent intensification of human activities and in particular changes in grazing activity are thought to have pronounced effects on Mediterranean biodiversity and ecosystems services, though the exact degree and nature of these impacts is not well understood. Nonetheless, understanding how human activities and in particular livestock grazing affect such services is critical if local communities are to make sustainable management decisions.

The central focus of this study is to assess the impacts of livestock grazing on the biodiversity and the associated ecosystem services in a typical Mediterranean ecosystem. Key research questions we investigate include:

1. What is the relationship between grazing intensity and species richness of primary producers, primary consumers, and secondary consumers?
2. How does grazing intensity affect provisioning of ecosystem services?
3. What constitutes sustainable levels of grazing?

2. Material and Methods

2.1 Study habitat and sites

This study focuses on the dwarf bush scrublands that are very widespread in warm arid regions (<600mm/year) of the Mediterranean Basin. This vegetation type, known under different names in various countries (‘phrygana’ in Greece, ‘baatha’ in the Middle East, ‘tomillares’ in Spain) consists of a diverse assemblage of woody, spinose and summer-deciduous perennials interspersed with a rich variety of annuals (Blondel &Aronson, 1999). In the Aegean Sea archipelago, phrygana composition varies according to geologic substrate, fire history and elevation with the main species being *Genista acanthoclada*, *Coridothymus capitatus, Sarcopoterium spinosum* and

Cistus creticus. In less disturbed and more productive areas, taller evergreen bushes such as *Pistacea lentiscus* and *Juniperus phoenicea* and *Quercus coccifera* become increasingly established. In the study region, phrygana habitat, while very widespread, tends to be restricted to elevated, sloping areas with shallow soil profiles, whereas the coastal plains have been converted for agricultural use.

We conducted this study in typical limestone phrygana habitats located on the large ($438km^2$) island of Naxos (Cyclades Isl., Central Aegean Sea, Greece) (Fig. 1). The island is covered by a mosaic of scrubland, relict oak forests at higher elevations and extensively used agricultural areas near the coasts. Data were collected in the field during the late spring-early summer season (May to July 2012).

2.2 Plots designs

On Naxos we established 12 rectangular study plots ($2,500m^2$ each). Study plots were selected randomly from a homogenous phrygana habitat and were matched for substrate (limestone), slope (<10%) and elevation (<400m asl.). Study plots were also chosen to span a range of grazing intensities ranging from areas that were ungrazed to areas subject to severe grazing intensity.

2.3 Stocking rate and grazing intensity

All plots were grazed on a year-round basis by resident mixed goat and sheep flocks. While stocking rate varied between study plots, type of animal husbandry did not: animals roamed the plots over the day and returned to a pen at night. Stocking rate (number of sheep and goats per $1,000m^2$) was determined by interviewing local shepherds about the size of the flock grazing an area and confirmed through field observations.

2.4 Biomass consumed

To obtain an estimate of the amount of biomass consumed by livestock in each study plot, we quantified the amount of dry dung found along two 50 x 0.8m transects placed randomly in each site. Because of the generally sparse ground cover, and the light substrate color against which dark dung pellets are easily distinguishable, careful visual searches are exhaustive (Herrick, 2005). Because animals remain on a property year-round, the amount of dung collected is a good estimate of the biomass consumed. Collected dung was weighed using a spring-loaded scale (Pesola) after it had been dried for one week - a point at which preliminary measurements had shown that there was no more additional weight reduction indicative of additional water loss.

2.5 Vegetation condition

A. Percent canopy cover, percent bare ground, and percent basal cover.

We quantified three vegetation characteristics (% canopy cover, % bare ground, and % basal cover) using the line-point intercept method (Lawrence, 2010) along two randomly selected 50m-long transects for each study plot. At 1m intervals along each transect, we dropped a pin tied to a string and recorded every plant species that was intercepted. For the canopy cover data we recorded at each pin-drop point the species of the first plant part (stem, leaf of plant base, whether dead or alive) touched by the pin. If no plant tissue was intercepted, a zero was recorded for this category. Canopy cover was calculated as the percentage of pin drops in a plot's two transects where vegetation canopy intercepted the pin. Percent canopy cover for each species was calculated as the number of pin drops that were intercepted by a particular species over the total number (100) of pin drops on a plot. Percent bare ground cover and percent basal cover were estimated in a similar fashion (Herrick, 2005); e.g. to estimate percentage bare ground versus basal cover, we recorded the number of times the dropped pin intercepted rock/stone, bedrock, soil or cryptobiotic crust versus a plant base.

Plant species richness was estimated for each plot as the average of the number of plant species encountered at 1m-interval assessments in each transects. Relative abundance was calculated as the number of observations of a particular species during pin-drops divided by the total number observations of all species. Number of species and relative abundance were then used to estimate Shannon-Wiener diversity indices (SWDI; Spellerberg & Fedor, 2003).

B. Vegetation biomass

Plant biomass was quantified on three, randomly selected 0.8 x 0.8m quadrates in each plot. In each quadrat, we clipped and collected all above-ground dead or alive plant biomass, which was then dried for two weeks (a period after which no further weight reductions were observed) and weighed using a spring-loaded scale (Pesola).

2.6 Floral resources

We determined percent flower cover by establishing three 50m transects per study plot and quantifying the presence of flower patches along these transects. A flower patch was defined as an aggregation of flowers where the distance between flowers was ≤2cm; only patches that were over 5cm across were recorded. Using the line-point intercept method we recorded species identity, as well as the beginning and end point of each flower patch, which was recorded if located within 2.5cm of either side of the transect (Lawrence, 2010). Percent flower cover for a transect was then estimated as the sum of the transect distances corresponding to flower patches underneath a transect line and divided by 50m. Overall percent flower cover for a study plot was calculated as the average of the individual flower cover values for each of the three transects on a plot.

Species-specific flower composition was determined by averaging the percent flower cover of each species across all three transects on a plot. We also quantified flower species richness by determining the number of species recorded in flower patches for each transect and then averaging across all transects in a study plot. Lastly, we calculated Shannon-Wiener biodiversity indices for flowers by using average percent flower cover of each species calculated from the flower composition (Magurran & McGill, 2010).

2.7 Soil stability

Surface soil is directly exposed to the action of the falling rainwater and its consistency is critical in determining amount of erosion. We collected 15 soil samples every 2m along a 30-meter long transect placed randomly in each study plot. Each sample consisted of a single, 8 x 8mm big surface soil fragment, that was collected at least 20cm away from any vegetation to avoid possible influence by nearby root systems (Herrick et al., 2005). If cryptobiotic crust was present, it was included in the sample. We dried the soil sample for 7 days before testing its stability by using the Bottle cap test (Gachene & Kimaru, 2003; Juo & Franzluebbers, 2003). Briefly, the soil fragment was placed in a bottle cap filled with water. After 30s, the soil sample was gently swirled for 5s. Based on the corresponding changes in soil structure, the sample was assigned to one of three categories: M (melted in first 30s); D (disintegrated upon swirling); and S (stable even after swirling). Soil stability was calculated as the percentage of “Stable” soil samples on each study plot.

2.8 Secondary Consumers

Secondary consumer, (i.e. wall lizards *Podarcis erhardii*) densities were measured using the transect method. Briefly, we recorded the number of lizards seen or heard over two 50m transects walked on each plot. Surveys were conducted during peak lizard activity periods (morning hours during May-June, the peak lizard mating season) and under favorable environmental conditions (sunny, 20-25°C and winds ≤10km/h). Plot lizard densities were the average of the individual transect surveys for each plot.

2.9 Arthropod Populations

To assess populations of arthropod pollinators, we used pan traps (Herrick et al., 2005) which we deployed during peak flowering season (May-June). Specifically, we captured pollinators using 400ml plastic bowls filled to ¾ volume with soapy water, and placed them on the flowering vegetation during wind-still days. Bowls were attached to the top of phrygana vegetation in a stable, horizontal position using metal wire. To account for possible variation in color preferences of different pollinator taxa, we used trios of plastic bowls of three specific colors (white, yellow and blue) that were positioned in equilateral triangles, 5m apart from each other. Four such sets of bowls were used in each plot where they were placed 15 m apart from each other and at least 5 m away from the plot edge. Pan traps were left out for 48hr, after which we collected, sorted and counted the arthropods captured in each traps; collected insects were assigned to order (*Coleoptera, Hymenoptera, Diptera, Lepidoptera, Hemiptera, Orthoptera, Odonata and Thysanura).* Hymenopterans were further grouped into more specific categories: domesticated bees, wild bees and wasps. Arthropods were dried for 7 days and biomass data were obtained using a digital balance. To account for seasonal variation in pollinator activity these capture sessions were repeated 3 times over the two month flowering season.

2.10 Pollinator visits

Pollinator visitation was determined by quantifying the number of pollinator visits to randomly selected flower patches on a study plot. Pollinator visitation rate was determined in multiple 0.8 x 0.8m quadrats on all but one of the study plots, (Katelymata, where flowers had all withered by the time observations took place). Because the vast majority of flowers in the area were either *Genista acanthoclada* or thyme (*Coridothymus capitatus*), we focused visitation rate measurements on these two species. To prevent observer bias, only a single person (WCC) quantified visitation rate; data were recorded from a distance of 2m. First we recorded the amount and species of open flowers in the quadrat. If blossoms were too dense to count, we used a 10 x 10 cm cardboard (based on previous measures known to represent ~30 blossoms) to estimate the area covered by flower patch and to obtain an estimate of the total number of flowers (Petanidou et al., 2008; Petanidou & Lamborn, 2005; Potts et al., 2006; Sjödin et al., 2007). Observations of pollinator visitation were then made for a 6 min time window during peak visitation hours (between 9 am and 5 pm) during the period between June 1st to July 7th. All of the observations were made on sunny days and under low wind conditions (≤2km/h). We recorded the total count of pollinators that landed on the flowers, as well as the identity of each pollinator to order, except for Hymenoptera where further distinctions were made between domesticated and wild bees, as well as wasps. If an individual pollinator landed on the same flower twice, this was recorded as two visits.

2.11 Statistical Analysis

Correlations and simple linear regressions were used to explain the association between livestock stocking rate and dung mass versus biomass removal, vegetation condition, floral resources, arthropod populations, and pollination service indicators. If normality assumptions were not met, data were log-transformed. To correct for elevated Type 1 errors during multiple comparisons we used the False Discovery Rate tests (Benjamini & Hochberg 1995). Zero-inflated negative binomial regression was used to analyze pollinator visitation rates, which are heavily skewed towards numerous zero-observations. In this approach, a count model indicates the dependent variable count predicted; the corresponding zero-inflation model gives the probability of an event (i.e. insect visit) happening.

3. Results

3.1 Stocking rate and grazing intensity

Average stocking rate on the 12 plots was 2.40±2.91 animals/1,000 m^2 (range 0-9 animals/1,000 m^2). Biomass consumed by livestock was measured as dry dung weights and averaged 500.53±841.28 g/100m^2 (range 0-1308.2 g/100m^2). Dung mass was positively related with stocking rate (r=0.60, p=0.024) (Appendix, Fig. A).

3.2 Canopy and basal cover (Erosion protection)

Average percentage of canopy cover across all study sites was 58.42±27.02 (range: 11-92%) and average percentage of basal cover across all sites was 23.96±18.80% (Range: 5-53%). Average percentage of bare ground was 7.92±8.34% (range: 1-31%). Stocking rate was negatively correlated to percent canopy cover (r=-0.78, p<0.01) (Fig.2), as well as percent basal cover (r=-0.56, p=0.03) (Appendix, Fig. B), and positively correlated to percentage of bare ground (r=0.83, p<0.01) (Appendix, Fig. C). Dung mass was negatively correlated with canopy cover (r=-0.81, p<0.01) and basal cover (r=-0.87, p<0.01) (Appendix, Fig. D, E). Dung mass was positively correlated with bare ground (r=0.64, p<0.01) (Appendix, Fig. F). The average percentage of soil stability was 78.45±14.25% (range: 45-100%). We did not find any relationship between grazing intensity (assessed through stocking rate and biomass consumed) and the soil stability.

3.3 Vegetation biomass (Productivity, Carbon sequestration)

The mean vegetation biomass among plots was 1,121.31±692.17g per m^2 (range: 162.50-1,873.17g per m^2). Across all plots, vegetation biomass decreased with stocking rate (r=-0.60, p=0.02) (Appendix, Fig. G). Vegetation biomass was also negatively correlated with dung mass (r=-0.79, p<0.01) (Appendix, Fig. H).

3.4 Species Richness and Diversity (Maintenance of biodiversity)

Plant species richness varied substantially between plots (average: 9.05±3.14 species/m^2; range: 4.69-15.63 species/m^2). The average transect plant species diversity (SWDI) was 1.63±0.30 (range: 1.08-2.11). Stocking rate was negatively related both to species richness (r=-0.58, p=0.03) (Appendix, Fig. I) and to species diversity (SWDI; r=-0.60, p=0.02) (Appendix, Fig. J). In contrast, dung mass was significantly related to species richness (r=-0.67, p=0.01) (Appendix, Fig. K) but not to SWDI (r=0.32, p=0.16) (Appendix, Fig. L).

3.5 Floral resources and pollinator populations (Pollination services and honey production)

A. Flower composition

The most common flower species on the study plots was conehead thyme *Coridothymus capitatus* (Labiatae) followed by spiny broom *Genista acanthoclada* (Fabaceae), with average occurrences of 29.64±14.95% and 19.13±14.19%, respectively (Fig. 4). Stocking rate was negatively correlated with overall flower cover (r=-0.61, p=0.02) (Appendix, Fig. M) and flower species richness *(*r=-0.52, p<0.05) (Appendix, Fig. N), but did not relate to the floral S-W diversity index (r=-0.24, p=0.31) (Appendix Fig. O). Dung mass was negatively correlated with flower cover (r=-0.86, p<0.01) (Appendix Fig. P), as well as with flower species richness (r=-0.78, p<0.01) (Appendix Fig. Q), and the floral S-W diversity index (r=-0.73, p<0.01) (Appendix Fig. R). Thus, floral composition became increasingly simplified with rising grazing intensity.

B. Pollinator populations

Across all sites the average number of pollinators captured daily per pan trap trio was 81.01±38.09 individuals and average pollinators~~s~~ biomass was 0.22±0.15g. *Hymenoptera* and *Diptera* were the most common orders (35.31±20.31% and 27.07±18.01 of individuals respectively). Total biomass of arthropods had no statistically significant relationship to stocking rate (Appendix Fig. T). In contrast, the relationship between arthropod numbers and stocking rate was U-shaped, with arthropod numbers first progressively declining with increasing stocking rate and then rising again rapidly at the site with the highest stocking rate [Lower Raini]) (R^2=0.487, $F_{2,9}$=6.21, p=0.02, for the quadratic model; Appendix, Fig. S). Although in this relationship there are high arthropod numbers both at low and high levels of grazing, there exist important differences in the taxonomic makeup of the arthropod communities at the two ends of the grazing spectrum. While in little-grazed heath communities *Hymenoptera* and *Diptera* are the major groups present, at the high-intensity grazing sites coleopterans - which are generally considered to be poor pollinators – predominate (Smith-Ramirez, *et* al, 2005). All of the apparent increase at heavily grazed areas stems from one site (Lower Raini) and there again is driven by the presence of very large numbers of a single species, *Mylabris quadripunctata* (Meloidae) which happened to experiencing a short but steep seasonal peak at the time of the sampling. When this plot is excluded from the analyses, the relationship between numbers of arthropods captured and stocking rate becomes monotonic as well. Amount of biomass consumed by livestock (i.e dung mass) was not significantly related to any of the arthropod populations metrics we used (arthropod numbers, biomass, species richness and arthropod SWDI; all p>0.05).

C. Pollinator visitation rates

We analyzed pollinator visitation rates using zero-inflated negative binomial models of pollinator visitation. We used the counts of pollinator visits as the dependent variable - in one model for wild pollinators only (which was comprised of wild bees, wasps (Hymenoptera), flies (Diptera), and beetles (Coleoptera)), and in another model only domesticated bees *(Apis mellifera*). *Coridothymus capitatus* flower count, *Genista acanthoclada* flower count, and stocking rate were used as the three independent explanatory variables. Zero-inflated negative binomial regression analyses generated two separate outputs: a count model, and a zero-inflation model. The count model reports log-transformed dependent variable prediction, which is the count number of events (visits). The zero-inflation model gives the logit-transformed dependent variable prediction, which is a probability of an event (visit) happening. Count model results showed that number of visits by wild pollinators was not significantly related to any of the three independent variables *(Coridothymus capitatus* flower count, *Genista acanthoclada* flower count, and stocking rate; Table 3A.) although there were marginally non-significant trends for visitation to decline both with increasing presence of *G. acanthoclada* (p=0.061) and with increasing stocking rate (p=0.07). For the zero-inflated model, none of the three dependent variables was significantly related to wild pollinator visitation rates.

Beyond the wild pollinators model described above, another zero-inflated negative binomial regression was performed for domesticated honeybee visits only (Table 3B.) in order to investigate which factors affect honeybees and the pollination and honey production services they provide. The count model revealed that number of honeybee's visits was negatively related to stocking rate. As stocking rate increased, the number of honeybee's visits decreased (r= −0.137±0.06 p=0.019). Furthermore, the zero-inflation model indicated that amount of thyme flower was positively related to the probability of honeybees being present during the survey period. This result also corresponds to the simple linear regressions of honeybee and wild pollinators' visits with stocking rate (Fig. 5), in which honeybee but not wild pollinators numbers are negatively correlated with grazing intensity.

3.6 Secondary consumers (Disease dilution)

The main species of secondary consumer across all our study sites is the Aegean Wall lizard *Podarcis erhardii* (Lacertidae). Lizard abundance, which varied substantially between transects (2.58±2.39 per plot, range: 0-7) had a hump-shaped relationship to stocking rate (R^2=0.504, $F_{2,9}$=4.579, p=0.042) for the quadratic model; Fig. 6), with lizard densities peaking at intermediate grazing densities and declining at the two ends of the grazing spectrum.

4. Discussion

The aim of this project was to evaluate the effects of livestock grazing on Mediterranean habitats and the ecosystem services these provide. Because this study evaluates the effects of livestock herbivory across multiple trophic levels, it allows for a more comprehensive understanding of the impacts of grazing on ecosystem services. This was accomplished by comparing species communities across a broad range of grazing regimes as determined both by stocking rates and by an independent measure of consumed biomass (Appendix Fig. A).

Effects on primary productivity and soils

The results of our study plot comparison indicate that plant aboveground biomass is negatively correlated with amount of plant biomass consumed by livestock (Appendix Fig. D). Furthermore, the relationship between stocking rate and plant biomass suggests that overgrazing at a given moment in time may not only diminish primary productivity, but also undermine the future grazing potential of this system. Thus, a decrease in standing biomass may not only be the direct consequence of biomass consumption and damage by livestock hoofs, but also be the result of prior negative feedback cycles where removal of plant matter leads to more open vegetation structure which in turn results in more desiccation and consequently less favorable conditions for vegetation growth. Both stocking rate, and amount of biomass consumed, were negatively associated with all Mediterranean heath vegetation indices measured, including vegetation biomass, percent canopy cover and percent basal cover. While these individual changes were not unexpected, what was surprising was the consistency of the *phrygana* community response across the range of sites, grazing intensities and vegetation metrics (Fig. 2; Appendix, Figs. A-H.).

Grazing activity has been frequently linked to soil erosion in Mediterranean ecosystems (Grove & Rackham 2001). Livestock such as goats may drive grazing range soil erosion not only through removal of vegetation cover, which shields the soil from the erosive impacts of the rain, but also by breaking up the soil surface with their hooves and therefore facilitating it washing away. In our study plots we found that while rising stocking rates were associated with reduced plant cover and increased bare ground, and therefore increase exposure of the ground to the elements (Appendix, Figs. C., F.), there was little evidence for the second causal pathway. Therefore, we found little evidence that trampling by livestock affected the structural stability of exposed surface soils in the area. The majority of exposed soils on the study plots irrespectably of grazing intensity could qualitatively be described as being consolidated and having a hard, almost impervious surface crust. Nonetheless, despite the apparently moderate destructive effects of livestock hooves on soil structural integrity, a process that became evident only at the highest stocking rates, livestock grazing should be considered an important driver of soil erosion in Aegean ecosystems, simply because it generates severe soil exposure via the removal of the protective phrygana vegetation.

Plant species richness and diversity are considered important linchpins of rangeland-provisioned ecosystem services (Balvanera et al. 2006). Although the number of species reported on here is, by the nature of the survey, limited to only a subset of the full plant community in an area, our study paints a clear and coherent picture of negative effects of livestock herbivory on mediterranean heath communities. As stocking rates increase, vegetation becomes rapidly simplified as numerous rarer plant species drop out and plant community degrades to a few core, grazing-resistant taxa (*Coridothymus, Genista, Calicotome, Sarcopoterium*) (Figure 3). This shift is driven by strong feeding preferences of livestock away from common, thorny bushes towards rarer, less defended taxa. Much of this transition can be attributed to the fact that goats are selective browsers that avoid hepatotoxicity from excessive amounts of plant allelochemicals by feeding on small quantities from a diversity of species.

Previous studies have suggested that disturbance such as grazing by native herbivores has the potential to promote plant diversity (Collins et al. 1998, Olff and Ritchie 1998). It might therefore reasonable to expect that some levels of livestock grazing will have positive effects on phryganic plant diversity. In contrast, our data suggest that grazing results in only few, if any, benefits for local plant communities. Herbivores can effect the vegetation in a multitude of ways, some positive and some negative. One the one side, ungulates may, by stopping the advance of late successional woody species, promote plant diversity, -- thus, by breaking up an otherwise closed shrub canopy they do promote a spatial heterogeneity that creates a plethora of ecological niches. On the other hand, goats appear to forage preferentially on more rare plant species, thus depressing community diversity. In this study system it appears that the second, selective foraging-mediated effect overshadows any positive outcomes that may stem from breaking up a closed shrub canopy.

Plant communities and the floral resources they represent are important both because they support critically important native and domesticated pollinators, and also because they form the basis of the local honey producing industry. In mediterranean ecosystems a large percentage of native plant species are not only pollinator-dependent but also produce prodigious amounts of floral resources in the form of flowers, nectar and pollen (Fielding and Turland, 2004). On our study plots floral diversity varied greatly and was strongly determined by prevailing intensity of goat and sheep browsing. On ungrazed plot transects, beyond the ubiquitous low woody bushes (*Genista, Coridothymus, Cistus,* Fig. 4), we regularly identified, significant numbers of several species of herbaceous annuals (*Teucrium, Helichrysum, Ballota*). As stocking rates increased, diversity decreased with the herbaceous taxa disappearing first (Appendix Fig. N), so that on the plots with the heaviest grazing, the only flowers we were able to document belonged to the spiny broom (*G. acanthoclada*) and to conehead thyme (*C. capitatus*), two of the most grazing-resistant perennials in the region.

Primary consumers

Aegean phrygana communities support diverse populations of pollinators (Petanidou and Ellis 1993). While we measured pollinator populations using several metrics (invertebrate numbers, biomass, species richness and SWDI), grazing intensity appears to have had a less pronounced or consistent impact on arthropod populations. Although we observed a negative effect of stocking rates on most metrics of arthropod presence, this did not hold true for amount of consumed biomass. Furthermore, the relationship between arthropod numbers and stocking rate was U-shaped, driven by very high numbers of pollinators at the most intensely grazed plot (Appendix, Fig. S). These large numbers were in turn caused by a pronounced but short-lived emergence of a single flower beetle species at that site during one of the sampling periods. If that outlier is removed, arthropod numbers follow the same negative relationship to stocking rate as the other arthropod variables. As grazing rates increased we also observed a progressive shift from groups that are considered to be good pollinators (such as *Hymenoptera* and *Diptera*) towards taxa such as *Coleoptera* that are more terrestrial, armored, resistant against water loss and overall less effective pollinators. Both the drop in overall pollinator numbers and the decline in their relative pollination effectiveness, point to an overall deterioration of the ecosystem services provided under more intense grazing regimes. The fact that we did not observe such pronounced effects of grazing on pollinator populations as on plant communities, can be attributed to two reasons. First, any livestock impacts on pollinators are going to be indirect and relative diffuse as they have to first be mediated through changes in vegetation. Secondly, changes in pollinator numbers are likely dampened by the fact that arthropods, being mobile, can easily disperse across the landscape from other areas that experience different grazing conditions.

Visitation rate by pollinators is a more direct assessment of pollination services and honey production. We found different patterns for wild versus domesticated (honey bees) pollinators. Wild pollinator hourly visits were not significantly related to either amount of *Genista* or *Coridothymus*, nor to prevailing grazing conditions. This may be attributable to the fact that this heterogeneous group of arthropods most likely has a diverse set of ecological needs (e.g. nesting sites) and as such is not apt to respond in a uniform fashion to livestock grazing and the presence of these two bush taxa.

On the other hand, number of hourly honeybee visits was positively related to amount of *Coridothymus* flowers and negatively related to grazing intensity. *Coridothymus capitatus* is a profuse nectaring plant that is widespread in island ecosystems; it is considered to be the foundation of Aegean apiculture and the main source for Greek thyme honey. As such, it is not surprising that honeybees, which are efficient and wide-ranging foragers, adapt their visit schedule to the presence of *C. capitatus* flowers on our study plots. In contrast, *Genista acanthoclada*, despite its even wider distribution and showy blooms does not produce much nectar and is of less importance to wild and domesticated pollinators alike. Beyond this, honeybee populations were less likely to forage in areas heavily grazed by livestock. This appears reasonable given the significantly reduced floral resources available in such areas and the aforementioned ability of honeybees to nimbly adjust their foraging behavior to locally available resources.

Secondary consumers

The main secondary consumers in Aegean heathlands are reptiles and in particular the ubiquitous Aegean Wall lizard *Podarcis erhardii*. Our data suggest that wall lizard abundance has a hump-shape relationship with stocking rate, meaning that the highest lizard densities were associated with intermediate levels of grazing. This pattern is best explained by the characteristics of lizard biology. Many lizard species depend of invertebrate populations (Ballinger 1977); because heavy grazing tends to impact invertebrate herbivores, it is expected to also exert a strong negative effect on resident lizard populations (Pringle et al. 2007). Beyond reducing the food supply, presence of livestock and ungulates may have additional negative effects on lizard populations that are not mediated through reduced food availability but rather through increased levels of ectoparasitism. Indeed, high livestock populations appear to foster elevated numbers of ticks (*Haemaphysalis* sp.) which also parasitize lizards. Such elevated tick burdens have been shown to undermine lizard body condition, as well as reproductive investment (J. Foufopoulos *pers. observ.*) and as such are likely to further impact lizard population densities in grazed areas.

In contrast, the decline of lizards at the lowest levels of the grazing spectrum is likely attributable to the thermal requirements of reptiles. Even in a relatively sunny environment like the Cyclades, reptiles require ample basking opportunities; as shown earlier, the least grazed sites are dominated by a thick and continuous layer of thorny vegetation that prevents sunlight from reaching the ground. Such dense vegetation is probably too shady and does not offer sufficient basking opportunities for lizards. As a result, different mechanisms probably limit lizards at the two opposite ends of the spectrum: at low grazing intensity, dense vegetation does not afford appropriate conditions to thermoregulate, while at high grazing conditions, decline of prey items, as well as too many ticks, likely limit lizard populations.

Mediterranean heathlands provide a wide range of ecosystem services that include provisioning of natural products such as honey, fuels, and aromatic herbs. They also protect areas from erosion, promote a stable water supply, and control pests. Although we evaluated only a subset of these services in relation to their sensitivity to livestock herbivory, we found that grazing has overall negative effects on these services. In particular, grazing by goats appears to undercut carbon sequestration, biomass production, maintenance of biodiversity and pollination services. In contrast, pest regulation mediated through lizard populations appear to be beneficially influenced at least to some intermediate levels of herbivory. While more research is needed to elucidate these relationships, our data suggest that livestock herbivory will likely have a more mixed effect on ecosystem services rendered by the local communities, especially as long at stocking rates remain moderate.

FIGURES

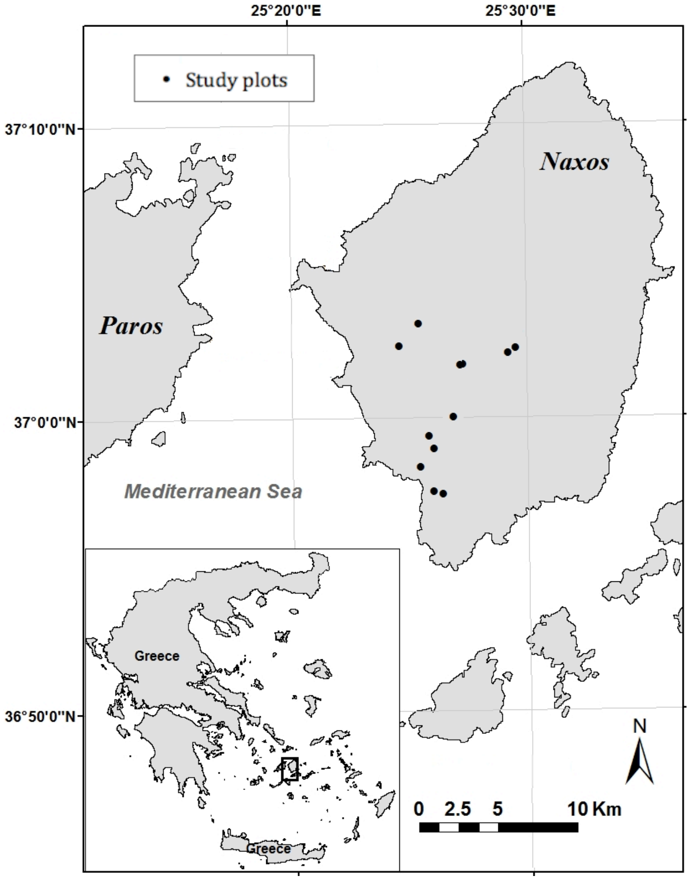

Figure 1. Map of the 12 study plots on the island of Naxos, Greece.

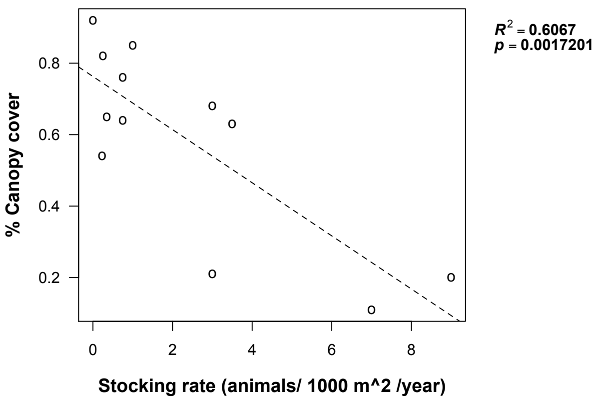

Figure 2. Canopy cover is negatively correlated with stocking rate (r=-0.78, p<0.02).

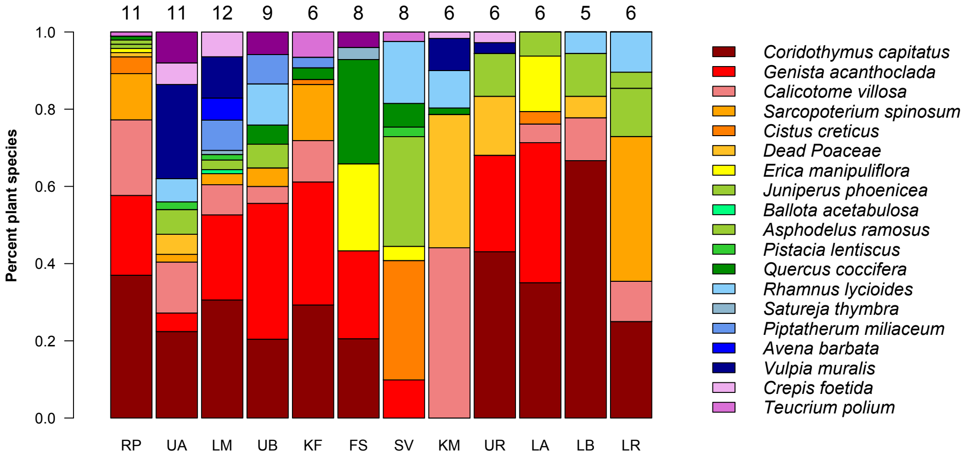

Figure 3. Bar chart of vegetation composition across the study plots from least to highest grazing intensity.

The y-axis gives the percentage occurrence of each plant species, while on the x-axis the 12 study plots are ranked in order of low (L-side) to high (R-side) stocking rate. Species identities are given in accompanying legend. The number above each bar gives total number of species. Species richness decreases as grazing is intensified. Additional graphical relationships are given in Figures I and K (Appendix).

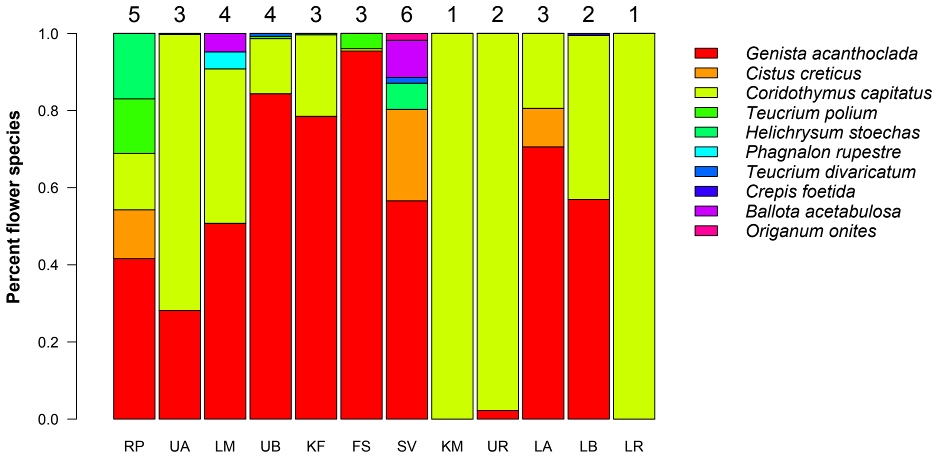

Figure 4. Flowering plant species composition across study plots from least to highest grazing intensity.

The y-axis gives relative composition of flowers detected on each plot (in %); on the x-axis study plots are ranked from low (L-side) to high (R-side) stocking rate. Species names are given in the legend. The number above each bar gives the total number of flowering species found on transects for each plot. Species richness decreases as grazing pressure intensifies.

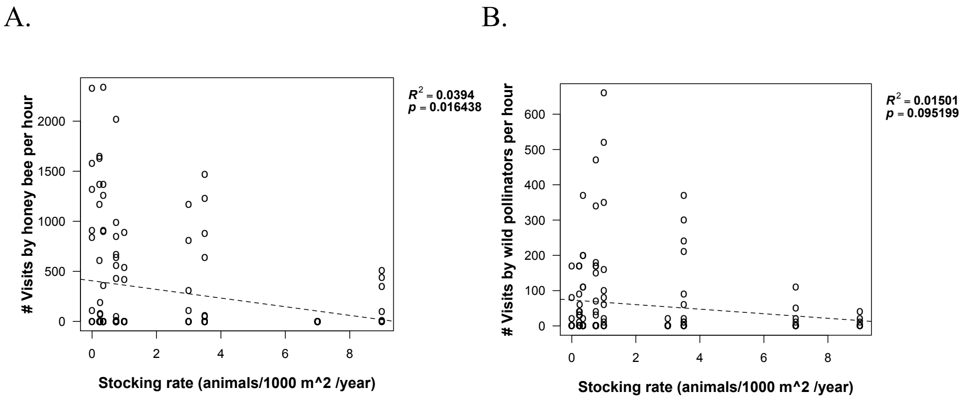

Figure 5. Relationship of A. domesticated bee visits (r=-20, p=0.02) and B. wild pollinators' visitation rate (r=-0.12, p=0.10) against stocking rate.

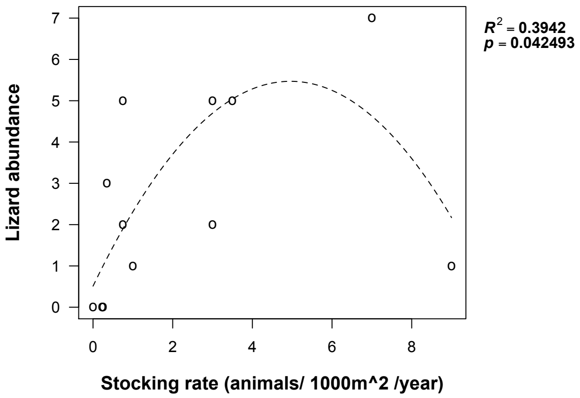

Figure 6. Lizard abundance (individuals seen per transect) relative to stocking rate. A quadratic function fits the data best and is shown here (R^2=0.504, *p=0.042*)

Table 1. Study plots and their physical characteristics.

Location	Abbreviation	Elevation	Aspect	Longitude	Latitude	Stocking rate (animals/ 1000^2 m/year)	lnDung mass (g)	Canopy Cover (%)	Basal cover (%)	Plant. Biomass (g/m^2)	Plant. Species	Invertebrates Biomass(g)	Soil Stability %	Lizard (indiv./ 100m)	S-W Vegetation	S-W Flower	S-W Invertebrates
Rachi Polychnitou	RP	202	NE	37.02708333	25.42141667	0	0.0	92.0%	44.0%	1780.21	7.5	0.15	100.0	0	1.70	1.49	0.94
Lower Agiassos	LA	18	W	36.97191667	25.42823333	3.5	3.4	63.0%	23.0%	1112.24	4	0.38	88.0	5	1.44	0.79	1.76
Upper Agiassos	UA	47	/	36.98076667	25.43258333	0.23	6.0	54.0%	8.0%	361.20	7.5	0.64	88.0	0	2.11	0.61	1.14
Katelymata	KM	76	/	36.98873333	25.42963333	3	5.7	68.0%	5.0%	800.26	5	0.20	76.0	2	1.30	0.00	1.42
Lower Raini	LR	48	/	36.9595	25.43301667	9	7.8	20.0%	8.0%	162.50	5	2.77	88.0	1	1.58	0.00	0.75
Upper Raini	UR	60	/	36.95876667	25.43656667	3	7.6	21.0%	3.0%	382.81	3.5	1.70	64.0	5	1.44	0.11	1.29
Upper Bazeos tower	UB	215	W	37.03418333	25.44853333	0.35	3.8	65.0%	22.5%	995.05	6.5	0.22	82.0	3	1.90	0.49	1.41

Lower Bazeos tower	LB	21	W	37.03405	25.44818333	7	6.3	11.0%	4.0%	523.70	3	0.10	76.0	7	1.08	0.71	1.56
Lower Marathós	LM	136	SW	37.00233333	25.44446667	0.25	0.0	82.0%	53.0%	2044.27	10	0.45	76.0	0	2.02	0.99	1.62
Stavropigi Vivlou	SV	164	NW	37.04238333	25.40975	1	4.0	85.0%	34.0%	1873.18	6.5	0.26	70.0	1	1.72	1.28	1.56
Koutsouria Filotiou	KF	330	NE	37.03941667	25.48341667	0.75	4.7	64.0%	31.0%	2031.51	4.5	0.22	45.4	2	1.59	0.20	1.57
Filoti Stadium	FS	351	SW	37.04121667	25.48575	0.75	3.1	76.0%	52.0%	1388.80	6.5	0.14	88.0	5	1.68	0.54	1.41

Table 2. Correlation table (Pearson product coefficients *r* [top of each cell] and correspond p-values [bottom of each cell] between the main variables measured in this study. Stocking rate and dung mass were log-transformed to satisfy criteria for normality. For each column as a group, bolded numbers are the ones that satisfy the false discovery rate test.

	LnStockingRate	LnDung mass	Canopy cover (%)	Soil+Rock	Basal cover (%)	Veg. Biomass	Veg. Sp. Richness	SWDI-Vegetation	Flower	Flower Sp. Richness	SWDI-flower	Invert. density	Invert. biomass	Invert. Richness	SWDI-Invertebrates	Secondary comsumers
lnStocking	1.00															
lnDung	0.558 (0.059)	1.00														
Canopy cover (%)	−0.651 (0.022)	**−0.825** **(0.001)**	1.00													
Soil+Rock	**0.730** **(0.007)**	**0.826** **(0.001)**	**−0.946** **(<0.001)**	1.00												
Basal cover (%)	−0.562 (0.057)	**−0.878** **(<0.001)**	**0.783** **(0.003)**	**−0.799** **(0.002)**	1.00											
Veg. biomass	−0.507 (0.092)	**−0.808** **(0.001)**	**0.806** **(0.002)**	**−0.722** **(0.008)**	**0.856** **(<0.001)**	1.00										
Veg. Sp. Richness	**−0.789** **(0.002)**	**−0.706** **(0.010)**	**0.689** **(0.013)**	**−0.791** **(0.002)**	**0.674** **(0.016)**	0.495 (0.102)	1.00									
SWDI-Vegetation	**−0.869** **(<0.001)**	−0.431 (0.162)	0.516 (0.086)	−0.583 (0.047)	0.478 (0.116)	0.302 (0.341)	**0.850** **(0.001)**	1.00								
Flower	**−0.711** **(0.009)**	**−0.870** **(<0.001)**	**0.681** **(0.015)**	**−0.699** **(0.011)**	**0.790** **(0.002)**	0.661 (0.019)	**0.781** **(0.003)**	**0.699** **(0.011)**	1.00							
Flower Sp. Richness	−0.522 (0.082)	**−0.803** **(0.002)**	0.634 (0.027)	−0.616 (0.033)	**0.731** **(0.007)**	0.727 (0.007)	0.530 (0.076)	0.454 (0.138)	**0.810** **(0.001)**	1.00						
SWDI-flower	−0.357 (0.254)	**−0.754** **(0.005)**	0.586 (0.046)	−0.622 (0.031)	0.601 (0.039)	0.582 (0.047)	0.513 (0.088)	0.311 (0.325)	0.657 (0.020)	**0.907** **(<0.001)**	1.00					
Invert. Density	−0.002 (0.996)	0.189 (0.556)	−0.135 (0.675)	0.129 (0.688)	−0.190 (0.555)	−0.324 (0.305)	0.262 (0.410)	0.374 (0.232)	−0.105 (0.746)	−0.047 (0.884)	0.052 (0.871)	1.00				
Invert. Biomass	0.456 (0.137)	**0.584** **(0.046)**	**−0.608** **(0.036)**	**0.653** **(0.021)**	−0.433 (0.160)	**−0.585** **(0.046)**	−0.214 (0.505)	−0.031 (0.924)	−0.352 (0.262)	−0.488 (0.108)	−0.501 (0.097)	**0.575** **(0.050)**	1.00			
Invert. Richness	−0.337 (0.285)	−0.070 (0.829)	0.111 (0.731)	−0.137 (0.672)	0.219 (0.494)	0.453 (0.139)	0.018 (0.957)	0.096 (0.767)	0.072 (0.824)	0.402 (0.195)	0.262 (0.410)	−0.195 (0.544)	0.167 (0.605)	1.00		
SWDI-Invertebrates	−0.159 (0.622)	−0.247 (0.438)	0.226 (0.481)	−0.220 (0.493)	0.219 (0.494)	0.434 (0.159)	−0.112 (0.730)	−0.174 (0.588)	0.252 (0.429)	0.257 (0.419)	0.154 (0.634)	**−0.905** **(<0.001)**	0.227 (0.478)	0.412 (0.184)	1.00	
Secondary comsumers	0.504 (0.094)	0.341 (0.277)	−0.520 (0.083)	0.472 (0.083)	−0.289 (0.121)	−0.329 (0.296)	**−0.731** **(0.007)**	**−0.691** **(0.013)**	−0.382 (0.220)	−0.244 (0.446)	−0.259 (0.415)	−0.623 (0.031)	−0.528 (0.078)	0.050 (0.877)	0.425 (0.169)	1.00
	← Log transformation[a] →		← No transformation →													

Table 3A. Effects of vegetation and landscape traits on wild pollinators' visitation rate (the visiting species are described in the content) as shown by a zero-inflated negative binomial regression. Top panel gives the result of the count model estimates while lower panel gives the zero-inflation model estimates. Bold numbers indicated significant relationships.

Zero-inflated negative binomial regression model of Wild pollinators			
Count model coefficients:			
	Estimates	Std. Error	*p*-value
C. capitatus	0.0007	0.0005	0.161
G. acanthoclada	−0.0005	0.0002	0.061
Stocking rate	−0.1268	0.0627	0.070
Zero-inflation model coefficients:			
	Estimates	Std. Error	*p*-value
C. capitatus	−0.0004	0.0008	0.598
G. acanthoclada	0.0006	0.0004	0.170
Stocking rate	0.0915	0.0770	0.235

Table 3B. Effects of vegetation and landscape traits on domesticated bee visitation rates as shown by a zero-inflated negative binomial regression. Top panel gives the result of the count model estimates while lower panel gives the zero-inflation model estimates. Bold numbers indicated significant relationships.

Zero-inflated negative binomial regression model of honeybee

Count model coefficients:

	Estimates	Std. Error	p-value
Intercept			
C. capitatus	0.0004	0.0005	0.419
G. acanthoclada	−0.0004	0.0003	0.161
Stocking rate	−0.1366	0.0581	**0.019**

Zero-inflation model coefficients:

	Estimates	Std. Error	p-value
(Intercept)			
C. capitatus	−0.0067	0.0014	**<0.0001**
G. acanthoclada	0.0005	0.0006	0.384
Stocking rate	0.0146	0.0900	0.871

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6. Appendix

A – Figures.

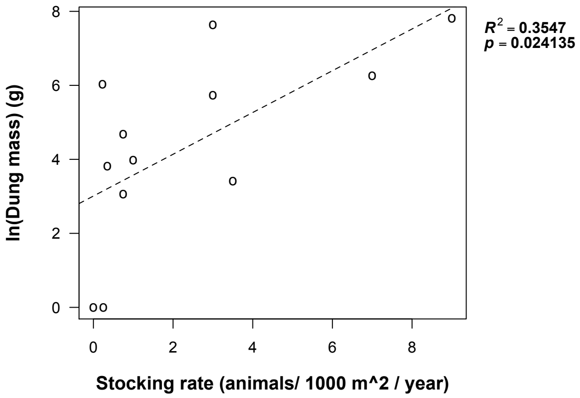


Fig. A. Dung mass on each study plot (log-transformed) is positively correlated with stocking rate.

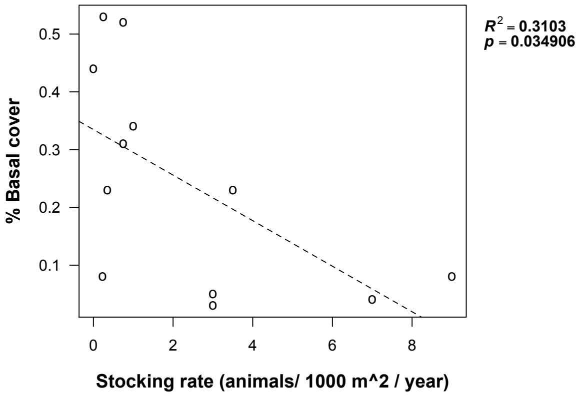


Fig. B. Percent basal cover is negatively correlated with stocking rate.

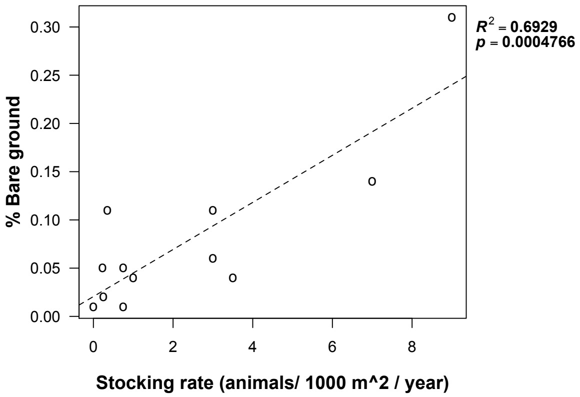


Fig. C. Percent bare ground is negatively correlated with stocking rate.

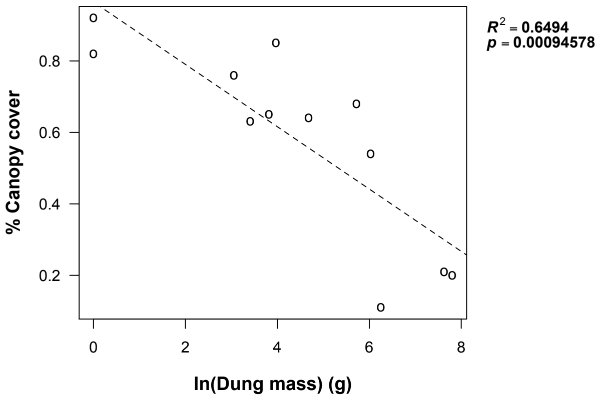


Fig. D. Percent Canopy cover is negatively correlated with dung mass.

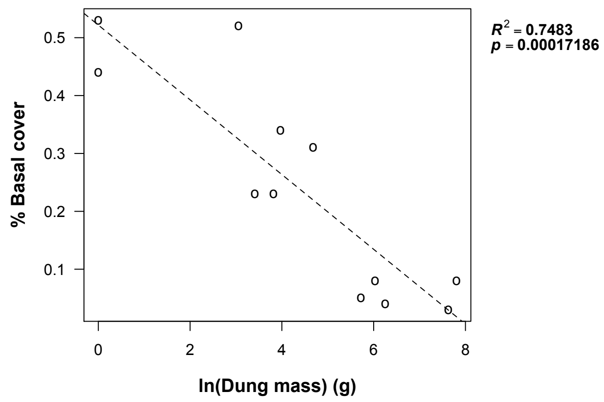


Fig. E. Percent basal cover is negatively correlated with dung mass.

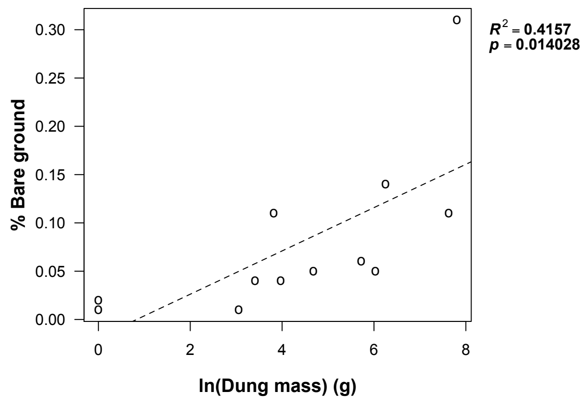


Fig. F. Percent bare ground is positively correlated with dung mass

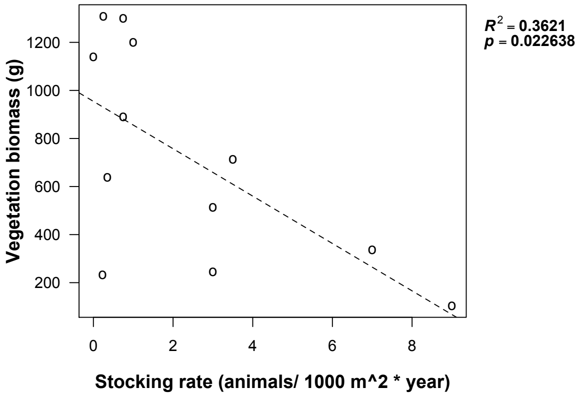


Fig. G. Vegetation biomass is positively correlated with stocking rate.

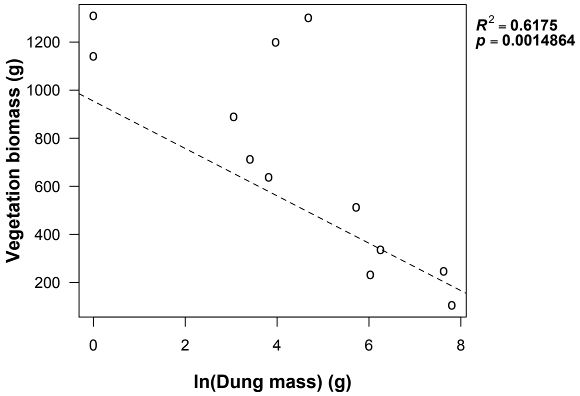


Fig. H. Vegetation biomass is positively correlated with dung mass.

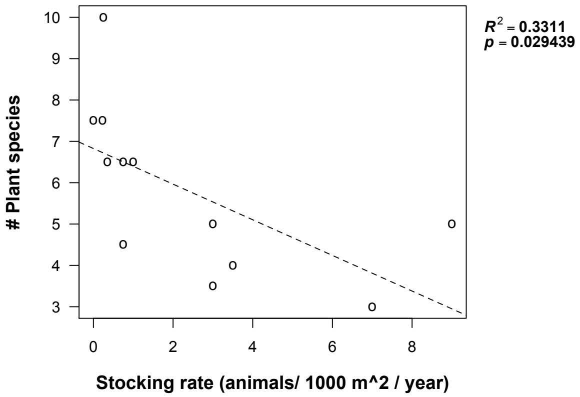


Fig. I. Plant species richness is negatively correlated with stocking rate.

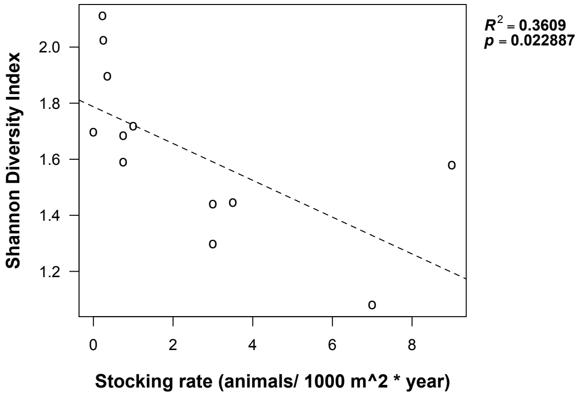


Fig. J. Plant species diversity is negatively correlated with stocking rate.

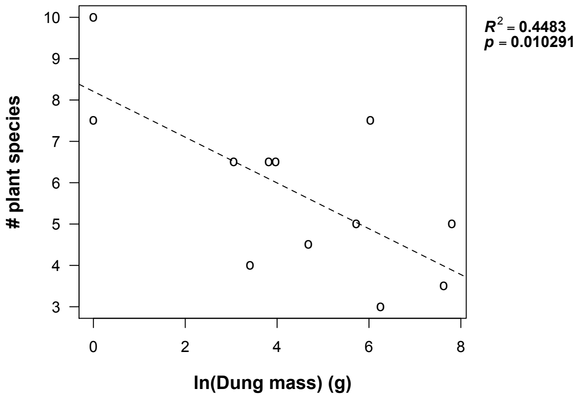


Fig. K. Plant species richness is negatively correlated with dung mass.

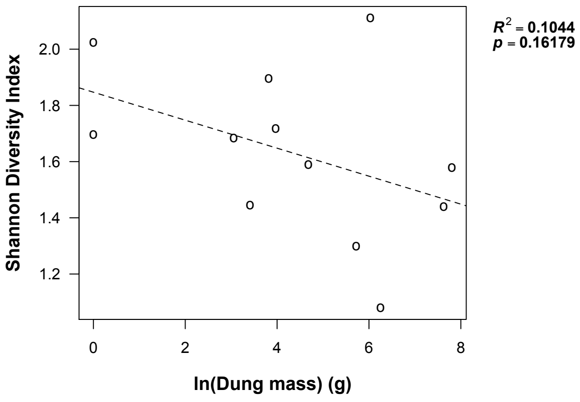


Fig. L. Plant species diversity is not correlated with dung mass.

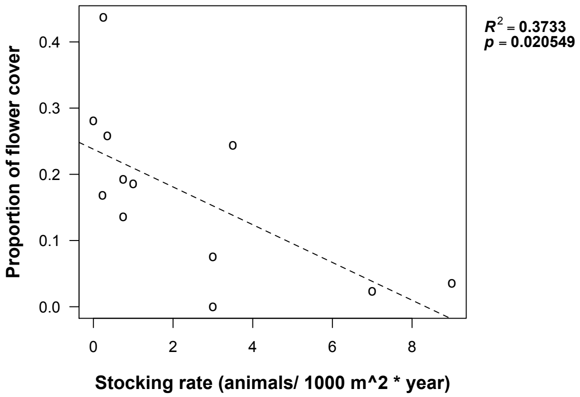


Fig. M. Flower cover is negatively correlated with stocking rate.

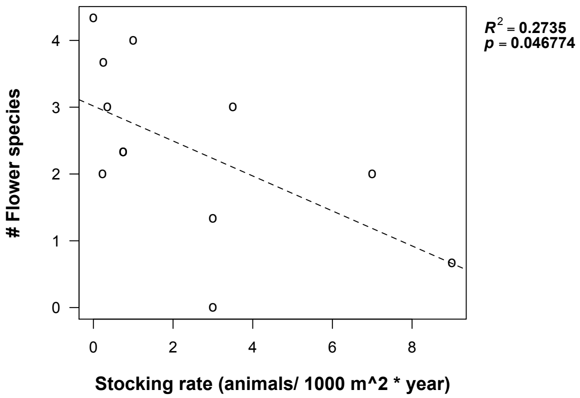


Fig. N. Flower species richness is correlated with stocking rate.

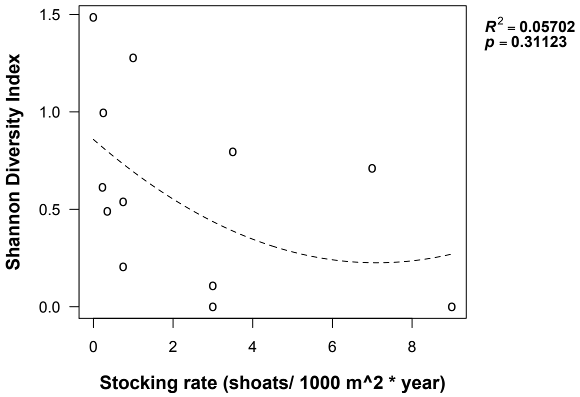


Fig. O. Flower diversity is not correlated with stocking rate.

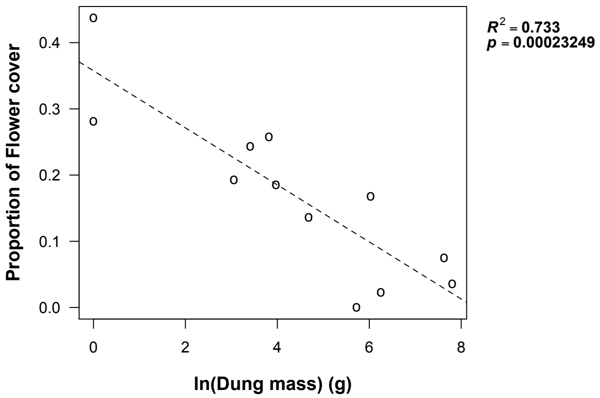


Fig. P. Flower cover is negatively correlated with dung mass.

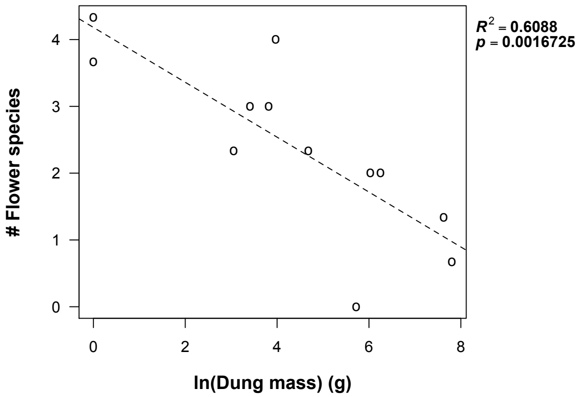


Fig. Q. Flower species richness is negatively correlated with dung mass.

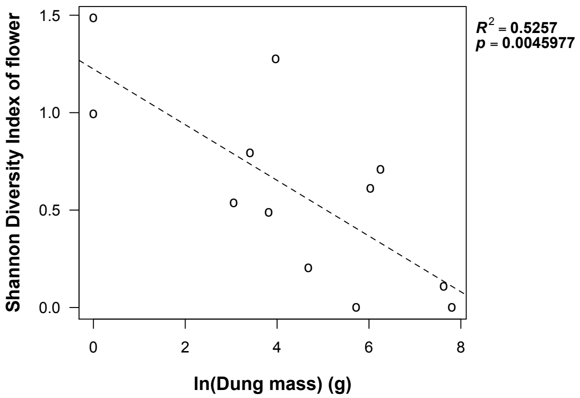


Fig. R. Flower species diversity is negatively correlated with dung mass.

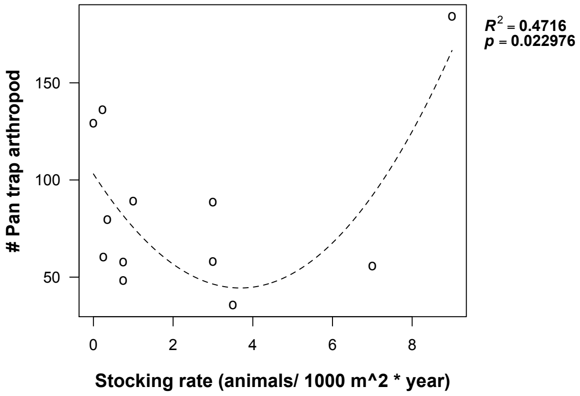


Fig. S. Arthropod numbers versus stocking rate.

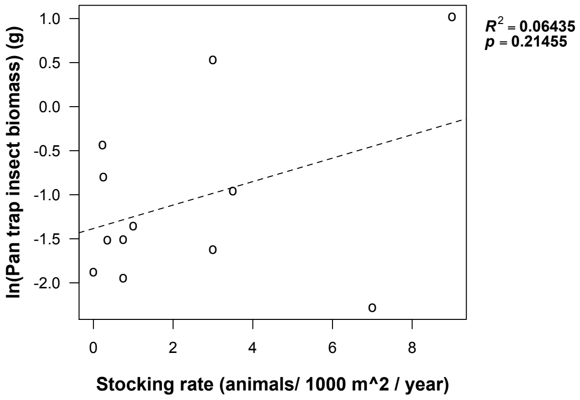
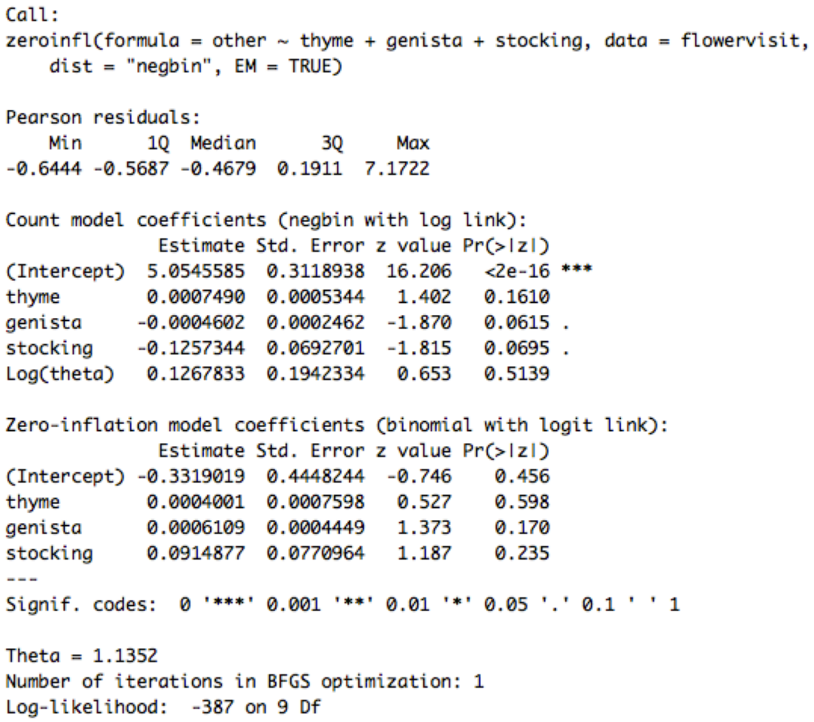


Fig. T. Arthropod biomass versus stocking rate**.**

APPENDIX

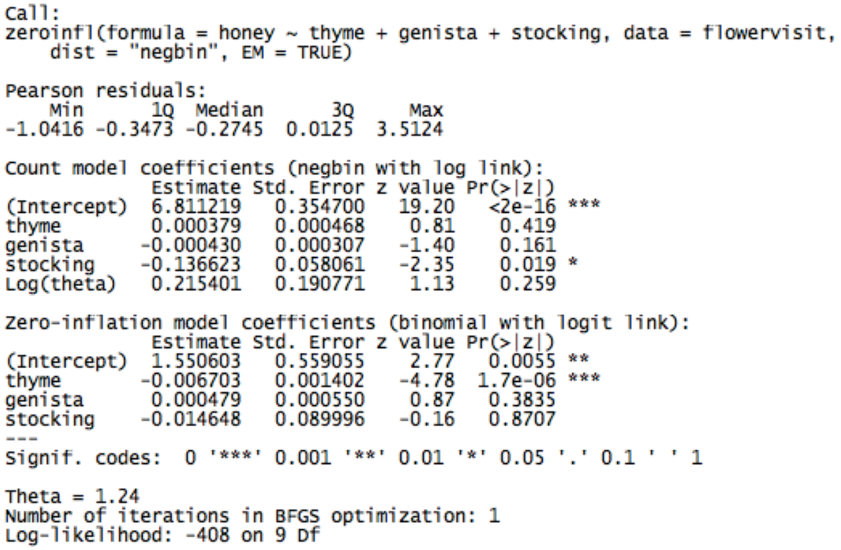
A. Statistical Tables

Full output of statistical model for wild pollinator visitation:



```
Call:
zeroinfl(formula = other ~ thyme + genista + stocking, data = flowervisit,
    dist = "negbin", EM = TRUE)

Pearson residuals:
    Min      1Q  Median      3Q     Max
-0.6444 -0.5687 -0.4679  0.1911  7.1722

Count model coefficients (negbin with log link):
              Estimate Std. Error z value Pr(>|z|)
(Intercept)  5.0545585  0.3118938  16.206   <2e-16 ***
thyme        0.0007490  0.0005344   1.402   0.1610
genista     -0.0004602  0.0002462  -1.870   0.0615 .
stocking    -0.1257344  0.0692701  -1.815   0.0695 .
Log(theta)   0.1267833  0.1942334   0.653   0.5139

Zero-inflation model coefficients (binomial with logit link):
              Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.3319019  0.4448244  -0.746    0.456
thyme        0.0004001  0.0007598   0.527    0.598
genista      0.0006109  0.0004449   1.373    0.170
stocking     0.0914877  0.0770964   1.187    0.235
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 1.1352
Number of iterations in BFGS optimization: 1
Log-likelihood:  -387 on 9 Df
```

Model for domesticated bees:



```
Call:
zeroinfl(formula = honey ~ thyme + genista + stocking, data = flowervisit,
    dist = "negbin", EM = TRUE)

Pearson residuals:
    Min      1Q  Median      3Q     Max
-1.0416 -0.3473 -0.2745  0.0125  3.5124

Count model coefficients (negbin with log link):
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  6.811219   0.354700   19.20   <2e-16 ***
thyme        0.000379   0.000468    0.81    0.419
genista     -0.000430   0.000307   -1.40    0.161
stocking    -0.136623   0.058061   -2.35    0.019 *
Log(theta)   0.215401   0.190771    1.13    0.259

Zero-inflation model coefficients (binomial with logit link):
             Estimate Std. Error z value Pr(>|z|)
(Intercept)  1.550603   0.559055    2.77   0.0055 **
thyme       -0.006703   0.001402   -4.78  1.7e-06 ***
genista      0.000479   0.000550    0.87   0.3835
stocking    -0.014648   0.089996   -0.16   0.8707
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Theta = 1.24
Number of iterations in BFGS optimization: 1
Log-likelihood: -408 on 9 Df
```