

**VERTEBRATE COMMUNITY RESPONSES TO LIVESTOCK GRAZING IN AN
ANCIENT MEDITERRANEAN RANGELAND SYSTEM: RETHINKING THE ROLE
OF GRAZING IN BIODIVERSITY CONSERVATION.**

by

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Abstract

Despite claims that livestock grazing may be a useful conservation tool for promoting biodiversity, the effect of livestock grazing on vertebrate populations remains controversial and poorly understood. This is particularly the case for Mediterranean ecosystems that have been grazed by livestock for thousands of years. The aim of my thesis is to understand: (1) the nature of the relationship between livestock grazing and vertebrate abundance and species richness and; (2) the mechanisms that drive this relationship.

Methods. I sampled small mammal, reptile, and passerine bird species across a range of livestock grazing intensities in a mediterranean pastoral system in the Aegean Sea (Greece). This study was conducted in a mediterranean summer-deciduous scrubland habitat with limestone substrate and shallow soils, which is widespread throughout the region. Using Generalized Linear Modeling (GLM), I determined the nature of the relationship between livestock grazing and vertebrate abundance and richness metrics. An information-theoretic approach was used to elucidate which habitat characteristics mediated by livestock grazing best predicted vertebrate responses.

Results. I found that terrestrial (small mammal and reptile) vertebrate responses to changing livestock stocking rate were different from those of passerine birds. Terrestrial species abundance decreased exponentially with increasing livestock stocking rate; however species richness exhibited a unimodal relationship with stocking rate, peaking at intermediate stocking rates. The response of terrestrial assemblages was best predicted by invertebrate food availability. Passerine bird species richness and abundance showed no relationship with levels of grazing, however avian population abundance and species richness were significantly correlated with vegetation structural heterogeneity.

Conclusions. My findings indicate that there is no ideal grazing level that optimizes vertebrate abundance and richness across different vertebrate groups. However light to intermediate grazing disturbance can be important in promoting terrestrial species richness, thus indicating that agricultural policy encouraging a mosaic of grazing intensities at the regional level could support diverse vertebrate assemblages.

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1. Introduction

Livestock grazing provides a globally important source of livelihoods, with 1.3 billion people relying on livestock as their principal source of subsistence (Steinfeld et al., 2006). However, livestock production is often viewed as environmentally unsound and a significant threat to ecosystem function. Pastureland is the single largest global form of land use, and the growing demand for livestock products, as well as the increasing amount of land designated for animal feed production (Steinfeld et al., 2006), have brought the negative impacts of livestock production into sharp focus. Deforestation, water pollution, erosion, biodiversity loss, and greenhouse gas emissions have all been attributed to the intensification of domestic grazing systems (Asner et al., 2004; Cole and Landres, 1996; Fleischner, 1994).

However, a growing number of studies have also documented the utility of grazing disturbance in creating and maintaining biodiversity (Fuhlendorf and Engle, 2001; Middleton, 2013). Disturbances such as mowing, grazing, and burning, have been shown to enhance species richness (Collins et al., 1998; Fynn et al., 2004), typically at intermediate intensities or frequencies (Connell, 1978; Grime, 1973; Huston, 1979). Commonly referred to as the Intermediate Disturbance Hypothesis (IDH) (Connell, 1978), the observed unimodal relationship between diversity and disturbance is often attributed to the effect of disturbance on competitive interactions such that moderate disturbance prevents competitive exclusion and allows for the coexistence of a greater number of species (Grime, 1973; Huston, 1979).

Although unimodal disturbance-diversity relationships have been observed among a variety of ecosystems, taxonomic groups, and disturbance types (Shea et al., 2004), the IDH has also received criticism (Adler et al., 2011; Fox, 2013) on both empirical and theoretical grounds. Recent meta-analyses indicate that unimodal disturbance-diversity relationships are rarely observed, with disturbance studies often finding neutral, positive, or negative relationships between disturbance and species richness (Hughes et al., 2007; Mackey and Currie, 2001). This range of disturbance-diversity relationships observed has been attributed to variations in methodology. For example, if a study only analyzes a narrow range of habitat types or disturbance intensities, or if an underlying environmental stressor limits diversity irrespective of disturbance regime, then the IDH may not be evident (Grime and Pierce, 2012). However, in addition to the lack of empirical support, Fox (2013) suggests that the theoretical underpinnings of why diversity responds unimodally to disturbance regimes are flawed. He suggests nature's response to disturbance is more complex than the proposed mechanisms of species co-existence in the presence of disturbance as outlined under the IDH. Yet, Pierce (2014) warns that abandoning IDH altogether may signal to policy makers that anthropogenic management of natural resources- such as grazing, burning, and mowing- are not important for conservation.

The majority of grazing disturbance literature concentrates on vegetative responses to livestock grazing (Milchunas and Lauenroth, 1993). There are relatively few studies on how grazing influences animal communities (Van Wieren and Bakker, 2008), most of which focus on invertebrates (e.g. Cagnolo et al., 2002; Gibson et al., 1992; Rickert et al., 2012; Vulliamy et al., 2006). How vertebrate assemblages respond to grazing disturbance is still poorly understood.

Several studies have shown grazing can have a negative impact on avian (Chamberlain and Fuller, 2000; Martin and McIntyre, 2007; Popotnik and Giuliano, 2000), reptile (Bock et al., 1990; Jones, 1981; Woinarski and Ash, 2002), and small mammal (Bock et al., 1984; Eccard et al., 2000; Heske and Campbell, 1991; Torre et al., 2007) abundance and richness, while others show the abundance of several species actually increase with livestock grazing (Bock et al., 1984; Dorrough et al., 2012; Medin and Clary, 1990). These studies are typically enclosure studies that compare vertebrate assemblages in grazed and ungrazed plots (e.g. Bock et al., 1990; Eccard et al., 2000a; Heske and Campbell, 1991; Jones, 1981; Torre et al., 2007; Woinarski and Ash, 2002). Such enclosure studies are unable to detect how assemblages respond to intermediate intensities or frequencies of grazing disturbance and do not account for the spatial and temporal variations in grazing pressure under natural pastoral systems (Butt and Turner, 2012). Additionally, these studies tend to focus one particular species or groups of animals, e.g. birds or small mammals (e. g. Bock et al., 1990; Eccard et al., 2000; Jones, 1981; Schmidt et al., 2005; Torre et al., 2007), which is less informative for conservation managers interested in conserving multiple species within naturally existing disturbance regimes.

Vertebrate-grazing studies often focus on the response of vertebrate communities to grazing pressure, but generally fail to investigate the mechanisms that drive these responses (Shea et al., 2004). While the IDH provides a useful starting place for understanding why disturbance can promote species co-existence, a growing number of field studies suggest that disturbance is a more complex phenomenon than the initial IDH acknowledges (Fox, 2013; Roxburgh et al., 2004; Shea et al., 2004). This should alert ecologists to the need of obtaining a more nuanced understanding of the mechanisms driving disturbance-diversity relationships. Understanding such mechanisms can ultimately help rangeland stakeholders and conservationists to manage the landscape in way that optimizes wildlife diversity and ecosystem function.

I focus this study on the Mediterranean Basin, a major biodiversity hotspot (Cuttelod et al., 2008), simultaneously threatened by grazing intensification and land abandonment (Perevolotsky and Seligman, 1998; Zervas, 1998). Livestock grazing has been a major activity in the region since antiquity, with archeological evidence of domesticated animals dating back to 6500 BC (Hadjigeorgiou, 2011). Given the long history of grazing, many Mediterranean scrubland species have adapted morphological and chemical defenses, such as spiny leaves, thorns, secondary chemical compounds, and below-soil perennating organs, that make these communities grazing-resistant (Sternberg et al., 2000). With urban relocation, high labor costs, the social devaluation of shepherding, and agricultural policies that encourage sedentary livestock systems, many areas along the northern rim of the Mediterranean have seen a shift from a mainly extensive/low-input system to intensive/high-input livestock practices (Hadjigeorgiou, 2011; Riedel et al., 2007; Strijker, 2005). Abandonment of pastoral lands can lead to woody plant encroachment resulting in reductions in biodiversity and increased wildfire risk (Asner et al., 2004; Sanderson et al., 2013; Zervas, 1998). On the other hand, intensification of livestock production can also result in biodiversity losses, desertification, and water pollution (Asner et al., 2004; Ilea, 2009). Understanding the impact of grazing in the Mediterranean is especially imperative, as this endemically rich region is vulnerable to both the ecological threats of undergrazing and overgrazing.

The objectives of this study were to: (1) determine the nature of the relationship between livestock grazing and vertebrate assemblages (see Appendix I) and (2) discover what mechanisms drive vertebrate assemblage responses to livestock grazing disturbance. In contrast to previous studies focusing on a single species or animal group, I examined the response of multiple vertebrate groups simultaneously to a broad spectrum of grazing intensities. I hypothesized vertebrate abundance would decrease with increasing livestock grazing, while vertebrate species richness would peak at intermediate livestock stocking rates.

To understand the mechanisms underlying the observed disturbance-diversity responses, I investigated a number of *a priori* hypotheses informed from the disturbance literature. These hypotheses suggest that grazing induces changes in food availability (Jones, 1981; Milchunas et al., 1998; Torre et al., 2007), vegetation cover (Bock et al., 1984; James, 2003; Popotnik and Giuliano, 2000), and vegetation structural heterogeneity (Grant et al., 1982; Martin and McIntyre, 2007) drive vertebrate diversity responses. Using an information-theoretic approach and Generalized Linear Modeling, I determined which habitat characteristics, modified through livestock grazing, best predicted vertebrate abundance and richness. Understanding what habitat characteristics best predict vertebrate abundance and richness is critical for informing land management strategies focused on promoting wildlife diversity and ecosystem function.

2. Methods

2.1 STUDY AREA

All fieldwork took place during May-July 2013 on the island of Naxos (446 km², 37°08'N, 25° 25'E). Naxos is the largest island in the Cyclades Cluster, an island archipelago located in the central Aegean Sea, Greece (Figure 1). Climatic conditions are typical of the Mediterranean region, with mild wet winters and warm dry summers (Nastos et al., 2010; Tselepidakis and Theoharatos, 1989). The island is comprised of limestone and flysch substrates and soil with a shallow profile. Maquis and phrygana are the dominant vegetation types on the island. Phrygana, the ecological equivalent of other mediterranean vegetation types including batha (Israel), tomillares (Spain), coastal sage (California), garrigue (France), and kwongan (SW Australia), consist of spiny, largely summer-deciduous aromatic shrubs. Vegetation on the study region is dominated by-common phryganic species including Conehead Thyme (*Coridothymus capitatus*), Aegean Broom (*Genista acanthoclada*), Prickly Burnet (*Sarcopoterium spinosum*), Pink Rock-Rose (*Cistus creticus*) and Spiny Broom (*Calicotome villosa*) with some maquis (woody shrubland) evergreen species interspersed including Kermes Oaks (*Quercus coccifera*), Mastic (*Pistacea lentiscus*) and Phoenician Junipers (*Juniperus phoenicea*). This type of scrubland vegetation is widespread throughout the Mediterranean Basin and home to a large number of endemic species (Grove and Rackham, 2003).

Naxos has a long history of grazing, with remains of domestic livestock found in the Neolithic layer of an archeological exploration of Zas Cave, Naxos (Halstead, 1996). Agriculture and animal husbandry are the main economic activities on Naxos, with wine, honey, and Naxian cheeses all important agricultural products of the island. Pastoralists generally maintain mixed flocks of sheep and goats; however, cattle and pigs are also present in the lowlands. The livestock are typically unfenced and graze on assigned land tracts that may or may not be owned by the pastoralists. Flocks of sheep and goats feed exclusively on natural pasture in the spring and summer, with minor amounts of supplemental feed used only when flocks are breeding, during the winter (Zervas, 1998).

2.2 STUDY PLOTS

Fifteen plots were established in low elevation regions of Naxos, to represent a continuum of livestock grazing intensities (Figure 1, Appendix II). Plots were controlled for vegetation type (phrygana), substrate (limestone), and elevation (30-350m), thus minimizing variation that may confound analyses. Plots were 100 x 100 m (1 ha) in size such that they were large enough to sample mobile vertebrate taxa while still being homogeneous with regards to grazing pressure, vegetation cover, and species composition. Within each plot, four 50 m transects were established in the four cardinal directions from the plot center to quantify habitat and invertebrate diversity.

For each plot, I assessed current grazing conditions and vertebrate population abundance and richness. I also collected data on habitat structure and invertebrate assemblages to explore potential mechanisms driving the relationship between livestock grazing and vertebrate populations (see Appendix II for detailed ecological study plot descriptions).

2.3 QUANTIFICATION OF GRAZING CONDITIONS

I used stocking rate as a measurement of livestock (goat and sheep) grazing pressure on each study plot. Stocking rate was defined as the number of goats and sheep stocked per hectare based on interviews with pastoralists and validated through my own flock counts, and adjusted for the duration of use. Modifications were made to account for over inflation due to livestock passing through the plot without grazing (Appendix III). Stocking rates were further validated by quantifying livestock dung mass and general reconnaissance (Jasmer and Holechek, 1984) which accounted for ground cover, vegetation height, and defoliation patterns in the area (see Appendix IV).

2.4 VERTEBRATE POPULATION MEASUREMENTS

Terrestrial Vertebrates

I used drift fences to survey ground dwelling reptiles and mammals. Fences were constructed on each plot using a three-fence array design (modified from Enge, 1997), with three 5m x 0.5m lengths of plastic mesh and four 8-liter buckets (Appendix V). Metal stakes were used to secure the fences at 1m-intervals. Buckets were sunk flush to the ground, and moist sponges and small rocks were placed in each bucket to prevent desiccation and overheating of animals. Each array was left open for a total of 20 trap nights during June and July and was checked daily. Animals were measured, marked using a permanent marker, and released at the point of capture.

Avian

Passerine species were surveyed twice at each plot in June and July 2013. Using a fixed radius point count method (modified from Hutto et al., 1986), a researcher stood at the center of each plot and recorded birds detected (visually and aurally) within a 50 m radius during a 10 minute observation period (Appendix V). Birds flying over the site were excluded from my analysis. Surveys were always conducted between 6:00-10:00h UTC and under similar weather conditions (clear, low winds and no precipitation).

2.5 HABITAT MEASUREMENTS

I collected a number of habitat condition measurements to assess how livestock grazing influences habitat structure and quality. These included: (1) vegetation biomass, (2) vegetation height, and, (3) shrub cover.

Vegetation biomass (kg/m²). Eight, randomly selected, 80 x 80 cm quadrats (two quadrats along each of the four transects per plot) were sampled. All vegetation within the quadrat was clipped to ground level. All living and dead plant matter was collected, dried in the sun until brittle, and weighed (modified from Gutiérrez and Meserve, 2000; Herrick et al., 2005). Aboveground biomass values, expressed as kg/m² were averaged for all quadrats in each plot.

Vegetation height (cm). Vegetation height was sampled at 5m intervals along 50m transects radiating from the center of the study plot in the four cardinal directions. Vegetation height was later classified into six height classes: No plant, <10cm, 10-50cm, 50cm-1m, 1-2m, and >2m (Riginos and Herrick, 2010). Height classifications were used to construct an index of vegetation structure heterogeneity, termed Foliage Height Diversity (*FHD*), at each site. FHD was calculated using the Shannon Index of Diversity (Magurran, 2004).

Shrub Cover was calculated using a gap intercept method (Herrick et al., 2005) to determine the amount of bare ground (gaps) greater than one meter between woody shrubs. Percent gap (% Gap) was calculated by dividing the number of recorded gaps by the total number of measurements on a plot. To obtain the % Shrub Cover, % Gap was subtracted from 100.

2.6 INVERTEBRATE POPULATION MEASUREMENTS

I installed 12 invertebrate pitfall traps at each site along each directional transect (three per transect at the 10, 30, and 50m points). Pitfall traps were constructed using 320mL plastic cups filled with 55mL of ethylene glycol (Formula Flu Antifreeze), to preserve invertebrate samples. Cups were sunk flush to the ground and under shrubs. Each cup was protected from livestock trampling by loosely placing 1-2 rocks over it and was left out for 10 consecutive trapping nights for a total of 120 trapping nights at each site. Invertebrates were identified to order and then dried for five hours under a heat lamp before being weighed. Invertebrate biomass (g) was averaged per site and invertebrate abundance and richness on the level of order were calculated. Invertebrates were further classified according to the presence or absence of chemical and morphological defenses to calculate the % of defended invertebrates at each site.

2.7 STATISTICAL ANALYSIS

Livestock Grazing-Environment Interactions

Spearman rank correlations were used to elucidate the relationship between livestock stocking rate and habitat and invertebrate measurements: vegetation biomass, foliage height diversity (FHD), vegetation species richness, shrub cover, and invertebrate biomass, richness, abundance, and % defended. I additionally looked at the correlation between each invertebrate order and stocking rate. Livestock stocking rate was \log_e -transformed to account for overdispersion of data.

Relationships between Livestock Grazing and Vertebrate Populations

The influence of grazing on vertebrate abundance and richness was assessed using Generalized Linear Modeling (McCullagh and Nelder, 1989). Because vertebrate abundance, as is often found with discrete count data, followed a Poisson error distribution, I used Poisson errors and a log link function when modeling abundance. Richness was normally distributed and was modeled with normal errors and an identity link function. To test for unimodality I compared a model using a second order term against a linear model. Model fit was assessed using an information-theoretic approach utilizing the Akaike Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson, 2002). The model with the lowest AIC_c score is the “best” model of those compared. To compare the various models, ΔAIC_c was calculated by subtracting the “best” model’s AIC_c score from the AIC_c of the model in question (Burnham and Anderson, 2002). If $\Delta_i < 2$, the model was considered well supported by my data. Akaike weights (w_i) and evidence ratios were used to determine the degree of certainty in model selection.

Mechanisms

After determining the relationship between livestock grazing and vertebrate richness and abundance for terrestrial and avian groups, I ran a number of *a priori* models to explore potential mechanisms that could explain how grazing influences these vertebrate populations (see Table 1).

3. Results

3.1 EFFECTS OF LIVESTOCK GRAZING ON VEGETATION TRAITS AND INVERTEBRATE NUMBERS

Livestock grazing significantly alters the Aegean landscape. With increasing stocking rate, both vegetation biomass ($r_s = -0.699$, $p = 0.004$, $n = 15$, Spearman) and shrub cover ($r_s = -0.790$, $p = 0.000459$, $n = 15$, Spearman), decreased significantly. Grazing was also associated with decreased plant species richness ($r_s = -0.890$, $p = 0.00009$, $n = 15$, Spearman). Invertebrate biomass increased with stocking rate ($r_s = 0.629$, $p = 0.016$, $n = 15$, Spearman), while invertebrate abundance and order richness were not significantly correlated with stocking rate ($r_s = 0.396$, $p = 0.144$, $n = 15$, Spearman and $r_s = 0.325$, $p = 0.237$, $n = 15$, Spearman, respectively). Three invertebrate orders were significantly correlated with livestock stocking rate. Blattodea abundance declined with livestock stocking rate ($r_s = -0.615$, $p = 0.015$, $n = 15$, Spearman), while Coleoptera ($r_s = 0.685$, $p = 0.005$, $n = 15$, Spearman) and Hemiptera ($r_s = 0.550$, $p = 0.033$, $n = 15$, Spearman) abundances increased with stocking rate. There were large shifts in invertebrate composition between ungrazed and grazed sites; with ungrazed sites dominated by Hymenoptera (45%) and Araneae (25%), while heavily grazed sites were dominated by Coleoptera (52%) and Hymenoptera (33%). There was also a notable increase in the percent of chemically and morphologically defended arthropods with livestock stocking rate ($r_s = 0.771$, $p = 0.003$, $n = 15$, Spearman).

3.2 VERTEBRATE POPULATIONS ACROSS STOCKING REGIMES AND PROXIMATE DRIVERS OF TERRESTRIAL VERTEBRATE AND AVIAN ABUNDANCE AND SPECIES RICHNESS

I recorded a total of 459 vertebrates (reptiles, mammals, and birds) representing 21 species (Appendix VI). Of these, 54% ($n = 250$, 9 species) were terrestrial vertebrates (reptiles and mammals) and 46% were passerine birds ($n = 209$, 12 species). Certain species were found on all sites, including the Aegean wall lizard (*Podarcis erhardii*) and the Sardinian warbler (*Sylvia melanocephala*). No site had all species present. Furthermore, sites with the richest avian assemblages such as Kokimas Galanadou with a species richness of 9, had low terrestrial vertebrate richness with only 3 species recorded. Several rare terrestrial vertebrate species, for example *Ablepharus kitaibelii* and *Sorex minutus*, were found only on grazed sites, whereas none of the less common species were found exclusively on ungrazed sites. In contrast, no such pattern was evident in birds, with several uncommon passerine species found exclusively on grazed (e.g. *Emberiza melanocephala*, *Saxicola torquata*) or ungrazed sites (e.g. *Miliaria calandra*, *Acanthis cannabina*) (Table 2).

Terrestrial Vertebrates

Terrestrial vertebrate abundance exhibited a negative linear relationship with livestock stocking rate (Table 3A and Figure 2A), which was best predicted by invertebrate biomass (Table 5A). Terrestrial vertebrate species richness displayed a unimodal relationship with stocking rate (Table 3B and Figure 2A) with richness peaking at a stocking rate of ca. 30-40 livestock/hectare.

Invertebrate biomass was the best predictor of this unimodal relationship between terrestrial vertebrate richness and livestock stocking rate, however foliage height diversity and the intercept only models also received considerable support with $\Delta AIC_c < 2$ (Table 5B).

Avian Species

Avian abundance and richness showed no clear relationship with stocking rate (Figure 2B), with the intercept only model providing the best model fit in both cases (Table 4). Avian abundance and richness were best predicted by foliage height diversity (FHD - a predictor of vertical structural heterogeneity), with some support that shrub cover may also be an important driver of avian abundance (Table 6). However, I found no clear relationship between livestock stocking rate and foliage height diversity (FHD) ($r_s = -0.051$, $p = 0.857$, $n = 15$, Spearman).

4. Discussion

4.1 RESPONSE OF VERTEBRATE ASSEMBLAGES TO GRAZING

Terrestrial Vertebrates

Disturbances, such as livestock grazing result, by definition, in damage or destruction of organisms (Mackey and Currie, 2001). Although vertebrates may not be directly harmed by a disturbance event given their mobility (Fuentes and Jaksic, 1988), disturbances such as livestock grazing can drastically alter resource and habitat availability, indirectly impacting these organisms. Changes in food availability, ground coverage, vegetation structure and soil compaction are all indirect ways in which livestock grazing is believed to alter small mammal and reptile populations (Bock et al., 1990; Jones, 1981; Schmidt et al., 2005; Torre et al., 2007). Although increases in population abundance among reptile species that prefer open habitat have been observed (Dorrough et al., 2012), most studies show decreased population sizes among reptiles (Bock et al., 1990; Jones, 1981; Woinarski and Ash, 2002) and small mammals (Eccard et al., 2000; Joubert and Ryan, 1999; Medin and Clary, 1990, 1989; Reynolds and Trost, 1980; Torre et al., 2007) with grazing. In agreement with this literature, I found that terrestrial vertebrate (reptiles and small mammals) abundance decreased with increased stocking rates.

Although previous grazing studies have speculated that food availability drives the decrease in small mammal and reptile abundance on grazed sites (e.g. Bock et al., 1990; Eccard et al., 2000), no empirical support is offered to back these assumptions. In this study, I find that invertebrate biomass was the best predictor of terrestrial vertebrate abundance. It is likely that invertebrate food availability is of functional importance given all of the terrestrial vertebrates in this study are to varying degrees insectivores (see Appendix VI). Interestingly, invertebrate biomass measured in pitfall traps actually increases with livestock stocking rate. Such increases in invertebrate biomass however may not necessarily reflect total arthropod numbers given that pitfall traps preferentially capture terrestrial taxa (W-C Cheng, *in prep.*). Utilizing a variety of invertebrate sampling methods (e.g. pan traps, sticky traps) that also trap insects living in the vegetation and likely susceptible to its removal, may reveal an overall decrease in invertebrate numbers with intensified livestock grazing. Additionally, the observed shifts in invertebrate community composition when stocking rate rises, towards more chemically and physically defended arthropods may account for the increase in invertebrate biomass on heavily grazed sites. This study supports the idea that grazing mediated changes in invertebrate populations are important drivers of terrestrial vertebrate abundance. Nonetheless, a finer taxonomic resolution (e.g. identifying invertebrates to the species level), a greater variety of invertebrate sampling methods, and a nuanced understanding of dietary preferences of the terrestrial species observed will help further elucidate the relationship between terrestrial vertebrate abundance and invertebrate populations.

Although sample sizes are too low to analyze each individual species' response to grazing, I did see evidence of species-specific grazing responses. For example, Aegean Wall Lizard (*Podarcis erhardii*) abundance decreased with stocking rate, while the abundance of the European snake-eyed skink (*Ablepharus kitaibelli*) increased with stocking rate. Despite reductions in overall population abundance, I found that terrestrial vertebrate richness peaked at intermediate stocking

rates in accordance with the IDH. This unimodal relationship was best predicted by invertebrate biomass, again suggesting the importance of grazing mediated changes in invertebrate populations. However, it is unclear how the increase in invertebrate biomass with grazing drives this unimodal response in terrestrial vertebrate richness. I hypothesize that either: (1) invertebrate biomass is just one of multiple mechanisms driving the response of terrestrial species richness (Roxburgh et al., 2004), or (2) invertebrate biomass is, in part, reflecting changes in invertebrate richness. My GLM analysis indicates foliage height diversity (FHD), a measure of vegetation structural heterogeneity, is also an important predictor of terrestrial vertebrate richness, giving some support to my first hypothesis. Sites with variation in vegetation structure presumably provide greater foraging and nesting opportunities, therefore supporting more diverse terrestrial vertebrates assemblages (Jones, 1981). As for the second hypothesis, although I found no significant relationship between stocking rate and invertebrate richness, previous studies have shown increases in invertebrate richness at intermediate levels of grazing disturbance (Milchunas et al., 1998). A finer taxonomic resolution (Cagnolo et al., 2002) and a variety of invertebrate sampling methods (e.g. pan traps, sticky traps) may reveal a significant unimodal relationship between grazing and invertebrate species richness in this system. An unanswered question is: is it a combination of the quantity of food available and changes in vegetation structure that drives terrestrial species richness responses to grazing or is invertebrate biomass acting as a surrogate for the heterogeneity of the food source available under different grazing regimes?

Avian

Avian species richness and population abundance, contrary to my expectations, did not show any significant relationship with stocking rate. I hypothesized that avian species richness, similar to terrestrial species richness, would peak at intermediate intensities of grazing, and be mediated through changes in vegetation structure (Collins et al., 1998; MacArthur and MacArthur, 1961; Watson, 1964). Additionally, I expected an overall decrease in total avian populations as seen in previous avian studies (James, 2003; Joubert and Ryan, 1999; Martin and McIntyre, 2007). However, I found that neither abundance nor richness were correlated with livestock stocking rates. Instead both avian abundance and richness were best predicted by vegetation structure complexity, a measurement of the microgeographic vegetation heterogeneity on a plot. Interestingly, the changes in vegetation structural heterogeneity were not related with livestock stocking rate and more likely the result of the history of management of an area. The lack of a significant relationship between avian assemblages and livestock grazing is likely because birds, by virtue of their greater mobility, select and use the landscape on a different, coarser scale than terrestrial vertebrates.

Although birds have been shown to respond both positively (e.g. Medin and Clary, 1990) and negatively (e.g. Popotnik and Giuliano, 2000) to livestock grazing, there are also a number of studies that suggest livestock grazing has no effect on bird communities. Reynolds and Trost (1980) found that avian richness was the same on grazed and ungrazed sagebrush sites in Idaho, which they attributed to the greater mobility of birds. Similarly, tree presence was found to be the most important factor for predicting bird presence in pastureland in Australia. Since grazing intensification did not impact tree presence, avian assemblages showed no response to changes in sheep and cattle grazing pressure (Dorrough et al., 2012). The bird species observed in this study tend to prefer open agricultural habitats (see Appendix VI). Therefore, these species are likely already adapted to a grazed landscape and small-scale changes in livestock intensification are

unlikely to impact these avian species. Utilizing a naturally occurring livestock grazing continuum, the study scale (1 ha plots) was chosen to reflect current grazing practices in the region. Comparing larger study plots with more homogenous grazing pressure may result in an observable relationship between grazing intensity and avian populations. It appears that the current grazing regime in the Mediterranean does not influence passerine richness or abundance, presumably because grazing does not significantly alter the food or habitat ability for avian species in the system at a regional level.

This study focused on vertebrate responses to current livestock grazing intensities. However, disturbance is a multifaceted phenomenon characterized by intensity, frequency, extent, duration, and timing (Miller et al., 2011). Although I detected no relationship between current stocking rates (disturbance intensity) and avian richness and abundance, it is possible that other aspects of grazing disturbance such as frequency or timing may be correlated with avian assemblages. Livestock grazing can alter vegetation structure and can create heterogeneous vegetation structures (Adler et al., 2001; Collins et al., 1998), which this study shows is important in determining species richness and abundance of bird populations. Therefore, I assume that while grazing does play a role in shaping vertebrate assemblages as mediated through vegetation structure, it is also possible that these changes in vegetation structure may be correlated with other disturbance measures such as the timing and frequency of grazing as well as non-grazing disturbances such as fire.

Future studies looking at multiple scales and disturbance characteristics are needed to gain a better understanding *if* and *how* avian populations respond to grazing disturbances. In the mean time, this study supports the growing literature showing the importance of vertical vegetation structural heterogeneity for supporting diverse avian populations (Lack, 1933; MacArthur and MacArthur, 1961; Tews et al., 2004; Watson, 1964), suggesting rangeland managers and conservationists should strive to create and maintain a diversity of vertical structures, especially in areas where avian populations are threatened.

Conclusions

In this study, I demonstrate distinct disturbance-diversity relationships for terrestrial and avian vertebrate groups and that disturbance responses are mediated through different grazing-mediated environmental changes. In a review of literature on richness-productivity relationships, Mittelbach et al. (2001) found that unimodal relationships were more common in aquatic vertebrates than terrestrial vertebrates. They suggest this may be due to the tendency for aquatic studies to look at the response of a trophic level while terrestrial studies focus on the response of a particular group of taxa (e.g. mammals, invertebrates, or birds). I found that insectivorous terrestrial vertebrates with similar dispersal abilities showed evidence of a unimodal disturbance-diversity response, while avian richness (which encompassed passerine species with varying dietary preferences) did not show a clear disturbance-diversity response. Although many mechanisms have been suggested to drive unimodal disturbance responses, (e. g. resource partitioning, competition-colonization trade-offs, temporal and spatial relative nonlinearity, and storage effects) (Connell, 1978; Miller and Chesson, 2009; Roxburgh et al., 2004) all of the mechanisms focus on competitive interactions. Given that vertebrate species vary significantly in terms of life history traits, physiology, morphology, and behavior, it is reasonable to assume

vertebrate groups are not limited by and competing over the same environmental factors. While moderate levels of grazing disturbance may benefit vertebrate assemblages, finding evidence of unimodal diversity-disturbance relationships among terrestrial vertebrates depends upon the methods of analysis, such as how species are grouped. Unimodal responses may only be evident when grouping species that have similar dietary or habitat preferences and are therefore in competition with each other. If disturbance enables co-existence through suppression of competitive dominants, the reduction in Sardinian Warbler (*Sylvia melanocephala*) numbers, a primarily insectivorous bird, is unlikely to benefit the predominately seed-eating Goldfinch (*Carduelis carduelis*). This study shows the importance of looking at a continuum of grazing intensities and the response of diverse species groups to truly understand the implications of livestock grazing in a system.

4.2 CONSERVATION IMPLICATIONS

The differential disturbance responses of terrestrial and avian vertebrate species suggest that there is no ideal livestock stocking rate that will maximize all vertebrate richness. My results indicate that small mammal and reptile species richness peaks at intermediate stocking rates (ca. 30-40 animals/hectare) and that there seems to be no significant response of avian assemblages to livestock grazing in this system. Taken together, this evidence suggests that grazing at light to moderate stocking rates in Mediterranean sclerophyllous scrub is not antithetical to, and may actually promote vertebrate conservation efforts. Nonetheless, these results need to be balanced with parallel considerations of the impacts of grazing on plant diversity and various other ecosystem services. This finding dovetails with previous claims that grazing can be an important conservation practice and that policy should encourage extensification of livestock practices rather than intensification and abandonment of pastoral lands (Middleton, 2013; Sanderson et al., 2013; Zervas, 1998). However, given that certain less common species were found exclusively on ungrazed or heavily grazed sites, I believe that a mosaic of grazing intensities would best support maximum vertebrate species richness. Such a grazing mosaic has been suggested for optimizing invertebrate (Gibson et al., 1992; Rickert et al., 2012) and bird richness (Milchunas et al., 1998) since a shifting mosaic of succession from disturbance provides habitat for multiple species, as well as conditions necessary for vertebrates that rely on various habitat characteristics throughout various life cycle stages. Although this study did not investigate the effects of fire disturbance on vertebrate populations, previous work has shown the importance of the interactions between fire and grazing disturbances (Fuhlendorf and Engle, 2001) and conservation managers should consider the combination of prescribed burns and livestock grazing as a way of creating and maintaining heterogeneous habitat.

I observed that diversity-disturbance relationships can take a variety of shapes, and found evidence for distinct mechanisms driving avian and terrestrial responses. All of this supports the need for more nuanced disturbance models than provided by the IDH. These results are useful in informing models that are better able to predict the impact of various disturbance regimes. Future studies should investigate a wider range of potential mechanisms, as well as different characteristics of grazing disturbance such as the influence of frequency and duration of livestock grazing on vertebrate populations.

The results of this study also underscore the importance of simultaneously investigating the response of multiple taxa to disturbance. Quantifying only avian population responses, would lead to the wrong conclusion that creating and maintaining vegetation structural heterogeneity is a management priority and that livestock grazing is not essential for conservation. However, by identifying invertebrate food availability as an important predictor for rich assemblages of terrestrial vertebrates, I recognized two different habitat characteristics that rangeland managers and conservationists should be aware of, and highlight the utility of limited livestock grazing as a useful conservation tool in Mediterranean scrublands.

Figures

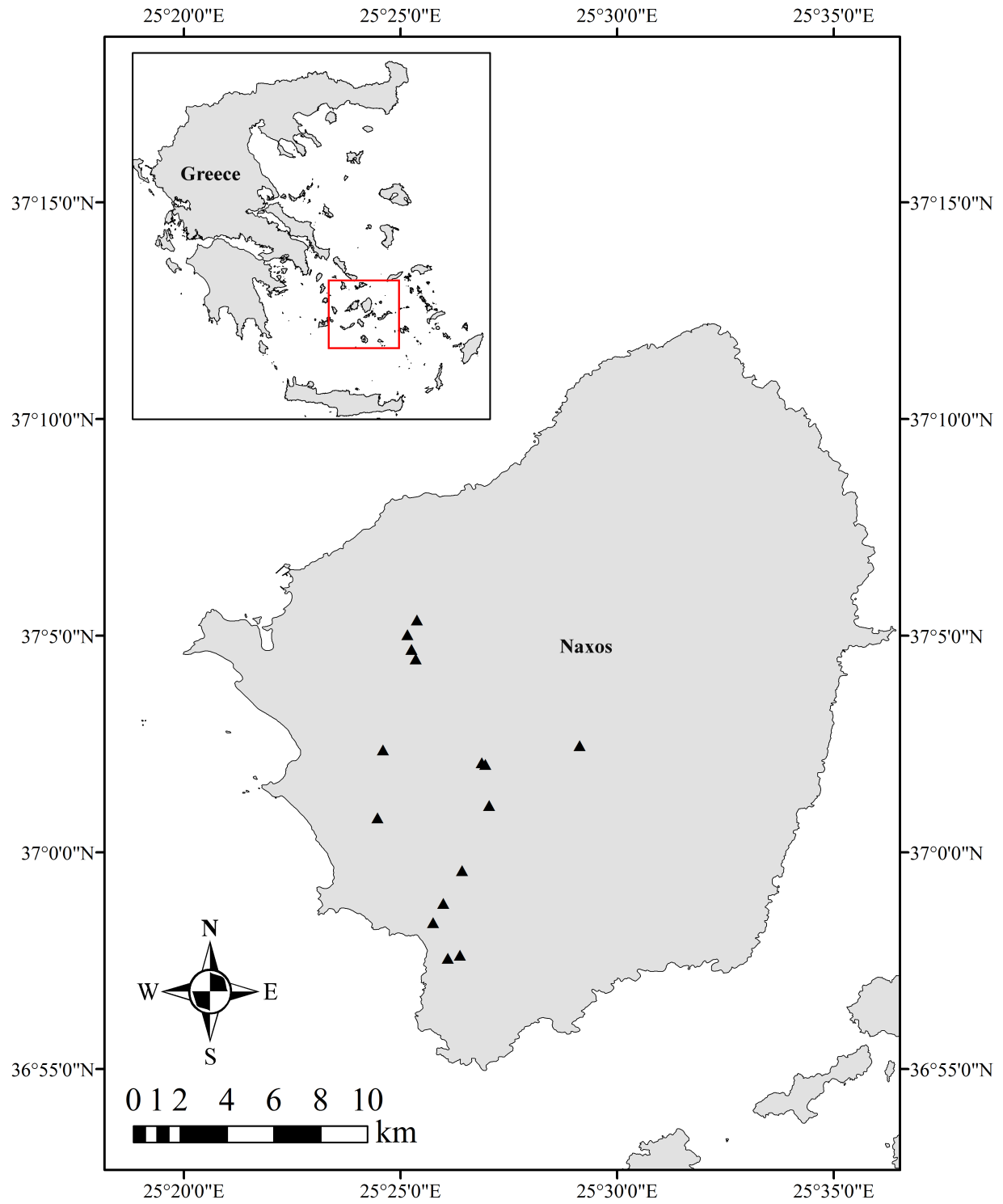


Figure 1. Map of Naxos Island. Study plots are indicated with triangles.

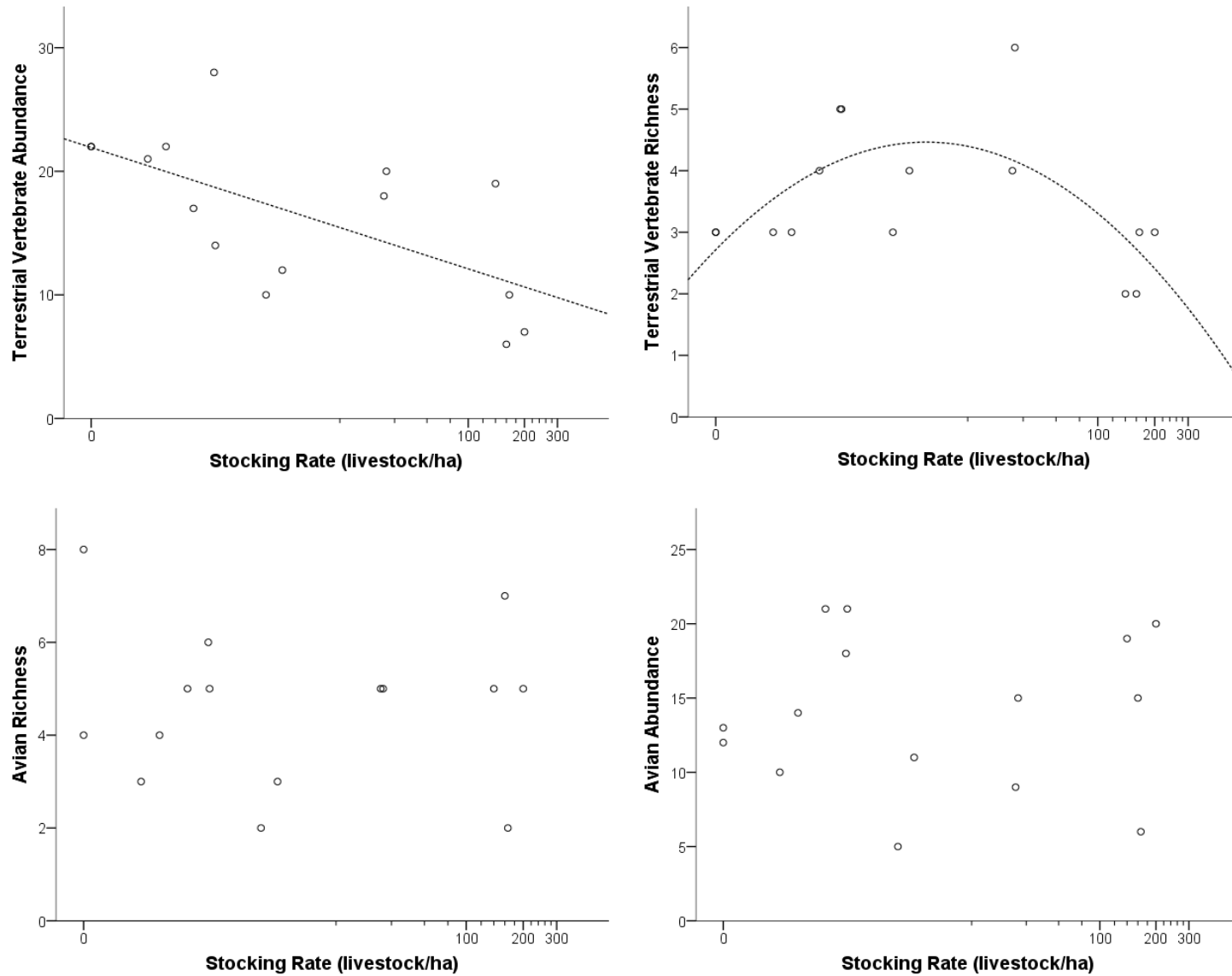


Figure 2. Relationship between livestock stocking rate (livestock/ha) and vertebrate wildlife population characteristics A. Terrestrial vertebrates: Abundance (left) and Species Richness (right). B. Birds: Abundance (left) and Species Richness (right). Dashed lines show the best model using an information-theoretic approach to multimodal inference. The absence of a dashed line indicates the null model (intercept-only) provided the best fit (as indicated by the lowest AIC_c score).

Tables

Table 1. *A priori* models corresponding to my hypotheses of potential mechanisms driving the grazing-vertebrate relationship.

Mechanism	Model
Food Availability	Vertebrate Richness/Abundance ~ Vegetation Biomass
Food Availability	Vertebrate Richness/Abundance ~ Invertebrate Biomass
Shrub Cover	Vertebrate Richness/Abundance ~ Shrub Cover
Vegetation Structural Heterogeneity	Vertebrate Richness/Abundance ~ FHD

Table 2. Vertebrate species assemblages by site. Species presence is indicated by an x. Sites are ranked in ascending order by stocking rate.

Site	Stocking Rate (livestock/ha)	Terrestrial									Avian										
		<i>Podarcis erhardii</i>	<i>Ablepharus kitaibelii</i>	<i>Cyrtodactylus kotschy</i>	<i>Hemidactylus turcicus</i>	<i>Lacerta trilineata</i>	<i>Eryx jaculus turcicus</i>	<i>Vipera ammodytes meridionalis</i>	<i>Crocidura suaveolens</i>	<i>Sorex minutus</i>	<i>Galerida cristata</i>	<i>Parus major</i>	<i>Saxicola torquata</i>	<i>Sylvia melanocephala</i>	<i>Lanius senator</i>	<i>Carduelis chloris</i>	<i>Carduelis carduelis</i>	<i>Acanthis cannabina</i>	<i>Miliaria calandra</i>	<i>Emberiza melanocephala</i>	<i>Emberiza cirius</i>
Kokimas Galanadou	0	x		x			x				x		x	x	x	x	x	x		x	x
Agios Dimitrios Galanadou	0	x				x			x				x		x			x			x
Lofos Galanadou	1	x		x		x							x	x							x
Agios Nikolaos Galanadou	1.5	x		x			x				x		x	x							x
Upper Agiassos	2.5	x		x		x	x				x		x	x					x		x
Upper Bazeos Tower	3.5	x	x	x					x	x			x	x					x	x	x
Stavropigi Vivlou	3.57	x		x		x		x					x	x	x						x
Koutsouria Filotiou	7.5	x		x									x	x							
Gialous Agiassou	9.38	x	x	x									x	x							
Lower Agiassos	35	x		x			x	x			x	x	x		x					x	
Platia Rachi	36.1	x		x	x		x		x	x			x	x	x				x		
Lower Bazeos Tower	140	x		x									x	x					x		x
Apaliros Castle	160	x		x									x	x	x					x	x
Agios Stefanos	166	x	x	x									x								
Hohlidia Agiassou	200	x	x										x	x	x						x

Table 3. GLM comparisons for the response of terrestrial vertebrate (small mammal and reptile) abundance (A.) and richness (B.) to changes in livestock stocking rates. Models are ranked in ascending order by ΔAIC_c . The log likelihood, deviance (D), AIC_c score, AIC_c weights (w_i) and evidence ratios are given for each model. Model variables include linear and squared terms for livestock stocking rate. TVA designates terrestrial vertebrate abundance while TVR designates terrestrial vertebrate richness.

	Log Likelihood	D	AIC_c	ΔAIC_c	w_i	Evidence Ratio
A. Terrestrial Vertebrate Abundance						
TVA ~ stocking_rate	-45.880	23.227	96.759	0.000	0.810	1.000
TVA ~ stocking_rate + stocking_rate ²	-45.749	22.966	99.680	2.921	0.188	4.308
TVA ~ intercept	-53.017	37.502	108.342	11.583	0.002	327.504
B. Terrestrial Vertebrate Richness						
TVR ~ stocking_rate + stocking_rate²	-18.028	9.717	48.055	0.000	0.647	1.000
TVR ~ intercept	-22.540	17.733	50.079	2.024	0.235	2.751
TVR ~ stocking_rate	-21.635	15.719	51.452	3.397	0.118	5.466

Table 4. GLM comparisons of the relationship of avian abundance (A.) and richness (B.) to livestock stocking rates. Models are ranked in ascending order by ΔAIC_c . The log-likelihood, deviance (D), AIC_c score, AIC_c weights (w_i) and evidence ratios are given for each model. Model variables include linear and squared terms for livestock stocking rate. AA designates avian abundance while AR designates avian richness.

	Log Likelihood	D	AIC_c	ΔAIC_c	w_i	Evidence Ratio
A. Avian Vertebrate Abundance						
AA ~ intercept	-47.570	29.035	97.448	0.000	0.725	1.000
AA ~ stocking_rate	-47.536	28.967	100.073	2.625	0.195	3.715
AA ~ stocking_rate + stocking_rate ²	-46.835	27.564	101.853	4.405	0.080	9.048
B. Avian Vertebrate Richness						
AR ~ intercept	-28.565	39.600	62.130	0.000	0.805	1.000
AR ~ stocking_rate	-28.560	39.572	65.301	3.171	0.165	4.882
AR ~ stocking_rate + stocking_rate ²	-28.372	38.594	68.744	6.614	0.030	27.303

Table 5. Model selection for predicting terrestrial (small mammal and reptile) richness (A.) and abundance (B.) as mediate through grazing-induced changes in habitat characteristics. Models are ranked in ascending order by ΔAIC_c . The log likelihood, deviance (D), AIC_c score, AIC_c weights (w_i) and evidence ratios are given for each model. Model variables include invertebrate biomass, foliage height diversity (FHD), vegetation biomass, and shrub cover. TVA designates terrestrial vertebrate abundance while TVR designates terrestrial vertebrate richness.

	Log Likelihood	D	AIC_c	ΔAIC_c	w_i	Evidence Ratio
A. Terrestrial Vertebrate Abundance						
TVA ~ invertebrate biomass	-37.376	10.378	79.843	0.000	1.000	1.000
TVA ~ shrub cover	-48.291	28.049	101.581	21.738	0.000	52,522.661
TVA ~ vegetation biomass	-50.797	33.063	106.595	26.752	0.000	644,351.717
TVA ~ intercept	-53.017	37.502	108.342	28.499	0.000	154,3402.573
TVA ~ FHD	-52.495	36.459	109.991	30.148	0.000	3,520,100.154
B. Terrestrial Vertebrate Richness						
TVR ~ invertebrate biomass	-20.616	15.585	49.631	0.000	0.387	1.000
TVR ~ intercept	-22.540	17.733	50.079	0.448	0.309	1.251
TVR ~ FHD	-21.576	15.586	51.325	1.694	0.166	2.333
TVR ~ vegetation biomass	-22.385	17.371	52.951	3.320	0.073	5.259
TVR ~ shrub cover	-22.504	17.649	53.189	3.558	0.065	5.924

Table 6. Model selection for predicting avian richness (A.) and abundance (B.) as mediated through grazing-induced changes in habitat characteristics. Models are ranked in ascending order by ΔAIC_c . The log-likelihood, deviance (D), AIC_c score, AIC_c weights (w_i) and evidence ratios are given for each model. Model variables include invertebrate biomass, foliage height diversity (FHD), vegetation biomass, and shrub cover. AA designates avian abundance while AR designates avian richness.

	Log Likelihood	D	AIC_c	ΔAIC_c	w_i	Evidence Ratio
A. Avian Abundance						
AA ~ FHD	-45.384	24.662	95.768	0.000	0.430	1.000
AA ~ shrub cover	-46.190	26.274	97.380	1.612	0.192	2.239
AA ~ intercept	-47.570	29.035	97.448	1.680	0.186	2.316
AA ~ invertebrate biomass	-46.485	26.865	97.971	2.203	0.143	3.009
AA ~ vegetation biomass	-47.562	29.018	100.124	4.356	0.049	8.829
B. Avian Richness						
AR ~ FHD	-22.880	18.556	53.941	0.000	0.971	1.000
AR ~ intercept	-28.565	39.600	62.130	8.189	0.016	60.009
AR ~ invertebrate biomass	-28.274	38.095	64.730	10.789	0.004	220.192
AR ~ vegetation biomass	-28.276	38.103	64.734	10.793	0.004	220.633
AR ~ shrub cover	-28.300	38.228	64.783	10.842	0.004	226.105

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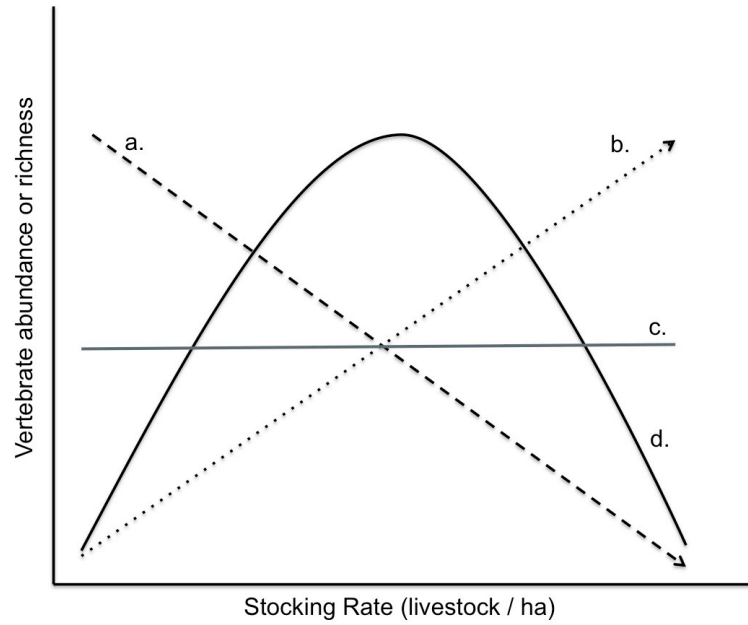
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APPENDICES

Appendix I. Hypothesized diversity-disturbance relationships for vertebrate species responses to livestock grazing: (a) negative linear, (b) positive linear, (c) neutral or (d) unimodal.



Appendix II. Location, elevation, aspect, vegetation characteristics, stocking rate and dung biomass for each study plot.

Name	Latitude	Longitude	Elevation (m)	Aspect	Primary Vegetation	Secondary Vegetation	Stocking Rate (livestock/ha)	Livestock Dung Biomass (g/m ²)
Kokimas Galanadou	N37°04.463'	E025°25.348'	179.53	N	<i>Genista/Calicotome/Cistus</i> Phrygana	Kermes Oak	0	0.00
Agios Dimitrios Galanadou	N37°04.758'	E025°25.378'	66.49	E	<i>Cistus/Calicotome</i> Phrygana	Pistacea	0	0.00
Lofos Galanadou	N37°04.682'	E025°25.256'	150.87	S	<i>Cistus/Calicotome</i> Phrygana	Kermes Oak	1	0.33
Agios Nikolaos Galanadou	N37°05.023'	E025°25.161'	54.86	W	<i>Genista</i> Phrygana	Pistacea	1.5	0.00
Upper Agiassos	N36°58.819'	E025°25.999'	32.87	S	<i>Coridothymus</i> Phrygana	Juniper	2.5	3.11
Upper Bazeos Tower	N37°02.026'	E025°26.963'	197.39	W	<i>Coridothymus/Genista</i> Phrygana	Kermes Oak/Juniper	3.5	1.33
Stavropigi Vivlou	N37°02.360'	E025°24.593'	170.38	E	<i>Cistus/Calicotome</i> Phrygana	Pistacea	3.57	1.00
Koutsouria Filotiou	N37°02.457'	E025°29.137'	326.25	E	<i>Coridothymus/Genista</i> Phrygana	Kermes Oak	7.5	2.94
Gialous Agiassou	N36°57.625'	E025°26.374'	54.86	S	<i>Coridothymus</i> Phrygana	Juniper	9.38	5.83
Lower Agiassos	N36.58.375'	E025.25.751'	55.42	W	<i>Coridothymus</i> Phrygana	Juniper	35	6.22
Platia Rachi	N37°00.794'	E025°24.470'	140.20	E	<i>Coridothymus/Genista</i> Phrygana	Juniper	36.1	2.39
Lower Bazeos Tower	N37°02.067'	E025°26.875'	206.65	W	<i>Coridothymus</i> Phrygana	Juniper	140	14.67
Apaliros Castle	N37°01.079'	E025°27.044'	206.95	N	<i>Coridothymus/Genista</i> Phrygana	None	160	16.72
Agios Stefanos	N36°59.578'	E025°26.421'	124.05	W	<i>Coridothymus</i> Phrygana	Juniper	166	59.33
Hohlidia Agiassou	N36°57.554'	E025°25.949'	61.63	N	Sparse <i>Coridothymus</i>	None	200	39.50

Appendix III. Modified Stocking Rate Calculation

I calculated stocking rate based on interviews with local pastoralists as follows:

Stocking Rate = Number of Goats and Sheep / Hectare (ha)

and subject to the following modifications:

(1) If animals merely passed through the plot I divided factor of ten. My calculations indicate this is representative of the fraction of time animals spent on the site while in transit (a tenth of a day).

(2) If animals were only present on a site for half the year, I corrected for this by dividing by a factor of two.

Appendix IV. Images of study plots showing different vegetation types along the grazing intensity gradient.



No Grazing



Light Grazing

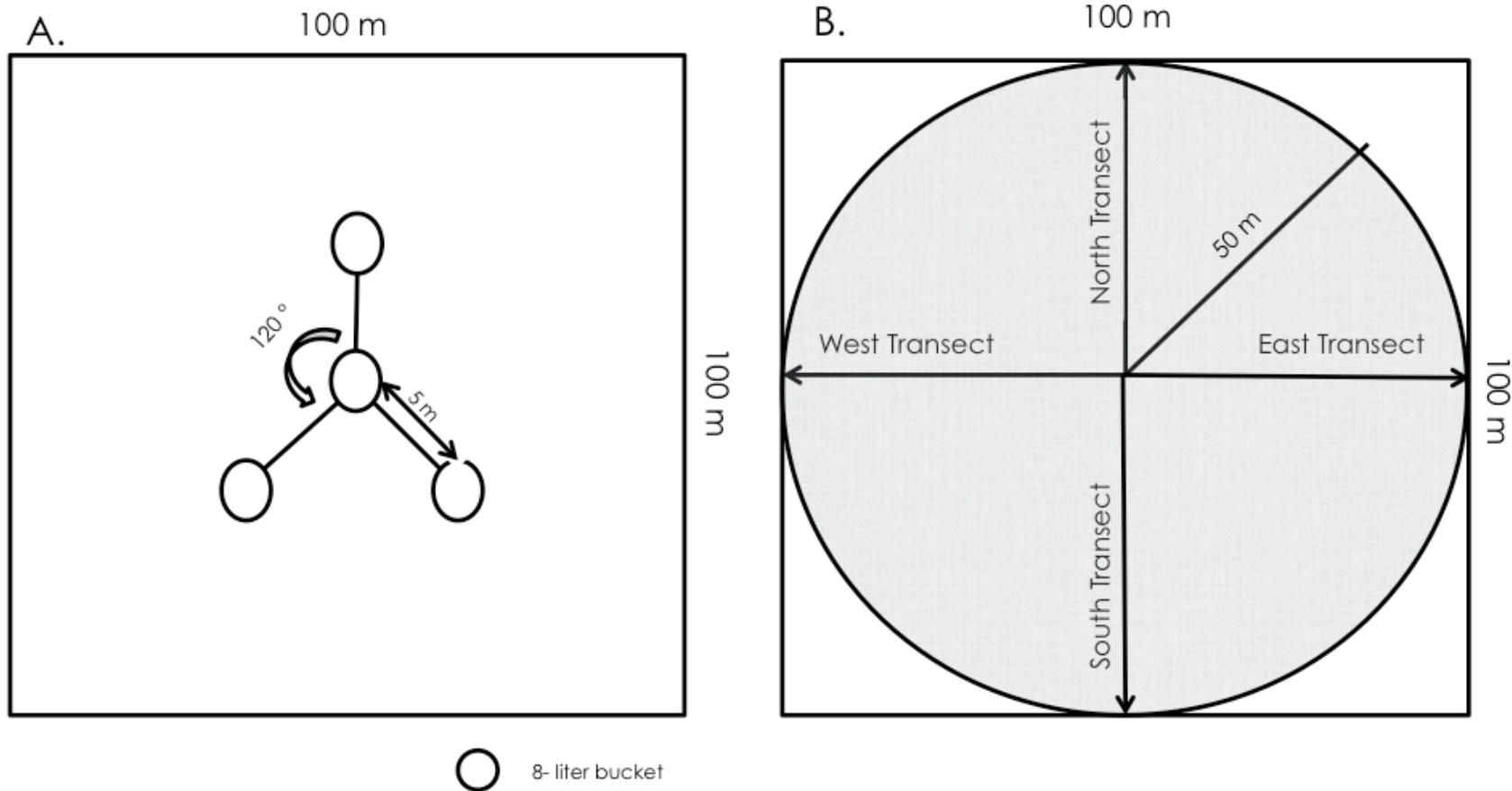


Moderate Grazing



Heavy Grazing

Appendix V. Implementation of vertebrate sampling methods: A) Schematic of drift fence trap array with the locations of 4 pitfall traps. B) Avian point count survey design. Avian point counts were made from the center of the plot, recording birds detected within a 50m radius (indicated in grey) during a 10-minute observation period.



Appendix VI. List of species observed during study and associated foraging guilds.

Latin Name	Common Name	Foraging Guild
<i>Sylvia melanocephala</i>	Sardinian Warbler	Insectivore
<i>Parus major</i>	Great Tit	Insectivore/Granivore
<i>Carduelis carduelis</i>	Goldfinch	Granivore/Omnivore
<i>Galerida cristata</i>	Crested Lark	Granivore/Omnivore
<i>Lanius senator</i>	Woodchat Shrike	Insectivore
<i>Acanthis cannabina</i>	Linnet	Granivore/Insectivore
<i>Miliaria calandra</i>	Corn bunting	Granivore/Omnivore
<i>Passer domesticus</i>	House Sparrow	Granivore
<i>Emberiza cirrus</i>	Cirl Bunting	Granivore/Omnivore
<i>Saxicola torquata</i>	Stonechat	Insectivore
<i>Carduelis chloris</i>	Greenfinch	Granivore/Omnivore
<i>Emberiza melanocephala</i>	Black-headed bunting	Granivore/Omnivore
<i>Crocidura suaveolens</i>	Lesser White Toothed Shrew	Insectivore
<i>Sorex minutus</i>	Eurasian Pygmy Shrew	Insectivore
<i>Lacerta trilineata</i>	Balkan Green Lizard	Insectivore
<i>Eryx jaculus turcicus</i>	Javelin Sand Boa	Carnivore/Insectivore
<i>Podarcis erhardii</i>	Aegean Wall Lizard	Insectivore
<i>Cyrtodactylus kotschy</i>	Kotschy's gecko	Insectivore
<i>Hemidactylus turcicus</i>	Mediterranean house gecko	Insectivore
<i>Ablepharus kitaibelii</i>	European Snake-Eyed Skink	Insectivore
<i>Vipera ammodytes meridionalis</i>	Long-nosed Viper	Carnivore/Insectivore