# Biodiversity Implications of Agricultural Terrace Abandonment in a Mediterranean Landscapes

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A thesis submitted in partial fulfillment

of the requirements for the degree of

Master of Science (School for Environment and Sustainability)

at the University of Michigan

August 2023

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**Abstract**
Dry-stone walls and terraces are a pervasive feature of traditional agriculture systems in many parts of the world and have been used to stabilize hilly slopes for millennia. They play a key role in reducing erosion, increasing rainwater infiltration, and increasing crop productivity. It has also been postulated that dry-stone wall terraces play a key role in increasing and helping to maintain biodiversity especially in the face of a changing climate. They are particularly common in the Mediterranean Basin where they often create a landscape-wide network of pharaonic proportions. Many of these terraces have been increasingly abandoned in recent years because of the high labor costs associated with their maintenance, and due to insufficient agricultural production on marginal lands. Little is known about how the abandonment process affects overall ecosystem function and biodiversity across multiple trophic levels. In this study conducted on the Aegean Island of Naxos, Greece, we build upon previous research which has demonstrated increased biodiversity in proximity to dry-stone walls. Previous research has suggested that terrace abandonment presents a serious threat to the ecological health of Mediterranean habitats (Deng et al., 2021; Newbold et al., 2020; Kruess and Tscharntke, 1994). Here we address two main issues regarding agricultural abandonment. First, we compare three distinct groups of terrace use: (1) active sites which are composed of plowed terraces and maintained supporting walls, (2) semi-active sites which are still plowed but whose supporting walls are not repaired, and (3) abandoned sites which are not used for cultivation, nor receive wall maintenance. Additionally, we use historical records to date the start of abandonment and study the impacts of age since abandonment on the present ecosystem. Measurements of biodiversity, such as reptile and arthropod species richness and population density, as well as measurements of vegetation were recorded to quantify the overall impacts of abandonment on biodiversity and ecosystem function over time. We find that terrace abandonment (via termination of agricultural production) and wall abandonment (via cessation of repairs) have varied effects on resident ecological communities. However, both conditions result in reduced biodiversity compared to actively managed fields. Also, effects vary by trophic level, with the strongest impacts on resident reptiles and arthropods, and the weakest on herbaceous plants. With increasing time since abandonment, we find significant increases in bush encroachment, and significant decreases in species richness and abundance among arthropod and reptile populations. This study suggests that maintenance of dry-stone wall terraces is an important component of ecological management in this region, as these agroecosystems contribute to a more multifunctional landscape.

**Key Words**: terrace abandonment, dry-stone walls, Mediterranean landscape, biodiversity, agriculture, land use change

## 1. Introduction

Dry-stone walls are used to create a network of agricultural terraces, to not only provide more surface for cultivation, but also to increase crop productivity, and to ensure the sustainability of agricultural activities (UNESCO - Intangible Cultural Heritage 2003; Lee and Kim, 2011). The practice of constructing agricultural dry-stone walls has been acknowledged by UNESCO as a culturally significant technique, evidenced by its inscription as an *Intangible Cultural Heritage of Humanity* (Jiménez de Madariaga, 2021). These structures are thought to have originated in Southeast Asia around five thousand 5,000 years ago, when proximity to steep mountainsides necessitated innovative agricultural approaches for communities lacking sufficient level arable land for cultivation. From there, dry-stone wall terracing spread to the Mediterranean and then expanded to other, more distant regions of the world (Price and Nixon, 2005). The global expansion and rise in incidence of terraced landscapes can be attributed to a scarcity of arable land, combined with population growth (Deng et al., 2021).

Dry-stone walls are a particularly common feature of agricultural terraces located in the Mediterranean Basin and some have been dated to the Bronze Age (Grove and Rackham, 2001). Areas such as the Mediterranean Basin constitute the cradle of western civilization and have supported complex human societies throughout millennia, despite conditions that are often marginal for agriculture. However, their increasing large-scale abandonment in recent years has precipitated significant concerns in regard to ecological impacts. Dry-stone walls are created by digging into a hillside, excavating any large rocks from the soil, and then using these rocks, together with others to construct a stone wall (Grove and Rackham, 2001). Because much of the Mediterranean consists of mountainous slopes, the presence of dry-stone walls is necessary in order to engage in any type of cultivation. For example, such terraces are often essential to the cultivation of regional staple crops such as wheat and olive trees.

While not strictly necessary for animal husbandry, agricultural terraces are often important for raising of livestock by providing flat and productive areas for small ruminant foraging. Dry-stone wall terraces are a significant landscape feature, functioning as productive systems and allowing for increased water and soil retention, in otherwise infertile areas. Dry-stone wall terraces have been shown to increase grain yields by 44.8% and soil moisture by 12.9%, supporting one of the most abundant group of crops in the Mediterranean (Deng et al., 2021). Specifically, the increased soil moisture held in these terraces creates more resilient crops, increasing survivability during droughts and resulting in a higher overall crop yields (Deng et al., 2021). Additionally, the construction and management of grain-bearing terraces modifies the soil profile which often has a high percentage of soil organic matter and nutrients compared to surrounding soils (Stanchi et al., 2012).

In addition to their primary function in facilitating husbandry, dry-stone wall terraces play an important role in supporting native biodiversity (Agnoletti et al., 2015; Arévalo et al., 2016). Considering lizards for example, of the 86 known subspecies of lizards found in Greece, 61 are endemic to the Aegean (Chondropoulos, 1986). Numerous studies document that many lizard species show a proclivity toward specialized elements of habitat structure due their needs as ectotherms to thermoregulate (Heatwole, 1977; Moermond, 1979; Christian et al., 1983; Grant and Dunham, 1988; Huey et al., 1989). Human-constructed rock walls have provided a suitable microhabitat for a variety of lizard species as they offer both cool, shady spaces within rock crevices, as well as warm, sunlit rock surfaces; therefore, providing lizards with a reliable mechanism to regulate their body temperature (Van Damme et al., 1989; Castilla and Bauwens, 1991). Additionally, such rock walls can serve as a refuge from predators such as snakes, another critical criterion considered in microhabitat selection (Martín and López, 1999). Prior research has found that lizards sometimes even prefer these man-made rock walls to their original, natural microhabitats (Salvador, 1974). Agricultural terraces located in the Mediterranean, as well as in other parts of Europe, are low-intensity production systems that, because of their ability to conserve natural resources, and their minimal environmental impact (e.g., through practices such as low external input use or intercropping), provide an abundant habitat for a diversity of plant, invertebrate and vertebrate taxa (Billeter et al., 2008). The importance of these traditional agroecosystems in supporting biodiversity, has become increasingly recognized in recent years as modern, high-intensity farming practices have led to significantly reduced levels of biodiversity world-wide (Arx et al., 2002). Terrace farming, therefore, represents not just an opportunity for sustainable food production, allowing for productive crop harvests on previously non-arable lands, but may also serve as a critical safeguard for local biodiversity that is threatened by changing climatic patterns (Newbold et al., 2020; Feng et al., 2017; Kosmowski, 2018). When actively maintained, dry-stone wall terraces provide a semi-natural environment that can support both humans, and high levels of biodiversity. However, land use change, specifically in the form of terrace abandonment and lack of maintenance, has potential to greatly reduce the productivity of previously supported ecosystems (Kruess and Tscharntke, 1994).

Although dry-stone wall terraces have been critical in supporting human societies in the Mediterranean over the last few millennia, many of them have been abandoned over the last century as a result of a dearth of interest in this type of labor intensive agriculture, urban expansion, and insufficient production compared to intensive forms of agriculture (Boccia et al., 2020; Schönbrodt-Stitt et al., 2013). Traditionally, dry-stone walls are created by meticulously stacking rocks which align with one another to create a system of support (UNESCO - Intangible Cultural Heritage 2003), that requires regular maintenance and repair. In many cases, the laborious wall maintenance is abandoned while plowing and harvesting continues each year, resulting in a partially abandoned terrace. However, agriculture on a partially abandoned terrace can only continue for so long, as wall maintenance abandonment eventually leads to progressive collapse. Dry-stone wall structures are susceptible to damage from rainfall infiltration, slope instability, erosion, and other environmental impacts, requiring regular upkeep to prevent soil loss or slope failure (Van Dijk and Bruijnzeel, 2003; Zuazo et al., 2005; Khanal and Watanabe, 2006). Eventually slope failure and erosion, which result from wall maintenance abandonment, inhibits harvesting and production, and all agricultural activity is abandoned. While some forms of agricultural abandonment result in a rebound of biodiversity due to improved soil quality and increased carbon sequestration (Wertebach et al., 2017), the same processes do not occur following agricultural terrace abandonment (Stavi et al., 2018). The features of dry-stone wall terraces which both foster biodiversity, and conserve water, soil and nutrients, tend to become degraded with progressive duration of abandonment, thereby negatively impacting microhabitat availability (Stavi et al., 2018).

In the last hundred years, agricultural production practices have experienced dramatic changes; most frequently visible are shifts to highly intensified systems and monocultures, leaving traditional systems, such as dry-stone wall terracing behind. The implications of agricultural intensification have negative consequences for biodiversity (Emmerson et al., 2016), as increased disturbance and chemical usage significantly reduces habitat quality and availability (Kruess and Tscharntke, 1994; Schweiger et al., 2005). The abandonment of traditional agriculture, in tandem with agricultural intensification, also has far-reaching ramifications.

Despite the fact that abandonment of dry-stone wall terraces has received relatively little attention, it has been shown to not only result in loss of food production potential, but also lead to substantial biodiversity declines due to habitat loss and reduced habitat quality (Kruess and Tscharntke, 1994; Uchida and Ushimaru, 2014). Unfortunately this phenomenon has not been studied extensively, particularly in the Mediterranean Basin, where agricultural terraces are not just widespread, but their abandonment represents an especially acute and rapidly worsening problem.

The Mediterranean is a biodiversity hotspot, and because many of the resident species have often small range sizes, they are at a higher risk of endangerment with increasing pressures of land use change and climate change (Newbold et al., 2020). Additionally, species with low abundance, such as those endemic to the Greek islands, as well as island endemics more broadly, are more susceptible to land use change (Suding et al., 2005). In the interest of preserving biodiversity in the Mediterranean, and in improving global conservation prioritization, this research aims at assessing the impacts of terrace abandonment by comparing actively used with partially and fully abandoned terraces on the island of Naxos, and more specifically, determine its effects on biodiversity.

Minimal prior research has assessed how terrace abandonment impacts ecosystem services, and most research on terrace abandonment focuses on the impacts on carbon sequestration, soil and water retention, as well as recreation (Garcia-Franco et al., 2014; He, 2010). While existing research supports the preservation of dry-stone wall terraces, there is also a need to better understand the implications of terrace abandonment on resident biodiversity. Furthermore, despite a number of mostly recent studies, it is clear that Mediterranean ecosystems have not been sufficiently studied, especially with regard to the ecology of endemic arthropods (Trihas and Legakis, 1991; Iatrou and Stamou, 1989; Kaltsas and Simaiakis, 2012). Whereas some literature exists on the abandonment impacts on biodiversity, such studies are limited to looking at impacts on individual species or individual trophic levels (Uchida and Ushimaru, 2014). Additionally, most studies on dry-stone wall terraces either study the positive impacts of active terraces, or the negative impacts of terrace abandonment, but do not compare active terraces to those which have been abandoned (Deng et al., 2021). In order to better understand the patterns associated with time since abandonment and build knowledge for potential efficient management strategies, we included sites with varying states of agricultural usage and abandonment in our study. Due to the high levels of terrace abandonment on Naxos, and the fact that the area is a biodiversity hotspot, it serves as an ideal location to evaluate the impacts of this type of land use change on various species microhabitats. Insights from this study can be applied to other regions of the world where terrace use is declining and provide insight as to how impacts of terrace abandonment on biodiversity may be exacerbated by climate change. The present study attempts to understand the implications of dry-stone wall terrace abandonment on biodiversity as well as understand the effects of terrace deterioration following abandonment on the Mediterranean environment. The study addresses the following questions:

(i) How does agricultural management status impact different types of biodiversity?

(ii) How does duration of abandonment affect different metrics of biodiversity, and are there different impacts on biodiversity comparing wall maintenance abandonment to plowing abandonment?

To answer these questions we compare a diversity of metrics across a group of dry-stone wall terraces ranging from fully abandoned terraces, terraces lacking wall maintenance, and active terraces, while accounting for confounding factors such as aspect, wall substrate composition, soil depth and slope. To quantify biodiversity we sampled arthropods, reptiles, insects and vegetation at each terrace site.

## 2. Methods

### *2.1 Study Area*

All fieldwork took place on the island of Naxos, (Cyclades, Aegean Sea, Greece) during the period of May-July 2022. The island is situated in the Mediterranean Basin, and belongs to a global biodiversity hotspot, with over 20,000 endemic plant species (CEPF 2017). Geologically, the island consists of a diversity of sedimentary rocks, mainly limestone and flysch (Vanderhaege et al., 2007). Much of the unplowed habitats in the Cyclades are covered by *phrygana*, a summer-deciduous, spinose, aromatic shrub community (Fielding and Turland, 2008). On the Cyclades, *phrygana* can be very species-rich (Fielding and Turland, 2008), and is typically dominated by tough cushion plants like *Genista acanthoclada, Coridothymus capitatus, Sarcopoterium spinosum, Cistus creticus* and *Erica manipuliflora*. Naxos has a Mediterranean climate; winters are mild and rainy, and summers are very arid and warm, with July and August being the hottest months (Theoharatos, 1978). Mean annual precipitation is approximately 360 mm (Nastos et al., 2010). The growing season on Naxos occurs in alignment with the rainfall distribution; germination of annuals, as well as re-growth of perennials commences typically after the first autumn rainfall (Sternberg et al., 2015).

### *2.2 Specific Study Sites*

We collected samples from 14 randomly selected study sites. However, to control for confounding factors and limit variability, we restricted site selection based on geologic substrate, type of agricultural use, and aspect. Specifically, study sites were included if walls were composed of limestone, the most common type of substrate on the island. To account for the effects of herbivory on vegetation structure, we only included sites which were subject to minimal or no livestock grazing. In addition, we selected sites with a broadly southern aspect (i.e., aspect ranging from SE to SW). Aspect was selected on the principle that south-facing slopes tend to be sunnier, drier, and likely to be more representative of typical future conditions as projected under warming climate scenarios (Alpert et al., 2002; Kitsara et al., 2021). Lastly, we selected sites which were intercropped with cereals, and without olive trees, as presence of such trees can have complex effects on ground vegetation cover. Management styles were consistent in that all actively plowed terraces were intercropped with various grains. These selection criteria helped to ensure sites were representative of typical conditions in the Cyclades today. Within each site, typically a field on a hillslope, we randomly selected 3 subsites, each consisting of a dry-stone wall, at least 20 m long, with an adjacent terrace. Photos were taken at each location, in addition to GPS point recordings, in order to visually and geographically document the terraces included in this study. Exact location of the study sites can be found in Figure 1.

### *2.3 Management Status and Age Delineation*

Given the patterns of field use observed previously on the island, we distinguished three distinct usage categories at increasing levels of agricultural disengagement: active agricultural use, plowing/no wall repair, and fully abandoned. Active status was assigned to sites where intercropped terraces with various grains were plowed annually, and where dry-stone walls were repaired following any type of damage. Plowing/no repair status was assigned to sites where intercropped terraces were actively being used for grain production, but where the dry-stone walls were not being repaired anymore. Typically, wall repair is abandoned due to the expensive labor cost, but grain harvest continues. Lastly, abandoned status was assigned to sites where all agricultural activity had ceased, the terraces were no longer used to grow crops, and the walls were not being repaired (see Figure 2). One important insight obtained early in this study was that site abandonment progressed in two predictable stages, in which first, wall repair was given up but terraces were still plowed, before eventually plowing and crop production were abandoned all together. Because wall repair is laborious and expensive, it is only done on terraces that generate income through agricultural production - indicating there were no sites where walls were repaired but agriculture was abandoned. Since effects of abandonment accrue over time, we also collected data on how long it had been since walls at a site were last repaired, and when terraces at each site were last plowed. This information was collected on site through community and landowner interviews, who had direct knowledge of the relevant usage history.

### *2.4 Wall Condition Measurements*

To obtain a comprehensive understanding of wall condition, we recorded multiple measurements along each dry-stone wall. First, a 20m long segment was selected randomly, and a transect was laid down along the length of that wall segment. Then, at every meter along the transect line, we collected binary data, (1/0), on presence of wall collapse. This was typically evidenced by rocks missing from the wall and having fallen into the terrace field below. These measurements of collapse were then used to calculate an average collapse percentage for each wall. In addition to the presence of damage, we also measured the maximum distance the rocks had fallen from the wall at each meter mark along the transect. This measurement was designated as the rubble distance. Considering that walls within and across sites had varying widths, rubble distance was measured starting at the edge of the wall closest to the adjacent field. To quantify the extent of loss of wall height, we also obtained multiple measurements of minimum and maximum height. To do so, we partitioned each wall into five equal 4m long segments. Within each segment the minimum height of the wall was recorded as well as the maximum height and the estimated maximum height. Estimated maximum height was collected in areas where rocks had fallen from the wall and the level of the terrace above indicated initial wall height. These height measurements were utilized to obtain an overall index score quantifying extent of wall disrepair. The Nossan Collapse Index (NCI) was established as a metric that comprehensively characterizes the overall condition of the wall. More specifically, the NCI is calculated using the following equation:

$$\text{NCI} = (\text{Minimum Wall Height}/\text{Estimated Maximum Wall Height}) \times 100$$

Possible NCI values range from 0-100, a higher value indicating better condition. We calculated NCI for each 4-meter segment using the associated wall heights, and then averaged the 5 NCI scores for each wall.

*2.5 Invertebrate Population Measurements*

To sample epigeous invertebrates, we placed two pitfall traps at each subsite (wall), one near, and one far from the wall. While the near pitfall trap was located within 30cm of the wall, the far pitfall trap was placed along the same perpendicular line away from the wall, but at a distance of 6 meters. Each pitfall trap was created by sinking a 475mL plastic cup into the soil to a depth of 10cm so that the top of the cup was flush with the soil surface. The traps were subsequently filled with approximately 100 ml of ethylene glycol (Woodcock, 2005; Schmidt et al., 2006), and partially covered with a flat rock which formed a raised lid above the cup opening. This elevated cover was resting on three smaller pebbles and prevented rain, stones, or soil from falling into the trap, all the while allowing invertebrates to crawl uninhibited into the trap (Gizicki et al., 2018). We retrieved the traps from each site after five days, and specimens were then rinsed with water before being stored in alcohol. Back in the lab, specimens from each trap were counted, and identified to morphospecies before being dried and weighed to obtain total biomass.

*2.6 Vertebrate Population Measurements*

To obtain reptile data at each subsite, we established one 20m transect line along each wall. Reptile presence was recorded along each transect by one of the authors, (HN), to reduce inter-observer variability (Donihue et al., 2015). Each transect was walked at a slow, consistent pace, and all reptiles detected within 3m distance on either side of the transect tape were counted. Reptile counts were conducted once at each wall during either morning or evening peak lizard activity periods (09.00 - 11.00 h, 17.00 - 19.00 h) and occurred during days of good weather (27-29C, sunny and trivial to no wind) (Donihue et al., 2015). We recorded both abundance of reptiles (i.e., number of individuals) as well as species detected.

*2.7 Habitat Measurements*

*Quantification of Vegetation*

Preliminary evidence on abandoned terraces suggested that vegetation characteristics (such as bush encroachment) varied based on distance from the wall, so we quantified vegetation characteristics in the context of distance relative to the nearest wall. As such, we sampled plant biomass and species richness at each subsite by recording species ID, and clipping all vegetation within two 60cm x 60cm squares (Gizicki et al., 2018), one close and one far from the wall. Thus, one square was placed close (30cm) to the wall, while the other square was placed far (6m) from the wall, along the same perpendicular line. To determine biomass, all vegetation within the square was clipped at ground level, collected and dried in direct sunlight outside in mesh bags until there was no weight loss, and then weighed using a spring-loaded balance (Pesola®).

Vegetation succession in the Cycladic *phrygana* is characterized by the invasion and progressive establishment of woody bushes at the expense of grasses and herbaceous annuals. To quantify the extent of bush encroachment we characterized the amount of woody perennials occurring at each of the study sites. Terraces were scored on a scale of 0 to 4, 0 being the complete absence of woody perennials, and 4 being fully overgrown (see Figure 3). Encroachment score for each subsite was determined independently by two researchers through a visual analysis.

*2.8 Statistical Analyses*

To determine the consequences of management status and age since abandonment (plowing and wall maintenance) on the condition of resident species communities, we compared 14 study sites across Naxos (see Figure 1). Because each site encompassed 3 individual subsites, each consisting of one focal study wall, a linear mixed effects model design was required for all analyses. For the various models created, each biodiversity metric was designated as a dependent variable, predicted by either age since abandonment or management status. Each model included either management status or age since abandonment as a fixed effect, site as a random effect, and distance as a covariate for relative vegetation and arthropod measures. Because distance was recorded at two constant measurements for all collected arthropod and vegetation data, it was included as a covariate in their associated models. All linear mixed models were run in R, utilizing the function '*lmer*' from the R package lme4 (Bates et al. 2015). When aggregated data are reported, mean values accompanied by SE are provided.

We selected a linear mixed effects model as the primary analysis mechanism to allow each specific study site to be incorporated as a random effect consistently among models, recognizing that data collected from walls located at the same site were more likely to have related data measurements. In order to ensure proper model selection, each mixed effects model was compared to a parallel null model, which was created by leaving out the fixed effect and then comparing the two models using the type II ANOVA function in R (CAR package v2.0-25). The comparisons using analysis of variance, provided us with AIC scores, Wald chi-square values for the fixed effect (either management status or abandonment age) and associated p values. For every comparative analysis, the linear mixed model with a lower AIC and a significant p value was selected to use in data interpretation. Tables 1 and 2 include ANOVA output of each linear model included in our study to aid in comprehension of fixed effect significance. In order to test for fit and model viability, residuals for each model were examined for linearity, normality, and homoscedasticity. Additionally, management status, age of plowing abandonment, and age of wall abandonment were utilized independently as fixed effects in separate mixed models. This was done to avoid multicollinearity as all three variables are highly correlated.

## 3. Results

*3.1 Effects of management status*

*Lizards*

We found significant differences in abundance and species richness among lizards inhabiting active, plowing/no repair and abandoned sites. Active sites had the highest lizard species richness and abundance. Management status significantly affected lizard species richness ($\chi^2(2) = 15.462$, $p = 0.0004$, $N = 42$). We found that active sites had the highest average species richness (2.33 ± 0.29 species/20m). Plowing/no repair sites had a significantly lower average species richness (1 ± 0.33 species/20m), and abandoned sites had the lowest average species richness (0.7 ± 0.31 species/20m) (see Figure 4). Similarly, in a parallel analysis using management status to predict lizard abundance, we found that status significantly affected lizard abundance ($\chi^2(2) = 11.598$, $p = 0.003$, $N = 42$). Mirroring species richness data we found that active sites had a significantly higher average lizard abundance (4.67 ± 0.76 indiv./20m). In contrast, plowing/no repair sites had lower abundances (2 ± 0.85, indiv./20m), while fully abandoned sites had the lowest averages (1.34 ± 0.80, indiv./20m) (see Figure 4).

*Arthropods*

Overall, we found significant differences in all measures of arthropod biodiversity among active, plowing/no repair and abandoned sites (see Figure 5). Status significantly affected arthropod abundance ($\chi^2(3) = 11.99$, $p = 0.007$, $N = 84$). Active sites had a significantly higher average arthropod abundance of individuals (83.47 ± 16.65 indiv., n = 84). Plowing/no repair sites had a lower average arthropod abundance (50.04 ± 18.15, indiv., n = 84), as did abandoned sites (26.96 ± 17.22, indiv., n = 84). This model also predicted that arthropods at a far distance had a higher average arthropod abundance (9.33 ± 0.80 indiv., n = 84). Management status significantly affected arthropod species richness ($\chi^2(3) = 22.09$, $p < 0.001$, $N = 84$). We found that active sites had a higher average arthropod species richness (12.7 ± 1.17 species, n = 84). Plowing/no repair sites had a lower average arthropod species richness (8.92 ± 1.26 species, n = 84), as did abandoned sites (6.29 ± 1.21 species, n = 84). This model also predicted that average arthropod species richness at a far distance is lower than at a close distance to the wall (0.25 ± 0.56, n = 84). Lastly, management status significantly affected arthropod biomass ($\chi^2(3) = 33.7$, $p < 0.0001$, $N = 84$). We found that active sites had a significantly higher average arthropod biomass (4.98 ± 0.43g, n = 84). Plowing/no repair sites had a lower average arthropod biomass of (0.71 ± 0.47g, n = 84), as did abandoned sites (0.46 ± 0.45g, n = 84). This model also predicted a lower average arthropod biomass at a far distance (0.29 ± 0.17g, n =84).

*Vegetation*

The linear mixed model we ran using management status and distance to predict vegetation biomass was significant, as indicated in Table 1. However, this can mainly be attributed to the significance of distance as a covariate. Our model predicted that average vegetation biomass at a far distance (5 meters) is significantly lower (249.22 ± 73.71 $g/m^2$, n = 84). With regard to management status, we found that active sites had an average vegetation biomass of 567.20 ± 222.9 $g/m^2$. Status affected vegetation biomass variably ($\chi^2(3) = 12.89$, $p = 0.005$, $N = 84$). Plowing/no repair sites had a lower average vegetation biomass (453.66 ± 245.78 $g/m^2$, n = 84), whereas abandoned sites had a higher average vegetation biomass (669.51 ± 233.16 $g/m^2$, n = 84), although neither were significant. Our model using status and distance to predict vegetation species richness, did yield significant differences among different management categories (Figure 6). Status significantly affected vegetation species richness ($\chi^2(3) = 25.99$, $p < 0.0001$, $N = 84$). We found that active sites had the highest average vegetation species richness (10.86 ± 0.9 species, n = 84). Plowing/no repair sites had a lower average vegetation species richness (4.44 ± 0.99 species, n = 84), as did abandoned sites (4.82 ± 0.94 species, n = 84). This model also predicted that average vegetation species richness at a far distance is lower than what was found at a close distance (1.05 ± 0.388 species, n = 84).

*3.2 Effects of Age since Plowing and Wall Abandonment*

*Lizards*

Both the age of plowing abandonment and age of wall repair abandonment were positively related to significant declines in lizard abundance. Our model including age of wall repair abandonment revealed a slightly higher rate of decline in lizard abundance. Age of wall maintenance abandonment significantly affected lizard abundance ($\chi^2(1) = 11.22$, $p = 0.001$, $N = 42$), lowering the number of lizards by 0.016 ± 0.004 individuals (Figure 7a) with each passing year since wall maintenance abandonment. Age of plowing abandonment significantly affected lizard abundance ($\chi^2(1) = 8.532$, $p = 0.004$, $N = 42$), lowering the number of lizards by 0.014 ± 0.004 individuals (Figure 7c) with each passing year since abandonment.

Similarly, both the age of plowing abandonment and age of wall repair abandonment were positively related to significant declines in lizard species richness. And again, wall repair abandonment revealed slightly a higher rate of decline in lizard species richness Age of plowing abandonment significantly affected lizard species richness ($\chi^2(1) = 7.57$, $p = 0.006$, $N = 42$), with the number of species declining by 0.006 ± 0.002 with each passing year since plowing abandonment (Figure 7d). Age of wall maintenance abandonment also significantly related to lizard species richness ($\chi^2(1) = 10.57$, $p = 0.001$, $N = 42$), lowering the number of species by 0.007 ± 0.002 with each increasing year since wall maintenance abandonment (Figure 7b).

*Arthropods*

Both the age of plowing abandonment and age of wall repair abandonment were positively related to declines in arthropod abundance, however, only the age of wall repair abandonment revealed significant declines in abundance. Age of plowing abandonment affected arthropod abundance ($\chi^2(2) = 5.25$, $p = 0.07$, $n = 84$), lowering the number of arthropods by 0.19 ± 0.095 individuals (Figure 8c) with each increasing year since plowing abandonment. This model also predicted that at age zero arthropod abundance at a far distance has an average of 17.04 ± 8.88 more individuals. Age of wall maintenance abandonment affected arthropod abundance ($\chi^2(2) = 7.502$, $p = 0.024$, $N = 84$), lowering the number of individuals by 0.26 ± 0.095 (Figure 8d) with each increasing year since wall maintenance abandonment. This model also predicted that at age zero arthropod abundance at a far distance has an average of 8.96 ± 6.89 more individuals.

Both the age of plowing abandonment and age of wall repair abandonment were positively related to declines in arthropod species richness, however, only the age of plowing abandonment revealed significant declines in species richness. Age of plowing abandonment affected arthropod species richness ($\chi^2(2) = 6.33$, $p = 0.042$, $N = 84$), lowering the number of species by 0.022 ± 0.007 (Figure 8e) with each increasing year since plowing abandonment. This model also predicted that at age zero, arthropod species richness at a far distance is an average of 0.3 ± 0.58 species fewer. Age of wall maintenance abandonment affected arthropod species richness ($\chi^2(2) = 2.137$, $p = 0.345$, $N = 84$), lowering the number of species by 0.014 ± 0.01

(Figure 8f) with each increasing year since wall maintenance abandonment. This model also predicted that at age zero arthropod species richness at a far distance is an average of 0.28 ± 0.58 species fewer.

Both the age of plowing abandonment and age of wall repair abandonment were positively related to declines in arthropod biomass, however neither model was significant. Age of plowing abandonment affected arthropod biomass ($\chi^2(2) = 3.229$, $p = 0.199$, $N = 84$), reducing their mass by 0.004 ± 0.005 g (Figure 8a) with each increasing year since plowing abandonment. This model also predicted that arthropod biomass at a far distance is an average of 0.29 ± 0.169 g greater. Age of wall maintenance abandonment affected arthropod biomass ($\chi^2(2) = 4.225$, $p = 0.121$, $N = 84$), reducing their mass by 0.007 ± 0.006 g (Figure 8a) with each increasing year since wall maintenance abandonment. This model also predicted that arthropod biomass at a far distance is an average of 0.29 ± 0.169 g greater.

*Vegetation*

Both the age of plowing abandonment and age of wall repair abandonment were positively related to declines in vegetation species richness with increasing time since abandonment. Age of plowing abandonment affected vegetation species richness ($\chi^2(2) = 7.653$, $p = 0.022$, $N = 84$), reducing the number of species by 0.008 ± 0.01 species (Figure 9c) with each increasing year since plowing abandonment. This model also predicted that vegetation species richness at a far distance is an average of 1.1 ± 0.387 lower. Age of wall maintenance abandonment affected vegetation species richness ($\chi^2(2) = 10.776$, $p = 0.005$, $N = 84$), lowering the number of species by 0.02 ± 0.01 (Figure 9d) with each increasing year since wall maintenance abandonment. This model also predicted that vegetation species richness at a far distance is an average of 1.1 ± 0.387 fewer.

Both the age of plowing abandonment and age of wall repair abandonment were positively related to increases in vegetation biomass. Age of plowing abandonment affected vegetation biomass ($\chi^2(2) = 10.861$, $p = 0.004$, $N = 84$), increasing mass by 0.7 ± 1.203 $g/m^2$ (Figure 9a) with each increasing year since plowing abandonment. This model also predicted that vegetation biomass at a far distance is an average of 249.22 ± 73.714 $g/m^2$ lower. Age of wall maintenance abandonment affected vegetation biomass ($\chi^2(2) = 10.776$, $p = 0.0046$, $N = 84$), increasing mass by 0.65 ± 1.305 $g/m^2$ (Figure 9b) with each increasing year since wall maintenance abandonment. This model also predicted that vegetation biomass at a far distance is an average of 249.217 ± 73.714 $g/m^2$ lower.

*Bush Encroachment*

Results from the linear mixed model using age of plowing abandonment to predict bush encroachment reveal significant increases in stage of bush encroachment with increasing time since abandonment. When using age of plowing abandonment to predict stage of bush encroachment we found that at age zero, when sites had not yet been abandoned, they had an average score of 0.98 out of 4 (SE = ± 0.409, n = 42). Age of plowing abandonment affected bush encroachment ($\chi^2(1) = 6.4202$, $p = 0.011$, $N = 42$), increasing score by 0.017 (Figure 10) with each increasing year since abandonment (SE = ± 0.006, n = 42).

## 4. Discussion

In this study we investigate the role of dry-stone wall terraces, a ubiquitous component of traditional agriculture in the Mediterranean Basin on resident biodiversity. Overall, our results reveal multiple significant relationships between the progression of abandonment and measurements of biodiversity. All analyses indicate a strong dependence of local plant and animal taxa on the presence of dry-stone wall terraces, and a decline in biodiversity with progressing stages of agricultural abandonment.

Both lizard abundance and lizard species richness declined significantly as an area became progressively abandoned. We found that lizard abundance and lizard species richness depend not just on the presence but also on the condition of the walls, and decline significantly with increasing time since plowing abandonment, as well as with increasing time since wall maintenance abandonment. Although both age of plowing abandonment and age of wall maintenance abandonment predicted declines in lizard biodiversity, age of wall maintenance abandonment resulted in higher rates of decline, which relates to the importance of these human constructed walls as a habitat to provide refuge from predators and a suitable location for thermoregulation (Van Damme et al., 1989; Martín and López, 1999). The lack of maintenance which results from agricultural abandonment reduces habitat suitability for lizard species because the availability of crevices to retreat to gets significantly reduced with time since abandonment. Because most dry-stone walls are created without any kind of binding agent (UNESCO, 2003), intense weather events, which are increasing in frequency, can have a severe negative effect on the rate of deterioration (Piervitali et al., 1998; Romero et al., 1998). As mentioned in our methods, sites were selected for sampling on the premise that walls were composed of limestone. Limestone is a porous substrate type that experiences decay and blistering as a result of calcite dissolution and granular disintegration (Robinson and Moses, 2002; Török, 2002; Sass and Viles, 2010). Therefore, when rocks toward the bottom of the wall begin to disintegrate, they impact the rocks on either side and above them, causing many to fall out of place and off the wall, as evidenced from many of the sites we sampled.

This reduction in habitat availability has potentially severe consequences for lizard populations. Previous research has found that among multiple species of lizards, microhabitat selection has a strong influence on morphological adaptations, allowing species to become more specialized in habitat navigation (Calsbeek and Irschick; Kohlsdorf and Navas, 2007; Revell et al., 2007). Further research has been conducted specifically on the morphological adaptations of *Podarcis erhardii*, a common species found in the Aegean and in our study, based on differences in microhabitat selection of areas with human constructed walls versus areas devoid of any walls (Donihue, 2016). This study indicates significant morphological and behavioral adaptations in Aegean Wall lizards based on occupied microhabitat. For example, lizards found at sites with dry-stone walls displayed more sit-and-wait hunting strategies, as opposed to active searching foraging behavior (Donihue, 2016). These findings, paired with the results from our study suggest potentially serious consequences for lizard survivability with the continuation of agricultural abandonment. Lizards that have foraging adaptations specialized for dry-stone wall microhabitats may struggle to forage as habitat availability declines, following increased incidence of terrace abandonment.

Similarly to lizards, arthropod abundance, species richness and biomass significantly declined as terrace status progressed from active to plowing/no repair, and then to abandoned. Although our models using age since abandonment (for both plowing and wall maintenance) did not yield significant relationships with any arthropod measurements, there were strong trends indicating a decline in arthropod biodiversity with increasing age since abandonment. One possible explanation for this is the reduction in soil water infiltration and storage which occurs following agricultural terrace abandonment. Water storage capacity diminishes with agricultural abandonment, as the erosion process leads to a significantly increased runoff coefficient and increased erosion (Koulouri and Giourga, 2007; Schönbrodt-Stitt et al., 2013). As previously stated, water retention is critical in Mediterranean climates which experience long summer droughts and minimal annual rainfall (Blondel et al., 2010; Theoharatos, 1978; Nastos et al., 2010), especially for arthropods which grow much slower when depending on plants under drought stress (Pérez-Fuertes et al., 2015; Pons and Tatchell, 1995).

Although not significant, our results indicated a notable decline in vegetation species richness, going from active to plowed without wall maintenance and fully abandoned sites. We also found a trending negative relationship between vegetation species richness and time since abandonment, for both plowing and maintenance abandonment, showing that vegetation species richness declined with age since abandonment. While many plant species native to this area have adaptations which allow them to survive in dry conditions, the availability of moist soil provides suitable habitat for a wider array of plant species and increases landscape heterogeneity. (Arévalo et al., 2016) Previous research shows presence of a bottom-up effect in Mediterranean agricultural systems, with increased water availability increasing vegetation species richness, which then increases resource availability for herbivores and their predators.

Vegetation biomass did not have any significant relationships to measurements of abandonment. However, there was a moderate positive trend showing increased vegetation biomass with increased time since abandonment, for both plowing and wall maintenance (Figures 9a, b). We also found there to be significantly reduced biomass at a farther distance from the wall. Both of these results align with our finding that bush encroachment increases significantly with increased time since plowing abandonment. *Phrygana,* as previously mentioned, are woody shrubs which are abundant in the Cycladic region, and absorb a significant amount of water and resources (Fielding and Turland, 2008). This likely explains the reduction in overall floral biodiversity with increasing time since abandonment, as woody perennials tend to outcompete most other herbaceous species. Because bush encroachment usually begins and is more pronounced at the base of the collapsed wall, this is likely why we found reduced biomass and species at a father distance from the wall (see Figures 9a, b, c, d).

As climatic conditions worsen and total annual rainfall continues to decline, the provision of maintained terraced hillsides, as areas which have significantly higher soil moisture retention and water storage capacities compared to areas without, will increase in significance (Feng et al., 2017; Kosmowski, 2018). Dry-stone walls increase water absorption in their below terraced fields by reducing hydrological connectivity, as the terrace intercepts the slope providing a flat surface for water to infiltrate (Gibson et al., 2018; Schilling and Jacobson, 2016). This increased water absorption produces better soil conditions resulting in more prosperous crop and vegetation growth (Duran Zuazo et al., 2019; Wang et al., 2019).

Several countries that have begun the process of terrace rehabilitation actions in order to preserve their cultural, sustainable and ecosystem services. (Bertolino and Corrado 2021; Bevan et al., 2013; Riccioli et al., 2011). The practice of cultivation on dry-stone wall terraces encourages a sense of community in rural agricultural areas, and preserves local tradition (Bertolino and Corrado 2021; Riccioli et al., 2011). From a hydrogeological standpoint, these terraces also help to prevent landslides and floods, and combat both erosion and desertification of the area (Bertolino and Corrado 2021). It is critical to note the role of these dry-stone wall terraces in the prevention of flooding, as climate change is leading to progressive increases in extreme rain events (Alpert et al., 2002). In the Mediterranean Basin, with the heavily documented trends of decreased total rainfall, increased annual temperatures, and increased incidence of extreme rain events, the preservation of dry-stone wall terraces presents itself as a critical mechanism to retain not only the cultural identity of the local area, but also the microhabitats of threatened species (Piervitali et al., 1998; Romero et al., 1998; Kadioglu et al., 1999). In alignment with our findings, other research on terrace abandonment in other countries has shown that as time since abandonment increases, these ecological benefits decline (Gallart et al., 1993).

In summary, we conclude that dry-stone wall terrace maintenance and preservation should be a main priority in the planning of biodiversity conservation in traditional Mediterranean agricultural systems. Dry-stone wall terraces are representative of how civilizations today and thousands of years ago have made the most effective use of their surroundings in a way that both benefited themselves and the environment (UNESCO - Intangible Cultural Heritage 2003). The results of this study, paired with the cultural significance of these structures emphasize the significance of their preservation. While the traditional act of dry-stone wall terracing with active maintenance has a multitude of positive impacts such as increased biodiversity, increased soil nutrient availability, reduced erosion risk, landscape heterogeneity, and others, the opposite is true with the abandonment of this form of agriculture. The process of abandonment has demonstrated negative impacts on biodiversity across multiple trophic levels included in our study. In a region that hosts a significant amount of endemic species and will continue to be heavily impacted by climate change, the preservation of ecosystems with demonstrated high levels of biodiversity, which decline significantly with land use change, should be prioritized in conservation efforts.

**Acknowledgements**

All field research described in our study was conducted with permission from private landowners and Naxian shepherds. This work was supported by the Program for Environment and Sustainability, Rackham Graduate School, University of Michigan International Institute, and the Modern Greek Department, who provided funding allowing us to conduct research on Naxos. I especially would like to thank fellow researchers and lab mates, Angelina Kossoff, and Ian Slack, for their unwavering support and motivation in the lab and in the field. We would also like to thank Jessica Villarel, Daly Kleaveland, Sagarika Kaushik and Nathan Michielsen for their assistance with field data collection.

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**Effects of Management Status on Biological Indicators**

| | *N* | $\chi^2$ | *df* | *p* |
|---|---|---|---|---|
| *Model (a): ~ Status \| Site* | | | | |
| Lizard Abundance | 42 | 11.598 | 2 | 0.003* |
| Lizard Species Richness | 42 | 15.462 | 2 | 0.0004* |
| *Model (b): ~ Status + Distance \| Site* | | | | |
| Arthropod Abundance | 84 | 11.99 | 3 | 0.007* |
| Arthropod Species Richness | 84 | 22.09 | 3 | < 0.0001* |
| Arthropod Biomass | 84 | 33.702 | 3 | < 0.0001* |
| Vegetation Species Richness | 84 | 25.99 | 3 | < 0.0001* |
| Vegetation Biomass | 84 | 12.89 | 3 | 0.005* |

**Table 1**. Results of two analyses testing for differences between active, plowing/no repair and abandoned sites in terms of various biological indicators. For arthropod abundance, arthropod species richness, arthropod biomass, vegetation species richness, and vegetation biomass the mixed models used include site status as well as the effects of distance away from the wall. Because all lizard metrics (lizard abundance, lizard species richness) were measured on the wall only, no distance effect is included. N indicates number of samples collected. An asterisk (*) indicates significance at the $p < 0.05$ level

## Effects of Abandonment Age on Biological Indicators

| | Plowing Abandonment | | | | | Wall Maintenance Abandonment | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *N* | $\chi^2$ | *df* | *p* | | *N* | $\chi^2$ | *df* | *p* |
| *Model (c): ~ Age Pl. \| Site* | | | | | *Model (e): ~ Age Mt. \| Site* | | | | |
| Lizard Abundance | 42 | 8.532 | 1 | 0.004* | Lizard Abundance | 42 | 11.22 | 1 | 0.001* |
| Lizard Species Richness | 42 | 7.57 | 1 | 0.006* | Lizard Species Richness | 42 | 10.57 | 1 | 0.001* |
| *Model (d): ~ Age Pl. + Distance \| Site* | | | | | *Model (f): ~ Age Mt. + Distance \| Site* | | | | |
| Arthropod Abundance | 84 | 5.25 | 2 | 0.07 | Arthropod Abundance | 84 | 7.503 | 2 | 0.024* |
| Arthropod Species Richness | 84 | 6.33 | 2 | 0.042 | Arthropod Species Richness | 84 | 2.137 | 2 | 0.345 |
| Arthropod Biomass | 84 | 3.229 | 2 | 0.199 | Arthropod Biomass | 84 | 4.225 | 2 | 0.121 |
| Vegetation Species Richness | 84 | 7.653 | 2 | 0.022* | Vegetation Species Richness | 84 | 10.776 | 2 | 0.005* |
| Vegetation Biomass | 84 | 10.86 | 2 | 0.004* | Vegetation Biomass | 84 | 10.776 | 2 | 0.0046* |

**Table 2.** Results of four analyses testing for the effects of duration of two different activities (duration of plowing abandonment - Left, and duration of wall maintenance abandonment - Right) on several key biological indicators. For arthropod abundance, arthropod species richness, arthropod biomass, vegetation species richness, and vegetation biomass the mixed models (Models *(d), (f)*) used include age of abandonment of plowing/wall repair, as well as the effects of distance away from the wall. Because all lizard metrics (lizard abundance, lizard species richness; Models *(c), (e)*), were measured on the wall only, no distance effect is included. N indicates number of samples collected. An asterisk (*) indicates significance of the predictor variable (age since last plowed or age since last wall maintenance) in predicting differences at the $p < 0.05$ level.

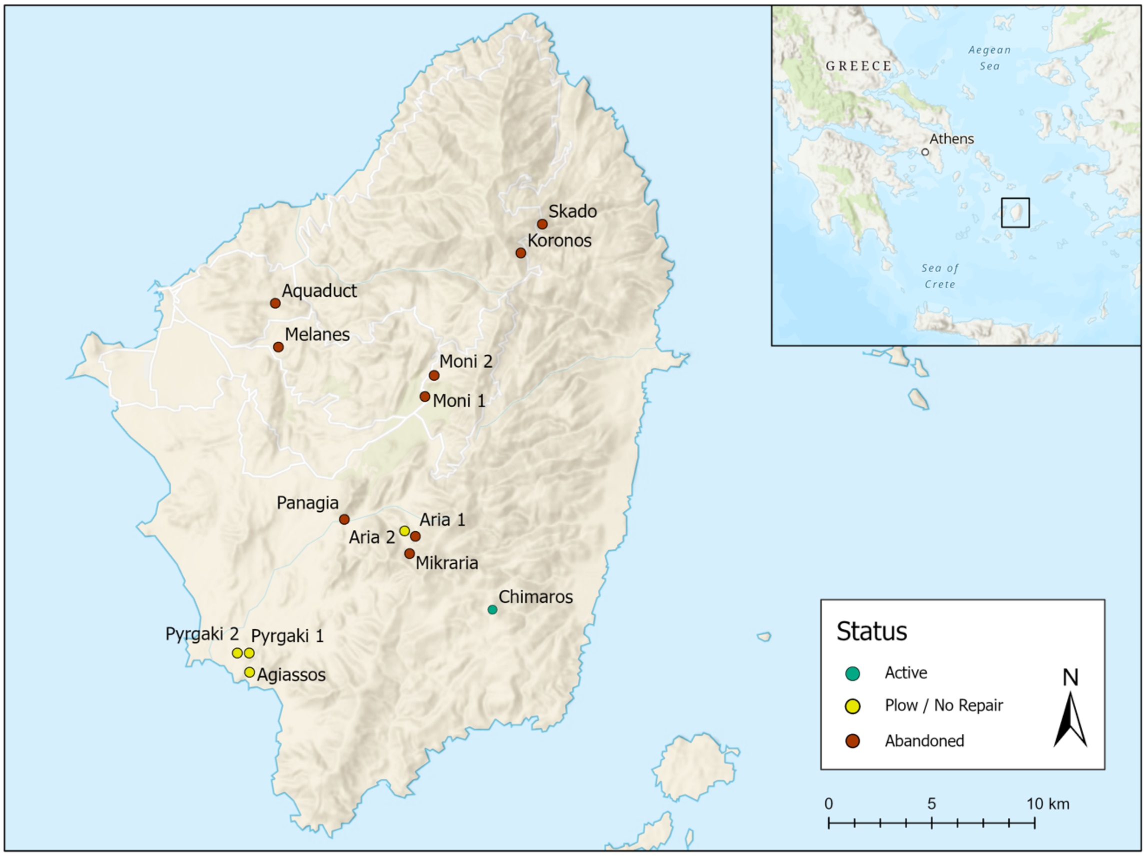


**Figure 1.** Map of the study locations on the island of Naxos (Cyclades, Aegean Sea, Greece). The inset map depicts the exact location of Naxos in the broader Mediterranean region. The approximate location of each site and its activity status are indicated by color in the inset legend. Specific study site coordinates are provided in in Appendix 1.

**Figure 2.** Examples of terrace activity status on Naxos. From left to right: Active, Plowing/No repair, Abandoned.

**Figure 3.** Stages of bush encroachment on the study sites on Naxos. Left: No bush encroachment (Score 0); Middle: Early/limited bush encroachment (Score 2); Right: Advanced/widespread bush encroachment (Score 4).

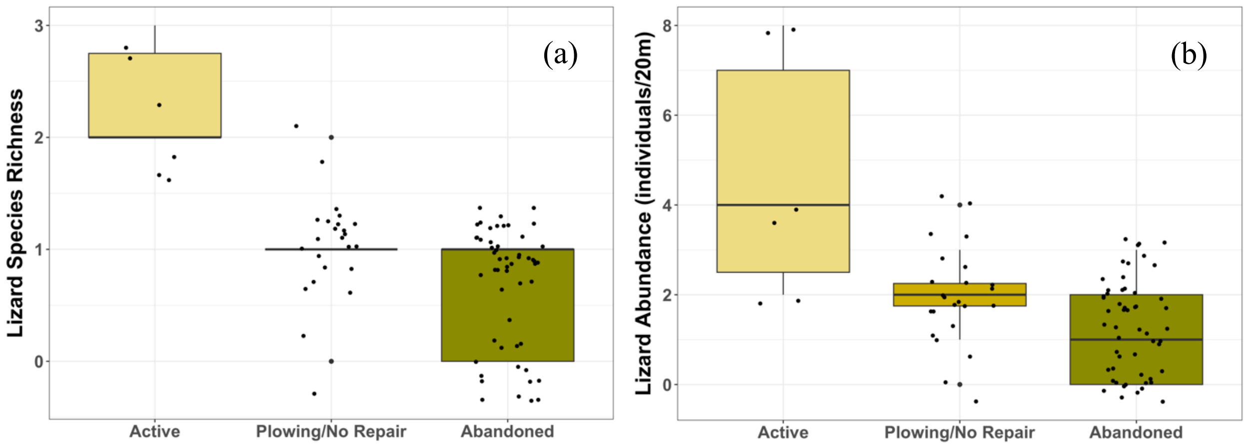


**Figure 4.** Distribution of lizard species richness (a), and lizard abundance by activity status (b).

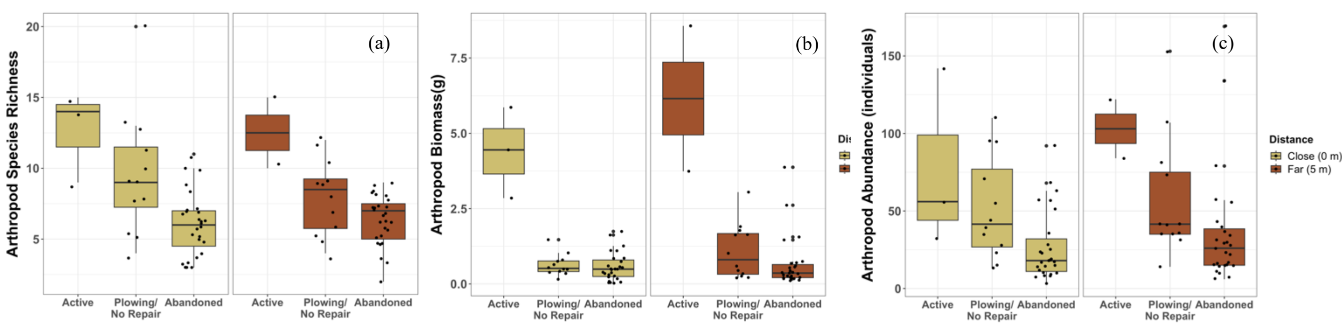


**Figure 5.** Distribution of arthropod species richness (a), arthropod biomass (b), and arthropod abundance (c), by site activity status and distance. Left (tan) panel in each pair shows data close to the walls, while Right (brown) panel shows data away from the walls.

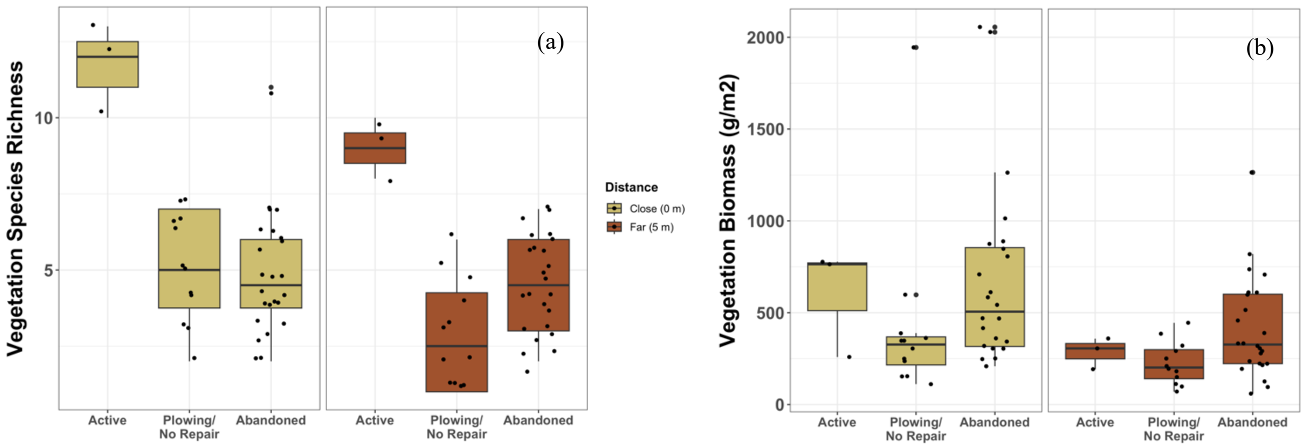


**Figure 6.** Distribution of vegetation species richness (a), and vegetation biomass (b), by activity status and distance. Left panels (tan) show data close to the walls, while Right panels show data away from the walls.

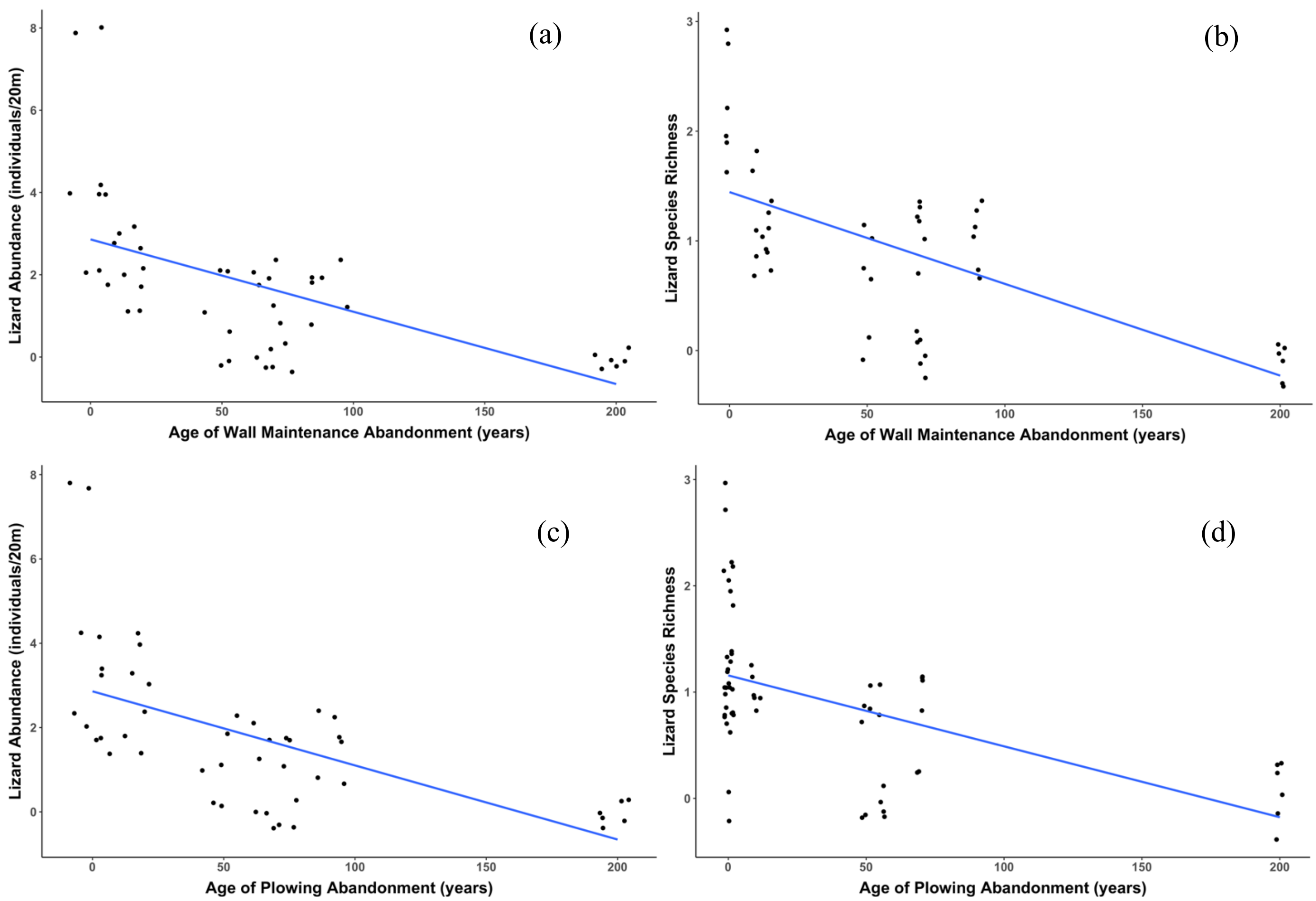


**Figure 7.** Effects of duration of agricultural abandonment on vertebrate populations. Top row: Lizard abundance (a) and lizard species richness (b) versus duration of wall maintenance abandonment. Bottom row: Lizard abundance (c) and lizard species richness (d) versus duration of plowing abandonment.

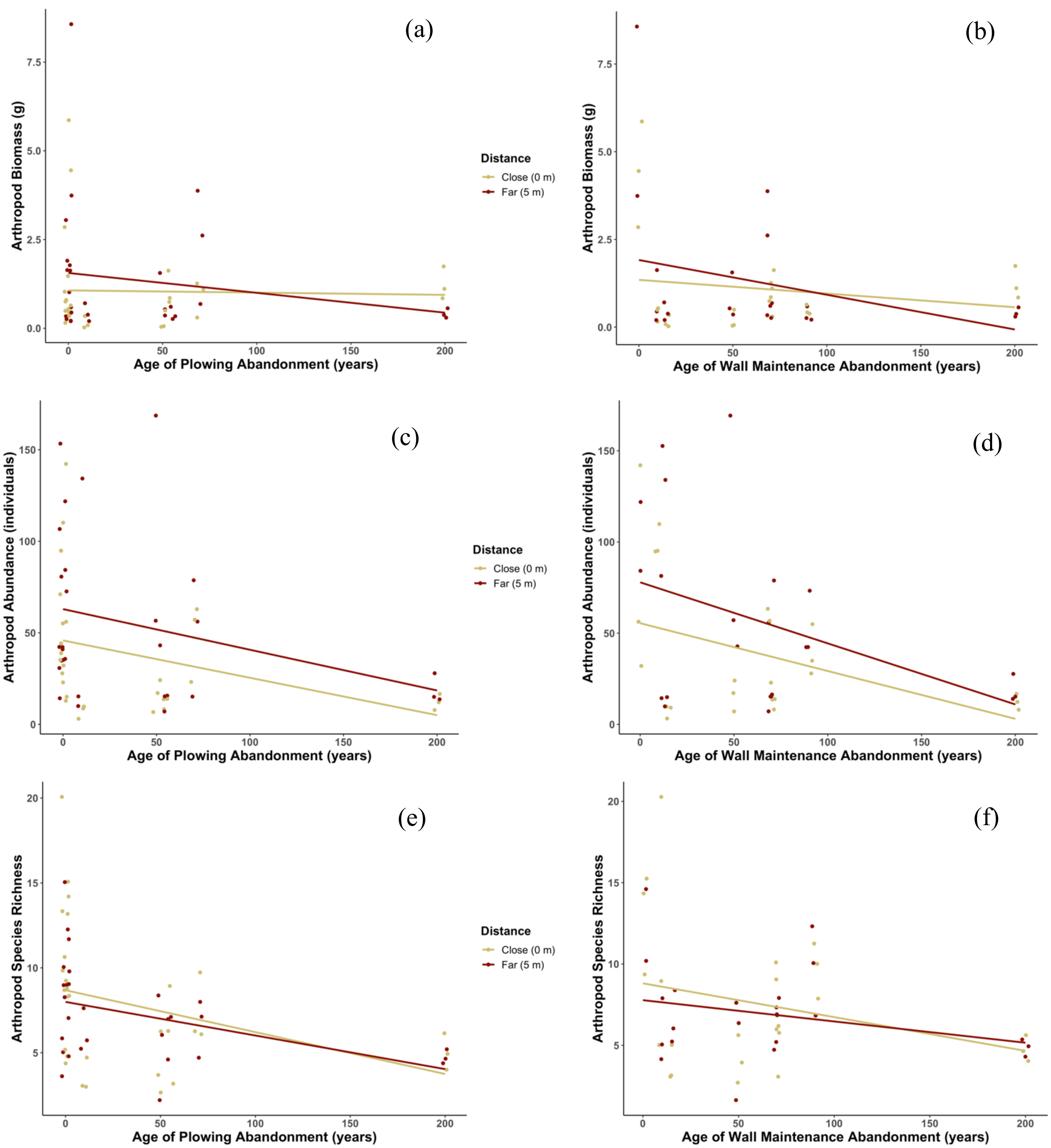


**Figure 8.** Effects of duration of agricultural abandonment on invertebrate populations. (a) Arthropod biomass versus age of plowing abandonment. (b) Arthropod biomass versus age of wall maintenance abandonment. (c) Arthropod abundance versus age of plowing abandonment. (d) Arthropod abundance versus age of wall maintenance abandonment. (e) Arthropod species richness versus age of plowing abandonment. (f) Arthropod species richness versus age of wall maintenance abandonment.

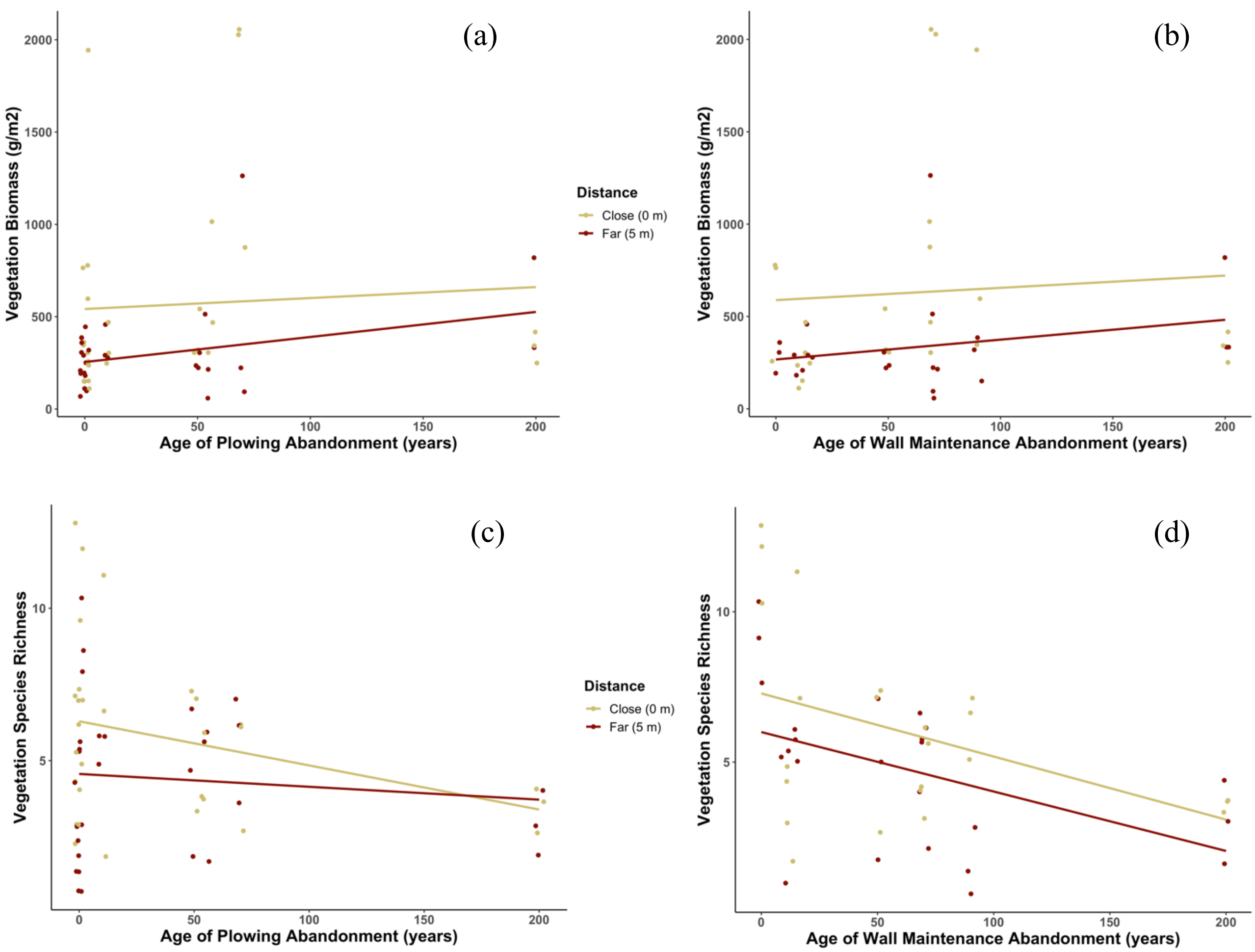


**Figure 9.** Effects of duration of agricultural abandonment on vegetation characteristics. (a) Vegetation biomass versus age of plowing abandonment. (b) Vegetation biomass versus age of wall maintenance abandonment. (c) Vegetation species richness versus age of plowing abandonment. (d) Vegetation species richness versus age of wall maintenance abandonment.

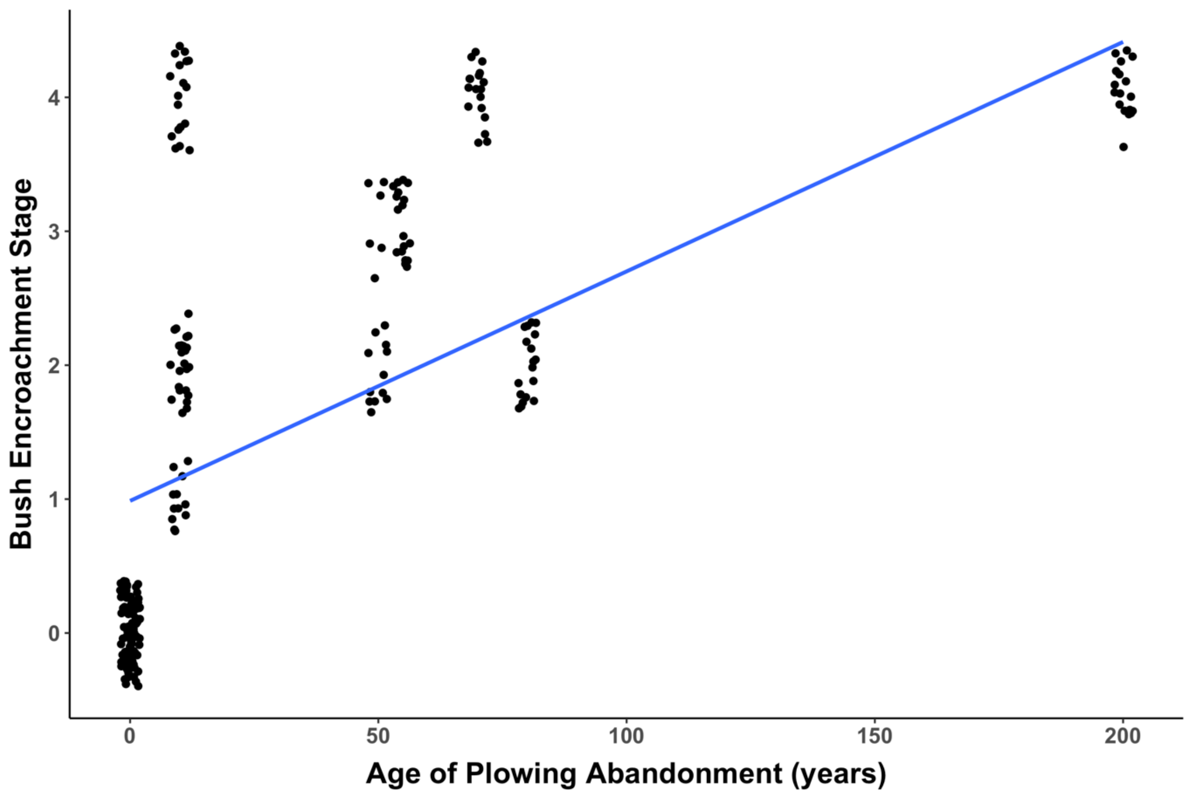


**Figure 10**. Bush encroachment state versus age of plowing abandonment.

| Site | Activity Status | Latitude | Longitude |
|---|---|---|---|
| Agiassos | Plowing/No Repair | 36.97443’ N | 25.41327’ E |
| Aquaduct | Abandoned | 37.10269’ N | 25.42459’ E |
| Aria 1 | Abandoned | 37.02251’ N | 25.4833’ E |
| Aria 2 | Plowing/No Repair | 37.023538’ N | 25.480992’ E |
| Chimaros | Active | 36.9962’ N | 25.51917’ E |
| Koronos | Abandoned | 37.120196’ N | 25.531666’ E |
| Melanes | Abandoned | 37.087513’ N | 25.425888’ E |
| Mikraria | Abandoned | 37.015708’ N | 25.483043’ E |
| Moni 1 | Abandoned | 37.07034’ N | 25.48974’ E |
| Moni 2 | Abandoned | 37.077603’ N | 25.493787’ E |
| Panagia | Abandoned | 37.02761’ N | 25.4546’ E |
| Pyrgaki 1 | Plowing/No Repair | 36.98126’ N | 25.40726’ E |
| Pyrgaki 2 | Plowing/No Repair | 36.981068’ N | 25.407996’ E |
| Skado | Abandoned | 37.130271’ N | 25.540933’ E |

**Appendix 1.** Coordinates of the 14 study sites on Naxos and their activity status.