

Ecological impacts of invasive rat removal on Mediterranean Sea islands

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Abstract

Travel and trade activities have caused the worldwide spread of invasive species possibly resulting in ecological disruption. Rats (*Rattus spp.*) are one of the most widespread invasive species as their broad diet allows them to take advantage of various food sources. On island ecosystems, rats are thought to increase predation pressure on native flora and fauna, compete with native species for resources, and alter island characteristics such as nutrient availability. Rat eradication projects are becoming a common means to restore island communities; however, management is labor intensive and expensive. This makes it critical that eradication efforts are studied to determine effectiveness and target sites for management.

This project evaluates the short-term impact of rat eradication on 15 islands supporting rats in the Aegean Sea (Greece): seven control and eight treatment sites. On each site, I collected baseline data on all levels of the islands food-web: vegetation biomass, invertebrate biomass and diversity, lizard density, and seabird abundance. Rats were then eradicated from all treatment islands using Brodifacoum baits. The same set of ecological data were collected one year following rat removal and changes were compared using control islands to correct for annual variation.

I found minimal changes in ecosystem condition following rat removal. I speculate that sites with a long period of rat colonization have lost species susceptible to rats and do not rapidly respond to eradication. Most study sites likely supported rats for many years. However, one treatment site was colonized by rats for only one year. This site shows a higher degree of positive change when compared to averages for control sites and other eradication islands. While more research is needed, it is possible that species vulnerable to rats persist on sites with a short period of rat colonization allowing for a quick recovery following eradication. It is also possible that, in the Aegean, one year is insufficient time for sites to respond to eradication.

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Introduction

Human activities have resulted in the intentional or unintentional introduction of numerous species outside of their natural ranges. In situations where these species become established in new habitats, they have the potential to alter ecosystems through increased competition with and predation on native taxa. Such invasive species are considered by the International Union for the Conservation of Nature (IUCN) to be a threat to multiple taxa around the world (Hilton-Taylor, 2009). However, overall effects on biodiversity are unclear and possibly dependent on the scale at which impacts are considered as invasive species have been found to decrease, increase, or have no effect on biodiversity (Murphy and Romanuk, 2014; Sax et al., 2002; Sax, 2003; Vellend et al., 2013).

Rats (*Rattus spp.*) are thought to be one of the most widespread exotic mammals. The spread of rats to new habitats, particularly isolated islands, dates back at least 3,000 years and has often been the result of shipping activities (Atkinson, 1985). Today, rats are found on over 80% of the world's major islands and island groups (Atkinson, 1985).

Rats have a broad diet allowing for the avoidance of density-dependent feedbacks with the decline of any one prey species (Atkinson, 1985; St. Clair, 2011). Rats have been found to feed on vegetation roots, leaves, bark, fruit, and seed (Allen et al., 1994; Shiels and Drake, 2011). Rats are also known to utilize invertebrate populations such as arthropods and terrestrial mollusks as a prey source (Cole et al., 2000; Lydeard et al., 2004). Furthermore, direct predation and competition for invertebrate prey sources is thought to have bottom-up impacts on the rest of the food-web affecting species such as resident reptiles (McCallum, 1986; Gasc et al., 2010).

On islands in particular, rats are believed to be one of the primary threats to nesting seabirds (Croxall et al., 2012). Rats have been found to prey on seabird eggs, chicks, and even adults (Jones et al., 2008). Their widespread occurrence in seabird breeding habitat makes them a likely contributor to the observed decline in seabird

populations (Jones et al., 2008). Decline of seabird colonies may have secondary effects on the rest of the island ecosystem as the birds import nutrients in the form of guano, fish scraps, and carcasses from the sea to the terrestrial environment (Fukami et al., 2006; Mulder et al. 2009). For instance, in a study on 11 islands in the Gulf of California, it was found that islands receiving guano input generally exhibited higher nutrient levels and greater plant productivity than sites without seabirds (Wait et al., 2003).

To deal with the conservation issues presented by invasive rodents, government agencies as well as non-governmental organizations are beginning to initiate eradication programs. However, eradication is both expensive and labor-intensive with cost and effort dependent on the size of the eradication site, mitigation required to protect non-target species, eradication method, site accessibility, and local regulations (Howald et al., 2007).

Furthermore, uncertainties remain with regard to the management of invasive species. For example, on seabird dominated islands, it is unclear if removing rats from a site where the colony has collapsed will result in the return of seabirds and subsequent restoration of the ecosystem (Mulder et al., 2009). It is also possible that the species composition of sites with longstanding invasions may shift towards taxa which are less affected by a particular invasive (Strayer et al., 2006). As a result, removing rats could only have limited effects especially on islands where rats have already caused susceptible native taxa to become locally extinct. This makes it necessary to monitor ongoing rat control efforts to assess ecological effects and determine the best use of management dollars.

In the past, many rat eradication monitoring efforts have focused on a single species of conservation concern or component of the island system rather than on entire ecosystem effects (Whitworth et al., 2005; St. Clair et al., 2011; Allen et al., 1994). Studies also tend to assess rat and eradication impacts by comparing sites of varying rat status such as those where rats have been removed with rat-free and invaded

sites rather than conducting before-and-after evaluations (St. Clair et al., 2011; Fukami et al., 2006).

The current project is designed to take advantage of a current large scale rat eradication operation to assess all levels of the island food-web on multiple islands before and one year after rat removal. Data will be compared across several treatment islands before and after rat eradication while using control sites to correct for annual variation. I predict that after rat eradication, increases will be visible throughout the island food-web as a result of a lack of rat predation on primary producers, primary consumers, and secondary consumers. Bottom up effects may also contribute to such increases as a lack of rat predation on plant matter will result in an increase in vegetation biomass leading to greater invertebrate biomass and lizard density. Furthermore, I predict that the lack of rat predation pressure on nesting seabirds after eradication will result in greater seabird abundance. This may restore the transfer of nutrients from the marine environment to the terrestrial island system. This increase in nutrient availability could then result in further increases in vegetation productivity reinforcing bottom-up effects on the food-web (Figure 1).

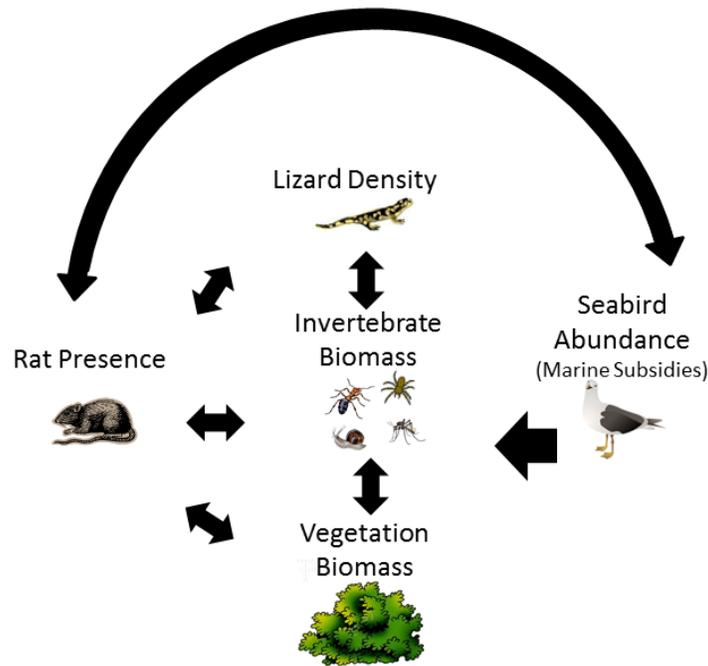


Figure 1: Typical Aegean study island food-web

Materials and Methods

Study Sites

I conducted this study in the NE Mediterranean Basin (Aegean Sea, Greece) (Figure 2). I worked on 15 rat-invaded islands uninhabited by humans off the coast of Greece and ranging in size from 0.005-2.71 km² (Figure 2, **Error! Reference source not found.**). These islands are located in six different regions or clusters named for the nearest large island (Skyros, Andros, Naxos, Paros, Schinoussa, Amorgos). While evidence is sparse, zooarchaeological data suggest that rats have been present in the Mediterranean for at least 2,000 years (Ruffino and Vidal, 2010). Historical records and genetic evidence suggest that *R. rattus* was transported via shipping activities; however, the warm Mediterranean climate may have also facilitated additional rat dispersal without human assistance (McCormick, 2003). Based on this, I assume that the majority of study islands have had a long history (greater than one year) of rat presence. The one exception is the island of Panagia where early surveys conducted by the Hellenic Ornithological Society (HOS, a Greek nonprofit organization) revealed the absence of rats until the summer of 2011.

All sites are located in the same climatic zone (thermo-Mediterranean climate) with humid yet arid (<590mm precip. annually) conditions (Gikas and Tchobanoglous, 2009). Local vegetation generally consists of a low, sclerophyllous, scrubby plant community called 'phrygana' (Vogiatzakis and Griffiths, 2008). Dominant taxa typically include thyme (*Coridothymus capitatus*), Phoenician juniper (*Juniperus phoenicea*) and lentisc (*Pistacea lentiscus*). Study islands are rocky with shallow soil profiles. Top native predators are generally resident populations of wall lizards (*Podarcis erhardi* or *P. gaigeae*; Lacertidae) found on all islands with the exception of Filiti.

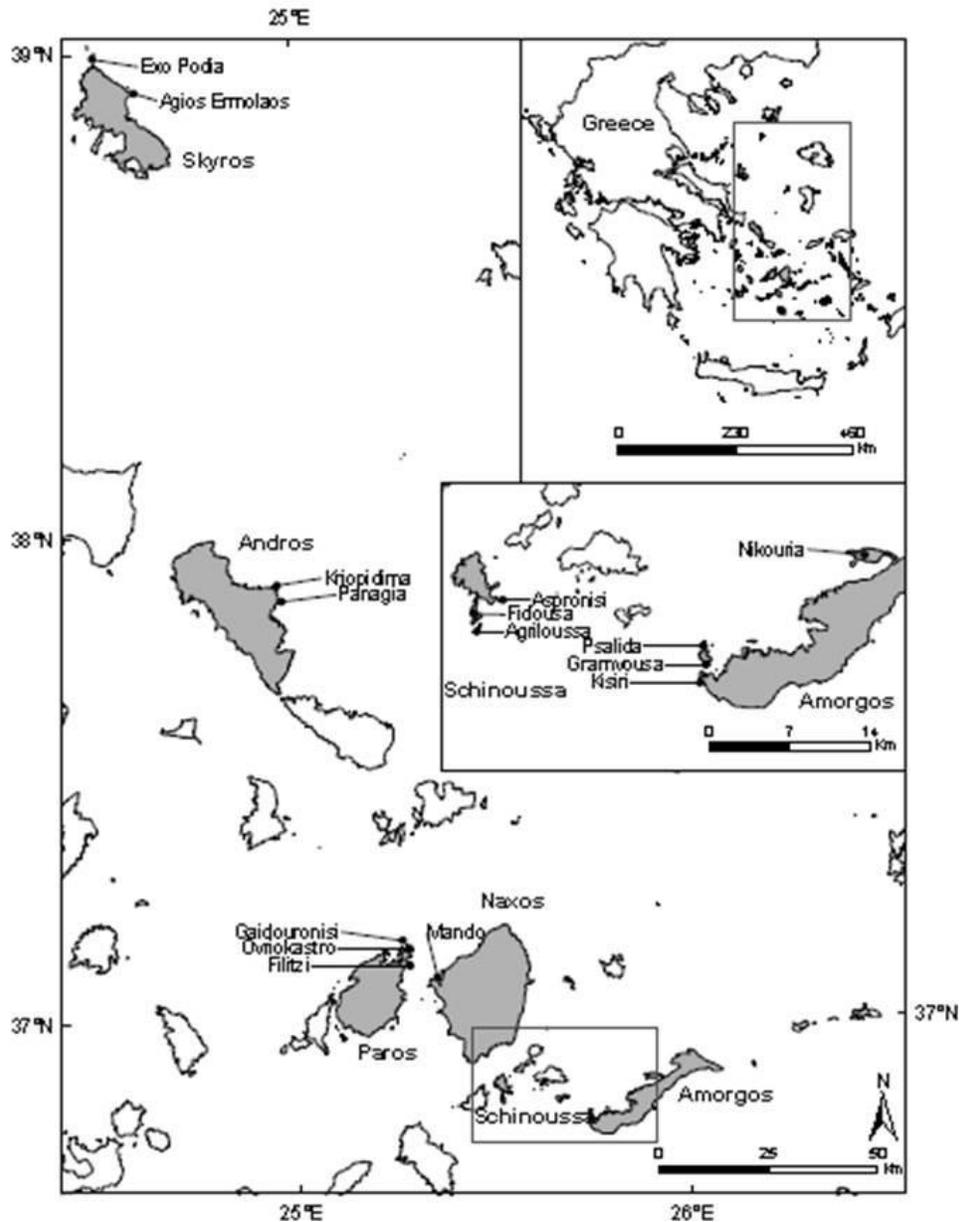


Figure 2: Study site locations. Bolded font represents island cluster.

Most of the islands in this study are used as nesting habitat by resident seabirds. The Aegean Sea harbors several species of breeding seabirds including the Audouin's Gull (*Larus audouinii*), Yellow-legged Gull (*Larus michahellis*), European Shag (*Phalacrocorax aristotelis*), Cory's Shearwater (*Calonectis diomedea*), and Yelkouan Shearwater (*Puffinus yelkouan*). Audouin's gull is a rare medium-sized ground-nesting seabird occurring only in the Mediterranean Sea and Atlantic Coast

of Morocco that has been the focus of extensive conservation efforts. The Yellow-legged gull is instead the most common gull species with a wide distribution in the SW Palearctic and a breeding focus in the Mediterranean Sea Basin. The shags which belong to the (*P. a. desmarestii*) sub-species are large seabirds that breed at low densities along rocky coastlines and islets. Cory's and Yelkouan shearwaters are pelagic seabirds that are colonial burrow-nesters on remote islets of the Mediterranean and East Atlantic (Fric et al., 2012).

Eleonora's falcons (*Falco eleonarae*) nest on two of the study islands. This species breeds solely in the Mediterranean, Canary Islands, and northwest Africa with the majority (>80%) of the global population nesting in the Aegean Sea region (Kassara et al., 2012). Eleonora's falcons, which hunt migrant fall songbirds, are unique among European birds because they breed in the fall. Nesting in synchrony, members of a colony match breeding activities to coincide with the wave of passerines moving southward across the Aegean Sea region (Kassara et al., 2012; Walter, 1979). Of the islands included in this study, Panagia and Exo Podia support the only two significant nesting colonies of Eleonora's Falcon.

Rat Eradications

Rat eradications were conducted on seven islands while eight other islands served as control sites (Figure 2, Appendix 1). On eradication islands, HOS staff deployed 2.5g pellets containing cereals, wax, and the second generation anticoagulant Brodifacoum (Taylor and Thomas, 1989). Pellets were placed inside plastic tubes to minimize bait exposure to non-target species and laid out on the island in a grid. Bait stations were monitored daily unless inclement weather restricted travel. The rate of bait removal was recorded and any pellets eaten were replaced. Rats were considered to have been eradicated once bait removal from stations ceased completely. Stations were monitored for one week following the last sign of rat activity to confirm eradication (Appendix 1). Eradication was generally achieved two to three weeks after the initial deployment of bait. Following rat eradication, permanent bait stations were placed on the island containing 10g bait blocks to prevent reinvasion and to monitor for future rat activity. Rat eradication success was also evaluated using sticks soaked in peanut oil, snap traps, and tracking

tunnels (Jakob Fric, pers. comm., 2014; Gillies and Williams, 2013; Taylor and Thomas 1989). Several months after eradication, presence or absence of rats was further confirmed on all islands by placing three 19x13.5x4.5 cm aluminum trays containing 600g sand mixed with 50g whole sunflower seed on each island for 11.8 ± 0.19 days in 2012 and 12.85 ± 0.20 days in 2013. Rat presence was determined from the presence of seed husks and rat feces in the trays.

Eight control islands were included in the study; these sites support rat populations that were not eradicated. Control sites were used to account for inter-annual variation unrelated to treatment (rat removal) that may have confounded the response variables and masked eradication effects.

To evaluate the impacts of rat eradication on islands, I determined changes on all trophic levels in the island ecosystem following rat removal (Figure 1 **Error! Reference source not found.**). This was done by collecting data on multiple ecosystem variables (vegetation biomass, snail abundance, invertebrate biomass, invertebrate diversity, lizard density, and seabird abundance) and comparing changes in each after eradication. Data was collected before and after rat removal on all islands with the exception of those in the Amorgos cluster where baseline data were collected late. Baseline data were collected in June 2012 on all four islands in this area. The three treatment sites in the Amorgos cluster were eradicated prior to this, in Feb 2012 (Gramvousa and Psalida), and November 2011 (Kisiri).

Vegetation

To quantify the effects of rats on island vegetation, plant biomass baseline data were collected on all study sites (March-July 2012); identical sampling was repeated post-eradication (May-June 2013). Where feasible, I attempted to match each 2013 island visit close to the date of the previous 2012 sampling.

For each island, plant biomass was assessed by sampling 3-5 sites (depending on island size) of representative vegetation. At each site, I established two abutting 80x80 cm sampling squares with similar vegetation composition and cover. To quantify

vegetation changes, I sampled one of the squares before and one after the eradication. During sampling, vegetation was clipped to ground level and all live and dead plant material was collected. The plant material was then dried and weighed (Guitérrez, J. and Meserve, 2000). Vegetation from islets in the Skyros cluster was dried in an oven for 60°C for 48 hours in 2012 and in 2013. All other vegetation was dried in the sun and during inclement weather, under heating lamps.

Invertebrates

Island arthropod communities were assessed by placing pitfall traps on all islands during baseline (March-July 2012) and post eradication (May- June 2013) sampling (St. Clair et al., 2011). Plastic cups approximately 7 cm wide and 11 cm deep were sunk under bushes into the ground, so that the lip of the cup was flush with the surface of the soil. Each cup was filled 2/3 with ethylene glycol due to its dual qualities as a preservative and its low rate of evaporation (Schmidt et al., 2006). The traps were then loosely covered with rocks to allow entrance of invertebrates but protect traps from being disturbed by non-target vertebrates. Invertebrates that fell into the cup were collected upon a return visit to the islands (12.75± 0.91 days in 2012 and 12.85±0.79 days in 2013). All collected invertebrates were, counted, dried and weighed to obtain biomass measurements. Biomass measurements were corrected for duration of sampling by dividing by the number of sampling days. Invertebrates were identified to order and a Shannon-Wiener diversity index was calculated.

Snails

Snails are a critical component of Aegean island species communities (Welter-Schultes and Williams, 1999). They are thought to be an important prey item for rats but are not commonly collected in pitfall traps (Chiba, 2010). To determine effects of rats on snail populations, I counted all live snails found within each 80X80cm vegetation plot at the time I collected plant biomass.

Secondary Consumers, Wall Lizards

Wall lizards (*Podarcis* sp.) are the top predators on all study islands. I determined wall lizard density along 100m transects before and after the eradication. Transects

were walked slowly and quietly and all lizards seen or heard were recorded (Buckley and Roughgarden, 2006). All transects were walked during March-July.

Seabird Sampling

All baseline seabird abundance data were collected prior to eradication from 2007-2012. Seabird colony sizes were estimated using adult bird counts or recording active nests (Fric et al., 2012). Nest or pair counts were converted to individuals by multiplying by 2. I considered all seabird data together as the dataset was not large enough to consider individual species effects (seabird data shown in Appendix). Data were categorized as pre- or post-eradication for analysis.

Eleonora's falcon colony monitoring

Long-term focal sampling of an Eleonora's falcon colony was conducted on the island of Panagia by HOS.

During multiple visits in the fall of each year (2006-2013 with the exception of 2009 and 2010), HOS biologists scoured the island and determined number of active nests and reproductive success. During a routine visit in the summer of 2011, rats were discovered on the island, which is located <100m from the larger, inhabited island of Andros. The island was therefore included in the eradication program and the full suite of island ecology baseline data were collected in March 2012 with the eradication taking place in the same month.

Falcon reproductive activities are typically assessed over a series of three visits, with the first in late August or early September to count active nests. A second visit is done to determine how many birds hatched from the nests and a third visit to see how many hatchlings survive to fledgling. Breeding success is then calculated as the number of fledglings divided by the number of active nests in each year (Jakob Fric, Pers. Comm.). I have included the findings from HOS surveys in **Error! Reference source not found.**

Statistical Analysis

I compared ecological changes from pre-to post-eradication in rat eradication islands relative to control islets using linear mixed models. This approach allowed

for the analysis of multiple sample plots nested within island sites. The following model was developed and run separately for each variable measured (vegetation biomass, invertebrate biomass, invertebrate diversity, snail biomass, snail count, lizard density, and seabird abundance).

Variable Measured ~ *Island Status* + *Year* + *Island Status*Year* + (1|*Island*)

Island status reflects the status of a site as either control or eradication while *Year* represents the timing of a measurement (before or after treatment). The *Island Status*Year* interaction allows us to compare the change on eradication islands before and after eradication with the change on control islands before and after eradication ie. this tests whether $\Delta_{\text{control}} = \Delta_{\text{eradication}}$. A random effect for *Island*, (1|*Island*), was included as data collected within the same island were not independent. If data were not normally distributed, a natural log transformation was applied.

As previously stated, the baseline data on four Amorgos islets (Gramvousa, Psalida, Kisiri) were collected after eradication. To investigate the sensitivity of the conclusions to the Amorgos islets, the analyses were repeated excluding all islets in the Amorgos cluster.

All analyses were run in R 2.14.2 (R Development Core Team, 2012). The lme4 and languageR packages were used in the linear mixed model analysis (Bates et al., 2012; Baayen, 2011).

Results

Success of Eradication

Occurrence of rat feces in seed trays was significantly different between control and eradication islands ($p < 0.01$, Pearson's Chi-squared test, $n = 37$). No rat feces were found on any treatment islands where trays were deployed after eradication. Seed tray data was not available for the Andros islets; however, on Panagia in the Andros cluster, rat absence was confirmed using the other methods (chewing sticks, snap

traps etc.). On the Andros control island (Kriopidima), continued rat presence was found in the form of freshly chewed plant seeds (Jakob Fric, Pers. Comm., 2014). Collectively, these results suggest that eradication efforts were successful.

Vegetation Biomass

There was no significant difference in the change in vegetation biomass (pre- vs. post eradication) when analyzing the entire dataset (Eradication islands changed from $310 \pm 47\text{g}$ to $464 \pm 65\text{g}$, while control islands from $330 \pm 55\text{g}$ to $353 \pm 64\text{g}$; $p=0.16$, $t=1.42$, linear mixed model, $n=127$). When removing the Amorgos islets from the analysis, a marginally significant difference was detected between control and eradication islands (Eradication islands changed from $279 \pm 68\text{g}$ to $521 \pm 93\text{g}$, while control islands changed from $312 \pm 62\text{g}$ to $316 \pm 70\text{g}$; $p=0.06$, $t=1.943$, linear mixed model, $n=95$). Specifically, a significant increase in vegetation biomass was detected following eradication on treatment islands ($p=0.02$, $t=2.28$, linear mixed model, $n=95$) while no such significant change was detected on control islands ($p=0.78$, $t=-0.28$, linear mixed model, $n=95$, Figure).

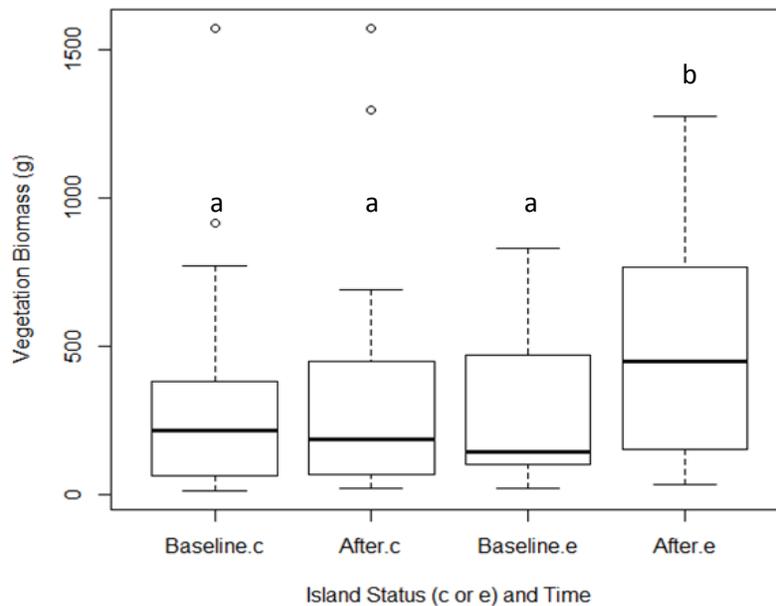


Figure 3: Vegetation biomass excluding the Amorgos islets
e=eradication, c=control islands, Baseline= before eradication, After=after eradication

Invertebrate Biomass and Diversity

When considering the entire dataset, the change in invertebrate biomass before and after rat eradication did not differ between control and eradication islands ($p=0.5$, $t=0.63$, linear mixed model, $n=125$). These results did not change when repeating the analysis without the Amorgos islets ($p=0.66$, $t=0.44$, linear mixed model, $n=98$).

There was also no significant difference in invertebrate diversity before and after eradication when analyzing the entire dataset ($p=0.26$, $t=-1.14$, linear mixed model, $n=122$) or when repeating the analysis without the Amorgos islets ($p=0.23$, $t=-1.21$, linear mixed model, $n=95$).

When looking specifically at snail count, there was no significant difference in the change observed before and after eradication on control versus eradication islands ($p=0.44$, $t=0.78$, linear mixed model, $n=71$). This treatment effect is also not significant when the analysis is repeated without the Amorgos islets ($p=0.76$, $t=0.31$, linear mixed model, $n=45$).

Lizard Density

I found no significant difference in lizard density before and after eradication between eradication and control islands, irrespective of whether the entire dataset was analyzed ($p=0.69$, $t=0.41$, linear mixed model, $n=56$) or when the analysis was repeated without the Amorgos islets ($p=0.59$, $t=0.54$, linear mixed model, $n=37$).

Seabird Abundance

There was no significant difference in change in seabird abundance before and after eradication on control vs. eradication islands ($p=0.66$, $t=0.45$, linear mixed model, $n=100$). Because seabird data were available before 2011, pre-eradication data were available for the Amorgos sites and so it was not necessary to repeat this analysis without the Amorgos islands.

Variable	Amorgos	Outcome	p value	t value	n
Vegetation Biomass	Included	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.16	1.42	127
Vegetation Biomass	Excluded	$-\Delta_{\text{control}}\neq\Delta_{\text{eradication}}$ $\Delta_{\text{control}}=0, \Delta_{\text{eradication}}>0$	0.06 0.78, 0.02	1.94 -0.28, 2.28	95
Invertebrate Biomass	Included	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.53	0.63	125
Invertebrate Biomass	Excluded	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.66	0.44	98
Invertebrate Diversity	Included	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.26	-1.14	122
Invertebrate Diversity	Excluded	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.23	-1.21	95
Snail Count	Included	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.44	0.78	71
Snail Count	Excluded	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.76	0.31	45
Lizard Density	Included	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.69	0.41	56
Lizard Density	Excluded	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.59	0.54	37
Seabird Abundance	Included	$\Delta_{\text{control}}=\Delta_{\text{eradication}}$	0.65	0.45	100

Table 1: Summary of linear mixed model statistics

Discussion

I found only relatively minor shifts across species communities following rat eradication on treatment islands (Table 1). When comparing each variable alone, I detected very few significant differences in ecosystem condition between eradication and control islands in the change from pre- to post-eradication. This is unexpected as other studies show recovery in vegetation cover, invertebrate abundance, reptiles, and seabirds following rat removal (Allen et al. 1994; St. Clair et al., 2011; Towns, 1991; Whitworth et al., 2005, Towns et al., 2006). Only vegetation biomass increased marginally on eradication islands. This change was detected only when excluding the Amorgos islands.

It is possible that the lack of significant vegetation recovery when looking at the entire dataset may be caused by an immediate onset of recovery prior to the delayed collection of baseline data on the Amorgos islands. This would have created an artificially elevated baseline against which post-eradication measurements were not differentiated.

It is also probable that the weak rat removal effects may be the result of the short sampling period. One year after treatment may not be enough time for vegetation and other ecosystem variables to recover following rat removal. This could particularly be the case in the arid systems of the Cycladic islands where vegetation growth is slow. Furthermore, bottom up effects of rats on higher trophic levels should be expected to be delayed relative to direct consumptive effects. Indeed in this study the only (marginally significant) effects I found were in plants, with no detectable effects on primary and secondary consumers (invertebrates and lizards respectively). It is therefore important for future similar projects to continue monitoring over several years to better quantify long-term effects of rat eradication.

Furthermore, sites with long-standing invasions may also have lost species that are particularly susceptible to rat activity. As a result, there may not be rapid recovery following eradication as only species able to coexist with rats remain. For instance, in the case of vegetation, the remaining species may be less palatable and slow growing as resources are invested into chemical defenses, woody structures, and thorns to deter predation (Yang et al., 2012). However, more research into the species composition of the islands is needed to confirm this.

The island of Panagia, where rats were present for a short time, shows higher average change across all variables than combined averages for control or other eradication sites (Appendix). It is possible that on this site, species vulnerable to rats were suppressed but not extirpated allowing Panagia to rebound quickly following rat removal.

The hypothesis that invading rats have long-term effects on island ecosystems is supported by previous studies, which demonstrate that introduced species have the capacity to alter community composition. For instance, invasive zebra mussels (*Dreissena polymorpha*) have been shown to cause phytoplankton communities to shift towards cyanobacteria in Lake Huron (USA) (Vanderploeg et al, 2001). In Australia, the introduction of cattle to savanna has led to a shift in vegetation composition from grasses to less palatable woody species (Sharp and Whittaker, 2003). A study in the Balearic Islands determined that vegetation composition was correlated with rat presence with some plant species favored and others depressed (Palmer and Pons, 2001). Lastly, a study in the Aleutian Islands demonstrated that rats have the capacity to indirectly alter species composition through predation. Rat predation on seabirds resulted in a reduction in seabird predation on grazing invertebrates leading to a shift in intertidal community composition from algae- to an invertebrate- dominated system (Kurle et al., 2008). However, it should be noted that my study includes only one site with a short period of rat colonization. More research using multiple sites of varying periods of rat colonization is needed.

Findings for two ecosystem variables in this study, snail abundance and seabird abundance, should be interpreted with caution. First, the lack of change observed in snail populations is unexpected. Out of all major taxonomic groups, mollusks have the greatest documented extinctions with nonnative predators such as rats cited as a major cause in the decline of native land snails (Lydeard et al., 2004). Rats in the Aegean readily consume snails: the most obvious marker of rat presence on the islands included in this study was the occurrence of preyed-upon snail shells. It is probable that the apparent lack of recovery in snail populations following rat eradication could be attributed to their unusual clumped distribution pattern. Snails on the study islands follow an extreme aggregation behavior where most of the population is concentrated in a few locations. Gastropods have been found to use chemoreception to cluster together around food sources and gather during breeding and aestivation periods (Croll, 1983; Fratini et al., 2001). These pronounced levels of spatial heterogeneity meant that my datasets had high levels of variance making it difficult to detect experimental treatment effects. More

comprehensive sampling would be needed on the study islands to determine rat impacts on snail populations.

Additionally, the lack of consistent effect of rat removal on Aegean seabirds may be attributable to the life history characteristics of the main bird species we focused on in this study. In other parts of the world, rats have been found to have negative impacts on seabirds through the predation of eggs, chicks, and occasionally adults (Seto and Conant, 1996; Jones et al., 2006; Jones et al., 2008). In many cases, the removal or control of rats results in increases in seabird populations and breeding success (Rayner et al. 2007; Imber et al.; 2000; Igual et al., 2006; Jouventin et al.; 2003). In contrast to these studies, we found at best a mixed effect of rats on Aegean seabirds. We did not detect any obvious effects of rat eradication on the most common species of seabirds (gulls and shags). Much of this lack of effect is likely attributable to the size-specific effects of rats on seabirds. A recent review of the literature reveals that the vulnerability of a seabird colony to rat predation is often species-specific. A meta-analysis by Jones et al. showed that smaller burrow-nesting seabirds are more susceptible to rat predation, whereas larger species such as gulls (Laridae) or shags (*Phalacrocorax* sp.) are less so (Jones et al., 2008). Three of the four focal seabird species in this study are larger-bodied and are thus expected to be resistant to rat predation. The last species, Cory's shearwater, is considered to be somewhat susceptible to rats (Martin et al. 2000) though it is possible that the lack of clear results may be simply attributable to the challenges of accurately surveying shearwater populations and the short duration of this study.

The Hellenic Ornithological Society observed a decline in Eleonora's falcon nesting and breeding success on Panagia following rat invasion and an increase following rat removal (Appendix 3). Rats have been found to prey on the eggs of ground nesting birds including Eleonora's falcons (Walter, 1979). Though, it is important to note that no control islands were used here and one cannot draw any statistical conclusions off this small set of data on Panagia. However, it is possible that the most immediate way to evaluate the impact of rats on seabirds is not via surveys of adult birds but rather through careful determination of breeding success similar to

the data collected on Eleonora's falcon. For instance, Cory's Shearwater breeding success has been found to mirror periods of rat control in a study on the Chafarinas Islands (Spain). While rates of egg predation did not vary with rat control; chick mortality was found to be high before rat control and low following management (Iguál et al., 2006). Future work should consider quantifying seabird breeding success and nesting habits when evaluating rat impacts particularly over the short term. Furthermore, studies should consider the possibility that rat predation on intact seabird eggs may vary across islands, as it has been shown to be a learned behavior and could vary across populations (Prieto et al., 2003).

In conclusion, the lack of consistent ecosystem response to rat eradication is possibly due to the short monitoring period of this study and changes in community composition on sites with long-standing invasion that favors species resistant to rat impacts. I recommend that future studies extend monitoring over several years and consider the duration of rat presence and island community composition where possible.

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Appendices

Appendix 1

Summary of Project Data (1)

Island	Status	Eradication Date	Eradication Confirmation	Island Area (km ²)	Time Period	Vegetation Biomass (mean±SE) (g)	Invertebrate Biomass (mean±SE)(g/day)	Invertebrate Diversity (mean±SE)(SWDI)
Gramvousa (Amorgos)	e	Feb-12	Y	0.820	Before	273.8 ± 75.8 (5)	0.014±0.010 (3)	0.645±0.359 (3)
					After	185 ± 51.3 (5)	0.017±0.008 (5)	1.331±0.089 (5)
Kisiri (Amorgos)	e	Nov-11	Y	0.016	Before	378.3± 129.12 (3)	0.005±0.001 (2)	1.375±0.098 (2)
					After	560.7± 163.3 (3)	.008±.001 (3)	1.355±0.060 (3)
Nikouria (Amorgos)	c	NA	NA	2.751	Before	432.6±91.5 (5)	0.142±0.034 (5)	0.914±0.093 (5)
					After	560.2±119.6 (5)	0.051±0.028 (4)	1.353±0.124 (4)
Psalida (Amorgos)	e	Feb-12	Y	0.032	Before	384.7±129.6 (3)	0.011±0.009 (2)	1.040±0.005 (2)
					After	476.7±94.8 (3)	.005±0.001 (3)	1.042±0.180 (3)
Kriopidima (Andros)	c	NA	NA	0.005	Before	397.7±51.8 (3)	0.002±0.002 (3)	0.487±0.487 (2)
					After	425.8±71.9 (3)	0.012±0.005 (5)	1.543±0.102 (5)
Panagia (Andros)	e	Mar-12	Y	0.012	Before	230.8±45.0 (4)	0.002±0.001 (3)	0.368±0.201 (3)
					After	626.0±139.6 (4)	0.049±0.0.033 (4)	1.025±0.325 (4)
Mando	c	NA	NA	0.043	Before	367.4±126.3 (5)	0.036±0.006(5)	0.928±0.164 (5)

Island	Status	Eradication Date	Eradication Confirmation	Island Area (km ²)	Time Period	Vegetation Biomass (mean±SE) (g)	Invertebrate Biomass (mean±SE)(g/day)	Invertebrate Diversity (mean±SE)(SWDI)
(Naxos)					After	644.0±190.1 (5)	0.024±0.020 (5)	0.934±0.201 (5)
Filitzi (Paros)	c	NA	NA	0.183	Before After	206.0±45.6 (5) 117.5±46.7 (4)	0.003±0.001 (7) 0.004±0.002 (4)	0.476±0.196 (7) 0.956±0.138 (4)
Gaidouronisi (Paros)	e	May-12	Y	0.144	Before After	95.2±23.9 (5) 318.6±139.9 (5)	0.019±0.006(7) 0.070±0.0056 (4)	0.819±0.155 (7) 0.9016±0.247 (5)
Ovriokastro (Paros)	e	Aug-12	Y	0.116	Before After	90.6±21.3 (5) 167.0±56.0 (5)	0.004±0.001 (6) 0.006±0.002 (5)	0.723±0.250 (6) 0.567±0.278 (5)
Agriloussa (Schinoussa)	c	NA	NA	0.088	Before After	109.0±59.5 (5) 77.0±31.8 (5)	0.011±0.009 (5) 0.005±0.003 (5)	0.440±0.440 (4) 0.798±0.250 (5)
Aspronisi (Schinoussa)	c	NA	NA	0.043	Before After	655.3±161.8 (3) 721.0±445.8 (3)	0.169±0.143 (3) 0.008±0.005 (3)	0.250±0.201 (2) 0.643±0.028 (3)
Fidousa (Schinoussa)	c	NA	NA	0.632	Before After	412.8±297.9 (5) 168±75.1 (5)	0.0152±0.011 (5) 0.001±0.001 (5)	0.174±0.174 (5) 0.413±0.169 (5)
Exo Podia (Skyros)	e	Nov-12	Y	0.138	Before After	760.9±39.8 (5) 994.7±119.0 (5)	6.872±1.587 (5) 0.531±0.073 (5)	0.018±0.018 (5) 0.152±0.101 (5)
Agios Ermolaos (Skyros)	c	NA	NA	0.005	Before After	144.2±44.7 (3) 170.2±21.5 (3)	0 (1) 0.017±0.017 (3)	0 (1) 0.187±0.187 (3)

Summary of Project Data (2)

Island	Status	Eradication Date	Eradication Confirmation	Island Area (km ²)	Time Period	Snail Count (mean±SE)(indiv.)	Snail Biomass (mean±SE)(g)
Gramvousa (Amorgos)	e	Feb-12	Y	0.820	Before	0 (5)	0 (5)
					After	2.8±1.960 (5)	0.268±0.235 (3)
Kisiri (Amorgos)	e	Nov-11	Y	0.016	Before	2.667±2.667 (3)	0.856±0.856 (3)
					After	4.667±4.177 (3)	2.186±1.953 (3)
Nikouria (Amorgos)	c	NA	NA	2.751	Before	0.200±0.200 (5)	0.035±0.035(5)
					After	0.200±0.200 (5)	0.0142±0.0142 (5)
Psalida (Amorgos)	e	Feb-12	Y	0.032	Before	NA	NA
					After	NA	NA
Kriopidima (Andros)	c	NA	NA	0.005	Before	NA	NA
					After	NA	NA
Panagia (Andros)	e	Mar-12	Y	0.012	Before	NA	NA
					After	NA	NA
Mando (Naxos)	c	NA	NA	0.043	Before	2±1.760 (5)	0.660±0.063 (5)
					After	4.2±2.973 (5)	0.221±0.173 (5)
Filitzi (Paros)	c	NA	NA	0.183	Before	NA	NA
					After	NA	NA
Gaidouronisi (Paros)	e	May-12	Y	0.144	Before	0 (5)	0 (5)
					After	2.6±1.29 (5)	2.1218±1.198 (5)
Ovriokastro	e	Aug-12	Y	0.116	Before	NA	NA

Island	Status	Eradication Date	Eradication Confirmation	Island Area (km ²)	Time Period	Snail Count (mean±SE)(indiv.)	Snail Biomass (mean±SE)(g)
(Paros)					After	NA	NA
Agrioussa	c	NA	NA	0.088	Before	NA	NA
(Schinoussa)					After	NA	NA
Aspronisi	c	NA	NA	0.043	Before	0 (3)	0 (3)
(Schinoussa)					After	0.333±0.333 (3)	1.645±1.645 (3)
Fidousa	c	NA	NA	0.632	Before	0.600±0.600 (5)	0.0552±0.0552 (5)
(Schinoussa)					After	1.200±0.800 (5)	0.0738±0.053 (5)
Exo Podia	e	Nov-12	Y	0.138	Before	0.250±0.250 (4)	0.027±0.027 (4)
(Skyros)					After	0.4±0.245 (5)	0.137±0.115 (5)
Agios Ermolaos	c	NA	NA	0.005	Before	NA	NA
(Skyros)					After	NA	NA

Summary of Project Data (3)

Island	Status	Eradication Date	Eradication Confirmation	Island Area (km ²)	Time Period	Lizard Density (mean±SE)(indiv./100m)	Seabird Abundance (Individuals all species)	Seabird Species Found (shag: s, yellow legged gull;y, Cory's shearwater: c, Audouin's gull: a)
Gramvousa (Amorgos)	e	Feb-12	Y	0.820	Before	2.333±0.333 (3)	10±10 (2)	s, y
					After	2.333±0.667 (3)	1 (1)	a
Kisiri (Amorgos)	e	Nov-11	Y	0.016	Before	0 (1)	49±24.705 (3)	a, y
					After	2±1 (2)	24± 12.741 (3)	s, a, y
Nikouria (Amorgos)	c	NA	NA	2.751	Before	6.75±0.854 (4)	NA	NA
					After	8±1.154 (3)	NA	NA
Psalida (Amorgos)	e	Feb-12	Y	0.032	Before	0 (1)	26.750±20.629 (3)	s,a, y
					After	1±1 (2)	18.5±18.5 (2)	y
Kriopidima (Andros)	c	NA	NA	0.005	Before	7.5±1.5 (2)	0 (1)	0
					After	2.5±2.5 (2)	31.5±23.5 (2)	y
Panagia (Andros)	e	Mar-12	Y	0.012	Before	15.5±6.5 (2)	29±29 (2)	s, y
					After	18.5±1.5 (2)	97.5±22.5 (2)	y
Mando (Naxos)	c	NA	NA	0.043	Before	5.5±0.5 (2)	NA	NA
					After	5.5±1.5 (2)	NA	NA
Filitzi (Paros)	c	NA	NA	0.183	Before	NA	318±15.567 (2)	s, y
					After	NA	159 (1)	s, y
Gaidouronisi	e	May-12	Y	0.144	Before	7.5±0.5 (2)	224±37.541 (3)	s, y

Island	Status	Eradication Date	Eradication Confirmation	Island Area (km ²)	Time Period	Lizard Density (mean±SE)(indiv./100m)	Seabird Abundance (Individuals all species)	Seabird Species Found (shag: s, yellow legged gull;y, Cory's shearwater: c, Audouin's gull: a)
(Paros)					After	6±0 (2)	50 (1)	y
Ovriokastro	e	Aug-12	Y	0.116	Before	3.5±3.5 (2)	242±49.487 (3)	s, y, c
(Paros)					After	3±0 (2)	104 (1)	s, y, c
Agriloussa	c	NA	NA	0.088	Before	8 (1)	40 (1)	y
(Schinoussa)					After	12.5±1.5 (2)	42 (1)	y
Aspronisi	c	NA	NA	0.043	Before	12 (1)	230(1)	y
(Schinoussa)					After	8±4 (2)	200 (1)	y
Fidousa	c	NA	NA	0.632	Before	0.5±0.5 (2)	NA	NA
(Schinoussa)					After	2±1 (2)	NA	NA
Exo Podia	e	Nov-12	Y	0.138	Before	4.5±2.5 (2)	97.333±0.882 (3)	s, y
(Skyros)					After	9 (1)	10 (1)	s, y
Agios Ermolaos	c	NA	NA	0.005	Before	9 (1)	4 (1)	s, y
(Skyros)					After	12±1 (2)	20 (1)	y

Appendix 2

Raw Seabird Data¹

Island	Status	Eradication	Year	Shag	Audouin's Gull	Yellow Legged Gull	Corys Shearwater
Gramvousa (Amorgos)	e	pre	2010	0	0	0	NA
Gramvousa (Amorgos)	e	pre	2011	4	0	16	NA
Gramvousa (Amorgos)	e	post	2013	0	1	0	NA
Kisiri (Amorgos)	e	pre	2007	0	0	0	NA
Kisiri (Amorgos)	e	pre	2009	0	68	0	NA
Kisiri (Amorgos)	e	pre	2010	0	78	1	NA
Kisiri (Amorgos)	e	post	2011	1	34	10	NA
Kisiri (Amorgos)	e	post	2012	0	1	0	NA
Kisiri (Amorgos)	e	post	2013	0	26	0	NA
Nikouria (Amorgos)	c	pre		NA	NA	NA	NA
Nikouria (Amorgos)	c	post		NA	NA	NA	NA
Psalida (Amorgos)	e	pre	2007	0	20	0	NA
Psalida (Amorgos)	e	pre	2009	0	0	0	NA
Psalida (Amorgos)	e	pre	2010	0	0	0	NA
Psalida (Amorgos)	e	pre	2011	17	0	70	NA
Psalida (Amorgos)	e	post	2012	0	0	0	NA

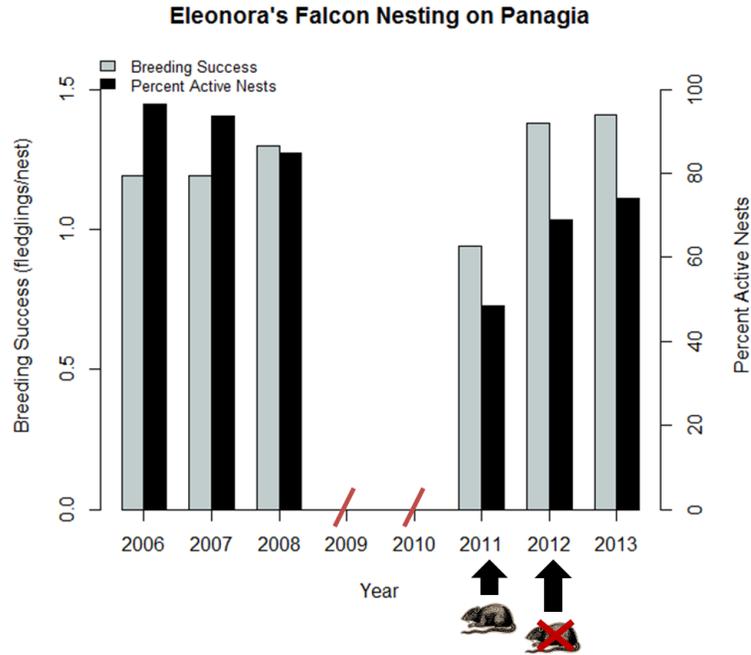
¹ NA designates a lack of observation or sites where a species was never found to be present. Under status c=control, e=eradication site. All seabirds are recorded as individuals.

Island	Status	Eradication	Year	Shag	Audouin's Gull	Yellow Legged Gull	Corys Shearwater
Psalida (Amorgos)	e	post	2013	0	0	37	NA
Kriopidima (Andros)	c	pre	2009	NA	NA	0	NA
Kriopidima (Andros)	c	post	2012	NA	NA	55	NA
Kriopidima (Andros)	c	post	2013	NA	NA	8	NA
Panagia (Andros)	e	pre	2009	8	NA	50	NA
Panagia (Andros)	e	pre	2010	0	NA	0	NA
Panagia (Andros)	e	post	2012	0	NA	75	NA
Panagia (Andros)	e	post	2013	0	NA	120	NA
Mando (Naxos)	c	pre		NA	NA	NA	NA
Mando (Naxos)	c	pre		NA	NA	NA	NA
Filitzi (Paros)	c	pre	2010	5	NA	300	NA
Filitzi (Paros)	c	pre	2011	9	NA	340	NA
Filitzi (Paros)	c	pre	2012	0	NA	300	NA
Filitzi (Paros)	c	post	2013	5	NA	154	NA
Gaidouronisi (Paros)	e	pre	2010	0	NA	150	NA
Gaidouronisi (Paros)	e	pre	2011	2	NA	270	NA
Gaidouronisi (Paros)	e	pre	2012	0	NA	250	NA
Gaidouronisi (Paros)	e	post	2013	0	NA	50	NA
Ovriokastro (Paros)	e	pre	2010	5	NA	200	0

Island	Status	Eradication	Year	Shag	Audouin's Gull	Yellow Legged Gull	Corys Shearwater
Ovriokastro (Paros)	e	pre	2011	1	NA	180	0
Ovriokastro (Paros)	e	pre	2012	10	NA	200	130
Ovriokastro (Paros)	e	post	2013	0	NA	90	14
Agrilou (Schinoussa)	c	pre	2012	NA	NA	40	NA
Agrilou (Schinoussa)	c	post	2013	NA	NA	42	NA
Aspronisi (Schinoussa)	c	pre	2012	NA	NA	230	NA
Aspronisi (Schinoussa)	c	post	2013	NA	NA	200	NA
Fidousa (Schinoussa)	c	pre		NA	NA	NA	NA
Fidousa (Schinoussa)	c	post		NA	NA	NA	NA
Ag. Ermolaos (Skyros)	c	pre	2010	1	NA	3	NA
Ag. Ermolaos (Skyros)	c	post	2013	0	NA	20	NA
Exo Podia (Skyros)	e	pre	2009	37	NA	59	NA
Exo Podia (Skyros)	e	pre	2010	28	NA	71	NA
Exo Podia (Skyros)	e	pre	2012	17	NA	80	NA
Exo Podia (Skyros)	e	post	2013	2	NA	8	NA

Appendix 3

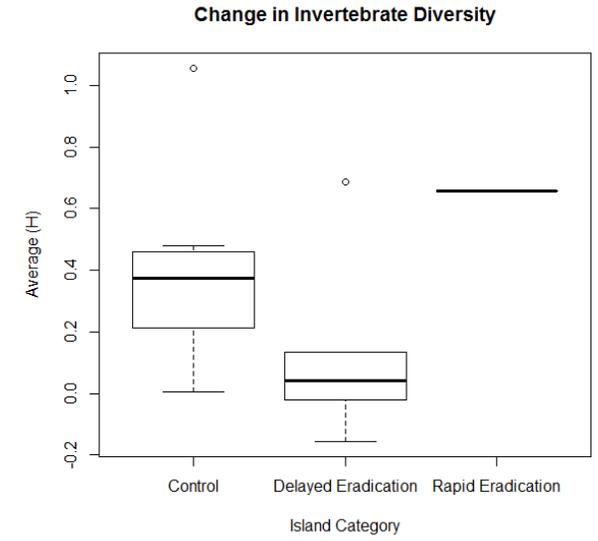
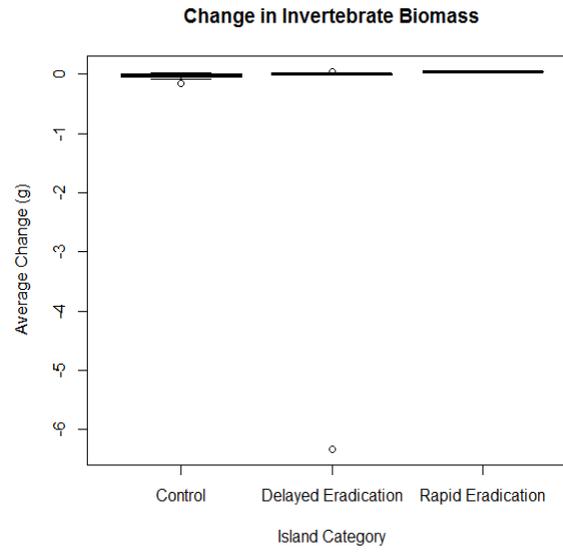
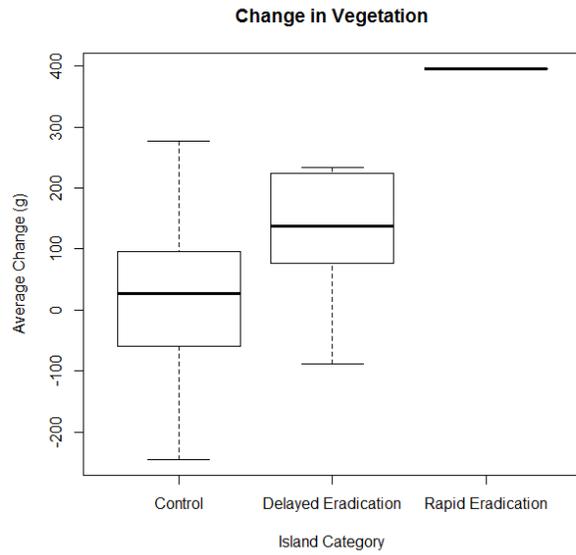
Eleonora's Falcon Data from the Hellenic Ornithological Society

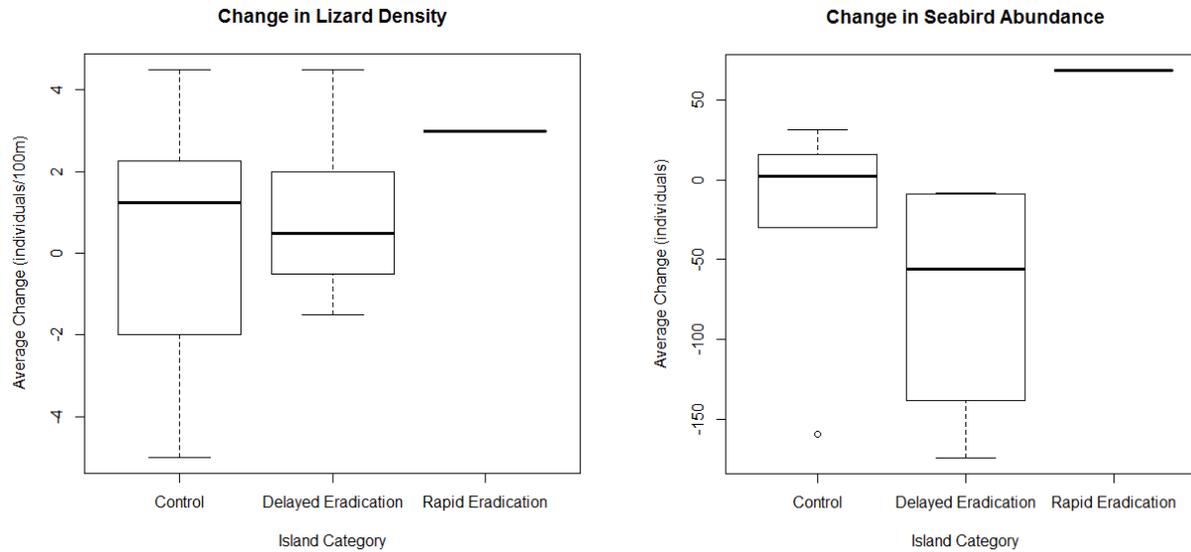


Year	2006	2007	2008	2011	2012	2013
Nesting Sites Checked	57	63	86	70	100	100
Active Nests	55	59	73	34	69	74
Percent Active (Active Nest/Nesting Sites Checked)*100	96.49	93.65	84.88	48.57	69	74
Fledglings (individuals)	65	70	95	32	95	104
Breeding Success (fledglings/nest)	1.18	1.19	1.30	0.94	1.38	1.41

Appendix 4

Average change on islands of varying eradication periods:





Average Change

Island Category	n	Change in Vegetation (g)	Change in invertebrate biomass (g/day)	Change in Invertebrate Diversity (H)	Change in lizard density (individuals/100m)	Average change in seabird abundance (individuals)
Control	8	19.84±54.15	- 0.03±0.02	0.39±0.11	0.18±1.33	-27.9±34.31
Delayed Eradication	6	119.87±49.60	-1.05±1.06	0.12±0.12	0.92±0.87	-73.60±29.00
Rapid Eradication	1	395.2	0.05	0.657	3	68.5

The average change across plots was calculated for each island by taking the difference between the island pre-eradication average and island post-eradication average. These values were then averaged by island category and one standard error from this mean was calculated