THE EFFECT OF INVASIVE LIVESTOCK ON SEABIRD-DERIVED NUTRIENT FLOWS ON MEDITERRANEAN ISLANDS

by

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ABSTRACT

Island ecosystems have been shown to be particularly vulnerable to biodiversity loss caused by the introduction of invasive species, such as goats (*Capra hircus*) and other livestock (Courchamp et al., 2003; D'Antonio & Dudley, 1995). Once established, goat populations exhibit high fecundity and can decimate vegetative communities if left unchecked (Schweizer et al., 2016). This has the potential to also impact the nutrient availability and trophic interactions within island ecosystems, which are often subsidized with inputs of marine nutrients via seabird deposition (Kazama, 2020). While the significance of seabird communities in the transportation of marine nutrients onto terrestrial ecosystems is widely known, little has been done to show if, and how, introduced livestock may disrupt these nutrient flows on small islands. In this study, we evaluated the effects of goat introduction and removal through whole island manipulation experiments. We found that the introduction of goats on islands had primarily negative effects on nesting seabird densities and marine nutrient subsidies. On the other hand, we did not detect significant effects of plant consumption and goat export on island nutrients. Studying how islands are affected by introduced goats pre- and post-eradication can inform management efforts for protecting endemic species, restoring degraded natural communities, and understanding the changes in nutrient cycling in these ecosystems.

INTRODUCTION

Islands are among the most important places for biodiversity conservation globally: while covering only about 5% of Earth's surface, they harbor about 40% of the planet's endangered species (Spatz et al., 2017). Islands harbor numerous endemic taxa, and their ecologies differ in often complex ways from those of mainland systems (D'Antonio & Dudley, 1995; Whittaker et al., 2023). These geographically isolated systems frequently rely on marine subsidies of nitrogen, phosphorus, and carbon, primarily imported either through seabirds or shore drift, to support their communities and maintain productive food webs (Anderson & Mulder, 2011; Hyndes et al., 2022; H. Jones et al., 2025; Polis & Hurd, 1996).

Nesting seabirds play a central role as mobile links between marine and terrestrial systems on small islets. By consuming marine prey - rich in carbon, nitrogen, phosphorus - and then depositing their feces (also termed "guano"), feathers, carcasses, and food scraps onto islands, they act as a biological pump, transporting marine nutrients into terrestrial ecosystems (Anderson & Mulder, 2011; De La Peña-Lastra, 2021; Hentati-Sundberg et al., 2020; Otero et al., 2018). These nutrients are especially concentrated around nesting colonies and progressively spread outward through both soil lixiviation processes as well as trophic interactions, influencing soil chemistry, plant productivity, and community composition (Forero & Hobson, 2003; Pascoe et al., 2022; Stadler et al., 2022). Ultimately, marine nutrient inputs mediated by seabirds not only enrich island soils but also fundamentally structure the productivity, species composition, and ecological functioning of island ecosystems (De La Peña-Lastra et al., 2020; Fukami et al., 2006; Kolb et al., 2011; Macias et al., 2018; Pascoe et al., 2021, p. 202). Because island systems depend so heavily on continued nutrient import, any decline of seabird populations (whether through habitat loss, predation by introduced mammals, or human disturbance) is thought to trigger sharp reductions in soil fertility and productivity, simplify plant communities, and diminish biodiversity (Croll et al., 2005; Maron et al., 2006; Pascoe et al., 2021) (Figure 1).

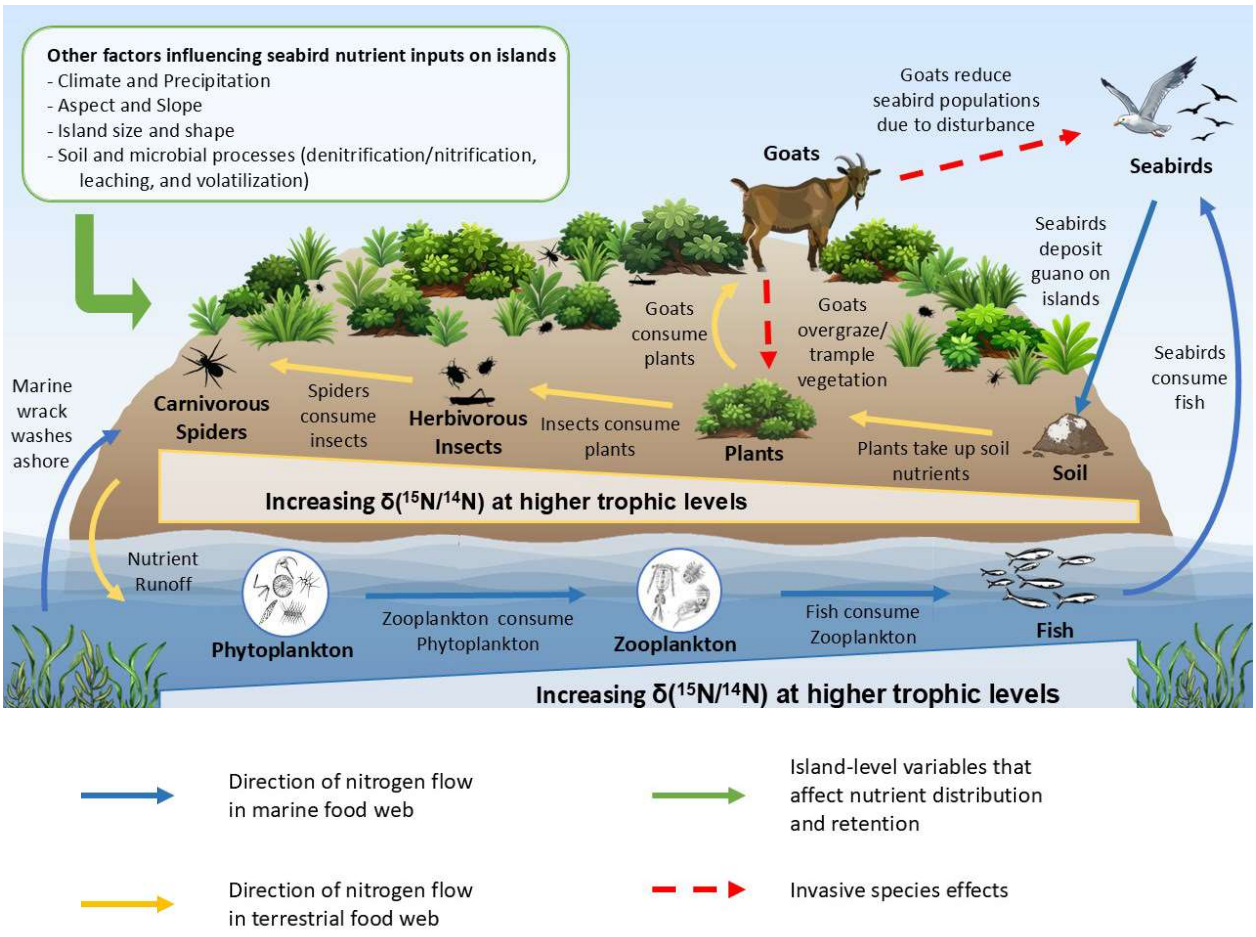


Figure 1. Conceptual diagram illustrating circular seabird-mediated nitrogen flow on islands. Solid arrows depict the movement and enrichment of heavier nitrogen (^{15}N) as it accumulates through marine (blue) and terrestrial (yellow) food webs. Solid green arrows represent additional environmental variables that may affect nutrient distribution and retention on the terrestrial island ecosystem. Dashed red arrows indicate invasive species effects on key ecosystem components. Seabirds and marine wrack serve as important vectors linking marine and terrestrial trophic systems by transporting marine-derived nutrients (i.e. ^{15}N) onto islands. These heavier isotopes subsequently return to the marine environment via terrestrial runoff, completing the nutrient cycle.

The Mediterranean Basin is recognized as one of the world's most important biodiversity hotspots, due to its remarkably high levels of endemism and species richness (Myers et al., 2000). This region contains over 13,000 known endemic plant species, as well as over 235 endemic vertebrates, many of which are restricted to the region's islands (Cuttelod et al., 2009; Myers et al., 2000). Situated within the north-eastern Mediterranean Basin, the Aegean Sea is characterized by complex archipelagos of mostly landbridge islands (Gaki-Papanastassiou et al., 2005; Sfenthourakis & Triantis, 2017). It contains over 7,000 islands

and islets, which vary broadly in terms of size, geologic substrate and history, distance to the mainland, vegetative cover, anthropogenic stressors, and actual species communities (Bergmeier et al., 2003; Simaiakis, 2014; Tzanoudakis & Panitsa, 1995).

Humans travelled and likely occupied all of the major Mediterranean islands for over 10,000 years, leaving a deep cultural and ecological imprint on even the more remote parts of the Basin (Carter et al., 2019; Cherry, 1981; Médail, 2017). Archaeological evidence shows that seafaring peoples were visiting and settling on Aegean Sea islands as early as the Neolithic, bringing along domesticated small ruminants that quickly became central to island subsistence economies (Bartolomé & Seguí, 2024; Hatziminaoglou & Boyazoglu, 2004). Goats *(Capra hircus)* in particular raised for their milk and meat, have served as an economically and culturally important cornerstone of human society in the Mediterranean region for centuries (Hatziminaoglou & Boyazoglu, 2004; Horwitz & Bar-Gal, 2006; Masseti, 2009; Morand-Fehr et al., 1983). Even the name 'Aegean' (Αίγαίον Πέλαγος) may derive from the ancient Greek word ***αἴγα***, meaning 'goat', underscoring the antiquity of goat husbandry in the archipelago (Ceccarelli, 2012). They have been released for varying periods of time on many, small, otherwise uninhabited islands in the Aegean Sea region.

Though humans have long occupied Mediterranean islands, their influence did not necessarily extend to small islets such as those used for this study. Because such islets have steep, rocky terrain, lack surface water, and are very inaccessible because of typically stormy seas, they have historically lacked both permanent human habitation and pervasive human activities (Knodell et al., 2022). Nevertheless, improved mechanized transportation in conjunction with control of piracy has allowed pastoralists, over the last century, to take advantage of these uninhabitable areas by transporting small ruminants seasonally to these islands. By placing, especially, goats (*Capra hircus*), a hardy livestock species with a generalist diet, on these islets for limited periods of time to graze, pastoralists can make land that would not be able to support traditional agricultural activity, productive (Constantakopoulou, 2020; Honigman, 2011). This practice, a form of transhumance, remains widespread throughout the Aegean and has been observed even

on larger islands at a more local scale, in which farmers move their livestock from the lowlands in the winter to mountain pastures in the summer (Forbes, 1995; Médail, 2017).

Goats have, because of their catholic forage preferences and their ability to persist seasonally without water, been able to thrive in various arid island environments and have been notorious for damaging vegetation cover(Chynoweth et al., 2013; Coblentz, 1978). Their introduction to islands has therefore been associated with overgrazing, shifts in species composition, loss of endemic taxa, and long-term soil loss due to wind erosion that can lead, in severe cases, to desertification (Arevalo et al., 2011; Bell, 1995; Hata et al., 2019). This not only diminishes terrestrial primary productivity but is also thought to interrupt the transfer of marine-derived nutrients that sustain island food webs (Bell, 1995; Forero & Hobson, 2003). Ultimately, these effects can persist even after goats have been removed from an area, with vegetation only partially recovering over time and native species richness remaining altered due to lack of recolonization on these insular systems (Capizzi, 2020; Gizicki et al., 2018; Pafilis et al., 2013; Phillips, 2010; Schweizer et al., 2016).

Conversely, some studies suggest that long-established goat populations may be ecologically beneficial in some areas, increasing plant species diversity through seed dispersal, suppressing aggressive invasive species through moderate grazing, and providing food resources (such as carcasses and dung) that support native scavengers and detritivores, serving almost as a ”keystone species” in some contexts (Bartolomé & Seguí, 2024; Gangoso et al., 2006). Regardless, goats remain the most ecologically destructive introduced species for island vegetation globally (Courchamp et al., 2003). Given these contrasting system-specific studies, a detailed understanding of the relationships of goats within a particular ecosystem, alongside intentional management -whether through population control, exclusion, or eradication – is critical for conserving and restoring vulnerable island ecosystems (Bartolomé & Seguí, 2024; BERMEJO & Lauenroth, 2012; Bodey et al., 2011; Phillips, 2010).

While impacts of introduced grazers on native plant communities and on soil loss have been commonly observed on island systems worldwide (Arevalo et al., 2011; Courchamp et al., 2003; Fernández-Lugo et al., 2013; Hata et al., 2019; Kossoff et al., 2024), much less is known about how they may alter nutrient cycling and stable isotope patterns on small seabird islands. Stable isotope analysis of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) provides a way to characterize these nutrient flows (Bodey et al., 2011; Forero & Hobson, 2003, 2003; Kelly, 2000). Heavier isotopes, such as ^{15}N and ^{13}C, accumulate at higher trophic levels and are more abundant near seabird colonies, reflecting the influence of marine nutrient input throughout an island's food web (Kazama, 2020; Pascoe et al., 2022). Understanding how nutrients move within small island ecosystems and how these flows may be disrupted by invasive herbivores is important to guide conservation, recovery efforts, and management efforts.

Invasive species can influence island food webs through either top-down (direct predation and removal of biomass) or bottom-up (loss of nutrient inputs). Ultimately, these forces can drive shifts in biomass, resources, and community structure, shaping ecosystems through fundamentally different mechanisms (Sánchez-Piñero & Polis, 2000; Wollrab et al., 2012). For example, bottom-up effects, which originate from changes in resource supply and are propagated upward through the food web, can occur when declines in seabird densities reduce the amount of nutrient subsidies delivered to islands. As seabird numbers decline, the total amount of allochthonous nutrients entering soil and plant communities decreases, leading to overall lower nutrient availability across all trophic levels.

In contrast, top-down forces, such as grazing, operate through direct consumption and removal of biomass of a 'bottom' tier organism (such as plants) by a 'top-tier' organism (e.g., goats). Herbivores often selectively feed on nutrient-rich plant tissues that are high in nitrogen. By doing so, they incorporate those nutrients into their bodies. Since goats are regularly moved from these islands and slaughtered off-site, the nutrients that they accrue in their bodies are exported along with them, hence reducing the island ecosystem's resource stocks (Leroux & Loreau, 2015). In systems where both seabird-mediated nutrient

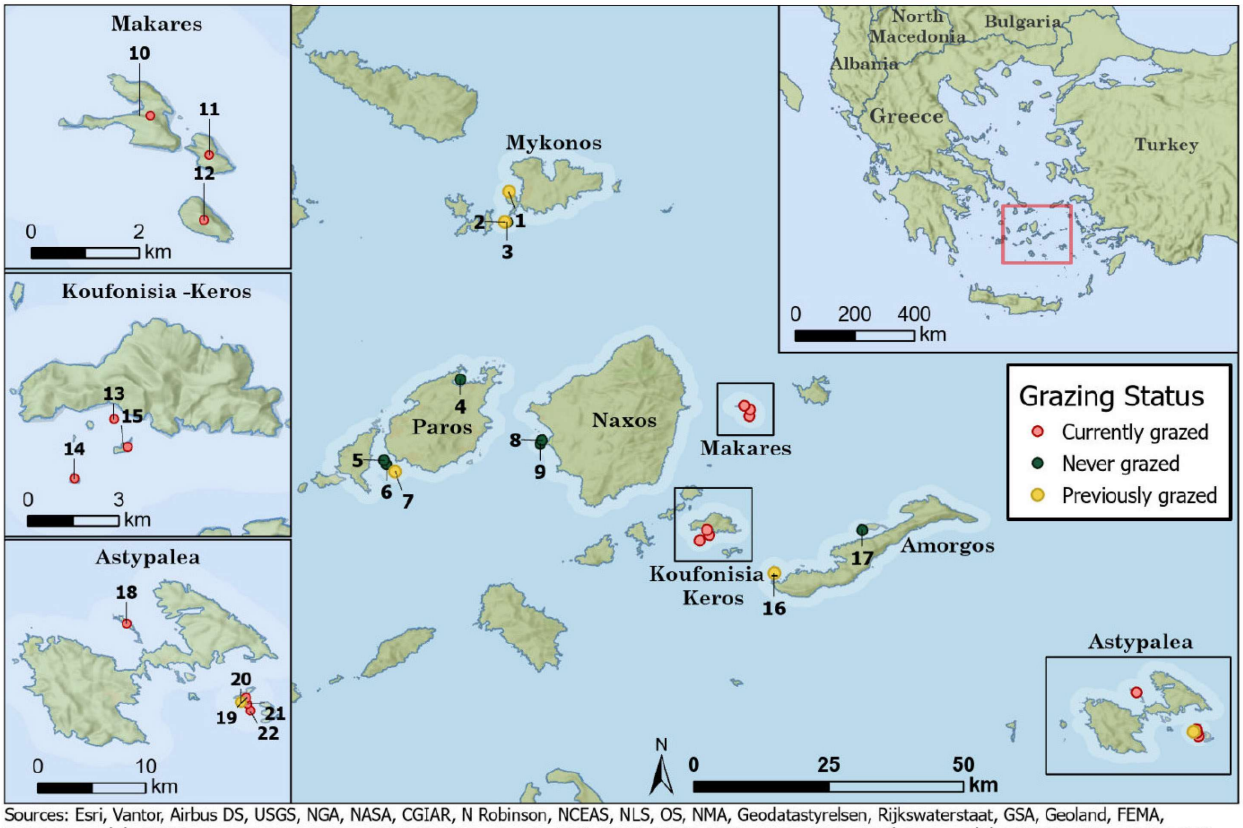
inputs and introduced livestock pressures vary, disentangling top-down from bottom-up drivers is critical for determining whether nutrient patterns reflect changes in resource supply, grazing pressure, or both. This is particularly important on small islets such as those in the Cyclades Archipelago, where nutrient cycles are highly reliant on allochthonous inputs by gulls (De La Peña-Lastra et al., 2020; Sekercioglu et al., 2016; Signa et al., 2012).

Here we use soil, plant, arachnid, guano, and goat dung samples from small Aegean islands (< 1km^2) to investigate how seabird-derived nutrients are distributed across trophic levels on islands differing in grazing history (never grazed, currently grazed, and previously grazed). We essentially use whole-island manipulations to test the hypothesis that concentrations of seabird-derived nutrients and isotopic enrichment will decline on islands where goats are present due to reductions in seabird density. If grazed islands have smaller seabird colonies, we predict that isotopic enrichment will decrease as island area increases.

MATERIALS AND METHODS

Study area

Fieldwork was conducted across the Cyclades Islands situated in the central Aegean Sea (Greece), between May and July 2023 [Figure 2].



Sources: Esri, Vantor, Airbus DS, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap, and the GIS user community, Sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community, Esri, USGS; SHI Ruixiang, LIU Chuang. Cyclades & Dodecanese [J/DB/OL]. Digital Journal of Global Change Data Repository, 2022.
Datum and Projection: WGS 1984
Created by: Brittany Amaral November 2025

Figure 2. Map of the study islands in the Cyclades Archipelago (Aegean Sea, Greece). Larger labeled islands (Mykonos, Paros, Naxos, Koufonisia-Keros, Makares, Amorgos, and Astypalea) represent main, human-inhabited, island clusters surrounded by uninhabited satellite islets. Circles indicate the study islets while color denotes grazing history: currently grazed islets (red) had active goat populations at the time of sampling; never grazed islets (green) had never supported goats; and previously grazed (yellow) islets have had goat populations removed. Study Islands are numbered as follows: Baos (1), Prasso (2), Krommydi (3), Agia Kali (4), Tourlos (5), Preza (6), Tigani (7), Parthenos (8), Mikri Vigla (9), Agios Nikolaos (10), Agia Paraskevi (11), Strongili (12), Mikri Plaka (13), Andreas (14), Loumboudiaris (15), Gramvoussa (16), Grambonissi (17), Megalo Fokonissi (18), Tigani (19), Moni (20), Ftheno (21), Chrondropoulo (22).

The Cyclades Archipelago is composed of 25 inhabited main islands surrounded by hundreds of smaller uninhabited islets and consists of varying geological substrates, including limestone, marble, granite, and schist (Evelpidou et al., 2021; Higgins, 2009; Torrent, 2005). These islands are surrounded by oligotrophic waters characterized by low primary productivity, and consequently relatively sparse fish stocks, as well as relatively low seabird densities comparative to the more nutrient-rich upwelling systems of the western Mediterranean Basin (Fric et al., 2013; Zotier et al., 1999). The region experiences a typical Mediterranean climate, defined by warm, dry summers and mild, rainy winters,

with strong winds that shape plant community structure (Suc, 1984; Vogiatzakis et al., 2016; Xoplaki, 2002). Vegetation across these islands consists largely of drought-adapted and salt-tolerant species, many of which are endemic islet specialists (Bergmeier et al., 2003; Montmollin & Strahm, 2005). The combination of aridity, thin soils, and salt spray produces vegetation that is spatially heterogeneous. Vegetation on the study islands is low, often dense, and the evergreen coastal heath is dominated by bushes of either *Pistacea lentiscus,* or *Atriplex recurva*. Near seabird colonies, vegetation was often also characterized by nitrophilous plant species (e.g. *Malva arborea)*.

The study islands have, because of their steep, rocky terrain, lack of surface water, and inaccessible nature, never had permanent human habitations (see Knodell et al., 2022). Nevertheless, improved motorized transportation in conjunction with government control of piracy, allowed pastoralists over the last century to take advantage of these uninhabitable areas by seasonally ferrying small ruminants to these islets. By bringing livestock and especially goats (*Capra hircus*), onto these islets for a limited period of time to graze, pastoralists were able to use land that would normally not be able to support traditional agricultural activity (Honigman, 2011). This practice, essentially a form of marine transhumance, exposed the study islands for the first time in their history to periods of intense overgrazing (Forbes, 1995; Médail, 2017).

Sampling was conducted on 22 islets that support breeding gull populations: 10 of these islands are currently grazed by goats, 7 have never been grazed by goats, and the remaining 5 were previously grazed by goats but have since had their populations removed [Table 1]. Grazing status and history were determined through interviews with local pastoralists and landowners. During field work and to ensure consistent sampling effort, we visited each islet for 1-4 hours, depending on size and available ambient conditions.

Island Number	Island Name	Grazing Status	Geologic Composition	Island Area (km^2)	Gull Count (indiv.)	Gull Density (indiv./km^2)
1	Baos	Previously grazed	Flysch	0.086	219	2535.46
2	Prasso	Previously grazed	Granodiorite	0.064	301	4687.16
3	Krommydi	Never grazed	Limestone	0.025	86	3418.53
4	Agia Kali	Never grazed	Granodiorite	0.013	4	305.67
5	Tourlos	Never grazed	Limestone	0.037	74	2001.41
6	Preza	Never grazed	Limestone	0.018	97	5468.49
7	Tigani (P)	Previously grazed	Limestone	0.084	15	178.55
8	Parthenos	Never grazed	Granodiorite	0.012	35	2914.24
9	Mikri Vigla	Never grazed	Granodiorite	0.007	34	4962.78
10	Agios Nikolaos	Currently grazed	Limestone	0.869	61	70.21
11	Agia Paraskevi	Currently grazed	Limestone	0.264	42	159.17
12	Strongili	Currently grazed	Limestone	0.364	308	846.17
13	Mikri Plaka	Currently grazed	Flysch	0.019	1	53.51
14	Andreas	Currently grazed	Limestone	0.047	14	296.40
15	Loumboudiaris	Currently grazed	Limestone	0.107	43	401.88
16	Gramvoussa	Previously grazed	Flysch/Marble	0.817	14	17.15
17	Grambonissi	Never grazed	Rhyolite	0.146	7	47.91
18	Megalo Fokonissi	Currently grazed	Limestone	0.689	16	23.21
19	Tigani (A)	Currently grazed	Limestone	0.079	16	203.77
20	Moni	Previously grazed	Limestone	0.014	8	555.90
21	Ftheno	Currently grazed	Limestone	0.028	7	252.70
22	Chondropoulo	Currently grazed	Limestone	0.014	14	991.71

Table 1. Summary of characteristics across 22 islets in the central Aegean Sea. Islands are listed with grazing status, geologic composition, total island area (km^2), island perimeter-to-area ratio, gull count (number of adult *L. michahellis*), and corresponding gull density (calculated as indiv./km^2). Grazing status represents 3 categories: never grazed (absence of goat populations both historic and present), currently grazed (grazing goat population during the sampling year), and previously grazed (islands on which goats have been removed for at least 20 years).

Seabird Population Size Estimation

The dominant seabird species nesting on the study islands is the Yellow-legged Gull (*Larus michahellis*), a widespread marine predator and scavenger in the Mediterranean with a generalist diet (Portolou et al., 2024; Zorrozua et al., 2024). These colonies have been shown to play an important role in the ecology of Mediterranean islets (García et al., 2002; Gizicki et al., 2018; Stadler et al., 2022). Colony size was estimated during nesting season through a minimum of two observational surveys conducted under appropriate ambient

conditions (see also Carlberg et al., 2022). Hence, counts were done using methods identical with Gizicki et al. (2018) and standardized census techniques described by (Walsh et al., 1995). Count data were then used to estimate gull density (individuals per km^2) for each island.

Field sample collection

Gull guano samples (n=22) were scraped from rocks near active nesting areas. Goat dung (n=8) was collected opportunistically, with each sample composed of at least 5 pellets from a single fecal pile. Soil samples (n=75) were collected after removing surface leaf litter and scraping the top layer to approximately 5cm depth. Each collection consisted of three subsamples spaced approximately 15 cm apart within the sampling area, and which were then combined into a single composite sample. All guano, dung, and soil samples were stored in sterile tubes, frozen during transport, and subsequently processed in a laboratory at Northern Illinois University.

Arachnids (n=30) were collected opportunistically by overturning rocks and hand-capturing individuals. After collection, specimens were stored in labeled tubes and frozen prior to processing. In the laboratory, specimens were rinsed in distilled water, and arachnid abdomens were removed to minimize isotopic bias from stomach contents.

Foliage samples of *Atriplex recurva* (n=19), *Malva arborea* (n=14), and *Pistacia lentiscus* (n=43) were collected across the islands. These three shrub species were selected due to their high prevalence in the Cyclades and distinct functional traits: *A. recurva* is a C4 perennial, *M. arborea* is a C3 nitrophilic biennial, and *P. lentiscus* is an evergreen C3 perennial. Upon collection, leaves were rinsed with distilled water, air-dried, and then frozen for transport in labeled ziploc bags.

All samples were oven-dried at 55 °C until reaching constant weight to remove residual moisture. Soil samples were homogenized using a 0.5 mm stainless-steel sieve. Gull guano, goat dung, soil, and arachnid samples were then finely ground using a pestle and mortar. For plant samples, petioles were removed after drying and the remaining leaf tissue was milled to a fine powder.

Due to ecological and logistical constraints inherent to small island systems, not all target plant taxa were found on every island. Islands with samples representing all trophic levels (soil, plant, and arachnid) and containing more than one of the target plant species were prioritized for stable isotope analysis.

Stable Isotope Analysis

Stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were conducted at the Northern Illinois University Stable Isotope Laboratory (DeKalb, IL, USA). Dried and homogenized samples of soil, vegetation, arachnid tissue, and gull guano were weighed (~1-10 mg), loaded into tin capsules, and analyzed using a Thermo Fisher Scientific MAT 253 and Delta Plus Advantage isotope ratio mass spectrometer coupled with a Costech ECS 4010 Elemental Analyzer. Isotopic ratios were expressed in delta (δ) notation in parts per thousand (‰) relative to international standards: Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric N_2 for nitrogen. Percent carbon (%C) and nitrogen (%N) were determined simultaneously during isotopic analysis. The C:N ratio was later calculated to assess the degree of organic enrichment and potential sources of nitrogen input across trophic levels.

Statistical analysis

All statistical analyses were performed in R (version 4.3.2; R Core Team, 2023). Prior to analyses, island area and gull density variables were log-transformed where appropriate to improve normality and reduce heteroscedasticity. Outliers were visually assessed and removed only when clearly attributable to measurement error or sample contamination. Duplicate samples were analyzed to ensure consistency among isotopic readings. Once measurement reliability was confirmed, only a single value per sample was retained for all subsequent statistical analyses.

To evaluate abiotic and biotic factors influencing seabird abundance, gull density (individuals km^2, log-transformed) was modeled as a function of log-transformed island area (km^2) and grazing status using linear models (lm). Differences in $\delta^{13}C$, $\delta^{15}N$, %C, and %N among sample types and grazing treatments were tested using linear mixed-effects

models (lmer in lme4) with islet identity included as a random effect to account for spatial non-independence. Best models were determined using Akaike's information criterion correcting for small sample size (AICc). Predicted relationships between gull density and explanatory variables were visualized using ggplot2, with 95% confidence intervals generated from model predictions. Isotopic niche space and trophic enrichment patterns were illustrated with bivariate $\delta^{13}C$– $\delta^{15}N$ plots. Significance was assessed at $\alpha = 0.05$ for all tests.

RESULTS

Gull Densities Across Islands

Gull densities varied considerably across the study islands (n = 22), with an overall mean of 884.622 ± 321.177 indiv./km^2 [Mean ± SE, range: 17.146-5,468.486 indiv./km^2, see Table 1.]. Grazed islands had on average much lower gull densities (307.212 ± 306.754 indiv./km^2) and were somewhat larger in area (0.014-0.869 km^2) compared to ungrazed islands, which had both a higher mean gull density of 2,175.597 ± 810.118 indiv./km^2 and smaller island areas (0.007-0.146 km^2). A one-way ANOVA indicated a significant effect of grazing status on island perimeter-to-area ratios (Grazing_status: df = 2, SS = 937.7, MS = 468.8, F = 4.499, p = 0. 025). Grazed islands exhibited lower perimeter:area (mean ± SE, range: 18.4 ± 9.285) relative to the smaller-sized ungrazed islands (32.554 ± 11.970). A post-hoc Tukey test indicated that never grazed islands differed significantly from both currently grazed (p =0.028) and previously grazed islands (p = 0.08) whereas currently grazed and previously grazed islands did not differ significantly (p > 0.05). Previously grazed islands displayed the lowest mean gull density (227.370 ± 137.648 indiv./km^2), while island areas (0.014-0.817 km^2) and perimeter:area (18.827 ± 9.278) were similar to those of currently grazed islands, reflecting the preference for introducing goats on larger islands that may have more resources to sustain a herd.

Model comparisons testing different hypotheses on the importance of island area and grazing status on gull densities are shown in Table 2. The best model (Table 2, 3), which

received 45% of the AICc weight, included only island area (km^2) as the strongest predictor of gull density. However, this model was not significantly different from the one including island area (km^2), grazing status, and the interaction between island area and grazing status as predictors of gull density (ΔAICc = 0.18). The full presentation of one of the two lowest AICc model (see Table 3) demonstrates that larger islands generally supported lower gull densities, indicating that gulls prefer smaller islands to nest on [Figure 3]. Furthermore**,** the statistically similar model including grazing status and the interaction term points to a pronounced detrimental effect of grazing goats on nesting gull density; a more attenuated impact of past grazing on gull density suggests that there is partial, and likely speedy, recovery of gull populations following cessation of stocking with island grazers (Table 3). The impacts of goat grazing on gulls appear to be more pronounced on small islands (see Table 3 and Figure 3) where the lack of space does not allow the animals to readily avoid each other.

Sample Size	Gull Density Model	d.f.	AICc	ΔAICc	Model Likelihood	AICc Weight	$R^2_{adj.}$
Islands	~ Intercept	1	53.46	8.17	0.02	0.01	0.000
(n=22)	~ Grazing	3	52.87	7.57	0.02	0.01	0.229
	~ Island Area	**2**	**45.30**	**0.00**	**1.00**	**0.45**	**0.382**
	~ Island Area + Grazing Status	4	47.83	2.53	0.28	0.13	0.466
	~ Island Area * Grazing Status	6	45.48	0.18	0.91	0.41	0.655

Table 2. AICc and ΔAICc values for linear models tested with independent variables (island area and grazing status) predicting gull density. "Best" model (highest AICc weight) is bolded.

Gull Density (log_{10}transformed individuals/km^2)					
Model (n=22)	**Variable**	**β**	**SE**	**t**	**p-value**
~ Island Area	(Intercept)	2.913	0.156	18.653	**<0.001***
(**AICc** = 45.30, $\mathbf{R^2_{adj.}}$= 0.382, **d.f.** = 20)	Island_size_km2	-1.752	0.498	-3.518	**<0.05***
~ Island Area * Grazing Status	Intercept	3.52459	0.24839	14.1899	**<0.001***
(**AICc** = 45.48, $\mathbf{R^2_{adj.}}$= 0.655, **d.f.** = 16)	Never :Currently Grazed	-1.055	0.327	-3.227	**<0.01***
	Never : Previously Grazed	-0.383	0.374	-1.025	0.320
	Island Area	-12.064	4.240	-2.845	**<0.05***
	Currently Grazed: Island Area	11.225	4.277	2.625	**<0.05***
	Previously Grazed : Island Area	9.757	4.307	2.265	**<0.05***

Table 3. Coefficients (β), error estimates (SE), t-values, and significance levels (p-value) for the top gull density models based on AICc (ΔAICc < 2).

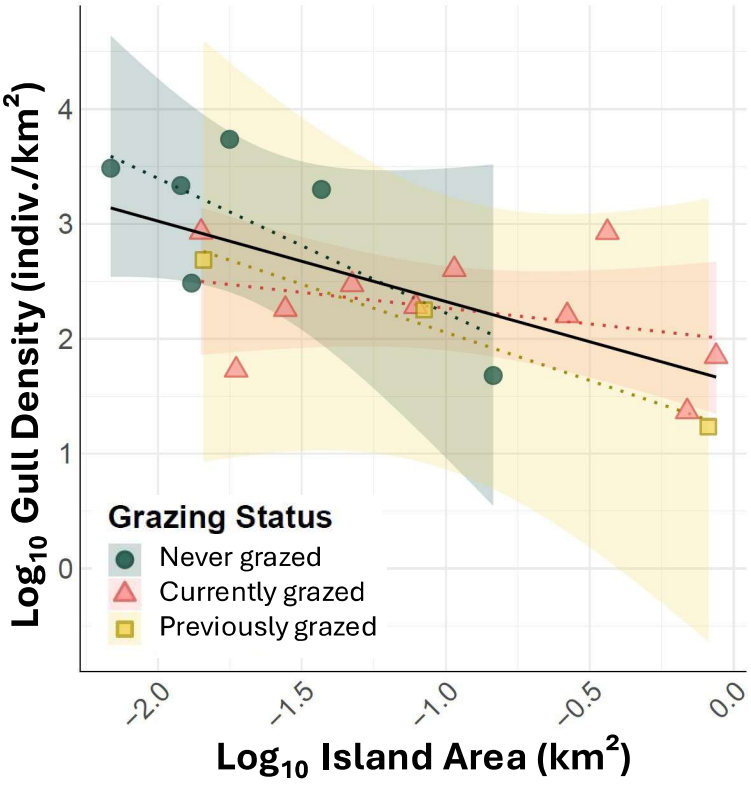


Figure 3. Gull density against island area for islands with different grazing practices. Shaded bands represent 95% confidence intervals. Slopes of lines differ, suggesting that the relationship between gull density and island area differs depending on an island's grazing status. Regression statistics: All islands (y=−0.72x+1.74, R^2=0.36, p=0.00313), not grazed (y=−1.14x+1.19, R^2=0.45, p=0.0986), currently grazed (y=−0.27x+1.99, R^2=0.12, p=0.323), previously grazed (y=−0.98x+1.62, R^2=0.4, p=0.254).

Total Nitrogen (%N)

Across all sample types, arachnids showed the highest values and the widest range of total nitrogen (%N) (11.34 ± 0.85% [mean and standard deviation]) [Table 4]. This matches the results of earlier research (Fagan et al., 2003), which found that %N increases with progressively higher trophic position. Gull guano contained higher and more variable total nitrogen (4.09 ± 1.75%), than goat dung (2.30 ± 0.49%), reflecting gulls' higher trophic positioning and opportunistic marine animal-based diet. *Atriplex recurva, Malva arborea,* and *Pistacia lentiscus* %N values overlapped with that of goat dung, as expected given the goats' herbivorous diet. Among plant species, *M. arborea* showed the highest range for total nitrogen (2.75 ± 1.40%) in line with being a known nitrophile. *P. lentiscus* exhibited the lowest %N values (1.20 ± 0.19%), typical of a slow-growing sclerophyll (Dogan et al., 2003; Rundel, 1988), while *A. recurva* had intermediate %N values (1.95 ± 0.73%).

Sample Type	n	%N	$\delta^{15}N$ (‰)	%C	$\delta^{13}C$ (‰)	C:N
Gull guano	22	4.09 ± 1.75	5.14 ± 1.01	26.57 ± 10.48	-23.45 ± 2.79	7.74 ± 4.35
Soil	75	0.38 ± 0.24	7.90 ± 3.55	4.70 ± 3.45	-22.56 ± 4.34	12.33 ± 6.23
A. recurva	19	1.95 ± 0.73	13.05 ± 2.78	33.19 ± 2.35	-14.62 ± 0.63	19.06 ± 6.39
M. arborea	14	2.75 ± 1.40	8.30 ± 6.43	40.79 ± 3.86	-28.08 ± 1.47	19.64 ± 11.35
P. lentiscus	43	1.20 ± 0.19	2.02 ± 1.98	49.27 ± 1.47	-27.44 ± 1.01	42.30 ± 7.49
Goat dung	8	2.30 ± 0.49	2.68 ± 2.60	47.45 ± 3.07	-28.22 ± 1.19	21.54 ± 5.20
Arachnids	30	11.34 ± 0.85	10.59 ± 4.41	45.15 ± 2.44	-24.21 ± 1.31	4.00 ± 0.29

Table 4. Mean and standard deviation of nutrient variables across each sample type

Gull density did not show a strong relation to %N across sample types, except for in *M. arborea,* which exhibited a statistically significant positive relationship indicating rising foliar nitrogen with increasing gull influence [Figure 4]. All other sample types showed weak or non-significant associations, suggesting limited transfer of seabird-derived nitrogen into those ecosystem components. Grazing effects on %N varied among taxa. Previously grazed islands consistently displayed lower %N than both grazed and ungrazed islands.

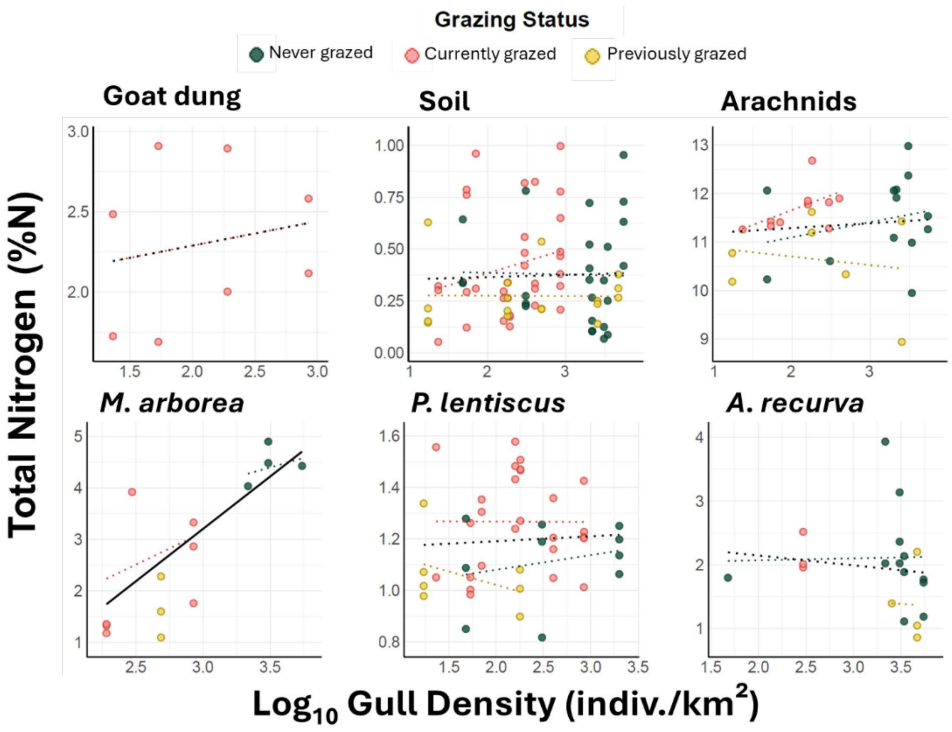


Figure 4. Multipanel scatterplots displaying relationships between gull density (log_{10}transformed individuals/km^2) and percent nitrogen (%N) across six sample types: goat dung, soil, arachnids, *M. arborea*, *P. lentiscus*, and *A. recurva*. Points represent measured %N values and colors indicate grazing status (grazed, ungrazed, previously grazed). Colored lines represent mixed-effects regression fits (incl. Island identity as a random effect) for each grazing category. Black lines represent summary mixed-effects regression fits (incl. island identity as a random effect) across all grazing categories. No significant associations were observed, however *M. arborea* shows a strong association between high gull density and %N on not grazed islands compared to lower values for currently grazed islands.

Model selection varied depending on sample type. Random island effects accounted for substantial variance in soil, *A. recurva,* and *P. lentiscus*. For *M. arborea*, gull density was the best predictor, whereas grazing status contributed strongly only for Arachnids [Table 5,6]. Given that we showed earlier that grazing status profoundly affects gull density numbers, this suggests that grazing indirectly affects nutrient levels through its influence on gull abundance, rather than goat presence directly affecting the amount of nitrogen in the system.

Sample Type	Total Nitrogen (%N) Model	d.f.	AICc	ΔAICc	AICc Weight	$R^2_{Marg.}$	$R^2_{Cond.}$
Soil	**(1 | Island)**	**3**	**1.107**	**0.000**	**0.947**	**0.000**	**0.266**
(n = 75)	Grazing Status + (1 | Island)	5	9.485	8.379	0.014	0.053	0.292
	Gull Density +(1 | Island)	4	7.525	6.418	0.038	0.001	0.282
	Gull Density + Grazing Status + (1 | Island)	6	15.634	14.527	0.001	0.058	0.308
	Gull Density * Grazing Status + (1 | Island)	8	24.311	23.205	0.000	0.073	0.340
A. recurva	**(1 | Island)**	**3**	**-14.298**	**0.000**	**0.865**	**0.000**	**0.324**
(n = 19)	Grazing Status + (1 | Island)	5	-9.711	4.587	0.087	0.213	0.374
	Gull Density +(1 | Island)	4	-8.360	5.938	0.044	0.003	0.352
	Gull Density + Grazing Status + (1 | Island)	6	-3.279	11.019	0.004	0.206	0.392
	Gull Density * Grazing Status + (1 | Island)	8	5.559	19.857	0.000	0.203	0.431
M. arborea	(1 | Island)	3	46.754	2.633	0.158	0.000	0.856
(n = 14)	Grazing Status + (1 | Island)	5	46.242	2.121	0.204	0.520	0.861
	Gull Density +(1 | Island)	**4**	**44.120**	**0.000**	**0.588**	**0.498**	**0.840**
	Gull Density + Grazing Status + (1 | Island)	6	49.310	5.190	0.044	0.498	0.873
	Gull Density * Grazing Status + (1 | Island)	7	53.010	8.890	0.007	0.405	0.896
P. lentiscus	**(1 | Island)**	**3**	**49.551**	**0.000**	**0.717**	**0.000**	**0.271**
(n = 43)	Grazing Status + (1 | Island)	5	53.077	3.526	0.123	0.151	0.381
	Gull Density +(1 | Island)	4	52.883	3.332	0.135	0.013	0.302
	Gull Density + Grazing Status + (1 | Island)	6	57.344	7.793	0.015	0.139	0.418
	Gull Density * Grazing Status + (1 | Island)	7	58.009	8.457	0.010	0.124	0.482
Arachnids	(1 | Island)	3	82.225	0.463	0.380	0.000	0.278
(n = 30)	**Grazing Status + (1 | Island)**	**5**	**81.762**	**0.000**	**0.478**	**0.217**	**0.349**
	Gull Density +(1 | Island)	4	85.888	4.125	0.061	0.008	0.306
	Gull Density + Grazing Status + (1 | Island)	6	85.548	3.786	0.072	0.222	0.382
	Gull Density * Grazing Status + (1 | Island)	8	89.704	7.941	0.009	0.243	0.427

Table 5. AICc and ΔAICc values for linear mixed effects models tested with independent variables (gull density, island area, grazing status) predicting total nitrogen (%N) for each sample type. For each model, "Island" is a random effect to account for non-independence of samples collected from the same islet. Marginal R^2 values indicate the proportion of variance explained only by model fixed effects (i.e. the independent variables), while conditional R^2 measure the proportion of variance explained by both fixed effects and random effects combined. All models reported lower marginal R^2 values compared to conditional R^2 values, meaning that the random effect (island identity) accounted for most of the variation within each sample type. Values and conditional "Best" models (highest AICc weight) are bolded.

Total Nitrogen (%)					
Sample Type	**Variable**	**β**	**SE**	**t**	**P-value**
Soil (n = 75)	(Intercept)	0.372	0.035	10.568	**< 0.001***
$R^2_{cond.}$ = 0.266 d.f.$_{resid.}$ = 72					
A. recurva (n = 19)	(Intercept)	1.952	0.204	9.572	**< 0.001***
$R^2_{cond.}$ = 0.324 d.f.$_{resid.}$ = 40					
M. arborea (n = 14)	(Intercept)	3.194	0.528	6.048	**< 0.01***
$R^2_{cond.}$ = 0.84 d.f.$_{resid.}$ = 10					
P. lentiscus (n = 43)	(Intercept)	1.195	0.039	30.447	**< 0.001***
$R^2_{cond.}$ = 0.271 d.f.$_{resid.}$ = 16					
Arachnids (n = 30)	Gull Density	0.149	0.244	0.609	0.553
$R^2_{cond.}$ = 0.349 d.f.$_{resid.}$ = 25	Currently Grazed	0.380	0.437	0.869	0.399
	Previously Grazed	-0.72	0.44	-1.61	0.13

Table 6. Estimated coefficients and associated errors for "best" total nitrogen (%N) model for each type of sample. Those marked with an asterisk (*) are significant ($p < 0.05$).

Nitrogen Isotope Ratios ($\delta^{15}N$)

Nitrogen isotope ratios varied substantially across the different sample groups (Figure 5). Arachnids had the second-highest mean $\delta^{15}N$ values (10.59 ± 4.41 ‰), reflecting their position as higher-level consumers [Table 4, Figure 5]. Gull guano (5.14 ± 1.01 ‰) exhibited higher $\delta^{15}N$ than goat dung (2.30 ± 0.49‰), also consistent with the gulls' higher trophic positioning. Among plants, *A. recurva* (13.05 ± 2.78 ‰) showed the highest mean $\delta^{15}N$ values, while *M. arborea* (8.30 ± 6.43 ‰) displayed the broadest range of $\delta^{15}N$ values. *P. lentiscus* (2.02 ± 1.98 ‰) showed the lowest mean enrichment $\delta^{15}N$ values.

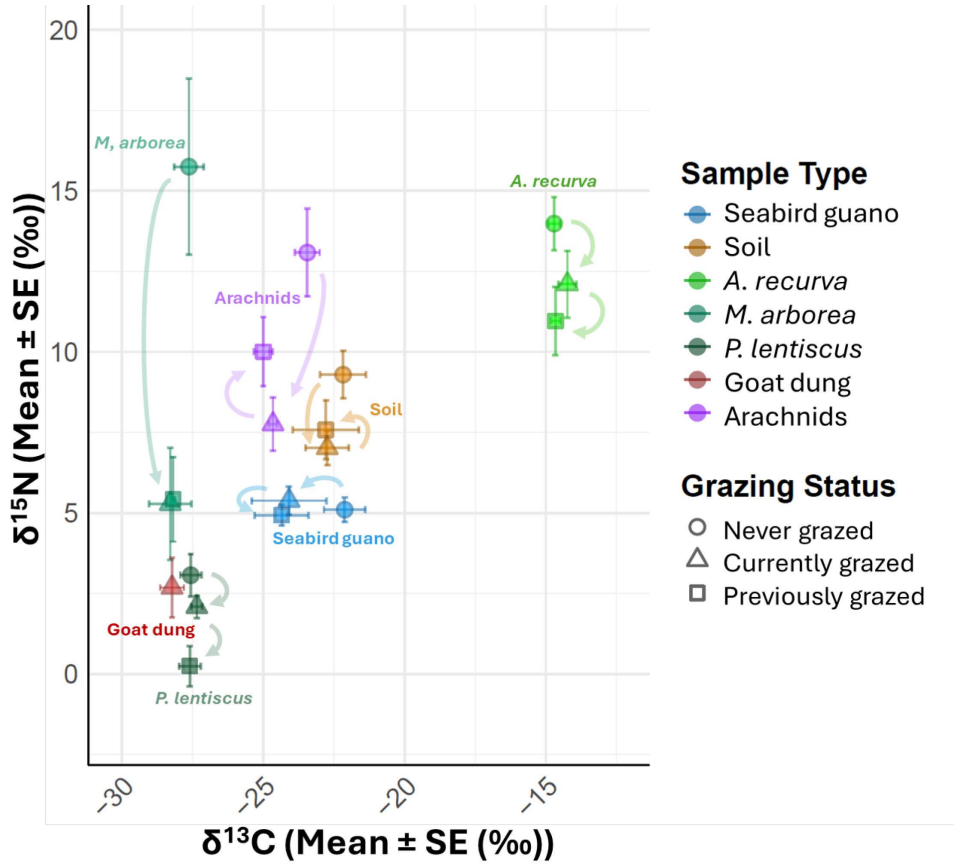


Figure 5. Isotopic niche plot showing means and standard error of each sample type separated by grazing status. Colors correspond to individual sample types. Shapes correspond to island grazing status. Arrows show directionality of grazing regime (starting with not grazed, followed by grazed, and lastly previously grazed) to better showcase the impact of goat introduction and then goat removal on the relative abundance of marine-derived nutrients in different components of island food webs.

Soil, *P. lentiscus,* and arachnids showed significant associations between grazing status, gull density, and $\delta^{15}N$ [Figure 6]. No significant associations were observed between grazing categories for *M. arborea* and *A. recurva*. Regression lines for $\delta^{15}N$ across grazing status categories and gull density overlapped closely, with similar intercepts and slopes, indicating the causative relationship between gull density and $\delta^{15}N$ did not change with grazing regime. (Figure 6). Hence, although ungrazed islands tended to show higher $\delta^{15}N$ across most sample types, these differences appear to be simply the result of the higher gull densities on these islands. Grazing status itself did not appear to have an additional, independent influence via direct top-down effects.

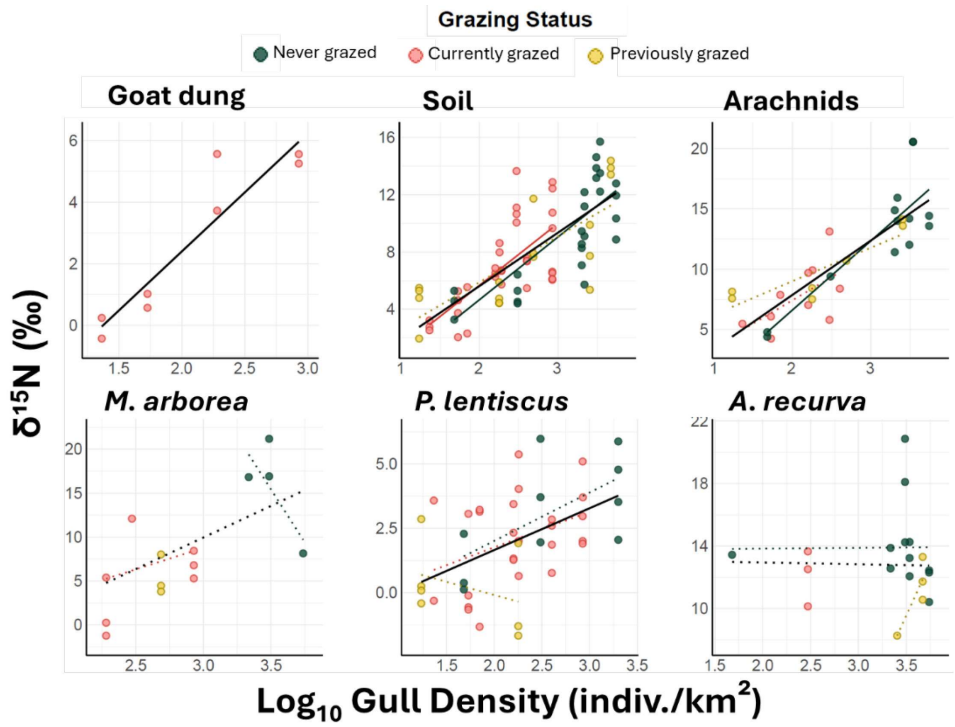


Figure 6. Relationships between gull density (log_{10}transformed individuals/km^2) and $\delta^{15}N$ (‰) across six types of samples: goat dung, soil, arachnids, *M. arborea, P. lentiscus, and A. recurva*. Circle colors indicate grazing status (grazed, ungrazed, previously grazed). Colored lines represent mixed-effects regression fits (incl. Island identity as a random effect) for each grazing category. Black lines represent summary mixed-effects regression fits (incl. island identity as a random effect) across all grazing categories. Solid lines represent significance ($p < 0.05$), and dotted lines represent non-significance ($p > 0.05$). Variation among grazing categories (slope of regression lines) suggests that an island's grazing status can influence isotopic signature strength of seabird-driven nitrogen inputs across island food webs.

Linear Mixed Effects Models identified gull density and grazing status as significant predictors of $\delta^{15}N$ across all sample types. The lowest AICc model across all sample types also included an interaction term between gull density and grazing status, suggesting that the strength of the relationship of gull density on $\delta^{15}N$ was varied among grazing categories, though these interactions were statistically insignificant [Table 7, 8].

Sample Type	$\delta^{15}N$ (‰) Model	df	AICc	ΔAICc	AICc Weight	$R^2_{Marg.}$	$R^2_{Cond.}$
Soil	(1 | Island)	3	336.250	23.105	0.000	0.000	0.846
(n = 75)	Grazing Status + (1 | Island)	5	332.525	19.379	0.000	0.092	0.858
	Gull Density + (1 | Island)	4	314.157	1.012	0.285	0.582	0.845
	Gull Density + Grazing Status + (1 | Island)	6	314.488	1.343	0.242	0.568	0.851
	Gull Density * Grazing Status + (1 | Island)	**8**	**313.145**	**0.000**	**0.473**	**0.556**	**0.855**
A. recurva	(1 | Island)	3	184.185	9.535	0.005	0.000	0.258
(n = 19)	Grazing Status + (1 | Island)	5	179.848	5.198	0.045	0.188	0.290
	Gull Density + (1 | Island)	4	177.373	2.723	0.155	0.244	0.248
	Gull Density + Grazing Status + (1 | Island)	6	176.983	2.332	0.189	0.293	0.293
	Gull Density * Grazing Status + (1 | Island)	**8**	**174.651**	**0.000**	**0.606**	**0.345**	**0.345**
M. arborea	(1 | Island)	3	86.985	5.920	0.020	0.000	0.844
(n = 14)	Grazing Status + (1 | Island)	5	82.065	1.000	0.237	0.342	0.856
	Gull Density + (1 | Island)	4	83.685	2.620	0.106	0.272	0.840
	Gull Density + Grazing Status + (1 | Island)	6	81.996	0.931	0.246	0.283	0.883
	Gull Density * Grazing Status + (1 | Island)	**7**	**81.065**	**0.000**	**0.391**	**0.368**	**0.883**
P. lentiscus	(1 | Island)	3	93.911	4.272	0.061	0.000	0.574
(n = 43)	Grazing Status + (1 | Island)	5	91.000	1.361	0.260	0.220	0.662
	Gull Density + (1 | Island)	4	94.558	4.920	0.044	0.000	0.619
	Gull Density + Grazing Status + (1 | Island)	6	92.516	2.877	0.122	0.203	0.694
	Gull Density * Grazing Status + (1 | Island)	**7**	**89.638**	**0.000**	**0.514**	**0.187**	**0.698**
Arachnids	(1 | Island)	3	163.749	23.236	0.000	0.000	0.808
(n = 30)	Grazing Status + (1 | Island)	5	156.652	16.140	0.000	0.260	0.823
	Gull Density + (1 | Island)	4	142.081	1.569	0.255	0.693	0.831
	Gull Density + Grazing Status + (1 | Island)	6	142.700	2.188	0.187	0.677	0.832
	Gull Density * Grazing Status + (1 | Island)	**8**	**140.512**	**0.000**	**0.558**	**0.702**	**0.837**

Table 7. AICc and ΔAICc values for linear mixed effects models that tested different hypothesis-driven predictions (effects of gull density, island area, grazing status) regarding $\delta^{15}N$ (‰) for each sample type. For each model, "Island" is a random effect to account for non-independence of samples collected from the same islet. Marginal R^2 values indicate the proportion of variance explained only by model fixed effects (i.e. the independent variables), while conditional R^2 measure the proportion of variance explained by both fixed effects and random effects combined. All models reported lower marginal R^2 values compared to conditional R^2 values, meaning that the random effect (island identity) accounted for most of the variation within each sample type. "Best" models (highest AICc weight) are bolded.

$\delta^{15}N$ (‰)					
Sample Type	**Variable**	**β**	**SE**	**t**	**P-value**
Soil (n = 75)	(Intercept)	-4.126	3.881	-1.063	0.303
$R^2_{cond.}$ = 0.885 d.f.$_{resid.}$ = 67	Gull Density	4.396	1.230	3.575	**< 0.01***
	Currently Grazed	1.116	5.134	0.217	0.831
	Previously Grazed	3.571	4.994	0.715	0.485
	(Interaction) Gull Density : Currently Grazed	-0.061	1.900	-0.032	0.975
	(Interaction) Gull Density : Previously Grazed	-1.178	1.671	-0.705	0.491
A. recurva (n = 19)	(Intercept)	13.708	5.847	2.344	0.067
$R^2_{cond.}$ = 0.345 d.f.$_{resid.}$ = 35	Gull Density	0.057	1.770	0.032	0.976
	Currently Grazed	-1.747	3.208	-0.545	0.619
	Previously Grazed	-51.411	54.154	-0.949	0.395
	(Interaction) Gull Density : Previously Grazed	13.445	15.231	0.883	0.427
M. arborea (n = 14)	(Intercept)	99.002	74.779	1.324	0.306
$R^2_{cond.}$ = 0.883 d.f.$_{resid.}$ = 7	Gull Density	-23.928	21.228	-1.127	0.367
	Currently Grazed	-105.125	81.092	-1.296	0.318
	Previously Grazed	-29.283	18.882	-1.551	0.253
	(Interaction) Gull Density : Currently Grazed	28.876	24.465	1.180	0.356
P. lentiscus (n = 43)	(Intercept)	-1.694	2.086	-0.812	0.422
$R^2_{cond.}$ = 0.698 d.f.$_{resid.}$ = 12	Gull Density	1.853	0.785	2.360	**< 0.05***
	Currently Grazed	0.686	2.609	0.263	0.794
	Previously Grazed	3.654	3.024	1.208	0.235
	(Interaction) Gull Density : Currently Grazed	-0.467	1.043	-0.448	0.657
	(Interaction) Gull Density : Previously Grazed	-2.879	1.480	-1.945	0.059
Arachnids (n = 30)	(Intercept)	-4.901	3.785	-1.295	0.219
$R^2_{cond.}$ = 0.837 d.f.$_{resid.}$ = 22	Gull Density	5.754	1.191	4.832	**< 0.001***
	Currently Grazed	5.191	5.983	0.868	0.400
	Previously Grazed	8.337	5.073	1.643	0.127
	(Interaction) Gull Density : Currently Grazed	-2.148	2.494	-0.861	0.403
	(Interaction) Gull Density : Previously Grazed	-2.967	1.798	-1.650	0.125

Table 8. Estimated coefficients and associated standard errors for the "best" $\delta^{15}N$ (‰) performing model for various types of samples. Those marked with an asterisk (*) and bolded are significant ($p < 0.05$).

Total Carbon (%C) and Carbon Isotope Ratios ($\delta^{13}C$)

P. lentiscus (49.27 ± 1.47%) and goat dung (47.45 ±3.07%) showed the highest %C, reflecting lignin-rich biomass and herbivory linkages (Massei et al. 2000). Arachnids (45.15 ± 2.44) also showed relatively high %C, whereas soils (4.70 ± 3.45%) had the lowest [Table 4]. Gull guano (26.57 ±10.48%) exhibited broad %C variability associated with an

opportunistic diet that is known to sometimes include significant amounts of plant matter (Carlberg et al., 2022). $\delta^{13}C$ values also varied strongly among plant species, reflecting different photosynthetic pathways (Forero & Hobson, 2003; Still et al., 2003). C_4 plants typically display less negative values ranging around −7‰ to −15‰ and C_3 plants are characterized by more negative values ranging about between −35‰ and −20‰ (Hyodo, 2015; Mulder et al., 2011; Still et al., 2003). This is consistent with our findings in which *A. recurva*, a C_4 plant, showed the most enriched $\delta^{13}C$ values (-14.62 ± 0.63‰), while *M. arborea* and *P. lentiscus* (both C_3 species) were lower (-28.08 ± 1.47‰ and -27.44 ± 1.01‰, respectively) [Figure 5].

Gull density did not significantly influence %C across sample types [Figure 7]. However, $\delta^{13}C$ values increased with gull density in arachnids, indicating greater incorporation of marine-derived inputs on islands with higher seabird abundance, though this pattern was not consistent across all sample types [Figure 8]. Grazing effects were not apparent in %C and $\delta^{13}C$ across sample types, except in arachnids [Figure 7, 8].

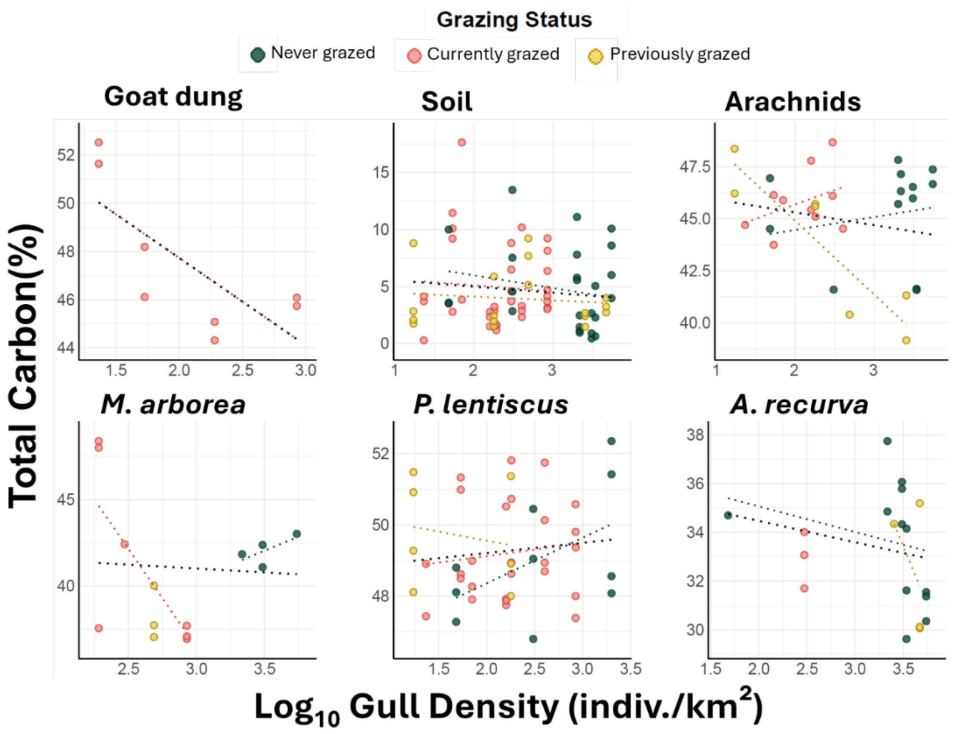


Figure 7. Relationships between gull density (log_{10}-transformed individuals km^2) and total carbon (%C) across six sample types: goat dung, soil, arachnids, *M. arborea*, *P. lentiscus*, and *A. recurva*. Points represent measured %C values and colors indicate grazing status (grazed, ungrazed, previously grazed). Colored lines represent mixed-effects regression fits (incl. Island identity as a random effect) for each grazing category. Black lines represent summary mixed-effects regression fits (incl. island identity as a random effect) across all grazing categories. Solid lines represent significance ($p < 0.05$) and dotted lines represent non-significance ($p > 0.05$). Regression equations, marginal R^2 values, and p-values for each grazing treatment are provided beneath each panel. No significant associations were observed between grazing categories, gull density, and percent carbon.

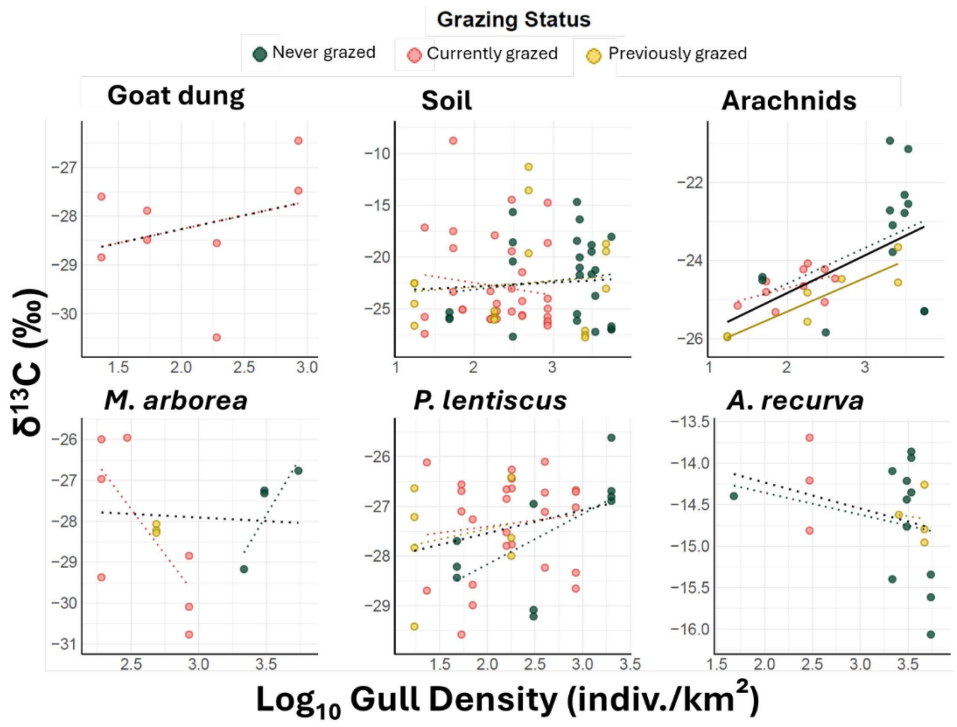


Figure 8. Relationships between gull density (log_{10}-transformed individuals km^2) and $\delta^{13}C$ (‰) across six sample types: goat dung, soil, arachnids, *M. arborea*, *P. lentiscus*, and *A. recurva* Points represent measured $\delta^{13}C$ values and colors indicate grazing status (grazed, ungrazed, previously grazed). Colored lines represent mixed-effects regression fits (incl. Island identity as a random effect) for each grazing category. Black lines represent summary mixed-effects regression fits (incl. island identity as a random effect) across all grazing categories. Solid lines represent significance ($p < 0.05$) and dotted lines represent non-significance ($p > 0.05$). Regression equations, marginal R^2 values, and p-values for each grazing treatment are provided beneath each panel. Arachnids exhibited the strongest positive $\delta^{13}C$ enrichment with increasing gull density, particularly in currently grazed sites, while plants and soil showed weak or inconsistent relationships across grazing categories.

C:N Ratios

C:N ratios were lowest in *M. arborea* and *A. recurva*, indicating higher nitrogen content and potentially greater palatability to grazers, aligning with our field research observations on their relative scarcity on grazed rather than ungrazed islands [Figure 9]. C:N declined with increasing gull density across most taxa, significantly so in *M. arborea (*$y = -16.27x + 65.97$, $R^2 = 0.49$, $p > 0.05$), suggesting enhanced nutrient availability from gull inputs on high-density islands.

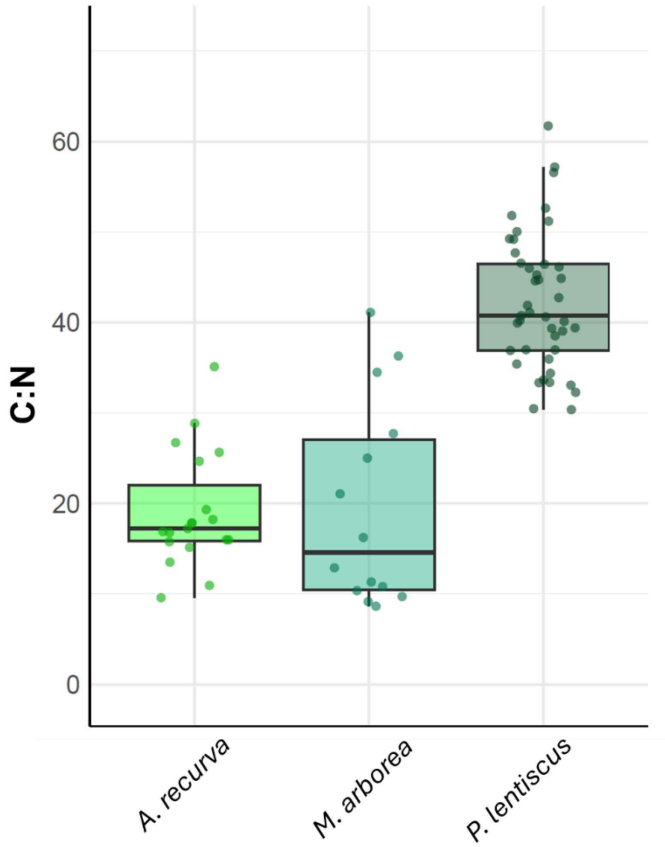


Figure 9. Boxplot displaying C:N ratio for each plant species (a) *A. recurva,* (b) *M. arborea*, (c) *P. lentiscus* with dots showing individual sample values. *P. lentiscus* shows the highest C:N, indicating that the foliar tissues have a substantially higher amount of carbon relative to nitrogen in comparison to the other two plant species.

DISCUSSION

The impact of invasive predators, such as rats and cats, on island systems is comparatively well known, with studies finding that their presence negatively affects islands in a variety of ways, including altering soil chemistry, reducing population abundance and species richness, and disrupting nutrient flow throughout island food webs (Bellingham et al., 2010; Courchamp et al., 2003; Drake et al., 2011; Fukami et al., 2006; Linhares & Bugoni, 2023). In contrast, the impacts of invasive grazers on such systems have not been studied as thoroughly, and many of their effects on nutrient flow dynamics are not well understood. Knowing how introduced herbivores, such as goats or sheep, affect island species communities is essential in order to not only protect these

communities but to also potentially inform pastoral management systems in a way that preserves ecological function and is sustainable in the long term.

Islands in the Mediterranean Basin have been subject to grazing by small ruminants for a very long period of time (Constantakopoulou, 2020; Hatziminaoglou & Boyazoglu, 2004; Horwitz & Bar-Gal, 2006; Lisiecki & Foufopoulos, 2022; Masseti, 2009). The focal islets of this study are all located in the vicinity of larger, inhabited islands, and many of them have been used by local shepherds for seasonal transhumance for over a century. Small livestock -typically goats, which are better adapted to arid conditions and rough terrain-, are transported annually by fishing boat to feed on the seasonal vegetation flush that occurs during and after the winter rain season (Coblentz, 1978). In essence, these mariner-shepherds perform a highly specialized form of seafaring transhumance, allowing their animals to take advantage of seasonally-available forage resources (Forbes, 1995). Length of stay of livestock on the islands varies depending on the amount of vegetation and the length of the growing season which may range between approximately 2 and 6 months. The rest of the year, the animals typically forage on a nearby larger island and may even receive complementary feeding to survive the dry season. Deploying livestock on these islets requires a complex set of specialized seafaring and animal husbandry skills that are gradually disappearing, explaining why some of the study islands are not grazed anymore.

The ecology of the study islands is shaped by the presence of nesting seabirds. Seabirds in general, and Yellow-legged Gulls in particular, act - by delivering notable amounts of N and P, in the form of food scraps, guano and carcasses - as mobile nutrient links between marine ecosystems and island food webs (De La Peña-Lastra, 2021; Hussein et al., 2021; H. Jones et al., 2025; Signa et al., 2012). We find that for the majority of measured C and especially N variables, density of gulls was among the strongest predictors of observed field values.

A variety of factors, both regional, as well as island-specific, determine size of a nesting gull colony. At the regional level, the number of fishing boats, as well as distance to the nearest garbage site have been shown to be associated with the size of resident gull

populations (Carlberg et al., 2022; Duhem et al., 2007, 2008; Zorrozua et al., 2024). Beyond this, we found that island size greatly affects the attractiveness of an island for nesting gulls: gulls are more likely to form dense colonies on smaller islands, probably because they offer more immediate access to the waters' edge.

Influence of Grazing Regime on Gull Density Patterns

Human-mediated changes, such as the introduction of livestock, can profoundly reshape island ecosystems, having both bottom-up and top-down ecological effects. In this study, we observed distinct declines of gull density on presently grazed islands relative to ungrazed ones. These declines in gull density among islands with differing grazing histories are consistent with previously reported long-term ecological impacts of goat introduction on islands (Schweizer et al., 2016) and align with patterns observed in other island systems where introduced herbivores have degraded nesting habitat and reduced seabird reproductive success (Bergmeier et al., 2003; Carlberg et al., 2022; Wright et al., 2010). Goat populations are known to reduce vegetative cover and destabilize soil, leading to increased erosion and ultimately reducing the number of ground-nesting seabirds such as the Yellow-legged Gull (*L. michahellis*) (Bell, 1995; Gizicki et al., 2018; Pafilis et al., 2013; Schweizer et al., 2016). Interestingly, Carlberg *et al.* (2022), found that livestock impact on gull nesting is not - as might be expected - mediated through vegetative cover destruction, but rather through a different mechanism, most likely on direct physical disturbance of incubating birds. In line with this observation, we detected more severe impacts of goat grazing on the gull populations of smaller islands, as expected if physical disturbance or trampling is the main problem for nesting seabirds.

Intermediate gull densities observed on previously grazed islands suggest at least partial recovery of collapsed seabird colonies following goat removal. This indicates that gull populations may respond positively and relatively quickly once grazing pressure is released and vegetation begins to recover. While invasive mammal presence influences on which specific islet within an island cluster gulls choose to nest, it is less likely to impact the total number of nesting birds in the region, which is more likely affected by regional

food-resource availability such as resident fish stocks, human landfills, and discard from fishing vessels. The fact that previously grazed islands have lower nesting gull densities relative to ungrazed islands implies that *full* ecosystem recovery may be slow or incomplete, potentially limited by long-term vegetation shifts induced during grazing periods (Capó et al., 2022; Gizicki et al., 2018; Glen et al., 2013; Prior et al., 2018)

Nitrogen Cycling and Marine-Derived Nutrient Inputs (General patterns in %N and $\delta^{15}N$)

We found comparatively weak effects of either seabird numbers or grazing regime on %N across most samples, but especially in soil. This suggests that whatever marine N subsidies are added by seabirds, they are lost quickly from the island either via microbial processes, leaching, or volatilization (Ramond et al., 2022). The last process may be particularly pronounced given the arid climate, lack of soil depth, and the widespread presence of limestone on the islands, a substrate known to have a higher pH facilitating ammonia volatilization of deposited guano (Austin et al., 2004; De La Peña-Lastra, 2021; Ochoa-Hueso et al., 2011; Torrent, 2005).

The three predominant plant taxa investigated here responded remarkably differently to changes in gull density. The only plant that reflected higher N inputs on gull colonies was *Malva arborea*, a specialized nitrophilous plant growing preferentially exactly at these sites. As a fast-growing, biennial C_3 species, *M. arborea* likely assimilates nitrogen rapidly through its shallow root system and high leaf turnover, making it a sensitive responder to localized guano enrichment. Conversely, *A. recurva* and *P. lentiscus* showed weaker responses in %N, possibly due to differences in physiology. The former, a halophytic C_4 shrub, maintains conservative nitrogen uptake and high water-use efficiency, while *P. lentiscus*, a slow-growing evergreen, tends to recycle nitrogen internally and may rely less on surface nutrient pulses while more clearly showing long-term enrichment effects (Brown, 1978; Thurner et al., 2025). While some of these differences in %N among the three plant species can probably be attributed to different growth forms and life history strategies, the location of plant occurrence also likely plays a role. Plants that grow

primarily in the vicinity of gull colonies (*M. arborea*) are more likely to show shifts in %N when gull numbers decrease, compared to those growing away from seabird sites (e.g. *P. lentiscus*).

Stable isotope analyses revealed clear trophic enrichment patterns - with arachnids often displaying the highest $\delta^{15}N$ and $\delta^{13}C$ values. In contrast, goat dung samples reflected an herbivorous diet largely consisting of *P. lentiscus* - and provided insight into how seabird activity influences island nitrogen dynamics. $\delta^{15}N$ increased with gull density across sample types, showcasing the incorporation of marine-derived nitrogen into the islands' food webs.

Arachnids consume multiple prey sources and preferentially integrate the higher-weight isotopes into their own tissues (Ambrose, 1991). This trophic amplification results in significantly higher $\delta^{15}N$ values relative to plants and soil and makes arachnids more responsive to subtle differences in nutrient sources across islands, even when primary producers (*A. recurva, M. arborea,* and *P. lentiscus*) show weaker or inconsistent patterns of $\delta^{15}N$ and $\delta^{13}C$ (Anderson & Polis, 1998; Sánchez-Piñero & Polis, 2000). $\delta^{15}N$ values of arachnids increased significantly with gull density, providing further evidence of marine nutrient transfer through the food web to upper trophic levels. This pattern also mirrors findings from other island ecosystems which show isotopic enrichment of arthropod consumers linked to seabird nutrient inputs (Pascoe et al., 2022).

Effect of grazing on Nutrient Availability (%N and %C) and Isotopic Signatures ($\delta^{15}N$ and $\delta^{13}C$)

We found that livestock grazing influenced nitrogen availability on small Mediterranean islands primarily indirectly by reducing the density of nesting gulls on goat-grazed islands. Grazing influenced %N and $\delta^{15}N$ levels differently across sample types, with some sample types exhibiting greater %N (e.g. *M. arborea)* or $\delta^{15}N$ (e.g. in soil, *P. lentiscus,* and arachnids) on ungrazed islands, while others showed the opposite or no notable difference. Islands with active grazing were, in general, significantly different from ungrazed islands, with grazing having a negative effect on levels of %N and $\delta^{15}N$. While

previously grazed islands were not quite statistically different from ungrazed islands, they did show somewhat lower %N and $\delta^{15}N$ values, suggesting that there may be legacy effects of grazing that may persist long after goats have been removed (Wright et al., 2010).

The general lack of direct grazing effects on $\delta^{13}C$ and %C indicates that carbon dynamics are less immediately sensitive to goat activity than nitrogen pathways. Nonetheless, the occurrence of lower C:N ratios on ungrazed islands indicates higher relative nitrogen enrichment, consistent with a more pervasive seabird influence.

Evidence of Recovery

The presence of intermediate gull densities and $\delta^{15}N$ enrichment levels on previously grazed islands provides evidence of recovery in both gull populations and nutrient dynamics following goat eradication. While these islands exhibited lower gull densities than ungrazed ones, linear mixed effects models revealed that previously grazed islands were not statistically different from ungrazed islands across all sample types (soil, *M. arborea, A.recurva, P. lentiscus*, and arachnids), arguing for the gradual reintegration of marine-derived nutrients through recolonizing seabirds. In-line with past research - in which islands following invasive species removal saw increases in seabird populations in as quickly as 20 years – we observed similar patterns following the removal of goats from islands in our study (Barbraud et al., 2021; H. P. Jones, 2010). Continued monitoring of these islands should help quantify recovery rates and identify ecological thresholds for restoration success.

Environmental constraints

Despite well-documented effects of goats on vegetation structure, canopy cover, and soil stability (Bell, 1995; Chynoweth et al., 2013; Gizicki et al., 2018; Schweizer et al., 2016), we found no support that top-down herbivory directly shapes the chemical signatures of nitrogen (%N, $\delta^{15}N$) and carbon (%C, $\delta^{13}C$) on these islands. This suggests that on our study islands, direct removal of plant tissue, altered litter inputs, or nutrient export via removed and slaughtered goats does not produce detectable shifts in bulk nutrient pools at the island level. Instead, any direct grazing effects appear to be overshadowed by

reductions in the magnitude of allochthonous nutrient inputs. Although seabirds exerted a clear influence on $\delta^{15}N$ enrichment across soil, plants, and arachnids, total nitrogen (%N) was less correlated with gull density than expected, especially in soil. This aligns with some studies reporting weak or inconsistent relationships between seabird presence and soil nutrient pools, even when strong $\delta^{15}N$ enrichment is observed (Markwell & Daugherty, 2002; Mulder et al., 2011; Orwin et al., 2016). At the same time, our findings contrast with various studies that have documented increases in %N alongside $\delta^{15}N$ in seabird-mediated environments (Leblans et al., 2014; Linhares & Bugoni, 2023; Mulder et al., 2011; Obrist et al., 2022; Polis & Hurd, 1996).

Several environmental and geomorphic processes may explain this weaker relationship. First, the arid Mediterranean climate and geology enhance volatilization of urea and ammonium from guano, which accelerates loss of N as gaseous NH_3 before it can be incorporated into soils or plant tissue (Ambrose, 1991; Blackall et al., 2007; Otero et al., 2018; Ramond et al., 2022; Sánchez-Piñero & Polis, 2000). The study islands are highly wind-exposed with minimal vegetation and often very fine, clay-rich surface soils – conditions that promote aeolian transport of nutrient-rich particles away from deposition sites (Evelpidou et al., 2021; Higgins, 2009; Torrent, 2005). Limestone substrates, which dominate much of the Cyclades, further elevate soil pH and increase volatilization of deposited guano relative to more acidic or organic-rich soils (Austin et al., 2004). Sites with shallow soils or large areas of exposed rock also have limited infiltration and retention capacity, increasing leaching or runoff losses of soluble N during occasional rainfall (De La Peña-Lastra et al., 2020; Ochoa-Hueso et al., 2011; Polis & Hurd, 1996).

Second, water availability is likely the most limiting factor of the study islets during the summer sampling period. In water-limited systems, plants often cannot take advantage of high nutrient inputs, resulting in a disparity between nutrient availability versus intake throughout the food web (Arevalo et al., 2011). Under drought conditions, microbial immobilization also declines, reducing the transfer of seabird-derived nitrogen into soil organic nutrient pools that can be taken up by plants (Austin et al., 2004).

CONCLUSION

Using whole island manipulations, and integrating gull density with island grazing data and stable isotope analysis, we show the importance of seabirds as bio-vectors linking marine and terrestrial nutrient pools as well as the impact of invasive livestock on these insular systems. Across trophic levels, gull density consistently emerged as one of the strongest predictors of $\delta^{15}N$ enrichment, and to a lesser degree %N, confirming their role as major biotic vectors transporting marine-derived nitrogen onto land. Seabird-driven nutrient subsidies elevate nitrogen availability and alter plant community composition (De La Peña-Lastra et al., 2020; Ellis, 2005; Mulder et al., 2011), whereas grazing acts as an opposing force by suppressing seabird populations and degrading habitat (Rosa García et al., 2012; Skarpe & Hester, 2008; Wright et al., 2010). We find that while the introduction of goats has clear effects on seabird density, the strong impact they have on vegetation structure (Gizicki et al., 2018; Rosa García et al., 2012; Schweizer et al., 2016), is not mirrored equally well in the isotopic signatures of the island's food web. Whatever effects small ruminants may have on N and C concentrations, they seem to be mediated primarily through declines in nesting seabirds rather than via direct effects through consumption and removal of plant tissues. In this sense, grazing acts as a deterrent for nesting seabirds, which in turn weakens the bottom-up nutrient subsidies these animals deliver. These findings suggest a broader pattern: nutrient dynamics on small, oligotrophic islands appear to be influenced by the presence of nutrient-importing biotic vectors (i.e. seabirds), and disruptions to those vectors can produce system-wide consequences. Grazers can therefore restructure nutrient landscapes by suppressing the orthogenic marine-nutrient pathway (Signa et al., 2012). The observed patterns emphasize that restoring seabird populations on Mediterranean islands requires not only the removal of invasive grazers but also the protection of nesting habitats and vegetative structure to facilitate ecosystem recovery (Wright et al., 2010).

In summary, our findings contribute to a growing body of evidence demonstrating that island nutrient dynamics are governed by the interaction of biotic vectors (seabirds, grazers) and abiotic constraints (island size, climate). In the Cyclades, management

actions targeting goat removal and seabird habitat restoration are essential to protect the endemic diversity and ecosystem function of these islets.

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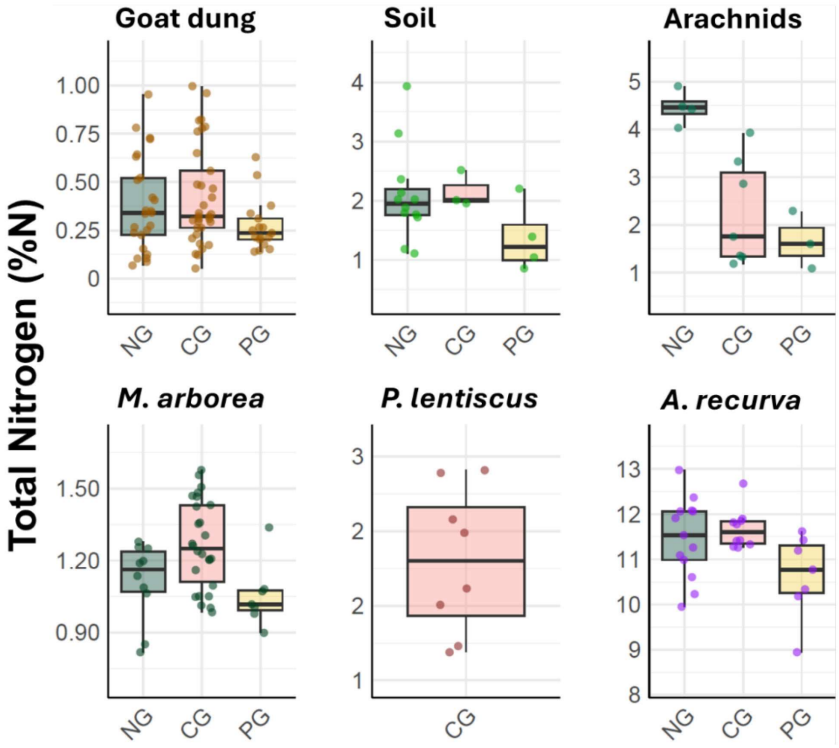
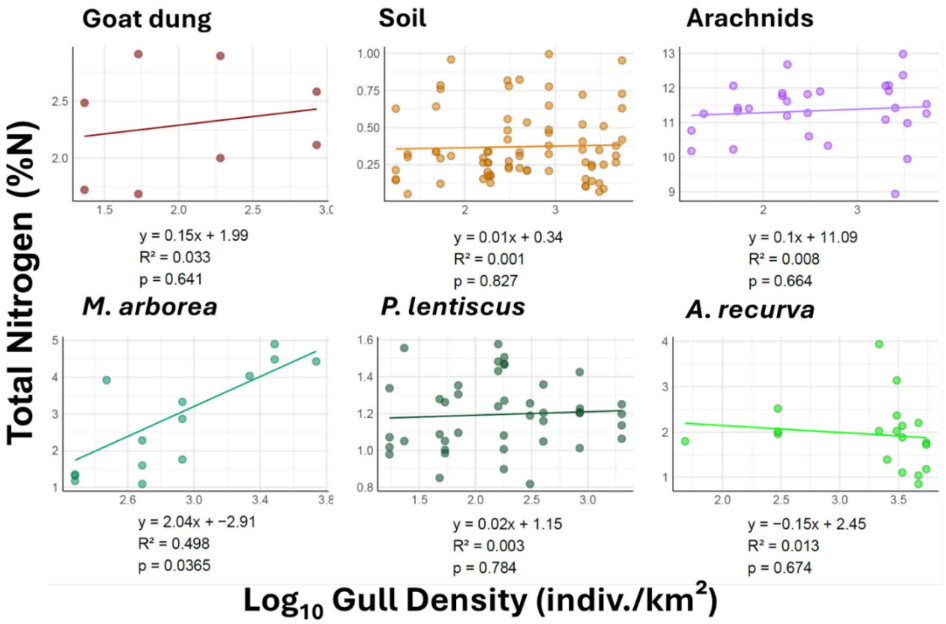
APPENDICES

Appendix A - Total Nitrogen (%N)

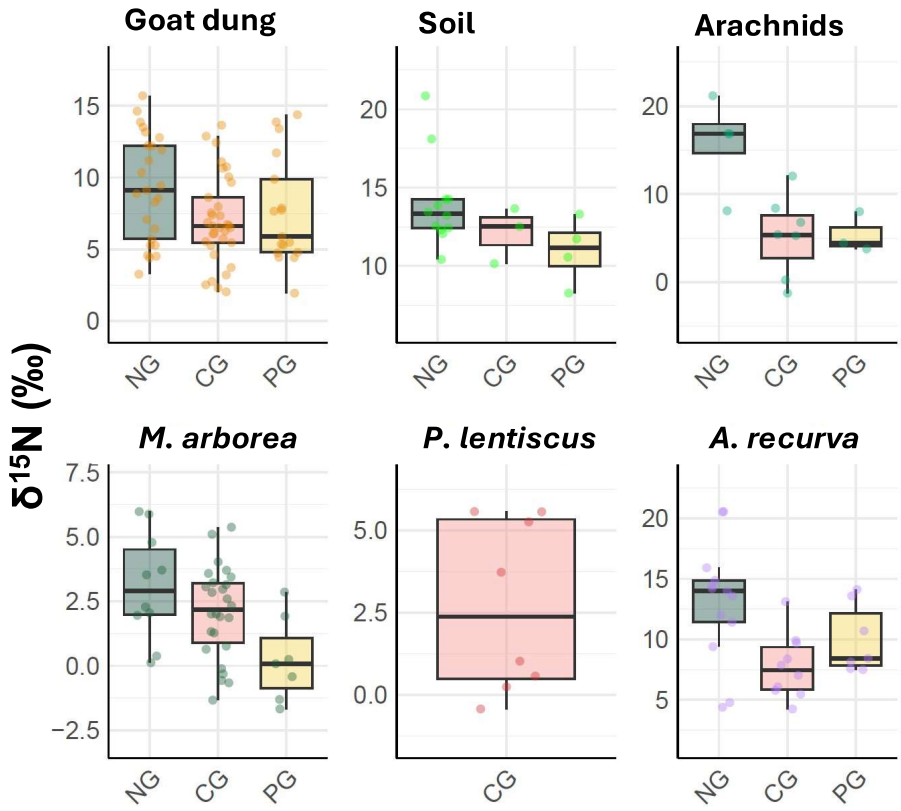


Appendix Figure A1. Boxplots displaying median and interquartile range of %N values for soil, *A. recurva, M. arborea, P. lentiscus,* goat dung, and arachnids across islands that are never grazed (NG), currently grazed (CG), or previously grazed (PG). Points represent individual samples and show variability of %N. Overall, %N varies among sample types but shows minimal differences among grazing categories within each type.

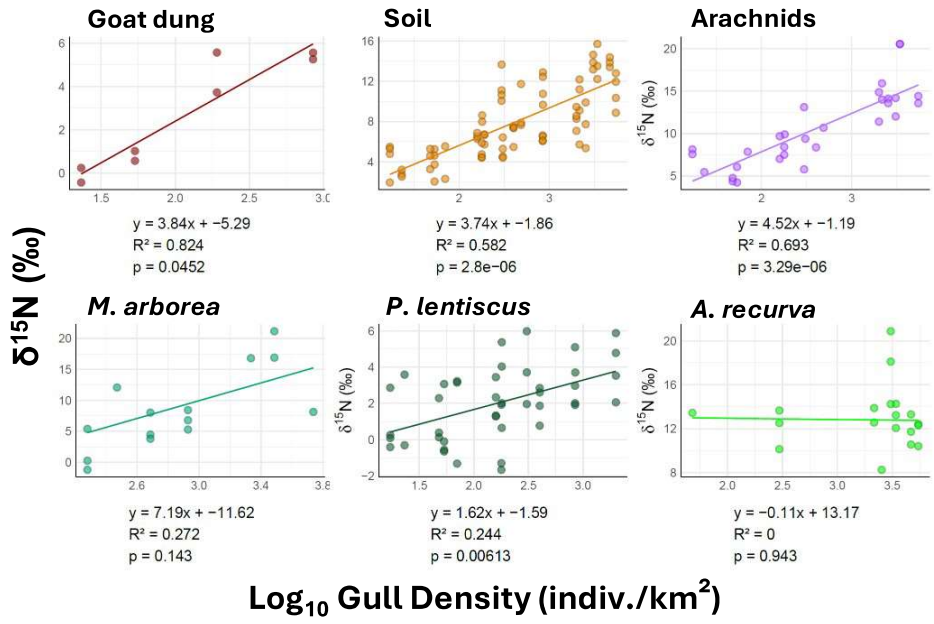


Appendix Figure A2. Multipanel scatterplots displaying relationships between gull density (log_{10}-transformed individuals km^2) and percent nitrogen (%N) for six representative components of the islets' food webs: soil, *A. recurva, M. arborea, P. lentiscus*, goat dung, and arachnids. Each panel shows individual sample values, the fitted linear regression line (with islet identity as a random effect), and corresponding regression statistics (slope, intercept, marginal R^2, and p-value). Among the sample types examined, only *M. arborea* exhibited a significant positive relationship between %N and gull density (p = 0.038), indicating elevated foliar nitrogen with increasing gull influence. All other sample types showed weak or non-significant associations, suggesting limited transfer of gull-derived nitrogen into those ecosystem components.

Appendix B - Isotopic Nitrogen ($\delta^{15}N$)



Appendix Figure B1. Boxplots displaying median and interquartile range of $\delta^{15}N$ values for soil, *A. recurva, M. arborea, P. lentiscus,* goat dung, and arachnids across islands that are never grazed (NG), currently grazed (CG), or previously grazed (PG). Points represent individual samples and show variability of $\delta^{15}N$. Overall, $\delta^{15}N$ varies among sample types but shows minimal differences among grazing categories within each type.



Appendix Figure B2. Relationships between gull density (log_{10}-transformed individuals km^2) and $\delta^{15}N$ (‰) for six representative components of the islets' food webs: soil, *A. recurva, M. arborea, P. lentiscus*, goat dung, and arachnids. Each panel shows individual sample values, the fitted linear regression line (with islet identity as a random effect), and corresponding regression statistics (slope, intercept, marginal R^2, and p-value). All sample types showed a positive correlation between gull density and $\delta^{15}N$, with only *A. recurva* and *M. arborea* showing non-significance ($p > 0.05$), suggesting limited integration of marine-derived nitrogen into their foliar tissue.

Appendix C - Total Carbon (%C)

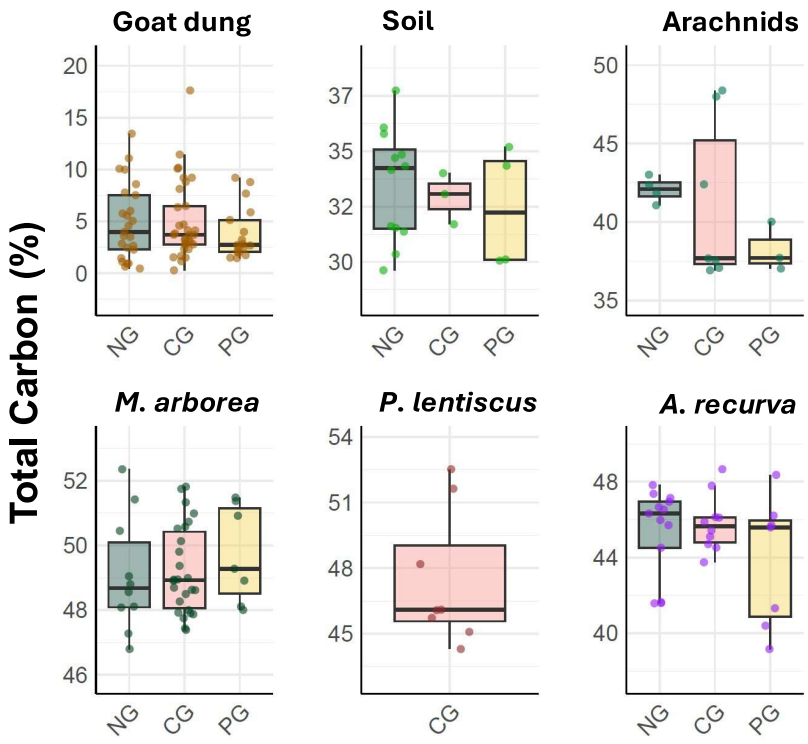
Sample Type	Total Carbon (%) Model	df	AICc	ΔAICc	AICc Weight	$R^2_{Marg.}$	$R^2_{Cond.}$
Soil	(1 | Island)	3	396.814	2.256	0.132	0.000	0.323
(n = 75)	Grazing Status + (1 | Island)	5	396.085	1.527	0.190	0.014	0.358
	Gull Density + (1 | Island)	4	397.284	2.726	0.104	0.013	0.344
	Gull Density + Grazing Status + (1 | Island)	6	396.353	1.795	0.166	0.025	0.377
	Gull Density * Grazing Status + (1 | Island)	**8**	**394.558**	**0.000**	**0.408**	**0.027**	**0.418**
A. recurva	(1 | Island)	**3**	**161.693**	**0.000**	**0.503**	**0.000**	**0.000**
(n = 19)	Grazing Status + (1 | Island)	5	164.369	2.676	0.132	0.019	0.023
	Gull Density + (1 | Island)	4	163.678	1.985	0.186	0.014	0.014
	Gull Density + Grazing Status + (1 | Island)	6	165.209	3.516	0.087	0.059	0.059
	Gull Density * Grazing Status + (1 | Island)	8	165.092	3.399	0.092	0.103	0.103
M. arborea	(1 | Island)	3	81.644	2.329	0.112	0.000	0.321
(n = 14)	Grazing Status + (1 | Island)	5	81.476	2.161	0.122	0.116	0.446
	Gull Density + (1 | Island)	4	81.928	2.613	0.097	0.003	0.364
	Gull Density + Grazing Status + (1 | Island)	**6**	**79.315**	**0.000**	**0.359**	**0.430**	**0.430**
	Gull Density * Grazing Status + (1 | Island)	7	79.606	0.291	0.310	0.486	0.486
P. lentiscus	(1 | Island)	3	89.832	0.954	0.209	0.000	0.430
(n = 43)	Grazing Status + (1 | Island)	5	90.075	1.197	0.185	0.026	0.541
	Gull Density + (1 | Island)	4	90.381	1.503	0.159	0.041	0.466
	Gull Density + Grazing Status + (1 | Island)	6	91.138	2.261	0.109	0.055	0.557
	Gull Density * Grazing Status + (1 | Island)	**7**	**88.878**	**0.000**	**0.337**	**0.084**	**0.615**
Arachnids	(1 | Island)	3	135.330	6.301	0.035	0.000	0.734
(n = 30)	Grazing Status + (1 | Island)	5	134.019	4.989	0.068	0.103	0.762
	Gull Density + (1 | Island)	4	136.099	7.069	0.024	0.038	0.748
	Gull Density + Grazing Status + (1 | Island)	6	134.571	5.541	0.051	0.142	0.770
	Gull Density * Grazing Status + (1 | Island)	**8**	**129.030**	**0.000**	**0.822**	**0.388**	**0.779**

Appendix Table C1. Full AICc and ΔAICc comparison for linear mixed effects models tested with independent variables (gull density, island area, grazing status) predicting total carbon (%C) for each sample type. For each model, "Island" is a random effect to account for the non-independence of samples collected from the same islet. Marginal R^2 values indicate the proportion of variance explained only by model fixed effects (i.e. the independent variables), while conditional R^2 measures the proportion of variance explained by both fixed effects and random effects combined. All models reported lower marginal R^2 values compared to conditional R^2 values, meaning that the random effect (island identity) accounted for most of the variation within each sample type. "Best" model (highest AICc weight) is bolded.

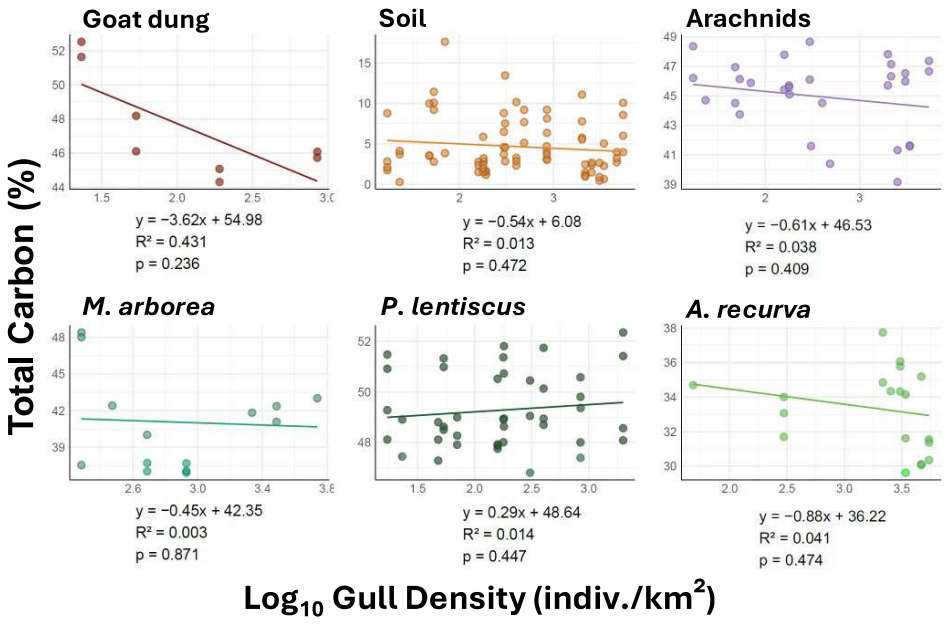
Total Carbon (%)

Sample Type	Variable	β	SE	t	P-value
Soil (n = 75)	(Intercept)	8.197	4.983	1.645	0.120
$R^2_{cond.}$ = 0.418 d.f.$_{resid.}$ = 67	Gull Density	-1.112	1.578	-0.705	0.491
	Currently Grazed	-2.001	6.590	-0.304	0.765
	Previously Grazed	-3.442	6.377	-0.540	0.597
	(Interaction) Gull Density : Currently Grazed	0.567	2.432	0.233	0.819
	(Interaction) Gull Density : Previously Grazed	0.788	2.137	0.369	0.717
A. recurva (n = 19)	(Intercept)	33.384	0.707	47.220	**< 0.001***
$R^2_{cond.}$ = 0 d.f.$_{resid.}$ = 40					
M. arborea (n = 14)	(Intercept)	76.288	12.966	5.884	**< 0.001***
$R^2_{cond.}$ = 0.43 d.f.$_{resid.}$ = 8	Gull Density	-9.744	3.665	-2.658	0.024
	Currently Grazed	-9.942	3.918	-2.537	0.029
	Previously Grazed	-11.851	3.853	-3.075	0.012
P. lentiscus (n = 43)	(Intercept)	45.804	1.833	24.983	**< 0.001***
$R^2_{cond.}$ = 0.615 d.f.$_{resid.}$ = 12	Gull Density	1.278	0.690	1.852	0.072
	Currently Grazed	2.676	2.293	1.167	0.251
	Previously Grazed	4.771	2.658	1.795	0.081
	(Interaction) Gull Density : Currently Grazed	-0.946	0.916	-1.033	0.308
	(Interaction) Gull Density : Previously Grazed	-1.788	1.301	-1.374	0.178
Arachnids (n = 30)	(Intercept)	43.481	3.416	12.727	**< 0.001***
$R^2_{cond.}$ = 0.779 d.f.$_{resid.}$ = 22	Gull Density	0.552	1.078	0.512	0.619
	Currently Grazed	0.126	5.290	0.024	0.981
	Previously Grazed	8.517	4.596	1.853	0.091
	(Interaction) Gull Density : Currently Grazed	0.434	2.195	0.198	0.846
	(Interaction) Gull Density : Previously Grazed	-4.109	1.631	-2.520	**< 0.05***

Appendix Table C2. Coefficients and error estimates for "best" total carbon (%C) model for each sample type. Those marked with an asterisk (*) are significant with a p-value less than 0.05.



Appendix Figure C1. Boxplots displaying median and interquartile range of %C values for soil, *A. recurva, M. arborea, P. lentiscus*, goat dung, and arachnids across islands that are never grazed (NG), currently grazed (CG), or previously grazed (PG). Points represent individual samples and show variability of %C. Overall, %C varies among sample types but shows minimal differences among grazing categories within each type.



Appendix Figure C2. Relationships between gull density (log_{10}-transformed individuals km^2) and percent carbon (%C) for six representative components of the islets' food webs: soil, *A. recurva, M. arborea, P. lentiscus*, goat dung, and arachnids. Each panel shows individual sample values, the fitted linear regression line (with islet identity as a random effect), and corresponding regression statistics (slope, intercept, marginal R^2, and p-value). All sample types except *P. lentiscus* have a slight negative slope. However, no significant associations between gull density and %C were observed.

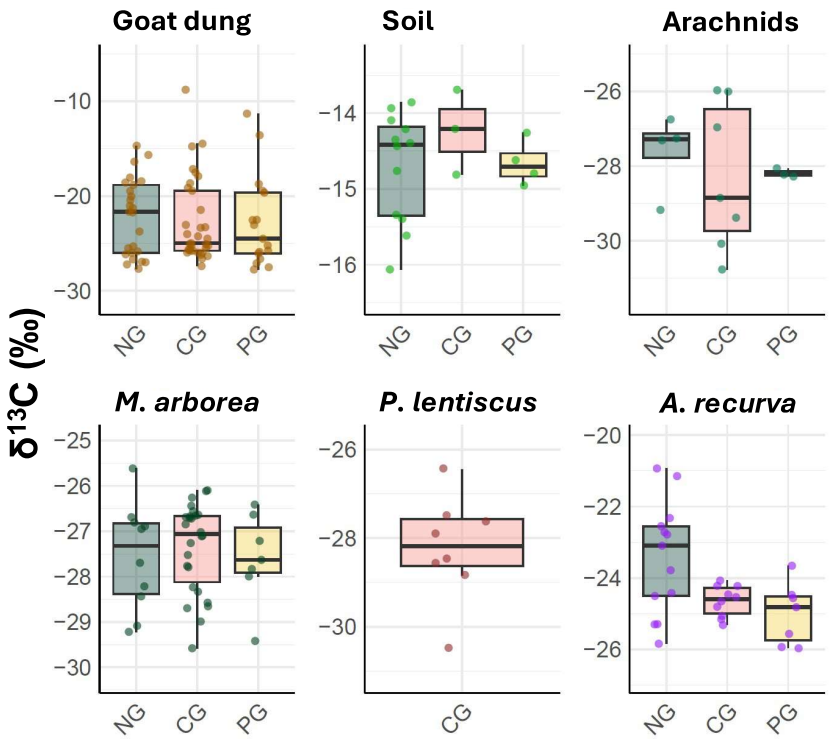
Appendix D - Isotopic Carbon ($\delta^{13}C$)

Sample Type	δ13C (‰) Density Model	df	AICc	ΔAICc	AICc Weight	$R^2_{Marg.}$	$R^2_{Cond.}$
Soil	(1 | Island)	3	430.056	4.085	0.077	0.000	0.324
(n = 75)	Grazing Status + (1 | Island)	5	428.829	2.857	0.142	0.004	0.360
	Gull Density + (1 | Island)	4	430.437	4.465	0.064	0.004	0.342
	Gull Density + Grazing Status + (1 | Island)	6	429.099	3.127	0.124	0.005	0.379
	Gull Density * Grazing Status + (1 | Island)	**8**	**425.972**	**0.000**	**0.593**	**0.019**	**0.416**
A. recurva	**(1 | Island)**	**3**	**129.853**	**0.000**	**0.448**	**0.000**	**0.068**
(n = 19)	Grazing Status + (1 | Island)	5	133.969	4.116	0.057	0.013	0.134
	Gull Density + (1 | Island)	4	130.026	0.173	0.411	0.077	0.084
	Gull Density + Grazing Status + (1 | Island)	6	133.855	4.002	0.061	0.100	0.143
	Gull Density * Grazing Status + (1 | Island)	8	135.750	5.896	0.023	0.130	0.172
M. arborea	**(1 | Island)**	**3**	**55.801**	**0.000**	**0.637**	**0.000**	**0.495**
(n = 14)	Grazing Status + (1 | Island)	5	59.916	4.115	0.081	0.010	0.644
	Gull Density + (1 | Island)	4	57.852	2.051	0.228	0.003	0.561
	Gull Density + Grazing Status + (1 | Island)	6	61.811	6.010	0.032	0.086	0.689
	Gull Density * Grazing Status + (1 | Island)	7	62.520	6.719	0.022	0.363	0.657
P. lentiscus	**(1 | Island)**	**3**	**40.522**	**0.000**	**0.746**	**0.000**	**0.497**
(n = 43)	Grazing Status + (1 | Island)	5	45.826	5.304	0.053	0.055	0.587
	Gull Density + (1 | Island)	4	43.261	2.739	0.190	0.078	0.517
	Gull Density + Grazing Status + (1 | Island)	6	49.765	9.243	0.007	0.084	0.617
	Gull Density * Grazing Status + (1 | Island)	7	50.521	9.999	0.005	0.070	0.673
Arachnids	(1 | Island)	3	94.438	5.202	0.051	0.000	0.797
(n = 30)	Grazing Status + (1 | Island)	5	93.484	4.248	0.081	0.217	0.810
	Gull Density + (1 | Island)	**4**	**89.236**	**0.000**	**0.681**	**0.360**	**0.810**
	Gull Density + Grazing Status + (1 | Island)	6	92.136	2.900	0.160	0.390	0.821
	Gull Density * Grazing Status + (1 | Island)	8	95.717	6.481	0.027	0.363	0.835

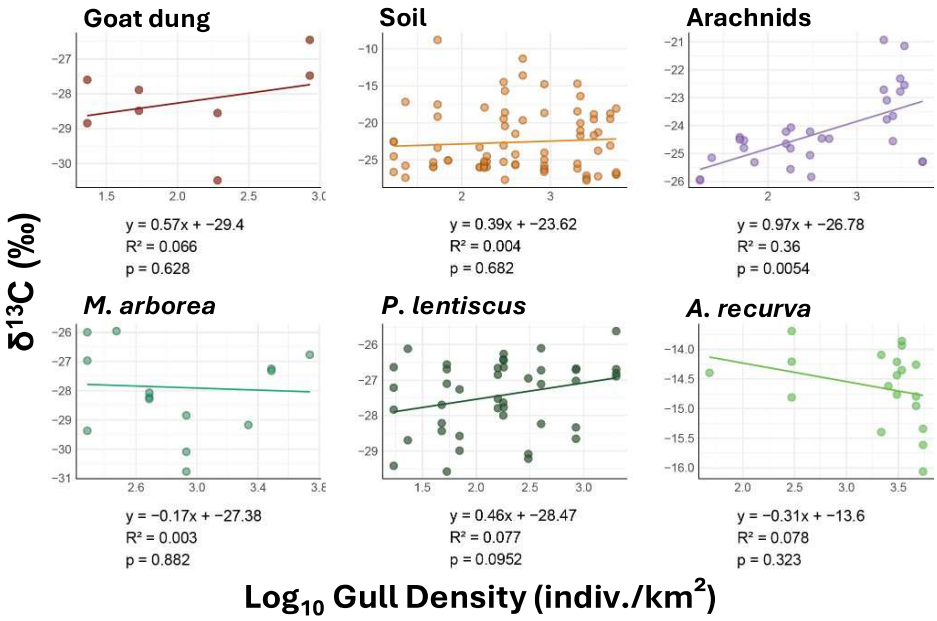
Appendix Table D1. Full AICc and ΔAICc comparison for linear mixed effects models tested with independent variables (gull density, island area, grazing status) predicting $\delta^{13}C$ (‰) for each sample type. For each model, "Island" is a random effect to account for non-independence of samples collected from the same islet. Marginal R^2 values indicate the proportion of variance explained only by model fixed effects (i.e. the independent variables), while conditional R^2 measure the proportion of variance explained by both fixed effects and random effects combined. All models reported lower marginal R^2 values compared to conditional R^2 values, meaning that the random effect (island identity) accounted for most of the variation within each sample type. "Best" model (highest AICc weight) is bolded.

δ13C (‰)					
Sample Type	**Variable**	**β**	**SE**	**t**	**P-value**
Soil (n = 75)	(Intercept)	-25.109	6.278	-4.000	**< 0.01***
$R^2_{cond.}$ = 0.416 d.f.$_{resid.}$ = 67	Gull Density	0.925	1.987	0.465	0.648
	Currently Grazed	4.786	8.302	0.577	0.572
	Previously Grazed	0.907	8.035	0.113	0.912
	(Interaction) Gull Density : Currently Grazed	-2.043	3.063	-0.667	0.514
	(Interaction) Gull Density : Previously Grazed	-0.307	2.692	-0.114	0.911
A. recurva (n = 19)	(Intercept)	-14.615	0.190	-76.894	**< 0.001***
$R^2_{cond.}$ = 0.068 d.f.$_{resid.}$ = 40					
M. arborea (n = 14)	(Intercept)	-27.914	0.506	-55.190	**< 0.001***
$R^2_{cond.}$ = 0.495 d.f.$_{resid.}$ = 11					
P. lentiscus (n = 43)	(Intercept)	-27.443	0.166	-164.879	**< 0.001***
$R^2_{cond.}$ = 0.497 d.f.$_{resid.}$ = 16					
Arachnids (n = 30)	(Intercept)	-26.776	0.808	-33.123	**< 0.001***
$R^2_{cond.}$ = 0.81 d.f.$_{resid.}$ = 26	Gull Density	0.975	0.303	3.215	**< 0.01***

Appendix Table D2. Coefficients and error estimates for "best" $\delta^{13}C$ (‰) model for each sample type. Those marked with an asterisk (*) are significant with a p-value less than 0.05.



Appendix Figure D1. Boxplots displaying median and interquartile range of $\delta^{13}C$ (‰) values for soil, *A. recurva, M. arborea, P. lentiscus*, goat dung, and arachnids across islands that are never grazed (NG), currently grazed (CG), or previously grazed (PG). Points represent individual samples and show variability of $\delta^{13}C$. Overall, $\delta^{13}C$ varies among sample types but shows minimal differences among grazing categories within each type.



Appendix Figure D2. Relationships between gull density (log_{10}-transformed individuals km^2) and $\delta^{13}C$ (‰) for six representative components of the islets' food webs: soil, *A. recurva, M. arborea, P. lentiscus*, goat dung, and arachnids. Each panel shows individual sample values, the fitted linear regression line (with islet identity as a random effect), and corresponding regression statistics (slope, intercept, marginal R^2, and p-value). All sample types except *A. recurva* have a slight positive slope. Arachnids were significantly positive with *P. lentiscus* showing near significance.

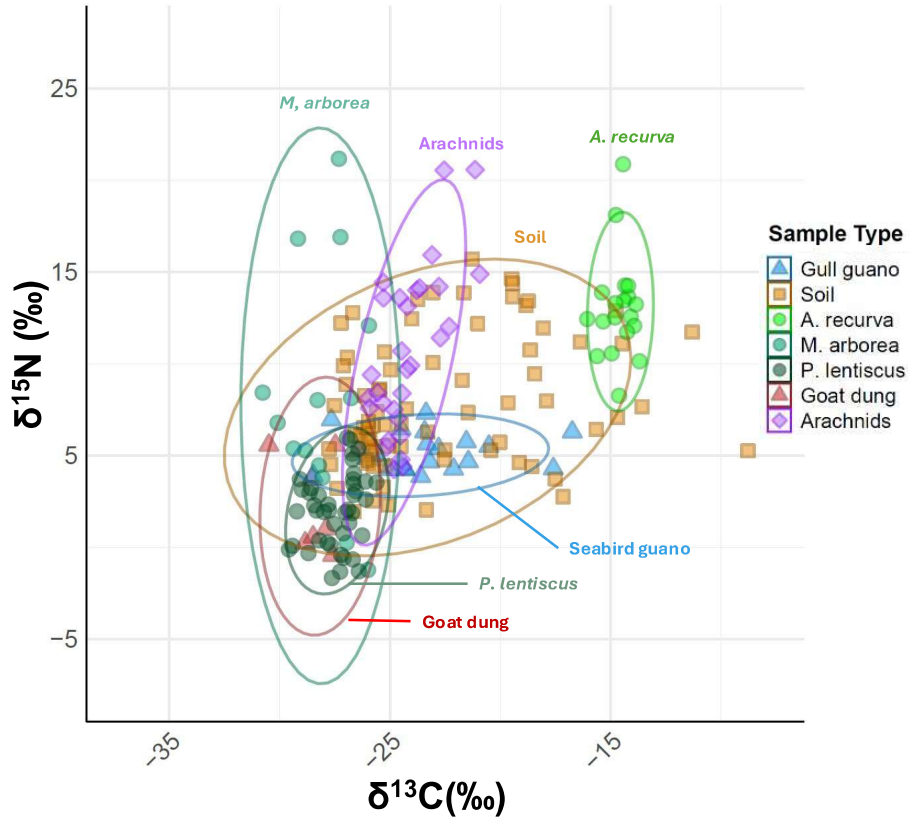
Appendix E – Supplementary Figures and Tables

Island Cluster	#	Island Name	Grazing Status	Geologic Composition	Latitude (Decimal Degrees - WGS 1984)	Longitude (Decimal Degrees - WGS 1984)	Island Perimeter (km2)	Island Area (km2)	Island Perimeter: Area	Gull Count (indiv.)	Gull Density (indiv./km2)
Mykonos	1	Baos	PG	Flysch	25.305492	37.442759	1.30	0.09	15.07	219	2535.46
	2	Prasso	PG	Granodiorite	25.298605	37.392335	1.61	0.06	25.06	301	4687.16
	3	Krommydi	NG	Limestone	25.302744	37.392027	0.83	0.03	33.03	86	3418.53
Paros	4	Agia Kali	NG	Granodiorite	25.22455	37.130141	0.49	0.01	37.22	4	305.67
	5	Tourlos	NG	Limestone	25.097738	36.995675	0.88	0.04	23.83	74	2001.41
	6	Preza	NG	Limestone	25.101456	36.989068	0.55	0.02	31.06	97	5468.49
	7	Tigani	PG	Limestone	25.116047	36.97652	1.33	0.08	15.77	15	178.55
Naxos	8	Parthenos	NG	Granodiorite	25.360664	37.028719	0.51	0.01	42.80	35	2914.24
	9	Miri Vigla	NG	Granodiorite	25.357809	37.023305	0.33	0.01	47.88	34	4962.78
Makares	10	Agios Nikolaos	CG	Limestone	25.695923	37.086595	7.80	0.87	8.98	61	70.21
	11	Agia Paraskevi	CG	Limestone	25.705722	37.080049	2.66	0.26	10.06	42	159.17
	12	Strongili	CG	Limestone	25.704822	37.069214	2.78	0.36	7.64	308	846.17
Koufonissi - Keros	13	Mikri Plaka	CG	Flysch	25.633824	36.879437	0.55	0.02	29.16	1	53.50
	14	Andreas	CG	Limestone	25.622114	36.861854	1.00	0.05	21.11	14	296.40
	15	Loumboudiaris	CG	Limestone	25.637848	36.871179	2.02	0.11	18.88	43	401.88
Amorgos	16	Gramvoussa	PG	Flysch/Marble	25.745804	36.807614	5.92	0.82	7.24	14	17.15
	17	Grambonissi	NG	Rhyolite	25.892366	36.879029	1.76	0.15	12.07	7	47.91
Astypalea	18	Megalo Fokonissi	CG	Limestone	26.34931	36.608847	9.28	0.69	13.46	16	23.21
	19	Tigani	CG	Limestone	26.448958	36.547102	1.13	0.08	14.39	16	203.77
	20	Moni	PG	Limestone	26.444478	36.543433	0.45	0.01	30.99	8	555.90
	21	Ftheno	CG	Limestone	26.450051	36.541905	0.68	0.03	24.62	7	252.70
	22	Chondropoulo	CG	Limestone	26.452407	36.536386	0.50	0.01	35.70	14	991.71

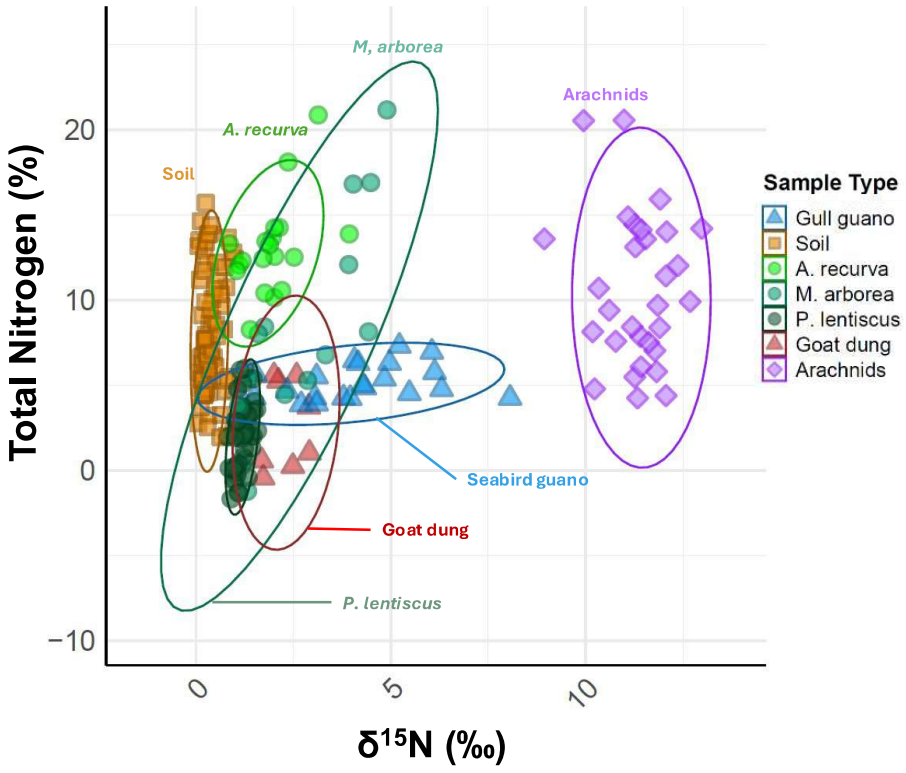
Appendix Table E1. Full table of Islet level characteristics and data

ANOVA	**Variable**	**d.f.**	**Sum of Squares**	**Mean Square**	**F-value**	**p-value$_{adj.}$**
	Grazing Status	2	937.7	468.8	4.5	**< 0.05***
Tukey's HSD	**Group Comparison**	**diff**	**lwr CI**	**upr CI**	**p-value$_{adj.}$**	
	NG : CG	-14.15	-26.935	-1.374	**< 0.05***	
	NG : PG	-13.73	-28.912	1.458	**< 0.05***	
	NG : PG	0.427	-13.777	14.632	0.997	

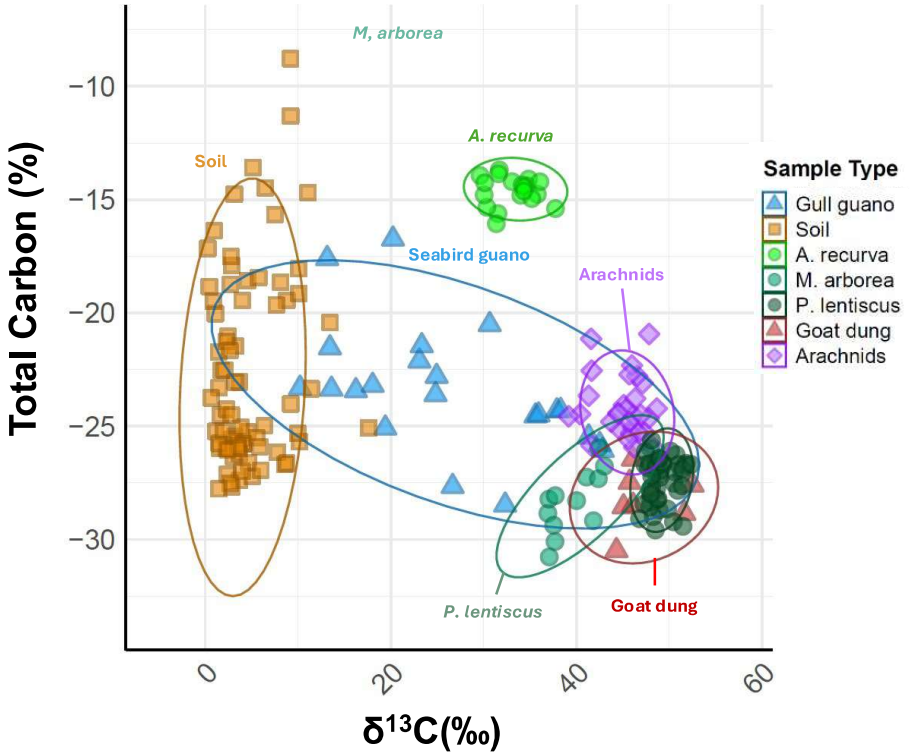
Appendix Table E2. Results of ANOVA and Tukey's Honestly Significant Difference post-hoc test for differences in Perimeter:Area ratio among grazing categories (NG = never grazed, CG = currently grazed, PG = previously grazed). Significant results ($p < 0.05$) are bolded and marked with an asterisk (*). Perimeter-to-area ratio of islands significantly differed across grazing histories ($F_{2,}$ = 4.5, $p < 0.05$). Tukey's post-hoc tests reveal that never-grazed islands differ significantly from both currently and previously grazed islands, whereas currently and previously grazed islands do not differ.



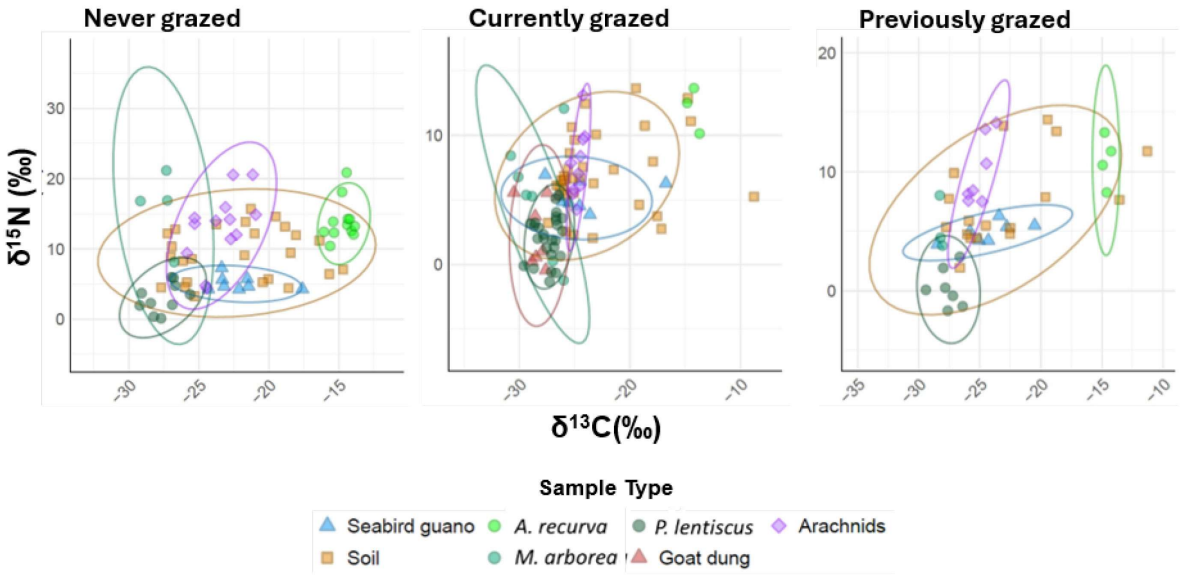
Appendix Figure E1. Bivariate plot showing $\delta^{13}C$ and $\delta^{15}N$ values for different types of samples. Points represent individual samples with different colors and shapes indicating distinct sample types. Colored ellipses depict the 95% confidence regions for each sample type, summarizing isotopic niche and variability. Isotopic signatures reflect differences in nitrogen and carbon sources, as well as trophic positioning of samples.



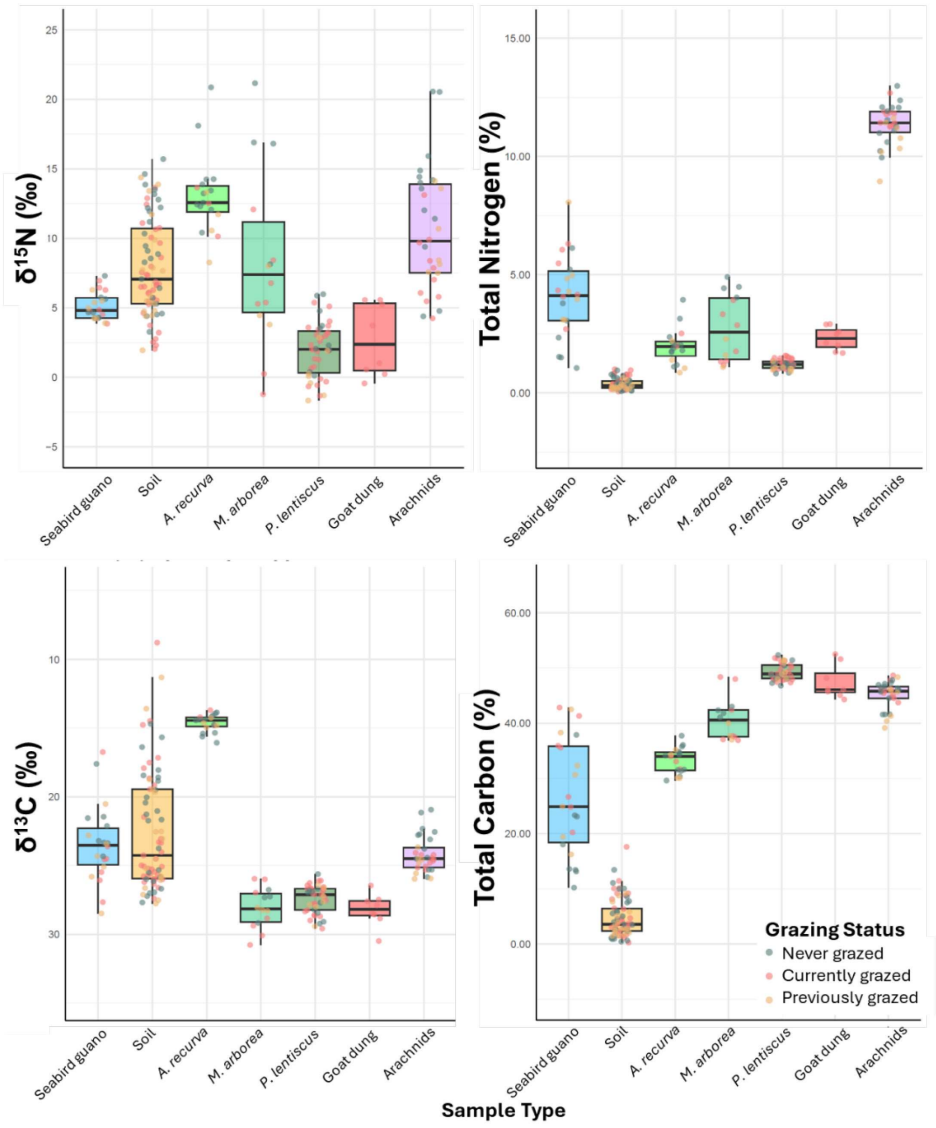
Appendix Figure E2. Bivariate plot showing total nitrogen (%N) and $\delta^{15}N$ (‰) values across different types of samples. Points represent individual samples with different colors and shapes indicating distinct sample types. Colored ellipses depict the 95% confidence regions for each sample type, summarizing isotopic niche and variability. Isotopic signatures reflect differences in nitrogen and carbon sources, as well as trophic positioning of samples.



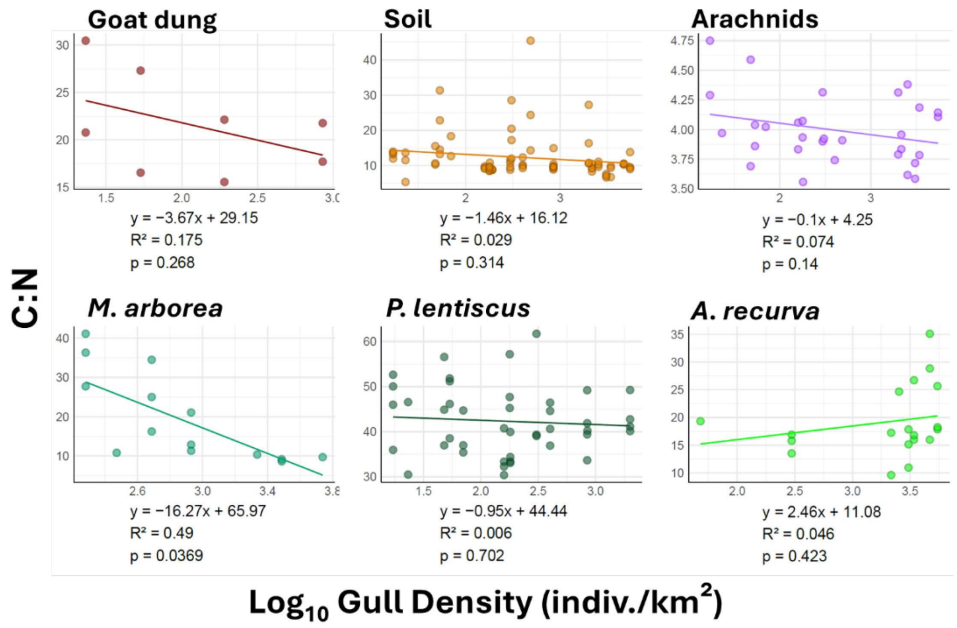
Appendix Figure E3. Bivariate plot showing %C and $\delta^{13}C$ values for different types of samples. Points represent individual samples with different colors and shapes indicating distinct sample types. Colored ellipses depict the 95% confidence regions for each sample type, summarizing isotopic niche and variability. Isotopic signatures reflect differences in nitrogen and carbon sources, as well as trophic positioning of samples and photosynthetic pathways of plants.



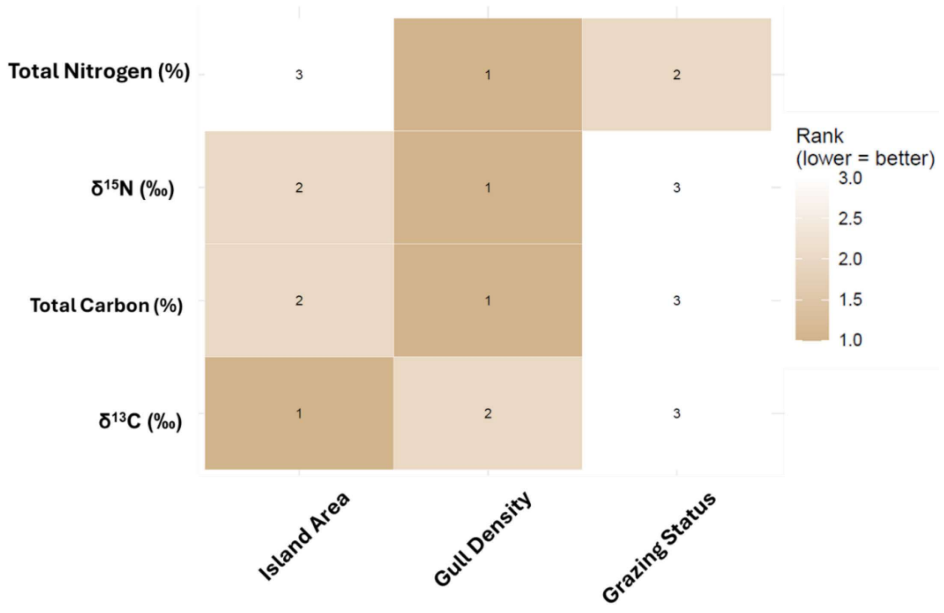
Appendix Figure E4. Multipanel bivariate scatter plots showing $\delta^{13}C$ and $\delta^{15}N$ values for different types of samples separated by island grazing status. Points represent individual samples with different colors and shapes indicating distinct sample types. Colored ellipses depict the 95% confidence regions for each sample type, summarizing isotopic niche and variability. Isotopic signatures reflect differences in nitrogen and carbon sources, as well as trophic positioning of samples.



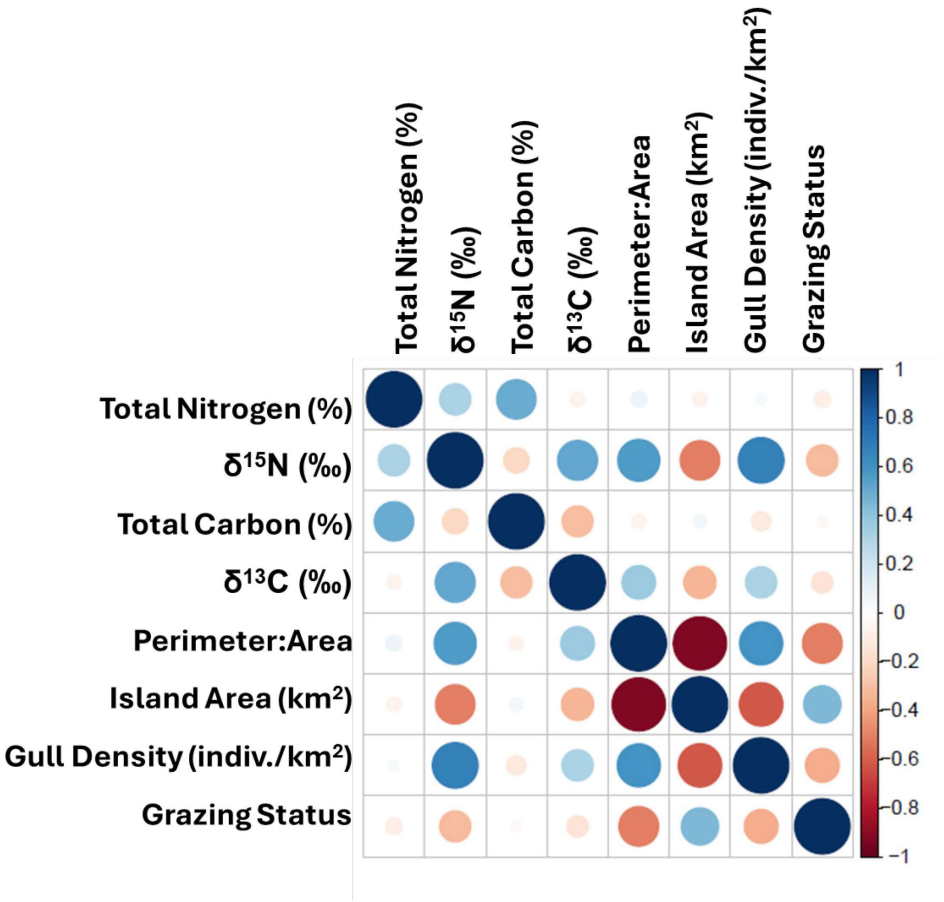
Appendix Figure E5. Multipanel boxplots displaying median and interquartile range of $\delta^{15}N$, %N, $\delta^{13}C$, and %C values for each sample type. Points represent individual samples with colors indicating grazing status of islands from which they were collected.



Appendix Figure E6. Relationships between gull density (log_{10}-transformed individuals km^2) and carbon to nitrogen ratio (C:N) across six sample types: soil, *A. recurva, M. arborea, P. lentiscus,* goat dung, and arachnids. Each panel shows individual sample values, the fitted linear regression line (with islet identity as a random effect), and corresponding regression statistics (slope, intercept, marginal R^2, and p-value). *M.* arborea shows a strong negative effect ($p < 0.05$) of gull density on C:N indicating that on islands with more dense gull populations, *M. arborea* intakes more nitrogen which is reflected in their foliar tissue.



Appendix Figure E7. Heatmap showing the relative importance (rank) of three predictor variables—Island Area, Gull Density, and Grazing Status—on four nutrient metrics (Total Nitrogen, $\delta^{15}N$, Total Carbon, and $\delta^{13}C$) based on AICc of univariate linear mixed models (with individual islet and sample type as a random effects). Darker shading represents a stronger predictor (lower rank value), and numbers within cells indicate each predictor's rank for that response variable.



Appendix Figure E8. Correlation matrix showing relationships among all nutrient and island-level variables, including total nitrogen (%), $\delta^{15}N$, total carbon (%), $\delta^{13}C$, perimeter-to-area ratio, island area (km^2), gull density (individuals/km^2), and grazing status. Circle size and color indicate the strength and direction of Pearson correlation coefficients (blue = positive correlation, red = negative correlation). Strong positive correlations are evident between total nitrogen and $\delta^{15}N$, as well as between total carbon and $\delta^{13}C$. Gull density is moderately related to island area and perimeter-to-area ratio, showing a preference for smaller islands with larger perimeter-to-area ratios. Grazing status exhibits weak correlations with most ecological variables, suggesting limited direct influence on nutrient or isotopic patterns at the island scale.

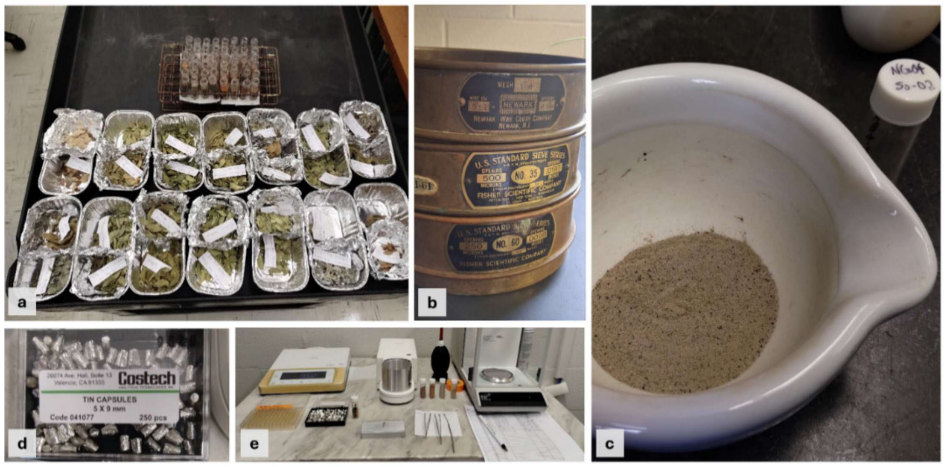
Appendix F – Photos



Appendix Figure F1. (a) Juvenile Yellow-legged Gull (*Larus michahellis*). To the right, are images of depression nests (b) surrounded by surrounded by *Malva arborea* on Mikri Plaka, a never grazed islands and (c) on uncovered on Prasso, a previously grazed islands.



Appendix Figure F2. To the left (a), a goat skull and remains found on Tigani (Astypalea). To the right, visual comparison of vegetation cover between (b) Strongillo an island with active goat grazing, and (c) Grambonissi, an island with no grazing history. Strongilo sparse, low-stature vegetation composed mainly of *Atriplex recurva*. Whereas Grambonissi features dense shrub cover dominated by *Pistacia lentiscus*.



Appendix Figure F3: Preparations for stable isotope analysis. All samples were labeled either using glass tubes marked with permanent marker (e.g. soil and arachnids) or with paper slips marked with both pencil and pen (e.g. foliar plant samples) (a). After drying, sifting (b), and being ground to a fine homogeneous powder (c), small portions of samples (1-10mg) were meticulously weighed and encapsulated in sterile tin capsules (d, e) in preparation for combustion through an elemental analyzer at Northern Illinois University.

Appendix G - R Code

```
####
# Notes on Script ---------------------------
####
# Full dataframes are named in all lowercase with underscores connecting words with data always at end (Example: iso_data)
# Subset dataframes that are incomplete or used as a step to making a larger dataframe may not follow this naming

### --- About data ---
# 30 islands sampled (13 currently grazed, 10 never grazed, 7 previously grazed)
# 22 islands analyzed (10 currently grazed, 7 never grazed, 5 previously grazed)
 # 211 samples total
   # Gull guano       (n=22)
   # Soil    (n=75)
   # Atriplex recurva              (n=19)
   # Malva arborea  (n=14)
   # Pistacia lentiscus           (n=43)
   # Goat dung        (n=8)
   # Arachnids        (n=30)

####
# Initial Set_up ------------------------------------------------------------
####
## Set working directory
setwd("C:/Users/DarkE/Documents/Graduate_Degree_UM/Masters_Thesis/Stable_Isotope_Data/Current")


## Install packages/Load library

# Package names
packages <- c("broom",
          "broom.mixed",
          "car",
          "colorspace",
          "corrplot",
          "cowplot",
          "dplyr",
          "emmeans",
          "ggplot2",
          "gridExtra",
          "lme4",
          "lmerTest",
          "multcomp",
          "MuMIn",
          "performance",
          "openxlsx",
          "readxl",
          "scales")

# Install packages not yet installed
installed_packages <- packages %in% rownames(installed.packages())
if (any(installed_packages == FALSE)) {
  install.packages(packages[!installed_packages])
}

# Packages loading
invisible(lapply(packages, library, character.only = TRUE))
```

```
## Read in data
clean_iso_data <- read_excel("Analysis_Data.xlsx")


####
# Factor levels ------------------------------------------------------------
####
clean_iso_data$Grazing_status <- factor(clean_iso_data$Grazing_status, levels = c("Never grazed","Currently
grazed","Previously grazed"))
clean_iso_data$Sample_type <- factor(clean_iso_data$Sample_type, levels = c("Gull guano","Soil","A. recurva","M.
arborea","P. lentiscus","Goat dung","Arachnids"))
clean_iso_data <- clean_iso_data %>%
 mutate(
  # Round or bin to nearest 0.5
  Island_degredation_cat = round(Island_degredation * 2) / 2,
  # Convert to factor with ordered levels 0, 0.5, ..., 5
  Island_degredation_cat = factor(Island_degredation_cat, levels = seq(0, 5, 0.5))
 )

####
# Assign order, colors, and shapes ----------------------------------------
####
## Assign colors
sample_colors <- c(
 "Gull guano"     = "#0096F2",  # clear blue
 "Soil"           = "#E68600",  # darker orange
 "A. recurva"     = "green",    # leaf green, bright
 "M. arborea"     = "#00A676",  # green-teal
 "P. lentiscus"   = "#145A32",  # dark evergreen
 "Goat dung"      = "#D32F2F",  # medium red
 "Arachnids"      = "#B47CFF"   # lavender purple
)

sample_outlines <- darken(sample_colors, amount = 0.3)

grazing_colors <- c(
 "Never grazed"     = "#0F4C3A",  # very dark green/teal
 "Currently grazed"  = "#fb908d",  # pale brick/rose red
 "Previously grazed" = "#F2D24B"   # saturated golden yellow
)

grazing_outlines <- darken(grazing_colors, amount = 0.3)

## Assign shapes
sample_shapes <- c(
 "Gull guano"    = 24,
 "Soil"          = 22,
 "A. recurva"    = 21,
 "M. arborea"    = 21,
 "P. lentiscus"  = 21,
 "Goat dung"     = 24,
 "Arachnids"     = 23
)

grazing_shapes <- c(
 "Never grazed"       = 21,
 "Currently grazed"   = 24,
```

```
  "Previously grazed"   = 22
)

####
# Set Graphing Limits ------------------------------------------------------
####
## Set limits for perc_N
y_min_percN = 0
y_max_percN = 15
x_min_percN = 0
x_max_percN = 15

## Set limits for dn15
y_min_dn15 = -5
y_max_dn15 = 25
x_min_dn15 = -5
x_max_dn15 = 25

## Set limits for perc_C
y_min_percC = 0
y_max_percC = 55
x_min_percC = 0
x_max_percC = 55

## Set limits for dc13
y_min_dc13 = -35
y_max_dc13 = -10
x_min_dc13 = -35
x_max_dc13 = -10

####
# Create Subsets ------------------------------------------------------------
####
###### Subset numeric data ######
## Subset numeric data
clean_iso_numeric <- clean_iso_data %>%
  select_if(is.numeric)

###### Subset by sample type #######
## Subset gull data
gull_iso_data <- clean_iso_data[clean_iso_data$Sample_type == "Gull guano", ]

## Subset Goat data
goat_iso_data <- clean_iso_data[clean_iso_data$Sample_type == "Goat dung", ]

## Subset Soil data
soil_iso_data <- clean_iso_data[clean_iso_data$Sample_type == "Soil", ]

## Subset plant data
plant_iso_data <- subset(clean_iso_data, Sample_type %in% c("A. recurva", "M. arborea", "P. lentiscus"))
#Rename Sample type column to Species
plant_iso_data <- plant_iso_data %>%
  rename(Species = Sample_type)

## Subset data for each plant species
recurva <- clean_iso_data %>% filter(Sample_type == "A. recurva")
arborea <- clean_iso_data %>% filter(Sample_type == "M. arborea")
lentiscus <- clean_iso_data %>% filter(Sample_type == "P. lentiscus")
```

```
## Subset Arachnids iso data
arachnids_iso_data <- clean_iso_data[clean_iso_data$Sample_type == "Arachnids", ]

###### Subset by grazing status ######
## Subset grazed islands
grazed_iso_data <- clean_iso_data[clean_iso_data$Grazing_status == "Currently grazed", ]

## Subset recovered islands
recovered_iso_data <- clean_iso_data[clean_iso_data$Grazing_status == "Previously grazed", ]

##Subset Never grazed islands
notgrazed_iso_data <- clean_iso_data[clean_iso_data$Grazing_status == "Never grazed", ]

###### Subset mean data ######
## Subset mean data (Group by Island and sample type while keeping specific columns)
mean_iso_data <- clean_iso_data %>%
 group_by(Island_code, Sample_type) %>%
 summarize(
  Cluster = first(Cluster),
  Island_name = first(Island_name),
  Geologic_composition = first(Geologic_composition),
  Island_size_m2 = first(Island_size_m_squared),
  Island_size_km2 = first(Island_size_km_squared),
  LogIsland_size_km2 = first(LogIsland_size_km_squared),
  Island_size_ha = first(Island_size_ha),
  perim_area_m2 = first(perim_area_m2),
  perim_area_km2 = first(perim_area_km2),
  Grazing_status = first(Grazing_status),
  mean_delta_15N = mean(Delta_15N, na.rm = TRUE),
  mean_percN = mean(Perc_N, na.rm = TRUE),
  mean_delta_13C = mean(Delta_13C, na.rm = TRUE),
  mean_percC = mean(Perc_C, na.rm = TRUE),
  mean_cn = mean(CN,na.rm = TRUE),
  Gull_count = first(Gull_count),
  Gull_density_km2 = first(Gull_density_m2),
  Gull_density_km2 = first(Gull_density_km2),
  LogGull_density_km2 = first(LogGull_density_km2),
  .groups = "drop"
 )

## Subset mean data for each sample type separated by grazing status
mean_grazing_data <- clean_iso_data %>%
 group_by(Sample_type, Grazing_status) %>%
 summarize(
  mean_d13C = mean(Delta_13C, na.rm = TRUE),
  mean_d15N = mean(Delta_15N, na.rm = TRUE),
  se_d13C = sd(Delta_13C, na.rm = TRUE) / sqrt(n()),
  se_d15N = sd(Delta_15N, na.rm = TRUE) / sqrt(n()),,
  .groups = "drop"
 )

## Subset mean gull island data data (One point per island)
gull_island_data <- clean_iso_data %>%
 group_by(Cluster, Island_name, Grazing_status) %>%
 summarize(
  Geologic_composition = first(Geologic_composition),
  Island_degredation = first(Island_degredation),
```

```
  Island_size_m2 = first(Island_size_m_squared),
  Island_size_km2 = first(Island_size_km_squared),
  LogIsland_size_km2 = first(LogIsland_size_km_squared),
  Island_size_ha = first(Island_size_ha),
  perim_area_m2 = first(perim_area_m2),
  perim_area_km2 = first(perim_area_km2),
  Grazing_status = first(Grazing_status),
  mean_delta_15N = mean(Delta_15N, na.rm = TRUE),
  mean_percN = mean(Perc_N, na.rm = TRUE),
  mean_delta_13C = mean(Delta_13C, na.rm = TRUE),
  mean_percC = mean(Perc_C, na.rm = TRUE),
  mean_cn = mean(CN,na.rm = TRUE),
  Gull_count = first(Gull_count),
  Gull_density_km2 = first(Gull_density_m2),
  Gull_density_km2 = first(Gull_density_km2),
  LogGull_density_km2 = first(LogGull_density_km2),
  .groups = "drop"
 )

###### Copy clean_iso_data, then remove fecal samples ######
## Remove guano (keep goat dung)
clean_iso_data2 <-  clean_iso_data %>% filter(!Sample_type == "Gull guano")

## Remove all fecal samples
clean_iso_data3 <- clean_iso_data %>% filter(!Sample_type %in% c("Goat dung","Gull guano"))

####
# Boxplots ----------------------------------------------------------------
####
###### %N ######
### Figure A1. Boxplot of %N by sample type and grazing status (One plot)
box_percN_multi <- ggplot(clean_iso_data2, aes(x = Grazing_status, y = Perc_N, fill = Sample_type)) +
 geom_boxplot(aes(fill = Grazing_status), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Sample_type), position = position_jitter(width = 0.2), size = 1, fill = NA, stroke = 1, alpha = 0.60,
show.legend = FALSE) +
 facet_wrap(~ Sample_type, scales = "free") +
 scale_fill_manual(values = grazing_colors)+
 scale_x_discrete(labels = c("Never grazed" = "NG",
                             "Currently grazed" = "CG",
                             "Previously grazed" = "PG")) +
 scale_color_manual(values = sample_outlines)+
 labs(title = "Percent Nitrogen (%) by Sample and Grazing Status", x = "Grazing Status", y = "Percent Nitrogen (%)") +
 theme_minimal()+
 scale_y_continuous(
  expand = expansion(mult = c(0.25, 0.25)),
  labels = number_format(accuracy = 0.01)) +
 theme(legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
     axis.text.y = element_text(size = 14),
     axis.line = element_line(color = "black", linewidth = 0.4),
     axis.title = element_text(size = 16, face = "bold"),
     plot.title = element_text(size = 18, face = "bold"),
     strip.text = element_text(size = 16, face = "bold"),
     panel.border = element_blank(),
     aspect.ratio = 1,
     panel.spacing = unit(1, "lines"))
```

```
#### Figure E5. Boxplots of δ15N by sample type and grazing status (Multiplots by sample type)
box_percN_all_sampletype <- ggplot(clean_iso_data, aes(x = Sample_type, y = Perc_N)) +
 geom_boxplot(aes(fill = Sample_type), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Grazing_status),
         position = position_jitter(width = 0.2),
         size = 1,
         fill = NA,
         stroke = 1,
         alpha = 0.6) +
 scale_color_manual(values = grazing_colors)+
 scale_x_discrete(labels = c("Never grazed" = "NG",
                     "Currently grazed" = "CG",
                     "Previously grazed" = "PG")) +
 scale_fill_manual(values = sample_colors) +
 labs(title = "Percent Nitrogen (%) by Sample Type",
    x = "Sample Type", y = "Percent N (%)", color = "Grazing Status") +
 theme_minimal()+
 #coord_cartesian(ylim = c(y_min_percN, y_max_percN))+
 #scale_y_continuous(breaks = seq(y_min_percN, y_max_percN, by = 5)) +
 scale_y_continuous(
  expand = expansion(mult = c(0.25, 0.25)),
  labels = number_format(accuracy = 0.01)
 ) +
 theme(legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
     axis.text.y = element_text(size = 14),
     axis.line = element_line(color = "black", linewidth = 0.4),
     axis.title = element_text(size = 16, face = "bold"),
     plot.title = element_text(size = 18, face = "bold"),
     strip.text = element_text(size = 16, face = "bold"),
     panel.border = element_blank(),
     aspect.ratio = 1,
     panel.spacing = unit(1, "lines"))

###### δ15N ######
### Figure B1. Boxplot of δ15N by sample type and grazing status (One plot)
box_dn15_multi <- ggplot(clean_iso_data2, aes(x = Grazing_status, y = Delta_15N, fill = Sample_type)) +
 geom_boxplot(aes(fill = Grazing_status), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Sample_type, fill = Sample_type), position = position_jitter(width = 0.2), size = 1,
        stroke = 1, alpha = 0.40, show.legend = FALSE) +
 facet_wrap(~ Sample_type, scales = "free") +
 scale_fill_manual(values = grazing_colors)+
 scale_color_manual(values = sample_colors, na.translate = FALSE)+
 scale_x_discrete(labels = c("Never grazed" = "NG",
                     "Currently grazed" = "CG",
                     "Previously grazed" = "PG")) +
 labs(title = "δ15N (‰) by Sample and Grazing Status",
    x = "Grazing Status",
    y = "δ15N (‰)",
    fill = "Grazing Status") +
 theme_minimal()+
 scale_y_continuous(expand = expansion(mult = c(0.25, 0.25))) +
 theme(legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
```

```
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      aspect.ratio = 1,
      panel.spacing = unit(1, "lines"))

## Figure E5. Boxplots of δ15N by sample type and grazing status (Multiplots by sample type)
box_dn15_all_sampletype <- ggplot(clean_iso_data, aes(x = Sample_type, y = Delta_15N)) +
 geom_boxplot(aes(fill = Sample_type), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Grazing_status),position = position_jitter(width = 0.2),size = 1, fill = NA, stroke = 1, alpha = 0.6) +
 scale_color_manual(values = grazing_colors)+
 scale_fill_manual(values = sample_colors) +
 scale_x_discrete(labels = c("Never grazed" = "NG",
                             "Currently grazed" = "CG",
                             "Previously grazed" = "PG")) +
 labs(title = "δ15N (‰) by Sample Type", x = "Sample Type", y = "δ15N (‰)") +
 theme_minimal()+
 coord_cartesian(ylim = c(y_min_dn15, y_max_dn15))+
 scale_y_continuous(
  expand = expansion(mult = c(0.25, 0.25)),
  labels = number_format(accuracy = 0.01)
 ) +
 theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      aspect.ratio = 1,
      panel.spacing = unit(1, "lines"))

###### %C ######
### Figure C1. Boxplot of %C by sample type and grazing status (One plot)
box_percC_multi <- ggplot(clean_iso_data2, aes(x = Grazing_status, y = Perc_C, fill = Sample_type)) +
 geom_boxplot(aes(fill = Grazing_status), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Sample_type), position = position_jitter(width = 0.2), size = 1,
         fill = NA, stroke = 1, alpha = 0.60, show.legend= FALSE) +
 facet_wrap(~ Sample_type, scales = "free") +
 scale_fill_manual(values = grazing_colors) +
 scale_x_discrete(labels = c("Never grazed" = "NG",
                             "Currently grazed" = "CG",
                             "Previously grazed" = "PG")) +
 scale_color_manual(values = sample_outlines)+
 labs(title = "Percent Carbon (%) by Sample and Island Type", x = "Island Type", y = "Percent Carbon (%)") +
 theme_minimal()+
 scale_y_continuous(
  expand = expansion(mult = c(0.25, 0.25)),
  labels = number_format(accuracy = 0.01)
 ) +
 theme(legend.position = "right",
```

```
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      aspect.ratio = 1,
      panel.spacing = unit(1, "lines"))

## Figure E5. Boxplots of %C by sample type and grazing status (Multiplots by sample type)
box_percC_all_sampletype <- ggplot(clean_iso_data, aes(x = Sample_type, y = Perc_C)) +
 geom_boxplot(aes(fill = Sample_type), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Grazing_status), position = position_jitter(width = 0.2), size = 1, fill = NA, stroke = 1, alpha = 0.6)
+
 scale_color_manual(values = grazing_colors)+
 scale_fill_manual(values = sample_colors) +
 scale_x_discrete(labels = c("Never grazed" = "NG",
                             "Currently grazed" = "CG",
                             "Previously grazed" = "PG")) +
 labs(title = "Percent Carbon (%) by Sample Type",
    x = "Sample Type", y = "Percent C (%)", color = "Grazing Status") +
 coord_cartesian(ylim = c(y_min_percC, y_max_percC))+
 theme_minimal()+
 scale_y_continuous(
  expand = expansion(mult = c(0.25, 0.25)),
  labels = number_format(accuracy = 0.01)
 ) +
 theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      aspect.ratio = 1,
      panel.spacing = unit(1, "lines"))

###### δ13C ######
### Figure D1. Boxplot of δ13C by sample type and grazing status (One plot)
box_dc13_multi <- ggplot(clean_iso_data2, aes(x = Grazing_status, y = Delta_13C, fill = Sample_type)) +
 geom_boxplot(aes(fill = Grazing_status), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Sample_type), position = position_jitter(width = 0.2), size = 1, fill = NA, stroke = 1, alpha = 0.60,
show.legend = FALSE) +
 facet_wrap(~ Sample_type, scales = "free") +
 scale_fill_manual(values = grazing_colors)+
 scale_color_manual(values = sample_outlines)+
 scale_x_discrete(labels = c("Never grazed" = "NG",
                             "Currently grazed" = "CG",
                             "Previously grazed" = "PG")) +
 labs(title = "δ13C (‰) by Sample and Grazing Status", x = "Grazing Status", y = "δ13C (‰)", fill = "Grazing Status") +
 theme_minimal()+
 scale_y_continuous(expand = expansion(mult = c(0.25, 0.25))) +
```

```
 theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      panel.spacing = unit(1, "lines"),
      aspect.ratio = 1)

## Figure E5: Boxplots of δ15N by sample type and grazing status (Multiplots by sample type)
box_dc13_all_sampletype <- ggplot(clean_iso_data, aes(x = Sample_type, y = Delta_13C)) +
 geom_boxplot(aes(fill = Sample_type), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Grazing_status), position = position_jitter(width = 0.2), size = 1, fill = NA, stroke = 1, alpha = 0.6)
+
 scale_color_manual(values = grazing_colors)+
 scale_fill_manual(values = sample_colors) +
 scale_x_discrete(labels = c("Never grazed" = "NG",
                     "Currently grazed" = "CG",
                     "Previously grazed" = "PG")) +
 labs(title = "δ13C (‰) by Sample Type",
    x = "Sample Type", y = "δ13C (‰)", color = "Grazing Status") +
 theme_minimal()+
 scale_y_continuous(expand = expansion(mult = c(0.25, 0.25))) +
 theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      panel.spacing = unit(1, "lines"),
      aspect.ratio = 1)

###### C:N ######
## Figure 9. Boxplots of Carbon-to-nitrogen ratio of each plant species (One plot)

box_CN_multi <- ggplot(clean_iso_data2, aes(x = Grazing_status, y = CN, fill = Sample_type)) +
 geom_boxplot(aes(fill = Grazing_status), alpha = 0.4, outlier.shape = NA, show.legend = FALSE) +
 geom_point(aes(color = Sample_type), position = position_jitter(width = 0.2), size = 1,
         fill = NA, stroke = 1, alpha = 0.60, show.legend = FALSE) +
 facet_wrap(~ Sample_type, scales = "free") +
 scale_fill_manual(values = grazing_colors) +
 scale_color_manual(values = sample_outlines)+
 scale_x_discrete(labels = c("Never grazed" = "NG",
                     "Currently grazed" = "CG",
                     "Previously grazed" = "PG")) +
 labs(title = "C:N Values by Sample and Island Type", x = "Island Type", y = "C:N") +
 theme_minimal()+
 #coord_cartesian(ylim = c(y_min_percN, y_max_percN))+
 #scale_y_continuous(breaks = seq(y_min_percN, y_max_percN, by = 5)) +
 scale_y_continuous(
```

```
   #breaks = seq(0, 5, by = 1),
   expand = expansion(mult = c(0.25, 0.25)),
   labels = number_format(accuracy = 0.01)
  ) +
  theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      panel.spacing = unit(1, "lines"),
      aspect.ratio = 1)

## Figure 9. Boxplot of CN of the plant species (One plot)
box_CN_plants <- ggplot(plant_iso_data, aes(x = Species, y = CN))+
  labs(title = "C:N by Plant Species", x = "Species", y = "C:N", fill = "Grazing Status")+
  geom_boxplot(aes(fill = Species), alpha = 0.4, outlier.shape = NA) +
  geom_point(aes(color = Species),
          position = position_jitter(width = 0.2),
          size = 1,
          fill = NA,
          stroke = 1,
          alpha = 0.60,
          show.legend = FALSE) +
  scale_fill_manual(values = sample_colors)+
  scale_color_manual(values = sample_outlines)+
  scale_x_discrete(labels = c("Never grazed" = "NG",
                      "Currently grazed" = "CG",
                      "Previously grazed" = "PG")) +
  theme_minimal()+
  #coord_cartesian(ylim = c(y_min_percN, y_max_percN))+
  #scale_y_continuous(breaks = seq(y_min_percN, y_max_percN, by = 5)) +
  scale_y_continuous(
   #breaks = seq(0, 5, by = 1),
   expand = expansion(mult = c(0.25, 0.25)),
   labels = number_format(accuracy = 0.01)
  ) +
  theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      panel.spacing = unit(1, "lines"))

###### Export Boxplots ######
pdf(file = 'Thesis_boxplots.pdf')
  print(box_percN_all_sampletype)
  print(box_percN_multi)
  print(box_dn15_all_sampletype)
```

```
 print(box_dn15_multi)
 print(box_percC_all_sampletype)
 print(box_percC_multi)
 print(box_dc13_all_sampletype)
 print(box_dc13_multi)
 print(box_CN_multi)
 print(box_CN_plants)

dev.off()

####
# Isotopic Niche Plots ----------------------------------------------------
####

###### Samples separate ######
## Figure E1. Isotopic niche plot all samples together (One plot)
isoniche_by_sample_ellipse <- ggplot(clean_iso_data, aes(x=Delta_13C, y=Delta_15N))+
 ggtitle ("All Samples by Sample Type")+
 labs(subtitle = "(Isotopic Niche: Carbon and Nitrogen)",
     x = "δ13C (‰)",
     y = "δ15N (‰)",
     fill = "Sample Type",
     color = "Sample Type",
     shape = "Sample Type") +
 geom_point(aes(fill = Sample_type, color = Sample_type, shape = Sample_type),
         size = 3,
         stroke = 1,
         alpha = 0.50) +
 coord_cartesian(ylim = c(y_min_dn15, y_max_dn15), xlim = c (x_min_dc13, x_max_dc13))+
 theme_minimal()+
 scale_x_continuous(
  breaks = seq(x_min_dc13, x_max_dc13, by = 10),
  expand = expansion(mult = 0.15)) +
 scale_y_continuous(
  breaks = seq(y_min_dn15, y_max_dn15, by = 10),
  expand = expansion(mult = 0.15)) +
 scale_color_manual(values = sample_outlines) +
 scale_fill_manual(values = sample_colors) +
 scale_shape_manual(values = sample_shapes) +
 stat_ellipse(aes(color = Sample_type, group= Sample_type), level = 0.95, geom = "path", linewidth = 0.75, alpha = 0.5)  +
 theme(legend.position = "none",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
     axis.text.y = element_text(size = 14),
     axis.line = element_line(color = "black", linewidth = 0.4),
     axis.title = element_text(size = 16, face = "bold"),
     plot.title = element_text(size = 18, face = "bold"),
     strip.text = element_text(size = 16, face = "bold"),
     panel.border = element_blank(),
     aspect.ratio = 1)

## Figure E4. Isotopic niche plot separated by grazing status (Multi-plot)
# For currently grazed islands
isoniche_grazed <- ggplot(grazed_iso_data, aes(x = Delta_13C, y = Delta_15N)) +
 ggtitle("Grazed Island Samples") +
 labs(subtitle = "(Isotopic Niche: Carbon and Nitrogen)",
     x = "δ13C (‰)",
```

```
    y = "δ15N (‰)",
    fill = "Sample Type",
    color = "Sample Type",
    shape = "Sample Type") +
  geom_point(aes(fill = Sample_type, color = Sample_type, shape = Sample_type),
         size = 3, stroke = 1, alpha = 0.50) +
  scale_color_manual(values = sample_outlines) +
  scale_fill_manual(values = sample_colors) +
  scale_shape_manual(values = sample_shapes) +
  stat_ellipse(aes(color = Sample_type, group= Sample_type), level = 0.95, geom = "path", linewidth = 0.75, alpha = 0.5)  +
  scale_x_continuous(expand = expansion(mult = c(0.1, 0.1))) +
  scale_y_continuous(expand = expansion(mult = c(0.1, 0.1))) +
  theme_minimal() +
  theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      aspect.ratio = 1)

# For previously grazed islands
isoniche_recovered <- ggplot(recovered_iso_data, aes(x = Delta_13C, y = Delta_15N)) +
  ggtitle("Recovered Island Samples") +
  labs(subtitle = "(Isotopic Niche: Carbon and Nitrogen)",
      x = "δ13C (‰)",
      y = "δ15N (‰)",
      fill = "Sample Type",
      color = "Sample Type",
      shape = "Sample Type") +
  geom_point(aes(fill = Sample_type, color = Sample_type, shape = Sample_type),
         size = 3, stroke = 1, alpha = 0.50) +
  scale_color_manual(values = sample_outlines) +
  scale_fill_manual(values = sample_colors) +
  scale_shape_manual(values = sample_shapes) +
  stat_ellipse(aes(color = Sample_type, group= Sample_type), level = 0.95, geom = "path", linewidth = 0.75, alpha = 0.5)  +
  scale_x_continuous(expand = expansion(mult = c(0.1, 0.1))) +
  scale_y_continuous(expand = expansion(mult = c(0.1, 0.1))) +
  theme_minimal() +
  theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      aspect.ratio = 1)

#For Never grazed islands
isoniche_notgrazed <- ggplot(notgrazed_iso_data, aes(x = Delta_13C, y = Delta_15N)) +
  ggtitle("Never grazed Island Samples") +
```

```
  labs(subtitle = "(Isotopic Niche: Carbon and Nitrogen)",
      x = "δ13C (‰)",
      y = "δ15N (‰)",
      fill = "Sample Type",
      color = "Sample Type",
      shape = "Sample Type") +
  geom_point(aes(fill = Sample_type, color = Sample_type, shape = Sample_type),
           size = 3, stroke = 1, alpha = 0.50) +
  scale_color_manual(values = sample_outlines) +
  scale_fill_manual(values = sample_colors) +
  scale_shape_manual(values = sample_shapes) +
  stat_ellipse(aes(color = Sample_type, group= Sample_type), level = 0.95, geom = "path", linewidth = 0.75, alpha = 0.5)  +
  scale_x_continuous(expand = expansion(mult = c(0.1, 0.1))) +
  scale_y_continuous(expand = expansion(mult = c(0.1, 0.1))) +
  theme_minimal() +
  theme(legend.position = "right",
      legend.text = element_text(size = 14),
      legend.title = element_text(size = 16, face = "bold"),
      axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
      axis.text.y = element_text(size = 14),
      axis.line = element_line(color = "black", linewidth = 0.4),
      axis.title = element_text(size = 16, face = "bold"),
      plot.title = element_text(size = 18, face = "bold"),
      strip.text = element_text(size = 16, face = "bold"),
      panel.border = element_blank(),
      aspect.ratio = 1)

###### Sample means and SE ######

### Fig 5. Means and SE of samples of each sample type separated by grazing status (One plot)
mean_isoniche_by_grazing_noarrows <- ggplot(mean_grazing_data, aes(x = mean_d13C, y = mean_d15N)) +
  ggtitle("All Samples by Sample Type") +
  geom_errorbar(aes(ymin = mean_d15N - se_d15N, ymax = mean_d15N + se_d15N,
                color = Sample_type), width = 0.2, alpha = 0.5) +
  geom_errorbar(aes(xmin = mean_d13C - se_d13C, xmax = mean_d13C + se_d13C,
                color = Sample_type), height = 0.2, alpha = 0.5) +
  geom_point(aes(fill = Sample_type, color = Sample_type, shape = Grazing_status),
           size = 3, stroke = 1, alpha =0.6) +
  # Arrows for grazing transition direction
  #geom_segment(data = arrow_df,
  #          aes(x = x_start_adj, y = y_start_adj,
  #              xend = x_end_adj, yend = y_end_adj,
  #              color = Sample_type),
  #          arrow = arrow(length = unit(0.25, "cm")),
  #          linewidth = 0.6, alpha = 0.6, show.legend = FALSE) +
  coord_cartesian(xlim = c(min(mean_grazing_data$mean_d13C) - 2, max(mean_grazing_data$mean_d13C) + 2),
                ylim = c(min(mean_grazing_data$mean_d15N) - 2, max(mean_grazing_data$mean_d15N) + 4)) +
  scale_color_manual(values = sample_outlines) +
  scale_fill_manual(values = sample_colors) +
  scale_shape_manual(values = c(21, 24, 22)) +
  labs(
    subtitle = "(Isotopic Niche: Carbon and Nitrogen)",
    x = expression(delta^13*C~"(Mean ± SE)"),
    y = expression(delta^15*N~"(Mean ± SE)"),
    shape = "Grazing Status",
    color = "Sample Type",
    fill = "Sample Type"
  ) +
```

```
 theme_minimal() +
 theme(legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
     axis.text.y = element_text(size = 14),
     axis.line = element_line(color = "black", linewidth = 0.4),
     axis.title = element_text(size = 16, face = "bold"),
     plot.title = element_text(size = 18, face = "bold"),
     panel.border = element_blank(),
     aspect.ratio = 1,
     strip.text = element_text(face = "bold", size = 12))

###### Export Isoniche Plots ######
pdf(file = 'Thesis_Isoniche_plots.pdf')
 print(isoniche_by_sample_ellipse)
 print(isoniche_grazed)
 print(isoniche_recovered)
 print(isoniche_notgrazed)
 print (mean_isoniche_by_grazing_noarrows)
dev.off()

####
# Composition Plots (Nitrogen and Carbon) ------------------------------
####
###### %N and δ15N ######
### Figure E2.Nitrogen composition vs isotopic signature plot (Single plot)
## Add ellipses for each sample type
Nitrogen_by_sample_ellipse <- ggplot(clean_iso_data, aes(x=Perc_N, y=Delta_15N, col=Sample_type,
shape=Sample_type))+
 ggtitle ("Composition Nitrogen")+
 labs(
  subtitle = "(Percent Nitrogen and Delta Values)",
  x = "Percent Nitrogen (%)",
  y = expression(delta^15 * "N (‰)"),
  legend = "Sample Type"
 ) +
 geom_point(aes(fill = Sample_type, shape = Sample_type, color = Sample_type),
        size = 3, stroke = 1, alpha =0.60)+
 scale_color_manual(values = sample_outlines) +
 scale_fill_manual(values = sample_colors) +
 scale_shape_manual(values = sample_shapes) +
 scale_x_continuous(expand = expansion(mult = c(0.1, 0.1))) +
 scale_y_continuous(expand = expansion(mult = c(0.1, 0.1))) +
 theme_minimal()+
 theme(legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
     axis.text.y = element_text(size = 14),
     axis.line = element_line(color = "black", linewidth = 0.4),
     axis.title = element_text(size = 16, face = "bold"),
     plot.title = element_text(size = 18, face = "bold"),
     panel.border = element_blank(),
     aspect.ratio = 1,
     strip.text = element_text(face = "bold", size = 12)) +
 stat_ellipse(aes(group = Sample_type, fill= Sample_type), level = 0.95, geom = "polygon", alpha = 0)
```

```
###### %C and  δ13C ######
### Figure E3. Carbon composition vs isotopic signature plot (single plot)
## Add ellipses for each sample type
Carbon_by_sample_ellipse <- ggplot(clean_iso_data, aes(x=Perc_C, y=Delta_13C))+
 ggtitle ("Composition Carbon")+
 labs(
  subtitle = "(Percent Carbon and Delta Values)",
  x = "Percent Carbon (%)",
  y = expression(delta^13 * "C (‰)"),
  shape = "Sample Type",
  color = "Sample Type",
  fill = "Sample Type"
 ) +
 geom_point(aes(fill = Sample_type, shape = Sample_type, color = Sample_type),
        size = 3, stroke = 1, alpha =0.60)+
 scale_color_manual(values = sample_outlines) +
 scale_fill_manual (values = sample_colors) +
 scale_shape_manual(values = sample_shapes) +
 scale_x_continuous(expand = expansion(mult = c(0.1, 0.1))) +
 scale_y_continuous(expand = expansion(mult = c(0.1, 0.1))) +
 stat_ellipse(aes(group = Sample_type, color = Sample_type), level = 0.95, geom = "path", alpha = 0.8, linewidth = 0.5)+
 theme_minimal()+
 theme(legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
     axis.text.y = element_text(size = 14),
     axis.line = element_line(color = "black", linewidth = 0.4),
     axis.title = element_text(size = 16, face = "bold"),
     plot.title = element_text(size = 18, face = "bold"),
     panel.border = element_blank(),
     aspect.ratio = 1,
     strip.text = element_text(face = "bold", size = 12))

###### Export Composition Plots ######
pdf(file = 'Thesis_composition_plots.pdf')
 print(Nitrogen_by_sample_ellipse)
 print(Carbon_by_sample_ellipse)
dev.off()

####
# Gull Density, Island Area, and Grazing Single plot ----------
####
### Fig 3. Grazing and Island size effect on gull density (Single plot)
# --- Step 1: Predictions per Grazing Status ---
stats_list <- list()
pred_lines <- list()

for (g in unique(gull_island_data$Grazing_status)) {
 sub_g <- subset(gull_island_data, Grazing_status == g)

 # Remove NA, NaN, Inf from BOTH variables
 sub_g <- sub_g %>%
  filter(
   is.finite(LogIsland_size_km2),
   is.finite(LogGull_density_km2)
  )
```

```
 if (nrow(sub_g) < 2) next

 # Fit linear model per grazing status
 model_g <- lm(LogGull_density_km2 ~ LogIsland_size_km2, data = sub_g)

 intercept <- coef(model_g)[1]
 slope <- coef(model_g)[2]
 r2 <- summary(model_g)$r.squared
 p_val <- summary(model_g)$coefficients[2, "Pr(>|t|)"]

 stats_list[[g]] <- paste0(
  g, ": y=", round(slope, 2), "x+", round(intercept, 2),
  ", R²=", round(r2, 2),
  ", p=", signif(p_val, 3)
 )

 # Prediction grid
 pred_data <- data.frame(
  LogIsland_size_km2 = seq(min(sub_g$LogIsland_size_km2),
                           max(sub_g$LogIsland_size_km2),
                           length.out = 100)
 )

 pred_interval <- predict(model_g, newdata = pred_data, interval = "confidence")
 pred_data$LogGull_density_km2 <- pred_interval[, "fit"]
 pred_data$pred_lower <- pred_interval[, "lwr"]
 pred_data$pred_upper <- pred_interval[, "upr"]
 pred_data$Grazing_status <- g

 pred_lines[[g]] <- pred_data
}

pred_lines_df <- do.call(rbind, pred_lines)
stats_text <- paste(unlist(stats_list), collapse = "\n")

# --- Step 2: Overall regression (ignoring Grazing Status) ---
overall_model <- lm(LogGull_density_km2 ~ LogIsland_size_km2, data = gull_island_data)
overall_pred <- data.frame(
 LogIsland_size_km2 = seq(min(gull_island_data$LogIsland_size_km2),
                          max(gull_island_data$LogIsland_size_km2),
                          length.out = 100)
)
overall_pred$LogGull_density_km2 <- predict(overall_model, newdata = overall_pred)

overall_stats <- paste0(
 "Overall: y=", round(coef(overall_model)[2], 2), "x+", round(coef(overall_model)[1], 2),
 ", R²=", round(summary(overall_model)$r.squared, 2),
 ", p=", signif(summary(overall_model)$coefficients[2, "Pr(>|t|)"], 3)
)

# --- Step 3: Plot ---
main_plot <- ggplot(gull_island_data, aes(x = LogIsland_size_km2, y = LogGull_density_km2)) +

 # Points
 geom_point(aes(fill = Grazing_status, color = Grazing_status, shape = Grazing_status),
         size = 3, alpha = 0.8, stroke = 1) +

 # Per-grazing regression ribbons
```

```
 geom_ribbon(data = pred_lines_df,
             aes(x = LogIsland_size_km2, ymin = pred_lower, ymax = pred_upper, fill = Grazing_status),
             alpha = 0.2, inherit.aes = FALSE) +

 # Per-grazing regression lines (lightly dotted)
 geom_line(data = pred_lines_df,
           aes(x = LogIsland_size_km2, y = LogGull_density_km2, color = Grazing_status),
           size = 1, linetype = "dotted", inherit.aes = FALSE, show.legend = FALSE) +

 # Overall regression line (solid black)
 geom_line(data = overall_pred,
           aes(x = LogIsland_size_km2, y = LogGull_density_km2),
           color = "black", size = 1) +

 # Scales
 scale_fill_manual(values = grazing_colors, name = "Grazing Status") +
 scale_color_manual(values = grazing_outlines, name = "Grazing Status") +
 scale_shape_manual(values = grazing_shapes, name = "Grazing Status") +

 # Labels
 labs(
  title = "Gull Density vs Island Area",
  subtitle = "(One Point per Island)",
  x = expression(Log[10]~"(Island Area km"^2~")"),
  y = expression(Log[10]~"(Gull density per km"^2~")")
 ) +

 theme_minimal() +
 theme(legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     axis.text.x = element_text(angle = 45, hjust = 1, size = 14),
     axis.text.y = element_text(size = 14),
     axis.line = element_line(color = "black", linewidth = 0.4),
     axis.title = element_text(size = 16, face = "bold"),
     plot.title = element_text(size = 18, face = "bold"),
     panel.border = element_blank(),
     aspect.ratio = 1)

# --- Step 4: Regression stats panel ---
stats_grob <- ggplot() +
 geom_text(aes(x = 0, y = 0, label = paste(overall_stats, "\n", stats_text)),
           hjust = 0, vjust = 1, size = 4) +
 theme_void()

###### Export plot ######
pdf(file = 'Thesis_gulldensity_islandarea_plot.pdf', width = 14, height = 8.5)
 grid.arrange(main_plot, stats_grob, ncol = 1, heights = c(3, 1))
dev.off()

####
# Gull Density and Island Area Multiplots ----------------------------
####
### Figures A2, B2, C2, D2, E4. Gull density and Island size effect on nutrients (Multiplots)
## List variables to plot
iso_vars <- list(
  "Delta_15N" = list(y_lab = expression(delta^15*N~"(‰)")),
  "Perc_N"    = list(y_lab = "Total Nitrogen (%)"),
```

```
  "Delta_13C" = list(y_lab = expression(delta^13*C~"(‰)")),
  "Perc_C"    = list(y_lab = "Total Carbon (%)"),
  "CN"    = list(y_lab = "C:N")
)

## Save function to create plots per variable
make_iso_plots <- function(var_name, y_label) {

  plots <- lapply(unique(clean_iso_data2$Sample_type), function(type) {

    # Subset
    subset_data <- clean_iso_data2 %>% filter(Sample_type == type)
    if(nrow(subset_data) == 0) return(NULL)

    # LMM with Island_name random effect
    model <- lmer(as.formula(paste(var_name, "~ LogGull_density_km2 + (1 | Island_name)")),
                  data = subset_data)

    # Fixed effects
    intercept <- fixef(model)[1]
    slope <- fixef(model)[2]

    # Marginal R²
    r2 <- r.squaredGLMM(model)[1]

    # P-value
    p_val <- summary(model)$coefficients[2, "Pr(>|t|)"]

    # Label text
    label_text <- paste0("y = ", round(slope, 2), "x + ", round(intercept, 2),
                         "\nR² = ", round(r2, 3),
                         "\np = ", signif(p_val, 3))

    # Prediction data
    pred_data <- data.frame(
      LogGull_density_km2 = seq(min(subset_data$LogGull_density_km2, na.rm = TRUE),
                                max(subset_data$LogGull_density_km2, na.rm = TRUE),
                                length.out = 100)
    )
    pred_data$pred <- predict(model, newdata = pred_data, re.form = NA)

    # Stats grob below
    stats_grob <- ggplot() +
      geom_text(aes(x = 0, y = -0.5, label = label_text), hjust = 0, vjust = 0.5, size = 3.5) +
      theme_void()

    # Main plot
    main_plot <- ggplot(subset_data, aes(x = LogGull_density_km2, y = .data[[var_name]])) +
      geom_point(shape = 21, size = 3, stroke = 1.2,
                 fill = sample_colors[[type]], color = sample_outlines[[type]], alpha = 0.6) +
      geom_line(data = pred_data, aes(x = LogGull_density_km2, y = pred),
                color = sample_colors[[type]], size = 0.8, inherit.aes = FALSE) +
      ggtitle(type) +
      labs(x = "Gull Density (km²)", y = y_label) +
      scale_x_continuous(expand = expansion(mult = c(0.5, 0.5))) +
      scale_y_continuous(expand = expansion(mult = c(0.5, 0.5))) +
      theme_minimal(base_size = 12) +
      theme(
```

```
      panel.background = element_rect(fill = "white", color = NA),
      plot.background = element_rect(fill = "white", color = NA),
      axis.line = element_line(color = "black", linewidth = 0.5),
      axis.title = element_text(size = 20, face = "bold"),
      axis.text = element_text(size = 14),
      plot.title = element_text(size = 18, face = "bold"),
      aspect.ratio = 1,
      legend.position = "bottom"
    )

  # Combine main plot + stats below
  plot_grid(main_plot, stats_grob, ncol = 1, rel_heights = c(3, 1))
 })

 Filter(Negate(is.null), plots)
}

## Generate plots for each variable
dn15_plots <- make_iso_plots("Delta_15N", expression(delta^15*N~"(‰)"))
percN_plots <- make_iso_plots("Perc_N", "Total Nitrogen (%)")
dc13_plots <- make_iso_plots("Delta_13C", expression(delta^13*C~"(‰)"))
percC_plots <- make_iso_plots("Perc_C", "Total Carbon (%)")
CN_plots <- make_iso_plots("CN", "C:N")

###### Export plots ######
pdf("Thesis_Gulldensity_isotope_plots_new.pdf", width = 15, height = 10)

 all_plots_list <- c(dn15_plots, percN_plots, dc13_plots, percC_plots, CN_plots)

 plots_per_page <- 6
 num_pages <- ceiling(length(all_plots_list) / plots_per_page)

 for (i in 1:num_pages) {
  start_idx <- (i - 1) * plots_per_page + 1
  end_idx <- min(i * plots_per_page, length(all_plots_list))
  plots_this_page <- all_plots_list[start_idx:end_idx]
  page_plot <- plot_grid(plotlist = plots_this_page, ncol = 3)

  title_page <- ggdraw() +
   draw_label("Thesis_gulldensity_nutrient_multiplots",
          fontface = 'bold', x = 0.5, hjust = 0.5, y = 0.99) +
   draw_plot(page_plot, y = 0, height = 0.95)

  print(title_page)
 }

dev.off()

####
# Gull Density, Island Area, and Grazing Multiplots ----------------------------
####
### Fig 4,6,7,8. Gull density, Grazing, and Island size effect on nutrients (Multiplots)
###### Export plots ######
build_grazing_multiplots <- function(data, response_var) {

 data <- data %>% mutate(Response = .data[[response_var]])

 plot_list <- lapply(unique(data$Sample_type), function(type) {
```

```
subset_data <- data %>% filter(Sample_type == type)
if (nrow(subset_data) == 0) return(NULL)

stats_list <- list()
pred_lines <- list()
line_types <- list()

# ---------- Per-Grazing Status Models ----------
for (g in unique(subset_data$Grazing_status)) {
  sub_g <- subset(subset_data, Grazing_status == g)
  if (length(unique(sub_g$Island_name)) < 2) next

  model_g <- lmer(Response ~ LogGull_density_km2 + (1 | Island_name), data = sub_g)
  slope <- fixef(model_g)[2]
  intercept <- fixef(model_g)[1]
  r2 <- r.squaredGLMM(model_g)[1]
  p_val <- summary(model_g)$coefficients[2, "Pr(>|t|)"]

  stats_list[[g]] <- paste0(
    g, ": y=", round(slope, 2), "x + ", round(intercept, 2),
    ", R²=", round(r2, 2), ", p=", signif(p_val, 3)
  )

  pred_df <- data.frame(
    LogGull_density_km2 = seq(min(sub_g$LogGull_density_km2, na.rm = TRUE),
                              max(sub_g$LogGull_density_km2, na.rm = TRUE),
                              length.out = 100)
  )
  pred_df$Response <- predict(model_g, newdata = pred_df, re.form = NA)
  pred_df$Grazing_status <- g

  pred_lines[[g]] <- pred_df
  line_types[[g]] <- ifelse(p_val < 0.05, "solid", "dotted")
}

pred_df <- do.call(rbind, pred_lines)
line_types <- unlist(line_types)

# ---------- Full Model ----------
full_model <- lmer(Response ~ LogGull_density_km2 + (1 | Island_name), data = subset_data)
full_pred <- data.frame(
  LogGull_density_km2 = seq(min(subset_data$LogGull_density_km2, na.rm = TRUE),
                            max(subset_data$LogGull_density_km2, na.rm = TRUE),
                            length.out = 100)
)
full_pred$Response <- predict(full_model, newdata = full_pred, re.form = NA)

f_slope <- fixef(full_model)[2]
f_int   <- fixef(full_model)[1]
f_r2    <- r.squaredGLMM(full_model)[1]
f_p     <- summary(full_model)$coefficients[2, "Pr(>|t|)"]

stats_list[["All islands"]] <- paste0(
  "All: y=", round(f_slope, 2), "x + ", round(f_int, 2),
  ", R²=", round(f_r2, 2), ", p=", signif(f_p, 3)
)
full_linetype <- ifelse(f_p < 0.05, "solid", "dotted")
```

```
  stats_text <- paste(unlist(stats_list), collapse = "\n")

  # ---------- Main Plot ----------
  main_plot <- ggplot(subset_data,
                aes(x = LogGull_density_km2, y = Response)) +
   geom_point(aes(color = Grazing_status, fill = Grazing_status),
           shape = 21, size = 3, stroke = 1, alpha = 0.8) +
   geom_line(data = pred_df,
           aes(y = Response, color = Grazing_status, linetype = Grazing_status),
           show.legend = FALSE,
           linewidth = 0.9) +
   geom_line(data = full_pred,
           aes(y = Response),
           color = "black",
           linewidth = 1.1,
           show.legend = FALSE,
           linetype = full_linetype) +
   scale_color_manual(values = grazing_outlines) +
   scale_fill_manual(values = grazing_colors) +
   scale_linetype_manual(values = line_types) +
   labs(title = type,
       x = "Log Gull Density (indiv./km²)",
       y = response_var) +
   theme_minimal() +
   scale_x_continuous(expand = expansion(mult = c(0.1, 0.1))) +
   scale_y_continuous(expand = expansion(mult = c(0.1, 0.1))) +
   theme(
     aspect.ratio = 1,
     axis.line = element_line(color = "black", linewidth = 0.6),
     axis.title = element_text(size = 18),
     axis.text.x = element_text(size = 14, angle = 45, hjust = 1, face = "bold"),
     axis.text.y = element_text(size = 14, face = "bold"),
     legend.position = "right",
     legend.text = element_text(size = 14),
     legend.title = element_text(size = 16, face = "bold"),
     panel.border = element_blank(),
     strip.text = element_text(size = 16, face = "bold"))

  # ---------- Stats Panel ----------
  stats_grob <- ggplot() +
   geom_text(
     aes(x = 0, y = 1, label = stats_text),
     hjust = 0,
     vjust = 1.2,
     size = 3,
     lineheight = 1
   ) +
   coord_cartesian(xlim = c(0, 1), ylim = c(0, 1), clip = "off")  +
   theme_void() +
   theme(plot.margin = margin(t = 5, r = 5, b = 5, l = 5))

  plot_grid(main_plot, stats_grob, ncol = 1, rel_heights = c(3, 1))
 })

 Filter(Negate(is.null), plot_list)
}
```

```
## RUN FOR ALL VARIABLES
gull_density_plots_d13C_grazing_new <- build_grazing_multiplots(clean_iso_data2, "Delta_13C")
gull_density_plots_percC_grazing_new <- build_grazing_multiplots(clean_iso_data2, "Perc_C")
gull_density_plots_d15N_grazing_new <- build_grazing_multiplots(clean_iso_data2, "Delta_15N")
gull_density_plots_percN_grazing_new <- build_grazing_multiplots(clean_iso_data2, "Perc_N")

## Save as list
all_multiplots <- list(
  "δ13C" = gull_density_plots_d13C_grazing_new,
  "%C"   = gull_density_plots_percC_grazing_new,
  "δ15N" = gull_density_plots_d15N_grazing_new,
  "%N"   = gull_density_plots_percN_grazing_new
)

##### Build multiplots function for response variables #####
pdf("Thesis_gulldensity_nutrient_grazing_multiplots.pdf", width = 15, height = 10)
plots_per_page <- 6

for (variable_name in names(all_multiplots)) {
  plots <- all_multiplots[[variable_name]]
  if (length(plots) == 0) next

  num_pages <- ceiling(length(plots) / plots_per_page)

  for (i in 1:num_pages) {
    start_idx <- (i - 1) * plots_per_page + 1
    end_idx   <- min(i * plots_per_page, length(plots))
    page_plots <- plots[start_idx:end_idx]

    page_plot <- plot_grid(plotlist = page_plots, ncol = 3)

    title_page <- ggdraw() +
      draw_label(
        paste("Gull Density vs", variable_name, "by Sample Type × Grazing Status"),
        fontface = "bold",
        x = 0.5, hjust = 0.5, y = 0.99, size = 18
      ) +
      draw_plot(page_plot, y = 0, height = 0.95)

    print(title_page)
  }
}

dev.off()

####
# Check island perimeter:area differences ----------------------------
####

###### Check Assumptions ######
## Shapiro-Wilk normality test
by(gull_island_data$perim_area_km2, gull_island_data$Grazing_status, shapiro.test)
  ## Note: all p-values >0.05 = perim_area_km2 is normally distributed within each grazing category.

## Levene's Test for Homogeneity of Variance (center = median)
leveneTest(perim_area_km2 ~ Grazing_status, data = gull_island_data)
  ## Note: p-value >0.05 = groups have statistically similar variances
```

```
###### ANOVA ######
anova_model_perimarea_grazing <- aov(perim_area_km2 ~ Grazing_status, data = gull_island_data)
summary(anova_model_perimarea_grazing)

###### Tukey Test ######
tuk <- TukeyHSD(anova_model_perimarea_grazing)
tuk

####
# Comparing Variables (Corrplot and Heatmap) ----------------------------
####
clean_iso_data3 <- clean_iso_data3 %>%
 mutate(
  Grazing_status_num = case_when(
   Grazing_status == "Never grazed" ~ 1,
   Grazing_status == "Currently grazed" ~ 2,
   Grazing_status == "Previously grazed" ~ 3,
   TRUE ~ NA_real_
  )
 )

###### Corrplot ######

### Figure E7. Corrplot on possible numerical predictors for each nutrient variable
# List of response variables
responses <- c("Perc_N" )

## List of predictors
predictors <- c("Perc_C" ,"Delta_13C", "Delta_15N","perim_area_km2", "LogIsland_size_km_squared",
           "LogGull_density_km2", "Grazing_status_num")

###### Export Corrplot ######
# Open PDF device
pdf("Thesis_correlation_plot_nutrients.pdf", width = 10, height = 10)  # adjust size as needed

# Set up 2x2 plotting grid
par(mfrow = c(2, 2), mar = c(1, 1, 2, 1))

# Loop over response variables
for (resp in responses) {

 # Select response + numeric predictors
 cor_data <- clean_iso_data3 %>%
  dplyr::select(all_of(resp), Delta_15N, Perc_C, Delta_13C, perim_area_km2, LogIsland_size_km_squared,
           LogGull_density_km2, Grazing_status_num)

 # Compute correlation matrix
 cor_matrix <- cor(cor_data, use = "pairwise.complete.obs")

 # Plot correlation
 corrplot::corrplot(cor_matrix, method = "circle",
            title = paste("Correlation with", resp))
}

###### Preliminary models for Nutrient LMMs ######
## Response variables
responses <- c("Delta_15N", "Perc_N", "Delta_13C", "Perc_C")
```

```
## Predictors
predictors <- c("Island_size_km_squared",
            "Gull_density_km2",
            "Grazing_status")

## Initialize results dataframe
aic_ranking_nutrients_lmm <- data.frame()

## Loop over responses
for (resp in responses) {

 # Fit LMMs for each predictor
 models <- lapply(predictors, function(pred) {
  formula <- as.formula(paste(resp, "~", pred, "+ (1|Sample_type) + (1|Island_name)"))
  lmer(formula, data = clean_iso_data3, REML = FALSE)
 })
 names(models) <- predictors

 # Compute AICc for each model
 aicc_values <- sapply(models, AICc)

 # Create dataframe for ranking
 df <- data.frame(
  Response = resp,
  Predictor = names(aicc_values),
  AICc = as.numeric(aicc_values)
 )

 # Rank predictors (lowest AICc = best)
 df <- df %>%
  arrange(AICc) %>%
  mutate(Rank = row_number())

 # Append to results
 aic_ranking_nutrients_lmm <- rbind(aic_ranking_nutrients_lmm, df)
}

## Print ranked predictors for each nutrient variable
print(aic_ranking_nutrients_lmm)

## Create nested order table
nested_order_table <- aic_ranking_nutrients_lmm %>%
 group_by(Response) %>%
 arrange(AICc) %>%
 summarise(Nested_Order = paste(Predictor, collapse = " -> "),
        .groups = "drop")

print(nested_order_table)

###### Heatmap for nutrient predictors ######
### Figure E7. Visualize best predictors for each nutrient variable
# Make sure Predictor is a factor so it appears in order in the plot
aic_ranking_nutrients_lmm <- aic_ranking_nutrients_lmm %>%
 mutate(Predictor = factor(Predictor, levels = predictors))

heatmap_nutrient_predictors <- ggplot(aic_ranking_nutrients_lmm,
                    aes(x = Predictor, y = Response, fill = Rank)) +
 geom_tile(color = "white") +
```

```
  scale_fill_gradient(low = "tan", high = "white",
                      name = "Rank\n(lower = better)") +
  geom_text(aes(label = Rank), color = "black", size = 5) +
  theme_minimal() +
  theme(axis.text.x = element_text(angle = 45, hjust = 1)) +
  labs(title = "Ranking of Predictors by AICc for Each Nutrient Variable",
       x = "Predictor",
       y = "Nutrient Variable")

###### Export Heatmap ######
pdf("Thesis_heatmap_nutrient_predictor_AICc.pdf", width = 11, height = 8.5)
print(heatmap_nutrient_predictors)
dev.off()

####
# Gull Density Linear Mixed Models (LMMs) ----------------------------------------------------------
####
# ---- Response variable
response <- "LogGull_density_km2"

# ---- Dataset
data <- gull_island_data

# ---- Fixed-effect model formulas
fixed_formulae <- list(
  "Intercept_only" = ~ 1,
  "Grazing"       = ~ Grazing_status,
  "Island_size"   = ~ LogIsland_size_km2,
  "Grazing_Island" = ~ Grazing_status + LogIsland_size_km2,
  "Interaction"   = ~ Grazing_status * LogIsland_size_km2
)

# ---- Function to safely fit fixed-effects-only models
fit_models <- function(data, response, formulas) {
  model_list <- list()

  for (nm in names(formulas)) {
    rhs <- as.character(formulas[[nm]])[2]  # right-hand side
    if (rhs == "1") {
      f <- as.formula(paste(response, "~ 1"))
    } else {
      f <- as.formula(paste(response, "~", rhs))
    }
    model_list[[nm]] <- lm(f, data = data)
  }

  return(model_list)
}

# ---- Function to compute AIC/AICc/weights and R²
compute_model_selection <- function(model_list) {
  n_vec <- sapply(model_list, nobs)
  aic_vals <- sapply(model_list, AIC)
  k_vals   <- sapply(model_list, function(m) length(coef(m)))
  resid_df <- sapply(model_list, function(m) m$df.residual)    # residual df

  # AICc
  aicc_vals <- aic_vals + (2 * k_vals * (k_vals + 1)) / (n_vec - k_vals - 1)
```

```
 # Weights
 delta_aic <- aic_vals - min(aic_vals)
 weight_aic <- exp(-0.5 * delta_aic) / sum(exp(-0.5 * delta_aic))

 delta_aicc <- aicc_vals - min(aicc_vals)
 weight_aicc <- exp(-0.5 * delta_aicc) / sum(exp(-0.5 * delta_aicc))

 # R²
 r2_vals <- sapply(model_list, function(m) summary(m)$r.squared)

 data.frame(
  Model = names(model_list),
  Model_Df = k_vals,
  Resid_Df = resid_df,
  AIC = aic_vals,
  Delta_AIC = delta_aic,
  Weight_AIC = weight_aic,
  AICc = aicc_vals,
  Delta_AICc = delta_aicc,
  Weight_AICc = weight_aicc,
  R2 = r2_vals
 )
}

# ---- Fit models
models <- fit_models(data, response, fixed_formulae)

# ---- Compute model selection
model_sel_table <- compute_model_selection(models)

# ---- Extract fixed effects
fixef_list <- lapply(names(models), function(nm) {
 m <- models[[nm]]
 fe <- broom::tidy(m)
 fe$Model <- nm
 fe
})

fixef_df <- bind_rows(fixef_list) %>%
 dplyr::select(Model, term, estimate, std.error, statistic, p.value)

# ---- Combine results
nested_model_summary_gulls <- model_sel_table %>%
 left_join(fixef_df, by = "Model") %>%
 mutate(Dataset = "Gull_island_summary",
      Response = response)

###### Export Heatmap ######
write.csv(nested_model_summary_gulls, "Thesis_gull_nested_models.csv", row.names = FALSE)

## Preview table
print(nested_model_summary_gulls)

####
# Nutient Linear Mixed Models (LMMs) ----------------------------------------------------------
####
```

```
options(na.action = "na.fail")  # Required for model.sel()

###### Set up variables and datsets ######
## RESPONSE VARIABLES
responses <- c("Delta_15N", "Perc_N", "Delta_13C", "Perc_C")

## Mapping short to full names
response_names <- c(
  "Delta_15N" = "Nitrogen Isotope Ratio (δ15N)",
  "Perc_N"    = "Total Nitrogen (%)",
  "Delta_13C" = "Carbon Isotope Ratio (δ13C)",
  "Perc_C"    = "Total Carbon(%)"
)

## PREDICTOR VARIABLES
predictors <- c(
  "Island_size_km_squared",
  #"perim_area_km2",
  #"Island_degredation",
  "Gull_density_km2",
  "Grazing_status"
  #"Rat_presence",
  #"Dist_landfill"
)

## DATASETS (sample types)
datasets <- list(
  Soil     = soil_iso_data,
  Atriplex = recurva,
  Malva    = arborea,
  Pistacia = lentiscus,
  Arachnids = arachnids_iso_data
)

###### Nutrient LMMs and AIC Table ######
## LMMs: Fit dynamic nested model hierarchy

###### Set up variables and datsets ######
## RESPONSE VARIABLES
responses <- c("Delta_15N", "Perc_N", "Delta_13C", "Perc_C")

## Mapping short to full names
response_names <- c(
  "Delta_15N" = "Nitrogen Isotope Ratio (δ15N)",
  "Perc_N"    = "Total Nitrogen (%)",
  "Delta_13C" = "Carbon Isotope Ratio (δ13C)",
  "Perc_C"    = "Total Carbon(%)"
)

## PREDICTOR VARIABLES
predictors <- c(
  "Island_size_km_squared",
  #"perim_area_km2",
  #"Island_degredation",
  "Gull_density_km2",
  "Grazing_status"
  #"Rat_presence",
  #"Dist_landfill"
```

```
)

## DATASETS (sample types)
datasets <- list(
 Soil     = soil_iso_data,
 Atriplex = recurva,
 Malva    = arborea,
 Pistacia = lentiscus,
 Arachnids = arachnids_iso_data
)

###### Nutrient LMMs and AIC Table ######

## LMMs: Fit dynamic nested model hierarchy
fit_dynamic_nested <- function(data, response_var, predictors) {

 # ---- Remove NAs
 data <- data[!is.na(data[[response_var]]), ]
 if (nrow(data) < 10) return(NULL)

 # ---- 1. Fit single predictor models for AIC ranking
 single_models <- list()
 for (pred in predictors) {
  fml <- as.formula(paste(response_var, "~", pred, "+ (1|Island_name)"))
  mod <- try(lmer(fml, data = data, REML = FALSE), silent = TRUE)
  if (!inherits(mod, "try-error")) single_models[[pred]] <- mod
 }
 if (length(single_models) == 0) return(NULL)

 # Rank predictors by AIC
 predictor_AIC <- sapply(single_models, AIC)
 ranked_predictors <- names(sort(predictor_AIC))

 # ---- 2. Build nested models
 model_list <- list()
 null_name <- "Null_Island"
 model_list[[null_name]] <- lmer(as.formula(paste(response_var, "~ (1|Island_name)")),
                        data = data, REML = FALSE)

 # Add first predictor
 model_list[[paste0("Model_", ranked_predictors[1])]] <-
  lmer(as.formula(paste(response_var, "~", ranked_predictors[1], "+ (1|Island_name)")),
       data = data, REML = FALSE)

 # Add progressively more predictors
 if (length(ranked_predictors) > 1) {
  for (k in 2:length(ranked_predictors)) {
   preds <- ranked_predictors[1:k]
   fml <- as.formula(paste(response_var, "~", paste(preds, collapse = " + "), "+ (1|Island_name)"))
   model_list[[paste0("Model_", paste(preds, collapse = "_"))]] <- lmer(fml, data = data, REML = FALSE)
  }
 }

 # ---- 3. Interaction model (≤ 3 predictors)
 if (length(ranked_predictors) <= 3) {
  int_terms <- paste(ranked_predictors, collapse = " * ")
  fml <- as.formula(paste(response_var, "~", int_terms, "+ (1|Island_name)"))
  int_model <- try(lmer(fml, data = data, REML = FALSE), silent = TRUE)
```

```
  if (!inherits(int_model, "try-error")) model_list$Interaction <- int_model
 }

 # Remove failed models
 model_list_fixed <- model_list[!sapply(model_list, is.null)]

 # ---- 4. AIC summary
 aic_raw <- MuMIn::model.sel(model_list_fixed)
 aic_df <- as.data.frame(aic_raw)
 aic_df$Model <- rownames(aic_df)
 rownames(aic_df) <- NULL
 aic_col <- grep("^AIC", colnames(aic_df), value = TRUE)

 # ---- 5. Classic AIC & residual df
 classic_aic <- sapply(model_list_fixed, AIC)
 df_resid <- sapply(model_list_fixed, function(m) stats::df.residual(m))

 # ---- 6. R² & sample sizes
 r2df <- data.frame(
  Model = names(model_list_fixed),
  n = sapply(model_list_fixed, nobs),
  df_residual = df_resid,
  R2m = sapply(model_list_fixed, function(m) MuMIn::r.squaredGLMM(m)[1]),
  R2c = sapply(model_list_fixed, function(m) MuMIn::r.squaredGLMM(m)[2])
 )

 # ---- 7. Extract model coefficient tables
 coef_tables <- dplyr::bind_rows(
  lapply(names(model_list_fixed), function(mn) {
   broom.mixed::tidy(model_list_fixed[[mn]], effects = "fixed") %>%
    dplyr::mutate(Model = mn)
  })
 )

 # ---- 8. Merge AIC, R², and coefficients
 summary_out <- aic_df %>%
  dplyr::mutate(AIC = classic_aic[Model]) %>%
  dplyr::select(dplyr::all_of(c("Model", "AIC", aic_col, "delta", "weight"))) %>%
  dplyr::left_join(r2df, by = "Model") %>%
  dplyr::left_join(coef_tables, by = "Model") %>%
  dplyr::relocate(dplyr::all_of(c("term", "estimate", "std.error", "df", "statistic", "p.value")),
           .after = weight)

 return(list(
  models = model_list_fixed,
  predictor_order = ranked_predictors,
  summary = summary_out
 ))
}

## APPLY FUNCTION TO ALL SAMPLE TYPES × RESPONSE VARIABLES
results <- list()
for (samp in names(datasets)) {
 for (resp in responses) {
  message("Running: ", samp, " × ", resp)
  res <- fit_dynamic_nested(datasets[[samp]], resp, predictors)
  results[[paste(samp, resp, sep = "_")]] <- res
 }
```

```
}

## COMPILE FULL SUMMARY TABLE
nested_model_summary_nutrients <- dplyr::bind_rows(
  lapply(names(results), function(name) {
    if (is.null(results[[name]])) return(NULL)
    parts <- strsplit(name, "_")[[1]]
    df <- results[[name]]$summary
    df$Sample_Type <- parts[1]
    response_short <- paste(parts[-1], collapse = "_")
    df$Response <- response_short
    df$Response_full <- response_names[[response_short]]
    df$Hierarchy <- paste(results[[name]]$predictor_order, collapse = " > ")
    df
  })
)

###### Export CSV ######
write.csv(nested_model_summary_nutrients, "Thesis_nutrient_nested_models.csv", row.names = FALSE)

## Return table
nested_model_summary_nutrients
```