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Contribution to the invertebrate fauna of the islets in the Inner Ionian Sea Archipelago, Greece

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ABSTRACT

Islets often host unique and fragile ecosystems, yet the invertebrate biodiversity of the Inner Ionian Sea Archipelago remains poorly documented. During a targeted expedition across ten islets between Lefkada, Kefalonia and mainland Greece, we conducted the first comprehensive survey of their terrestrial invertebrate fauna. Using hand collecting, net sweeping and substrate sieving, we recorded 222 taxa spanning multiple phyla (Arthropoda, Mollusca, Annelida). Most of these records are deemed new for the region, even though several of the taxa are regarded as well-established since they have an extended distribution in western Greece. Species richness varied substantially among islets, with Kalamos hosting the highest number of taxa (72) and the unnamed islet near Kastos the lowest (11). Multivariate analyses using selected arthropod taxa based on presence–absence data revealed several faunal clusters, although low statistical support suggests considerable heterogeneity among islets. Diversity metrics indicated that Alafonisi exhibited the greatest taxonomic distinctness, whereas Mermygkas showed the most homogeneous fauna. Several endemic and regionally significant species were detected, including multiple Ionian endemics and taxa newly recorded for the archipelago. The results highlight the conservation importance of these small landmasses, which harbour distinct assemblages shaped by isolation, geomorphology, human activity and potential species transfers via boats or grazing animals. This study provides a foundational dataset for future biogeographical, ecological and taxonomic research in the Ionian region and underscores the value of islets as natural laboratories of biodiversity. Finally, the study provides the first standardised Darwin Core dataset for the region, establishing a foundational resource for future ecological, taxonomic, and biogeographical research.

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Introduction

Even though islets have a small size, they often harbour unique ecosystems as they may support rare or endemic species (Matthews and Triantis 2021; Whittaker *et al*. 2023; Rios *et al*. 2024). Their isolation makes them natural laboratories for research on topics such as speciation, adaptation and evolution (Whittaker *et al*. 2017). Islets are regarded as biodiversity hotspots and their study has provided insight into ecosystem dynamics and how they are impacted by changes in climate and land uses (Fernández-Palacios *et al*. 2021; Rozzi *et al*. 2023; Rios *et al*. 2024). As islets represent fragile ecosystems highly susceptible to anthropogenic disturbance, they are early victims of direct or indirect human activities, e.g. pollution, land use changes, invasive species, etc. (Rozzi *et al*. 2023; Llorente-Culebras *et al*. 2024; Xiong *et al*. 2024).

Research on islets in the Mediterranean, and especially around the Aegean and Ionian Archipelagos, has been a subject of study for the past decades (Triantis *et al*. 2008; Papadopoulou *et al*. 2010; Sfenthourakis and Triantis 2017; Itescu *et al*. 2020; Proios *et al*. 2024; Santi *et al*. 2024) but specific work on the invertebrate fauna

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assemblages of the Ionian islets has been limited to non-existent. Only scattered data from random collections have been recovered from the bibliography (Rähle 1979; Tzortzakaki 2012; Gittenberger 2015).

Very little taxonomical research has been conducted on these islets in the past, leaving a big gap in our knowledge of these islands' biodiversity. The collected material plays an important role by helping us fill in those gaps in the knowledge of biodiversity, zoogeography and even taxonomy of the invertebrate fauna of western Greece. This study aimed at creating a first catalogue of invertebrate biodiversity from the islets of the inner Ionian Sea and establishing a baseline for future monitoring for these fragile ecosystems.

Materials and methods

The Inner Ionian Sea Archipelago consists of multiple small rocky islets lying between Lefkada, Kefalonia and mainland Greece. During this expedition, a total of 10 different islets were censused for invertebrates. The islets were selected based on their accessibility by the vessel and dingy used in this expedition. In addition, there were weather parameters as well as logistics constraints allowing or excluding visits to certain islets in the region. All collecting effort was performed within a few days during May 2023 as the financial capabilities of the project could not allow for repeated visits for collection. In some cases, only one point from a relatively large islet was censused while, in other, islets were revisited during the few days period. The islets visited during the expedition are shown in Figure 1 with the sampling sites indicated as red circles, while the metadata associated with the collecting effort are provided in Supplementary Table S1.

Invertebrates were collected predominately using the following methods: hand collection with the use of an aspirator or tweezer, net sweeping and collection from substrate by sieving. At least one substrate specimen was collected from every visited islet. Most of the collected specimens were preserved in 95% ethanol. Ethanol injections were performed in some specimens (like slugs) to preserve their internal

Figure 1. The islets in the Inner Ionian Sea Archipelago. Sampling sites are indicated with a red circle. The inlet map indicates the study area relating to mainland Greece. (Map generated with QGIS ver. 3.44.2). (Author's work/source: authors).

structure. Some insects (Hymenoptera: Apoidea, Orthoptera and Lepidoptera) were first killed in a freezer and subsequently fixed in position. Dry specimens were also collected, such as Mollusca shells or bones collected accidentally with the substrate samples. These were simply stored in ziplock bags with metadata labels alongside them. The soil samples were only examined after the expedition was over. The samples were sieved using a 2 mm sieve. Soil samples were then stored for potential future research, especially towards their abiotic properties.

Specimens were identified to the lowest possible taxonomic level but even higher levels than genus always refer to distinct morphospecies (i.e. a record on Aphididae contains only one morphospecies and not several grouped into the family). Several identification keys and online resources were used in the identification process (e.g. Willemse 1985; Bosmans and Chatzaki 2005; Willemse *et al*. 2018; Borowiec and Salata 2022, 2025; WSC 2025).

In order to better understand the biogeographical processes for the study area, we selected only arthropod taxa suitably targeted by our collecting methods. For the statistical analysis (UPGMA Clustering, biodiversity indices) we used PAST ver.5.0.2 software (Hammer *et al*. 2001). We also performed additional statistical analyses (NMDS, ANOVA) using R Statistics ver.4.5.2 for Windows running on RStudio ver. 2026.01.0 + 392 utilising the [vegan ver.2.7–2] library. The map was created using QGIS ver.3.44.2 (QGIS.org 2025). Finally, graphs were created on MS Excel ver. 2510 (Microsoft 365 Ent.).

Data resources

The collection information including taxa identified, as well as all relevant metadata for the collection effort at each point visited, are presented in a Darwin Core MS Excel file deposited here: https://doi.org/10.5281/zenodo.17502534. For the full list of references used in identifying the specimens collected please refer to Supplementary material 1.

Taxon treatments

Specimens were collected from several major taxonomic groups, as presented below.

Arthropoda

Collembola

Springtails (Collembola) were obtained from soil samples from eight different islets.

Chelicerata

- **Acariformes-Parasitiformes**

Soil mites were found in soil samples from five different islets. The acariform family Trombidiidae was found in Kythros and Provati, while the parasitiform family Parasitidae was found in Formicoula, Kalamos and Kythros.

- **Pseudoscorpiones**

Pseudoscorpions were only collected from two islets (Formicoula and Kythros). In Kythros however, two Pseudoscorpiones morphospecies were found, one from the base of the cliff on the northern side of the islet and another from the islet's small cave.

- **Araneae**

Spider species were found in 12 different localities. The species are the following:

  - *Anagraphis* cf. sp. from Kalamos.
  - *Araneus angulatus* from Kalamos, Kythros and Provati.
  - *Araneus circe* from Atokos.
  - *Cyrba algerina* from Alafonisi, Atokos, Kalamos and Provati.
  - *Cyrtocarenum cunicularium* from Alafonisi, Kalamos and Kythros.
  - *Habrocestum* sp. from Atokos.

- *Haplodrassus* sp. from Alafonisi and Kalamos.
- *Hasarius adansoni* from Kalamos.
- *Hogna graeca* from Provati.
- *Hogna radiata* from Meganisi.
- *Kochiura aulica* from Alafonisi.
- *Leptorchestes* sp. from Provati.
- *Loxosceles rufescens* from Formicoula and Kalamos.
- *Lycosidae* from Alafonisi and Kythros.
- *Maimuna vestita* from Alafonisi.
- *Neoscona adianta* from the Mermygkas.
- *Ozyptila sanctuaria* from Provati.
- *Palpimanus gibbulus* from Alafonisi.
- *Philaeus chrysops* from Alafonisi, Kalamos, Kythros and Provati.
- *Runcinia grammica* from Kalamos.
- *Saitis* sp. from Kalamos.
- *Scytodes thoracica* from Alafonisi.
- *Steatoda* cf. *triangulosa* (juveniles) from Formicoula.
- *Xysticus kochi* from Alafonisi.
- *Zelotes* sp. from Provati.

- **Opiliones**

Opiliones were only found on Kalamos; both on the beach visited at 05.v (one Opilionidae, maybe *Opilio* sp.) and along the trail visited at 07.v (*Rafalskia* sp., *Mediostoma* sp. and an unidentified species).

- **Scorpiones**

Only two scorpion species were found during the expedition on two different islets. The common *Aegeobuthus gibbosus* was found on Kythros while the Ionian endemic *Euscorpius* cf. *corcyraeus* on Kalamos.

Diplura

Two Diplura species were found during the expedition, both in soil samples from Formicoula islet (one Campodeidae and one Japygidae).

Insecta

Coleoptera. The Coleoptera taxa found during the expedition were the following:

- Alaeocharinae from Kythros.
- Anobiinae from Kythros.
- Anthicinae from Kythros.
- *Blaps* sp. from the small caves in Kythros.
- *Carabus (Tomocarabus) convexus* from Kalamos.
- *Cephennium* sp. from Kalamos.
- *Cetonia* cf. *aurata* from Kalamos.
- *Ceutorrhynchus* sp. from the Mermygkas.
- *Clanoptilus* sp. from Kythros.
- Cryptocephalinae (faecal cases) from Kythros and Prasonisi.
- *Cryptocephalus (Burlinius)* sp. from the Mermygkas.
- *Dasytes* sp. From Formicoula and Meganisi.
- Dasytinae from Meganisi and Provati.
- *Hymenalia* cf. sp. from Kythros and Provati.
- *Hymenalia* sp. from Kythros and Prasonisi.
- *Hymenorus* cf. sp. from Prasonisi

- *Jekelius (Jekelius) brullei brullei* from Kalamos and Provati.
- *Lagria* sp. from Kalamos and Meganisi.
- *Macrolenes dentipes* from Kythros.
- *Nephus* sp. from Kythros.
- Nyctophilidae (larva) from Meganisi.
- *Ochthebius* sp. from the Mermygkas.
- *Oedemera (Oedemera) flavipes* from Kalamos, Kythros, Meganisi and Provati.
- *Oedemera rufofemorata rufofemorata* from Formicoula, Mermygkas, Kalamos and Prasonisi.
- *Omophlus* sp. from Meganisi and Provati.
- *Otiorhynchus* cf. *lugens* from Kythros.
- *Otiorynchus lugens* from the Mermygkas.
- *Pedinus* sp. from Kalamos and Provati.
- *Polydrusus* sp. from Alafonisi and Meganisi.
- *Raiboscelis azureus* from Alafonisi.
- *Raiboscelis* cf. sp. from Provati.
- *Rhagonycha* cf. sp. from Kalamos,
- *Stenopterus rufus* from Provati.
- *Stenosis* sp. from Kythros.
- Tenebrionidae (larva) from Prasonisi.
- *Tropinota* cf. *squalida* from Meganisi.
- Xantholinini cf. from Provati.

Dermaptera

Only one earwig species was found (in the small Mermygkas islet) and unfortunately only dead females were obtained so a secure identification was not possible.

Dictyoptera

Two Dictyoptera species (the common cockroach *Loboptera decipiens decipiens* and the endemic subterranean termite *Reticulitermes urbis*) seemed to be very common as they were found in many islets. Two other Dictyoptera were collected during the expedition, one *Ectobius* sp. from Provati and *Ameles spallanzania* from Alafonisi (from the later only two old oothecae were found).

Diptera

The Diptera taxa found during the expedition are the following:

- Bombyliidae from Provati.
- *Calliphora* sp. from Prasonisi.
- Cecidomyiidae from Alafonisi, Mermygkas, Kythros, and Provati.
- *Chloromyia* sp. from Kythros and Meganisi.
- *Drosophila* sp. from the Mermygkas, Kalamos and Kythros.
- *Episyrphus balteatus* from Formicoula.
- *Fannia* sp. from Kythros.
- *Nephrotoma* sp. from Meganisi.
- *Sargus bipunctatus* from Meganisi.
- Stratiomyidae from Kythros.
- Tephritidae from the Mermygkas, Kythros and Meganisi.
- *Tipula* ssp. from Alafonisi, and Atokos.

Embioptera

Only one specimen of Embioptera was collected during the expedition, a female *Haploembia solieri*, common in western Greece, from the small satellite islet near Kastos.

Hemiptera

Hemiptera species were found in 10 different localities. The species are the following:

- Aphididae from the Mermygkas, Kalamos, and Kythros.
- *Closterotomus annulus* from Meganisi.
- *Eulachnus* cf. sp. from Kythos.
- *Gonocerus* cf. *insidiator* (only nymphs) from Provati.
- Membracoidea from Mermygkas, Kalamos, and Kythros.
- *Micrelytra fossularum* from Alafonisi.
- *Phytocoris* sp. from Meganisi.
- *Rhynocoris rubricus* from Kythros.
- *Scantius aegyptius* from Meganisi.
- *Trioza* sp. from Mermygkas.

Hymenoptera

Formicidae species were found on every collection site with many morphospecies being present on many different islets. On the other hand, winged Hymenoptera were present on six islets.

The ant taxa recorded were:

- *Aphaenogaster balcanica* from Meganisi and Kalamos.
- *Camponotus kiesenwetteri* from Formicoula.
- *Camponotus lateralis* from Formicoula.
- *Camponotus oertzeni* from Formicoula, Mermygkas, Kalamos and Atokos.
- *Crematogaster schmidti* from Formicoula, Kalamos, Atokos and Alafonisi.
- *Crematogaster sordidula* from Meganisi and Provati.
- *Lepisiota melas* from Formicoula, Prasonisi and Alafonisi.
- *Lepisiota nigra* from Atokos.
- *Pheidole pallidula* from Formicoula, Kalamos, Provati, Atokos, Kythros, Alafonisi and the unnamed islet close to Kastos.
- *Plagiolepis perperamus* from Meganisi, Formicula and Kalamos.
- *Tetramorium diomedeum* from Kalamos.
- *Tetramorium immigrans* from Prasonisi.
- *Tetramorium kephalosi* from Meganisi.

Lepidoptera

Various Lepidoptera species were recorded from 10 localities. Butterflies such as the common *Euchloe ausonia, Maniola jurtina* and the elusive *Papilio alexanor* were found on Meganisi as well as *Thymelicus* sp. on Kythros where it was very common. Regarding moths, *Ophiusa tirhaca* was found on Mermygkas, *Lasiocampa trifolii* and a *Leucania* sp. (only weathered wings inside a small cave) on Kythros, *Lymantria dispar* on Meganisi (on a *Quercus coccifera* tree) and *Euproctis chrysorrhoea* (larvae) on the small satellite islet near Kastos.

Neuroptera

The most common Neuroptera were from the family Chrysopidae and were found in Alafonisi and Formicoula. More specifically, the species *Distoleon tetragrammicus* was found on Alafonisi, and a *Libelloides* sp. on Kythros. Although the latter was very common on the islet, we were unable to collect or photograph any specimen.

Orthoptera

Orthoptera were found in eight different localities, with common taxa being the genera *Eupholidoptera* and *Calliptamus*. Unfortunately, during the time of the expedition very few adult specimens were found and most of the specimens observed and collected were still nymphs. The collected taxa were *Chorthippus biguttulus biguttulus* from Alafonisi, a *Myrmecophilus* sp. (nymph) from Formicoula, *Acrometopa servillea macropoda*

from Meganisi, *Stenobothrus ribicundulus* from Provati, *Poecilimon laevissimus* from Kythros, *Calliptamus* sp. (nymphs) from Provati, Kalamos and the unnamed islet east of Kastos, *Tettigonia viridissima* from Provati, *Eupholidoptera* cf. *megastyla* (nymphs) from Kalamos and Provati and *Leptophyes punctatissima* from Kalamos and Tettigoninae nymphs from Meganisi and Provati.

Zygentoma

Zygentoma were found on nine different islets, with the most common species being *Allacrotelsa kraepelini*. Other species found were *Tricholepisma gyriniformis* on Atokos, *Ctenolepisma ciliata* on Kalamos and Provati, *Proatelurina pseudolepisma* on Meganisi and a *Ctenolepisma* sp. on the small satellite islet near Kastos.

Isopoda

A total of 18 different Isopoda species were found in nearly all of the visited localities, with the most common being the endemic *Armadillidium arcadicum*, present almost everywhere, followed by the cosmopolitan *Porcellionides pruinosus*. Other species found are:

- *Agabiformius lentus* found on Mermygkas, and Meganisi.
- *Armadillidium beieri* on Kythros and Kalamos.
- *Armadillidium epiroticum* on Kalamos, newly recorded for the Ionian region.
- *Armadillidium frontemarginatum*, a species endemic to the Ionian Sea Archipelago, found on Meganisi and Kalamos.
- *Armadillidium granulatum* found on Meganisi.
- *Armadillidium marmoratum* on Provati.
- *Armadillidium vulgare*, a cosmopolitan species found on Alafonisi, and Meganisi.
- *Chaetophiloscia cellaria* on Prasonisi.
- *Chaetophiloscia elongata* on the satellite islet near Kastos.
- *Chaetophiloscia leucadia*, a species endemic to the Ionian Sea Archipelago, found on Formicoula and Meganisi.
- *Ligia italica*, a halophilous species common throughout Greece, found on Kythros.
- *Orthometopon dalmatinum*, a common species in western Greece, found on Formicoula and Provati.
- *Platyarthrus* cf. *werneri*, a myrmecophilous species living inside ant nests, found on Atokos.
- *Porcellio achilleionensis*, a species endemic to western Greece, found on Kalamos.
- *Porcellio lamellatus*, a species living in close vicinity to the sea, found in Formicoula, Mermygkas and the islet near Kastos.
- *Stenophiloscia glarearum*, a halophilus species found on a beach in Alafonisi.
- *Trachelipus palustris* found on Meganisi.

Myriapoda

Chilopoda. Chilopods were found in eight different islets. The species found are:

- *Bothriogaster signata* on Kalamos and Provati.
- *Cryptops parisi* on Kalamos, Kythros and Meganisi.
- *Eupolybothrus littoralis* on Meganisi.
- Geophilomorpha (juvenile) on Prasonisi.
- *Lithobius* cf. *erythrocephalus* on Formicoula (two juveniles).
- *Pachymerium ferrugineum* on Alafonisi.
- *Pleurolithobius jonicus* on Meganisi.
- *Scolopendra cingulata* on Alafonisi, Atokos, Kalamos, Kythros, Meganisi and Prasonisi.
- *Scutigera coleoptrata* on Formicoula.

Diplopoda

Diplopod species were found in nine different localities:

- *Chromatoiulus podabrus* on Alafonisi, Kalamos and Meganisi.
- *Diplopoda* ssp. on Atokos, Kythros, Prasonisi and Provati.
- *Byzantorhopalum (Ioniulus)* sp. on Kalamos (either a new location for *Byzantorhopalum (Ioniulus) leucadium*, endemic to Lefkada, or a new species).
- *Pachyiulus varius* on Meganisi.
- *Polyxenus* cf. *chalcidicus* on Formicoula.
- *Polyxenus* cf. *lagurus* on Kythros.

Mollusca

The molluscan taxa found during the expedition are the following:

- *Platyla similis* on Kythros.
- *Albinaria contaminata florisi* on Atokos (endemic to the island, described in 2015).
- *Albinaria contaminata interjecta* on Kalamos and Kythros.
- *Albinaria leonedani* on Prasonisi and Provati (a species that was described in 2015 from the nearby islet of Kastos. These are the second and third localities where the species has been found).
- *Albinaria senilis leucadia* on Alafonisi, Kythros, and Meganisi.
- *Allaegopis ionicus* on Kalamos.
- *Caracolina lenticula* on Kalamos.
- *Cecillioides acicula* on Kythros.
- *Cecillioides michoniana/veneta* on Prasonisi.
- *Cecillioides* sp. on Kalamos.
- *Cernuella* sp. (juveniles) on Meganisi.
- *Cernuella virgata* on Kalamos and Provati.
- *Chondrina arcadica* on Kythros.
- *Chondrus zebrula* on Kalamos.
- *Cochlostoma tesselatum* ssp. on Alafonisi, Atokos, Formicoula, Kalamos, Kythros, Meganisi, Prasonisi, islet near Kastos and Provati.
- *Cornu aspersum* on Meganisi.
- *Granopupa granum* on Kythros and Prasonisi.
- *Hypnophila zacynthia* on Kythros and Meganisi.
- *Limax conemenosi* on Kalamos.
- *Lindholmiola corcyrensis* on Alafonisi, Kalamos, Kythros, and Meganisi.
- *Lindholmiola lens* on the islet near Kastos and Provati.
- *Mastus* cf. *grandis* on Mermygkas and Prasonisi.
- *Mastus grandis* on Alafonisi and Formicoula.
- *Mediterranea ionica* on Kythros, Prasonisi and Provati.
- *Microxeromagna loweii* on Kythros.
- *Monacha claustralis* on Meganisi.
- *Monacha parumcincta* on Alafonisi, Formicoula, Mermygkas, Kythros, Meganisi, Prasonisi and Provati.
- *Myosotella myosotis* on Alafonisi.
- *Papillifera papillaris papillaris* on Meganisi.
- *Poiretia compressa* on Atokos, Kalamos, Kythros, Prasonisi, and Provati.
- *Pomatias elegans* on Atokos, Kythros, and Provati.
- *Rupestrella philippii* on Provati.
- *Rupestrella rhodia* on Kythros.
- *Schistophallus cyprius* on Meganisi.
- *Stigmatica stigmatica* ssp. on Formicoula, Kalamos and the islet near Kastos.
- *Stigmatica stigmatica miles* on Alafonisi, Kythros, and Meganisi.
- *Tandonia sowerbyi* on Meganisi.
- *Tandonia* sp. on Kythros.
- *Trochoidea pyramidata* on Formicoula and Mermygkas.

- *Truncatellina callicratis* on Kythros and Prasonisi.
- *Truncatellina rothi* on Atokos and Formicoula.
- *Tuncatella subcylindrica* on Alafonisi.
- *Vitrea contracta* on Kalamos.
- *Vitrea selecta* on Atokos and Provati.
- *Vitrea subrimata* on Prasonisi.
- *Xerotricha conspurcata* on Meganisi.

Annelida

The only earthworm species found during the expedition was an Enchytraeidae found on Mermygkas, Prasonisi and Provati islets.

Analysis

Records of each taxon were transformed into a presence/absence data matrix using MS Excel, as well as recording the approximate area for each islet in km^2, resulting in Table 1. The highest number of morpho/species was that on Kalamos islet (72), while the lowest number was recorded from the Unnamed islet close to Kastos (11). We performed a multivariate clustering analysis with Paired group (UPGMA) algorithm based on the Jaccard similarity index with 999 permutations, resulting in the graph of Figure 2 when using the presence/absence data for all taxa collected from the islets. Due to the low support of our dendrogram, we performed a Non-metric Multidimensional Scaling (NMDS) analysis to provide a complementary perspective on faunal dissimilarities (Figure 3). The NMDS ordination (Stress = 0.116) yielded a configuration consistent with the hierarchical clustering, offering additional spatial context for the observed community patterns. The horizontal axis (NMDS1) represents the primary gradient of species change across the Ionian islets. Moving from right to left (from Mermygkas towards Meganisi) shows a clear shift in community structure. The tight clustering of islets within the blue ellipse (the Atokos-Prasonisi group) aligns with the groupings identified in the UPGMA analysis, even where nodal support was limited. Meganisi remains a distinct faunal outlier, consistently separated from the central clusters across both dimensions.

When computing beta diversity (per Whittaker 1960), Meganisi showed the highest score relating to the fauna recorded from the unnamed islet close to Kastos (0.74545) while Atokos had the lowest one in relation to the same islet (0.46667). When checking Shannon H' diversity index, Kalamos had the highest score (3.829) while the unnamed islet close to Kastos had the lowest, at 2.565. To evaluate the ecological significance of the clusters identified in the NMDS, we performed a one-way ANOVA comparing species richness across the three islet groups (Cluster A, Cluster B, and Outliers) (Figure 4). Prior to the analysis, the assumptions of normality and homogeneity of variances were assessed using Shapiro-Wilk and Levene's tests, respectively; both were met ($p > 0.05$). The ANOVA results (Table 2) confirmed that differences in species richness between the NMDS-defined groups are statistically significant ($F_{(2, 7)} = 13.82$, $p = 0.0037$). This result, coupled with the high spatial overlap in the NMDS, suggests that the low bootstrap support (26–31%) in the hierarchical clustering for Cluster A is likely a reflection of a largely shared and statistically uniform species pool among

Table 1. Number of morpho/species and approximate area for each visited islet. (Author's work/source: authors).

Islet name	Morpho/Species	Area (km^2)
Kalamos	70	24.9
Meganisi	54	22.3
Atokos	18	4.5
Kythros	63	0.74
Formicula	35	0.1
Provati	46	0.1
Prasonisi	23	0.03
Alafonisi	40	0.014
Mermygkas	24	0.006428
un-named islet	11	0.001644

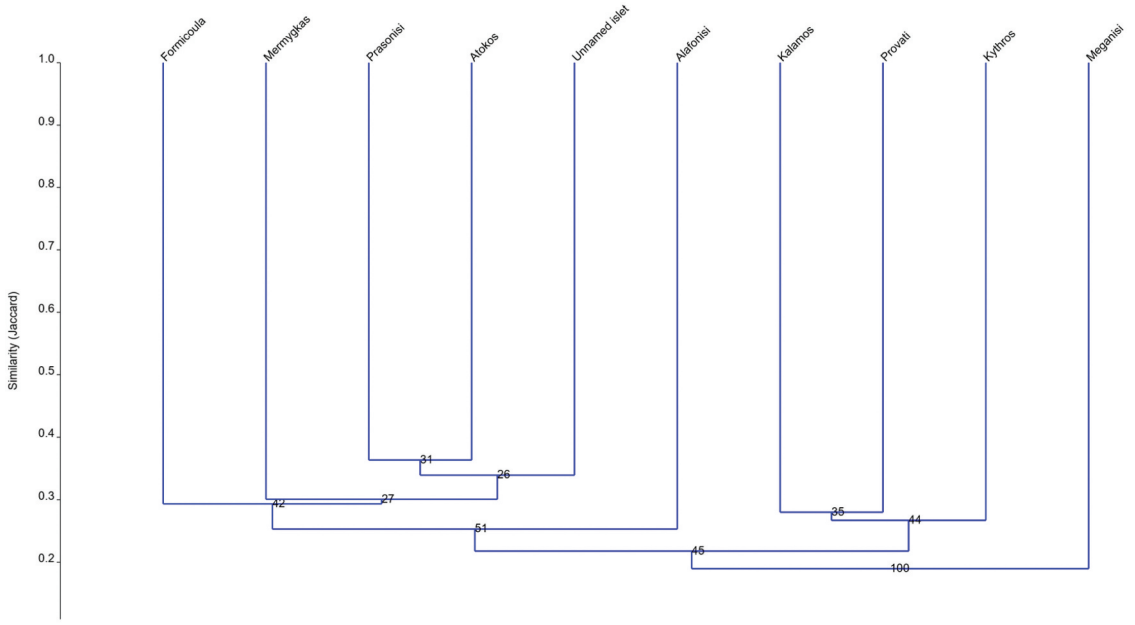

Figure 2. UPGMA dendrogram of invertebrate community similarity across 10 Ionian islets. A UPGMA dendrogram organizing the islets into a hierarchical structure based on the Jaccard similarity index, which quantifies biological overlap between locations. The branching patterns identify groups with similar species compositions, while the numerical values at each node indicate the statistical confidence of these groupings based on 999 permutations (n = 10). The low similarity levels at which major branches merge reflect high beta diversity, suggesting that most islands maintain relatively distinct ecological communities. (Author's work/source: authors).

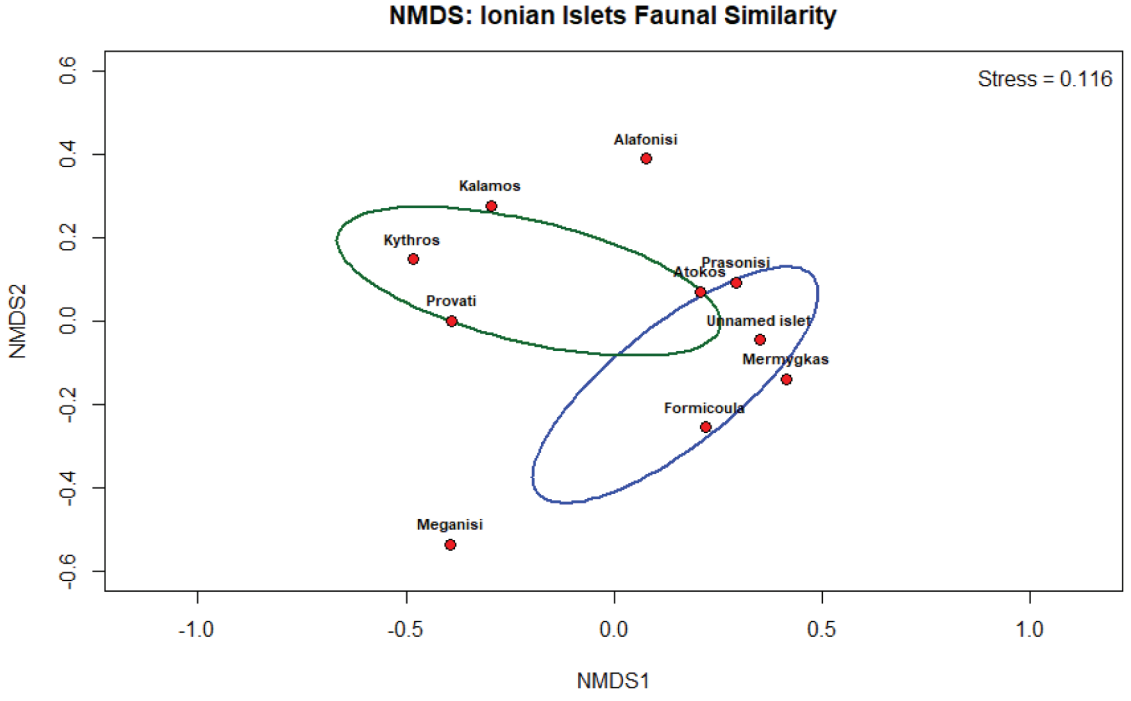

Figure 3. Non-metric Multidimensional Scaling (NMDS) ordination of invertebrate community composition across 10 Ionian islets based on Jaccard dissimilarity. Axes are constrained to −0.8 to 0.8 (NMDS1) and −0.6 to 0.6 (NMDS2) to highlight central clustering. Ellipses represent 95% confidence areas for faunal groups. The low stress value (0.116) confirms that the ordination accurately reflects the faunal relationships, supporting the outlier status of Meganisi observed in hierarchical clustering. (Author's work/source: authors).

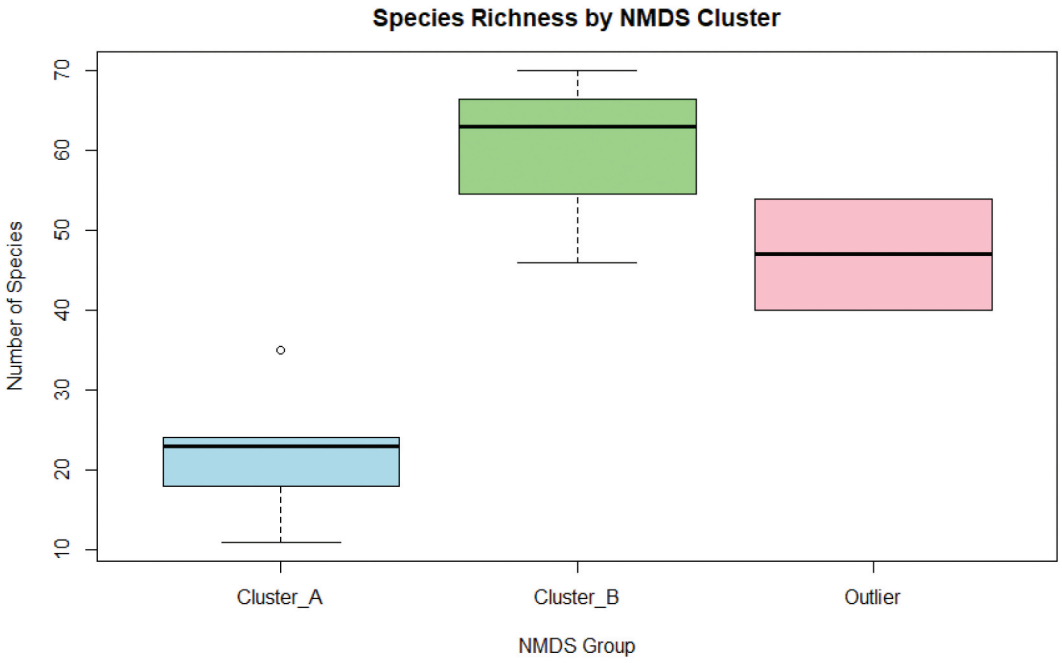

Figure 4. Comparison of species richness among NMDS-defined islet clusters. Boxplots display the distribution of species richness across identified groups (n = 10). High-diversity Cluster B differs significantly from the low-diversity Cluster A, based on a one-way ANOVA between clusters ($F_{(2, 7)} = 13.82$, $p = 0.0037$). The statistical uniformity within Cluster A explains the low bootstrap support (26–31%) in hierarchical clustering, as these islets share a heavily overlapping species pool. (Author's work/source: authors).

Table 2. One-way ANOVA results comparing species richness across NMDS clusters. (Author's work/Source: authors).

Source of Variation	df	Sum of Squares	Mean Square	F-statistic	p-value
Group	2	2816.93	1408.47	13.82	**0.00371043****
Residuals	7	713.47	101.92	NA	NA

those islets. Taxonomic distinctness (Δ^+) was examined with the islet of Mermygkas indicating the most homogeneous fauna (2.731) while Alafonisi had the highest level of taxonomic distinctness (3.808). The results for this measurement are plotted in Figure 5.

Discussion

Many of the islets visited during this expedition were censused for the first time. The expedition recorded 222 taxa (species/subspecies/morphospecies) of terrestrial invertebrates. Of those, Kalamos harbours the highest number of arthropods with 72 in total, followed closely by Kythros and Meganisi with 66 and 55, respectively. On the unnamed satellite islet close to Kastos (approx. 0.0026 km^2), only 15 species/morphospecies of invertebrates were recorded (11 of those were arthropods). Even though the close proximity to the adjacent island of Kastos of approx. 50 m can account for the species located there, it is also evident that even such small land entities can accommodate microhabitats suitable for several taxa.

Our analysis reveals several clusters of islets based on their faunal similarity but also cannot fully justify the irregular grouping for a number of those islets. This unevenness is furthermore supported by the low confidence between clusters when accounting for the statistical permutations performed during the analysis. While the UPGMA dendrogram exhibited low bootstrap support for several internal nodes, the NMDS ordination (Stress = 0.116) provides a robust alternative visualisation of faunal relationships. The close spatial proximity of islets within Cluster A (e.g. Atokos, Prasonisi, and Mermygkas) suggests a high degree of taxonomic homogeneity. In this context, the low bootstrap values do not indicate a lack of relationship, but rather a lack of hierarchical structure; the islets are so faunally similar that they form a cohesive cluster rather than a distinct series of branching events. The significant overlap between the 95% confidence ellipses for

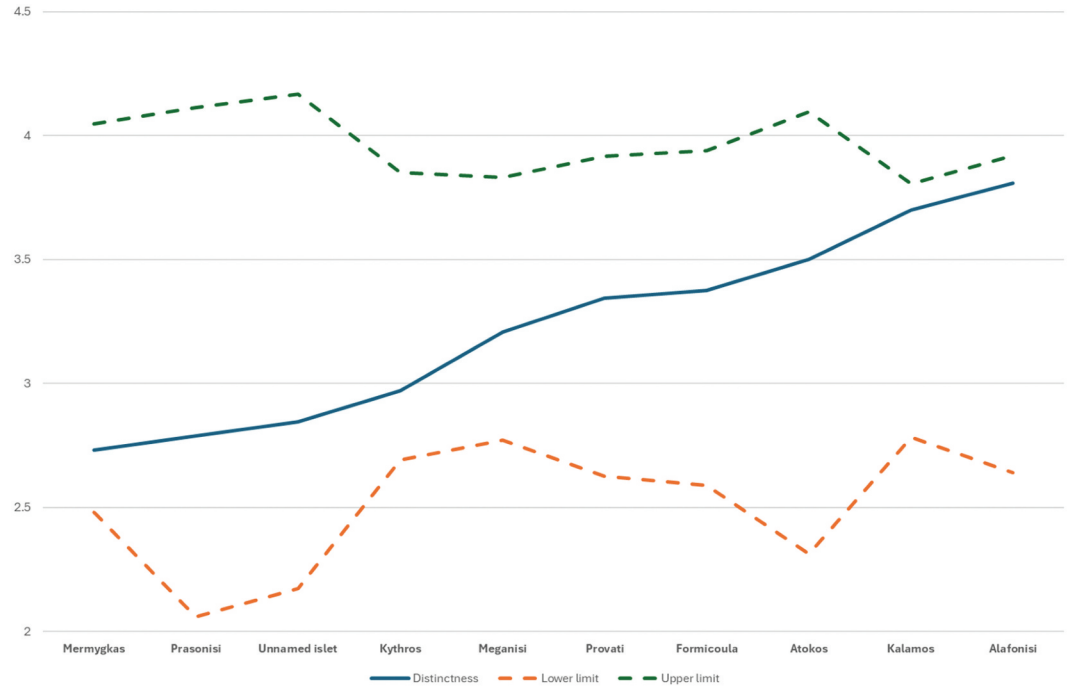

Figure 5. Average Taxonomic Distinctness (Δ^+) across the Ionian islets (n = 10). Plot displaying the Taxonomic Distinctness (Δ^+) across the islets, with the blue line representing the average evolutionary relatedness between species at each site. The dashed green and Orange lines establish the 95% confidence funnel. All islets (n = 10) fall within these limits, indicating that their taxonomic diversity is statistically typical of the regional species pool, regardless of their total species count. (Author's work/source: authors).

the central islets suggests they draw from a common regional species pool. The NMDS highlights that the 'uncertainty' in the dendrogram's branching is likely a reflection of nestedness, where smaller islets host a subset of the species found on larger ones. Because the dissimilarities between these pairs are negligible, the hierarchical model struggles to resolve a single 'parent' islet, whereas the NMDS successfully captures this community stability within a two-dimensional gradient.

Considering that the whole area is a hotspot for small boat island-hopping for recreational purposes, there are strong possibilities that species were unintentionally transferred between the islets and have managed to create viable populations there (Hulme 2009; Gippet *et al*. 2019; Athinaiou *et al*. 2024). This process could very well be taking place for hundreds (if not thousands) of years, creating the faunal matrix existing today (Constantakopoulou 2024). In addition, several of the smaller islets have been utilised by goat herders as feeding grounds for their herds; especially during the summer months. This practice contributes to the transfer of animals clinging to the herd while, at the same time, the goats have an effect on the flora arrangement and thus the animal composition for each islet (Rambo and Faeth 1999; Kruess and Tscharntke 2002; Pafilis *et al*. 2013).

Under a similar notion, the temporal aspect of our collection effort was limited due to the mission constraints. Although our effort took place during early spring – a period regarded as the most productive for terrestrial biodiversity in the Mediterranean area (Colombini *et al*. 2002; Legakis and Adamopoulou 2005; Petanidou *et al*. 2008) – it was still extremely confined to one or two days per collection site. The timing of our effort surely affected the species number as well as the community composition, with some species that potentially have presence on the islets not being collected at this time due to their seasonal biological cycle.

Our findings highlight the distinct biogeographical character of the Ionian islets compared to the well-studied Aegean archipelago. While the Aegean is a global hotspot for paleo-endemism by hosting ancient lineages that survived in isolation for millions of years, the Ionian islets follow a 'land-bridge' model (Valli *et al*. 2019). The Ionian islets exhibit higher total species richness but lower narrow-range endemism. They act as a faunal reservoir for Western Greek and Adriatic lineages. Conservation priority here shifts from protecting 'individual rare species' to maintaining the metapopulation connectivity between islets and the mainland

(Iliadou *et al*. 2014). The conservation of Ionian terrestrial arthropods must account for the high level of human-mediated connectivity. Because small boat traffic and seasonal grazing are prevalent, these islets are at higher risk for invasive species homogenisation (Athinaiou *et al*. 2024). In the Ionian, where precipitation is higher, the faunal composition is heavily dependent on the lushness of the vegetation. As noted, over-grazing by goats doesn't just remove plants; it collapses the micro-habitats (shade, moisture, leaf litter) that support terrestrial arthropods (Pafilis *et al*. 2013). The Hellenic state has intensified the conservation and protection of the area incorporating the islets of the inner Ionian Sea by a series of Ministerial Decrees (i.e. 123711/3066/Government Gazette 953/31.12.2024), with the Environmental Impact Assessment for the newly established Ionian Sea Marine Park currently (January 2026) in print. The Marine Park will include the islets visited on our expedition.

Biodiversity of islets is a topic that has several appearances in the recent bibliography, especially as a concept of a unique habitat entity within a larger ecosystem frame (Moniz *et al*. 2012; Closset-Kopp and Decocq 2015; Rajesh *et al*. 2022; Orczewska *et al*. 2024). These areas are indeed hotspots of unique and irreplaceable evolutionary life acting as centres of endemism and evolution. They harbour species with unique adaptations which offer essential ecosystem services. At the same time, they can be extremely vulnerable to various threat levels and should be regarded as focal points for conservation priorities.

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Author contributions

CRediT: **Christos Georgiadis:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing; **Nikolaos Manolas:** Data curation, Investigation, Resources, Writing – original draft, Writing – review & editing; **Leonidas-Romanos Davranoglou:** Investigation, Resources, Writing – review & editing; **Jakovos Demetriou:** Investigation, Resources, Writing – review & editing; **Georgios Kakiopoulos:** Investigation; **Evangelos Koutsoukos:** Investigation, Resources, Writing – review & editing; **Eva Tankovic:** Conceptualization, Funding acquisition, Investigation, Project administration, Writing – review & editing; **Georgios Karris:** Conceptualization, Supervision, Writing – review & editing.

Disclosure statement

No potential conflict of interest was reported by the authors.

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Data availability statement

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/records/17628776.

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