An analysis of the distributions of the native and naturalised snake species in the Maltese archipelago

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This work is a dissertation-style report prepared by Eleanor Dobbs for the purpose of providing an update on academic research activities undertaken from 2021 onwards.

The document is a work in progress as of 19th March 2025 and is **not** for widespread distribution. The initial research findings have not yet been subject to independent peer review, although the intention will be to publish this work via normal academic channels in due course.

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Abstract:

Globally, numerous reptile species are at risk of extirpation due to human influence on natural landscapes. However, snakes remain poorly studied relative to other squamates, thus ascertaining population distributions is critical for their conservation. The Maltese Islands have two native and two naturalised snake species and using a complementary methodology of citizen science and fieldwork, locality records were collated across the three main islands of the Maltese archipelago. *Hierophis viridiflavus* was the most common, and the only species native to all three islands. *Telescopus fallax* and *Zamenis situla* were believed to be isolated to the island of Malta, but this paper is the first to report individuals found on Gozo, possibly due to accidental relocation. *Hemorrhois algirus*, the rarest of the four species, remains largely confined to the localities surrounding Floriana. Based on anecdotal information, *Z.situla* sightings have substantially reduced in agricultural landscapes and the data suggests a notable shift into urban landscapes. All the Maltese snake species show tendencies to use dry stone walls as critical refuge sites, with *Z.situla* records also distributed significantly closer to water streams than the other resident species. *T. fallax* presence maps demonstrated a much more widespread distribution than previous estimates, and these data provide the first insight into the distribution of the elusive *H. algirus*. The collective influence of resource type and use across different habitats may also represent key factors in explaining presence in future research. In the wake of further habitat loss and fragmentation, all species need urgent intervention and improvements to urban planning to accommodate movements of terrestrial species.

Key Words: Snakes, Maltese Archipelago, Distributions, Citizen Science, Urban, Habitat type

Introduction

Reptiles are an understudied, megadiverse, and unevenly globally distributed taxon which play critical roles in ecosystems (Valencia-Aguilar et al., 2015). Amidst the reports of declines in reptile species, squamate populations have historically received little attention (Todd et al., 2010), with only 3.4% included in the 2004 IUCN Global Species Assessment (Baillie et al., 2004). Furthermore, amongst the almost 10,000 squamate species assessed to date, 1,472 remain data deficient (Cox et al., 2022).

Currently, 60% of snake species are purported as being highly threatened (Cox et al., 2022), and population data remains scarce (Moura et al., 2016). As a result, they are often excluded from large scale studies seeking to identify biodiversity and distribution patterns (Moura et al., 2016). However, despite the limited research determining whether snake populations are in decline, a consensus among herpetologists worldwide postulates that snakes are disappearing, with sharp and synchronous declines already evidenced in some species (Gibbons et al., 2000; Seigel & Mullin, 2009; Reading et al., 2010). Research spanning the last decade has provided compelling reports that reptiles are extremely sensitive to anthropogenic landscape alteration and exceptionally high rates of urbanisation across the globe represent a pertinent threat to snake species (Cordier et al., 2021). Throughout European temperate zones, the chief threats faced by snake populations are habitat loss, degradation, and fragmentation, with 75% of species threatened by agriculture alone (Todd et al., 2010; Cox et al., 2022). Restricted geographic ranges, coupled with specific habitat requirements also put snake species at risk from additional threats attributed to their habitat specificity (Todd et al., 2010). Although in Europe, habitat alteration may be the primary cause of these declines, additional factors such as shifts in prey availability, habitat edge destruction, environmental contamination, disease, roadkill, invasive species, and global climate change may also be facilitating losses (Gibbons et al., 2000; Reading et al., 2010; Cox et al., 2022). Snakes are also vulnerable to population declines attributed to traits that enhance a species' sensitivity to extinction such as relatively long lifespans, exclusively carnivorous diets, and low reproductive outputs (Scott & Seigel, 1992; Dodd, 1993; Greene, 1997). Thus, snakes are believed to have a greater vulnerability to extinction than many other taxa (Lyet et al., 2013). Larger species of snake also typically require larger areas of suitable habitat coverage and disperse over greater distances, so without the presence of sufficient habitat corridors, they are at increased risk of road mortality and extirpation due to lack of available conducive habitat (Andrews et al., 2008).

Highlighting threats to snake populations is critical for their conservation. However, accurately detecting population declines often remains difficult as snakes are challenging study subjects attributed to their low population densities, extended periods of inactivity, and cryptic behavioural habits (Gibbons et al., 2000).

Furthermore, few long-term studies have successfully researched demographic patterns of change in natural populations (Gibbons et al., 2000). Many snake species also remain data deficient, with 17% having outdated assessments and only 2% having time series data (Saha et al., 2018; Cox et al., 2022). Ultimately, these limitations have resulted in the IUCN species extinction risk assessment for snakes being poorly evaluated (Böhm et al., 2013). Ecologists are faced with the added dilemma that many snake observations are anecdotal and without accurate data on demography, individual dispersal, and habitat preference, their distributions can be challenging to ascertain (Filippi and Luiselli, 2000).

The Mediterranean Basin has been drastically altered by anthropogenic activity (Blondel and Aronson, 1999) and yet it is still recognised as a significant biodiversity hotspot (Myers et al., 2000). The substantial changes in land use across the Mediterranean has impacted biodiversity with 14% of reptile species under threat of extinction and snakes are in notable decline (Brooks et al., 2002; Santos et al., 2022). Habitat alteration can considerably alter the dietary habits of snake species (Capizzi et al., 2008) with urbanisation across the Mediterranean coastal belt also facilitating a general decline affecting entire species assemblages (Santos et al., 2007). Equally, as many snake species remain unassessed and data deficient, those with localised small ranges, such as Malta, may be inherently at higher risk of extinction (Meiri, 2016). This paper will therefore be the first to combine large scale citizen science and fieldwork to analyse the distribution of the unique assemblage of snake species found on the Maltese archipelago.

The herpetofauna of the Maltese archipelago is represented by 10 terrestrial species (Vella et al., 2020). The four snake species all belong to the Colubridae family (Schembri, 1984); and include the native *Hierophis viridiflavus* and *Zamenis situla,* and the naturalised *Hemorrhois algirus* and *Telescopus fallax,* the latter both believed to have been accidentally introduced during the First World War (Borg, 1939). To date, the information available to accurately assess the conservation threats and subsequent status of Maltese snakes is scant. However, the limited published literature has already highlighted the threats posed to the resident snake populations through urbanisation and habitat loss (Lanfranco, 1955; Savona-Ventura, 1985).

Hierophis viridiflavus or Western whip snake (*Serp iswed* in Maltese), is the largest of the four resident Maltese species and is believed to be both common and the only species known to reside on all three inhabited Maltese islands (Schembri, 1984). *Zamenis situla* or leopard snake *(Lifgha* in Maltese) was described as scarce in Malta in 1996 and its distribution across the island of Malta remains largely unknown (Dossier on Wild Fauna in the Maltese Islands: Capture, Killing and Exploitation, 2011). *Telescopus fallax* or the European cat snake (*Qattas, Teleskopu,* or *Serp* in Maltese) is the only predominantly nocturnal species found in Malta and was historically considered the rarest of the four resident species (Achille, 2015). It was also assigned rare status in Malta in

1996 and is locally considered Vulnerable (Dossier on Wild Fauna in the Maltese Islands: Capture, Killing and Exploitation, 2011). Malta represents the only European station for the elusive *Hemorrhois algirus* or Algerian whip snake (*Serp l-Ahdar* in Maltese) and it has remained largely confined to the localities surrounding Floriana since its theorised accidental introduction alongside *T.fallax* (Borg, 1939). *Hemorrhois algirus* was last assessed by the IUCN in 2004, whilst the other three species were assessed in 2008 (Dossier on Wild Fauna in the Maltese Islands: Capture, Killing and Exploitation, 2011; see Rugiero et al., 1998; Naumov & Tomovic, 2007; Achille, 2015; Speybroeck et al., 2016 for more detailed descriptions of morphology, phylogeny, life history, and ecology for all four species).

This assemblage of snake species does not exist anywhere else in the world and are isolated to a small island ecosystem with increasing anthropogenic pressures. This paper therefore aims to remediate the lack of data on the distributions of the Maltese snake populations, describe their known presence across the archipelago, and discern how natural and man-made landscape properties may be influencing their distributions. From this, future research can ascertain range-wide and localised declines, more accurately designate conservation statuses, and devise appropriate conservation intervention methods to ensure the longevity of these species. The primary objectives at a species level include deducing exactly which species exist on each of the primary Maltese islands and provide the first distribution assessment of the understudied *H. algirus* in Europe.

Materials and Methods

Study Region

The Maltese archipelago (35.9375° N, 14.3754° E) is situated in the central Mediterranean, 96 km south of Sicily (Stevens et al., 1995). Despite their small size, the Maltese islands (316 km^2) consist of various habitat types and diverse flora and fauna (Schembri, 1994), and consists of three inhabited islands: Malta (245.7 km^2), Gozo (67.1 km^2), and Comino (2.8 km^2) (Schembri, 1994). Malta's most characteristic vegetation communities are those that pertain to the sclerophyll series. The four communities; woodland remnants, maquis, garigue and steppe undergo vegetational succession in response to both natural and man-made disturbance and often occur in mosaic patterns (Fourth National Report to the CBD – Republic of Malta, 2010). However, the islands are also represented by coastal, rupestrian, and freshwater communities (Schembri, 1994). Malta's exceptionally high population density has also facilitated the creation of areas with dense urban infrastructure (Schembri, 1994).

Citizen Science Data

Citizen-science data was primarily obtained by mining the social media platform Facebook. Various Facebook groups were identified as hotspots for frequent snake sighting related posts such as herpetological groups, wildlife groups, nature groups, and agricultural groups. These were backdated and records were qualified for exact location, time, and date, as well as photographic evidence or additional information. The groups were closely monitored for new posts. Geographic location was qualified using Google Maps and species identification was validated by two herpetologists where photos were provided. Where photographs were not provided, the species identification was validated based on the description of the specimen. Records were initially plotted on Google Maps. Unknown specimens were not included as part of the records. The online species record database iNaturalist was also used to obtain records of snakes and only records with photographs of the snake were included in the research.

Surveying

Fieldwork surveys were conducted between 18 April 2022 and 28 June 2022. The islands of Malta, Gozo, Comino, and Cominotto were surveyed. Trackless Visual Encounter Survey (VES) were used (Lardner et al., 2019) to identify snake presence. After analysing the preliminary citizen science and literary data, we highlighted areas where presence had either never been recorded or had previously been confirmed but had not been qualified in recent years. From these areas, survey locations were decided based on accessibility. Surveys were conducted twice a day, 5 days a week for approximately 2-hours, including one morning (0700– 0900 hrs) and one afternoon survey (1500 – 1700 hrs). Twice a week, night-time trackless VES were conducted between 2100 – 2300 hrs. When a snake was sighted, the species, time, temperature, humidity, GPS location, and date were recorded. Sloughs were also collected with GPS location and suspected species identification recorded.

GIS Maps

Map products and their analyses were created in the GIS software Quantum GIS (QGIS) version 3.16 Hannover (www.qgis.org). The database was composed by GPS point locality record, collected in geodetic reference WGS84. To reduce the cartographical distortions of Europe, the maps were projected in Universal Transverse Mercator projection, ETRS89 UTM zone 33N (EPSG code: 3045; https://spatialreference.org/ref/epsg/3045/html/).

Snake record data were transformed into a grid where individual points were overlapped with the 500 m x 500 m UTM grid. For each species, each grid was assigned either a value of 0 or 1, respectively for absence and presence, and distribution maps were compared with those based on the data provided by the Environment and Regulatory Authority Malta (ERA).

Habitat type at the study area was determined through the CORINE Land Cover 2018 database (version 2020_20u1) (EEA, 2019). A total 19 classifications were used to depict the snake's habitat preference. The total area covered by the terrestrial components was computed using QGIS, subsequently deriving the percentage coverage of the features containing snake record. Water courses (Valley Management Unit – Parks Malta, 2020) and water features (NTM, 2019) for the archipelago of Malta were considered, including 8 classes: ponds, dams, quarries, reservoirs, rock pools, salt pans, wetlands and other.

The level of urbanisation was derived from the Urban Atlas LCLU 2018 database (EEA, 2020). Geographical coverage of this database included only the main island of Malta. Seven out of 25 classes were selected from the database. The presence of snakes within the different degree of urbanisation was derived and coverage percentage of each species computed.

Snakes' proximity to roads and water features were derived through the vector analysis tool "Distance to the nearest hub (hub to line)". The line files were converted to points with 1 m resolution, and the distance between each record and the closest feature point was calculated. Cover percentages of the gridded snakes' distributions were computed by overlaying the 500 m x 500 m grid with the base map of the Maltese archipelago. Each independent snake sighting was correlated to terrain elevation. The elevation layer is a digital elevation model (DEM) of the Maltese archipelago (25 m cell size), made available through the European organisation Copernicus (EEA, 2016).

Statistical Analysis

All statistical analysis was carried out using R (version 4.1.3; R Core Team, 2023). Data manipulation and transformation were undertaken using packages "dplyr" and "tidyverse" (Wickham et al., 2023; Wickham et al., 2019). To assess homogeneity of variance between species Levene's test from the "car" package was used (Fox and Weisberg, 2019). Due to differences between the variance of species, Welch's (analysis of variance) ANOVA was used, alongside Games-Howell post-hoc tests (Kassambara, 2023). Additionally, to determine difference between species relative abundance to categorical variables, such as habitat and urban type, Fisher's

Exact Test was used. Only 26% of records were included in the urban density analysis. All visualisations were created using “ggplot2” (Wickham, 2016).

Ethical considerations

This study obtained full approval from the University of Kent, School of Anthropology and Conservation Research Ethics Committee. The fieldwork portion of the research was carried out under license pertaining to the Environment Protection Act (CAP.549) and issued by the Environment and Resources Authority (ERA) in Malta (Permit number: EP 1652/21; Approved Documents: EP 1652/21/1E/5A). The study also adhered to best practice protocols outlined by both authorities in terms of conservation focus and prioritisation of animal welfare.

Results

A total of 920 specimens were recorded across the Maltese islands. The records dated from 11 January 2003 to 26 July 2023, and included 469 *H. viridiflavus* (13.5% deceased), 216 *Z. situla* (22.7% deceased), 198 *T. fallax* (11.6% deceased), and 37 *H. algirus* (18.9% deceased). Three *Z. situla*, one *T. fallax*, and 93 *H. viridiflavus* specimens were recorded on Gozo. Only *H. viridiflavus* was recorded on Comino (n=12) and no snakes were reported on Cominotto. A total of 15 snakes were recorded on surveys (12 *H. viridiflavus*, 1 *Z. situla*, 2 *T. fallax*) with an additional 4 snakes (1 *Z. situla*, 1 *T. fallax*, 1 *H. viridiflavus*, and 1 *H. algirus*) recorded as rescues. 97.9% of records were from Citizen Science data.

Habitat type

The two native species and *T. fallax*, demonstrated the highest occupancy frequencies across agricultural, discontinuous urban, and sclerophyllous vegetation landscapes, illustrating a clear pattern that the three most widely distributed species inhabit both natural and anthropogenically altered landscapes. Figure 1 shows the coverage of each habitat type across the islands, demonstrating that occupancy is high in the human-altered and widely distributed habitats. Whereas lower occupancy was reported in the smaller natural habitat fragments such as forests and sparsely vegetated areas. Figure 1 shows that *Hierophis viridiflavus* inhabit more habitat types than the other three species. Although appearing to occupy similar habitats, *T. fallax* and *H. viridiflavus* demonstrated a greater presence in sclerophyllous vegetation than *Z. situla*. *Hemorrhois algirus* exhibited exclusive occupation of urban areas with limited expansion across habitat types and proportionally dominated green urban and discontinuous urban fabric areas. *Z. situla* and *T. fallax* showed a greater presence in discontinuous urban areas than *H. viridiflavus,* with the latter species also having a notably higher presence in agricultural landscapes than the former two species.

Proximity to natural streams and water features

The highest number of records were reported to be 100-500 m from a water stream (28.3%), 44.6% of which were *H. viridiflavus.* Only 6.7% of snakes were recorded within a 0-20 m proximity to a water stream, the greatest proportion of which were *H. viridiflavus* (71.0%). *Zamenis situla* were, however, found significantly closer on average to water streams than the other three species (F(3,177)=12.6, p<0.001; 699.50m ± 48.40). Compared to 1051.16m ± 47.99 for *H. viridiflavus*; 994.89m ± 73.80 for *T. fallax* and 1179.34m ± 87.25 for *H. algirus*.

Figure 2 shows locations of each type of water feature present across the archipelago. Only one individual snake (*H. viridiflavus*) was recorded within a 0-20 m proximity of a water feature, which was a reservoir. Overall, most snakes were recorded closest to reservoirs and dams across all ranges. A substantially larger proportion of *T. fallax* and *H. viridiflavus* records were located around wetland sites than *Z. situla.*

Road proximity

Figure 3 shows reported snake presence in relation to the Maltese road network. 83.8% of snake records were located less than 100 m from a road, with the greatest proportion of snake records found within the shorter proximity ranges to roads, 0-5 m (22.4%) and 10-50m (32.7%). With increasing distances from road features, fewer snakes were recorded with 1.7% and 0.3% snake records reported between 250-500 m and 500 m+ distances, respectively. Most snakes occurred on or around residential (29.2%) and unclassified roads (20.4%). Statistical analysis revealed that snake species were significantly different in relation to their distance from roads (F(3)=1.21, p=0.307), however post-hoc tests did not reveal significance between any species pair (p>0.05).

The three most widely distributed species were found predominantly within 10-50 m and 0-5 m road proximities to any road type. A greater abundance of *T. fallax* were found in the 50-100 m and 100-250 m ranges compared to *Z. situla,* but ultimately showed no pattern in road proximity as the species was reported in similar abundances across all ranges, except 250-500 m and +500 m. *Z. situla* records were primarily found within a 10-50 m proximity (34.2%), with the greatest proportion of *H. algirus* located 10-50 m from a road (42.9%).

Urban Density

Figure 4 shows that of the records found in urban areas, the highest abundance of snakes was found in 'industrial, commercial, public, military, and private units' (26.2%) with discontinuous very low-density urban fabric (<10%) demonstrating the lowest abundance of snake records (1.0%). The two native species showed a clear trend for occupying areas represented by higher urban density, whilst *T. fallax* was reported in greater proportions in the median urban density classes. All the Maltese snake species distributions expanded over the three densest urban fabric classes, whilst *H. algirus* demonstrated a stronger presence in green urban localities. Only *T. fallax* and *Z. situla* were found across all the analysed urban classes, and anecdotal data revealed that both species are often found in residential dwellings.

Elevation

The maximum height of the Maltese islands is 253 m. Considering the highest abundance of snakes was recorded at the 50-100 m elevational range (32.2%), the results showed a clear trend for the snakes to be present in areas of median elevational ranges. The lowest abundance was recorded at a 5-10 m elevation range (3.7%). *Hemorrhois algirus* were predominantly found across the 10-50 m range (80.0%). The other three species were found across all elevational ranges. No significant differences in elevation were reported between all four species (PWC, $p > 0.05$)

Species Distributions

Figures 5 and 6 show the distributions of the four resident Maltese species. *H. viridiflavus* had the largest area of occupancy of 183.4 km^2 (across all three islands), whilst *H. algirus* had the lowest occupancy size of 4.75 km^2. *Zamenis situla* occupancy was 54.0 km^2 and was also almost double that of the *T. fallax* distribution (28.0 km^2). The previous distribution estimates provided by ERA saw the native species distributions as 316 km^2 for *H. viridiflavus* and 106.08 km^2 for *Z. situla* (only Malta). In terms of the naturalised species, *T. fallax* was reported to occupy 37.03 km^2 (only Malta), whilst distribution estimates for *H. algirus* were not included. Overlaps with our data and ERAs previous projections showed a 14.8% similarity for *H. viridiflavus* (59.5 km^2), 13.4% (14.3 km^2) for *Z. situla*, with the lowest occupancy similarity demonstrated by *T. fallax*, overlapping by only 9.5% (3.5 km^2). There was no distribution overlap represented by all four species based on these data.

Figure 1. Habitat classifications of the Maltese archipelago following the CORINE Land Cover 2018 database (version 2020_20u1) (EEA, 2019). The grid (500 m x 500 m squares) contains a coloured dot for the presence of the related snake species: (white) *Hemorrhois algirus*, (red) *Telescopus fallax*, (yellow) *Zamenis situla*, (blue) *Hierophis viridiflavus*. Map generated on QGIS version 3.16 Hannover (www.qgis.org).

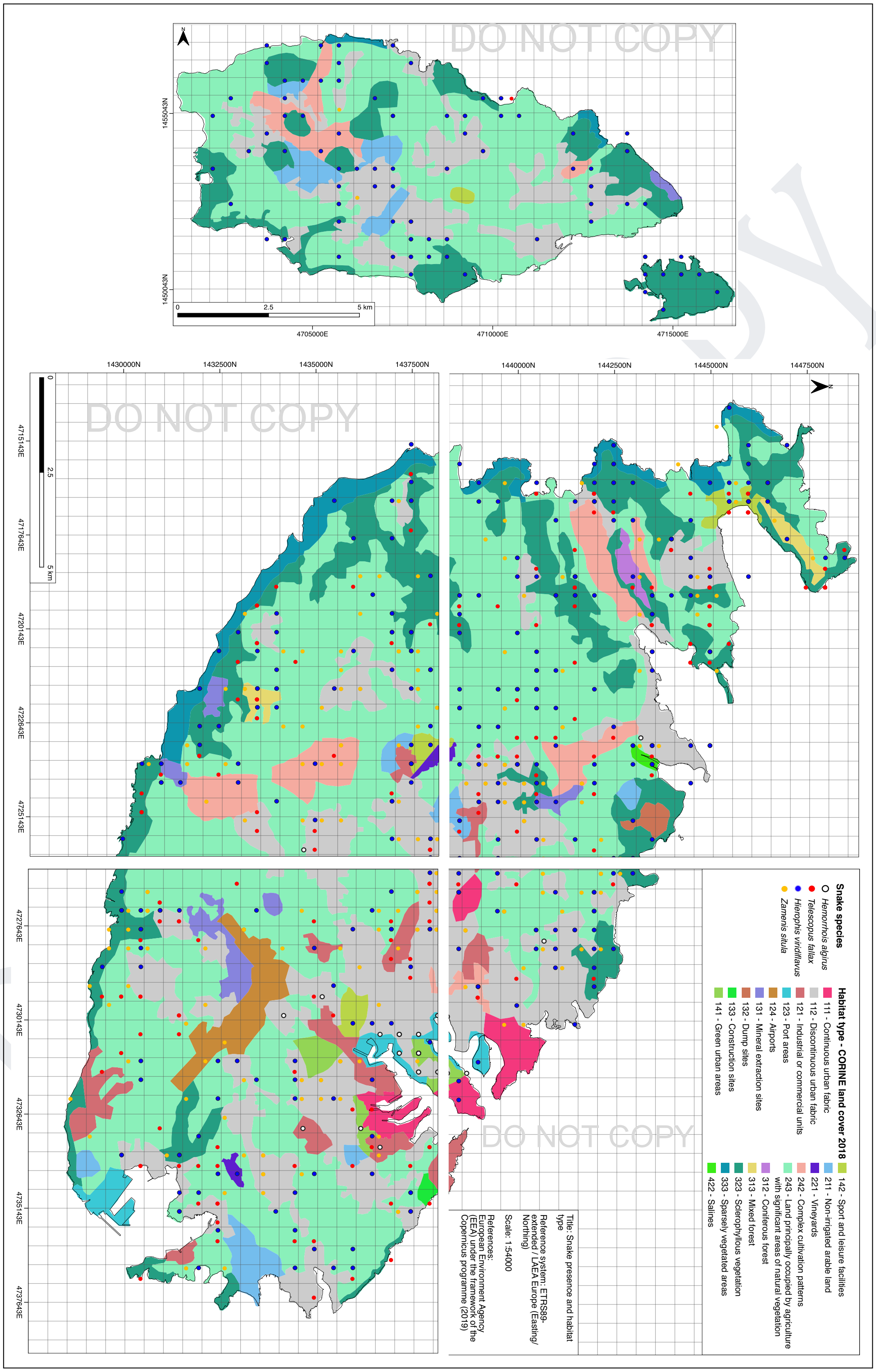


Figure 2. Snake location in relation to: water features of the Maltese archipelago. Map generated on QGIS version 3.16 Hannover (www.qgis.org).

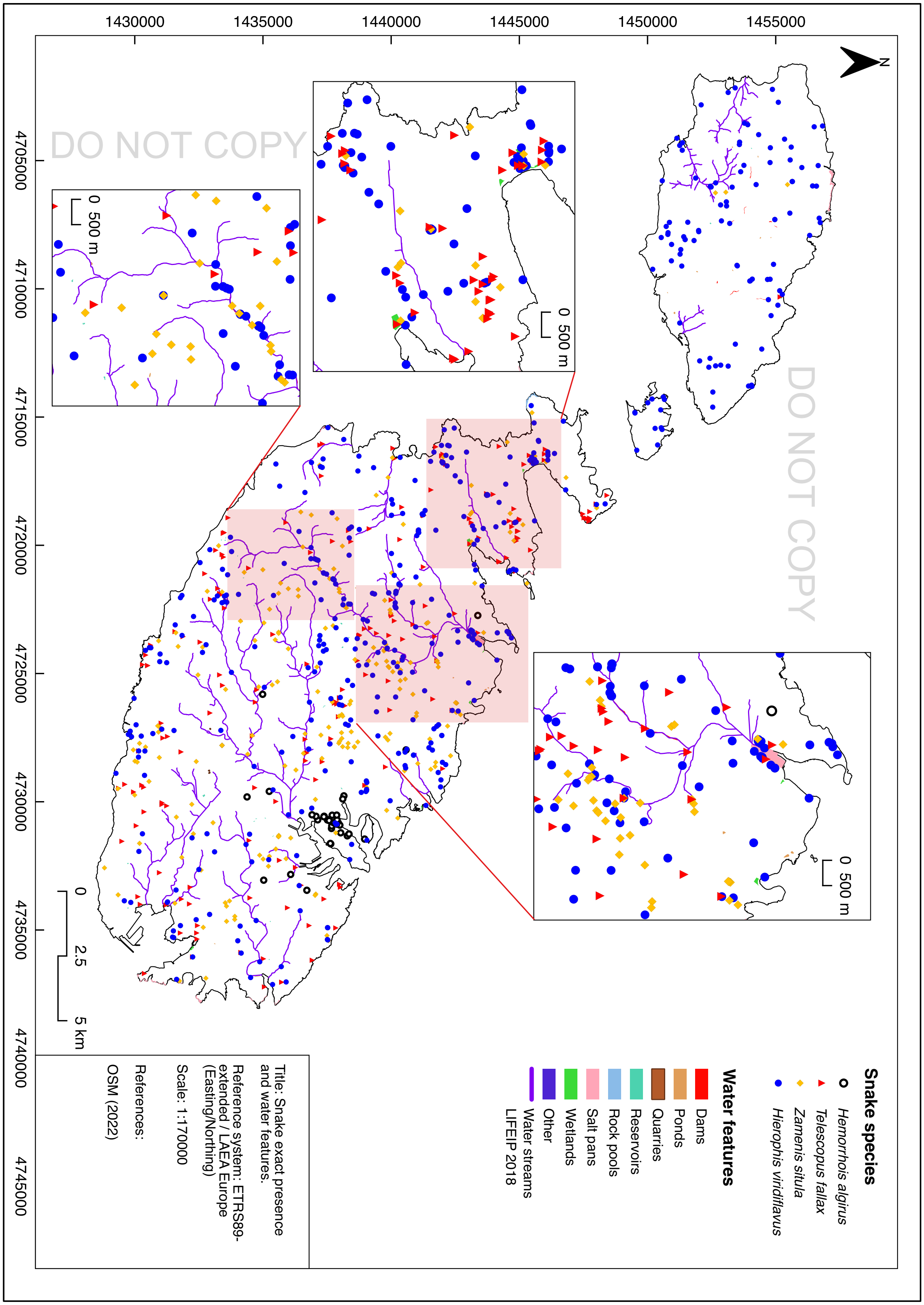


Figure 3. Snake location in relation to the road network of the Maltese archipelago. Map generated on QGIS version 3.16 Hannover (www.qgis.org).

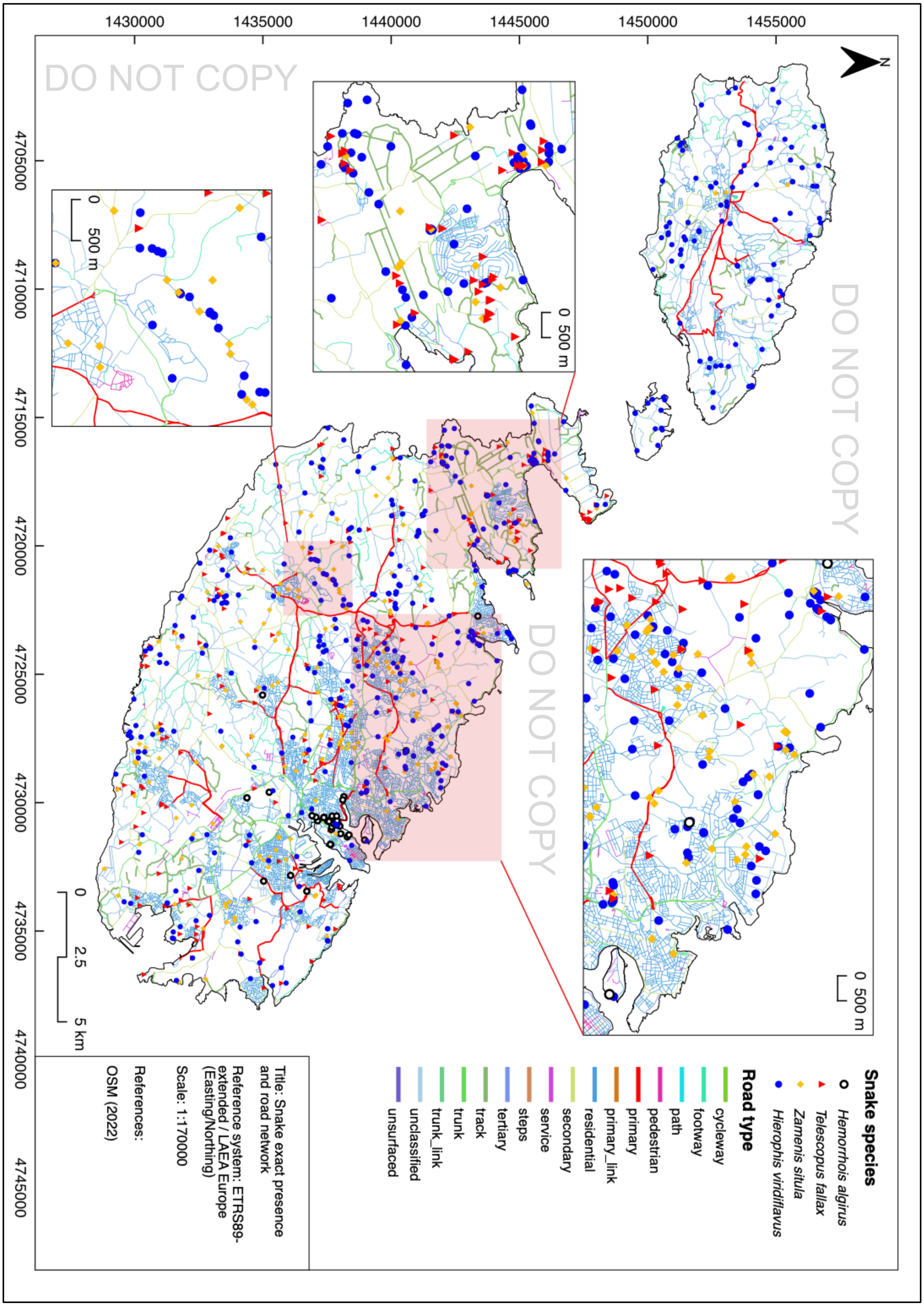
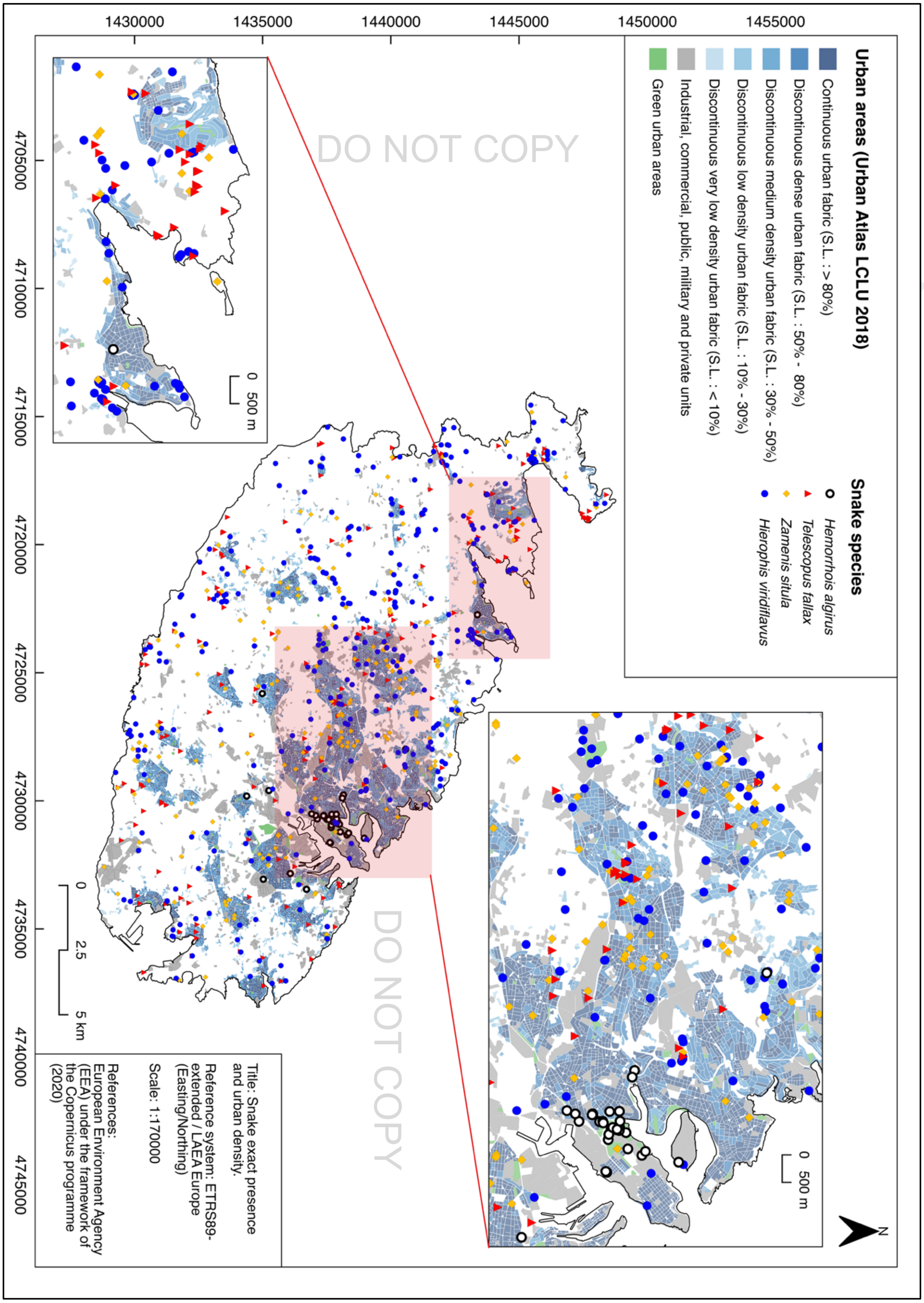


Figure 4. Snake location in relation to urban density of the Maltese archipelago. Urban classification followed the 7 classes of the Urban Atlas LCLU 2018 database (EEA, 2020). Map generated on QGIS version 3.16 Hannover (www.qgis.org).



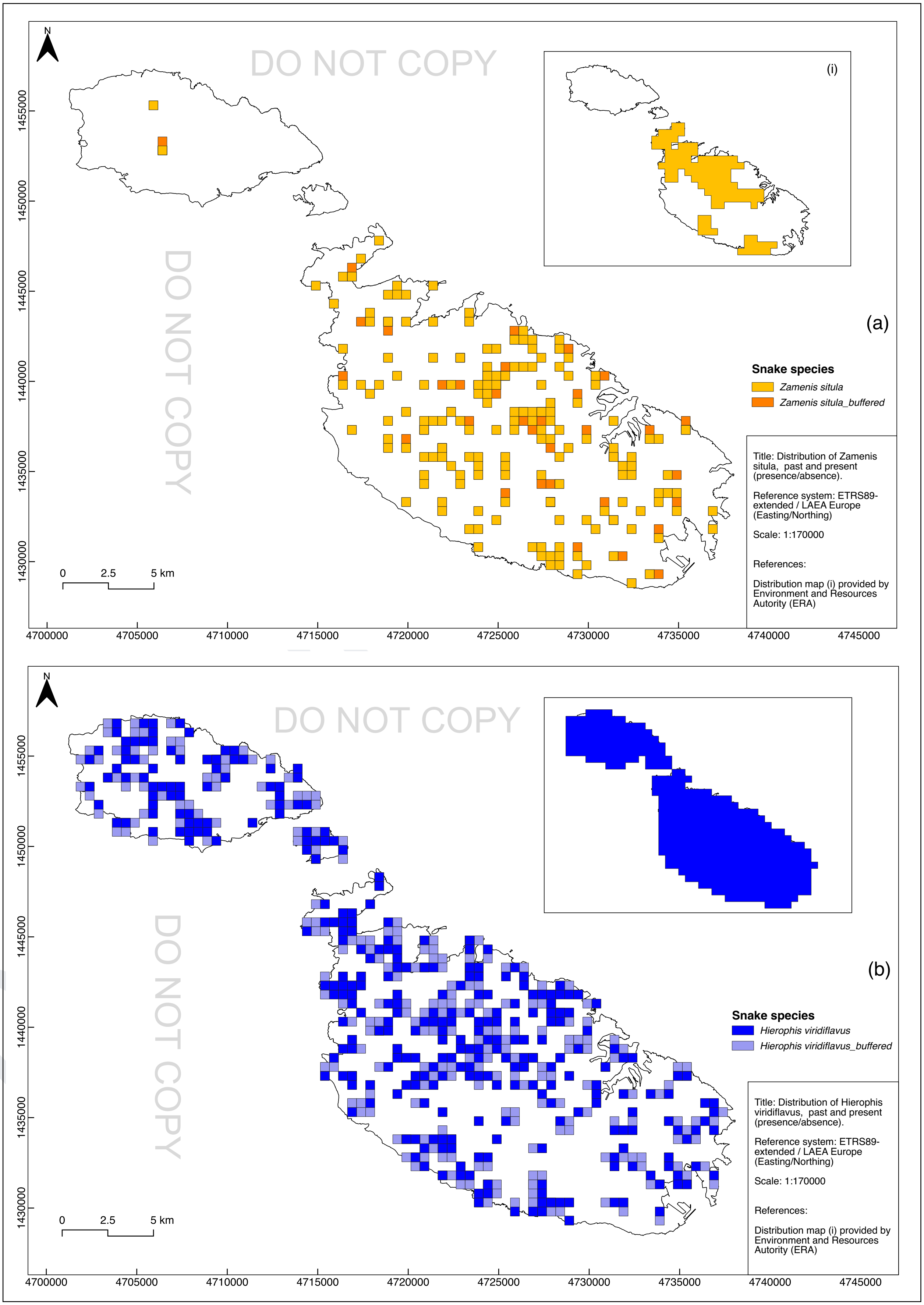


Figure 5. Native snake distribution gridded at 500 m x 500 m squares resolution: (a) *Zamenis situla*, and (b) *Hierophis viridiflavus*. The inset maps represent the past species distribution made available by the Environment and Resources Authority (ERA) through personal communication. The light blue and orange squares represent the buffered presence of the snakes, based on the 0.114Km^2 and 0.022Km^2 travel distance respectively for *Hierophis viridiflavuss* and Zamenis situlas. Map generated on QGIS version 3.16 Hannover (www.qgis.org)

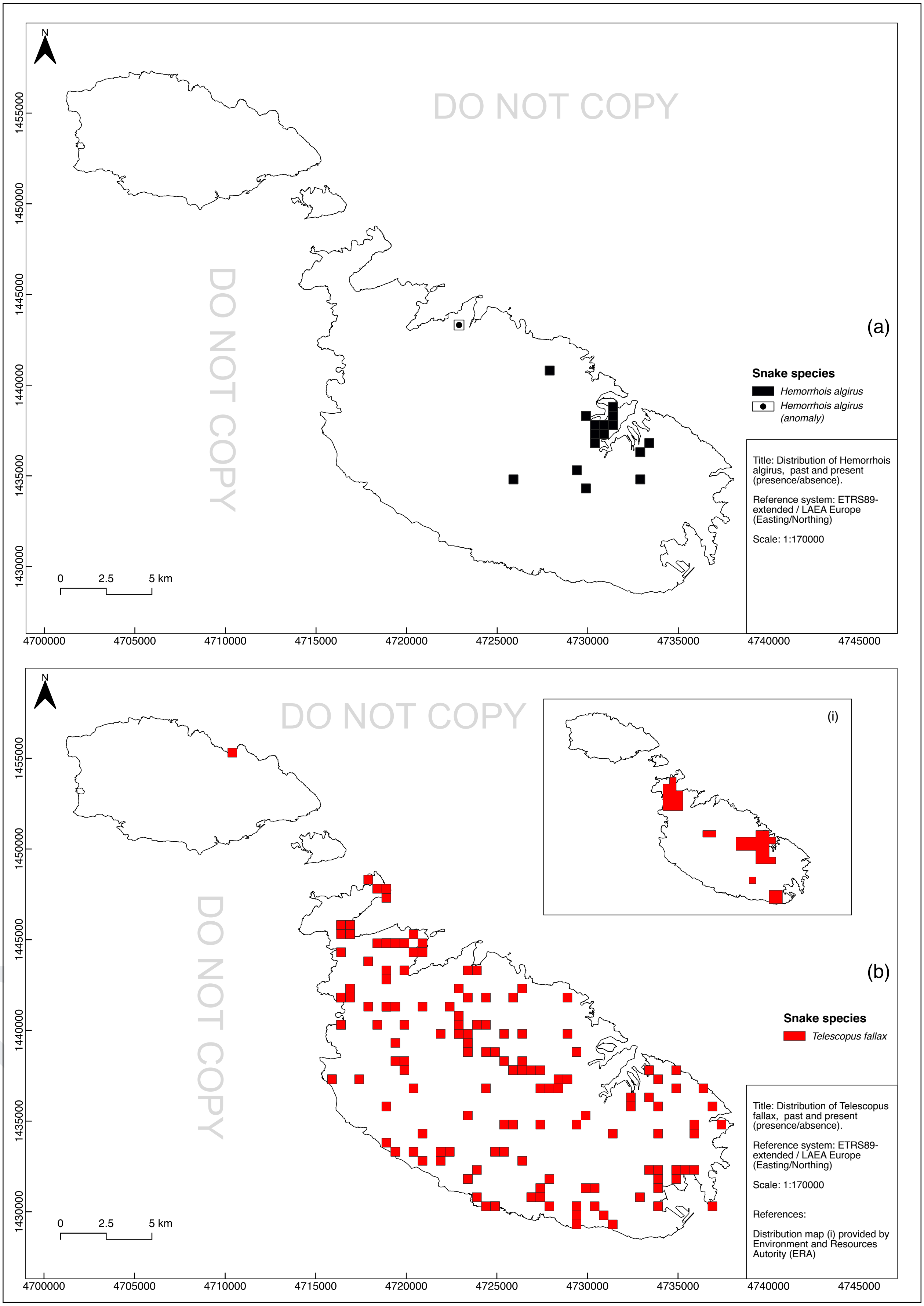


Figure 6. Naturalised snake distribution gridded at 500 m x 500 m squares resolution: (a) *Hemorrhois algirus*, and (b) *Telescopus fallax*. The inset maps represent the past species distribution made available by the Environment and Resources Authority (ERA) through personal communication. Notice that (a) presents an anomalous location of *Hemorrhois algirus* (black square, green hashed). Map generated on QGIS version 3.16 Hannover (www.qgis.org)

Discussion

Our study represents the largest known database of snake occurrence across the Maltese archipelago to date. We detected similar habitat type use between the three most widely distributed species, with presence concentrated in agricultural land, discontinuous urban fabrics, and sclerophyllous vegetation. However, the native species occupied a wider array of habitat types, and the presence maps indicate that their known range, based on these data, were substantially larger than that of their non-native counterparts. *H. viridiflavus* was the most widely distributed species and these data reinforce the notion that it is not only common but is relatively abundant across all three Maltese islands. The largest of the Maltese snake species, *H. viridiflavus* may require larger tracts of conducive habitat and move more extensively, evidenced by its greatest presence recorded in agricultural landscapes which represent the most extensive habitat type across the archipelago (Schembri, 1984; Andrews et al., 2008). The larger distributional range in comparison to the other three species could therefore be a result of established correlations between body and home range size (Reed & Shine, 2002). Moreover, the species distributions calculated in this study can only account for the specimens recorded. Therefore, each species actual range may be greater. *Hierophis viridiflavus* is also considered as having a low risk of extinction throughout the rest of its Mediterranean range attributed to its wide-ranging distribution and capacity to adapt to anthropogenically modified areas (Achille, 2015). However, *H. viridiflavus* and *Z. situla* are both sensitive to isolation which affects their presence throughout other parts of their native range (Luiselle & Capizzi, 1997). Their restriction to small fragments within intensively cultivated landscapes in Italy, did not limit their capacity to reach high population sizes and densities due to substantial rates of immigration from surrounding populations through natural corridors (Luiselli & Capizzi, 1997). Yet, this is not reflected in the Maltese populations as there is no capacity for natural immigration due to the island's isolation from mainland Europe, and urban areas continue to encroach on natural landscapes, further contributing to the view that widespread species can still be vulnerable (Lyet et al., 2013).

Based on the species area relationship (Connor & McCoy, 1979), all four species may not be able to persist in the smaller natural fragments of woodlands in high abundances and instead rely on larger conducive habitat types, most of which are anthropogenically modified across the archipelago. *Zamenis situla* and *Telescopus fallax* demonstrated a strong preference for both discontinuous urban and agricultural habitats (37.5% and 37.0%, respectively), suggesting that both species have a capacity to persist in varying degrees of anthropogenically modified landscapes. *Telescopus fallax* showed a greater presence in sclerophyllous vegetation than *Z. situla,* an observation which may be a result of *T. fallax* primarily predating on other reptile species, whilst *Z. situla* largely predates rodents (Stevens, 1995). *Telescopus fallax* distribution is also now much more widespread than previous reports and has expanded its occupation to include the western coast of

Malta, far beyond its original theorised introduction site of Floriana (Borg, 1939). This may, however, be a result of its elusive behaviour and evading detection which may have compromised the accuracy of previous presence estimates and thus exaggerating the disparity between historic and current distributions. Moreover, these data may contribute to the theory that *T. fallax* has been present in Malta for much longer than previously thought. *Hemorrhois algirus* however*,* is still recognised as an exceptionally rare snake in Malta and was represented by substantially fewer records than the other three species. Despite being isolated to a small area of Malta characterised by few habitat types, *H. algirus* appears to persist in anthropogenically altered landscapes and has carved out a niche occupying green urban areas. Whether the capacity of *H. algirus* to persist in a restricted locality is by choice, or a consequence of being unable to naturally disperse due to the presence of urban barriers remains unknown. Therefore, more locality data is required to accurately elucidate whether the species could be expanding its range and deduce the drivers behind why it has historically remained so isolated. This isolation also puts this species at severe risk of extirpation.

Species of many taxa may also select specific features of a given environment, man-made or natural, which provide it with the appropriate necessities for survival (Carpenter, 1952). For example, the importance of man-made structures is emphasised by Capula et al. (1997), reporting that over 70% of *H. viridiflavus* reports were observed in dry-stone walls and rocky sites surrounded by spiny shrubs. Both *T. fallax* and *Z. situla* are also known to colonise areas with dry stone walls, with the former species also often finding refuge in rock cavities and interstitial spaces across its native range (Achilles, 2015). These structures are common across Malta and Gozo and are primarily used to border pastures in agricultural landscapes (Vella and Garrido, n.d). It is evidenced that the three most widespread species may demonstrate variation in refuge choice based on maturity, as juveniles are regularly observed occupying the rubble walls. The utilisation of these walls also provides further explanation for the substantial proportion of records across these three species being found in agricultural landscapes, suggesting refuge type within habitats may influence presence. *Telescopus fallax* adults are also often observed in the dry-stone walls, behaviour which may be due to their nocturnal habits and continued predation on the gecko species once they mature. The utilisation of rock formations, man-made or natural for refuge is not unique to the Maltese islands and is also evidenced in the nocturnal broad-headed snake (*Hoplocephalus bungaroides*) (Webb & Shine, 2000). This species uses sandstone rocks as diurnal retreat-sites, yet their prolific removal for ornamental gardens has resulted in substantial declines through reduction in prey availability (Shine & Fitzgerald, 1989; Webb & Shine, 2000). Thus, the recent use of concrete to stabilise the traditional Maltese walls (*personal observations*) may facilitate similar outcomes by reducing prey and refuge availability and forcing snakes, particularly *T. fallax,* outside of their established niche.

Hierophis viridiflavus occupy similar habitat niches in Malta as those present across much of its native range. However, the species strong presence in agricultural landscapes in Malta may also be attributed to its use of agricultural irrigation systems which represent non-natural but semi-permanent water sources across Malta (*personal observations*). Therefore, although *Z. situla* were found significantly closer to streams than the other species (PWC, $p<0.001$), it may not be an accurate indicator of how water dependence limits snake species distribution in Malta. Instead, different species may rely on different habitats to exploit water availability, with *Z. situla* clearly associated with natural water sources. Figure 4 does appear to show that many individual snake records were located around water streams, however, due to the high temperatures recorded in warmer seasons, these are typically not permanent water features. Therefore, the substantial presence of all species in urban fabrics may also be related to water availability as anecdotal information revealed they will drink water from garden ponds and fountains. Moreover, this may explain why anecdotal data from local farmers across Malta highlighted that far fewer *Z.situla* had been seen in agricultural areas in the last 10 years. Snake presence may therefore be attributed to biological significance, as resource availability such as water, refuge, and prey may be affecting snakes' utilisation of certain habitats seeking to exploit specific resources.

In terms of elevation, the higher abundances of snakes found within the 50-100 m range may be due to the majority of Malta being represented by this elevation. A confounding issue with this study, however, may be that detection rates were biased as more people would frequent areas of low or median elevations as higher elevations such as the west coast of Malta are less populated. The Maltese islands are also very small, and temperature and humidity differed negligibly across the islands on most days. Therefore, abiotic factors may have been more associated with increased detectability rather than representing elements that influence presence. Moreover, despite continued survey efforts, it was concluded that due to its small size, Cominotto would be unable to support large herpetofauna such as snakes.

As Malta continues to experience an unprecedented rate of urban expansion (Caruana, 2020), the resident species are vulnerable to loss of conducive habitat and subsequent range contraction. It is therefore no surprise that the Maltese snakes are demonstrating high occupancy across urban areas, with no natural habitat types being represented by all four species. The positive response to urbanisation may be attributed to increased resources at moderate levels of urban density, for example gardens, and parks where some habitats are retained (Luck & Smallbone, 2010). Moreover, urban greenspaces are representing critical refuge sites for urban dwelling wildlife (Koenig et al., 2001), as evidenced by 40.5% of *H. algirus* being reported in these localities. However, this may also be a result of the species isolation and the physical barriers preventing dispersal. Native species also respond positively to the retention of vegetation (Luck & Smallbone, 2010), as evidenced within moderately urban dense areas (discontinuous dense and medium urban fabrics) such as Birkirkara reporting relatively high abundances of snakes, particularly *Z. situla* (See Figure 4). The preservation of gardens, courtyards, and green urban sites in these townships can therefore support snake populations by maintaining resource availability, but the utility of these resources is dictated by the capacity of snakes to traverse the landscape (Luck & Smallbone, 2010). The Maltese snakes, however, may be struggling to survive in areas such as St. Julians and Sliema as they are represented by extremely infrequent snake reports, likely due to lack of conducive habitat and extremely dense urban infrastructure. This suggests that there may be a limit on an urban area's capacity to support snake populations as development continues.

Citizen science data was fundamental for evidencing snake sightings in both rural and urban landscapes. Farmers for example reported seeing fewer *Z. situla*, yet there were increasing reports of the species being found in people's homes. In Greece, the species is often found in urban dwellings, likely attributed to their prey preference for small rodents (Stevens, 1995). These observations further support a pattern of range shifting from rural to anthropic environments for species such as *Z. situla* in the wake of rapid urbanisation. Some species may also be able to persist in urban environments by avoiding encounters with humans (Shine and Fitzgerald, 1996). The elusive and nocturnal habits of *T. fallax* likely resulted in reduced detection rates in comparison to the diurnal species and coupled with the concept of imperfect detectability may have resulted in an underestimation of its true distribution (Durso & Siegel, 2015). The same may be true of *Z. situla* as the species' equally elusive behaviour and low population densities can hinder detection and limit the accuracy of population and distribution estimates (Polyakova et al., 2019). Therefore, as urbanisation continues to encroach on natural habitats, the risk of human-wildlife conflict may further influence their population declines as anecdotal data revealed that the persecution of snakes was not uncommon across the Maltese islands.

Roads represent another man-made feature of a snake's environment, with 1 out of 8 snake records reported within a 5 m radius of a road, indicating that snakes are likely to be present across the dense road network and within the habitats adjacent to them. Paterson et al (2021) reported that road density was a strong predictor of reptile occupancy and *H. viridiflavus* are regularly observed exhibiting male-male combat behaviour on roads during breeding season (Achille, 2015). Local farmers have also reported that snakes are often seen crossing unpaved roads when moving between agricultural fields. However, these observations may not be a result of roads directly influencing presence, but rather demonstrates that the dense road network present across Malta has inevitably become a prominent feature of each species range. *Hierophis viridiflavus* are also highly thermophilic and have been repeatedly observed basking on open roads (Bonardi et al., 2008). Therefore, it is highly probable that roads will impact snake distributions and individual dispersal capacity by creating barriers to migration and facilitating higher degrees of mortality (Quintero-Ángel et al., 2012). Roads also cause changes in species movement patterns, and can restrict access to water and prey, illustrating they may influence variation in habitat use based on resource availability across Malta. Moreover, *H.algirus* appears almost entirely isolated due to the dense road network across Malta, especially around Floriana. Therefore, potentially reducing the impact of biotic and abiotic pressures as influencing factors in their distribution.

A limitation of these observations, however, is that in terms of detectability bias, it was important to recognise that people utilise roads more often than rural spaces, thus snakes may have been more likely to be detected in areas with more roads.

Despite providing the first confirmed presence of *T. fallax* and *Z. situla* on Gozo, it remains unknown whether the species have naturalised or whether the more likely explanation of accidental relocation is the reason. Various reports include seeing snakes in cars across Malta, therefore it is likely that the specimens found on Gozo were accidentally transported via vehicles, and *H. viridiflavus* remains the only true native species on all three islands. This hypothesis is also supported by the presence of a dead (roadkill) *H. algirus* specimen recorded in Bugibba in the northeast of Malta as seen in Figure 6 far from its currently established range. The relocation of reptiles is also reported in New Zealand with various snake species being accidentally imported via motor vehicles (Gill et al., 2001). Thus, increases in the road network in Malta is likely to facilitate more incidences of accidental relocations of snakes outside of their established ranges. As these data are the first to report relocations of this nature in Malta, they demonstrate the importance of recognising the threat posed by roads and vehicles in transporting invasive species as well as the resident species across the archipelago.

This paper provides the most accurate distribution estimates of all four species to date, including the first analysis of *H. algirus* distribution in Europe. The exact spread of the species distributions remains slightly ambiguous due to imperfect detectability; however, these maps ultimately provide an updated repertoire of presence for the native species and demonstrate that *T. fallax* has substantially expanded its range compared to previous assessments. The results also critically illustrate a rural to urban shift for the Maltese snakes as they are being forced to adapt to the rapid urbanisation of the islands, behaviour which will undoubtedly put all species at risk from a multitude of threats. The critical element of citizen science also proved invaluable in providing accurate locality records for all four species and elucidated important insights into factors that may be influencing distributions, as well as providing the first qualified records of *Z. situla* and *T. fallax* on Gozo. In the future, this data can be used in conjunction with further research to explore the causes of mortality in snakes, create species distribution models, and campaign for the implementation of eco-centric urban planning to safeguard snake populations from the varied threats resulting from urban expansion and habitat loss across the Maltese Archipelago.

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