

Title

Novel Bayesian analysis of presence-only data highlights distinctiveness of Maltese fossil record compared to Sicily

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Abstract

1. Presence-only datasets are common in a wide range of ecological studies, including the identification of faunal or botanical species in fossil records. Inherently lacking sample sizes, these data are an information-impoverished analogue of count data. Consequently, presence-only data are important but poorly exploited resource that are typically only used qualitatively.
2. We propose a novel Bayesian method which accounts for all compositional count possibilities in presence-only data to probabilistically predict the future discovery of a new species, and test for differences between datasets.
3. We apply this to Malta's fossil record to (i) test the consensus view that its Pleistocene fauna was the same as Sicily's, given the frequent periods of low sea levels when a land bridge existed between them; and (ii) determine how under-sampled Malta is compared to Sicily.
4. We establish that the faunal composition of Malta and Sicily did differ significantly in all Pleistocene sub-periods. We predict 0.427% (95% CI = 0% to 2.1%) of future Maltese fossil recoveries will yield new undiscovered species, which is 13 times more probable than for Sicily.
5. Our results indicate substantial long-term ecological and evolutionary differences existed between Malta and Sicily despite frequent Pleistocene land bridges. Our prediction of new species discoveries provides a robust quantitative foundation for further fieldwork on Malta.

Keywords

Bayesian; MCMC; mean likelihood estimator; missingness; presence-only data;

Introduction

Ecological context

The current state of Malta and Sicily as distinct islands has not always been the case. For 2.5-million-years Europe has been dominated by recurrent glacial periods when vast amounts of water locked in polar ice drastically depleted Mediterranean Sea levels, joining these islands together. By the Late Pleistocene, the Maltese Islands featured one of the highest rates of faunal endemism in the

Mediterranean (Van Der Geer 2021), yet the remarkable natural history of this Mediterranean 'Galapagos' remains poorly understood. Attempts to use the palaeontological record to connect vertebrates with their environmental settings have been limited by the destruction of most of the original early fossil sites, rendering a modern, high-resolution evaluation of chronology and context impossible. Faunal turnovers are clearly attested, yet there is little understanding of the contemporaneity of different species, or the timing and causes of extinctions and extirpations since chronologies are largely only relative approximations. As a result, Malta has played only a minor role in the reconstruction of broader, regional biogeographic and evolutionary patterns, and has typically been viewed as an extension of a larger Sicilian story since Pohlig (1893) (e.g. Hunt & Schembri 1999, Bonfiglio et al. 2002, Marra 2013).

Fossils of many faunal species have been found on both Malta and Sicily, suggesting dispersal during glacial periods, when low sea levels exposed land bridges or island 'stepping stones'. However, the direction, frequency and timing of such events remain to be established. Observed differences between Maltese and Sicilian fossil records have generally been attributed to limited sampling, particularly on Malta where known sites are sparse. However, substantial separation has also been hypothesised, with morphological similarities between fossil taxa instead attributed to convergent evolution (Herridge 2010). Untangling these processes is particularly challenging given the problematic nomenclatures used (e.g. see Herridge (2010) and Van Der Geer (2021) for discussion), and ultimately require further palaeontological investigation through the discovery and careful excavation of new sites. It remains unclear if and why some species have so far been discovered only on one island or the other. Therefore, it is both a starting point and a soluble statistical problem to use the current best available data to determine whether the difference between observational records is merely the consequence of a sampling bias or shows genuine faunal differences between Malta and Sicily during the Pleistocene.

Statistical context

Any test for a statistically significant difference in fauna between Malta and Sicily must first assume a null hypothesis that both had the same species. It must then evaluate if the observed number of differences could happen by chance, given the number of samples. The fewer the samples, the greater the chance of observing more differences under this null. However, reliable sample sizes such as NISP (Number of Identified/Individual Specimens) are not available for the available faunal fossil record of Malta and Sicily. This is fairly typical for prehistoric faunal assemblages. Apart from the fact that many species are difficult to identify, research agendas typically lead to more interest in establishing where and when species existed, and are less interested in quantifying the fossils once their presence has been established. Unfortunately, presence-only data pose a major challenge for any statistical analysis. For example, compressing the observed sample sizes of species A ($n = 50$) and species B ($n = 1$) into merely the presence of A and B causes a massive and irreversible loss of information content, informing us merely that at least one fossil of each was identified. The true counts can be handled as free parameters in a model, but there remains an infinite number of count combinations of A and B that satisfy their presence condition.

As such, the key statistical contribution of this paper is in the design of an appropriate model that properly accounts for all possibilities that give rise to the observed presence/absence, allowing us to test these differences and provide quantitative predictions of future discoveries. This can be achieved effectively if we incorporate two further pieces of information. Firstly, we can include prior estimates of the *relative frequencies* of species that have been identified as present. Surprisingly this provides information about both the total number of samples, and about the number of fossils from new species that have not yet been discovered – the missingness. This is because the presence of a rare species in our data is better explained by a larger number of fossil samples, and a larger number of samples reduces the chance of any further undiscovered species. Secondly, we can include a prior estimate of the total number of fossil samples that have been recovered from each island. Even the most conservatively broad range provides a hugely

informative limit on what is otherwise only constrained to be equal or greater than the number of identified species.

The necessarily subjective nature of these two priors may be of concern to the frequentist who values only the data, but within a Bayesian inferential framework these prior beliefs work extremely well in conjunction with the data to reveal a tightly constrained parameter space. The precision of these estimates can be greatly improved if we also have *absence data* i.e., species that can be reasonably assumed to exist, but have not yet been observed. For example, under the null hypothesis that the true faunal composition of Sicily and Malta were the same, any species observed in Sicily but not on Malta can be considered absent from the Malta dataset. This generates a statistical tension whereby the absence of common species is better explained by fewer samples, whilst the presence of rarer species is better explained by more samples.

Geological and evolutionary context

Today, Malta is a small archipelago with an area of just 316 km² in central Mediterranean. However, during periods of low sea level from the Middle Pleistocene onwards, it was either a much larger island or a south-eastern peninsula of a connected Sicily-Italy. The size of Malta and its land bridge or 'stepping stone' island connections to the European mainland can be estimated using the bathymetry of the Malta Plateau, the now underwater region between Malta and Sicily. As a structurally elevated submarine shelf covering an area of 10,700 km², the Malta Plateau is a seaward extension of the Hyblean plateau from Sicily and is located at bathymetric depths ranging from 100 m to 150 m (Bishop & Debono 1996; Micallef, Berndt & Debono 2011; Reyes Suarez *et al.* 2019). The north-western side of the Plateau is bounded by submarine ridges with depressions reaching depths of 1700 m. The Maltese archipelago represents the part of the Plateau that emerged in the early Messinian c.6 million years ago (Pedley & Clarke 2002). However, the quantified absence of any Early Pleistocene fossils on Malta, and complete lack of any geological deposits dating to this period may suggest that Malta was either mainly submerged during this timeframe, or a smaller/more difficult to reach island.

Projecting the current bathymetry into the past is problematized by tectonic changes owing to Malta's proximity to the subduction boundary between the African and European plates. Patterns of tectonic instability since the Late Pleistocene have been inferred in the region of western and south-eastern Sicily using seismic and global positioning system (GPS) data (Oldow *et al.* 2002; Anzidei *et al.* 2014). However, over the last 125 thousand years (kyr), the Maltese archipelago has been generally observed as tectonically stable (Pedley & Clarke 2002; Galea 2007; Serpelloni *et al.* 2007; Furlani *et al.* 2013; 2021). Therefore, post-125-kyr estimates of the changing coastal morphology of Malta and its connections based on past periods of Mediterranean sea-level changes may be fairly reliable, and have been supported by underwater surveys (Siddall *et al.* 2003; Lambeck & Purcell 2005; Lambeck *et al.* 2011; Furlani *et al.* 2013; Micallef *et al.* 2013; Zecchin *et al.* 2015; Foglini *et al.* 2016; Benjamin *et al.* 2017; Antonioli *et al.* 2018; Furlani *et al.* 2018; Antonioli *et al.* 2021). On this basis, the most recent period of land connection and subsequent inundation occurred during the Last Glacial Maximum (LGM, 20 ka), when an exposed Malta Plateau acted as a connecting land bridge (90 km long and 40 km wide) between Sicily and Malta at 130 m isobath (Furlani *et al.* 2013; Micallef *et al.* 2013; Foglini *et al.* 2016). Post-LGM glacial melting increased sea-levels at an average rate of 5 mm per annum (Lambeck *et al.* 2011) and from 12.9 ka, the Malta Plateau was completely submerged by successive events of glacio-eustatic sea-level rise. This most recent cycle of connection and inundation is a model for previous cycles, although pre LGM tectonic changes cannot be ruled. During the greatest glacial extremes of the Pleistocene, sea levels periodically dropped to at least 120 m below current sea level, coinciding with Marine Isotope Stage (MIS) 16 (c. 630 ka; early Middle Pleistocene) (Bintanja, Van De Wal & Oerlemans 2005), MIS 12 (c. 460 ka; Middle Pleistocene), and a drop in sea level to 130 isobath in MIS 6 (c. 140 ka), which likely represents the most recent substantial land connection prior to the LGM (Benjamin *et al.* 2017). Other more recent dips such as c.100m around 80 ka may not have been sufficient to maintain a complete land

bridge, but rather may have exposed a series of islands linking a larger Malta with Sicily. Thus, Malta is likely to have had a semi-permeable relationship with Sicily between 140 and 20 ka, with stepping stone islands likely acting as a filter in faunal exchanges.

These changes provide a plausible mechanism for significant faunal differences between Malta and Sicily. Periodic changes in climate and sealevel, and possibly tectonics, created a frequently changing ecological landscape, which in turn would change selective pressures. The separation of islands and loss of habitat diversity from higher sea levels during warmer interglacial periods would have permitted divergent evolutionary trajectories and independent extinctions, despite the fact that the faunal units or biozones of Malta and Sicily have been regarded as being the same since the early 20th century (Busk 1868; Adams 1870). This is due to the fact that a smaller terrestrial surface area would have reduced carrying capacity and population sizes, exacerbating evolutionary change further through increased genetic drift and stochastic extinction processes, while the greater isolation would have impeded new colonisations to replace extinct or extirpated species.

Materials and Methods

Pleistocene palaeontological faunal fossil data of Malta and Sicily

We used the faunal lists of Van Der Geer et al. 2021, which reflects the most comprehensive collation of faunal literature to date for the Siculo-Maltese region for broad sub-periods of the Pleistocene. These were integrated into an updated taxonomic and stratigraphic framework (see also SI). These are summarised for Malta and Sicily as Early Middle Pleistocene (EMP), Late Middle Pleistocene (LMP) and Late Pleistocene (LP). Additionally, fossil records from the Early Pleistocene (EP) are available for Sicily, but despite extensive surveying, no geological deposits from this period have been found on Malta. Therefore, *a priori* we assume Malta was submerged during the EP and housed no terrestrial species.

The biostratigraphy on Malta is primarily based on the cave of Għar Dalam (SE Malta, Birzebbugia) which has a relatively well-preserved Late Middle Pleistocene-Holocene stratigraphic sequence and has been extensively excavated (Van Der Geer 2021). The youngest layer in this limestone cave is an archaeological layer, which dates to the mid-Holocene and yielded remains of domestic animals, which we exclude. Għar Dalam yielded mainly megafauna (*Hippopotamus*, *Palaeoloxodon*, *Cervus*, *Canis*) and few small mammals. As a consequence, their biostratigraphic position is inferred from co-occurring megafauna at their localities, e.g. the dormice *Leithia melitensis* from Mnajdra, Tal-Ġnien fissure, Wied Inċita and Bengħajsa Gap, *L. cartei* from Mnajdra, *Maltamys gollcheri* from Mnajdra, and *M. wiedincitensis* from Wied Inċita (for details, see SI). *Maltamys gollcheri* is sometimes considered a junior synonym of *Leithia cartei* (Zammit-Maempel & De Bruijn 1982), whilst we follow the view that *Maltamys* sp.–*wiedincitensis*–*gollcheri* are chronospecies and *Leithia cartei* is a distinct species (Masini et al. 2008). The elephant genus *Palaeoloxodon* is referred to as *Elephas* in older literature. We also drop subgenus level e.g., *Microtus* instead of *Pitimys* for the Maltese vole.

The current biozones of Sicily — also known as Faunal Complexes — are mainly based upon new arrivals and extinction events of megafauna in combination with stratigraphical data (Bonfiglio, Marra & Masini 2000; Bonfiglio et al. 2002; Masini et al. 2008). The earliest insular biozone, the Early Pleistocene Monte Pellegrino fauna, named after its single site (Kotsakis 1978) has so far no equivalent on Malta. Yet, it already contains early forms of the two giant dormouse lineages that are shared between Sicily and Malta, starting in the early Middle Pleistocene. An even older biozone, the Messinian, late Turolian (MN 13) Gravitelli fauna (Seguenza 1902) is excluded here as it represents a Eurasian mainland fauna. Also excluded here is the Castello Faunal Complex of the terminal Pleistocene (likely coinciding with the Last Glacial Maximum) as this fauna belongs to the pan-Eurasian mammoth steppe fauna.

The biochronology of Sicily and Malta is inextricably linked with the presence of dwarf elephants, although only one taxon – *Palaeoloxodon falconeri* -- is chronologically diagnostic. Initially, three dwarf Maltese elephant species were recognised: *Palaeoloxodon melitensis*, *P. falconeri* and *P. mnaidriensis* (see SI for details). The first is considered a junior synonym of the second (Ambrosetti 1968) as the material cannot be properly separated based on body size. Confusingly, the three elephant species names that were defined based on Maltese fossils, have since been applied to elephant remains from Sicily, with *P. mnaidriensis* used for larger-sized (ca. 2m tall), and *P. falconeri* for small-sized (ca 1m tall), dwarf elephants (following Vaufreyc 1929). In addition, a fourth, large-sized subspecies (*P. antiquus leonardi*) has been recognised at a Sicilian late Middle Pleistocene deposit (Aguirre 1969). Its fossils occur together with remains of middle-sized species at Contrada Fusco near Siracuse, indicating they might represent male individuals, as elephants are highly sexually dimorphic in size. We here exclude *leonardi* from our overviews.

The large-sized dwarf elephant from Sicily, referred to *P. mnaidriensis*, likely represents a separate species from the medium-sized *P. mnaidriensis* described from Maltese material (Herridge 2010), thus in the literature, it is often placed in quotation marks or prefixed with *aff.* to indicate taxonomic uncertainty. Here, we keep the name, pending a revision of the Siculo-Maltese elephant phylogeny, and use it to refer to the large-sized dwarf elephants on Sicily and Malta, in line with common usage. This ongoing taxonomic uncertainty in the most-studied Siculo-Maltese taxonomic group, dwarf elephants, is likely indicative of similar issues across the many taxa that have lack any kind of taxonomic scrutiny. However, this shared faunal framework summarised in van der Geer *et al.* 2021 continues to inform biogeographic and biostratigraphic inference in the region, potentially overestimating the similarities between the island faunas. Here we ask the question: even under this assumption of shared faunal history, which should over-emphasise co-occurrence of taxa, are Malta and Sicily's Pleistocene fauna similar?

Prior beliefs of relative frequencies

Our estimates of the relative frequencies of each species are presented as integer ratios with respect to the rarest species (relative frequency = 1, see table 1). These prior beliefs are provided by author AvdG who formed these estimates using expert knowledge of trophic pyramids, predator-prey dynamics, modern species analogues, NISP counts of comparative fossil assemblages, and differential taphonomic loss. This prior knowledge is by definition subjective; so as a sensitivity test, we also use a second set of prior estimates from author EYH, ensuring complete independence between authors. They are similar in their ranking of the relative frequencies of species but differ quantitatively by an order of magnitude (biggest ratio of 100:1 rather than 1000:1).

species	name	Prior beliefs of relative species frequencies		Early Pleistocene (EP)		Early Middle Pleistocene (EMP)		Late Middle Pleistocene (LMP)		Late Pleistocene (LP)	
		AAEvdG	EYH	Sicily		Sicily	Malta	Sicily	Malta	Sicily	Malta
<i>Pellegrinia panormensis</i>	Gundi	700	100	x							
<i>Mustelercta arzilla</i>	Marten	5	50	x							
<i>Leithia sp.</i>	Dormouse	800	100	x							
<i>Hypolagus peregrinus</i>	Hare	600	80	x							
<i>Apodemus maximus</i>	Giant fieldmouse	1000	100	x							
<i>Asoriculus burgioi</i>	Shrew	500	100	x							
<i>Maltamys cf. gollcheri</i>	Dormouse	800	100	x							
<i>Leithia melitensis</i>	Giant Dormouse	800	80			x	x				
<i>Palaeoloxodon falconeri</i>	Dwarf Elephant	300	10			x	x				
<i>Leithia carteri</i>	Giant Dormouse	800	80			x	x	x	x		

<i>Maltamys gollcheri</i>	Dormouse	800	80			x	x				
<i>Crocidura esuae</i>	White-toothed Shrew	500	100			x	x	x	x		
<i>Lutraeximia trinacriae</i>	Sicilian Otter	5	1			x		x			
<i>Tyto mourechauvireae</i>	Large Barn Owl	5	1			x					
<i>Cygnus equitum</i>	Small swan	10	20			x					
<i>Grus melitensis</i>	Giant Crane	10	20			x	x	x	x		
<i>Athene trinacriae</i>	Owl	5	1			x					
<i>Testudo hermanni</i>	Hermann's Tortoise	7	10	x		x		x		x	
<i>Testudinidae sp.</i>	Giant Tortoise	50	60			x					
<i>Lutra euxena</i>	Maltese Otter	5	1				x		x		
<i>Maltamys wiedincitensis</i>	Dormouse	800	100				x	x	x		x
<i>Hippopotamus pentlandi</i>	Dwarf Hippo	300	10					x			
<i>Palaeoloxodon mnaidriensis</i>	Dwarf Elephant	300	10					x	x	x	
<i>Hippopotamus melitensis</i>	Dwarf Hippo	300	10						x		
<i>Microtus melitensis</i>	Vole	800	80						x		
<i>Grus grus</i>	Common Crane	10	20						x		
<i>Centrochelys robusta</i>	Giant Tortoise	50	60						x		
<i>Microtus pauli</i>	Burrowing vole	800	80						x		
<i>Dama carburangelensis</i>	Fallow Deer	100	40					x		x	
<i>Bos primigenius</i>	Aurochs	100	20					x		x	
<i>Cervus elaphus</i>	Red Deer	100	40					x	x	x	
<i>Sus scrofa</i>	Wild Boar	100	40					x		x	
<i>Ursus arctos</i>	Brown Bear	1	1					x		x	x
<i>Bison priscus</i>	European Bison	100	20					x		x	
<i>Canis lupus</i>	Wolf	1	1					x	x	x	
<i>Panthera leo</i>	Lion	1	1					x		x	
<i>Crocuta crocuta</i>	Spotted Hyena	1	1					x		x	
<i>Lepus europaeus</i>	Brown Hare	600	80							x	
<i>Erinaceus europaeus</i>	European hedgehog	75	80					x			
<i>Emys orbicularis</i>	European pond turtle	7	60					x			
<i>Cygnus falconeri</i>	Giant Swan	10	20					x	x		
<i>Equus hydruntinus</i>	Wild Ass	100	10							x	
<i>Apodemus sylvaticus</i>	Common Fieldmouse	1000	100							x	
<i>Microtus savii</i>	Pine Vole	800	80							x	
<i>Crocidura sicula</i>	Sicilian Shrew	500	100							x	x
<i>Equus caballus</i>	Horse	100	10							x	
<i>Crocidura sicula calypso</i>	Gozitan Shrew	500	100								x
<i>Cervus sp</i>	Dwarf Deer (medium)	300	40								x
<i>Cervus sp</i>	Dwarf Deer (small)	300	40								x
<i>Cervus sp</i>	Dwarf Deer (tiny)	300	40								x
<i>Microtus melitensis</i>	Burrowing vole	800	80								x
<i>Rhinolophus hipposideros</i>	Lesser horseshoe bat	25	80								x
<i>Vulpes vulpes</i>	Red Fox	1	10							x	x

Table 1: Species identified as present (x) on the islands of Malta and / or Sicily during the four broad Pleistocene periods. Prior beliefs of the relative frequencies of each species were obtained independently from authors AvdG and EYG. These are qualitatively similar in terms of their ranking but differ quantitatively by and order of magnitude.

Estimating missingness

Consider the simpler problem of how to use *counts* of fossils to quantify numbers of species that existed but have not yet been discovered. With the accumulation of many specimens we can become increasingly confident that no further undiscovered species exist, since the absence of evidence increasingly becomes evidence of absence as sample sizes increase. Equivalently, the chance of discovering a new species is greater if we have observed very few specimens so far. We can model this as a vast urn containing balls (specimens) of many different colours (species). We then propose the existence of one further colour, which aggregates all remaining species that have not been observed, which we call the missingness. This missingness proportion of balls in the urn remains a free parameter in the model to be indirectly estimated (a percentage between 0% and 100%). Once a missingness percentage is proposed, it is trivial to convert the relative frequencies of the observed species to proportions, to ensure 100% of the balls have been appropriately assigned to either an observed species or missingness. For example, if two species are observed which we believe existed with a relative frequency of 1 to 10, and 3% missingness is proposed, the urn comprises 8.82%, 88.18% and 3% of each type respectively.

The likelihood of any proposed urn configuration (the probability of observed *counts* given some proposed urn proportions and missingness) can be calculated exactly using the multinomial distribution. However, there are many possible urn configurations that could lead to the same observed data, therefore there is always a range of possible true values of missingness. Fig 1 illustrates this for the simple case of just two species (A and B) believed to have been present with equal frequency, under all combinations of data between 0 and 10 samples each, and five discrete proposed values of missingness.

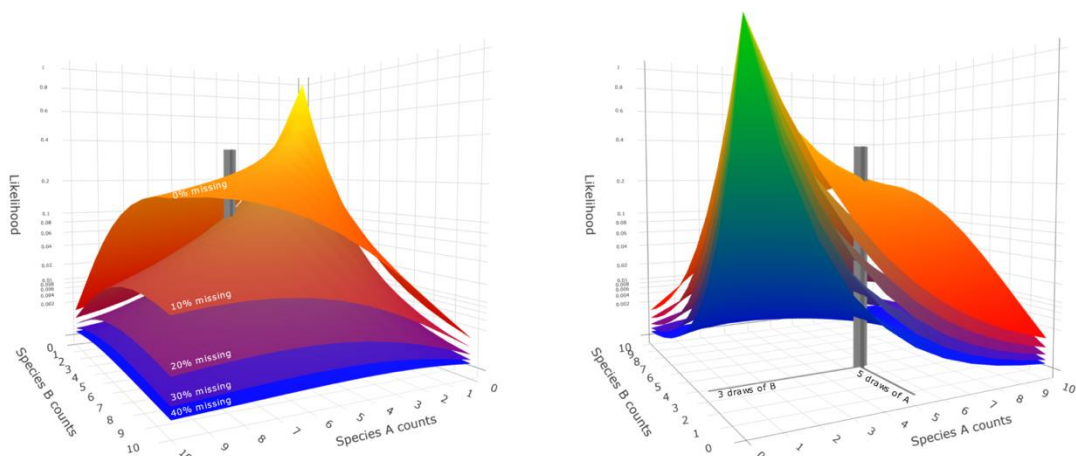
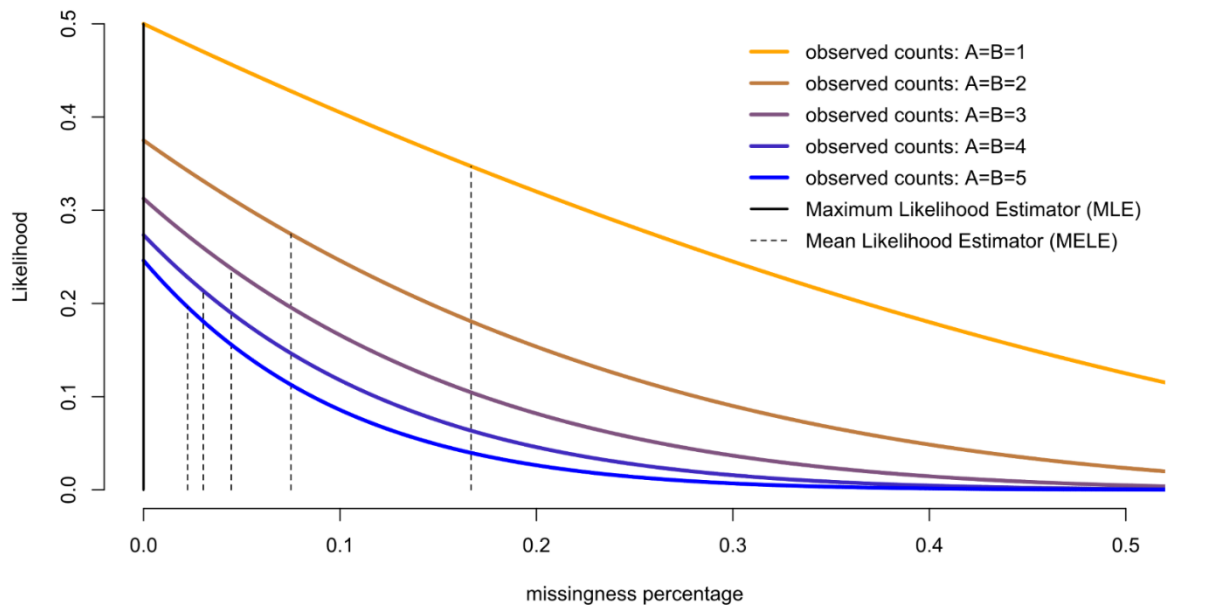


Fig 1: Two views of the same five likelihood surfaces, illustrating how confident we can be in a model of both species A and B being present with equal frequencies, under various combinations of observed counts and proposed missingness.

Notice that likelihoods always increase as the number of observations reduces. This is because it is more probable to observe one of each from two draws, than two of each from four draws, and certain to observe nothing from zero draws. Notice also that the surface with zero missingness always has a higher likelihood. This might seem strange – surely if I draw only two samples and each is a different species, I should expect to find a new species soon if I continue drawing from the urn? The solution to this counterintuition is two-fold. Firstly, we are interested in the probability of drawing these two *specific* species, not *any* two (we will later specify prior beliefs on the proportions of *specific* species), so the chances of drawing two specific species from a possible two species is higher than drawing the same two from a possible three species. Secondly, and most importantly, this type of problem is served poorly by a point estimate,

and even if a point estimate was desired, the maximum likelihood estimator (MLE) is not the best estimator. This is because the MLE always sits at the limit of the distribution, and therefore does not represent the expected value which is somewhere within the distribution. Instead, Fig 2 shows the likelihood curves for different observed counts of A and B, and the Mean Likelihood Estimator (MELE) which is equivalent to the Bayes estimator with a uniform prior (McLeod & Quenneville 2001).



Mean likelihood estimator (MELE) which provides the expected value,

Fig 2: Intuitively there is a high chance of a new species C existing if we have only observed one count each of A and B, and a tiny chance of a new species C existing if we have observed thousands of A's and B's. Yet the MLE is always zero (solid vertical line). In contrast, the MELE provides an estimate of the expected missingness value (dashed vertical line), which is much greater with fewer observations.

Calculating likelihoods from Presence-only data

By definition, presence-only data does not include the number of samples for each species, and there are an infinite number of possible draws that satisfy the observation of being present. We resolve this by first introducing one further parameter – the total number of draws D , which must be an integer greater or equal to the number of species observed. For any proposed value for D we can then generate all possible combinations of species counts that sum to D and calculate a likelihood for each combination. For example, if we propose four draws ($D=4$) from two species (A and B), the three (unordered) sets AAAB, AABB, AB BB are plausible explanations for the observation that species A and B were both present. Since all these combinations are possible, the overall likelihood becomes the sum of the likelihoods of each combination.

In practice this approach is intractable for even moderate values of D due to the huge number of compositional sets determined by

$C(n,r)C(n,r)$ where $n=D-1$ and $r=\text{number of species}$. Instead, we devise an efficient algorithm written in R (see SI for functions written in R) (Team 2013) that utilises the inclusion – exclusion principle so that only 2^r combinations need be generated, no matter how large D . For example, there are $C(499,10)C(499,10) = 2.4 \times 10^{20}$ compositional sets that satisfy 500 draws from 10 species, but our algorithm only requires $2^9 = 512$ combinations to be calculated. The need for this additional parameter (D) couples with the poorer information content of presence data to generate huge equifinality, with a vast array of parameter combinations being almost identically probable. For example, Fig 3 illustrates that if five species have been observed, likelihoods reach near certainty under zero missingness with any number of draws above c.50. Clearly point estimates cannot represent this uncertainty. Nevertheless, the maximum likelihood explanation is that we have exhaustively sampled (a huge number of balls were drawn) and there are no further

species to be found. However, a *better* explanation using the MELE is that 13 fossils were drawn and 6.6% of fossils in the urn belong to as yet undiscovered species (Fig 3 left), or in the case of one species *a priori* believed to be 10 times more common than the others, the better explanation is that 34 fossils have been drawn with 2.7% belonging to new species (Fig 3 right).

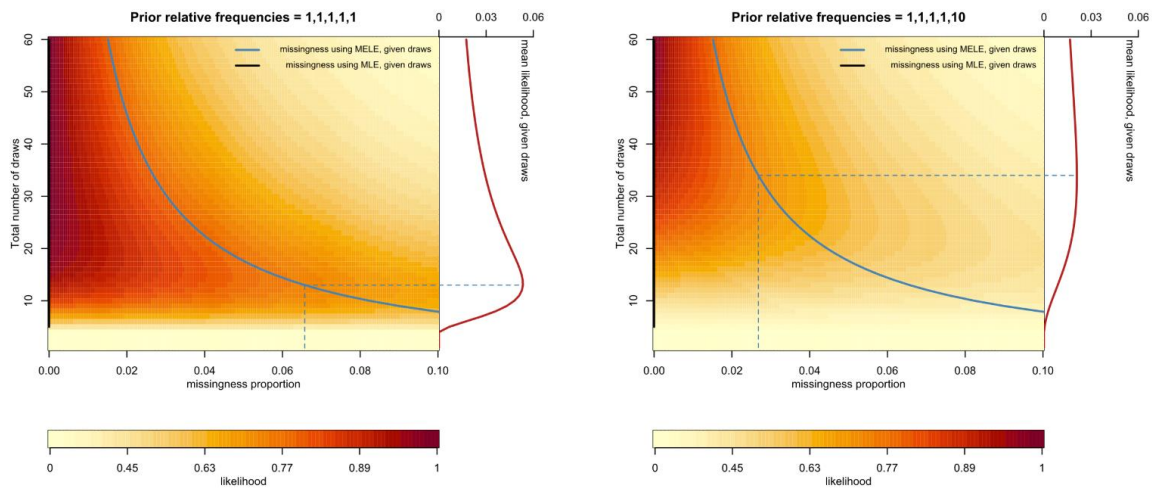


Fig 3: Likelihood surfaces illustrate the substantial equifinality in presence data, since there are many possible combinations of missingness and the number of draws that can result in the same observation of five species being present. Nevertheless, if point estimates are required, mean likelihood estimates (MELE) are superior to maximum likelihood estimates (MLE) for this type of problem. Left: five species are observed where all are *a priori* believed to be present with equal frequencies. Right: the same five species where one is *a priori* believed to be ten times more common than the others. In both cases the best MLE point estimate is an infinite number of draws with zero missingness (an exhaustive search where all species have been found). In contrast, the best MELE point estimate is 13 draws with a further 6.6% of samples in the urn belonging to as yet unobserved species (left), and 34 draws with a further 2.7% in the urn belonging to as yet unobserved species.

Known absence

If more than one sample set is available *for the same ecological unit*, we gain the advantage that a species that is present in one set but absent in another provides additional constraints to the parameters. For example, under the null hypothesis that the land bridge between Sicily and Malta was substantial and persistent enough to ensure the same fauna on both, species present on Sicily that have not been observed on Malta are now known to be absent from the Maltese data, despite being hypothesised to have existed. Therefore, the failure to have observed them is best explained by fewer draws, which generates more statistical tension. Fig 4 illustrates this effect for just two toy presence sample sets, such that set 1 comprises species A, B, D, F, G whilst set 2 comprises species A, B, C, E. We apply our prior beliefs in the relative frequencies of A, B, C, D, E, F, G as 10, 8, 4, 3, 2, 1, 1 respectively, and an uninformative prior on the total number of draws. This results in a 3D likelihood manifold with regard to the total draws from set 1, total draws from set 2, and the common missingness (species in neither set), which we illustrate using 2D and 1D marginal distributions.

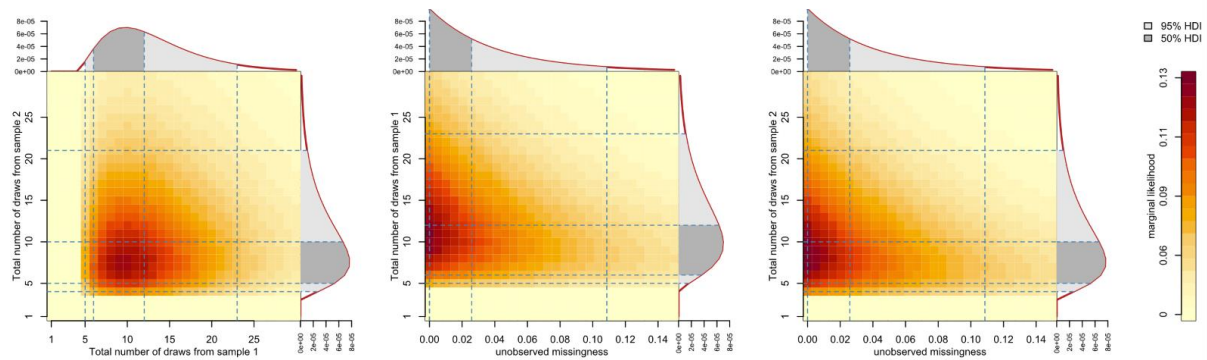


Fig 4: All three marginal 2D and 1D distributions of the 3D likelihood manifold, illustrating the joint likelihoods of i) the total number of draws from sample set 1; ii) the total number of draws from sample set 2; and iii) the proportion of missingness, given two pieces of information: a) the observation species A, B, D, F and G were present in sample set 1, and species A, B, C and E were present in sample set

2; and b) prior beliefs that the true relative proportions of species A, B, C, D, E, F, G are 10, 8, 4, 3, 2, 1, 1 respectively. This heavily constrains 3D parameter space, providing estimates that the total number of draws in sample 1 is 5 to 23 (95% HDI), total number of draws from sample set 2 is (4 to 21 95% HDI), and the unobserved missingness is 0 to 11% (percentage of the urn that belong to new species). 95% and 50% highest density estimates are illustrated for 1D marginals only.

Prior beliefs of total number of fossils

Parameter estimates can be greatly improved with the inclusion of a prior estimate of the total number draws D . These can be easily incorporated within the Bayesian framework by multiplying the likelihood distribution by a probability distribution that describes our *a priori* belief of D , which we use within an MCMC framework to sample from the posterior distribution. Our prior estimates (independent for each period for each island) were provided by authors AvdG, who has expert knowledge of the archiving of fossil assemblages (see table 2). The ranges are deliberately wide to ensure conservative results and represent AvdG's 95% confidence intervals of the true number of fossils that are identifiable to species level that have been discovered. In their raw form these are simply upper and lower boundaries, but we also incorporate a central tendency to represent AvdG's belief that values near the middle of the range are more probable than values near the boundaries. This is achieved by converting the raw ranges to the 95% quantiles of a unimodal distribution. A Gaussian distribution is inappropriate for this since the true number of samples cannot be negative, instead we use a Gamma probability distribution.

Period	Island	Prior number of fossil samples		Gamma probability distribution parameters	
		lower	upper	shape	rate
EP	Sicily	500	2000	14.44314	0.01305
EMP	Malta	20	150	7.15700	0.10596
	Sicily	2000	4000	55.88176	0.01925
LMP	Malta	500	2000	14.44314	0.01305
	Sicily	1000	5000	10.87494	0.00424
LP	Malta	500	2000	14.44314	0.01305
	Sicily	5000	10000	55.88176	0.00770

Table 2: Prior beliefs of the total number of fossil samples identifiable to species level recovered in each period for each island. Lower and upper values represent the raw ranges that encompass the true number of fossils, with 95% confidence. These are then converted to Gamma distribution parameters (shape and rate) to also incorporate the central tendency of this prior probability distribution, such that values near the boundary are less probable.

Parameter estimates using MCMC

All parameters were estimated using Markov Chain Monte Carlo (MCMC) using the Metropolis-Hastings algorithm (Hastings 1970). The three independent search types are summarised in Table 3, repeated for each period independently (EMP, LMP and LP) plus EP for the independent hypothesis on Malta. Each was performed using AvdG's prior frequencies and repeated as a sensitivity test using AYH's prior frequencies. We ran 100 chains to avoid the need for thinning (Link & Eaton 2012), and each chain was run for 100,000 steps, with the first 1000 discarded for burn-in. Both the starting parameters and the jump sizes of each parameter proposal were tuned by repeating this entire process until convergence and reasonable acceptance ratios (c.20-55%).

Hypothesis	Parameters	Parameter description
Null	missingness D_{malta} D_{sicily}	Proportion of undiscovered fossils belonging to species not yet found on Malta or Sicily Total number of fossils so far drawn from Malta Total number of fossils so far drawn from Sicily
Malta Independent	missingness D	Proportion of undiscovered fossils belonging to species not yet found on Malta Total number of fossils so far drawn from Malta
Sicily Independent	missingness D	Proportion of undiscovered fossils belonging to species not yet found on Sicily Total number of fossils so far drawn from Sicily

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Table 3: Summary of the independent parameter searches performed for each of the Palaeolithic time periods.

Null hypothesis test

Our objective is to test if the number of species differences between Sicily and Malta (present on one but not the other) could have occurred under the null hypothesis that Sicily and Malta had the same fauna. We test this for each period (EMP, LMP, LP) independently, by first performing a parameter search under the null (see Table 3), then randomly sample parameter sets the joint posterior distribution. Each parameter set is used to generate an integer number of observations for each species (for Malta and Sicily separately) by randomly sampling from the multinomial distribution such that size = D and the multinomial probabilities use the species frequency priors and the missingness. Integers are then compressed to presence – absence, and our summary statistic is the total number of species differences between Sicily and Malta. When repeated for 100,000 sampled parameter sets, this provides a summary statistic distribution under the null hypothesis, which can be compared with the same statistic from the observed data. Finally, we calculate the p-value as the proportion of null samples that generate more (or the same) differences as the observed data.

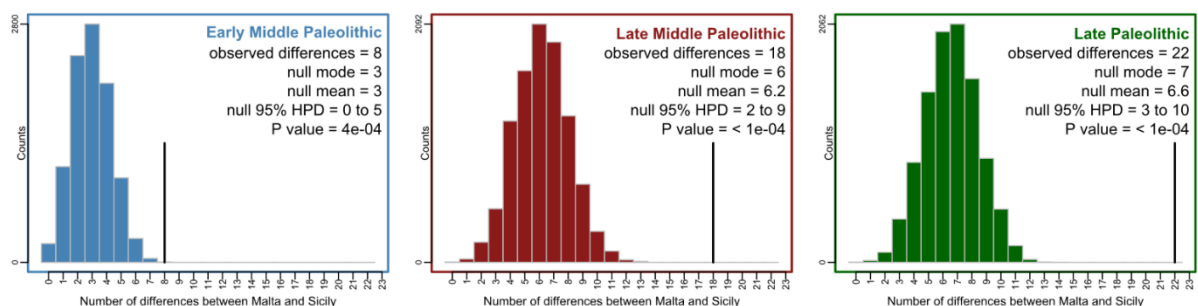
Alternative hypothesis

If the null hypothesis can be rejected, we instead accept the alternative hypothesis that the faunal compositions of Malta and Sicily differed, and we can instead directly use our missingness parameter to infer the proportion of new fossils belonging to undiscovered species. From this we derive the number of new fossils to be found before we should expect a better than even chance of discovering a new species.

Results

Null hypothesis test

The null hypothesis can be unequivocally rejected for all three time periods tested (EMP, LMP, LP). Fig 5 illustrates the observed number of species differences between Malta and Sicily compared to the null distribution of differences, generated from the joint posterior parameter distributions. In the cases of LMP and LP, not a single iteration of the MCMC chain under the null model generated more differences than observed (18 differences from 26 species, and 22 differences from 25 respectively) and in the case of EMP around 0.04% of simulations were as extreme (8 differences). Since we reject the null hypothesis, no direct inferences can be drawn from the parameter estimates under the null. Nevertheless, the additional absence data clearly has a huge constraining influence on parameter space, and shows that precise estimates can be achieved in other applications where there are known absences (Fig S11). As a sensitivity test, we repeated using our independent set of priors for the species' frequencies from author EYH (Fig S12), which also leads to rejection of the null hypothesis for all three time periods.



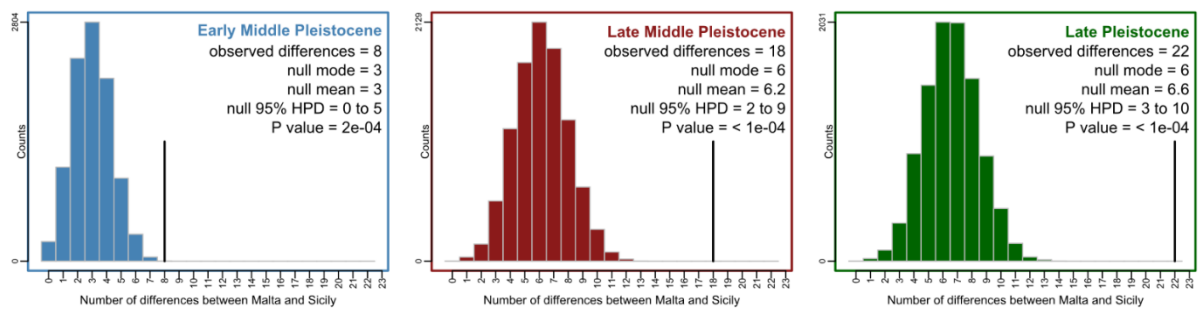


Fig 5: Null distributions of the number of species differences between Sicily and Malta, for each time period tested independently. In each case the observed number of species differences (vertical black line) is significantly greater than can be expected under the null.

Alternative hypothesis parameter estimates

Having rejected the null hypothesis, the alternative hypothesis that species composition differed between islands requires independent parameters for Sicily and Malta. Fig 6 illustrates and summarises these posterior estimates. Missingness represents the probability of the next fossil being a new species, which is substantially higher for Malta in all periods. Most notably, this probability is slightly over 1% for the Early Pleistocene. A quantitative comparison with Sicily's missingness indicates this potential for the discovery of a new species is several times greater on Malta than Sicily for all periods, with mean missingness of Malta divided by mean missingness of Sicily = 30.6, 2.4 and 6.4 for EMP, LMP and LP respectively. Overall (equally weighting all three periods) this is 13.16 times greater probability of discovering a new species on Malta.

These missingness probabilities can be used in the Geometric distribution to predict how many fossil draws should be expected before there is a better than even chance of discovering a new species. In the case of Malta EMP, the mode estimate is just 16 new draws (50% CI = 13 to 88), suggesting further excavation work of (yet to be discovered?) EMP deposits on Malta is highly likely to yield important new discoveries.

Our sensitivity test repeats all these independent hypothesis tests using our alternative prior beliefs provided by author EYH (Fig S13), and result in remarkably similar estimates despite these priors differing by an order of magnitude. This suggests that although this Bayesian framework has incorporated several relevant prior beliefs, ultimately these results are dominated by the data. Indeed, the alternative priors provide slightly higher estimates of missingness on Malta (1.127%, 0.098% and 0.098% for EMP, LMP and LP respectively), suggesting our results may even be slightly too conservative.

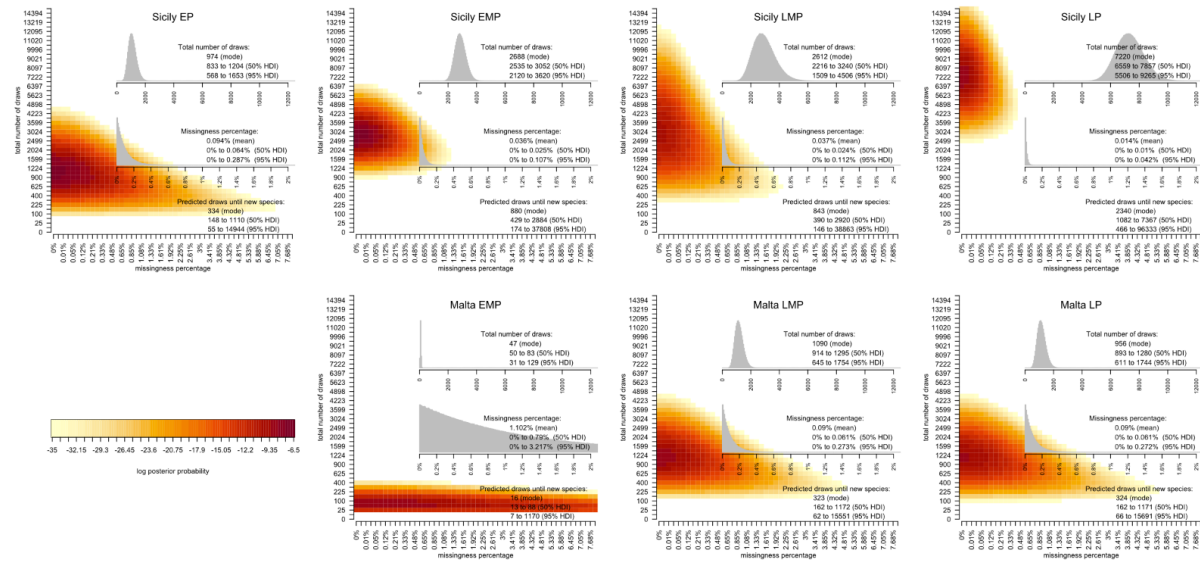


Fig 6: Posterior parameter estimates under the alternative hypothesis that the faunal composition of Sicily and Malta differed.

Discussion

We have developed a new inferential framework with wide application in the palaeontological sciences, that can estimate the probability of new species discoveries. Our approach is of particular relevance in the context of excavation planning, in situations where opportunities for excavation are limited, or in places where there has been a substantial destruction of sites, for example due to over-development.

With reference to our case study, our results indicate that Malta and Sicily differed in their faunal ecologies over the Middle and Late Pleistocene, and also that a number of new species are yet to be discovered, especially on Malta. While our model assumes equivalence of fauna at times when Malta and Sicily were contiguous, the connection to Malta may have been less of a conduit than currently understood. For example, it remains possible that land bridges during periods of low sea level only existed for very brief periods, or were partial, consisting of ‘stepping stone’ islands. It is also possible that connections featured barriers such as rivers (see, e.g. Pedley et al., 2002), swampy regions or other challenging terrains. Our model also does not take into account the opposing forces of evolution (species gain) and extinction (species loss) of taxa down-stream of those time periods where Malta and Sicily were connected. Nevertheless --and despite the fact that similarities between the islands are likely overemphasised given the assumption of shared taxonomic history -- our results represent the first quantitative effort to compare the two islands’ faunas, and indicate that Malta had its own island ecosystem. Indeed, although low in diversity, Malta features some of the highest rates of endemism for its size in the Mediterranean during the Middle to Late Pleistocene (see, e.g. van der Geer et al., 2020). Malta’s fauna should no longer be seen as simply an extension of Sicily’s.

Determining the reasons for these differences, and the nature of Malta’s connections and disconnections with surrounding regions represents a key future goal. Related to this, is the need to unravel the true phylogeny and taxonomic status of similar-sized animals on Malta and Sicily (e.g. elephants, dormice). Were they really the same species, or just species on convergent evolutionary trajectories? Such revisions may yet yield even greater differences between Sicily and Malta.

Ground truthing our predictions through further excavations is the next step in model validation. However, recent preliminary test excavations in Malta led by ES suggest the discovery of two new species in a trench just 1m x 1 m in area, and excavated to a depth of 1 m. Formal descriptions of these discoveries are forthcoming. However, the discovery of *Meles meles* (European badger) in Holocene deposits dating to 7.5 ka and associated with Neolithic ‘Red Skorba’ pottery, and the

discovery of *Varanus* sp. (monitor lizard) in deeper deposits dating to 13 ka, is certainly consistent with the predictions made here. Neither of these species are known in Malta today, nor have they been previously been recorded on the Islands. Notably, both species are unknown on Sicily. European badgers are present on the Italian mainland today and are a European species not known from Africa. They may therefore have been introduced by people. However, monitor lizards are an Afro-Asiatic species that have not been present in Europe since the Middle Pleistocene. Its survival in Malta up to 13 ka therefore represents a substantially younger date for this species in Europe. Planned larger and more extensive excavations will provide a more robust empirical test for the utility of our model. Together with preliminary results from Malta, we anticipate that future excavations will yield new species and greater faunal diversity, shedding light on a globally unique ecosystem.

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Conflict of interest statement

The authors have no conflicts of interest to declare.

Author contributions

ES, AvdG, EYH and AT conceived of the project. AvdG and EYH collated the data, generated the taxonomic framework and provided prior beliefs; ES, AvdG and AT led the writing of the manuscript; AT conceived and implemented the methodology. ES led the fieldwork leading to the discovery of new species described, together with NV, RG, JB and HG. EYH identified the new species. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Algorithm to calculate likelihood of presence-only data

The function *method.1()* provides an intuitive compositional approach to calculating the probability of presence-only data, where *draws* = the total number of samples, and *probs* is a vector of *S* + 1 probabilities defining the relative frequency of all *S* observed species and the last value of *probs* is the proposed missingness. In contrast, the function *method.2()* utilizes the inclusion – exclusion principle to provide the same result with massively less computational cost. However, *method.2()* can be vulnerable to catastrophic cancellation from floating point limits, therefore our complete algorithm also incorporates minor modifications to handle the final summation more precisely (see functions.R).

```
method.1 <- function(draws, probs){
  require(arrangements)
  x <- cbind(compositions( draws, length(probs) - 1), 0)
  res <- sum(apply(x, 1, dmultinom, prob=probs))
  return(res)}
```

```
method.2 <- function(draws, probs){
```

```

require(arrangements)
N <- length(probs)
expr <- list()
coef <- rep(c(1,-1),length.out=N)
if(N==1){
  k1 <- 1 - probs
  res <- sum(k1^draws)
}
if(N>1){
  for(n in 1:N){
    k1 <- 1 - rowSums(cbind(v=combinations(probs[1:(N-1)], k=n-1), probs[N]))
    expr[[n]] <- coef[n] * (k1^draws)
  }
  res <- sum(unlist(expr))
}
return(res)}

```

Null parameter estimates

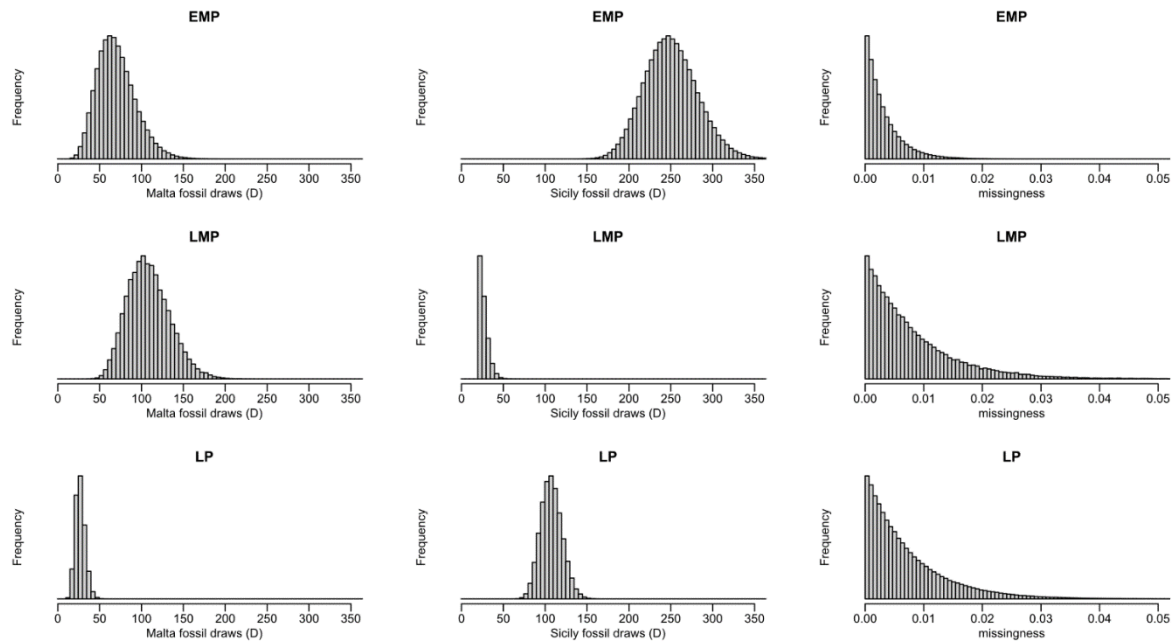
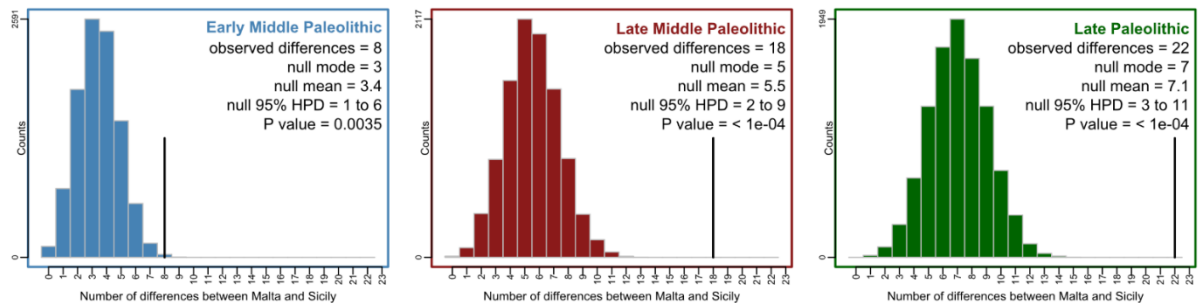


Fig S11: Marginal posterior parameter estimates under the null hypothesis.

Null hypothesis sensitivity test



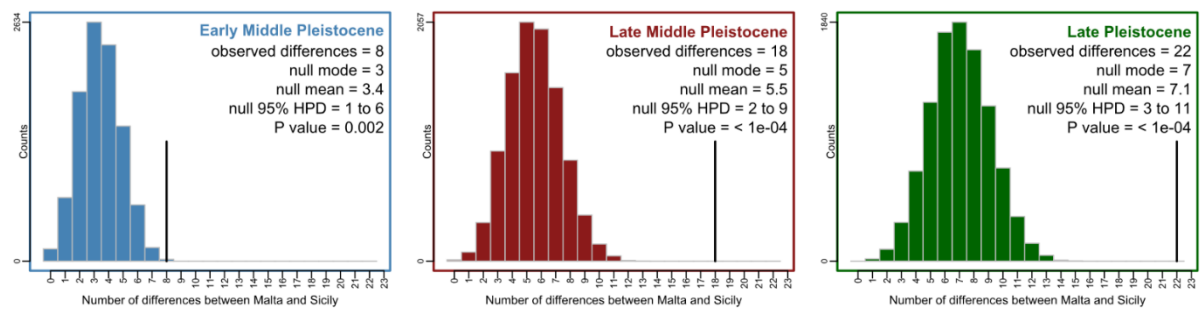


Fig SI2: Sensitivity test using our second independent set of prior beliefs of species frequencies from author EYH. Null distributions of the number of species differences between Sicily and Malta, for each time period tested independently. In each case the observed number of species differences (vertical black line) is significantly greater than can be expected under the null.

Independent hypothesis sensitivity test

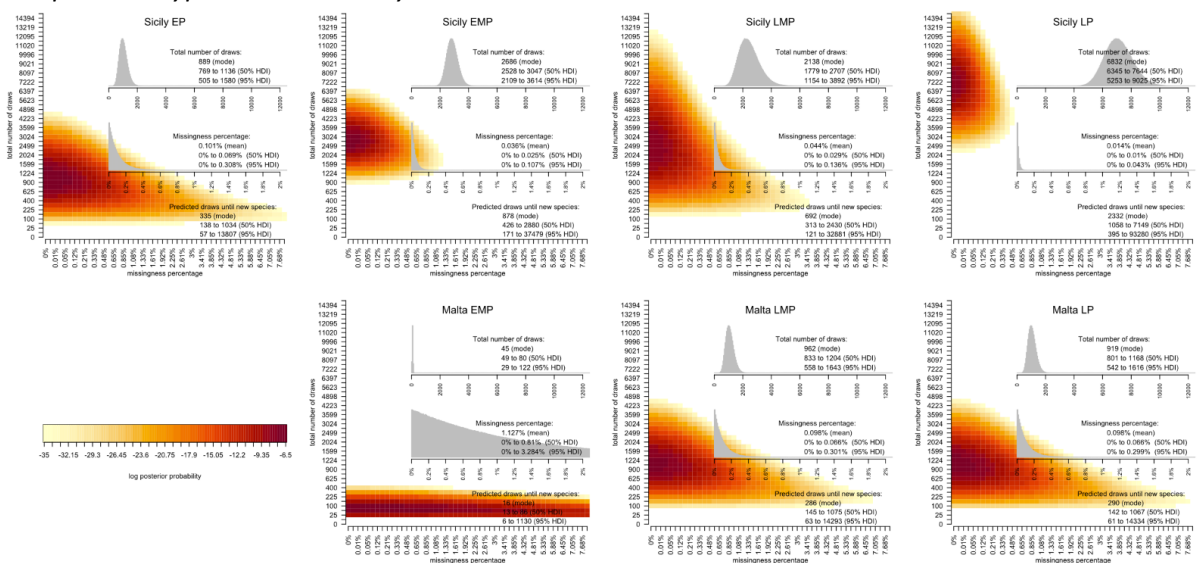


Fig SI3: Sensitivity test using our second independent set of prior beliefs of species frequencies from author EYH.

Taxonomy and biostratigraphy of Maltese species

In the second half of the 19th century, three dwarf elephants were formally described for Malta, and ascribed to the genus *Elephas*, at the time a wastebin taxon for elephants that are currently known as *Elephas*, *Loxodonta*, *Mammuthus*, *Palaeoloxodon*. All Sicilian and Maltese dwarf elephant species fall today under *Palaeoloxodon*, the genus of straight-tusked elephants. The three Maltese species described were: *Elephas falconeri* by Busk in 1867, *E. melitensis* by Falconer (in Busk 1867) (posthumously; mentioned in 1862) (both from material from Zebbuġ “Cave”); and *E. mnaidriensis* by Adams in 1870, from material from Mnajdra Gap, Benghajsa Gap, Gandia. Busk (1867) suggested the two ‘diminutive’ forms, *melitensis* and *falconeri* differed postcranially, with the former more similar to the African elephant, while the latter resembled the Asian, and that one ‘probably exceeded the other in size’ (Busk 1867, p. 230). Adams (1874) indicated that the specimens he referred to *mnaidriensis* were of larger size than *melitensis*, and cast doubt on Busk’s interpretation of the presence of a second small-sized taxon. Vaufreys (1929) erroneously reinterpreted the Maltese taxonomy, applying the names *falconeri*, *melitensis*, and *mnaidriensis* to small-, medium- and large-sized forms respectively, to reflect the three size classes he perceived in the Sicilian material he worked on, and then further applied these names to elephant finds of approximately similar sizes from e.g. Crete and Cyprus. This sized-based scheme was also used for other Mediterranean Islands (e.g. Tilos). However, on Sicily and Malta this shared, size-based taxonomy has persisted, with

melitensis falling out of use owing to limited recognition for the existence of a medium-sized dwarf elephant. However, the Sicilian material referred to *mnaidriensis* by Vaufrey, and most later authors, is much larger in size than the original *mnaidriensis* material described by Adams, and likely not conspecific (or contemporaneous). There is thus a pre- and post-1929 difference in usage for *mnaidriensis* in the literature. Maglio (1973) in his review of elephant species retained this practice, dismissing the idea that each island colonisation is a unique process resulting in an independent lineage on each island without any genetic contact between the separate islands, but it has now been largely abandoned reflecting the understanding that dwarfing evolved independently on each island. Part of the confusion is based upon the large size variation which is common in elephants today, both the African and the Indian species, as well in extinct species like the woolly mammoth (*Mammuthus primigenius*). Elephant cows stop growing at an earlier age than bulls, and as a consequence, full-grown bulls may stand 1 m taller at the shoulder than cows. The measurements of *P. falconeri* by Ambrosetti (1968) from Spinagallo cave (Sicily) reflect this bimodality. Roth (1990) estimated that bulls and cows stood on average 130 cm and 100 cm at the shoulder respectively. Since then, *melitensis* is considered a junior synonym of *falconeri*. Contemporaneity of two dwarf elephant species on Malta is extremely unlikely, given the limited surface area of the island. Only on islands the size of Java or larger did this occur, and in these cases the species belong to different genera (van der Geer et al. 2017). The only explanations of two species having been reported together at a single locality is either a taxonomic error due to sexual dimorphism or the mixing together of differently aged faunas. In the reconstruction of the biostratigraphy of Malta, we used the cave of Għar Dalam for reference, as this site has the best preserved Late Middle Pleistocene-Holocene stratigraphic sequence. Voles (*Microtus*, subgenus *Pitymys*) and white-toothed shrews (*Crocidura*) were recovered from this cave, but dormice are lacking, except for *Leithia cartei*. This species and the other three dormouse species have been recovered from other Maltese sites. *Leithia melitensis* has been described from Zebbuġ, Mnajdra, Tal-Ġnien, Wied Inċita, Gandia and perhaps Bengehisa Gap; *Leithia cartei* from Zebbuċ and Mnajdra; *Maltamys gollcheri* from Mnajdra; and *M. wiedincitensis* from Wied Inċita. Mnajdra also yielded the vole *Microtus pauli*, indicating a late Middle Pleistocene age for its small mammal assemblage. Gandia (*L. melitensis*) likely dates to this epoch as well, based on the occurrence of *P. mnaidriensis*. Wied Inċita lacks diagnostic taxa and has been assigned a Pleistocene age (Daams and de Bruijn 1995). Otter remains (*Lutra euxena*; type locality Tal-Ġnien; Pleistocene) were identified from Għar Dalam cave as well. Despite their unusually large size (own observation), they are included here conservatively in Table 1 for the LMP, anticipating a revision of the carnivore remains. Small red foxes (*Vulpes vulpes*) from an unknown Maltese locality (Bate 1920) are here assigned to the Late Pleistocene, in agreement with the Sicilian faunas; an earlier occurrence is unlikely given the absence of this species from other Mediterranean islands that were not connected to the mainland. *Microtus pauli* and *M. melitensis* are here regarded chronospecies, following Malec and Storch (1970). The extant shrews of Sicily and Malta (and Gozo) all belong to the species *Crocidura sicula*, which likely derived from the Pleistocene species *C. esuae*, present on both islands. Genomic evidence from DNA shows that the latter species might have evolved from the Saharan shrew *C. tarfayaensis* (Dubey et al. 2007), with the split dating back to the Messinian, indicating an arrival of the ancestor of the extant shrews already during the Monte Pellegrino faunal stage of Sicily. Since the split between the Maltese and Sicilian populations was dated to the Middle Pleistocene, the Late Pleistocene species of both islands is here considered conspecific with the extant species. Bird fossils are extremely rare and fragmented, and hence their occurrence is incomplete as indeterminable elements and elements with unresolved or open taxonomy are not included here. Giant swans (*Cygnus falconeri*) have been reported from Zebbuġ as well (Parker 1865), a site with *falconeri*, indicating an earlier occurrence of giant swan in Malta than on Sicily. The bat fossil record is even more fragmentary nature; bats have been recovered from EMP ("several species of bats") and LP ("Chiroptera") Sicilian deposits (Bonfiglio et al. 2001), but have not been identified taxonomically.

In general, by lack of a robust geochronology of Maltese fossiliferous deposits, we here necessarily adopt a conservative approach by assuming arrival from Sicily and contemporaneous but not earlier

occurrences where precise data are lacking. We acknowledge that in this way our results are biased towards a greater similarity between Malta and Sicily, but are of the opinion that an overly conservative approach is the best practice with the current data issues of geochronology, stratigraphy and taxonomy.

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