

Hidden signatures of the Mesolithic-Neolithic transition in Iberia: The pine marten (*Martes martes*, Linnaeus 1758) and beech marten (*Martes foina*, Erxleben, 1777) from Cova Fosa (Spain)

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ABSTRACT

Zooarchaeological and palaeontological records indicate that whereas the pine marten (*Martes martes*, L.) constitutes a genuine element of the European fauna, the beech marten (*Martes foina*) is a recent colonizer whose invasion was fostered by the spread of the Neolithic economies. In this paper: (1) we provide the first direct radiocarbon date for the appearance of the beech marten in the Iberian Peninsula and Europe, (2) assess the evolution of the abundances of the two species in the eastern Iberian site of Cova Fosca (13,360-4,522 cal BC), and (3) explore the causes that may have played a role in the expansion of the beech marten and the retreat of the pine marten to the northern fringe of the Iberian Peninsula. Our study suggests that whereas the beech marten might have benefited from landscape transformations that the Neolithic agropastoral communities fostered, hunting pressure along with a combination of natural and anthropic landscape changes that took place in eastern Iberia after the onset of the Neolithic (*ca.* 5,600 cal BC onwards) may have sealed the fate of the pine marten in the region.

Keywords: *Martes martes*, *Martes foina*, palaeoenvironment, Mesolithic-Neolithic transition, Iberian Peninsula

1. AIMS AND SCOPE

The Mesolithic-Neolithic transition constitutes one of the major landmarks of human evolution. Given the environmental changes the shift from hunting and gathering to production economies brought about, it is no wonder that the phenomenon allows for a multifarious approach that ranges from the strictly cultural to the strictly biological (Cortés *et al.*, 2012). From a zoological standpoint, the focus was laid on the faunal turnover that witnessed a substitution of the game animals –ungulates for the most part-by domestic stocks, likewise dominated by the ungulates. Without denying the merits of this approach, we know that many other groups of animals –vertebrates as well as invertebrates- can document the Mesolithic-Neolithic transition, both at the level of cultural/economic changes as well as at the level of the environment (Harris, 1996; Sánchez, 2004; Cortés *et al.*, 2012). In this paper we will assess this transition in a site located on the Eastern Iberian Peninsula through the two species of martens that

presently occur in Western Europe: the pine marten (*Martes martes*, Linnaeus 1758) and the beech marten (*Martes foina*, Erxleben 1777).

The archaeozoological and paleontological record of these medium-sized mustelids is comparatively sparse in both Europe and Iberia, and in many cases the finds have been only reported at the level of the Genus (i.e. *Martes* sp.) (Sommer and Benecke, 2004; Llorente *et al.*, 2011; see Appendix 3). One of the reasons that accounts for the latter situation has to do with the difficulty of discriminating osteologically the two species (Anderson, 1970; Libois, 1991; Ambros and Hilpert, 2005; Llorente, *et al.*, 2011). Still, when the paleontological and archaeological finds do allow for species identification, a recurrent pattern emerges. In this way, all of the Upper Pleistocene finds of martens in Western Europe correspond either to the pine marten or to its putative ancestral species *Martes vetus*, Kretzoi (1933), whose record in the Iberian Peninsula extends back to the Middle Pleistocene (Kurtén, 1965; Guérin and Patou-Mathis, 1996; García, 2003; Sommer and Benecke, 2004; Pascal, *et al.*, 2006). In addition, all throughout Western Europe, the archaeological record exclusively documents the hunting of pine martens, in particular during the Mesolithic period (Trolle-Lassen and Königsson, 1986; Trolle-Lassen, 1987; Zeiler, 1987; Grundbacher, 1992; Rowley-Conwy, 1994-1995; Charles, 1997; Strid, 2000; Chiquet, 2004; Richter, 2005a). The absence of the beech marten from the British islands was one of the clues that suggested the species to be a post-6 ky BC colonizer of the European continent (Masseti, 1995a; 1995b; 1998; Yalden, 1999; Masseti, 2009), and the comparatively recent dates of the source finds of beech martens in Europe seemed lend weight to such hypothesis (Appendix 3). But it was recently that a paper provided compelling data that evidenced the European dispersal of *M. foina* to be associated with the spread of the Neolithic agropastoral communities, a process that started on the Near East around the seventh millennium BC (Llorente *et al.*, 2011). For such reason, as is the case with the imported sheep and goat, the beech marten qualified as yet another faunal bio-indicator for revealing the existence of a Neolithic economy in a given European territory.

An issue that needs to be settled concerns the reasons for why the species would have associated with the agropastoral economies. Human translocations explain the presence of the beech marten on the Mediterranean islands (Masseti, 1995a, 1995b). Still, at the scale of the European continent, the rapidity with which this dispersal took place would demand such an enormous number of translocation events so as to render humans unlikely as the sole agent responsible for the beech marten's wave of spread. For such reason, one needs to assume that the habits of this carnivore somehow predisposed (i.e. "pre-adapted") it to benefit from those environmental changes the Neolithic settled way of life brought about. A second that phenomenon that begs for an explanation in the Iberian Peninsula concerns the fates of the pine and beech martens, that appear to have followed diametrically opposed pathways during these past millennia. Indeed, when one confronts the archaeological records with present day distributions, it seems evident that the beech marten has proved to be a most successful colonizer whereas the pine marten suffered a drastic contraction of territory during the second half of the Holocene (Figure 1). The timing and reasons for such divergent trajectories appear to run parallel, on the one hand, with the expansion of anthropized landscapes (i.e. meadows, farmlands, urban areas), and with a clearance of forests on the other, the latter phenomenon probably coupled to no small extent with the expansion of those anthropized environments. Whether correlations here imply causation for the changing distributions of the two marten species, however, remains open to debate and will be

one of the issues to be addressed in this paper. The involvement of the beech marten in the contraction of the pine marten distribution remains nevertheless questionable since current data in sympatry areas do not reveal clear competition between the two species (Delibes, 1983; Posluszny, *et al.*, 2007; Rosellini, *et al.*, 2008). Such coexistence therefore calls upon some sort of niche segregation taking place at the level of the eco-morphologies and behavior. Indeed, and given that both species are reported as eclectic in their trophic spectra, the few radio-tracking studies (Marchesi, *et al.*, 1989) and molecular identification of scats (Posluszny *et al.*, 2007) in areas of sympatry evidenced the pine marten to be more carnivorous and the beech marten more generalist despite major overlaps. In particular, these studies revealed beech martens to concentrate to a larger extent than pine martens on rapidly renewing resources, as is the case of insects and certain fruits. In fact, differences in the use of micro-habitat and the circadian activity have been considered to lie behind the sympatry between the species of the Genus *Martes* (Zielinski and Duncan, 2004). These results bear important implications in the context of our research.

Strictly cultural reasons may likewise explain the present-day success of the beech marten and the long-term decline of the pine marten. Hunting is a case in point. As said, pine martens from archaeological sites throughout Europe evidence traces of skinning since the Upper Paleolithic, and it is them, not beech martens, the ones that have well documented historical and ethnographic records of hunting for pelts (Delort, 1978). Is the absence of evidence of systematic hunting in the beech marten a reflection of reality? Could it be that overhunting depleted pine marten populations favoring the occupation of their niche by the beech marten? When dealing with these issues one needs to contend with the idea that the disappearance of the pine marten at a given archaeological sequence after the onset of the Neolithic may simply be a construct due to the disappearance of the hunter-gatherer way of life, not evidence of a local extinction event. Such contingencies make it all the more difficult to spot unequivocal evidence for the involvement of people when trying to track down local extinction events or translocations through time.

Armed with these provisos in mind, in this paper we will consider a case study from the Levantine region of the Iberian Peninsula where the aforementioned issues can be explored in more detail.

2. THE SITE OF COVA FOSCA

The site of Cova Fosca (Ares del Maestre, Castellón), is located at 900 m.a.s.l on an steep ravine of the Maestrazgo Mountains (Iberian Range) in Eastern Spain that lies *ca.* 40 km away from the Mediterranean coast (Olària, 1988; Llorente *et al.*, 2014). The site saw campaigns in the 1970s and 1980s (Olària, 1988) but our study concerns the excavations that took place between 1999 and 2003 at the entrance of the rock shelter (i.e. Sector C). This is a terrace whose pronounced slope occasionally provoked an irregular layering of the deposits where a few levels exhibited tilting and non-homogeneous development (i.e. varying depths at different points) (Llorente, 2007; Morales Muñoz, *et al.*, 2008; Olària and Jener, 2008; Llorente *et al.*, 2014). It was for this reason that an exhaustive program of radiocarbon dates was carried out to clear any potential disconformities existing in the chronostratigraphic column.

Cova Fosca's Sector C (CFSC, from here onwards) incorporates 34 levels that range from the Late Magdalenian (13,360 cal BC) to the Middle Neolithic (4,850-4,522 cal BC) (Olària, 2000; López and Olària, 2008; Llorente, 2010; Llorente *et al.*, 2011, 2014) in what appeared to constitute an intermittent sequence of human occupation of a small (i.e. 20 m deep x 27 m wide) rock shelter, whose roof reaches from 5 m to 2 m in height (Olària, 1988).

All sediments from the 1999-2003 campaigns were sieved through a 0.5 mm and 0.3 mm meshes. Such meticulous screening explains the richness and diversity of the faunal collections. Indeed, with close to 95,000 remains retrieved and ca.130 species of vertebrates and mollusks identified, the faunas from CFSC constitute the largest faunal assemblage thus far retrieved in the Iberian Holocene (Llorente *et al.*, 2014). The carnivore collection in particular stands not only among the largest for Iberian Prehistory but also as the most diversified one for this group in the Iberian Holocene. (Llorente, 2015).

Given that ungulates made up approximately 60% of the NISP (Number of identified specimens), their remains exhibited high frequencies of anthropic marks, and non-identified remains where ungulates for the most part with identical traces of human manipulation, one can safely consider the vast majority of the deposits to be anthropic in nature (Aura *et al.*, 2002; Llorente, 2010; Llorente *et al.*, 2014). Although alternative agents such as nocturnal preybirds and natural deaths might have occasionally contributed some of the micro-vertebrate accumulations, most of the carnivore remains appeared to have been accumulated by humans as well (Llorente, 2010, 2015). Of particular interest here is the standardized skinning process of medium-size carnivores. This has been documented throughout the chrono-cultural sequence, evidencing the persistence of a hunter-gatherer tradition at CFSC after the appearance of the domestic stocks (i.e. the Neolithic), a matter of far-reaching consequences in the context of this paper (Llorente, 2015).

Such fortunate combination of features, and the fact that, of all Iberian sites where both marten species have been documented, this happens to be the only one covering a time interval of ca. 9,000 years, allows one to explore the abundances of the two mustelids from a diachronic standpoint. In this paper we would specifically like to address the following issues:

- (1) Whether the beech marten's earliest presence at CFSC was coincident with the earliest evidences of the Neolithic economies there,
- (2) Whether trends of changing abundances existed in the marten species and, in case so,
- (3) Whether those trends hint at cultural, paleo-environmental, or biological causes, or to a particular combination of them.

As we intended to frame the biological causes from the standpoint of competitive interactions between the two species and of changes taking place in the landscapes, in addition to the zooarchaeological analysis, two additional lines of enquiry were incorporated to our study. These include: (a) an actualistic study that explored whether differences existed in the occupation and use of space when the pine and beech marten coexist, and (b) a diachronic assessment of the vegetation from eastern Iberia during the first half of the Holocene, aimed at revealing changes in the biotopes that could have benefited one species at the expense of the other.

3. METHODS

3A. Zooarchaeology

For identification purposes, use was made of the collections of Arturo Morales-Muñiz housed at the Laboratorio de Arqueozoología-Universidad Autónoma de Madrid (LAZ-UAM), as well as of criteria taken from the literature (Frechkop, 1959; Anderson, 1970; Altuna, 1973; Hans and Steiner, 1986; Libois, 1991; Grundbacher, 1992; Ambros and Hilpert, 2005; Montero, 2008; Llorente *et al.*, 2011).

Abundances were calculated following the classical estimators in archaeozoology, as are the aforementioned NISP and the MNI (Minimum number of individuals) (Reitz and Wing, 1999). In addition to epiphyseal fusion calendars of the major limb bones (unpublished data from the LAZ-UAM reference collection), age was estimated through tooth eruption and wear, as well as with data on the development of crests and closure of the cranial sutures as described by Ryabov (1975) and the work on *Martes americana* by Brassard and Bernard (1939).

Taphonomic analyses aim at determining the heterogeneity of the samples, detection of any intrusive elements, and specification of agents responsible for the accumulation of the faunal assemblages. To this end, the taphonomic groups described by Gautier (1987) and the typology of marks, as specified by Liesau (1998) and Pérez-Ripoll (1992), were used. Marks were analyzed with the aid of a Wild M5A stereomicroscope and later compared with those recorded on carnivores from Mesolithic and Neolithic sites of Scandinavia and the Iberian Mediterranean region by Trolle-Lassen (1987) and Pérez-Ripoll (1992) respectively.

3B. The ecological model: an actualistic analytical tool

To approach the interaction between the pine and the beech martens we carried out an actualistic study in the province of Asturias (Northern Spain). This region was selected because: (1) it is one of the few areas of the Iberian Peninsula where both marten species still inhabit in sympatry, (2) it features a range of altitudes from the coastline up to *ca.* 2,500 m that creates a high diversity of habitats, and (3) this combination of features occurs over a well-defined, *ca.* 10,600 km², territory that turns the region into a micro-scale model of sorts to assess how the two marten species might have interacted in the past over a larger scale scenario under equivalent ecological conditions.

A database of 163 beech marten and 279 pine marten quotes was gathered between 1973 and 2014 through sighting records, roadkills and camera trapping. In the case of the latter, only inter-annual quotes derived from a permanent located camera have been used in order to avoid duplicate information from the same individual. Other records, including observations from wildlife care centers, have been incorporated into the database. Habitat types and altitude were recorded whenever possible. The former were classified into five categories: deciduous forest, pine forest, shrubland and anthropized areas (i.e. including grazing grasslands and urbanized areas). Habitat surface and its estimated range have been taken from the *Cartografía Temática Ambiental del Principado de Asturias* (INDUROT).

The relationship of each species with the type of habitat and altitude was analyzed through two statistical tests, establishing as the limit of significance a *p*-value of 0.05:

- A χ^2 test was applied in order to detect whether each species used the territory as one would be expected on the sole basis of altitude and habitat availability. Expected frequencies were thus obtained by multiplying the records for each species by the frequency of availability that each type of altitude and habitat feature on the territory.

-Fisher's exact probability test was applied as an *a posteriori* test to detect where abundance differences in altitude and habitat between the species were found.

Circadian activity was studied through an exhaustive camera trapping program in the municipality of Cudillero (100 m.a.s.l), where both marten species appear, between the years 2011 and 2014. For standardizing recordings, annual mean values of the orto and sunset were set between 8 and 19 hours of solar time, respectively. Circadian activity constitutes a key parameter for not only exploring the degree of competition between the two marten species, but also the reasons for the expansion of the beech marten. Indeed, though the beech marten dispersal runs parallel with the spread of the Neolithic landscapes (Llorente *et al.*, 2011), the establishment of this species on a particular territory could have occurred: (a) either passively, as an opportunistic colonization of newly emerged empty niches in habitats previously altered by the agropastoral communities, or (b) through an active role of humans, who might have intentionally translocated beech martens at a certain time or place. The "passive dispersal scenario" would gain support if the beech marten were to exhibit a predominantly nocturnal activity allowing it to prosper inconspicuously in anthropic environments, an issue of utmost importance in the context of our research.

3C. Palynology

A total of 18 published pollen records have been selected to reveal what sorts of habitats were available for the two marten species in Eastern Iberia during the first half of the Holocene. This selection met three criteria: (a) records had to be high resolution ones, covering the chronological (i.e. Early-Middle Holocene) and cultural (i.e. Mesolithic-Early Neolithic transition) frames we intended to explore, (b) highland records from either the core study area (i.e. the Southern Iberian Range) or the Baetic Range, with similar ecological characteristics (i.e. existence of the supra- and oromediterranean bioclimatic belts with *Pinus nigra* subsp. *salzmanii* from limestone environments and a Holocene vegetation history with a similar evolutionary dynamics), and (c) lowland records from areas where the earliest evidences of Neolithic communities have been documented in Eastern Iberia. This is the case of the Mediterranean coastal plains and of the inner valleys featuring fertile soils.

4. RESULTS

4A. Zooarchaeology

At CFSC, marten remains have been identified on a total of 15 levels (Table 1). These include 1 Middle Neolithic level (47-125 cm below surface), 9 Early Neolithic levels (125-255 cm below surface), 2 Mesolithic levels (255-298 cm below surface), and a further 3 from the Epipaleolithic (298-388 cm below surface).

The combined total of remains from the genus *Martes* at CFSC amount to almost 14% of all the carnivores therein retrieved (Table 1). Given that non-diagnostic bones from this Genus -such as ribs and vertebra- must have been *per force* allocated within the

unidentified carnivore category, the NISP of +100 remains undoubtedly represents an underestimation of the number of marten remains in the samples. Still, given that *Martes* is one of the rarest carnivore taxa throughout the Iberian Peninsula during the Pleistocene and Holocene, whose finds seldom incorporate more than one bone, the size of this collection is remarkable (Table 1, Appendices 1, 2, and 3). Given that from the Epipaleolithic to the Early Neolithic a substantial fraction of this collection bear marks of manipulative operations associated with skinning (Figure 2), one may postulate at CFSC the existence of a specialized pelt procurement activity, hitherto undocumented in Iberia despite its long record in Europe, where *M. martes* was but one in a long list of species (Trolle-Lassen and Königsson, 1986; Trolle-Lassen, 1987; Grundbacher, 1992; Rowley-Conwy, 1994-1995; Charles, 1997; Strid, 2000; Chiquet, 2004; Richter, 2005b; Llorente *et al.*, 2011; Llorente, 2015).

Of those remains within the Genus *Martes* that could be identified to species, pine martens constituted the bulk of the samples (+95%) and were documented all throughout the chrono-stratigraphic sequence (Table 1). Beech marten remains have been only documented in two levels. The earliest record (i.e. one radius and one ulna from level -242/-255 for an MNI = 1) corresponded with the level postulated by the excavators to constitute the cultural transition from the Mesolithic to the Neolithic at CFSC. The second record (a fibula from level -211/ -220) was safely placed within the Early Neolithic package. Relevant now is that a radiocarbon date we have obtained on the beech marten's radius confirms the presence of *M. foina* in the earliest moments of the Neolithic at CFSC (Poz-68357: 6255±35 BP; 5316-5076 cal BC at 95.4% probability). This radiocarbon date sets a direct baseline for the appearance of the beech marten in Iberia and in Europe. The earliest evidence of the domestic stocks at CFSC (i.e. 10 sheep remains), on the other hand, appeared in level -235/-242, lying immediately above the aforementioned "transition" level. That the radiocarbon date taken on one of these sheep bones derived from a slightly earlier time, though still within the same temporal frame, as the beech marten's radius (Poz-62966: 6420±50BP; 5477-5318 cal BC at 95.4% probability), is most relevant. Although the slight discordance of the two dates may reflect contrivances having to do with the aforementioned tilted layering of the levels on the slope at the entrance of the shelter (see above), the data not only evidence that the domestic stocks appeared on the region previous to the carnivore, but also that the beech marten is one of the earliest bio-indicators of the Neolithic world in the area as well.

Concerning pine marten frequencies through time, one remarks that its diachronic abundance at CFSC peaks to *ca.* 15% of the carnivore' samples during the Mesolithic, then plummets to almost half that value in the ensuing Early Neolithic, despite its far higher NISPs, and decreases further still in the Middle Neolithic horizon that ends the sequence (Figure 3).

Finally, in terms of cohorts (i.e. age groups), adults, meaning animals above 2 years, monopolize the sample. Indeed, out of 17 individuals only one specimen from the Epipaleolithic (a mandible from level -365/-388) corresponded to a 2-month old animal. Interestingly, and given that pine marten cubs do not leave the nest until their third month of life (Barja, 2008), the possibility exists that this young animal might simply represent a natural death accumulation. This is reinforced by the fact that breeding pine marten females select shelters for nesting when the temperature is cold, which was the case for the Epipaleolithic at Cova Fosca (Zalewski, 1997; Barja, 2008; Sesé, 2011).

4B. Actualistic ecological model

The results of our actualistic study carried out in the province of Asturias are presented in Tables 2 and 3, and in Figure 4. Three parameters of that study are addressed in this paper, namely:

1. Altitude: altitude quotes reveal the presence of both martens from sea level to the supra-forestral level but there seems to exist a preferential range of altitudes for each species (Table 2: p-values). χ^2 tests suggests a significant difference existing between the observed and the expected frequencies in altitude preference in the case of the beech marten ($\chi^2 = 135,05$; d.f.= 4; $p < 0,00001$) but not in the case of the pine marten ($\chi^2 = 1,4$; d.f.= 4; $p < 0,8442$). The frequency of the beech marten is higher than expected in the lowlands (especially below the 200 m.a.s.l) becoming lower than expected as soon the 400 m.a.s.l threshold is reached (Table 2).

2. Habitat: In the case of the biotopes occupied by the two species, our data revealed highly significant differences between the observed records and those expected on the basis of the available relative area that each of these biotopes covers in the province of Asturias (Table 3). In this way, it seems clear that the pine marten is far more common in deciduous forests whereas in disturbed (i.e. anthropized) biotopes beech martens are significantly more abundant. The data also evidence significant differences in the case of shrublands and pine forests (the later mostly immature, under regimes of 40 year cycles of woodcutting operations) that favor the beech marten and hint at its reported condition as a colonizer of non-mature ecosystems (Figure 4).

Most of the cases of sympatry were recorded in the countryside (10) and the deciduous forests (8). To explain such coexistence in the case of the countryside is not difficult as this anthropized habitat -featuring meadows, farmland, hedges and stone walls in addition to isolated trees and woodland pockets- exhibits such a structural complexity that allows for the presence of favorable and contiguous microhabitats. The coexistence of the two species in the deciduous forests, on the other hand, appears more problematic in that this habitat seems mostly conducive for the presence of the pine marten. It is for this reason that Pilot *et al.* (2007) argue that it is the fragmentation, however incipient, of the woodlands what explains such recurrent coexistence. Without denying this possibility, we believe that other factors of displacement, as is the case of feeding habits and circadian rhythms, may also hold a clue to explain the presence of the beech marten in the deciduous forests.

3. Circadian rhythm: Beech martens were predominantly recorded between 6pm and 4am throughout the year (237 night records *vs.* 63 diurnal records) with maximum values between 10 pm and 2 am. There were no such clear activity preferences in the case of the pine marten, which has been shown to be active during both nighttime and daytime (63 records *vs.* 46 respectively). Though previous studies consider the pine marten as mainly nocturnal, these studies considered nighttime the range from 5pm to 7pm (Clevenger, 1993; Zalewski, 1997; Berdión-Grados, 2005; Barja, 2008). If this time range were to be considered daytime, as we had done in our study, a far more “diurnal” pattern would emerge for the pine marten. Indeed, some of these authors mention that during the heat period (i.e. end of the summer) the pine marten exhibits a peak of activity from 8 am to 8 pm (Zalewski, 1997; Barja, 2008). The complementary activity patterns found in our study are significantly different between the two species

(Exact Probability Fisher test p-value < 0.0001) and, for such reason, what seems clear is that the beech marten is a far more nocturnal animal when compared to the pine marten. We believe this diachrony in the activity patterns of the two species facilitates their coexistence under conditions of syntopy as has been repeatedly (Kronfeld-Schor and Dayan, 2003; Zielinski and Duncan, 2004).

4C - Palynological data

During the temporal interval ranging from 8,770-5,500 cal BC forests dominated all lowland environments (Table 4). In the fertile valleys, the pollen records from Navarrés (Carrión and van Geel, 1999), Villena (Yll *et al.*, 2003), Salines (Burjachs *et al.*, 1997) and Les Alcusses (Tallón *et al.*, 2014) show that pre-Neolithic forests were dominated by pines (*Pinus nigra* and *P. pinaster* or *P. halepensis* near the coast) with scattered occurrences of both evergreen and deciduous *Quercus*. Some palynological records from coastal areas, such as those from Cova de les Cendres (Dupré, 1986), Xàbia (Viñals *et al.*, 1993), Elx (Burjachs *et al.*, 1997) and Casablanca-Almenara (Planchais and Parra, 1984) reveal a dominance of evergreen oak forests (*Quercus ilex* and *Q. coccifera*), accompanied by *Pinus halepensis* and a xerothermophilous *maquia* dominated by *Olea*, *Pistacia*, *Phillyrea*, *Arbutus*. No symptom of anthropization is documented at this time at either the inner valleys or the coastal areas.

Beginning with the Neolithic *ca.* 5,600-5,000 cal BC, the existing pollen records (Table 4) point to anthropogenic modifications taking place in the vegetation of the coastal areas and inner valleys (Cruz-Berrocal *et al.*, 2014). From the second half of the 6th millennium cal BC, the environmental impact of agropastoral communities is hinted at mostly by the rapid decline of forests, in particular pine and riparian woodlands. At this time, an expansion of grasslands in both the inner valleys and coastal areas was fostered, mostly through anthropic fires (e.g. Navarrés, Casablanca-Almenara, Les Alcusses, Xàbia, Cendres, L'Or). This resulted in the development of a thermophilous *maquia* (mainly *Olea* and *Pistacia* sp.) as well as of anthropic-nitrophilous and anthropozoogenous communities whose appearance coincides with the earliest evidences of agriculture (*Cerealia* pollen type) and pastoral activities. The replacement of pines by evergreen *Quercus* woodlands during the first half of the 5th millennium cal BC, on the other hand, is due primarily to the warmer and wetter conditions prevailing in Eastern Iberia at this time (Carrión, 2002; Gil-Romera *et al.*, 2010b). As mentioned, the rapid contraction of the forests and expansion of the grasslands (Poaceae) during the Early Neolithic may have been related to the intensification of forest clearance. The increasing levels of coprophilous and carbonicolous fungi, linked with grazing and fire, are likewise related to regional clearing processes (Gil-Romera *et al.*, 2010a). Cereal cultivation in the region is verified through the carpological record at the start of the second half of 6th millennium cal BC (Zapata, *et al.*, 2004).

In the case of the highlands, the picture is slightly changed on a temporal basis but essentially holds. In the high-mountain areas of the Baetic Range (Table 4), the pollen records of Siles, El Sabinar, Villaverde and Cañada de la Cruz (Segura mountains) (Carrión *et al.*, 2001a, 2001b, 2004; Carrión, 2002), Cañada del Gitano (Baza mountains) (Carrión *et al.*, 2007) and Gádor (Gádor mountains) (Carrión *et al.*, 2003) show that forests were dominated by pines (probably *Pinus nigra*) from the 7th to the 4th millennia cal BC, with some presence of *Pinus pinaster*, deciduous *Quercus* and other mesophytes (*Corylus*, *Betula*, *Fraxinus*, *Acer*) from the 6th millennium cal BC

onwards. The progressive replacement of pine forests by mesophilous species after *ca.* 5400 cal BC is viewed as a response to increased water availability (Gil-Romera *et al.*, 2009). Even if there is no firm palynological evidence of human disturbance at this time, the sporadic presence of anthropozoogenous taxa (e.g. *Plantago*) and coprophilous fungi (Sordariaceae) since *ca.* 5500 cal BC reveal some pastoral pressure, but the major transformation of the landscapes did not take place until the 3rd millennium cal BC (i.e. the Argar culture). It is at this time when anthropogenic fires increased significantly, depleting pine woodlands and extending pastures that came to dominate the landscape (López-Sáez *et al.*, 2010; Fierro *et al.*, 2011).

A similar pattern is documented in the Southern Iberian Range (Table 4), where pollen records from Cova Fosca (Yll, 1988), Ojos del Tremedal (Stevenson, 2000) and Villarquemado (Aranbarri *et al.*, 2014) show a remarkable prevalence of pine woodlands (*Pinus nigra/sylvestris*) around 5830 cal BC, as these communities are highly resilient. From that date onwards, the vegetation of these mountains was characterized by an expansion of mesophytes and Mediterranean taxa (particularly evergreen *Quercus*) whereas *Pinus nigra/sylvestris* forests decreased. This indicates both higher temperatures and moister conditions, but also upland tree colonization associated with the upward shift of the supramediterranean vegetation belt (Rubiales *et al.*, 2010).

5. DISCUSSION

From the above mentioned data, it appears that the environment around Cova Fosca must have suited the pine marten all throughout the chronological sequence under consideration. In terms of altitude, for example, the 900 m where the site is located correspond with the threshold where the frequencies of pine martens start to surpass those of beech martens in the province of Asturias (Table 2). Such altitude is not the most adequate one for the beech marten that in our study systematically featured its highest abundances below 200 m. If only for this reason, one would expect the beech marten to be a rare occurrence around Cova Fosca as seems indeed to have been the case. In terms of habitat types, Cova Fosca was conducive for pine marten requirements all throughout this portion of the Holocene. As was seen (Figure 3), pine martens peaked during the Mesolithic, which is the time when not only woodlands are documented to reach their maximum development around Cova Fosca (i.e. +75% of the pollen assemblages; Table 4) but also when other forest bio-indicators, such as woodland birds, peak as well (i.e. *ca.* 78% of the avian community; Figure 6). Moreover, given that pine forests dominated woodlands in the Eastern Iberian highlands from 8,770-5,500 cal BC (i.e. more than 90% of all the tree pollen; Table 4), and that Iberian pine martens thrive in mature pine forests from Galicia (NW Spain) to the Pyrenees (Ruiz-Olmo *et al.*, 1988; Barja, 2008), those high frequencies of *M. Martes* during the Mesolithic suggest that the pine forests around Cova Fosca had to be mature. Indeed, the low frequencies that in Asturias both marten species exhibit in pine forests (Figure 4) are probably due to the fact that these are immature (i.e. less than 40 years old).

The woodland signature at Cova Fosca was still strong during the Early Neolithic, and although there existed an evident decline of the woodlands (i.e. less than 40% of the pollen; Table 4) and of woodland birds (i.e. 62%; Figure 6) at that time, those declines do not explain the drastic drop attested in the frequencies of the pine marten (Figure 3).

This same reasoning applies to the Middle Neolithic, when pine martens reached their minima yet pollen records revealed an upland shift of the tree line, not a contraction of the woodlands (Table 4). When one considers that the end of the archaeological sequence at CFSC (i.e. ca. 4,500 cal BC) predates the 3rd millennium cal BC, when drastic human landscape transformations are documented for the eastern Iberian highlands, one is left with scarce ground to argue that landscape changes lie behind the decline of the pine marten at Cova Fosca. Yet the trend of decreasing abundance is so clear that it begs for an explanation. Alternative explanatory causes need to be taken into account.

The most evident alternative is hunting. If one considers, as the faunal and taphonomic evidences suggest, that humans were the major agent behind this activity, specifying whether those people were hunter-gatherers or herders (i.e. the agropastorals that reached Cova Fosca) would prove crucial to determine whether such hunting could have been an occasional or systematic activity. Obviously, only hunter-gatherers could be responsible for the hunting taking place before the Neolithic. After this time, things would be more difficult to settle. Still, even though herders can hunt small and medium sized carnivores, the usually elusive, nocturnal, and solitary habits of most these, make it difficult for a herder, normally fixed to an area by his flock, to hunt them through tracking. The age structure of the pine martens may help us decide on the matter. Indeed, if herders did hunt at Cova Fosca, then trapping, rather than tracking, should have been the most commonly deployed strategy (Boza, 2008). As traps are fixed devices, trap captures constitute broad-spectrum, non-selective (i.e. random) samplings of populations, where taxa, cohorts and sexes are each cropped as a function of their existing frequencies in the sampled area. Only unexperienced, sick and weak animals are bound to be captured in higher proportions than those dictated by mere chance alone. From this perspective, the fact that 16 out of 17 pine marten individuals from CFSC were adults, and large-sized, hints at a selection of prime adults, probably males, that would run counter to any random captures scenario (Montero, 2008). Of particular relevance here is the absence of juvenile individuals and sub-adults (i.e. animals below 15 months), which happen to be both unexperienced and frequent in natural pine marten populations (Barja, 2008). Likewise noteworthy is the fact that the only infantile may represent an intrusion (i.e. a natural death; see above). Such a skewed age profile speaks of a selective hunting strategy exerted by expert hunters, knowledgeable in both the behavior and specific territories of the pine martens living around the shelter. That hunter-gatherers were the ones carrying out this hunting is additionally evidenced by the presence of anthropic marks aimed at fur procurement in the pine marten bones (Figure 2). Fur would be, in principle, a commodity for which herders should have had far easier alternatives at their disposal.

Both lines of evidence reinforce more conventional signatures of the hunter-gatherer economy at Cova Fosca. These include the diversity and frequencies of the wild game species, their skeletal and age profiles and, above all, the fact that the processing of the pine marten, as was the case with the remaining carnivores, was homogeneous throughout the sequence (Llorente *et al.*, 2014; Llorente, 2015). Such array of faunal signatures suggests the persistence of a hunter-gatherer way of life at Cova Fosca that kept on after the appearance of the Neolithic people in the region. This hunting activity on the part of hunters might explain why the sharp drop in pine marten frequencies documented during the Early Neolithic took place against a background of increasing number of carnivores (i.e. 4.3% vs. 1.8%; see Table 1) (Morales *et al.*, 2008; Llorente *et*

al., 2009, 2014; Llorente, 2015). At any rate, what one can certainly postulate at this point is that hunting pressure at Cova Fosca kept on throughout the 9,000 years of the occupation, so that hunting should definitively be a phenomenon to be reckoned with when considering the factors contributing to the local extinction of the species.

At CFSC, beech martens made only a futile appearance during the Early Neolithic. It might thus be no coincidence that the only other remain of the species was reported inside the shelter by Estévez (1988) from another Early Neolithic level (Level I) (Olària, 1988) indicate that the beech marten, though infrequent, inhabited the area for a prolonged period of time. As data presently stand, there is no evidence to indicate that the species reached to the Middle Neolithic. Although one can argue that there might exist both stochastic (i.e. sample size) and deterministic reasons (i.e. no hunting of the species) to explain such scarcity, the sporadic presence of beech martens at CFSC, the fact that only pine martens are recorded at the end of the sequence, and the lack of evidence of beech martens becoming more frequent through time, all hint at an absence of causal links between the trajectories of the two mustelids at the site. Indeed, when the data from our actualistic study are considered in the light of this research, one can hardly find an argument to imply the beech marten in the diminishing frequencies of the pine marten through time. The ways through which the two species resolve their coexistence when in sympatry, and the fact that often both seem to thrive in the same area, suggests that there exists no causal link arguing for the beech marten displacing the pine marten under any specific circumstances. This, obviously, in no way diminishes the importance that other factors, such as its nocturnal habits, its preference for disturbed habitats or the tolerance the animal exhibits when it approaches human settlements, playing a role in dictating its accommodation to the new environmental scenarios that have turned it into the most successful member of its Genus at present.

6. CONCLUSIONS

Through an absolute dating of its remains, our study has evidenced that the appearance of the beech marten at Cova Fosca followed shortly after the arrival of the Neolithic communities to the area. Such result reinforces the correlation established throughout Western Europe in a previous study and postulates a continental route for the dispersal of the species into the Iberian Peninsula. The essentially nocturnal habits of the beech marten that the camera trapping study evidenced may have helped it to become an inconspicuous companion of humans in the disturbed landscapes that the Neolithic communities fostered. The lack of ethnographical and zooarchaeological evidences of the beech marten being exploited by humans, suggests that its dispersal additionally took advantage of the commensal rodents, insects and cultigens linked to these agricultural landscapes.

In the case of the pine marten, the decrease in numbers that our study revealed can be tentatively assigned to over-hunting, probably coupled, in due time, with a human-mediated deforestation process in the area. We believe that pine marten hunting probably had reduced the populations by the end of the Neolithic to the extent of rendering the surviving populations extremely vulnerable to the devastating landscape transformations known to have occurred since the start of the 3rd millennium BC. We therefore believe it was a combination of cultural and environmental factors what sealed the fate of the pine marten in this part of the Iberian Peninsula. As any tentative

scenario, this one will necessarily need to remain open until new data are gathered that could verify it.

To confirm that the fate of the pine marten at Cova Fosca was sealed before the beech marten set foot on it and that the latter was not involved in the former's replacement, would suggest that the courses taken by the two mustelids need not be considered in the light of competitive displacement scenarios. The popular belief that colonizer species necessarily replace their putative equivalents needs thus to be called into question. This is an issue that, on a general basis, has been forcefully argued by Thompson (2014).

The differences that dictate how people dealt with apparently identical species in the past are often not only culturally dictated thus difficult to explain in the absence of pertinent actualistic data, but also of far-reaching consequences. The beech and pine martens are difficult to discriminate osteologically, and despite differences existing in their biologies, activity patterns, or quality of their pelage for that matter, one would expect them to have been treated by people in essentially the same manner. Why pine martens have been systematically hunted whereas beech martens qualified as vermin at best is most puzzling yet undoubtedly explains why one is presently a threatened species while the other thrives all around.

To end, and given that past human behaviors are often so elusive and difficult to reveal, one should think that combining as many different perspectives as possible will help the analyst solve some of the problems he/she confronts. The patterns zooarchaeologists find are likewise difficult to evaluate in the absence of the appropriate context that only present-day studies offer. Finally, the conservation effort should greatly benefit from lessons learned from the archaeological record that provides a temporal frame that often proves crucial to address current problems from a long-term perspective. For all these reasons, combining archaeological data with neontological studies should prove essential to get a more precise picture of past scenarios and to clarify the nature of the problems that many species face today. We hope this paper will have contributed to fulfilling some of these aims.

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TABLE LEGENDS

Table 1- Marten, carnivore and mammal NISPs at Cova Fosca sector C according to cultural horizon. Marten MNIs are provided within brackets.

Table 2- Observed vs. expected frequencies of pine and beech martens according to altitude ranges in the province of Asturias. Differences of abundance within each category for the two species have been obtained by Fisher's exact probability test.

Table 3- Observed vs. expected frequencies of pine and beech martens according to habitat type in the province of Asturias. Expected frequency values were obtained from the relative available area of each kind of habitat in the province. Differences of abundance within each category for the two species have been obtained by Fisher's exact probability test.

Table 4- Main palynological features for South-Eastern Iberia (ca. 8,770-5,000 cal BC).

FIGURE LEGENDS

Figure 1- Present day distributions (shaded areas) and archaeological presence (dots) of the pine marten (A) and beech marten (B) in the Iberian Peninsula. Pleistocene records of *Martes* sp. were taken to represent pine marten. Number 13 indicates the site of Cova Fosca. Details of sites and chronologies are provided in Appendices 1, 2 and 3.

Figure 2- Distribution of anthropic marks in the pine marten collections from Cova Fosca sector C. Incisions and peeling marks are associated with skinning operations.

Figure 3- NISP frequencies of pine and beech martens through time at Cova Fosca sector 3C (percentages estimated from the total of identified carnivore remains; see Table 1).

Figure 4- Frequencies of the beech and pine martens in the province of Asturias according to habitat type.

Figure 5- Pollen records quoted in the text. **Baetic Range:** 1, Siles; 2, Cañada de la Cruz; 3, El Sabinar; 4, Villaverde; 5, Cañada del Gitano; 6, Gádor; **Coastal areas:** 7, Casablanca-Almenara; 8, Elx; 9, Cova Cendres; 10, Xàbia; **Inner valleys:** 11, Navarrés; 12, Salines; 13, Villena; 14, Cova de l'Or; 15, Les Alcusses; **Southern Iberian Range:** 16, Ojos del Tremedal; 17, Villarquemado; 18, Cova Fosca.

Figure 6- Proportions of woodland avian taxa at Cova Fosca sector C. Included in this group are 18 species of birds that nest in trees, including woodpeckers (*Picidae*), hawfinch (*Coccothraustes coccothraustes*) and jay (*Garrulus glandarius*). Lesser spotted woodpecker (*Picus minor*) photo by Francisco Gutiérrez.

TABLES

TAXON	Epipalaeolithic	Mesolithic	Early Neolithic	Middle Neolithic	TOTAL
<i>Martes martes</i>	3 (2)	5 (2)	56 (12)	1 (1)	65 (17)
<i>Martes foina</i>	0	0	3(2)	0	3 (2)
<i>Martes</i> sp.	4 (2)	1 (1)	28 (5)	0	33 (7)
Total <i>Martes</i> spp.	7	6	87	1	101
Total id Carnivores	25	32	671	13	740
Total id mammals	3596	1767	15605	3894	24862

Table 1

Species	<i>M. foina</i>		<i>M. martes</i>		p-value
	Observed	Expected	Observed	Expected	
Altitudes (m.a.s.l)					
0-200	85	30.2	50	47,1	<0,00001
200-400	31	30.6	53	47,8	0,7076
400-800	31	50.7	76	79,0	0,0154
800-1200	11	30.7	47	47,9	0,0007
>1200	3	18.9	25	29,4	0,0021
Total	161	161.1	251	251	-

Table 2

Species Habitat	<i>M. foina</i>		<i>M. martes</i>		Fisher's test
	Observed	Expected	Observed	Expected	
Deciduous forest	23	42.2	123	103.8	0.0002
Pine forest	9	6.1	12	14.9	0.4285
Shrubland	11	8.9	20	22.1	0.5231
Anthropized areas	26	11.8	15	29.2	0.0499
Total	69	69	170	170	-

Table 3

Region	Mesolithic (ca. 8770-5500 cal BC)	Early Neolithic (ca. 5600-5000 cal BC)
Coastal areas	Evergreen <i>Quercus</i> (30-40%) <i>Pinus halepensis</i> (20%) Xerothermophilous <i>maquia</i>	Evergreen <i>Quercus</i> (<40%) <i>Pinus halepensis</i> (<10%) ↑↑Xerothermophilous <i>maquia</i> <i>Cerealia</i> ↑↑ Poaceae Anthropozoogenous taxa Coprophilous fungi
Inner valleys	<i>Pinus nigra</i> (>60%) <i>Pinus pinaster</i> (<5%) Evergreen <i>Quercus</i> (<2%) Deciduous <i>Quercus</i> (<2%)	<i>Pinus nigra</i> (>20%) <i>Pinus pinaster</i> (<5%) Evergreen <i>Quercus</i> (20-30%) Deciduous <i>Quercus</i> (>5%) Xerothermophilous <i>maquia</i> <i>Cerealia</i> ↑↑ Poaceae Anthropozoogenous taxa Coprophilous fungi
Southern Iberian Range	<i>Pinus nigra/sylvestris</i> (>60%) <i>Pinus pinaster</i> (5%) Deciduous <i>Quercus</i> (<5%) Evergreen <i>Quercus</i> (<5%) Steppe elements Recurrent wildfires (↑microcharcoals)	<i>Pinus nigra/sylvestris</i> (30%) <i>Pinus pinaster</i> (<5%) Deciduous <i>Quercus</i> (5%) Evergreen <i>Quercus</i> (20%)
Baetic Range	<i>Pinus nigra/ P. halepensis</i> (>60%) <i>Pinus pinaster</i> (<5%) Deciduous <i>Quercus</i> (<5%) Recurrent wildfires (↑microcharcoals)	<i>Pinus nigra</i> (50%) <i>Pinus pinaster</i> (5-10%) Deciduous <i>Quercus</i> (10%) Anthropozoogenous taxa Coprophilous fungi

Table 4

APPENDIX 1 - CATALOGUE OF PINE MARTEN FINDS IN IBERIA

Code	Site	Location	Period	NISP	Reference
1	Ekain	Deva, Guipúzcoa	Magdalenian	?	Altuna, 1984, 2010
2	Marizulo	Urnieta, Guipúzcoa	Mesolithic	2	Arribas, 2004
			Neolithic	2	
			Bronze	3	
3	Santimamiñe	Kortezubi, Vizcaya	Post-Azilian	1	Castaños, 1986
			Iron Age- Chalcolithic	3	
			Superficial?	2	
4	Albiztey	Abadiano,	Chalcolithic-	1	Castaños, 1986

		Vizcaya	Bronze		
5	Goikolau	Berriatua, Vizcaya	Roman	2	Castaños, 1986
			Chalcolithic	1	
6	Sierra de Gibujo	Guillarte, Álava	Mesolithic (7350 ±150BP)	5	Altuna, 1974
7	Zatoya	Abaurrea Alta, Navarra	Early Neolithic	14	Mariezkurrena and Altuna, 1989
			Laminar Epipalaeolithic-Post-Azilian	18	
			Azilian	12	
8	Abauntz	Arraitz, Navarra	Epipaleolithic	1	Altuna <i>and</i> Mariezkurrena, 1983
			Early Neolithic	1	
			Roman	1	
9	Aizpea	Arike, Navarra	Epipalaeolithic	3	Castaños, 2001a
10	Hornos de la Peña	San Felices de Buelna, Cantabria	Aurignacian	?	Yravedra, 2010
11	Cabezo de Amoreira	Muge, Portugal	Mesolithic	3	Lentacker, 1990-1991
12	Cova del Avellaner	La Garrocha, Girona	Early Neolithic	3	Altuna & Mariezkurrena, 2009
13	Cova Fosca	Ares del Maestre, Castellón	Epipaleolithic	3	This paper
			Mesolithic	5	
			Early Neolithic	56	
			Middle Neolithic	1	

APPENDIX 2 - CATALOGUE OF FINDS FROM *Martes* sp IN IBERIA

Code	Site	Location	NISP	Chronology	Reference
1	Ekain	Deba, Guipúzcoa	2	Aurignacian(+ 30.600 BP)	Altuna & Mariezkurrena, 1984, 2010
3	Santimamiñe	Kortezubi, Vizcaya	2	Asturian	Castaños, 1986
			1	Magdalenian	
13	Letzetxiki	Mondragón, Guipúzcoa	1	Upper Aurignacian	Altuna, 1972
14	Laminak II	Berriatua, Vizcaya	2	Azilian	Castaños, 1994
15	Las Pajucas	Lanestosa, Vizcaya	1	Mesolithic	Altuna, 1967, 1972
8	Abauntz	Arraitz, Navarra	1	Magdalenian	Altuna <i>et al.</i> , 2001-2002
16	A Valiña	Castroverde, Lugo	8	Chatelperronian (<i>ca.</i> 31 Ky BP)	Fernández-Rodríguez, 2010
17	Cueva de Valdegoba	Huércemes, Burgos	?	Musterian (OIS 3-6) 73±2 Ky	Aguirre, 1989 ; Arribas, 2004
18	Oliveira	Torres Novas, Portugal	1	Musterian (<i>ca.</i> 35,000 BP)	Zilhão, 2010
	Peña Larga	Cripán, Álava	3	Bronze	Castaños, 1999

	Urtao II	Oñate, Guipúzcoa	4	Chalcolithic	Mariezkurrena, 1989
	Pico Ramos	Muskiz, Vizcaya	2	Chalcolithic	Castaños, 1995
	Arenaza	San Pedro de Galdames, Vizcaya	1	Neolithic (3015 ± 195)	Arribas, 2004
	Cueva de los Gitanos	Sámano, Cantabria	2	Neolithic	Altuna & Mariezkurrena, 2009
	Aldeacueva	Carranza, Vizcaya	4	Chalcolithic	Altuna, 1967, 1972
	Los Husos I	Elvillar, Álava	2	Neolithic	Altuna & Mariezkurrena, 2009
			1	Chalcolithic	
	Abrigo de la Peña	Marañón, Navarra	1	Neolithic	Castaños, 1986
			5	Chalcolithic	
	Atxuri	Baztán, Navarra	5	Neolithic- Chalcolithic	Castaños, 1986
			1	Superficial?	
	Sagastigorri	Kortezubi, Vizcaya	1	Bronze-Roman	Castaños, 1986
	Santimamiñe	Kortezubi, Vizcaya	2	Superficial?	Castaños, 1986
			2	Iron Age-Roman	
			18	-Chalcolithic - Bronze	

APPENDIX 3 - CATALOGUE OF BEECH MARTEN FINDS IN IBERIA

Code	Site	Location	NISP	Cronology	Reference
13	Cova Fosca	Ares del Maestre, Castellón	1	5,260±70 BC; 5,150±70 BC Neolithic (Level I)	Estévez, 1988
			1	Early Neolithic (5,310-5,040 cal BC; 5,300-5,010 cal BC)	Llorente et al., 2011
19	Chaves	Bastarás, Huesca	15	Neolithic 4,800-4,300 BC	Castaños, 2004
20	Cova Verda	Sitges, Barcelona	¿	Middle and Late Neolithic (5,000-4,000 BC)	Rubio, 1989
21	Cubío Redondo	Matienza, Cantabria	6	Neolithic 5,000-4,000 BC	Castaños, 2001b
22	Lumentxa	Lekeitio, Vizcaya	1	Bronze	Altuna, 1972

Figure 1
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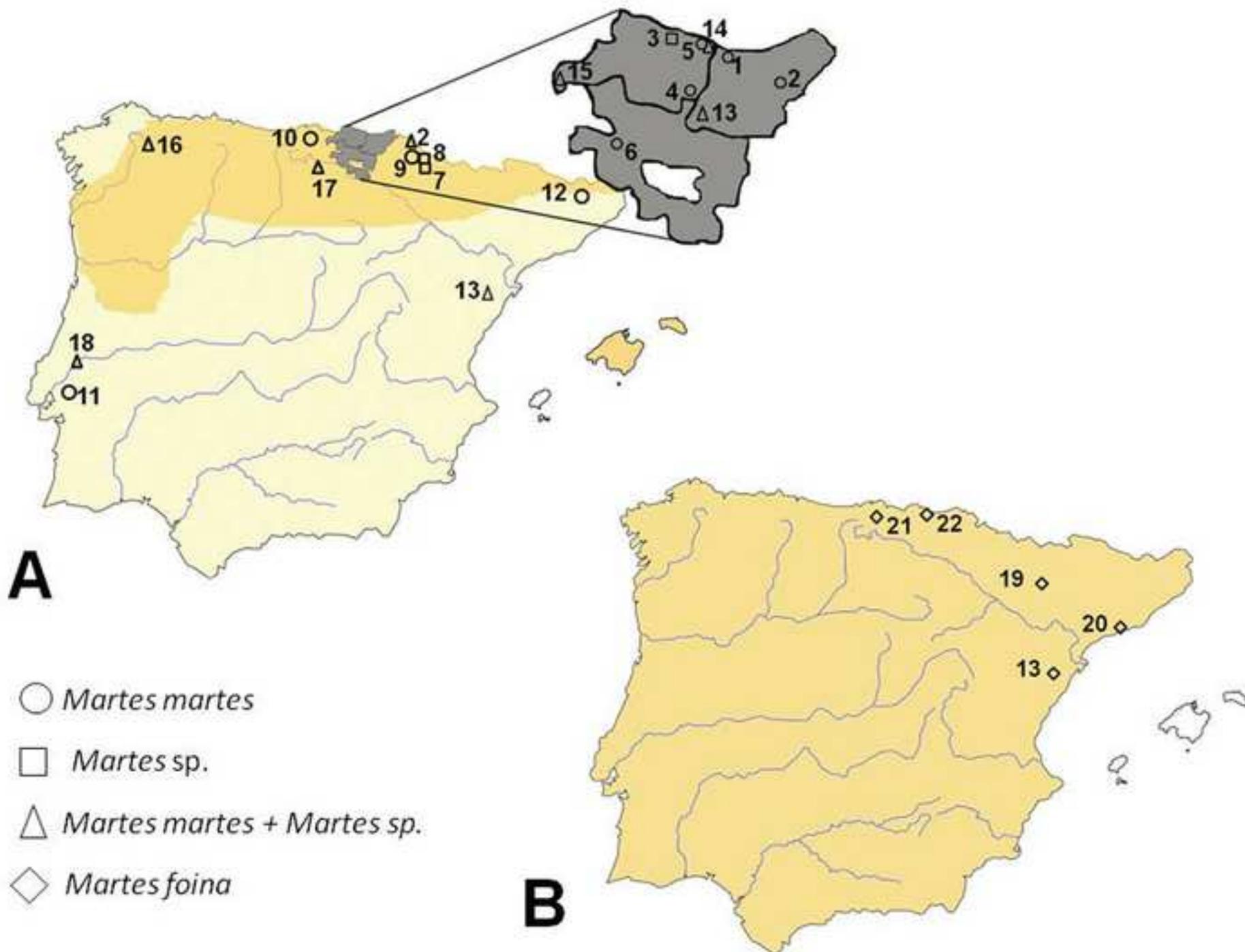


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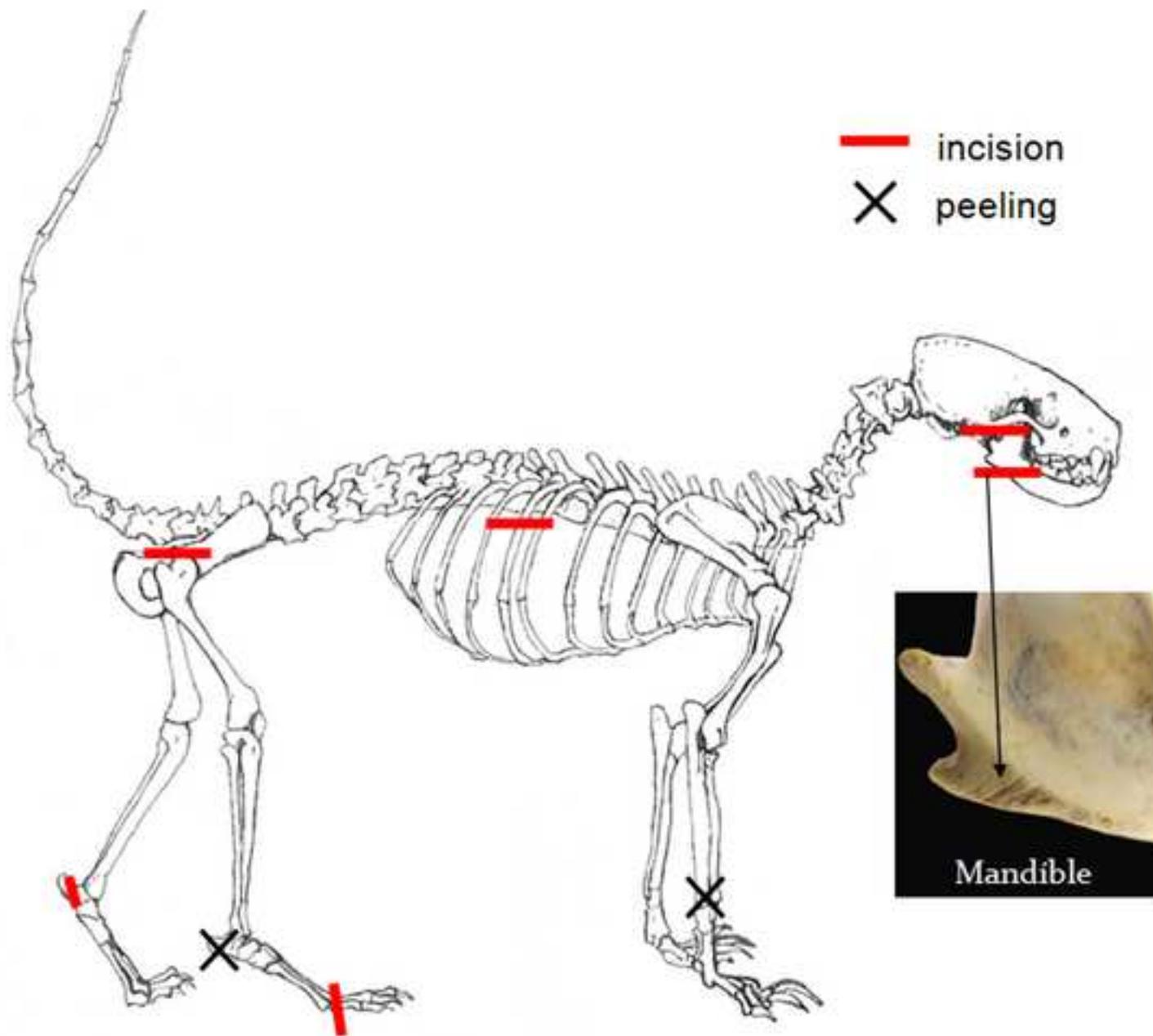


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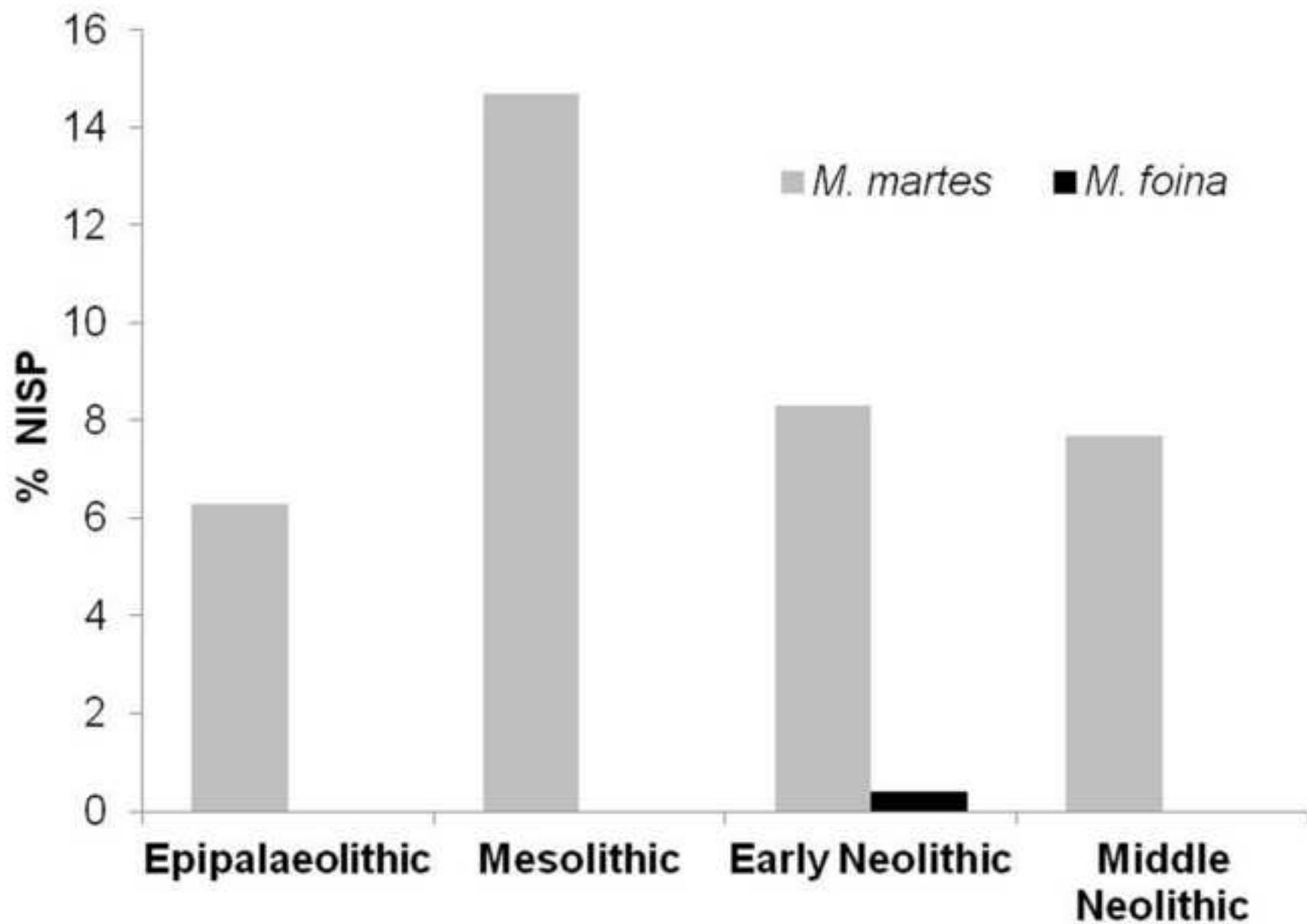


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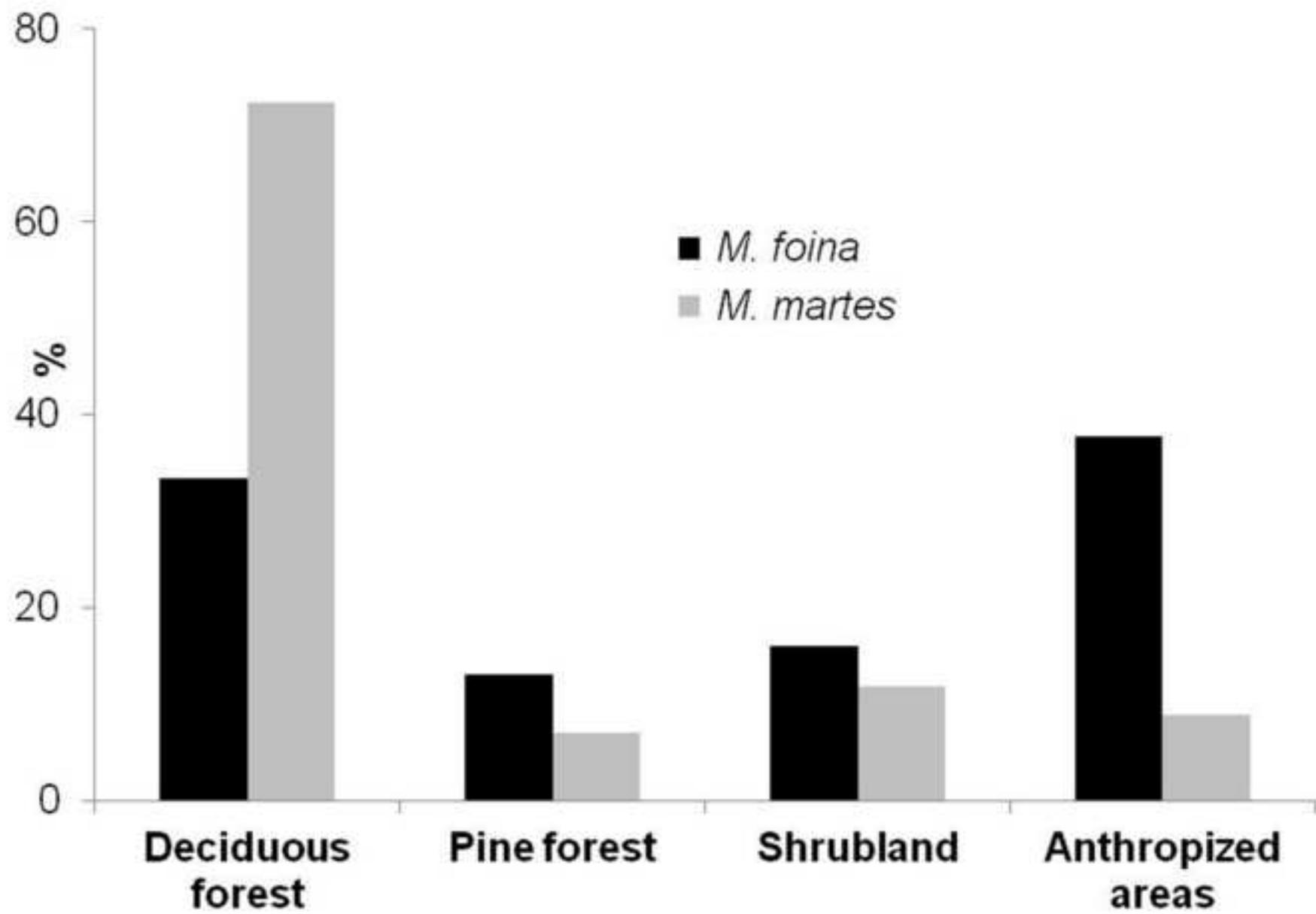


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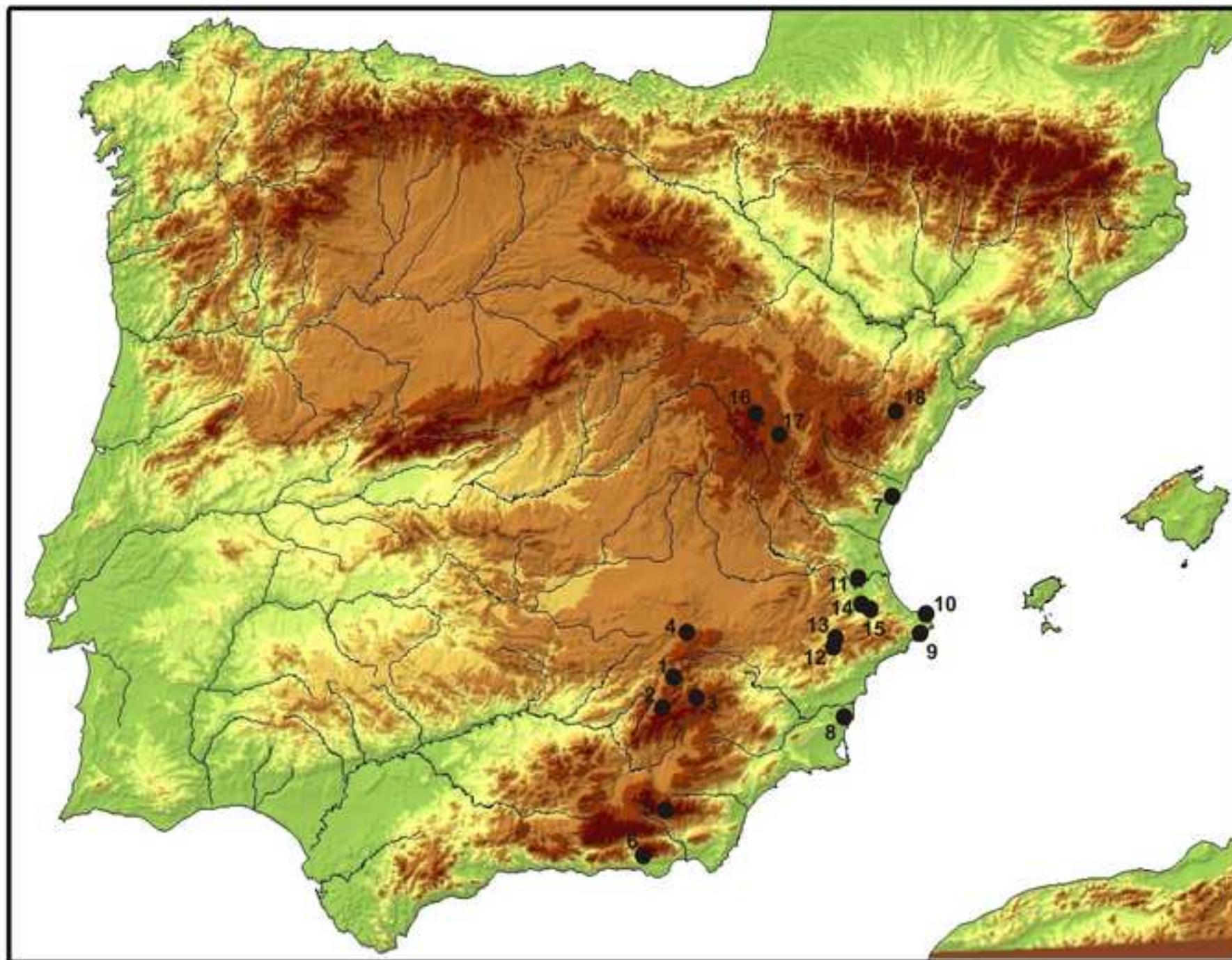


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