



Invited review

Human impact and ecological changes during prehistoric settlement on the Canary Islands

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ABSTRACT

Oceanic islands remained free of humans until relatively recent times. On contact, humans encountered pristine environments with unique ecosystems and species highly vulnerable to novel impacts. In the course of rendering an island habitable, the new settlers transformed it through fire, deforestation, hunting and introduction of pests and weeds. The result, as described for many oceanic islands globally, has been a catastrophe for biodiversity. Here we present the case of the Canary Islands, an Atlantic archipelago renowned for its exceptional biodiversity, and show that these islands have been no exception to the general rule. We review the archaeological, palaeoecological, palaeontological and ecological literature for the archipelago and discuss the ecological consequences – in particular habitat transformation and biodiversity loss – of human settlement. In contrast to previous views that prehistoric humans had only limited impacts on these islands, we show that vegetation change, increased fire, soil erosion, species introductions and extinctions follow the familiar oceanic pattern. Timing of human settlement of the Canary Islands has been controversial, with revised archaeological dates suggesting a relatively late arrival at the beginning of the Common Era, while palaeoecological and palaeontological evidence favours a presence several centuries earlier. While the matter is still not settled, we suggest that settlement sometime between 2400 and 2000 cal years BP is a possibility.

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1. Introduction

Oceanic islands were inaccessible to humans until relatively recent times (Keegan and Diamond, 1987). From the moment that humans began to cross wide extents of open ocean, they started to transform island environments. The effects of human presence on islands often become apparent in the early stages in the colonization process, even before permanent settlement (i.e. visitation

stage: see Wood et al., 2017). Later, when permanent settlement by technological advanced populations occurs, anthropic environmental changes are always evident. However, key processes – such as the rate of forest loss or species introduction – do not necessarily depend on timing of settlement or the size or technical level of the colonizing population (Wood et al., 2017).

Prehistoric settlement and its consequences for island environments is not as well understood as later events because of the absence of written archives and the continuing loss of ancient settlement sites and natural deposits. Nevertheless, archaeological and palaeoecological studies provide abundant evidence for the magnitude of human impact and the rapidity with which may occur on islands worldwide (Burney, 1997; Rick et al., 2013; Braje et al., 2017; Nogué et al., 2017). Humans impact directly on the

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environment through the exploitation of species (hunting, fishing and gathering) and indirectly, through habitat transformation (felling, burning, farming and erosion) and introduction of exotic species. These latter may predate, compete or hybridize with island native species, and introduce diseases, parasites and vectors, reducing population sizes and threatening the species survival (e.g. Steadman, 1995; Prebble and Dowe, 2008) and ecosystem integrity (e.g. Wilmshurst et al., 1997; Hunt and Lipo, 2010).

The Canary Islands, at the eastern margin of the North Atlantic, was one of the few archipelagos in the region to have been colonized in prehistoric times. The first Canarian inhabitants are known as Canarian aborigines or Canarian natives, or sometimes referred to as "Guanches" (strictly speaking the name for the inhabitants of the island of Tenerife). The time of their arrival is poorly constrained and still debated (see del Arco et al., 1997; Atoche, 2008; Arnay-de-la-Rosa et al., 2009; Atoche and Ramírez, 2011; Rando et al., 2014; Velasco, 2014; Atoche and Ramírez, 2017; Fregel et al., 2019; Velasco et al., 2019). However, most authors agree that there was effective settlement of all the islands at around or after the beginning of the common era (CE) which implies a Canarian prehistoric period of at least 1400 years, that is until 1402 CE when Normans arrived in Lanzarote to begin their conquest. According to modern and ancient human DNA analysis of Canarian natives, the original prehistoric settlers were of Libyan-Berber stock from North-West Africa (Flores et al., 2001; Maca-Meyer et al., 2004; Fregel et al., 2009, 2015, 2019).

The aftermath of prehistoric human impact on islands has been reviewed for other groups of islands and oceans (e.g. Athens and Ward, 1993; Burney, 1997; Fitzpatrick and Keegan, 2007; Prebble and Wilmshurst, 2009; Rick et al., 2013; Wood et al., 2017). The Atlantic archipelagos have received less attention, perhaps because of the scarce and scattered information available. In a previous review on the Canary Islands, Morales et al. (2009) focused on the relationship between Canarian aborigines and their environment from an archaeological perspective, providing detailed information on native and introduced species used by aborigines. Here, we expand on this previous review, including available data from palaeoecological, palaeontological and archaeological studies carried out in the Canary Islands over the last decades. We focus on ecological processes (i.e. vegetation dynamics, fire regime, soil erosion, species introduction, extinctions and extirpations), and their consequences for human-mediated transformation of the environment during the prehistoric period.

How human societies colonised and transformed biotas and ecosystems of pristine islands worldwide, and in turn how these new environmental settings have transformed those societies, is a topic of increasing interest. Some recent works discuss the transformation of pristine island landscapes to satisfy human needs (Huebert and Allen, 2016) and the consequences of species extinction and the introduction of weeds, pests and domestic and commensal animals (Athens, 2009; Prebble and Wilmshurst, 2009; Leppard and Birch, 2016). Others deal with topics such as the timing of colonization (Alcover, 2008; Wilmshurst et al., 2011; Siegel et al., 2005; Mitchell, 2019), how humans have adapted to the new insular environments (Kirch, 2007; Leppard, 2017), and the demographic and genetic consequences for the founder populations (Moore, 2001). Some authors argue that understanding the processes of island colonization is a useful proxy for future human colonization of "islands" beyond the Earth (e.g. the Moon, Mars) (Fitzpatrick and Erlandson, 2018). Whatever the approach, human colonization of islands is best addressed through the study of archaeological, palaeontological and palaeoecological evidence combined.

2. Impact on ecosystems

2.1. Changes in vegetation

The Canary Islands host a unique set of native vegetation types. The dominant types are: two shrubland ecosystems, that of the coast adapted to dry and warm climate, and that of the summit to dry and cold conditions; and three forest ecosystems, thermophilous woodland, subtropical evergreen laurel forest, and endemic Canarian pine forest (for detailed descriptions see del Arco et al., 2010).

Unlike many regions which have abundant, well preserved fossil sites, the Canary Islands have few suitable sites, and little is known about their long-term vegetation history. However, through investigations of the few available lake and crater sedimentary sequences and their plant microfossils it has been possible to reconstruct past environments and describe their dynamics and trajectories up until the present day (Fig. 1). Sedimentary records from the mid elevations of the islands of Tenerife (de Nascimento et al., 2009), La Gomera (Noguér et al., 2013) and Gran Canaria (de Nascimento et al., 2016) cover a period of some thousands of years, including the period before the arrival of first Canarian settlers, thus providing the evidence for their impact on the vegetation.

On Tenerife, the forest surrounding La Laguna (at some 600 m a.s.l.) included typical evergreen laurel forest species, such as *Morella faya*, *Erica* spp., *Ilex cf. canariensis*, *Picconia excelsa*, *Prunus lusitanica* and *Viburnum rigidum* among others. Relatively high pollen percentages of two arboreal Fagaceae genera, oaks (*Quercus* sp.) and hornbeams (*Carpinus* sp.) occur as well. Oak and hornbeams had not previously been considered as native to the islands but must have grown in the forest around La Laguna before human arrival, at least locally. It is unclear whether they were a separate community or if they were part of the laurel forest, the pine forest or the thermophilous woodlands.

On La Gomera, the vegetation which before colonization surrounded Laguna Grande (ca. 1,200 m a.s.l.) was made up mainly of *Erica* spp. and *Morella faya* together with other species typical of the laurel forest and thus resembled the present-day forest communities. On Gran Canaria, sediments from Laguna de Valleseco (ca. 900 m a.s.l.) were dominated by pollen of *Juniperus cf. turbinata* and *Phoenix canariensis*, with only a sparse representation of laurel forest species and high percentages of shrub and herbaceous types, suggesting the surrounding vegetation was thermophilous woodland. Therefore, at two of the sites, the present-day vegetation is completely different from the community inferred from the fossil record. In Tenerife, the shift towards current vegetation began some 2000 years ago, presumably when the island was already inhabited. The forest composition changed through the progressive decline of the Fagaceae trees (*Quercus* sp. and *Carpinus* sp.), whose pollen signal vanished completely by 700 to 400 years ago. From this point on, the forest composition was typical of the laurel forest with *Morella faya* the dominant tree. In the centuries immediately after the conquest, the forest was largely eliminated, only a few trees of *Laurus novocanariensis* remaining within the area of abandoned plots and houses that now occupy the centre of the city of La Laguna (de Nascimento et al., 2009).

On Gran Canaria, the two dominant arboreal species, palms and juniper trees, began to decline some 2300 years ago, ultimately being almost entirely replaced by shrubby and herbaceous vegetation. Although occurring several centuries before the oldest indications of humans in the Gran Canaria archaeological record (Velasco, 2014; Velasco et al., 2019), this vegetation change suggests that the island may have been settled at this time. Later, around 1800 years ago, there is a clear cereal pollen signal,

indicating agricultural activity in the area lasting at least 200 years. The original forest did not recover and was replaced by secondary vegetation similar to that now seen around the Laguna de Valleseco (de Nascimento et al., 2016). On La Gomera, however, there is no sign of significant reduction in forest cover or change in its composition after the date of first human arrival (Nogué et al., 2013).

These palaeoecological records show environmental transformation began during the early phases of human colonization, as can be seen in changes in the forest species composition and opening of the canopy, as at La Laguna in Tenerife, and complete forest clearance as occurred at the Laguna de Valleseco on Gran Canaria. However, these transformations were not uniform over the entire archipelago, nor did they have the same impact on all vegetation communities. While deforestation reached its highest levels during the historical period (Parsons, 1981; Santana, 2001; Rodríguez and Naranjo, 2005) in some places, as shown in the La Gomera pollen record, forest has remained intact up until the present.

2.2. Modification of the fire regime

The natural fire regime before the historic period is poorly known. The most Mediterranean-like vegetation types (i.e. the pine forest) have species with the fire-resistant traits expected in fire-prone ecosystems (Méndez et al., 2015), and we assume this to be the case also for the thermophilous woodland. The other vegetation types are less prone to fire as they either grow in more humid areas (laurel forest) or have lower biomass (coastal and summit scrubs).

The same three records analysed for pollen show a significant increase in the concentration of charcoal beginning about 2300–2000 years ago (de Nascimento et al., 2009, 2016; Nogué et al., 2013) (Fig. 1). At an additional site on Gran Canaria (La Calderilla) surrounded by pine forest, the charcoal record showed a fire phase at 2280–2000 years cal BP that appears to have initiated forest decline (Ravazzi et al. submitted). Charcoal concentrations were much lower before this period, and the vegetation experienced less frequent but probably more extensive fires. Volcanic activity and lightning are the only sources of natural ignition in the Canaries, but neither are frequent, and large amounts of biomass accumulate between fires. Fires when they occurred were thus large and may have burnt for several days. In La Laguna (Tenerife) and Laguna de Valleseco and La Calderilla (Gran Canaria) fires became more frequent from the beginning of the colonization period. At Laguna Grande (La Gomera) fires were infrequent even after human arrival. Charcoal analysis shows that from about 1900 years ago fires occurred throughout the three islands, indiscriminately affecting various vegetation types, including pine forest, laurel forest and thermophilous woodland. This new regime of elevated fire frequency was maintained through the entire prehistoric period without ever returning to pre-human levels. In the case of La Gomera, the Laguna Grande site has a cool, wet climate and was not a preferred area for human settlement, which may explain its low fire frequency.

The increase in fire frequency, without parallel in the millennia before settlement, is clear evidence for the importance of fire to the Canarian natives. These abrupt increases in charcoal in the fossil record at the same time that pollen of arboreal species declines shows continuous anthropogenic fire which, in combination with tree felling, pastoralism and agriculture, reduced and degraded forest over large areas of these islands.

2.3. Soil erosion

Increased soil erosion is another consequence of human

activities on islands (Burney et al., 2001; McWethy et al., 2009). Erosion follows deforestation or the loss of vegetation cover through fire, logging, overgrazing and ploughing. All these activities occurred in the Canaries. Sedimentological analysis of archaeological layers in Lanzarote (Criado and Atoche, 2003, 2004) show, from very early stages in the human occupation of the area, an increase in the sediment grain size indicating a rapid, chaotic influx of material caused by intense animal trampling of the nearby slopes. Other indications of erosion are increases: i) of carbonates freed by the erosion of deeper soil layers; ii) of iron and manganese, produced by destruction of clay soils; and iii) in the rate of sedimentation pointing to intense, rapid erosion. The geomorphological study of various archaeological sites in Gran Canaria also suggest a relationship between erosion and the first settlement of the island (Criado and Hansen, 2002).

An increase in sedimentation rates after human occupation can also be detected in the La Laguna sedimentary record (de Nascimento et al., 2009) and Laguna Grande (Nogué et al., 2013), although these accelerate during the historical period. Deforestation of the slopes and mountains surrounding La Laguna probably increased sedimentation (Criado, 2002). Although the forests of La Gomera remained almost intact, the immediate surrounds of Laguna Grande were subject to a certain level of exploitation and clearing which would have increased local erosion.

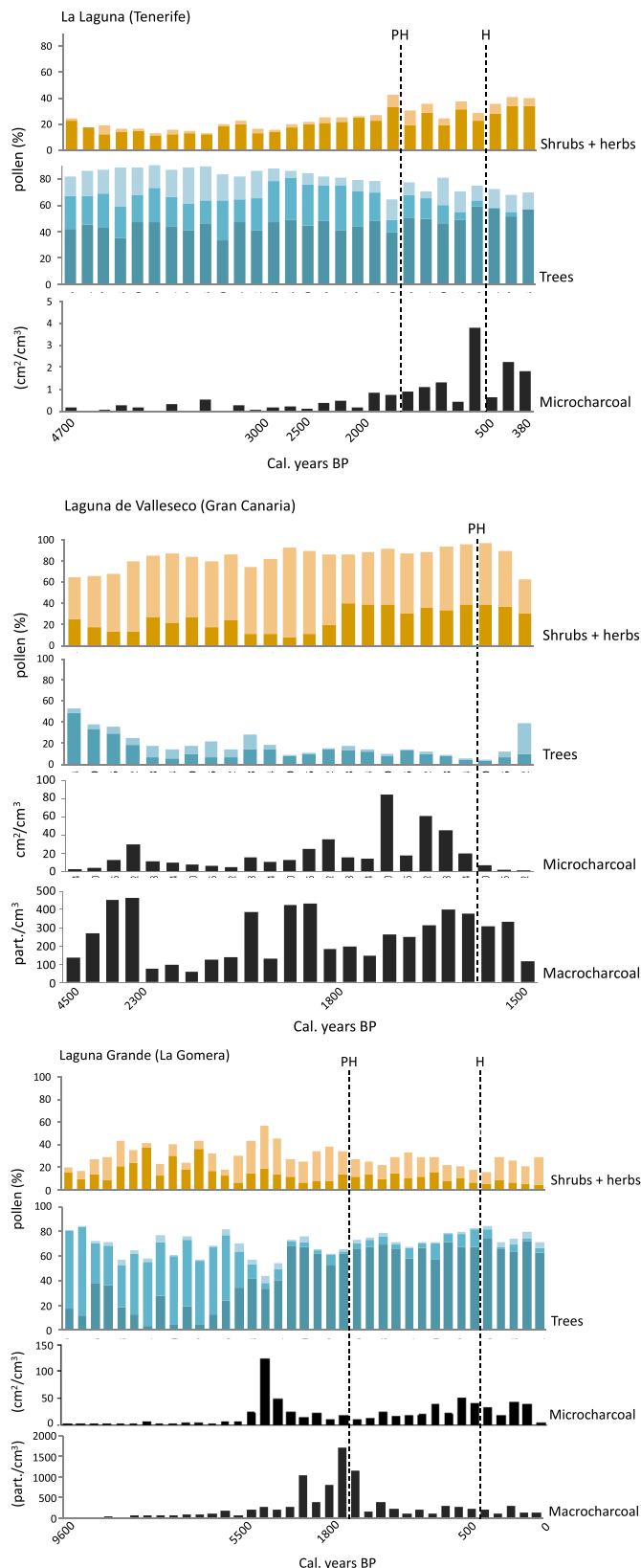
3. Introduced species

3.1. Introduced animals

The first Canarian settlers brought with them domestic plants and animals and practiced agriculture and animal husbandry (Figs. 2 and 3, Table 1, Table S1). Goats (*Capra hircus*), sheep (*Ovis aries*) and pigs (*Sus domestica*) were introduced to all the islands; dogs (*Canis familiaris*), also were present on all islands with the exception of El Hierro; while the prehistoric introduction of cats (*Felis catus*) is uncertain, although some bones have been assigned to this species on Tenerife and La Palma (Machado, 2007; Morales et al., 2009).

Pastoralism was one of the main economic activities on all the islands and introduced herbivores, especially goats and sheep, provided the settlers with skins, bones, horns, meat and milk, the last two fundamental to the Canarian diet (González-Reimers et al., 2001; Velasco, 2001; Arnay-de-la-Rosa et al., 2009, 2010, 2011). The Canarian aborigines practiced a form of transhumance, in which the animals were continually moved over long distances tracking changes in vegetation productivity by grazing the coastal areas in winter and the summits in summer (Pais, 1996a). However, stock management was complex being strongly influenced by the steep, much divided landscape and also the social organization of each island which in their turn determined the nature and extent of movements (Velasco et al., 1999).

A recent analysis of archaeological remains from various human settlements across La Gomera showed that, at times, living spaces were shared with animals. As well, the presence of pens close to these sites points to other pastoral practices in which animals were moved seasonally over small distances but remained close to settlements (Hernández-Marrero et al., 2016). Similarly, in La Palma, two types of pastoral management have been described which depended on access to the high-altitude pastures. The distances involved in movement from the lower elevation settlements to the peaks were much shorter in the south of the island and could be completed within the one day, while in the north, the terrain being more rugged, they were much longer, which forced the shepherds to move with their flock during the summer season (Pais, 1996a). The mobility of these flocks of goats and sheep shows that this



pastoralism must have had a very significant effect on virtually all the island vegetation communities from the very beginning of colonization.

Pigs were third in importance as livestock after goats and sheep and their bones are abundant in the fossil record (Atoche, 2003; Alberto et al., 2015; Hernández-Marrero et al., 2016). Free-roaming pigs graze widely as they have an omnivorous diet consisting of roots, fruits, shoots, herbs, mushrooms, invertebrates and remains of other animals that they find in forest understories. Analogy with wild pigs, or domestic pigs free to roam over large areas as in the Iberian *dehesa* system, suggests that the pigs introduced by the Canarian aborigines were raised mostly in the laurel forest zone (Pais, 1996b) whether this was through being pastured or as feral animals that were eventually harvested. The laurel forest under-story is rich in roots, fruits, fern rhizomes and invertebrates, and exploitation by pigs would have had a significant impact on the regeneration dynamics of the forest, particularly through the consumption of fruits, shoots and roots as well as through trampling, increasing seedling mortality, decreasing the litter cover and accelerating soil erosion. Consumption and trampling would have also affected the forest litter and soil invertebrate community. Pigs were also common in the eastern islands (Atoche, 2003) where laurel forest was scarce, which suggests that these animals could take advantage of other vegetation types, as well as possibly being raised in pens close to settlements.

In order to understand the impact of pre-Hispanic pastoralism, the density of the stock maintained on each island, changes over time, the distribution and intensity of grazing in the various vegetation communities, and the ways in which the Canarian aborigines created and maintained grazing lands need to be addressed. Grazing animals were introduced at the time of first settlement (Delgado et al., 2000; Ferrando et al., 2015; Olalde et al., 2015). In pre-human times the islands lacked terrestrial mammals with the exception of two species of giant rat (*Canariomys bravoi* and *C. tamarani*), the lava mouse (*Malpaisomys insularis*) and the Canarian shrew (*Crocidura canariensis*). The introduction of larger domestic mammalian herbivores may have had a severe initial impact, especially on those endemic plants not adapted to herbivory and possibly driving some to extinction. However, the fossil record of plant extinctions is sparse and therefore we cannot be sure of the impact of herbivores during the initial contact period. Other practices associated with the management of stock, such as the use fire and clearing of forest to encourage pasture, must have had a significant impact on the cover and composition of the vegetation communities as well.

Some authors suggest that the prolonged effect of herbivory together with the increased frequency of fires after human arrival are the primary cause of species impoverishment in some ecosystems. For example, the pine forests are characterized by a very species poor understory, and many endemic species are now found only in areas inaccessible to stock (Nogales et al., 1992; Rodríguez-Piñero and Rodríguez-Luengo, 1993; Garzón-Machado et al., 2010; Irl et al., 2014). Which stage of the human settlement of the Canaries has produced the greatest impact is uncertain because pastoralism has continued throughout the historic period right up until the present day. However, without doubt, the importance of herding as a Canarian economic activity suggests that from the very beginning of colonization the countryside had to be cleared,

Fagaceae trees (medium blue), other forest types (light blue). Gran Canaria: thermophilous woodland (dark blue), other forest types (light blue). La Gomera: laurel forest (dark blue), Canarian willow and palm communities (medium blue), other forest types (light blue). PH: prehistoric period, H: historic period. The prehistoric period for each island has been delimited according to the earliest dates from the archaeological record following Fig. 2 and Table 1.

Fig. 1. Main vegetation changes (inferred from pollen percentage) and changes of fire regime (inferred from charcoal concentration) that occurred on the islands of Tenerife, Gran Canaria and La Gomera (Canary Islands), over the last thousand years (cal years BP). Yellow bars represent pollen types assigned to shrubs (dark yellow) and herbs (light yellow). Blue bars represent pollen types from trees, with different shades of blue for the main forest types found on each site. Tenerife: laurel forest (dark blue),

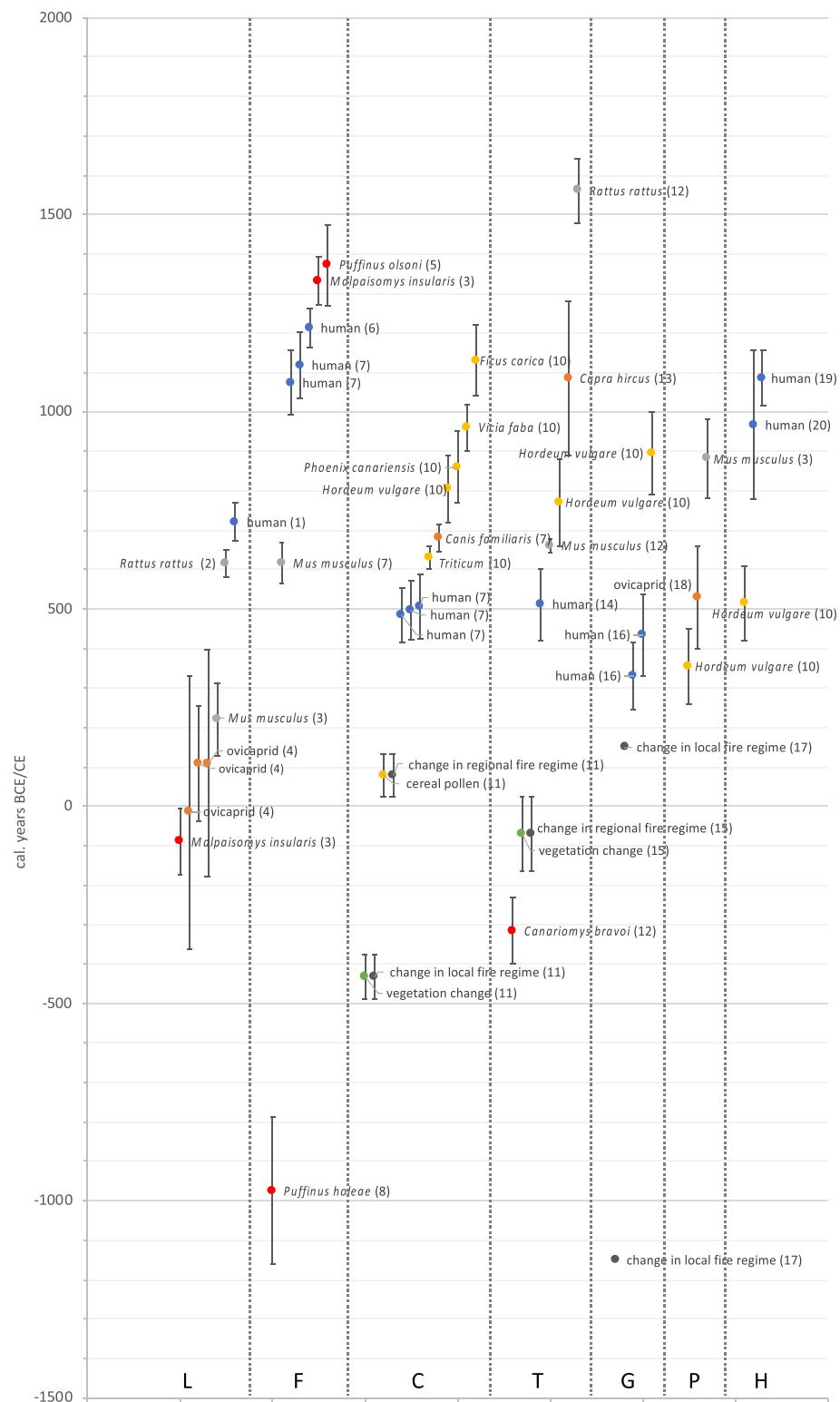


Fig. 2. Selection of ^{14}C dates as calibrated ages 2σ range (cal years BCE/CE), from archaeological (bones, teeth, tissues, seeds), palaeontological (bones) and palaeoecological (sediments) samples available from the Canary Islands (L: Lanzarote, F: Fuerteventura, C: Gran Canaria, T: Tenerife, G: La Gomera, P: La Palma, H: El Hierro). Archaeological dates represent the first record available of human remains (blue), domestic animals (orange), cultivars (yellow) and alien commensals species (grey). Palaeontological dates represent the latest available record of animal extinct species (red). Palaeoecological dates represent changes in pollen composition (green), detection of cereal pollen (yellow) and changes in charcoal abundance (black). Numbers in brackets indicate source references included in Table 1.

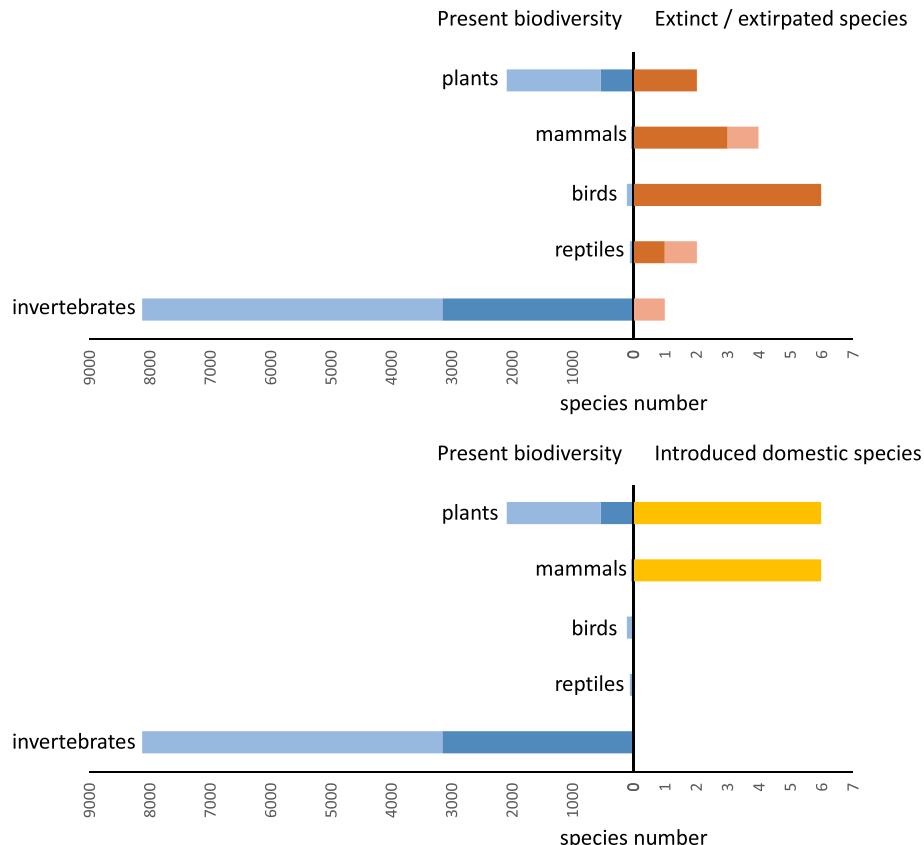


Fig. 3. Number of native (light blue) and endemic (dark blue) species from several taxonomic groups (plants, mammals, birds, reptiles, invertebrates) in the Canary Islands at present, and number of extinct (dark orange) and extirpated (light orange) species, and introduced domestic species by taxonomic group in the prehistoric period. For detail on species see sections 2.2 and 4, and Table S1.

especially of the denser shrubland and forest, to permit free movement of animals and provision of seasonal pastures.

The European introduction of the rabbit (*Oryctolagus cuniculus*) in the 15th century and more recently game animals for sport such as the Mouflon (*Ovis orientalis*) and the Barbary sheep (*Ammotragus lervia*) in the 20th century, have increased the threat to the flora of the Canary Islands (Nogales et al., 2006) as these feral animals are not subject to any type of management except when they are harvested. Given these circumstances it is difficult to estimate the relative impact of these introduced species.

As well as domestic animals, the first inhabitants of the islands accidentally introduced rodents. Introduced rodents are believed to have caused disequilibrium in many populations of native species as a result of competition for resources, predation and transmission of diseases. Moreover, predation on fruit and seedlings may have negatively affected the regeneration of numerous plant species. The house mouse (*Mus musculus*) was probably inadvertently introduced by the first inhabitants to all the islands although its remains have only been found on some of them (Fuerteventura, Lanzarote, Tenerife, La Palma and El Hierro) (Machado, 2007; Alcover et al., 2009; Morales et al., 2009; Rando et al., 2014). The house mouse coexisted during some centuries with a species of endemic rodent, the lava mouse (*Malpaisomys insularis*), which lived on Fuerteventura, Lanzarote, and some of the northern islets of the Chinijo archipelago. The house mouse may have been a competitor and transmitter of new diseases to the lava mouse, although it did not cause its extinction, at least on the islands. On the islets, however, it has been hypothesized that the introduction of the house mouse and the consequent increase in prey for its usual predator (the barn

owl, *Tyto alba*) unleashed hyper-predation. In this particular case, the introduced prey species (house mouse) is well adapted to a high level of predation while the native species (the lava mouse) does not have the same recovery capacity because of its low reproductive rate and thus high levels of predation ultimately leads to its extinction (Rando et al., 2011). The introduction of the house mouse may have had a similar effect on other endemic mammals such as the giant rat of Tenerife (*Canariomys bravoi*) (Rando et al., 2014), or the Canarian shrew (*Crocidura canariensis*) that was extirpated on some islets (Rando et al., 2011).

Two species of rats were introduced by Europeans to the Canaries: the black rat (*Rattus rattus*) and Norwegian rat (*Rattus norvegicus*). The haplotype pattern of the present-day populations of black rat show differences between the eastern islands (Lanzarote and Fuerteventura) and the others, suggesting a double colonization following the route of the Norman-Castilian conquerors (López et al., 2013). Populations of black rats on El Hierro share haplotypes with the eastern islands and probably were derived from Norman ships visiting the island, these having already introduced the same species of rat during their campaigns in Lanzarote and Fuerteventura at the beginning of the 15th century. Nevertheless, remains of black rat have been found in archaeological sites on Lanzarote some 1300 years before present, that is before the arrival of the Normans, suggesting the previous introduction of this rat, at least to this island (Atoche, 2009; Rando et al., 2011). The Norwegian rat is a much more recent introduction, probably in the 18th century (Nogales et al., 2006).

These rats are among the most damaging exotic invaders in the world. They are omnivorous consuming plants (fruits, seeds, leaves,

Table 1

List of selected ^{14}C dates and calibrated ages at 2σ range (cal years BCE/CE) from archaeological, palaeontological and palaeoecological samples available from the Canary Islands. The island: Isl. (L: Lanzarote, F: Fuerteventura, C: Gran Canaria, T: Tenerife, G: La Gomera, P: La Palma, H: El Hierro), site, type of deposit: Dep. (AR: archaeological, PA: palaeontological, PE: palaeoenvironmental), type of sample, related human activity, lab code and source reference are shown. Reference number (Ref.) is used in Fig. 2.

Dep.	Isl.	Site	Sample	Proxy/Activity	Age (^{14}C yr BP)	Lab code	Calibrated ages 2σ range (cal years BCE/CE)	Reference	Ref.
AR	L	Zonzamas	human bone	human occurrence	1281 ± 20	D-AMS 015885	671–770 cal CE	Santana et al., 2017	1
AR	L	Caldera de Tinache	<i>Rattus rattus</i> bone	first record of alien commensal species	1460 ± 25	KIA-36265	580–650 cal CE	Rando et al. (2011)	2
AR	L	El Bebedero	<i>Mus musculus</i> bone	first record of alien commensal species	1815 ± 25	KIA-36470	128–313 cal CE	Alcover et al. (2009)	3
AR	L	El Bebedero	ovicaprid bone	introduction of domestic species/livestock	1895 ± 120	GrN-19195	177 cal BCE – 395 cal CE	Atoche and Ramírez (2017)	4
AR	L	Caldera de Tinache	ovicaprid bone	introduction of domestic species/livestock	1890 ± 60	Beta-172349	38 cal BCE – 252 cal CE	Atoche and Ramírez (2017)	4
AR	L	El Bebedero	ovicaprid bone	introduction of domestic species/livestock	1980 ± 140	GrN-19194	361 cal BCE – 332 cal CE	Atoche and Ramírez (2017)	4
PA	L	Jameo de la Puerta Falsa	<i>Malpaisomys insularis</i> bone	last record of an extinct endemic species	2075 ± 25	KIA-36469	174–4 cal BCE	Alcover et al. (2009)	3
PA	F	Cueva de Las Moscas	<i>Puffinus olsoni</i> bone	last record of an extinct endemic species	1265 ± 25	KIA-29159	1270–1475 cal CE (2σ calib. interv. Marine 04.14C $\Delta R = 257 \pm 67$)	Rando and Alcover (2007)	5
PA	F	Cueva del Llano Huriamen	<i>Malpaisomys insularis</i> bone	last record of an extinct endemic species	670 ± 35	KIA-30983	1271–1394 cal CE	Alcover et al. (2009)	3
AR	F	Huriamen	human bone	human occurrence	830 ± 30	Beta-384060	1161–1264 cal CE	Fregel et al. (2019)	6
AR	F	La Tonina	human bone	human occurrence	910 ± 30	Beta-392420	1033–1204 cal CE	Velasco et al. (2019)	7
AR	F	Huriamen	human teeth	human occurrence	980 ± 30	Beta-384060	993–1155 cal CE	Velasco et al. (2019)	7
PA	F	Cueva de Villaverde	<i>Mus musculus</i> bone	first record of alien commensal species	1415 ± 40	KIA-30994	565–669 cal CE	Alcover et al. (2009)	3
PA	F	Islote de Lobos	<i>Puffinus holeae</i> bone	last record of an extinct endemic species	3395 ± 30	KIA-36249	1159–790 cal BCE (2σ calib. interv. Marine 04.14C $\Delta R = 257 \pm 67$)	Rando and Alcover (2010)	8
AR	C	Cenobio de Valerón	<i>Ficus carica</i> seed	introduction of cultivars/agriculture	890 ± 30	Beta-384698	1040–1220 cal CE	Naranjo and Rodriguez, 2015	9
AR	C	Dunas de Maspalomas	<i>Vicia faba</i> seed	introduction of cultivars/agriculture	1050 ± 30	Beta-359512	900–1020 cal CE	Morales et al. (2017)	10
AR	C	La Cerera	<i>Phoenix canariensis</i> date	harvesting of native plants	1180 ± 30	Beta-302327	770–950 cal CE	Morales et al. (2017)	10
AR	C	Dunas de Maspalomas	<i>Hordeum vulgare</i> seed	introduction of cultivars/agriculture	1200 ± 30	Beta-359513	720–890 cal CE	Morales et al. (2017)	10
AR	C	Guayadeque	<i>Canis familiaris</i> bone	introduction of domestic species	1340 ± 30	Beta-510720	645–715 cal CE	Velasco et al. (2019)	7
AR	C	La Cerera	<i>Triticum aestivum/durum</i> seed	introduction of cultivars/agriculture	1410 ± 30	Beta-302329	600–660 cal CE	Morales et al. (2017)	10
AR	C	Acusa	human tissue	human occurrence	1540 ± 30	Beta-510717	426–588 cal CE	Velasco et al. (2019)	7
AR	C	Guayadeque	human tissue	human occurrence	1550 ± 30	Beta-468991	424–572 cal CE	Velasco et al. (2019)	7
AR	C	Arguineguín?	human bone	human occurrence	1570 ± 30	Beta-391059	417–554 cal CE	Velasco et al. (2019)	7
PE	C	Laguna de Valleseco	bulk sediment	change in regional fire regime	1919 ± 24	UBA-16255	26–131 cal CE	de Nascimento et al. (2016)	11
PE	C	Laguna de Valleseco	bulk sediment	introduction of cultivars/agriculture (cereal pollen)	1919 ± 24	UBA-16255	26–131 cal CE	de Nascimento et al. (2016)	11
PE	C	Laguna de Valleseco	bulk sediment	change in local fire regime	2344 ± 26	UBA-16256	488–376 cal BCE	de Nascimento et al. (2016)	11
PE	C	Laguna de Valleseco	bulk sediment	change in vegetation	2344 ± 26	UBA-16256	488–376 cal BCE	de Nascimento et al. (2016)	11
AR	T	Arenas 1	<i>Rattus rattus</i> bone	introduction of alien commensal species	325 ± 30	KIA-40844	1479–1644 cal CE	Rando et al. (2014)	12
AR	T	Hoya Brunco	<i>Capra hircus</i> skin	introduction of domestic species/livestock	930 ± 110	M-1055	890–1280 cal CE	del Arco et al. (1997)	13
AR	T	Chinguaro	<i>Hordeum vulgare</i> seed	introduction of cultivars/agriculture	1260 ± 40	Beta-261243	660–880 cal CE	Morales et al. (2017)	10

(continued on next page)

Table 1 (continued)

Dep.	Isl.	Site	Sample	Proxy/Activity	Age (^{14}C yr BP)	Lab code	Calibrated ages 2σ range (cal years BCE/CE)	Reference	Ref.
AR	T	La Fortaleza	<i>Mus musculus</i> bone	introduction of alien commensal species	1365 ± 20	KIA-40847	641–679 cal CE	Rando et al. (2014)	12
AR	T	Capricho	human bone	human occurrence	1540 ± 40	Beta-368410	421–601 cal CE	Arnay-da-la-Rosa et al., 2017 in Fregel et al. (2019)	14
PE	T	La Laguna	bulk sediment	change in fire regime	2045 ± 30	POZ-13147	165 cal BCE – 24 cal CE	de Nascimento et al. (2009)	15
PE	T	La Laguna	bulk sediment	change in vegetation	2045 ± 30	POZ-13147	165 cal BCE – 24 cal CE	de Nascimento et al. (2009)	15
PA	T	Barranco Las Moraditas	<i>Canariomys bravoii</i> bone	last record of an extinct endemic species	2275 ± 25	KIA-36264	400–231 cal BCE	Rando et al. (2014)	12
PA	T	Arenas 3	<i>Gallotia goliath</i> bone	last record of an extinct endemic species	4895 ± 40	KIA-47429	3769–3636 cal BCE	Rando et al. (2014)	
PA	T	Cueva del Viento	<i>Carduelis aurelioii</i> bone	last record of an extinct endemic species	11460 ± 60	KIA-30992	11477–11257 cal BCE	Rando et al. (2010)	
AR	G	Alto del Garajonay	<i>Hordeum vulgare</i> seed	introduction of cultivars/agriculture	1130 ± 40	Beta-206015	790–1000 cal CE	Morales et al. (2017)	10
AR	G	El Pescante	human bone	human occurrence	1640 ± 40	Beta-232016	332–538 cal CE	Hernández-Marrero et al. (2016) in Fregel et al. (2019)	16
AR	G	El Pescante	human bone	human occurrence	1700 ± 40	Beta-232015	246–416 cal CE	Hernández-Marrero et al. (2016) in Fregel et al. (2019)	16
PE	G	Laguna Grande	bulk sediment	change in local fire regime	958 ± 23/3890 ± 26	UBA-18409/UBA-17219	1150 cal BCE (interpolated from age-depth model)	Nogué et al. (2013)	17
PE	G	Laguna Grande	bulk sediment	change in local fire regime	958 ± 23/3890 ± 26	UBA-18409/UBA-17219	150 cal CE (interpolated from age-depth model)	Nogué et al. (2013)	17
AR	P	Barranco de la Baranda	<i>Mus musculus</i> bone	first record of alien commensal species	1140 ± 25	KIA-36254	782–981 cal CE	Alcover et al. (2009)	3
AR	P	El Tendal	ovicaprid bone	introduction of domestic species/livestock	1530 ± 70	Ua-10225	400–660 cal CE	Soler et al., 2002	18
AR	P	El Tendal	<i>Hordeum vulgare</i> seed	introduction of cultivars/agriculture	1660 ± 40	Beta-206154	260–450 cal CE	Morales et al. (2017)	10
AR	H	Punta Azul	human bone	human occurrence	970 ± 30	Beta-382740	1016–1155 cal CE	Ordóñez et al., 2017 in Fregel et al. (2019)	19
AR	H	Hoyo de Los Muertos	human bone	human occurrence	1050 ± 60	CSIC-144	778–1155 cal CE	Martín de Guzmán, 1976 in Velasco et al. (2019)	20
AR	H	La Lajura	<i>Hordeum vulgare</i> seed	introduction of cultivars/agriculture	1530 ± 40	Beta-261244	420–610 cal CE	Morales et al. (2017)	10

stems), invertebrates and vertebrates. They are a major threat to birds living on predator-free islands through their consumption of eggs, chicks and occasionally adults (Nogales et al., 2006). The introduction of rats to the Canaries, and especially the black rat, is considered the principal cause of the extinction of numerous bird species (Illera et al., 2012), and the most probable cause of the extinction of the lava mouse (*Malpaisomys insularis*) in Fuerteventura and Lanzarote (Rando et al., 2011). However, it is not clear if the black rat coexisted with the giant endemic rats (López-Jurado and López-Martínez, 1991; Bocherens et al., 2006; Rando et al., 2014). Other studies show the present-day impact of the black rat on the vegetation, in particular in the laurel forest where they consume tree fruits and by competing with native fruit-eating birds disrupt the dispersal network altering the regeneration and ultimately the makeup of the forest (Delgado, 2002; Traveset et al., 2009). The Norwegian rat differs from the black rat as it is mainly associated with rural and urban settlements and is rarely encountered in well preserved natural environments where its impact is quite limited (Nogales et al., 2006).

The cat (*Felis catus*) has the greatest impact of all feral mammals at present. In contrast to dogs (*Canis familiaris*), which are incapable of self-maintaining wild populations, these felines have maintained wild populations since introduction, being present in all the zonal

ecosystems. Their diet depends for the most part on the ecosystem they occupy (Nogales and Medina, 2009), birds, reptiles, rabbits, rats, and mice making up their prey. While it is clear that they pose a risk to reptiles and endemic birds, they help control populations of exotic herbivores (rabbits, mice) and predators (rats) that are themselves a threat to the native flora and fauna. While dogs, and possibly cats, were introduced on various islands during the prehistoric period, it is not known what may have been their impact.

3.2. Introduced plants

Vegetables and cereals made up an important part of the Canarian aborigine diet. The cultivation and gathering of various species of plants, both introduced and native, has been attested in the archaeological sites by seeds or carbonized remains and documented in the historic record (Figs. 2 and 3, Table 1, Table S1). In agreement with the historic descriptions, the first Canarians used plants not only as food, but also for forage, fuel, tools, construction materials and for a number of chemical substances (Morales, 2003).

From the study of seeds in archaeological sites it can be concluded that agriculture was widely practiced among the Canarian aborigines, although the degree to which it was developed varied greatly between the islands, being much more extensive in

Gran Canaria than elsewhere while in the eastern islands there is scarcely any evidence for it (Morales et al., 2009, 2017). The first Canarians cultivated cereals, mostly barley (*Hordeum vulgare*) in all the central and western islands, and to a lesser extent wheat (*Triticum durum*), but barely on La Gomera and none on El Hierro. They also cultivated legumes, such as beans (*Vicia faba*), lentils (*Lens culinaris*) and peas (*Pisum sativum*) on La Palma, Tenerife and Gran Canaria, and figs (*Ficus carica*) were introduced to Gran Canaria. Gran Canaria is the only island in which all these seeds and fruits have been found and also is the only one with prehistoric granaries (Morales et al., 2009, 2014). In fact, the analysis of the prehistoric palaeodiet of the first inhabitants of Gran Canaria shows that vegetable products, in combination with sea food (shellfish and fish) were the everyday staples (Velasco, 2001; Arnay-de-la-Rosa et al., 2010). Considering the differences in importance of agriculture between islands and periods (Morales et al., 2017) the island most impacted by this activity was Gran Canaria. The first chronicles from this island (Cioranescu, 2004) describe valleys with cultivations including irrigation systems. For this to happen the forests and shrubs that made up the original vegetation must have been cleared, the soil worked and water sources and springs channelled. The initial effects of these activities resulted in a reduction of vegetation cover with subsequent loss of biodiversity and soil erosion. Alteration of the hydrological regime in some areas may have locally affected moisture-loving vegetation and freshwater invertebrates.

4. Exploitation of native species

Besides the introduction of agriculture and stock raising, the first Canarians also exploited the local resources through hunting, fishing and gathering (Table S1). There is a range of evidence as to their consumption of marine and terrestrial foods including activities such as shellfish gathering, coastal fishing, and the sporadic consumption of reptiles, birds and mammals. Middens in coastal areas show that the Canarian aborigines collected huge quantities of shellfish and fish (Rodríguez and Navarro, 1999; Navarro et al., 2001; Galván et al., 2005) these foods forming a substantial part of their diet as has been shown by paleodiet studies based on isotopic ratios and the elemental composition of their bone remains (Velasco, 1998; González-Reimers et al., 2001; Arnay-de-la-Rosa et al., 2009, 2010).

Among the most common species found are gastropods and marine bivalves, such as limpets (*Patella* spp.), sea snails (*Osilinus atratus*), rock snails (*Stramonita haemastoma*), periwinkles (*Littorina striata*), dove snails (*Columbella adansonii*), the Canarian abalone (*Haliotis tuberculata*) and the spiny oyster (*Spondylus senegalensis*). These molluscs may have also provided dyes and shells for ornaments. Remains of crabs, as well as sea urchins and fish such as the parrotfish (*Spurisoma cretense*), moray eels (*Muraena* spp.), grouper (*Epinephelus marginatus*), the seabream (*Diplodus sargus*), comb grouper (*Mycteropterus fusca*) and the barred hogfish (*Bodianus scrofa*) appear frequently in archaeological sites (Rodríguez, 1996). The abundance of these shell middens and the importance of marine sources in the Canarian diet are indicative of intense exploitation of these resources during the prehistoric period which, while not causing extinctions, must have contributed to decreases in populations and reduction in the size of some species. An example of the pressure placed on some of these species is the large limpet (*Patella candei candei*) that in the past was probably on all the islands but at present is only on Fuerteventura, and even here many of the original populations have disappeared (Weber and Hawkins, 2002; Navarro et al., 2005).

The presence of a few remains of the Mediterranean monk seal (*Monachus monachus*) in caves and shell middens indicates that the

first Canarians probably hunted this species (López et al., 1995). The extirpation of the monk seal from the Canaries occurred during the historic era (Cioranescu, 2004) and has been attributed to the European colonizers, although possibly the first settlers reduced its range until it was confined to the uninhabited islet of Lobos, to the north of Fuerteventura, an islet that the Castilians so named (*lobo de mar* is a word for monk seal in Spanish) because it was abundant there (López et al., 1995).

Canarian aborigines may have also hunted terrestrial vertebrates to complement their protein diet, favouring in this case species of a larger size. When the first humans arrived, the Canaries were populated by various species of giant lizards: on Tenerife *Gallotia goliath*, that perhaps also inhabited La Palma, and *G. intermedia*; on El Hierro *G. simonyi*; on La Gomera *G. bravoana*; and on Gran Canaria *G. stehlini* (Maca-Meyer et al., 2003; Cox et al., 2010; Mateo et al., 2011). The remains of these species appear in archaeological deposits mixed up with other faunal refuse from food consumed at the site (e.g. Alberto, 1998; López-Jurado et al., 1999; Martín et al., 1999; Hernández-Marrero et al., 2016), and occasionally, as in the case of *G. stehlini*, the bones show signs of human consumption (Martín et al., 1999).

Giant rats inhabited the central islands of the archipelago, *Canariomys tamarani* in Gran Canaria and *C. bravoi* in Tenerife. These rodents were 30 cm long and weighed about a kilogram (López-Martínez and López-Jurado, 1987; Michaux et al., 2012) and may have been hunted as terrestrial animals of this size were uncommon in the islands thus the rats should have been an attractive prey item. However, although giant rat bones have been found in archaeological deposits (López-Jurado and López-Martínez, 1991; Alberto, 1998; Galván et al., 1999), there is no direct evidence for human consumption. In spite of efforts to obtain new dates for the giant rat of Tenerife and revision of existing dates, it has not been possible to demonstrate that this species co-existed with humans. It is possible that the bones were pre-human and mixed with archaeological remains during occupation of the sites (Rando et al., 2014).

The early Canarians almost certainly hunted birds as broken bones with cuts and charring have been found in various archaeological sites, indicating human consumption. Some of the most common bones found in these sites belong to the common buzzard (*Buteo buteo*), Scopoli's shearwater (*Calonectris diomedea*), various pigeon species (*Columba* spp.), the crow (*Corvus corax*), the Canary Island quail (*Coturnix gomerae*), the kestrel (*Falco tinnunculus*) and the lava shearwater (*Puffinus olsoni*) (Alcover and Florit, 1989; Rando and Perera, 1994; Rando et al., 1996, 1997). However, birds were not a significant part of the early Canarian diet in comparison with marine animals and domestic mammals, whose remains are much more abundant in archaeological deposits (Alcover and Florit, 1989; Rando et al., 1997).

The first Canarians also exploited the local vegetable resources as is shown by seeds and charcoal found in archaeological sites. Among the seeds of native plants are found those of the Canarian palm (*Phoenix canariensis*), whose fruits (támaras) were consumed. Other trees whose fruits were commonly gathered are *Visnea mocanera* and *Pistacia atlantica*. Frequently found also are seeds of various woody legumes (*Adenocarpus* sp., *Chamaecytisus* sp., *Retama rhodorhizoides*, *Spartocytisus* sp.), that may have been used for forage; plants with medicinal or aromatic properties such as *Neochamaelea pulverulenta*; and tree species such as *Juniperus turbinata*, *Lauraceae* spp., and *Pinus canariensis*, that were probably collected for firewood. Also common are the seeds of ruderal herbaceous plants such as *Fumaria* sp., *Galium aparine*, *Silene gallica*, and *Rumex* sp., that may have been used as forage or stock bedding or simply accidentally included with other plants of interest (Morales, 2003, 2009; Morales et al., 2007, 2011, 2014, 2017).

Charcoal macroremains found in numerous archaeological sites throughout the archipelago show that the first Canarians used trees and shrubs for firewood (Machado, 2007). About 24 tree species and 26 shrub species have been identified from hearths in settlement sites. Among the plants most commonly collected are tree species of the laurel forest such as *Arbutus canariensis*, *Erica arborea*, *Heberdenia excelsa*, *Ilex canariensis*, *Laurus novocanariensis*, *Morella faya*, *Persea indica*, *Picconia excelsa*, *Salix canariensis*, and *Visnea mocanera*. Among the species belonging to the thermophilous woodlands, charcoal of *Juniperus turbinata*, *Olea cerasiformis* and *Phoenix canariensis* have been found. Also frequent is charcoal of woody species of the pine forests especially the Canarian pine (*Pinus canariensis*), as well as shrubs such as *Adenocarpus* spp. or *Cistus monspeliensis*. Finally, charcoal of species of the secondary shrublands also occur such as *Euphorbia* spp., *Hypericum* spp., *Rumex lunaria*, and *Pteridium aquilinum*.

The species identified from charcoal in archaeological sites can be used to infer the surrounding vegetation. Changes in the species composition of charcoal have been interpreted as a reduction or exhaustion of local species through over-exploitation, they being replaced as a source of wood by other more distant species (Machado, 2007). Some examples come from sites in the mid elevations of La Palma and Tenerife where there is a progressive decline in charcoal of thermophilous woodland species, the closest vegetation to the sites, and an increase in charcoal from the laurel forest species (Machado et al., 1997; Machado and Ourcival, 1998; Machado, 2007). In coastal sites in Gran Canaria, charcoal is found of species from communities growing at higher elevations such as *Arbutus canariensis*, *Erica* sp., *Olea cerasiformis*, *Picconia excelsa*, *Pinus canariensis*, *Rhamnus glandulosa*, *Salix canariensis*, and *Visnea mocanera* (Machado, 2007). Something similar happened on El Hierro, where charcoal of juniper and pine, as well as laurel forest species are found in settlements of the lower zones (Machado, 2007). Recent studies from Gran Canaria show the different uses made of each species, and how aborigines preferentially exploited Canarian pine (*Pinus canariensis*) for the construction of granaries, as well as in funerary and domestic contexts. Secondary species like fig (*Ficus carica*) and laurel (*Laurus novocanariensis*) co-dominate with *Pinus canariensis* depending on the site and were used in barn construction, while dragon tree (*Dracaena draco*) was more common at burial sites. Dragon tree wood may have had both a ritual meaning and a clear practical purpose as it is very light, so useful for carrying a corpse to caves difficult of access (Vidal-Matutano, 2019).

The complete replacement of some species at some sites suggests that they may have disappeared at local to regional scales. This is the case for the Canarian pine and the Canarian juniper (*Juniperus cedrus*), that made up the most common charcoal until 650–550 years BP at Las Cañadas (the summit of Tenerife) but after this date was replaced by local shrubs as the principal source of firewood (Machado and Galván, 1998). However, in a second locality at Las Cañadas (Chasogo) dated around the 500–400 years BP, a recent charcoal study of temporary occupation sites indicates an abundance of *Pinus canariensis* together with woody legumes, which suggests pine forests were close at hand (Vidal-Matutano et al., 2019). While in Fuerteventura the charcoal record shows that thermophilous woodlands underwent a decline from about 1000 years BP, it also indicates the extirpation of trees such as *Arbutus canariensis*, *Persea indica* and *Pinus canariensis* from the island (Machado, 2007).

5. Extinct species

The Canary Islands have experienced a number of extinctions and also of extirpations of animals and plants, which are attributed

to humans. Among the vertebrates, birds have the largest number of documented extinctions, followed by mammals and reptiles, while the impact of the first colonists on invertebrates is virtually unknown (Figs. 2 and 3, Table 1).

There is only one example of an extirpation in the Canarian invertebrate fauna. The large limpet (*Patella candei candei*) was gathered intensively leading to its disappearance from all the islands (Weber and Hawkins, 2002; Navarro et al., 2005) with the exception of some populations remaining on Fuerteventura. Although the exploitation of this mollusc began during the prehistoric period, it continued through the historical period resulting in the present-day situation where the species is listed as in danger of extinction in the Spanish Threatened Species List (<http://www.mapama.gob.es/>) and appears as a vulnerable species in the Canarian Protected Species List (<http://www.gobiernodecanarias.org/>). It is still present on the Portuguese archipelago of Selvagens, some 150 km north to Tenerife.

According to fossil records and molecular analysis, the endemic reptile species, *Gallotia goliath*, the giant lizard of Tenerife, is the only extinct species of reptile (Maca-Meyer et al., 2003). This species was present on Tenerife and perhaps also on La Palma (see Mateo et al., 2001), La Gomera and El Hierro (Maca-Meyer et al., 2003). Some authors argue that on La Gomera the fossil remains could belong to a second extinct species, *G. bravoana*, distinct from the recently discovered giant lizard of La Gomera, *G. gomerana* (Martín and Rando, 2006). If this is so, it is a second case of extinction in the genus *Gallotia*. However, recent molecular studies of fossil remains of the giant lizard of La Gomera suggests that *G. bravoana* and *G. gomerana* are actually the same species (Mateo et al., 2011). Thus, there has been no extinction but a case of a 'Lazarus species', that is a species considered extinct has been rediscovered (Nogales et al., 2001). An extinct giant lizard was also described for La Palma from subfossil remains, and proposed as a subspecies of El Hierro giant lizard *G. simonyi avarita* (Mateo et al., 2001), which would represent a subspecies extinction. Finally, a subspecies of El Hierro giant lizard, *G. simonyi simonyi* may have disappeared from the population living on offshore rocks (Roques de Salmor), while the second subspecies *G. simonyi machadoi* survives on the island today (Maca-Meyer et al., 2003). In any case, the taxonomic status of the species of the genus *Gallotia*, extinct as well as extant, needs revision. The extinction of *G. goliath* is attributed to humans, but apart from occasional consumption, we do not know what effect the first Canarians had on these species. The arrival of Europeans probably had a much greater effect with the introduction of its main predator, the cat (Medina and Nogales, 2009), and to a minor extent, dogs and rats, as well as degradation of its habitat (Rando, 2003).

Three of the species of giant lizard that survive in the Canaries, *G. simonyi*, *G. bravoana* and *G. intermedia*, suffered an impact similar to *G. goliath* and today are found in small populations in inaccessible areas. The reduction of their distribution and population size was such that the three species were considered extinct and have only been rediscovered and described recently (Böhme and Bings, 1975; Hernández et al., 2000; Nogales et al., 2001). The three species are considered at risk of extinction in the Spanish Threatened Species List (<http://www.mapama.gob.es/>), while in the Canarian Protected Species List *G. intermedia* and *G. simonyi* are listed as vulnerable species, and *G. bravoana* as a species at risk of extinction (<http://www.gobiernodecanarias.org/>). Their populations have suffered a loss of genetic diversity which will be addressed through recovery plans although there have only been studies on *G. bravoana* (Gonzalez et al., 2014). In the case of *G. bravoana*, recent molecular studies suggest that the loss of genetic diversity has occurred over a lengthy period, so the influence of natural factors such as climate change in the reduction of

distribution and population size cannot be ruled out (Gonzalez et al., 2014). Finally, there is no evidence for direct consumption of these species by the early Canarians, and we may assume that although they may have suffered a certain amount of reduction initially, their decline was due to the arrival of the Europeans.

As well as a reduction in population size, a diminution in the body sizes of the lizard community on each island has been noted. This size reduction results from differential pressure on the largest individuals within the same species. For example, *G. stehlini*, *G. simonyi* and *G. bravoana* at present have a smaller size than their respective fossil remains (Barahona et al., 2000; Mateo et al., 2011; Pérez-Méndez et al., 2015). Another process that leads to a reduction in size of present day lizards is defaunation that is, the loss of animals, in this case those of the larger sizes, through extinction or reduction of their populations so that the most abundant populations come to be those of medium or small size (Pérez-Méndez et al., 2015). Reduction in size has in its turn consequences for the vegetation communities because the Canarian lizards are frugivores and seed dispersers for numerous native plants. A well studied example is the dispersal of *Neochamaelea pulverulenta*, an endemic Canarian plant, present in Gran Canaria, Tenerife and La Gomera, that depends exclusively on lizards for effective dispersal of its seeds. After defaunation and reduction in size of its dispersers, the dispersal of seeds and recruitment of seedlings is less effective, thus diminishing population genetic diversity and connectivity for this plant species (Pérez-Méndez et al., 2015, 2016, 2018).

Birds without doubt have experienced the greatest number of extinctions in the Canary Islands, with at least 12 species extinct or extirpated, 7 of them endemic (Illera et al., 2012). Some of these extinctions are the result of the impact that apparently began with the arrival of the first Canarians and continued with the arrival of the Europeans. In spite of the evidence for consumption by humans of some species (Rando and Perera, 1994), the main causes of the extinctions can be attributed to other indirect impacts of human activities, mainly the introduction of exotic species, new parasites and diseases and the destruction of habitat. Certain characteristics such as ground nesting, reduced flying ability and large size are associated with extinction of some Canarian birds (Illera et al., 2016).

The lava shearwater (*Puffinus olsoni*) was hunted and eaten by humans (Alcover and Florit, 1989; Rando and Perera, 1994). Given the estimated date of the extinction of this bird (700–500 years cal BP) it must have co-existed with the first Canarians for 1000 years during which time they may have decimated the species through hunting, although the house mouse as an occasional predator of eggs and chicks may also have had some effect (Rando and Alcover, 2007). However, the date of its extinction is close to the time of the arrival of the Europeans which suggests that introduction of rats and cats during the conquest is the most probable cause of extinction. Factors such as their relatively smaller size and nesting behaviour (i.e. in rough lava fields and inaccessible caves) may have contributed to its survival until European arrival (Rando and Alcover, 2007).

The extinction of the second species of shearwater, the dune shearwater (*Puffinus holeae*), happened much earlier (the youngest remains are dated at 3100–2700 years cal BP), and may have coincided with the initial stages of human settlement of the eastern islands (Rando and Alcover, 2010). Although no bones have been found with indications of human consumption, the dune shearwater was a prime target because of its size, (larger than that of the lava shearwater) and ease of capture as it nested in accessible dunes. Moreover, both species were philopatric, that is, they remained close to the area where they hatched or returned to that location to breed, which made the colonies more vulnerable to new predators. The absence of dune shearwater remains in

archaeological sites suggests that extinction during the initial stages of settlement was rapid leaving virtually no trace (Rando and Alcover, 2010).

The extinction of the Canary Island quail (*Coturnix gomerae*) is also linked to human impact as bones of this species have been found with signs of human consumption. As with the shearwaters, it was an easy prey due to its reduced flying ability and its terrestrial habits (Jaume et al., 1993). However, the date of extinction is not known.

Three passerine species, *Emberiza alcoveri* (Rando et al., 1999), *Carduelis triasi* (Alcover and Florit, 1987) and *C. aurelio* (Rando et al., 2010), became extinct in the Canaries before the arrival of Europeans. *E. alcoveri* was wingless and flightless while *C. triasi* and *C. aurelio* had limited flying ability making them vulnerable to predators. This suggests that the three species succumbed shortly after the arrival of humans. The single date available for *C. aurelio* shows it was present in the islands 13,400 years ago (Rando et al., 2010) but we do not know the date or cause of extinction.

For the remainder of the extinct or extirpated birds, the timing and cause of extinction is ambiguous with the exception of those in the historic record (Illera et al., 2012). The last extinction of a bird in the Canaries was that of Canary Island oystercatcher (*Haematopus meadewaldoi*), a species of eastern islands and islets. While a very recent extinction, probably at the beginning of the 20th century, one of the principal causes of its decline was the over-exploitation of the large limpet (an essential part of its diet) which began during the prehistoric period (Hockey, 1987).

Of the few native mammal species occurring in the Canaries before the arrival of humans (seven bats, two rats, a mouse, a shrew and a seal) three have become extinct and another three have been extirpated. The three extinct mammal species in the Canaries are rodents: the giant rats of Gran Canaria (*Canariomys tamarani*) and Tenerife (*C. bravoi*), and the lava mouse (*Malpaisomys insularis*) (López-Jurado and López-Martínez, 1991; Rando et al., 2011, 2014).

The extinction of the giant rats has been attributed to the impact of the first human settlers, although as we mentioned in the discussion of the exploitation of native species there is no direct evidence for their consumption. Neither can it be confirmed that these species co-existed with humans, at least in the case of the better studied giant rat of Tenerife (Rando et al., 2014). However, its most recent dates (c. 2400–2200 years cal BP) make it more probable that it became extinct during the earliest stage of human settlement rather than during the historic period, suggesting that it vanished rapidly leaving almost no trace in the palaeontological or archaeological record. Among the most probable causes of its extinction are the introduction of species by the first settlers, the house mouse (*Mus musculus*) having the greatest impact due to its rapid expansion and high population density leading to hyperpredation, introduction of new parasites and diseases, or competition for resources. We cannot discount either the role of other introduced species such as goats, sheep, and pigs in degrading its habitat or sporadic hunting by humans for food. We have less information on the Gran Canaria giant rat and it has been suggested that its extinction was a consequence of hunting by humans or even because it was preyed on by dogs introduced by the first settlers (López-Jurado and López-Martínez, 1991).

The extinction of the lava mouse (*Malpaisomys insularis*) has been an asynchronous process driven by a series of local extinctions and extirpations of isolated populations as a result of distinctive causes (Rando et al., 2011). Before the arrival of humans, the lava mouse inhabited Lanzarote and Fuerteventura and at least two islets, La Graciosa and Lobos. On the larger islands it was present until at least 700–550 years cal BP on Fuerteventura, and until 2120–1950 years cal BP on Lanzarote. In spite of the difference in the possible date of extinction of the lava mouse between these

islands the cause was probably the same, the introduction of the black rat (*Rattus rattus*) which occurred at least six centuries apart, being earlier in Lanzarote. Both introductions occurred when the islands were already populated and therefore the extinction of the lava mouse is not directly attributable to the Canarian aborigines. However, in the case of the islets, the extirpation of the lava mouse probably occurred earlier. The most recent date for the bones of the lava mouse from the islets is quite old, some 6650–6500 years cal BP on La Graciosa, and therefore natural causes cannot be ruled out. An alternative hypothesis is that the lava mouse which lived on the islets suffered from the effects of the introduction of the house mouse which occurred in prehistoric times, some 1290 years cal BP. In this case, in a situation where the carrying capacity is limited by the size of the islets, the house mouse could have acted as an invasive species with a higher reproductive rate and a greater resilience to predation in contrast to the lava mouse which having small populations and a low reproductive rate, was more vulnerable to hyper-predation by barn owls (Rando et al., 2011).

Of the native mammal species, two extirpations may have been initiated during prehistoric times. The Mediterranean monk seal (*Monachus monachus*), whose extirpation from the Canaries finally happened during historical times (López et al., 1995), was possibly hunted also by the first settlers. The Canary Island shrew (*Crocidura canariensis*), whose extirpation from La Graciosa and Alegranza islets seems to have followed the introduction of the house mouse about 1290 years ago, was probably eliminated through hyperpredation as described for the lava mouse, although in this case it did not become extinct because it survives on Lanzarote and Fuerteventura and the islets of Lobos and Montaña Clara (Rando et al., 2011). The third case of mammal extirpation is recent. The bat Kuhl's pipistrelle (*Pipistrellus kuhlii*) was probably extirpated from Lanzarote by use of pesticides and elimination of its natural habitat (Trujillo and Barone, 1991).

In contrast to the animal kingdom there is little evidence for the impact that the first settlers may had on Canarian plants and only two possible cases of extinction have been suggested. Pollen from the Fagaceae family belonging to the genera *Carpinus* and *Quercus*, is abundant in the record from La Laguna, showing that these plants were present from at least 4700 years cal BP (de Nascimento et al., 2009). From about 2000 years ago, the pollen signal of both genera progressively reduces at the same time that there was an abrupt increase in fire events on the island, suggesting that the first settlers used fire from the beginning to open up the vegetation cover. This transformation of the forest resulted in the disappearance of these trees although we do not know what species they were, which communities did they belonged to and if they were more widespread in the past. Charcoal from *Arbutus canariensis*, *Persea indica*, and *Pinus canariensis*, tree species which no longer occur naturally in Fuerteventura, suggest that extirpations have occurred in the Canaries (Machado, 2007). With the exception of these records there are no other examples of plant species extinctions attributable to the first Canarians, but we can infer that the impact of fire and the introduction of herbivores had negative consequences for the most vulnerable plant species which lacked defences against herbivores or fire-adaptive traits.

Palaeoecological, palaeontological, and archaeological research is therefore beginning to show that the magnitude of the aboriginal impact on the pristine environments of the Canary Islands was similar to the impacts arising from other first settlers of oceanic archipelagos, in particular those of the well studied Mediterranean (e.g. Alcover, 2008; Leppard and Birch, 2016), Caribbean (e.g. Higuera-Gundy et al., 1999; Siegel et al., 2015), Melanesian and Polynesian (e.g. Kirch, 2007; Prebble and Wilmshurst, 2009) prehistoric societies.

6. Contribution of palaeoenvironmental data to establishing timing of the Canary Island settlement

Dating the first arrival of humans on islands is challenging when archaeological evidence is scarce or based on dating of unreliable material (e.g. ambiguous traces of human activities, radiocarbon dating of long-lived organisms), providing poorly constrained chronologies that may differ by several centuries depending on the source (e.g. Siegel et al., 2015; Mitchell, 2019). There have been efforts to apply criteria based on chronological hygiene (i.e. by discarding material not rigorously treated for contamination or with high in-built age, rejecting samples collected from disturbed layers, and accounting for lab errors) to reconstruct robust chronologies on islands (Alcover, 2008; Wilmshurst et al., 2008, 2011).

In the Canaries, the colonization chronology is still unresolved. A date around the second half of the first millennium BCE has been traditionally used as a consensus timing for the settlement of the archipelago. However, recent reviews of radiocarbon dates and newly dated material have shown that the oldest dates for Canarian colonization are unreliable; when these are excluded the prehistoric period is shortened by several centuries (Atoche, 2008; Rando et al., 2014; Velasco, 2014; Fregel et al., 2019; Velasco et al., 2019). In the latest review, including a total of 434 radiocarbon dates, by applying chronological hygiene criteria, Velasco et al. (2019), proposed a permanent settlement of the islands after the second and third century CE.

Palaeoecological data can be an additional and reliable line of evidence to identify human colonization events on islands, especially during early colonization when groups of settlers are small and leave few archaeological traces (McGlone and Wilmshurst, 1999; Athens, 2009; Prebble and Wilmshurst, 2009; Siegel et al., 2015). Palaeoenvironmental and palaeontological data regarding habitat modification, introduction of domestic and commensal species and extinction or extirpations of the native ones, combined with archaeological evidence, might help framing the timing for the archipelago colonization.

According to the dates reviewed by Velasco et al. (2019), the earliest evidence of human presence based on radiocarbon dated human remains (bone, teeth and tissues), comes from the island of La Gomera (246–416 cal CE), followed by Gran Canaria (417–554 cal CE), Tenerife (421–601 cal CE), Lanzarote (671–770 cal CE), El Hierro (778–1155 cal CE), and Fuerteventura (993–1155 cal CE), while there are no dated human remains for La Palma (see Fig. 2, Table 1). Introduction of domestic species provides evidence for earlier human occurrence. For instance, radiocarbon dates from cereal (barley) seeds provide the earliest dates for La Palma (260–450 cal CE) and El Hierro (420–610 cal CE). Bones of ovicaprids predate by several centuries the dates of human occurrence for the island of Lanzarote (361 cal BCE – 332 cal CE) and provide an early date for La Palma (400–660 cal CE). The introduction of commensal species is also a reliable indicator of human colonization. Based on both palaeontological and archaeological records the remains of introduced rodents provide dates that also precede human dates by several centuries for the islands of Lanzarote, where the house mouse was first recorded between 128 and 313 cal CE, and the black rat between 580 and 650 cal CE, and Fuerteventura, with a first record of the house mouse between 565 and 669 cal CE.

Evidence from the palaeoecological record based on habitat and fire regime modifications provides earlier dates yet again for the detection of human occurrence (see Fig. 2, Table 1). Changes in forest composition along with shifts in fire regimes, occur between 488 and 376 cal BCE in Gran Canaria and between 165 cal BCE and 24 cal CE in Tenerife, preceding by almost 900 and 400 years respectively the earliest archaeological evidence (human bones) for

Gran Canaria (417–554 cal CE), and Tenerife (421–601 cal CE). In Gran Canaria, pollen from cereals was also detected between 26 and 131 cal CE, coinciding with shifts in the fire regime at regional scale, some 400 years earlier than the oldest human date found for the island. In La Gomera, two shifts in fire regime at local scale were detected at 1150 cal BCE and 150 cal CE, the most recent is about 200 years older than the earliest archaeological evidence of human presence on the island (246–416 cal CE).

Therefore, there are significant differences between the timing on human occurrence based on palaeoecological and archaeological evidence. These discrepancies may be explained by the bulk sediment palaeoenvironmental samples containing old, inwashed carbon, while the strict criteria of chronological hygiene recently applied to archaeological data, where any date coming from charcoal or wood has been discarded, may have resulted in too severe pruning of the chronology. Such age differences are less marked or non-existent when dates retrieved from charcoal and wood found at archaeological sites are considered. A wood sample from Cueva del Rey in Gran Canaria dated between 245 and 537 cal CE (Velasco et al., 2019), is closer in time (although still a few centuries later) to dated evidence for human activity (deforestation, increase of fire events and cultivation of cereals) in the palaeoecological record in Laguna de Valleseco. In Tenerife, the oldest dates from archaeological sites based on charcoal (740–429 cal BCE) and wood (390–60 cal BCE) (del Arco et al., 1997) suggest an early presence of humans before the initiation of changes in forest composition and fire regime detected at La Laguna at the beginning of the CE.

These uncertainties could be partly solved by the identification of short-lived species from dated wood and charcoal remains. However, obtaining identifiable plant remains from the sediments used for palaeoenvironmental reconstructions is extremely difficult considering the low organic content and lack of macrofossils that characterizes this type of sediments in the Canaries.

The latest records of extinct species are in general asynchronous with archaeological evidence of human settlement in the islands (Fig. 2, Table 1). In Tenerife, where remains of three extinct species have been radiocarbon dated, several millennia separate the ages of the most modern remains of the slender-billed greenfinch (*Carduelis aurelio*), 11477–11257 cal BCE, and the Tenerife giant lizard (*Gallotia goliath*), 3769–3636 c BCE, from the oldest archaeological remains (421–601 cal CE). The last record of the giant rat (*Canariomys bravoi*) (400–231 cal BCE) is at least 600 years older than dated human occurrence. In Fuerteventura, the two extinct shearwaters have been dated, the dune shearwater (*Puffinus holeae*) showing an early last occurrence, 1159–790 cal BCE, that predates by more than one millennium the earliest evidence of settlement based on the occurrence of house mouse (565–669 cal CE). The last record for the lava shearwater (*Puffinus olsoni*) is much more recent (1270–1475 cal CE) and probably concurrent with the arrival of Europeans on the island. Similarly, the extinct lava mouse (*Malpaisomys insularis*) from the eastern islands has a recent last record in Fuerteventura (1271–1394 cal CE) and an earlier last record in Lanzarote (174–4 cal BCE), the latter coinciding with evidence of initial prehistoric settlement of the island based on ovicaprid bones (361 cal BCE – 332 cal CE). Despite the difficulty of linking the extinction of these species with prehistoric settlement by dating alone, palaeontologists maintain that is highly likely that these species were driven to extinction by direct or indirect human influences during the prehistoric period (Rando and Alcover, 2010; Illera et al., 2012; Rando et al., 2014).

From the summary of radiocarbon dates shown in Fig. 2, it is evident that the palaeontological and palaeoecological records provide evidence of humans in the archipelago several centuries and even millennia before the earliest dates from the archaeological sites. As recognised elsewhere, the time elapsed between early

signs of human impact as detected in the palaeoecological record and the identification of human presence by archaeological materials may differ by several centuries (Athens, 2009; Siegel et al., 2015).

If an analysis is made of the earliest archaeological evidence of undisputable human presence in the Canaries, that is ovicaprid bone dates from Lanzarote (El Bebedero, 361 cal BCE – 332 cal CE) and human bone dates from La Gomera (El Pescante, 246–416 cal CE), a striking pattern of colonization emerges. The sequence suggests a colonization from Lanzarote, in the east, to La Gomera, in the centre-west, skirting the larger, higher islands of Gran Canaria and Tenerife that offered more resources than the smaller islands. Moreover, Fuerteventura, which is the closest to the African continent would also have been bypassed. The three skipped islands are visible from either Lanzarote or La Gomera but, according to the archaeological record, those islands were colonized some two to five centuries later (Fig. 2, Table 1). The earlier dates provided by the palaeoecological and palaeontological records, with abundant indications of habitat transformation and biotic impacts, may give us a hint of an earlier colonization of the major and central islands, closer in time to the settlement of Lanzarote.

An important limitation in the application of palaeoecological studies to the colonization chronology of the Canaries is the few studied sites and the scarce data available from them. The palaeontological record is also limited by the few remains that have been dated. Hopefully, more palaeontological and palaeoecological studies and more archaeological excavation on those islands with few dated records (i.e. La Palma, El Hierro), will improve the chronology and clarify the pattern of human settlement of the Canary Islands and its environmental consequences.

What seems to be clear is that a series of environmental changes, interpreted from independent lines of evidence (animal extinctions, changes in vegetation composition, forest clearance, introduction of domestic animals and cultivars, and modification of the fire regime), began a few centuries before or around the beginning of the CE and continuing through the prehistoric period.

7. Conclusions

The Canarian first settlers found on their arrival pristine environments characterized by distinctive ecosystems and endemic species that had evolved in the absence of humans over more than 20 My. In order to survive, the settlers cleared the original densely forested ecosystems by fire and felling leading to enhanced erosion rates and charcoal depositions in sediments. By modifying the habitat they, and their domestic and commensal animal species, extinguished, extirpated or reduced population and/or body sizes of several endemic species.

A number of animal species have disappeared; at the very least a giant lizard, two giant rats, a mouse and several bird species. Predation or harvesting by humans or introduced mammals as well as habitat alteration appear to be the main causes. Plants are not well represented in the Canarian fossil record and, although we know oak and hornbeam were eliminated on Tenerife, it is highly likely that more plant species were driven to extinction through fire, grazing and clearance. If so, this raises the possibility that a number of terrestrial invertebrates were lost as well.

Some decades ago, it was widely assumed that the prehistoric Canarians lived in harmony with their environment and significant ecological impacts began with the Norman-Castilian conquest. Recent research has shown that the early Canarians, just like other societies that colonized oceanic islands, had substantial and damaging impacts on their environments. We expect that future findings and the application of novel methods in palaeoecology will consolidate this new paradigm.

Credit author statement

Lea de Nascimento: conceptualization, investigation, writing - original draft, writing - review & editing, visualization. Sandra Nogué: investigation, writing - review & editing. Agustín Narango-Cigala: investigation, writing - review & editing. Constantino Criado: investigation, writing - review & editing, visualization. Matt McGlone: writing - original draft, writing - review & editing. Enrique Fernández-Palacios: investigation, writing - review & editing. José María Fernández-Palacios: conceptualization, investigation, writing - original draft, writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

- Alberto, V., 1998. Los otros animales. Consumo de *Gallotia goliath* y *Canariomys bravoi* en la prehistoria de Tenerife. *El Mus. Canar.* 53, 59–86.
- Alcover, J.A., Florit, X., 1987. Una nueva especie de *Carduelis* (Fringillidae) de La Palma. *Viera* 17, 75–86.
- Alcover, J.A., Florit, X., 1989. Els ocells del jaciment arqueològic de La Aldea, Gran Canària. *Butll. Inst. Catalana Historia Nat.* 56, 47–55.
- Alcover, J.A., 2008. The first Mallorcans: prehistoric colonization in the Western Mediterranean. *J. World PreHistory* 21, 19–84.
- Alcover, J.A., Rando, J.C., García-Talavera, F., Hutterer, R., Michaux, J., Trias, M., Navarro, J.F., 2009. A reappraisal of the stratigraphy of Cueva del Llano (Fuerteventura) and the chronology of the introduction of the house mouse (*Mus musculus*) into the Canary Islands. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 277, 184–190.
- Alberto, V., Navarro, J.F., Castellano, P., 2015. Los registros faunicos de las aras de sacrificio del Alto de Garajonay (La Gomera, Islas Canarias). *Zephyrus* LXXVI, 159–179.
- Arnay-de-la-Rosa, M., Gámez-Mendoza, A., Navarro-Mederos, J.F., Hernández-Marrero, J.C., Freig, R., Yanes, Y., Galindo-Martín, L., Romanek, C.S., González-Reimers, E., 2009. Dietary patterns during the early prehispanic settlement in La Gomera (Canary Islands). *J. Archaeol. Sci.* 36, 1972–1981.
- Arnay-de-la-Rosa, M., González-Reimers, E., Yanes, Y., Velasco-Vázquez, J., Romanek, C.S., Noakes, J.E., 2010. Paleodietary analysis of the prehistoric population of the Canary Islands inferred from stable isotopes (carbon, nitrogen and hydrogen) in bone collagen. *J. Archaeol. Sci.* 37, 1490–1501.
- Arnay-de-la-Rosa, M., González-Reimers, E., Yanes, Y., Romanek, C.S., Noakes, J.E., Galindo-Martín, L., 2011. Paleonutritional and paleodietary survey on prehistoric humans from Las Cañadas del Teide (Tenerife, Canary Islands) based on chemical and histological analysis of bone. *J. Archaeol. Sci.* 38, 885–895.
- Arnay-de-la-Rosa, M., González, E., Navarro, J.F., Criado, C., Clavijo, M.A., García, C., Marrero, E., Pou, S., 2017. Estudios sobre el patrimonio arqueológico del Parque Nacional del Teide. Proyectos de investigación en parques nacionales. In: Amengual, P. (Ed.), *Naturaleza y Parques Nacionales. Serie Investigación en la Red: 2012–2015*. Organismo Autónomo Parques Nacionales, Madrid, pp. 107–129.
- Athens, J.S., Ward, J.V., 1993. Environmental change and prehistoric Polynesian settlement in Hawai'i. *Asian Perspect.* 32, 205–223.
- Athens, J.S., 2009. *Rattus exulans* and the catastrophic disappearance of Hawai'i's native lowland forest. *Biol. Invasions* 11, 1489–1501.
- Atoche, P., 2003. Fenómenos de intensificación económica y degradación medioambiental en la protohistoria canaria. *Zephyrus* 56, 183–206.
- Atoche, P., 2008. Las culturas protohistóricas canarias en el contexto del desarrollo cultural mediterráneo: propuesta de fasificación. In: González, R., López, F., Peña, V. (Eds.), *Los Fenicios Y El Atlántico. Centro de Estudios Fenicios y Púnicos*, Madrid, pp. 317–344.
- Atoche, P., 2009. Estratigrafías, cronologías absolutas y periodización cultural de la protohistoria de Lanzarote. *Zephyrus* 63, 105–134.
- Atoche, P., Ramírez, M.A., 2011. Nuevas dataciones radiocarbónicas para la protohistoria canaria: el yacimiento de Buenavista (Lanzarote). *Anu. Estud. Atl.* 57, 139–169.
- Atoche, P., Ramírez, M.A., 2017. C¹⁴ references and cultural sequence in the Protohistory of Lanzarote (Canary Islands). In: Barceló, J.A., Bogdanovic, I., Morell, B. (Eds.), *Actas del Congreso de Cronometrías para la Historia de la Península Ibérica (IberCrono 2017)*. CEUR-WS, Barcelona, pp. 272–285.
- Barahona, F., Evans, S.E., Mateo, J.A., García-Márquez, M., López-Jurado, L.F., 2000. Endemism, gigantism and extinction in island lizards: the genus *Gallotia* on the Canary Islands. *J. Zool.* 250, 373–388.
- Bocherens, H., Michaux, J., García Talavera, F., Van der Plicht, J., 2006. Extinction of endemic vertebrates on islands: the case of the giant rat *Canariomys bravoi* (Mammalia, Rodentia) on Tenerife (Canary Islands, Spain). *Comptes Rendus Palevol* 5, 885–891.
- Böhme, W., Bings, W., 1975. Zur frage des Überlebens von *Lacerta s. simonyi* Steindachner (Sauria: Lacertidae). *Salamandra* 11, 39–46.
- Braje, T.J., Thomas, P.L., Fitzpatrick, S.M., Erlandson, J.M., 2017. Archaeology, historical ecology and anthropogenic island ecosystems. *Environ. Conserv.* 44, 286–297.
- Burney, D.A., 1997. Tropical islands as paleoecological laboratories: gauging the consequences of human arrival. *Hum. Ecol.* 25, 437–457.
- Burney, D.A., James, H.F., Burney, L.P., Olson, S.L., Kikuchi, W., Wagner, W.L., Burney, M., McCloskey, D., Kikuchi, D., Grady, F.V., Gage, R., Nishek, R., 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecol. Monogr.* 71, 615–641.
- Cioranescu, A., 2004. Crónicas francesas de la conquista de Canarias. *Le Canarien. Ediciones Idea, Cabildo Insular de Tenerife, Santa Cruz de Tenerife.*
- Cox, S.C., Carranza, S., Brown, R.P., 2010. Divergence times and colonization of the Canary Islands by *Gallotia* lizards. *Mol. Phylogenet. Evol.* 56, 747–757.
- Criado, C., 2002. Breve e incompleta historia del antiguo lago de la ciudad de San Cristóbal de La Laguna. *Concejalía de Cultura y Patrimonio Histórico Artístico, San Cristóbal de La Laguna.*
- Criado, C., Hansen, A., 2002. Sobre la posibilidad de una morfodinámica inducida por la población prehistórica en la isla de Gran Canaria. *Tábora* 11, 87–94.
- Criado, C., Atoche, P., 2003. Estudio geoarqueológico del yacimiento de El Bebedero (siglos I a.C. a XIV d.C., Lanzarote, Islas Canarias). *Cuaternario Geomorfol.* 17, 91–104.
- Criado, C., Atoche, P., 2004. ¿Influyó la ganadería de los Mahos en el deterioro paleoambiental de la isla de Lanzarote? *Tenique* 6, 137–157.
- del Arco, M.C., del Arco, M.M., Atiénzar, E., Atoche, P., Martín, M., Rodríguez, C., Rosario, C., 1997. Dataciones absolutas en la prehistoria de Tenerife. In: Atoche, P., Millares, A., Lobo, M. (Eds.), *Homenaje a Celso Martín de Guzmán. Universidad de Las Palmas de Gran Canaria, Las Palmas de Gran Canaria*, pp. 65–77.
- del Arco, M.J., González-González, V., Garzón-Machado, V., Pizarro-Hernández, B., 2010. Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodivers. Conserv.* 19, 3089–3140.
- de Nascimento, L., Willis, K.J., Fernández-Palacios, J.M., Criado, C., Whittaker, R.J., 2009. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *J. Biogeogr.* 36, 499–514.
- de Nascimento, L., Nogué, S., Criado, C., Ravazzi, C., Whittaker, R.J., Willis, K.J., Fernández-Palacios, J.M., 2016. Reconstructing Holocene vegetation on the island of Gran Canaria before and after human colonization. *Holocene* 26, 113–125.
- Delgado, J.V., Perezgrovas, R., Camacho, M.E., Fresno, M., Barba, C., 2000. The Wool-Less Canary Sheep and their relationship with the present breeds in America. *Animal Genet. Resour. Inf.* 28, 27–34.
- Delgado, J.D., 2002. Interaction between introduced rats and a frugivore bird-plant system in a relict island forest. *J. Nat. Hist.* 36, 1247–1258.
- Ferrando, A., Manzana, A., Jordana, J., Capote, J., Pons, A., País, J., Delgado, T., Atoche, P., Cabrera, B., Martínez, A., Landi, V., Delgado, J.V., Argüello, A., Vidal, O., Lalueza-Fox, C., Ramírez, O., Amills, M., 2015. A mitochondrial analysis reveals distinct founder effect signatures in Canarian and Balearic goats. *Anim. Genet.* 46, 452–456.
- Fitzpatrick, S.M., Erlandson, J.M., 2018. Island archaeology, model systems, the Anthropocene, and how the past informs the future. *J. Island Archaeol.* 13, 283–299.
- Fitzpatrick, S.M., Keegan, W.F., 2007. Human impacts and adaptations in the Caribbean Islands: an historical ecology approach. *Earth Environ. Sci. Trans. Roy. Soc. Edinburgh* 98, 29–45.
- Flores, C., Maca-Meyer, N., Pérez, J.A., Cabrera, V.M., 2001. The peopling of the Canary Islands: a CD4/Alu microsatellite haplotype perspective. *Hum. Immunol.* 62, 949–953.
- Fregel, R., Pestano, J., Arnay-de-la-Rosa, M., Cabrera, V.M., Larruga, J.M., González, A.M., 2009. The maternal aborigine colonization of La Palma (Canary Islands). *Eur. J. Hum. Genet.* 17, 1314–1324.
- Fregel, R., Cabrera, V.M., Larruga, J.M., Hernández, J.C., Gámez, A., Pestano, J.J., Arnay, M., González, A.M., 2015. Isolation and prominent aboriginal maternal legacy in the present-day population of La Gomera (Canary Islands). *Eur. J. Hum. Genet.* 23, 1236–1243.
- Fregel, R., Ordóñez, A.C., Santana-Cabrera, J., Cabrera, V.M., Velasco-Vázquez, J., Alberto, V., Moreno-Benítez, M.A., Delgado-Darias, T., Rodríguez-Rodríguez, A.,

- Hernández, J.C., País, J., González-Montelongo, R., Lorenzo-Salazar, J.M., Flores, C., Cruz-de-Mercadal, M.C., Álvarez-Rodríguez, N., Shapiro, B., Arnay, M., Bustamante, C.D., 2019. Mitogenomes illuminate the origin and migration patterns of the indigenous people of the Canary Islands. *Plos One* 14 (3), e0209125.
- Galván, B., Hernández, C.M., García, J.C., Mesa, E.M., Rodríguez, E.C., Barro, A., Alberto, V., Afonso, J.A., González, G., 2005. Los concheros de La Fuente. Consideraciones metodológicas y resultados preliminares. *Revista Tabona* 13, 103–141.
- Galván, B., Hernández, C., Velasco, J., Alberto, V., Borges, E., Barro, A., Larraz, A., 1999. Orígenes de Buenavista del Norte. De los primeros pobladores a los inicios de la colonización europea. Ayuntamiento de Buenavista del Norte, Santa Cruz de Tenerife.
- Garzón-Machado, V., González-Mancebo, J.M., Palomares-Martínez, A., Acevedo-Rodríguez, A., Fernández-Palacios, J.M., del-Arco-Aguilar, M., Pérez de Paz, P.L., 2010. Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. *Biol. Conserv.* 143, 2685–2694.
- González-Reimers, E., Velasco-Vázquez, J., Arnay-de-la-Rosa, M., Santolaria-Fernández, M., Galindo-Martín, L., 2001. Paleonutritional analysis of the pre-hispanic population from Fuerteventura (Canary Islands). *Sci. Total Environ.* 264, 215–220.
- Gonzalez, E.G., Cerón-Souza, I., Mateo, J.A., Zardoya, R., 2014. Island survivors: population genetic structure and demography of the critically endangered giant lizard of La Gomera, *Gallotia bravoana*. *BMC Genet.* 15, 121.
- Hernández, E., Nogales, M., Martín, A., 2000. Discovery of a new lizard in the Canary Islands, with a multivariate analysis of *Gallotia* (Reptilia: Lacertidae). *Herpetologica* 56, 63–76.
- Hernández-Marrero, J.C., Navarro-Mederos, J.F., Trujillo-Mora, J.M., Cancel, S., Machado-Yanes, C., País, J., Morales, J., Rando, J.C., 2016. An approach to prehistoric sheepherding in La Gomera (Canary Islands) through the study of domestic spaces. *Quat. Int.* 414, 337–349.
- Higuera-Gundy, A., Brenner, M., Hodell, D.A., Curtis, J.H., Leyden, B.W., Binford, M.W., 1999. A 10,300 ^{14}C yr record of climate and vegetation change from Haiti. *Quat. Res.* 52, 159–170.
- Hockey, P.A.R., 1987. The influence of coastal utilisation by man on the presumed extinction of the Canarian Black Oystercatcher *Haematopus meadewaldoi* Bannerman. *Biol. Conserv.* 39, 49–62.
- Hubert, J.M., Allen, M.S., 2016. Six centuries of anthropogenic forest change on a Polynesian high island: archaeological charcoal records from the Marquesas Islands. *Quat. Sci. Rev.* 137, 79–96.
- Hunt, T.L., Lipo, C.P., 2010. Revisiting Rapa Nui (Easter Island) "Ecocide". *Pac. Sci.* 63, 601–616.
- Illera, J.C., Rando, J.C., Richardson, D.S., Emerson, B.C., 2012. Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. *Quat. Sci. Rev.* 50, 14–22.
- Illera, J.C., Spurgin, L.G., Rodríguez-Expósito, E., Nogales, M., Rando, J.C., 2016. What are we learning about speciation and extinction from the Canary Islands? *ARDEOLA* 63, 15–33.
- Irl, S.D.H., Steinbauer, M.J., Messinger, J., Blume-Werry, G., Palomares-Martínez, A., Beierkuhnlein, C., Jentsch, A., 2014. Burned and devoured—introduced herbivores, fire, and the endemic flora of the high-elevation ecosystem on La Palma, Canary Islands. *Arctic Antarct. Alpine Res.* 46, 1–11.
- Jaume, D., McMinn, M., Alcover, J.A., 1993. Fossil birds from the Bujero del Silo, La Gomera (Canary Islands), with a description of a new species of Quail (Galliformes: Phasianidae). *Boletín do Museu Municipal do Funchal* 2, 147–165.
- Keegan, W.F., Diamond, J.M., 1987. Colonization of islands by humans: a biogeographical perspective. *Adv. Archaeol. Method Theor.* 10, 49–92.
- Kirch, P.V., 2007. Three islands and an archipelago: reciprocal interactions between humans and island ecosystems in Polynesia. *Earth Environ. Sci. Trans. Roy. Soc. Edinburgh* 98, 85–99.
- Leppard, T.P., 2017. The biophysical effects of Neolithic island colonization: general dynamics and sociocultural implications. *Hum. Ecol.* 45, 555–568.
- Leppard, T.P., Pilaar Birch, S.E., 2016. The insular ecology and palaeoenvironmental impacts of the domestic goat (*Capra hircus*) in Mediterranean Neolithization. In: Ghilardi, M., Leandri, F., Bloemendal, J., Lespez, L., Fachard, S. (Eds.), *Géoarchéologie des îles de Méditerranée*. CNRS Editions, Paris, pp. 47–56.
- López, L.F., González, J., Hildebrant, S., 1995. La foca monje y las Islas Canarias. Biología, ecología y conservación de una especie mística. Consejería de Política Territorial, Gobierno de Canarias, Las Palmas de Gran Canaria.
- López, M., Foronda, P., Feliú, C., Hernández, M., 2013. Genetic characterization of black rat (*Rattus rattus*) of the Canary Islands: origin and colonization. *Biol. Invasions* 15, 2367–2372.
- López-Jurado, L.F., López-Martínez, N., 1991. Presencia de la rata gigante extinguida de Gran Canaria (*Canaryomys tamarae*) en una cueva de habitación aborigen. *El Mus. Canar.* 48, 19–22.
- López-Jurado, L.F., García-Márquez, M., Mateo, J.A., 1999. Descripción de la distribución primitiva del lagarto gigante de El Hierro y de su regresión histórica. *Monogr. Herpetol.* 4, 17–25.
- López-Martínez, N., López-Jurado, L.F., 1987. Un nuevo múrido gigante del Cuartenario de Gran Canaria *Canaryomys tamarae* nov. sp. (Rodentia, Mammalia). Interpretación filogenética y biogeográfica. *Doñana - Acta Vertebr.* 2, 1–66.
- Maca-Meyer, N., Carranza, S., Rando, J.C., Arnold, E.N., Cabrera, V.M., 2003. Status and relationships of the extinct giant Canary Island lizard *Gallotia goliath* (Reptilia: Lacertidae), assessed using ancient mtDNA from its mummified remains. *Biol. J. Linn. Soc.* 80, 659–670.
- Maca-Meyer, N., Arnay, M., Rando, J.C., Flores, C., González, A.M., Cabrera, V.M., Larruga, J.M., 2004. Ancient mtDNA analysis and the origin of the Guanches. *Eur. J. Hum. Genet.* 12, 155–162.
- Machado, M.C., 2007. Una visión de las Islas Afortunadas, a partir de los restos arqueológicos. *Revista Tabona* 15, 71–90.
- Machado, M.C., Galván, B., 1998. La vegetación en el valle de Chafarí (Las Cañadas del Teide, Tenerife), antes de la conquista castellana. *Cuaternario Geomorfol.* 12, 117–125.
- Machado, M.C., Ourcival, J.M., 1998. La evolución de la vegetación del Norte de Tenerife (Islas Canarias) durante el período prehistórico. Aportación antracológica. *Arqueología Espacial* 19–20, 249–260.
- Machado, M.C., del Arco, M.C., Vernet, J.-V., Ourcival, J.-M., 1997. Man and vegetation in northern Tenerife (Canary Islands, Spain), during the prehispanic period based on charcoal analyses. *Veg. Hist. Archaeobotany* 6, 187–195.
- Martín de Guzmán, C., 1976. Fechas de Carbono-14 para la arqueología prehistórica de las Islas Canarias. *Trabajos de Prehistoria* 33, 318–328.
- Martín, A., Rando, J.C., 2006. On the scientific name of the extant giant lizard of La Gomera (Canary Islands): *Gallotia gomerana* Hutterer, 1985 vs. *G. bravoana* Hutterer, 1985 (Reptilia: Lacertidae). *Vieraea* 34, 65–70.
- Martín, E., Velasco, J., Alberto, V., 1999. Excavaciones arqueológicas en Risco Chimirique (Tejeda, Gran Canaria). Primeros resultados. *Vegueta* 4, 57–74.
- Mateo, J.A., García, M., López, L.F., Barahona, F., 2001. Descripción del lagarto gigante de La Palma (Islas Canarias) a partir de restos subfósiles. *Rev. Española Herpetol.* 15, 53–59.
- Mateo, J.A., Crochet, P.A., Afonso, O.M., 2011. The species diversity of the genus *Gallotia* (Sauria: Lacertidae) during the Holocene on La Gomera (Canary Islands) and the Latin names of Gomeran giant lizards. *Zootaxa* 2755, 66–68.
- McGlone, M.S., Wilmsurst, J.M., 1999. Dating initial Maori environmental impact in New Zealand. *Quat. Int.* 59, 5–16.
- McWethy, D.B., Whittle, C., Wilmsurst, J.M., McGlone, M.S., Li, X., 2009. Rapid deforestation of South Island, New Zealand, by early Polynesian fires. *Holocene* 19, 883–897.
- Medina, F.M., Nogales, M., 2009. A review on the impacts of feral cats (*Felis silvestris catus*) in the Canary Islands: implications for the conservation of its endangered fauna. *Biodivers. Conserv.* 18, 829–846.
- Méndez, J., Morales, G., de Nascimento, L., Otto, R., Gallardo, A., Fernández-Palacios, J.M., 2015. Understanding long-term post-fire regeneration of a fire-resistant pine species. *Ann. For. Sci.* 72, 609–619.
- Michaux, J., Hautier, L., Hutterer, R., Lebrun, R., Guy, F., García-Talavera, F., 2012. Body shape and life style of the extinct rodent *Canariomys bravoi* (Mammalia, Murinae) from Tenerife, Canary Islands (Spain). *Comptes Rendus Palevol* 11, 485–494.
- Mitchell, P., 2019. Settling Madagascar: when did people colonize the world's largest island? *J. I. Coast Archaeol.* <https://doi.org/10.1080/15564894.2019.1582567>.
- Moore, J.H., 2001. Evaluating five models of human colonization. *Am. Anthropol.* 103, 395–408.
- Morales, J., 2003. De textos y semillas. Una aproximación etnobotánica a la prehistoria de Canarias. *El Museo Canario, Las Palmas de Gran Canaria*.
- Morales, J., 2009. Las evidencias carpológicas. In: González, P., Moreno, M.A., Jiménez, A.M. (Eds.), *El yacimiento arqueológico de La Cerera, un modelo de ocupación en la isla de Gran Canaria*. Cabildo de Gran Canaria, Las Palmas de Gran Canaria, pp. 277–297.
- Morales, J., Alberto, V., Rodríguez, A., 2007. Intervención arqueológica en el yacimiento de Belmaco (campaña del año 2000). Nuevas aportaciones al estudio de macrorrestos vegetales en la isla de La Palma. *Revista de Estudios Generales de la Isla de La Palma* 3, 135–160.
- Morales, J., Rodríguez, A., Alberto, V., Machado, C., Criado, C., 2009. The impact of human activities on the natural environment of the Canary Islands (Spain) during the pre-Hispanic stage (3rd–2nd Century BC to 15th Century AD): an overview. *Environ. Archaeol.* 14, 27–36.
- Morales, J., Navarro-Mederos, J.F., Rodríguez-Rodríguez, A., 2011. Plant offerings to the Gods: seed remains from a pre-Hispanic sacrificial altar in La Gomera Island (Canary Islands, Spain). In: Fahmy, A.G., Kahilheber, S., D'Andrea, A.C. (Eds.), *Windows of the African Past. Current Approaches to African Archaeobotany*. Africa Magna Verlag, Germany, pp. 67–78.
- Morales, J., Rodríguez-Rodríguez, A., González-Marrero, M.C., Martín-Rodríguez, E., Henríquez-Valido, P., del-Pino-Curbelo, M., 2014. The archaeobotany of long-term crop storage in northwest African communal granaries: a case study from pre-Hispanic Gran Canaria (cal. AD 1000–1500). *Veg. Hist. Archaeobotany* 23, 789–803.
- Morales, J., Rodríguez, A., Henríquez-Valido, P., 2017. Agricultura y recolección vegetal en la arqueología prehistórica de las Islas Canarias (siglos III–XV d.C.): la contribución de los estudios carpológicos. In: Fernández, J., Mujika, J.A., Arrizabalaga, Á., García, M. (Eds.), *Miscelánea en homenaje a Lydia Zapata Peña (1965–2015)*. Servicio Editorial de la Universidad del País Vasco, Bilbao, pp. 189–218.
- Naranjo, Y., Rodriguez, A., 2015. Artefactos e instrumentos de piedra en un espacio de almacenamiento colectivo. El caso de El Cenobio de Valeron (Gran Canaria, España). *Munibe Antropología – Arqueología* 66, 291–308.
- Navarro, J.F., Hernández, C.M., Barro, A., Borges, E., Hernández, J.C., Alberto, V., 2001. La Fortaleza de Chipude y los concheros de Arguamul al cabo de tres décadas: viejos problemas, nuevas identificaciones. *Spal. Revista de Prehistoria y Arqueología* 10, 327–341.
- Navarro, P.G., Ramírez, R., Tuya, F., Fernandez-Gil, C., Sanchez-Jerez, P., Haroun, R.J.,

2005. Hierarchical analysis of spatial distribution patterns of patellid limpets in the Canary Islands. *J. Molluscan Stud.* 71, 67–73.
- Nogales, M., Marrero, M., Hernández, E.C., 1992. Efecto de las cabras cimarronas (*Capra hircus*) en la flora endémica de los pinares de Pajonales, Ojeda e Inagua (Gran Canaria). *Botánica Macaronésica* 19–20, 79–86.
- Nogales, M., Rando, J.C., Valido, A., Martín, A., 2001. Discovery of a living giant lizard, genus *Gallotia* (Reptilia: Lacertidae), from La Gomera, Canary Islands. *Herpetologica* 57, 169–179.
- Nogales, M., Rodríguez-Luengo, J.L., Marrero, P., 2006. Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mamm. Rev.* 36, 49–65.
- Nogales, M., Medina, F.M., 2009. Trophic ecology of feral cats (*Felis silvestris f. catus*) in the main environments of an oceanic archipelago (Canary Islands): an updated approach. *Mamm. Biol.* 74, 169–181.
- Nogué, S., de Nascimento, L., Fernández-Palacios, J.M., Whittaker, R.J., Willis, K.J., 2013. The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. *J. Ecol.* 101, 368–377.
- Nogué, S., de Nascimento, L., Froyd, C.A., Wilmshurst, J.M., de Boer, E.J., Coffey, E., Whittaker, R.J., Fernández-Palacios, J.M., Willis, K.J., 2017. Island biodiversity conservation needs palaeoecology. *Nat. Ecol. Evol.* <https://doi.org/10.1038/s41559-017-0181>.
- Olalde, I., Capote, J., Del-Arco, M.C., Atoche, P., Delgado, T., González-Anton, R., País, J., Amills, M., Lalueza-Fox, C., Ramírez, O., 2015. Ancient DNA sheds light on the ancestry of pre-hispanic Canarian pigs. *Genet. Sel. Evol.* <https://doi.org/10.1186/s12711-015-0115-7>.
- Ordóñez, A.C., Freigal, R., Trujillo-Mederos, A., Hervella, M., de-la-Rúa, C., Arnay-de-la-Rosa, M., 2017. Genetic studies on the prehispanic population buried in Punta Azul cave (El Hierro, Canary Islands). *J. Archaeol. Sci.* 78, 20–28.
- Pais, J., 1996a. Los asentamientos pastoriles prehistóricos del reborde montañoso que contornea la caldera de Taburiente. *Revista Taborno* 9, 149–164.
- Pais, J., 1996b. La economía de producción en la prehistoria de la Isla de La Palma. La Ganadería. Dirección General de Patrimonio Histórico, Gobierno de Canarias, Santa Cruz de Tenerife.
- Parsons, J.J., 1981. Human influences on the pine and laurel forests of the Canary Islands. *Geogr. Rev.* 71, 253–271.
- Pérez-Méndez, N., Jordano, P., Valido, A., 2015. Downsized mutualisms: consequences of seed dispersers' body-size reduction for early plant recruitment. *Perspect. Plant Ecol. Evol. Systemat.* 17, 151–159.
- Pérez-Méndez, N., Jordano, P., García, C., Valido, A., 2016. The signatures of Anthropocene defaunation: cascading effects of the seed dispersal collapse. *Sci. Rep.* 6, 24820.
- Pérez-Méndez, N., Jordano, P., Valido, A., 2018. Persisting in defaunated landscapes: reduced plant population connectivity after seed dispersal collapse. *J. Ecol.* 106, 936–947.
- Prebble, M., Dowe, J.L., 2008. The late Quaternary decline and extinction of palms on oceanic Pacific islands. *Quat. Sci. Rev.* 27, 2546–2567.
- Prebble, M., Wilmshurst, J.M., 2009. Detecting the initial impact of humans and introduced species on island environments in Remote Oceania using palaeoecology. *Biol. Invasions* 11, 1529–1556.
- Rando, J.C., Rodríguez, A.C., País, F.J., Navarro, J.F., Martín, E., 1996. Los restos de aves del yacimiento arqueológico de "El Tendal" (La Palma, Islas Canarias). *El Mus. Canar.* 51, 87–102.
- Rando, J.C., López, M., Jiménez, M.C., 1997. Bird remains from the archaeological site of Guinea (el Hierro, canary islands). *Int. Osteoarchaeol.* 7, 298–302.
- Rando, J.C., 2003. Protagonistas de una catástrofe silenciosa. Los vertebrados extintos de Canarias. *El Indiferente* 14, 4–15.
- Rando, J.C., Alcover, J.A., 2007. Evidence for a second western Palaearctic seabird extinction during the last Millennium: the Lava Shearwater *Puffinus olsoni*. *Ibis* 150, 188–192.
- Rando, J.C., Alcover, J.A., 2010. On the extinction of the dune shearwater (*Puffinus holeae*) from the Canary Islands. *J. Ornithol.* 151, 365–369.
- Rando, J.C., Perera, M.A., 1994. Primeros datos de ornitofagia entre los aborígenes de Fuerteventura (Islas Canarias). *ARCHAEFAUNA* 3, 13–19.
- Rando, J.C., López, M., Seguí, B., 1999. A new species of extinct flightless passerine (Emberizidae: *Emberiza*) from the Canary Islands. *Condor* 101, 1–13.
- Rando, J.C., Alcover, J.A., Illera, J.C., 2010. Disentangling ancient interactions: a new extinct passerine provides insights on character displacement among extinct and extant island finches. *PLoS One* 5, e12956.
- Rando, J.C., Alcover, J.A., Michaux, J., Hutterer, R., Navarro, J.F., 2011. Late-Holocene asynchronous extinction of endemic mammals on the eastern Canary Islands. *Holocene* 22, 801–808.
- Rando, J.C., Alcover, J.A., Galván, B., Navarro, J.F., 2014. Reappraisal of the extinction of *Canariomys bravoi*, the giant rat from Tenerife (Canary Islands). *Quat. Sci. Rev.* 94, 22–27.
- Ravazzi C., Mariani M., Criado C., Garozzo L., Naranjo-Cigala A., Perez-Torrado F.J., Pini R., Rodriguez-Gonzalez A., Nogué S., Whittaker R.J., Fernández-Palacios J.M., de Nascimento L. submitted for publication The Influence of Natural Fire and Cultural Practices on Island Ecosystems: Insights from a 4800 Year Record from Gran Canaria, (Canary Islands).
- Rick, T.C., Kirch, P.V., Erlandson, J.M., Fitzpatrick, S.M., 2013. Archeology, deep history, and the human transformation of island ecosystems. *Anthropocene* 4, 33–45.
- Rodríguez, C.G., 1996. La pesca entre los canarios, guanches y auritas: las ictiofaunas arqueológicas del Archipiélago Canario. *Cabildo Insular de Gran Canaria, Las Palmas de Gran Canaria.*
- Rodríguez, O., Naranjo-Cigala, A., 2005. *Paisajes, Geografía, Etnobotánica y Geobotánica. El azúcar y su cultura en las islas atlánticas. Canarias siglos XVI al XX.* Ayuntamiento de Los Llanos de Aridane, La Palma.
- Rodríguez, A., Navarro, J.F., 1999. La industria malacológica de La cueva de El Tendal (San Andrés y Sauces, isla de La Palma). *Vegueta* 4, 75–100.
- Rodríguez-Piñero, J.C., Rodríguez-Luengo, J.L., 1993. The effect of herbivores on the endemic Canary flora. *Boletín do Museo Municipal do Funchal* 2, 265–271.
- Santana, A., 2001. Evolución del paisaje de Gran Canaria (siglos XV-XIX). Ediciones del Cabildo de Gran Canaria, Las Palmas de Gran Canaria.
- Santana, J.A., Moreno, M.A., Suárez, I., Mendoza, F., Alberto, V., 2017. Zonzamas: un yacimiento singular en la isla de Lanzarote. Nuevos datos arqueológicos. *XXII Coloquio de Historia Canario-Americana* 1–18.
- Siegel, P.E., Jones, J.G., Pearsall, D.M., Dunning, N.P., Farrell, P., Duncan, N.A., Curtis, J.H., Singh, S.K., 2015. Paleoenvironmental evidence for first human colonization of the eastern Caribbean. *Quat. Sci. Rev.* 129, 275–295.
- Soler, V., Navarro, J.F., Martín, E., Castro, J.A., 2002. Aplicación contrastada de técnicas de datación absoluta al yacimiento "Cueva del Tendal", isla de La Palma (Islas Canarias). *Revista Taborno* 11, 73–86.
- Steadman, D.W., 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets archaeology. *Science* 267, 1123–1131.
- Traveset, A., Nogales, M., Alcover, J.A., Delgado, J.D., López-Darias, M., Godoy, D., Igual, J.M., Bover, P., 2009. A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). *Biol. Invasions* 11, 1653–1670.
- Trujillo, D., Barone, R., 1991. La fauna de quirópteros del Archipiélago Canario. In: Beníz, J., de Paz, O. (Eds.), *Los murciélagos de España y Portugal. ICONA, Colección Técnica. Ministerio de Agricultura, Pesca y Alimentación*, Madrid, pp. 94–111.
- Velasco, J., 1998. Economía y dieta de las poblaciones prehistóricas de Gran Canaria una aproximación bioantropológica. *Complutum* 9, 137–159.
- Velasco, J., Hernández, C.M., Alberto, V., 1999. Consideraciones en torno a los sistemas productivos de las sociedades prehistóricas canarias: los modelos de Tenerife y Gran Canaria. *Vegueta* 4, 33–56.
- Velasco, J., 2001. Dieta, nutrición y economía de las poblaciones prehistóricas de Gran Canaria, Tenerife, La Palma y El Hierro: un enfoque bioantropológico. *Vector plus: miscellanea científica – cultural* 17, 19–29.
- Velasco, J., 2014. El tiempo de los antiguos canarios. *Boletín Electrónico de Patrimonio Histórico* 2, 12–14.
- Velasco, J., Alberto, V., Delgado, T., Moreno, M., Lecuyer, C., Richardin, P., 2019. Poblamiento, colonización y primera historia de Canarias: el C14 como paradigma. *Anu. Estud. Atl.* 66, 1–24.
- Vidal-Matutano, P., 2019. Pinos y dragos en la vida y la muerte de los indígenas canarios. *Pellagofio* 79. <https://pellagofio.es/islas/arqueologia/pinos-y-dragos-en-la-vida-y-la-muerte-de-los-indigenas-canarios/>. (Accessed 1 November 2019).
- Vidal-Matutano, V., Alberto-Barroso, V., Marrero, E., García, J.C., Pou, S., Arnay de la Rosa, M., 2019. Vitrified wood charcoal and burnt bones from the pre-Hispanic site of Chasogo (Tenerife, Canary Islands, Spain). *J. Archaeol. Sci.* 28, 102005.
- Weber, L., Hawkins, S., 2002. Evolution of the limpet *Patella canaliculata* d'Orbigny (Mollusca, Patellidae) in Atlantic archipelagos: human intervention and natural processes. *Biol. J. Linn. Soc.* 77, 341–353.
- Wilmshurst, J.M., McGlone, M.S., Partridge, T.R., 1997. A late Holocene history of natural disturbance in lowland podocarp/hardwood forest, Hawke's Bay, New Zealand. *N. Z. J. Bot.* 35, 79–96.
- Wilmshurst, J.M., Anderson, A.J., Higham, T.F.G., Worthy, T.H., 2008. Dating the late prehistoric dispersals of Polynesians to New Zealand using the commensal Pacific rat. *Proc. Natl. Acad. Sci. Unit. States Am.* 105, 7676–7680.
- Wilmshurst, J.M., Hunt, T.L., Lipo, C.P., Anderson, A.J., 2011. High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. *Proc. Natl. Acad. Sci. Unit. States Am.* 108, 1815–1820.
- Wood, J.R., Alcover, J.A., Blackburn, T.A., Bover, P., Duncan, R.P., Hume, J.P., Louys, J., Meijer, H.J.M., Rando, J.C., Wilmshurst, J.M., 2017. Island extinctions: processes, patterns, and potential for ecosystem restoration. *Environ. Conserv.* 44, 348–358.