

A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean)

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Abstract Invasions of alien rodents have shown to have devastating effects on insular ecosystems. Here we review the ecological impacts of these species on the biodiversity of the Balearic and the Canary Islands. A total of seven species of introduced rodents (two rats, three mice, one dormouse, and one squirrel) have been

recorded (six in the Balearics and four in the Canaries). Some of them can occasionally be important predators of nesting seabirds, contributing to the decline of endangered populations in both archipelagos. Rats are also known to prey upon terrestrial birds, such as the two endemic Canarian pigeons. Furthermore, rats actively consume both vegetative and reproductive tissues of a high number of plants, with potential relevant indirect effects on vegetation by increasing erosion and favoring the establishment of alien plants. In the Balearics, rats and mice are important seed predators of endemic species and of some plants with a restricted distribution. In the Canaries, rats intensively prey upon about half of the fleshy-fruited tree species of the laurel forest, including some endemics. In both archipelagos, alien rodents disrupt native plant–seed dispersal mutualisms, potentially reducing the chances of plant recruitment at the same time that they modify the structure of plant communities. We further suggest that alien rodents played (and play) a key role in the past and present transformation of Balearic and Canarian native ecosystems.

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Introduction

Insular ecosystems are susceptible to species introductions mainly due to (1) the particular species

composition and extant functional types, which differs significantly from the mainland, (2) the type of interactions—often quite peculiar—which have evolved in them over thousands or millions of years, and (3) the intrinsic traits of native species (absence of defenses in front to predators/herbivores, etc.). Alien mammals have reportedly caused the most stunning of ecological disturbances from biological invasions, which can be partly attributed to the general absence of naturally occurring terrestrial mammals on most remote islands (Atkinson 2001). Invasions by rodents, in particular, have often been pointed out as those showing the most devastating effects on invaded habitats (Atkinson 1985; Courchamp et al. 2003). Rodent species usually show high fecundities, can be important herbivores (often also acting as seed predators), and can further affect the flora and fauna indirectly by promoting an increase in erosion and a decline of soil fertility. This in turn favors the success (or spread) of new exotic species, promoting what has been named an *invasional meltdown* (Simberloff and Von Holle 1999).

While the impact of introduced rodents on seabird communities in islands throughout the world has received much attention (e.g., Atkinson 1985; Penloup et al. 1997; Fukami et al. 2006), their effects on vegetation (and in particular, on endemic and/or threatened plants) have barely been examined. Moreover, despite the fact that alien rodents can potentially affect the populations of a number of invertebrate species, as it has been reported for some groups from continental areas (e.g., Parmenter and MacMahon 1988), few studies have investigated such effect on insular environments (but see Cheylan 1982; Palmer and Pons 1996; review in Towns et al. 2006). Disruptions of plant–animal mutualisms (mainly pollination and seed dispersal) due partly or totally to alien rodents have also been documented, mainly from some islands like New Zealand and other South Pacific oceanic islands (review in Traveset and Richardson 2006).

Our goal in the present work is to analyze the ‘state of the art’ on the presence of alien rodents and their impacts on the past and present biodiversity of two Spanish archipelagos, one at the Western Mediterranean Sea, the Balearic Islands, and the other in the eastern part of the Atlantic Ocean, the Canary Islands. Both archipelagos harbor high biodiversity richness, with a high fraction of endemic species, and

are thus considered as biodiversity hot-spots (Médail and Quézel 1999). We review the literature published to date, with the main goal that this information can be useful for scientists and conservation biologists interested in the biodiversity of both archipelagos and islands in general.

The archipelagos

The Balearic archipelago (39.00°N and 1.42°E; around 4,961 km²) consists of two main groups of islands at the eastern coast of the Iberian Peninsula (193 km distant to the mainland) in the Western Mediterranean Sea. The Gymnesian Islands, in the east, are Mallorca, Menorca, and Cabrera, whereas the Pityusic Islands, in the west, are Eivissa and Formentera, and all the islands are surrounded by a number of islets (Fig. 1). At the south of Mallorca, there is also the small archipelago of Cabrera, which today is a national park.

The Canarian archipelago consists of seven main volcanic islands (27–29°N and 13–18°W; 7,500 km²) off the Atlantic coast of northwest Africa (100 km distant from the mainland). La Palma, El Hierro, La Gomera, and Tenerife are referred to as the western Canaries, while Lanzarote, Fuerteventura, Gran Canaria, and their islets form the eastern Canaries. The uninhabited islets north of Lanzarote (Alegranza, Montaña Clara, La Graciosa, and East and West Rocks) are included in the Archipelago Chinijo (Fig. 1).

Rodents of the Balearic Islands

Current fauna

The current rodent fauna of the Balearic Islands consists of six species belonging to two families (Myoxidae and Muridae) (e.g., Alcover 1979, 1983; see Table 1). The number of rodent species per island ranges from one at the smaller islets containing rodents (only a few islets are free of rodents) to six at Mallorca and Menorca. The two main Pityusic Islands contain five species each. The islets with only one species are always inhabited by the black rat *Rattus rattus* or by the house mouse *Mus musculus domesticus*.

All the Balearic living rodents have been introduced by humans at different times since the

Fig. 1 Map of the Balearic and the Canarian archipelagos. The islands in the Balearics are: *Ma* Mallorca, *Me* Menorca, *Ei* Eivissa, *Fo* Formentera and *Ca* Cabrera. In the Canaries, *L* Lanzarote, *F* Fuerteventura, *C* Gran Canaria, *T* Tenerife, *G* La Gomera, *P* La Palma, and *H* El Hierro

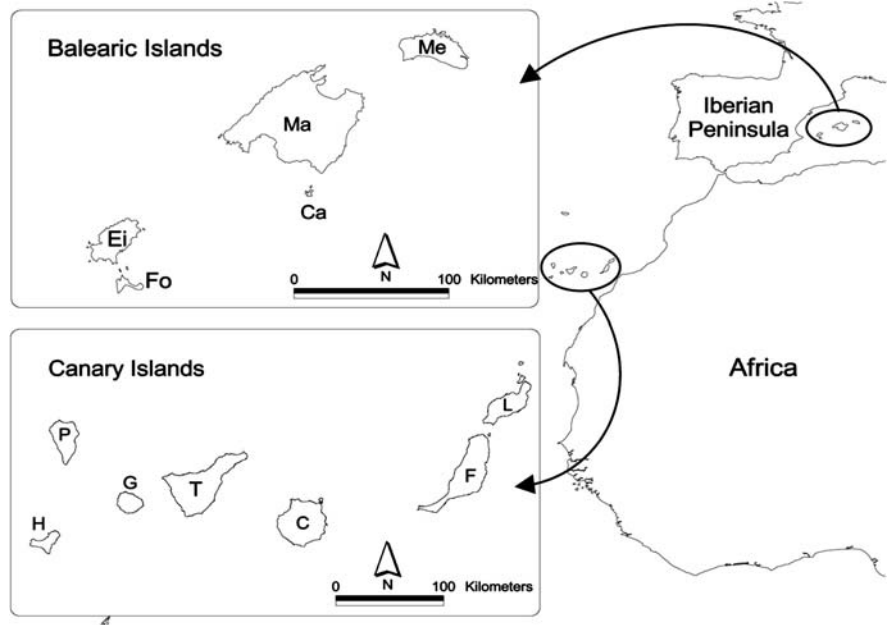


Table 1 List and distribution of invasive non-native rodents present in the Balears and the Canary Islands

Species	Balearic Islands					Canary Islands							≈ Introduction date	Native range	
	Ma	Me	Ca	Ei	Fo	L	F	C	T	G	P	H			
<i>Eliomys quercinus</i>	x	x	†	†	x	-	-	-	-	-	-	-	-	Before 2040 B.C., estimated: ca. 2300–2200 B.C.	Europe
<i>Apodemus sylvaticus</i>	x	x	†	x	x	-	-	-	-	-	-	-	-	Before 2040 B.C., estimated: c. 2300–2200 B.C.	Europe
<i>Rattus rattus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	B: before 90 B.C. C: ≥15th century	South-East Asia
<i>Rattus norvegicus</i>	x	x	-	x	x	x	x	x	x	x	x	x	x	B: ≥18th century C: ≥18th century	Asia (China)
<i>Mus musculus domesticus</i>	x	x	x	x	x	x	x	x	x	x	x	x	x	B: before 90 B.C. C: <300 AD	Asia
<i>Mus spretus</i>	x	x	-	x	-	-	-	-	-	-	-	-	-	Prehistoric times (probably at the Talaiotic period, Iron Age)	North Africa
<i>Atlantoxerus getulus</i>	-	-	-	-	-	?	x	?	-	-	-	-	-	1965	Northwest Africa (Morocco and Algeria)

Ma Mallorca, *Me* Menorca, *Ca* Cabrera, *Ei* Eivissa, *Fo* Formentera, *L* Lanzarote, *F* Fuerteventura, *C* Gran Canaria, *T* Tenerife, *G* La Gomera, *P* La Palma and *H* El Hierro

B Balearic Islands, **C** Canary Islands

x, presence; -, absence; †, disappeared; ?, to be confirmed

archipelago was settled, about 4,300–4,200 years ago (Bover and Alcover 2008). Despite the abundant palaeontological/archaeological documentation and the also profuse information on some aspects of the

rodent biology and ecology in the Balearics (Alcover 1983), we still know rather little on their food habits and their impact on ecosystems (e.g., Kahmann and Lau 1972). Some studies have examined such impact

by means of exclosures, although they have not discriminated among the rodent species involved (e.g., Lázaro et al. 2006; Rodríguez-Pérez and Traveset 2007; Santamaría et al., in preparation). Other works have also inferred effects of rats on plants, invertebrates, and birds by comparing rat-infested islets with rat-free islets, but without performing any analysis of stomach contents (e.g., Palmer and Pons 1996).

The first human settlers documented on the Balearic Islands introduced domestic stock along with two wild rodent species: the garden dormouse, *Eliomys quercinus*, and the wood mouse, *Apodemus sylvaticus* (Alcover et al. 2001). At least during one millennium, these two species appear to be the sole rodent species inhabiting the Balearic archipelago (Alcover, unpublished data).

Eliomys quercinus is currently living in Mallorca, Menorca, and Formentera. According to the fossil record (bone remains), it disappeared from Eivissa and Cabrera at unknown historical times (Alcover and Kahmann 1980; Alcover 1993) probably due to the later introduction of predators like genets, *Genetta genetta*, or stone martens, *Martes foina* (the latter only in Eivissa), or even due to the introduction of pathogens arrived along with the alien rodents.

Apodemus sylvaticus lives on the same islands as *E. quercinus*, but is still present in Eivissa. Its bone remains are abundant on deposits of Cabrera, from where it disappeared at an unknown time (Alcover 1980, 1993), possibly for the same reasons of the disappearance of *E. quercinus*, and even for its direct co-occurrence with *R. rattus*. Nowadays, *A. sylvaticus* is the most abundant small mammal in the Balearic Islands, being distributed over all ecosystems although it is especially frequent in shrublands (macchias).

There is no strong evidence of the presence of other introduced animals on the Balearics during the second millennium cal B.C. From indirect chronological data obtained in Menorca, a new wave of animal immigrants seems to have arrived during the second half of the first millennium cal B.C., probably as a result of the influence of the Roman expansion (Reumer and Sanders 1984; Sanders and Reumer 1984). The introduction of *R. rattus* and *M. m. domesticus* into the Balearics is related to the Roman expansion in the Mediterranean. The

Algerian mouse, *Mus spretus*, is also present in the Roman Age layers in Menorca, and partial evidence—without strong chronological reliability—points out that its arrival might have occurred before that of *R. rattus* and *M. m. domesticus*, certainly in prehistorical times long after the arrival of the first invasive rodents. *Mus spretus* is currently distributed over all habitats, achieving the highest densities in some xeric macchias and in cereal crops (Alcover 1979).

Finally, the Norwegian rat, *Rattus norvegicus*, is a very late immigrant in the Balearics. It is present in the four main islands, and although Alcover (1979) claimed its presence in the Cabrera harbor, no remains exist supporting this view. Currently, this species has not been detected in this island (Alcover 1993; and recent campaigns, McMinn, pers. comm.). The species is spread around towns and farms, living in wild conditions only in some marshes. Due to its water requirements (e.g., Lesser 2003; Sellami et al. 2005), this species is presumably unable to successfully colonize the small and very dry Balearic islets.

Fossil fauna

Before human arrival, the Balearic archipelago was inhabited by three endemic land mammals, namely *Myotragus balearicus* (a dwarf goat with rodent-like incisors, weighing over 40 kg), a shrew *Asoriculus hidalgoi* (= *Nesiotites hidalgoi*), and the Balearic dormouse, *Eliomys morpheus* (= *Hypnomys morpheus*). The former is considered as a key species in the Balearic ecosystems (e.g., Palmer et al. 1999), whereas the ecological role of *E. morpheus* is widely unknown. This extinct rat-size dormouse, weighing about 200–240 g (Mills 1976) inhabited the Gymnesic Islands (see Table 1) over all the Pliocene and Pleistocene, and its extinction is probably related to human arrival (Bover and Alcover 2008). By contrast, the Pityusic Islands lacked terrestrial mammals during the upper Pleistocene; they were actually the sole Mediterranean archipelago lacking terrestrial mammals during this period. The ecology of these islands, thus, is thought to have been highly peculiar (Palmer et al. 1999). Their free rodent condition is reflected in the fossil avifauna, which contains thousands of seabird bones and an endemic flightless rail (McMinn et al. 2005).

Rodents of the Canary Islands

Current fauna

Four alien rodent species are currently found in the Canaries (Table 1). Three belong to the Muridae family: *R. rattus*, *R. norvegicus* and *M. m. domesticus*, while the fourth is of the Sciuridae family: the Barbary ground squirrel *Atlantoxerus getulus*. *Rattus rattus* are distributed throughout rural and natural environments, whereas *R. norvegicus* is mainly located in towns, villages, and sometimes in coastal areas; both species are relatively abundant in these habitats. *Mus m. domesticus* is present in all Canarian habitats, being rather abundant in most of them except the laurel forest. *Atlantoxerus getulus* is widespread and relatively abundant throughout the semi-desert Fuerteventura, occurring only in organic-sandy habitats at low densities (López-Darias and Lobo, 2008), and has also been recorded (1996–2006) in Gran Canaria, although it has not definitively established in this island (Calabuig and López-Darias, pers. obs.). Recently it has been detected in the xeric Lanzarote (López-Darias, pers. obs.). While *M. m. domesticus* was brought to the Canaries about two millennia ago (Carrascosa and López-Martínez 1988), the introduction of the two rats probably took place after 14th-century European contact (see Nogales et al. 2006). The squirrel, by contrast, arrived in the Canaries in 1965 (Machado 1979; Machado and Domínguez 1982).

In the context of rodents of the Macaronesian archipelagos (Azores, Madeira, Salvages, Canaries and Cape Verde), the Canary Islands constitute the best studied, although many aspects are yet scarcely known. Different types of herbivory (consumption of leaves, shoots, fruits, or seeds) have been described as major impacts caused by *R. rattus* in natural habitats (Delgado 1997, 2000, 2002; Godoy 2001; Salvande et al. 2001, 2003; Gómez and Fernández 2003) as well as in cultivated areas near towns and villages (Pérez Padrón and Miralles Ciscar 1974). Other studies have examined the effect of direct predation by rats upon both vertebrate and invertebrate fauna (Hernández et al. 1999; Delgado et al. 2005; Lorenzo, pers. comm.). There is a small amount of data on the distribution and population status of rodents, mainly for *R. rattus* (Hernández et al. 1999; Contreras, pers. comm.).

Fossil fauna

The fossil record reveals the existence of three extinct endemic murids: two species of giant rats—one from Tenerife (*Canariomys bravoii*) and one from Gran Canaria (*C. tamarani*) (Crusafont-Pairo and Petter 1964; López-Jurado and López-Martínez 1991; Michaux et al. 1996)—and the lava mouse *Malpaisomys insularis* from Fuerteventura, Lanzarote, and surrounding islets (Carrascosa and López-Martínez 1988; Hutterer et al. 1988; Michaux et al. 1991, 1996; Boye et al. 1992; Montgelard 1992; López-Martínez et al. 1998; Renaud and Michaux 2004). By contrast, the western Canary Islands (La Palma, La Gomera and El Hierro), the most isolated from the African continent, show a total absence of non-flying terrestrial mammals in their native fauna (Table 1).

Evidences of ecological impacts

Predation by rodents on seabirds

A number of studies on the impacts of introduced predators on island ecosystems have reported a negative impact on seabird ecology (Norman 1975; Moors and Atkinson 1984; Moors et al. 1992; Hobson et al. 1999; Martin et al. 2000; Towns et al. 2006). Insular flightless birds as well as seabirds such as petrels and shearwaters (Procellariiformes) are particularly vulnerable as they usually exhibit a long reproductive cycle, ground nesting habitat, low fecundity, and virtually no adaptations against terrestrial predators (Iguar et al., 2007). From an evolutionary perspective, the introduction of alien predators probably makes the philopatric behavior of seabirds a maladaptive response (Spear et al. 1998; Schlaepfer et al. 2005).

Petrels and shearwaters, in particular, are vulnerable to predation by rodents only during the reproductive period, but different species are affected in different stages of the breeding cycle. Small-size birds are susceptible during the whole breeding period, because adults, eggs, and chicks can be successfully preyed upon (Moors and Atkinson 1984; Atkinson 1985; Martin et al. 2000). By contrast, medium and large-size species are mainly affected after incubation because adults are able to defend eggs against predator intrusions during incubation

(Igal et al. 2006). Large eggs, such as those of Audouin's gulls (*Larus audouinii*), are also neglected by rats because of their size (Prieto et al. 2003). Other groups of seabirds, like gulls (Laridae) and shags (Phalacrocoracidae), are less vulnerable to rodent predation due to the longer parental care, the lower nest site fidelity, and the placement of nest in open microhabitats, which are less exposed to predation (Martin et al. 2000).

Both rodent densities and habitat features of colonial seabirds are known to influence the effects of predation (Moors et al. 1992; Igal et al. 2006). These effects, in turn, depend upon factors such as the availability of alternative food resources (e.g., vegetal material) (Cheylan 1985, 1988) and the colony physical characteristics (e.g., ground or forest complexity and nest accessibility increase nest detection and search time by predators; Hernández et al. 1999; Igal et al. 2007). The latter could be considered a dilution effect which can explain the lower probability of predation in high-density areas of colonies (Hamilton 1971; Imber 1978; Seto and Conant 1996; Imber et al. 2000; Igal et al. 2007), and even the possibility that rats become specialist predators on chicks. Predator effects on populations further depend on the scale and evolution of the rodent invasion, on the proportion of the population affected, and on the population sensitivity to demographic parameters (fecundity, dispersal, and survival) mostly affected by predation (Lebreton and Clobert 1991).

Predation by rats

Rats are among the main predators implicated in documented extirpations of local seabird populations occurring in different archipelagos (Norman 1975; Moors and Atkinson 1984; Tucker and Heath 1994; Courchamp et al. 2003). The main effect on seabird demography is the reduction of individual breeding success by predation on eggs or chicks (Thibault 1995; Seto and Conant 1996; Amengual and Aguilar 1998; Jouventin et al. 2003; Igal et al. 2006). In small species, moreover, rats can also decrease adult survival by direct predation on incubating birds (Atkinson 1985) or restrict their distribution (Mitchell and Newton 2004).

In the Balearics, predation by *R. rattus* on chicks or eggs is one of the main problems in the

conservation of seabirds considered either vulnerable or threatened (Viada et al. 2006). In small islands of both archipelagos, there is a clear negative association between presence of *R. rattus* and occurrence of small seabird species (Amengual and Aguilar 1998; Martin et al. 2000). For example, in the Cabrera Archipelago, the European storm petrel (*Hydrobates pelagicus*) disappeared from two islets during the 1970s after their colonization by *R. rattus* (Araujo et al. 1977; Amengual and Aguilar 1998; Amengual et al. 2000). In the main Canary Islands, Martín et al. (2002b) reported seabird population extirpations, attributing them to both *R. rattus* and *R. norvegicus*, and also to other introduced mammals such as feral cats (*Felis catus*). Likewise, the current distribution of small Procellariiformes (*Bulweria bulwerii*, *Pelagodroma marina*, *H. pelagicus*, and *Oceanodroma castro*) in the Canary Islands is mainly restricted to islets and rocks where rats are absent (Martín et al. 2002b).

Although predation on medium and large-sized species affects mainly chicks, the depressed breeding performance could eventually lead to a significant reduction in population densities and even the dispersion of the whole population from small islands. *Rattus rattus* are reported to reduce productivity and ultimately population size of the large *C. diomedea* in different Mediterranean islets (Thibault 1995; Martin et al. 2000; Igal et al. 2006). In the Balearic archipelago, this seabird has disappeared from islets with high *R. rattus* densities, such as L'Imperial islet of Cabrera Archipelago (Amengual and Aguilar 1998), its abundance has been significantly affected (Martin et al. 2000), or the species is still present but with populations with low breeding success (López-Jurado et al. 1992; Amengual and Aguilar 1998; Rodríguez et al. 2000). A negative effect of *R. rattus* on other medium-sized seabirds is not so clearly documented. In the critically endangered Balearic shearwater (*P. mauretanicus*), the presence of *R. rattus* in an island does not necessarily entail its disappearance (although it has disappeared from small islets with rats, such as Illa de ses Rates; Amengual and Aguilar 1998) and the effect on its productivity is not obvious (Amengual and Aguilar 1998; Martin et al. 2000; Louzao et al. 2006). Population density and reproductive success of the Balearic shearwater seems to be low in islets without any rat-control campaigns (Igal et al. 2004; Ruiz and

Marti 2004) but there is no available empirical evidence confirming this. From the fossil record, we know that *Puffinus nestori*, the ancestor of *Puffinus mauretanicus*, did actually coexist with native rodents (*Eivissia canarreiensis* and cf. *Hypnomys* sp., Alcover and Agustí 1985) in the island of Eivissa during the upper Pliocene (Alcover 1989), although the interactions between these species are totally unknown.

In the Canary Islands, recent studies on the impacts of invasive rodents upon Cory's shearwaters' (*Calonectris diomedea*) colonies in Gran Canaria reveal that rats and mice are the main cause of failure of the over 53% ($n = 80$) of unsuccessful nests (Luzardo and López-Darias, pers. obs.). Furthermore, predation by *R. rattus* upon Manx shearwater (*Puffinus puffinus*) chicks recorded in laurel forests of Tenerife Island (Hernández et al. 1990) was probably the main cause of local population declines (Martín and Lorenzo 2001).

Predation by other small rodents

Detailed studies on the effects of small rodents are lacking both in the Balearic and the Canary Islands. Egg predation by *M. m. domesticus* has been recorded for crevice nesting-seabird species (Cuthbert and Hilton 2004), although this phenomenon is scarcely documented. In the Canary Islands, Martín et al. (2002a) recorded a high level of predation by *M. m. domesticus* upon artificial nests (containing quail eggs) in the small islet of Alegranza (near Lanzarote), which harbors one of the most important colonies of breeding seabirds (*B. bulwerii*, *C. diomedea*, *Puffinus assimilis*, *P. marina*, *H. pelagicus* and *O. castro*) and where rats are absent.

Predation by rodents on other bird species

Predation by rodents on species other than seabirds has been much less documented (but see Penloup et al. 1997; Brown et al. 1998; Hernández et al. 1999; Innes et al. 2004; Tweed et al. 2006). In the Balearic Islands, information about rodent predation on non-seabird species is particularly scarce, and it is only available for birds breeding at marine cliffs. For instance, predation by *R. rattus* on eggs and chicks of Eleonora's falcon (*Falco eleonorae*) is documented at the Dragonera Natural Park (Viada et al. 2006).

Martin et al. (2000) point out that the common swift (*Apus apus*) is present but with lower densities at some islands of the Cabrera Archipelago with rat presence.

A study carried out in the Canary Islands showed that nest predation, mainly by *R. rattus*, on the two endemic pigeons (*Columba junoniae* and *C. bollii*) can reach up to 88% (Hernández et al. 1999); according to these authors, *R. rattus* is the main cause of the scarcity of *C. junoniae*, which breeds on the ground, in some islands such as Tenerife. On the other hand, *R. norvegicus* seems to be one of the most likely responsible for the disappearance of the endemic lesser short-toed lark, *Calandrella rufescens rufescens*, from northern Tenerife (Lorenzo, pers. comm.). In another recent study, Delgado et al. (2005) report different patterns of predation on artificial avian nests by *R. rattus* in fragmented laurel forests in the Canary Islands. Furthermore, in Fuerteventura Island, *A. getulus* has been recently proved to predate upon eggs in artificial nests (López-Darias, pers. obs.), as well as upon real trumpeter finch (*Bucanetes githagineus*) nests (Barbosa et al. 2006). However, real impacts of this invasive squirrel upon the breeding passerines of the island are unknown and would be worth exploring.

Effects on the non-bird fauna (invertebrates, lizards, other mammals)

Compared to the studies performed on the effect of alien rodents on native avifauna, relatively little has been done to assess the potential impacts on other 'smaller' fauna in island ecosystems. With regards to the invertebrate fauna, a unique study in the Balearic archipelago performed in about 50 islets showed that *R. rattus* has caused a decrease of endemic tenebrionid beetles, while enhancing the abundance of some other non-endemics (Palmer and Pons 1996). In the Canary Islands, *R. rattus* is known to predate upon the gastropod species of *Hemicycla* and *Plutonia* genus in the laurel forest (Godoy 2001). In Fuerteventura Island, *A. getulus* was described as a predator of terrestrial gastropod species (Machado and Domínguez 1982). The recent discovery in the squirrels' stomachs of certain species of tremadota (Brachylaimidae), which are dependent on gastropods at the end of their life cycle, further supports the predation on these animals (López-Darias et al.

2008). The squirrel impact upon gastropods, a group with an important fraction of endangered endemic species, is certainly worth to explore and quantify.

The impact of rats on lizard populations in the Balearics has been recently investigated. A survey in the Gymnesic Islands points out that the presence of *R. rattus* is negatively correlated with densities of the endemic *Podarcis lilfordi* (Pérez-Mellado, pers. comm.). In the Canaries, rats and mice are also considered as potential predators of eggs and juveniles of the six endemic lizard species belonging to the genus *Gallotia* (three of these are endangered giant lizards).

Very little is known about current invasive rodent effects upon other mammals. However, they could have been one of the main causes for the extinction of endemic rodents in the past. The introduction of pathogens by alien rodents is considered as a likely cause of the extinction of the Balearic and Canarian endemic small mammals (e.g., Boye et al. 1992; Rando 2003; Bover and Alcover 2008; Rando et al., unpublished). The vectors of introduction of such pathogens would have been rats and mice, in the Canary Islands, and the *E. quercinus* and/or the *A. sylvaticus* in the Balearics. Current impacts on living mammals, some of them also endemic and endangered (e.g., the Canarian shrew *Crocidura canariensis*), remain unknown. In Fuerteventura, the presence of the alien squirrel seems to affect the abundance of the also alien European rabbit (*Oryctolagus cuniculus*) (López-Darias and Lobo, 2008).

Herbivory

Plant matter can constitute an important fraction of the diet of the most common alien rodents. Specifically for rats, vegetation can make up to 73–99% of stomach contents (Cheylan 1982). Despite this, data on the effect of rats on vegetation is very patchy. The first study providing empirical data, which clearly shows an effect of rat presence on floristic composition, was done in the Balearics by Palmer and Pons (2001). The presence of rats in small islets appeared to depress some plant species (*Beta vulgaris*, *Medicago citrina*, *Lavatera arborea*, *Silene sclerocarpa*, etc.) while favoring other plants (*Whitania frutescens*, *Olea europaea*, *Ephedra fragilis*, *Echium parviflorum*, etc.), and similarity indexes were higher for pairs of islands (either both rat-infested or both

rat-free) than for island pairs where only one island was rat-infested. Other studies carried out in the Balearic Islands on the reproductive ecology of endemic plants or plants with restricted distributions in the Western Mediterranean, have shown an important role of rodents as seed predators. For some of these species, post-dispersal seed predation actually represents an important bottleneck in the plant regeneration process. For instance, over 80% of the seeds of *Buxus balearica* (Lázaro et al. 2006), *Rhamnus ludovici-salvatoris* (Traveset et al. 2003) and *Daphne gnidium* (Rodríguez-Pérez and Traveset 2007) are preyed upon by rodents (presumably *A. sylvaticus* given the forest habitat where these shrubs are usually found) in the northern mountain chain of Mallorca. Between 40 and 60% (depending upon year) of seeds of the threatened shrub *Daphne rodriguezii* are also killed by *R. rattus* in Illa den Colom islet, offshore Menorca (Rodríguez and Traveset, pers. obs.). A large fraction (over 90%) of seeds of the rare shrub *M. citrina* in Cabrera Island is consumed by either rats or mice (Santamaría et al., unpublished). Other species like *Rhamnus alaternus*, *Cneorum tricoccon* or *Paeonia cambessedessi* have also shown high levels (ca. 50%) of seed predation by rodents, although in these cases it is less clear that rodents are limiting their regeneration (Traveset, unpublished). In a recent experiment carried out in Cabrera Island, the exclusion of rats appears to result in a greater seedling survival of species such as *Cistus monspeliensis* (Santamaría et al., unpublished).

Stephanodonty in the lava mouse (*M. insularis*) from the eastern Canary Islands suggests that this species was adapted to a grass or vegetarian diet (Renaud and Michaux 2004). The extinct giant rat from Tenerife (*C. bravoii*) has been reported to be mainly herbivorous (Bocherens et al. 2003, 2006) and was probably a laurel forest dweller (López-Martínez and López-Jurado 1987), exploiting canopy fruits, seeds, and leaves rather than understory grasses. Unfortunately, we do not have a clear picture yet of the role that such extinct rodents played on the structure and dynamics of pristine Canarian habitats.

In island forests worldwide, *R. rattus* is known as consumers and destroyers of plant material, affecting support, photosynthetic and reproductive parts, from buds, leaves and bark, stems, roots and rhizomes, to flowers, fleshy fruits, seeds and seedlings (Campbell 1978; Cuddihy and Stone 1990; Sugihara 1997).

Rattus rattus has been interacting with the Canarian native forests probably since the arrival of Europeans. In the laurel forest, where rats reach maximum densities, practically no common tree species escape their injuries, chiefly by *R. rattus* (Table 2). Rats affect plants in many ways, foraging and nesting activities being particularly relevant in the Canaries. Reports from Garajonay National Park (La Gomera, Bañares and Barquín 1982; Gómez and Fernández 2003) have described intense defoliation (*Heberdenia excelsa*, *Picconia excelsa*), terminal branch cutting (*H. excelsa*, *Ocotea foetens*, *Persea indica*, *P. excelsa*) and debarking (*Laurus novocanariensis*) caused by *R. rattus*. Bark damage in *P. excelsa* and *H. excelsa* coincides with drought periods (Gómez and Fernández 2003), which may even worsen the growth rate of trees. In addition, fruit ramets of *Viburnum rigidum* are cut and abandoned by rats (Delgado 2000), which decrease the potential dispersal of seeds.

Experimental evidence suggests that browsing by introduced herbivores responds to leaf nutrient and secondary metabolites, and such behavior may force favorable nutritional changes in leaves (Kuhajek et al. 2006). In the Canary Islands, the trees *Ocotea*, *Persea*, *Apollonias*, and *Laurus* (Pedro et al. 2001) share many diterpenes and essential oils. *Rattus rattus* becomes intoxicated by ingestion of *Persea* leaves, stems and fruits that are rich in ryanoid diterpenes (González-Coloma et al. 1990, 1992). Nutritional benefits may override the negative effects of secondary metabolites in *R. rattus*. Rat impacts on the aerial parts of *Persea* peak in April–May and in October, probably tracking the temporal variation in chemical composition (González-Coloma et al. 1990; Gómez and Fernández 2003). Non-systematic records of rat husking stations in Tenerife laurel forests have revealed broken seeds and exocarp remains of several species (e.g., *Laurus*, *Viburnum*, *Picconia*; Delgado 2000), which may have been left apart to allow volatilization of toxins before consumption (McConkey and Drake 2003).

Fruit and seed removal by rats is to some extent selective (Delgado 2000; McConkey and Drake 2003). In field trials offering whole fruits of *Viburnum*, *Laurus* and *Persea* to free-ranging *R. rattus*, they ate preferentially the two former species (>55% consumption) over the latter (<17%) (Delgado 2000). Seed destruction was higher in *Viburnum* (>50%) than in the two lauraceous trees (<5%). Despite ripe

Persea fruits lack the above-mentioned secondary metabolites (Fraga and Terrero 1996), rats did not select them in field trials (Delgado 2000). *Viburnum rigidum* fruits contain glucosides and are laxative (Pérez de Paz and Medina 1988), but rats seemed to select their fruits against those of *Persea* and *Laurus* (Delgado 2000). In experiments performed on the laurel forest ground with seeds from six native fleshy-fruited plants (*Myrica faya*, *Ilex canariensis*, *V. rigidum*, *P. excelsa*, *L. novocanariensis* and *Apollonias barbujana*), predation intensity by *R. rattus* was highest in *M. faya* (52.6%) and lowest in *A. barbujana* (9.9%) (Godoy 2001). In seed-selection trials using pairs of seeds on the laurel forest ground, Godoy (2001) found that rats consumed larger quantities of small-seeded species (*I. canariensis*, *Ilex perado*, *M. faya* and *Prunus lusitanica*), than of large-seeded species (lauraceous trees: *P. indica*, *A. barbujana* and *L. novocanariensis*). Size thus seemed to be a determinant in seed selection. However, seed chemical composition, and especially the content of secondary compounds could also affect consumption. Experiments simultaneously offering seeds of both *M. faya* and *P. excelsa* to rats suggested that seed density had no significant impact on predation behavior (Godoy 2001).

Predation by *R. rattus* on seeds of several trees and shrubs is intense and widespread at the archipelago scale. In four of these islands, *R. rattus* predated more than 70% of *I. canariensis* seeds at the post-dispersal phase (Salvande et al. 2006). The highest predation was found in the laurel forest of Tenerife, whereas the lowest intensity was found on El Hierro. In the former, *R. rattus* caused serious depletion of fruit crops in a bird-dispersed shrub (*V. rigidum*), critically limiting fruit resources for its legitimate seed-disperser, the robin *Erithacus rubecula* (Delgado 2002). The continental seed-dispersal system established between the robin—the main seed disperser—and the shrub receives little predation impact (at least by these rodents, present in these mainland areas) but a consistent bird visitation and thus dispersal (Herrera 1995). On the contrary, the invaded island system is characterized by very low visit rates by birds (at least on forest interior plants) and rapid fruit depletion by rats (Delgado 2002).

In other oceanic islands, rats (*R. exulans* and *R. rattus*) have been reported to limit plant recruitment (New Zealand, Campbell 1978; Hawaii, Cuddihy and

Table 2 Summary on the effects of predation by rats on laurel forest tree species and their reproductive strategies

Tree species	Fruit type	Plant regeneration strategy ^a			Black rat effects ^b						
		Seed bank	Seedling bank	Suckling bank	Fruit pulp predation	Seed predation	Unripe fruits	Defoliation	Debarking	Seed dispersal	
<i>Apollonia barbujana</i>	Bacca	-	+	+	+	+	+				Probable
<i>Arbutus canariensis</i>	Berry-like drupe	-	-	+	+	+	Probable				Probable
<i>Euphorbia mellifera</i>	Capsule	+	?	-	-	+	+		+	+	Probable
<i>Heberdenia excelsa</i>	Drupe	-	+	-	-	+	+		+	+	Probable
<i>Ilex canariensis</i>	Drupe	-	-	+	+	+	+				Probable
<i>Ilex perado</i>	Drupe	-	-	+	+	+	+				Probable
<i>Laurus novocanariensis</i>	Bacca	-	+	+	+	+	+		+	+	Probable
<i>Myrica faya</i>	Pseudodrupe	+	-	+	+	+	+				
<i>Ocotea foetens</i>	Bacca	-	+	+	+	+			+		
<i>Pearsea indica</i>	Bacca	-	+	+	+	+	+		+	+	Probable
<i>Picconia excelsa</i>	Drupe	-	+	-	-	+	+		+	+	Probable
<i>Pleiomeris canariensis</i>	Drupe	-	-	+	+	+	+				
<i>Prunus lusitanica</i>	Drupe	-	-	+	+	+	+				
<i>Rhamnus glandulosa</i>	Drupe	-	+	-	-						
<i>Sambucus palmensis</i>	Drupe	?	+	?	?	?	Probable		Probable		
<i>Sideroxylon marmulano</i>	Drupe	?	?	?	?	?					
<i>Viburnum rigidum</i>	Drupe	-	+	-	-	+	+			+	Probable
<i>Visnea mocanera</i>	Capsule	-	+	+	+	+	+				

^a Fernández-Palacios and Arévalo (1998), Arévalo et al. (1999), Arévalo and Fernández-Palacios (2003), Fernández-Palacios et al. (2004)

^b Banières and Barquín (1982), Contreras (pers. comm.), González-Coloma et al. (1992), Delgado (1997, 2000, 2002), Godoy (2001), Gómez and Fernández (2003), Salvade et al. (2006)

Stone 1990, and references therein; Tonga Islands, McConkey and Drake 2003); seed predation by rats, specifically, causes important declines in the populations of some plant species (New Zealand, Allen et al. 1994; Campbell and Atkinson 2002). Neither in the Balearic Islands nor in the Canary Islands has a detailed study been developed yet to test the effects of predation by rats on plant recruitment and regeneration.

Disruption of plant–animal mutualistic interactions

The dispersal success of a plant can be modified by introduced herbivores (e.g., rats, goats, parrots) either directly by consuming vegetative or reproductive parts and decreasing seed-dispersal rates, or indirectly by negatively affecting populations of native legitimate dispersers (Traveset and Richardson 2006). Mutualistic disruptions caused by rodents from other islands have shown to alter the populations of native seed dispersers, which in turn act as seed dispersers of a number of plants (Kelly et al. 2006).

In the Mediterranean islands, *R. rattus*, along with the also invasive rabbit, *O. cuniculus*, disperse the seeds of the ice plant *Carpobrotus* spp. (Aizoaceae), a group of South African species particularly invasive in other regions with Mediterranean climate. This contributes to the expansion of this alien plant along the Californian coast (D'Antonio 1990) and on Mediterranean islands (Bourgeois et al. 2005) including the Balearics (B. Padrón et al., unpublished). Such *invasional meltdowns* disrupt native plant–animal mutualisms because they modify the structure of native plant communities and the foraging behavior and movement patterns of the mutualistic animals. Because of the relatively lower species richness and the presence of endemic generalists (Olesen et al. 2002), we would expect a stronger effect of such invader complexes on islands. Further studies that explore the impact of such invasive species on the structures of either pollination or dispersal webs are needed, as ecologists have only just begun to explore this facet of biological invasions.

In the Canary Islands, and previously mentioned, *R. rattus* is a clear disruptor of native seed dispersal systems but especially in the laurel forest. Most of the disperser agents that participate in these mutualistic systems are birds. In most seed-dispersal systems of

the different tree species, this ecological process has been poorly studied and quantitatively evaluated. In some cases (e.g., *V. rigidum*), the seed-predation effect is important, surpassing 44% of the crop and consuming the pulp of another 32.4% of fruits (Delgado 1997, 2002). In coastal shrubland environments, rodents prey upon the seeds of the old Canarian endemism *Neochamaelea pulverulenta* (Cneoraceae). This plant is only dispersed by the endemic lizard's genus *Gallotia* and this strong and relict interaction might partly be disrupted by such rodents (Valido 1999).

The Barbary ground squirrel appears to disrupt dispersal systems of native plants, such as *Rubia fruticosa*, *Asparagus nesiotetes*, and *Lycium intricatum*, in Fuerteventura (Nogales et al. 2005; López-Darias and Nogales, 2008). These authors counted an important number of native plant seeds and found a high percentage of broken seeds in the scats of this squirrel. Furthermore, the ingestion of native seeds by this species negatively affects their viability (Nogales et al. 2005) and their germination percentage (López-Darias and Nogales, 2008). On the other hand, this squirrel facilitates the seed dispersal of some introduced plants (e.g., *Opuntia maxima*), representing thus an example of an *invasional meltdown* (Simberloff and Von Holle 1999).

Lastly, the interaction between *M. m. domesticus* and the seeds of the invasive cactus *Opuntia dillenii*, mainly found in Canarian coastal areas, is worth mentioning (Nogales, pers. obs.). Although native lizards effectively disperse a high number of its seeds, spreading it in xeric habitats, this rodent preys upon the seeds and might well contribute to limit the expansion of this plant. The importance of this effect, however, has not been deeply studied.

Past and present implications of alien rodent expansion for biodiversity in the Balearic and Canary Islands

The consequences for biodiversity of the introduction of alien rodents on the Balearic and Canarian ecosystems are not easy to predict. A rough view can only be approached from the available knowledge on the effect that these animals have had in other islands and on the biology of the different species. We can thus only provide *termini ad quem* or

the most likely scenarios of interest to conservation biologists.

We first need to consider the historical factors involved in each island or group of islands. For instance, a group of islands in each archipelago (the Pityusic Islands in the Balearics, and La Palma, El Hierro and La Gomera, the western Canary Islands) had no native terrestrial mammals at the time of human colonization. This allows for predicting that the stronger effect of mammal invaders should have occurred on those islands, similar to what has been reported from other islands like Hawaii (Athens et al. 2002) or Easter Island (Hunt 2007). There were no native mammals before human arrival in any of these Pacific archipelagos, and huge changes in their vegetation structure and composition have directly derived from the action of rodents. Alien rodents have existed in the Pityusics for ca. 4,300 years, whereas they arrived to the western Canary Islands much more recently, ca. 2,000 years ago. It thus seems reasonable to think that they are largely responsible for changes in the vegetation structure and species composition that have occurred for such a long time. By killing large amounts of seeds and seedlings, and indirectly influencing the demography of other seed consumers like granivorous birds or ants, alien rodents may have been acting as keystone species in the functioning of many if not all ecosystems in both archipelagos. The consequences of rodent herbivory on vegetation in the islands free of native mammals before rodent arrival should be reflected in palaeontologic deposits. Unfortunately, however, no pollen cores are currently available from these islands to confirm such hypothesis.

The ecosystems of the eastern Balearic Islands, on the other hand, evolved along millions of years with the presence of an herbivorous (partially omnivore) rodent, *E. morpheus*. After human arrival, this species was initially replaced by two introduced rodents, *E. quercinus* and *A. sylvaticus*. To some extent, these alien species—mainly the former—possibly acted as ecological equivalents of *E. morpheus*, and thus their impact on vegetation might have been similar to that of the species they replaced. Despite the shape of its jaw suggests a more herbivorous diet than in the recent *E. quercinus*, the wide range of isotopic values of $\delta^{13}\text{C}$ obtained from samples ($n = 4$) of *E. morpheus* suggests that it had an omnivorous diet (Bover and Alcover 2008). We might thus expect that

their impact on the Mallorcan natural vegetation did not differ significantly from that exerted by the replaced native species. By contrast, the disappearance of *M. balearicus* was probably a major cause of vegetation change in the Gymnesic Islands (Palmer et al. 1999).

The effect of alien rodents will vary depending upon the particular regeneration strategies of the species. In the case of the laurel forest of the Canary Islands, for instance, predation by *R. rattus* on fleshy-fruited plants might dramatically limit seed production, changing regeneration and forest succession patterns (Fernández-Palacios and Arévalo 1998). However, some trees display prevalent asexual regeneration (vegetative sprouts or suckers) and do not rely largely on seed banks (i.e., *P. lusitanica*, *I. canariensis*, *I. perado*) (Fernández-Palacios and Arévalo 1998; Arévalo and Fernández-Palacios 2003; Fernández-Palacios et al. 2004), and thus seed predation by rats in such species can be of secondary importance compared to tree species which are dependent on seed/seedling banks for recruitment (Arteaga et al. 2006). On the other hand, species with a seedling bank (Lauraceae, *Laurus*, *Persea*, *Apollo-nias* and *Ocotea*; Oleaceae, *Picconia*) are candidates to suffer strong seed limitation. Those tree species with a seed bank—but not a seedling bank—such as *M. faya*, could also experience the highest impact on long-term regeneration by seed; however, regeneration in *M. faya* is vegetative and depends mostly on a sucker reservoir, which lessens the immediate impact of seed predation by rats on such species. We also need to know the extent of seed-predation impact on the seed banks and plant recruitment patterns at local and regional scales, and to establish links between predation activities by rodents on plants, plant seed dispersers, and their combined incidence.

Another effect of rodent introduction in islands initially free of them concerns the demography of seabirds. In Eivissa, for instance, large seabird colonies were present before human arrival, evidenced by tens of thousands of fossil bones (Alcover et al. 1994). Nowadays, all colonies in that island have been totally extirpated, alien rodents being probably partly responsible for that. Rodents may have also contributed to the disappearance of *Pterodroma* sp. (Procellariiformes) from El Hierro; this species bred in the island before human arrival (Rando 2002).

In our view, the *R. rattus* emerges as the most evident devastating rodent species in the Balearic and Canary Islands. This species is known to be a good swimmer that facilitates its expansion to close islands and islets once introduced to a main island by humans. It is actually one of the most invasive species worldwide, and its effects on the flora and fauna have been documented in a great number of studies (Atkinson 1985; Courchamp et al. 2003), including the two archipelagos dealt in this review. *Rattus rattus* may have been responsible for the extirpation of many seabird populations, even the extinction of the lava shearwater *Puffinus olsoni* (Rando and Alcover, 2008), and their pathogens may even have caused extinctions of native rodents (Rando et al., unpublished) or local extirpations of other introduced rodents (e.g., Alcover 1980, 1993).

The late arrival of *R. norvegicus* into the Balearics and Canaries seems to have had a more limited impact on the ecology of these islands, despite its strong impact on other island ecosystems has been extensively reported (e.g., Thorsen et al. 2000; Towns et al. 2006). In the Balearics, the species has hardly adapted to xeric—the most dominant—environments; it is practically present only in marshes, and its effects on breeding birds or other prey have not yet been documented. In the Canaries, this rat is more linked to towns and villages and all seems to indicate that wild fauna near these places have suffered its influence (e.g., seabirds and some populations of *C. r. rufescens*).

We can further speculate that the later arrival of *M. spretus* into Mallorca, Menorca and Eivissa, as well as the subsequent arrival of *M. m. domesticus* into the Balearic Islands and into Fuerteventura and Lanzarote (inhabited by another murid, the endemic lava mouse *Malpaisomys insularis*) had a relatively small influence on the ecology of these islands. We know from the fossil record that there were barn owls (*Tyto alba*) in all these islands, which possibly limited the population growth of *Mus* spp. Even though these small rodents might have had a negative impact on different invertebrate species and perhaps even on some vertebrates (e.g., the endemic Canarian quail *Coturnix gomerae* might have been affected by *M. m. domesticus*), we believe they played an overall small role in the functioning of the ecosystems. It is also true, however, that we do not have empirical data on their densities in different habitats, and we thus might

be underestimating their local importance at some sites.

From a conservation viewpoint, rodent population traits make an absolute eradication to be plausible only in isolated and small islets but extremely expensive and unviable in islands and large islets (Donlan et al. 2003; Jouventin et al. 2003; Orueta et al. 2005). For seabirds breeding in small islands, rat-control campaigns are probably the best management solution. The positive association between rat-control effort and the breeding success of some species of shearwaters (Thibault 1995; Amengual and Aguilar 1998; Igual et al. 2006) actually justifies such eradications campaigns. Nevertheless, several studies suggest that the knowledge of the true effects in populations, the influence of habitat features, and the capacity of rat populations to recover, must be taken into account when planning a rat-control program (Igual et al. 2006; Towns et al. 2006). With regards to lizard populations, rat eradication campaigns in the Balearic Islands might also be negatively affecting lizard populations, suggesting that the chemical method (poison) used in the eradication might increase lizard mortality as well (Pérez-Mellado, pers. comm.). In other oceanic islands like New Zealand, populations of some lizard species have rapidly responded after rat eradications (Towns et al. 2006). Although there is not much information available in the Canaries and the Balearics, preliminary information leads us to predict that the lizard population densities in both archipelagos, at least in some islets, would also rise after rat eradication. Despite numerous completed eradications of rodents, especially in New Zealand, there are few publications that describe the benefits, mainly because of the overwhelming task of measuring change at the ecosystem level (Donlan et al. 2003), especially for some very long-lived species that may take decades to respond (Towns et al. 2006).

In conclusion, fossil records and current ecological impacts suggest that *R. rattus* has probably been the rodent invader with the worst consequences for the Balearic and Canarian native ecosystems, although the role played by other alien rodents was not negligible. Nevertheless, for both archipelagos, we do need most evidence of the rodent effects on biodiversity, by measuring the response by species and assemblages after rodent removal. As for many other studies, this task will be more plausible if we

choose those groups of organisms that show a higher vulnerability to rodent presence, for instance, terrestrial flightless invertebrates, lizards, small terrestrial birds with weak flight and ground-nesters, surface-nesting seabirds, plants with fleshy fruits or with palatable seedlings, etc. (Townes et al. 2006). However, from a conservationist viewpoint, our compilation reveals that rodents cause enough ecological impacts to justify economical investment in rodent management (control or eradication) especially in the small islets of both the Balearic and the Canary archipelagos.

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