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MISSING SPECIES IN SÃO SEBASTIÃO ISLAND, SOUTHEASTERN BRAZIL

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ABSTRACT

São Sebastião Island or Ilhabela is a large (336 km²) island on the northern coast of the state of São Paulo that, despite its area and being mostly covered by forest, presents an impoverished mammal and bird fauna compared to the facing mainland. Absent species are mostly mammals weighting more than 1 kg and two larger opossums, and forest birds belonging to the large ground insectivore, understory insectivore, bamboo / vine tangle insectivore and frugivore guilds. Although human disturbance probably account for some absences, especially of larger mammals, and past higher sea levels for others, most are best explained by a former pronounced shrinking of the forest cover, probably associated to drier climatic conditions during the last glacial period, and the drier character of its forests when compared to the mainland.

Keywords: Mammals, birds, fauna, São Sebastião Island, Brazil, Ilhabela, island biogeography.

INTRODUCTION

The composition of island biotas depend on the combined effects of immigration and extinction, directly related to island size and isolation. Larger islands are more likely to host a more diverse and stable biota than smaller ones, a trend also patent when one compare less isolated against more isolated islands (Arrhenius 1921, MacArthur and Wilson 1967, Brown and Kodric-Brown 1977, Connor and McCoy 1979). Both subtle habitat differences

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between islands and the mainland (Lack 1976, Simberloff 1995) and life history traits of the species influencing their colonizing and persistence habilities (Banfield 1954, MacArthur and Wilson 1967, Diamond *et al.* 1976, Lomolino 1982, 1986, 1994) are important factors influencing the composition of an island fauna.

Such knowledge has been used in conservation science and provide guidelines for predicting long term processes relevant to the conservation and management of natural areas (see Soulé and Wilcox 1980, Harris 1984).

Studies on the vertebrate fauna on land-bridge islands isolated at the end of the last Ice Age have been made in a number of tropical and subtropical settings (summary in Diamond 1984), including eastern Brazil (Müller 1966, 1968, Fernandez *et al.* 1988, Coelho *et al.* 1991). This area lies within the Atlantic Forest domain, characterized by high species diversity and endemism (Cracraft 1985, Fonseca 1985) and also by heterogenity of habitats found along the gradient from sea level to the ridges of the mountains stretching along the coast.

Although exploited by European colonizers since the 1500's, the Atlantic Forest has suffered a major decline only in the present century, due to the expansion of agriculture and, more recently, to urban development. Presently less than 8% of it remains, almost all of which in the mountains, with less than 1% being considered primary forest (SOS Mata Atlântica 1993). The remaining pockets of forest are increasingly becoming isolated from each other and most are smaller than 1,000 km^2. Making things worse few pockets, including most protected areas, conserve the entire habitat gradient from lowland to montane forest. Considering the situation, it is not surprising that the Atlantic Forest has been considered a global conservation priority (SOS Mata Atlântica 1993).

Several islands in southeastern Brazil still have an extensive covering of Atlantic Forest. These islands are considered to have been isolated from the mainland since 10,500 BP or later, and have suffered the effects of extractivism or/and low technology agriculture, earlier by indigenous peoples and later by European colonists, for the last 400 years or more.

Both isolation and human impact are factors influencing almost all protected areas in the Atlantic Forest domain, so those islands can be used to predict the long-term future of protect areas and of the Atlantic Forest as a whole.

Methods

São Sebastião Island (23°50'S, 45°20'W), best known as Ilhabela, lies

in the northern coast of São Paulo state, southeastern Brazil. It is one of the largest Brazilian islands, with 336 km^2, being isolated from the mainland by a channel 1.76-3.5 km wide and 4.5-46 m deep across it (Ângelo 1989). The island is considered to have been isolated for about 7,000 years, with the raising of sea level after the last glaciation. Sea level has reached peaks above the present three times, at 5,100 years BP (5 m above present level), 3,600 BP (3 m) and 2,500 BP (2 m), alternating with periods when sea level was close to the present (Flexor *et al.* 1984).

The island faces the town of São Sebastião at the mainland, whose environs are mostly urban. Only the sothwestern corner of the island faces a forested area in the mainland, north of Maresias beach, where the Serra do Mar massif reaches the sea.

The island raises steeply from the sea, with a mean altitude of 900 m and with its highest peak reaching 1,379 m and being higher than the Serra do Mar. Ilhabela's rugged relief (and also the sister islands of Búzios and Vitória) was formed by alcaline eruptive rocks that broke through Pre-Cambrian gnaisses during vulcanic episodes about 81 million years ago. Those younger rocks make most of the island's peaks being, to a certain degree, surrounded by the older gnaisses and granites (Projeto RADAMBRASIL 1983).

There are only two reasonably flat areas at sea level forming coastal plains similar to the ones in the mainland, the largest at the west side of the island, 5 km^2 (Perequê plain), the other on the east side, only with 1 km^2 (Castelhanos plain). These plains were drowned during periods of higher sea levels. There are many perennial creeks and streams all over the island, most with their courses interrupted by frequent waterfalls. Only on the coastal plains are there lenthic watercourses.

Climate is mild tropical, with a mean temperature of 22^{o}C and an annual rainfall around 1,350 mm. Due to the island's altitude, causing a noticiable rain-shadow effect and the predominance of winds from the south and southeast, precipitation is greater on the east and south faces of the island, the northwest face being the driest. There is a well defined dry season from May to August, although mist occurs at the higher peaks year-round.

There is still no detailed study of the island's vegetation. Undisturbed areas, mostly above 500 m, are covered by primary or old secondary forest with canopy higher than 15-20 m and scattered stands of giant bamboo, *Guadua* sp., resembling forests at similar altitude in the Serra do Mar. Lower areas still bear the marks of disturbance, being covered by forest where fast-growing trees like *Schizolobium parahyba, Piptadenia gonoacantha* (Leguminosae), *Croton* spp (Euphorbiaceae), and *Ficus* spp (Moraceae) dominate, or by anthropogenic grassland dominated by the "sapé" grass *Imperata brasiliensis.*

Compared to the mainland the forests at Ilhabela are drier, with fewer epiphytes and myrtaceous trees and the conspicous absence of the palm *Euterpe edulis*, an abundant species in the mainland and found in neighboring but far smaller Búzios Island. On the northwest face the forest has a decidedly semideciduous character during the dry season, a large percentage of the trees (mostly *P. gonoacantha*) losing their leaves.

Ilhabela was colonized in the late 18th century. From the late 19th to the mid 20th century the island was a great producer of sugarcane and cofee, what meant the virtual extirpation of the forests below 300 m and, in some places higher to 500 m. This means a 30% loss in forested area (see França 1954, Müller 1966). During this period the more accessible forests were also selectively logged to the point that, accordng to França (1954), local fishermen could no longer find trees large enough to build dugout canoes.

During the peak of sugarcane agriculture, the island had more than 10,000 people, a number that dropped to less than half after the plantations declined in the mid 20th century. The number grew only after the island became a summer resort in the 1970's, 14,000 people now living there.

After the decline of large-scale agriculture the forest has recovered in some areas but most areas below 150-200 m and those around settlements, including "traditional" fishermen or "caiçara" villages, are still covered by "sapezal" (anthropogenic grassland) due to the annual fires set by people and to subsistence agriculture (on the association between "traditional agriculture" techniques and "sapezal" grassland, see the comments of Lobato 1983, p. 141). Nowadays human occupation is greatest close to the sea along the western face of the island, where the town of Ilhabela is located, with a few caiçara villages in the eastern and southern faces of the island. Some villages are remnants of larger settlements that owed their existence to sugarcane agriculture, timber exploration or commercial fishing, all activites now gone.

The mountains along the middle of the island have no inhabitants and, together with part of the lower areas, are considered a preserve (Ilhabela State Park). More detailed information on São Sebastião island is found in França (1954), Müller (1966) and Olmos (1994).

Ilhabela has been a collecting locality by museum personnel since the late 19th century (Ihering 1897, Luederwaldt 1929), who already pointed the puzzling absences of several species of animals. Ihering (1897) listed 14 bird species collected in the island and 12 mammals reported, observed and/or collected. Luederwaldt (1929) lists 115 birds (including 17 sea and shore bird species) and 16 land mammal species, including a *Didelphis marsupialis* found dead on the beach. Müller (1966) conducted a more intensive study on the vertebrate fauna of Ilhabela, but the lack of time (he spent only three months

in the island) and accessibility to more distant parts of the island made him miss many species. In all he recorded 145 birds (including sea and shore birds) and 17 land mammals (including introduced rodents).

Data Collecting and Analyses

Due to the lack of known paleontological or archaeological sites in the island, I assume that Ilhabela had a fauna similar to the mainland prior to isolation, a reasonable assumption due to the island's size, topography and short distance from the mainland.

Faunal listings of mammals (excluding bats) and birds were made for Ilhabela from published information (Ihering 1897, Luederwaldt 1929, Müller 1966, 1968), museum records (specimens housed in the Museu de Zoologia da Universidade de São Paulo - MZUSP), live trapping (for small mammals) and direct observations in 1993-1994, when the author was resident in Ilhabela and able to work all over the island. Records were also kept of animals captured, found dead or otherwise reported by state park personnel.

Listings for Ilhabela were compared to the known mammal and bird communities in the mainland, as recorded through similar methods along several years of residence and work in the region and with the data available for the islands of Rio de Janeiro (Fernandez *et al.* 1988, Coelho *et al.* 1991), which have similar origin and history. Species absences, discrepancies and ecological differences among mainland and insular populations were recorded.

Analyses excluded sea birds, and some wide ranging groups not dependent on forest habitats like herons, ducks and shorebirds.

Results

Mammals

Ilhabela shows an impoverished mammal fauna, with only 23 recorded species (Table 1), while in the mainland 40 or more are to be expected. I once found a dead coypu *Myiocastor coypus* on the beach, but it probably came from the mainland, as seems it was the case of Luederwaldt's *Didelphis*.

The island has none of the larger terrestrial herbivores like deer *Mazama americana* and *M. guazoubira*, peccaries *Tayassu tajacu* and *T. pecari*, and tapir *Tapirus terrestris*. Absent species are also rabbits *Sylvilagus brasiliensis*, agoutis *Dasyprocta agouti*, anteaters *Tamandua tetradactyla*, sloths *Bradypus variegatus* and hairy porcupines *Sphiggurus insidiosus*.

Among the carnivores the only confirmed species are the ocelot *Felis pardalis*, the oncilla, *Felis tigrina* and the otter *Lutra longicaudis*, the latter living both along the seashore and in streams. Ihering (1897) reported giant otters *Pteronoura brasiliensis* being seen in the channel, but the species is unknown from coastal areas in eastern Brazil.

There are non conclusive records of racoons *Procyon cancrivorus* and tayras *Eira barbara*, but I believe them to be present in low densities. Foxes *Cerdocyon thous*, coatis *Nasua nasua*, weasels *Galictis vittata* and cats other than the above are unknown in Ilhabela. Only one primate species has been found in the island, the capuchin monkey *Cebus apella*. Although there are rumours of wooly spider-monkeys *Brachyteles arachnoides* in Ilhabela, no positive evidence could be found.

The small mammals show a nearly complete faunal complement, and a few additional species are likely to be found with greater trapping effort. Interesting absences are the black-eared opossum *Didelphis marsupialis*, whose absence was already noted by Luederwaldt (1929), the brown four-eyed opossum *Metachirus nudicaudatus* and, perhaps, the tick-tailed opossum *Lutreolina crassicaudata*. The former is said to have been introduced around the town of Ilhabela about 10 years ago, but I have never recorded it. Another introduced species is an unidentified wild cavy, restricted to grassy areas.

Birds

Like mammals, land birds show an impoverished fauna at Ilhabela, with only 209 recorded species (Table 2), while over 300 are expected in a similarly sized forested area in the mainland. Published surveys carried in the Atlantic Forest of São Paulo have found fewer species only because of limited time of research (see Willis and Oniki 1981, Höfling and Lencioni 1992). Additional species, especially birds able and willing to cross the channel, are likely to be recorded in the future but I am confident my results reflect the general trends of the community.

Some of the most conspicous absences are many low canopy and understory furnariids, ant-birds and tyrannids like *Anabazenops fuscus, Syndactila rufisuperciliata, Automolus leucophtalmus, Heliobletus contaminatus, Batara cinerea, Mackenziana leachi, Formicarius colma, Hylopezus nattereri, Grallaria varia, Hemitriccus* spp, *Myiornis auricularis, Phylloscarthes* spp (except for *Phylloscarthes oustaleti*), and *Ceratotriccus furcatus*. Most of those species are easily found just across the channel, in the Serra do Mar.

Another group with remarkable absences are the large frugivores like *Crypturellus* spp. (although *Tinamus solitarius* is commom in the island), *Penelope* spp., *Ramphastos vitellinus, Bailonius bailoni* and *Pyroderus*

scutatus. Other puzzling absences are forest falcons *Micrastur* spp. and icterids like *Cacicus* spp. and *Icterus cayanensis*.

It is interesting that species that in the north coast of São Paulo (and/or elsewhere) are restricted to lowland and low montane forest, like *Drymophila squammata*, *Carpornis melanocephalus*, *Leucopternis lacernulata* (Müller's record from Ilhabela seems, from description, to best refer to *L. polionota*), *Crypturellus noctivagus* and *Tachyphonus cristatus* are absent from the island.

The presence of a few species is based on only one or two records and I doubt Ilhabela supports resident or viable populations of those species. Most are known altitudinal migrants like *Phaetornis eurynome*, *Phibalura flavirostris*, *Procnias nudicollis*, *Lipaugus lanioides*, *Legatus leucophaius* and *Thlypopsis sordida*, or wandering species like the lowland forest-restinga endemic *Tangara peruviana* and the hummingbird *Colibri serrirostris*. The sole records of *Cranioleuca pallida* and *Neopelma aurifrons* may reflect true rarity, although the former may have been a vagrant (see Willis 1979).

Some never duplicated records by Müller (1966) may indicate truly rare species, like *Aramides cajanea*, *Glaucis hirsuta*, *Myrmotherula minor*, *Manacus manacus* and *Cnemotriccus fuscatus*, but considering my search effort and the readily identifiable vocalizations of most of those species, I believe some of them may have been misidentified or actually no longer occur in the island, as are some birds recently extinct or near so due to the cage-bird trade (*Oryzoborus angolensis*, *Sicalis flaveola* and *Cyanocompsa brissoni*).

Two open habitat species, *Falco sparverius* and *Zenaida auriculata*, were recorded by Luederwaldt (1929) and Müller (1966) but I could not find them in the island, although they are still present in the facing mainland, so I consider them extinct.

Discussion

Mammals

Ihering (1897) has an account of a jaguar *Panthera onca* being clubbed to death in Ilhabela after crossing the channel from the mainland. He also says that deer, otters and giant otters were seen swimming in the channel several times.

It seems clear that colonization and genetic flow of strong-swimming mammals were possible until fairly recently, in the hypothesis the island had no populations on its own. The channel is no barrier to larger animals like peccaries, tapirs, deer and larger cats, and probably also to smaller ones like agoutis, sloths and tamanduas, which are known to swimm well. The question is why none of those species managed to have populations in Ilhabela to the present.

According to Diamond (1984) larger mammals, carnivores and habitat specialists are among the most extinction-prone species after habitat fragmentation. I believe the absence of the larger herbivores and carnivores from Ilhabela may have two reasons. First, the island size and habitat complexity (a result of its topography) at some moment of its history may have not been enough to support viable populations of some species along its 7,000 years or so of isolation. This may explain the absence of *Felis yagouaroundi*, *Cerdocyon thous* and *Sylvilagus brasiliensis*, species living in mosaics of open and edge habitats (Emmons and Feer 1990, Redford and Eisenberg 1992, pers. obs.) that likely occupied only a small part, or were absent, when the island was completely covered by forest before the 18th century.

Another factor, that I believe had a most important role, is the human impact. Ilhabela was already used, but apparently not permanently inhabited, by hunter-gatherer indians during the 1500's (França 1954). Also, shell middens at Búzios island, a few miles east of Ilhabela, point to an occupation of the coastal islands of São Paulo dating from thousands of years, as similar archaeological sites in Rio de Janeiro are known to date from 7,900 to 1,400 years B.P. (Kneip and Pallestrini 1989).

During the peak of sugarcane agriculture a fairly large percentage of the island's forests was cleared, including all of the freshwater swamps on the coastal plains. Also, there was a large human population etching its living in the island, many of them in a subsistence way that has persisted among the artisanal fishermen to this day. At the same time the mainland facing the island was also developed for agriculture (França 1954).

Habitat destruction, both in the island and in the mainland, source of colonizing individuals, coupled with subsistence hunting probably account for the asence of species like *Tapirus terrestris, Tayassu* spp. and, maybe, primates other than *Cebus,* if present (see Bodmer *et al.* 1988a, b). Deer and agouti absence may be due to the same reasons. Large carnivores would follow the fate of their prey.

In Ilhabela, among the larger mammals, only *Cunniculus paca* and *Hydrochaerus hydrochaeris* occur but seem nowhere common (during my residence in Ilhabela I found tracks of the first once and of the latter three times), the same occuring with *Felis tigrina* and *F. pardalis* (one and three records, respectively).

The rareness of the larger rodents seems to be largely a result of hunting, as they are among the favorite targets of poachers (pers. obs.), and in the absence of larger predators should attain somewhat high population densities, as it happens in other localities (Glanz 1990, pers. obs.). It is interesting to point that freshwater swamps, optimum habitat for capybaras, are reduced to a

patch of 5 ha at most, amid an urban area, the remaining capybara population living around fast-flowing streams in the forest, something I have also observed in the Serra do Mar.

The absence of some species is harder to explain, perhaps owing to random events like disease or the number of "stranded" individuals when the island became isolated, or perhaps to a former drastic shrinking of the island's forests. Those are *Didelphis marsupialis, Metachirus nudicaudatus, Tamandua tetradactyla, Bradypus variegatus, Nasua nasua, Galictis vittata* and *Sphiggurus insidiosus*. Their absence is puzzling, especially of *Didelphis*, considering the island's size and the fact that some species, like opossums and sloths, attain higher densities in isolated woodlots and islands than in continuous forest, apparently due to lower predator pressure (Fonseca and Kierulf 1989). *Metachirus* is mostly restricted to lowland and low montane forest in the facing mainland (pers. obs.), its absence likely owing to lack of habitat (see under Birds).

Absence from the island seems largely correlated with body size. All absent species weigh more than 1 kg (with *Sphiggurus* at the limit), except *Didelphis, Metachirus* and *Lutreolina*. The extant small mammal fauna is fairly diverse, being comparable to some of the richest areas in the Atlantic forest (Fazenda Intervales, Olmos 1991) and even exceeding some mainland localities (Juréia Ecological Station, Bergallo 1994), although some wet montane forest species like the rodents *Delomys dorsalis* and *Oryzomys ratticeps* are lacking.

Compared to Grande island (better known as Ilha Grande), not too far to the north (Fernandez *et al.* 1988), Ilhabela has a greater number of species, although that may be due to a smaller collecting effort. It is interesting that Ilha Grande has no larger mammals except for otters (specimen at the MZUSP), ocelots, pacas and agoutis, all found in Ilhabela except for the latter. It is interesting that both *Didelphis* and *Metachirus* occur in Ilha Grande, while at Ilhabela their niches are filled by *Philander opossum*.

The patterns of absence at Ilha Grande seem similar to Ilhabela, but more extreme. The larger distance from the mainland, smaller area (170 km^2) and even greater human impact probably explain the low diversity of its mammal community.

Birds

Absence patterns of birds have particularities when compared to mammals, as many species do cross the channel to and from the mainland, forming continuous populations, as most parrots and hawks. Many of the absent species are birds eating large insects in or near the ground, understory insecti-

vores and bamboo/vine tangle insectivores (categories follow Willis 1979).

Large understory insectivores like *Batara cinerea, Mackenziana leachii, Hylopezus nattereri* and *Grallaria varia* are among the extinction-prone species in isolated small woodlots (Willis 1979) but it is surprising that their diversity is so low in a large island like Ilhabela. Willis (1979) suggests this group to be extinction-prone due to the generally low population densities and sedentary habits, making them vulnerable to low food supplies or other catastrophic events affecting an isolated forest. Nevertheless, to apply such a model to Ilhabela present difficulties unless the forest occupied a far smaller portion of the island in the past.

Such low diversity may be compensated by increased densities of the remaining species compared to the mainland. It is my feeling that *Chamaeza campanisoma, Pyriglena leucoptera, Merulaxis ater* and *Sclerurus scansor* have higher densities in Ilhabela than in the mainland, all occuring from sea level to high in the mountains.

Understory and bamboo/vine insectivores show a similar pattern of lower species diversity, this being one of the facts that more strongly call the attention of ornithologists visiting the island. This is hard to explain, as the group as a whole is not particularly extinction-prone (Willis 1979). Both this and the former group are made of species very unlikely to cross a 2 km sea channel, so recolonization after local extinction is not likely. Like some ground insectivores, a few species of understory insectivores seem to occur at higher densities at Ilhabela, namely *Dysthamnus mentalis, Drymophila ferruginea* and *Basileuterus culicivorus.*

Large frugivores in the island present some interesting patterns. All expected species of parrots are found there, with the possible exception of *Triclaria malachitacea*, a forest species unlikely to try to cross the channel, something all the other psitacids do to this day (Müller 1966, pers. obs.).

One of the most interesting results is the absence of the smaller tinamous *Crypturellus* spp. coupled with the presence of the larger *Tinamus solitarius*, exactly the opposite of what has been observed by Willis (1979) in isolated woodlots. Another puzzling fact is the absence of *Penelope* spp., species known to be resilient to moderate levels of hunting and habitat disturbance, with the presence of the more extinction-prone *Pipile jacutinga* which, although rare, has breeding populations in Ilhabela despite the absence of the palm *Euterpe edulis,* said to be a keystone resource for the species (Collar *et al.* 1992).

A group of species whose absence is more easily explainable are the birds restricted to the lowlands (see Results), to which the recently vanished *Aramides cajanea, Myrmotherula minor* and *Manacus manacus*, restricted to such habitats along the coast of São Paulo, must be added. I believe this group

of species disappeared due to lack of habitat caused both by raisings of the sea level a few thousand years ago and, more recently, by agriculture and urban developments. Some of those extinctions seem to have occured quite recently.

The absence of *Aramides cajanea* is worth detailing. It was present until at least 1964 (Müller 1966) and is still found in smaller islands around Ilhabela like Búzios, Vitória and Alcatrazes, where it is the sole large ground insectivore and can be found in forest far from the water and also on the rocks along the seashore, but always close to the trees. In the mainland the species is restricted to swamps and mangroves, a situation that probably occured in Ilhabela, its disappearence there owing to the recent destruction of the wetlands.

Some species show an apparent niche expansion in the absence of lowland cogenerics. In Ilhabela, where *Drymophila squamata* is absent, *D. ferruginea* is found at sea level, something that does not occur in the facing mainland. The same has been observed with *Carpornis cucullatus*, a montane species ranging to sea level in the absence of *C. melanocephalus*. In the absence of *Ramphastos vitellinus* (which strangely seems not to have crossed the channel), *R. dicolorus* is found year-round at sea level, and not only during the winter as in the mainland. I have captured the montane antbird *Mackenziana severa* among bushes a few meters from the beach, but this is a different case as the absent cogeneric is also a montane species.

On the other hand, lowland *Ramphodon naevius* is found up to at least 700 m, the lack of other hermit hummingbirds (at least in numbers larger than an occasional straggler) allowing such niche expansion.

Compared to the available data on Ilha Grande, Ilhabela has a far more diverse avifauna, but that locality seems to have not been adequately studied, any comparision can only be at best provisional.

Ilhabela shows a simplified mammal and bird communities compared to the facing mainland. The absence of some species, especially larger mammals and some birds, is explainable by overhunting and the loss of lowland and low montane habitats to agriculture starting in the 19th century. Extinctions continue to the present as a result of low population sizes and factors like hunting (still occuring despite being illegal) and random habitat variations, but documentation of recent colonizations is not available due to lack of more complete previous data.

Hunting, perhaps coupled with some environmental factor, seems to keep the populations of species like capuchin monkeys, pacas, capybaras and guans (but not tinamous) in low numbers even in the absence of large cats, a situation when higher population densities of the rodents are to be expected (see Glanz 1990) and despite the present hunting pressure being smaller than it used to be a few years ago (M. Dias de Melo pers. com., pers. obs.). My

feeling is the populations of larger rodents, monkeys, guans and also of wild cats are so reduced that it will take a considerable time for the effects of protection to be felt, if they are not already below viable numbers and we are being witness to their gradual extinction, as happened with recently extinct birds like *Manacus manacus* due to low altitude forest clearence decades before their final demise.

Past events of sea level raising probably also played a hole by eliminating the lowland endemic components of the communities, leading to replacements by montane species.

Nevertheless, there are many absence patterns not solely explainable by human impact and raisings of the sea level. These suggest the occurence of some catastrophic event able to extinguish a wide variety of animals from opossums to insectivore birds, or that Ilhabela had its forest drastically reduced in the past to the point that some forest-dependent species populations were no longer viable.

Ab'Saber (1977) proposed that during the last glacial period precipitation along the southern Brazilian coast was considerably lower, and the Atlantic Forest reduced to islands atop higher elevations like the Serra do Mar. Low altitude areas were covered by xeric vegetation resembling the present-day caatinga, a remnant still persisting around Cabo Frio in Rio de Janeiro.

Ilhabela, due to its altitude, probably kept a forested "island" at its higher elevations during that period. Nevertheless this island was probably small enough to account for the extinction of many of the species missing today, both mammals and birds, most of which would be effectively isolated from populations in other forested patches. Ecological factors like competitive exclusion, epidemics and founder population size, and random catastrophic events, like frost (see Heyer *et al.* (1988) for an account of amphibian extinctions), fire and, perhaps, human activities, would have more accute and longer-lasting effects on isolated populations living in smaller forest islands.

It is also probable that in the past, as today, the forest "island" in Ilhabela was drier when compared to the Serra do Mar, due to its physical setting and precipitation patterns. If it was the case during the last glacial, as seems likely, this habitat difference may have been a key factor in the extinction process and in preventing colonization. The absence of some species, like sloths, rodents restricted to wet montane forest and some understory insectivore birds, may be due to this factor.

The importance of subtle habitat differences in explaining the composition of island avifaunas was first advanced by Lack (1976) but generally ignored, only to be recently resurrected (Simberloff 1995). This habitat effect may well be working today, as the forests of the island's north and west faces

are noticeable drier due to the rain shadow effect and may be suboptimal habitats for some colonizing individuals.

In the well known Barro Colorado Island, bird extinctions are biased towards species with populations varying most or which are shortest-lived. More specialized species, like some antbirds, have also became extinct (Willis 1974, Karr 1990). Although there is no comparable information for Atlantic Forest birds, it is possible that the same patterns are repeated in Ilhabela.

Some explanations for the bird extinctions in Barro Colorado, like ecological truncation (Willis 1974), increased nest predation (Louiselle and Hopes 1983) and lack of moist refugia during dry periods (Willis 1974, Karr 1982), may also explain part of what happened in Ilhabela, especially the last. The impossibility of identifying a sole proximate cause for the extinctions at Barro Colorado after such long a research time in the area gives a clue of the complexity of the factors influencing extinction in insular habittats.

All land mammals presently found in Ilhabela are able to cross the channel (capybaras and otters), can survive in fairly small forest patches surrounded by xeric or open habitats, or are habitat generalists. *Didelphis marsupialis* is the sole species for whose absence an explanation is still wanting, unless an epidemic has occurred. It is important to notice that *Didelphis* (and also *Metachirus*) populations in southeastern Brazil are known to suffer wide oscillations, especially in isolated woodlots (Fonseca and Kierulff 1989, Cerqueira *et al.* 1993, Bergallo 1994), a characteristic of many bird species recently extinct in Barro Colorado Island (Karr 1990) and that may be important in explaining mammal extinctions too.

With the post glacial warming the sea level rose and the forest habitat expanded, excluding xeric-adapted species but maintaining the isolation of the species unable to cross the channel. Such a model, coupled with the habitat differences between Ilhabela and the mainland, explains the absence of many of the species not presently found in Ilhabela, while the more recent sea level risings and human impact account for the others.

A piece of evidence strenghtening the view that Ilhabela had a fairly long period when its forest was isolated is the presence of the endemic echimiid rodent *Nelomys thomasi* (Ihering 1897) related to, but distinctive from, mainland *N. nigrispina* (Olmos unpublished data), and restricted to forest and forest-edge habitats.

Nevertheless, the reason many species able to cross the channel have been unable to establish themselves is unclear. Hermit hummingbirds, icterids, forest-falcons and many other species would apparently be undeterred by a 1.76 km channel and are able to use a wide range of forest types, but they are absent or represented by stragglers. Other puzzling aspect, still in need of an

Table 1. Native land mammals (excluding bats) recorded from Ilhabela.

Species	Source
Caluromys philander	Luederwaldt 1929, pers. obs.
Philander opossum	pers. obs.
Marmosops microtarsus	MZUSP collection
Marmosops incanus	pers. obs.
Monodelphis cf. americana	pers. obs.
Dasypus novencinctus	Müller 1966, pers. obs.
Cebus apella	Luederwaldt 1929, Müller 1966, pers. obs.
Lutra longicaudis	Luederwaldt1929, pers. obs.
Felis pardalis	Luederwaldt 1929, pers. obs.
Felis tigrina	Luederwaldt 1929, Müller 1966, pers. obs.
Sciurus ingrami	Luederwaldt 1929, Müller 1966, pers. obs.
Oligoryzomys nigripes	Luederwaldt 1929, MZUSP collection
Oryzomys nitidus	Ihering 1897, MZUSP collection, pers. obs.
Holochilus brasiliensis	Luederwaldt 1929
Nectomys squamipes	Luederwaldt 1929, MZUSP collection, pers. obs.
Oxymycterus hispidus	Luederwaldt 1929, MZUSP collection
Akodon cf. cursor	pers. obs.
Thaptomys nigrita	pers. obs.
Hydrochaerus hydrochaeris	Luederwaldt 1929, pers. obs.
Agouti paca	Ihering 1897, Müller 1966, pers. obs.
Nelomys thomasi	Ihering 1897, MZUSP collection, pers. obs.
Proechimys iheringi	Luederwaldt 1929, MZUSP collection, pers. obs.
Kannabateomys amblyonyx	pers. obs.

Table 2. Bird species recorded from Ilhabela. Source indicates more recent record.

Species	Source	Species	Source
Tinamus solitarius	Müller 1966, pers. obs.	*Chaetura cinereiventris*	Müller 1966, pers. obs.
Coragyps atratus	Müller 1966, pers. obs.	*Chaetura andrei*	pers. obs.
Cathartes aura	Müller 1966, pers. obs.	*Ramphodon naevius*	pers. obs.
Elanoides forficatus	Müller 1966	*Glaucis hirsuta*	Müller 1966
Harpagus diodon	pers. obs.	*Phaethornis eurynome*	pers. obs.
Harpagus bidentatus	pers. obs.	*Eupetomena macroura*	pers. obs.
Buteo magnirostris	pers. obs.	*Melanotrochilus fuscus*	Müller 1966, pers. obs.
Buteo albicaudatus	pers. obs.	*Colibri serrirostris*	Müller 1966, pers. obs.
Buteo brachyurus	pers. obs.	*Anthracothorax nigricollis*	pers. obs.
Leucopternis polionota	Müller 1966, pers. obs.	Lophornis chaybea	Müller 1966, pers. obs.
Spizastur melanoleucos	pers. obs.	*Thalurania glaucopis*	Müller 1966, pers. obs.
Spizaetus tyrannus	pers. obs.	*Amazilia brevirostris*	pers. obs.
Milvago chimachima	Müller 1966, pers. obs.	*Amazilia fimbriata*	Müller 1966, pers. obs.
Caracara plancus	Müller 1966, pers. obs.	*Amazilia lactea*	pers. obs.
Falco deiroleucos	pers. obs.	*Clytolaema rubricauda*	pers. obs.
Falco sparverius	Müller 1966	*Calliphlox amethystina*	Müller 1966
Pipile jacutinga	Müller 1966, pers. obs.	*Trogon viridis*	pers. obs.
Odontophorus capueira	Müller 1966, pers. obs.	*Trogon rufus*	Müller 1966, pers. obs.
Rallus nigricans	Müller 1966, pers. obs.	*Trogon surrucura*	pers. obs.
Aramides cajanea	Müller 1966	*Ceryle torquata*	pers. obs.
Laterallus viridis	pers. obs.	*Chloroceryle amazona*	Müller 1966, pers. obs.
Laterallus melanophaius	pers. obs.	*Chloroceryle americana*	Müller 1966, pers. obs.
Porphyriops melanops	Müller 1966	*Chloroceryle inda*	Müller 1966, pers. obs.
Fulica armilata	Müller 1966	*Baryphtengus ruficapillus*	pers. obs.
Columba plumbea	Müller 1966, pers. obs.	*Selenidera maculirostris*	Müller 1966, pers. obs.
Columbina talpacoti	Müller 1966, pers. obs.	*Ramphastos dicolorus*	Müller 1966, pers. obs.
Leptotila verreauxi	Müller 1966, pers. obs.	*Picumnus temmincki*	Müller 1966, pers. obs.
Leptotila rufaxilla	pers. obs.	*Picumnus cirratus*	Müller 1966, pers. obs.
Zenaida auriculata	Müller 1966	*Colaptes campestris*	Müller 1966, pers. obs.

Table 2. Continued

Species	Source
Pyrrhura frontalis	Müller 1966, pers. obs.
Forpus xanthopterygius	Müller 1966, pers. obs.
Brotogeris tirica	Müller 1966, pers. obs.
Touit surda	pers. obs.
Pionopsitta pileata	pers. obs.
Pionus maximiliani	Müller 1966, pers. obs.
Amazona farinosa	Müller 1966, pers. obs.
Piaya cayana	pers. obs.
Crotophaga ani	Müller 1966, pers. obs.
Guira guira	pers. obs.
Tapera naevia	Müller 1966, pers. obs.
Tyto alba	pers. obs.
Otus choliba	pers. obs.
Pulsatrix koeniswaldiana	pers. obs.
Speotyto cunicularia	pers. obs.
Rhinoptynx clamator	pers. obs.
Lurocalis nattereri	pers. obs.
Nyctidromus albicollis	Müller 1966, pers. obs.
Nyctiphrynus ocellatus	pers. obs.
Hydropsalis brasiliana	Müller 1966, pers. obs.
Streptoprocne zonaris	Müller 1966, pers. obs.
Myrmotherula minor	Müller 1966
Herpsilochmus rufimarginatus	pers. obs.
Drymophila ferruginea	Müller 1966, pers. obs.
Drymophila ochropyga	pers. obs.
Terenura maculata	pers. obs.
Pyriglena leucoptera	Müller 1966, pers. obs.
Myrmeciza loricata	Müller 1966, pers. obs.
Chamaeza campanisoma	Müller 1966, pers. obs.
Colaptes melanochloros	pers. obs.
Celeus flavescens	Müller 1966, pers. obs.
Melanerpes flavifrons	pers. obs.
Veniliornis spilogaster	Müller 1966, pers. obs.
Campephilus robustus	Müller 1966, pers. obs.
Dendrocolaptes platyrostris	Müller 1966, pers. obs.
Dendrocincla fuliginosa	pers. obs.
Sittasomus griseicapillus	Müller 1966, pers. obs.
Lepidocolaptes fuscus	Müller 1966, pers. obs.
Synallaxis spixi	Müller 1966, pers. obs.
Synallaxis ruficapilla	Müller 1966, pers. obs.
Cranioleuca obsoleta	pers. obs.
Anabacerthia amaurotis	pers. obs.
Philydor atricapillus	Müller 1966, pers. obs.
Philydor liechtensteini	pers. obs.
Philydor rufus	pers. obs.
Sclerurus scansor	Müller 1966, pers. obs.
Lochmias nematura	Müller 1966, pers. obs.
Mackenziana severa	pers. obs.
Dsythamnus mentalis	pers. obs.
Myrmotherula gularis	Müler 1966, pers. obs.
Elaenia flavogaster	Müller 1966, pers. obs.
Camptostoma obsoletum	pers. obs.
Leptopogon amaurocephalus	pers. obs.
Pipromorpha rufiventris	pers. obs.
Phaeoprogne tapera	pers. obs.
Progne chalybea	Müller 1966, pers. obs.
Notiochelidon cyanoleuca	Müller 1966, pers. obs.
Stelgidopteryx ruficollis	Müller 1966, pers. obs.

Table 2. Continued

Species	Source
Conopophaga melanops	Müller 1966, pers. obs.
Conopophaga lineata	Müller 1966, pers. obs.
Merulaxis ater	Müller 1966, pers. obs.
Scytalopus speluncae	pers. obs.
Laniisoma elegans	MZUSP collection
Carpornis cucullatus	Müller 1966, pers. obs.
Phibalura flavirostris	Müller 1966
Lipaugus lanioides	pers. obs.
Pachyramphus polychopterus	Müller 1966, pers. obs.
Tityra cayana	pers. obs.
Procnias nudicollis	pers. obs.
Chiroxiphia caudata	Müller 1966, pers. obs.
Manacus manacus	Müller 1966
Neopelma aurifrons	pers. obs.
Piprites chloris	pers. obs.
Schiffornis virescens	Müller 1966, pers. obs.
Colonia colonus	Müller 1966, pers. obs.
Knipolegus nigerrimus	Müller 1966, pers. obs.
Fluvicola nengeta	pers. obs.
Machetornis rixosus	pers. obs.
Sirystes sibilator	pers. obs.
Muscivora tyrannus	Müller 1966, pers. obs.
Tyrannus melancholicus	Müller 1966, pers. obs.
Empidonomus varius	pers. obs.
Legatus leucophaius	Müller 1966
Megarhynchus pitangua	Müller 1966, pers. obs.
Myiodynastes maculatus	pers. obs.
Myiozetetes similis	Müller 1966, pers. obs.
Pitangus sulphuratus	Müller 1966, pers. obs.
Attila rufus	pers. obs.
Thryothorus longirostris	Müller 1966, pers. obs.
Troglodytes aedon	Müller 1966, pers. obs.
Platycichla flavipes	Müller 1966, pers. obs.
Turdus rufiventris	Müller 1966, pers. obs.
Turdus amaurochalinus	Müller 1966, pers. obs.
Turdus albicollis	Müller 1966, pers. obs.
Anthus lutescens	Müller 1966, pers. obs.
Anthus correndera	Müller 1966
Cyclarhis gujanensis	Müller 1966, pers. obs.
Vireo olivaceus	pers. obs.
Molothrus bonariensis	pers. obs.
Gnorimopsar chopi	Müller 1966, pers. obs.
Parula pitiayumi	pers. obs.
Geothlyps aequinoctialis	Müller 1966, pers. obs.
Basileuterus culicivorus	pers. obs.
Basileuterus rivularis	pers. obs.
Coereba flaveola	Müller 1966, pers. obs..
Chlorophanes spiza	Müller 1966, pers. obs.
Dacnis cayana	Müller 1966, pers. obs.
Euphonia chlorotica	pers. obs.
Euphonia pectoralis	pers. obs.
Pipraidea melanonota	pers. obs.
Tangara seledon	Müller 1966, pers. obs.
Tangara cyanocephala	Müller 1966, pers. obs.
Tangara peruviana	pers. obs.
Thraupis sayaca	Müller 1966, pers. obs.
Thraupis cyanoptera	pers. obs.
Thraupis ornata	pers. obs.
Thraupis palmarum	Müller 1966, pers. obs.
Ramphocelus bresilius	Müller 1966, pers. obs.

Table 2. Continued

Species	Source
Myiarchus ferox	Müller 1966, pers. obs.
Myiarchus swainsonii	Müller 1966
Contopus cinereus	pers. obs.
Empidonax euleri	MZUSP collection, pers. obs.
Cnemotriccus fuscatus	Müller 1966
Myiobius barbatus	pers. obs.
Myiophobus fasciatus	Müller 1966
Hirundinea ferruginea	Müller 1966, pers. obs.
Platyrrinchus mystaceus	Müller 1966, pers. obs.
Tolmomyias sulphurescens	pers. obs.
Todirostrum poliocephalum	pers. obs.
Phylloscarthes oustaleti	Müller 1966, pers. obs.
Serpophaga subcristata	pers. obs.
Sicalis flaveola	Müller 1965
Haplospiza unicolor	pers. obs.
Zonotrichia capensis	Müller 1966, pers. obs.
Passer domesticus	Müller 1966, pers. obs.
Estrilda astrild	pers. obs.
Orthogonys chloricterus	Müller 1966, pers. obs.
Habia rubica	Müller 1966, pers. obs.
Tachyphonus coronatus	Müller 1966, pers. obs.
Trichothraupis melanops	Müller 1966, pers. obs.
Hemithraupis ruficapilla	pers. obs.
Thlypopsis sordida	pers. obs.
Saltator similis	Müller 1966, pers. obs.
Pitylus fuliginosus	pers. obs.
Cyanocompsa brissonii	Müller 1966
Volatinia jacarina	pers. obs.
Sporophila frontalis	pers. obs.
Sporophila caerulescens	Müller 1966, pers. obs.
Oryzoborus angolensis	Müller 1966

explanation, is the extinction of the adaptable *Falco sparverius* and *Zenaida auriculata*.

The present faunal composition of Ilhabela is a puzzling problem that can not be explained by a single factor. Multiple causes are implied, some of them from the distant past, others being the result of man's usually negative relationship with his environment. Further studies in Ilhabela are worth carrying, especially to understand how the ecosystem adjusted to the lack of so many species belonging to important groups like polinators, seed dispersers and predators.

The fact of such a large island being species-poor compared to the mainland makes one wonder about the future of the Atlantic Forest, reduced to isolated patches that continue to suffer the effects of extractivism and habitat degradation even in protected areas, most of which are badly designed and do not cover the necessary habitat gradients. The impoverishment we now observe in Ilhabela may turn out to be the destiny of what is left of the Atlantic Forest.

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