Island biogeography of the Japanese terrestrial mammal assemblages: an example of a relict fauna

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Abstract

Aim The aim of this paper is to provide a review of the biogeography of the terrestrial mammalian fauna from the Japanese islands.

Location The Japanese archipelago is located off the eastern coast of Asia. It extends over a distance of approximately 2000 km in length, from north to south, and comprises more than 3900 islands of widely differing areas.

Methods The list of the living and Quaternary mammalian fauna of Japan and its geographical distribution was compiled from various published works. Introduced species, marine mammals and bats were not considered in this study. Simpson and Jaccard indices were used to quantify the similarities between the fauna from twelve selected islands from the Japanese archipelago. Regression lines and Pearson correlation coefficients were used to describe the relations between species richness and various geographical factors of the islands, such as area or descriptors of isolation. Lastly, we used the method proposed by Atmar & Patterson (1993) to measure the degree of nestedness of the Japanese terrestrial mammalian fauna.

Results Species richness on islands is highly correlated with island size. However, this study reveals the importance of non-equilibrium effects. At a large scale, the current distribution of mammals in Japan seems to be due to selective post-glacial extinction processes. A large proportion of the Japanese mammals are endemic forms, and extinctions were not balanced by the colonization of species from the Asiatic mainland. In addition, we show the major role played by inter-island dispersal processes, in particular from larger islands towards smaller ones, that are mainly effected by the presence of deep marine channels between islands.

Main conclusions The present distribution of the terrestrial mammalian fauna from Japan is thus mainly the result of post-glacial extinctions that were not compensated for by colonization of new species from the faunal Asiatic mainland source pool. However, this study emphasizes the importance of inter-island dispersal processes.

Keywords
Island biogeography, terrestrial mammals, Japan, land-bridge islands.

INTRODUCTION

The Japanese archipelago is a long chain of islands located off the eastern coast of Asia, and includes four main islands: Hokkaido, Honshu, Shikoku and Kyushu (Fig. 1).

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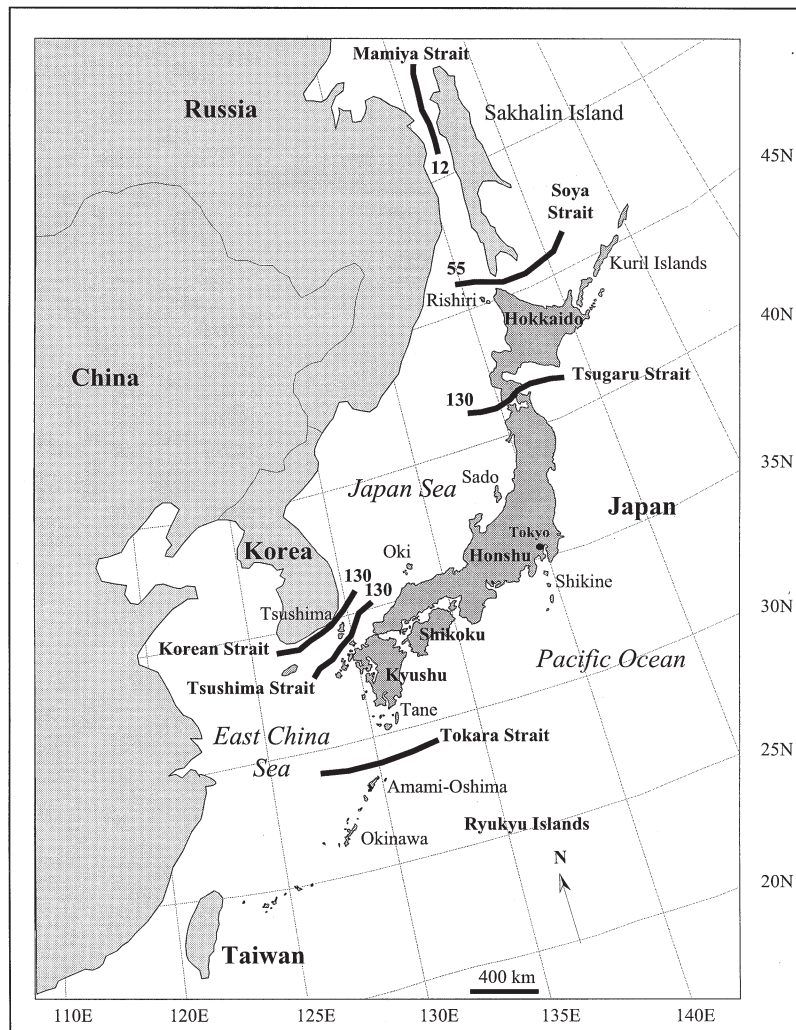
These four islands extend over a distance of about 2000 km in length, and Japanese islands collectively cover a surface area of 377,000 km², between 120°E and 150°E, and 22°N and 45°N. Except for the Ruykyu islands in south, most of this area falls within the Palearctic region of Corbet (1978). The Japanese archipelago comprises more than 3900 islands of widely different areas, ranging from less than 1 km² to more than 230,000 km². Additionally, geological evidence shows that these islands experienced various histories, some of them being

Figure 1 Geographical setting of the Japanese archipelago. Numbers indicate the depth of the tectonic straits in metres.

connected to each other or to the adjacent Asiatic mainland, while others remained isolated during the whole Quaternary. All the Japanese islands but the Ryukyu islands are landbridge islands *sensu* Lawlor (1986), i.e. they were connected to the Asian mainland during Late Pleistocene and the maximum water depth surrounding these islands does not exceed 130 m. The Ryukyu islands are surrounded by deeper marine straits and were not connected to the mainland during maximum sea-lowering, and so are considered true oceanic islands. The peculiarities of the Japanese mammalian fauna have long been recognized (Wallace, 1892; Kuroda, 1939). The aim of this paper is to provide a review of biogeography of the terrestrial mammalian faunas found on the islands of the Japanese archipelago, using classical biogeographical approaches.

METHODS

The list of the living terrestrial mammalian fauna of Japan and its geographical distribution was compiled from data in

Nowak & Paradiso (1990), Corbet & Hill (1992), Wilson & Reeder (1993), Abe (1994) and Dobson (1994). The species status of some taxa is still controversial, and the most conservative assessment was used for the present study. The faunal list considered is very close to the most recent one proposed by Abe (1994). Introduced species such as *Suncus murinus, Oryctolagus cuniculus, Callosciurus erythraeus, Ondatra zibethicus, Rattus rattus, Mus musculus, M. caroli, Myocastor coypus, Procyon lotor* and *Canis familiaris* are not included in this analysis. *Rattus norvegicus* was included because it is considered as a native species of Japan since it is also known in fossil Quaternary localities (Kowalski & Hasegawa, 1976; Kawamura, 1989). Marine mammals (pinnipeds, cetaceans and the sea otter *Enhydra lutris*) and bats were ignored because of their high ability to disperse. The extinction of the wolf, *Canis lupus,* occurred in Japan within historical time because of human hunting (Dobson, 1994) and was thus included as an element of the living mammalian fauna in Japan. Records for the Quaternary

mammalian fauna were obtained from the reviews of Kamei (1981), Hasegawa *et al*. (1988) and Kawamura *et al*. (1989).

In order to quantify the similarities between the fauna of selected islands of the Japanese archipelago, we computed the Simpson's similarity index following the formula $R_S = C/N$, where C is the number of taxa (here species) shared, and N the number of species in the smaller fauna. We also computed another faunal similarity index, the Jaccard index, which is one of the faunal similarity indice recommended by Janson & Vegelius (1981). The formula for the Jaccard index is: $R_J = C/(C + N_a + N_b)$, where C is the number of species shared by the two localities a and b, N_a the number of species found in locality a but not in locality b and N_b the number of species found in locality b but not in locality a. The matrix of Simpson and Jaccard indices were then subjected to an average linkage cluster analysis (UPGMA). The twelve islands considered were the following: Hokkaido, Rishiri, Honshu, Shikoku, Kyushu, Sado, Oki, Tsushima, Tane, Shikine, Amami-Oshima and Okinawa (Fig. 1).

To describe the relationship between island area and species richness, regression lines were computed using the least-squares method on log-transformed variables. We also used Pearson correlation coefficients to describe the relationships between island area, diversity, maximum elevation of the island, maximum depth between islands, and distance between islands or from an island to the mainland. Finally, a stepwise multiple regression analysis was performed to quantify the effect of isolation on island richness. All the statistical analyses were computed using Systat Software version 5.2.1.

Lastly, we used the method proposed by Atmar & Patterson (1993) to measure the nestedness of the presence-absence matrix of the Japanese mammalian fauna. The metric used is T, the 'matrix temperature', which ranges from 0° for a perfectly nested matrix to 100° for a matrix that is completely disordered. The statistical significance of the T-value computed was assessed by a Monte Carlo simulation, using the 'Nestedness Calculator' of Atmar & Patterson (1995).

PRESENT AND QUATERNARY ENVIRONMENTS OF THE JAPANESE ISLANDS

Palaeogeography of the Japanese area during Quaternary
The Japanese islands are located along the boundaries of the Eurasian, North American, Pacific Ocean and Philippine Sea plates (Fig. 2) and the landforms of Japan have been strongly influenced by the movements of these plates (Ota & Omura, 1991; Jolivet & Tamaki, 1992).

The Japanese area was situated adjacent to the Korean Peninsula, until the opening of the Sea of Japan. This opening began at about 25 Ma in the north-eastern part of Japan, but only at about 16 Ma in the south-western area (Hayashida & Ito, 1984; Otufuji *et al*., 1985; Hayashida, 1986; Hayashida & Fukoi, 1991; Hayashida *et al*., 1988; Jolivet & Tamaki, 1992). The isolation of Japan was accentuated by a marine transgression during late Early
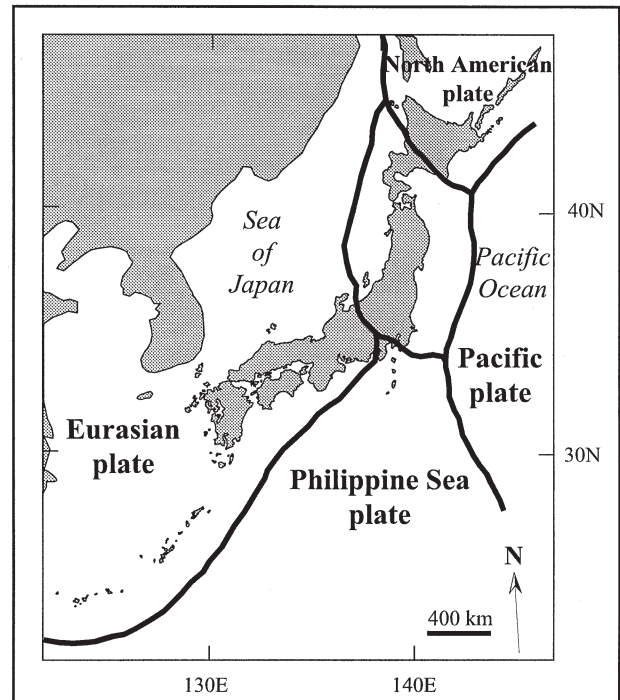

Figure 2 Tectonic setting of the Japanese islands. Lines represent the limit between tectonic plates (modified, after Ota & Omura, 1991).

Miocene (Hayashida & Ito, 1984; Otofuji *et al*., 1985; Hayashida, 1986; Hayashida & Fukui, 1991). On the basis of these geological data, the living Japanese fauna is assumed to have originated in the Middle-Late Miocene.

Since this period, Hondo (i.e. Honshu, Shikoku, Kyushu and small adjacent islands) has spent long periods isolated from the mainland. However, since the opening of the Japan Sea, many land-bridge connections have occurred between Hondo and the Asiatic continent (Kawamura, 1991; Fig. 3). These connections are supported by the presence in the Quaternary fauna of some continental elements, such as *Stegodon* which migrated from south China to Japan during the maximum sea lowering in Middle Pleistocene, or *Equus* which migrated from the northern part of the continent through Sakhalin island to Hokkaido and Hondo in Late Pleistocene, during the Würm sea level lowering about 20,000 years BP (Kamei, 1962; Kawamura, 1991).

Many recent works have estimated sea-level changes in Japan during the whole Quaternary (Fig. 3). During most of the Pleistocene, sea level was more than 55 m below its current position (Burckle, 1992) and such a sea level drop allowed a connection between Hokkaido and the continent, via the Sakhalin island. Estimations of the maximum sea lowering in Middle Pleistocene varies within the range from −130 m to −140 m (Fujii, 1990; Oshima, 1990). Subsequently, the lowest sea level stand of the Würm is estimated from −85 m to −130 m (Kamei & Res. Group for Biogeography from Würm glacial, 1981; Chappell & Shackleton, 1986;
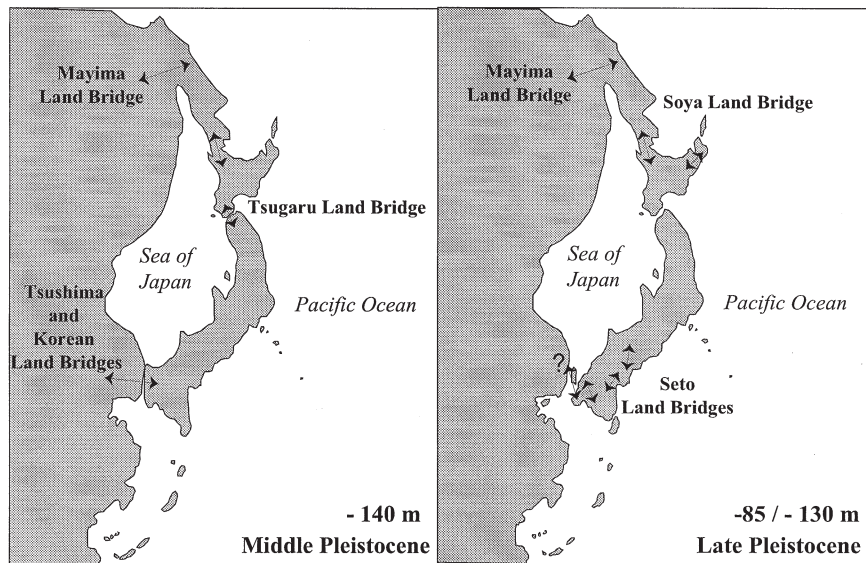
Figure 3 Palaeogeography of the Japanese archipelago during the two sea level lowerings of Middle Pleistocene and Late Pleistocene (modified, after Dobson, 1994).

Morley *et al*., 1986; Fujii, 1990; Oshima, 1990; Burckle, 1992; Keigwin & Gorbarenko, 1992; Tushingham & Peltier, 1993). However, it is still difficult to quantify these sea-level drops since the Japanese islands are located in one of the most tectonically active regions, and significant subsidence has been evidenced in Japan since the Miocene (Hashimoto, 1991). The deepest straits between Hondo and the Asiatic Mainland are the Tsushima strait and the Korean strait (130 m) in South-west Japan (Keigwin & Gorbarenko, 1992; Fig. 1), and the existence of a land-bridge connection in that place during Late Quaternary is still controversial. Stable isotopic analyses on oxygen from cores in the Sea of Japan indicated that the Sea of Japan has always been connected to the Northern Pacific Ocean throughout the Quaternary (Keigwin & Gorbarenko, 1992), i.e. the Tsushima strait and/ or the Korean strait have never been completely closed. This hypothesis is also corroborated by the analysis of pollen and radiolarian abundances in Japan Sea cores (Morley *et al*., 1986). On the contrary, the Ryukyu islands evidently remained isolated throughout the Quaternary, which is reflected in the high degree of endemism of the mammalian fauna. However, Hasegawa (1980) suggested the existence of a partial connection between the Ryukyu islands and the mainland during the Würm maximum sea lowering suggested by the appearance of the wild boar, *Sus*, in Late Pleistocene fossil layers. This emphasizes the recent discovery of some vole (*Microtus*) species in a Late Pleistocene locality of the Ryukyu islands (Kaneko & Hasegawa, 1995). Whether the occurrence of the genera *Sus* and *Microtus* in the Ryukyu islands is due to accidental human introduction or not is difficult to know.

Climate and vegetation of the Japanese area

The climate of Japan is predominantly a mid-latitude oceanic climate, with relatively abundant precipitation (1000 to more

than 4000 mm/yr), and a small annual mean temperature variation. Average January and July temperatures range from 5.3 °C to 25 °C in the warm-temperate zone (southern Honshu, Shikoku and Kyushu), from −1.0 °C to 22.4 °C in the cool-temperate zone (northern Honshu) and from −6.2 °C to 17.8 °C in the subarctic zone (Hokkaido).

The four main biogeographic regions of Japan support four different prevailing vegetation types (Fig. 4). The first is Hokkaido where a subboreal coniferous forest is the main vegetation with some montane forests at high elevations. This vegetation is characterized by the assemblage of *Picea*, *Abies* and *Tsuga*. In Northern Honshu, the dominant vegetation is temperate deciduous broadleaf forest, characterized by the assemblage of *Quercus*, *Fagus* (Fagaceae) associated with conifers such as *Cryptomeria* and *Pinus*. In Southern Honshu, Shikoku and Kyushu, the vegetation is dominated by a warm-temperate evergreen broadleaf forest which includes *Castanopsis*, *Quercus*, *Cryptomeria* and *Sciadopitys* (Morley *et al*., 1986; Heusser, 1992a, 1992b). The Ryukyu islands are characterized by a tropical rain forest (Dobson, 1994).

These vegetation types were similar during the latest glacial, although their distributions were different, with a displacement of the vegetation zones towards the south and lower elevations (Fig. 4). During that time, the extension of the evergreen broadleaf forest was thus extremely reduced (Dobson, 1994). Pollen analyses from some bore holes in the Sea of Japan indicated a shift from a vegetation dominated by the association of *Quercus*/*Cryptomeria* (temperate forest), to a more open environment dominated by herbs and the association of *Picea*/*Abies*/*Tsuga* (subboreal coniferous forest) during last glacial time, 20,000 years BP (Morley *et al*., 1986; Heusser, 1992a). The most striking observation about the palaeoenvironment of the Japanese area, as indicated by
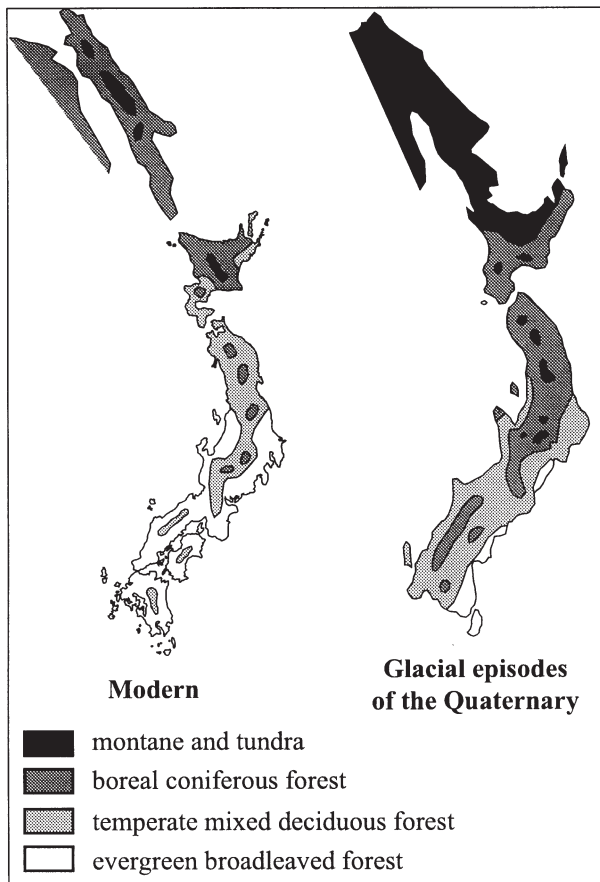
Figure 4 Main vegetation zones in Japan today and during the Last Glacial Age (after Dobson, 1994).

extant and fossil mammal faunas, is that these faunas have always been dominated by temperate forest elements, with a lot of indigenous forest dweller species (Kowalski & Hasegawa, 1976; Kawamura, 1989, 1991).

RESULTS AND DISCUSSION

Composition of the mammal fauna of the Japanese islands

Living mammals of the Japanese islands number 129 species (Wilson & Reeder, 1993; Abe, 1994), and most of them inhabit temperate to warm forests (Kowalski & Hasegawa, 1976; Kamei *et al*., 1987, 1988). This mammalian fauna is characterized by a high degree of endemism, and is assumed to have originated in the Middle-Late Miocene (Kamei *et al*., 1988).

The terrestrial mammal fauna of Japan is composed of seven orders and ninety species (Table 1). Among these orders, the Chiroptera, Rodentia and Insectivora are the most successful

groups, representing 38%, 21% and 19% of the total number of species, respectively. The Carnivora follow in species richness, while the remaining three orders (Lagomorpha, Artiodactyla and Primates) represent only a small proportion of the Japanese terrestrial mammalian fauna. Overall, the total percentage of endemic species is 40%, which is relatively high and characteristic of island faunas. Heaney (1986: Table 6) found the endemism of nonvolant mammals varied from 0% to 72% for various Philippine islands, and from 29% to 79% for various island groups. Among small mammals, the Rodentia have the highest proportion of endemics with 63.15% of the species being known only in the Japanese islands.

Pattern of distribution of the modern terrestrial mammal fauna

A review of distribution patterns among terrestrial mammals in Japan has recently been published (Dobson, 1994). The Japanese islands can be divided into three biogeographic regions based on the present-day distribution of terrestrial mammals (Kawamura, 1991; Dobson, 1994): Hokkaido and adjacent small islands, where the fauna is mostly similar to those of adjacent Asian continent; Hondo (Honshu – Shikoku – Kyushu and adjacent small islands) which is dominated by endemic species; Ryukyu Islands, where the fauna includes highly endemic forms (Kawamura, 1991).

The two biogeographic regions of Hokkaido and Hondo are separated by the Tsugaru tectonic strait, while the regions of Hondo and the Ryukyu Islands are separated by the Tokara strait, which demarcates the Palearctic from the Oriental or Indo-Malayan regions (Tokuda, 1941; Kaneko, 1985; Corbet & Hill, 1992; Fig. 1).

The mammalian terrestrial nonvolant species composition of twelve selected islands of the Japanese archipelago is presented in the Appendix. We used two indices of similarity for these twelve islands, the Simpson's index and the Jaccard index, to quantify the faunal similarities between the three biogeographic regions of the Japanese archipelago.

The results of both these similarity indices analyses strongly support the existence of three biogeographic regions (Fig. 5). The two islands, Okinawa and Amami-Oshima from the Ryukyu islands, are very similar. The second region is represented by Hokkaido and Rishiri island which is located north-west of Hokkaido. The third region consists of all the islands included in the Hondo area that were considered for this analysis. It is interesting to point out one peculiarity of this last region which is revealed by both indices. Within the Hondo area, the Tsushima island falls outside the main group formed by the other islands. These results suggest a strong influence of the existence of deep tectonic straits between islands on overall faunal similarity.

In order to determine the precise patterns of distribution of the terrestrial mammals in Japan, we investigated the relationships between area, species richness, and proportion of endemic species (Table 2).

Table 1 Composition of the mammal fauna of the Japanese islands, introduced species excluded. The fauna is dominated by small mammals, with a high degree of endemism (40%).

	No. of species	% species	No. of endemics	% endemics
Chiroptera	34	37.8	10	29.4
Rodentia	19	21.1	12	63.1
Insectivora	17	18.9	9	52.9
Carnivora	12	13.3	1	8.3
Lagomorpha	4	4.4	2	50.0
Artiodactyla	3	3.3	1	33.3
Primates	1	1.1	1	100.0
Total	90		36	40.0

Island area and species diversity

Species-area curve

For terrestrial non volant mammals (except Chiroptera), the number of species on an island is highly correlated with island area, with a correlation coefficient of 0.905 ($P < 0.001$; Fig. 6).

The relationship between species number (NSP) and island area (AREA) can be expressed by the following equation: $LogNSP = 0.599 + 0.232 LogAREA$ (Eq. 1). The slope of the regression line is 0.232. There is no *a priori* biological significance of the absolute value of the slope (Connor & McCoy, 1979; Lawlor, 1986), but the value of 0.232 obtained falls within the interval computed for other landbridge islands (Lomolino, 1986). Lawlor (1986) proposed a higher value of
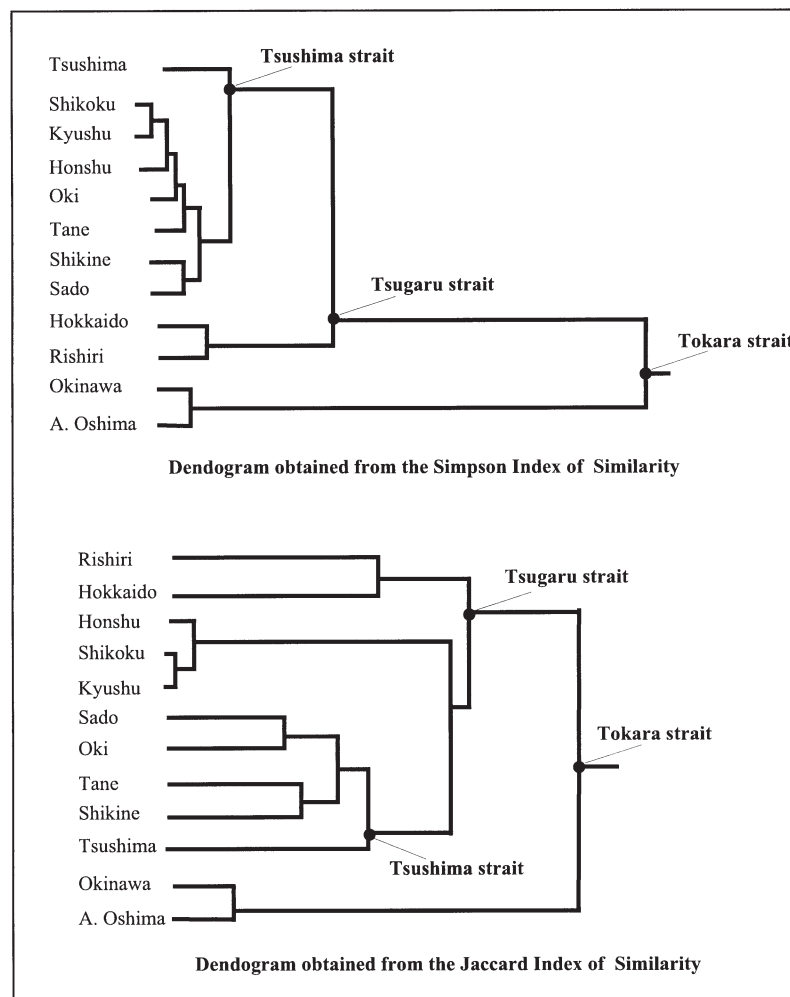

Figure 5 Faunal similarity between twelve selected islands of the Japanese archipelago. The two dendrograms based on Simpson and Jaccard similarity indices are concordant with the existence of three main biogeographic provinces which are demarcated by tectonic straits.
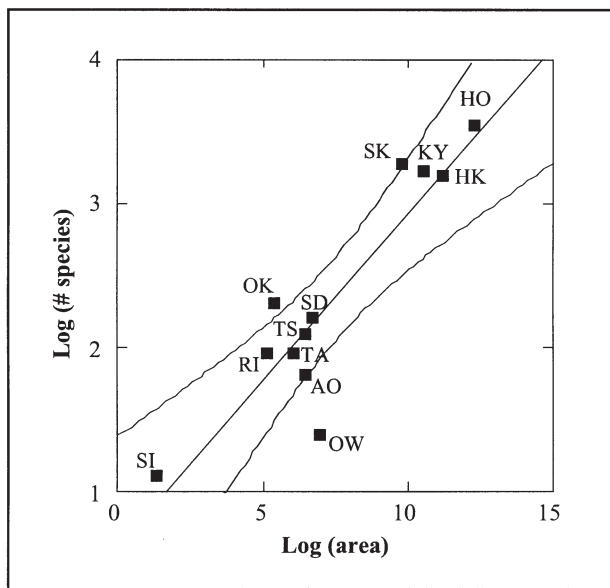
Figure 6 Relationship between species richness and island area for twelve selected islands of the Japanese archipelago. The relationship is highly significant ($P < 0.000$) and the value of the slope (0.232) falls within the interval computed for landbridge islands. Abbreviations for island names are the following: HK, Hokkaido; RI, Rishiri; HO, Honshu; SK, Shikoku; KY, Kyushu; SD, Sado; OK, Oki; TS, Tsushima; TA, Tane; SI, Shikine; OW, Okinawa; AO, Amami-Oshima.

0.347 based on fifteen islands of the Japanese archipelago that represent the same range of areas than in the present work (from 4 km² to more than 210,000 km²). Since his work, however, many advances have been made in the knowledge of systematic and geographical distribution of the Japanese mammals (Abe, 1994; Dobson, 1994).

Effect of isolation on diversity
The islands of Amami-Oshima and Okinawa (Ryukyu islands) are depauperate in number of species (Table 2, Fig. 6). These two islands are very far from the mainland (more than 600 km) and are surrounded by the 500 m bathymetric line. Interestingly, some fossil arvicolid rodents from the Late Pleistocene were

recently discovered in the Ryukyu Islands (Kaneko & Hasegawa, 1995). Even if this fossil assemblage was not actually found on the islands of Okinawa or Amami-Oshima, it is not improbable that some arvicolid rodents could also have occurred on these two islands during the Late Pleistocene. Under this hypothesis, the living fauna of the Ryukyu islands would be a relict of a more diverse one that occurred during the Pleistocene and suffered extinction unbalanced by colonization because of their great isolation. Adding the two fossil rodent species to the number of species present on both Okinawa and Amami-Oshima islands makes the values for these islands fall within the 95% confidence of the regression line computed for all the twelve islands considered (Eq. 1). These results are thus in accordance with a nonequilibrium (relict) model.

Effect of land-bridge connections on diversity
The island of Oki (North of western Honshu) supports more species than expected based on its area (Table 2, Fig. 6). The oceanic trench between Honshu and Oki island is less than 90 m in depth and the distance from Oki to Honshu is very small (63 km). As a consequence, some land bridge connections must have occurred between this small island and Honshu during last Glacial Age, thus allowing some immigrant species from Honshu to colonize Oki island.

Island area and abundance of endemic species

Island area and number of endemic species to Japan are significantly correlated ($Log\#END = 0.136 + 0.187$ LogArea, $R = 0.649$, $P < 0.022$; Fig. 7A). It can be noticed that the two islands of Hokkaido and Rishiri have a low number of endemic species, when compared to area and also a very low proportion of endemics (Fig. 7A and B). When not taking into account these two islands, the relationship between area and number of endemic species is stronger ($Log\#END = 0.164 + 0.214$ LogArea, $R = 0.820$, $P < 0.004$). This result support the hypothesis of the occurence of a continuous land bridge connection between Hokkaido and the Asiatic mainland through the Sakhalin island during the whole Pleistocene. In contrast, the island of Sado has a high number of endemic species relative to its area. Despite its very small distance to the main island of Honshu (32 km), Sado Island is isolated by a deep marine channel (between 400 and 500 m) and probably

Table 2 Area, composition of the terrestrial mammalian fauna, and geographical parameters from 12 selected islands of the Japanese archipelago, introduced species excluded. Di: minimum distance to the mainland or to the nearest larger island; Dm: minimum distance to the mainland; Maxdepth: maximum depth between an island and the mainland or the nearest larger island; Elevation: maximum elevation; Latitude: mean latitude (North).

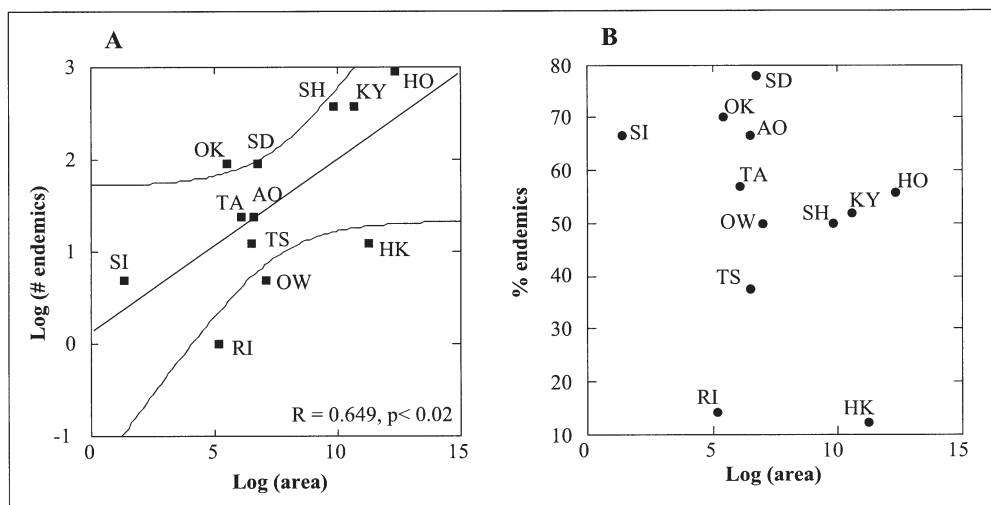|	Area (km²)	No. of sp.	No. of sp. end. to Japan	% sp. end. to Japan	Di (km)	Dm (km)	Max depth (m)	Elevation (m)	Latitude (°N)
Hokkaido	78511	24	3	12.5	24	285	130	2290	43.5
Rishiri	183	7	1	14.3	21	255	75	1719	45
Honshu	230510	34	19	55.9	184	184	130	3776	37.5
Sado	857	9	7	77.8	32	674	450	1173	38
Oki	243	10	7	70.0	63	316	85	608	36
Shikine	4	3	2	66.7	41	867	350	50	34.5
Shikoku	18765	26	13	50.0	6	245			

Figure 7 Relationship between number of endemic species in the fauna and island size (A) and between the proportion of endemics and island size (B). The two islands Hokkaido (HK) and Rishiri (RI) support a very small proportion of endemics. Abbreviations for island names are the same as in Figure 6.

lacked a land bridge connection during the Pleistocene to the main island of Honshu. In this case, isolation seems to have promoted endemism, with six of the nine species that occur on Sado being endemic to Japan, and one shrew (*Sorex sadonis*) restricted to Sado Island. Finally, Tsushima Island is separated from Honshu by a strait of 130 m in depth, and from Korea by a strait of 130 m as well. The maximum sea lowering during the Middle Pleistocene (around 150,000 years BP) was estimated at 130 m ± 10 m below its current position (Oshima, 1990) and the depth of the next sea-lowering during Late Pleistocene (around 20,000 years BP) is still under discussion, and values varies from –85 m to –130 m in the Sea of Japan (Fig. 3; Chappell & Shackleton, 1986; Morley *et al.*, 1986; Fujii, 1990; Oshima, 1990; Burckle, 1992; Keigwin & Gorbarenko, 1992; Tushingham & Peltier, 1993). Some palaeoceanographic studies recently suggested that the Korean strait between Korea and Tsushima was never completely closed during the maximum sea lowering of the Late Pleistocene (Morley *et al.*, 1986; Fujii, 1990; Oshima, 1990). Additionally, the analysis of faunal similarity of the Japanese islands clearly indicates the peculiarity of Tsushima when compared to the whole Hondo area (Fig. 5). However, the relatively low proportion of endemic species suggests a short period of isolation for Tsushima Island. Additionally, the species *Prionailurus bengalensis* is found in Tsushima Island and originates from the Asiatic adjacent mainland. All these observations support the existence of a land bridge connection between Tsushima Island and Korea during the Pleistocene, whereas a connection between Tsushima Island and Honshu seems less likely.

Effect of isolation on diversity

Environmental parameters other than area can greatly influence the species richness of a given island. A second prediction of

the MacArthur & Wilson (1967) model is that the number of species on islands decreases with isolation.

Three variables can be used to quantify the isolation of a given island (Table 2): Dm, the minimum distance from this island to the mainland; Di, the minimum distance from this island to the mainland or a larger island; and Maxdepth: the maximum depth of marine channel between this island and the closest larger island. Two other environmental parameters were also considered: the maximum elevation of a given island, which is supposed to be related to the environmental heterogeneity, and the mean latitude of this island (Table 2).

The matrix of Pearson correlation coefficients between all these variables is given for log-transformed variables in Table 3. Species richness was significantly correlated with island area ($P < 0.001$), elevation ($P < 0.01$), and maximum depth ($P < 0.05$). Additionally, there was no significant relationship between species richness and isolation expressed by distance, whether it was distance to the mainland or distance to the closest larger island. Finally, the negative correlation with richness was stronger for distance to the mainland than for interislands distance. This corroborates the geological hypothesis that all the Japanese islands are of the same age, and had a common faunal source area, i.e. the adjacent mainland, during the last sea-level drop of Late Pleistocene.

Following the method proposed in Crowell (1986), we computed a stepwise multiple regression analysis to test for the effect of the variable MaxDepth on species richness (Table 4). Maximum depth to the closest island, MaxDepth, was entered just after area in the model, and as isolation expressed by MaxDepth increases, species richness decreases (coefficient of –0.280, $P < 0.005$). The best multivariate model that explains species richness on a given island can be expressed by the following equation: Log (#sp.) = 2.269 + 0.198 Log (Area) –0.280 Log (MaxDepth) ($R = 0.964$, $P < 0.000$). This result

Table 3 Pearson correlation matrix of environmental parameters and species richness for 12 selected islands of the Japanese archipelago, for log-transformed variables. Species richness is highly correlated to area and elevation. * $P <0.05$; ** $P<0.01$; *** $P<0.001$

	No. of sp.	Di	Dm	Max depth	Elevation	Latitude
Area	0.905***	−0.237	−0.445	−0.370	0.854***	0.137
No. of sp.		−0.467	−0.525	−0.643*	0.826**	0.376
Di			0.275	0.704*	−0.229	−0.282
Dm				0.611*	−0.495	−0.312
Max depth					−0.413	−0.438
Elevation						0.400

Table 4 Results of a stepwise multiple regression analysis. Species richness can be explained by area and maximum depth to the closest island (Max depth) which is entered into the model in second rank

Parameter	Coefficient	P	Contrib. to R^2
Log (Area)	0.198	0.000	0.818
Log (Max depth)	−0.280	0.005	0.111

points to the strong influence of deep oceanic channels as barriers to colonization of small islands.

Island area and species composition

Community structure
The relationship between island area and the proportion (expressed in percentage of species) of primates, lagomorphs and artiodactyls was not significant (R = 0.12, $P>0.70$; R = 0.14, $P>0.66$ and $R = 0.26$, $P>0.41$, respectively). Smaller islands tend to support a higher proportion of insectivores, although this relationship was not significant ($R = −0.55$, $P>0.06$). By contrast, small islands are impoverished in carnivores and support larger rodent faunas. As island size increases, proportion of rodents in the mammalian fauna decreases ($R = −0.82$, $P< 0.001$), while proportion of carnivores increases ($R = 0.72$, $P< 0.008$). This is in accordance with the prediction that carnivores as well as large bodied mammals will suffer higher extinction rates on small islands than herbivores or small mammals.

We ranked islands by increasing species richness, and species were ranked by increasing occurrence frequency (Fig. 8). Patterson & Atmar (1986) used this particular representation to describe the nested community structure of land-bridge islands. In order to quantify the degree of nestedness of the Japanese fauna, we used the Nestedness Calculator described in Atmar & Patterson (1995). The matrix temperatures that reflect the degree of nestedness of the fauna were computed for the whole set of data that includes twelve islands from all the Japanese area, but also for a subset of eight islands located in the Hondo area that does not include Hokkaido and Rishiri islands located in most Northern Japan, and Okinawa and Amami-Oshima islands from the Ryukyus islands, in South. For the two data sets, the probability to find as highly nested matrix at random are very low. Monte-Carlo simulations gave P-values of 2.24e-10 for the twelve islands set, and 9.13e-13 for the eight islands subset (Fig. 8). However, the matrix temperature computed for all the twelve islands from Japan is still quite high (19.9°), whereas this value is very low when

considering only islands from the Hondo area (7.28°). Low temperatures reflect a strong degree of nestedness and are typical of relict faunas and floras (Wright *et al.*, 1998). This result supports the existence of different biogeographic regions in Japan. The relatively high *T*-value found for all the Japanese archipelago can be easily explained by the different geographical histories of the Japanese fauna. Whereas the Ryukyus islands are highly isolated, Hokkaido and small adjacent islands were more often connected to the adjacent mainland during the Quaternary, which should have promote species turnover in this region. In contrast, the high degree of nestedness found for Hondo area indicates that the fauna was initially homogenous before the fragmentation of the Japanese archipelago into several islands. There are, however, a few exceptions in our data set.
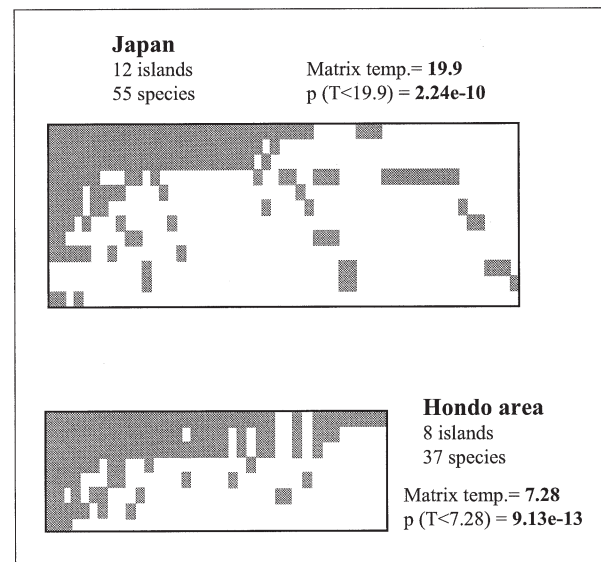

Figure 8 Matrix of presence-absence of terrestrial mammalian species for twelve islands in Japan (above), and for eight islands within the Hondo area (below). Islands are arranged by increasing species richness, while species are arranged by increasing frequency occurrence. All the two data sets show a significant degree of nestedness, but the subset of eight islands has a very low matrix temperature (high degree of nestedness) wich is typical for relict faunas. The matrices temperatures and associated probabilities were computed using the Nestedness Calculator of Atmar & Patterson (1995).

Deviations from perfect nestedness

Human populations can disturb the distribution of mammals and cause extinctions by hunting. They can also promote introductions from the mainland, or from a large island to a smaller one. Within the Hondo area, the pattern of perfect nestedness is disrupted by species endemic to a single island (*S. sadonis, S. suaevolens*) which can be explained by the local differentiation of species. The cat *P. bengalensis* is present only on Tsushima Island and is clearly a Korean form (Imaizumi, 1970). It is quite surprising to find the mole *M. tokudae* on both Honshu and Sado islands as it seems that Sado was never connected to other islands, even during the last maximum sea-lowering. One hypothesis is that this species was introduced to Sado Island by humans in historical times. The distribution pattern of the vole *P. smithii* is not in accordance with the general pattern of perfect nestedness since it is present only on the largest island Honshu and the small neighbouring island of Oki. In that case, two hypotheses, a land bridge connection between Oki and Honshu or a human introduction of that vole in Oki, are possible. Under the hypothesis of perfect nestedness, the deer *Cervus nippon* should be present in Oki and Sado islands. The great isolation of Sado Island should have prevented this species from colonizing, while the small area of Oki may have been a limiting factor to its long-term establishment on the island. An alternative hypothesis is the local extinction of the deer which is very sensitive to human disturbance (Dobson, 1994). The vole *Microtus montebelli* appears to have been carried by human agent very recently to Sado Island (Dobson, 1994). Finally, it is difficult to interpret the absence of the widespread species, *Crocidura dsinezumi*, on Tsushima Island.

Extinctions of the Pleistocene fauna

Data from Hasegawa (1977), Kamei (1981), Kawamura *et al*. (1989) and Kawamura (1991) were compiled to constitute the composition of the Quaternary terrestrial mammal fauna of Japan. The Early Pleistocene fauna is a temperate forest type fauna largely shared with those of North China (*Elaphurus, Cervus, Mammuthus* . . .). However, these forms are mostly endemic at the specific level, which indicates that the Japanese islands were already isolated from the mainland. The Middle Pleistocene fauna is dominated by temperate forest forms and endemic species, and is also characterized by the presence of living species (*Apodemus argenteus* and *A. speciosus, Sorex shinto, Crocidura dsinezumi, Canis lupus* . . .). The Late Pleistocene fauna is characterized by the appearance of a few large herbivorous steppe forms (*Equus, Bison* . . .) that migrated from the north, via Hokkaido. After the extinction of many species between 20,000 BP and 10,000 BP, possibly accentuated by human hunting, the Holocene fauna became almost identical to that of the present day.

The following part is limited to the study of the mammalian fauna from Hondo area which shows the most complete fossil record.

The difference between Pleistocene and modern mammal

Table 5 Number of living and extinct genera of terrestrial mammals in Hondo area. The fauna suffered almost 50% of extinction since the establishment of the fauna, in Early Middle Pleistocene

	No. living	No. extinct	No. total	% extinction
Rodentia	9 (33.33)	3 (12.50)	12	25
Insectivora	6 (22.22)	3 (12.50)	9	33.33
Carnivora	7 (25.93)	1 (4.17)	8	12.50
Lagomorpha	1 (3.70)	0	1	0
Artiodactyla	3 (11.11)	10 (37.04)	13	76.92
Proboscidea	0	3 (12.50)	3	100
Perissodactyla	0	3 (12.50)	3	100
Primates	1 (3.70)	0	1	0
Total	27	24	51	47.06

faunas is quite striking (Table 5). Whereas the modern fauna is dominated by small mammals (Rodentia, Insectivora and Lagomorpha), the Early Pleistocene fauna is dominated by large herbivores (Artiodactyla and Proboscidea) in relative proportion of genera (Fig. 9). Artiodactyls suffered a high degree of extinction at the end of the Pleistocene, 76.9% of the fossil genera being absent from the living fauna (Table 5). The Proboscidian genera *Stegodon* and *Mammuthus* became extinct at the end of the Middle Pleistocene, while the remaining genus, *Palaeloxodon*, remained present until the end of the Pleistocene. Perissodactyls (*Rhinoceros, Dicerorhinus* and *Equus*), were represented in the Middle and Late Pleistocene faunas but all these taxa became extinct in Japan during Holocene. Carnivores became quite abundant in Middle Pleistocene, and only one genus (*Panthera*) out of nine became extinct recently. Lagomorphs (*Lepus*) and Primates (*Macaca*) have never been well represented in the Japanese fauna, each of them accounting for one genus. Concerning small mammals, the number of genera of Rodents and Insectivores was less reduced than for large mammals, 33.33% and 25% of the genera being extinct, respectively (Table 5). However, the composition in genera has changed, and some speciation have occurred among rodents (from *Clethrionomys japonicus*, an extinct species, to the extant species *Phaulomys smithii and P. andersoni*).

There was thus a shift from palaeocommunities dominated by large mammals to modern communities dominated by small mammals (Fig. 9). The extinction of large bodied mammals during the last 10,000 years is probably associated with the progressive shift from a cold to a warm temperate climate and corroborates the general rule that large bodied mammals are more susceptible to extinction than small ones.

For terrestrial mammalian species, we found a reduction of 47.06%, from fifty-one to twenty-seven genera, between the Quaternary and the living faunas (Table 5). We can estimate that the last land bridge connection between the Japanese archipelago and the Asiatic mainland, via Hokkaido and Sakhalin islands occurred during the sea-lowering of the late Pleistocene (around 20,000 years BP). This is attested by the migration from north to Honshu of large boreal herbivores at that time. This low sea-stand was followed by a transgression, and Honshu remained isolated from the mainland until nowadays. The extinction rate of the Japanese fauna can thus
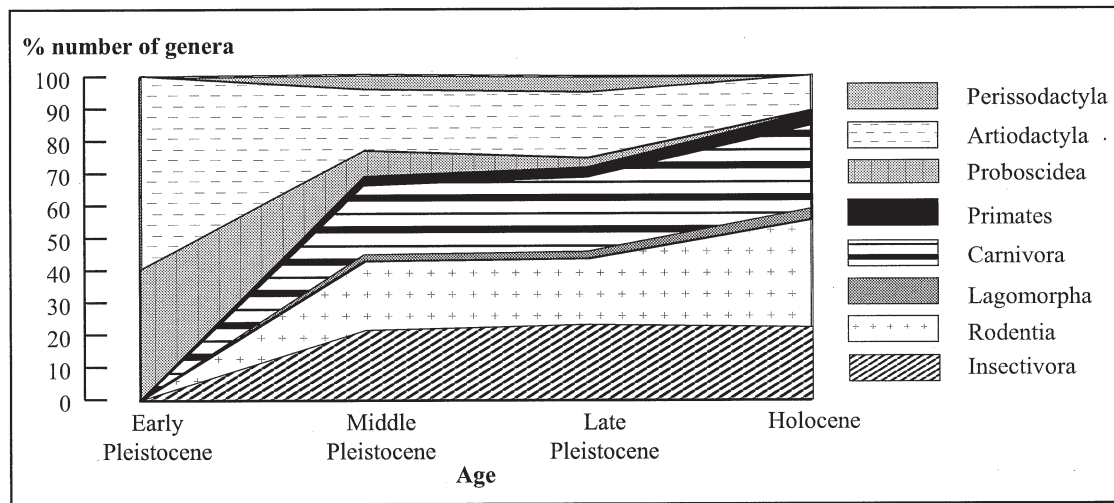
Figure 9 Evolution of the Pleistocene Japanese terrestrial mammalian fauna in proportion of genera. There is a shift from a fauna dominated by large herbivores to a fauna dominated by small mammals.

be estimated at about twelve genera per 10,000 years, knowing that the extinction rate was not constant and that most of the extinctions events occurred 10,000 BP.

CONCLUSION

The present day Japanese terrestrial mammal fauna is characterized by a high degree of endemism at the species level (40%) and is dominated by small mammals (rodents and insectivores).

The mammal composition of twelve selected islands of the Japanese archipelago revealed that large bodied mammals and carnivores have been more sensitive to extinction than small mammals. This result is in accordance with the rules that govern the persistence of species on land-bridge islands suggested by Brown (1971) and are similar to those found in SE Asia archipelagos (Heaney, 1986) and for the small mammals of the Rocky Mountains (Patterson, 1984).

The first prediction of the MacArthur & Wilson equilibrium theory (1963; 1967) is upheld. The species richness on island increases with island area ($R = 0.905$). However, there were some deviations from this general rule. In particular, we showed the relative importance of interisland colonization on richness, which can be favoured by land-bridge connections, or prevented by deep marine channels. The slope of the regression line between species richness and area is intermediate between low values computed for mainland and higher ones found for true oceanic islands. This intermediate value falls within the interval proposed by Lawlor (1986) for typical land-bridge islands.

The second prediction of the MacArthur & Wilson (1967) theory is that the number of species on an island is inversely related to its distance from the primary faunal source area. This prediction was not confirmed in our study, whether we considered distance to the mainland or distance to the closest larger island. On the contrary, oceanic depth between islands played a significant role in regulating richness, following that

of area. This result emphasizes the major role played by interisland colonization events on diversity, both within evolutionary and historical time scales.

Another prediction of the equilibrium theory is that small area promotes endemism, and we found the island size to be significantly correlated with the number of endemic species. In addition, we showed that endemism was related to the presence of deep oceanic channels.

The nonrandom pattern of distribution of mammals on islands within Hondo area demonstrates the importance of postglacial selective extinctions that are not balanced by colonization or local speciation processes (Patterson & Atmar, 1986; Atmar & Patterson, 1993; Wright et al., 1998). This observation is in accordance with the fossil record which assess for the existence of some local extinctions unbalanced by colonization or speciation processes, and is illustrated by the extinction of most of the large mammal fauna after the last Glacial, or by the extinction of the vole in the Ryukyu islands.

The present distribution of the terrestrial mammal fauna in Japan is thus the result of postglacial extinctions which were not compensated for by colonization of new species from the faunal source pool. Our study emphasized the potential role played by interisland colonizations, from larger islands to smaller ones. We couldn't decide whether the immigrant populations are long-term resident species or are implicated in a continuous extinction-colonization cycle. The proximity of a small island to a larger one indeed increases the probability of dispersal, if deep-sea trenches do not separate them, whereas the small area of the island reached cannot allow the long-term establishment of new taxa. In order to test for these two hypotheses, we suggest a study of the phenotypic variation (especially the size) of a particular taxon within the Japanese archipelago. A species which has become established on a small island isolated from the larger island should indeed present some morphological differences from the population on the larger island (source area), whereas there should be no

differences between the two populations under the hypothesis of a continuous colonization-extinction cycle.

ACKNOWLEDGMENTS

REFERENCES

Abe, H. (1994) *A pictorial guide to the mammals of Japan*, 195 pp. Tokaidi University Press, Tokyo (in Japanese).

Atmar, W. & Patterson, B.D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia,* 96, 373–382.

Atmar, W. & Patterson, B.D. (1995) *The nestedness temperature calculator: a Visual Basic program, including 294 presence–absence matrices*. AICS Research, Inc., University Park, NM and Field Museum, Chicago (http://aics–research.com/nestedness/tempcalc.html).

Brown, J.H. (1971) Mammals on mountaintops: non-equilibrium insular biogeography. *Am. Nat.* 105, 467–478.

Burckle, L.H. (1992) Diatom biostratigraphy: leg 128. *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 127/128, Part 1 (ed. by K. A. Pisciotto, J. C. Ingle Jr, M. T. VonBreymann, J. Barron *et al.*), pp. 359–363. College Station, TX (Ocean Drilling Program).

Chappell, J. & Shackleton, N.J. (1986) Oxygen isotopes and sea-level. *Nature*, 324, 137–140.

Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species-area relationship. *Am. Nat.* 113, 791–833.

Corbet, G.B. (1978) *The mammals of the Palearctic region: a taxonomic review*. British Museum (Nat. Hist.), London.

Corbet, G.B. & Hill, J.E. (1992) *The mammals of the Indomalayan region: a systematic review*, 488 pp. Oxford University Press, Oxford.

Crowell, K.L. (1986) A comparison of relict versus equilibrium models for insular mammals of the Gulf of Maine. *Biol. J. Linnean Soc.* 28, 37–64.

Dobson, M. (1994) Patterns of distribution in Japanese land mammals. *Mammal Rev.* 24, 91–111.

Fujii, S. (1990) Changes of the palaeoenvironment along the Japan Sea since the Early Pleistocene. *Quat. Res. (Daiyonki-Kenkyu),* 29, 173–182 (in Japanese, English summary).

Hasegawa, Y. (1977) History and distribution of vertebrates. *Quaternary studies in Japan* (ed. by Japan Ass. Quat. Res.), pp. 227–243. University of Tokyo Press, Tokyo (in Japanese).

Hasegawa, Y. (1980) Note on vertebrate fossils from Late Pleistocene to Holocene of Ryukyu Islands, Japan. *Quat. Res. (Daiyonki-Kenkyu)* 18, 263–267 (in Japanese, English summary).

Hasegawa, Y., Tomida, Y., Kohno, N., Ono, K., Nokariya, H. & Uyeno, T. (1988) Quaternary vertebrates from Shiriya area, Shimokita Peninsula, northeastern Japan. *Mem. Nat. Sci. Mus.* 21, 17–36 (in Japanese, English summary).

Hashimoto, M. (1991) *Geology of Japan*, 249 pp. Terra Scientific Publishing Company, Tokyo.

Hayashida, A. (1986) Timing of rotational motion of Southwest Japan inferred from paleomagnetism of the Setouchi Miocene Series. *J. Geomag. Geoelectr.*, 38, 295–310.

Hayashida, A. & Fukui. T. (1991) Paleomagnetism of the early Miocene Kani Group in Southwest Japan and its implication for the opening of the Japan Sea. *Geophys. Res. Letts*, 18, 1095–1098.

Hayashida, A. & Ito, Y. (1984) Paleoposition of Southwest Japan at 16 Ma: implication from paleomagnetism of the Miocene Ichishi Group. *Earth Planet. Sci. Letts*, 68, 335–342.

Hayashida, A., Otofuji, Y.I. & Torii, M. (1988) Paleoposition of Southwest Japan and Convergence between Eurasia and Pacific plates in pre-Neogene time. *Modern Geol.*, 12, 467–480.

Heaney, L.R. (1986) Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. *Biol. J. Linnean Soc.* 28, 127–165.

Heusser, L.E. (1992a) Neogene palynology of holes 794A, 795A, and 797B in the Sea of Japan: stratigraphic and paleoenvironmental implications of the preliminary results. *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 127/128, Part 1 (ed. by K. A. Pisciotto, J. C. Ingle Jr, M. T. VonBreymann, J. Barron *et al.*), pp. 325–339. College Station, TX (Ocean Drilling Program).

Heusser, L.E. (1992b) Preliminary results of high-resolution pollen analyses of selected Pleistocene intervals from holes 798A, 798B, and 798C. *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 127/128, Part 1 (ed. by K. A. Pisciotto, J. C. Ingle Jr, M. T. VonBreymann, J. Barron *et al.*), pp. 317–324. College Station, TX (Ocean Drilling Program).

Imaizumi, Y. (1970) Land mammals of the Tsushima Islands, Japan. *Mem. Nat. Sci. Mus*. 3, 160–176 (in Japanese, English summary).

Janson, S. & Vegelius, J. (1981) Measures of ecological association. *Oecologia*, 49, 371–376.

Jolivet, L. & Tamaki, K. (1992) Neogene kinematics in the Japan Sea region and volcanic activity of the northeast Japan arc. *Proceedings of the Ocean Drilling Program, Scientific Results*, Vol. 127/128, Part 2 (ed. by K. Tamaki, K. Suyehiro, J. Allan, M. McWilliams *et al.*), pp. 1311–1331. College Station, TX (Ocean Drilling Program).

Kamei, T. (1962) Some problems on the succession of the Quaternary mammalian faunas in Japan. *Earth Sci. (Chikyu-Kagaku),* 60/61, 23–34 (in Japanese, English summary).

Kamei, T. (1981) Faunal succession of Pleistocene mammals in the Japanese islands: an aspect. *Quartärpaläontologie*, 4, 165–174.

Kamei, T. & Res. Group for Biogeography from Würm glacial (1981) Fauna and flora of the Japanese islands in the last glacial time. *Quat. Res. (Daiyonki-Kenkyu),* 20, 191–205 (in Japanese, English summary).

Kamei, T., Kawamura, Y. & Taruno, H. (1987) Quaternary environments and the migration of mammals to the Japanese islands. *Abstr. Int. Union Quat. Res., XIIth Int. Congr.*, 197.

Kamei, T., Taruno, H. & Kawamura, Y. (1988) Implication of mammal fauna for the Quaternary geohistory of the Japanese islands. *Quat. Res. (Daiyonki-Kenkyu).* 26, 293–303 (in Japanese, English summary).

Kaneko, Y. (1985) Geographical distribution of terrestrial mammals in Japan and ecological distribution of small field rodents in Shikoku. *Contemporary mammalogy in China and Japan* (ed. by T. Kawamichi), pp. 28–32. Mammalogical Society of Japan, Tokyo.

Kaneko, Y. & Hasegawa, Y. (1995) Some fossil arvicolid rodents from the Pinza-Abu cave, Miyako island, the Ryukyu islands, Japan. *Bull. Biogeogr. Soc. Japan,* 50, 23–37.

Kawamura, Y. (1989) Quaternary rodent faunas in the Japanese islands (Part 2). *Memoirs of the Faculty of Science*, LIV, 1–235.

Kawamura, Y. (1991) Late Pleistocene to Holocene mammalian faunal succession in the Japanese islands, with comments on the Late Quaternary extinctions. *Abstr. Int. Union Quat. Res., XIIIth Int. Congr.*, 160.

Kawamura, Y. (1991) Quaternary mammalian faunas in the Japanese islands. *Quat. Res. (Daiyonki-Kenkyu).* 30, 213–220.

Kawamura, Y., Kamei, T. & Taruno, H. (1989) Middle and Late Pleistocene mammalian faunas in Japan. *Quat. Res. (Daiyonki-Kenkyu).* 28, 317–326 (in Japanese, English summary).

Keigwin, L.D. & Gorbarenko, S.A. (1992) Sea level, surface salinity of the Japan Sea, and the Younger Dryas event in the Northwestern Pacific Ocean. *Quat. Res. (N.Y),* 37, 346–360.

Kowalski, K. & Hasegawa, Y. (1976) Quaternary rodents from Japan. *Bull. Natn. Sci. Mus., Series C (Geol.).* 2, 1–70.

Kuroda, N. (1939) Distribution of mammals in the Japanese Empire. *J. Mammal.* 20, 37–50.

Lawlor, T.E. (1986) Comparative biogeography of mammals on islands. *Biol. J. Linnean Soc.* 28, 99–105.

Lomolino, M.V. (1986) Mammalian community structure on islands: the importance of immigration, extinction and interactive effects. *Biol. J. Linnean Soc.* 28, 1–21.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution,* 17, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography.* Princeton University Press, Princeton.

Morley, J.J., Heusser, L.E. & Sarra, T. (1986) Latest Pleistocene and Holocene palaeoenvironment of Japan and its marginal sea. *Palaeogeogr., Palaeoclim., Palaeoecol.* 53, 349–358.

Nowak, R.M. & Paradiso, J.L. (1990) *Walker's mammals of the World,* 1629 pp. Johns Hopkins University Press, Baltimore.

Oshima, K. 1990) The history of straits around the Japanese islands in the Late-Quaternary. *Quat. Res. (Daiyonki-Kenkyu).* 29, 193–208 (in Japanese, English summary).

Ota, Y. & Omura, A. (1991) Late Quaternary shorelines in the Japanese islands. *Quat. Res. (Daiyonki-Kenkyu).* 30, 175–186.

Otufuji, Y.-I., Hahashida, A., Torii, M. (1985) When was the Japan Sea opened?: paleomagnetic evidence from Southwest Japan. *Formation of active ocean margins* (ed. by N. Nasu et al.), pp. 551–556. Terra Scientific Publishing Company (TERRAPUB), Tokyo.

Patterson, B.D. (1984) Mammalian extinction and biogeography in the Southern Rocky Mountains. *Extinctions* (ed. by M. H. Nitecki), pp. 247–293. University of Chicago Press, Chicago.

Patterson, B.D. & Atmar, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linnean Soc.,* 28, 65–82.

Tokuda, M. (1941) A revised monograph of the Japanese and Manchou-Korean Muridae. *Biographica, Transact. Biogeogr. Soc. Japan,* 4, 1–156.

Tushingham, A.M. & Peltier, W.R. (1993) Implications of the radiocarbon timescale for ice-sheet chronology and sea-level change. *Quat. Res. (N.Y.),* 39, 125–129.

Wallace, A. R. (1892) *Island life,* 2nd edn, 563 pp. MacMillan, London.

Wilson, D.E. & Reeder, D.M. (1993) *Mammal species of the World. A taxonomic and geographic reference,* 1206 pp. Smithsonian Institution Press, Washington.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. & Atmar, W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia,* 113, 1–20.

BIOSKETCH

Virginie Millien-Parra is a graduate student. Her thesis topic is rodent community size structure and its evolution on islands, based on a synthesis of paleontological, ecological and biogeographical approaches. She has published on the effect of competition between species on rodent community size structure and on morphological and size evolution of rodent species on islands. Her current research aims to identify the role of competition in the composition and evolution of mammal communities on islands.

Appendix Terrestrial mammalian species for twelve selected islands in the Japanese archipelago, introduced species excluded. * denote species endemic to the Japanese archipelago. Abbreviations for island names are the following: HK, Hokkaido; RI, Rishiri; HO, Honshu; SK, Shikoku; KY, Kyushu; SD, Sado; OK, Oki; TS, Tsushima; TA, Tane; SI, Shikine; OW, Okinawa; AO, Amami-Oshima.

Species	HK	RI	HO	SK	KY	OK	SD	TS	SI	TA	AO	OW
RODENTIA												
Apodemus argenteus*	+		+	+	+	+	+	+		+		
A. peninsulae	+											
A. speciosus*	+	+	+	+	+	+	+	+	+	+		
Clethrionomys rufocanus	+	+										
C. rutilus	+											
Diplothrix legatus											+	+
Glirulus japonicus*			+	+	+	+						
Microtus montebelli*			+		+		+					
Phaulomys andersoni*			+									
P. smithii*			+			+						
Petaurista leucogenys*			+	+	+							
Pteromys momonga*			+	+	+							
P. volans	+											
Rattus norvegicus	+	+	+	+	+	+	+	+	+	+		
Sciurus lis*			+	+	+							
S. vulgaris	+											
Tokudaia muenninki*												+
T. osimensis*											+	
Tamias sibiricus	+	+	+	+	+							
PRIMATES												
Macaca fuscata*			+	+	+					+		
LAGOMORPHA												
Lepus brachyurus*			+	+	+	+	+					
L. timidus	+											
Ochotona hyperborea	+											
Pentalagus furnesi											+	
INSECTIVORA												
Crocidura dsinezumi*	+		+	+	+	+	+		+	+		
C. horzfieldii											+	+
C. orii											+	
Chimarrogale platycephara			+	+	+							
Euroscaptor mizura*			+									
Mogera robusta			+	+	+	+				+		
M. tokudae*			+				+					
M. wogura*			+	+								
Sorex gracillumus	+											
S. hosonoi*			+									
S. minutissimus	+	+										
S. sadonis*							+					
S. shinto	+		+	+								
S. suaevolens*								+				
S. unguiculatus	+	+										
Urotrichus pilirostris*			+	+	+							
U. talpoides*			+	+	+	+		+				
CARNIVORA												
Canis lupus	+		+	+	+							
Mustela erminea	+		+									
M. nivalis	+		+									
Meles meles			+	+	+							
Martes melampus			+	+	+			+				
M. zibellina	+											
Nictereutes procyonoides	+		+	+	+	+	+					
Prionailurus bengalensis								+				
Ursus arctos	+											
U. thibetanus			+	+	+							
Vulpes vulpes	+	+	+	+	+							
ARTIODACTYLA												
Cervus nippon	+		+	+	+			+		+		
Sus scrofa			+	+	+						+	+
Capricornis crispus*			+	+	+							