Preface to the Second Number of the Special Issue: Natural Environmental and Biotic Features and Ecological History of Biotic Migrations and Invasions into the Japanese Archipelago from Geological to Modern Ages

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Prologue

Modern biological invasions in Japan are having various types of serious impacts on ecosystems and human life, and appropriate countermeasures are urgently needed (Washitani, 2004). In contrast, when historically viewed on a much longer time scale, major factors responsible for the unique indigenous flora and fauna of contemporary Japan included geo-biotic exchanges with the Eurasian Continent accompanied by intermittent isolations of the Japanese Archipelago, as well as its unique environmental conditions.

In the present essay, as a preface to the second number of the special issue, 'Biological invasion in Japan,' I will briefly summarize the natural environmental features, including geological, climatic and biotic, and the geological-ecological histories of the Japanese Archipelago, which have also interacted with human history and are relevant to the biotic exchanges with Eurasian Continent, in order to contrast them with modern biological invasions.

Key words: biological invasion, ecological history, migration

1. Geo-biotic Histories, Environmental Features and Biota

1.1 Geological origins of the Japanese Archipelago

The distribution of volcanic and sedimentary rocks in northeastern and lowland Japan suggests the date of formation of the geological basis of the present Japanese Archipelago was in the Miocene era (approximately 22 million years ago) (Taira, 1983). The Sea of Japan is a young marginal basin located between Japan and the Asian Continent and is inferred to have been formed in the middle Miocene, i.e., about 15 million years ago (Chinzei, 1991). Before that geological age, the Japanese islands were not separated from the Eurasian Continent, but formed the eastern end of the continent.

During earlier geological ages, parts of the Japanese Archipelago were assembled at the eastern border of the Eurasian Continent through stepwise fusions of landmasses conveyed by oceanic plate movement (Hashimoto, 1991). The first arrival of a landmass, which had been derived from an old equatorial continent, was dated to the beginning of the Mesozoic era. The second arrival occurred in the Jurassic to early Cretaceous era when the main parts of the present Honshu, Shikoku, and Kyushu were assembled. At the next stage during the Cretaceous to Miocene era, the southwestern borders of Honshu, Shikoku and Kyushu and the main part of Hokkaido were added.

Deviation of magnetism of early Miocene rocks from that of older rocks supports the hypothesis that the Japanese Archipelago was located closer to the Asian continent before the middle Miocene when the southwestern and northeastern halves independently started to rotate clockwise and counterclockwise, respectively, to settle in the present position and configuration (Otofuji & Matsuca, 1984). This model well explains the current topographic and petrologic coincidences that can be recognized between the continental and Japanese coastlines facing the Sea of Japan.

The present island arc/submarine trench system became active at the beginning of the Tertiary (approximately 30 million years ago), when the basic nature of the relative movements of the Pacific plate and Eurasian plate was fixed.

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1.2 Volcanoes and rich natural disturbances

Natural or human disturbances play important roles in dynamic transitions of local biota, including biological invasions, through the generation of well illuminated gaps within dense vegetation or the release of resources occupied by competitive dominant species. Volcanic and seismic activities and flooding are the main causes of large-scale natural disturbances, which are major natural driving forces for biological invasions or transitions.

Around the globe, the spatial distribution of volcanoes is remarkably uneven, and more than 80% are clumped along continental borders or island arcs adjacent to trenches where ocean plates sink beneath continental plates (Machida, 2002). The Japanese Archipelago, which forms a northeast-southwest arc stretching along the eastern end of the Eurasian Continent over approximately 2,400 km, consists entirely of relatively new volcanic belts along a conspicuous plate subduction zone, where the plates of the western Pacific Ocean, i.e., the Pacific and Philippine plates, sink beneath the North American and Eurasian plates, respectively. Therefore, the Archipelago is especially rich in natural disturbances accompanying volcanic and seismic processes. More than the one tenth (86 out of 800 total) of active volcanoes in the world, including both active and dormant ones, are found along two lines consisting of the eastern and western Japanese volcanic zones (Sakaguchi *et al.*, 1976) where one-tenth of the portion of the earth energy responsible for volcanic eruptions and earthquakes is emitted, despite covering only 1/400 of the total land area of the globe (Ito, 1987).

Many volcanoes have their peaks at elevations above 3,000 m. Representative of those is Mt. Fuji, the highest mountain in Japan, rising to 3,776 m on the Pacific coast in central Honshu, the last eruption of which was recorded in 1707. Volcanic ash and other volcanic ejecta that are widely found in strata throughout the Japanese Archipelago enable us to infer the times, scales and impacts of past volcanic eruptions. The most violent eruption that occurred within the recent 10,000 years was that of the Kikai caldera in the sea near southern Kyushu located between the south end of Kyushu and Yakushima Island and dated back to 6,300 years ago (Machida, 2001). During the eruption, the pyroclastic flow spread across the sea not only to the mountain ranges of Yakushima Island but also an immense tract of the southern Kyushu region. One can easily imagine disasters sweeping away all animals and plants within range and vast void niches formed for biological invasions. On a time scale of tens of thousands of years, volcanic activities are likely to be one of the most important factors influencing the biota of the Archipelago.

Volcanic ash soils named andisols that are characterized by black color and fine particle size, and thus have large specific surface areas are widely distributed across temperate humid Japan, covering one-sixth of the total land surface and 27% of all agricultural lands (Takahashi & Shoji, 2002; Shoji & Takahashi, 2002).

1.3 Active geomorphological processes and rapid rivers

The mountainous condition of the Japanese Archipelago is the natural consequence of frequent volcanic eruptions and seismic activity. The mountains tend to be formed by volcanic ejecta or seismic land upheavals. More than three-quarters of the land surface of Japan consists of mountains that form the solid backbone of the Japanese Archipelago, while flat lands, including plateaus and lowlands, occupy only 26% of the total land area of Japan.

Due to steep mountainous topographies and climatic conditions with abundant precipitation, aquatic soil erosion and sedimentation occur actively throughout Japan. The volume of gravel and sand removed by erosion along a representative rapid river, the Kurobe River of central Honshu, is estimated to be as large as 6,000 m^3/km^2 per year (Hamada & Nakamura, 1999). Such a high erosion rate is globally exceptional. Active production and sedimentation of gravel, sand, silt and clay are the most conspicuous features of rapid Japanese rivers, and most plains in Japan are deltas or alluvial fans formed by riparian sedimentation during the recent 10,000 years (Kodansha International, 1999). Deposition of alluvial sediments as thick as 50-90 m is exceptionally rare world wide, but rather common in lowland Japan.

Various types of geomorphic processes on various scales which prevail over the islands result in a fine-grained mosaic of physical land conditions, in other words, highly spatially heterogeneous environmental conditions. Both scenic beauty and frequent natural disaster are the results of high geomorphic activities of the Japanese Archipelago. In addition to frequent disturbances, spatially heterogeneous environmental conditions consisting of a fine-grained mosaic are the most pronounced feature of the Japanese natural environment, enhancing biological diversity.

1.4 Climatic features

The present climate of Japan is generally temperate with annual mean temperatures of 10-18°C, although there are large seasonal fluctuations in both temperature and precipitation (Fukui, 1977). Compared to other regions at the same latitude, Japan is characterized by abundant annual precipitation and a large annual fluctuation of temperature characterized by summer heat comparable to the tropics and winter chilling comparable to the frigid zone (Kira *et al.*, 1976).

In addition to such a large thermal fluctuation, there are marked seasonal changes due to alteration of the circulation system. A global circulation pattern characterized by tropical monsoon systems is basically constant year round, but in the northern hemi-

sphere entire circulation systems shift north during summer (Study Group for Climate Impact and Application, 2002, 2004). Japan is located just at the latitudinal zone where tropical circulation systems alternate with subtropical, and extra-tropical with polar seasonally (Hamada & Nakamura, 1999). Therefore, within the range of the Japanese Archipelago, tropical circulation prevails in summer, but extra-tropical circulation, in autumn, winter, and spring. The meteorology under the influence of the tropical circulation system is characterized by the absence of fronts and migratory anticyclones. The weather is relatively invariable day-to-day, but variable within a day. In contrast, the extra-tropical circulation system brings about cyclically changing weather with a cycle of several days, according to the migration of fronts and migratory anticyclones from west to east.

In addition to the marked seasonality, there are great spatial thermal variations over the islands, which occur both horizontally (depending on latitude) and vertically (depending on altitude). An altitude a little below 2,000 m on the northern island of Hokkaido thermally corresponds that of 3,000 m in central Honshu. Mountainous tundra characterized by dwarf pine vegetation of Japanese stone pine (*Pinus pumila*) occurs above the altitude of 3,000 m in Honshu, but above 1,500 m in Hokkaido (Fukui, 1977).

Throughout the archipelago, annual precipitation generally ranges from 1,000 to 2,500 mm with an average of 1,700 mm (Fukui, 1977). Seasonal precipitation patterns contrast between the Pacific Ocean and the Japan Sea sides due to the monsoon, i.e., prevailing winds changing direction seasonally (southwest in summer vs. northeast in winter) as well as the presence of mountains along the backbone of the mainland (Yoshino, 1980a,b). The winter monsoon, from late September to late March, deposits rain and snow on the Japan Sea side and brings dry, windy weather to the Pacific side. In contrast, the summer monsoon from mid-April to early-September brings rain to the Pacific coast. Destructive typhoons often occur in late summer and early fall, causing natural disturbances such as landslides and floods.

In addition to this overall pattern, minor climatic variations resulting from the topographical complexity of the islands widen the range of variation of climatic conditions in Japan (Sakaguchi *et al.*, 1976). For example, a drier climate with annual precipitation of less than 1,000 -1,600 mm prevails in the area around the Seto inland sea, while annual precipitation reaches more than 8,000 mm in the mountainous regions of Yakushima Island off southern Kyushu (Hamada & Nakamura, 1999).

Abundant rainfall and prevailing mild temperatures throughout most of the country produce a lush vegetation cover and enable a variety of crops to be raised, except on mountainous terrain or in waterlogged regions.

1.5 Biomes

Biomes are major communities of plants and animals sharing similar life forms and environmental conditions. Individual biomes characterized by dominant types of vegetation are largely determined by major climatic conditions.

Most areas of Japan are blessed with abundant precipitation and temperatures mild enough to foster forests. Forest vegetation varies according to the great spatial thermal variations over the islands (Kira *et al.*, 1976), which occur both vertically (depending on latitude) and horizontally (depending on altitude). The warmth index (WI), the yearly accumulation of monthly mean temperatures in excess of 5°C (Kira & Yoshino, 1967), is useful for predicting the major biome types of a given region: WI>=180, subtropical evergreen forests; 180>WI>=80, warm temperate broad-leaved evergreen forests; 80>WI>=45, cool temperate broad-leaved deciduous forests; 45>WI>=15, sub-arctic coniferous evergreen forests; and WI<15, alpine tundra found at high altitudes.

The range of broad-leaved evergreen forests extends from Kyushu to Honshu's northern lowlands. Moving northwards along the Japanese Archipelago, the evergreen-deciduous demarcation descends gradually from above 1,000 m in Kyushu to sea level in northern Honshu. Representative deciduous trees are beech (*Fagus crenata*), katsura (*Cercidiphyllum japoicum*), maples such as *Acea japonicum* and *Acea mono*, oak (*Quercus mongolica*), and birch (*Betula ermanii*); while coniferous trees such as *Abies sacalinensis* and *Picea jezoensis* predominate in the north and on the eastern periphery of Hokkaido up to an altitude of 700 m (Kira *et al.*, 1976). There are semitropical rainforests in the Rukyu and Bonin (Ogasawara) islands of southern Japan.

Such a wide range of climatic conditions enables biological invasions from various climatic zones to occur with ease. Moreover, currently, the heat island phemomenon in mega-cities, where alien plants or animals are first introduced, is likely to facilitate the establishment subtropical animals and plants.

The large difference in winter snowfall between the Pacific and Japan Sea sides affects the actual ranges of individual biomes and also the distribution of tree species. Heavy snowfall on the side facing the Japan Sea results in specific adaptation in plants, and we can find certain evolutionary group pairs, ecotypes or species, one distributed only on the side facing the Pacific Ocean and the other, only on the side facing the Japan Sea (Ohwi, 1953). Susceptibility to biological invasions is likely to be somewhat lower in the regions facing the Japan Sea, where only plants and animals adapted to heavy snow can attain high fitness.

2. Japanese Biota and Factors Responsible for its Diversity

2.1 Species richness patterns

Ecologists have been trying hard to understand and theorize global biodiversity patterns such as spatial variability of species richness. A currently influential hypothesis is the so-called 'species richness-energy hypothesis' (Currie, 1991) or more generally, the 'species richness-climate hypothesis' (Rosenzweig, 1995). The hypothesis predicts that regional species diversity increases with increasing heat and water availability (Kerr, 2001). The empirical patterns of many taxonomic groups including terrestrial insects, vertebrates, and plants, and marine and aquatic taxa across most of the world strongly support this model (Gaston, 2000), although various other factors affecting regional or local species richness are well known (Rosenzweig, 1995; Huston, 1994).

The Japanese Archipelago is generally temperate, so intermediate species richness is expected according to the general 'species richness-energy' hypothesis (Huston, 1994). However, if the current species richness is compared with those of other island countries in temperate regions such as the British Isles and New Zealand, marked species richness, both total and per area, can be observed for mammals, reptiles, amphibians, freshwater fishes, and vascular plants (Table 1). Dragonfly taxa are notable, consisting of nearly 200 species (Sugimura *et al.*, 1999). In addition to climatic variability due to the large south-north range and geographical variation, active natural disturbances and fine-grained spatial heterogeneities resulting from unique geomorphic conditions would also be partially responsible for the biological diversity of the Japanese Archipelago.

Moreover, the biological-geographical history including that of human-nature interactions greatly influences the current pattern of regional species diversity, since species diversity is affected by the balance among immigration, speciation and extinction. As to extinction and immigration (transportation), humans have been exerting huge influences since prehistoric ages as will be described later.

The wealthy flora and fauna of the country embracing more than five thousand wild vascular plant species, 188 mammals, 250 breeding birds, 87 reptiles, 61 amphibians (WRI, 2001), and 197 dragonflies (Ishida, 1996), are ascribed not only to the various modes and scales of the present environmental variability throughout the country, but also to its unique land and biotic histories, as described below. Moreover, it is also related to the fact that the islands were least affected by the last glaciations, so that tertiary floral and faunal components have been well preserved.

2.2 Geographic separation leading to diversification

Populations of plants or animals of the same origin that have become mutually isolated due to geographical separation or other reasons are expected to evolve along different paths, not only by chance but also as the result of different environmental conditions exerting different selective forces (Hey, 2001; Tuewlli *et al.*, 2001).

Plate tectonic landmass movement and other geomorphic processes as well as colonization of organisms into the new regions provide opportunities for producing 'geographically separated conditions' facilitating species diversification. In addition, geomorphic processes and climatic changes may bring out new selective forces for biological diversification. Although species differ greatly in their abilities to disperse and adapt to new environments, and thus respond to environmental changes differently, large-scale geomorphic events such as landmass movement or the formation of geographic barriers, i.e., seas, continents and mountain ranges affects the whole biota.

At the beginning of the Triassic, the present continents of the world were part of one large super-continent named Pangaea, which covered about one-quarter of the Earth's surface. Late in the Triassic Period (245 to 208 million years ago), Pangaea began to break apart and its segments, Laurasia (the origin of all the present-day northern continents) and Gondwanaland (the origin of all of the present-day southern continents), gradually separated, resulting in the formation of the Atlantic Ocean. Probably reflecting the Pangaea splitting events, we can recognize floral or faunal regions characterized by their distinctive plant or animal life. The present geographical position of Japan can hardly explain the marked resemblance of its flora to that of Atlantic America, or that of the Himalayan region, but we can predict the similarities when considering the origin of the Japanese Archipelago as a result of landmass assemblies and splitting.

Table 1 Current species richness compared with those of two other island countries in temperate regions, as the British Isles and New Zealand (according to the data table from WRI 2001).

	Japan		British Isles		New Zealand	
Area (km^2)	378,000		244,000		270,000	
Taxa	All species	Endemic species	All species	Endemic species	All species	Endemic species
Land Mammalia	97	38 (39.2)	50	0 (0.0)	2	2 (100.0)
Breeding Aves	247	17 (6.9)	230	1 (0.4)	150	74 (49.3)
Reptilia	63	36 (57.1)	8	0 (0.0)	52	48 (92.3)
Amphibia	55	49 (89.1)	7	0 (0.0)	3	3 (100.0)
Vascular plants	5,300	1,800 (34.0)	1,623	16 (1.0)	2,382	1,942 (81.5)

2.3 Endemism and conditions responsible for preserved biota

Although the flora and fauna are closely related to those of continental East Asia due to the geological history, the endemism of both the flora and fauna of Japan is remarkable. We have 188 mammal species including 42 (22%) endemics (WRI, 2001). The Japanese mammalian fauna shares 41% of its species with East Russia, 34% with Korea, 40% with continental China, 12% with Taiwan, and 9% with Southeast Asia.

In any taxonomic group, the numbers of total species and endemics are high, but amphibian and dragonfly richness is especially noteworthy. The close combination of woodlands and wetlands is the most conspicuous feature of Japanese landscapes. Amphibians and dragonflies are strongly associated with such a combination of landscape components. One of the old names for Japan is AKITSUSHIMA meaning 'The Island of the Dragonfly' (Hearn, 1901). Japan has continued to be a woodland country rich in wetlands at least for 10,000 years, even since the human activities came to prevail in the archipelago. Such continuity has well preserved the ancient biota including forest plants and animals, which escaped the impacts of Quaternary climatic changes, repeated alternations of warming and glaciation, by shifting their range to the north or south along the islands, extending 2,000 km in a southwest to northeast direction.

The wealthy tree flora is well preserved, consisting of approximately a thousand species including many relict endemics, and is remarkable if compared with that of the British Islands, which preserve only 143 tree species surviving the losses during the Wuerm and Riss Ice Ages (Hamada & Nakamura, 1999).

The flora of the cool temperate regions, including the mountainous heights of southwestern Japan and hills and lowlands of northeastern Japan, contains many species and genera endemic to Japan or East Asia (Nakanishi *et al.*, 1983), and this is especially tune of areas with abundant precipitation. An endemic species group, called the 'Sohayaki' elements, is found in the southwestern mountainous regions on the side facing the Pacific Ocean, while the 'Japan Sea' elements are distributed in snowy mountains on the side facing the Japan Sea (Ohwi, 1953). The cool temperate deciduous forests are characterized by tertiary circa-Arctic elements, many of which are now distributed in East Asia and North America, in an isolated manner. The flora of the warm temperate regions, in low altitude southwestern areas, has fewer but a considerable proportion of endemics. Compared to the temperate regions, the sub-frigid regions at high altitudes in the central part of Honshu embrace much fewer endemics and the flora is enriched by circa-Arctic elements, which are widely distributed around the Arctic (Ohwi, 1953).

In addition to many endemics on the islands, Japan's flora and fauna contain many components common to easten continental Asia, because compared to whole length of the history of continuity, only a brief time has lapsed since the complete separation of the Japanese Archipelago from the continent.

2.4 Vegetation and disturbances

Species compositions of individual communities tend to adjust to the particular types and frequencies of disturbances occurring in the region, as such individuals and species best adapted to those types and frequencies have the highest survival rate and reproductive success, so that they dominate the community. The establishment of equilibrium conditions is prevented when disturbances in combination with environmental fluctuations suppress competing species, altering the balance of competitive interactions (Huston, 1994).

Biodiversity of the Japanese Archipelago would have been enhanced by the active natural disturbances caused by frequent typhoons, and high volcanic, seismic and geomorphic activities causing landslides, fires, storms and flooding, which destroy established vegetation on various spatial and temporal scales, increasing α-diversity, as well as increasing β-diversity through enhanced regional or local environmental heterogeneity. The Japanese flora contains many disturbance tolerant or even dependent plant species (Washitani, 2001).

In primeval ecosystems, natural disturbances play vital roles in maintaining a shifting mosaic of habitat patches and contribute to retention of a subset of the natural biodiversity (Huston, 1994). If natural processes are left in complete absence of disturbances, light-demanding species, which can grow only in sunny habitats, are lost as succession proceeds.

2.5 Vegetation and natural and anthropogenic disturbances

Even today, intensive exploitation of the land for agriculture has been mostly confined to densely populated lowlands and hilly regions of the islands, though conifer plantations occupy more than half of the mountainous regions at the sacrifice of natural vegetation (Ministry of Environment, 2002).

Humans have influenced the Japanese Islands for at least tens of thousands of years, and now none of its ecosystems is entirely wild or natural. Japanese ecosystems have been subjected to a long history of human interventions, but humans have been only one among many influences, including active natural disturbances.

Clearing primeval forests to develop agricultural lands and settlements may have led to the extinction of closed-canopy specialist species. However, certain types of human intervention played certain roles in preserving local flora and fauna of older ages against the natural courses of ecosystem change due to non-anthropogenic climatic changes. Intermittent clearing of woods would serve to maintain the deciduous forests even after domination by northwardly advancing

broad-leaved evergreen forests due to climatic warming, which started about 10,000 years ago. Deciduousness is the necessary condition for preserving many plants and insects adapted to deciduous forests of cooler temperate climates (Moriyama, 1988). It is increasingly recognized that the sensitivity of species to current threats may reflect 'extinction filters' imposed by past events (Balmford, 1996).

Active natural disturbances prevailing in the Japanese Archipelago which destroy established vegetation, i.e., floods, landslides, volcanic eruptions and associated fires, have continuously exerted selective forces for disturbance-resilience or resistance of species. Simultaneously, by creating gaps or void niches, frequent disturbances have facilitated biological invasions.

3. Chronology of Biotic Exchanges and Invasions

3.1 Migrations and isolations during glacial and interglacial ages

It is well known that the climate cycle of the alternation of glacial and interglacial ages, which has repeated seven times during the past 700,000 years, greatly influenced biotic communities around the globe, and that the evolution and development of hominids were also governed by such environmental fluctuations (Pavlov *et al.*, 2001).

The lower sea level during glacial periods generated land bridges connecting the Japanese Archipelago to the Eurasian Continent, one between the Korean Peninsula and Kyushu and the other, between Sakhalin and Hokkaido (Nogami *et al*., 1980). These conditions may have elicited active biotic migrations. Many colonization events including those of humans from the continent may have occurred and profoundly affected the Japanese fauna and flora of later ages. Extant and extinct mammals may have migrated from the Asian Continent through the land bridges.

Fossil mammoths, which have been excavated from southeastern Hokkaido, and a fossil elephant, *Palaeodoxodon naumanii,* excavated from various regions of Japan, suggest that large mammals could move from the continent by land when the Japanese islands were connected to the continent (Kamei, 1991). *P. naumanii* is inferred to have moved from northern China 300,000 years ago by the southern route and first entered Kyushu. The fossil elephants lived in the Japanese Archipelago until approximately 16,000 years ago, when a cooler climate intermittently prevailed and fostered coniferous forests of Pinaceae, Taxodiaceae, and Cupressaceae, which covered the present warm temperate regions. Fossil evidence suggests that in the same era, big horn deer, Japanese deer, brown bears, rabbits, mice, and bean geese lived with *P. naumanii* (Kawamura, 1991). Migrations of large mammals may also facilitate the migration of plants through seed dispersal mechanisms which depend on mammals (Washitani, 2002).

Fossil records suggest that *P. naumanni* rapidly declined during the last interglacial period. The climate was fairly mild, so climate factors are inconceivable as the major factor in its extinction. Active human hunting (Cardillo & Lister, 2002) is evidenced by stone and bone tools yielded with the elephant bones, including knives and scrapers, and suggest that was among the reasons for extinction of active hunting of *P. naumanni* by Paleolithic man (Kamei, 1991).

During the last ice age which lasted from 20,000-18,000 years BP, thick ice sheets covered Canada, Greenland and Scandinavia and more than 30% of the land area of the world was covered by glacial ice. The sea level was depressed by 80-130 m globally, as a counter-balance against ice sheet development. In the Japanese Archipelago, however, glaciers were poorly developed due to a somewhat dry climate (Nogami, 1998), and older flora and fauna survived the age well. In central Japan, the ice sheet covered only mountain peaks above an altitude of 2,500 m, and a large part of the region escaped the influence of glaciers.

Post-ice age warming caused extensive marine transgression with a 40 m sea level elevation in total during the 4,000 years from 10,000 year ago when the sea level rose continuously by 1 cm per year. In the early Jomon period, i.e., 6,000 years ago, the climate was relatively warm and the sea level was about 3 m higher than now (Hamada, 1999).

3.2 Pre-historic migrations of humans and large mammals

When and who first lived in the Japanese Archipelago is the most fascinating question enthralling not only anthropologists and archeologists but also the general public. Current interdisciplinary research activities concerning this question (Omoto, 1996; Urabayashi & Tozawa, 2001; Baba, 2001), which include genetic analysis of old human bones with DNA markers, have revealed dynamic human migrations and interactions in and around the pre-historic scene of the Japanese Archipelago (Fig. 1).

Numerous stone tools dated back to 10,000 to 30,000 years ago have been found through recent archeological excavations throughout the Japanese Archipelago (Okamura, 2000), but no firm evidence of old human settlements in Lower and Middle Paleolithic Japan has been obtained until today.

Underground preservation of old bones is extremely difficult in the acidic soils prevailing over the Japanese Islands, so old human bones are rarely found and only in special regions or under conditions such as in limestone soil or shell heaps (Amano, 2001). Although more than 5,000 Paleolithic remains have been found throughout the Archipelago, only one fossil human skeleton of that age (dated to 18,000 years ago) is available for sufficient analysis. The nearly complete set of fossil human bones called 'Minatogawa hominid,' which were excavated from a site on

Okinawa Island (Baba, 2001), was recently demonstrated to be morphologically and genetically similar to the Wajaku hominids who lived in prehistoric Indonesia（Tagaya, 2001）. However, the sample size is too small to permit any statistical analysis, and large ambiguity still remains on his relation to later Japanese such as the Jomon or other Asian hominids.

A specific type of fine stone razors found with many Paleolithic remains throughout Japan suggests the immigration of mammoth hunters from Siberia during the coldest period of the latest Ice Age (Urabayashi & Tozawa 2001). The stone razors, which were designed to be used by setting into bone arrow heads just like modern replaceable razor blades, were a unique invention of prehistoric Siberian mammoth hunters, who left remains at the Marita site near Irkutsk that can be dated back to about 20,000 years ago (Kimura, 2001). They hunted mammoths and reindeer, ate meat, and utilized fur, bones, and horns to manufacture housing, tools, accessories, etc. The fine stone razors, which probably were essential to mammoth hunting, started to be used in Siberia about 21,000 years ago, while the oldest stone razor of this type found in Japan dates to approximately 20,000 years ago.

During that period（20,000-18,000 years ago）, the globe was in the worst part of the last Ice Age, and vast tracts of Siberia were covered with so called 'mammoth steppe,' a grassland that mainly consisted of *Poa*, *Carex* and *Eriphorum* (Kawamura, 2001). Together with woolly rhinoceros, reindeer, bison, wild horses, arctic foxes and wolverines, mammoths inhabited the middle and northern latitudes of Eurasia, and extended their range into the cool steppes of North America where average temperatures were 7 or 8 degrees colder than today（Urabayashi & Tozawa, 2001）.

The supposed age of mammoth migration from Siberia to northern Japan is also around 20,000 years ago when the habitat of the mammoth, i.e., drier steppes with scattered conifers or open woodlands, reduced in area and/or shifted southwards (Kawamura, 2001). During the coldest period of the latest Ice Age, open woodlands or Mammoth steppes advanced to cover not only Hokkaido but also the northern part of Honshu. With such an environmental change in mind, it is easy to imagine that mammoths migrated to northern Japan along with mammoth hunters, pursuing the game.

At the end of the glacial age 10,000 to 13,000 years ago the mammoths became extinct. Slaughtering by hominids in combination with climatic changes is thought to be partially responsible for the extinction (Kawamura, 2001).

3.3 Prehistoric human life facilitating biotic migration

The Japanese Neolithic Age, the Jomon period and the Yayoi period are characterized by unique types of earthenware common to the remains of the ages. The Jomon（meaning 'cord marks' in Japanese）type of pottery with cord mark patterns pressed into the clay, were first discovered in the early Meiji Period by an American zoologist Edward Sylvester Morse who taught zoology at Tokyo Imperial University as a professor (Sahara, 1998a). Since the first discovery of Jomon pottery by Morse near Tokyo, numerous Jomon type potteries have been excavated from all over Japan. The period of Jomon pottery usage began about 12,000 years ago and lasted to 2,300 years ago.

Simpler potteries having bullet-shaped bases without special surface patterns, which are presumed to be an ancestral type for the Jomon ones, were unearthed from several remains dated to about 13,000 years ago. Representative clay pottery without cord marks, dated 12,000 years ago, was excavated from Shinjuku in Tokyo (Abe, 2001). This type of pottery is very similar to the world's oldest earthenwares found in Siberian remains located in the Amur basin, but are much thinner and have bullet-shaped bases, suggesting that the earthenware was used to boil food by placing it over a fire（Abe, 2001）.

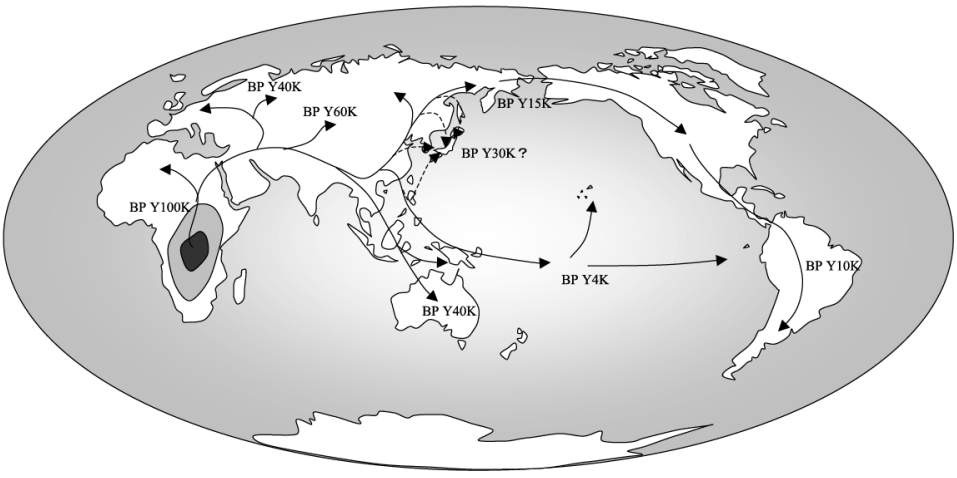

Fig. 1 Prehistoric global migrations of *Homo sapiens* and interactions around Japan (redrawn from Baba, 2001).

The descendents of mammoth hunters migrated from Siberia with their fine razor stones and bullet-shaped potteries, probably facing dramatic climatic changes due to global warming, and had to modify their lifestyle and culture to fit well in their new environment (Urabayashi & Tozawa, 2001). Arid, cool steppes were rapidly disappearing and gradually displaced by dense forests. Such environmental changes caused extinctions of large mammals, which were grazers strongly depending on the grasslands. The Jomon people had to innovate their dietary life drastically, and one of the solutions to the challenge may have involved cooking techniques with fire.

In addition to the above-mentioned evidence (i.e., the shared features of stone tools and earthenware), morphological and genetic analyses of old human bones also suggest Paleolithic human immigration from Siberia to the Japanese Archipelago before the beginning of the Jomon period.

The first old human bones were excavated by E. S. Morse who found seven sets of human bones from a shell midden site in Omori, southern Tokyo, in 1877. Since then, several thousand sets of Jomon human bones have been excavated from various regions of Japan (Amano, 2001). Old bones of the Jomon people have been found all over the Japanese Islands, from the north end of Hokkaido to south end of Southeastern Islands.

Multivariate craniofacial analysis and genetic analysis with DNA markers strongly suggest a close relationship between the Jomon and existent mongoloids of Siberia and other regions of the east Eurasian continent (Omoto, 2001). Shinoda（cited by Omoto, 2001）compared mitochondrial DNA sequences registered in a DNA bank for the Jomon and modern peoples of various areas of the World and obtained exciting results. Among 29 Jomon investigated, 17 shared identical sequences with the existent Buryats living near Lake Baikal, and three others, with Koreans, Taiwan Chinese and Thais, respectively.

The results strengthened the inference that the Jomon, or proto-Japanese, may have had multiple origins, but possibly one of the dominant lineages was descendants from Paleolithic Siberian mammoth hunters. They partially merged with peoples from other continental Asian regions and spread throughout the archipelago (Tozawa, 2001), gradually adapting to the islands' natural environments. The Ainu, a minority race of northern Japan, is known to be genetically and craniofacially close to the prehistoric Jomon (Brace *et al.*, 2001). Linguistic evidence also suggests that a certain people speaking a language belonging to the Ural-Altaic family moved eastward across Siberia and entered Japan via Sakhalin Island and Hokkaido (Amano, 2001).

A recent investigation based on craniofacial morph-metric comparisons（Brace *et al*., 2001）also showed that the prehistoric Jomon and the Ainu of contemporary Japan are actually closer to prehistoric and existent European groups than the core populations of continental Asia. Along with the Ainu and the Jomon, the Polynesians of Oceania are shown to be close to Eurasians. The study also revealed that American natives living in the border region between Michigan and Alberta, Canada, are very similar to the Jomon and the Ainu. Figure 1 is a schematic representation of the placement of the original populations involved in the thus presumed initial human expansions and their subsequent movements and combinations（Brace *et al*., 2001）.

Therefore, it is suggested that the Japanese Archipelago was a focal place, where Paleolithic peoples with different migration histories interacted, and merged, and the dominant group was people closely associated with those starting on the trip to the New World, with some among them migrating afterwards to South Asia and Polynesia. Such dynamic human migrations might be accompanied by both intentional and unintentional plant and animal migrations, as described later.

Most modern Japanese are genetically not so close to the Jomon. After the end of the Pleistocene, development of agriculture led to a major expansion of the core population of continental East Asia, and many immigrants from the continent entered in the Japanese Archipelago (Tozawa, 2001). Immigrant lineages had become dominant in the Yayoi period, as described later.

3.4 Presumed plant transportation by prehistoric humans

Dynamic migrations of mammals including hominids during and after the last Ice Age should have been accompanied by dispersal of the seeds of grassland plants as well as ruderals, a type of weedy plant. Ruderals are plants that grow on well-illuminated nutrient rich sites such as bare grounds formed by trampling by mammalian herds, whose discharge of bodily wastes creates especially nutrient-rich conditions (Grime, 1979).

The dynamic Paleolithic migrations and/or range expansions of mammals including humans surely helped such sun-loving nutrient-consuming plants that disperse their seeds by hitchhiking on mammals externally or internally. In addition to clinging to wooly body parts, adhesion to legs or hoofs of mammals with mud is thought to be one of the most effectual means of seed dispersal for ruderals（Fenner, 1985）. Upright-standing humans with an exceptionally large foot sole area relative to body size may be the most efficient seed dispersers for such plants.

The Ice Age, when land bridges or shallows connected the Asian continent with the Japanese Archipelago (Fig. 2), was a great migration age, when plants and animals including hominids actively migrated long distances. Short grass steppes or tundra could be more easily traversed by large mammals, including humans, than forests, although only species

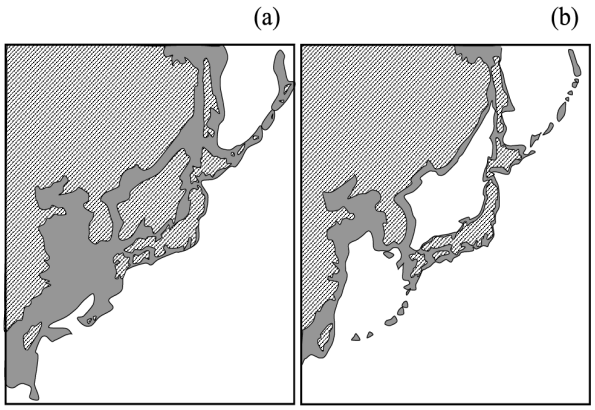

Fig. 2 Japan in early diluvium, approximately a million years ago (a) and land bridges or shallows connecting the Japanese Archipelago to the continent during the Würm Ice Age about 20,000-30,000 years ago (b) (redrawn from Hamada & Nakamura, 1999).

which had adapted to cooler climates, could actively migrate.

Intentional introduction of plants probably originated just at the time when people first appreciated the roles of seeds or other dispersal agents in plant reproduction, although we can only resort to imagination to reconstruct such a history of the relationship between humans and plants.

Patches or layers containing high densities of plant seeds found among Jomon remains are interpreted as debris from squeezing berries to make juice or wine. The discarded seeds were those of *Sambucus*, *Raps*, *Actinidia, Morus,* and *Vites* species (Tsuji, 1999). These shrubs and vines grow vigorously after fires or clearing of forests. Gaps created by natural or human disturbances would be a food reservoir for easy collecting of delicious berries. People not only acted as effective seed dispersers, but also unintentionally or intentionally prepared suitable habitats for these plants.

3.5 Active trade with the Asian continent

The Sannai Maruyama site in Aomori Prefecture, one of the most representative Jomon remains, contains various types of dwellings, apparently accommodating approximately 500 people at its peak (Watanabe, 2001). Various trade items excavated from the site, jade beads, raw amber, projectile points attached with asphalt and pottery with patterns created by pressing cone shells from the southwestern sea, suggest active trade across the Japan Sea by dugout canoe.

Even after separation of the islands from the Eurasian Continent because of sea elevation due to global warming after the last Ice Age, active movement of people and cultures may have continued. Rice cultivation was probably introduced from South China more than 2,500 years ago (Urabayashi, 2001). Jomon rice is thought to have been introduced from the Yunnan region, through southern mountainous regions and the Shandong Peninsula. In the Jomon period, rice was generally cultivated in burned fields with other miscellaneous cereals, but some paddies of the period have been also unearthed (Urabayashi, 2001).

The Yayoi culture, which arose first in Kyushu about 2,200 years ago while the Jomon culture was still undergoing development in other parts of the Japanese Islands, spread gradually eastward to overwhelm the Jomon culture as it went, until it reached the northern part of Honshu (Tozawa, 2001). The name Yayoi derived from the name of a town in Tokyo where, in 1884, pottery of this type was first found and drew the attention of scholars. Yayoi pottery was fired at higher temperatures than Jomon pottery and was produced by turning on wheels (Sahara, 1998b).

During the Yayoi period, irrigated rice cultivation became commoner and commoner (Urabayashi, 2001). Analysis of plant opals, which are microfossils derived from grass leaf tissues, is helpful in revealing or ascertaining sites where ancient paddy fields were located (Fujiwara, 1998). With the help of analytic techniques, more than 100 paddy remains of the Yayoi era (BC 3c - late AC 3c) have been excavated (Amano, 2001). The remains are located in lowlands or valleys, where irrigation and drainage are feasible, benefiting from the natural topography. These constitute evidence demonstrating that rice cultivation spread rapidly in the Yayoi period. Rapid development of agriculture would be associated with the introduction of ironware.

Probably certain paddy weeds were unintentionally introduced accompanying rice introduction (Maekawa, 1943). However, they are originally wetland plants, and considering the floristic resemblance of Japan and continental Asia, it is difficult to conclude that they had never been native to Japanese wetlands.

3.6 Ancient to pre-modern agricultural ages

Similarly to human histories of many other regions, from an ecological viewpoint, Japanese history can be broadly divided into the three familiar periods of hunter-gatherer, agricultural and industrial societies (Totman, 2000). In Japan, a Japanese-style agricultural system which was established in the Yayoi period on the basis of the Jomon legacy and items imported from continental East Asia lasted to the early 20th century, when eddies of violent industrialization shattered the traditional agricultural systems together with their rural communities.

The early centuries of land clearance and low-intensity tillage significantly altered landscapes by opening many scattered lowland areas to sunlight. Moreover, the adoption of Chinese architectural practices and the creation of a succession of densely populated capital cities in the Kinai Basin led to deforestation of the basin, frequent eruption of wildfires that swept through areas of recently created scrub growth, and erosion leading to gradual degradation of soil and downstream flooding (Totman, 2000). By the eleventh century, human exploitation had almost completely

stripped the basin of its old-growth forests and damaged enough soil in the metropolitan region so that the ruling elite was unable to maintain the level of resource extraction essential to its urban civilization. However, many regions outside the Kinai might well have preserved the integrity of their ecosystems to modern ages (Totman, 2000).

After the age of warfare, Japanese society entered an intensive agricultural stage (Tanaka, 2000), and feudal rulers governed the agricultural communities. As the agricultural society developed and its systems became refined, farmers became tied to their villages more and more tightly. The agricultural society was sustained by yields or outputs from regional ecosystems, similarly to hunter-gather societies, while the current industrial society is sustained by current output from spatially and temporally remote ecosystems, i.e., biological output from different regions and yields from ancient biomass (coal, oil and gas).

During the long-standing agricultural age, Japan experienced many inland wars, through which the warrier class took over real control form the Tenno (Emperor) court nobles. However, the country totally escaped foreign invasion. The risk of subjection to foreign rulers was first heightened after the Chinese Sung dynasty was overrun in 1279 by the Mongol armies of Kublai Khan, who dispatched invading armies to northern Kyushu several times (Murai, 2001). The last dispatched fleet was reported to contain 140,000 fighters, mostly Chinese, on 4,400 vessels. Dogged resistance and a fortuitous typhoon, which has been called 'divine wind' in later legend, wrecked the invading force on the beaches, and Japan could evade the Mongol invasion.

3.7 National seclusion and escape from European colonization

Pressure from abroad greatly increased after the first arrival of Europeans on Tanegashima, an island off the south of Kyushu in 1542, when a Chinese ship with three Portuguese crew members drifted ashore at the island and guns and gunpowder as well as Christianity were first introduced to Japan (Kamigaito, 2000). Nagasaki port was opened to foreign trade in 1570, and the Portuguese entered the harbor (Harada, 1999). Firearms and new religions were accepted by the Japanese in the midst of a warring state period and had great influences on Japanese society.

"After nearly a hundred years of Christianity and foreign intercourse, the only apparent results of this contact with another religion and civilization were the adoption of gunpowder, and firearms as weapons, the use of tobacco, and the habit of smoking, the making of sponge-cake (still called Castira—the Japanese form of Castile), the naturalization into the language of a few foreign words, the introduction of new and strange forms of disease, among which the Japanese count the scourge of venereal virus, and the permanent addition to that catalogue of terrors which priest and magistrate in Asiatic countries ever hold as weapons to overawe the herd." (Griffis, 1883)

Hideyoshi Toyotomi, a prominent warrior who stopped the warring state and brought the entire country under his control licensed both domestic and foreign trading ships, and Ieyasu Tokugawa who established the Tokugawa Shogunate systematized this licensing by issuing sealed letters (Harada, 1999). However, in the 1630s, the Tokugawa Shogunate forbade foreign trade to avoid a tangle of foreign complications that involved unruly European, Japanese, and other Asian traders as well as an increasing Manchu assault on Korea and Ming China. Japanese were forbidden to go abroad. In 1639, Portuguese ships were excluded from Japanese ports, and only the Dutch and Chinese were allowed to trade, and they were only allowed to trade, at an isolated port located in Nagasaki. Therefore, foreign trade was restricted until modern trade officially began in 1859 (Harada, 1999).

3.8 Opening the country and avenues to industrialization

During the agricultural periods, especially the period of Japan's isolation, biological invasions were likely to be rather trivial issues. However, 19th century European imperialism, which was itself driven primarily by the carrot and stick of early industrial empowerment and Western Europe's ecological limitations, disturbed the Tokugawa political order by depriving it of the stable and non-threatening geopolitical context in which it had operated (Totman, 2000). The European intrusion also brought in not only its wake, but also the rudiments of an alternative to intensive agriculture: namely, industrialization. From the 1860s onward, Japanese leaders and an ever-growing portion of the general populace began to tackle the task of developing their own industrializing order with enthusiasm. In the late Edo period, active introduction of European plants and animals was made and some were naturalized later. White clover (*Trifolium repens* L) is believed to have been first introduced when it was used as packing for boxes containing earthenware imported from Holland (Osada, 1976), although later repetitive intentional introductions as pasture plants or soil erosion prevention material are rather responsible for the current day prevalence of the species.

Japan's modern foreign trade officially began in 1859. Until then the Tokugawa Shogunate (1603-1867) had maintained a policy of National Seclusion (Asao, 1998). With the signing of the Harris Treaty (United States—Japan treaty of Amity and Commerce) in July 1858, Japan opened its doors to Western commerce.

The Meiji revolution was a new departure for industrialization of Japan. The society that hitherto had been sustained by current output of the regional ecosystem gave way to one that depends on a combination of current biological output from remote places and yields from ancient biomass, i.e., fossil fuels

(Totman, 2000). It definitely opened the age of rapid biological invasion into Japan.

Achieving equality with the West was one of the primary goals of the Meiji leaders. Treaty reform, aimed at ending the foreigners' judicial and economic privileges provided by extraterritoriality and fixed customs duties, was sought as early as 1871 when the Iwakura mission went to the United States and Europe (Inoo, 1995). The Western powers insisted, however, that they could not revise the treaties until Japanese legal institutions were thoroughly reformed along European and American lines. In this context, 'Westernization' of social systems became synonymous with the modernization that was the prerequisite to industrialization of Japan. Many of Japan's leaders at that time had gone abroad to embassies and on study tours, and the government had actively hired foreign advisors and employees to help in the development of new governing and educational institutions and new commercial and industrial ventures. By 1875 some 520 foreign employees, mostly European, already worked for the government, while hundreds more were under taking private services, mainly as engineers and teachers (Griffis, 1883).

The efforts of central government were fully rewarded and in 1894, the treaty provisions for extraterritoriality were formally changed (Inoo, 1995). Meiji leaders encouraged study abroad, and promoted the learning of foreign languages and translation of European books. They accepted the introduction of such cultural elements as contemporary European food, dress, architecture, art, music, dance, drama, literature and philosophy as well as science (Hearn, 1904). Westernization gradually penetrated all social and daily life of the Japanese especially in the new metropolitan Tokyo.

3.9 Westernization and active biotic introduction

Japan was thus among the world's first societies to industrialize along with parts of Europe and North America (Totman, 2000). With the slogan 'Japanese sprit with Western learning,' the government as well as economic and academic circles strived to introduce western cultures, technologies, and goods including numerous biotic items. Therefore, the rush to introduce exotic plants and animals led to naturalization of many such introduced species. The first naturalization of most contemporarily common non-native plant species occurred in the Meiji period (Washitani, 2002). Since that period, the number of naturalized species has constantly increased. Several *Solidago* species including *Solidago altissima,* one of the most notorious invasive plants in current-day Japan, were first introduced as ornamental plants at that time (Osada, 1976).

A pathogenic nematode (*Bursaphelenchus xylophilus*) that was unintentionally brought from North America and has caused tremendous damage to pine plantations throughout Honshu, Shikoku and Kyushu, especially in recent years, was first recorded in Nagasaki in 1905. It is thought to have invaded by hiding in imported wood for shipbuilding (Tomigashi, 2002).

Successful establishment of introduced species requires suitable habitats where they can live and reproduce. Distributions of most naturalized species were principally confined to areas subjected to intensive human interventions for industrialization or urbanization (Washitani & Morimoto, 1993). During the early modern industrial stage 1868-1945, agricultural techniques changed only incrementally and in rather familiar ways (Totman, 2000), and intact SATOYAMA landscapes with wealthy indigenous biodiversity (Washitani, 2001) were likely to be well preserved. Not only primeval forests but also intact SATOYAMA landscapes were relatively resistant to invasions by newcomers, though constantly influenced by humans in order to extract bio-resources such as fuels, fertilizer, and building materials (Washitani, 2001).

In the course of the early modern industrial development of Japan, after fostering light industry, especially the textile industry, during 1897-1906, the government led development of basic industries such as railroads and mining. Railways opened routes for invasive plant species to invade throughout the country. *Erigeron canadensis*, which was unintentionally introduced from North America and spread along the railways in those days, was called the 'railway plant' in Japanese (Osada, 1976). The plant was regarded as a symbol of the early modern industrial development of Japan.

Japan's heavy industries, such as iron/steel and shipbuilding, grew rapidly from the 1930s (Kodansha International, 1999). Remarkable industrial development resulted in domestic shortages of raw materials and markets. The need to secure raw materials and markets in a hostile international trading environment led to efforts to form the so-called 'Greater East Asia Co-prosperity Sphere' in the years immediately preceding World War II. Imperialism accompanied by militarism stirred up Japanese pride and the will to invade other Asian countries. Increased fur demand related to military invasions of North China elicited introduction of fur animals such as *Myocaster coypus*, which become naturalized after the war (Murakami, 2002).

The war was ended by the holocaust of the atomic bombs dropped on Nagasaki and Hiroshima. The fall webworm, *Hyphantria cunea*, which greedily strips a wide range of deciduous trees, especially cherry trees, was thought to be introduced attached to propaganda bills the US Air Force distributed by airplane or intermingled with US Army munitions (Gomi, 2002).

3.10 Post-war economic growth and increased invasions

As a result of its defeat, Japan was subjected to the Allied Occupation, which lasted from August 1845 to

April 1952. Japan concluded a security treaty with the United States that permitted US military bases to remain on Japanese soil in return for an American commitment to protect Japan from foreign aggression. US military bases are thought to be among the major gates for unintentional introduction of various exotic plants and animals. An example is *Polypedates leucomystax*, which was first recorded the early 1960s in Okinawa where US armed forces were based and is thought to have been introduced from Indochina attached to military items (Ohta, 2002a). During 28 years from 1945 to 1973, the Okinawa Islands were newly invaded by a total of 12 nonindigenous insect species, half of which were first found in the vicinity of the US military bases (Kiritani, 2002).

During post war food shortage (1945 to 1955) more than 25 species of cereal weevils invaded Japan via cereal imports (Kiritani, 2002).

The Korean War (1950-1953) brought about a rush of special military procurements to support US and United Nations forces, enabling Japanese industry to climb out the stagnation. Naturalization of various alien plants and animals became tangible in the post-war era (Osada, 1976; Miyashita, 1977).

The rapid growth and bubble economy from the mid-1960s brought about a new rush of naturalization of introduced plants and animals especially those from the United States of America, the major trade counterpart exporting biotic items including cereals to Japan (Washitani, 2002).

Biological invasion depends on both opportunities for invasion and the presence of habitats or niches where the introduced species can establish. An example of establishment through intentional introduction for farming can be found in *Rana catesbeiana,* which was actively introduced for meat production (Hasegawa, 1999), though the attempt was soon abandoned. The species is now one of the most common amphibian species in various aquatic habitats, is an extraordinarily strong competitor species (Kiesecker *et al.*, 2001) and is thought to threaten native amphibians (Ohta, 2002b).

Chances for invasion may be extraordinarily elevated if the plants or animals are intentionally introduced in large amounts continuously into the region, including vast areas of unoccupied habitats. As such, active introduction of non-native pasture grasses for various construction projects has caused serious problems of invasions of such grasses as *Eragrostis curvula* (Muranaka & Washitani, 2004) and several varieties of *Festuca* into wide ranges in Japan (Washitani, 2002).

The most notorious invaders attracting serious public concern are introduced freshwater fishes of the sunfish family native to North America. These fishes have been repeatedly released into lakes and ponds for sport fishing and have multiplied explosively (Yodo, 2002), preying on a wide range of native species including aquatic fishes and insects such as dragonfly larva (Suda, 2002). The large-mouth bass, reported in only 23 prefectures of Japan in early 1970s, is now distributed to all 49 prefectures.

During and after the rapid economic growth which started in the 1960s, Japanese landscapes were greatly changed by various types of development projects according to a national plan to 'remodel the Japanese archipelago' (Tanaka, 1972), which was inevitably accompanied by drastic landform changes. Surging waves of development projects for construction of dams, ports, roads, industrial complexes, residential areas, and recreational facilities such as golf courses, destroyed large tracts of various types of natural or semi-natural habitats such as woodlands, wetlands, beaches, floodplains, and grasslands, leaving unoccupied sunlit habitats where invasive alien plant species could easily establish large seed sources. Rural landscapes today are bright with escaped exotic ornamental plants, such as *Slidago altissima* and *S. gigantean* var. *leiophylla, Coreopsis lanceolata*, *Rubeckia laciniata, Aster novae-angliae*, and *Aster novi-belgii*, most of which were introduced from North America in the Meiji or Taisho periods, and we totally miss native wild flowers familiar to elderly persons.

Anthropogenic landscape changes in concert with active intentional and unintentional introductions associated with economic globalism are likely to be most responsible for the current rush of invasions. The rapid decline of native species replaced by prevailing non-native species throughout the landscape is a major aspect of the current biodiversity crisis of Japan.

Epilogue

Within less than 150 years, Japan has been transformed from a closed country of self-sustainable agricultural communities depending solely on regenerative bio-resources to one of the big industrial countries exploiting resources worldwide. During this period, naturalized alien species increased tremendously. Today, in concert with other factors causing environmental deterioration, invasive alien species profoundly threaten the biodiversity and integrity of Japanese ecosystems, especially those in fresh water and agricultural landscapes. Social concern about the problems has been growing rapidly (Washitani, 2004), and Japanese society at last has started groping for effective countermeasures to the problems (Mito & Uesugi, 2004), though whether or not we can establish appropriate countermeasures depends largely on the scientific understanding of the problems by the general public as well as the officials responsible for the matter. I hope the present special issue will play an important role in promoting such a wide scientific understanding.

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