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WHY ISLANDS?

José María Fernández-Palacios

Abstract. Ever since the first transoceanic expeditions (XV century) islands worldwide have attracted the interest of voyagers, and, in recent centuries (XVIII-XX) especially from biogeographers, evolutionary biologists and ecologists. Some islands' and archipelagoes' special features, such as their quite diverse origin, their geographical settings and locations, their life cycle, their history, their well defined limits and, especially, their isolation, have made them outstanding life museums and laboratories. Using a wide variety of data from such islands, various different ecological and evolutionary hypotheses can be, and have been, tested. In fact, many fundamental theoretical concepts, central to the understanding of scientific disciplines such as ecology, biogeography, genetics, evolution and vulcanology, have resulted mainly or exclusively from island research.

Keywords. Islands, museums, evolutionary laboratories, explosive radiation, biodiversity, conservation biology.

Resumen. Ya desde las primeras expediciones transoceánicas (siglo XV), las islas de todo el mundo atrajeron el interés de los viajeros y particularmente en siglos recientes (XVIII-XX) el de los biogeógrafos, biólogos evolutivos y ecólogos. Algunos de los particulares rasgos de islas y archipiélagos, tales como su muy diverso origen, sus características geográficas, sus ciclos vitales, su historia, sus bien definidos límites y, especialmente, su aislamiento, han hecho de las islas extraordinarios laboratorios y museos vivientes. Empleando una amplia variedad de datos de tales islas, varias hipótesis ecológicas y evolutivas pueden y han sido probadas. De hecho, muchos conceptos teóricos fundamentales, centrales en la comprensión de disciplinas científicas como la ecología, la biogeografía, genética, evolución y vulcanología, han surgido principal o exclusivamente de la investigación insular.

Palabras clave. Islas, museos, laboratorios evolutivos, radiación explosiva, biodiversidad, biología de la conservación.

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Resum. Ja des de les primeres expedicions transoceàniques (segle XV), les illes de tot el món van atreure d'interès dels viatgers i particularment, en segles recents (XVIII-XX), el dels biogeògrafs, biòlegs evolutius i ecòlegs. Alguns dels particulars trets d'illes i arxipèlags, tals com el seu molt divers origen, les seves característiques geogràfiques, els seus cicles vitals, la seva història, els seus ben definits límits i, especialment, el seu aïllament, han fet de les illes extraordinaris laboratoris i museus vivents. Emprant una àmplia varietat de dades de illes, diverses hipòtesis ecològiques i evolutives poden i han estat provades. De fet, molts conceptes teòrics fonamentals, centrals en la comprensió de disciplines científiques com l'ecologia, la biogeografia, la genètica, l'evolució i la vulcanologia, han sorgit principal o exclusivament de la investigació insular.

Paraules clau. Illes, museus, laboratoris evolutius, radiació explosiva, biodiversitat, biologia de la conservació.

INTRODUCTION

In a broad sense, an island can be defined, in relation to a focal individual, population or species, as any favorable place (e.g. territory, lake, or even a vagrant animal) located within a surrounding hostile environment. For dwellers of real islands (patches of land surrounded by water), the hostile environment is the water surrounding them (whether ocean, sea, lake or river), whereas for habitat islands the unfavorable environment may be agricultural land, urban area, industrial land or a degraded stage of the same ecosystem. Mountain tops or 'sky islands' are summits separated from similar summits by valleys containing very different climates, whereas seamounts with illuminated summits are separated from similar seamounts by dark abysms, making them habitat islands beneath the sea. Even a single flower can constitute an island for its animal dwellers, separated from other flowers by open space; or a vagrant animal, an island for the parasites it hosts. In this essay I nevertheless limit my scope to real islands, without forgetting that the majority of concepts developed in island biology are valid for all island types.

How many islands are there?

Although real islands are considered to comprise ca. a 5 % of land above sea-level, the actual number of real islands is far from being known. Listed in the Island Directory (UNEP 2009) there are 17 islands larger than 100,000 km^2, 59 larger than 10,000 km^2, 241 larger than 1,000 km^2, 797 larger than 100 km^2, 246 larger than 10 km^2 and 176 larger than 1 km^2 and 50 larger than 10 ha. But very probably this last total, where the highest number of islands is to be expected, is highly inaccurate. In Indonesia alone there are 17,507 islands (of which 8,844 have been named and 6,000 are inhabited!) and another 7,017 in the Philippines, according to Wikipedia.org. In Finland there are 190,000 lakes and within them 180,000 islands; similarly, in Canada, with at least 32,000 lakes larger than 3 km^2, 50,000 lake and ocean islands have been reported (Wikipeda.org). Other clusters of numerous islands include the South China Sea (30,000), the Stockholm archipelago (24,000), Japan (6,852), the Aaland archipelago (6,500), the Aegean archipelago (6,000), the Chinese Zhoushan islands (4,700), the Australian Great Barrier (3,800), the Maldives (1,322) and the Dalmatian coast in Croatia (1,185), just to include those clusters with more than thousand islands and islets. Even a country without ocean coasts, like Switzerland, has some 35 lake islands (Wikipedia.org). Furthermore there are approximately 30,000 known seamounts in the world's oceans. My guess is that there should be more than one million real islands and seamounts in the world.

New Guinea (785,753 km^2) is considered to be the largest island. Although Greenland is larger (2,166,086 km^2) it is actually a set of islands united by an ice cap. Numerous islands are also hidden beneath Antarctica's ice. By contrast, Australia is widely considered to be the smallest continent; at 7 686 850 km^2 it is an order of magnitude larger than the largest island, New Guinea. Furthermore, islands are home to ca. 10% of the world's human population (some 600 million people) as well as one fourth of the world's sovereign states and their combined land area and exclusive economic zone takes up over one sixth of the Earth's surface.

As each island constitutes a unique geological and biological 'natural experiment', it is easy to understand **why islands** have attracted interest ever since the first transoceanic expeditions (XV century), first from voyagers, and in recent centuries (XVIII-XX) from biogeographers, evolutionary biologists and ecologists. Some of the islands' and archipelagos' special features, such as their diverse origin, their geographical settings and locations, their dynamic history and, especially, their persistent isolation through time, have made them outstanding life museums and laboratories. Using a wide range of evidence from islands, various different hypotheses about biological processes can be, and have been, tested (Mayr 1967).

Island features

Some important island features that make them biologically interesting study systems include: i) the lower biological complexity of island communities when compared to equivalent mainland ones, ii) their clearly defined limits (the shore, for real islands), iii) the availability of a large range of whatever properties are studied (area, age, altitude, isolation, latitude, richness, etc.) and iv) the availability of many replicates (although these are never perfect replicates).

As we have already see, island area varies from New Guinea (792,500 km^2) to rocks less than 100 m^2 (ten orders of magnitude). Island age varies from ca. 150 My (Madagascar) to just a few years (e.g. Surtsey, born in 1963). Island altitude varies from peaks higher than 4000 m (New Guinea, Borneo, Taiwan, Hawaii) to flat atolls just centimeters above the sea level. Isolation varies from more than 4000 km (Marquesas) to hundreds of m (Anglesey, Sicily, Sakhalin, etc.). Finally, island latitudes range from 84° N (Oodak, Greenland, the world's northernmost emerged land) to 81°S (Berkner Island, Antarctica).

Other important island features include the tempering effect exerted by the surrounding ocean, which causes smaller climatic fluctuations (e.g. seasonal) than continental areas of similar latitude. In oceanic islands, periodic volcanic renovation, frequently supplies new land for colonisation. But perhaps the outstanding characteristic of islands is their great dynamism, by no means comparable with continental dynamic rhythms, which extend over eras. I explore this insular feature in the next paragraphs.

Real islands have been categorized according to their origins ever since the first golden age of island studies –which we may consider as beginning with the pioneer work by Johann Reinhold Forster (1778) and continuing during the XIX century, with outstanding island researchers such as Leopold von Buch (1825), Charles Darwin (1859), Joseph Dalton Hooker (1866) and Alfred Russel Wallace (1891).We can distinguish three main types of island (Whittaker and Fernández-Palacios 2007):

i) Oceanic or volcanic islands. These emerged because of the accumulation of volcanic material through millions of years of activity in ocean floors and have thus never been connected to any mainland. These islands are typically small, high, isolated and tend to form archipelagos. Their life span can vary from days (Sabrina, Azores, 1889) to 30 My (Salvajes, Macaronesia). They are necessarily populated via long distance dispersal. Despite sharing a volcanic origin, the ultimate mechanisms of such islands' birth vary widely, including intra-plate hot-spot archipelagos (Hawaii, Society, Austral, Marquesas, Madeira, Canaries, Cape Verde, Guinean Gulf Islands, Mascarenes), volcanic arcs caused by subduction at convergent plate boundaries (e.g. the Aleutians, Kuril, Marianas, Kermadec, South Sandwich, Lesser Antilles), and volcanic activity related to mid-oceanic sea-floor spreading at divergent plate boundaries (e.g. Azores, Tristan da Cunha, Ascension, St. Helena, Fernando de Noronha, St. Paul, Amsterdam) or related to a triple plate junction archipelago (Galápagos). Some cases, such as Iceland, involve a combination of such mechanisms (Iceland). Finally, the type of the volcanic eruption responsible (either Hawaiian, Strombolian, Vulcanian, Pelean or Plinian) also differentiates islands.

Although sometimes considered a different group, atolls are actually a particular kind of oceanic island because their characteristic coral reefs develop on already submerged basaltic skeletons of old oceanic islands. This only occurs if mean annual sea temperature reaches a certain level, restricting coral reefs to warm tropical, and the warmest of subtropical, waters. Atolls, very frequent in the Indian (Lakshadweep, Maldives, Chagos) and Pacific (Tuamotu, Kiribati, Tuvalu, Tokelau, Caroline Islands, Marshall Islands) Oceans, are only represented in the Caribbean Sea by a few Colombian atolls (Providencia and San Andrés) and in the Atlantic Ocean by the Brazilian Atol das Rocas.

ii) Continental islands or land-bridge islands. These are continental peninsulas that have been isolated from the rest of the continent by rising sea level, usually related to glaciations. They tend to persist as islands only during interglacials, until the next glaciations lowers sea levels again, restoring them to their peninsular status. Among them we can include large islands such as the British Isles, Wrangel, Severnaya Zemlya, Novaya Zemlya, New Siberian Islands, Newfoundland, all the Canadian islands in Nunavut and in the Northwest Territories, Bahamas, Falkland, Tierra del Fuego, Chiloé, Sakhalin, Sri Lanka, Sumatra, Java, Borneo, New Guinea, Tasmania and, especially, innumerable small islands interspersed with the large ones in the clusters just mentioned.

iii) Continental fragments or micro-continents. These are islands that split apart from the continent to which they once belonged, because of tectonic processes (especially seafloor spreading). Islands of this type tend to be large and, importantly, long lasting, sometimes even achieving ages exceeding 100 million years, as in the case of Madagascar. Other examples of this island type include Kerguelen, Seychelles, Formosa, New Caledonia, New Zealand, the great Antilles, Corsica, Sardinia, Sicily, Crete, Cyprus and South Georgia.

Some island groups, most notably Japan, the Philippines and Indonesia, have both a continental origin and intense island-arc volcanic activity linked to the presence of subduction trenches, resulting in complex continental-volcanic islands that do not easily fit into with the above classification. Similarly, several Pacific archipelagos (including Fiji, Vanuatu and Tonga), located between Australia and the so-called "Andesite line" (a geologically important loop separating the basaltic inner Pacific Ocean basin from the andesitic margins of the ocean), also have mixed continental and volcanic origin.

Biogeographical setting

For oceanic islands, their location, which as we have seen can be almost anywhere (within a plate or at divergent or convergent plate boundaries), is a crucial feature defining the composition of their biota. Isolation from the closest mainland largely determines the degree of endemicity that a island group will harbor. However, the number of potential colonization sources is also important. For instance, Hawaii harbors huge endemicity, which is due to its central Pacific location. This central location also means that colonization has been from several mainland sources (North America, Asia, Australasia). The result is a very different taxonomic balance of its biota in comparison, for instance, with the Galápagos or Canary islands. These archipelagos, being much closer to continents, both have lesser endemicity, although still impressive, but also much more skewed taxonomic balance towards South America and the Mediterranean basin, respectively. Finally, latitudinal location constrains islands' species richness, both through the size of the mainland species pool available and because of the climatic conditions on the islands. For instance, Anak Krakatau, Indonesia (6° S) and Surtsey, Iceland (63° N) (Figure 1) share very similar origins, ages, areas, isolations, altitudes and shapes, but greatly diverge in both their species composition and, especially, in their species richness, Anak Krakatau being much more species rich.

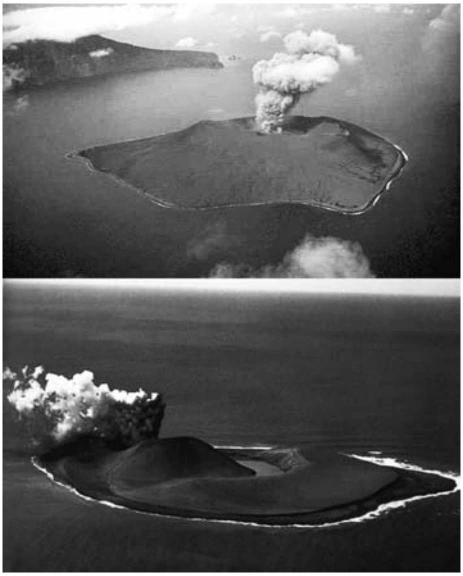

Fig. 1- Both Anak Krakatau, Indonesia (1939) (above) and Surtsey, Iceland (1963) (below) exemplify the most famous cases of new-born islands where colonization is being monitored

Furthermore, the emergence of an archipelago can connect two different, but neighboring, biogeographical kingdoms, as is the case for the Aleutians island arc, connecting the Palaeartic (Siberia) with the Nearctic (Alaska), and the Indonesian chain, connecting the Indo-tropical with the Australian ones. In both cases a double dispersal filter effect has been reported, resulting in the prevalence within a specific insular biota of species phylogenetically related to their closest mainland (Carlquist 1965). Finally, several archipelagos spread linearly at increasing distances from the mainland within a single biogeographic realm can act as unidirectional dispersal filters, as happens with Micronesia, Melanesia and Polynesia within the Pacific Ocean. Here, it has been shown (Williamson, 1981) that the further into the ocean an archipelago is located, the fewer representatives of a specific taxonomic group have been able to colonized it.

Island dynamism

Continental or land-bridge islands are highly dynamic and tend to be by far the most ephemeral islands within the real islands family, although they typically remain as emerged land for very long periods of time. Although some volcanic islands, such as Sabrina, lasting just a couple of weeks, are even more ephemeral, they do not get meaningfully populated during their short existences, thus losing their biogeographical interest. Most land-bridge islands have achieved their current insular condition only a few millennia ago, after the onset of the last interglacial period, and will lose it again in a few more millennia, with the arrival of the next glaciation. Before their most recent birth as islands, since at least the Eemian interglacial (ca. 127 Ky BP) these land-bridge islands (e.g. the British Islands, Sumatra, Java, Borneo, Newfoundland, Tierra del Fuego, Malvinas, Tasmania or New Guinea) were instead prominent peninsulas, sometimes even beneath the ice caps, of Europe, Indochina, Labrador, Patagonia or Sahul (the Pleistocene continent including the current Australia, New Guinea and Tasmania), respectively (Figure 2). This peninsula–island seesawing has happened perhaps as many as 20 (or maybe even 30) times in the Quaternary (Lisiecki and Raymo 2007). Islands of this type are extremely numerous, perhaps comprising more than 95 percent of all existing islands; each of the island clusters mentioned above contains more than 1,000 islands of this type.

A life span of ca. 15 Ky, coupled with usually low isolation – narrow water gaps, never deeper than 120 m – is not sufficient for evolutionary processes to produce new species, so continental islands rarely include a significant neoendemic element in their biotas. Speciation processes that start shortly

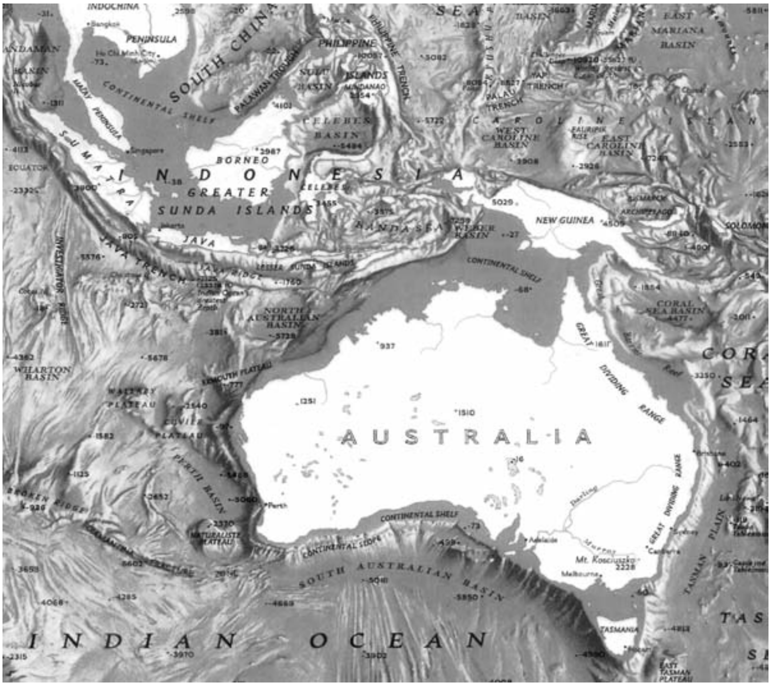

Fig. 2- The reiterative island-peninsular shift of land-bridge islands in the Pleistocene is exemplified in the Australasian region by the Sahul Pleistocene continent (Australia, Tasmania and New Guinea) and by the Indonesian Pleistocene peninsula (Sumatra, Java and Borneo)

after island isolation are cut short by genetic dilution once the mainland population rejoins the diverging insular population. Thus the endemism in the small number of continental islands that have relatively high degrees of endemism, such as Sumatra, Java, Borneo and New Guinea, should be attributed to the outstanding diversity of the tropical forests that those islands host, containing many narrow-ranged species, and to their large areas (making them more likely to contain entire species ranges), rather than to isolation.

On the other hand, continental fragments (or 'micro-continents') are by far the most persistent of islands, sometimes lasting more than a 100 million years. As seen already, they were formerly parts of a mainland, but achieved their insular status because of seafloor spreading, and not eustatic sea level transgressions as with continental islands. The formation of new oceanic crust in a rift valley divides the mainland and eventually causes such isolation of continental fragments. When these fragments are smaller than New Guinea the convention is to call them islands, although the same tectonic process also originate new continents. A spectacular example was the break-up of Gondwanaland, which started ca. 200 My BP, yielding both the new continents of Africa, South America, Sahul and India, and the islands that form Antarctica, Seychelles, Kerguelen, Madagascar, New Caledonia and New Zealand. Although there are not many islands of this type (perhaps fewer than 100 worldwide) they are mostly large islands and support vast numbers of endemic species (both relict and resulting from genetic drift). Therefore they contribute a disproportionately large share of world biodiversity.

As the seafloor spreading will continue as long as the Earth's interior fuel (decay of K, Th and U radio-isotopes) lasts, logically we expect that some of these continental fragments will collide in the future with other continents or continental fragments, so that new larger islands or continents will be formed through accretion. This has happened repeatedly in the history of Earth, including the collision of India with Eurasia ca. 60 My BP. Before that, India had acted as a 'biotic ferry' during a solitary voyage of 70 My (Ali and Aitchison, 2008) (Figure 3). The collision caused the uplift of the Tibetan Plateau and the Himalayan mountain chain, still in formation. Another example is the much more recent (2.5 My BP) collision of North America with South America, an event that is considered to have started the Pleistocene glaciation cycles (Uriarte 2003). Besides the outstanding geological and climatic consequences of such events, the primary biological consequences of these collisions are the biotic interchanges made possible: biotas that have developed in isolation for tens of millions of years are connected.

Nevertheless, by far the highest insular dynamism is associated with the oceanic islands. These islands behave in the long run almost as living beings, as they are born, grow, erode and finally

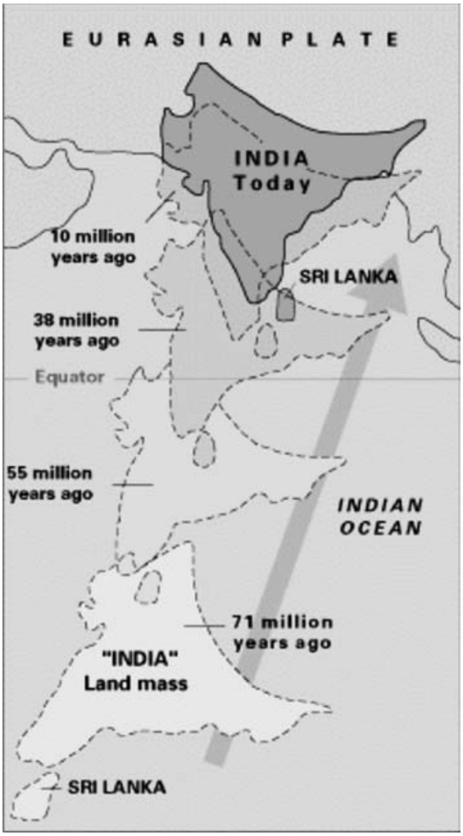

Fig. 3- Continental fragments as biotic ferries. India's 70 Million years trip from Gondwanaland to Eurasia, creating the Himalayan chain after the collision

die, disappearing under the sea, where they remain as seamounts unless they are subducted beneath continental crust. The duration of their life span as islands varies, depending on different factors, such as the intensity of the erosion processes (wetter climates cause faster erosion rates) and the chemical composition of the substrates, but usually volcanic islands last no longer than 5-15 My. An outstanding exception involves the older Macaronesian islands, with some of them (Selvagens, Fuerteventura or Sal) achieving ages greater than 20 My, because the volcanic activity that originated them in the past has persisted for an unusually long time because of the very slow rotation of the African plate (Geldmacher et al. 2001) and the inexistence of a significant subsidence in this zone of the Atlantic (Carracedo 2006).

Furthermore, new volcanic islands are frequently born all over the world, recent ones including Anak Krakatau (1930), Tuluman (1960), Surtsey (1963), Motmot within the Wisdom lake in Long Island off New Guinea (1968). Others are completely sterilized, such as the three older Krakatau islands in 1883 (Rakata, Sertung and Panjang); from a biogeographical point of view this is equivalent to resetting the chronometer to zero. There are perhaps ca. 2,000 islands of this type around the world, but as happen with the fragments they contribute as well disproportionally to the earth species richness, and as we are going to see later, with the conservation concerns as well.

Different phases in a hot-spot island life cycle

Hot-spot volcanic islands behave in the long run rather like biological individuals: they are born, grow, acquire a maximum area and altitude, before being eroded and subsiding, ending up just under the sea, where erosion is not more functional (Menard, 1986) (Figure 4). This series of events has recently

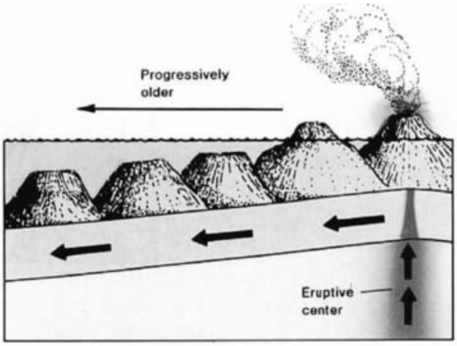

Fig. 4- Hotspot originated islands are born and grow while located over the mantel plume (right of the graph) and later, as they move away begin to be eroded until disappearing under the sea level where they rest as seamounts. If the oceanic floor subsidence is important (as happen in this graph) the seamounts will progressively sink beyond the photosynthetic zone (left of the graph)

been called the 'oceanic island ontogeny' (Stuessy, 2007) or the oceanic 'island life cycle' (Whittaker et al., 2007, 2008). Furthermore, volcanic islands are usually subject to a series of catastrophic events during their lifespans, which make them clearly different from other island groups. Six different phases may be distinguished in a hot-spot island cycle (Fernández-Palacios and Whittaker, in press; Fernández-Palacios, in press): a) birth and submarine construction; b) emersion and subaereal construction; c) erosion and dismantling prevalence; d) basal plain; e) terminal disappearance and f) guyot (from the Swiss geologist Arnold Guyot, meaning a flat-summit seamount) (Figure 5).

It is possible to exemplify the different phases of the oceanic island life cycle coexisting in a hot-spot archipelago, but only if the archipelago has been built over a very long time span, as with Hawaii in the Pacific Ocean, and the Canaries and Madeira in the Atlantic Ocean. Figure 6 shows the evolution of the Madeiran and the Canarian archipelagos through time. The phase

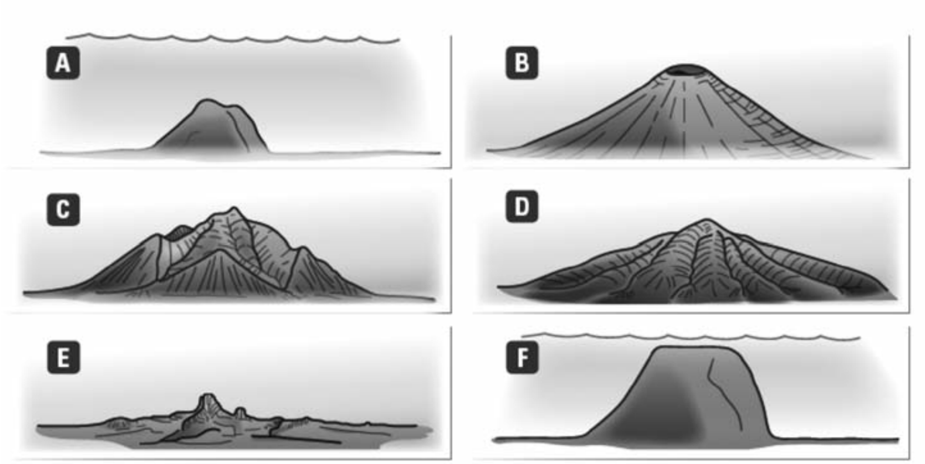

Fig. 5- The six stages recognized in the volcanic island cycle: a) birth and submarine construction; b) emergence and subaereal construction; c) erosion and dismantling dominant; d) reduction to a low-lying plain; e) terminal disappearance and f) guyot (flat-summit seamount) (Fernández-Palacios y Whittaker, 2010)

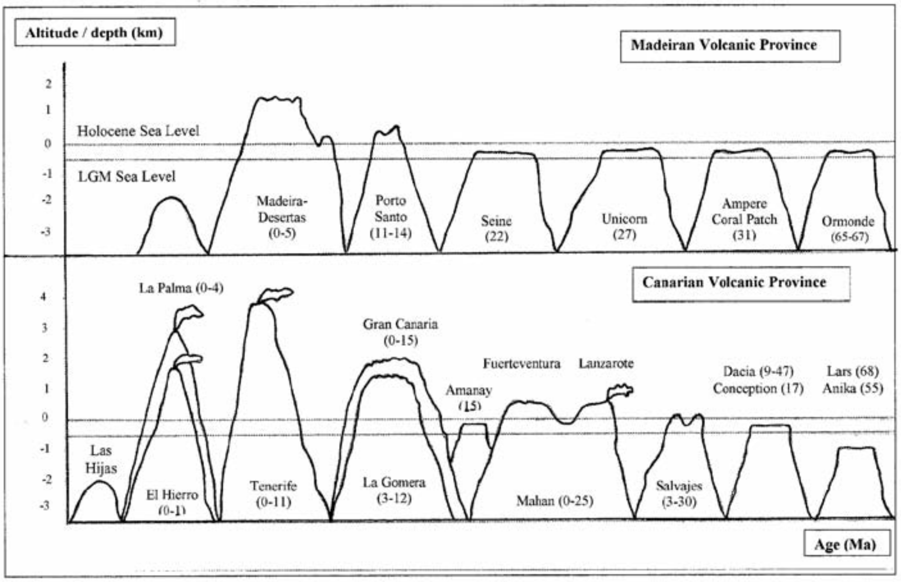

Fig. 6- Islands and seamounts constituting the Madeiran and Canarian archipelagos. In brackets are the ages of their first and last volcanic activity (Fernández-Palacios et al., in press)

(a) "birth and submarine construction" is represented by sea-mounts not yet emerged (such as Las Hijas in the Canaries), seamounts that are thought to be located above the mantle plume that has enable the existence of the archipelagos. La Palma, El Hierro and Tenerife represent accurately the "emersion and subaereal construction" phase (b), where the islands are still being built, as their recent volcanic activity testifies. These islands achieve globally significant heights, both above sea level (at 3718m, Teide on Tenerife is the highest mountain in Spain) and, especially, above the ocean floor, which in this part of the Atlantic is ca. 3-4 km below sea level. These first two phases are not represented today in the Madeiran archipelago.

The "erosion and dismantling" phase (c) is well represented by Madeira itself in the Madeiran archipelago and by Gran Canaria and La Gomera in the Canaries, both being volcanic buildings that have in the past had a much larger height and area, and where destructive processes today dominate constructive ones (except for the northeastern part of Gran Canaria where volcanic activity, although not historical, still occurs). It is in this phase that the islands achieve their maximal structural complexity (Whittaker et al., 2007, 2008), and, despite losing the summit ecosystems to erosion, still keep an important number of single-island endemics.

The "basal plain" phase (d) is well represented in Madeira by Porto Santo and Selvagem Grande and in the

Canaries by Mahan (the single volcanic building that includes both Lanzarote and Fuerteventura). Nevertheless, Mahan, and especially Lanzarote, still maintains very important volcanic activity that is rejuvenating the island. Despite having been much higher in the past (Fuerteventura, today only 800 m high is thought to have been 3300 m high in its past (Stillman, 1999)), today only low-altitude habitats are present. The "terminal disappearance" phase (e) is exclusively represented by La Salvajita and Ilheu de Fora, in the Selvagens archipelago, islets belonging politically to Madeira but built by the Canarian hot spot (Geldmacher et al. 2001). They are fragmented structures, lower than 30 m, that will soon disappear under the sea.

Finally, the "guyot" phase (f) is exemplified in Macaronesia by several flat-topped seamounts such as Seine, Coral Patch and Unicorn in the Madeiran Volcanic Province, and Amanay, Conception and Dacia in the Canarian province. These contrast with the Hawaiian sector of the Pacific Ocean, where subsidence of the Pacific floor causes the guyots to be drawn several hundred meters below sea level (Price and Elliot-Fisk 2004). In Macaronesia ocean floor subsidence is very scarce or even non-existent (Carracedo 2006) and the guyots maintain their summits within the photic (illuminated) zone, which extends to ca. 150 m depth.

If the summits of guyots are no more than 120 m below present-day sea level, as many of them are, they emerge and submerge repeatedly during Pleistocene glacial–interglacial cycles. When above sea level, they can constitute chains of 'stepping stone' islands that, in the case of Macaronesia may have more effectively connected the present-day archipelagos with each other and with Iberia and North Africa. When submerged, as today, these guyots constitute submarine islands with illuminated summits, where photosynthetic benthic communities thrive, isolated from similar ones by abyssal (3-4 km) depths. It is known from recent studies (e.g. Beck et al. 2002) that these submerged guyots harbor endemic biota, mainly invertebrate species, which may or may not be shared with nearby, similar submarine summits.

During the formation of a volcanic island, as it grows progressively in altitude, climatic conditions not previously present on the island (usually increased precipitation and humidity coupled with decreased temperature) gradually appear. These new conditions are exploited either by incoming species with appropriate ecological tolerances or, more usually in very remote islands, by marginal populations of widespread, generalist species that radiate adaptively to form new, more specialist species. If there are more similar islands nearby with climatic conditions, these new species may disperse and occupy these habitats. After some time, species occupying the same habitat in different islands may diverge to become new species, a phenomenon that has been called geographic speciation or inter-insular vicariance. This is most likely when, as commonly happens, the ecological specialization to the higher-altitude conditions is accompanied by reduced dispersal ability. Thus the same functional type may be present on several islands but as different species.

Later, as the island ages further, erosion increasingly dissects its landscape, forming huge ravines that greatly complicate the island topography and isolate formerly continuous populations, providing new opportunities for speciation through intra-insular vicariance. During this stage the island tends to achieve its maximal topographic complexity and biodiversity (Whittaker et al. 2007, 2008).

Finally, as erosion continues, the summit and mountain ecosystems progressively disappear. Unless the endemic, high-altitude specialist species are able to migrate to similar ecosystems in adjacent islands – which they cannot do when similar ecosystems do not exist there, or when the species cannot disperse that far – these species will be lost when their ecosystems disappear from the island.

Furthermore, volcanic islands, at least during their youth, are repeatedly subject to eruptions, which simultaneously destroy extant ecosystems and create new terrain to colonize. Subsequently the new terrain offers new opportunities for pioneer species, either native or immigrant. Often the new volcanic terrain is not homogeneously covered by barren lava, but contains patches of the former ecosystem that was not destroyed. These older 'islands' within a recent lava sea (known as kipukas in Hawaii or islotes in the Canaries) (Figure 7) constitute refugia from which the survivors can colonize and build the new ecosystem. But kipukas are also important from a genetic point of view, because they constitute the remaining populations and are subject to stochastic genetic bottlenecks, in which survival is not related to ability to withstand local conditions, but instead to the chance of their location when the lava came.

Fig. 7- *kipuka* in the Big Island (Hawaii) surrounded by a recent lava flow

Giant gravitational landslides constitute perhaps the most important type of catastrophic event affecting oceanic islands. We know today (Carracedo and Tilling 2003) that such events, which can strike from the initial subaereal phases to island senescence, can destroy significant parts of an island in just a few minutes. These events also produce mega-tsunamis that impact on the coasts of neighboring islands or mainland, destroying their coastal ecosystems. The ecological destruction again produces new terrain for native or immigrant species to colonize.

Features of volcanic island ecosystems

Although volcanic island ecosystems tend to have similar structure and function to the closest mainland ecosystems, their isolation excludes the participation of many common continental animal and plant species. The new insular building has to be constructed with the available bricks: those species that have been able to reach the island. It is common for some dominant mainland plant species, including those typically forming the main three-dimensional structure of the ecosystems) to fail to colonize, causing the insular ecosystems to have significantly different physiognomy.

Perhaps one of the more conspicuous examples of the influence of remoteness in the ecosystem functioning is an interesting successional characteristic of remote islands' forests called stand-level forest die-back (Mueller-Dombois, 1988). Basically, this phenomenon involves a demographically based event: the near-simultaneous death of the pioneer cohort that originally colonized the new volcanic terrain. This can destroy forest stands on remote islands when there is a lack of replacement of pioneers because mid- and late-succession (typically with shorter dispersal distances) have failed to colonize. This interesting process has been described for *Metrosideros* forest in Hawaii (Mueller-Dombois, 1988) and *Scalesia* forest in the Galápagos Islands (Lawesson, 1988), but not in the Canaries, where an important array of mid- and late-successional tree species are present, probably because of the lesser isolation.

The limited extent of many island habitats, reflecting the small area and great topographic complexity typical of oceanic islands, coupled with big variation in physical and chemical substrate properties, results in a limited recurrence of similar habitats across an archipelago. Even when similar habitats do recur in an archipelago, often intra- and inter-island vicariance result in relatively few shared species.

Volcanic islands also have interesting idiosyncrasies of nutrient cycling and limitation (Vitousek, 2004): young volcanic soils tend to be limited by N content and old ones by P content (Walker and Syers, 1976), so the highest carrying capacities are reached at middle age. Even so, the ecological principles governing continental ecosystems also tend to govern island ecosystems (Mueller-Dombois, 1992).

Ecological processes occurring on islands

The bulk of the short-term (ecological time-scale) changes occurring on islands, which in the long run create the basis for evolutionary processes to act, result from species impoverishment related to dispersal filters differentially affecting the continental species. The species impoverishment results not only in fewer species in some guilds, but also in a skewed or biased representation of the continental guilds on the islands, a phenomenon called ‘disharmony’. Thus entire functional groups (ecological disharmony) or taxonomic groups (taxonomical disharmony) can be absent from the insular communities. Both the species impoverishment within represented guilds and the disharmony lead to relaxation of inter-specific competition and therefore to increased intra-specific competition, through a demographic process called ‘density compensation’. In density compensation, similar resource levels used in the islands, but by fewer species than in the continent, lead to higher population sizes and densities (MacArthur et al. 1972) of individual species on the islands.

In this biotic context, under the intense pressure of high intra-specific competition, those individuals that successfully exploit new resources will tend to gain a selective advantage, increasing the likelihood of the species undergoing ecological release and a niche shift. Bizarre behavior, such as pollination by reptiles, has this origin and has so far only been described in islands and some peninsulas (Olesen and Valido, 2003).

When a species finds and uses a so-far underexploited resource on an island (for example a granivorous bird using a particular-sized fruit), facilitated by the absence of species that exploit the resource elsewhere, selection gradually shifts some of the characters used for the exploitation of the new resource to new dimensions that better match the new context (in our example, bill size may change). This was documented for several species of Darwin’s finches by David Lack (1947) in his seminal study of vacant trophic niches in the Galápagos Islands; he called it ‘character divergence’ or ‘character displacement’ (Grant and Grant, 2008).

When species disperse to islands, either from the continent or from other islands, they leave behind them, wholly or in part, their biotic context, including their pollinators, dispersers, competitors, prey, predators, parasites or diseases. Once on the new island, they typically find a new, simpler biotic context, where several, if not all, of the previously co-occurring species are not present because of their failure to cross the water gaps. Instead, other insular species perform specific mutualistic, competitive or predatory activities. In the case of plants, this causes simplification of species–specific pollination and dispersal webs. In the island ecosystem super-generalist species (perhaps lizards or birds) may pollinate or disperse even the newest plant arrivals. Sometimes one species may even perform both services simultaneously, a phenomenon called ‘double mutualism’.

Islands as evolutionary laboratories: long term (evolutionary time-scale) changes occurring in islands

As well as preserving relict species, museum-like, micro-continents and oceanic islands function as evolutionary laboratories, where new species – neoendemics – are continuously being formed. Several evolutionary processes promote such speciation, all sharing the necessity for long-term isolation in an environmentally adequate context, where natural catastrophes (often causing species extinctions) continuously create new space, resources and opportunities.

If the island is young and large, in the first phases of the island life cycle, it will typically be high enough to include several altitudinal zones, in which new forms of the original colonizers, much better adapted to the specific conditions existing at each altitude, will thrive, originating new species through adaptive radiation. Medium-aged islands tend to retain most of their maximum altitude, again sustaining a range of altitudinal zones and promoting adaptive radiation, but their deep erosion also offers a dissected landscape where a second mechanism, (intra-island) vicariance, can create new species that exploit the same habitat or niche, but in different parts of an island. The radiation of an ancestral colonizer in new lineages, regardless of the ultimate mechanism involved, is called cladogenesis (Stuessy et al. 1990). Finally, a species invading an old, small, flat, near-homogeneous oceanic islands (usually in the last island life-cycle phases) may well populate the whole island and, over time, will diverge from the ancestral colonizer without radiating into several new forms – a process called anagenesis (Stuessy et al. 1990). If, by whatever mechanism, the progenitor species survives with little change alongside species derived from it, the process is called anacladogenesis.

Island rule

The 'island rule', a term coined by Leigh van Valen (1973), is an evolutionary phenomenon that affects different taxa in different islands. Basically it comprises a series of conspicuous changes undergone by island inhabitants, compared with their mainland counterparts or ancestors. These include shifts in body size, loss of dispersal ability (often to the point of flightlessness), the appearance of secondary woodiness in plant taxa derived from herbaceous continental ancestors, diminution of the clutch size, behavioral tameness and several others.

Size shifts in animals probably constitute the most impressive island rule pattern, and can be manifest as either gigantism or dwarfism (Lomolino, 2005). It has long been considered that small animals (e.g. rodents, lizards, insects or birds) tend to shift towards gigantic forms on islands, as a consequence of either the shift to available resources usually exploited in the continents by larger animals, or release from predation, in both cases the continental natural enemies not having colonized the islands. Unfortunately, most of the best examples of gigantism have vanished after the human settlement of many islands, including the Malagasy giant lemurs (*Archaeoindris*, *Palaeopropithecus* and *Megaladapis*) and elephant birds (*Aepyornis spp.*), the New Zealand moas (*Dinornis spp.*), the Mauritian dodo *(Raphus cucullatus*), the West Indian giant hutia (*Amblyrhiza inundata*), the Canarian giant tortoise (*Testudo* *burchardii*) and rats (*Canariomys spp*.), the Corsican giant shrew (*Nesiotites corsicanus*) and the Capeverdian skink (*Macroscincus coctei*), among many other impressive examples. Still extant examples of gigantism include the Galápagos and Aldabra tortoises (*Geochelone nigra* and *G. gigantea* respectively), the Little Barrier Island (New Zealand) giant weta (*Deinacrida heteracantha*), the Angel Island chuckwalla (*Sauromalus hispidus*), the Solomon Islands giant skink (*Corucia zebrata*) and the New Caledonian giant gecko (*Rhacodactylus leachianus*).

By contrast, dwarfism is thought to be common in large animals that, once on islands, tend to diminish their sizes, because of either resource deficit or release from predation. Superb examples of now-extinguished dwarfism include several species of Pliocene-Pleistocene Mediterranean (Cyprus, Crete, Sardinia, Sicily, Malta, Cyclades and Dodecanese Islands) dwarf elephants; dwarf wooly mammoths in Sardinia, St. Paul off Alaska, the Californian Channel Islands and Wrangel Island; the Balearic mouse-goat (*Myotragus balearicus*) and Flores Man (*Homo floresiensis*). Still extant dwarfisms include the Spitzbergen reindeer (*Ranginfer tarandus platyrynchus*).

Secondary woodiness – the emergence of woody structures in island plants with immigrant herbaceous ancestors – has appeared repeatedly in different taxa and island groups, probably resulting from a release in islands from the harsher continental climate conditions (Carlquist 1974). Clades with secondary woodiness representatives include the Hawaiian *Scaevola*, *Silene* and *Cyanea*, the Macaronesian *Sonchus*, *Limonium, Echium* and *Argyranthemum*, the Juan Fernández Islands woody lettuces (*Dendroseris*) and the St. Helena sunflower trees (*Psiadia, Commidendron, Petrobium, Senecio* and *Melanodendrum*).

Flightlessness and other reduction in flying ability in island animals is another typical insular feature that has appeared many times in a wide range of island taxa, including insects and birds. Remarkable examples in insects include the New Zealand wetas (Anostostomatidae, Rhaphidophoridae) and the Canarian *Acrostira* (Pamphagidae) species. Among birds, the dodos, elephant birds, moas and the Rodrigues Solitaire (*Pezophaps solitaria*) have become flightless. Flightlessness has even been documented in passerines, such as the famous Stephen island wren (*Traversia lyalli*) that was eliminated by a single cat (named Tibbles), and the not-so-famous Canarian long-legged bunting (*Emberiza alcoverii*), also now extinct.

Islands as outstanding biodiversity holders: Speciation machines and museums

Oceanic islands, micro-continents and lakes contribute disproportionately to world biodiversity, given their combined area. Much of this contribution comes from cases of so-called 'explosive radiation' (Table 1), which are a typical result of persistent isolation in a heterogeneous and complex environment, as explained above. Outstanding examples of such radiation in the animal world include Hawaiian *Drosophila* fruit flies, African Great Lakes cichlid fish, Madagascan lemurs, Caribbean *Anolis* lizards, New Zealand land snails and New Guinean microhylid frogs. In the plant world, palms show explosive radiation both in Madagascar (*Dypsis*) and in the Caribbean (*Coccothrinax* and *Copernicia*), and examples for dicotyledons include several Hawaiian (*Cyanea, Cyrtandra, Haplostachys*), New Caledonian (*Phyllanthus, Psychotria, Pittosporum*) and Macaronesian (*Aeonium, Sonchus, Echium*) clades (Table 1).

Island group or lake	Animal taxa	Plant taxa
African Great Lakes	Cichlidae fishes (ca. 1500)	
New Zealand	Land snails (ca. 1000) Cicadas (40) Diplodactylid geckos (37)	
Hawaii	*Drosophila* flies (ca. 1000) Trigonidiine Crickets (173) Honeycreeper birds (ca. 60)	*Brighamia, Cyanea, Clermontia, Delissea, Lobelia, Trematolobelia* (Campanulaceae) (125) *Cyrtandra* (Gesneriaceae) (58) *Haplostachys, Phyllostegia, Stenogyne* (Lamiaceae) (57) *Melicope, Platydesma* (Rutaceae)(52)
Caribbean islands	*Anolis* lizards (ca. 400)	*Coccothrinax* palms (48) *Copernicia* palms (19)
Madagascar	Lemurs (99) Vangidae birds (21)	*Dypsis* Palms (ca. 150)
New Caledonia	*Diplodactylid* geckos (58) *Lygosomine* skinks (51)	*Phyllanthus* (111) *Psychotria* (85) *Pittosporum* (50)
Macaronesia	*Laparocerus* beetles (126) *Dysdera* spiders (53) *Napaeus* snails (70)	*Aeonium clade* (Crassulaceae) (55) *Sonchus* clade (Asteraceae) (35) *Echium* (Boraginaceae) (29)
Galápagos	Darwin's finches (15)	
New Guinea	Microhylid frogs (215)	
Mascarenes	*Phelsuma* geckos (40)	

Table 1. Selected examples of explosive radiation in island and lake taxa, which contribute significantly to world biodiversity. The number of known species is given in brackets, including both extant and extinct species (various sources)

Islands as museums

Volcanic islands and, particularly, micro-continents can act as natural history 'museums', where species long ago extinguished in the continents still form part of the extant biota. The role of islands as refugia for paleoendemic species results from several phenomena. First, the buffer effect exerted on islands by the oceans provides them with milder climates than those experienced on the continents at the same latitudes. This has been especially important in the climate shifts experienced in the Pleistocene. Secondly, many oceanic islands have steep topography and attain high altitudes, allowing short-distance altitudinal migration by species, to track suitable climatic conditions for their ecological requirements. Again, this is particularly important when climate changes. Thirdly, the reduced inter-specific competition characteristic of many oceanic islands can allow the survival of forms already outcompeted by evolutionary novelties on continents. Finally, small islands and islets located off mainland or larger islands can act as refugia for species already extinguished by humans on the mainland, by hunting or the introduction of exotic species.

Such insular paleoendemisms, some of them bizarre, include more than twenty laurel forest tree species in Macaronesia, among them *Pleiomeris, Persea, Visnea, Ocotea, Apollonias* and *Heberdenia*, (Fernández-Palacios 2009), the Galápagos and Aldabra giant tortoises (*Geochelone* spp.), the Tuatara (*Sphenodon* spp.) in islets off New Zealand and the Balearic lizard (*Podarcis lilfordi*) in islets off Mallorca and Menorca.

Archipelagos as speciation machines

Archipelagos have been likened to speciation machines (Rosenzwieg, 1995), in the sense that new endemic species, generated from few colonization events, are continuously produced in them. Several archipelago characteristics create suitable conditions for this evolutionary phenomenon, including: i) natural fragmentation (into islands) of the available land; ii) long-term isolation; iii) high altitudes of volcanic islands enabling important habitat heterogeneity; iv) the complex intra-island landscape created once destruction processes begin to dominate; v) emergence of islands in sequence (in hot spot archipelagos); and vi) eustatic sea-level changes in the Pliocene-Pleistocene.

The combination of these factors facilitates a wealth of ecological, biogeographic and evolutionary processes, resulting in high rates of speciation. Within a single high island, adaptive radiation (Figure 8) may generate new species exploiting several habitats and niches from the island coast to the summit. If the island is heavily dissected by erosion but still retains relatively high altitude, intra-island vicariance among different ravines or slopes will be present as well. Vicariance may also occur when island fusion and fission (for example, resulting from changes in the sea level) happen repeatedly. We know that vicariance has been much more effective in creating new species in oceanic archipelagos than adaptive radiation has (Funk and Wagner, 1995).

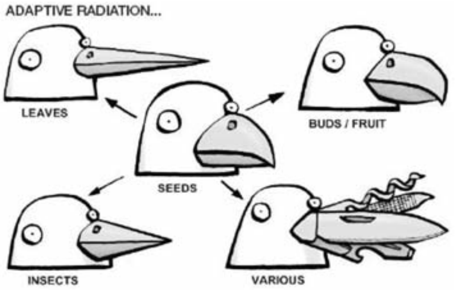

Fig. 8- The adaptive radiation consists in the development from a common ancestor of several new species which are specialized in the exploitation of the different available resources. The Hawaiian honeycreepers constitute one of the more spectacular adaptive radiations examples worldwide

When movements between islands within the same archipelago happen only infrequently, the picture complicates further. Additional processes to consider include: i) double invasions (a second invasion of the same ancestor, long after the first one, which by then has originated a new species); ii) the progression rule (colonization of newer islands from older ones); and iii) retrocolonization (the colonization by a new species of the island which its ancestor stem from). Depending on the specific circumstances of the new islands colonized, all these processes may be related to either adaptive radiation or vicariance. If sexual selection and hybridization introgression are also added to the speciation equation, one can understand why the more explosive examples of radiation worldwide tend to be insular or lacustrine.

Islands as a paradigm of conservation biology concerns

Collectively, the world's islands represent an outstanding example of major concerns in Conservation Biology, as they simultaneously host huge amounts of endemic species and are seriously threatened. Nevertheless, it is important to realize that even before the human colonization of islands worldwide, extinction was a major force shaping insular communities. We now know that, at least for large, high and old archipelagos, a large proportion of the endemic species, both in the flora and in the fauna, are single-island endemics (SIEs). SIEs are species restricted to a single island, usually the island where they originated (in which case they are neoendemics). Furthermore, most of these species have few (often just one) populations, comprising only a few hundred individuals or fewer, so that even without the dramatic impact of humans, SIEs are always prone to extinction. Eruptions, large landslides, tsunamis, droughts and hurricanes were all significant threats to endemic island species long before the human colonization islands worldwide. Nevertheless, the arrival of humans has been associated with an increase in extinction of four orders of magnitude over the natural rates affecting island endemics (Groombridge and Jenkins 2002).

Although containing just 5 % of the Earth's land surface, island extinctions account for more than 500 (60%) of the ca. 850 known extinctions occurring after 1600 AD (Primack and Ros 2002).

Those data include 60% of the mammal species lost, 79% of the mollusks, 81 % of the birds, 84 % of the insects and 95% of the reptiles, but only 36% of the plants. Tellingly, Lord Howe Island (10 km^2), off Australia, has had more historic extinctions of endemic bird than Asia and Africa put together! (figure 9).

Fig. 9- Lord Howe island, Australia (10 km^2) account for more known endemic land bird extinctions than Asia and Africa together

Human activities – especially destroying or transforming habitats, hunting, collecting, burning and introducing exotic species and diseases – have had well documented impacts on the endemic biota of islands. These impacts include extinctions of charismatic species, not least many of those already mentioned as outstanding examples of the island rule, such as the Madagascan elephant bird (*Aepyornis*), the New Zealand moas (*Dinornis*), the Hawaiian honeycreepers (Drepanididae), the Balearic mouse-goat (*Myotragus balearicus*), the Mauritius dodo (*Raphus cuculatus*), the North Atlantic great auk (*Pinguinus impennis*) and the Commander Islands (Steller's) sea cow (*Hydrodamalis gigas*) in the animal realm, and the Easter Island palm (*Paschalococos disperta*) and the St. Helena arboreal sunflowers (Asteraceae) in the plant world, just to mention some of the more spectacular cases. Simultaneously, many other species that are not charismatic but undoubtedly playing important roles in their natural ecosystems, have also been driven extinct by human activities on islands.

Many of the best examples of catastrophic invasions by species accidentally introduced by humans again come from islands. The Pacific Brown snake (*Boiga irregularis*) led to ca. 10 extinctions in the avifauna of Guam (Rodda et al. 1999). The Macaronesian faya tree (*Myrica faya*) in Hawaii is another good example, its success being attributed to its ability to fix nitrogen; this has multiplied by four the levels of nitrogen in its new ecosystem (Vitousek and Walker 1989). The *Myrica faya* invasion has facilitated the subsequent invasions, mediated by feral pigs, by several continental weeds that are better adapted to such high nitrogen concentrations than the native plants. Lakes account for impressive extinctions caused by species introduced by humans, the best known example being the extinction of ca. 200-300 haplochromid cichlid fish species in Lake Victoria after the introduction (for economic reasons) of the Nile perch (*Lates niloticus*) to the lake (Groombridge and Jenkins 2002). Thousands of other insular species all over the world are currently threatened with extinction.

All these reasons, and others, explain why within the 34 *Conservation International* (2005) biodiversity hot-

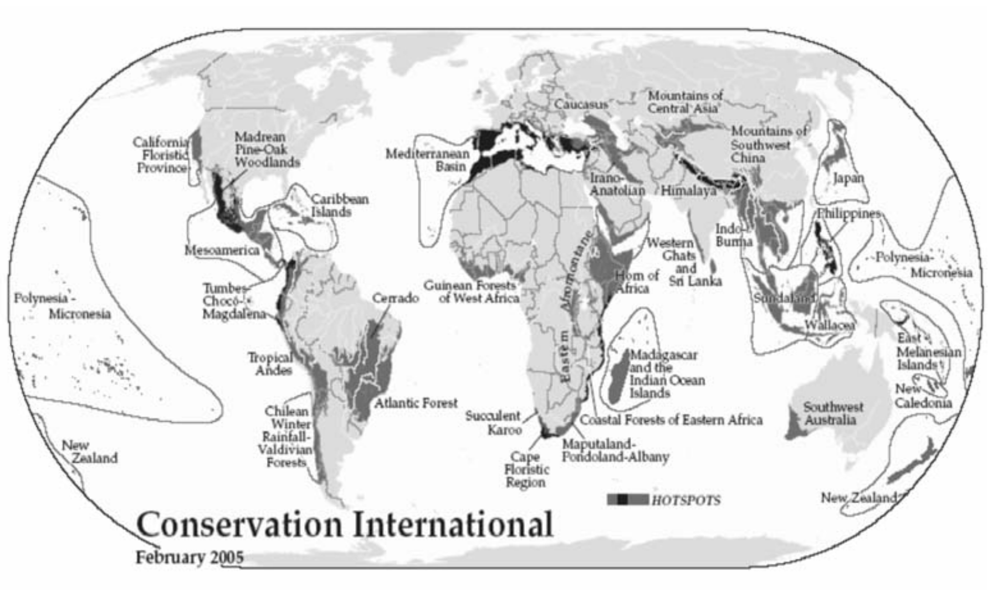

Fig. 10- The 34 *Conservation International* (2005) biodiversity hotspots

spots (which cover just 2.3% of the Earth's surface and are home to over the 50% of the world's plant species and 42% of terrestrial vertebrates; http://www.biodiversityhotspots.org) nine hotspot are composed exclusively of islands: (1) the Caribbean islands, (2) Madagascar and adjacent islands (the Comoros, Mascarenes, and Seychelles), (3) East Melanesia, (4) Japan, (5) New Caledonia, (6) New Zealand, (7) the Philippines, (8) Polynesia-Micronesia and (9) Wallacea. Three more have a substantial proportion of their diversity within islands: (10) the Mediterranean basin (including the Atlantic islands of Macaronesia), (11) the Western Ghats and Sri Lanka and (12) Sundaland (figure10).

To conclude, we can say for sure that research on islands has been invaluable for the development and enrichment of several scientific disciplines. Many concepts that have emerged mainly or exclusively from island research are today crucial for the understanding of various biological (Ecology, Biogeography, Evolution, Genetics, Conservation Biology) and geological (Vulcanology, Geomorphology) disciplines (table 2).

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Ecology	taxon cycle, r versus K strategies selection, primary succession, character displacement, species–area relationships, niche shift, stand-level forest die-back, ecological release, density compensation, double mutualism
Biogeography	long-distance dispersal, stepping stones, colonization, immigration, turnover, species impoverishment, disharmony, relictualism, palaeoendemisms, dispersal filters, kipuka, rescue effect, target area
Evolution	geographic speciation, founder principle, inbreeding depression, adaptive radiation, introgression, genetic revolution, neoendemisms, island rule
Conservation Biology	metapopulations, fragmentation, relaxation, extinction, invasion, invasional meltdown, reserve design
Vulcanology	hot spots, mega-landslides, tsunamis, guyot, island arcs

Table 2. Selected scientific concepts of different disciplines resulting mainly or exclusively from island research

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