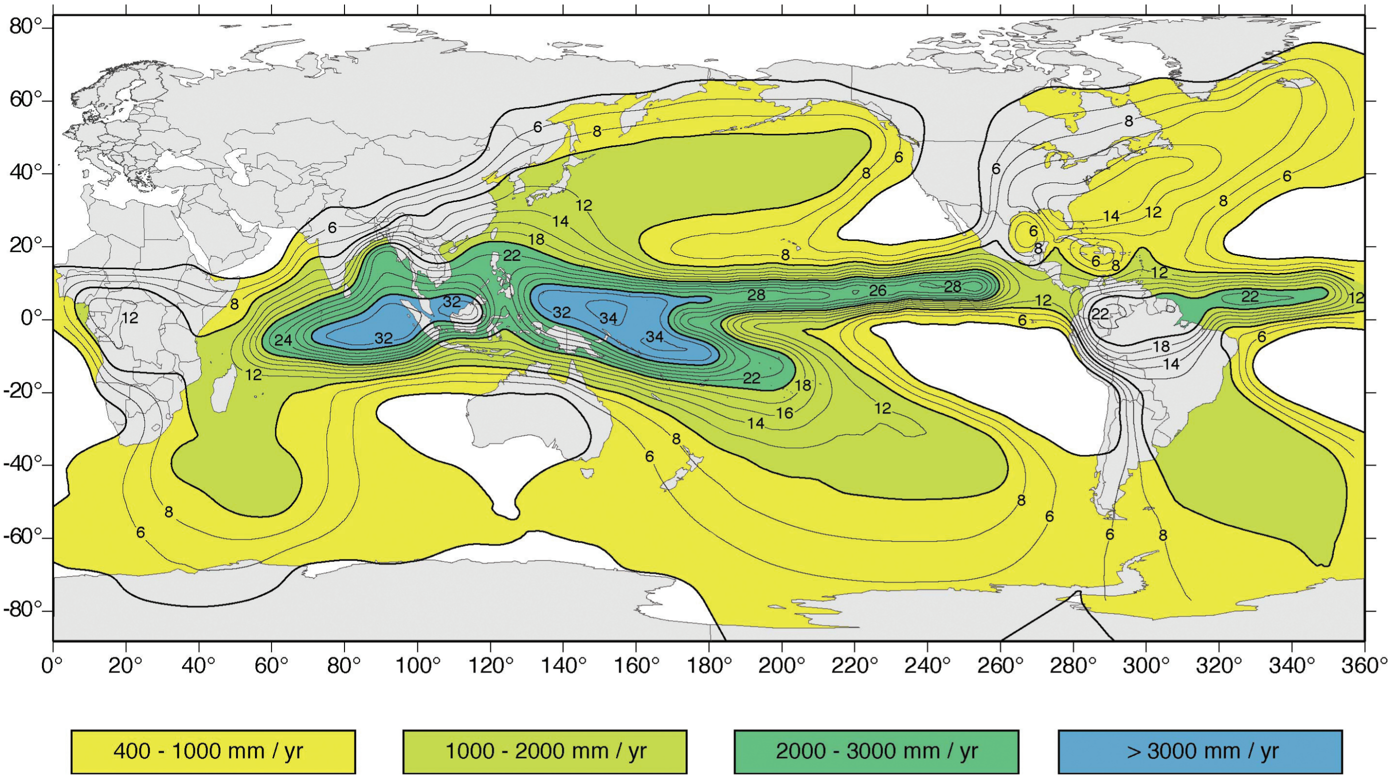

FIGURE 4 Average annual rainfall in millimeters per year for the 17-year period from 1979 to 1995. Interpolated and modified from Xie and Arkin (1997).

high tide. This is to say nothing of the threats to healthy coral growth posed by high water temperatures and possible increasing acidification of the ocean. Very high carbon dioxide levels probably occurred during the Cretaceous, a time of global warmth but also of very healthy populations of calcareous animals and plants. Whatever trends toward major acidification in the Cretaceous world existed were partly offset by dissolution of calcareous sediments on the deep seafloor. Ultimately, the same balancing may happen in the modern ocean, but this will take time. Over the shorter term, Waterworld awaits.

SEE ALSO THE FOLLOWING ARTICLES

Darwin and Geologic History / Makatea Islands / Marshall Islands / Motu / Reef Ecology and Conservation

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ATOMIC TESTING

SEE NUCLEAR BOMB TESTING

AZORES

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The Azores are a remote and geologically recent archipelago consisting of nine volcanic islands located in the North Atlantic Ocean (Fig. 1). Of the 4467 species and subspecies of terrestrial plants and animals known to inhabit this archipelago, 420 are endemics. These islands were discovered in the fifteenth century, and more than 500 years of human settlement have taken their toll on the local fauna and flora. Approximately 70% of the vascular plants and 58% of the arthropods found in the Azores are exotic, many of them invasive, and only 20% of the archipelago's terrestrial realm is protected, which raises serious long-term conservation concerns for the Azorean endemic biota.

GEOLOGICAL SETTING AND ENVIRONMENT

The Azorean archipelago is located in the North Atlantic Ocean, at the junction of the Eurasian, African, and North American plates (Fig. 1). The archipelago consists of nine volcanic islands, aligned on a west-northwest–east-southeast trend, which are divided into three groups: the western group of Corvo and Flores; the central group of Faial, Pico, Graciosa, São Jorge, and Terceira; and the eastern group of São Miguel and Santa Maria (Fig. 1). The largest island is São Miguel (745 km^2), and the smallest is Corvo (17 km^2). Santa Maria is the southern- and easternmost island (37° N, 25° W), Flores is the westernmost (31° W), and Corvo (39°42′ N) is the northernmost island. Pico has the highest elevation point (2351 m above sea level), and Graciosa the lowest (402 m above sea level). Five other islands have elevations near 1000 m above sea level. The three island groups are separated by 1000–2000-m-deep sea channels, except for Faial and Pico islands, between which the channel is, in many parts, only 20 to 50 m deep. The Azores are separated from the most western point of mainland Europe (i.e., Cabo da Roca, Portugal) by 1390 km. Located in the Atlantic Ocean at a mean latitude of 38°30′ N, the Azores enjoy a distinctly oceanic climate. The insignificant variation in the seasonal temperature and the high humidity and precipitation that characterize the archipelago's climate are mostly due to the influence of the Gulf Stream, which transports warm waters and humid air masses and is responsible for the high-pressure systems over the Azores.

Geologically, the Azores comprise a 20–36-million-year-old volcanic plateau; the oldest rocks (composing Santa Maria Island) emerged 8.120 million years ago, whereas the youngest (forming Pico Island) are about 250,000 years old. The geostructural environment of the Azores Plateau, defined by the 2000-m bathymetric contour line, is dominated by the confluence of the American, Eurasian, and African lithospheric plates. Thus the Azores are characterized by high volcanic activity typical of a ridge-hotspot interaction (i.e., a hotspot on a slow-moving plate). As opposed to the Hawaiian islands, which are chronologically arranged, the Azorean islands do not show any correlation between their distances to the hotspot and their individual ages of emergence. The eastern parts of all Azorean islands are geologically the oldest, which is the result of the particular seismovolcanic mechanisms of this archipelago. This tectonic feature is responsible for many volcanic eruptions (e.g., Capelinhos, Faial Island, 1957–1958) and tectonic earthquakes (e.g., Terceira and São Jorge islands, 1980; Faial and Pico islands, 1998).

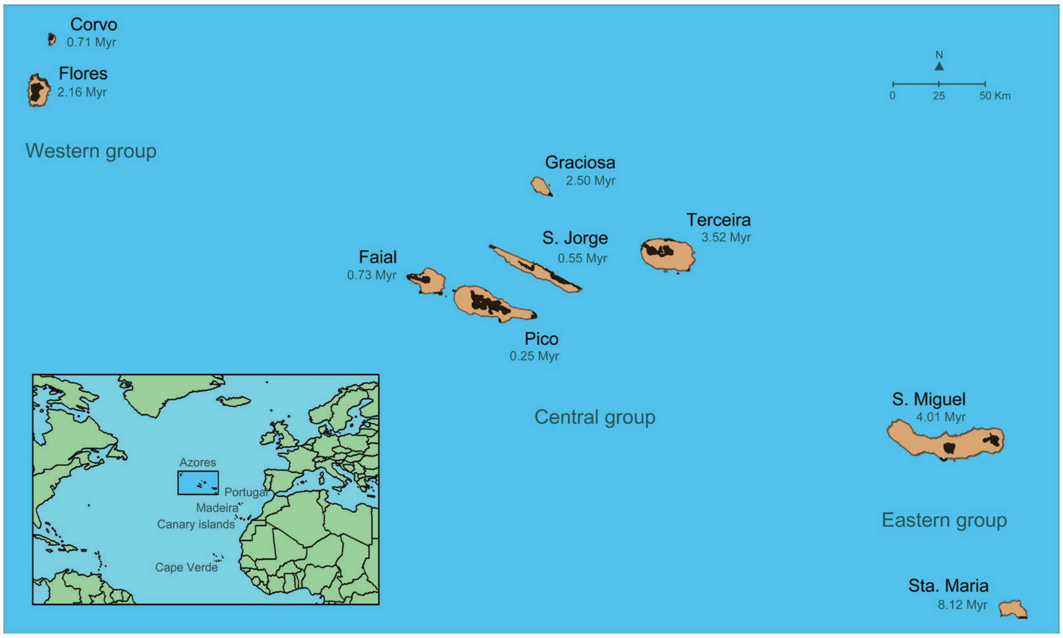

FIGURE 1 The location of the Azorean archipelago in the North Atlantic, and the nine islands of the Azores with estimated geological age. Shaded areas correspond to protected island areas based on recent IUCN classification (almost 20% of the total territory of the archipelago).

As a result of several recent historical lava flows, there is a great concentration of lava tube caves and pits in the Azores. A total of 250 underground cavities, including lava tubes, volcanic pits, pit-caves, and sea-erosion caves, are known to exist on the Azores, creating many kilometers of cave passages, extraordinary geological formations, and unique fauna adapted to caves.

Regarding native plant communities, laurisilva,—a humid evergreen broadleaf laurel forest—was considered in the past to be the predominant vegetation form in the Azores. However, more recent studies have shown the existence of a wide variety of plant communities, including coastal vegetation, wetland vegetation (lakeshore and seashore communities and a variety of bogs), several types of meadows, and different types of native scrub and forest. Moreover, the Azorean laurisilva differs from that found on Madeira and on the Canary Islands, as it includes a single species of Lauraceae, several species of sclerophyllous and microphyllous trees and shrubs, and luxuriant bryophyte communities, covering all available substrata. In contrast to other Macaronesian archipelagoes, the Azores only has one endemic genus of vascular plants (*Azorina*). After human settlement, other types of vegetation cover have become progressively dominant. Presently, they include pastureland, production forest (mostly with *Cryptomeria japonica*), mixed woodland (dominated by nonindigenous taxa), field crops and orchards, vineyards, hedgerows, and gardens.

OVERALL BIODIVERSITY: SPECIES INHABITING THE AZORES

The terrestrial flora and fauna of the archipelago were recently listed (summary in Table 1). It is believed that the Azores, especially the younger islands, are not saturated with species. The islands are probably in a nonequilibrium condition as a consequence of (1) the dispersal difficulties imposed by the isolation of the archipelago, which are much greater than the dispersal abilities of a wide range of taxa; (2) the vicissitudes of the Pleistocene environment; (3) the destructive influence of volcanic activity; and, more recently, (4) the impact of human activities.

TABLE 1
Number of Currently Known Terrestrial Species and Subspecies in the Fauna and Flora of the Azores

	Total	Endemic
Algicolous fungi	1	0
Lichenicolous fungi	22	0
Lichens	551	12
Bryophyta	438	9
Plantae	947	68
Nematoda	80	2
Annelida	21	0
Mollusca	111	49
Arthropoda	2227	267
Chordata	69	13
Total	4467	420

NOTE: Table based on the catalog of Borges *et al.* (2005).

BIOGEOGRAPHY

Even factoring out the area of the islands, the native fauna and flora of the Azores is impoverished when compared to the other Macaronesian archipelagoes (Madeira and the Canary Islands). For example, the number of Azorean endemic species is about three times less than the number of endemics of the Madeira archipelago (three times smaller but older and nearer to the mainland) and ten times less than the number of endemics of the Canary Islands (three times larger). Given the isolation of the Azores, the ancestors of all the terrestrial endemic species found in the archipelago had to travel over a significant water distance (more than 1200 km) from neighboring Europe and about 800 km from Madeira Island. Additionally, colonization of the Azores has occurred over a short geological period, since the oldest island (Santa Maria) emerged 8.12 million years ago. Accordingly, it is of no surprise that the only indigenous terrestrial vertebrates are bats (two species) and birds (16 species). Nevertheless, the presence of many endemic flightless beetles in the Azores, whose ancestors are believed to have also been flightless, suggests that long-distance ocean dispersal, by air and on the water surface (rafting), must have been an important colonization mechanism. Most storms and prevailing winds come from the West, but the Azorean biota is mainly of Palearctic and Macaronesian origin. A similar situation occurs with the Azorean terrestrial molluscs, which are clearly of Palearctic origin and, at the same time, exhibit Macaronesian relationships in some taxa: *Leptaxis* lives also in Madeira, and *Napaeus* in the Canary Islands. The preferred explanation for this "anomaly" is the large distance to the American continent and the possibility that the paleo-winds may have blown in a different direction from the current prevailing winds. However, a simpler explanation for the biota composition of the Azores is the arrival of colonizers through "sandstorm" dispersal originally coming from the Sahara. Clear exceptions to the Palearctic/Macaronesian origin can only be found in organisms with great dispersal abilities, such as bryophytes, some species of which, found in the Azores, are unequivocally of American origin.

The most general pattern in ecology is the species-area relationship (SAR). Considering only the area above an altitude of 300 m (because native habitats can only be found above that elevation in almost all Azorean islands), a significant relationship is observed in the Azores for indigenous bryophytes, vascular plants, and arthropods, but not for land molluscs (Fig. 2). Arthropods show the steepest slope of the SAR curves, which implies a higher beta-diversity for this group and, consequently, a more heterogeneous species composition among the islands. However, the time factor should be accounted for in the case of endemics; this could explain the absence of SAR for land snails, as small, older islands (e.g., Santa Maria) harbor more endemic species.

Some of the most diverse Azorean genera with endemic species are also diverse in Madeira and the Canary Islands (e.g., the beetles *Trechus* and *Tarphius,* the hemipteran *Cixius,* and the land-snails *Napaeus* and *Plutonia*), thus reinforcing the hypothesis of a Macaronesian interarchipelago dispersal.

EVOLUTION

There are several aspects of the evolutionary history of the Azorean biota that are still not clear. Traditionally, many biologists considered the Azorean and the Macaronesian endemic flora in general to be ancient, consisting of many paleoendemic species, relicts of the vegetation that originally covered most of Western Europe during the Tertiary period. However, there is increasing evidence from molecular data that many of the endemic Macaronesian plant species are the result of in situ evolution after a relatively recent colonization (neoendemics). This theory may also apply to invertebrates (e.g., arthropods and terrestrial molluscs), in which colonization followed by isolation has led to the evolution of a highly original neoendemic fauna. The most diverse genera in the Azores belong to the animal realm (classes Gastropoda and Insecta). Molecular data on insects show that many endemic species belonging to speciose genera are monophyletic in the Azores (e.g., *Tarphius, Trechus, Hipparchia*), thus implying that all species within a particular genus originated by speciation events occurring after the arrival of a single ancestor to the archipelago. In spite of some evidence that evolution has proceeded to a subgeneric level in some land molluscs (e.g., *Macaronapaeus, Atlantoxychilus, Drouetia*), natural arrival to the Azores is an uncommon event, and most of the Azorean endemics are neoendemics. Thus, dispersal limitation may be viewed as one of the main driving forces that has shaped the Azorean native biota. Available data suggest that the "progression rule"

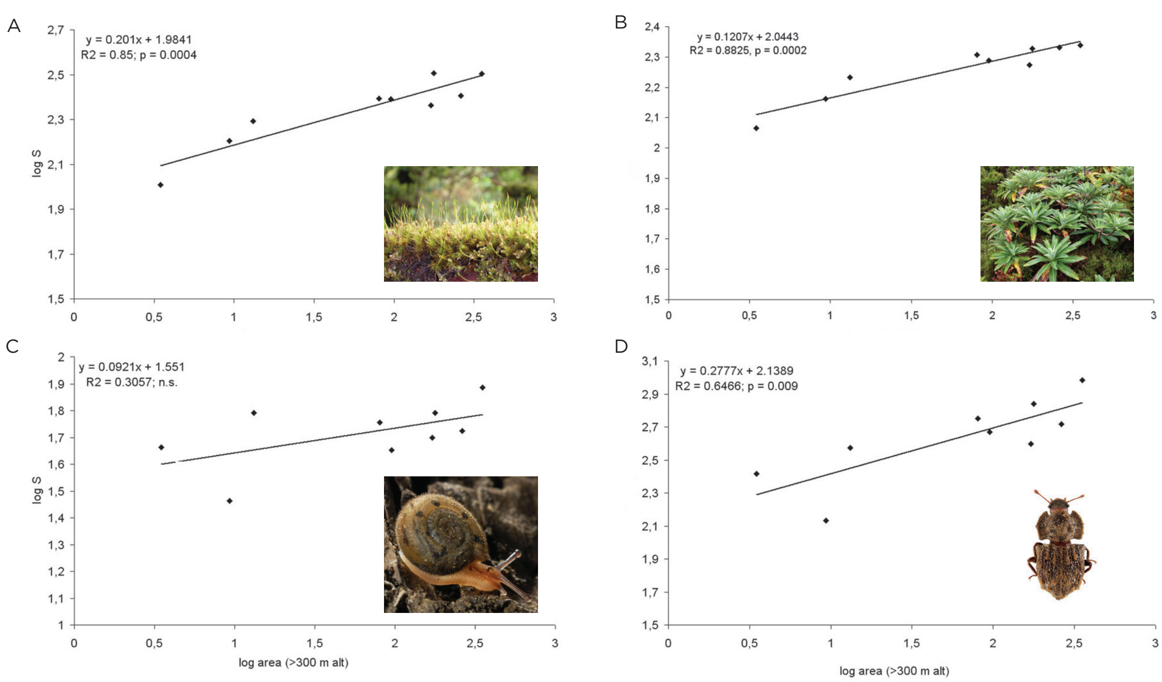

FIGURE 2 Species-area curves for (A) indigenous bryophytes, (B) vascular plants, (C) terrestrial molluscs, and (D) arthropods (see text for further explanations).

(i.e., a nonstochastic pattern of colonization from older to younger islands) applies to the Azores: Santa Maria has generally been the first to be colonized, accompanied by subsequent lineage splitting as individuals disperse to the younger western islands. Future phylogenetic studies, aimed at understanding patterns of dispersal, colonization, and speciation in the Azores, should clarify the presence of more complex patterns within and among island speciation as well as the possibility of back colonization events from younger to older islands.

The high volcanic activity in the Azores is responsible for the formation of new habitats, such as lava tubes and volcanic pits, from which 20 neoendemic troglobitic arthropod species have been described to date. These cave-limited species exhibit different levels of adaptation to the underground environment and therefore constitute an excellent opportunity to investigate ongoing evolutionary processes. Many of the cave species known to occur in the Azores belong to genera that have representatives in the troglobitic fauna of other Macaronesian islands (e.g., the Canary Islands), thus serving as a model for further studies of inter-archipelago speciation.

An interesting example of an island syndrome in the Azores is given by the damselfly *Ischnura hastata* (Insecta, Odonata): There is no evidence of parthenogenetic populations in the New World, so the Azorean populations probably developed parthenogenesis after colonization.

CONSERVATION REMARKS

The relatively high level of endemism in the Azores gives to the archipelago's biota great conservation relevance. Its preservation has also been recognized by the local government through the establishment of protected areas for conservation purposes since the early 1980s. The Azorean Protected Areas Network is currently being reformulated according to IUCN criteria and includes 23 Sites of Community Importance and 15 Special Protected Areas, which are part of the NATURA 2000 network of nature protection areas. Most of this protected area includes the richest sites in endemic arthropods and also in rare European bryophyte species, but the area does not protect all native fauna and flora.

Although expanding, unregulated tourism has not yet raised conservation concerns in the archipelago. Fragmentation and degradation of habitats together with the spread of nonindigenous species are the greatest threats to the terrestrial biodiversity in the Azores. Intentional introduction of many plant species for agriculture, forestry, and aesthetic purposes has had an enormous impact on the current flora of these islands. Many of the imported species "escaped into the wild," and a considerable proportion have become naturalized, causing problems in agriculture and forestry. The impact of these species—in particular, invasive vascular plants, which are disrupting native plant communities with unknown consequences for overall native biodiversity—is of great concern. A negative impact on the indigenous community of phytophagous insects is expected, as well as changes in vegetation structure, difficulties in the regeneration of endemic species, and competition for dispersal agents, leading to a reduction in the frequency and abundance of indigenous plant taxa. Humans are clearly implicated in the establishment of exotic species: 70% of the vascular plants and 58% of the arthropod species and subspecies have been introduced on purpose or as stowaways. Moreover, the density of human population is correlated with the diversity of exotic taxa (vascular plants: $r = 0.86$; $p = 0.003$; arthropods: $r = 0.93$; $p = 0.0002$), and there is a remarkable correlation between the richness of exotic plant species and that of exotic arthropod species ($r = 0.96$; $p < 0.0001$).

Protected areas are strategically important in order to guarantee a successful management of biodiversity conservation policy in the Azores. Progress in the conservation of Azorean biodiversity depends predominantly on long-term studies on the distribution and abundance of focal species and the control of invasive species. This research requires serious commitment from scientists, politicians, and the general public. The definition of genetic units for conservation purposes in the Azores is also extremely important, particularly for widespread endemic species. For some of those endemics that are geographically structured, part of their genetic variability is locally endangered due to threats to specific populations or to the refuge-type distribution. The conservation of the Azorean natural heritage will largely depend on the definition of a global and integrated global strategy focusing on the management of both indigenous and nonindigenous species, and paramount attention needs to be paid to the implementation of a sustainable use of the archipelago's natural resources, including its biodiversity, in a trade-off with human activities and increasing inhabitants' commitment to environmental values.

SEE ALSO THE FOLLOWING ARTICLES

Canary Islands, Biology / Fragmentation / Lava Tubes / Madeira / Species–Area Relationship

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