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SPECIAL ISSUE: INTRODUCTION

The Canaries: an important biogeographical meeting place

We were delighted on two counts to be able to act as the conveners of the third biennial meeting of the International Biogeography Society (IBS) in Puerto de la Cruz, Tenerife in January 2007. First, the conference facilities generously provided for our use by the Cabildo Insular de Tenerife made an excellent venue for the free-flowing discussion with colleagues old and new that is the hallmark of a good academic meeting, while the symposia and poster presentations alike were of a uniformly high standard. In short, it was acknowledged by those attending to be a thoroughly successful meeting, which showed biogeography to be a dynamic and exciting discipline and demonstrated that the still recent initiative of launching the IBS in 2000 was long overdue. Second, holding the meeting in the Canary Islands provided an opportunity to bring the archipelago to the attention of the biogeographical community, hopefully generating wider interest in the biogeography, ecology, evolution and conservation of the wonderful diversity of ecosystems and species found within the archipelago.

This brief introduction is divided into two parts. First, we provide a brief comment focused on the content of this Special Issue, and second, we provide a short overview of the special biogeographical setting of the Canary Islands, emphasizing the pressures on the natural environment today and some of the measures in place for the conservation of nature within the archipelago.

PART I: UP FOR DEBATE – FUTURE DIRECTIONS FOR BIOGEOGRAPHY?

The conference was organized around five thematic sessions under the headings of (1) An integrative view of ecogeographic 'rules', (2) Quaternary impacts on Holarctic biogeography, (3) Island biogeography, (4) Maritime connectivity: reconciling models of dispersal and vicariance with evidence of biogeographical structure in a continuous environment, and (5) Separating historical from environmental effects on species distributions. An indication of the diversity and substance of the presentations at the meeting is represented in this collection of papers, which are drawn from each of these themes. Most of the papers herein derive from key-note presentations, but one derives from a poster presentation, one from a presentation during a panel discussion on the theme 'Biogeography in the public eye', and finally we have included a specially commissioned Commentary (Mackey, 2008) focusing on the contribution by Patten & Smith-Patten (2007).

Geographical gradients in species richness have long fascinated biogeographers and ecologists, with recent work capitalizing on newly available spatial data sets and advances in spatial analytical techniques (e.g. Diniz-Filho & Bini, 2005; Rangel *et al.*, 2006) to offer substantial advances in understanding. In this Special Issue, Svenning *et al.* (2008) provide an illustration of a further recent development (Hawkins *et al.*, 2006), integrating evolutionary structure with the spatial analysis in their examination of palm species richness gradients across the New World. While finding support for the significance of climate, especially the mechanisms invoked in water–energy dynamics theory (O'Brien, 2006), their analysis also emphasizes the role of long-term environmental change, in the form of Late Tertiary orogeny. The importance of the changing elevation of landmasses is even more strongly emphasized in Patten & Smith-Patten's (2007) analyses of biotic boundaries in Neotropical avifauna. Their paper demonstrates a contrasting approach to that of Svenning *et al.* (2008) in that they use species location data rather than trusting in the species-range map data commonly used in spatial analyses of diversity gradients, and it demonstrates a contrasting approach to spatial analysis in their use of Monmonier's algorithm. In a further illustration of the methodological diversity of biogeographical analyses of relationships between taxa and area, both Waters (2007) and Sanmartín *et al.* (2008) offer approaches to using molecular phylogenies to infer the relative roles of dispersal and vicariance between and among continents and islands. Their work is part of a growing resurgence of interest in long-distance dispersal as a valid mechanism (alongside vicariance mechanisms) within biogeographical science, and of a growing awareness of the importance of incorporating general patterns of environmental history in island biogeographical and evolutionary models (e.g. Carine *et al.*, 2004; Carine, 2005; Whittaker *et al.*, 2007, 2008).

Also on the theme of environmental change, but with a more recent focus, both Magri (2007) and Bhagwat & Willis (2008) provide substantive contributions to an understanding of the role of glacial/interglacial climate cycles in shaping the composition of European fauna and flora. Both papers emphasize that elements of the post-glacial biota of north-western Europe persisted through unfavourable glacial periods not just in distant southern refugia, but also farther north, dispersed across landscapes at low densities or in pockets of favourable microclimates. These findings deserve to be carefully considered by those attempting to use so-called bioclimatic envelope models to forecast future species responses to global climate change (e.g. Araújo & Guisan, 2006; Araújo *et al.*, 2006; Randin *et al.*, 2006). The pioneering attempt by Bhagwat & Willis (2008) to identify the species traits that favoured persistence in western Europe through the Pleistocene also deserve close attention: what sort of a guide do their findings provide on how temperate communities may respond not to a cooler climate but to a substantially warmer one? This seems an area worthy of further consideration from biogeographers.

There has recently been a considerable resurgence of interest among biogeographers in ecogeographical rules such as Bergmann's rule, Jordan's rule, and the Island rule (e.g. Meiri & Dayan, 2003; Lomolino *et al.*, 2006; Meiri *et al.*, 2006;

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Price & Phillimore, 2007). Gaston *et al.* (2007) neatly define these 'rules' collectively as being about spatial patterns in biological traits. Many of these rules have been around for a long time, and there is generally something in them, but, as both Gaston *et al.* (2007) and McDowall (2007) emphasize, the patterns of variation involved typically turn out to be more complex than originally envisaged, and also typically involve co-variation with other biological traits on the one hand, and co-variation amongst potential causal environmental variables on the other (e.g. see Guillaumet *et al.*, 2007; Meiri *et al.*, 2008). Equally important is that these rules, however they may originally have been defined, are frequently being addressed at a number of taxonomic levels, typically both intra-specific, and inter-specific, thus posing significant challenges to those attempting to synthesize findings in this area. Both McDowall (2007) and Gaston *et al.* (2007) rise to these challenges, and identify some key research priorities for the future.

Although much of the conference focused on the underlying pre-human signal inherent within biogeographical data, the application of biogeography in the Anthropocene was a theme continued from the previous meeting of the society (Riddle, 2006), represented in this Special Issue notably in the form of Blondel's (2007) synthesis of human impacts on the ecology and environment in the Mediterranean, and in the advocacy for biogeographical analyses in conservation decision-making evident in other papers in the Special Issue (e.g. Patten & Smith-Patten, 2007; Bhagwat & Willis, 2008). However, of all of the papers in the Special Issue, perhaps the most important message for the biogeographical community is to be found in Ladle's (2008) critique of the public representation of biogeography. His finding that biogeography has a low public profile will come as no great surprise to most biogeographers, but nonetheless provides painful evidence that ours is a largely cryptic discipline. The failure of practising biogeographers to promote public awareness of their work more effectively under the label biogeography may also be linked in some way, as Ladle suggests, to our failure to penetrate school curricula (at least this seems to be the case in the UK). Although the evidence from this Special Issue is of a vibrant, intellectually challenging and exciting discipline, Ladle demonstrates that we need to do much more outreach and public dissemination work to establish the relevance of biogeography in the public sphere (see also Whittaker *et al.*, 2005). Certainly, we would anticipate public outreach to be an important emerging role for a maturing IBS, and one that we would hope to address further at the fourth biennial IBS meeting, which will take place on the Yucatan Peninsula of Mexico in January 2009. We return to this theme again, briefly, at the end of the second section of this Introduction to the Special Issue.

PART II: THE GLOBALIZATION OF THE CANARY ISLANDS – IMPLICATIONS FOR BIODIVERSITY

This section of the paper is based on the first presentation at the IBS meeting, in which the first author (JMFP) provided an overview of the Canary Islands, their geo-environmental history, biodiversity value,

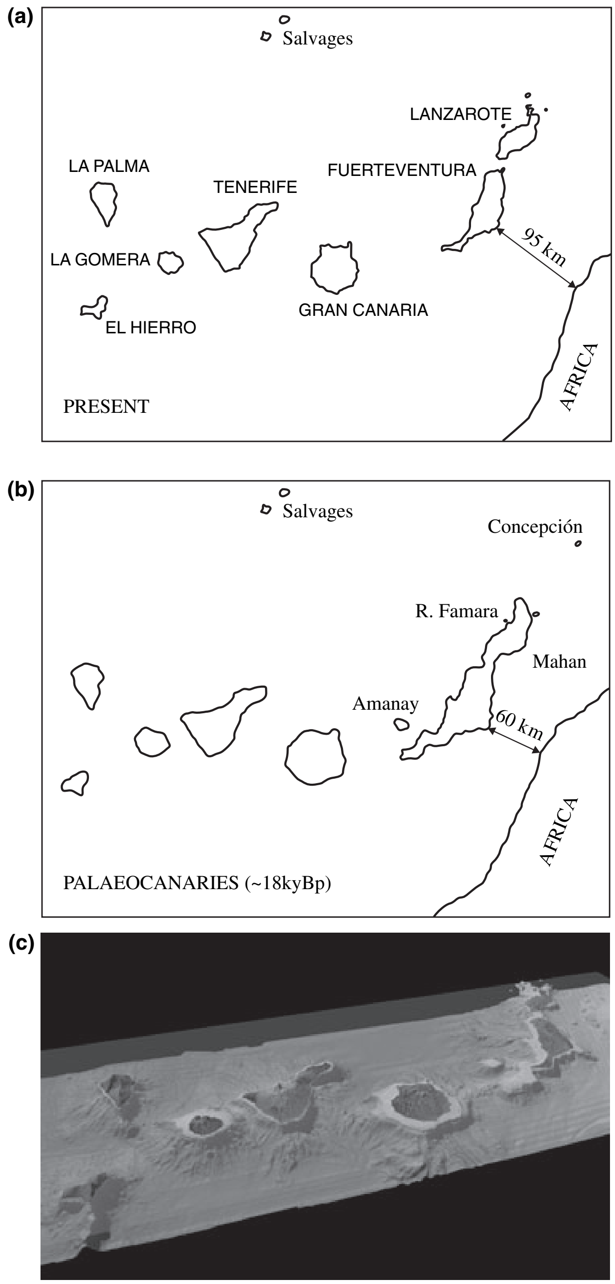

Figure 1 The Canary Islands (a) today and (b) at the time of the sea-level minimum of the Last Glacial (modified from García-Talavera, 1999), and (c) in relief, showing the bathymetry of the archipelago (with the kind permission of Juan Acosta, Multibean Mapping Group, Instituto Español de Oceanografía, Madrid, Spain).

human colonization, environmental challenges, and conservation responses. There is also much to say about recent advances in the understanding of the biogeography of the Canary Islands, in which great strides have been made in the last 20 years, in large measure through the application of modern molecular phylogenetic analyses. For further detail on these advances and innovative analyses based on these data, see Sanmartín *et al.* (2008).

Geo-environmental setting and biodiversity attributes of the Canary Islands

The Canary Islands constitute a volcanic archipelago located off the West Saharan coast of north-west Africa (Fig. 1). The islands are characterized by outstanding biodiversity, featuring high levels of endemism, including both palaeo- and neo-endemic forms, and spectacular radiations in many animal and plant lineages, distributed across an impressive array of major ecosystem types from semi-desert through sub-tropical broadleaved evergreen woodlands and xeric endemic pine woodlands to high-altitude sub-alpine and alpine environments. This diversity is underpinned and explained by a combination of geological and geographical characteristics (Table 1), including: (1) the subtropical location (27–29° N) of the archipelago; (2) the unusual longevity (16–20 Myr) of the older islands (for volcanic oceanic islands); (3) the high altitudes achieved by the central and western islands (> 1500 m a.s.l., with the highest point on Tenerife, the Teide peak of 3718 m a.s.l., also being the highest point in the Atlantic Ocean); (4) the influence of the North-East trade winds and of the Canarian cool marine current; and (5) the intermediate degree of isolation, varying between some 60 km at low sea-level stands and 95 km today (García Talavera, 1999), generating a less disharmonic biota (*sensu* Whittaker & Fernández-Palacios, 2007) than found in Hawaii, but enough restrictions on gene flow to enable the evolution of high in situ diversity (Table 2).

Although the oldest parts of the archipelago date back over 10 Myr, the geological context of the islands is one of ever-changing circumstances. For instance, within just the last 2 Myr (the Pleistocene and Holocene) major events have included: (1) the emergence of new islands (La Palma and El Hierro) and islets (Alegranza, Montaña Clara, La Graciosa, Lobos) in the western and eastern extremes of the archipelago, respectively; (2) the partial destruction of some islands as a result of mega-landslides that have formed huge scar-valleys (La Orotava, Güímar, Icod in Tenerife; Taburiente, Cumbre Nueva in La Palma; and Las Playas, El Julan, El Golfo in El Hierro) (Whelan & Kelletat, 2003; Whittaker & Fernández-Palacios, 2007); and (3) the influence of the glacial/inter-glacial cycles of the Pleistocene. These cycles have driven eustatic sea-level fluctuations, which have periodically doubled and then halved the area of the archipelago, implying variations in the maximum island altitude of more than 100 m, and shortening the distances among islands and with the continent significantly. The low sea-level stands of the Pleistocene also resulted in: (1) the emergence of Amanay Island, currently a sand bank off the north coast of Fuerteventura; (2) the joining together of Lanzarote, Fuerteventura and their islets, to form the large East Canarian Ridge Island, also known today as Mahan (Fig. 1b, 1c); and (3) the emergence of a chain of stepping-stone islands that provided enhanced dispersal opportunities between the Canaries, Madeira, the Azores and the Iberian Peninsula (García Talavera, 1999). Carine's

Table 1 Selected geographical data for the Canaries (source: Fernández-Palacios *et al.*, 2004).

Island	Area (km^2)	Altitude (m)	Coastal perimeter (km)	Distance from Africa (km)	Maximum age (Myr)
Tenerife	2034	3718	269	284	11.5
Fuerteventura	1655	807	255	95	20.5
Gran Canaria	1560	1948	197	196	14.5
Lanzarote	807	670	203	125	15.5
La Palma	708	2426	126	416	1.7
La Gomera	370	1487	87	333	12
El Hierro	269	1501	95	383	1.1
La Graciosa	27.5	266	28	151	0.04
Alegranza	10.2	289	14	168	0.04
Lobos	4.4	122	9	123	0.05
Montaña Clara	1.3	256	4	159	0.03
Canaries	**7447**	**3718**	**1291**	**95**	**20.5**

Table 2 Canarian biodiversity (animals, plants, fungi and algae), including introduced species. Endemism levels are high within the terrestrial biota (27.55%) but low within the marine biota (0.03%). Sources: Martín *et al.* (2005b) for terrestrial and Moro *et al.* (2003) for marine species.

Taxonomic group	Number of terrestrial species	Number of endemic terrestrial species	Percentage endemism within terrestrial species	Number of native marine species	Total number of species
Arthropoda	7198	2768	38.46	1096	**8294**
Mollusca	242	198	81.82	1170	**1412**
Other invertebrates	158	8	5.06	992	**1150**
Vertebrates	136	21	15.44	717	**853**
Bryophyta	478	10	2.09	0	**478**
Vascular plants	2037	524	25.72	3	**2040**
Fungi	3079	143	4.64	22	**3101**
Algae*	?	–	–	1149	**1149**
Total/Average	**13,328**	**3672**	**27.55**	**5149**	**18,477**
Number of genera	5260	121	2.30	2575	**7835**
Number of families	1248	0	0	1091	**2339**

*Including diatoms and dinoflagellata.

(2005) 'colonization window hypothesis' posits that the events listed above provide episodes in which the opportunities to colonize the Canary Islands are significantly enhanced, resulting in discrete waves of colonization, followed by subsequent evolutionary change: he exemplifies this model with data for Canarian *Convolvulus*. Along similar lines, but focusing just on the emergent geological pattern, Whittaker *et al.* (2007, 2008) argue that the sequential ontogeny of each island within such archipelagos drives changes in the dominant processes and patterns of island evolution, providing a long-term evolutionary model for oceanic islands, again illustrated (in part) by data from the Canaries.

The catalogue of Canarian species includes 18,477 species, comprising 13,328 terrestrial (Izquierdo *et al.*, 2004) and 5149 marine species (Moro *et al.*, 2003). In addition to numerous Macaronesian endemic species, 121 genera, 3836 (3672 terrestrial + 164 marine) species and *c.* 600 subspecies are exclusive to the archipelago (Tables 2 & 3). In fact, despite some three centuries of attention from natural scientists, the species catalogue for the Canaries is far from being complete. New species or subspecies are being described from the archipelago at a rate of about one species every six days over the last two decades (Martín *et al.*, 2005b), among them vertebrates such as the Canarian shrew (*Crocidura canariensis*), the Teno (Tenerife) and La Gomera giant lizards (*Gallotia intermedia* and *G. gomerana*, respectively), as well as two trees, the Grancanarian dragon-tree (*Dracaena tamaranae*) and the round-leaf fire tree (*Myrica rivas-martinezii*). This trend is likely to continue in the near future, with new discoveries most likely in habitats such as steep cliffs, forest canopies and in the floor of the sea-channels separating the islands.

Arguably, the Canarian biota can be considered the most biodiverse of any political unit within Spain or within the European Union, including not only large numbers of species, and of endemic species, but also outstanding examples of archipelagic radiations (Table 4) – in both the animal and plant kingdoms. For example, the *Hemycicla* snails and *Laparocerus* weevils respectively comprise 76 and 68 species within endemic monophyletic clades, and succulent rosette-forming members of the plant family Crassulaceae in the genera *Aeonium, Monanthes, Aichryson* and *Greenovia* include at least 50 species within endemic monophyletic clades (Izquierdo *et al.*, 2004).

Table 3 Canarian terrestrial biodiversity (animals, plants and fungi), indicating the distributional status of the species. Sources: Izquierdo *et al.* (2004), Martín *et al.* (2005b), Whittaker & Fernández-Palacios (2007).

Island	Single island endemisms (SIEs)	Multiple island endemisms (MIEs)	Total Canarian endemic species	Non-endemic native species	Total native species	Introduced species	Total number of species
Lanzarote	104	391	495	1628	2123	336	2459
Fuerteventura	128	413	541	1768	2309	364	2673
Gran Canaria	694	626	1320	3503	4823	886	5709
Tenerife	823	1208	2031	5758	7789	1604	8853
La Palma	244	812	1056	3802	4858	576	5434
La Gomera	268	795	1063	2975	4042	492	4534
El Hierro	110	549	659	1780	2439	314	2753
Canaries	**2371**	**1301**	**3672**	**8222**	**11,894**	**1434**	**13,328**

Table 4 Canarian endemic species belonging to the more species-rich endemic (bold) and non-endemic invertebrate and vascular plant genera (sources: Oromí & Báez, 2001; Izquierdo *et al.*, 2004).

Animal genus	Species number	Plant genus	Species number
Hemicycla	76	*Aeonium*	28
Laparocerus	68	*Echium*	23
Attalus	51	*Sideritis*	23
Dolichoiulus	46	*Argyranthemum*	19
Napaeus	45	*Sonchus*	18
Dysdera	43	*Lotus*	17
Oecobius	35	*Limonium*	16
Cardiophorus	31	*Cheirolophus*	15
Tarphius	30	*Micromeria*	14
Acalles	27	*Crambe*	12
Cyphopterum	24	*Pericallis*	12
Calathus	24	*Aichryson*	11
Spermophorides	22	*Convolvulus*	10
Hegeter	22	*Helianthemum*	9
Obelus	21	*Monanthes*	9
Nesotes	20	*Euphorbia*	9
Porcellio	18	*Teline*	8
Plutonia	18	*Polycarpaea*	8
Asianidia	17	*Descurainia*	7
Oxypoda	16	*Tolpis*	7
Pholcus	16	***Atalanthus***	6
Pachydema	16	***Parolinia***	6
Issus	15	*Bystropogon*	5

The Canarian terrestrial zonal ecosystems include up to six recognized formations from coast to summit (Table 5): (1) the sub-desert coastal scrub, with strong affinities to the nearest African mainland ecosystems, dominated by succulent endemic *Euphorbia* shrubs and today highly threatened by the pressure of continuing urban expansion driven by the tourist industry; (2) the thermophilous woodlands, the most Mediterranean-like ecosystems of the Canaries, which have almost disappeared as a result of anthropogenic clearance; (3) the laurel-forest, the sub-tropical ecosystem of the archipelago, shared with Madeira and the Azores and a relict of a forest type formerly (in the Miocene and Pliocene) widely distributed in Southern Europe and North Africa, which is today recovering as a result of the abandonment of agriculture in the mid-altitudinal belt; (4) the Canarian pine forest, once greatly reduced but exten-

Table 5 A zonal classification of Canarian ecosystems and their distribution within the archipelago.

Zonal ecosystem name	Island distribution	Approximate altitudinal range (m a.s.l.)	Characteristic plant species
Sub-desert coastal scrub	All islands and islets	Windward: 0–300 Leeward: 0–500	*Euphorbia balsamifera* *Euphorbia canariensis*
Thermophilous woodland	The seven large islands	Windward: 300–500 Leeward: 500–900	*Juniperus turbinata* *Olea europaea*
Broadleaved-evergreen (Laurel) forest	Central and western islands	Windward: 500–1200	*Laurus novocanariensis* *Myrica faya*
Pine forest	The four highest islands	Windward: 1200–2000 Leeward: 900–2200	*Pinus canariensis*
Summit scrub	La Palma and Tenerife	> 2000	*Spartocytisus supranubius* *Adenocarpus viscosus*
Peak ecosystem	Tenerife	> 2700	*Viola cheiranthifolia*

Table 6 The shift of the economic development model (1960–2006) on the Canaries from an agricultural base to mass tourism (source: Fernández-Palacios *et al.*, 2004). 2006 data have been obtained from various official electronic sources.

Property	1960	1970	1980	1990	2000	2006
Population (M)	0.94	1.17	1.44	1.64	1.78	1.99
Number of tourists (M)	0.07	0.79	2.23	5.46	12.0	12.5
Population density (inhabitants km^{-2})	130	155	189	206	231	266
Cultivated area (K ha)	95	68	60	49	46	46
Oil consumption (K oil equiv. ton.)	–	827	1442	2473	3155	?
Electric energy consumption (GW)	–	890	1680	3423	6292	8278
Concrete consumption (M ton.)	–	0.76	1.22	1.57	2.65	2.43
Number of cars (M)	0.02	0.08	0.28	0.5	1.08	1.30
Active population in agriculture (%)	54	28	17	7	6	4.6
Active population in services (%)	27	46	55	62	70	?
Unemployment (%)	2	1	18	26	13	11.5
Female life expectancy (years)	65	75	77	80	82	83
Literacy (%)	36.2	–	91.7	95.7	96.4	?
Per capita income (K dollars)	4.3	8.8	11.4	15.4	17.2	25.8

sively reforested in the last sixty years; (5) the summit scrub, dominated by endemic cushion-like legumes; and, finally, (6) exclusively represented in the highest slopes of the Teide volcano, the alpine Peak ecosystem (Fernández-Palacios *et al.*, 2004).

Human colonization and its aftermath

Although the timing of human colonization remains uncertain, it is considered that, some time during the first millennium BC, people of Berberic culture arrived on the Canaries from North Africa (Cabrera, 2001). The Guanche, as they became known, introduced goats, sheep, pigs and dogs, and developed a society based largely on shepherding, which persisted until the Castilians conquered the archipelago during the 15th century. The introduction of large vertebrate herbivores to island ecosystems that had evolved for millions of years in the absence of predators, and the use of fire to convert woodland to other land use, including pasturages, undoubtedly had huge impacts on the ecology of the islands, including the disappearance of entire forest types and dominant tree species within the thermophilous woodland belt (L. de Nascimento *et al.*, submitted). The Castilian conquerors shifted this animal-based subsistence model to a new agriculture-based development model that led to the logging of almost all of the mid-altitude forests (thermophilous woodlands and laurel forests), where their settlements were established (Cabrera, 2001), and the eventual loss of most of the pine woodlands. The agricultural model was highly dependent on the economic success of a limited array of export crops, (wine, sugar cane, bananas, tomatoes), which have shown a pattern of boom-and-bust over time that might be described as cycles of near-monoculture. Finally, the third great shift in the Canarian economy occurred only 50 years ago, when the mass-tourism model, today implanted in the eastern and central islands almost exclusively, replaced the agriculture model, with the latter persisting as a dominant force only in the three small western islands.

This last shift in economic development has abruptly transformed both Canarian society and Canarian landscapes (Table 6), resulting in the emergence of new environmental problems that threaten both ecosystem and species diversity. For instance, although the birth rate of the Canarian population (1.26 children/women) is clearly under the replacement level, an annual population growth of *c.* 50,000 people has yielded a population of 2 million inhabitants, which is double the population of the archipelago as recently as the 1960s. Furthermore, the islands are visited by about 12 million visitors a year (0.3 million daily), resulting in a *de facto* population of 2.3 million inhabitants. This equates to a population density of about 300 people per square kilometre, which is unevenly distributed within and between islands: some 87% of the population are concentrated in Gran Canaria and Tenerife, with densities of approximately 500 people per square kilometre. This population needs increasing space for residence and infrastructure, energy (so-called 'clean energy' accounting for only 1% of the production), food and water resources, and is simultaneously producing increasing volumes of domestic waste.

The image of the construction crane stalking the coastal zone of Tenerife consuming territory is one familiar to the attendees of the IBS meeting, as it has been to any visitor in the past quarter century. As a consequence of this evidently unsustainable rush for growth, half of the Canarian agricultural area (50,000 ha) has been abandoned in the last five decades, whereas the coastal ecosystems have been and still are being systematically replaced by tourist resorts and infrastructure (highways, airports, harbours, golf courses, etc.). The energy consumption has multiplied by 10 in the last 50 years (from 0.7 to 7GW), with 99% of the electricity production based on imported fossil fuels. Furthermore, about 130 hm^3 $year^{-1}$ of waste water is produced, of which 60% is delivered to the sea without treatment, and the islands are home to some 1.2 million cars, more than 12,000 km of paved roads, and some 500,000 tourist beds. Today, it can be calculated that each Canarian citizen contributes to global climatic change by means of the emission of 25 kg CO_2 day^{-1}, and produces *c.* 5 kg waste day^{-1}, of which 1.5 kg is classified as urban waste (Fernández-Palacios *et al.*, 2004).

The upshot of these changes has been a wholesale shift in the nature and geography of the human impact on Canarian landscapes, alongside a shift in which the archipelago has moved from being a net exporter to a net importer of food. On Tenerife, the upper regions, which were once devastated by overgrazing and cutting, have now largely been handed over to replanting (especially in the endemic Canary Island pine belt) and to conservation. The laurel forest belt, although reduced to perhaps 20% of its original area, is stable in area and has protected status. Many areas once in cultivation in the more humid parts of the lowlands are gradually being recolonized by a mix of native and exotic plants, or else are being built on. As current mass tourism favours the sunniest environments, it is in the dry lowlands that the pressure is now greatest, with some of the biggest tourist developments severely impacting on the most arid areas, previously only sparsely populated.

Although many Canarian endemic species are today on the brink of extinction (Martín *et al.*, 2005b) (Table 7), the list of known species extinctions is fortunately not as great as in other similar volcanic archipelagos, such as Hawaii, the Mascarenes and the Caribbean islands (Groombridge & Jenkins, 2002; Whittaker & Fernández-Palacios, 2007). Nevertheless, the high biodiversity value (especially high endemism) and high level of threat to Canarian biodiversity has led to the designation of Canarian sites in several prominent conservation prioritization schemes, and to the incorporation of the whole archipelago in the recently expanded 2005 version of Conservation International's hotspots scheme (http://www.conservation international.org), as a part of an intrusion into the Atlantic Ocean of the so-called Mediterranean Basin hotspot, which now embraces the Macaronesian archipelagos of the Azores, Madeira, the Canaries and Cape Verde Islands.

Conservation efforts

Two main approaches to the conservation of the Canarian natural heritage have been developed by the various administrations (European, Spanish, Canarian and Insular) active in the archipelago (Tables 8 & 9): (1) protection of the land and marine territories through the establishment of networks of protected areas; and (2) protection of species through the establishment of several catalogues of threatened species.

There are three overlapping protected-area networks within the Canaries: (1) the Canarian network (Red Canaria de Espa-

Table 7 Canarian endemic species considered extinguished or critically endangered as a result of anthropogenic activities. Plant names in italics, animal names in roman font. (sources: Bañares *et al.*, 2004; Martín *et al.*, 2005b).

Extinguished	< 25 individuals	< 50 individuals	< 100 individuals
Kunkeliella psilotoclada	*Lotus eremiticus*	*Bencomia sphaerocarpa*	*Myrica rivas-martinezii*
Normania nava	*Ilex perado* ssp. *lopezlilloi*	*Lotus pyranthus*	*Euphorbia mellifera*
Aeonium mascaense	*Lotus berthelotii*	*Crambe wildpretii*	*Cheirolophus santos-abreui*
Helianthemum cirae	*Lotus maculates*	*Limonium dendroides*	*Cheiroplophus sventenii* ssp. *gracilis*
Canaryomis bravoi	*Dorycnium spectabile*	*Globularia ascanii*	*Bencomia brachystachya*
Canaryomis tamarani	*Helianthemum bystropogophyllum*	*Tanacetum oshanahanii*	*Limonium relicticum*
Malpaisomys insularis	*Pericallis hadrosoma*		*Dracaena tamaranae*
Coturnix gomerae	*Sideritis amagroi*		*Globularia sarcophylla*
Puffinus olsoni	*Solanum vespertilio* ssp. *doramae*		*Helianthemum inaguae*
Saxicola dacotiae murielae			*Solanum lidii*
Haematopus meadewaldoi			*Lotus kunkelii*
Phylloscopus canariensis exsul			*Helianthemum gonzalezferreri*
Gallotia maxima			*Onopordon nogalesii*
Pseudomyas doramensis			*Plantago famarae*
Criptella famarae			Neophron percnopterus majorensis
Xeroyticha arguineguinensis			Gallotia bravoana

Table 8 Numbers of Canarian species for particular taxa that are listed in particular Catalogues of Protected Species (Rodríguez Luengo *et al.*, 2003; Martín *et al.*, 2005a). Many species are listed in more than one catalogue, so that the total number considered threatened may be estimated as approximately 465 species.

Taxonomic group	Spanish Catalogue	Canarian Catalogue	EU Birds Directive	EU Habitat Directive
Seaweeds	–	15	–	–
Ferns	1	14	–	4
Higher plants	69	233	–	68
Invertebrates	11	77	–	–
Fishes	1	9	–	–
Reptiles	11	12	–	15
Birds	55	65	28	–
Mammals	23	25	–	36
Total	**173**	**450**	**28**	**123**

Table 9 Designations within the Canarian Protected Areas Systems (from Whittaker & Fernández-Palacios, 2007).

Name	Characteristics	No.
National Park (Spanish and Canarian networks)	Large areas relatively untransformed by human activity, with high importance owing to the singularity of their biota, geology or geomorphology and representing the main natural Spanish ecosystems	4
Natural Park (Canarian network)	Large areas with similar characteristics to the National Parks, being representatives of the Canarian natural heritage	12
Rural Park (Canarian network)	Large areas where agricultural and livestock activities coexist with zones of a great natural and ecological interest	7
Integral Natural Reserve (Canarian network)	Small natural areas protecting populations, communities, ecosystems or geological elements deserving special value for their rareness or fragility. Only scientific activities allowed	11
Special Natural Reserve (Canarian network)	Similar to the former, but allowing educational and recreational activities together with scientific ones	15
Site of Scientific Interest (Canarian network)	Small isolated sites comprising populations of threatened species	21
Natural Monument (Canarian network)	Small areas characterized by geological or palaeontological elements of special singularity	52
Protected Landscape (Canarian network)	Areas with outstanding aesthetic or cultural values	27
Special Area of Conservation (SAC) (EU Natura 2000 network)	Areas that contribute in a valuable manner to maintaining or restoring natural habitat types or species to a favourable conservation status. The 151 terrestrial SACs largely overlap with the Canarian network of protected areas, adding 300 km^2, but the 23 marine SACs contribute an additional 1800 km^2 of protected marine ecosystems	174
Special Protected Area (EU Natura 2000 network)	Areas that contribute to preserving, maintaining or restoring the diversity and extension of the proper habitats for the 44 Canarian bird species included in the European directives	27
Biosphere Reserves (UNESCO network)	Areas protecting spaces where human activity constitutes an integral component of the territory, and where the management should focus on the sustainable development of the resources	4
World Heritage Site (UNESCO network)	Outstanding natural areas with unique features on a global scale	2
Ramsar Convention Protected Wetlands (UNESCO network)	Wetlands offering important ecological services, such as the regulation of water regimes, as well as important sources of biodiversity	1

cios Naturales Protegidos); (2) the European Union Natura 2000 network; and (3) UNESCO sites (biosphere reserves, World Heritage sites and Ramsar wetlands). Together they comprise 13 distinct designations of protected area (Santana *et al.*, 2006; Whittaker & Fernández-Palacios, 2007) (Table 9), which impose varying degrees of land-use planning and protection, from strict nature reserves on the one hand, to zones in which agriculture and livestock grazing are an intrinsic part of an integrated development model on the other. The protected-area estate includes four National Parks (Cañadas del Teide in Tenerife, Caldera de Taburiente in La Palma, Garajonay in La Gomera and Timanfaya in Lanzarote), and, excluding the Biosphere Reserves designation, which includes the entire islands of Lanzarote, La Palma and El Hierro, and the south-west part of Gran Canaria, the protected territory embraces *c.* 45% of the terrestrial surface area of the archipelago and about 1800 km^2 of marine protected areas. Considered by island, the percentage of protected areas varies from 28% for Fuerteventura to 60% for El Hierro.

In terms of species protection efforts, Canarian species are listed within both the Spanish Catalogue of Threatened Species (Bañares *et al.*, 2004), and the Canarian Catalogue of Threatened species, as well as within the annexes of both the Birds and Habitat European Union Directives (Martín *et al.*, 2005a). Altogether, some 465 Canarian endemic species or Canarian populations of charismatic species (such as the Cetacean species inhabiting the sea channels between the islands) are protected (Table 8). Of these 465 species, approximately 175 are classed as threatened by extinction (some of these are listed in Table 7).

A governmental proposal for the withdrawal of about 56% of the species included in the Canarian Catalogue has recently been published (Martín *et al.*, 2005a). This action was based on a four-year monitoring and assessment project. The authors concluded that, in about 200 cases, although the species concerned were restricted to only a few populations, the populations were healthy and stable. In addition, some 40 species previously listed as endangered were removed from that list based on, for example, changed assessments of whether they were endemic, taxonomic clarification of status, etc.

Although some species populations may be healthier than once thought, and although intensive conservation efforts may be pulling some endangered species back from the brink of extinction, many others species remain acutely at risk (Bañares *et al.*, 2004). In addition, the islands support large numbers of non-native introduced species, and their continued introduction, alongside the continued wholesale transformation of natural environments, especially in the coastal zone, is to be anticipated. The political imperatives within the archipelago remain focused on short-term economic interests and a model of increased tourism, development and urbanization. This economic model casts a dense shadow of uncertainty over the future of the natural resource base and biodiversity of the archipelago, particularly of the warm, dry climate belt so popular with European tourists. Despite attempts to provide legal protection for biodiversity and to invest in environmental conservation at various political levels, the pressures on the natural resources of the Canary Islands continue to increase (García Falcón & Medina Muñoz, 1999). These pressures include efforts to reduce the protection afforded to particular protected areas that have potential commercial value for development. Nonetheless, the various networks of protected areas and other conservation measures show how it is possible to tailor protected-area models to an insular context; without these legal instruments, the future of many Canarian endemic species and ecosystems would indeed be bleak.

Looking to the future

Despite the general recognition of the Canaries as Europe's most outstanding biodiversity centre, and despite the efforts of various administrations in the protection of this unique heritage, the levels of environmental concern shown by Canarian society as a whole currently appear insufficient to generate fundamental shifts in the pattern of resource exploitation. Given the continuation of an economic development model based on increasing concentrations of population, and the reception of huge numbers of tourists, without clear signals of a serious shift to a sustainable development model it seems that pressure can only grow on the natural resources, in terms of space, buildings, infrastructure, energy, water, and food. A substantial change in the direction of this pattern of development and consumption is surely needed if the unique natural heritage of these islands is not to be squandered, with the consequent detrimental costs for the quality of life on offer to the people of the Canaries. At the same time, Canarian society itself is in flux, with large movements of people in to and (to a degree) out of the archipelago, leading to cultural as well as economic and environmental change. The challenge for those interested in the conservation of nature and of biodiversity is how to promote an increased valuation of these natural resources amongst the public and polity.

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REFERENCES

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33,** 1677–1688.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33,** 1712–1728.

Bañares, A., Blanca, G., Güemes, J., Moreno, J.C. & Ortiz, S. (eds) (2004) *Atlas y libro rojo de la flora vascular amenazada de España*. Ministerio de Medio Ambiente, Madrid.

Bhagwat, S.A. & Willis, K.J. (2008) Species persistence in northerly glacial refugia of Europe: a matter of chance or biogeographical traits? *Journal of Biogeography*, **35,** 464–482.

Blondel, J. (2007) On humans and wildlife in Mediterranean islands. *Journal of Biogeography*, doi:10.1111/j.1365-2699.2007.01819.x.

Cabrera, J.C. (2001) Poblamiento e impacto aborigen. *Naturaleza de las Islas Canarias. Ecología y conservación* (ed. by J.M. Fernández-Palacios & J.L. Martín Esquivel) pp. 241–246. Turquesa Ediciones, Santa Cruz de Tenerife.

Carine, M.A. (2005) Spatio-temporal relationships of the Macaronesian endemic flora: a relictual series or window of opportunity? *Taxon*, **54,** 895–903.

Carine, M.A., Russell, S.J., Santos-Guerra, A. & Francisco-Ortega, J. (2004) Relationships of the Macaronesian and Mediterranean floras: molecular evidence for multiple colonizations into Macaronesia and back-colonization of the continent in *Convolvulus* (Convolvulaceae). *American Journal of Botany*, **91,** 1070–1085.

Diniz-Filho, J.A.F. & Bini, L.M. (2005) Modelling geographical patterns in species richness using eigenvector-based spatial filters. *Global Ecology and Biogeography*, **14,** 177–185.

Fernández-Palacios, J.M., Arévalo, J.R., Delgado, J.D. & Otto, R. (2004) *Canarias: ecología, medio ambiente y desarrollo*. Centro de la Cultura Popular de Canarias, La Laguna.

García Falcón, J.M. & Medina Muñoz, D. (1999) Sustainable tourism development in islands: a case study of Gran Canaria. *Business Strategy and the Environment*, **8,** 336–357.

García Talavera, F. (1999) Consideraciones geológicas, biogeográficas y paleoecológicas. *Ecología y Cultura en Canarias* (ed. by J.M. Fernández-Palacios, J.J. Bacallado and J.A. Belmonte), pp. 39–63. Cabildo Insular de Tenerife, Santa Cruz de Tenerife.

Gaston, K.J., Chown, S.L. & Evans, K.L. (2007) Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, doi:10.1111/j.1365-2699.2007.01772.x.

Groombridge, B. & Jenkins, M.D. (eds) (2002) *World atlas of biodiversity: earth's living resources in the 21st century*. UNEP World Conservation Monitoring Centre, University of California Press, Berkeley, CA.

Guillaumet, A., Ferdy, J.-B., Desmarais, E., Godelle, B. & Crochet, P.-A. (2007) Testing Bergmann's rule in the presence of potentially confounding factors: a case study with three species of *Galerida* larks in Morocco. *Journal of Biogeography*, doi:10.1111/j.1365-2699.2007.01826.x.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography*, **33,** 770–780.

Izquierdo, I., Martín, J.L., Zurita, N. & Arechavaleta, M. (eds) (2004) *Lista de especies silvestres de Canarias. Hongos, Plantas y animales terrestres 2004*. Gobierno de Canarias, Santa Cruz de Tenerife.

Ladle, R.J. (2008) Catching fairies and the public representation of biogeography. *Journal of Biogeography*, **35,** 388–391.

Lomolino, M.V., Sax, D.F., Riddle, B.R. & Brown, J.H. (2006) The island rule and a research agenda for studying ecographical patterns. *Journal of Biogeography*, **33,** 1503–1510.

Mackey, B.G. (2008) Boundaries, data and conservation. *Journal of Biogeography*, **35,** 392–393.

Magri, D. (2007) Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2007.01803.x.

Martín, J.L., Fajardo, S., Cabrera, M.A., Arechavaleta, M., Aguiar, A., Martín, S. & Naranjo, M. (2005a) *Evaluación 2004 de especies amenazadas de Canarias*. Gobierno de Canarias, Santa Cruz de Tenerife.

Martín, J.L., Marrero, M.C., Zurita, N., Arechavaleta, M. & Izquierdo, I. (2005b) *Biodiversidad en Gráficas. Especies silvestres de las Islas Canarias*. Gobierno de Canarias, Santa Cruz de Tenerife.

McDowall, R.M. (2007) Jordan's and other ecogeographical rules, and the vertebral number in fishes. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2007.01823.x.

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30,** 331–351.

Meiri, S., Dayan, T. & Simberloff, D. (2006) The generality of the island rule re-examined. *Journal of Biogeography*, **33,** 1571–1577.

Meiri, S., Meijaard, E., Wich, S.A., Groves, C.P. & Helgen, K.M. (2008) Mammals of Borneo – small size on a large island. *Journal of Biogeography*, in press.

Moro, L., Martín, J.L., Garrido, M.J. & Izquierdo, I. (eds) (2003) *Lista de especies marinas de Canarias (algas, hongos, plantas y animales) 2003*. Gobierno de Canarias, Santa Cruz de Tenerife.

O'Brien, E.M. (2006) Biological relativity to water–energy dynamics. *Journal of Biogeography*, **33,** 1868–1888.

Oromí, P. and Báez, M. (2001) Fauna invertebrada nativa terrestre. *Naturaleza de las Islas Canarias. Ecología y conservación* (ed. by J.M. Fernández-Palacios & J.L. Martín Esquivel) pp. 205–212. Turquesa Ediciones, Santa Cruz de Tenerife.

Patten, M.A. & Smith-Patten, B.D. (2007) Biogeographical boundaries and Monmonier's algorithm: a case study in the northern Neotropics. *Journal of Biogeography*, doi: 10.1111/j.1365-2699.2007.01831.x.

Price, T.D. & Phillimore, A.B. (2007) Reduced major axis regression and the island rule. *Journal of Biogeography*, **34,** 1998–1999.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33,** 1689–1703.

Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. & Bini, L.M. (2006) Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15,** 321–327.

Riddle, B.R. (2006) Conservation biogeography: Frontispiece. *Journal of Biogeography*, **33,** 2025–2026.

Rodríguez Luengo, J.L., García Casanova, J., Díaz, G. & Delgado, A. (eds) (2003) *Fauna y Flora de Canarias en el catálogo nacional de especies amenazadas*. Gobierno de Canarias, Santa Cruz de Tenerife.

Sanmartín, I., van der Mark, P. & Ronquist, F. (2008) Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands. *Journal of Biogeography*, **35,** 428–449.

Santana, A., Villalba, E. & Arcos, T. (2006) *La red Natura 2000 de Macaronesia y los espacios naturales protegidos de Canarias. Veinte años de planificación*. Gobierno de Canarias, Las Palmas de Gran Canaria.

Svenning, J.-C., Borchsenius, F., Bjorholm, S. & Balslev, H. (2008) High tropical net diversification drives the New World latitudinal gradient in palm (Arecaceae) species richness. *Journal of Biogeography*, **35,** 394–406.

Waters, J.M. (2007) Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *Journal of Biogeography*, doi:10.1111/j.1365-2699.2007.01724.x.

Whelan, F. & Kelletat, D. (2003) Submarine slides on volcanic islands – a source for mega-tsunamis in the Quaternary. *Progress in Physical Geography*, **27,** 198–216.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

Whittaker, R.J., Araújo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M. & Willis, K.J. (2005) Conservation biogeography: assessment and prospect. *Diversity and Distributions*, **11,** 3–23.

Whittaker, R.J., Ladle, R.J., Araújo, M.B., Fernández-Palacios, J.M., Delgado, J. & Arévalo, J.R. (2007) The island immaturity – speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. *Ecography*, **30,** 321–327.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, in press.