Journal of Biogeography, **26**, 813–823

Historical processes and environmental factors as determinants of inter-island differences in endemic faunas: the case of the Balearic Islands

M. Palmer, G. X. Pons*†, I. Cambefort and J. A. Alcover* *EP 90 Lab. Entomologie, Museum National d'Histoire Naturelle, 45, rue Buffon, F-75005 Paris, France, and * Institut Mediterrani d'Estudis Avançats (IMEDEA; CSIC-UIB), Ctra. Valldemossa km 7.5, E-07071 Palma de Mallorca, Spain*

Abstract

Aim We describe current interisland similarities of endemic faunas, and elucidate the significance of historical factors and environmental ones in determining the pattern found.

Location The six major islands of the Balearics (Western Mediterranean).

Methods An extensive review of all the endemic fauna ranging from platyhelminthes to mammals is made. From 568 presumed endemic species and subspecies, 230 full species with neither taxonomic nor distributional uncertainty are chosen. Inter-island similarities are determined using such a presence-absence matrix. Finally, relationships between the matrix of faunistic similarity and a number of matrices measuring environmental and historical factors are elucidated.

Results Endemic fauna similarities depend clearly on historical factors. Dependence on environmental factors is unclear. Moreover, endemic fauna reveals two clear-cut clusters of islands within the Balearics: the Gymnesic Islands, in the NE, and the Pityusic Islands in the SW. Historical factors cluster the Balearic Islands in the same way. Contrasting, environmental variables show smoothed, no significant differences among the Gymnesics and the Pityusics.

Main conclusions Pre-human flora (palynology) and fauna (bird and mammal fossil record) suggest that environmental differences among the Gymnesics and the Pityusics have now been reduced in comparison to the environmental differences at the Pleistocene and Holocene boundary. This environmental homogenization is likely related with human invasion. Historical effects of prehuman differences between Gymnesic and Pityusic Islands are still recognizable on endemic fauna. In contrast, there is no historical effects on interisland similarities using currently breeding birds (as an example of organisms well-dispersed and related to vegetation type). We explain the pattern of interisland similarities of endemic fauna as the result of the independent histories among the two islands groups. Contrasting, successive colonizations and extinctions would determine interisland similarities of breeding birds.

Keywords
Endemic species, extinction, human impact, palaeoenvironment, Balearic Islands.

Correspondence: M. Palmer, Institut Mediterrani d'Estudis Avançats (IMEDEA; CSIC-UIB), Ctra. Valldemossa km 7.5, E-07071 Palma de Mallorca (SPAIN). E-mail: ieampv@ps.uib.es.
† Current address: Dept. Earth Sciences, Univ. Illes Balears.

INTRODUCTION

Endemic species are key elements for elucidating biogeographical features of faunas and floras (Myers & Giller, 1988). Species' origin (vicariance *v.* dispersal) can be elucidated from palaeogeographical data (e.g. Palmer & Cambefort, 1997). Conversely, species confined to discrete areas contain information for describing the hierarchical organization of these areas, and allow us to test their association with historical processes (e.g. Brown & Gibson, 1983; Oosterbroek & Arntzen, 1992; Anderson, 1994; Sfenthourakis, 1996; Wang *et al.*, 1996) or to environmental factors (e.g. Palmer & Pons, 1996a).

Here, we propose a synthetic approach: our goal is to elucidate the significance of historical and environmental factors in determining the faunistic interisland similarities within the six major islands of the Balearics (Western Mediterranean). Data on species' specific history can be obtained directly from the fossil record, or indirectly, by phylogenetic inference. However, a fossil record from the Balearics is only available for vertebrates (Alcover *et al.*, 1981) and land snails (Cuerda, 1975; Paul & Altaba, 1992); and there are few published phylogenetic analyses that include species from the Balearics (e.g. Oosterbroek & Arntzen, 1992; Arntzen & García-París, 1995; Altaba, 1997; Palmer & Cambefort, 1997). One way to circumvent such gaps is to restrict the analysis to the endemic fauna. Previous analyses concerning the origin of the fauna and flora from the Balearics (Colom, 1957; Cardona & Contandriopoulos, 1979; Cardona, 1979) either include introduced species or do not consider fifty-five species described after 1979, or both. Instead, we propose to analyse a subsample of the authochtonous fauna represented only by the updated endemic species list.

DATA COLLECTION

We investigated the endemic fauna of the six major islands of the Balearics. This is the most isolated archipelago in the Western Mediterranean. Two separate subarchipelagos are usually recognized within the Balearics (Pityusic and Gymnesic Islands, Fig. 1). First, a list of all possible endemic species was made consisting of 568 species and subspecies (Pons & Palmer, 1996). Taxa were deleted from this list according to the following six criteria: (1) subspecies, such as the twenty-seven subspecies of *Podarcis pityusensis* Boscá (Sauria: Lacertidae) inhabiting single islets; (2) species synonymized with others with a wider distributional range (e.g. *Philoctetes friesei* Mocsary, Hymenoptera: Chrysididae, described from Mallorca and found to be identical to *P. abeillei* Mingo, a widely distributed species); (3) species with doubtful taxonomic status, such as *Deronectes brannani* Schaufuss (Coleoptera: Dytiscidae), considered identical to the widely distributed *D. moestus* by Franciscolo (1979); (4) species described from the Balearics and recently discovered elsewhere (e.g. *Bythinus bicornis* Reitter [Coleoptera: Pselaphidae], described from Mallorca and recently found in the Iberian Peninsula); (5) species described before 1930, and never mentioned again in the literature; for example, the five *Sagaritis* species (Hymenoptera: Ichneumonidae) described by Kriechbaumer (1894); and (6) species known only in the Balearics but known to have been recently introduced. One example is *Brachylaima ruminae* Mas-Coma and Montoliu (Trematoda: Brachylaimidae), known only from Formentera. This species probably has a wider distributional range because it is a parasite of *Rattus rattus* L., a nonendemic mammal with few dispersal constraints. *R. rattus* was introduced to the Balearics by the Romans (Reumer & Sanders, 1984). Formentera (as Eivissa) lacked nonflying mammals before the arrival of humans (Alcover *et al.*, 1994) and consequently no mammalian parasites were present there. These deletions have only been possible by obtaining the advice and suggestions of more than forty taxonomists mentioned in Pons & Palmer (1996). New species, ecological and distributional data published later have also been included (Gaju-Ricart *et al.*, 1995; Jaume & Boxshall, 1995; 1996a,b; Canzoneri & Rallo, 1996; Gómez-Zurita *et al.*, 1996; Jäch *et al.*, 1996; Lehrer, 1996).

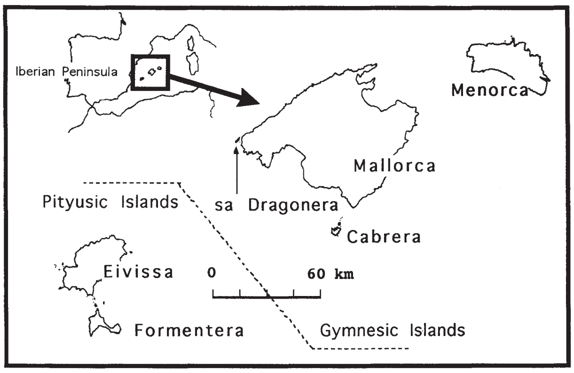

Figure 1 Location of the Balearic Archipelago in the Western Mediterranean. Note that Eivissa is the Catalan name for the Island called Ibiza in Spanish.

DATA ANALYSIS

Our study focuses on the relationships between the endemic fauna and some independent variables. Therefore, a multiple regression model is used. The dependent variable is defined by the matrix of similarities between all island pairs (ENDEMIC). Inter-islands similarities are determined by the difference (observed – expected) number of species co-occurrences. Expected co-occurrences are obtained by a randomization procedure (ISLDRAND, Manly, 1995) that switches rows and columns of the observed presence-absence matrix (i.e. fixing marginal totals). We use such an unconventional measurement because other similarity indices seems to depend on sample size and diversity (Wolda, 1981). The index used here seems to be size and area-independent (Appendix 1). Manly (1995) also provides a test statistic for identifying items with unusual patterns of co-occurrences. ISLDRAND allows up to 160 species. To circumvent such a constraint, we have included in the analysis (1) the species present in more than one island (73) and (2) 10 successive random samples of 160 species (70%).

We tested the association between the endemic faunal similarity and some independent variables. The first, TIME, Million years (ln-transformed) since the last land connection between islands pairs as an estimation of the shared history of those island pairs (based on Busack, 1986; Petitpierre *et al*., 1987; Oosterbroek & Arntzen, 1992; Beerli *et al*., 1996). Geographical distance, in km (ln-transformed) is the second independent variable considered (DISTANCE). Shared degree of vegetation types constitutes the third independent variable (VEGETATION). Specification of vegetation communities is based on plant associations, i.e. vegetation communities harboring some characteristic species, with comparable landscape settings and with comparable habitats belong to the same association (Folch, 1982). Similar specifications are used to assess environmental factors which determine vertebrate species' distributions (e.g. Romero & Real, 1996). Presence and absence of associations throughout the six Balearic islands are based on Folch (1982), updated by Bibiloni (personal communication). There are eighty-one associations in the Balearics (ranging from sixty-nine in Mallorca to nine in sa Dragonera). Similarity among island pairs was measured by the same (observed – expected) number of species co-occurrences. Similarly, this procedure was repeated using breeding bird communities (BIRDS). The presence or absence of currently breeding birds on the six islands is based on Muntaner (1984) updated by Avellà *et al*. (1997). Very recently introduced species such as the monk parakeet *Myiopsitta monachus* (Boddaert) were excluded. Species number of breeding birds in the Balearics is ninety-five (ranging from ninety-two in Mallorca to twenty-six in Cabrera). It is important to remark that vegetation types and breeding birds are used only as estimates of general environmental similarity. Finally, area differences among island pairs (AREA, km^2, ln-transformed) is the last independent variable considered.

Preliminary pairwise correlation analyses of the independent variable were done by univariate Mantel tests. All variables are distances or similarities. We used PERMUTE! 3.4 alpha (available via anonymous ftp by P. Casgrain 1998) that normalizes all variables before calculations. One tailed tests were based on 10,000 iterations.

Some pairs of the independent variables are collinear (Table 1). VEGETATION could be considered uncorrelated with TIME only if the Bonferroni adjustment is applied ($P = 0.048$; Table 1). However, BIRDS and VEGETATION are correlated, and BIRDS is preferred as environmental estimator because it is clearly independent of historical effects ($P = 0.105$; Table 1). Considering DISTANCE, the pattern for breeding birds suggests that colonization is not distance-dependent because off the small scale of interisland distances. Endemic fauna is not distance-dependent for the opposite reason: all interislands distances are effective geographical barriers. After successive deletions of collinear variables, the multivariate model used for testing the historical and environmental effects on endemic fauna is composed by TIME and BIRDS. Permute! computes multiple regression coefficients of the independent variables. It permutes at random columns and rows of the original dependent matrix, recomputing the regression coefficients *k* times, where *k* is the number of permutations (10,000).

Table 1 Correlation between independent variables. Probability values of univariate Mantel tests based on 10,000 iterations.

	Time	Distance	Vegetation	Birds
Distance	0.017			
Vegetation	0.048	0.053		
Birds	0.105	0.096	0.001	
Area	0.134	0.034	0.318	0.299

RESULTS

A complete list of all 230 endemic species included in the analysis after reducing the original larger list is found in Table 2. Of the species, 157 (68%) inhabit a single island. The remaining seventy-three (32%) are distributed among two to six islands. The pattern of species co-occurrences departs significantly from the usually expected. Probability values are highly significant for all the six islands (Table 3). Such departures are related to differences between the Gymnesic Islands (Mallorca, Menorca, Cabrera and sa Dragonera) and the Pityusic Islands (Eivissa and Formentera). There are only seventeen endemic species which inhabit both a Pityusic island and a Gymnesic island. The number of observed co-occurrences among Mallorca and Eivissa is fourteen (from 22.8 expected co-occurrences). Contrasting, the number of observed co-occurrences within subarchipelagos are larger than expected (e.g. Eivissa *v.* Formentera; twenty-two observed and 9.5 expected, and Mallorca *v.* Menorca; thirty-seven and 27.9).

The main habitats or communities at present in the Balearics are oak woodlands, *Olea europaea* L. shrublands, *Rosmarinus officinalis* L. shrublands, lagoons, dunes, rocky seashores, mountain tops, mountain streams and caves. Excluding caves and considering only species with data available for habitat preferences, the distribution of endemic species throughout the major habitat types reveals an unexpected pattern: evergreen oak (*Quercus ilex* L.) woodland (considered the climax habitat in the Balearics; Bolos & Molinier, 1958; Rivas-Martínez *et al*., 1992) contains only twenty-four endemic animal species (only four of which are specific to such a habitat). By contrast, ninety-five endemic species can be found on seashores (thirty-four of which are specific). The endemic fauna from shrublands (both *Olea* and *Rosmarinus*-shrubland) seems to be composed of generalist species (ninety) since only three are exclusive to shrublands.

The main finding presented here is the result of bivariate regression. The dependent variable (i.e. endemic fauna similarities) is significantly correlated with historical factors (i.e. the first independent variable). Partial coefficient (*b*) for TIME differs significantly from $b = 0$ in all the tests performed (Table 4). However, there are not strong evidences on the significance of environmental factors (i.e. the second independent variable). BIRDS' effect is significant using the seventy-three species found in more than one island. Contrasting, none of the ten tests using random samples of 160 species is significant (Table 4).

It is important to emphasize that BIRDS (now as dependent

Table 2 Endemic species of the Balearic Islands. Presence and absence from the two subarchipelagos (Gymnesic Islands and Pityusic Islands) are indicated. Mallorca (Ma), Menorca (Me), Cabrera (Ca), sa Dragonera (Dr), Eivissa (Ei) and Formentera (Fo).

		Gymnesics				Pity	
		Ma	Me	Ca	Dr	Ei	Fo
STRONGYLIDA	Strongyloides ophiusensis Roca and Hornero 1992	0	0	0	0	1	1
OXYURIDA	Spauligodon cabrerae Castaño, Zapatero and Solera 1988	0	1	1	0	1	0
PLOIMA	Lecane margalefi De Manuel 1994	1	0	0	0	0	0
HAPLOTAXIDA	Allolobophora mediterranea Oerley 1881	1	1	0	0	0	0
STYLOMMATOPHORA	Oxychilus lentiformis Kobelt 1882	1	1	1	1	0	0
STYLOMMATOPHORA	Oxychilus pytiusanus Riedel 1969	0	0	0	0	1	1
STYLOMMATOPHORA	Vitrea gasulli Riedel and Paul 1977	0	0	0	0	1	0
STYLOMMATOPHORA	Rupestrella moraguesi (Kobelt 1882)	1	0	0	0	0	0
STYLOMMATOPHORA	Trochoidea caroli (Dohrn and Heynemann 1862)	0	0	0	0	1	1
STYLOMMATOPHORA	Trochoidea claudinae (Gasull 1963)	1	0	0	0	0	0
STYLOMMATOPHORA	Trochoidea ebusitana (Jaeckel 1952)	0	0	0	0	1	1
STYLOMMATOPHORA	Trochoidea frater (Dohrn and Heynemann 1862)	1	0	1	1	0	0
STYLOMMATOPHORA	Trochoidea nyeli (Mittre 1844)	1	1	1	0	0	0
STYLOMMATOPHORA	Trochoidea pietroi (Hidalgo 1878)	1	0	0	0	0	0
STYLOMMATOPHORA	Allognathus graellsianus (Pfeiffer 1848)	1	0	0	0	0	0
STYLOMMATOPHORA	Iberellus balearicus (Ziegler 1853)	1	0	0	1	0	0
STYLOMMATOPHORA	Iberellus companyonii Aleron 1837	1	1	1	0	1	1
STYLOMMATOPHORA	Iberellus pythiusensis Bofill and Aguilar-Amat 1924	0	0	0	0	1	0
STYLOMMATOPHORA	Iberellus tanitianus Forés and Vilella 1993	0	0	0	0	1	0
STYLOMMATOPHORA	Limax majoricensis Heynemann 1863	1	0	1	0	1	1
CYCLOPHOROIDA	Tudorella ferruginea Lamarck 1823	1	1	1	1	0	0
TRUNCATELOIDEA	Belgrandiella edmundi Boeters 1984	1	0	0	0	0	0
ARANEAE	Nemesia brauni Koch 1882	1	1	1	0	0	0
ARANEAE	Harpactea dufouri Thorell 1873	1	1	1	1	1	1
ARANEAE	Theonoe major Denis 1961	0	1	0	0	0	0
ARANEAE	Lepthyphantes balearicus Denis 1961	0	1	0	0	0	0
ARANEAE	Zodarion mallorca Bosmans 1994	1	0	0	0	0	0
ARANEAE	Malthonica balearica Brignoli 1978	1	1	1	1	0	0
ARANEAE	Hahnia hauseri Brignoli 1978	1	0	1	1	0	0
PSEUDOSCORPIONES	Chthonius balearicus Mahnert 1977	1	0	0	0	0	0
PSEUDOSCORPIONES	Chthonius bellesi Mahnert 1989	0	1	0	0	0	0
PSEUDOSCORPIONES	Chthonius cabreriensis Mahnert 1993	0	0	1	0	0	0
PSEUDOSCORPIONES	Chthonius ponsi Mahnert 1993	0	0	1	0	0	0
PSEUDOSCORPIONES	Acanthocreagris balearica (Beier 1961)	0	1	0	0	0	0
PSEUDOSCORPIONES	Neobisium monasterii Mahnert 1977	1	0	0	0	0	0
PSEUDOSCORPIONES	Roncus neotropicus Redikorzev 1937	1	0	0	0	1	0
PSEUDOSCORPIONES	Roncus vidali Lagar 1972	1	0	0	0	0	0
PSEUDOSCORPIONES	Allochernes pityusensis Beier 1961	0	0	0	0	1	0
PSEUDOSCORPIONES	Pselaphochernes balearicus Beier 1961	1	0	0	0	0	0
PSEUDOSCORPIONES	Dactylochelifer balearicus Beier 1961	0	1	0	0	1	0
PSEUDOSCORPIONES	Dactylochelifer besucheti Mahnert 1976	1	0	0	0	0	0
OPILIONES	Scotolemon balearicus Rambla 1977	1	0	0	0	0	0
OPILIONES	Scotolemon krausi Rambla 1972	1	0	1	0	1	0
OPILIONES	Dasylobus ferrugineus Thorell 1876	1	0	1	1	1	0
OPILIONES	Phalangium clavipus Roewer 1911	1	0	0	0	0	0
ACARI	Steganacarus balearicus Pérez-Iñigo 1969	1	0	0	0	0	0
ACARI	Ctenobelba parafoliata Pérez-Iñigo 1991	0	1	0	0	0	0
ACARI	Pseudoamerioppia balearica (Pérez-Iñigo 1991)	0	1	0	0	0	0
ACARI	Pergalumna minoricana Pérez-Iñigo 1991	0	1	0	0	0	0
COPEPODA	Diacyclops balearicus Lescher-Moutué 1978	1	0	0	0	0	0
COPEPODA	Ginesia longicaudata Jaume and Boxshall 1977	1	0	0	0	0	0
COPEPODA	Speleophria gymnesica Jaume and Boxshall 1996	1	0	0	0	0	0
COPEPODA	Speleophriopsis balearicus Jaume and Boxshall 1996	1	0	0	0	0	0
COPEPODA	Troglocyclopina balearica Jaume and Boxshall 1996	1	0	0	0	0	0
COPEPODA	Superornatiremis mendai Jaume 1997 in press	1	0	0	0	0	0
COPEPODA	Intercrusia garciai Jaume 1997 in press	1	0	0	0	0	0
COPEPODA	Neoechinophora xoni Jaume 1997 in press	1	0	0	0	0	0
THERMOSBAENACEA	Tethysbaena scabra (Pretus 1991)	1	1	1	1	0	0
ISOPODA	Metacirolana ponsi Jaume and Garcia 1992	0	0	1	0	0	0
ISOPODA	Spelaeoniscus coiffaiti Vandel 1961	0	1	0	0	0	0
ISOPODA	Agabiformius manacori (Racovitza 1907)	1	0	0	0	0	0
ISOPODA	Porcellio balearicus Cruz and Garcia 1992	1	0	0	0	0	0
ISOPODA	Armadillidium pretusi Cruz 1990	1	0	0	0	0	0
ISOPODA	Armadillidium serrai Cruz and Dalens 1990	0	1	0	0	0	0
ISOPODA	Armadillidium strinatii Vandel 1961	0	1	0	0	0	0
HYMENOPTERA	Pseudepipona gineri (Schulthess-Schindler 1934)	0	0	0	0	1	0
HYMENOPTERA	Mimesa palliditarsis Saunders 1904	1	0	0	0	0	0
HYMENOPTERA	Halictus dubitabilis Saunders 1904	1	0	0	0	0	0
HYMENOPTERA	Halictus hollandi Saunders 1904	1	0	0	0	0	0
HYMENOPTERA	Halictus microcardia Pérez 1895	0	0	0	0	1	0
HYMENOPTERA	Anthophora balearica Friese 1896	1	1	0	0	1	0
COLEOPTERA	Reicheia balearica Español 1974	1	0	0	0	0	0
COLEOPTERA	Broscus insularis Piochard 1867	1	0	0	0	0	0
COLEOPTERA	Duvalius balearicus Henrot 1964	1	0	0	0	0	0
COLEOPTERA	Trechopsis ferreresi (Lagar 1975)	1	0	0	0	0	0
COLEOPTERA	Hypotyphlus menorquensis (Coiffait 1961)	0	1	0	0	0	0
COLEOPTERA	Orthomus balearicus (Piochard 1867)	1	1	0	0	0	0
COLEOPTERA	Henrotius jordai (Reitter 1914)	1	0	0	0	0	0
COLEOPTERA	Percus plicatus Dejean 1828	1	1	0	1	0	0
COLEOPTERA	Percus espagnoli Lagar 1965	0	0	1	0	0	0
COLEOPTERA	Platyderus balearicus Jeanne 1970	0	0	0	0	1	0
COLEOPTERA	Platyderus formenterae Jeanne 1988	0	0	0	0	0	1
COLEOPTERA	Platyderus majoricus Jeanne 1988	1	0	0	0	0	0
COLEOPTERA	Acinopus pilipes Piochard 1867	1	1	0	0	0	0
COLEOPTERA	Scybalicus minoricensis Vives and Vives 1994	0	1	0	0	0	0
COLEOPTERA	Hydraena balearica D'Orchymont 1930	1	1	0	0	1	0
COLEOPTERA	Limnebius minoricensis Jäch, Valladares and García-Avilés 1996	0	1	0	0	0	0
COLEOPTERA	Catops zariquieyi Jeannel 1936	1	0	0	0	0	0
COLEOPTERA	Neuraphes navasi Español 1940	0	0	0	0	1	0
COLEOPTERA	Cephennium minoricum Besuchet	0	1	0	0	0	0
COLEOPTERA	Cephennium franciscae Besuchet	0	1	0	0	0	0
COLEOPTERA	Lobrathium bellesi Bordoni 1977	1	0	0	0	0	0
COLEOPTERA	Medon subterraneum Coiffait 1969	0	0	0	0	1	0
COLEOPTERA	Paratyphlus cristobali Coiffait 1959	0	1	0	0	0	0
COLEOPTERA	Paratyphlus menorquensis Coiffait 1959	0	1	0	0	0	0
COLEOPTERA	Paratyphlus besucheti Coiffait 1970	1	0	0	0	0	0
COLEOPTERA	Paratyphlus mallorcensis Coiffait 1955	1	0	0	0	0	0
COLEOPTERA	Bacillopsis balearica (Breit 1908)	1	0	0	0	0	0
COLEOPTERA	Astenus lepidulus Normand 1945	0	0	0	0	1	0
COLEOPTERA	Atheta bellesi Benick 1990	1	0	0	0	0	0
COLEOPTERA	Entomoculia ebusica Coiffait 1973	0	0	0	0	1	0
COLEOPTERA	Omalium espanoli (Jarrige 1952)	1	0	0	0	0	0
COLEOPTERA	Hypomedon mallorcensis Coiffait 1969	1	0	0	0	0	0
COLEOPTERA	Lesteva balearica Lohse 1962	1	0	0	0	0	0
COLEOPTERA	Typhlosorius ibizensis Coiffait 1973	0	0	0	0	1	0
COLEOPTERA	Xantholinus balearicus Coiffait 1962	1	1	0	0	0	0
COLEOPTERA	Faronus espanoli Normand 1945	0	0	0	0	1	0
COLEOPTERA	Faronus insignis Besuchet 1958	1	1	0	0	0	0
COLEOPTERA	Leptobythus palaui Jeannel 1955	1	0	0	0	0	0
COLEOPTERA	Bythinopsis balearica Jeannel 1961	0	1	0	0	0	0
COLEOPTERA	Decatocerus pityusensis Besuchet 1958	0	0	0	0	1	0
COLEOPTERA	Geopselaphus balearicus Besuchet 1969	1	0	0	0	0	0
COLEOPTERA	Thorectes balearicus López-Colón 1984	1	0	0	0	0	0
COLEOPTERA	Elaphocera capdeboui Schaufuss 1882	1	0	1	1	0	0
COLEOPTERA	Elaphocera ibicensis Escalera 1926	0	0	0	0	1	1
COLEOPTERA	Syncalypta jordai Reitter 1910	1	0	0	0	0	0
COLEOPTERA	Olimnius echinatus Berthélemy 1979	1	1	0	0	0	0
COLEOPTERA	Attalus gineri Escalera 1942	0	0	0	0	1	0
COLEOPTERA	Abromus palaui Español 1945	1	0	0	0	0	0
COLEOPTERA	Helioctamenus hippopotamus Schaufuss 1882	1	1	0	0	0	0
COLEOPTERA	Mordellistena ermischi Compte 1966	0	0	0	0	1	0
COLEOPTERA	Mordellistena balearica Compte 1985	1	0	0	0	0	0
COLEOPTERA	Microhoria balearica (Pic 1904)	1	0	0	0	0	0
COLEOPTERA	Pachychila sublunata Solier 1935	1	0	1	1	1	1
COLEOPTERA	Tentyria ophiusae Codina 1918	0	0	0	0	1	1
COLEOPTERA	Tentyria schaumi Kraatz 1865	1	1	1	1	0	0
COLEOPTERA	Alphasida ibicensis Pérez Arcas 1868	0	0	0	0	1	1
COLEOPTERA	Alphasida depressa Solier 1836	1	1	0	0	0	0
COLEOPTERA	Asida barceloi Pérez Arcas 1868	1	0	0	1	0	0
COLEOPTERA	Asida ludovici Escalera 1925	0	0	0	0	1	1
COLEOPTERA	Asida cardonae Pérez Arcas 1868	1	1	0	0	0	0
COLEOPTERA	Asida moraguesi Schaufuss 1879	1	0	0	0	0	0

Table 2 *contd*

ISOPODA	Ballodillium pilosum Vandel 1961	1	1	1	0	0	0
ISOPODA	Trogloianiropsis lloberai Jaume 1995	1	0	1	0	0	0
ISOPODA	Balearonethes sesrodesanus Dalens 1977	1	0	0	0	0	0
ISOPODA	Haplophthalmus chisterai Cruz and Dalens 1989	1	0	0	0	0	0
ISOPODA	Trichoniscus dragani Tabacaru 1974	1	0	0	0	0	0
AMPHIPODA	Metacrangonyx longipes Chevreux 1909	1	1	0	0	0	0
AMPHIPODA	Salentinella formenterae Platvoet 1984	0	0	0	0	0	1
AMPHIPODA	Psammogammarus burri Jaume and Garcia 1992	0	0	1	0	0	0
AMPHIPODA	Pseudoniphargus daviui Jaume 1991	0	0	1	0	0	0
AMPHIPODA	Pseudoniphargus pedrerae Pretus 1990	0	0	0	0	1	1
AMPHIPODA	Pseudoniphargus pityusensis Pretus 1990	0	0	0	0	1	1
AMPHIPODA	Pseudoniphargus racovitzai Pretus 1990	1	0	0	0	0	0
AMPHIPODA	Pseudoniphargus triasi Jaume 1991	0	0	1	0	0	0
AMPHIPODA	Rhipidogammarus variicauda Stock 1978	1	0	0	0	0	0
AMPHIPODA	Bogidiella balearica Dancau 1973	1	0	0	0	0	0
AMPHIPODA	Bogidiella torrenticola Pretus and Stock 1990	1	0	0	0	0	0
MYSIDACEA	Burrimysis palmeri Jaume and Garcia 1993	0	0	1	0	0	0
POLYXENIDA	Lophoproctus pagesi Condé 1981	1	0	0	0	0	0
IULIDA	Nemasoma coiffaiti (Demange 1961)	0	1	0	0	0	0
IULIDA	Schyzophyllum ibizanum Verhoeff 1924	0	0	0	0	1	0
GLOMERIDA	Glomeris ibizana Verhoeff 1924	0	0	0	0	1	0
CRASPEDOSOMATIDA	Strongylosoma soderlundi Verhoeff 1924	0	0	0	0	1	0
GEOPHILOMORPHA	Himantariella balearica Capuse 1975	1	0	0	0	0	0
GEOPHILOMORPHA	Nesoporogaster excavatum Verhoeff 1924	0	0	0	0	1	0
GEOPHILOMORPHA	Pachymerium dragani Capuse 1975	1	0	0	0	0	0
LITHOBIOMORPHA	Lithobius clarcki Eason 1975	1	0	0	0	0	0
LITHOBIOMORPHA	Lithobius dragani Negrea and Matic 1973	1	0	0	0	0	0
LITHOBIOMORPHA	Lithobius fagei Demange 1961	1	1	0	0	0	0
LITHOBIOMORPHA	Lithobius georgescui Negrea and Matic 1973	1	0	0	0	0	0
LITHOBIOMORPHA	Lithobius vivesi Serra 1983	1	0	0	0	0	0
PROTURA	Eosentomon coiffaiti Condé 1961	0	1	0	0	0	0
COLLEMBOLA	Pseudosinella subcentralis Gamma 1985	1	0	0	0	0	0
COLLEMBOLA	Hypogastrura pityusica Ellis 1974	0	0	0	0	1	0
COLLEMBOLA	Deutonura ibicensis (Ellis 1974)	0	0	0	0	1	0
COLLEMBOLA	Pratanurida menorquina Arbea and Jordana 1990	0	1	0	0	0	0
COLLEMBOLA	Neosminthurus natalicius Ellis 1974	0	0	0	0	1	0
DIPLURA	Plusiocampa breuili Condé 1954	0	0	0	0	1	0
DIPLURA	Plusiocampa fagei Condé 1954	1	0	0	0	0	0
DIPLURA	Homojapyx espanoli (Pagès 1950)	1	0	0	0	0	0
THYSANURA	Lepismachilis affinus Gaju-Ricart, Bach, Molero and Mora 1993	1	0	0	0	0	0
THYSANURA	Lepismachilis gimnesiana Mendes 1981	1	0	0	0	0	0
THYSANURA	Machilis dragani Hollinder 1973	1	0	0	0	0	0
THYSANURA	Machilis hauseri Mendes 1981	1	0	0	0	0	0
THYSANURA	Praemachiloides insularis Gaju-Ricart et al. 1995	0	0	0	0	0	1
BLATTOPTERA	Phyllodromica adspersa (Bolívar 1897)	1	1	0	0	0	0
BLATTOPTERA	Phyllodromica llorenteae Harz 1971	1	1	0	0	0	0
ORTHOPTERA	Steropleurus balearicus Bolívar 1878	1	1	0	0	0	0
ORTHOPTERA	Euchorthippus angustulus Ramme 1931	1	0	0	0	1	1
HEMIPTERA	Velia hoberlandi Tamanini 1951	1	1	0	0	0	0
HOMOPTERA	Hysteropterum gravesteini Dlabola 1975	1	0	0	0	0	0
DIPTERA	Bibio gineri Gil 1932	0	0	0	0	1	0
DIPTERA	Machimus ibizensis Gil 1932	0	0	0	0	1	0
DIPTERA	Medetera roghii Rampini and Canzoneri 1979	0	1	0	0	0	0
DIPTERA	Hydrellia mayoli Canzoneri and Rallo, 1996	1	0	0	0	0	0
DIPTERA	Azorastia gemmae Carles-Tolrá 1994	0	0	0	0	1	0
DIPTERA	Thoracochaeta palpebris Carles-Tolrá 1994	0	0	0	0	1	0
DIPTERA	Dicranomyia staryi Geiger and Mentl 1994	1	0	0	0	0	0
DIPTERA	Stilpon intermedius Raffone 1994	1	0	0	0	0	0
DIPTERA	Pandelleola resnikae Lehrer 1996	1	0	0	0	0	0
DIPTERA	Salemea bolivari (Gil 1932)	1	0	1	0	1	0
PLECOPTERA	Leuctra balearica Pardo and Zwick 1993	1	0	0	0	0	0
LEPIDOPTERA	Ardania balearica Falcovisch 1978	1	0	0	0	0	0
LEPIDOPTERA	Stollia betae Falcovisch 1978	1	0	0	0	0	0
LEPIDOPTERA	Opercovalva mallorcae Guzman 1975	1	0	0	0	0	0
HYMENOPTERA	Entamobora pseudoplicata (Wolf 1961)	0	1	0	0	1	0
HYMENOPTERA	Pompilus poultoni Saunders 1904	1	0	0	0	0	0
HYMENOPTERA	Ancistrocerus ebusitanus Lichtenstein 1884	1	0	1	0	1	0
COLEOPTERA	Asida planipennis Schaufuss 1869	1	1	1	1	0	0
COLEOPTERA	Asida mater Escalera 1925	0	0	0	0	1	1
COLEOPTERA	Akis bremeri Ardoin 1979	0	0	0	0	0	1
COLEOPTERA	Pimelia criba Solier 1836	1	1	0	0	0	0
COLEOPTERA	Pimelia elevata Sénac 1887	0	0	0	0	1	1
COLEOPTERA	Isocerus balearicus (Schaufuss 1879)	1	0	0	0	0	0
COLEOPTERA	Dendarus depressus Reitter 1915	1	1	1	0	0	0
COLEOPTERA	Heliopathes balearicus Español 1955	0	0	0	0	1	1
COLEOPTERA	Phylan mediterraneus (Piochard 1869)	0	0	0	0	1	1
COLEOPTERA	Phylan semicostatus (Mulsant and Rey 1854)	1	1	1	1	0	0
COLEOPTERA	Phylan nitidicollis (PérezArcas 1872)	0	0	1	0	0	0
COLEOPTERA	Phaleria pujeti Español 1955	1	1	0	0	1	0
COLEOPTERA	Pseudosericius ibicensis Español 1955	0	0	0	0	1	0
COLEOPTERA	Alphitophagus xaxarsi Reitter 1914	1	0	0	0	0	0
COLEOPTERA	Probaticus balearicus Español 1980	0	0	0	0	0	1
COLEOPTERA	Nesotes viridicollis (Schaufuss 1869)	1	1	1	1	1	1
COLEOPTERA	Pachybrachys anoguttatus Suffrian 1866	1	1	0	0	0	0
COLEOPTERA	Timarcha balearica Gory 1829	1	1	0	0	0	0
COLEOPTERA	Cyrtonus majoricensis Breit 1908	1	0	1	1	0	0
COLEOPTERA	Cryptocephalus majoricensis LaFuente 1918	1	0	0	1	0	0
COLEOPTERA	Cryptocephalus tramuntanae Petitpierre 1993	1	0	0	0	0	0
COLEOPTERA	Scythropus lopezi Hoffmann 1956	1	0	0	0	0	0
COLEOPTERA	Geonemus palaui Español 1951	0	0	0	0	1	0
COLEOPTERA	Geonemus caudulatus Fairmaire 1891	1	0	0	0	0	0
COLEOPTERA	Brachycerus balearicus Bedel 1874	1	0	1	0	0	0
COLEOPTERA	Pseudotorneuma zariquieyi Roudier 1954	0	0	0	0	1	0
COLEOPTERA	Pseudotorneuma besucheti González 1966	1	0	0	0	0	0
COLEOPTERA	Cycloderes espanoli Roudier 1954	0	0	0	0	1	1
SQUAMATA	Podarcis lilfordi (Eisentraut 1928)	1	1	1	1	0	0
SQUAMATA	Podarcis pityusensis (Einsentraut 1930)	0	0	0	0	1	1
SALIENTA	Alytes muletensis (Sanchiz and Adrover 1977)	1	0	0	0	0	0

Table 3 Endemic fauna. Estimated significance levels (*P* in %) of the statistics used (Manly, 1995), for six individual islands. The estimated significance levels are mean values for 100 replicates of serial test with a series of length of $n = 10000$. The critic value for 5% with Bonferroni adjustment are 5/6 = 0.8%. Above, *P*-values using seventy-three endemic species found in more than one island. Below, mean and max *P*-values of ten random subsamples of 160 species taken from the 230 endemic species.

		Mallorca	Menorca	Cabrera	sa Dragonera	Eivissa	Formentera
73 species		0.02	0.03	0.03	0.03	0.02	0.02
160 species	mean	0.031	0.183	0.12	0.085	0.031	0.042
	max	0.04	0.79	0.43	0.12	0.04	0.05

Table 4 Multivariate Mantel tests based on 10000 iterations. TIME is M years from the last land connection between islands pairs. BIRDS is the matrix of inter-island breeding bird similarity measured by (observed–expected) number of co-occurrences. The dependent variable is the matrix of interisland endemic faunal similarity measured by (observation–exp.) number of co-occurrences. Above, results using seventy-three endemic species found in more than one island. Below, results of ten random subsamples of 160 species taken from the 230 endemic species. Partial coefficient for independent variables (*b*) and the probability that $b = 0$ are indicated.

	Time		Birds	
	b	Prob	*b*	Prob
73 species	−0.786	0.003	0.293	0.004
160 species	−0.804	0.022	0.174	0.141
	−0.783	0.007	0.237	0.060
	−0.846	0.018	0.138	0.177
	−0.909	0.026	0.026	0.396
	−0.836	0.021	0.136	0.194
	−0.776	0.022	0.173	0.161
	−0.789	0.027	0.168	0.165
	−0.845	0.026	0.111	0.251
	−0.850	0.019	0.124	0.209
	−0.817	0.019	0.152	0.158

variable of an univariate Mantel test) is itself independent of TIME (Table 1). Moreover, environmental variables do not show significant clustering among the Gymnesic and the Pityusic subarchipelagos (Table 5). There is, however, a trend of tiny islands (Cabrera and sa Dragonera) for displaying a more similar than expected set of vegetation types (Table 5). This fact could be explained by increased relative importance of littoral habitats in tiny islands (Wiggins & Møller, 1996). The significant departure from the expected pattern of co-occurences for breeding birds from Formentera (Table 5) is not related to differences among the Gymnesics and the Pityusics. The departure among Formentera and Eivissa (forty observed and 35.0 expected) could be related to some local factor because the opposite trend among Formentera and the Gymnesics has not been detected (e.g. Mallorca *v.* Formentera; forty observed and 40.9 expected, and Menorca *v.* Formentera; thirty-six observed and 36.8 expected).

DISCUSSION

An important trend emerges from the multivariate analysis of the endemic fauna from the Balearics: islands with stronger palaeogeographic relationships (i.e. connected by land bridges more recently) have a more similar endemic fauna. In contrast, extant bird fauna seems independent of palaeogeographic relationships between islands. Environment could play a complementary role in determining similarities of endemic fauna. However, environmental variables do not show the clear cluster among the Gymnesic and the Pityusic Islands revealed by endemic fauna.

Interpretation of the above trends is only possible from palaeoenvironmental knowledge. There are no comprehensive past vegetation data for the Balearic Islands. However, some features from the prehuman palaeoenvironment (upper Pleistocene and early Holocene) suggest huge differences from the living scenario. Palynological data demonstrates (i) that the vegetation in Mallorca during the upper Pleistocene and early Holocene was roughly similar to the vegetation in Menorca, and (ii) that such vegetations were clearly different from the present ones. The differences were not small changes in plant species composition, but they suggest that some currently relict vegetation types could have been more widely distributed in the past (Pérez-Obiol *et al.*, 1996). Conversely, ever-green oak woods (currently presumed to be the climax vegetation) could have been little developed or absent at the Holocene (Yll *et al.*, 1994). Unfortunately, there are no palynological data from the Pityusic Islands. However, the vertebrate fossil record from upper Pleistocene and early Holocene allows us to conclude that the palaeoenvironment of the Pityusic Islands was very different

Table 5 Breeding birds and vegetation types. Estimated significance levels (P in percentage) of the statistics used (Manly, 1995), for six individual islands. The estimated significance levels are mean values for 100 replicates of a serial test with a series length of $n = 10000$. The critic value for 5% with Bonferroni adjustment are 5/6 = 0.8%.

	Mallorca	Menorca	Cabrera	sa Dragonera	Eivissa	Formentera
Birds	78.53	49.28	57.13	4.89	1.65	0.29
Vegetation	2.61	4.19	0.03	0.02	46.65	10.48

Table 6 Current and prehuman (Pleistocene–Holocene boundary) species from Mallorca (Gymnesics) and Eivissa (Pityusics), expressed as number of species and number of endemics.

	Gymnesic Islands		Pityusic Islands	
	Prehuman	Present	Prehuman	Present
Mammals	3/3	13/0	0/0	9/0
Reptiles	1/1	11/1	1/1	4/1
Amphibians	1/1	4/1	0/0	2/0
Land snails	12/12	72/9	7/7	49/7

from that of the Gymnesic Islands. Evidence emerges from the fossil record of mammals and birds (Alcover *et al*., 1981; Alcover *et al*., 1994). According to the mammal fossil record, the Gymnesic Islands were inhabited by three land mammals including *Myotragus balearicus* Bate (Artiodactyla, Caprinae). Such a dwarf caprine was endemic to the Gymnesics, but absent from the Pityusics. *M. balearicus* displays a number of apomorphies considered as adaptations to island environments achieved in the absence of carnivorous mammals (e.g. ever-growing incisors and shortened legs). Bovids are not common components of islands biotas, and *M. balearicus* must be considered, *sensu* Power *et al.* (1996), a *key* species shaping the environment in the Gymnesic prehuman ecosystems (Delvosalle & Duvigneaud, 1967; Schüle, 1993; Alcover *et al*., 1999; Seguí & Alcover, in press). In contrast, Eivissa and Formentera lacked nonflying mammals during the upper Pleistocene and early Holocene (being the only Mediterranean islands to display this feature, Alcover *et al*., 1994). According to the fossil bird record, bird communities in Mallorca and Eivissa during the upper Pleistocene and early Holocene were structured in very different ways. On Eivissa, e.g. Anseriformes were the most important middle-sized grazers and sea eagles were the top predators (Seguí & Alcover, in press). Bird communities are usually correlated with vegetation (Cody, 1985; Welsh & Lougheed, 1996). Based on the fact that the bird and mammal communities from the Gymnesic and Pityusic Islands were different during the upper Pleistocene and early Holocene, a difference in the past vegetation (and in the past environment) of these islands should be inferred.

The scenario shown by these palaeontological data suggests that the faunistic and floristic differences between the Gymnesic and the Pityusic Islands were stronger in the past than today. Human colonization has brought about selective extinction of some endemic species and colonization of a number of widespread species (e.g. Table 6). The negative effect of human-associated introduced fauna on the insular endemic fauna has been documented by Palmer & Pons (1996a, b) and Pons & Palmer (1999) for the small islands of the Balearics. Other known remarkable ecological changes that took place after the arrival of humans were the dramatic reduction of *Buxus balearicus* Lam. woods (Pérez-Obiol *et al*., 1996) and some changes in mutualistic relationships. *Cneorum triccocon* L. (Cneoraceae) seems to have been dispersed only by lizards before humans arrival. However, lizards became extinct on Mallorca after the introduction of weasels (*Mustela nivalis* L.), and *C. triccocon* is currently dispersed by pine martens (*Martes martes* L.) (Traveset, 1995).

Endemic species in the Balearics are currently more abundant in marginal habitats such as seashores or mountain tops. Some of them have been displaced toward such marginal habitats (e.g. *Alytes muletensis* Sanchiz and Adrover, widely distributed in Mallorca before human colonization, but nowadays restricted to isolated streams in the northern mountains of Mallorca).

Low dispersal capability of endemic species explains the persistence of between subarchipelagos (i.e. Pityusic and Gymnesic Islands) differences. In contrast, similarity based on bird presence or absence is not correlated with palaeogeographic relationships. The composition of bird fauna (and of other well-dispersed organisms) on individual island seems to covary with environmental changes brought about by local extinctions and colonizations by another set of species (e.g. Lugo, 1988; Pons & Palmer, 1999).

The data presented here underline the importance of knowing the past when interpreting a contemporary fauna, its affinities and the key factors determining its maintenance. Past events could be critical when islands and endemic species are involved. Conservation programs should be in accordance with history as well as present environments.

ACKNOWLEDGMENTS

This paper has benefited from the comments and critical review of G. Bibiloni, P. Casgrain, D. Jaume, B.F.J. Manly, L. Marcus, S. Morand, J.A. Rosselló. K. Taylor, P.Y. Sondaar and M. Williamson. All SYSTAT calculations have been done by A. Traveset. We are specially indebted to all taxonomists mentioned in Pons & Palmer (1996). We are grateful to the Laboratoire d'Entomologie of the MNHN (Paris), the IMEDEA-CSIC (Palma de Mallorca), and to the CICYT (Spain; AMB96–0843 and PB97–1173 research projects) and the DGICYT (Spain; FPI-Ext. grant to M. Palmer) for its financial support.

REFERENCES

Alcover, J.A., McMinn, M. & Altaba, C.R. (1994) Eivissa: a Pleistocene oceanic-like island in the Mediterranean sea. *Res. Exploration,* **10**, 236–238.

Alcover, J., Moyà-Solà, S. & Pons-Moyà, J. (1981) *Les quimeres del passat*. Ed. Moll. Palma.

Alcover, J., Pérez-Obiol, R., Yll, E.-I. & Bover, P. (1999) The diet of *Myotragus balearicus* Bate 1909 (Artiodactyla: Caprinae), an extinct bovid from the Balearic Islands: Evidence from coprolites. *Biol. J. Linnean Soc.* **66**, 57–74.

Altaba, C.R. (1997) Phylogeny and biogeography of midwife toads (*Alytes*, Discoglossidae): a reappraisal. *Contr. Zool.* **66**, 257–262.

Anderson, S. (1994) Area and Endemism. *Q Rev. Biol.* **69**, 451–471.

Arntzen, J.W. & García-París, M. (1995) Morphological and allozyme studies of midwife toads (genus *Alytes*), including the description of two new taxa from Spain. *Contr. Zool.* **65**, 5–34.

Avellà, F., Muñoz, A., Garcias, P. & Jurado, J.R. (1997) *Atles dels aucells nidificants de Mallorca i Cabrera 1983–94*. G.O.B.ed. Palma de Mallorca.

Beerli, P., Hotz, H. & Uzzell, T. (1996) Geologically dated sea barriers calibrate a protein clock for Aegean water frogs. *Evolution,* **50**, 1676–1678.

de Bolòs, O. &. Molinier, R. (1958) Recherches phytosociologiques dans l'île de Majorque. *Coll. Bot.* **5**, 699–863.

Brown, J.H. & Gibson, A.C. (1983) *Biogeography.* The CV Mosby Company, St. Louis.

Busack, S.D. (1986) Biogeographic analysis of the herpetofauna separated by the formation of the strait of Gibraltar. *Natl Geogr. Res.* **2**, 17–36.

Canzoneri, S. & Rallo, G. (1996) Nuove ricerche preliminari condotte nelle Isole di Maiorca e Minorca e descrizione di una nuova specie (Diptera, Ephydridae). *Boll. Soc. Hist. Nat. Balears,* **39**, 101–110.

Cardona, M.A. (1979) Consideracions sobre l'endemisme i l'origen de la flora de les Illes Balears. *Bull. Inst. Cat. Hist. Nat.* **44**, 7–15.

Cardona, M.A. & Contandriopoulos, J. (1979) Endemism and the Evolution in the Islands of the Western Mediterranean. *Plants and islands* (ed. by D. Bramwell), pp. 133–169. Academic Press. London.

Cody, M.C. (1985) *Habitat selection in birds.* Academic Press, New York.

Colom, G. (1957) *Biogeografía de las Baleares.* Edit. Estudi General Lul.lià, Palma de Mallorca.

Cuerda, J. (1975) *Los tiempos cuaternarios en Baleares.* Edit. Institut d'Estudis Baleàrics, Palma de Mallorca.

Delvosalle, L. & Duvigneaud, J. (1967) Voyage à Majorque. Compte Rendue botanique des excursions. *Les Naturalistes belgues,* **48**, 365–388.

Folch, R. (1982) *La vegetació dels Països Catalans.* Ed. Ketres, Barcelona.

Franciscolo, M.E. (1979) *Fauna d'Italia: Haliplidae, Hygrobiidae, Gyrinidae, Dytiscidae.* Ed. Calderini, Bologna.

Gaju-Ricart, M., Bach de Roca, C., Molero-Baltanás, R. & Mora-Carmona, R. (1995) Descripción de *Praemachiloides insularis* sp. n. de las Islas Baleares (Microcoryphia: Machilidae). *Bol. Asoc. Española Entom.* **19**, 163–172.

Gómez-Zurita, J., Sacarés, A. & Petitpierre, E. (1996) Chrysomelidae de sa Dragonera. *Boll. Soc. Hist. Nat. Balears,* **39**, 129–134.

Jaccard, P. (1908) Nouvelles recherches sur le distribution florale. *Bull. Soc. Vaudoise Sci. Nat.* **44**, 223–270.

Jäch, M., Valladares, L.F. & García-Avilés, J. (1996) *Limnebius minoricensis* sp. n. (Coleoptera: Hydraenidae) from the Balearic Islands, Spain. *Aquat Insects,* **18**, 113–116.

Jaume, D. & Boxshall, D. (1995) *Stygocyclopia balearica*, a new genus and species of calanoid copepod (Pseudocyclopiidae) from anchialine caves in the Balearic Islands (Mediterranean). *Sarsia,* **80**, 213–222.

Jaume, D. & Boxshall, D. (1996a) A new genus and two new species of cave-dwelling Misophrioid copepods from the Balearic Islands (Mediterranean). *J. Nat. Hist.* **30**, 989–1006.

Jaume, D. & Boxshall, D. (1996b) Two new genera of cyclopinid copepods (Crustacea) from anchialine caves on western Mediterranean and eastern Atlantic islands. *Zool. J. Linnean Soc.* **117**, 283–304.

Kriechbaumer, N. (1894) Himenópteros nuevos de Mallorca recogidos por D. Fernando Moragues (presbítero). *Anales Sociedad Española Historia Natural,* **3**, 239–253.

Lehrer, A.Z. (1996) Trois sarcophagines méditerranéennes nouvelles (Diptera, Sarcophagidae). *Mitt. Schweizerischen Entomol. Ges.* 69, 261–270.

Lomolino, M.V. (1996) Investigating causality of nestedness of insular communities: selective inmigrations or extinctions? *J. Biogeogr.* **23**, 699–703.

Lugo, A.E. (1988) Estimating reductions in the diversity of tropical forest species. *Biodiversity* (ed. by E. O. Wilson), pp. 58–70. National Academy Press, Washington D.C.

Manly, B.F.J. (1995) A note on the analysis of species co-ocurrences. *Ecology,* **76**, 1109–1115.

Muntaner, J. (1984) Some faunal and biogeographic considerations on the avifauna of Eivissa. *Biogeography and ecology of the Pityusic Islands* (ed. by H. Kuhbier, J. A. Alcover and C. Guerau d'Arellano), pp. 527–563. Dr. Junk Publisher, The Hague.

Myers, A.A. & Giller, P.S. (1988) *Analytical biogeography.* Chapman & Hall, London.

Oosterbroek, P. & Arntzen, P. (1992) Area-cladograms of circum-Mediterranean taxa in relation to the Mediterranean paleogeography. *J. Biogeogr.* **19**, 3–20.

Palmer, M. & Cambefort, Y. (1997) Aptérisme et diversité dans le genre *Thorectes* Mulsant 1842 (Coleoptera: Geotrupidae): Une étude phylogénétique et biogéographique des espèces méditerranéennes. *Ann. Soc. Entom. France,* **33**, 3–18.

Palmer, M. & Petitpierre, E. (1993). Els coleòpters de Cabrera: llista faunística i perspectives d'estudi. *Història Natural de L'arxipèlag de Cabrera* (ed. by J. A. Alcover, E. Ballesteros and J. J. Fornós), pp. 383–407. CSIC – Edit. Moll, Mon. Soc. Hist. Nat. Balears, 2, Palma de Mallorca.

Palmer, M. & Pons, G.X. (1996a) Diversity in Western Mediterranean Islets: effects of rat presence on a beetle guild. *Acta Oecologica,* **17**, 297–305.

Palmer, G.X. & Pons, G.X.. (1996b) Variacions estacionals de l'abundància dels Tenebrionidae (Coleoptera) a l'Illa del Toro (Mallorca). *Boll. Soc. Hist. Nat. Balears,* **39**, 167–175.

Paul, C.R.C. & Altaba, C.R. (1992) Els mol.luscs terrestres fòssils de les illes Pitiüses. *Boll. Soc. Hist. Nat. Balears,* **35**, 141–170.

Pérez-Obiol, R., Yll, R.R., Pantaleon-Cano, J. & Roure, J.M. (1996) Historia de *Buxus* y *Corylus* en las Islas Baleares durante el Holoceno. *Biogeografía Pleistocena-Holocena de la Península Ibérica* (ed. by P. Ramil-Rego, C. Fernández-Rodríguez and M. Rodríguez-Guitián), pp. 87–97. Xunta de Galicia, Santiago de Compostela.

Petitpierre, E., Arranz, E. & Terrasa, B. (1987) Population genetics of Western Mediterranean insular lizards. *Genét. Ibér.* **39**, 453–471.

Pons, G.X. & Palmer, M. (1996) *Fauna endèmica de les Illes Balears.* IEB COPOT- SHNB, Mon. Soc. Hist. Nat. Balears, 5, Palma de Mallorca.

Pons, G.X. & Palmer, M. (1999) Invertebrats endèmics i illes: Introduccions i extincions als illots de Cabrera (Illes Balears). *Ecologia de les Illes* (ed. by J. A. Alcover). SHNB-IEB, Ed. Mon. Soc. Hist. Nat. Balears, 6, Palma de Mallorca, pp. 105–122.

Power, M., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Scott Mills, L., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. (1996) Challenges in the Quest for Keystones. *Bioscience,* **46**, 609–620.

Real, R. & Vargas, R. (1996). The probabilistic basis of Jaccard's Index of similarity. *Syst. Biol.* **45**, 380–385.

Reumer, J.W.F. & Sanders, E.A.C. (1984) Changes in the vertebrate fauna of Menorca in prehistoric and classical times. *Z. F. Säugetierkunde,* **49**, 321–325.

Rivas-Martínez, S., Costa, M., Soriano, P., Pérez, R., Llorens, L. & Rosselló, J.S. (1992) Datos sobre el paisaje vegetal de Mallorca e Ibiza (Islas Baleares, España). *Itinera Geobotanica,* **6**, 5–98.

Romero, J. & Real, R. (1996) Macroenvironmental factors as ultimate determinants of distribution of Common Toad and Natterjack Toad in the South of Spain. *Ecography,* **19**, 305–312.

Schüle, W. (1993) Mammals, vegetation and the initial human settlement of the Mediterranean Islands: a paleoecological approach. *J. Biogeogr.* **20**, 399–412.

Seguí, B. & Alcover, B. (in press) Comparison of paleoecological patterns in insular bird faunas: a case-study from the western Mediterranean and Hawaii. *Smithsonian Contr. Paleobiol.* in press.

Sfenthourakis, S. (1996) A biogeographical analysis of terrestrial isopodes (Isopoda, Oniscoidea) from the central Aegean Islands (Greece). *J. Biogeogr.* **23**, 687–698.

Traveset, A. (1995) Seed dispersal of *Cneorum tricoccon* L. (Cneoraceae) by lizards and mammals in the Balearic islands. *Acta Oecologica,* **16**, 171–178.

Wang, Q., Thornton, Q.B. & New, T.R. (1996) Biogeography of the phoracantine beetles (Coleoptera, Cerambycidae). *J. Biogeogr.* **23**, 75–94.

Welsh, D.A. & Lougheed, S.C. (1996) Relationship of bird community structure and species distribution to two environmental gradients in the North Boreal forest. *Ecography,* **19**, 194–208.

Wiggins, D.A. & Møller, A.P. (1996) Island size, isolation, or interspecific competition? The breeding distribution of the *Parus* guild in the Danish archipelago. *Oecologia,* **111**, 255–260.

Wilkinson, L. (1992) *SYSTAT for Windows, Version 5* edn. SYSTAT Inc. Evaston.

Wolda, H. (1981) Similarity indices, sample size and diversity. *Oecologia (Berl.),* **50**, 296–302.

Yll, E., Pérez-Obiol, R. & Julià, R. (1994) Vegetation change in the Balearic islands (Spain) during the Holocene. *Histor. Biol.* **9**, 83–89.

BIOSKETCHES

Born in 1945, **Y. Cambefort** is currently working on dung beetles natural history (taxonomy, phylogeny and biogeography) as well as on their symbolic significance. He is the co-editor of *Dung-beetle ecology* (1991) and the author of *Le scarabée et les dieux* (1994)

The common interest of **J. A. Alcover, G. X. Pons** and **M. Palmer** is insularity. They are trying to find synthetic answers from their alpha-taxonomy specialization: pre-human mammals and birds, spiders and beetles. Their contributions usually focus on western Mediterranean historical biogeography and insular evolutionary biology. J. Alcover has edited five books on islands. He is on the scientific staff of CSIC, Spain. G. X. Pons and M. Palmer are junior scientists and they are temporarily linked to the IMEDEA-CSIC. They have published a book on endemic fauna from the Balearic Islands.

Appendix I A number of similarity indices for presence/absence data are revised by Wolda (1981) demonstrating that diversity and sample size can affect them. Species number and diversity are constrained on islands. Accordingly, we use an unconventional measure of interisland similarity that seems area-independent (i.e. independent of the species numbers displayed by the island pair under comparison). The measurement is simply the (observed–expected) co-occurrences. Pair wise expected co-occurrences is provided by a generalized Monte Carlo testing procedure (Manly, 1995). Marginal totals (both species abundance and species number in each island) are fixed following Manly (1995) and Real & Vargas (1996). Here, we test the behaviour of the similarity measurement used in a number of scenarios.

1. We follow Wolda (1981) for testing sample size effect. An hypothetical fauna distributed adjusted to a log series is used in the analyses. This fauna has 100,000 individuals and 150 species (alpha = 17.3). Four random samples of different size are taken without replacement (2000, 1000, 500 and 250 individuals) with five replicates for each. Mean species number for each of the four sample sizes are 93.0, 82.1, 70.0, and 54.8 ISLDRAND (Manly, 1995) provides the pairwise expected number of co-occurrences used for determining the index under testing. An squared 20*20 (four samples sizes by five replicates) symmetric matrix of pairwise (observed–expected) number of co-occurrences is obtained. Multidimensional scaling (SYSTAT 5; Wilkinson, 1992) to one dimension is used for obtaining a single value for each of the twenty items. One-way ANOVA of these values is the final output detailed below.

ANALYSIS OF VARIANCE

Source	Sum-of-squares	DF	Mean-square	*F*-ratio	*P*
Dependent variable: (Observed -expected) co-occurrences					
Sample size	1.245	3	0.415	0.354	0.787
Error	18.755	16	1.172		
Dependent variable: Jaccard index					
Sample size	17.237	3	5.746	33.274	<0.001
Error	2.763	16	0.173		

Differences between size categories are clearly not significant. Similar output using Jaccard index (Jaccard, 1908) has been added for comparative purposes. In the case of using Jaccard index, smaller samples tend to display smaller similarity.

2. Diversity effects have been tested by a similar procedure. Three faunas with the same 150 species, with the same rank of species abundances, and distributed adjusted to a log series are used in the analyses. These faunas have 10^6, 10^5 and 10^4 individuals and 150 species (alfa = 13.4, 17.3 and 25.0). Five replicates of a sample size of 2000 individuals is taken without replacement. Mean species number for each of the three diversity types are 75.6, 91.6 and 118.4. Similarly, pairwise expected number of co-occurrences is provided by ISLDRAND (Manly, 1995). An squared 15*15 (three diversities by five replicates) symmetric matrix of pairwise indices is obtained. Multidimensional scaling to one dimension is used for obtaining a single value for each of the fifteen replicates. One-way ANOVA of the values obtained is the final output detailed below.

ANALYSIS OF VARIANCE

Source	Sum-of-squares	DF	Mean-square	*F*-ratio	*P*
Dependent variable: (Observed–expected) co-occurrences					
Diversity	2.767	2	1.384	1.357	0.294
Error	12.233	12	1.019		
Dependent variable: Jaccard					
Diversity	13.909	2	6.955	76.519	<0.001
Error	1.091	12	0.091		

Differences between samples extracted from the three faunas are clearly not significant. Using Jaccard index, samples with smaller diversity tend to display smaller similarity.

3. Looking for Type II errors, two faunas with the same diversity (150 species and 1000 individuals; alfa = 48.9), distributed adjusted to a log series are used in the analyses. These two faunas displayed the same 150 species, but different (at random) rank of species abundance. Our purpose is to test the capability of the index for detecting differences among similar faunas. Following the same procedure described above, differences among faunas are significant using the index under testing. Notice the extreme conditions of high similarity among faunas, high diversity and small sample size (ten replicates of only twenty-five individuals from each of the two faunas). However, the index failed in finding significant differences among the two faunas with tiny sample sizes ($n < 10$ individuals).

ANALYSIS OF VARIANCE

Source	Sum-of-squares	DF	Mean-square	*F*-ratio	*P*
Dependent variable: (Observed–xpected) co-occurrences					
Fauna	10.748	1	10.748	20.909	< 0.001
Error	9.252	18	0.514		
Dependent variable: Jaccard Index					
Fauna	11.378	1	11.378	23.752	< 0.001
Error	8.622	18	0.479		

4. The index is tested with an additional hypothetical fauna, structured in a different way. The probability of extracting a species in a sample is the same for all species and depends only on the sample size. Mean species number of the for sizes used (five replicates each) are 88.4, 71.8, 48.6, and 34.4.

ANALYSIS OF VARIANCE

Source	Sum-of-squares	DF	Mean-square	*F*-ratio	*P*
Dependent variable: (Observed–expected) co-occurrences					
Species number	0.084	3	0.028	0.023	0.995
Error	19.916	16	1.245		
Dependent variable: Jaccard Index					
Species number	12.427	3	4.142	8.753	0.001
Error	7.573	16	0.473		

The results clearly show that the index under testing is not dependent of the number of species. Contrasting, Jaccard index is size-dependent.

5. We also test the effect of species number with a data set showing nestedness (Lomolino, 1996). The data are presences–absences of tenebrionid beetles on fourteen islets at the Cabrera Archipelago (Balearic Islands, Western Mediterranean; Palmer & Petitpierre, 1993). As in the cases above, ISLDRAND provides the pairwise expected number of co-occurrences used for determining the index under testing (i.e. (observed–expected) number of co-occurrences). An squared 14*14 (fourteen islands), symmetric matrix of all pairwise indices is obtained. Multidimensional scaling (SYSTAT) to one dimension allows to obtain a single value for each of the fourteen islands. Regression of these values on the number of species on each island is the final output displayed below.

REGRESSION ANALYSIS

Variable	Coefficient	*T*	*P*(2 tail)
Dependent variable: (Observed–expected) co-occurrences			
Squared R:.069	*n* = 14 islands		
Constant	0.647	0.874	0.399
Species number	−0.156	−0.944	0.364
Dependent variable: Jaccard Index			
Squared R:.483	*n* = 14 islands		
Constant	1.711	3.108	0.009
Species number	−0.413	−3.355	0.006

Similarities measured using the new index show no dependence with the number of species. Contrasting, Jaccard index depends on the species number of the islands being compared

6. Finally, we test linearity of the index. As a criterion we use fifteen samples of 100 species. The number of species both samples have in common decrease linearly from 99 to 86. The values obtained are regressed with the number of species in common. The results confirm the linearity of the two indices.

REGRESSION ANALYSIS

Variable	Coefficient	*T*	*P*(2 tail)
Dependent variable: (Observed–expected) co-occurrences			
Squared R: 1.000	*n* = 15 samples		
Constant	8.000	0.49e+04	< 0.000
Shared species	4.320	0.26E+04	< 0.000
Dependent variable: Jaccard Index			
Squared R: 1.000	*n* = 15 samples		
Constant	8.000	240.824	< 0.000
Shared species	4.319	130.010	< 0.000