Genes, geology and biodiversity: faunal and floral diversity on the island of Gran Canaria

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Abstract

Genes, geology and biodiversity: faunal and floral diversity on the island of Gran Canaria.— High levels of floral and faunal diversity in the Canary Islands have attracted much attention to the archipelago for both evolutionary and ecological study. Among the processes that have influenced the development of this diversity, the volcanic history of each individual island must have played a pivotal role. The central island of Gran Canaria has a long geological history of approximately 15 million years that was interrupted by violent volcanism between 5.5 and 3 million years ago. Volcanic activity is thought to have been so great as to have made all plant and animal life virtually extinct, with survival being limited to some coastal species. The implication from this is that the higher altitude laurel forest and pine woods environments must have been re–established following the dramatic volcanic period. This paper reviews the evidence for this using recent molecular phylogenetic data for a number of plant and animal groups on the island of Gran Canaria, and concludes that there is general support for the hypotheses that the forest environments of Gran Canaria post–date the Roque Nublo eruptive period.

Key words: Gran Canaria, Phylogeography, Biodiversity, Ecology, Evolution.

Resumen

Genes, geología y biodiversidad: diversidad de la fauna y flora de la isla de Gran Canaria.— La extensa diversidad de la flora y fauna de las Islas Canarias ha convertido el archipiélago en un centro de especial interés para los estudios sobre evolución y ecología. De entre los procesos que han influido en el desarrollo de esta diversidad, cabe destacar el importante papel que ha desempeñado la historia volcánica de cada una de las islas. La isla principal del archipiélago, Gran Canaria, tiene una larga historia geológica de aproximadamente unos 15 millones de años, que fue interrumpida por un violento volcanismo que tuvo lugar hace entre 5,5 y 3 millones de años. Se considera que la actividad volcánica fue de tal magnitud, que prácticamente extinguió toda la vida vegetal y animal de las islas, a excepción de unas pocas especies costeras que lograron sobrevivir. De ello puede deducirse que los entornos de mayor altitud, como los bosques de laureles y pinos, seguramente se reestablecieron tras el dramático período volcánico antes mencionado. En este trabajo, se revisa la evidencia de ello mediante el análisis de datos filogénicos moleculares recientes de una serie de grupos de plantas y animales de la isla de Gran Canaria, y se demuestra la validez general de la hipótesis que sostiene que los entornos forestales de Gran Canaria son posteriores al ciclo eruptivo de Roque Nublo.

Palabras clave: Gran Canaria, Filogeografía, Biodiversidad, Ecología, Evolución.

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Introduction

The Canary Islands (fig. 1) are increasingly being utilised for evolutionary studies of colonisation and speciation (for a review see JUAN et al., 2000), the attraction stemming from the great diversity within the flora and fauna of the archipelago. The Canary Islands are characterised by a high level of species endemism, and groups of closely related species are often characterised by a diversity of both morphological and ecological types. The rich biodiversity of the Canarian archipelago is undoubtedly attributed in part to the diversity of habitats present. The Canary Islands have a subtropical climate with warm temperatures that show little seasonal variation. The climate is strongly influenced by the humid trade winds from the northeast, which in combination with the altitude of the volcanoes and the drier northwest winds blowing at higher levels produce an inversion zone and marked vegetational zones. Five vegetational zones can be recognised: 1. Arid subtropical scrub up to 250m; 2. Humid and semi–arid subtropical scrub and woods from 250 to 600m; 3. Humid laurel forest in the cloud belt from 600 to 1,000 m; 4. Humid to dry temperate pine forest from 1000 to 2,000 m; 5. Dry subalpine scrub over 2,000 m.

Although individual islands are characterised by a diversity of habitats the extent of these on each island differs, and this can be attributed to both natural and non–natural causes. For example, due to their low elevation the eastern islands of Fuerteventura and Lanzarote are naturally lacking forest habitats. In contrast forest environments occur naturally on the island of Gran Canaria, but the extent of these has been drastically reduced by human activity. Only a small percentage of the

original *Pinus canariensis* forest, totalling about 12,000 ha remains, and this is fragmented (PÉREZ DE PAZ et al., 1994). There is now almost no low-land thermophilous forest and of the once exten-sive laurel forest there remain only two fragments amounting to approximately 130 ha. Not surpris-ingly, Gran Canaria is characterised by a large number of plant species recognised as endangered or threatened (AIZPURU et al., 2000).

The laurel forest and pine woods have been viewed as a relict flora (CIFFERI, 1962), proper to the Tertiary and thus constituting the oldest island environments (MACHADO, 1976). In fact many plant genera from Macaronesia (Canary Islands, Ma-deira, Azores, Selvagens, and Cape Verde Islands) have been considered relict survivors from the Tertiary period. This hypothesis of a relict origin for many elements of the Macaronesian flora can be traced back to the end of the last century (ENGLER, 1879) and has continued to win favour with more modern biogeographers (e.g. WULF, 1943; LEMS, 1960; CIFERRI, 1962; MEUSEL, 1965; TAKHTAJAN, 1969; BRAMWELL, 1972, 1976; HUMPHRIES, 1976; SUNDING, 1979; CRONK, 1992). Evidence for a relict origin comes from fossil data suggesting that many groups now found in the laurel forests and sclerophilous zones of Macaronesia were appar-ently lost from the flora of Europe at the end of the Tertiary and in the Pleistocene due to climate change. The woody habit of many Macaronesian plants has also been viewed as an ancestral trait that identifies them as a relict flora.

Recent molecular phylogenetic studies have sought to test this hypothesis of a relict origin for a number of plant groups and, perhaps surprisingly, little evidence has come to light (see EMERSON, 2002 for a review). This does not rule out the possibility of a component of the Canary Island
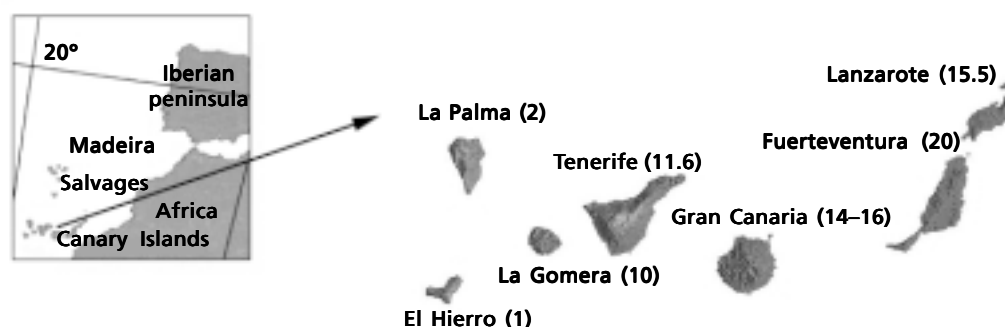

Fig. 1. The Canary Islands. Numbers in parentheses refer to the proposed maximum geological ages for each of the Canary Islands, estimated in millions of years.

Fig. 1. Las islas Canarias. Los números entre paréntesis se refieren a los máximos períodos geológicos propuestos para cada una de las islas, estimados en millones de años.

flora being relicts from the tertiary, and indeed molecular data can not exclude this for the laurel forest endemic *Ixanthus viscosus* (Gentianaceae) (THIV et al., 1999) and molecular phylogenetic data support a relict origin for the monotypic genus *Allagopappus* (FRANCISCO–ORTEGA, 2001). Similar to *Allagopappus*, molecular data also describe basal phylogenetic positions for the monotypic genus *Plocama* (BREMER, 1996; ANDERSSON & ROVA, 1999) and *Lavatera phoenicea* (RAY, 1995) supporting a possible relict origin for these taxa.

An old age for the forest environments may also lead to older associations within these environments for the animal species inhabiting them. It is interesting that in the laurel forests of the Canarian archipelago many insect groups reach their maximum of endemicity (MACHADO, 1976), an observation supporting the antiquity of the laurel forest environment (EMERSON et al., 1999). However, this observation of high endemicity is just that, suggestive but not conclusive. To test the general hypothesis that the forest environments are relictual a molecular phylogenetic approach is required to generate age estimates for the origin of species groups confined to the forest environments. A suitable island for testing this general hypothesis is that of Gran Canaria. The island of Gran Canaria has a maximum subaerial age of approximately 15 million years (My) (HOERNLE et al., 1991), making it the geologically oldest island with forest environments. One may argue that the limited laurel forest remaining may introduce a bias due to a concomitant species loss with deforestation. This analysis is restricted to laurel forest data for Coleoptera, for which it has been noted that there is frequent sympatry of closely related species (MACHADO, 1976), and for which many species have managed to survive in deforested areas, through use of alternative humid habitat (P. Oromí, pers. comm.).

It is generally accepted by geologists that the recent eruptive period that formed the Roque Nublo agglomerate complex (from 5.5 million years ago (Mya) to 3 Mya) was very explosive (PÉREZ–TORRADO et al., 1995). It is very probable that the whole vegetation of this island, except possibly some coastal species, went extinct (ARAÑA & CARRACEDO, 1980; MARRERO & FRANCISCO–ORTEGA, 2001). Given this consideration we can define two hypotheses with regard to the antiquity of the forest environments in Gran Canaria that can be tested with molecular phylogenetic data:

Hypothesis 1 (H_1): The forest environments of Gran Canaria are ancient and survived through the Roque Nublo eruptive period. If this is true then sequence divergence estimates for some species groups inhabiting the forests should pre–date the end of the Roque Nublo eruptive period (3 My).

Hypothesis 2 (H_2): The forest environments of Gran Canaria post–date the Roque Nublo eruptive period. If this is true then no age estimates for species groups inhabiting the forests should

pre–date the end of the Roque Nublo eruptive period (3 My).

Recent molecular phylogenetic analyses of plant and animal groups on the Canary Islands provide a number of data sets for testing which of the two hypotheses (H_1, H_2) best fit the forest environments of Gran Canaria. What follows is a review of these studies with an assessment of their support for H_1 or H_2, and a comparative assessment of data for non–forest organisms.

Flora and fauna of the pine and laurel forests

Laurus azorica

Laurus azorica (Canary Island laurel) is one of two species in the genus and is native to the Canary Islands, Madeira and the Azores. The second species, *L. nobilis*, is found in southern and western Europe, including all the Mediterranean area and the Atlantic coast of France and the Iberian peninsula (ARROYO–GARCÍA et al., 2001). The common ancestor of both species was broadly distributed in Europe from the Miocene until the Pleistocene (BARBERO et al., 1981). *Laurus azorica* is one of the defining species of the laurel forests of the Canary Islands. Recently ARROYO–GARCÍA et al., 2001 have undertaken an amplified fragment length polymorphism (AFLP) analysis to establish genetic similarities among populations of both species of *Laurus*. Genetic similarities between each pair of samples were calculated using the number of shared amplification products using the Dice (SNEATH & SOKAL, 1973) which were then represented as a dendrogram (fig. 2). From figure 2 it is clear that the genetic diversity encompassed by *L. azorica* falls within the greater genetic diversity exhibited by *L. nobilis*. In fact allelic variation exhibited by *L. azorica* is nested within that of *L. nobilis* from the Iberian peninsula and it appears that *Laurus* in Madeira and the Canary Islands may have been the result of two recent independent colonisations from Iberia. Although there is no means of calibrating divergence times from the dendrogram in figure 2, the genetic patterning is indicative of the Macaronesian *Laurus* being recently derived from *L. nobilis*. ARROYO–GARCÍA et al. (2001) suggest that laurel in the Canary Islands is more likely to be the result of a recent range expansion from the continent, and although the evidence is indirect, it is more consistent with H_2.

Calathus

The genus *Calathus* (Coleoptera) is represented by 24 species in the Canary Islands. Most species are in the monteverde, which is composed of laurel forest and fayal–brezal (the vegetation occurring above and around the laurel forest proper), and a few are found in pine forest. Several species are
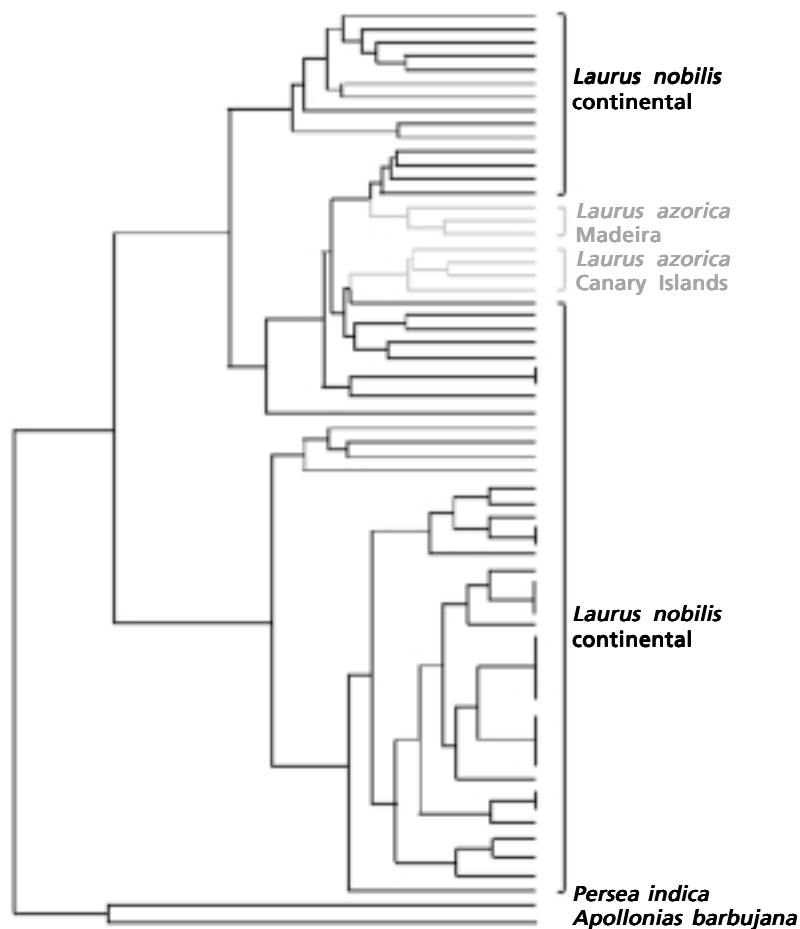
Fig. 2. Dendrogram constructed from AFLP data for genotypes of *Laurus nobilis* (black bars) and *L. azorica* (gray bars). Modified from ARROYO–GARCÍA et al. (2001).

Fig. 2. Dendrograma construido a partir de los datos AFLP para genotipos de Laurus nobilis *(barras negras) y de* L. azorica *(barras grises). Modificado de* ARROYO–GARCÍA *et al. (2001).*

found below these montane forest environments in the lowland thermophilous forest (now open areas due to deforestation). Three species occur on the island of Gran Canaria, two occurring in the laurel forest (*C. canariensis* and *C. appendiculatus*) and one occurring outside the laurel forest (*C. angularis*). Recent phylogenetic analyses by EMERSON et al. (1999, 2000a), using mitochondrial DNA (mtDNA) cytochrome oxidase I and II genes (COI and COII), have identified these three species as monophyletic. Studies by DESALLE et al. (1987) and BROWER (1994) have shown that mtDNA in arthropods evolves at a rate of 2 and 2.3% per My respectively. EMERSON et al. (1999) have applied an average of these, 2.15% per My, leading them to conclude that the observed mtDNA diversity among the species dates back only some 750,000 years (yr). Although it can not be ascertained with any certainty when the island of Gran Canaria was

colonised, the phylogenetic relationships of the three species lend support to H$_2$.

Nesotes

The genus *Nesotes* (Coleoptera) is represented on the Canary Islands by 19 species and 2 subspecies, but recent molecular phylogenetic analyses indicate that alpha taxonomy underestimates the real number of species (REES et al., 2001a, 2001b). There are five species on the island of Gran Canaria inhabiting a range of niches, including xeric coastal areas (*N. lindbergi* and *N. fusculus*), open areas and pine forests (*N. quadratus* and *N. piliger*) and laurel forest (*N. conformis*). The molecular phylogenetic analyses of REES et al. (2001a, 2001b), using mtDNA COII gene sequences, have identified the Gran Canarian species to be a monophyletic group resulting from a
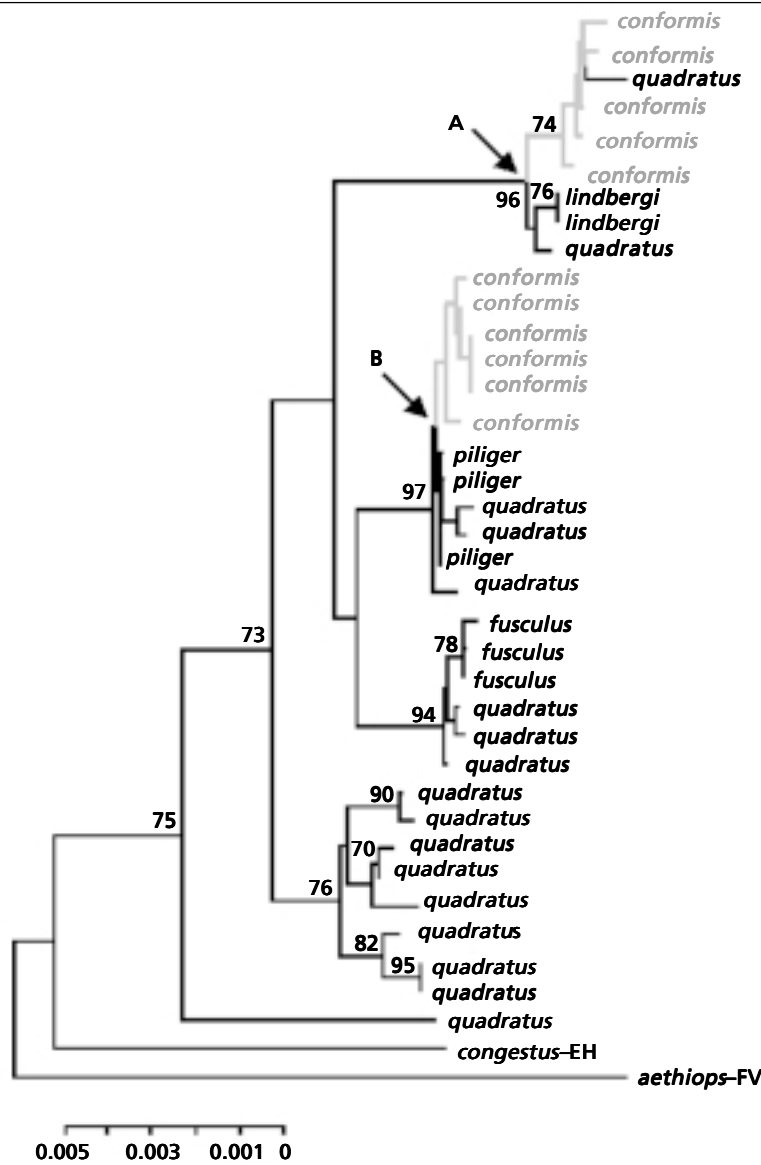
Fig. 3. Neighbour joining tree of maximum likelihood distances for *N. conformis*, *N. quadratus*, *N. piliger*, *N. lindbergi* and *N. fusculus* using mtDNA sequence data. Bootstrap values are indicated for nodes gaining more than 70% support (1,000 reps). *Nesotes conformis* lineages are shown in gray. Age estimates for nodes A and B are discussed in the text. Modified from REES et al. (2001b).

Fig. 3. Árbol por agrupación de vecinos de distancias máximas de verosimilitud para N. conformis*,* N. quadratus*,* N. piliger*,* N. lindbergi *y* N. fusculus*, utilizando la secuenciación de ADNmt. Los valores iniciales de ceba (valores "bootstrap") se indican para los nodos que cuentan con un apoyo de más del 70% (1.000 reps). Los linajes de* Nesotes conformis *se indican en gris. Las estimaciones de edad para los nodos A y B se discuten en el texto. Modificado de* REES *et al. (2001b).*

single colonisation event. Their conclusion is that this group is the result of a recent diversification of a widespread *N. quadratus* type ancestor, typical of open areas, followed by morphological adaptation to laurel, pine and coastal environments. The maximum genetic distance

(maximum likelihood) within the Gran Canarian clade is 7.1% (Tamura Nei model with invariant sites and gamma shape parameter). For the purposes of this paper it is useful to apply the 2.15% per My rate estimate for arthropods (DESALLE et al., 1987; BROWER, 1994) to test sup-

port for each of the two hypotheses. Ideally one would like to use specific rate estimates for each group of species analysed, for the particular mitochondrial gene analysed. In the absence of such specific rate estimates the general rate estimate of 2.15% per My is used with the caveat that individual groups analysed are likely to have specific rate estimates that vary around the general rate estimate, and should thus be viewed with caution. The 7.1% maximum divergence of the Gran Canarian *Nesotes* gives an estimated age of 3.3 My for the most recent common ancestor (MRCA) of this group. To estimate the approximate ages of laurel forest lineages from the tree in figure 3, the tree has been calibrated with the 3.3 My age estimate for the MRCA, and the non parametric rate smoothing (NPRS) method of SANDERSON (1997) has been applied (see EMERSON et al., 2000b). This method smoothes local transformations in rate as rate changes over the tree. Essentially this method replaces the constraint of a constant rate across a tree with a much weaker constraint on how rates vary, but one that is still sufficient to allow the estimation of divergence times. This generates maximum age estimates of 1 My and 0.9 My for nodes A and B on figure 3, indicating that the laurel forest of Gran Canaria has only recently been colonised by *Nesotes*, and supporting H_2.

Tarphius

The genus *Tarphius* (Coleoptera) is represented by 29 species on five of the Canary Islands. The *Tarphius* are hygrophilic fungivorous beetles, intimately associated with the monteverde forest, with some species also occurring in the pine forests, and a few species in other mesic environments (e.g *T. supranubius* in subalpine *Adenocarpus viscosus* shrubs). Four species occur on Gran Canaria; *T. moyanus* is known only from the laurel forest, *T. huggerti* is known only from areas of monteverde that have now been deforested, *T. piniphilus* occurs in the pine forest of Tamadaba, and *T. canariensis* occurs in the laurel forest. Of the four, the first three are restricted to Gran Canaria but *T. canariensis* also occurs on Tenerife, and La Palma. Recent molecular phylogenetic analyses of the *Tarphius* using mtDNA COI and COII gene sequence data (EMERSON et al., 2000c and unpublished data) have identified that the four species of Gran Canaria are the result of two independent colonisation events, one involving *T. canariensis* and the other giving rise to the other three species. Using a combination of the phylogeographic pattern for *T. canariensis*, geological data, the biogeography of the remaining species and estimated divergence times, EMERSON et al. (2000c) have estimated that the genetic diversity present within Gran Canarian *T. canariensis* dates back 1.8 My, and the maximum age for the colonisation of Gran Canaria by *T. canariensis* is, at the most, 2.4 My suggesting a post–Roque Nublo origin. The clade of the three

remaining Gran Canarian species has a maximum genetic divergence of 4.7 % (Emerson et al., unpublished data). Applying the 2.15% per My rate for arthropod mtDNA evolution suggests an age estimate of 2.2 My for the MRCA of the three remaining species. Although it can not be ascertained when the island of Gran Canaria was colonised, the recent diversification of the three species lends support to H_2.

Steganacarus

Oribatid mites of the genus *Steganacarus* are macrophytophages requiring forest soils rich in organic substances (RAJISKI, 1967). The genus comprises approximately 50 species, with three endemic to the Canary Islands, two of which occur on Gran Canaria. *Steganacarus guanarteme* is endemic to Gran Canaria, while *S. carlosi* is also found on the islands of Tenerife and La Gomera. A molecular phylogenetic analysis using mtDNA COI gene sequences (SALOMONE et al., 2002) has identified *S. guanarteme* and *S. carlosi* from Gran Canaria to be monophyletic. Although it can not be concluded when Gran Canaria was colonised, applying the 2.15% per My rate for arthropod mtDNA evolution suggests an age estimate of 1.6 My for the MRCA, supporting a post–Roque Nublo origin.

Pinus canariensis

Pinus canariensis is endemic to the central (Gran Canaria, Tenerife) and western (La Palma, El Hierro and La Gomera) Canary Islands, where it comprises one of the two dominant forest types in the archipelago. Distinctive features of the species are the thick bark, underlain by epicormic buds, and the capacity for basal resprouting; adaptations that enable this pine to survive the moderately intense fires associated with the ongoing volcanic activity of the islands (KEELY & ZEDLER, 1998). A recent molecular phylogenetic assessment of Eurasian pines (WANG et al., 1999) using sequence data from 4 chloroplast genes (*rbcL*, *matK*, *trnV* intron, and *rp120–rp18* spacer) identifies *P. canariensis* to belong to clade of six closely related species including *P. heldreichii*, *P. pinea*, *P. pinaster*, *P. brutia* and *P. halepensis*.

Within the Pinaceae several conflicting attempts have been made to calibrate from the fossil record. WANG et al. (2000) have used a 140 My age for the split of the genus *Pinus* from the other Pinaceae to calibrate their phylogeny of the Pinaceae. However the same estimate derived from MILLER (1988) has also been used by SAVARD et al. (1994) to date the origin of the Pinaceae itself. KUTIL & WILLIAMS (2001) suggest the genus *Pinus* probably emerged within the Pinaceae during the Jurassic period approximately 195 million years ago, but there is no fossil evidence supporting this conjecture. The earliest known pine from the fossil record, *P. belgica* (ALVIN, 1960) dates back to the Early

Cretaceous approximately 130 Mya, and I use this as a conservative calibration for the origin of the genus *Pinus* for dating divergence times within the genus. Using sequence data for rbcL and matK from WANG et al. (1999) maximum likelihood distances were calculated using PAUP* v.4.0b10 with parameters obtained from Modeltest v.3.06 (POSADA & CRANDALL, 1998). The Modeltest program tests the fit of 56 models of DNA sequence evolution using likelihood values obtained from PAUP* for each of the models (SWOFFORD, 1998). Genetic divergences between *P. canariensis* and two non–*Pinus* members of the Pinaceae, *Picea abies* and *Pseudotsuga menziesii* are 4.540% and 4.291% respectively. Using the average of these (4.415%) and calibrating with the 130 My fossil record for *P. belgica* gives an estimated absolute nucleotide substitution rate of 0.034% per My. Genetic divergence between *P. canariensis* and the continental species *P. pinaster* is 0.085%, and applying the divergence rate of 0.034% per My generates an estimated divergence time of 2.5 Mya between *P. canariensis* and *P. pinaster*. A genetic divergence of 0.17% between *P. canariensis* and *P. pinea* generates an estimated divergence time between these two lineages of 5 Mya. Although these age estimates indicate nothing specifically about *P. canariensis* on Gran Canaria, they do suggest the *P. canariensis* forest ecosystem is rather young (2.5–5 My) compared with the geological age of the archipelago.

Brachyderes

The genus *Brachyderes* (Coleoptera) is found predominantly in the Iberian peninsula and North Africa, with some species extending their ranges into France and northern Italy. The genus is also represented on four of the seven Canary Islands, and current taxonomy describes these as four subspecies of *B. rugatus* (PALM, 1976), although previous treatments have described the four as distinct species (LINDBERG & LINDBERG, 1958). *Brachyderes rugatus* is primarily associated with *Pinus canariensis* and its distribution is broadly correlated with the range of *P. canariensis*. A recent molecular phylogenetic analysis of the Canary Island *Brachyderes* using mtDNA COII gene sequence data (EMERSON et al., 2000b) has been able to use a combination of phylogeographic pattern and the geological ages of islands to estimate the ages of origin of each subspecies on each island, indicating that Gran Canaria was colonised by the ancestor of *B. r. calvus* at least 2.6 Mya.

Brachyderes rugatus, along with eight other species, belongs to the subgenus *Brachyderes*, and limited sampling of the eight continental congenerics suggests the colonisation of Gran Canaria could be much older than 2.6 My. Sequence data for three of these other species, *B. pubescens*, *B. grisescens* (EMERSON et al., 2000b), and *B. incanus* (Emerson, unpublished data) indicate a deep divergence of

the *B. rugatus* lineage. Using the minimum genetic distance (maximum likelihood with parameters determined by Modeltest) between *B. rugatus* and the continental species (32%), and applying the 2.15% per My rate for arthropod mtDNA evolution, suggests a conservative age estimate of 15 My for the MRCA of *B. rugatus* and the continental species. However, it is inappropriate to draw such conclusions with less than 40% of the continental species having been sequenced (EMERSON, 2002).

It is interesting that the minimum age estimate of 2.6 My for the colonisation of Gran Canaria by *Brachyderes* (EMERSON et al., 2000b) is surprisingly similar to the 2.5 My minimum age estimate for the divergence of *P. canariensis* from continental *Pinus* species (see above). The phylogeographic pattern for *B. r. calvus* on Gran Canaria suggests the contemporary population is the result of a much more recent expansion out of a geographically restricted area in the region of Juncal (fig. 4). Although it can not be ascertained when the island of Gran Canaria was colonised, the phylogeographic pattern for *B. r. calvus*, and the recent age estimate for its host plant, *P. canariensis* lend support to H_2.

Non–forest flora and fauna

It could be argued that measures of genetic diversity observed within the laurel and pine forest ecosystems of Gran Canaria may be typical for the flora and fauna of Gran Canaria as a whole. A number of recent molecular phylogenetic analyses of Gran Canarian taxa occurring exclusively outside the forest ecosystems provide a comparative assessment of the genetic diversities of the forest and non–forest ecosystems.

Pimelia

The genus *Pimelia* (Coleoptera) has 14 taxa described in the Canary Islands, with all endemic to single islands with the exception of one species that occurs on two islands. Five taxa occur on the island of Gran Canaria, three are strictly coastal (*P. estevezi*, *P. granulicollis*, *P. sparsa albohumeralis*), one occurs in dry lowland environments (*P. sparsa serrimargo*), and the fifth inhabits dry high altitude environments (*P. sparsa sparsa*). A molecular phylogenetic analysis using mtDNA COI gene sequence data has identified these five taxa and *P. fernandezlopezi* from La Gomera to be monophyletic, indicating the five Gran Canarian taxa resulted from within island diversification following a single colonisation event (JUAN et al., 1995). Using the maximum genetic distance (maximum likelihood with parameters determined by Modeltest) between Gran Canarian species (19.6%), and applying the 2.15% per My rate for arthropod mtDNA evolution, suggests an age estimate of 9 My for the MRCA of the Gran Canarian taxa. This age estimate indicates
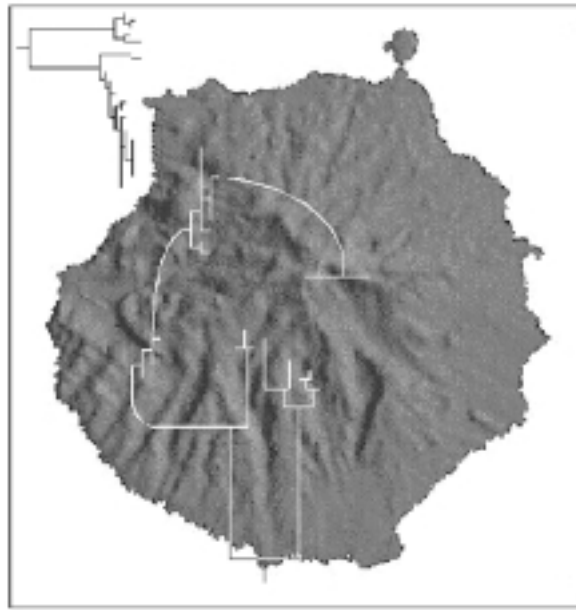
Fig. 4. Phylogeography of *Brachyderes rugatus calvus* haplotypes on Gran Canaria. Branch lengths are not proportional to maximum likelihood branch lengths which are given in the top left inset. Modified from Emerson et al. (2000b).

Fig. 4. Filogeografía de los haplotipos de Brachyderes rugatus calvus *de Gran Canaria. Las longitudes de las ramas no son proporcionales a las longitudes de las ramas de máxima probabilidad, que se indican en el recuadro izquierdo superior. Modificado de* Emerson *et al. (2000b).*

that the genus *Pimelia* was established on Gran Canaria prior to the Roque Nublo eruptive period. Further to this the genetic distance of 8.15% between the high altitude species *P. sparsa sparsa* and the closely related *P. sparsa serrimargo* suggests an age estimate of 3.8 Mya for the divergence of these two species, close to the end of the Roque Nublo eruptive period.

Hegeter

The genus *Hegeter* (Coleoptera) is endemic to Macaronesia with 23 species, 21 of which occur exclusively on the Canary Islands. Most species are xerophilic and present at low altitudes, but some are present in the high altitude volcanic zones (Juan et al., 1996). A molecular phylogenetic analysis of
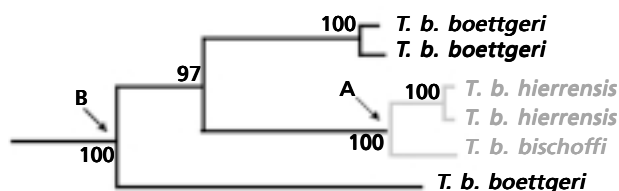

Fig. 5. A neighbour joining tree of phylogenetic relationships among species of *Tarentola* from Gran Canaria, El Hierro and the Selvages, with bootstrap values (1,000 reps). Age estimates for nodes A and B are discussed in the text. Modified from Carranza et al. (2000).

Fig. 5. Árbol por agrupación de vecinos de relaciones filogenéticas entre varias especies de Tarentola *de Gran Canaria, El Hierro y las Islas Selvagens, con valores iniciales de ceba (valores "bootstrap", 1.000 reps.). Las estimaciones de edad para los nodos A y B se discuten en el texto. Modificado de* Carranza *et al. (2000).*

Table 1. Estimated ages in millions of years (My) for Gran Canarian taxa analysed in this study, and their correspondence to the Roque–Nublo eruptive period occurring from 5.5–3.0 million years ago: Ae. Age estimate; PstRN. Post–Roque Nublo; RN. Roque–Nublo; PreRN. Pre-Roque Nublo.

Tabla 1. Estimaciones de edades expresadas en millones de años (My) para los taxones de la isla de Gran Canaria analizada en este estudio, y su correspondencia con el ciclo eruptivo de Roque-Nublo que tuvo lugar hace 5,5–3,0 millones de años: Ae. Edad estimada; PstRN. Posterior a Roque Nublo; RN. Roque Nublo; PreRN. Previo a Roque Nublo.

Environments / taxa	Ae	PstRN	RN	PreRN
Pine and laurel forest				
Laurus azorica	not calibrated	✓		
Calathus	0.75 My	✓		
Nesotes	1 My	✓		
Tarphius	2.4 My	✓		
Steganacarus	1.6 My	✓		
Pinus canariensis	2.5–5 My	?	?	
Brachyderes	2.6 My	✓		
Non–forest				
Pimelia	9 My			✓
Hegeter	10.9 My			✓
Tarentola	5.3–6.7 My			✓
Chalcides	4.8–5.6 My		✓	

the Canary Island *Hegeter* using mtDNA COI gene sequence data included five of the six species from Gran Canaria. Although lacking bootstrap support, monophyly for the Gran Canarian species is favoured. Using the maximum genetic distance (maximum likelihood with parameters determined by Modeltest) between Gran Canarian species (23.5%), and applying the 2.15% per My rate for arthropod mtDNA evolution, suggests an age estimate of 10.9 My for the MRCA of the Gran Canarian taxa. Similarly to the result for the *Pimelia*, this age estimate indicates that the genus *Hegeter* was established on Gran Canaria prior to the Roque Nublo eruptive period. Although two of the five species can be found in mountainous, deforested areas, they are not restricted to this habitat and also occur in xerophilous low or medium altitude habitats (JUAN et al., 1996). The species not included in the study of JUAN et al. (1996), *H. abbreviatus*, is recorded as only occurring in humid forest environments (JUAN et al., 1996), and it would be interesting with regard the hypotheses being tested here to know the phylogenetic placement, and approximate divergence time of this species.

Tarentola

The gekkonid genus *Tarentola* comprises around 22 species that occur in North Africa, the coastal districts of the Mediterranean sea and Macaronesia, with an isolated species in Cuba and the Bahamas, and a further recently described species in Jamaica that is probably extinct. A single species of *Tarentola*, *T. boettgeri boettgeri* occurs on the island of Gran Canaria, and typical of species within this genus it is found in dry, non–forest environments, from sea level to altitudes of 1500 m (BARBADILLO et al., 1999). Several recent molecular phylogenetic analyses of the *Tarentola* using mtDNA 12S and cytb sequence data, and sequence data from the nuclear c–mos gene (CARRANZA et al., 2000, 2002) have helped to clarify the origins of the Macaronesian taxa. Within the Macaronesian islands DNA sequence diversity within *T. b. boettgeri* on Gran Canaria clearly indicates an origin by a single colonisation event, with *T. b. hierrensis* from El Hierro, and *T. b. bischoffi* from the Selvages being included within this clade (fig. 5). Using sequence data for the mtDNA cytb gene, the greatest genetic distance among Gran Canarian haplotypes (maximum likelihood with parameters determined by Modeltest) is 16.8%. CARRANZA et al. (2000) conclude that *T. b. hierrensis* from El Hierro is the result of a colonisation from the Selvages involving the ancestor of *T. b. bischoffi*. Assuming El Hierro was colonised not long after its appearance, node A in figure 5 provides a maximum age estimate for this event,

allowing for unsampled or extinct lineages from the Selvages (see EMERSON et al., 2000b, EMERSON, 2002). Calibrating this node with the estimated 1.1 My age of El Hierro (GUILLOU et al., 1996) generates a cytb divergence rate estimate of 2.5% per My for *Tarentola*. Applying this rate to the observed 16.8% divergence within Gran Canarian *T. b. boettgeri* generates an age estimate of 6.7 My for the MRCA of this species. This compares well with an estimate of 5.3–6.7 My for the MRCA of *T. b. boettgeri* generated by CARRANZA et al. (2002). Both of these age estimates suggest that *T. b. boettgeri* was established on Gran Canaria prior to the Roque Nublo eruptive period.

Chalcides

The skink genus, *Chalcides*, contains at least 19 species, with the majority occurring in Morocco, and three endemic species in the Canary Islands. A single species, *C. sexlineatus*, occurs on the island of Gran Canaria, occurring in dry and mesic open areas from the coast to elevations over 1,000 m. The monophyly of *C. sexlineatus* has been verified by a molecular phylogenetic analysis using mtDNA sequence data from 12S RNA, 16S RNA, and cytb (BROWN & PESTANO, 1998), revealing substantial within island genetic diversity of *C. sexlineatus*. A follow–up study using only 12S RNA sequence data (PESTANO & BROWN, 1999) sampled *C. sexlineatus* more intensively and identified three deep mitochondrial lineages within the island. The authors suggest that *C. sexlineatus* may have survived through the Roque Nublo eruptive period with a restricted distribution in the south–east of the island. Genetic distance estimates (maximum likelihood with parameters determined by Modeltest) for taxa spanning the root of the tree for *C. sexlineatus* are typically between 6–7% (with a maximum value of 12.6%). Although it is understood that 12S rRNA evolves at a slower rate than many protein coding mtDNA genes, rate estimates within the reptiles are lacking. However a recent study of grass lizards (*Takydromus*), LIN et al. (2002) have estimated a divergence rate of 1.25% per My for the 12srRNA gene. Applying this rate to genetic divergence estimates within *C. sexlineatus* generates an approximate age of 4.8–5.6 My for the MRCA (with a maximum estimate of 10.1 My), suggesting *C. sexlineatus* was already established on Gran Canaria in the early part of the Roque Nublo eruptive period.

Conclusion

The violent eruptions on the island of Gran Canaria that formed the Roque Nublo agglomerate complex, 5.5–3 Mya, were very explosive (PÉREZ–TORRADO et al., 1995), leading to the speculation that they would have led to massive extinction within the island, with species survival being limited to the coastal environment (ARAÑA & CARRACEDO, 1980; MARRERO & FRANCISCO–ORTEGA, 2001). The implication from this is that the higher altitude laurel forest and pine wood environments must have been re–established following the dramatic volcanic period. An assessment of recent molecular phylogenetic analyses for plant and animal groups associated with these forest ecosystems finds general support for the hypothesis that the forest environments of Gran Canaria post–date the Roque Nublo eruptive period (table 1). No definitive evidence exists for these species groups predating the end of the Roque Nublo eruptive period (3 My). Four species groups occurring exclusively outside the forest ecosystems have also been analysed. Three of these provide evidence for an origin predating the Roque Nublo eruptive period, and the fourth, *Chalcides*, may have an origin at the beginning of the Roque Nublo eruptive period.

These results are compatible with a general prediction, based on the volcanic history of the island, that biodiversity on Gran Canaria, as measured by genetic diversity, is lower within the laurel forest and pine wood ecosystems compared to that of non–forest ecosystems. It will be interesting to see whether future molecular phylogenetic analyses of other species groups on the island of Gran Canaria add further support to the findings of this paper.

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