



Inferring dispersal: a Bayesian approach to phylogeny-based island biogeography, with special reference to the Canary Islands

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ABSTRACT

Aim Oceanic islands represent a special challenge to historical biogeographers because dispersal is typically the dominant process while most existing methods are based on vicariance. Here, we describe a new Bayesian approach to island biogeography that estimates island carrying capacities and dispersal rates based on simple Markov models of biogeographical processes. This is done in the context of simultaneous analysis of phylogenetic and distributional data across groups, accommodating phylogenetic uncertainty and making parameter estimates more robust. We test our models on an empirical data set of published phylogenies of Canary Island organisms to examine overall dispersal rates and correlation of rates with explanatory factors such as geographic proximity and area size.

Location Oceanic archipelagos with special reference to the Atlantic Canary Islands.

Methods The Canary Islands were divided into three island-groups, corresponding to the main magmatism periods in the formation of the archipelago, while non-Canarian distributions were grouped into a fourth 'mainland-island'. Dispersal between island groups, which were assumed constant through time, was modelled as a homogeneous, time-reversible Markov process, analogous to the standard models of DNA evolution. The stationary state frequencies in these models reflect the relative carrying capacity of the islands, while the exchangeability (rate) parameters reflect the relative dispersal rates between islands. We examined models of increasing complexity: Jukes–Cantor (JC), Equal-in, and General Time Reversible (GTR), with or without the assumption of stepping-stone dispersal. The data consisted of 13 Canarian phylogenies: 954 individuals representing 393 taxonomic (morphological) entities. Each group was allowed to evolve under its own DNA model, with the island-model shared across groups. Posterior distributions on island model parameters were estimated using Markov Chain Monte Carlo (MCMC) sampling, as implemented in MrBayes 4.0, and Bayes Factors were used to compare models.

Results The Equal-in step, the GTR, and the GTR step dispersal models showed the best fit to the data. In the Equal-in and GTR models, the largest carrying capacity was estimated for the mainland, followed by the central islands and the western islands, with the eastern islands having the smallest carrying capacity. The relative dispersal rate was highest between the central and eastern islands, and between the central and western islands. The exchange with the mainland was rare in comparison.

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Main conclusions Our results confirm those of earlier studies suggesting that inter-island dispersal within the Canary Island archipelago has been more important in explaining diversification within lineages than dispersal between the continent and the islands, despite the close proximity to North Africa. The low carrying capacity of the eastern islands, uncorrelated with their size or age, fits well with the idea of a historically depauperate biota in these islands but more sophisticated models are needed to address the possible influence of major recent extinction events. The island models explored here can easily be extended to address other problems in historical biogeography, such as dispersal among areas in continental settings or reticulate area relationships.

Keywords

Bayesian inference, Canary Islands, carrying capacity, dispersal rates, island biogeography, stochastic models.

INTRODUCTION

After being relegated to a simple 'footnote acknowledgment' (Lynch, 1989) in biogeographical papers for a long time, dispersal is again receiving increased attention as a fundamental process explaining the distribution of organisms (de Queiroz, 2005; McGlone, 2005; Riddle, 2005; Cowie & Holland, 2006). This trend can be observed in the large number of phylogeny-oriented articles published since 2004 in this journal and in *Systematic Biology* with the word 'dispersal' in their abstract (54 and 48, respectively; more than one per month). The change is so noticeable that one may speak of a paradigm shift in historical biogeography from the vicariance approach, in which distributions were mainly explained as the result of geological isolating events (Nelson & Platnick, 1981), to one where dispersal takes a more prominent, or even primary role, in explaining current distribution patterns (de Queiroz, 2005). This shift in perspective ('counter-revolution', de Queiroz, 2005) has mainly been brought about by the popularization of molecular systematics and the possibility of estimating divergence times using molecular clocks. Many plant and animal lineages, whose distributions were originally explained by vicariance, appear to be too young to have been affected by the postulated geological events, suggesting their current distribution patterns are the result of dispersal (e.g. Baum *et al.*, 1998; Waters *et al.*, 2000; Cooper *et al.*, 2001; Arensburger *et al.*, 2004; Renner, 2004). Even the biotic patterns of regions such as the Southern Hemisphere, traditionally considered as the prime example of the vicariance scenario, appear to have been shaped in large part through trans-oceanic dispersal (Winkworth *et al.*, 2002; Vences *et al.*, 2003; Sanmartín & Ronquist, 2004; Sanmartín *et al.*, 2007).

This shift in perspective in empirical studies, however, has not been accompanied by a concomitant shift in theoretical and methodological approaches to biogeographical analysis. Cladistic biogeography (Humphries & Parenti, 1999) consid-

ered dispersal as a rare and chance phenomenon, incapable of explaining general, shared distribution patterns across groups. Biogeographical analysis was based on finding a general pattern of area relationships among the groups analysed, which was then interpreted as evidence of a common sequence of vicariance events dividing an ancestral biota. If dispersal was incorporated into biogeographical reconstructions (as in 'phylogenetic biogeography', Van Veller *et al.*, 2003), it was usually in the form of *ad hoc* explanations to explain departure from a strict vicariance model (Brooks & McLennan, 2001; Brooks *et al.*, 2001), or from a combination of vicariance and geodispersal (i.e. range expansion in response to the disappearance of a dispersal barrier) represented by the backbone of the area cladogram (Wojcicki & Brooks, 2005). These methods have in common that they are designed to find patterns of area relationships without explicitly making any assumptions about the underlying evolutionary processes; information about the biogeographical processes that have generated the patterns is ignored when constructing the general area cladogram (Ebach *et al.*, 2003) or inferred *a posteriori* when comparing the area cladogram to the patterns of individual groups (Wojcicki & Brooks, 2005).

In recent years, new methods of biogeographical inference have been developed that allow integration of all relevant biogeographical processes (i.e. dispersal, extinction, vicariance, and duplication) directly into the analysis through the use of explicit process models – the event-based approach. Each process is assigned a cost inversely related to its likelihood, and the analysis consists of finding the minimum-cost, most parsimonious explanation for the observed distribution pattern (Page, 1995, 2003; Ronquist, 1995, 1997, 1998, 2003; Page & Charleston, 1998; Sanmartín & Ronquist, 2002; Sanmartín, 2006). Event-based reconstructions specify both the ancestral distributions and the events responsible, thus making it easier to compare alternative evolutionary/biogeographical scenarios. Probably the most important contribution of event-based methods to analytical historical biogeography

was the possibility to detect patterns of ‘concerted’ dispersal. This refers to repeated, *directional* dispersal resulting from common constraints, such as prevailing winds and ocean currents, and generating shared distributional patterns across multiple organism groups (Sanmartín & Ronquist, 2004; Sanmartín *et al.*, 2007). For the first time, both vicariance and dispersal hypotheses were amenable to analytical testing (Sanmartín *et al.*, 2007).

Although event-based methods represent an important advance over traditional, cladistic–vicariance approaches, they still have several limitations. Like most phylogeny-based inference methods used currently in biogeography, they are founded on the parsimony principle. This means that the cost of the events cannot be estimated directly from the data but must be fixed beforehand using *ad hoc* procedures such as permutation-based significance tests (Ronquist, 2003; Sanmartín & Ronquist, 2004). For example, parsimony-based tree fitting under the four-event model (Ronquist, 2003) requires vicariance to have a lower cost than dispersal in order to distinguish phylogenetically constrained distribution patterns from random patterns but the exact optimal cost ratio is difficult to determine – see Ronquist (2003) and Sanmartín *et al.* (2007) for more details. Another problem, due to the use of the parsimony or cost-minimization principle itself, is that the number of dispersal events is typically underestimated in event-based reconstructions (Sanmartín & Ronquist, 2004). Dating of divergence times and phylogenetic uncertainty (i.e. tree is not known without error) are other important factors that are difficult, if not impossible, to incorporate within the parsimony context.

Statistical approaches to biogeographical analysis, which model dispersal as a discrete-state stochastic process, have been proposed in recent years. For example, Huelsenbeck *et al.* (2000) developed a Bayesian tree fitting method that models host switching (dispersal) as a stochastic process capable of disrupting the topological congruence between the organism phylogeny and the host (area) cladogram, i.e. in the absence of dispersal the two cladograms are identical (Huelsenbeck *et al.*, 2000). Similarly, Ree *et al.* (2005) suggested a likelihood alternative to dispersal–vicariance analysis that models dispersal and extinction as stochastic anagenetic events occurring along internodes, while vicariance and duplication are treated as cladogenetic events responsible for the inheritance of biogeographical ranges. The advantage of these methods over event-based biogeography is that they allow biogeographical parameters of interest, such as dispersal rates, to be estimated directly from the data without the inherent bias of the parsimony approach.

A dispersal-based biogeography?

Any of the mixed dispersal–vicariance methods described above, however, still assume vicariance as the primary explanation for shared distribution patterns, either by requiring a lower cost for vicariance than for dispersal (Ronquist, 2003), by assuming biogeographical congruence as the default

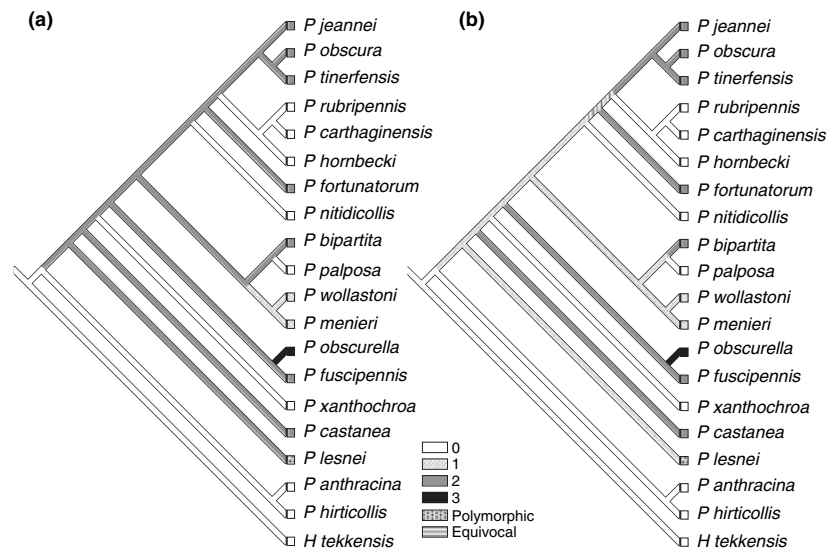
background pattern requiring no stochastic modelling (Huelsenbeck *et al.*, 2000), or by considering dispersal as a stochastic process with no direct role in cladogenesis (Ree *et al.*, 2005). This situation contrasts with the increasing interest among biogeographers for the development of methods of biogeographical inference that give dispersal primacy over vicariance in explaining general biogeographical patterns (McDowall, 2004; de Queiroz, 2005; Riddle, 2005; Cowie & Holland, 2006).

Probably no other scenario is more appropriate for this dispersal-based biogeography than oceanic islands. Oceanic archipelagos of volcanic origin such as hotspot or arc archipelagos arose directly from magma rising up through the ocean and never had any geological connection to a continental landmass. Hence, their current biodiversity and observed biogeographical patterns is fundamentally the product of over-water dispersal (Cowie & Holland, 2006). Examples of this type of archipelago are the Hawaiian Islands in the Pacific Ocean, the Mascarene Archipelago in the Indian Ocean, or the Atlantic Canary Islands (see below). Dispersal is typically considered the key process generating biological diversity in islands (Emerson, 2002; Lomolino *et al.*, 2005; Cowie & Holland, 2006), even though vicariance is sometimes invoked to explain within-island (Juan *et al.*, 2000) or even inter-island speciation (e.g. Pleistocene fluctuating sea levels among the central Hawaiian Islands; Cowie & Holland, 2006). Moreover, dispersal in island systems seems to be capable of producing non-stochastic, highly concordant distribution patterns such as those expected from vicariance. For example, the predominant mode of colonization in hotspot archipelagos such as the Hawaiian Islands is the ‘stepping-stone model’, in which the pattern of island colonization follows the sequence of island emergence, with geologically younger islands more recently colonized than older ones. Most Hawaiian groups are apparently descendants of a single colonization event that follows this pattern of stepwise dispersal (Funk & Wagner, 1995). Mixed dispersal–vicariance methods such as those discussed above would not be appropriate for reconstructing this type of highly congruent, non-stochastic dispersal patterns because these methods do not associate dispersal with cladogenesis (Ree *et al.*, 2005) or because they give vicariance the primary role in explaining shared distribution patterns (Ronquist, 2003).

Inferring dispersal: ancestral-state inference methods

Current research on island evolutionary biogeography focuses mainly on reconstructing patterns of island colonization in individual (Goodson *et al.*, 2006) or multiple (Emerson, 2002; Carine *et al.*, 2004) groups. The most common approach is to use some type of ‘ancestral character state’ inference method to reconstruct the number and sequence of dispersal/colonization events (Funk & Wagner, 1995; Népoukroeff *et al.*, 2003). Parsimony mapping of the ‘biogeographical character’ onto a phylogenetic tree – independently derived from morphological or molecular data – is by far

Figure 1 Parsimony-based optimization of the geographic distribution of the Canary Island species of *Pachydemia* (Coleoptera, Scarabaeoidea) and related African species, onto a morphology-based phylogeny (one of three most parsimonious trees, I. Sanmartín, unpublished data); Outgroup: *Hemictenius tekkensis*. (a) Fitch (unordered) optimization; (b) Wagner (ordered) optimization. The Wagner optimization is four steps longer than the Fitch optimization. Area codes: (0) Mainland: Africa/Asia Minor; (1) eastern Canary Islands (Lanzarote and Fuerteventura); (2) central Canary Islands (Gran Canaria, Tenerife, La Gomera); (3) western Canary Islands (La Palma, El Hierro); (polymorphic) widespread in two or more island groups.



the most popular approach (Funk & Wagner, 1995, and references therein; Moore *et al.*, 2002; Allan *et al.*, 2004; Goodson *et al.*, 2006). Often, intricate colonization pathways are directly deduced from the topology of the tree, leading to conclusions that are difficult to justify (see Emerson, 2002, for examples). A more sophisticated approach is to use phylogenetic programs, such as PAUP or MacClade, to optimize ancestral areas onto the internal nodes of the tree. This analysis consists of finding the reconstruction with the minimum number of character state changes (i.e. dispersal events) required to explain the distributions of the terminal taxa on the phylogenetic tree (Fig. 1). Different parsimony criteria can be used to implement alternative dispersal models: for example, Fitch Parsimony is appropriate for an unconstrained-dispersal model in which all transitions (dispersals) have the same cost (Fig. 1a; e.g. Moore *et al.*, 2002; Goodson *et al.*, 2006), while Wagner Parsimony may be used for a stepping-stone, sequential model in which dispersal is primarily from one island to an adjacent one along the island chain (Fig. 1b). Testing models against each other, however, is more problematic since the Fitch unconstrained model will always be more parsimonious – require fewer steps – than the Wagner ordered model (Fig. 1a,b). A more serious drawback of the parsimony approach is its disregard of two important sources of error (Ronquist, 2004): the uncertainty associated with estimating ancestral states on a given tree – only minimum-change reconstructions are evaluated even when alternative reconstructions could be almost as likely (e.g. Goodson *et al.*, 2006) – and the error in the phylogenetic estimate, since ancestral states are usually reconstructed on a single best tree assuming the phylogeny is known without error. This last source of error could be easily incorporated into the analysis if instead of a single input tree we use a set of weighted trees expressing our confidence in the different clades in the tree (Ronquist, 2003). For example, Huelsenbeck & Imennov (2002) inferred the geographic distribution for the most recent common ancestor to hominids by integrating over trees drawn from the posterior distribution of a Bayesian

Markov Chain Monte Carlo (MCMC) analysis. They weighted each tree according to its posterior probability and then used Fitch optimization to reconstruct ancestral states on each of the trees. Their approach has the advantage that it incorporates topological uncertainty into the reconstruction but it ignores the error associated with reconstructing the evolution of a character on a given phylogenetic tree, which may be a more critical source of uncertainty. This is because information about ancestral states of a particular character comes only from the character itself, whereas the information about phylogenetic relationships is typically based on large sets of characters (Ronquist, 2004).

Parametric statistical approaches such as maximum likelihood (ML) (Pagel, 1994, 1999; Schultz *et al.*, 1996; Schluter *et al.*, 1997; Mooers & Schluter, 1999) offer the advantage over parsimony methods that they use an explicit stochastic model of evolution and branch length information to estimate the probability of change between ancestral states along a given branch – that is, they can account for the fact that changes are more likely along long branches than along shorter ones. Given a tree topology, branch lengths and the distribution of each species, the maximum likelihood approach finds the value of the biogeographical parameters that maximize the probability of observing the data. Since all alternative reconstructions are evaluated in estimating the relative probabilities of ancestral states, ML analyses do incorporate uncertainty in ancestral state reconstruction (Pagel, 1994, 1999). However, ancestral state changes are typically reconstructed over a fixed tree topology with fixed branch lengths (Nepokroeff *et al.*, 2003; Outlaw *et al.*, 2003), in which case the phylogenetic uncertainty is ignored. These methods also typically ignore the error associated with estimating the parameters in the substitution model(s).

Bayesian inference allows us to relatively easily incorporate both sources of uncertainty through random sampling from the posterior probability distribution of the phylogeny and other model parameters using the MCMC technique (see below). Unlike maximum likelihood, Bayesian analysis treats a

model parameter as a random variable, whose posterior probability distribution we want to estimate (Holder & Lewis, 2003). This is done by integrating (marginalizing) over all possible values for the other parameters in the model, including the tree topology. Thus, an important property of Bayesian analysis is that inferences on model parameter estimates (i.e. the marginal posterior probabilities) are independent of the underlying phylogeny (Pagel *et al.*, 2004). The posterior probability distribution on a model parameter is typically summarized in the form of the mean and 95% credibility interval (the middle 95%) of the MCMC samples of that parameter.

Bayesian approaches to ancestral state reconstruction have been proposed in recent years (Huelsenbeck & Bollback, 2001; Pagel *et al.*, 2004) and even applied to biogeographical inference (Olsson *et al.*, 2006). These approaches model dispersal as a Markov chain stochastic process involving the transition between two or more discrete states with different rates or probabilities (Pagel *et al.*, 2004). However, when applied to biogeography, these approaches are usually based on the simplest model of dispersal (equal probabilities for all transitions) and have only been applied to single, individual groups (e.g. Olsson *et al.*, 2006). Here, we extend this approach to more complex dispersal models and to biogeographical analysis across many groups of organisms evolving on different trees, resulting in a general methodology for statistical analysis of island biogeography based on phylogenies and distributional data.

BAYESIAN ISLAND MODELS: MODELLING ISLAND EVOLUTION

We will focus here on models that we refer to as 'static-island models'. In these very simple models, islands are considered discrete geographic units whose relationships are constant through time. Islands are assumed to be older than the organisms inhabiting them and we ignore any change within the islands through time (e.g. island size); the islands just form the background against which colonization patterns are studied. This may seem too simplistic because we know that island size in archipelagos, such as the Canary Islands, has changed over time through erosion and volcanic activity (e.g. Tenerife) and that some of the Canary Islands became connected in times of low sea levels (i.e. the islands of Fuerteventura and Lanzarote during the Pleistocene; Fernández-Palacios & Andersson, 1993). However, this simplification is a useful starting point for more complex models and does not require incorporating time-related or area-related processes such as extinction.

To model the transitions (dispersals) between the islands, we used discrete-state continuous time Markov chain models, mathematically equivalent to those used to model DNA evolution. At the heart of any continuous-time Markov chain are the instantaneous rates of change from one state to another, here collected in the Q matrix. Assume we are studying four islands: A, B, C and D. In the most generalized model we examined, the rate of dispersal from island i to island

j during some infinitesimal time period dt is given by the instantaneous rate matrix:

$$Q = \begin{pmatrix} & [A] & [B] & [C] & [D] \\ [A] & - & \pi_{B|A}r_{AB} & \pi_{C|A}r_{AC} & \pi_{D|A}r_{AD} \\ [B] & \pi_{A|B}r_{AB} & - & \pi_{C|B}r_{BC} & \pi_{D|B}r_{BD} \\ [C] & \pi_{A|C}r_{AC} & \pi_{B|C}r_{BC} & - & \pi_{D|C}r_{CD} \end{pmatrix}$$

where $\pi_{B|A}r_{AB}$ is the probability of moving from island A to island B. This model is completely analogous to the General Time-Reversible (GTR) model used in molecular evolution. The number of islands (states) is completely arbitrary; we use four here for simplicity. There are two different parameters in this model:

1. π_i is the *relative carrying capacity*, defining the steady state relative species richness of island i , that is, the proportion of the total island lineages we expect to find on island i at equilibrium conditions (all Markov processes tend to converge to an equilibrium). It is analogous to the stationary state frequencies in a DNA substitution model. Note that accurate estimation of the relative carrying capacity assumes unbiased sampling of lineages across islands.
2. r_{ij} is the *relative dispersal rate*, corrected for relative carrying capacities, between islands i and j or, in other words, the relative rate of exchange between these two states in the model. The r_{ij} parameters are analogous to the exchangeability parameters, sometimes referred to as relative substitution rates, in the GTR model, and to some extent to the migration parameters used in metapopulation models.

It is important to note that the instantaneous dispersal rates in the model described above are percentage rates. Assume, for instance, that we were interested in the absolute dispersal rate from island i to island j at some point in time. The percentage dispersal rate is $\pi_j r_{ij}$ (from the Q matrix) and the absolute rate is obtained by multiplying this rate with the total number of lineages on the source island, island i . At equilibrium conditions, this number is $N\pi_i$, where N is the total number of lineages on all islands at this point in time. To accommodate for variation among groups in overall dispersal rate, we incorporate a group-specific overall dispersal rate, m , in this to give a total dispersal rate of

$$C_{ij} = N\pi_i\pi_jr_{ij}m$$

The colonization rate for island i (i.e. the probability of island i being colonized by a given group of organisms), C_i , is the sum of contributions from all $(N - 1)$ surrounding source islands, weighted by their relative carrying capacities and relative rates of dispersal to island i , and multiplied by the relative carrying capacity of the recipient island i and the group-specific dispersal rate m , that is

$$C_i = N\pi_i \left(\sum_{j \neq i} \pi_j r_{ij} \right) m$$

The formula above is very similar to the equation used in metapopulation theory (Hanski, 1994, 1998, 2001) for calcu-

lating the probability of colonization of a given patch. The Incidence Function Model (IFM) (Hanski, 2001) is a stochastic occupancy model that models the presence/absence of a species in a habitat patch. In this model, the probability of colonization of a given patch i is dependent on the connectivity of the patch, which is given by the Connectivity Index (Hanski, 2001):

$$S_i = \left(\sum_{j \neq i} e^{-\alpha d_{ij}} p_j A_j \right)$$

where d_{ij} is the distance between patches i and j , p_j is the probability of occupancy of patch j , and A_j is the area of patch j . Both p_j and A_j are directly related to the expected population size of patch j (Hanski, 2001; Wahlberg *et al.*, 2002), which in turn is related to the resources available in the patch. Their product is comparable to our island carrying capacity in that both measure intrinsic island qualities. The distance-dependent term $e^{-\alpha d_{ij}}$ can be compared to our relative dispersal rate parameter in that it is a characteristic of pairs of islands. This term decreases with increasing isolation (d_{ij} being the distance between islands i and j), as one might expect for our dispersal rate parameter. It also depends on a species-specific component (α), the inverse of the 'species-specific average migration rate', which measures the immigration ability of the focal species (Hanski, 2001). This component of the exponential term of the metapopulation model is similar to our m parameter. There is a second component to the IFM, which is the probability of establishment and survival once dispersed (probability of successful dispersal). This involves an extinction probability ($E_i = e/A_i$) that is an inverse function of the population size of the receiving patch i , which in turn is assumed to be proportional to the area of the patch, A_i (Wahlberg *et al.*, 2002). In contrast, the dispersal rates estimated in our model represent the probability of a lineage colonizing a new island and subsequently surviving and diversifying there. Thus, our phylogenetically-derived dispersal rates can be said to include implicitly both the colonization and the extinction components. This also means that the actual number of dispersal (migration) events will be underestimated in our model because only those migrants whose lineages survive through time will be recorded in the phylogeny.

Despite the similarities, there are also some fundamental differences between the IFM and our model. The basic units in the IFM model are individual organisms, whose history is not taken into account, and the dispersal processes take place over relatively short time periods (ecological time). Our model is explicitly historical, it is based on evolutionary lineages as the basic units, and it models dispersal over longer time periods.

Other dispersal models related to ours are those used in coalescent-based population genetics (Beerli & Felsenstein, 1999, 2001). These models do take genealogical history into account but they make a number of assumptions about population-level parameters or phenomena, such as the effective population size and the coalescent process, which may be difficult to model realistically across a larger

phylogeny encompassing many populations or species. Furthermore, it is typically assumed in these models that each population corresponds to an island, which may often be inappropriate for problems in historical biogeography. In general, the population genetic approach would seem appropriate for problems with a few closely related populations and short- to intermediate-time scales, whereas our approach would be more appropriate for large phylogenies and longer time scales.

Island models

By exploring constrained versions of the generalized model described above, it is possible to get at several intuitively important factors characterizing the biogeographical history of a set of islands (Fig. 2).

For example, in the simplest possible model (Fig. 2a), equivalent to the Jukes & Cantor (1969) DNA substitution model (Jukes–Cantor (JC)), all the islands have the same carrying capacity and all dispersals occur at the same rate. This is a very simplistic model in which all islands are considered equivalent (also called the N-island model) regardless of area size or distance between the islands.

In the 'Equal-in' model (Fig. 2b), equivalent to the F81 or 'equal input' substitution model (Felsenstein, 1981), the carrying capacities differ between the islands but all dispersal rates are equal. An alternative model of intermediate complexity is to assume uniform carrying capacities and unequal dispersal rates, but we regard this as a less plausible model biologically and do not consider it further here. Finally, in the model equivalent to the General Time Reversible model (GTR, Tavaré, 1986), also known as the full model (Fig. 2c), each island has a different carrying capacity and dispersal (exchangeability) rates potentially differ between all pairs of islands.

Any of these three dispersal models can be easily transformed into a stepping-stone or sequential-dispersal variant (Fig. 2d–f), in which the instantaneous rates of dispersal between non-adjacent islands, the rates that are not adjacent to the diagonal of the Q matrix, are zero. For instance, the instantaneous rate matrix for the stepping-stone version of the GTR model is:

$$Q = \begin{pmatrix} [A] & [B] & [C] & [D] \\ [A] & - & \pi_{B \rightarrow A} & 0 & 0 \\ [B] & \pi_{A \rightarrow B} & - & \pi_{C \rightarrow B} & 0 \\ [C] & 0 & \pi_{B \rightarrow C} & - & \pi_{D \rightarrow C} \end{pmatrix}$$

Similar static-island models have been used in the past. For example, Peter Beerli's MIGRATE (Beerli, 2006) uses ML or Bayesian MCMC to estimate effective population sizes and past migration rates between n island populations by assuming migration matrix models of varying complexity (e.g. full model, N-island model, stepping-stone model, etc). Nekroeff *et al.* (2003) used models similar to ours in maximum likelihood-based ancestral area reconstruction for the Hawai-

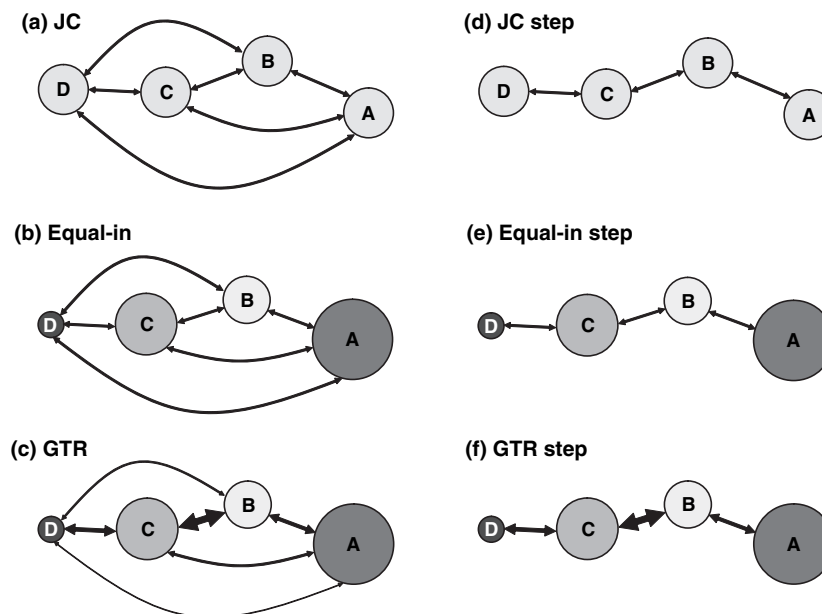


Figure 2 Bayesian Island Models: Each circle represents an island; circle size represents the relative carrying capacity of the island (expected number of lineages at equilibrium); arrow width represents the relative dispersal rate between two single islands. (a) Jukes–Cantor (JC) model: all carrying capacities equal, all dispersal rates equal. (b) Equal-in model: unequal carrying capacities, equal dispersal rates. (c) General Time Reversible (GTR) model: unequal carrying capacities, unequal dispersal rates. (d–f) Stepping-stone variant of each model. (d) JC step: all carrying capacities equal, dispersal rates equal between adjacent islands, zero between non-adjacent islands. (e) Equal-in step: unequal carrying capacities, all dispersal rates equal between adjacent islands, zero between non-adjacent islands. (f) GTR step: all carrying capacities unequal, all dispersal rates unequal between adjacent islands, zero between non-adjacent islands.

ian plant genus *Psychotria*. They divided the archipelago into four island-groups and used a GTR-like dispersal model to estimate maximum-likelihood probabilities of ancestral island distributions on the phylogeny. To our knowledge, however, the current study represents the first time such models are used in a classical historical biogeography context, where dispersal processes are estimated across a large number of groups evolving on different phylogenies.

Calculating dispersal rates across groups

When the same stochastic dispersal model is applied across different groups of organisms, as in our approach, the problem of scaling dispersal rates arises. First, because the molecular characters of each group evolve at their own rate, the branch lengths, which are expressed in terms of the expected number of substitutions per site, need not be comparable across groups. Second, the evolutionary rate might vary across lineages within each tree, making it difficult to translate branch lengths into relative time units. Third, the age of the studied groups could vary widely. Finally, even if we had accurately dated trees, the dispersal rates would probably be different among groups.

To address these problems, we used a simplistic approach. We enforced a strict molecular clock for all the organismal phylogenies and introduced a group-specific dispersal rate scaler (m_i), which measured the dispersal rate as the expected number of dispersals, in a single lineage, from the root to the

tip of the tree. This scaler is the product of the dispersal rate and the age of the group, and thus accommodates variation across groups in both of these parameters. The variation in evolutionary rate across groups was accommodated by a second group-specific scaler (μ_i) associated with the molecular clock tree (see below). To obtain absolute rates of dispersal, we would have needed to calibrate the trees with some internal calibration point (e.g. fossils and maximum age of islands) but we did not explore that here.

Setting the analysis

Figure 3 illustrates the model structure of the analysis. Consider one data set for each group of organisms, containing a molecular partition (DNA sequences, restriction sites, protein data, etc.) and a biogeographical partition. Whereas the molecular partition contains hundreds or thousands of characters, the biogeographical partition contains only one (island distribution). Although the biogeographical partition may appear equivalent to a discrete morphological character, as discussed by Lewis (2001), it is more comparable to a molecular character in that the state labels 0, 1, 2, etc., are not arbitrary. This means that we can generalize stationary state frequencies (carrying capacities) and exchangeability rates across groups. The substitution model of the molecular partition is allowed to differ among groups (GTR_1 , GTR_2 , etc., Fig. 3), whereas the biogeographical model of island evolution is shared across groups (IM ,

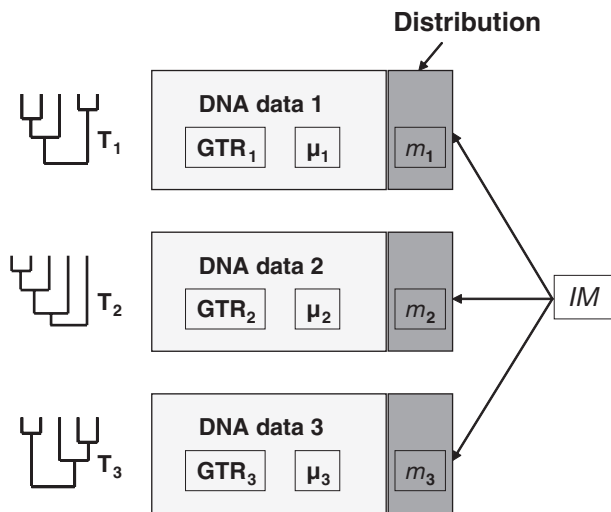


Figure 3 Schema representing the model structure of a Bayesian island biogeography analysis, as implemented in MrBayes 4.0. There is one data set for each group of organisms, containing a molecular partition (DNA sequences, restriction site, etc.) and a biogeographical partition (character ‘island distribution’). The substitution model of the molecular partition is allowed to differ among groups (GTR_1 , GTR_2 , etc.), whereas the biogeographical model of island evolution (IM) is shared across groups. To compare dispersal rates across groups, a separate molecular clock is enforced for each group (T_1 , T_2 , etc.). Two group-specific rate scalars are introduced: a mutation rate scaler (μ_i) that scales the clock tree to produce branch lengths measured in expected number of substitutions per site; and a dispersal rate scaler (m_i) that scales the tree to produce branch lengths measured in terms of the number of expected successful colonization events (dispersal). The ratio between the two scalars, m_i/μ_i , is equivalent to the number of expected dispersals per number of expected substitutions per site. The two scalars together accommodate variation in age, evolutionary rate, and relative vagility across groups. Abbreviations: IM , island model; m_i , overall dispersal rate; μ_i , mutation rate.

Fig. 3). In practice, this means that phylogenetic inference is independent for each group (i.e. each data set is allowed to evolve on its own topology with its own set of branch lengths), while biogeographical inference is based on all groups analysed together.

As described above, we used two tree height scalars for each group in the analysis. One (the mutation rate μ_i) scales the clock tree (which has unit height) to produce branch lengths measured in expected number of substitutions per site, the other (overall dispersal rate, m_i) scales the tree to produce branch lengths measured in terms of the number of expected successful colonization events (dispersals). The ratio between the two scalars, m_i/μ_i , is equivalent to the number of expected dispersals per number of expected substitutions per site. Note that the two scalars together accommodate variation across groups in date of first diversification, molecular substitution rate, as well as relative vagility.

Bayesian estimation of parameters

Bayesian inference is based on calculating the posterior probability of a hypothesis from the likelihood of the data (i.e. the probability of observing the data given the hypothesis) and a *prior* probability that expresses our previous knowledge about the hypothesis (the model parameters), using Bayes’ theorem:

$$f(\theta/D) = [f(D/\theta) \times f(\theta)]/f(D)$$

The denominator, also called model likelihood, is a multi-dimensional integral and summation of the probability of the data over all parameters in the model. Typically, it cannot be estimated analytically so it is estimated using a sampling technique called Markov Chain Monte Carlo (MCMC). Basically, we construct a Markov chain that traverses the universe of our composite (phylogenetic–biogeographical) model including all possible values for the topology, branch lengths, and the parameters of the substitution model for each group of organisms, as well as the parameters of the biogeographical model (i.e. island carrying capacities and dispersal rates), which are shared across groups. In each cycle (generation) of the Markov chain, the values of one or several parameters are changed to a new state according to some stochastic proposal mechanism (the Metropolis–Hastings algorithm). Changes that improve the likelihood of the model are always accepted; otherwise, they are accepted with a probability proportional to the ratio of the likelihood of the new state compared with that of the previous state in the chain (Holder & Lewis, 2003; Nylander *et al.*, 2004; Pagel *et al.*, 2004). If the Markov chain is allowed to run long enough, it reaches a stationary distribution. At stationarity, the Markov chain samples trees and other model parameters from the posterior probability distribution of the composite model. Thus, if stationarity is reached, the MCMC sample of values should ideally approximate the posterior distribution of the model. Because the Markov chain samples simultaneously from the posterior density of trees, and the posterior probability distribution of the parameters in the molecular and biogeographical models, we can estimate the joint probability distribution of the biogeographical parameters and the tree and molecular substitution parameters. By integrating out the other parameters (trees and molecular substitution variables), we can obtain marginal probability distributions for the parameters in our biogeographical model. These parameter estimates are independent from – they accommodate the uncertainty in – the underlying phylogenies and molecular models.

In this sense, our approach is different from that of Pagel *et al.* (2004). They separated the estimation of the phylogeny from estimation of the model of character evolution by running first the phylogenetic Markov chain and then using the MCMC sample of phylogenies to run the character-model Markov chain. They argue that if the character studied is highly homoplastic (as distribution probably is), including the character could distort the estimate of the posterior probability of trees. The standard Bayesian approach, which is the one we adopt, instead focuses on the posterior distribution resulting

from simultaneous consideration of all the processes that are modelled. After all, if we can use stochastic models to estimate biogeographical scenarios, why should the biogeographical estimates not influence the phylogenies? In practice, however, it is unlikely that a single distribution character will have any measurable influence on the phylogenetic estimates when combined with numerous molecular characters.

INFERRING DISPERSAL RATES AND MODES OF COLONIZATION IN THE CANARY ISLANDS

To test the stochastic island models and the Bayesian MCMC approach in inferring colonization rates, we applied the method to an empirical data set consisting of published phylogenies of animals and plants endemic to the Canary Islands.

The Canary Islands

After the Hawaiian Islands, the Canary Islands are probably the best studied volcanic island system in the world, both in terms of their geological history (Ancochea *et al.*, 2006) and the phylogenetic origin of their biota (Juan *et al.*, 2000; Emerson, 2002). They are a volcanic archipelago forming a chain of seven islands and several islets located 110 km from the northwestern coast of Africa (Fig. 4). The islands are separated by deep oceanic trenches (up to 3000 m deep) and have never been connected to any continental landmass, although during periods of low sea level (Pleistocene), the coast lines of Lanzarote and Fuerteventura were much closer to the African coast (as close as 65 km, Carine *et al.*, 2004) than they are today. The latter islands are also separated by the shallowest waters (< 200 m deep) and probably formed one large island in the past (Fernández-Palacios & Andersson, 1993).

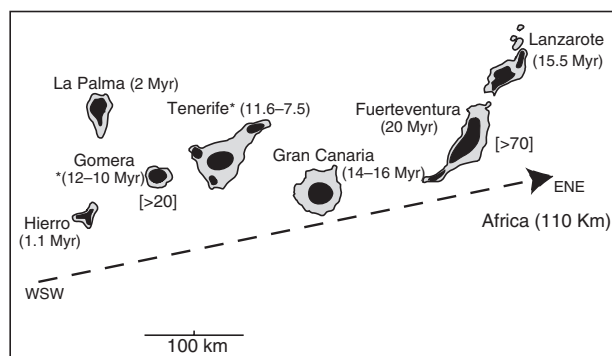


Figure 4 Map of the Canarian archipelago indicating the major volcanoes and the age of the islands in million years (Myr). Ages of islands indicated by * differ among authors (Carracedo *et al.*, 1998; Anguita & Hernán, 2000), (maximum age of basal shield between brackets). The dashed line represents the direction of the moving African Plate according to the hotspot hypothesis (Carracedo *et al.*, 1998, see text).

All the islands were formed in the past 20 Myr, with the easternmost islands of Fuerteventura and Lanzarote being the oldest, while the westerly islands of La Palma and El Hierro are the youngest (Fig. 4). Island formation is controversial. The most accepted theory is that the archipelago was formed in a sequence as a result of the African Plate slowly moving north-eastward over a volcanic hotspot in the Atlantic Ocean (Holik *et al.*, 1991; Carracedo *et al.*, 1998; Guillou *et al.*, 2004; Paris *et al.*, 2005). Several anomalies, however, distinguish the Canary Islands from other hotspot archipelagos such as the Hawaiian Islands (Anguita & Hernán, 2000). All islands show gaps in their volcanic activity, up to several millions of years, which do not fit the classical hotspot model of Wilson (1963). Moreover, the easternmost and oldest islands of Fuerteventura and Lanzarote, presumably no longer in contact with the volcanic hotspot, are still active and have had eruptions in the past 0.1 Myr (Coello *et al.*, 1992), which could have partially wiped out their original flora and fauna (Juan *et al.*, 1998, 2000). There are also anomalies in the correlation between the age of the island and the geographic distance to the hotspot characteristic of the Hawaiian archipelago. For example, the western island of La Gomera should be closer to the present location of the volcanic hotspot (now under El Hierro; Carracedo *et al.*, 1998) than Tenerife but according to recent K–Ar dating (Anguita & Hernán, 2000; Ancochea *et al.*, 2006) La Gomera (14–10 Myr), or at least its submarine stage (> 20 Myr), could be older than Tenerife (11.8–7.5 Myr, Fig. 4). The case is similar for Lanzarote (15 Myr) and Fuerteventura (20 Myr; 70 Myr for the basal complex, Anguita & Hernán, 2000). Some authors have explained these anomalies by the slow movement of the African Plate (1.9 cm year) resulting in poor correlation between geographic position and age (Carracedo *et al.*, 1998; Guillou *et al.*, 2004), but alternative scenarios have also been proposed: a propagating fracture from the Atlas Mountains (Anguita & Hernán, 1975) and uplifted tectonic blocks (Araña & Ortiz, 1991). Recently, Anguita & Hernán (2000) proposed a unifying theory in which the Canary Islands originated from a mantle thermal anomaly, probably an old hotspot that was revived by a propagating fracture from the rising Atlas Mountains, and further uplifted by tectonic forces (Anguita & Hernán, 2000). Ancochea *et al.* (2006) also propose a temporal sequence of volcanic activity in the Canary Islands that fits better with a history of irregular orogenic pulses (tectonic-controlled volcanism) than with a moving hotspot. In general, all geological studies agree on the existence of a general east-to-west progression in the age of the islands but there is little agreement as to the maximum ages for the subaerial stage of each island (Anguita & Hernán, 2000; Paris *et al.*, 2005; Ancochea *et al.*, 2006). Despite this uncertainty, many biogeographical studies in the Canary Islands assume that the temporal evolution of the archipelago is well known and use the age of the islands as calibration points to place ‘maximum age constraints’ at some nodes in the phylogeny, which are used in turn to generate maximum age estimates for the rest of the nodes (e.g. Emerson *et al.*, 2000a; Emerson & Oromí, 2005; Contreras-Díaz *et al.*, 2007).

If the islands are older than assumed, divergence times will be underestimated, with the error being larger, the more distal from the root node is the calibration point (Emerson, 2002). Ignoring geological uncertainty is a common problem of current historical biogeography. Despite great advances in incorporating phylogenetic and dating uncertainty (Bell & Donoghue, 2005), integrating the error associated with palaeogeographical reconstructions into biogeographical analysis remains an outstanding problem.

Colonization patterns

Like the Hawaiian Archipelago, the Canary Islands present a large diversity of habitats, ranging from open xeric environments to lowland scrub to pine forests to sub-alpine vegetation, as well as the two most distinctive ecosystems, the endemic laurel humid forests (*laurisilva*) and the volcanic lava caves, which are also the most threatened by human activity (Juan *et al.*, 2000). The high diversity of habitats, geological isolation from any major landmass, interspecific competition, and adaptive radiation (Francisco-Ortega *et al.*, 2000; Juan *et al.*, 2000; Carine *et al.*, 2004; Silvertown, 2004) are some of the causal factors that have been suggested to explain the high levels of endemism found in the archipelago – around 50% of the terrestrial invertebrate fauna and more than 20% of the native flora (50% of the native vascular flora, Santos-Guerra, 2001) are endemic (Izquierdo *et al.*, 2001). Interest in the origin of the Canarian biota has significantly increased in recent years, with phylogenetic studies now published for numerous groups of Canarian plants and animals (see Appendix S1 in Supplementary Material). In some of these taxa, the predominant mode of colonization is the stepping-stone colonization sequence from older to younger islands characteristic of Hawaiian groups. However, the longer history, more complex volcanic activity and closer proximity to the mainland (Juan *et al.*, 2000) make multiple independent colonization events by related lineages (e.g. Emerson *et al.*, 2000b), and even back-colonization to continental areas (e.g. Moore *et al.*, 2002), more likely in the Canary Islands than in the Hawaiian Archipelago. Hence, whereas most groups in Hawaii are descendants of a single colonization event, many endemic groups in the Canaries seem to be non-monophyletic (Appendix S1). It is therefore important when modelling dispersal in the Canary Islands to include the adjacent areas in the model and to identify in the phylogeny the closest non-Canarian relative of each Canarian group. This is often complicated by the fact that not all continental relatives are included in the published data sets (e.g. Moore *et al.*, 2002; Emerson & Oromí, 2005), or by the ambiguity and lack of support of phylogenetic relationships at basal nodes, which often make conclusions on monophyly and geographical ancestry tentative (Emerson, 2002). Extinction of continental relatives during post-Miocene aridification could also explain the apparent monophyly of Canarian lineages (Emerson, 2002). It seems, however, that in general, the majority of studied Canarian groups have their

closest relatives on the adjacent continents, North Africa or southern Europe (in particular the Iberian Peninsula) or in other Macaronesian islands such as Madeira, Cape Verde or the Azores (Carine *et al.*, 2004; see Appendix S1). Only a few groups show closer relationships to far-off areas, such as South Africa (Mort *et al.*, 2001).

Colonization patterns in the Canary Islands are usually more complex than the stepping-stone model characteristic of the Hawaiian Archipelago. Figure 5 attempts to summarize the main models of species diversification that have been discussed for the Canarian biota (see also Appendix S1). The first two models are variants of the stepping-stone model and can also be found in the Hawaiian biota (Roderick & Gillespie, 1998). Model I ('single species per island', Fig. 5a) assumes stepwise colonization with concomitant speciation, resulting in a single species on each island; proposed examples include the endemic lizard *Gallotia* (Thorpe *et al.*, 1993). Model II ('multiple species per island: within-island diversification', Fig. 5b) also starts with stepwise colonization with speciation but this is followed by multiple speciation events within each island, usually by adaptive radiation, resulting in each species having its closest relative on the same island; examples include the beetle genus *Pimelia* (Tenebrionidae) (Juan *et al.*, 1995). Model III (Fig. 5c) is characteristic of the Canarian Archipelago and postulates independent colonization events from the mainland or even back-colonization of continental areas, usually followed by within-island radiation; examples include the beetle genus *Calathus* (Carabidae) (Emerson *et al.*, 2000b). Finally, 'inter-island colonization of similar ecological zones' (Francisco-Ortega *et al.*, 2001) seems to be the primary mode of species diversification in Canarian plants (Model IV, Fig. 5d). In this uniquely Macaronesian pattern, independent lineages have radiated through the archipelago by colonizing similar habitats on different islands, i.e. each species has its closest relative in a different island but occupying a similar habitat; examples include the endemic genus *Bystropogon* (Trusty *et al.*, 2005). In other plant groups, species diversification has followed a combination of Model IV and Model II (i.e. within-island adaptive radiation: species have their closest relative in the same island); examples include the genera *Sonchus* (Kim *et al.*, 1996) and *Sideritis* (Barber *et al.*, 2000, 2007). In contrast, the stepping-stone colonization model (Model I) seems to be rare in plants (Appendix S1). Although not represented here, hybridization seems to be another important factor driving species diversification in Canarian plant lineages (Herben *et al.*, 2005; Barber *et al.*, 2007).

MATERIALS AND METHODS

Data set

Aligned molecular data matrices for Canarian organisms were obtained from the original authors or more often from web data bases such as ALIGN (EMBL) or TREEBASE; the latter was more useful because matrices could be directly exported as

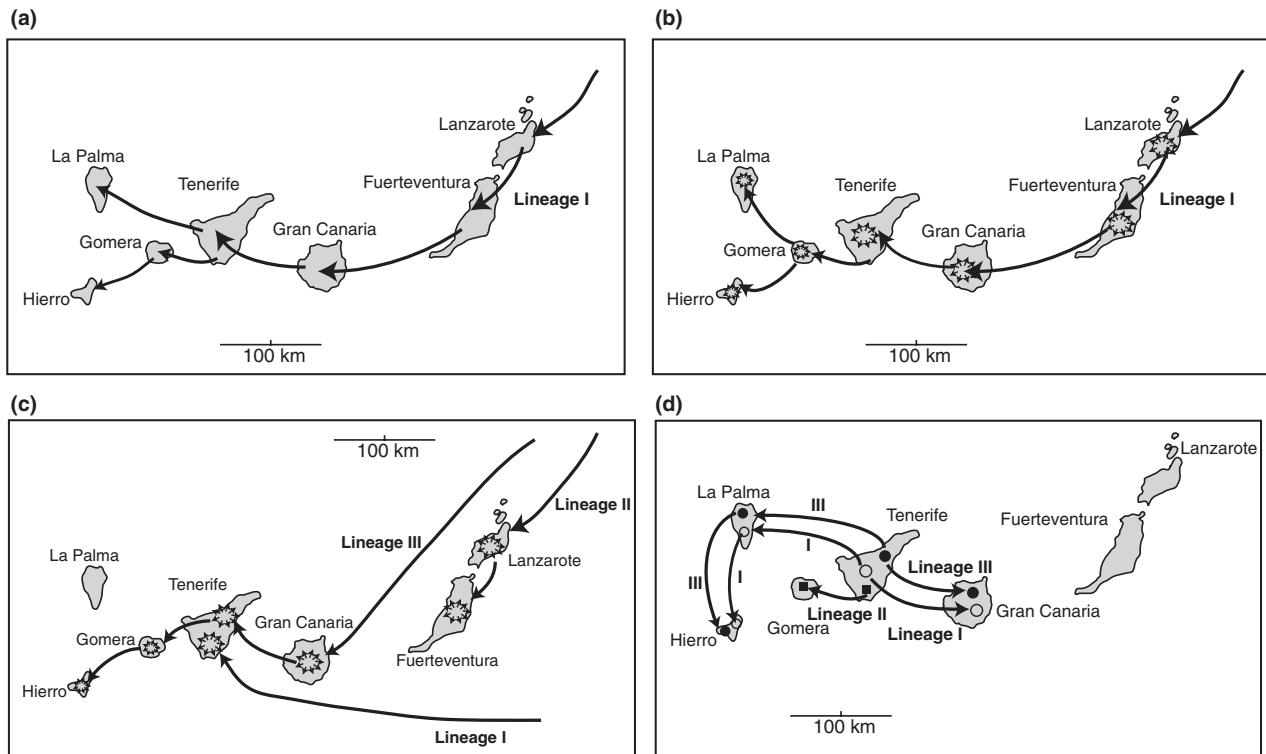


Figure 5 Some common modes of species diversification in Canarian animals and plants. (a) Model I: Stepwise colonization with concomitant speciation resulting in a single species on each island. (b) Model II: Stepwise colonization with speciation followed by within-island speciation; each species has its closest relative in the same island. (c) Model III: Multiple independent colonization events from the mainland (or even back-colonization events of continental areas), followed by within-island speciation. (d) Model IV: Inter-island colonization between similar ecological habitats; each species has its closest relative in a different island but occupying a similar habitat (geometric symbols). The last mode of speciation is common in plants.

Nexus files. Unfortunately, the format used in GenBank to store aligned matrices (PopSet) did not preserve, when exported, the original alignment (indels and deletions were removed), so we could not use any of the several Canarian data sets stored in this data base. Surprisingly, despite the rich phylogenetic literature on the Canary Island biota, very few original data sets were available. In total, we obtained 14 original aligned matrices, corresponding to 13 groups, six plant and seven invertebrate animal groups (Table 1). The final data set consisted of 954 taxa/individuals, although the number of putative ‘taxonomic entities’ (species/subspecies/variants) represented in the analysis was much smaller, 393 (Table 1). This was because many species were represented in the data set by several individuals: in some cases the species was widespread in several islands (e.g. Allan *et al.*, 2004; Table 1) but more often the monophyly of the species was being questioned (e.g. Meimberg *et al.*, 2006). Paraphyletic species seem to be common in island studies. Given the extent of morphological convergence that has been documented in islands, careful sampling across the geographical distribution of each species is considered crucial for assessing phylogenetic and colonization patterns in island groups (Emerson, 2002). We therefore preferred to use the complete original data sets for our analyses, even if there are sometimes multiple individuals per

species such as in the most phylogeography-oriented studies (e.g. Moya *et al.*, 2006). All included data sets had complete or near-complete (90%) sampling of Canarian endemics (Table 1).

Biogeographical areas

The Canary Islands were divided into three island-groups according to the geological period when the main volcanic activity responsible for the subaerial edifices took place (Ancochea *et al.*, 2006); these also coincide with the aftermath of the three main compressive phases at the Atlas Mountains (Anguita & Hernán, 2000). Thus, we considered an eastern island-group: Fuerteventura–Lanzarote (Oligocene–Early Miocene); a central island-group: Gran Canaria–Tenerife–La Gomera (Mid–Late Miocene); and a western island-group: La Palma–El Hierro (Pliocene–Pleistocene). We included a fourth ‘mainland-island’ group to account for the fact that many Canarian radiations are non-monophyletic (e.g. Allan *et al.*, 2004; Emerson *et al.*, 2000b). In most cases, the ‘mainland’ area was North Africa, the Iberian Peninsula or other Macaronesian islands (e.g. Madeira). However, a few groups included other areas such as tropical Africa (Percy & Cronk, 2002) or even Australia (Percy, 2003). The reason we

Table 1 List of published phylogenetic studies used in the analysis. 'No. species' refers to the number of taxonomic (morphological) entities (species/subspecies/variants) included in each study. 'No. taxa' refers to the number of individual sequences included in each study (see text).

Groups	Reference	Data (length)	No. species	No. taxa	Distribution [‡]			
					M	E	C	W
Plants								
<i>Sideritis</i> (Lamiaceae)	Barber <i>et al.</i> (2000)	Restriction sites (432)	34	54	6	2	37	9
<i>Tolpis</i> (Asteraceae)	Moore <i>et al.</i> (2002)	Restriction sites (224)	20	31	13	0	9	9
Genisteae (Fabaceae)	Percy & Cronk (2002)	ncDNA (637)	36	50	31	0	14	7*
<i>Lotus</i> (Fabaceae) [†]	Allan <i>et al.</i> (2004)	ncDNA (721)	52	52	36	2	11	4*
<i>Bystropogon</i> (Lamiaceae)	Trusty <i>et al.</i> (2005)	nc/cpDNA (1485)	15	20	6	0	8	6
<i>Micromeria</i> (Lamiaceae)	Meimberg <i>et al.</i> (2006)	cpDNA (2983)	15	28	4	2	17	8*
Animals								
<i>Pimelia</i> (Tenebrionidae)	Contreras-Díaz <i>et al.</i> (2003), Moya <i>et al.</i> (2006)	mtDNA (726, 197)	14	173	0	3	130	40
Arytaininae (Psylloidea)	Percy (2003)	mtDNA (981)	62	84	47	0	26	12*
<i>Calathus</i> (Carabidae)	Emerson <i>et al.</i> (2000b)	mtDNA (1611)	37	72	18	4	48	2
<i>Nesotes</i> (Tenebrionidae)	Rees <i>et al.</i> (2001)	mtDNA (675)	23	174	9	14	109	42
<i>Tarphius</i> (Colydiidae) [†]	Emerson & Oromí (2005); Emerson <i>et al.</i> (2000a) (<i>T. canariensis</i> -complex)	mtDNA (1041)	31	133	6	0	96	31
<i>Trechus</i> (Carabidae) [†]	Contreras-Díaz <i>et al.</i> (2007)	ncDNA (459)	22	51	11	0	28	13*
<i>Dolichoilulus</i> (Julidae, Myriapoda) [†]	I. Sanmartín (unpublished data)	mtDNA (2122)	32	32	3	2	25	2
Total			393	954	190	29	558	185

*Some taxa are widespread in more than one group of islands (usually between central and western).

[†]Data sets where there is significant undersampling of non-Canarian Macaronesian endemics.

[‡]M, mainland; E, east; C, central; W, west.

chose this extremely simplified model with only three island groups and one outside area is that our approach infers parameters of fairly complex substitution models from a single character, albeit coded for several groups, suggesting that we may run into problems with over-parameterization. Our results also seemed to indicate that the most complex of the examined models represented the extreme limit of the

resolving power of our data (see below). Larger data sets assembled in the future should allow the exploration of more complex and realistic island models. We want to point out, however, that there is nothing in theory or in our algorithmic implementation in MrBayes 4.0 that limits this type of analysis to models with four islands. Table 2 lists the island groups used here as well as some of their physical characteristics.

Table 2 Geographic units (island-groups) used in the analysis and some of their physical characteristics.

Island-groups	Area (km ²)	Minimum geographic distance to other 'island groups' (km)			
		Mainland	Eastern	Central	Western
'Mainland'	9,000,000		110 (NA–FU)	110 (NA–FU)	110 (NA–FU)
Eastern islands	2521			81 (FU–GC)	324 (FU–LP)
Central islands	3968				86 (GO–LP)
Western islands	1007				

Island-groups: 'Mainland' (Macaronesia and continental areas, mainly North Africa and Iberian Peninsula), 'Eastern islands' (Lanzarote and Fuerteventura), 'Central islands' (Gran Canaria, Tenerife and La Gomera), 'Western islands' (La Palma and El Hierro). 'Area' is the sum of the areas of all islands in each island group; for North Africa we have used as a proxy the area covered by the Saharan desert (which covers most of North Africa) because of the difficulties with adopting a more geopolitical definition. 'Minimum geographic distance to other island groups' is the present minimum geographic distance between the mainland and the nearest island in each island-group or between the two nearest islands in any two island-groups (source: Fernández-Palacios & Andersson, 1993). Island abbreviations: FU, Fuerteventura; GC, Gran Canaria; GO, Gomera; LP, La Palma; NA, North Africa.

Distribution data were obtained from the original articles and complemented with the help of online data bases such as Euro+Med Plantbase (<http://www.emplantbase.org/home.html>), Flora Europaea Database (rbg-web2.rbge.org.uk), Fauna Europaea (<http://www.fauaenr.org>), the Missouri Botanical Garden's VAST database (<http://mobot.mobot.org/W3T/Search/vast.html>), etc. Taxon sampling in our data set (Table 1) agrees well with current estimates of biological diversity among the three island groups, showing the highest diversity for the central islands and the lowest for the eastern islands (Izquierdo *et al.*, 2001). In contrast, non-Canarian Macaronesian endemics seem to be undersampled in some of our data sets (see Table 1) and continental relatives are probably undersampled in all our data sets.

Analysis

All models and Bayesian MCMC sampling algorithms were implemented in MrBayes 4.0 (the source code and executables used for this study are available by request from the first author; the official release of MrBayes 4.0 is expected in the summer of 2008; see <http://www.mrbayes.net> for up-to-date information). We used the GTR substitution model for all molecular partitions consisting of DNA sequence data, and the binary Equal-in model for all restriction site partitions. Six different biogeographical models were tested: JC, JC step (stepping stone variant), Equal-in, Equal-in step, GTR, and GTR step. MCMC sampling was run for 20 million generations in two independent analyses, without Metropolis coupling, except for the GTR model, where we used four runs of 30 million generations each. Each analysis was started from different, randomly chosen topologies, and the results were compared across runs to verify that the model likelihoods and samples of model parameters were similar. The chains were sampled every 100th generation and burn-in was set to 2 million generations in all cases. The software Tracer v. 2.1 (Rambaut & Drummond, 2005) in combination with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) was used to monitor the behaviour – performance of these analyses – in particular with regard to mixing, convergence among runs and effective sample size of parameter estimates (see Appendix S2). Bayes factors were used for model comparison. Model likelihoods for calculation of Bayes factors were estimated using the harmonic mean of the likelihood values sampled from the stationary phase of the MCMC run (Newton & Raftery, 1994).

RESULTS

The trace plots for the Bayesian MCMC analyses indicated stationarity and convergence to similar likelihood values among runs for all models except the JC step model, for which the likelihood values of one chain appeared to become fixed for a long period after the chosen burn-in, indicating slow mixing. Samples of all model parameters were compared using the Potential Scale Reduction Factor (PSRF), which is expected to approach 1.0 as independent runs converge. The

Table 3 Bayes Factor comparison of different models of island evolution. Models have been ordered according to increasing model likelihood (harmonic mean). A difference larger than five between two model likelihoods indicates 'very strong support for the model with the highest likelihood' (Kass & Raftery, 1995).

Island model	Ln model likelihood
JC step	-101704.09
Equal-in	-101667.87
JC	-101649.92
Equal-in step	-101628.31
GTR	-101624.19
GTR step	-101618.94
	*(-101642.9)

*Model likelihood for the 'long analysis' (30 million generations, four runs); see text.

PSRF was 1.02 or lower for almost all model parameters except some GTR rate (exchangeability) parameters for small data sets or particularly conserved gene regions, where these values were sometimes difficult to estimate accurately. The exception to this rule was the JC step model, where the mixing problems in one chain caused significant heterogeneity between the two runs. Since the JC step model was clearly not the best for our data, we did not pursue the problem further by running longer Markov chains or by pooling the results from more runs. Tracer plots showed good mixing and large effective sample sizes (> 300 for each run) for all biogeographical parameter estimates in the GTR model (Appendix S2).

The negative log of the model likelihoods for the different island models, estimated using the harmonic mean method, ranged from -101,704 to -101,618 (Table 3). The JC step model was the worst, followed by the Equal-in model and the JC model. The best models were (in order of increasing likelihood) the Equal-in step model, the GTR model, and the GTR step model. However, the variance in estimated model likelihoods between runs was large compared with the differences between the models, and the values for different models often overlapped. For instance, of the four runs for the GTR model, three had estimated model likelihoods between the two values for the GTR step model – the arithmetic mean of the model likelihoods was actually higher for the GTR model (-101364.89) than for the GTR step model (-101380.92) – while one of the estimated model likelihoods for the Equal-in step model was better than the worst estimated value for the GTR model. A longer analysis of the GTR step model (30 million generations and four independent runs as in the GTR model) gave identical results to the shorter analysis, except that the model likelihood was this time lower than that of the GTR model (Table 3). Considering all this, the Bayes factor comparison among models must be regarded as tentative at best. Possibly, by identifying gaps with respect to the log likelihoods, one can take them to indicate that there are three different groups of models: (1) the

Table 4 Bayesian estimates (mean, standard deviation and 95% credibility interval of the posterior probability distribution) of the parameters of the three best biogeographic island models for our data set.

Model	Mean	Standard deviation	95% credibility interval		PSRF
			Lower	Upper	
EQUAL-IN STEP					
π_M	0.656	0.055	0.542	0.751	1.001
π_E	0.021	0.005	0.012	0.034	1.000
π_C	0.249	0.054	0.157	0.361	1.002
π_W	0.074	0.016	0.046	0.110	1.000
GTR					
π_M	0.633	0.096	0.413	0.785	1.006
π_E	0.012	0.006	0.004	0.026	1.006
π_C	0.208	0.041	0.138	0.299	1.001
π_W	0.147	0.076	0.050	0.343	1.006
r_{ME}	<1.0E-6	<1.0E-6	<1.0E-6	<1.0E-6	1.000
r_{MC}	0.026	0.013	0.010	0.058	1.009
r_{MW}	<1.0E-6	<1.0E-6	<1.0E-6	<1.0E-6	1.000
r_{EC}	0.788	0.096	0.562	0.921	1.005
r_{EW}	<1.0E-6	<1.0E-6	<1.0E-6	<1.0E-6	1.000
r_{CW}	0.187	0.093	0.058	0.407	1.004
GTR STEP					
π_M	0.166	0.003	0.034	0.410	1.023
π_E	0.007	0.047	0.003	0.012	1.006
π_C	0.167	0.098	0.094	0.277	1.007
π_W	0.661	0.131	0.418	0.800	1.013
r_{ME}	0.353	0.131	0.147	0.660	1.022
r_{EC}	0.635	0.007	0.328	0.839	1.021
r_{CW}	0.012	0.055	0.004	0.027	1.006

π_i , island carrying capacity; r_{ij} , relative dispersal rate; M, mainland; E, Eastern islands; C, Central islands; W, Western islands; PRSF, Potential scale reduction factor. This parameter is used for convergence diagnostics; a value close to 1.0 indicates a good sampling from the posterior probability distribution of the parameter.

Equal-in step model, the GTR model, and the GTR step model, fitting the data best; (2) the Equal-in and JC model with intermediate fit; (3) and the JC step model with the poorest fit. Note that Bayesian model comparisons do not necessarily favour parameter-rich models. Thus, it is quite possible that the true model likelihood is higher for a stepping-stone model than for its corresponding ‘full’ model. In fact, the stepping-stone model is expected to have a higher model likelihood when dispersals are exclusively between adjacent islands because the more general model has to spread its prior probability over more parameters, lowering its marginal likelihood.

The estimated biogeographical parameters in the GTR model and the Equal-in step models agree well with each other and with external evidence regarding Canary Island biogeography. In both models, the estimated relative carrying capacity is large for the mainland (Table 4; Figs 6 & 7). Of the islands, the central group has the largest carrying capacity followed by the western islands, with the carrying capacity of the eastern islands being much smaller than that of the others.

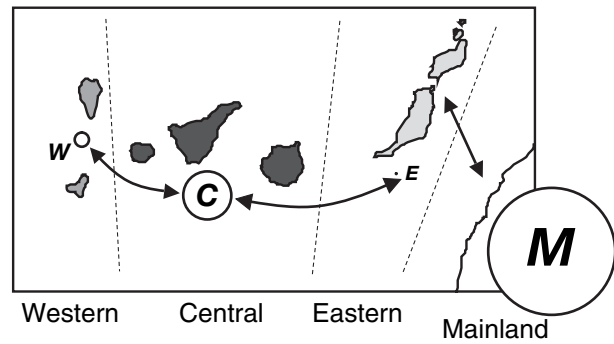


Figure 6 Estimated relative carrying capacities for the Canary Islands based on a data set of 13 Canarian plant and animal phylogenies and using the Equal-in step Bayesian island model. The Canary Islands were divided into three island-groups (‘Eastern’, Lanzarote and Fuerteventura; ‘Central’, Gran Canaria, Tenerife and La Gomera; and ‘Western’, La Palma and El Hierro); ‘Mainland’ represents non-Canarian distributions (continental areas and Macaronesia). The size of the circles is roughly proportional to the estimated relative carrying capacity for each island-group (see Table 4). The arrow width represents the relative dispersal rate, here 1/3 because the dispersal rate is the same for all island groups and dispersal is only allowed between adjacent island groups (‘step model’, see Fig. 2e).

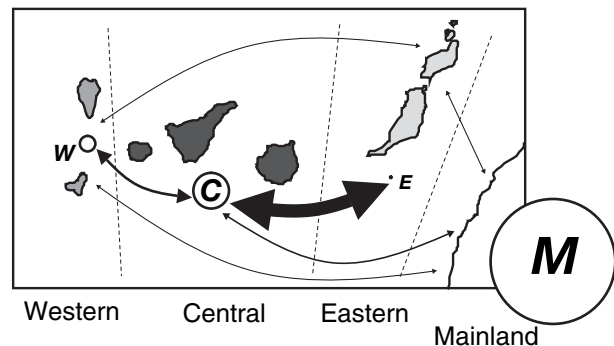


Figure 7 Relative carrying capacities and dispersal rates estimated for the GTR Bayesian island model based on a data set of 13 Canarian plant and animal phylogenies (see Fig. 6 for further explanation).

In the Equal-in step model, the dispersal rate is of course constrained to be the same between the mainland and the eastern islands, the eastern and central islands, and the central and western islands, with all other instantaneous dispersal rates being zero (Fig. 6). In contrast, the GTR model accommodates variation among the rates, but the estimated values agree with the step model in that most of the exchange is occurring between two of the predicted stepping stones: (1) the eastern and central islands; and (2) the central and western islands (Fig. 7). However, the rate of exchange with the mainland is very low in comparison, with only the dispersal rate between the central islands and the mainland being larger than 1.0E-6. The instantaneous rate of exchange between the western and eastern islands is also less than 1.0E-6.

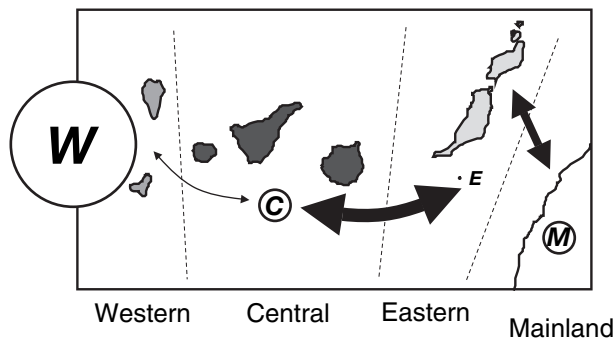


Figure 8 Relative carrying capacities and dispersal rates estimated for the GTR step Bayesian island model based on a data set of 13 Canarian plant and animal phylogenies (see Fig. 6 for further explanation). In this model dispersal is only allowed between adjacent island-groups.

The parameter estimates under the GTR step model imply a very different scenario (Table 4, Fig. 8). In this scenario, the relative carrying capacity is largest for the western islands (0.66), followed by the central islands (0.17) and the mainland (0.17). The relative carrying capacity of the eastern islands is low (0.007), similar to the results for the Equal-in step and GTR models. The dispersal rate is high between the eastern and central islands (0.64) and between the mainland and the eastern islands (0.35), while it is very low between the central and western islands (0.01). The GTR and GTR step scenarios are not as different as they may first seem, because the same number of predicted dispersal events can result from either a high carrying capacity and a low dispersal rate or a low carrying capacity and a high dispersal rate. However, we suspect that the estimated parameters under the GTR step model represent a spurious result. The effective sample size for several biogeographical parameter estimates in this model was low (< 200 , Appendix S2), possibly because of a correlation between the estimated carrying capacities and the dispersal rates (Appendix S2). Thus, there are difficulties to disentangle these two parameters in the GTR step model and it is at least possible that values close to the unconstrained GTR model are underrepresented in our samples. More importantly, however, we note that the carrying capacities of the islands in the GTR and Equal-in step models fit better with the sampling frequencies (Table 1) than do the carrying capacities of the GTR step model. These are all equilibrium models, and if they fit the data well we should expect a reasonable fit between the carrying capacities and the sampling frequencies (see below). Presumably, untangling dispersal rates from carrying capacities is difficult with our relatively modest data set and can only be done appropriately when permitting all dispersal paths between island groups and the mainland under the GTR model. The GTR step model forces dispersal events between the mainland and the central islands to go through the 'intermediate state' of the eastern islands (Fig. 8) but this is unsupported by the data under simple parsimony optimization and the unconstrained (GTR) dispersal model shows extremely

low probability of dispersal ($< 1.0E-6$) between the mainland and the eastern islands (Table 4). In the following discussion, we will therefore focus entirely on the results of the GTR and Equal-in step models.

Because the estimates of island model parameters are based on only one character per studied organism group, one might expect a large variance. However, some of the posterior distributions are actually reasonably narrow (Table 4, Appendix S2). For instance, the relative carrying capacity of the central islands in the GTR model is 0.21 ± 0.04 , with a 95% credibility interval of (0.14, 0.30). The carrying capacity of the western islands is 0.15 ± 0.08 (0.05, 0.34) and of the eastern islands is 0.01 ± 0.006 (0.004, 0.03). The two highest exchange rates in the GTR model are between the eastern and central islands, being 0.79 ± 0.10 (0.56, 0.92) of the total, and between the central and western islands, being 0.19 ± 0.09 (0.06, 0.41). Similar variances and credibility intervals are obtained with the Equal-in step model (Table 4). The GTR scatterplots (Appendix S2) show no apparent correlation between the highest dispersal rates (eastern-central and central-western) and the relative carrying capacities, indicating that at least for this model we can tease apart the two.

In comparing the carrying capacities and dispersal rates with island areas and inter-island distances (Table 2), we focused on the GTR model. The former are in rough agreement with the size of the unit areas in that the relative carrying capacity of the mainland was inferred to be more than three times that of the largest island-group carrying capacity (Table 4). However, for the island-groups there does not seem to be a good correlation between the estimated carrying capacities and the island size [the small sample size ($n = 3$) did not allow statistical testing of the significance of the correlation]. For example, the eastern islands occupy an area of 2521 km² (Table 2) but have a lower carrying capacity (0.01) than the much smaller western island-group (1007 km², 0.15; Tables 2 & 4). Instead, the estimated carrying capacities agreed better with the sampling density in our analysis (i.e. number of taxa included in each island-group), in which the western islands are represented by six times more taxa than the eastern islands (Table 1).

In contrast, there seems to be a reasonably strong correlation between the relative dispersal rates in the GTR model and the minimum inter-island distances (Spearman's $R = -0.82$, $P = 0.04$, $n = 6$). For example, the two highest exchange rates were between two sets of nearest neighbour island-groups: the eastern and central islands, and the central and western islands, which are separated by less than 90 km, whereas dispersal between the eastern islands and the far-off western islands (324 km, Table 2) was lower than $1.0E-6$ (Table 4). On the other hand, the exchange of lineages with the mainland occurs at a much lower rate than expected by the geographic distance (it is only 110 km between Fuerteventura and North Africa but more than 300 km between Fuerteventura and the western islands). It is worth noting, however, that some of the colonization events from the mainland, or back-colonizations to the mainland, involve other areas than North Africa (e.g.

Iberian Peninsula and Macaronesia) and thus occur over much longer distances.

DISCUSSION

Until recently, studies of island biogeography have been limited to describing patterns of colonization of individual groups using phylogenetic data and parsimony-based approaches (e.g. Goodson *et al.*, 2006). Only a few studies have focused on extracting generalities from individual patterns and on using these to analyse the processes responsible for island evolution, such as the relative role played by inter-island colonization vs. within-island diversification (Funk & Wagner, 1995; Emerson, 2002). So far, however, there have been no serious attempts to formulate stochastic models that describe the evolution of an island biota from a phylogenetic perspective. In general, historical, phylogeny-based island biogeography remains in a largely 'descriptive' stage, in which each taxon is treated as a special case. This contrasts with the ecological perspective on island biogeography, where MacArthur & Wilson's (1967) Dynamic Theory of Island Biogeography and later modifications (e.g. Rosenzweig, 1995; Whittaker, 1998; Heaney, 2000; Lomolino, 2000; and recently Emerson & Koln, 2005) have played an integral part in studies of the evolution of island biotas and have been tested across multiple groups and island ecosystems (e.g. Schoener & Schoener, 1983; Azera *et al.*, 2007). Similarly, it has become clear that we need a more theoretical, model-based approach to island historical biogeography, one which allows us to make predictions that can later be tested using empirical data, for example, the putative correlation between carrying capacity and island size. In this sense, the Bayesian stochastic island models described here can be considered as a first step in this direction.

Canary Island biogeography

Despite its limited scope (we use over-simplified models and only a small proportion of Canarian phylogenies are represented in our analysis), the results presented here suggest that the Canary Islands fit to some extent the classical stepping-stone model characteristic of hotspot archipelagos such as the Hawaiian Islands, in that the main exchange of organismal lineages is occurring between adjacent island groups, i.e. between the eastern and central islands and the central and western islands (Fig. 7). This is also evident in the good fit of the data to the step models, the step versions of the Equal-in and GTR models being among the three best models in the Bayes Factor model comparison (Table 3). In contrast, the low colonization rate between the mainland and the eastern islands in the GTR model does not fit the stepping-stone scenario well but it is possible that this is due to significant recent extinction of lineages in the eastern islands.

An alternative explanation for the dispersal patterns is that the central islands are acting as 'centres of diversification and dispersal' within the archipelago, as has been suggested by other

authors (Francisco-Ortega *et al.*, 2002; Allan *et al.*, 2004). For example, a pattern often described in Canarian biogeographical studies is stepwise dispersal from the large, central islands in the east (Tenerife and Gran Canaria) to the smallest islands of La Palma and El Hierro in the west (e.g. Thorpe *et al.*, 1993; Rees *et al.*, 2001; Percy & Cronk, 2002; Allan *et al.*, 2004; see Appendix S1). The central islands also show the highest carrying capacity in our equilibrium dispersal models, supporting their role as diversification centres, and they show the highest rate of exchange with the mainland (Table 4). Distinguishing this type of dispersal scenario – dispersal eastward and westward from the central islands – from the classic east-to-west stepwise colonization model would require a much larger data set with more dispersal events and a finer division of the islands than the one used here. It also requires the development of time-irreversible dispersal models in which dispersal rates are allowed to be asymmetric between the islands (in preparation). These models are more parameter-rich than the time-reversible models examined here, suggesting that a larger data set may be needed for these analyses.

The highest dispersal rate in our analysis is found between the central and the eastern islands. This may seem surprising because Lanzarote and Fuerteventura are the least represented islands in our data set (Table 1) and in general among published phylogenies: many island radiations have no members in these islands (e.g. *Tolpis*, Moore *et al.*, 2002; Genistea, Percy & Cronk, 2002; *Tarphius*, Emerson & Oromí, 2005). Notice, however, that the dispersal rates estimated by our model are *relative* dispersal rates, that is, they are the rate of dispersal *per* island inhabitant. The absolute number of dispersals between Lanzarote and Fuerteventura and the central islands is probably small but, in relation to their carrying capacities, the dispersal rate between the eastern and the central islands has been higher than between the richer western and central islands.

The low carrying capacity estimated here for Lanzarote and Fuerteventura is also at odds with their relatively large size and older age (Table 2; Fig. 4). However, it agrees well with the lower species richness recorded in these islands compared with that of the more western islands (Fernández-Palacios & Andersson, 1993; Izquierdo *et al.*, 2001). This difference has often been explained in terms of ecological diversity: Lanzarote and Fuerteventura are drier and more flat than the other islands and they lack the high elevations exposed to the humid northeasterly trade winds that have engendered a wide range of ecological diversity in the higher and more western islands. An alternative explanation is that this poverty is the result of historical extinction events that may have partly wiped out the biota of these islands (Juan *et al.*, 1998). The volcanoes in these two islands are still active and Lanzarote has experienced at least one major volcanic eruption in historical times (the eruption of Timanfaya in 1730), whereas the last volcanic activity in Fuerteventura was probably about 35,000 years ago (Coello *et al.*, 1992). The recent volcanic activity could have created empty ecological niches, which could have been filled by colonizers from the central islands. This appears to have happened in several groups (e.g. *Sideritis*, Barber *et al.*, 2000;

Micromeria, Meimberg *et al.*, 2006). In either case, it should be noted that Fuerteventura and Lanzarote contain some areas that are very rich in endemics (e.g. Jandía in Fuerteventura, Juan *et al.*, 1998) and that some groups do have their highest diversity in these islands (Izquierdo *et al.*, 2001).

The low dispersal rates we found between the mainland and the Canary islands suggest that inter-island dispersal has been more important than multiple independent colonizations from the mainland in promoting diversification in the Canary Islands, in agreement with previous studies (Francisco-Ortega *et al.*, 2002; Carine *et al.*, 2004). Some additional lines of evidence also support our conclusion. For example, despite the fact that many Canary Island plant assemblages are paraphyletic (Appendix S1), most Macaronesian assemblages are monophyletic, i.e. the result of a 'single introduction event' (e.g. *Bystropogon*, Trusty *et al.*, 2005; *Sideritis*, Barber *et al.*, 2000; *Tolpis*, Moore *et al.*, 2002). An exception is *Lotus* (Allan *et al.*, 2004).

Geographical isolation alone cannot explain the unexpected low number of mainland colonizations because the Canary Islands are separated by only 100 km from coastal Africa. Interspecific competition by niche preemption (Silvertown, 2004) or extensive hybridization masking later colonization events (Herben *et al.*, 2005) have to be invoked instead. Under-sampling of continental relatives and mainland extinctions following increased post-Miocene aridification are other alternative explanations (Emerson, 2002). Mainland extinction is certainly a possibility with respect to back colonizations. However, in a reversible model this should be indicated by a lower than expected carrying capacity for the mainland and not by a lower exchangeability rate. In conclusion, it must be noted that our study represents just a very small percentage of published Canarian phylogenies. In addition, low nodal support in some trees makes conclusions on monophyly of Canarian groups and other relationships tenuous (see Appendix S1). A much larger data set would be needed to make strong general inferences on the biogeographical history of the Canarian biota. For example, irreversible dispersal models have twice as many parameters as the GTR model, suggesting the need for at least twice the number of taxa studied here. A large data set would also be needed to analyse biotic relationships between the Canary Islands and adjacent regions in more detail (e.g. Macaronesia, Southern Europe) or to compare colonization patterns among different types of organisms, for example plants versus animals. Given the large number of phylogenies already published (Appendix S1), this should be feasible in the near future.

A model-based approach to biogeography

Model-based approaches to historical biogeography, such as event-based parsimony or likelihood methods, have been criticized in the literature, mainly by proponents of phylogenetic biogeography (Brooks *et al.*, 2001; Van Veller *et al.*, 2003; Wojcicki & Brooks, 2005), for being methods that search for simple explanations ('simplicity biogeography', Brooks, 2005).

By constraining the data to fit a simple evolutionary model, they over-simplify the data and potentially ignore its complexity (Van Veller *et al.*, 2003; Wojcicki & Brooks, 2005; Brooks, 2005). We see our models, however, not as constraints but as a way of estimating one's confidence in alternative hypotheses tested on the data (Pagel *et al.*, 2004). In Bayesian approaches, the observed data are treated as fixed and we allow the hypothesis on those data (the model parameters) to vary and let the shape of the posterior distribution tell us in which hypotheses to have more confidence (Pagel *et al.*, 2004). Bayesian model comparison also provides a way to statistically address the robustness of support for alternative evolutionary models (Holder & Lewis, 2003; Ronquist, 2004). For example, Bayes factors can be used to compare alternative island models for a particular group and then use the selected model to reconstruct ancestral distributions on the group's phylogeny. However, the most important advantage of Bayesian approaches over parsimony methods, such as those used in phylogenetic biogeography, is their ability to account for phylogenetic and parameter uncertainty. Instead of using the best tree and the most optimal reconstruction of ancestral areas and biogeographical events for each group, we estimate probabilities that are integrated over all alternative phylogenies and all alternative hypotheses of the evolutionary processes that generated the data (Pagel *et al.*, 2004). Bayesian MCMC methods are especially powerful for this type of analysis. Since they allow calculating the marginal probabilities of parameters instead of point estimates, they are more robust to over-parameterization – low ratio between data and number of parameters – than maximum likelihood methods (Holder & Lewis, 2003; Ronquist, 2004). This makes Bayesian analysis especially appropriate for dealing with the complex, parameter-rich models described here.

In a more philosophical sense, the main appeal of model-based approaches lies precisely in their simplicity. They allow us to formulate clear, testable predictions that can later be examined across a broad range of taxonomic groups and geographic regions (Lomolino *et al.*, 2005). Without this ability to generalize and statistically test across groups, we are left with case-by-case (historically contingent) explanations (e.g. Brooks, 2005).

All models start in a simplified form and are later refined by subsequent research (Brown & Lomolino, 2000). The Island Equilibrium Theory of MacArthur & Wilson was criticized for its simplicity but it spurred a series of new empirical studies that sought to corroborate or refute the model, which led in turn to subsequent modification and improvement of the model (Lomolino, 2000). DNA substitution models also evolved over time from the simple JC model to more complex models such as the GTR model. Although our Bayesian Island models are admittedly very simple, we see them as a foundation to which new variables or biological parameters (e.g. within-island speciation and catastrophic extinction) should be added. Future work, for example, could include the development of dynamic island models, in which the size of the islands, their carrying capacities, or the dispersal rates between adjacent islands were allowed to vary across time.

Another exciting development would be to explicitly model speciation and extinction using birth–death models, while simultaneously considering inter-island dispersal events. This should allow us to directly examine the proposed diversification models for the Canary Islands (Fig. 5).

Bayesian analyses based on dynamic island models could also help in conservation decisions. For example, applied to a large data set of dated Canarian phylogenies, they could help to distinguish between the two different scenarios for the low species diversity of Lanzarote and Fuerteventura described above. If their poverty of biological diversity is due to limited habitat complexity, we should expect to observe a low carrying capacity and lineages of varying age. On the contrary, if the cause was the extinction of a large part of their flora and fauna due to recent volcanic activity, we would expect a higher carrying capacity, and a mix of a few old lineages with a flurry of recent colonizers. In the former case, we would be dealing with an endangered, ‘relict’ biota, which should be protected against extinction. In the latter case, the biota is composed of more opportunistic elements, which will do well without human intervention. This is obviously somewhat simplistic because Lanzarote and Fuerteventura do contain areas that are both species-rich and old (see above) but it does show that these kinds of studies could have important conservation implications.

The Bayesian island-models described here are not necessarily limited to island systems but may also be applied to other dispersal-based scenarios. For example, numerous studies have shown that mountain biotas behave like insular systems in terms of species–area and species–isolation relationships, endemism, and the influence of disturbance and other long-term processes (Lomolino *et al.*, 1989). Our dispersal-based models are also well suited to marine biogeography, in which dispersal is the main explanation for biogeographical patterns (Briggs, 2006). Finally, dynamic island models could also be used to analyse ‘reticulate biogeographical scenarios’ like those postulated for the Northern Hemisphere (Sanmartín *et al.*, 2001; Donoghue & Smith, 2004; Ree *et al.*, 2005). For example, we could assume a few distinct time periods, of predetermined or estimated time duration, and allow different transition rates between these time periods to reflect the changing continental configurations.

In summary, although much work remains to be done, we believe that the Bayesian statistical approach to island biogeography described here could become a versatile additional tool in the toolbox of historical biogeographers.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of published phylogenies of Canarian radiations and some of their biogeographical characteristics (e.g. main mode of species diversification).

Appendix S2 Tracer plots for the GTR and GTR step island analyses.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01885.x> (This link will take you to the article abstract).

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