

Current Biology

Equilibrium Bird Species Diversity in Atlantic Islands

Highlights

- The idea that species diversity on islands is at equilibrium is controversial
- We reconstruct temporal diversity dynamics of birds in the islands of Macaronesia
- Bird diversity has achieved and maintained equilibrium state for long periods
- Supports MacArthur and Wilson's island biogeography theory, which turns 50 this year

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In Brief

50 years ago, MacArthur and Wilson proposed the influential idea that species diversity on islands is at equilibrium. Using phylogenies and modeling, Valente et al. show that four Atlantic archipelagos (Azores, Canary Islands, Cape Verde, and Madeira) have achieved and maintained an equilibrium number of bird species over millions of years.



Equilibrium Bird Species Diversity in Atlantic Islands

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SUMMARY

Half a century ago, MacArthur and Wilson proposed that the number of species on islands tends toward a dynamic equilibrium diversity around which species richness fluctuates [1]. The current prevailing view in island biogeography accepts the fundamentals of MacArthur and Wilson's theory [2] but questions whether their prediction of equilibrium can be fulfilled over evolutionary time-scales, given the unpredictable and ever-changing nature of island geological and biotic features [3–7]. Here we conduct a complete molecular phylogenetic survey of the terrestrial bird species from four oceanic archipelagos that make up the diverse Macaronesian bioregion—the Azores, the Canary Islands, Cape Verde, and Madeira [8, 9]. We estimate the times at which birds colonized and speciated in the four archipelagos, including many previously unsampled endemic and non-endemic taxa and their closest continental relatives. We develop and fit a new multi-archipelago dynamic stochastic model to these data, explicitly incorporating information from 91 taxa, both extant and extinct. Remarkably, we find that all four archipelagos have independently achieved and maintained a dynamic equilibrium over millions of years. Biogeographical rates are homogeneous across archipelagos, except for the Canary Islands, which exhibit higher speciation and colonization. Our finding that the avian communities of the four Macaronesian archipelagos display an equilibrium diversity pattern indicates that a diversity plateau may be rapidly achieved on islands where rates of in situ radiation are low and extinction is high. This study reveals that equilibrium processes may be more prevalent than recently proposed, supporting MacArthur and Wilson's 50-year-old theory.

RESULTS

The biogeographical region of Macaronesia [8], located in the Northeast Atlantic Ocean, comprises four main volcanic island chains—the Azores, Madeira, the Canary Islands, and Cape Verde (Figure 1; Table 1). In our analyses, we focus on bird species whose ecology is broadly comparable to that of a typical songbird, and therefore we exclude birds of prey and rails. We also exclude marine, aquatic, migratory, and introduced species. To estimate times of colonization and speciation of Macaronesian birds, we reconstructed and dated phylogenies covering all known colonization events of native terrestrial birds from our focal group in the islands—including many that had never before been studied (Table S1). We identified a total of 91 independent colonization events (Table S2): 15 on the Azores, 46 on the Canary Islands, ten on Cape Verde, 19 on Madeira, and one on the Selvagens (a small archipelago that we do not include in the main analyses; see STAR Methods). The colonization events comprise 63 species, of which 29 are endemic to a single archipelago, two are endemic to Macaronesia (Berthelot's pipit and the island canary), and 32 are non-endemic (also occur in the continent). We identified only two occasions of cladogenetic events that have extant descendants on the islands, both within the Canary Islands: the blue tits (*Cyanistes*) group of the central islands and one within the blue chaffinches (*Fringilla*; Table S3). The times of colonization of the archipelagos obtained in our Bayesian dating analyses are shown in Figure 1 and Table S2. The average age of colonization of Macaronesia is 0.97 (± 0.15) mega-annum (Ma) (Figure S1; Table 1). Endemic species are significantly older (2.71 [± 0.54] Ma) than non-endemic species (mean 0.54 [± 0.07] Ma) ($p < 0.001$). An analysis of variance revealed no significant differences in colonization times between island chains for both endemic ($p = 0.79$) and non-endemic ($p = 0.69$) species.

To estimate rates of colonization, extinction, cladogenesis, and anagenesis we used DAISIE (dynamic assembly of islands through speciation, immigration, and extinction), an island biogeography process-based model [5]. DAISIE estimates rates of island biota assembly—including extinction—based on phylogenetic information, with high precision [5, 11]. Here we develop a new multi-archipelago version of DAISIE that allows us to test whether the different island groups are governed by the same

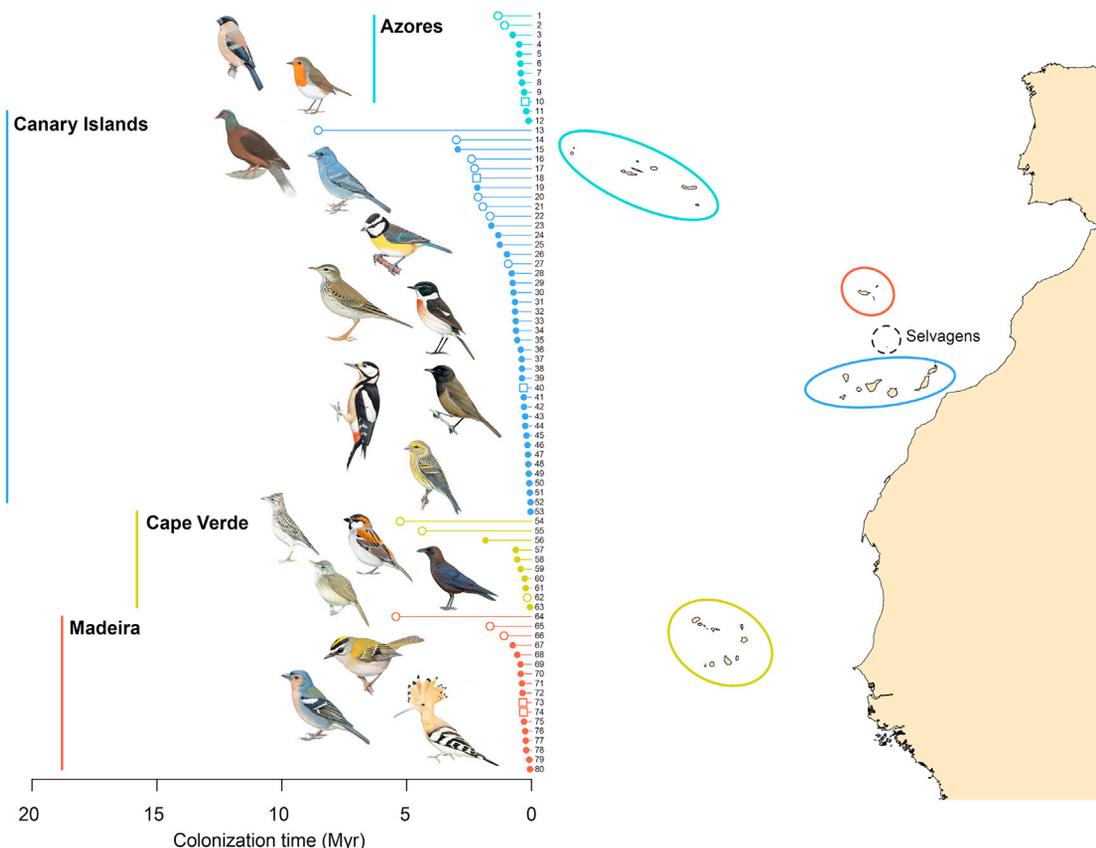


Figure 1. Colonization Times of Macaronesian Bird Taxa and Map of Macaronesia

The vertical lines show the maximum geological ages of the archipelagos. Filled circles, non-endemic species; unfilled circles, endemic species; unfilled squares, Macaronesian endemic. Numbers next to the colonization events correspond to codes in Table S2. 95% confidence intervals for the estimates are given in Table S2. Bird drawings were used with permission from [10]. See also Table S2.

macroevolutionary process. We treat each of the archipelagos as an “island,” because the importance of the archipelago as the relevant unit in island biogeography is increasingly recognized [12, 13] and birds are vagile taxa that disperse relatively frequently between islands of the same archipelago [14].

Using the Bayesian information criterion (BIC), the preferred multi-archipelago DAISIE model is M17, a model with six parameters (Table S4 and S5; Figure 2). Two models that are very similar to M17—M15 and M24 (Table S5)—also carry a large proportion of BIC weight and cannot be ruled out (see STAR Methods). According to the M17 model, all Macaronesian islands share the same macroevolutionary rates for extinction—1.05 events per lineage per Ma—and anagenesis—0.51 events per lineage per Ma (Table S5). Further, in the Azores, Cape Verde, and Madeira, cladogenesis is absent and colonization rate is 0.05 events per mainland lineage per Ma (equivalent to 15 events per Ma given a mainland pool size of 300 species). The exception is the Canary Islands, which have a different (non-zero) rate of cladogenesis (0.13 events per lineage per Ma) and a higher rate of colonization (0.15 colonization events per mainland lineage per Ma, equivalent to 45 colonization events per Ma). The M17 model is diversity independent (there are no negative feedbacks of diversity on rates of colonization and cladogenesis). A bootstrap analysis using multiple simulated datasets revealed

that the model performs well, recovering correct parameter values with little bias (Figure S2).

The preferred model for all archipelagos is an equilibrium model because the rate of extinction exceeds the rate of cladogenesis [11]. Simulations of total species diversity through time reveal a general pattern of the number of species in the four Macaronesian archipelagos rapidly reaching an asymptotic phase (Figure 3). The four island chains are thus currently at equilibrium, and this state has been maintained over millions of years.

DISCUSSION

Our molecular phylogenetic dating analysis of the terrestrial avian community of Macaronesia covering all known extant and extinct colonization events provides a valuable temporal context for understanding the biogeographical and diversification history of the islands [9, 15]. Fitting of the new multi-archipelago DAISIE models to these phylogenetic data revealed striking homogeneity in rates of bird species accumulation in the Macaronesian bioregion (Figure 2), with diversity resulting from essentially the same biogeographical process. Indeed, three of the archipelagos (the Azores, Cape Verde, and Madeira) are governed by the same macroevolutionary dynamics model (Table S5). The Canary Islands form the only exception: although they

Table 1. Macaronesia Archipelago Characteristics and Mean Colonization Times

| | Archipelago | | | | |
|----------------------------|-----------------|-------------|----------------|-------------|-------------|
| | Macaronesia | Azores | Canary Islands | Cape Verde | Madeira |
| Species (total) | 63 | 15 | 49 | 10 | 19 |
| Endemic species (total) | 31 | 5 | 16 | 3 | 5 |
| Colonizations (total) | 91 | 15 | 46 | 10 | 19 |
| Species (extant) | 50 | 12 | 42 | 10 | 16 |
| Endemic species (extant) | 21 | 2 | 11 | 3 | 3 |
| Colonizations (extant) | 78 | 12 | 39 | 10 | 16 |
| Known extinct species | 13 | 3 | 7 | 0 | 3 |
| Radiations | 2 | 0 | 2 | 0 | 0 |
| Island age (Ma) | 29 ^a | 6.3 | 21 | 15.8 | 18.8 |
| Distance to continent (km) | 96 | 1365 | 96 | 568 | 633 |
| Colonization Time (Ma) | | | | | |
| All taxa | 0.97 (0.15) | 0.52 (0.11) | 1.09 (0.23) | 1.38 (0.6) | 0.76 (0.31) |
| Endemic | 2.71 (0.54) | 1.21 (0.13) | 2.86 (0.84) | 3.27 (1.57) | 2.73 (1.36) |
| Non-endemic | 0.54 (0.07) | 0.39 (0.06) | 0.66 (0.12) | 0.58 (0.22) | 0.34 (0.05) |

Times were obtained in the divergence dating analyses (the SE is indicated in parentheses).

^aAge of the Selvagens archipelago.

share the same rate of extinction and anagenesis as all other island chains (Figure 2), they exhibit substantially higher rates of cladogenesis and colonization. In addition, whereas in the other three archipelagos the preferred model was one with no cladogenesis, the phylogenetic data of Canarian birds was best fit by a model in which endemic diversity is generated both through cladogenesis and anagenesis. The reason that in situ radiation seems to take place in the Canary Islands while being absent in the other archipelagos may be linked to the fact that the Canaries have by far the largest area of all Macaronesian archipelagos [9], which may have facilitated allopatry, a key factor in triggering avian radiations [16]. Indeed, the archipelago has been the setting for multiple radiations across other taxonomic groups [17, 18].

The results regarding the rates of colonization and extinction are striking. While the higher rate of colonization of the Canaries may be expected given their proximity to the African continent (only 96 km), the homogeneity in rates that we found for the other three archipelagos is unexpected. A decline of immigration rates with increasing distance from a source pool is a standard feature of most island biogeography models [4, 12, 19]. However, we find no support for archipelagos with very different levels of isolation (Table 1) having been colonized at different rates by birds. It appears that for a vagile group such as birds, the distance-colonization relationship may be more complex than previously thought—birds that are able to cross a certain distance threshold may be able to reach various mid-isolation islands with a similar probability [16, 20]. Strictly speaking, we cannot rule out the possibility that differences in the avifaunas of the mainland source areas—e.g., in the proportion of species able to reach and successfully establish islands whose environment is different from the continent—may have cancelled out differences in distance. However, this requires a quite tight negative correlation between the size of the mainland species pool of potential colonizers and dispersal distance, for which we see no straightforward explanation.

Regarding extinction, the homogeneity in rates across the four archipelagos is also surprising, particularly given the differences in area between them. Models with differential extinction all performed poorly (Table S5) and the precision of our extinction estimates was high (Figure S2), supporting the robustness of this result. The influence of latitude, climate, and intra-archipelagic connectivity, which may have enabled greater gene flow and rescue of small populations in the smaller archipelagos, most likely overwhelmed the negative effect of area on extinction.

As expected, species that have been classified as endemics mostly show deep levels of divergence from continental relatives (Figures 1 and S1; Table 1). The oldest extant endemic species in each of the archipelagos are the Azores chaffinch (*Fringilla m. moreletii*), the laurel pigeon of the Canary Islands (*Columba junoniae*), the Razo lark of Cape Verde (*Alauda razae*), and the Madeira firecrest (*Regulus madeirensis*) (Table S2). Interestingly, among the taxa with deep divergences, we also find some to which species status has not been assigned and are considered subspecies, despite their being older than some archipelagic endemics. For example, the European robin subspecies *Erithacus rubecula* subsp. *marionae* [21] of the Canary Islands colonized the archipelago almost 3 Ma ago and forms a well-supported monophyletic clade. We investigated whether taxonomic scheme affected our results and found that treating taxa with deep divergences as endemics led to increased estimates of anagenesis in DAISIE but did not affect the preferred model (see STAR Methods).

Tests of diversity equilibrium on islands have traditionally been conducted over ecological timescales [22], as MacArthur and Wilson's mathematical work focused on extinction versus immigration. However, in *The Theory of Island Biogeography* [1], they explicitly considered the speciation phase and adaptive radiation—i.e., evolutionary processes. Formal tests of this theory on evolutionary timescales were unfeasible until recently because they required information on events that took place in the geological past [3]. In the 21st century, the mainstream of the field of island biogeography has fully incorporated the

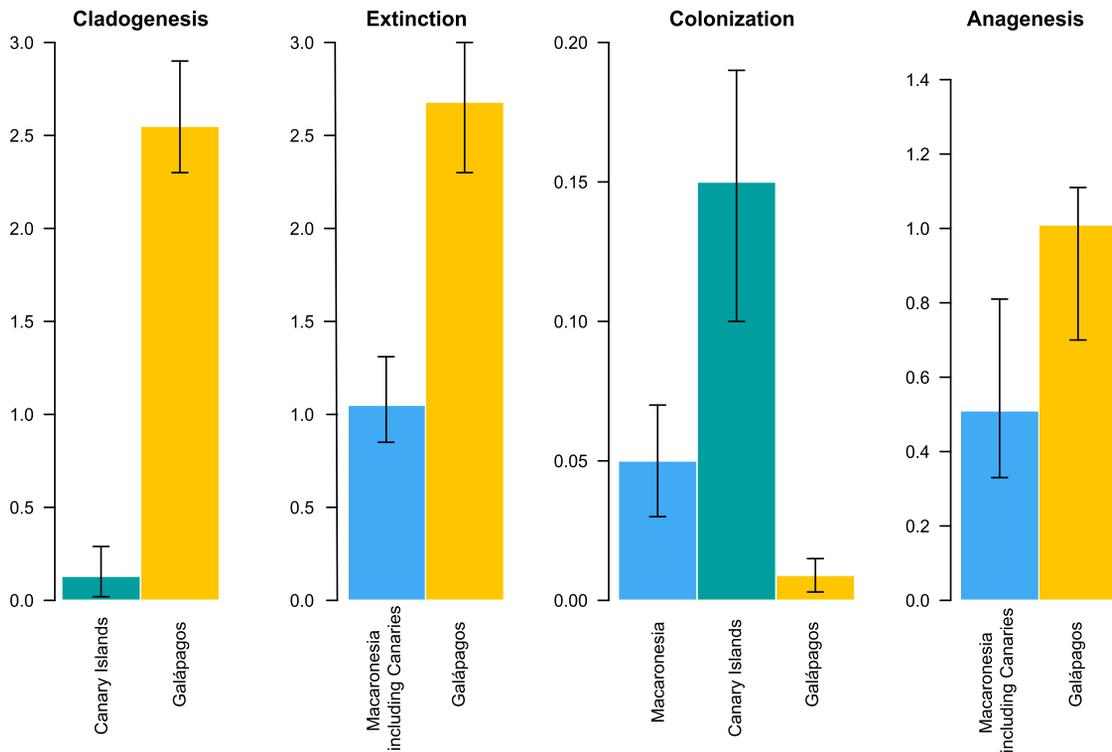


Figure 2. Maximum-Likelihood Estimates of the Rates of Cladogenesis, Extinction, Colonization, and Anagenesis for Macaronesia

Estimated in DAISIE using the M17 model and for the rates previously found in Galápagos birds [5]. Rates are shown in events per lineage per million years. Error bars show the 2.5th–97.5th percentiles of bootstrap analyses. See also Tables S5 and S6.

evolutionary aspects of MacArthur and Wilson’s theory [2, 5, 19, 23]. In a series of pioneering studies, Ricklefs and Bermingham fitted colonization-extinction models (excluding speciation) to species accumulation curves from several insular communities, finding evidence for evolutionary equilibrium in the number of independent island colonist lineages of Hawaiian birds, West Indian reptiles, and New Zealand ferns, but not in Lesser Antillean birds [14, 24–26]. More recently, the development of the DAISIE model has allowed explicit consideration of speciation via in situ radiation (cladogenesis) and anagenesis, enabling tests of equilibrium not just in the number of lineages, but also in total species diversity. The previous applications of this method have either found no evidence for equilibrium dynamics—in Galápagos birds [5]—or found diversity to be much below equilibrium—in Greater Antillean bats [11].

Our results reveal that the avifauna of each of the four Macaronesian archipelagos has independently achieved a diversity steady state and is at a macroevolutionary equilibrium. The preferred model was diversity independent, indicating that equilibrium does not arise through negative diversity feedbacks, as is the case in other vertebrate insular groups [27, 28]. Instead, total species richness has reached a plateau in the four island groups (Figure 3) because the rate of extinction is higher than the rate of speciation [11]. By incorporating speciation, our study reveals that a macroevolutionary equilibrium can be achieved in the total number of species.

The finding that Macaronesian birds are at equilibrium contrasts with the results of the only other avian study to assess

equilibrium including speciation on the Galápagos avifauna, which found no evidence for steady-state dynamics. However, the Galápagos is an atypical archipelago in that it supports two large endemic radiations of birds [16]. In fact, despite being rich in bird species, oceanic islands are generally home to few or no avian radiations—most of their endemic bird species show an anagenetic pattern, i.e., they have no close relatives on the same island or archipelago [16, 29, 30]. Whereas in the Galápagos the rate of cladogenesis in birds was high enough to overcome the balancing effects of extinction—leading to non-asymptotic behavior of the species through time plot (Figure 3)—in Macaronesia the rates of in situ radiation are too low to allow positive diversification rates. Only two clades, the chaffinches and the blue tits, have undergone cladogenesis within the bioregion, producing two and three species, respectively. These “radiations” are modest when compared to the highly diverse Darwin’s finches [31]. Thus, the key to achieving equilibrium appears to be a lack of opportunities for in situ diversification in an archipelagic context. The ability of birds to fly and disperse between islands within an archipelago is potentially the main cause for low rates of cladogenesis in most archipelago lineages of birds [16, 30]. In addition, extrinsic factors such as island configuration, connectivity, and climate (mostly temperate in Macaronesia) may also have contributed to preventing lineage splitting or survival of incipient allopatric species [16].

Recent verbal and simulation models have suggested that speciation and colonization processes on volcanic islands may operate at rates that are too slow to allow the realized species

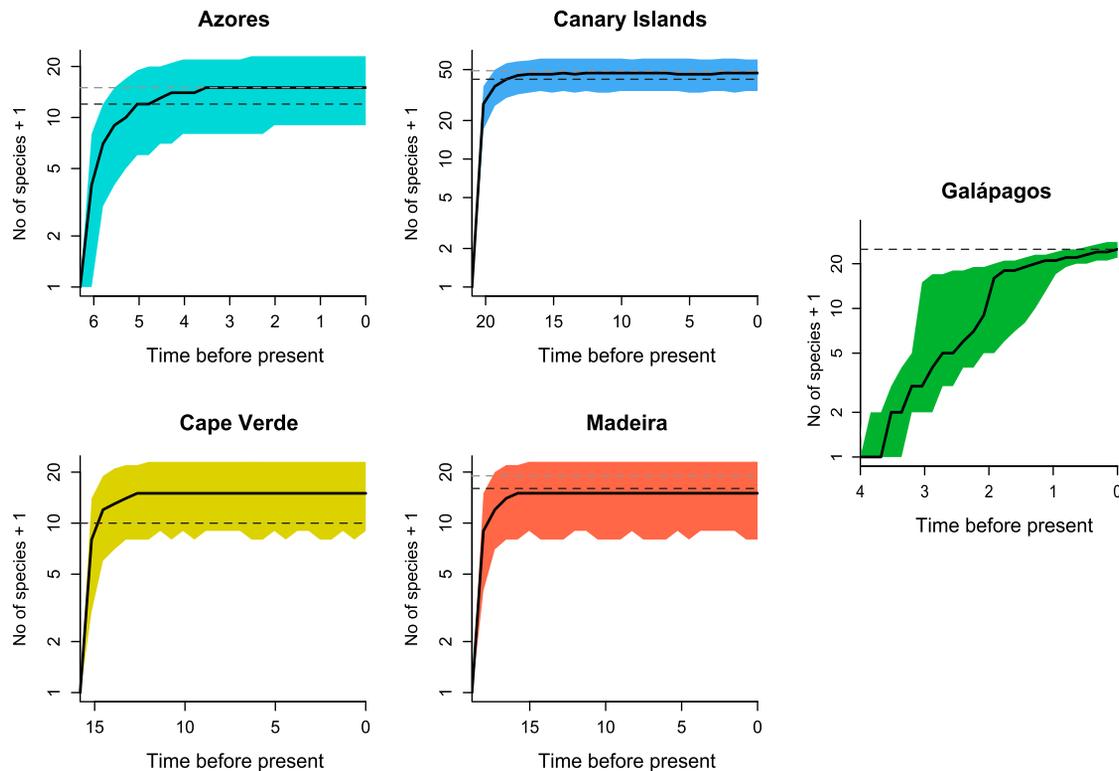


Figure 3. Number of Species through Time in Each of the Archipelagos

Based on 5,000 datasets simulated with the maximum-likelihood (ML) parameters of the best DAISIE model (M17). Black line shows median value across simulations, and the colored areas show the 2.5th–97.5th percentiles. The inset shows the same plot for the Galápagos Islands [5]. Gray dashed line, pre-human diversity; black dashed line, contemporary diversity (excluding extinct species). Time is shown in Ma. See also Table S5.

diversity to match the theoretical equilibrium or carrying capacity in a context of ongoing geological change and environmental fluctuations [3, 4, 23, 32], i.e., the concept of unattained equilibrium [2]. As a result, the current prevailing view in island biogeography accepts the essentials of MacArthur and Wilson’s theory (e.g., colonization and extinction depend on island isolation and size) but doubts that their prediction of equilibrium can be fulfilled over long timescales [2]. Indeed, in Macaronesia, detailed paleogeographic reconstructions have provided support for disequilibrium models, by revealing pronounced geological instability as well as variable levels of connectivity between landmasses [8, 33]. Surprisingly, our results in birds suggest that equilibrium in this vertebrate group may be attained within a relatively short time frame. When rates of cladogenesis are low (as in the Canary Islands) or absent (as in the Azores, Cape Verde, and Madeira), the pace of approach to equilibrium is determined almost solely by the rate of extinction [4, 11]. The rate of colonization does affect the approach to equilibrium in the number of non-endemic species, but not in the number of endemic species (see STAR Methods). Thus, archipelagos with high rates of natural extinction may rapidly reach equilibrium regardless of how often they are colonized, potentially outpacing major geological change that may otherwise deter steady state. While volcanic activity and sea level fluctuations have certainly had a dramatic effect on insular diversity on short timescales [3, 13, 33], the good fit of the model in our analyses suggests that such events may have limited impact on diversity at longer scales.

Influenced by the equilibrium theory of island biogeography, research on insular communities in the 20th century was arguably dominated by an equilibrium perspective [32]. However, in recent years, the idea that islands tend toward a dynamic equilibrium diversity that is maintained over extended periods has increasingly been replaced by a non-deterministic disequilibrium view, in which diversity is constantly tracking a theoretical equilibrium that is never reached [2, 3, 6, 7, 11]. Our results do not support this trend, by suggesting the avifaunas of four oceanic archipelagos have achieved and maintained a diversity steady state for millions of years. The findings on the birds of these North Atlantic islands are particularly relevant because they are representative of the typical oceanic island—they are rich in endemic bird species but poor in in situ avian radiations. This suggests that the pattern of long-term evolutionary diversity steady state being achieved in a short period of time may be the case for many more islands. Future studies on the avifaunas of other island systems worldwide may reveal that MacArthur and Wilson’s predicted equilibrium is widespread.

STAR METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures and six tables and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2017.04.053>.

AUTHOR CONTRIBUTIONS

L.V. designed the study, performed the analyses, and wrote the original draft. R.S.E. developed new statistical tools and contributed to study design. R.T. supervised the molecular analyses and contributed to study design. J.C.I. provided expertise on Macaronesian birds and conducted the fieldwork. K.H., T.P., and J.C.I. performed the laboratory work.

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STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|--|--|---|
| Biological Samples | | |
| Avian blood samples used for DNA isolation | This paper | Table S1 |
| Chemicals, Peptides, and Recombinant Proteins | | |
| DNeasy Blood & Tissue Kit | QIAGEN | Cat#69506 |
| MyTaq DNA Polymerase | Bioline GmbH | Cat#BIO-21107 |
| Exonuclease I | New England Biolabs GmbH | Cat#M0293L |
| Antarctic Phosphatase | New England Biolabs GmbH | Cat#M0289L |
| BigDye Terminator v3.1 Cycle Sequencing Kit | ThermoFisher Scientific – Applied Biosystems | Cat#4337455 |
| Deposited Data | | |
| New cytochrome- <i>b</i> sequences | This paper | GenBank accession numbers in Table S1 |
| 25 Maximum clade credibility trees | This paper | Deposited in Mendeley Data, http://dx.doi.org/10.17632/62p6fsnyfz.3 |
| Optimizations of the 50 candidate models | This paper | Deposited in Mendeley Data, http://dx.doi.org/10.17632/r9wt6x7d92.2 |
| Oligonucleotides | | |
| L14841: AAAAAGCTTCCATCCAACATCTCAGCATGATGAAA | [34] | N/A |
| L14995:GCCCCATCCAACATCTCAGCATGATGAAACTTCCG | [35] | N/A |
| H15767: ATGAAGGGATGTTCTACTGGTTG | [36] | N/A |
| H15917: TAGTTGGCCAATGATGATGAATGGGTGTTCTACTGGTT | [35] | N/A |
| H16065: GAGTCTTCAGTCTCTGGTTTACAAGAC | [37] | N/A |
| L-cytB_Passer: CACAGGCCTAATTAAGCCTACCT | This paper | N/A |
| H-cytB_Passer: TTGARAATGCCAGCTTTGGGAG | This paper | N/A |
| L-cytB-Mot: CCAAATYGTACAGMCTCCTG | This paper | N/A |
| H-cytB-Mot: GGTGAATGAGGCTAGTTGCCCA | This paper | N/A |
| Software and Algorithms | | |
| DAISIE R package v.1.4 | This paper; [5] | http://cran.r-project.org/web/packages/DAISIE/ |
| BEAST 2 | [38] | http://www.beast2.org |
| Geneious 8 | [39] | http://www.geneious.com |
| jModeltest 2.1.5 | [40] | https://github.com/ddarriba/jmodeltest2 |

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Luis Valente (luis.valente@mf-n-berlin.de).

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Sampling overview

We downloaded cytochrome-*b* (cyt-*b*) sequences from 1,001 individuals from a total of 397 species of Macaronesian taxa and their closest continental relatives from GenBank. In addition, we produced new sequences from 99 fresh samples from 44 species collected in Macaronesia, Europe and North Africa ([Table S1](#)). We cover 27 new Macaronesian colonization events that had never before been sampled and greatly expand the sampling of continental relatives.

Taxon sampling

Our sampling focuses on the native resident terrestrial birds from the four main archipelagos that make up Macaronesia – Azores, Canary Islands, Cape Verde, Madeira (Figure 1, Table S2). We based the taxon lists for each of the archipelagos on recent checklists (Refs [41–43], Avibase (<http://avibase.bsc-eoc.org>) and African Bird Club (<https://www.africanbirdclub.org>). For each taxon from each archipelago we aimed to sample individuals from the archipelago as well as from the taxon's closest relatives outside the archipelago. If the taxon was a species endemic to the archipelago, we sampled multiple individuals from that species, as well as from the most closely related species as identified based on available phylogenetic or taxonomic information. If the taxon was not endemic, we sampled individuals from population(s) of the archipelago as well as populations of the species from nearby regions (either from other archipelago or from the continent). The vast majority of Macaronesian birds have a Palearctic origin [9], and we thus focused our sampling from outside Macaronesia on the closest mainland regions in Africa and Europe, with particular focus on the Iberian Peninsula and Morocco.

The small archipelago of Selvagens is also part of Macaronesia but only one taxon of our focal group has colonized the islands (*Anthus berthelotti*). We exclude this archipelago from the main analyses because, given its very small area, extinction rates are likely high and colonization rates low, and thus this data point would potentially add more noise than power to the analyses. However, we did sample *Anthus berthelotti* individuals from Selvagens and we provide the estimated age of colonization of this species in the results for reference (Table S2).

METHOD DETAILS

DNA sequences

We conducted analyses using the mitochondrial cytochrome-*b* gene (*cyt-b*) because 1) *cyt-b* is considered a reliable marker for use as molecular clock, as heterogeneity in its substitution rate has been shown to be very low across avian lineages [44, 45]; 2) the gene is the most widely used sequenced marker in avian studies and sequences are available from previous studies for the majority of our target taxa; 3) previous studies of Macaronesian birds have found concordance between colonization time estimates obtained using only *cyt-b* and using multiple markers [46, 47]; 4) using other less-commonly used markers would have required obtaining hundreds of additional bird DNA samples.

Although our age estimates are based on a single mitochondrial marker we believe that the inclusion of multiple markers would not significantly alter our age estimates – indeed, a recent phylogenomic study of blue tits (*Cyanistes*) from the Canary Islands found that a multi-marker dataset did not yield significantly different colonization times from those previously obtained using cytochrome-*b* [46, 47]. As our approach uses bird sequences from multiple studies we decided to favor larger taxonomic sampling over greater genetic coverage, and in this respect our dataset is unique among phylogenetic syntheses of island birds in its taxonomic completeness. Focusing on a single well-understood marker with the most well-established molecular clock in birds [44, 45] allowed us to obtain relative ages that are comparable across taxa and avoid issues associated with calibration in the absence of fossils.

Sequence data: GenBank

We used Geneious 8 [39] to conduct an extensive search of GenBank for *cyt-b* sequences of Macaronesian and non-Macaronesian taxa fitting the criteria described in the previous section. We also downloaded sequences from outgroup taxa, selecting the sequences with the top similarity scores in the output of BLAST queries. In total, we downloaded 1,001 *cyt-b* sequences from GenBank, including 397 species across 76 genera and 43 of the independent colonization events. The availability of *cyt-b* sequences in GenBank varied greatly according to taxon. For some taxa, sequences from both archipelago and close relatives from outside the archipelago were already available (e.g., from detailed phylogenetic/phylogeographic analyses, such as *Serinus canarius* [48] and *Sylvia spp.* [49]). In other cases, the target species had been sampled, but only from the continent and not from Macaronesia (e.g., *Alaemon alaudipes*, *Emberiza calandra*, *Motacilla cinerea*). In others, the sampling of the continental relatives was very poor or only from very distant regions (e.g., *Eremopterix nigriceps*, *Streptopelia decaocto*, *Turdus merula*). Finally, for two species there were no previous *cyt-b* sequences available on GenBank (*Corvus ruficollis*, *Passer iagoensis*). For one of the species, *Sturnus vulgaris*, *cyt-b* sequences were not available in GenBank from target populations. However, many NADH dehydrogenase 2 (ND2) sequences were available for this species, and we therefore used this marker for this species. GenBank accession numbers and geographical origin for all downloaded sequences are available on the maximum clade credibility trees deposited online.

Sequence data: new sequences

Overall, sequences available on GenBank covered only 55% of the extant Macaronesia independent colonization events. We thus aimed to substantially improve the sampling by producing new sequences for several Macaronesian taxa and their close relatives from continental regions. We focused on the Macaronesian archipelagos as well as in the Iberian Peninsula and North Africa. New samples were obtained during field trips conducted by JCI between 2008 and 2016 to the Azores, Canary Islands, Cape Verde, Madeira, Selvagens, Iberian Peninsula and Morocco. Individuals were captured using mist-nets or spring traps baited with larvae. Blood samples (c. 40 μ L) were taken by brachial venipuncture, diluted in ethanol in a microfuge tube and stored at room temperature. Birds were released at the point of capture. Further samples were obtained from: Alex Tavares (Cape Verde); Ángel Moreno, David P. Padilla, and Mariano Hernández (Canary Islands); J.L. Tella (Iberian Peninsula, Morocco, Mauritania), and Guillermo López (Iberian Peninsula). Sample information and GenBank accession numbers for all new specimens are provided in Table S1.

DNA was extracted from blood samples using QIAGEN DNeasy Blood and Tissue kits (QIAGEN, USA). The *cyt-b* region was amplified using the following primers: L14841 (AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA) [34]; L14995 (GCC CCA TCC AAC ATC TCA GCA TGA TGA AAC TTC CG) [35]; L15308 (GGC TAT GTC CTC CCA TGA GGC CAA AT); H15767 (ATG AAG GGA TGT TCT ACT GGT TG) [36]; H15917 (TAG TTG GCC AAT GAT GAT GAA TGG GTG TTC TAC TGG TT) [35] and H16065 (GAG TCT TCA GTC TCT GGT TTA CAA GAC) [37]. For species of *Motacilla*, *Passer* and *Petronia* we found that the above primers also amplified nuclear mitochondrial DNA segments (NUMTs). In order to avoid NUMTs, we designed the following new primers that were specific to mitochondrial *cyt-b* copies: L-cytB_Passer (CAC AGG CCT AAT TAA AGC CTA CCT), H-cytB_Passer (TTG ARA ATG CCA GCT TTG GGA G, L-cytB-Mot (CCA AAT YGT TAC AGG MCT CCT G), H-cytB-Mot (GGT GAA TGA GGC TAG TTG CCCA).

Polymerase chain reactions (PCR) were set up in 25 μ L total volumes including 5 μ L of buffer MyTaq, 1 μ L (10 μ M) of each primer, and 0.12 μ L MyTaq polymerase. PCRs were performed with the following thermocycler conditions: initial denaturation at 95°C for 1 min followed by 35 cycles of denaturation at 95°C for 20 s, with an annealing temperature of 48°C for 20 s, and extension at 72°C for 15 s min and a final extension at 72°C for 10 min. Amplified products were purified using Exonuclease I and Antarctic Phosphatase, and sequenced at the University of Potsdam (Unit of Evolutionary Biology/Systematic Zoology) on an ABI PRISM 3130xl sequencer (Applied Biosystems) using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). We used Geneious 8 to edit chromatograms and align sequences. Alignment was unambiguous in all cases.

In total, we added 99 new *cyt-b* sequences from 44 different species, covering an additional 27 Macaronesian colonization events that had never before been sampled. The new sequences increase the sampling of *cyt-b* for extant colonization events from the existing 55% (43/78 colonization events) to 90% (70/78). We also substantially increased sampling of continental relatives, adding 39 new *cyt-b* sequences from the Iberian Peninsula and North Africa, covering 28 species.

Phylogenetic analyses

In order to estimate the times of colonization and speciation of Macaronesian birds, we produced dated phylogenetic trees in BEAST 2 [38]. We produced an alignment for each genus, with the exception of the following genera, which were combined into a single alignment: *Columba* and *Streptopelia*, because they are the only genera from order Columbiformes in our analyses; *Passer* and *Petronia* because they belong to sister clades; the five genera of the lark family Alaudidae (*Alaemon*, *Alauda*, *Ammomanes*, *Calandrella* and *Eremopterix*) because they were recently analyzed in a family-wide phylogenetic analysis [50]. In total we produced and analyzed 25 alignments leading to 25 phylogenies (trees deposited Mendeley Data). For each alignment we performed substitution model selection in jModeltest [40] using the Bayesian information criterion (models for each alignment available in Mendeley Data).

We used rates of molecular evolution for avian *cyt-b* sequences, which have been shown to evolve in a clock-like fashion at an average rate of ~2% per Ma [44]. Recent analyses have confirmed the suitability of *cyt-b* as a molecular clock in birds [45]. We used the average *cyt-b* molecular clock rate for the relevant bird order estimated by [44]: Passeriformes – 2.07% (0.01035 substitutions per site per Ma); Columbiformes 1.96% (0.0098); and Piciformes – 3.30% (0.0165). We applied a Bayesian uncorrelated lognormal relaxed clock model. For each analysis, we ran four independent chains of 10 million generations, with a birth-death tree prior. Convergence of chains and appropriate burn-ins were assessed with Tracer and maximum clade credibility trees with mean node heights were produced in Tree Annotator. We produced 25 maximum clade credibility trees (deposited in Mendeley Data) which were used to extract branching times for island species. Data points from taxa of the same archipelago were then assembled together into archipelago-specific datasets which were analyzed with DAISIE.

Colonization times

For the majority of colonization events, we sampled two or more individuals from each archipelago (Table S2). In most of these cases, the individuals from the same archipelago formed a monophyletic clade, and we used the stem age of this clade as the time of colonization. For 20 colonization events – all of which corresponded to non-endemic species – the multiple individuals from the same archipelago were embedded in a well-supported clade (PP > 0.99) containing other individuals from that species from other regions. Most of these groupings were young (average age 530,000 years), and within-clade resolution was very poor. We therefore assume that the fact that the individuals do not form a distinctive clade is due to incomplete lineage sorting or insufficient phylogenetic information rather than evidence for multiple colonization events by that species. For all such cases we took the age of the most recent common ancestor of the clade containing the individuals from the same archipelago as a maximum age of colonization, and applied the “Non_endemic_MaxAge” option in DAISIE, which integrates over the possible colonization times between the present and the upper bound.

For eight of the extant colonization events, no sequences of individuals from the archipelago were available on GenBank and we were not able to obtain samples for new sequencing. However, for these cases we sampled individuals from the same species from different archipelagos and/or from the mainland, and we thus used the most recent common ancestor of these individuals as an upper bound for the age of the colonization event, using again the “Non_endemic_MaxAge” option in DAISIE.

Treatment of extinct species

Thirteen taxa have gone extinct from Macaronesia (Tables 1 and S2), and their extinction has been linked to human activities [9, 51]. As anthropogenic extinctions do not count toward the natural background rate of extinction, we explicitly include these species in the analyses, treating them as though they had survived until the present following the approach of Valente et al. [11]. Of the 13 extinct species, two taxa have been extirpated from the islands but are still extant elsewhere (the wood pigeon from Madeira, and the alpine

chough from the Canary Islands). We included these extirpated species in the phylogenetic analyses mentioned above because we sampled sequences from extant populations from other regions and were able to place an upper bound on the time of colonization. From the taxa that have gone completely extinct we were able to obtain samples from an extinct population of the lesser short-toed lark (*Calandrella rufescens rufescens*) from the Canary Islands.

The remaining ten extinct species (Table S2) are only known from fossils or subfossils and we were therefore not able to obtain sequences from them. The ten species were endemic to the archipelago where they occurred and were not closely related to extant species, having most likely resulted from independent colonization events. In order to incorporate these taxa into the analyses we modified the DAISIE framework to allow for a new type of data point corresponding to unsampled endemic species. Given that the age of colonization of these extinct species is unknown, the method assumes they could have colonized anytime between the maximum age of the archipelago and the present. We ran DAISIE analyses including and excluding extinct species and found that the main results were not affected – we thus report only the results including extinct species.

QUANTIFICATION AND STATISTICAL ANALYSIS

DAISIE analyses

DAISIE is a dynamic stochastic island biogeography model [5]. The general DAISIE framework [4, 5] assumes that each species on the mainland (source pool) is equally likely to colonize the island, at a per lineage rate γ (which applies to the number of species on the mainland). Colonization includes both dispersal and successful establishment. Each species present on the island is equally likely to go extinct, at a per lineage rate of μ . Island endemic species can be gained through speciation via anagenesis (where an island population diverges through time and becomes reproductively isolated from the mainland source population, without increase in island species diversity), which occurs at a per lineage rate λ^a ; or via cladogenesis (where one island taxon splits into two island endemic species), which occurs at a per lineage rate λ^c . In models including diversity-dependence (M42-M48 and M50 in Table S5), γ and λ^c decline linearly with the number of species on the island, depending on K' , the maximum number of niches on the island that could be attained in the absence of extinction.

We developed a new multi-archipelago version of DAISIE that allows different archipelagos to share all or some macroevolutionary rates. This leads to substantial increase in the number of potential data points used for maximum-likelihood optimization, and allows us to test whether rates differ between archipelagos. We used this updated version of the DAISIE R package to estimate archipelago-wide diversification and biogeographical rates. We fitted and compared a large set of candidate models that differed in the number of parameters shared between archipelagos (Tables S4 and S5). We estimated the following parameters: rate of colonization (γ), extinction (μ), speciation via cladogenesis (λ^c), speciation via anagenesis (λ^a) and diversity-limits (K'). Model parameters were estimated via maximum likelihood by fitting models to the times of colonization and branching for each of the archipelagos.

We assumed a static mainland pool size of 300 species, approximately the number of species of our target group found in Europe and North Africa. Mainland pool size affects DAISIE estimates of colonization rate, which decline with increasing pool size, but not the other rates (extinction, cladogenesis and anagenesis).

We used the following published geological ages for the archipelagos: Azores - 6.3 Ma [52]; Canary Islands – 21 Ma [53]; Cape Verde - 15.8 Ma [54]; Madeira – 18.8 Ma [55]. We fitted models to a consensus dataset representing the colonization and branching times obtained in the maximum clade credibility trees from BEAST 2 and including extinct species. For each model, we ran maximum-likelihood optimizations with 20 different, random, initial starting conditions to ensure searches were not trapped on local suboptima.

Model comparison was done using BIC, because in DAISIE this criterion has lower error rates [5] and penalizes more complex models. The preferred model using BIC was M17 (discussed in the main text), but two other models – M15 and M24 – also carry a large proportion of BIC weight. M15 has an additional anagenesis parameter for the Canary Islands, which is lower than on the other archipelagos; M24 has a single cladogenesis parameter applying to all archipelagos. Our main conclusions – that the four archipelagos are at equilibrium and that the Canaries exhibit exceptional dynamics – are supported by all three models, and thus we focus on the results of M17 as this model has one parameter less than the second best model (M15), it was marginally preferred using BIC in the main analyses and strongly preferred in the analyses assuming a ‘phylogenetic’ taxonomic scheme (BIC weight for M17 was 0.74, versus 0.02 for M15 and 0.09 for M24).

We assessed bias and precision of the ML inferences using a parametric bootstrap approach (Figure S2). We simulated 1,000 datasets for each archipelago with the parameters of the M17 model and then estimated the ML parameters from each of the simulated datasets and compared them with the simulated values.

Equilibrium

We simulated islands with the ML parameters of the preferred models for each archipelago. For each model, we simulated 5,000 island biota from the birth of the archipelago to the present (Figure 3). This enabled us to assess visually whether the number of species has achieved an asymptotic value, i.e., equilibrium. We additionally used a deterministic equation available within the DAISIE package [11] to calculate the expected total species diversity at equilibrium for each of the archipelagos. The expected number of species at equilibrium is 46 species for the Canary Islands and 14 species each for Azores, Cape Verde and Madeira. Because equilibrium is dynamic, species richness stochastically fluctuates around these values [5]. Therefore, at a particular point in time there can be diversity undershoots (e.g., Cape Verde) or overshoots (e.g., Madeira) with respect to the equilibrium value (Figure 3).

Recent extinctions caused by humans have affected how distant the system is to the theoretical equilibrium [11] – for example, as a result of the loss of seven species from the Canary Islands by extinction, contemporary diversity (42 species) is currently below equilibrium (46 species), whereas pre-human diversity was actually above equilibrium (49 species) (Figure 3).

The rate of colonization can affect the rate of approach to equilibrium of non-endemic species (i.e., equilibrium in the number of non-endemics is reached more rapidly under higher colonization), but does not influence equilibrium in endemic species, which in diversity-independent models is determined by the rate of cladogenesis and extinction (see equations in [11]). Because in the preferred model extinction is estimated to be (much) higher than cladogenesis, the time to reach equilibrium in the total number of species is solely determined by extinction – i.e., higher rates of colonization would not lead to equilibrium being reached more quickly.

Taxonomy and species status

The taxonomy and status (endemic/non-endemic) of many Macaronesian taxa is ‘work in progress’ by the ornithological community, as more morphological and molecular studies become available [43, 56]. To account for taxonomic uncertainty, we analyzed data-sets assuming three alternative classification schemes: 1) ‘conservative’ classification, based on the Clements checklist [57], which does not confer species status to many Macaronesian endemic taxa; 2) ‘current’, which takes into account recent molecular and morphological results from Macaronesian bird studies [43]; and 3) ‘phylogenetic’, under which we consider as endemic species cases where a taxon from an archipelago forms a well-supported monophyletic group older than 1 Ma on our maximum credibility BEAST trees. The taxa for which alternative taxonomies were used are shown in Table S6. The preferred DAISIE model under the ‘current’ and ‘phylogenetic’ classification schemes was the M17 model (Table S5; Mendeley Data, <http://dx.doi.org/10.17632/r9wt6x7d92.1>), whereas for the ‘conservative’ scheme the preferred models were M43 and M44, which show very similar BIC weights (Mendeley Data, <http://dx.doi.org/10.17632/r9wt6x7d92.1>). M43 is a diversity-dependent version of M17. M44 is similar to M43 but the Canary Islands differ only in the rate of colonization; the rate of cladogenesis is equal and non-zero across all archipelagos (Table S4). Because the ‘conservative’ scheme is not up to date with recent findings, and because the ‘phylogenetic’ scheme is too liberal, we favor the ‘current’ scheme. In any case, the results for the three alternative classification schemes are fully in agreement with respect to our main conclusions (equilibrium in all four archipelagos has been achieved, homogeneity in rates across archipelagos and the Canary Islands have decoupled dynamics) and therefore in the main text we discuss only the results of the ‘current’ classification scheme. The results of the optimizations of the 50 candidate models for the ‘conservative’ and ‘phylogenetic’ schemes have been deposited in Mendeley Data whereas those for the ‘current’ scheme are provided in Table S5.

DATA AND SOFTWARE AVAILABILITY

The new DNA sequences produced in this study were deposited in GenBank. Accession numbers are given in Table S1.

The 25 maximum credibility trees from BEAST are deposited in Mendeley Data at <http://dx.doi.org/10.17632/62p6fsnyfz.3>. These include GenBank numbers and geographical origin of all individuals as well as information on the models and molecular rates used to build each tree.

The results of the optimizations of the 50 candidate models for the ‘conservative’ and ‘phylogenetic’ schemes are deposited in Mendeley Data at <http://dx.doi.org/10.17632/r9wt6x7d92.2>.

New computer code was implemented in a new version of DAISIE R package available in: <http://cran.r-project.org/web/packages/DAISIE/>.