Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles

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Abstract

Lesser Antillean anoles provide classic examples of island radiations. A detailed knowledge of their phylogeny and biogeography, in particular how the age of species relate to the ages of their respective islands and the age of their radiation, is essential to elucidate the tempo and mechanisms of these radiations. We conduct a large scale phylogenetic and phylogeographic investigation of the Lesser Antillean anoles using multiple genetic markers and comprehensive geographic sampling of most species. The multilocus phylogeny gives the first well-supported reconstruction of the interspecific relationships, and the densely sampled phylogeography reveals a highly dynamic system, driven by overseas dispersal, with several alternative post-dispersal colonisation trajectories. The age of these anole radiations corresponds with the ancient Miocene Island arc, but the ages of extant species are relatively young (about the age of the younger arc, or less). The species age is compatible with other small terrestrial amniotes. The difference between the age of the radiation and the age of the extant species suggests substantial species turnover on older arc islands, most likely through competitive replacement. Although extant anoles are extremely speciose, this may represent only a fraction of their biodiversity over time. While several cases of paraphyly enable us to infer some recent colonization events, the relatively young age of extant species, the high levels of species turnover through time, and the absence of the younger arc in the early and middle stages of the radiation, does not allow the early inter-island colonization to be reliably inferred. Reproductive isolation in allopatry takes a very considerable time (in excess of 8my) and sympatry appears to occur only late in the radiation. The resolved multilocus phylogeny, and relative species age, raise difficulties for some earlier hypotheses regarding size evolution, and provide no evidence for within-island speciation.

Keywords	Anolis; multilocus phylogeny; Lesser Antilles; species age; species turnover; island colonization.
Taxonomy	Biological Sciences, Evolutionary Biology, Phylogeny, Island Biogeography, Speciation
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Dear Editor

We are submitting the manuscript entitled “Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles” to be considered for publication in the journal Molecular Phylogeny and Evolution.

We provide the first resolved multilocus species tree for these radiations and combine this with a series of densely sampled phylogeographic analysis within-species to indicate species age. We relate this to geological data. This allows us to deduce considerable species turnover on older islands and show that attempts to define early-stage colonization sequence are spurious and that the classic evolution of size in these radiations needs to be reconsidered. We show recent colonization events (via paraphyly) and that reproductive isolation and subsequent sympatry require a very considerable amount of time in allopatry.

We trust this will be of interest to a wide audience.

Yours

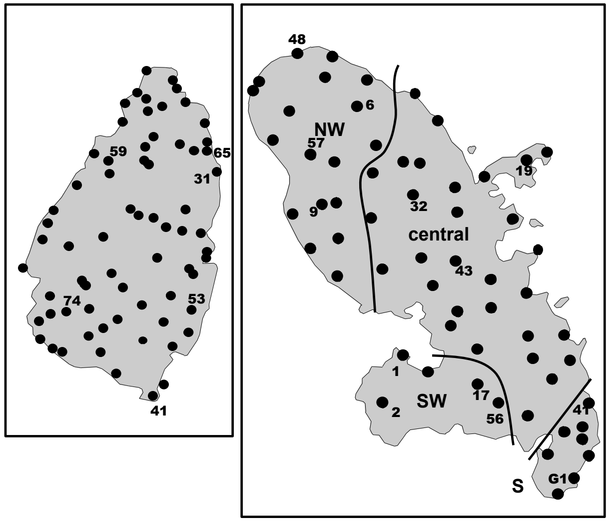
Roger S Thorpe, Corresponding author.

Highlights

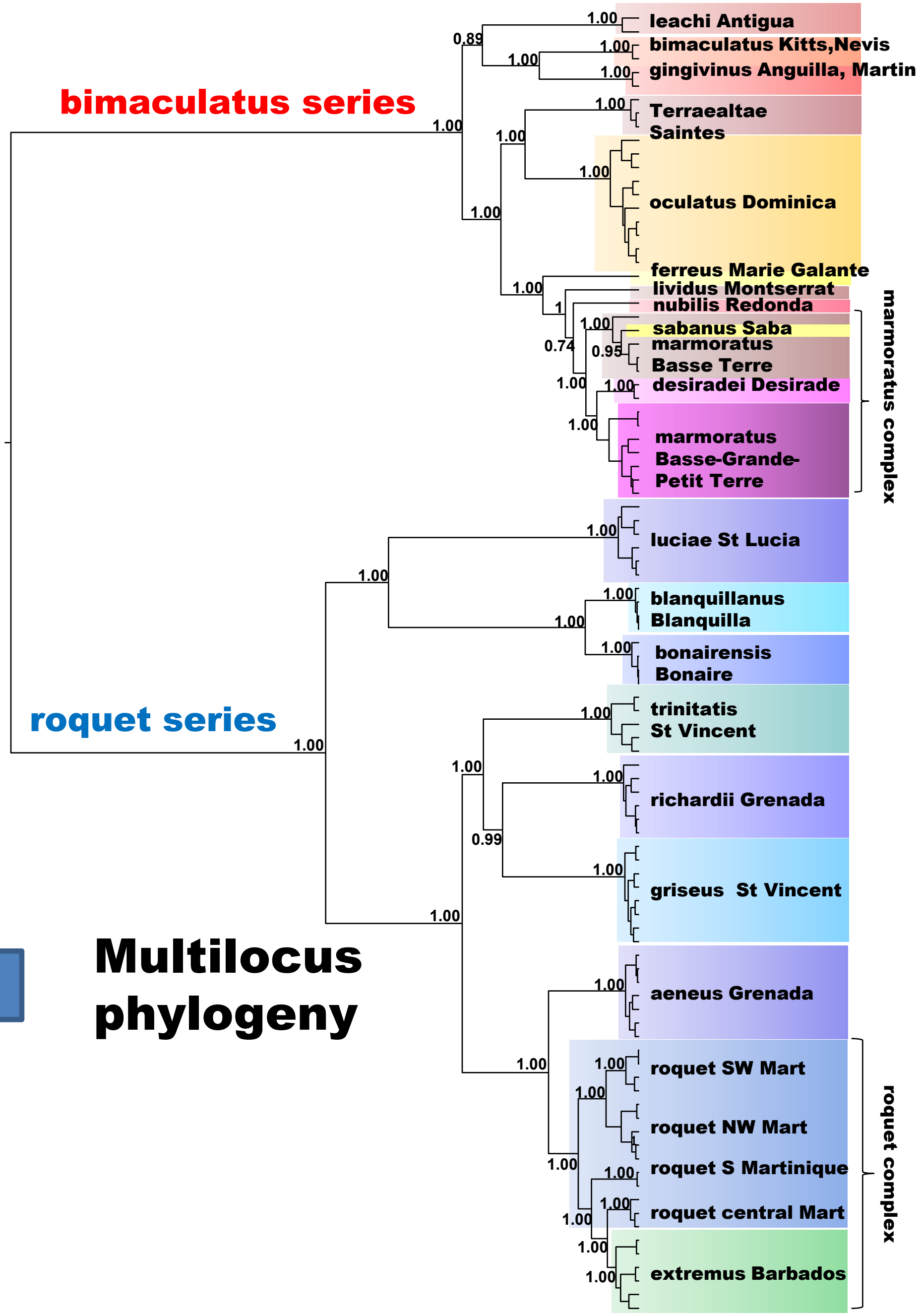
- A multilocus study provides a resolved phylogeny for Lesser Antillean anoles.
- Dense phylogeographic sampling within-species indicates the age of species.
- Old radiations are composed of young species, with species turnover on older islands.
- Reproductive isolation occurs only after a very prolonged time in allopatry.
- Only recent colonization events can be deduced from the phylogeny.

Lesser Antillean anoles

Dense phylogeographic sampling



Multilocus phylogeny



Graphical abstract legend

A combination of a resolved multilocus phylogeny and dense phylogeographic sampling indicates species age and recent colonization events

Multilocus phylogeny, species age and biogeography of the Lesser Antillean anoles.

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Declaration of interest: None

ABSTRACT

Lesser Antillean anoles provide classic examples of island radiations. A detailed knowledge of their phylogeny and biogeography, in particular how the age of species relate to the ages of their respective islands and the age of their radiation, is essential to elucidate the tempo and mechanisms of these radiations. We conduct a large scale phylogenetic and phylogeographic investigation of the Lesser Antillean anoles using multiple genetic markers and comprehensive geographic sampling of most species. The multilocus phylogeny gives the first well-supported reconstruction of the interspecific relationships, and the densely sampled phylogeography reveals a highly dynamic system, driven by overseas dispersal, with several alternative post-dispersal colonisation trajectories. The age of these anole radiations corresponds with the ancient Miocene Island arc, but the ages of extant species are relatively young (about the age of the younger arc, or less). The species age is compatible with other small terrestrial amniotes. The difference between the age of the radiation and the age of the extant species suggests substantial species turnover on older arc islands, most likely through competitive replacement. Although extant anoles are extremely speciose, this may represent only a fraction of their biodiversity over time. While several cases of paraphyly enable us to infer some recent colonization events, the relatively young age of extant species, the high levels of species turnover through time, and the absence of the younger arc in the early and middle stages of the radiation, does not allow the early inter-island colonization to be reliably inferred. Reproductive isolation in allopatry takes a very considerable time (in excess of 8my) and sympatry appears to occur only late in the radiation. The resolved multilocus phylogeny, and relative species age, raise difficulties for some earlier hypotheses regarding size evolution, and provide no evidence for within-island speciation.

Keywords
Anolis, multilocus phylogeny, Lesser Antilles, species age, species turnover, island colonization.

1. Introduction

Island archipelagoes tend to be biodiversity hotspots (Myers et al*.,* 2000), and have been the focus of many evolutionary studies. The production of that biodiversity (that is, the radiation of a group in an archipelago by classical geographic Darwinian evolution) can be thought of as loosely following a series of stages. First, the initial colonization of an island in the archipelago; second, the dispersal among islands, third the divergence of the various isolated (allopatric) island forms into separate species; and last the continued inter-island colonization resulting in independent species living in sympatry (Losos and Ricklefs, 2009). The highly speciose anoles in the Lesser Antillean archipelago provide examples of island radiations where the tempo and mode of this process can be studied. Here, we investigate these radiations using a well- resolved multilocus molecular phylogeny, and densely sampled phylogeography, to elucidate these processes and expose the utility and limitations of these methods.

Anoles are small, neotropical/subtropical, insectivorous tree lizards that are the subject of numerous evolutionary and ecological studies (Losos, 2009). The genus (*sensu lato*) is very speciose, and we follow Losos (2009), Poe (2013) in treating *Anolis* as a single genus with the main clades recognised as series (but see Nicholson et al*.,* 2012, and Poe et al., 2017). The northern Lesser Antilles (Dominica northwards) are inhabited by the *bimaculatus* series, and the southern Lesser Antilles (Martinique southwards) and associated islands, are inhabited by the *roquet* series (Fig. 1). We use the term series, because of its convenience in distinguishing between various phylogenetic levels; for example the name *roquet* is used at three levels, 1) for the *roquet* series occupying the southern Lesser Antilles, 2) for the *roquet* complex that includes *A. extremus* from Barbados, and 3) for the nominal species *A. roquet* on Martinique.

Phylogenetic studies (e.g. Nicholson et al., 2005) show that the Lesser Antillean *bimaculatus* and *roquet* series are as distantly related as anoles can be, and must have colonised this island chain independently. Both *roquet* and *bimaculatus* series are monophyletic, and exclusively Lesser Antillean, in the sense that they do not naturally have extant members in South America, or Greater Antilles, respectively. They do however, have sister taxa in South/Central America and the Greater Antilles respectively, which suggests they may be the product of single colonizations of the Lesser Antilles (northern *bimaculatus* from the Greater Antilles, and southern *roquet* from South America), with subsequent divergence within their mutually exclusive northern and southern sections of the island chain.

The Lesser Antilles are composed of two volcanic arcs, which are superimposed from Martinique southwards. The older outer arc is Eocene to Miocene (Wadge, 1994) and is currently represented by relatively low elevation islands, while the younger, inner arc is composed of mountainous islands that arose between 8 my ago in the late Miocene and the present (Bouysse, 1984), with most islands being 5 my old or younger (Briden et al., 1979). Both arcs are a product of subduction of the Atlantic Ocean crust under the Caribbean plate (Maury et al., 1990), with a subsequent independent volcanic origin of each island. The exceptions to this are Barbados, which is an accretionary prism (Speed, 1994), and the very ancient La Desirade (Briden et al., 1979). Also, two species from the *roquet* series are found south of the Lesser Antilles on continental shelf islands off the South American coast (Blanquilla and Bonaire). In any event, although the situation may be complicated by instances of island coalescence, the islands and island banks (e.g. St Kitts/Nevis bank) have generally arisen independently from the sea over time (Surget-Groba and Thorpe, 2013), so that overseas inter-island colonization is a dominant feature of the biogeography of these anoles.

Each Lesser Antillean island, or island bank, has either one or two endemic anole species, with no significant island or islet uninhabited (Fig.1). Females may lay a series of single eggs every six weeks or so, with adults living a few years. There can be high population densities (Malhotra and Thorpe, 1991) and population turnover, and aspects of their life history (e.g. sperm storage and multiple inseminations) are compatible with a facility to colonize among islands and rapidly expand population size (Eales et al., 2010). Even so, these are low-vagility animals, with the per-generation gene exchange among islands effectively close to zero compared to the massive population turnover within an island. Numerous studies (Thorpe et al., 2015 and references therein) have shown that while there may be distinct phylogeographic divisions, and (largely unrelated) geographic variation in quantitative traits within an island species, morphological continuity among geographic sites testifies to their conspecificity (see, however, Thorpe et al., 2010 for Martinique).

Thus, Lesser Antillean anoles generally represent a system in which allopatric species are isolated from one another on separate islands/island banks with deep sea between, with the potential for gene flow between species effectively zero throughout their entire evolutionary histories. Where two species occur in sympatry on a single island, they maintain morphological distinctiveness in widespread syntopy and without evidence of gene flow (Thorpe et al., 2015) and can therefore be considered to have independent evolutionary trajectories. In these cases, phylogenetic studies have shown that these island/island-bank species are mutually monophyletic. The exceptions to this general rule are multispecies complexes (*roquet* and *marmoratus* complexes), where precursor islands may coalesce resulting in secondary contact of previously allopatric “species”, and nominal species may be paraphyletic (Materials and Methods).

These Lesser Antillean anole radiations have been used to study character displacement and alternative theories of size evolution (Losos, 2009), as well as infer colonization sequence (Stenson et al., 2004; Losos, 2009). Among other factors these studies have been limited by poorly resolved phylogenies and poor sampling of many island species. Here we provide a well resolved, multilocus (mtDNA and five nDNA genes) phylogeny and, in a supporting analysis, dense sampling of numerous species to give a robust estimate of within-species divergence, and a perspective on the age of these species.

2. Materials and methods

2.1 Molecular methods

DNA sequences consisted of published sequences (Thorpe et al., 2015, and references therein) and novel sequences generated for this study. Total DNA was extracted from autotomised tail tip tissue using a high salt method (Aljanabi and Martinez, 1997). Fragments of the mitochondrial cytochrome b (cyt b) gene and nuclear genes genes 3’ nucleotidase (NT3), prolactin receptor (PRLR), G protein-coupled receptor 149 (R35), recombination activating gene 1 (RAG1), and Rhodopsin, were then PCR amplified using the cyt b primers in Thorpe *et al.* (2015); the PRLR and NT3 primers in Townsend *et al.* (2008); the R35 primers in Leaché (2009); the RAG1 primers Mart_FL1 and Amp_R1 described in Crottini et al. (2012) and Hoegg et al. (2004); and the Rhodopsin primers Rod3 and Rod4 in Glor et al. (2004). Reactions were performed in 11 µl volumes, comprising ABgene ReddyMix™ PCR Master Mix (cat. no. AB-0575/LD/A), 0.27µM of each primer and ~10-20 ng of template DNA. Products from PCR were cleaned using the enzymes exonuclease 1 and thermo-sensitive alkaline phosphatase, and direct sequencing carried out by Macrogen Inc. (dna.macrogen.com) using both forward and reverse primers. Sequence chromatograms were proof-read, aligned and checked for unexpected stop codons or frameshift mutations using the software CodonCode Aligner version 3.5.6.

2.2 Phylogenetic methods

There were two primary phylogenetic analyses. The first (Analysis 1) aims to produce a well resolved interspecific phylogeny, the second (Analysis 2) aims to produce a robust estimate of the age of individual species in relation to the age of the appropriate anole radiation (series or clade).

2.2.1 Phylogenetic methods Analysis 1: Multilocus tree.

In order to maximize the possibility of producing a phylogenetic tree with resolved inter-specific relationships, the mtDNA gene cytochrome b, and five single-copy nuclear genes (NTF3, PRLR, R35, RAG1, Rhodopsin) were used. Previous studies (Thorpe et al., 2015 and references therein) have revealed the phylogeographic structure within well sampled individual species. For Analysis 1, where there are numerous collection sites within a species, sites were selected to represent these major phylogeographic regions. Other species have fewer collection sites per island. The geographic sampling of DNA sequences is shown in Fig. 2. All species from the *roquet* series, together with *A. oculatus*, and *A. marmoratus* from the *bimaculatus* series, have multiple sites per species. All other species from the *bimaculatus* series are represented by at least one site per island/islet.

All well-recognized, nominal, species are included for both series, and putative species from precursor islands, e.g., the four lineages on Martinique in secondary contact after the coalescence of the precursor islands (Thorpe et al., 2010), are treated as separate entities. For the *roquet* series these are *A. luciae* from St Lucia, *A. trinitatis* (smaller) and *A. griseus* (larger) from St Vincent, *A. aeneus* (smaller) and *A. richardii* (larger) from Grenada, *A. bonairensis* from Bonaire, *A. blanquillanus* from Blanquilla, *A. extremus* from Barbados, and NW Martinique *A. roquet*, SW Martinique *A. roquet*, S Martinique *A. roquet* and central Martinique *A. roquet* from Martinique. The Barbados species *A. extremus* (nested within Martinique roquet) and the four Martinique lineages are hereafter referred to as the *roquet* complex. The *bimaculatus* series excludes the small bodied *wattsi* clade, which is sister to the remaining larger bodied *bimaculatus* series (Poe et al., 2017). The species included are, *A. leachi* from Barbuda and Antigua, *A. bimaculatus* from the St Kitts and Nevis bank, *A. gingivinus* from Anguilla and St Martin, *A. terraealtae* from Les Saintes group of small islands, *A. oculatus* from Dominica, *A. ferreus* from Marie Galante, *A. lividus* from Montserrat, *A. nubilis* from Redonda, *A. sabanus* from Saba, *A. desiradei* from La Desirade, western *A. marmoratus* from west and central Basse Terre, eastern *A. marmoratus* from Grande Terre, eastern Basse Terre, and Petite Terre. The population from the islets of Petite Terre off Grande Terre are not recognized in this study as a nominal species, but are sampled. The populations from the islets of Îlet-à-Kahouanne and Tête-à-Anglais off northern Basse Terre are not recognized as nominal species and not included. The multispecies complex of *A. sabanus*, eastern *A. marmoratus,* western *A. marmoratus*, and *A. desiradei* is hereafter referred to as the *marmoratus* complex (Fig. 2).

Phylogenetic analysis of the concatenated cyt b and nuclear datasets were conducted using a Bayesian method with a Yule tree prior in BEAST v. 1.8.2. (Drummond et al., 2012). Heterozygous positions in nuclear sequences were treated as missing data. Datasets were partitioned by gene and each assigned separate molecular clock and substitution models, with the latter selected under the Bayesian Information Criterion in MEGA5 (Tamura et al., 2011). Preliminary runs with relaxed clock models failed to reject non-zero evolutionary rates and so strict clock models were utilised. MCMC chains ran for sufficient length to achieve convergence and sufficient sampling of all parameters (ESS > 200), verified using the program TRACER v. 1.6 (Rambaut et al., 2014). The maximum clade-credibility (MCC) tree was obtained and annotated with relevant statistics from the posterior sample of trees using the program TREEANNOTATOR. Additional phylogenetic estimates were also conducted under maximum likelihood (ML) using RAxML-HPC2 8.2.3 (Stamatakis 2014) on the CIPRES Portal (Miller et al., 2010) using the iguanid *Polychrus marmoratus* as the outgroup. The dataset was partitioned as described above and the ML tree estimated using a GTR+G models and clade support assessed by 500 bootstrap replicates using a GTR+CAT model (which approximate the GTR+G model while offering greatly increased computational speed). We additionally analysed the aligned nuclear sequences using identical methods to check for consistency between relationships inferred using only nuclear sequences with those inferred using the complete dataset.

2.2.2 Phylogenetic methods Analysis 2: Molecular dating

The extent of molecular divergence between a pair of extant species may give an upper bound to the time of their divergence, but this will tend to be exaggerated by deep lineage coalescence, and especially by the extinction of any intermediate species. The latter may be a particular problem in radiations with considerable species turnover and lead to a gross overestimation of the age of a species. Assuming complete lineage sorting following colonization, and no subsequent bottlenecking, the extent of divergence within a species should give a more realistic estimate of time of colonization and origin, but will be underestimated by lineage extinction resulting from genetic drift, and or under-sampling within the species. The latter can be managed by comprehensively sampling the geographic range of a species, as this will minimize the possibility of not sampling a major divergent phylogeographic lineage. For this analysis, we employed just the cyt b gene, because mtDNA will more closely match population divergence and be less prone to incomplete lineage sorting due to lower effective size (Ne) in comparison to nuclear markers. Moreover, it allowed us to efficiently maximize the number of sites with sequences, thereby minimizing the problem of under-sampling within-species divergence. Hence for Analysis 2, the number of sites per species was maximized (Fig 2). Sample site numbers for Analysis 2 that are not also used in Analysis 1 are given for each species in Thorpe et al. (2015), or Appendix A in supplementary materials. This gave us dense to very dense sampling for all the *roquet* series species (even the small island of Blanquilla has several sampled sites and St Lucia has over 80), with *A. oculatus* (Dominica), and the western and eastern *A. marmoratus* from the *bimaculatus* series, being well sampled.

We calibrated our Analysis 2 phylogenetic tree by constraining the age of the tree root. This age was estimated by reanalysis of the dataset and calibrations used in a previous phylogenetic study of iguanian lizards (Townsend et al., 2011), in order to recover the mean age of the *Anolis* crown group. Based on reanalysis of the Townsend et al. (2011) dataset, we calibrated the *Anolis* tree root using a normal prior with a mean age of 44.9 mybp and a 95% confidence interval of 36.1–53.3my (T. Townsend, pers. comm.).

3. Results

3.1 Analysis 1: Multilocus tree

We generated a combined total of 2453bp DNA sequence from five single copy nuclear genes (621 bp of NTF3, 516 bp of PRLR, 344 bp of R35, 729 bp of RAG1, 330 bp of Rhodopsin), for the numbered sites in Fig 2, together with 1041 bp mitochondrial DNA (cyt b) sequences for these sites. Concatenated analysis of nuclear sequences without mitochondrial DNA gave a phylogeny with well supported interspecific relationships above the level of species complexes (Appendix B in supplementary materials). While concatenated analysis of all sequences provided complete resolution (posterior clade probabilities all >0.95) of interspecific relationships within the *roquet* series and almost complete resolution within the *bimaculatus* series (except at the *nubilis* and *marmoratus* node) (Fig. 3). The topology was confirmed by the congruent maximum likelihood tree (Appendix C in supplementary materials). The analysis 1 phylogeny supported the monophyly of almost all nominal species with multi-individual sampling, except where there are multispecies complexes. In the *bimaculatus* series, the *marmoratus* complex has *A. sabanus* (Saba) nested within the western *marmoratus* (Basse Terre) lineage rendering it paraphyletic, and *A. desiradei* as sister to the eastern *marmoratus* (Grande Terre plus) lineage. The *roquet* complex contains *A. extremus* (Barbados) nested among the Martinique "species" from the precursor islands, with the central Martinique *A. roquet* as the sister lineage.

Within the *roquet* series, a major division exists between the lineage (*A. luciae, bonairensis, blanquillanus*) and the lineage (*A. roquet*, e*xtremus, trinitatis, aeneus, richardii, griseus*). Notably these two primary lineages within the *roquet* series do not inhabit geographically distinct regions. The lineage (*A. roquet*, e*xtremus, trinitatis, aeneus, richardii, griseus*) then splits into a lineage (*A. trinitatis, richardii, griseus*) from the more southerly LA islands of St Vincent and Grenada, and a more widely distributed lineage (*A. roquet*, e*xtremus, aeneus*) from Martinique, Barbados and Grenada. The large species of *A. richardii* and *A. griseus,* from Grenada and St Vincent respectively, are sister taxa, while the small species (*A. aeneus, A. trinitatis*) are not. Neither of the large and small pairs on St Vincent (small *A. trinitatis,* large *A. griseus*), and Grenada (small *A. aeneus,* large *A. richardii*) are sister species. All these major divisions of the *roquet* series are well supported.

However, in the *bimaculatus* series there are some geographic trends. The northern species *A. leachi, A. bimaculatus,* and *A. gingivinus* (from Barbuda/Antigua, St Kitts/Nevis, Anguilla/St Martin respectively) group together, as do those from the more southerly regions of the *bimaculatus* series range, that is, *A. terraealtae* (Les Saintes) and *A. oculatus* (Dominica). The species from the more central part of the *bimaculatus* series range, *A. ferreus, A. lividus, A. nubilis*, and the *marmoratus* complex, also group together.

One of the purposes of the multilocus Analysis 1 is to contribute to defining the evolutionary units or "species" to be dated in Analysis 2. For the *roquet* series the nominal species *A. luciae, A. trinitatis, A. griseus, A. aeneus, A. richardii, A. bonairensis,* and *A. blanquillanus* are reciprocally monophyletic and on this criteria are not excluded from the dating in Analysis 2. *Anolis extremus* (Barbados) is nested inside the four major lineages of the *roquet* complex from Martinique in conformity with previous studies (Thorpe and Stenson, 2003; Thorpe et al., 2010; Surget–Groba and Thorpe, 2013). Investigations of the geology, phylogeography and population genetics of this complex elucidate how the four *roquet* "species" occupied four of the precursor islands (NW Martinique, SW Martinique, S Martinique and central Martinique) that have geologically recently joined to form current day Martinique resulting in secondary contact with varying degrees on introgression. The nominal species *A. extremus* evolved on Barbados after having probably been colonized from the central Martinique precursor island. Consequently, these five reciprocally monophyletic lineages are regarded as independent entities for the purposes this study, and join the seven nominal species above in being eligible for dating in Analysis 2.

The species of the *bimaculatus* series are less well sampled and the situation is more complex. The Dominican species (*A. oculatus*) is monophyletic and is eligible for inclusion in the dating analysis. The situation with the *marmoratus* complex is less well studied than the *roquet* complex. Once again there appears to be two broad reciprocally monophyletic allospecies associated with precursor islands of Basse Terre and Grand Terre (although the Grande Terre plus outlying islands lineage now also occupies eastern Basse Terre). However, *A. sabanus,* while being distinctly different in appearance*,* is not reciprocally monophyletic with the Basse Terre lineage, but is nested within it. Moreover, *A. desiradei* and Grande Terre *A. marmoratus* are sister lineages nested within the *marmoratus* complex. The recognition of these allopatric species inevitably has arbitrary aspects, and this allows various interpretations of the evolutionary units to be dated.

3.2 Analysis 2: Molecular dating

We assembled a dataset of 459 mitochondrial DNA sequences from the *roquet* and *bimaculatus* series, comprising 1041bp of aligned cyt b sequence (all sites in Fig. 2). We found high levels of haplotype diversity. Sequences from 339 individuals of nine species in the *roquet* series yielded 319 unique cyt b haplotypes. Reduced sampling for the *bimaculatus* series prevents a robust comparison, but the rates of haplotype discovery in the two well-sampled species suggests similar levels of diversity. The large-sample, single-gene Yule tree (Appendix D in supplementary materials) is generally congruent with the reduced-sample, multilocus tree from Analysis 1.However, details of the *marmoratus* complex from the *bimaculatus* series differ. Here, the western *A. marmoratus* lineage (Basse Terre) is no longer monophyletic, since two individuals from western Basse Terre join *A. nubilis* (Redonda) as an out-group to the otherwise congruent *marmoratus* complex. Hence, the inclusion of western *A. marmoratus* as an evolutionary unit to be dated is compromised, as is the dating of the whole *marmoratus* complex, as these units include the nominal species *A. nubilis* in contradiction to the multilocus tree.

For the *roquet* series, the *roquet* complex is eligible to be dated, as potentially are the “species” NW *A. roquet,* SW *A. roquet* , S *A. roquet* , central *A. roquet*, *A.* e*xtremus, A. trinitatis, A. aeneus, A. richardii, A. griseus, A. luciae, A. bonairensis, and A. blanquillanus*. However, the latter has to be excluded because there are too few samples within the species to adequately sample the diversity, and S Martinique and central Martinique *roquet* have to be excluded because of the potential for bottlenecks reducing the within species diversity. Although the central Martinique lineage now occupies quite a large area, the lack of phylogeographic structure (Thorpe and Stenson, 2003; Thorpe et al., 2010), and relative low diversity, is suggestive of bottlenecking. However, this still allows a strong sample of species to be dated within the *roquet* series. The situation with the *bimaculatus* series is less useful. The species *A. leachii, A. bimaculatus, A. ferreus, A. nubilis, A. sabanus*, and *A. terraltae*, are not sufficiently well sampled to allow robust dating based on within-species diversity. Moreover, the diversity of those on the smaller islands and islets (e.g. Redonda, Les Saintes) may be impacted by bottlenecking. Dating of some of the components of the *marmoratus* complex is also difficult given the complications explored above (incongruence, outliers and species limits).

The median and 95% HPD of the appropriate time to most recent common ancestor (TMRCA) dates are given in Table 1, and illustrated in Fig 4. The age of the *roquet* series, based on within-series divergence is about 32 mybp, while the *bimaculatus* series, using the same criteria is younger at about 22 mybp. The age of the eligible species in the *roquet* series (NW *A. roquet,* SW *A. roquet* , *A.* e*xtremus, A. trinitatis, A. aeneus, A. richardii, A. griseus, A. luciae,* and *A. bonairensis*) are all under 5 my with an mean age of 2.5 my. Hence, the well sampled individual species in the *roquet* series are very much younger than the series itself: on average only a thirteenth of the age of their series. Even the multispecies *roquet* complex is only 7.6 my old, approximately a quarter of the age of its series.

The Dominican anole (*A. oculatus*) from the *bimaculatus* series is relatively young at just under 4 my and the eastern *A. marmoratus* lineage (Grande Terre plus offshore islets) dates at a very similar 4.4my. If the incongruent *A. nubilis*+outliers are excluded, the western

A. marmoratus lineage (western Basse Terre plus *A. sabanus*) is also a comparable 3.6 my old. The *marmoratus* complex is 6.9 my old if the *A. nubilis*+outliers are excluded, and 7.6 my if not. In any event there a few species to be robustly dated, but, one again, they are much younger than the age of the series (about a fifth depending on the definition of a "species").

4. Discussion

4.1 Species relationships

Earlier molecular phylogenies of Lesser Antillean anoles relied heavily on mtDNA analyses (Creer et al., 2001; Stenson et al., 2004), although other data (allozymes for the former, microsatellites for the latter) were included. These studies of the *bimaculatus* (Stenson et al., 2004) and *roquet* (Creer et al., 2001) series were far less well resolved and supported than the current multilocus study, which has only one key node with relatively poor support (in the *bimaculatus* series) (Fig. 3). Even so there is broad congruence between the trees from these earlier studies and the multilocus tree. They do, however, differ in node support and in the important detail of the topology. A recent phylogeny of all extant *Anolis* species (Poe et al., 2017), based on mtDNA and a nuclear exon, failed to resolve the relationships within either the *roquet* or *bimaculatus* series as the nodes were generally very poorly supported at this level. The *bimaculatus* and *roquet* phylogenies of Poe et al. (2017) are notably incongruent with the well-supported phylogeny in this study.

One novel aspect of the resolved *roquet* series phylogeny is that the two larger species (*A. griseus*, St Vincent: *A. richardii*, Grenada) are sister taxa, and that neither of the two species pairs on St Vincent (*A. griseus* and *A. trinitatis*), or Grenada (*A. aeneus, A. richardii*), are sister taxa. There is evidence from Thorpe et al. (2010) and Surget-Groba et al. (2012), that there can be notable reduction in gene flow between populations from different habitat types within an island. However, this study does not provide phylogenetic/biogeographic evidence of within-island speciation.

One of the better known aspects of Lesser Antillean anole biogeography is the tendency for solitary anoles to be of intermediate size while with sympatric pairs one tends to be large and the other small. However, this is not absolute and there are several problems with this characterization, not the least when alternative hypotheses (e.g. character displacement versus size assortment) are to be rigorously tested. Roughgarden and Pacala (1989) suggest that the size differential in sympatric pairs is due to secondary colonization by larger anoles driving the original anole to become smaller to avoid competition, and subsequently being driven extinct. This study does not support of this hypothesis, as although on St Vincent the smaller congener is older, on Grenada, it is the larger of the pairs which is older. Analysis of size evolution across these radiations requires fully-resolved species trees, and the absence of these inevitably imposed limits on earlier attempts at to test causal hypotheses (Butler and Losos, 1997; Creer et al., 2001). Further phylogenetic challenges to the analysis of this relative size evolution come from the limited number of independent evolutionary events (degrees of freedom) available. The resolved phylogeny of the *roquet* series in this study indicates that the current larger species are sister taxa and evolved only once, and while an analysis of the *bimaculatus and wattsi* series requires a similarly resolved species tree, it is apparent that the small-bodied wattsi group is monophyletic (Nicholson et al, 2012) and small body size likely evolved only once. This natural limit to the number of independent evolutionary events may restrict the power of a statistical test. Another challenge is the difference between absolute size and relative size. While it is clear that in both series, one of the sympatic pairs is relatively larger and the other relatively smaller, this does not hold well for inter-island comparisons when sizes are treated as categorical (small, intermediate, large). For example, *A. aeneus* may be categorized as small (Losos, 2009), and is smaller than its sympatric congener on Grenada, but it is still a robust and fairly large anole of comparable size to those classified as intermediate, such as the *roquet* species from Martinique (Appendix E in supplementary materials). Field experiments have shown size to be a target of selection (Thorpe et al., 2005a), and size may vary substantially within a species, showing considerable sexual, spatial and temporal variation. Males are generally substantially larger than females across all species for both radiations, and certain ecotypes within a species (e.g. montane ecotypes in Dominica and Basse Terre) may be notably larger than others (Thorpe et al*.,* 2015). Studies have also shown considerable temporal variation in some, but not all, Lesser Antillean species, with subfossils of some Late Pleistocene species from the *bimaculatus* series were larger than current forms, for example *A. ferreus* (Marie Galante) were 25% larger (Bochaton *et al.*, 2017) and *A. leachii* 60% larger (Losos, 2009) in thev relatively recent past. These factors are all further complicated by the practical issues of quantifying size parameters in an organism with indeterminate growth, and the prospect of evolutionary steps being overwritten by species turnover. Consequently, there is much more to be done in critically analyzing this phenomena using well resolved species trees, adequate sampling at various levels, and taking into account the above issues.

The recognition of allopatric species has an arbitrary element to it, which is exposed in both the *roquet* and *marmoratus* complexes. In the *roquet* complex, *extremus* from Barbados in nested among the previously allopatric lineages of the Martinique *roquet* nominal species. However, detailed population genetic study (Thorpe et al., 2010) shows that, generally, the different lineages within this nominal species exchange nuclear genes where they meet, as if they were conspecific. *Anolis roquet* on Martinique are regarded as nominally conspecific, while *A. extremus,* at least as phylogenetically divergent as most Lesser Antillean anoles, is found on distant Barbados (with no real prospect of genetic exchange with the Martinique populations) and is regarded as a sound nominal species. The situation in the less well-studied *marmoratus* complex from the *bimaculatus* series is even more complex. In a parallel situation to that in the *roquet* complex, there are two prospective precursor islands, Basse Terre and Grande Terre, which have recently approached, but are currently separated by a narrow, shallow, channel. As in the *roquet* complex these precursors have matching lineages (albeit with less lineage – precursor congruence) without evidence of complete genetic isolation where they meet on easterrn Basse Terre (Malhotra, 1992). Hence they are nominally conspecific as *A. marmoratus*. Also *A. desiradei* (La Desirade) is sister to the Grande Terre *A. marmoratus* lineage and is therefore nested inside the *marmoratus* complex. The La Desirade population is quite phylogenetically divergent to its sister lineage and here is regarded as a separate species. Although the Saban population is phylogenetically nested within Basse Terre *A. marmoratus*, it is morphologically distinct, and at a considerable geographic distance, and is regarded as the species *A. sabanus*. The population from the islets of Petite Terre (off shore to Grande Terre) are not phylogenetically divergent and we do not recognize these as separate species based on current available information. We did not include the populations from the islets of Îlet-à-Kahouanne and Tête-à-Anglais offshore to north Basse Terre, but see no published evidence to warrant their recognition as separate species (Meiri, 2016), and its phylogenetic relationships in Poe et al. (2017) are very poorly supported, make little geographic sense, and have little phylogenetic congruence with this, or previous, studies.

4.2 The evolutionary and geological timescale

The *roquet* and *bimaculatus* (excluding the *wattsi* group) series arose around 32 and 22 mybp respectively (Fig. 4, Table 1) after the origin of the older outer arc of Lesser Antillean islands in the Eocene to Miocene (Wadge, 1994), but before the origin of the younger inner arc (Bouysse, 1984). These geological dates are compatible with the invasion of the older arc from the south (S America) by the *roquet* series, and from the north (Greater Antilles) by the *bimaculatus* series, that is, step one in the above model. The subsequent invasion of the younger arc, once again by the *roquet* series in the south, and *bimaculatus* series in the north (step 2), could be achieved once the individual younger islands arose (circa <8 mybp). The difference in age of the two series is misleading, and it does not mean that the *roquet* series invaded the Lesser Antilles before the *bimaculatus* series. The *wattsi* complex of small northern anoles, which are phylogeneytically (Poe et al., 2017) and morphologically distinct from the more morphologically robust *bimaculatus* series, are not included in this analysis. Their inclusion as part of the *bimaculatus* series would increase the diversity, and hence estimated age, of this series. The current north-south distribution of anoles in the Lesser Antilles is not shown in other animal groups and, given the dynamics of species turnover, we cannot necessarily assume that the relative distribution of these two series has been stable over time.

Based on within-species divergence, the extant species are estimated to have arisen after the geological origin of their respective islands (Fig 4, Table 1, Appendix F in supplementary materials), as one would expect if the dating of the origin of both island and species is correct. One notable exception to this is *A. extremus* on Barbados. Barbados, unlike most other Lesser Antillean islands is not volcanic in origin, but is an accretionary prism covered by sedimentary rock. Although the underlying rock is ancient it is thought that it uplifted only recently (Bender et al., 1979) and the sedimentary capping suggests an age of emergence about a 0.5 to 1.0 milion years (Speed, 1994). There is substantial, hierarchal phylogeographic structure in *A. extremus* within Barbados (which is compatible with the slightly greater, between-species divergence, within the *roquet* complex) (Table 1). There are no suitable series of adjacent islets to act as alternative refugia with divergent populations from which mainland Barbados could be recolonized. Hence, the situation cannot readily be explained by anything other than at least some of the Barbados accretional prism being above water and inhabitable for much longer than 1mybp. This is discussed in detail in Thorpe et al. (2005b) and the dates for the *roquet* complex and its constituent lineages, including *extremus* from Barbados, are compatible with the previous focused studies (i.e. 95% limits generally overlap).

Both the geological and molecular dating in the *marmoratus* complex and associated islands are complicated. La Desirade (Maury et al., 1990) is very ancient (predating the origin of all the lineages discussed here), while the dating of Grande Terre is complicated in a similar way to that of Barbados:- that, is the underlying rocks may be older, but it has a more recent sedimentary limestone cap and one cannot be sure that none of Grande Terre (or in this case, any other associated island or islet within easy colonization distance) was not above water and available for the *marmoratus* complex to inhabit. Consequently, the best date available is that of high elevation Basse Terre dated at 4-6 mybp (Maury, 1990). These geological dates overlap the 95% HPD values for the complex (all lineages), although they are below the mean value. However, here the phylogenetic information may be less reliable (in contradiction to the multilocus study) as another species (*A. nubilis*) and two Basse Terre specimens are included as outliers in this complex. This will exaggerate the within-complex divergence, and once these are excluded the geological dates are more compatible with the within-complex, and within-“species” ages of 6.9 mybp for the *marmoratus* complex, and 3.6 mybp for the western *A. marmoratus* (Basse Terre, Saba).

One of the notable facets of Table 1 is the discrepancy between the age of a species estimated from within species divergence, compared to the age estimated from between-species divergence. While in some situations (such as the *roquet* complex) between-species divergence is no greater than within-species divergence than one would expect, in others the discrepancy is very notable. For example, the within-species divergence of *A. luciae* is likely to be reliable as it is based on exhaustive phylogeographic sampling, with little likelihood of bottlenecking having occurred on this large, high-elevation island. The within-species estimate for the age of *A. luciae* is only 3.3my (2.3 - 4.3 95% HPD), while the between-species estimate is 23.4 (17.2- 29.6 95% HPD). While this is an extreme case, it nevertheless holds true as a generalization for situations where the phylogeny, phylogeographic sampling, and insensitivity to bottlenecking, allow meaningful estimates of within-and among species divergence (e.g., *A. luciae, A. trinitatis, A. griseus, A. aeneus, A. richardii,* and *A. oculatus*). It is clear that using between-species divergence to estimate species age could lead to a very misleading, gross over-estimation. On small, or low-elevation, islands bottlenecking can potentially greatly reduce within-species divergence so that species age cannot be reliably estimated from within-species divergence. In these situations, and where phylogeographic sampling does not allow an estimate of within-species divergence, then at least between species divergence may give an upper bound to the species age, however unrealistic it is as an estimate of the real age. However, considerable caution is required when using these inter-species estimates, because they can give ages greater than the age of the island, emphasizing their unreliability.

4.3 Species age and inter-island colonization

The other, and perhaps most important revelation from Table 1, is the age of the species compared to the age of the entire series. While the series are Oligocene in origin, the species are Pleistocene to Pliocene, with even the large species complexes no older than very late Miocene. The average age of a species in the *roquet* series (excluding underestimations due to potential bottlenecking or inadequate sampling) is only about 8% of the age of the series. Although it is an extreme case, we use *A. luciae* from St Lucia as an example, because it is exhaustively sampled and therefore unlikely to give an underestimate of species age due to inadequate sampling. St Lucia combines both young and old arc elements, and is dated at about 18 mybp (Briden et al., 1979), while the current extant species age is estimated at only 3.3 my old. Could St Lucia have been unoccupied by anoles prior to the establishment of *A. luciae* ? This is most unlikely, given the complete occupation of every island and islet in the Lesser Antilles. Given the size and elevation of the island, and the phylogeographic structure of the species, it is also unlikely that bottlenecking has substantially underestimated species age. This study provides no evidence of within–island speciation, so serially repeated *in situ* within-island speciation, with the new species repetitively replacing the old, is also an unlikely explanation. It is also unlikely that the species age (estimated by mtDNA) has been grossly under-estimated by serially repeated, or at least recent, selective sweeps eradicating all earlier haplotypes. The most likely explanation is that there is species turnover with the island being occupied by a series of different anoles through time with colonizers replacing residents by competitive exclusion, perhaps (but not necessarily) with additional factors, such as disease and extreme physical events (volcanism, hurricanes), impacting the process. We are not aware of any anole extirpations due to recent hurricanes, volcanism or disease, and even the massive volcanic event in Dominica 28 ky ago did not expurgate *A. oculatus* (Malhotra and Thorpe, 2000). These additional proximal reasons may be irrelevant to the broad picture of competitive replacement by new colonizers. In any event, the age of the Lesser Antillean anole species is not exceptional, and is what one would expect for a small terrestrial amniote. The species ages in this study are compatible with estimates of mean species age in other northern hemisphere squamates of 3.3 my (Dubey and Shine, 2010), the average persistence time of an island population of birds in the Lesser Antilles of about 2 my, (Ricklefs and Bermingham, 2007), and a modal age of 1-2 my for small North American mammals (Prothero 2014). What emerges is that the current biogeographic pattern, in geological terms, is likely to be just a temporary time-slice of a very dynamic situation, with substantial species turnover throughout the long life of the radiations.

Species turnover has important implications, not least for attempts to understand the colonization sequence within the Lesser Antilles (i.e. step 2 inter-island colonization). As the *bimaculatus* series phylogenetically splits into northern, middle and southern islands, it is tempting to interpret this as an earlier-to-later colonization sequence from north to south down the Lesser Antillean chain (Stenson et al*.*, 2004). However, given that 1) the younger arc did not exist at the origin of either of the series, and 2) that the species involved in the early inter-island colonization sequence no longer exist, attempts to reconstruct these early stages (Stenson et al., 2004; Losos, 2009) are inevitably spurious.

Although reconstructing the early stages of inter-island colonization may be problematic, recent events, such as paraphyly (where one island species is nested inside another island species) may enable some recent inter-island colonizations to be reconstructed (Fig. 5). Indeed, if no species or haplotypes were lost, one would expect the phylogeny for a radiation to be a complete, sequential, pectinate comb with each species nested inside the next. In fact, paraphyly appears to be relatively rare, the early events being eradicated by lineage loss and species turnover. There are a few examples of species paraphyly established here (the number depending on the arbitrary recognition of allopatric species). The Barbados anole is nested within the nominal (paraphyletic) *A. roquet* species, and *A. sabanus* (Saba) and *A. desiradei* (La Desriade) are nested within the nominal (paraphyletic) *A. marmoratus* species.

The origin and colonization sequence of the four *A. rouqet* lineages on the respective precursor islands of Martinique, and *A. extremus* from Barbados, are discussed in detail in Thorpe et al. (2010) and Surget-Groba and Thorpe (2013). Barbados appears to have been colonized from the relatively distant Martinique complex (Fig 5), being a sister lineage to the central Martinique lineage within the *roquet* Martinique complex (Thorpe and Stenson, 2003; Thorpe et al., 2010; Surget-Groba and Thorpe, 2013). The colonization sequence within this complex suggested by Thorpe et al. (2010) and Surget-Groba and Thorpe (2013) is the divergence of the south and southwest *A. roquet* on their respective precursor islands, the colonization of the central Martinique precursor from the south Martinique precursor, the subsequent colonization of Barbados from this central Martinique, and the colonization of the northwest Martinique precursor from the southwest Martinique precursor.

In the *marmoratus* complex, from the northern *bimaculatus* series, nominal species on small islands are nested inside a nominal species from a main island complex, with primary lineages that may correspond to precursor islands. Unlike the situation in Martinique where the four lineages correspond very closely with the four precursor islands, here there are two primary parapatric lineages (western and eastern *marmoratus*) that correspond less closely with the two presumed precursor islands of Basse Terre and Grande Terre. In this case eastern *A. marmoratus* (primarily Grande Terre) extends substantially into eastern Basse Terre (Fig. 2B, 5). The two main islands, Basse Terre and Grande Terre, currently approach at a narrow, low elevation isthmus, but presumably these were separate islands in the past. While alternative scenarios are possible, the simplest explanation is that the western and eastern lineages diverged on Basse Terre and Grande respectively after about four to six million years ago when they were both emerged separate islands (Fig. 5), and the eastern lineage, based originally in Grande Terre, has subsequently spread into eastern Basse Terre. Subsequently to this east–west split, La Desirade was colonized from eastern *A. marmoratus* on Grande Terre, and geographically distant Saba was relatively recently colonized from western *A. marmoratus* on Basse Terre (Fig 5). It is also reasonable to assume that Petite

Terre has recently been colonized by eastern *A. marmoratus* on adjacent Grande Terre, as it is nested within this lineage (Fig. 5). Although the critical populations of *A. marmoratus* (i.e, those involved in the eastern and western *marmoratus* contact) have not been the subject of similar population genetic research as *A. roquet* (Thorpe et al., 2010), morphological continuity among eastern and western lineage populations (Malhotra, 1992) suggests the situation is the same as in Martinique. Hence, we have nominal species that are nested inside, and are phylogenetically shallower than, the main island primary lineages which are formally treated as conspecific.

Examples of similar cases of paraphyly exist in other Lesser Antillean lizards. For example, west Basse Terre also appears to be the source of the Dominican gecko (*Sphaerodactylus fantasticus*) as the Dominican population is nested within the western Basse Terre lineage for these geckos (Thorpe et al., 2008), while the Dominican lineage of *S. festus* is nested within the northern Martinique lineage (Surget-Groba and Thorpe, 2013). In all these cases, a prerequisite for paraphyly to be exposed is multiple sampling of each island species. In the *bimaculatus* series several species are represented by only single samples, so even if paraphyly existed with extant species it would not be exposed by this study.

Without paraphyly it can be difficult to infer the colonization process even with sister species. The large-bodied *A. richardii* (Grenada and Grenadines) and *A. griseus* (St Vincent) are sister species, but their age is similar (2.4 and 2.1 my respectively) so it is not possible to know whether the colonization direction was from Grenada/Grenadines to St Vincent, or *vice versa*, or even from a third, now extinct species on another island. Similarly, the islands of the South American coast (Bonaire and Blanquilla), and St Lucia form a distinct lineage in the *roquet* series (dated by internal divergence at around 23 mybp). While it is reasonable to expect that these offshore S American island were colonized from the Lesser Antilles species, the divergence of this *luciae/bonairensis/blanquillanus* clade, and the *bonairensis/blanquillanus* clade (similarly dated at around 7 mybp) substantially predates the age of *A. luciae* precluding it as the colonizer. Given the suspected species turnover, the colonizer of these S. American islands could have come from any of the (presumably) Lesser Antilles occupied at the time by members of this clade of the *roquet* series.

4.4 Potential dispersal outcomes

It is clear that in Lesser Antillean anoles, and we expect in other radiation, Step 2 is not simply a question of the original colonizer dispersing to a series of empty islands in sequence. In the potential colonization of an unoccupied island, the two possible outcomes would be success or failure. We have no evidence on how frequently natural extinction of these species occurs, without congeneric competition, leaving islands unoccupied. However, given the high population densities and the current occupation of every island, perhaps most colonization attempt will be from one occupied island to another. And here we postulate five potential outcomes from such a process.

A) The colonizing species is reproductively isolated from the resident species and becomes extinct due to stochastic early extinction, or being out-competed by the resident. It is axiomatic that this can leave no obvious biogeographic signature, even if it is a frequent outcome.

B) The colonizing species (small founder population) interbreeds freely with the resident species, resulting in introgression. The colonizer may leave no obvious genetic signature if the colonizer's genes are too rare to be detected, or are lost due to drift or negative selection. The evidence that allopatry over substantial time does not necessarily result in reproductive isolation (Thorpe et al., 2010) suggests this may be a very frequent outcome. An example of this may be the Caravelle Peninsular population of *A. roquet*, as it is the only Martinique precursor island population without its own distinct genetic lineage. It appears that when this precursor island joined the central Martinique region its anole population was replaced by the central Martinique population. Given the general lack of reproductive isolation among these precursors (Thorpe et al., 2010) it is likely to be introgression rather than an example of process A above, except if the Caravelle Peninsula was occupied by a different species, very divergent from the *roquet* complex.

C) The colonizing species (very large founder population or island coalescence) interbreeds to varying extents with the other or resident species, resulting in varying degrees of introgression, but recognition as a single nominal species. This leaves a genetic and biogeographic signature and each anole series in the Lesser Antilles appears to provide an example of this. The extent of introgression between the four precursor Martinique island population of the nominal species *A.roquet*, is an example (Thorpe et al., 2010; Surget Groba et al., 2012). The colonization of eastern Basse Terre from adjacent Grande Terre by the eastern *A. marmoratus* may be an example of a large founder population, or past island coalescence.

D) The colonizing species is reproductively isolated from the resident and outcompetes and replaces the resident. The ongoing invasion of *A. cristatellus* in Dominica and its replacement of the similar (intermediate) sized, syntopic, resident *A. oculatus* in the south west of the island is direct evidence of at least the first stage of this process (Eales et al., 2010; Malhotra *et al.,* 2007). This is also what is inferred for the St Lucian populations (see above), and may have occurred frequently on the older arc islands. Theories, such as size assortment (Losos, 2009), suggest that an intermediate (solitary) anole could not successfully invade when an island is already occupied by an anole of the same size, but the evidence here does not support this.

E) The colonizing species is reproductively isolated from the resident species and survives and coexists in sympatry with it (Step 4). In the north of the northern Lesser Antilles the sympatry of the smaller-bodied *watttsi* group with the relatively larger *bimaculatus* series provides an example. In the south of the southern Lesser Antilles the species pairs on Grenada (*A. aeneus* –smaller, *A. richardii* -larger) and St Vincent (*A. trinitatis* –smaller, *A. griseus*-larger) provide additional examples. The estimated age of the species suggests that the smaller *A.trinitatis* was the resident in St Vincent before the colonization by *A.griseus*. In Grenada the estimated age of the species are closer and overlap, but the larger *A. richardii* is slightly older and may perhaps have been the resident while *A. aeneus* was the colonizer. It is not possible to know the extent of sympatry in the past, or if these islands are currently saturated with sympatric pairs. One likely case is Marie Galante which has a large anole (*A. ferreus*), but no smaller partner. It is not apparent why some islands have two species and some just one. There is a geographic trend, with the southern islands of the south series, and some northern islands of the north series having two species, while the central islands in the chain (both series) have just a single species. However, this does not appear to have anything to do with the age of the current extant species, island age, or island size.

We can gain an insight into the relative frequency of types C (introgression) and D/E (replacement/sympatry) by dating the outcomes from island coalescence, natural sympatry and artificial (invasive species) sympatry. The secondary contact after the coalescence of precursor island populations from Martinique, even after about 8 my of divergence (Table 1), show widespread introgression of varying degrees, and always more than across ecotones within a single lineage (Thorpe et al., 2010). Even at about 10 my divergence the invasive species of *A.aeneus* and *A. trinitatis* in Trinidad show some hybridization (Hailey et al., 2009). However, the naturally occurring sympatry on St Vincent (*A. trinitatis, A. griseus*) and Grenada (*A.richardii, A. aeneus*) occurs after about 15 and 20 my divergence respectively. Similarly, there is no introgression between the invasive *A. extremus* and resident *A. luciae* on St Lucia after about 32 my divergence (Giannassi et al., 1997). In the northern Lesser Antilles the small-bodied *watts*i group is naturally sympatric with the larger bodied *bimaculatus* series. Since the *wattsi* group and *bimaculatus series* are reciprocally monophyletic (Poe et al., 2017) their divergence must be greater (perhaps much greater) that the within-*bimaculatus* series divergence of 22 my. Hence, it appears that allopatric isolation does not rapidly result in reproductive isolation and that more than 8, but less than 15 my of divergence, is required to achieve this. Consquently, for these anole radiations, introgression is a far more likely outcome in the first half of the radiation process, than replacement or sympatry if the colonized island is already occupied.

4.5 Conclusions from the island radiation model and Lesser Antillean anoles

One can infer several stages of the radiation model in the Lesser Antillean anole radiations. Step 1, the initial colonization (the southern *roquet* series radiation from S. America, the northern *bimaculatus* series from the Greater Antilles) is uncontroversial. Step 2, inter-island dispersal can be inferred for relatively recent events e.g., Barbados from Martinique at circa 3 mybp, (or even later in precursor island coalescence), but is opaque, or overwritten by species turnover, in the early stages of the radiation (i.e., 8-32 mybp). The phylogeographic and quantitative trait divergence within an island species (Step 3) is well documented (Thorpe et al., 2015 and references therein), but a very long time (in excess of 8 my) is required for reproductive isolation. Step 4, (sympatry) is evidenced in a few instances, but these are all quite old (the youngest at 15 my divergence), never involve more than two species, and are inferred to occur only in the second half of the radiation process.

The genus *Anolis sensu* Losos (2009) is regarded as the most speciose amniote genus with around 400 extant species. This study suggests that, at least in the case of the Lesser Antilles and associated islands, estimates based on extant species may greatly under-estimate the number of species and diversity through geological time. However, this may not reflect the situation in the larger islands of the Greater Antilles, where extinction rates at equilibrium in these multispecies anole communities may be low (Rabosky and Glor, 2010).

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Appendices A, B, C, D, E, & F. Supplementary material

Supplementary data associated with this article can be found, in the online version, at

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Table 1 Estimate of ages of Lesser Antillean islands and the *Anolis* species occupying them. Estimate of island and species age from densely sampled island species. Species = nominal species or previously allopatric "species" from precursor islands. Island age = geological island age in million years from literature. Within = within series/species divergence with 95% HPD in brackets, * = sampling inadequate for meaningful estimate. Among = among Series/species with 95% HPD in brackets. [1] These are allopatric "species" (from precursor island) in the *roquet* complex *sensu* Thorpe et al. (2015). [2] The range of the Central Martinique form also includes the Caravelle peninsula which is Oligocene (ca <34mybp). [3] Central and South Martinique include some low elevation areas which may have been under water until recently, and there is no strong phylogeographic structure. Hence these "Within" dates may be underestimates due to bottlenecking. [4] Martinique includes precursor islands from both the younger and older arcs. [5] Barbados is ancient rocks with some more recent limestone capping suggesting recent emergence, but the deep well-structured phylogeography suggests this species has been diverging in-situ for longer (Thorpe et al., 2005b). [6] In the south the younger arc is superimposed on the older arc so cited geological dates may reflect either young arc (St Vincent, Grenada) or older arc (St Lucia) volcanicity. [7] Bonaire and Blanquilla are old islands with younger limestone without sufficient data to confidently indicate a date of origin or emergence, although on the latter, low-elevation island populations may have been bottlenecked. [8] Marie Galante is mid Miocene overlain by more recent deposits (Martin-Kaye, 1969). [9] The range of the *marmoratus* complex includes both Basse Terre (younger arc), and Grande Terre, together with some allopatric populations on islands that can be very ancient (e.g., La Desirade). La Desirade may be Mesozoic, i.e., earlier than the rafiation so this date is not used. Moreover, Grande Terre may be Lower to Mid Miocene (Martin-Kaye, 1969), but it thought to have emerged more recently (Maury et al., 1990). Dating the range of the nominal species is therefore complicated, and here we just consider the younger arc island, Basse Terre, with its main lineage distributed over the centre and west of the island at 4-6mybp (Maury et al*.,* 1990) for the complex and its components. [10] One specimen among several, for both localities 2 and 7 in western Basse Terre (maBT02_08 and maBT07_39 respectively), join incongruently (with Analysis 1) with *A. nubilis* (Appendix D in supplementary materials), rather than others from the same site or the western *marmoratus* lineage. This would artificially increase both the age of the complex and the eastern *marmoratus* lineage and they are excluded. Their inclusion would increase the age of the complex slightly to 7.6 mybp.

Island/series	Species	Island age	Reference	Yule Within	Yule Among
roquet series				31.60 (23.8-39.1)	43.6 (34.8-52.6)
NW Martinique	NW Mart [1]	7.1	Briden et al 1979	2.38 (1.57-3.29)	4.19 (2.93-5.56)
SW Martinique	SW Mart[1]	8.3	Briden et al 1979	1.73 (1.07-2.45)	4.19 (2.93-5.56)
Central Martinique	Central Mart[1]	12.8-15.9[2]	Briden et al 1979, Wadge 1994	1.46 (0.97-2.00) [3]	4.08 (2.96-5.29)
S Martinique	S Mart[1]	<34	Wadge 1994	1.40 (0.86-1.97) [3]	5.94 (4.35-7.65)

All Martinique	*roquet*	<34[4]	Wadge 1994	7.56 (5.65-9.65)	10.1 (7.40-12.81)
Barbados	*extremus*	[5]	Speed 1994, Thorpe et al 2005	3.35 (2.37-4.33)	4.08 (2.96-5.29)
St Lucia	*luciae*	18.3[6]	Briden et al 1979	3.30 (2.27-4.33)	23.4 (17.2-29.6)
St Vincent	*trinitatis*	3.5[6]	Maury et al 1990	4.23 (2.99-5.64)	15.4 (1.5-19.6)
St Vincent	*griseus*	3.5[6]	Maury et al 1990	2.12 (1.40-2.90)	15.4 (1.5-19.6)
Grenada	*aeneus*	>5[6]	Maury et al 1990, Martin-Kaye 1969	1.82 (1.20-2.47)	10.1 (7.4-12.81)
Grenada	*richardii*	>5[6]	Maury et al 1990, Martin-Kaye 1969	2.44 (1.66-3.26)	19.9 (15.0-25.1)
Bonaire	*bonairensis*	-[7]		1.21 (0.74-1.78)	7.22 (5.10-9.59)
Blanquilla	*blanquillanus*	-[7]		0.60 (0.33-0.91)	7.22 (5.10-9.59)
bimaculatus series				22.1 (16.8-27.8)	43.6 (34.8-52.6)
St Martin Bank	*gingivinus*	37	Briden et al 1979, Maury et al 1990	*	14.5 (9.91-20.0)
Saba	*sabanus*	0.4	Roobol and Smith 2004	*	2.12 (1.42-2.92)
Kitts Nevis bank	*bimaculatus*	3.4	Maury et al 1990	*	14.5 (9.91-20.0)
Antigua Barbuda Bank	*leachi*	40	Briden et al 1979	*	19.6 (14.9-24.6)
Redonda	*nubilis*	<1.5	Maury et al 1990	*	5.96 (4.21-7.97)
Montserrat	*lividus*	4.4	Briden et al 1979, Maury et al 1990	*	9.37 (6.95-12.0)
Illes des Saintes	*terraealtae*	4.7	Maury et al 1990	*	13.6 (10.1-17.3)
Marie Galante	*ferreus*	[8]		*	12.0 (8.87-15.2)
Guadeloupe (excl I d Saintes, Marie	*marmoratus complex*[9,10]	(4-6)	Maury et al 1990	*6.91 (5.12-8.74)	7.61 (5.55-9.81)

Galante)					
Grande Terre + East BT + Petite Terre+Desirade	Eastern *marmoratus*+ *desiradei* [9]	(4-6)	Maury et al 1990	5.74 (4.12-7.37)	6.91 (5.12-8.74)
Desirade	*desiradei* [9]	mesozoic	Maury et al 1990	*	5.74 (4.12-7.37)
Grande Terre +eastern BT+ Petite Terre)	Eastern *marmoratus*[9]	(4-6)	Maury et al 1990	4.40 (3.10-5.77)	5.74 (4.12-7.37)
Basse Terre (+Saba)	Western *marmoratus*[10]	4-6	Maury et al 1990	3.62 (2.48-4.82)	6.91 (5.12-8.74)
Dominica	*oculatus*	<5	Maury et al 1990, Martin-Kaye 1969	3.98 (2.85-5.18)	13.6 (10.1-17.3)

Figure 1. Islands and *Anolis* species (in italics) in the Lesser Antilles and associated islands. The *bimaculatus* series is north, and the *roquet* series, south of the dashed line. The insert shows Bonaire and Blanquilla off the South American coast. The *wattsi* complex is not included.

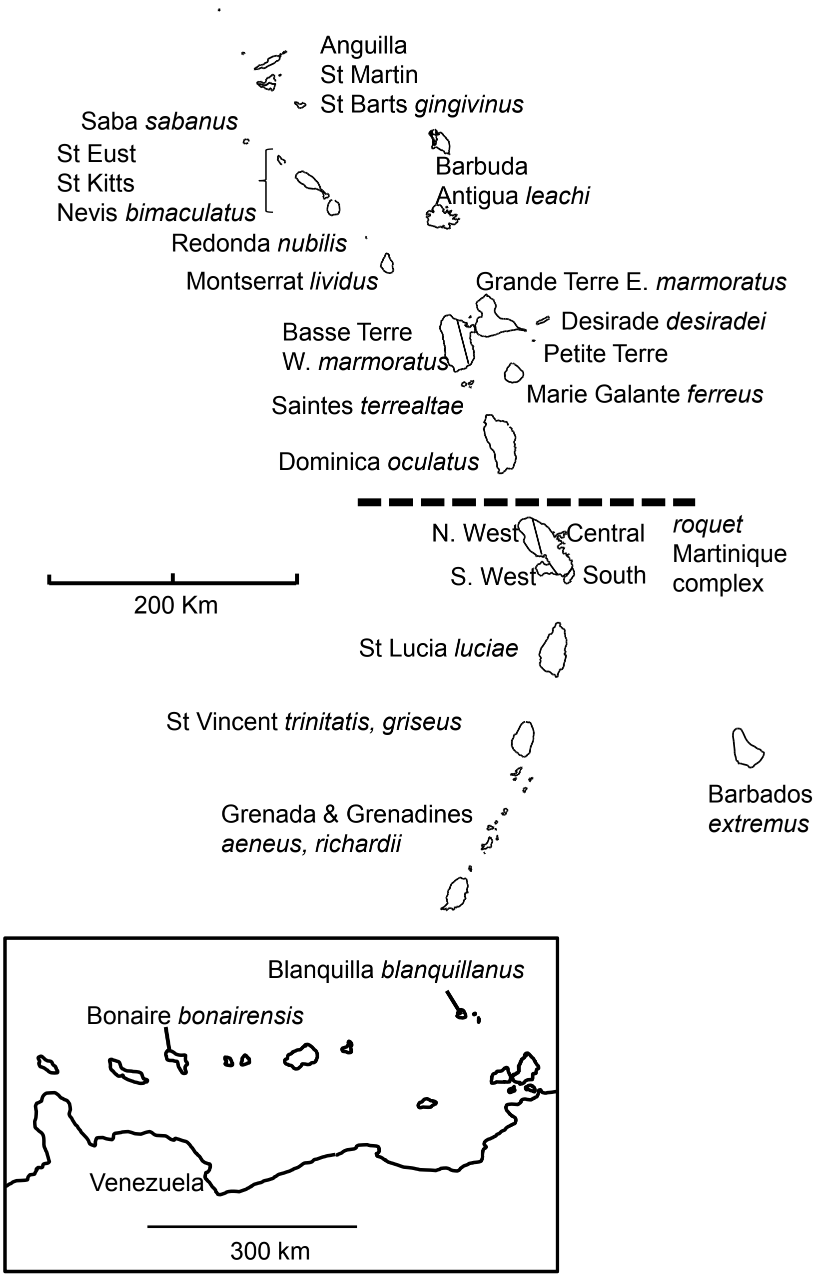
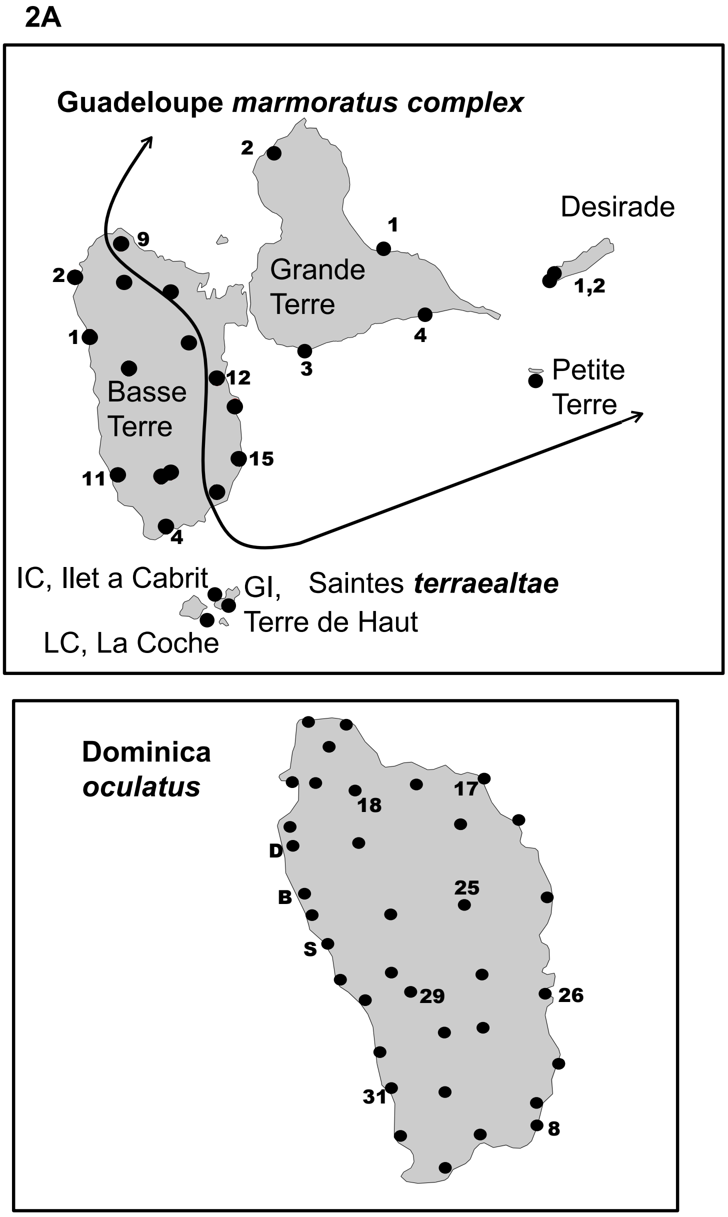


Figure 2. Islands with multiple sampling localities. 2A. *bimaculatus series.* 2B *roquet* series. Not to scale. Localities employed in analysis 1 are numbered; additional localities (Analysis 2) are un-numbered. The lines in Guadeloupe and Martinique indicate the components of the *marmoratus* and *roquet* complexes respectively. On the multiple species islands of St Vincent and Grenada *A. trinitatis*, *A. griseus, A*, *aeneus* and *A. richardii* localities are indicated by t, g, a and r respectively. The identity of all localities and the primary lineages of species are found in Thorpe et al. (2015) for *A. marmoratus* on Basse Terre, *A. oculatus, A. trinitatis, A. richardii, A. aeneus* and *A. luciae*; in Thorpe *et al.* (2005) for *A. extremus*; in Thorpe and Stenson (2003) for the *roquet* complex on Martinique; in Thorpe (2017) for *A. bonairensis*; and in Appendix A in supplementary materials for *A. blanquillanus* and eastern *A. marmoratus*.



2B

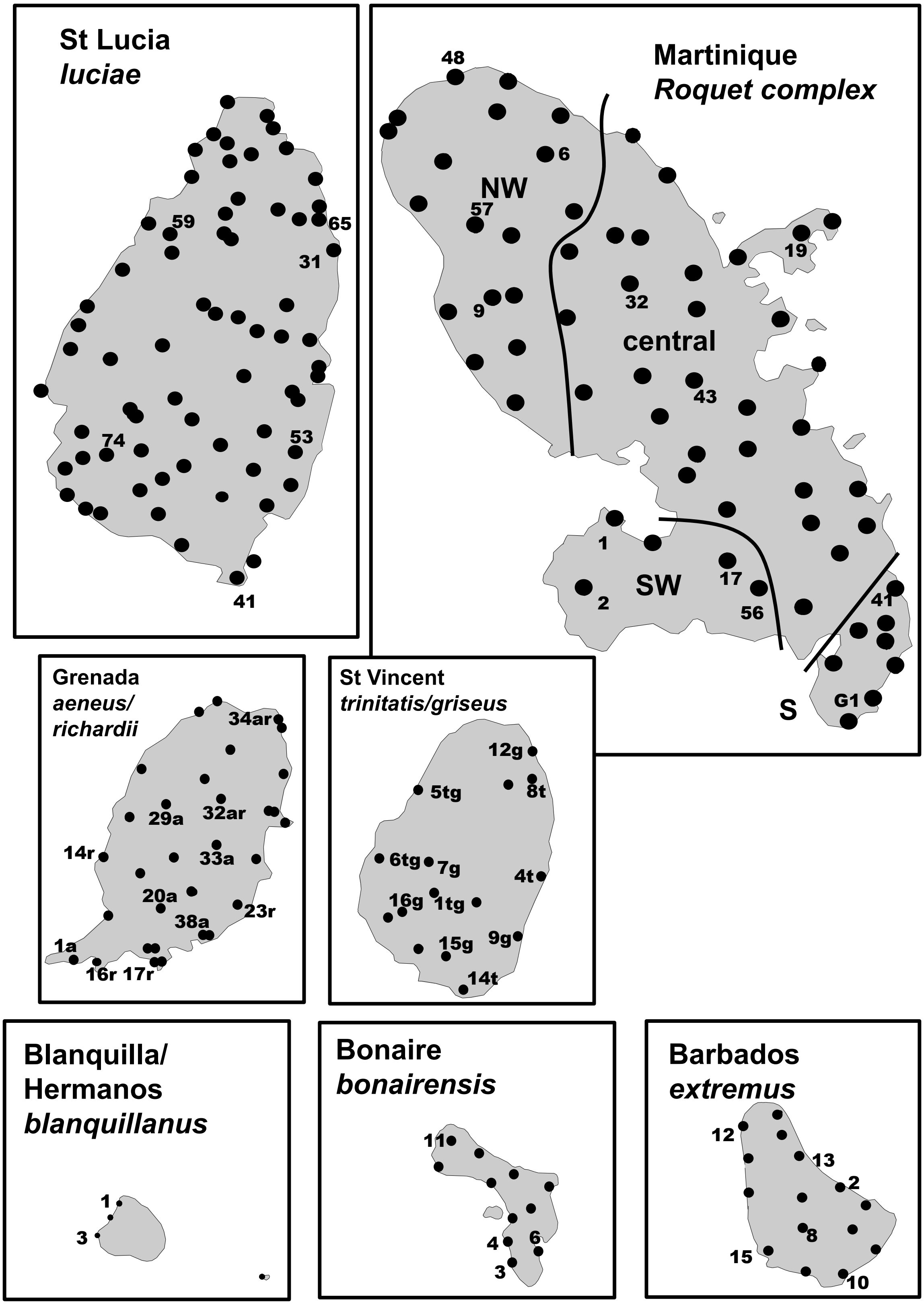

St Lucia
luciae
59
65
31
74
53
41
Martinique
Roquet complex
48
6
NW
57
9
19
32
central
43
1
2
SW
17
56
41
G1
S
Grenada
aeneus/
richardii
34ar
29a
32ar
14r
33a
20a
23r
38a
1a
16r
17r
St Vincent
trinitatis/griseus
12g
5tg
8t
6tg
7g
4t
16g
1tg
9g
15g
14t
Blanquilla/
Hermanos
blanquillanus
1
3
Bonaire
bonairensis
11
4
6
3
Barbados
extremus
12
13
2
8
15
10

Figure 3. Analysis 1 Total evidence phylogeny of Lesser Antillean anoles based on concatenated mitochondrial and nuclear genes. Number at nodes indicate posterior clade probabilities at the level of nominal species, putative precursor "species", and complexes, or above. The species name, island and (where appropriate) locality number are indicated at terminal nodes.

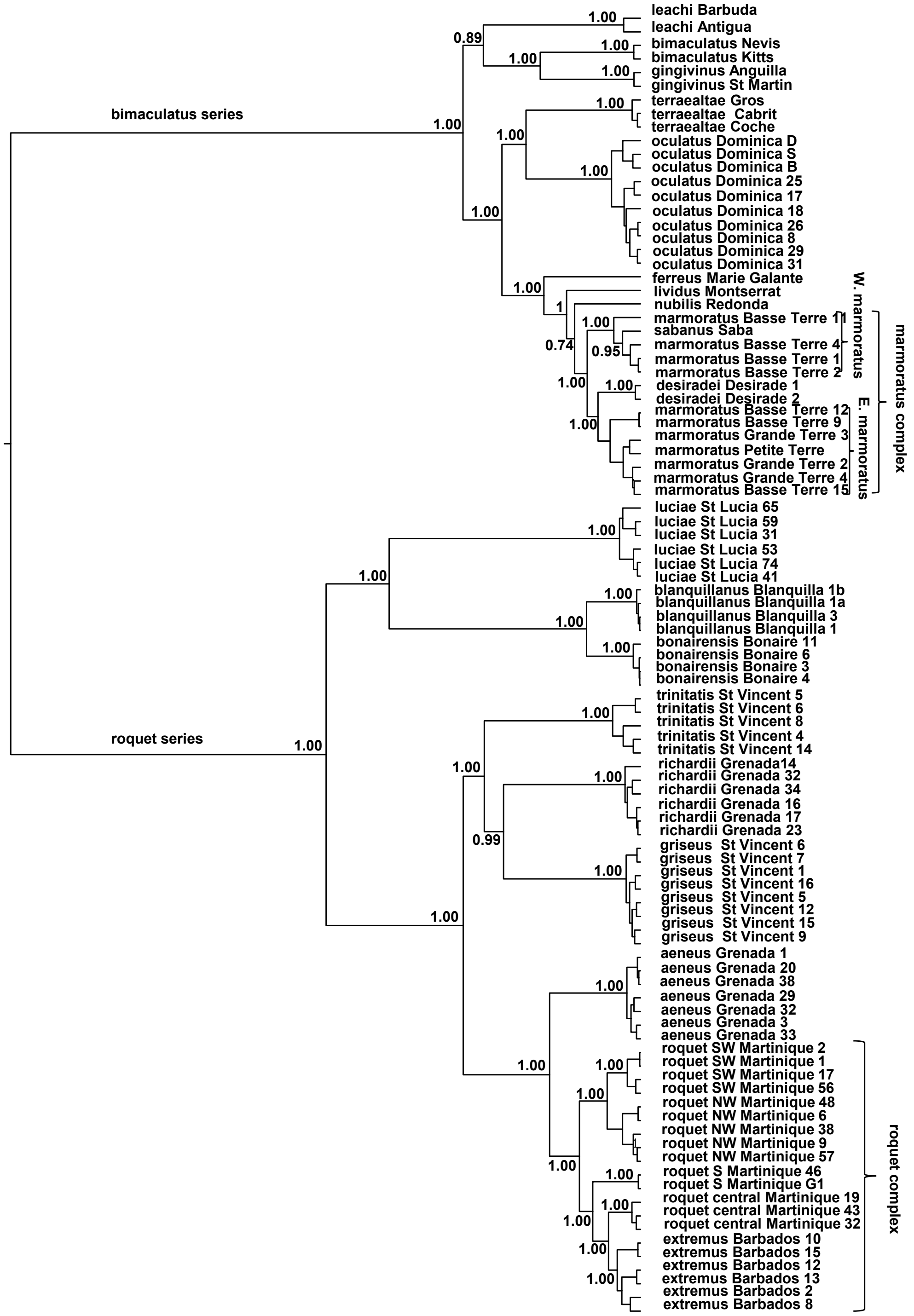


Figure 4. Age of series, species complexes and of substantially sampled species in relation to island ages. The x axis represents time in millions of years before present. Series, species and their islands are listed on the right. For each species and series, points and thick solid bars show the median and 95% HPD of the within species or series TMRCA, respectively. Points with thin dashed lines show the median and 95% HPD of the divergence time between species and their nearest extant relative. Black squares show the ages of islands (with arrow indicating the off-scale, possible, Mesozoic origin of La Desirade). [1] See Table 1 for comments on the age of the *marmoratus* complex.

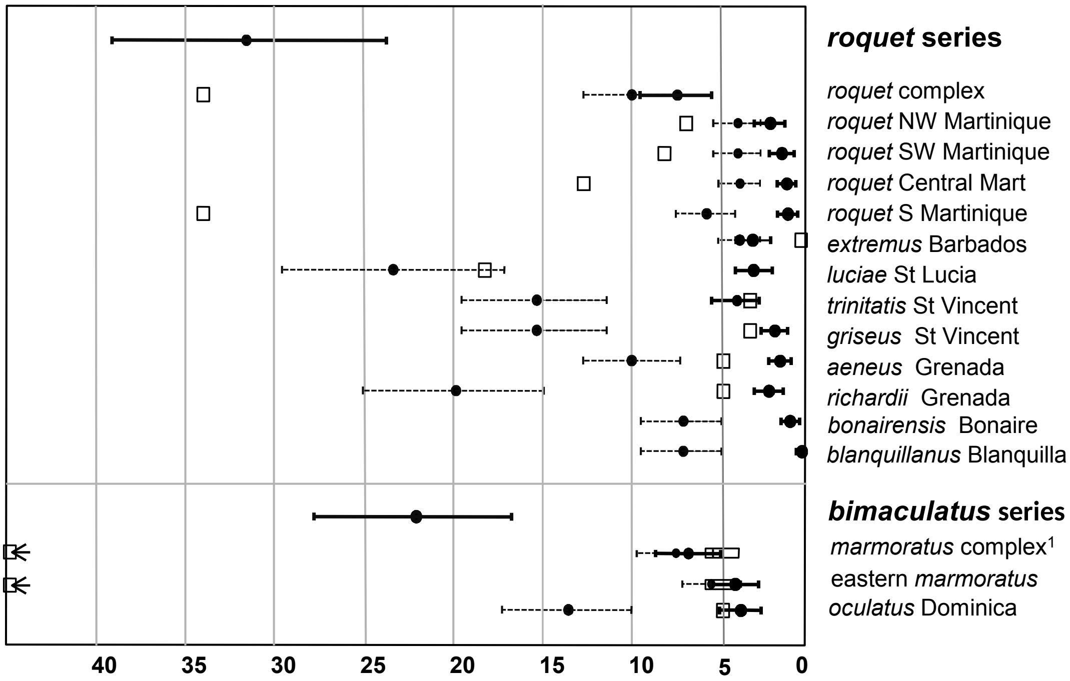
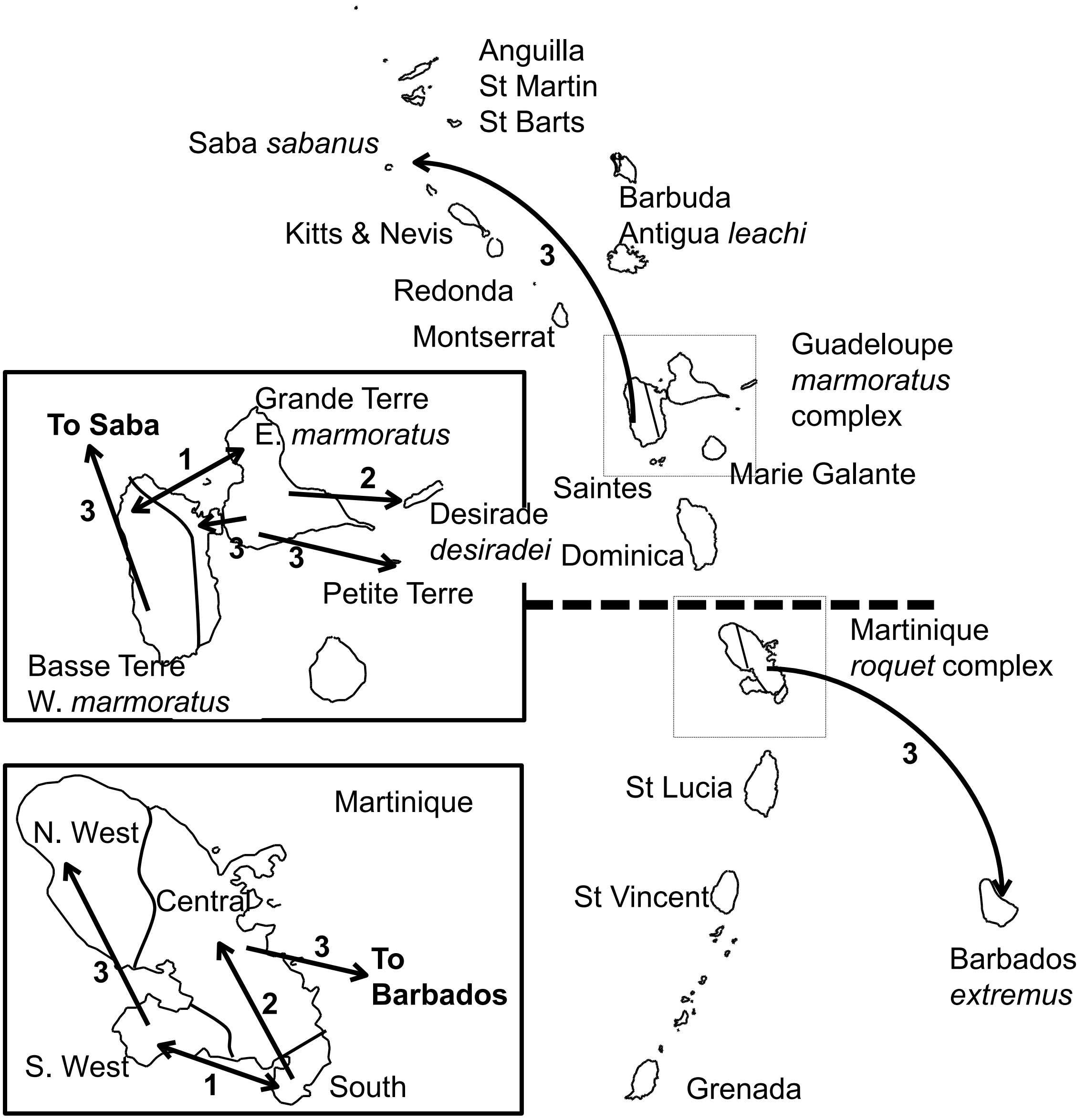
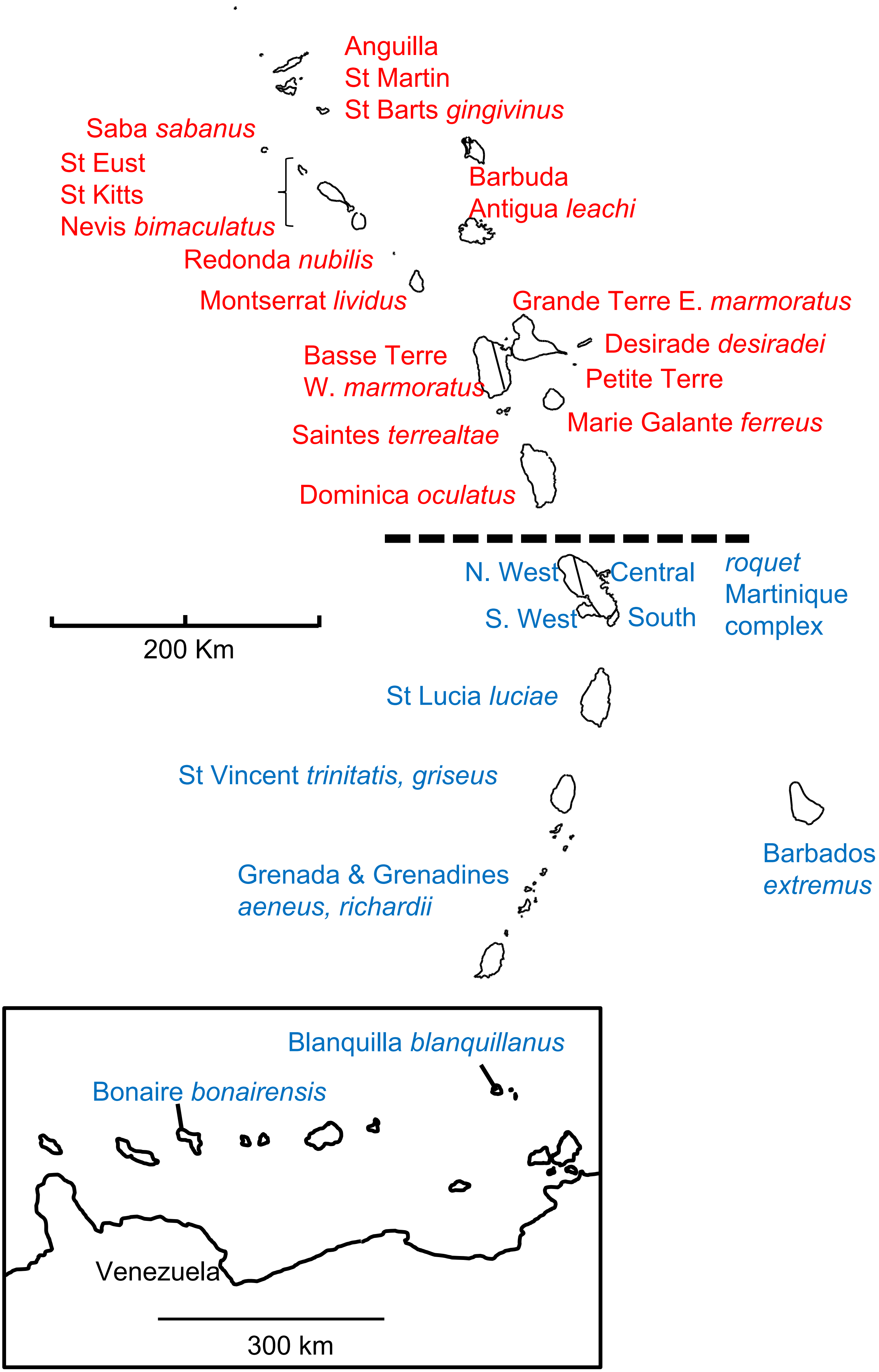
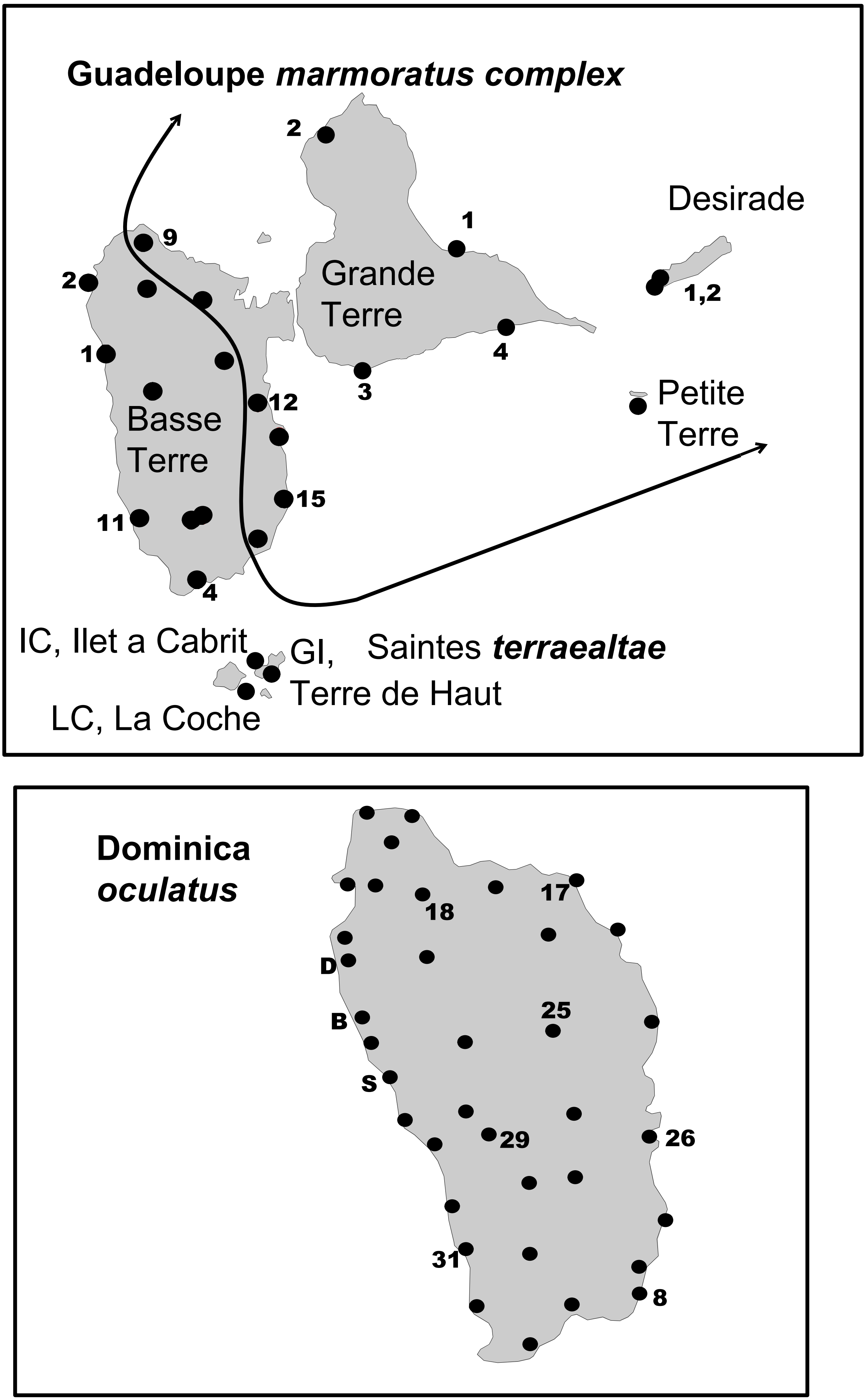


Figure 5. Relatively recent colonization events suggested by paraphyly. There are two long-distance events (colonization of Saba and Barbados) and a series of short distance colonizations from large islands to adjacent smaller islands/islets. In the *marmoratus* complex, 1), the divergence between the Basse Terre and Grande Terre allopatric lineages, is 2), followed by the colonization of La Desirade from Grande Terre, and more recently 3) the colonization of Saba from the Basse Terre (western *marmoratus*) lineage, the colonization of Petite Terre from the Grande Terre (eastern *marmoratus*) lineage, and the spread of the eastern *marmoratus* lineage into eastern Basse Terre. In the *roquet* complex, 1) the divergence of the South Martinique and SW Martinique lineages is followed by 2) the colonization of central Martinique from south Martinique, and then 3) the colonization of NW Martinique from SW Martinique, and colonization of Barbados from central Martinique.

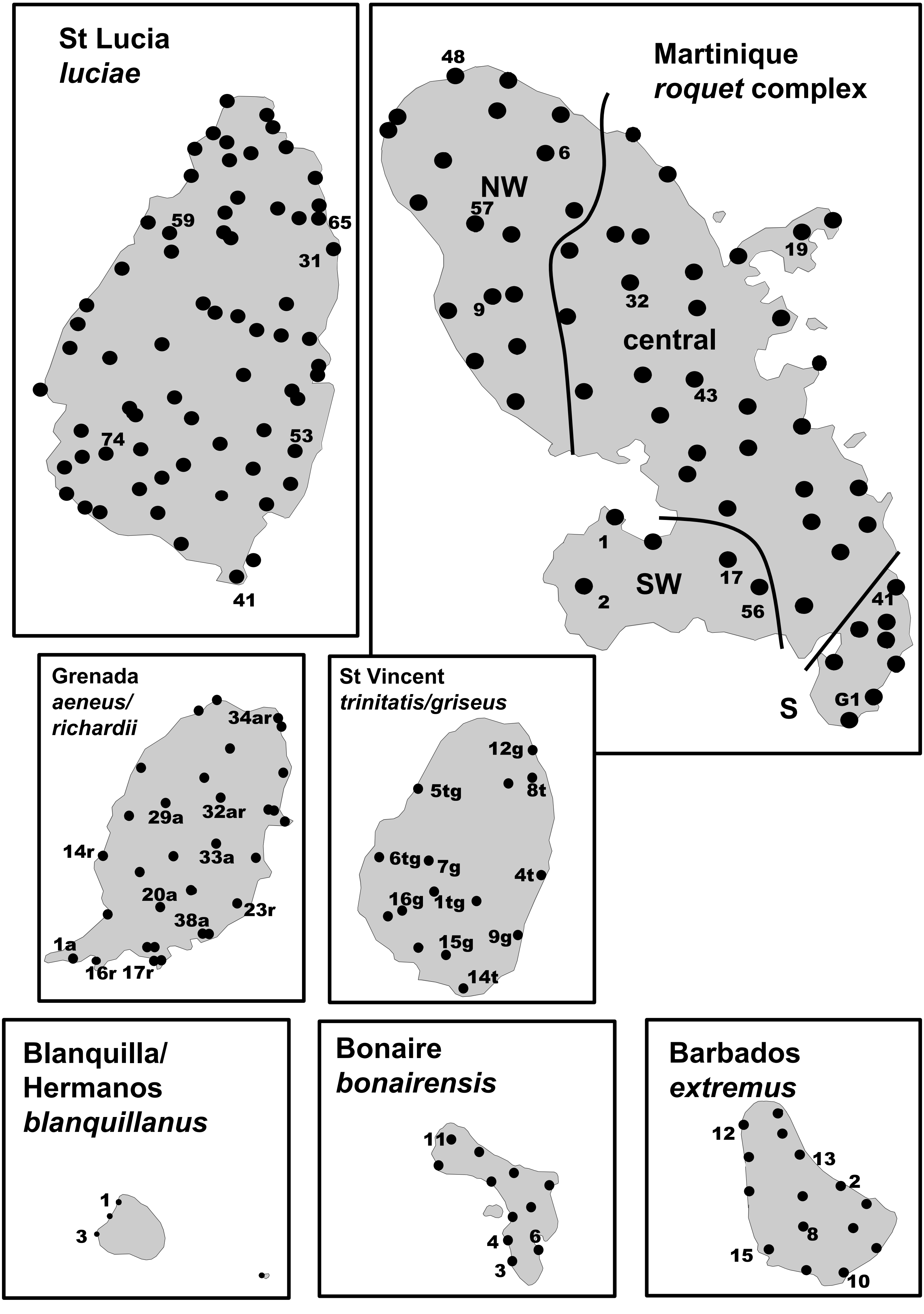


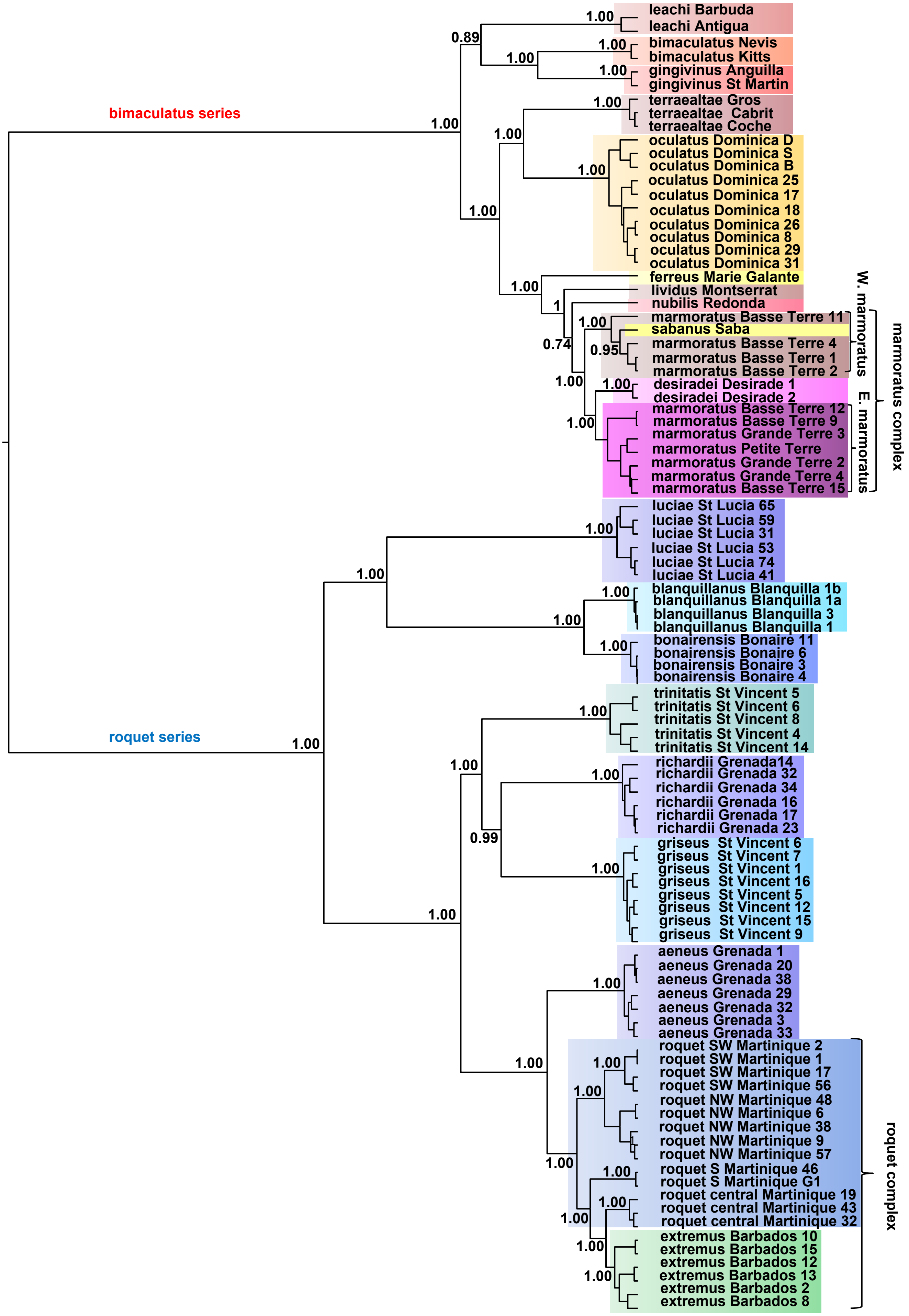

Anguilla
St Martin
St Barts *gingivinus*
Saba *sabanus*
St Eust
St Kitts
Nevis *bimaculatus*
Barbuda
Antigua *leachi*
Redonda *nubilis*
Montserrat *lividus*
Grande Terre E. *marmoratus*
Desirade *desiradei*
Basse Terre
W. *marmoratus*
Petite Terre
Marie Galante *ferreus*
Saintes *terrealtae*
Dominica *oculatus*
N. West
Central
roquet
Martinique
complex
S. West
South
200 Km
St Lucia *luciae*
St Vincent *trinitatis, griseus*
Barbados
extremus
Grenada & Grenadines
aeneus, richardii
Blanquilla *blanquillanus*
Bonaire *bonairensis*
Venezuela
300 km

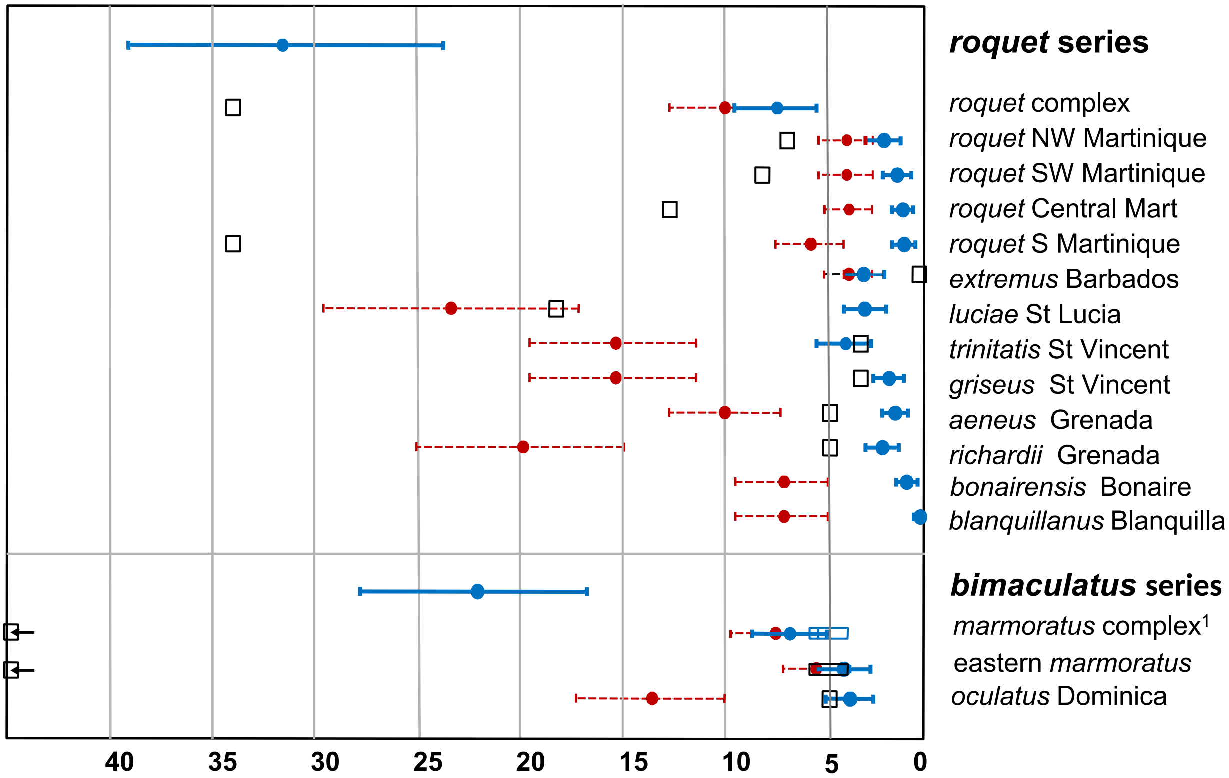
2A


Guadeloupe *marmoratus complex*
Desirade
1,2
Grande Terre
2
1
4
3
Petite Terre
Basse Terre
9
2
1
12
15
11
4
IC, Ilet a Cabrit
GI, Terre de Haut
Saintes ***terraealtae***
LC, La Coche
Dominica *oculatus*
17
18
D
B
25
S
29
26
31
8

2B


St Lucia
luciae
59
65
31
74
53
41
Martinique
roquet complex
48
6
NW
57
9
19
32
central
43
1
SW
2
17
56
41
S
G1
Grenada
aeneus/
richardii
34ar
29a
32ar
14r
33a
20a
23r
38a
1a
16r
17r
St Vincent
trinitatis/griseus
12g
5tg
8t
6tg
7g
4t
16g
1tg
15g
9g
14t
Blanquilla/
Hermanos
blanquillanus
1
3
Bonaire
bonairensis
11
4
6
3
Barbados
extremus
12
13
2
8
15
10


bimaculatus series
roquet series
1.00
0.89
0.74
0.95
0.99
1
leachi Barbuda
leachi Antigua
bimaculatus Nevis
bimaculatus Kitts
gingivinus Anguilla
gingivinus St Martin
terraealtae Gros
terraealtae Cabrit
terraealtae Coche
oculatus Dominica D
oculatus Dominica S
oculatus Dominica B
oculatus Dominica 25
oculatus Dominica 17
oculatus Dominica 18
oculatus Dominica 26
oculatus Dominica 8
oculatus Dominica 29
oculatus Dominica 31
ferreus Marie Galante
lividus Montserrat
nubilis Redonda
marmoratus Basse Terre 11
sabanus Saba
marmoratus Basse Terre 4
marmoratus Basse Terre 1
marmoratus Basse Terre 2
desiradei Desirade 1
desiradei Desirade 2
marmoratus Basse Terre 12
marmoratus Basse Terre 9
marmoratus Grande Terre 3
marmoratus Petite Terre
marmoratus Grande Terre 2
marmoratus Grande Terre 4
marmoratus Basse Terre 15
W. marmoratus
E. marmoratus
marmoratus complex
luciae St Lucia 65
luciae St Lucia 59
luciae St Lucia 31
luciae St Lucia 53
luciae St Lucia 74
luciae St Lucia 41
blanquillanus Blanquilla 1b
blanquillanus Blanquilla 1a
blanquillanus Blanquilla 3
blanquillanus Blanquilla 1
bonairensis Bonaire 11
bonairensis Bonaire 6
bonairensis Bonaire 3
bonairensis Bonaire 4
trinitatis St Vincent 5
trinitatis St Vincent 6
trinitatis St Vincent 8
trinitatis St Vincent 4
trinitatis St Vincent 14
richardii Grenada14
richardii Grenada 32
richardii Grenada 34
richardii Grenada 16
richardii Grenada 17
richardii Grenada 23
griseus St Vincent 6
griseus St Vincent 7
griseus St Vincent 1
griseus St Vincent 16
griseus St Vincent 5
griseus St Vincent 12
griseus St Vincent 15
griseus St Vincent 9
aeneus Grenada 1
aeneus Grenada 20
aeneus Grenada 38
aeneus Grenada 29
aeneus Grenada 32
aeneus Grenada 3
aeneus Grenada 33
roquet SW Martinique 2
roquet SW Martinique 1
roquet SW Martinique 17
roquet SW Martinique 56
roquet NW Martinique 48
roquet NW Martinique 6
roquet NW Martinique 38
roquet NW Martinique 9
roquet NW Martinique 57
roquet S Martinique 46
roquet S Martinique G1
roquet central Martinique 19
roquet central Martinique 43
roquet central Martinique 32
extremus Barbados 10
extremus Barbados 15
extremus Barbados 12
extremus Barbados 13
extremus Barbados 2
extremus Barbados 8
roquet complex


roquet series
roquet complex
roquet NW Martinique
roquet SW Martinique
roquet Central Mart
roquet S Martinique
extremus Barbados
luciae St Lucia
trinitatis St Vincent
griseus St Vincent
aeneus Grenada
richardii Grenada
bonairensis Bonaire
blanquillanus Blanquilla
bimaculatus series
marmoratus complex1
eastern marmoratus
oculatus Dominica
40
35
30
25
20
15
10
5
0

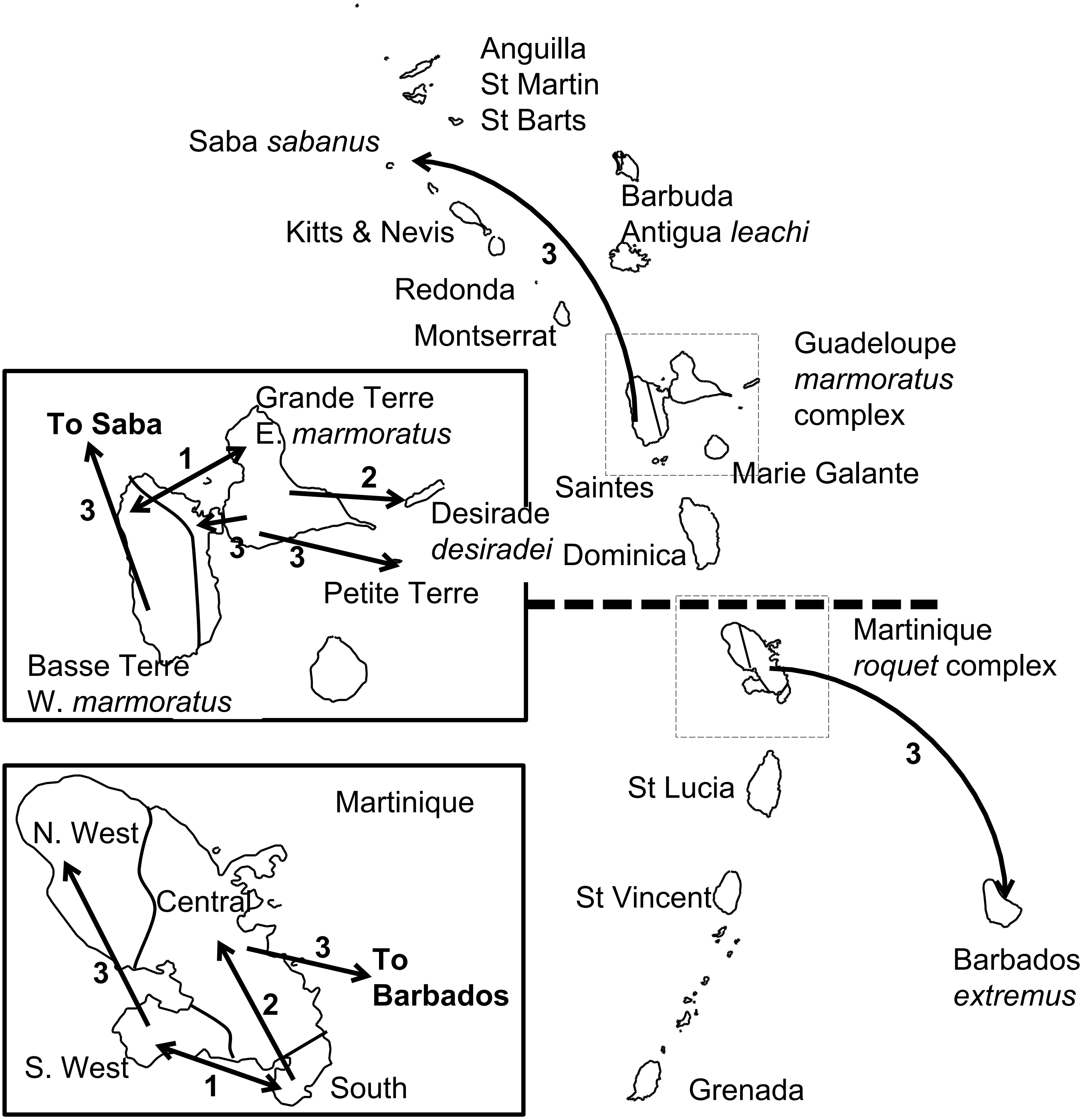
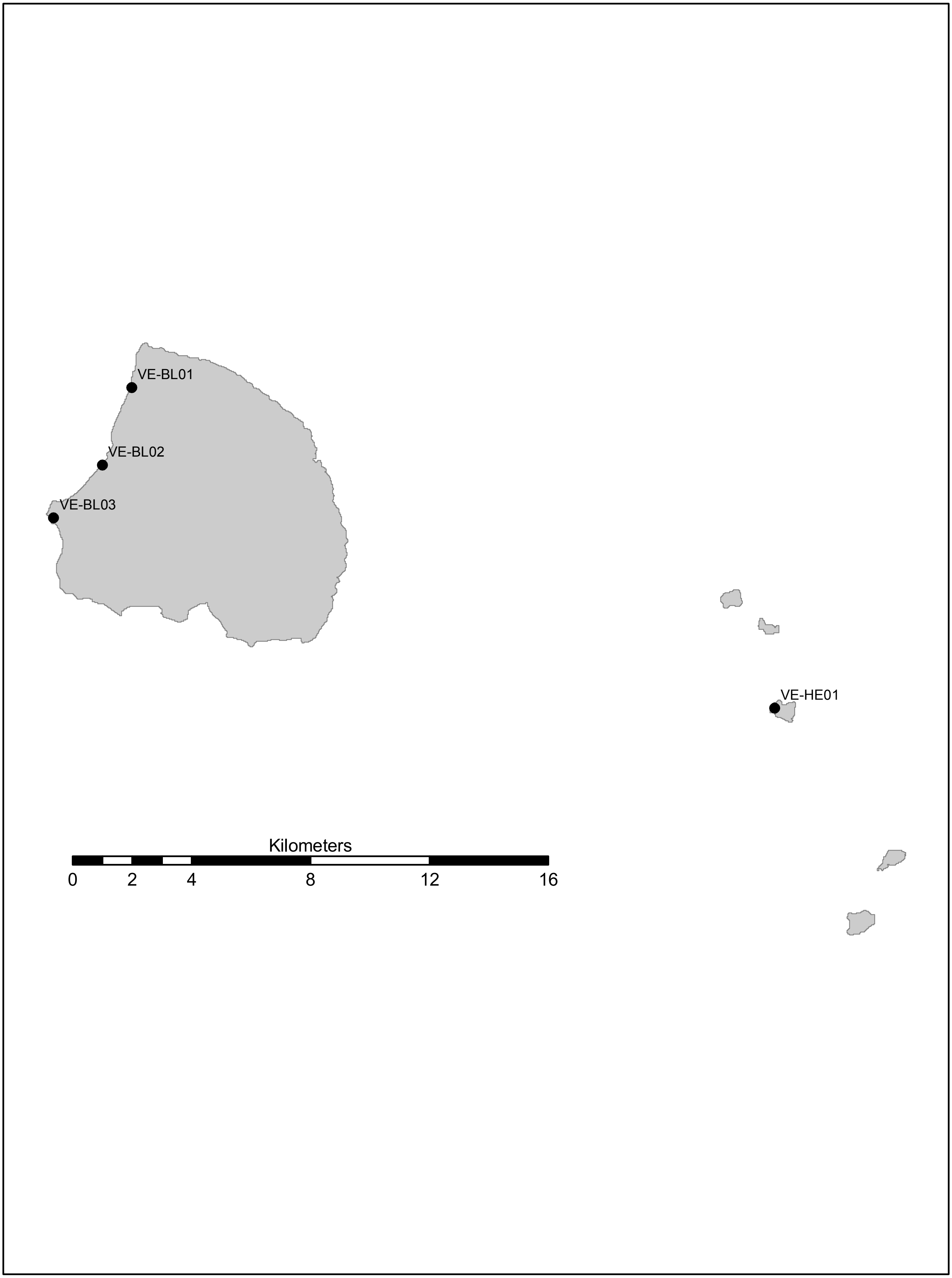

Anguilla
St Martin
St Barts
Saba *sabanus*
Barbuda
Antigua *leachi*
Kitts & Nevis
3
Redonda
Montserrat
Guadeloupe
marmoratus
complex
To Saba
Grande Terre
E. *marmoratus*
1
3
2
Desirade
desiradei
3
3
Petite Terre
Basse Terre
W. *marmoratus*
Saintes
Marie Galante
Dominica
Martinique
roquet complex
3
St Lucia
St Vincent
Barbados
extremus
Grenada
Martinique
N. West
Central
3
To
Barbados
3
2
S. West
1
South

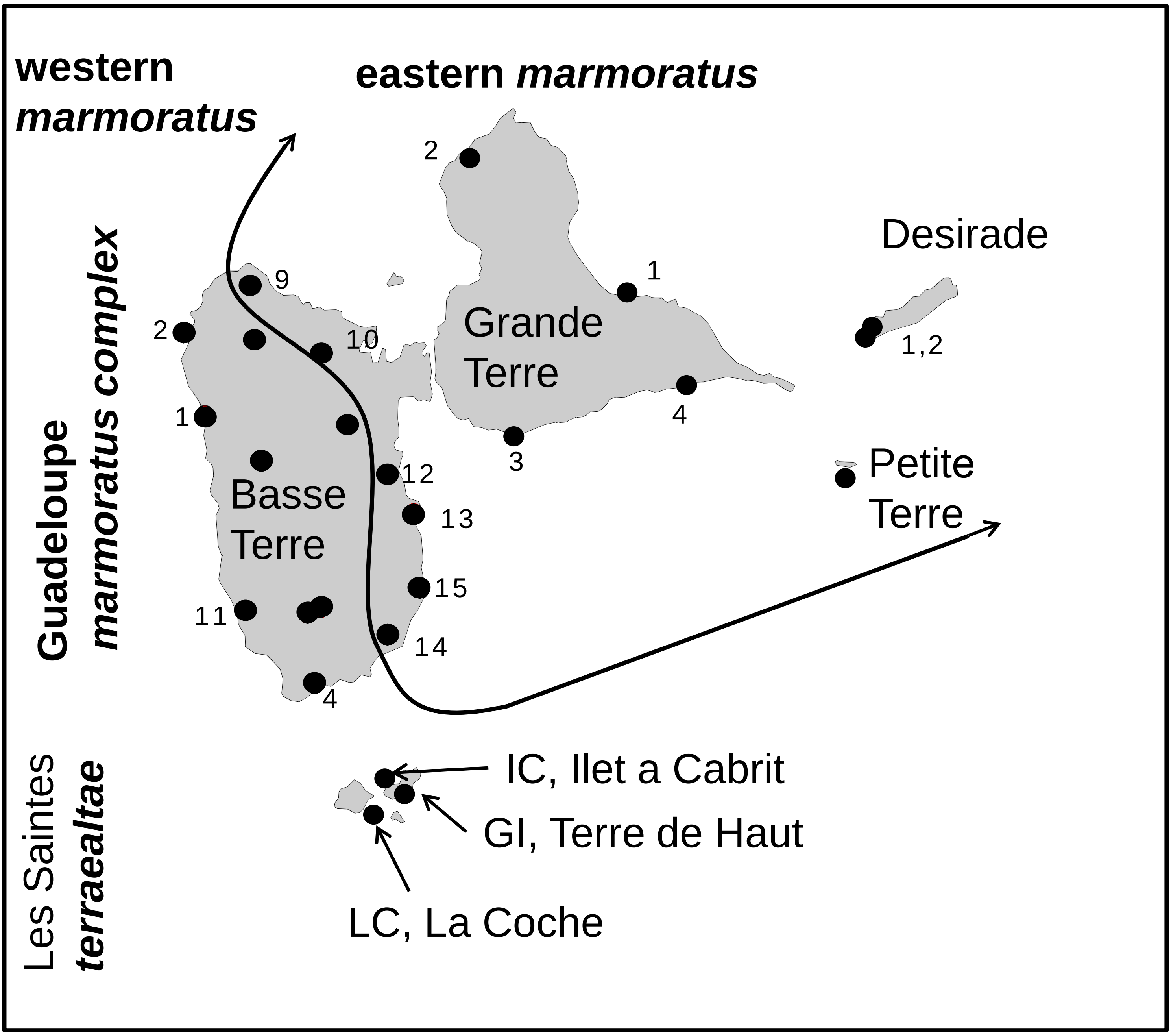
Table 1 Estimate of ages of Lesser Antillean islands and the *Anolis* species occupying them. Estimate of island and species age from densely sampled island species. Species = nominal species or previously allopatric "species" from precursor islands. Island age = geological island age in million years from literature. Within = within series/species divergence with 95% HPD in brackets, * = sampling inadequate for meaningful estimate. Among = among Series/species with 95% HPD in brackets. [1] These are allopatric "species" (from precursor island) in the *roquet* complex *sensu* Thorpe et al. (2015). [2] The range of the Central Martinique form also includes the Caravelle peninsula which is Oligocene (ca <34mybp). [3] Central and South Martinique include some low elevation areas which may have been under water until recently, and there is no strong phylogeographic structure. Hence these "Within" dates may be underestimates due to bottlenecking. [4] Martinique includes precursor islands from both the younger and older arcs. [5] Barbados is ancient rocks with some more recent limestone capping suggesting recent emergence, but the deep well-structured phylogeography suggests this species has been diverging in-situ for longer (Thorpe et al., 2005b). [6] In the south the younger arc is superimposed on the older arc so cited geological dates may reflect either young arc (St Vincent, Grenada) or older arc (St Lucia) volcanicity. [7] Bonaire and Blanquilla are old islands with younger limestone without sufficient data to confidently indicate a date of origin or emergence, although on the latter, low-elevation island populations may have been bottlenecked. [8] Marie Galante is mid Miocene overlain by more recent deposits (Martin-Kaye, 1969). [9] The range of the *marmoratus* complex includes both Basse Terre (younger arc), and Grande Terre, together with some allopatric populations on islands that can be very ancient (e.g., La Desirade). La Desirade may be Mesozoic, i.e., earlier than the rafiation so this date is not used. Moreover, Grande Terre may be Lower to Mid Miocene (Martin-Kaye, 1969), but it thought to have emerged more recently (Maury et al., 1990). Dating the range of the nominal species is therefore complicated, and here we just consider the younger arc island, Basse Terre, with its main lineage distributed over the centre and west of the island at 4-6mybp (Maury et al., 1990) for the complex and its components. [10] One specimen among several, for both localities 2 and 7 in western Basse Terre (maBT02_08 and maBT07_39 respectively), join incongruently (with Analysis 1) with *A. nubilis* (Appendix D in supplementary materials), rather than others from the same site or the western *marmoratus* lineage. This would artificially increase both the age of the complex and the eastern *marmoratus* lineage and they are excluded. Their inclusion would increase the age of the complex slightly to 7.6 mybp.

Island/series	Species	Island age	Reference	Yule Within	Yule Among
roquet series				31.60 (23.8-39.1)	43.6 (34.8-52.6)
NW Martinique	NW Mart [1]	7.1	Briden et al 1979	2.38 (1.57-3.29)	4.19 (2.93-5.56)
SW Martinique	SW Mart[1]	8.3	Briden et al 1979	1.73 (1.07-2.45)	4.19 (2.93-5.56)
Central Martinique	Central Mart[1]	12.8-15.9[2]	Briden et al 1979, Wadge 1994	1.46 (0.97-2.00) [3]	4.08 (2.96-5.29)
S Martinique	S Mart[1]	<34	Wadge 1994	1.40 (0.86-1.97) [3]	5.94 (4.35-7.65)

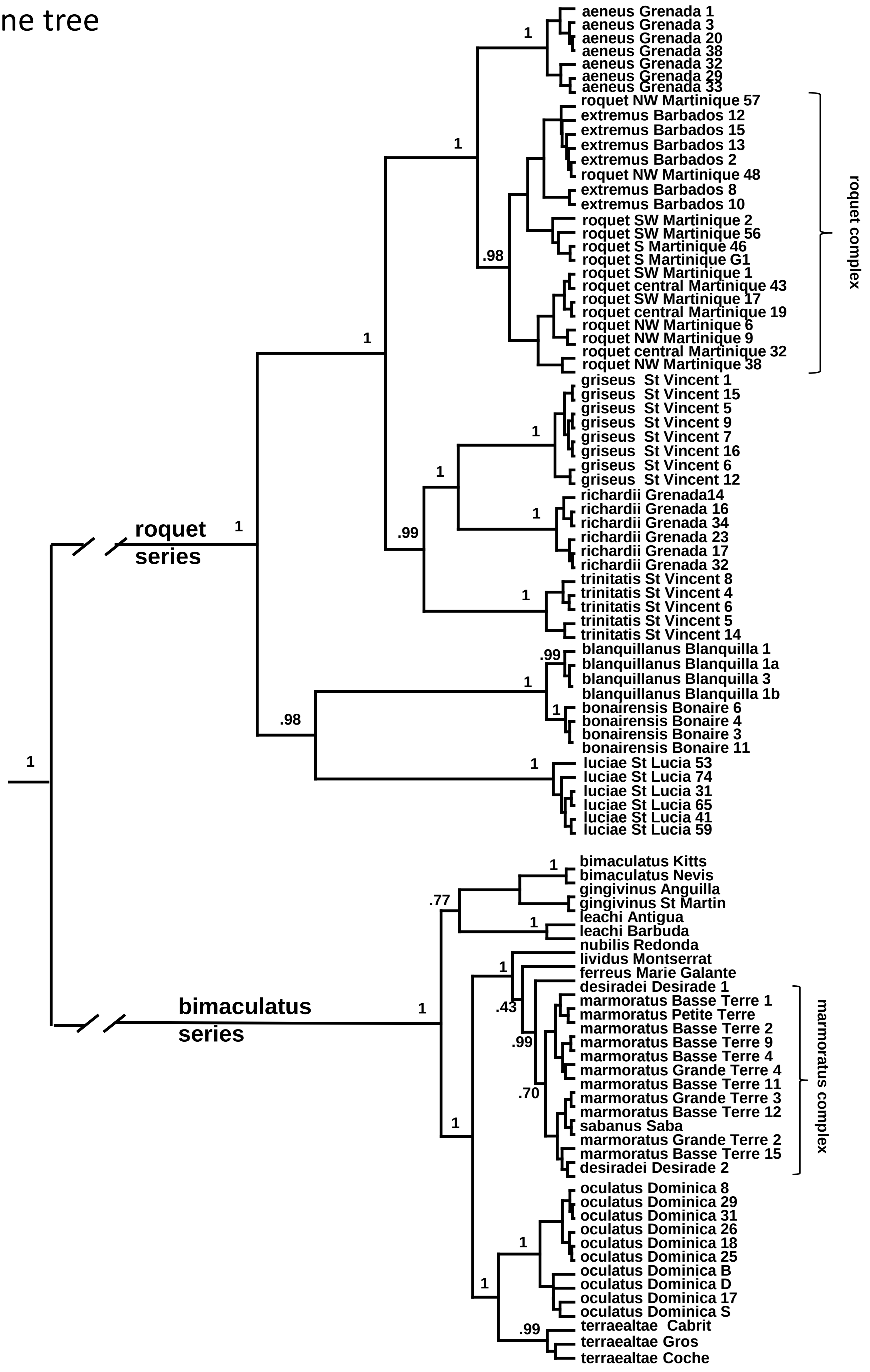
All Martinique	*roquet*	<34[4]	Wadge 1994	7.56 (5.65-9.65)	10.1 (7.40-12.81)
Barbados	*extremus*	[5]	Speed 1994, Thorpe et al 2005	3.35 (2.37-4.33)	4.08 (2.96-5.29)
St Lucia	*luciae*	18.3[6]	Briden et al 1979	3.30 (2.27-4.33)	23.4 (17.2-29.6)
St Vincent	*trinitatis*	3.5[6]	Maury et al 1990	4.23 (2.99-5.64)	15.4 (1.5-19.6)
St Vincent	*griseus*	3.5[6]	Maury et al 1990	2.12 (1.40-2.90)	15.4 (1.5-19.6)
Grenada	*aeneus*	>5[6]	Maury et al 1990, Martin-Kaye 1969	1.82 (1.20-2.47)	10.1 (7.4-12.81)
Grenada	*richardii*	>5[6]	Maury et al 1990, Martin-Kaye 1969	2.44 (1.66-3.26)	19.9 (15.0-25.1)
Bonaire	*bonairensis*	-[7]		1.21 (0.74-1.78)	7.22 (5.10-9.59)
Blanquilla	*blanquillanus*	-[7]		0.60 (0.33-0.91)	7.22 (5.10-9.59)
bimaculatus series				22.1 (16.8-27.8)	43.6 (34.8-52.6)
St Martin Bank	*gingivinus*	37	Briden et al 1979, Maury et al 1990	*	14.5 (9.91-20.0)
Saba	*sabanus*	0.4	Roobol and Smith 2004	*	2.12 (1.42-2.92)
Kitts Nevis bank	*bimaculatus*	3.4	Maury et al 1990	*	14.5 (9.91-20.0)
Antigua Barbuda Bank	*leachi*	40	Briden et al 1979	*	19.6 (14.9-24.6)
Redonda	*nubilis*	<1.5	Maury et al 1990	*	5.96 (4.21-7.97)
Montserrat	*lividus*	4.4	Briden et al 1979, Maury et al 1990	*	9.37 (6.95-12.0)
Illes des Saintes	*terraealtae*	4.7	Maury et al 1990	*	13.6 (10.1-17.3)
Marie Galante	*ferreus*	[8]		*	12.0 (8.87-15.2)
Guadeloupe (excl I d Saintes, Marie	*marmoratus complex*[9,10]	(4-6)	Maury et al 1990	*6.91 (5.12-8.74)	7.61 (5.55-9.81)

Galante)					
Grande Terre + East BT + Petite Terre+Desirade	Eastern *marmoratus*+ *desiradei* [9]	(4-6)	Maury et al 1990	5.74 (4.12-7.37)	6.91 (5.12-8.74)
Desirade	*desiradei* [9]	mesozoic	Maury et al 1990	*	5.74 (4.12-7.37)
Grande Terre +eastern BT+ Petite Terre)	Eastern *marmoratus*[9]	(4-6)	Maury et al 1990	4.40 (3.10-5.77)	5.74 (4.12-7.37)
Basse Terre (+Saba)	Western *marmoratus*[10]	4-6	Maury et al 1990	3.62 (2.48-4.82)	6.91 (5.12-8.74)
Dominica	*oculatus*	<5	Maury et al 1990, Martin-Kaye 1969	3.98 (2.85-5.18)	13.6 (10.1-17.3)


VE-BL01
VE-BL02
VE-BL03
VE-HE01
Kilometers
0
2
4
8
12
16


western *marmoratus*
eastern *marmoratus*
Guadeloupe *marmoratus complex*
Les Saintes ***terraealtae***
Desirade
Grande Terre
Basse Terre
Petite Terre
2
9
2
10
1
1
1,2
4
3
12
13
15
11
14
4
IC, Ilet a Cabrit
GI, Terre de Haut
LC, La Coche

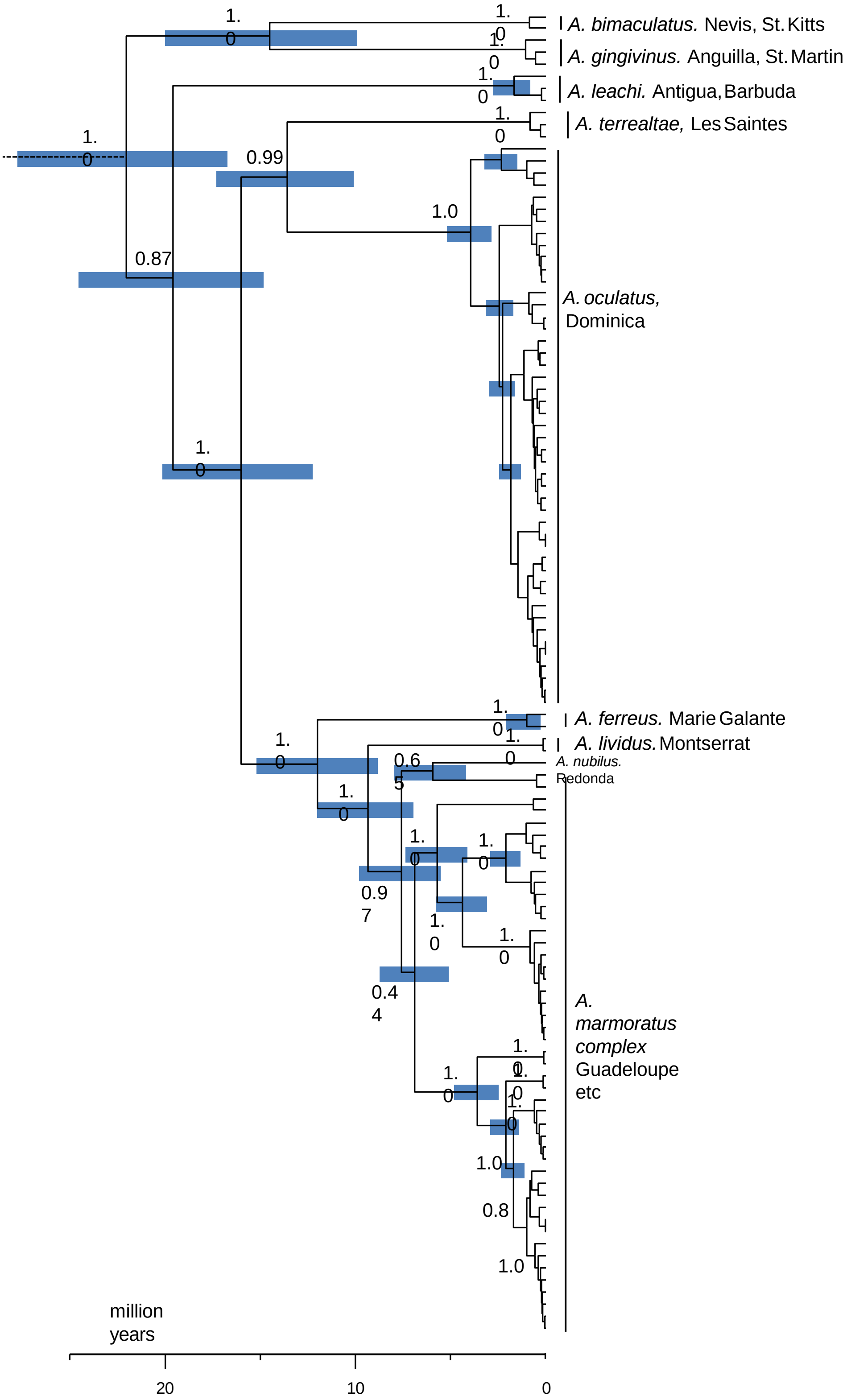
Concatenated nuclear gene tree



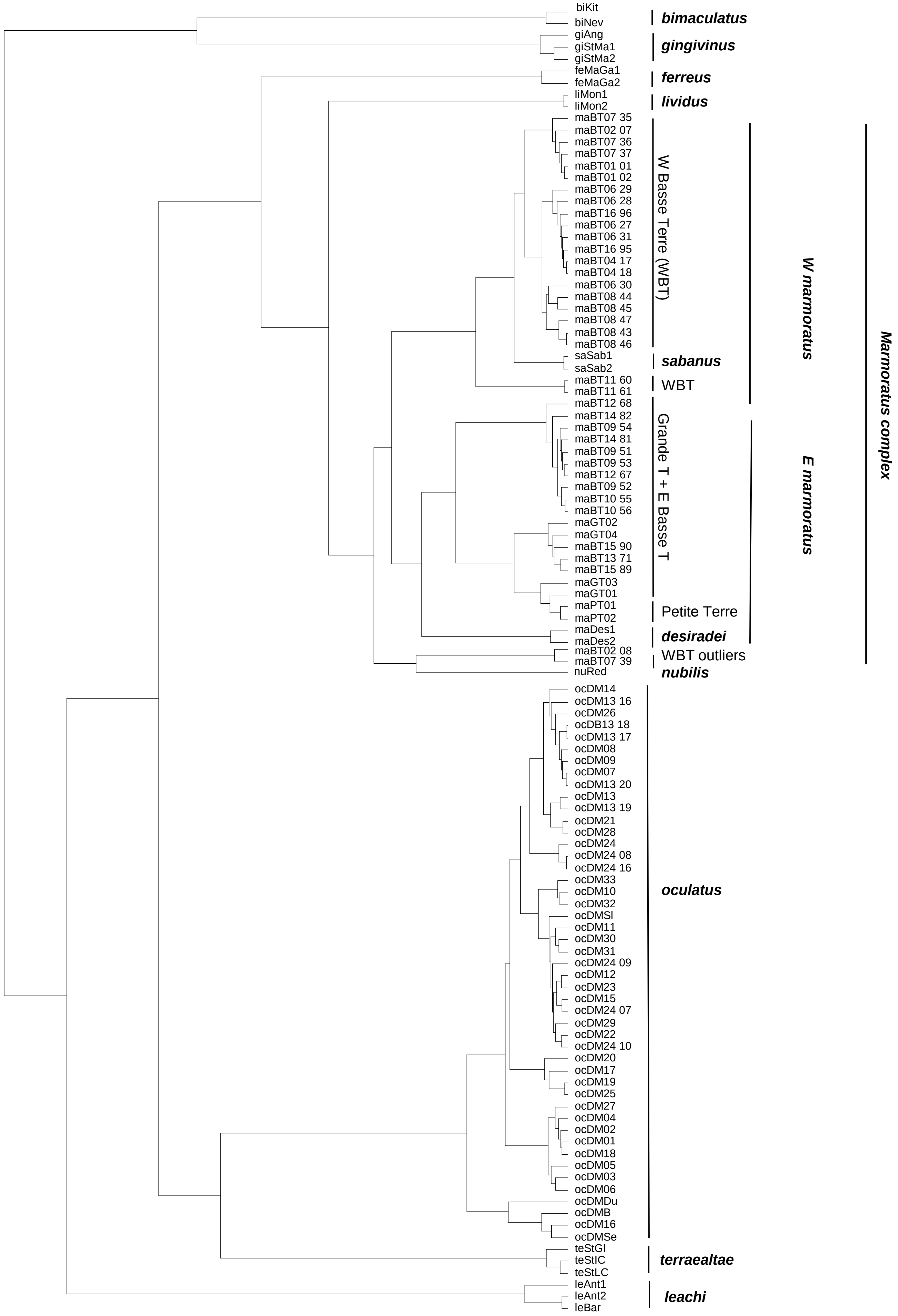
Maximum likelihood tree.
concatenated cyt b and nuclear datasets

Yule mtDNA gene tree, *bimaculatus* series section

95% HPD divergence time (blue bar) and posterior probability for key nodes.
See B1 (below) for details of individuals



Section B1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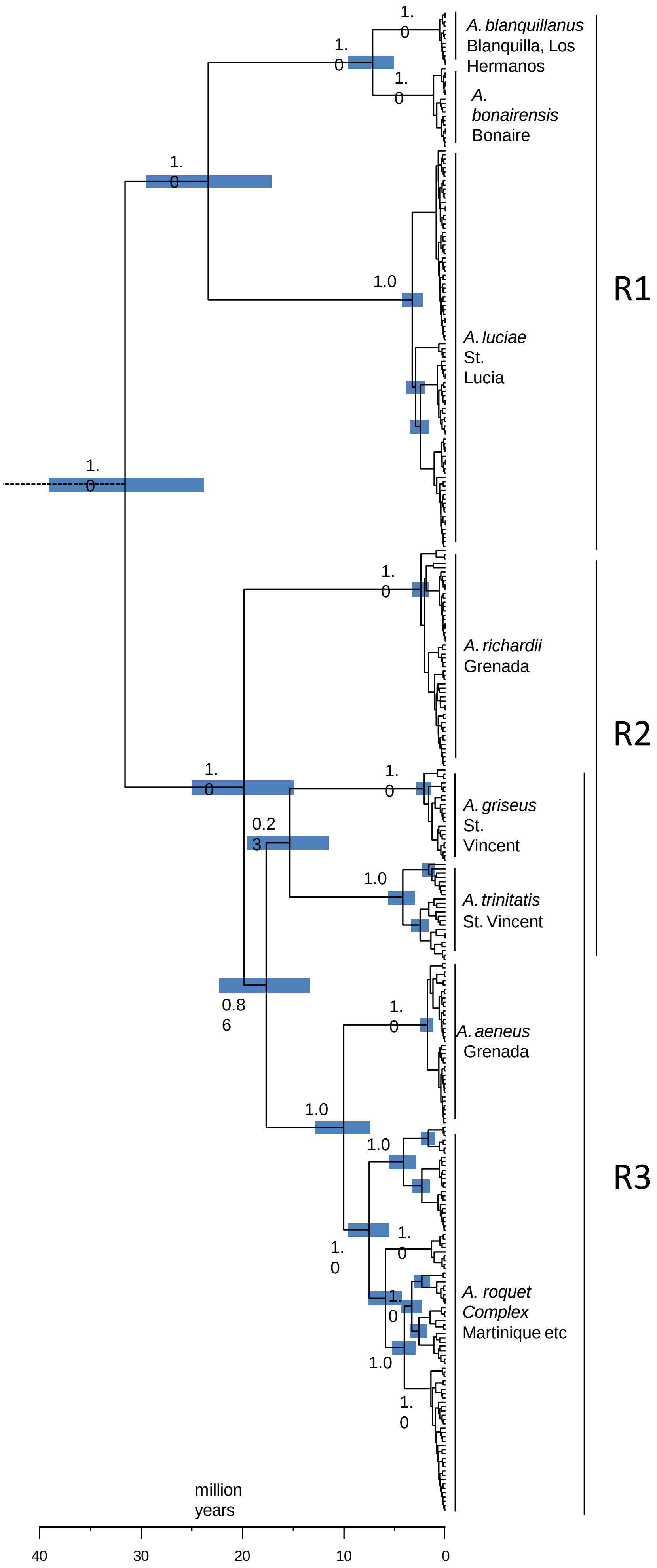
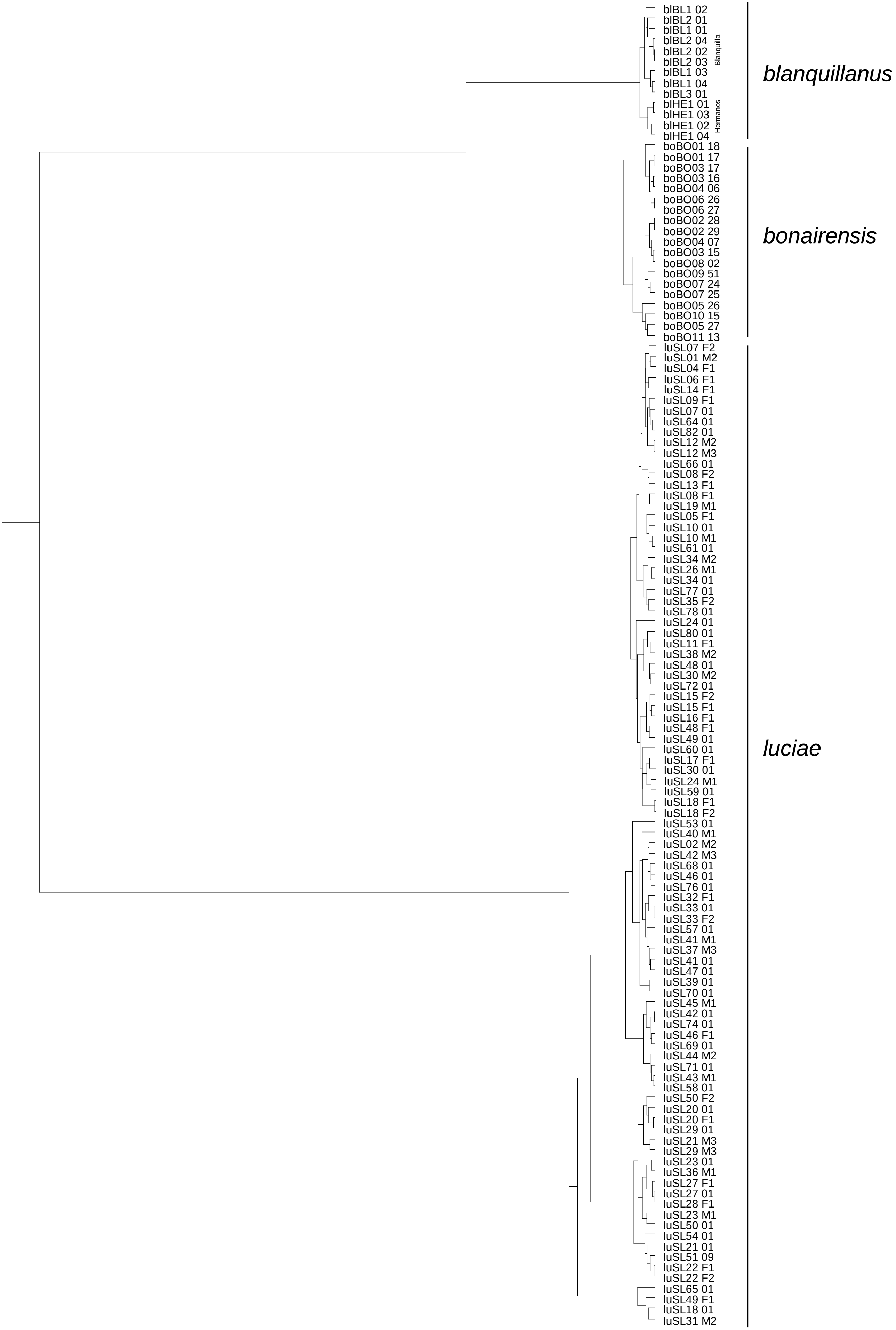
bimaculatus
giAng
giStMa1
giStMa2
gingivinus
feMaGa1
feMaGa2
ferreus
liMon1
liMon2
lividus
maBT07 35
maBT02 07
maBT07 36
maBT07 37
maBT01 01
maBT01 02
maBT06 29
maBT06 28
maBT16 96
maBT06 27
maBT06 31
maBT16 95
maBT04 17
maBT04 18
maBT06 30
maBT08 44
maBT08 45
maBT08 47
maBT08 43
maBT08 46
W Basse Terre (WBT)
saSab1
saSab2
sabanus
maBT11 60
maBT11 61
WBT
W marmoratus
maBT12 68
maBT14 82
maBT09 54
maBT14 81
maBT09 51
maBT09 53
maBT12 67
maBT09 52
maBT10 55
maBT10 56
maGT02
maGT04
maBT15 90
maBT13 71
maBT15 89
maGT03
maGT01
Grande T + E Basse T
maPT01
maPT02
Petite Terre
maDes1
maDes2
desiradei
E marmoratus
maBT02 08
maBT07 39
WBT outliers
Marmoratus complex
nuRed
nubilis
ocDM14
ocDM13 16
ocDM26
ocDB13 18
ocDM13 17
ocDM08
ocDM09
ocDM07
ocDM13 20
ocDM13
ocDM13 19
ocDM21
ocDM28
ocDM24
ocDM24 08
ocDM24 16
ocDM33
ocDM10
ocDM32
ocDMSl
ocDM11
ocDM30
ocDM31
ocDM24 09
ocDM12
ocDM23
ocDM15
ocDM24 07
ocDM29
ocDM22
ocDM24 10
ocDM20
ocDM17
ocDM19
ocDM25
ocDM27
ocDM04
ocDM02
ocDM01
ocDM18
ocDM05
ocDM03
ocDM06
ocDMDu
ocDMB
ocDM16
ocDMSe
oculatus
teStGl
teStlC
teStLC
terraealtae
leAnt1
leAnt2
leBar
leachi

Yule mtDNA gene tree, *roquet* series section

95% HPD divergence time (blue bar) and posterior probability for key nodes.
See R1-R3 (below) for details of individuals



Section R1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blBL2 01
blBL1 01
blBL2 04
blBL2 02
blBL2 03
blBL1 03
blBL1 04
blBL3 01
blHE1 01
blHE1 03
blHE1 02
blHE1 04
Blanquilla
Hermanos
blanquillanus
boBO01 18
boBO01 17
boBO03 17
boBO03 16
boBO04 06
boBO06 26
boBO06 27
boBO02 28
boBO02 29
boBO04 07
boBO03 15
boBO08 02
boBO09 51
boBO07 24
boBO07 25
boBO05 26
boBO10 15
boBO05 27
boBO11 13
bonairensis
luSL07 F2
luSL01 M2
luSL04 F1
luSL06 F1
luSL14 F1
luSL09 F1
luSL07 01
luSL64 01
luSL82 01
luSL12 M2
luSL12 M3
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luSL59 01
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luSL46 01
luSL76 01
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luSL41 M1
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luSL41 01
luSL47 01
luSL39 01
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luSL45 M1
luSL42 01
luSL74 01
luSL46 F1
luSL69 01
luSL44 M2
luSL71 01
luSL43 M1
luSL58 01
luSL50 F2
luSL20 01
luSL20 F1
luSL29 01
luSL21 M3
luSL29 M3
luSL23 01
luSL36 M1
luSL27 F1
luSL27 01
luSL28 F1
luSL23 M1
luSL50 01
luSL54 01
luSL21 01
luSL51 09
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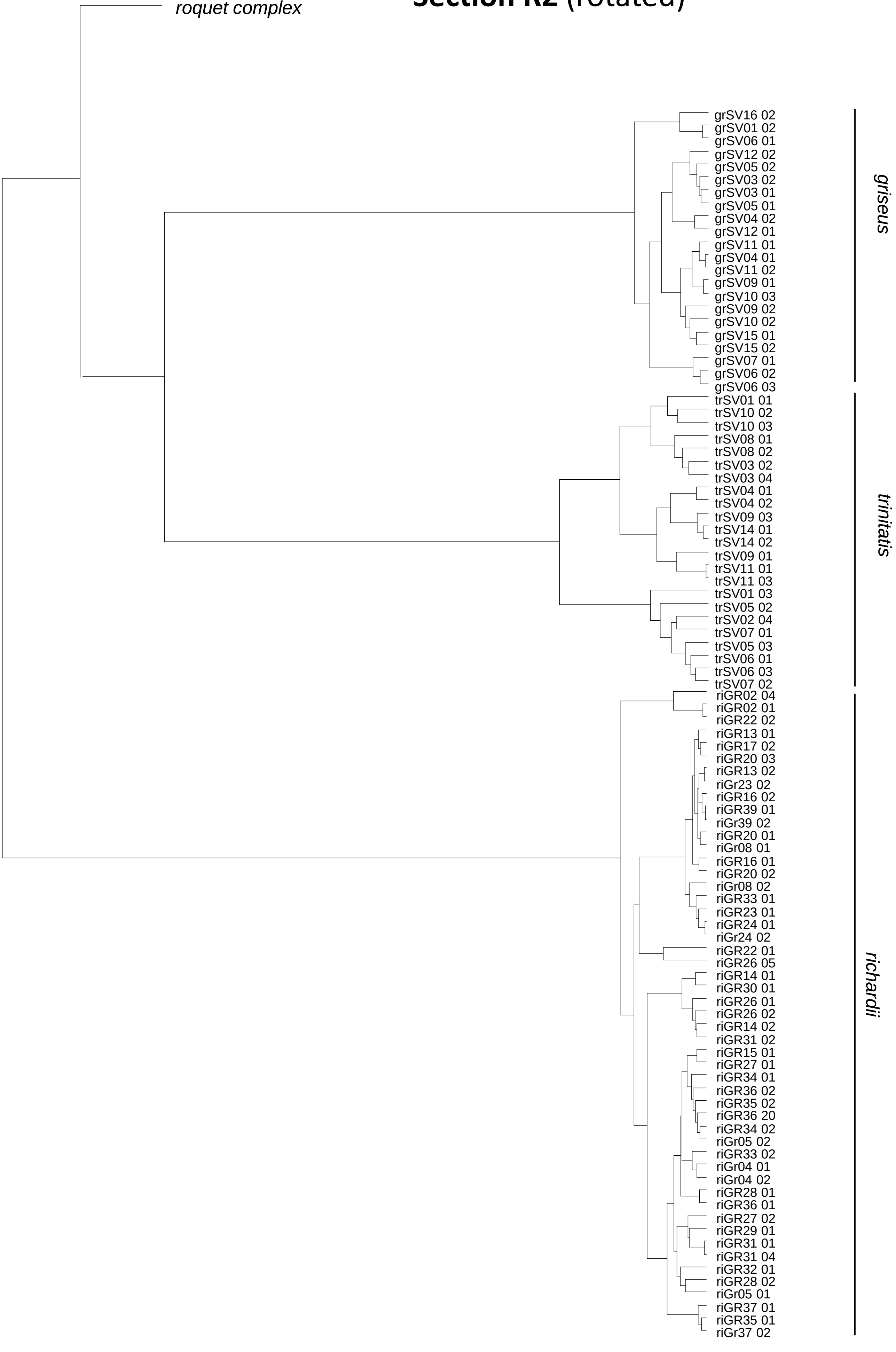
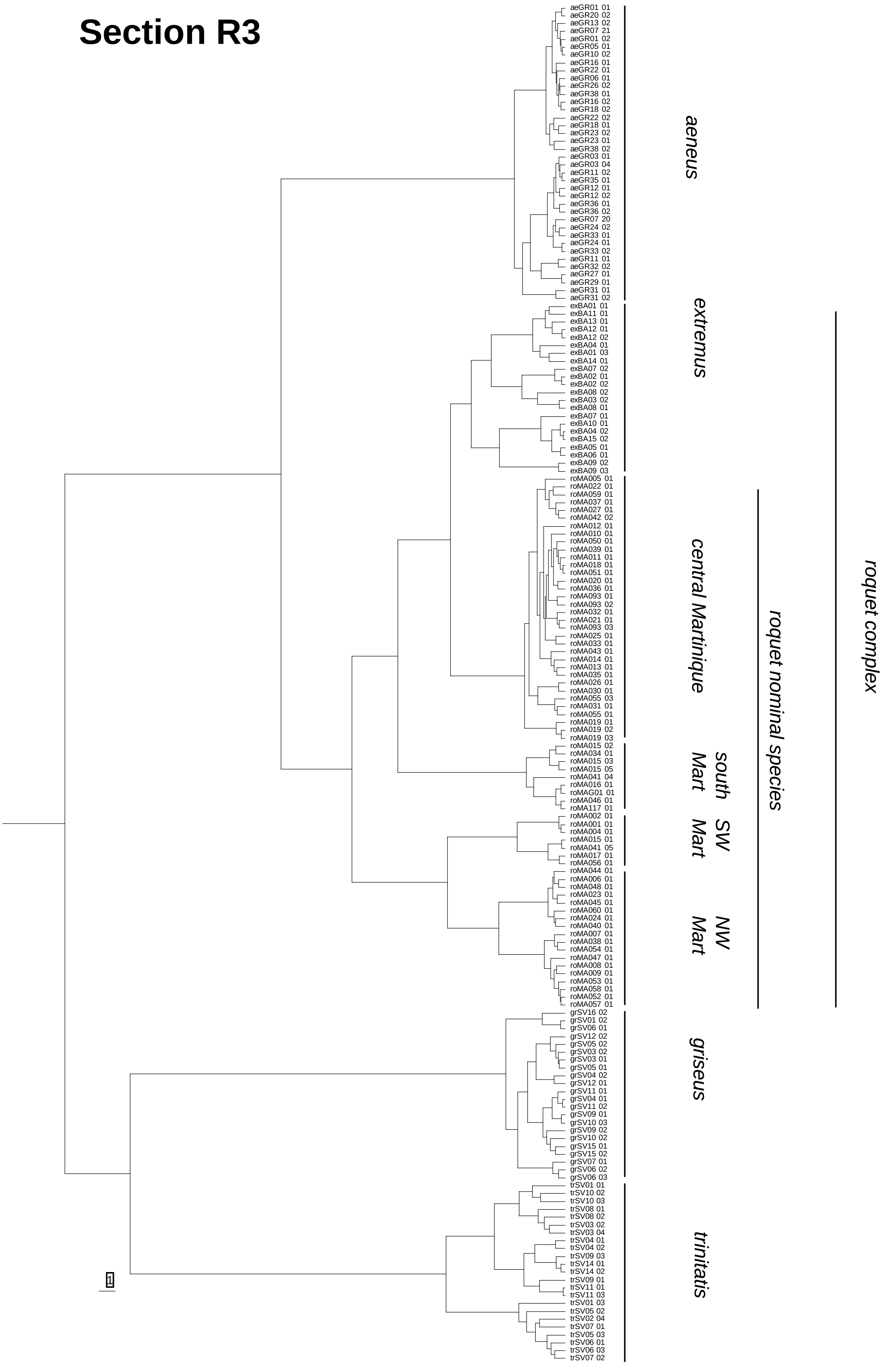
luSL65 01
luSL49 F1
luSL18 01
luSL31 M2
luciae

Section R2 (rotated)



Section R3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aeGR20 02
aeGR13 02
aeGR07 21
aeGR01 02
aeGR05 01
aeGR10 02
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aeGR22 01
aeGR06 01
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aeGR38 01
aeGR16 02
aeGR18 02
aeGR22 02
aeGR18 01
aeGR23 02
aeGR23 01
aeGR38 02
aeGR03 01
aeGR03 04
aeGR11 02
aeGR35 01
aeGR12 01
aeGR12 02
aeGR36 01
aeGR36 02
aeGR07 20
aeGR24 02
aeGR33 01
aeGR24 01
aeGR33 02
aeGR11 01
aeGR32 02
aeGR27 01
aeGR29 01
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aeGR31 02
exBA01 01
exBA11 01
exBA13 01
exBA12 01
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exBA07 02
exBA02 01
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aeneus
extremus
central Martinique
south Mart
SW Mart
NW Mart
roquet nominal species
roquet complex
griseus
trinitatis
1

Online size analysis

As anoles have asymptotic growth the five largest specimens (SVL) were selected from the sample of ten per site and site means , and 95% confidence limits (CIs) given. All localities are low elevation. The *aeneus* samples are from Morne Rouge and Fort Jeudy, Grenada (Thorpe et al 2015), the *roquet* complex samples are from south Martinique (site 4 transect VIII), and central Martinique (site 8 transect I) from Thorpe et al (2010), and from northwest Martinique NW Martinique (site 1 combined transect) from Surget-Groba et al (2012). Although *A. aeneus* and *A. roquet* may be put in different size categories (small and intermediate, respectively), they are approximately the same size with overlapping 95% CIs.

species	*aeneus*	*aeneus*	south Mart *roquet*	central Mart *roquet*	NW Mart *roquet*
site	Morne Rouge	Fort Jeudy	site 4 Trans VIII	site 8 Trans I	site 1 Comb Trans
mean SVL 95%CI	68.4 (66.5-70.3)	71.5 (70.1-72.8)	69.8 (68.7-70.9)	71.6 (69.5-73.7)	70.7 (70.0-71.4)

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Table 1 Estimate of island and species age.

Island/series	Species	Island age	Reference	Yule Within	Yule Among
roquet series				31.60 (23.8-39.1)	43.6 (34.8-52.6)
NW Martinique	NW Mart [1]	7.1	Briden et al 1979	2.38 (1.57-3.29)	4.19 (2.93-5.56)
SW Martinique	SW Mart[1]	8.3	Briden et al 1979	1.73 (1.07-2.45)	4.19 (2.93-5.56)
Central Martinique	Central Mart[1]	12.8-15.9[2]	Briden et al 1979, Wadge 1994	1.46 (0.97-2.00) [3]	4.08 (2.96-5.29)
S Martinique	S Mart[1]	<34	Wadge 1994	1.40 (0.86-1.97) [3]	5.94 (4.35-7.65)
All Martinique	*roquet*	<34[4]	Wadge 1994	7.56 (5.65-9.65)	10.1 (7.40-12.81)
Barbados	*extremus*	-[5]	Speed 1994, Thorpe et al 2005	3.35 (2.37-4.33)	4.08 (2.96-5.29)
St Lucia	*luciae*	18.3[6]	Briden et al 1979	3.30 (2.27-4.33)	23.4 (17.2-29.6)
St Vincent	*trinitatis*	3.5[6]	Maury et al 1990	4.23 (2.99-5.64)	15.4 (1.5-19.6)
St Vincent	*griseus*	3.5[6]	Maury et al 1990	2.12 (1.40-2.90)	15.4 (1.5-19.6)
Grenada	*aeneus*	>5[6]	Maury et al 1990, Martin-Kaye 1969	1.82 (1.20-2.47)	10.1 (7.4-12.81)
Grenada	*richardii*	>5[6]	Maury et al 1990, Martin-Kaye 1969	2.44 (1.66-3.26)	19.9 (15.0-25.1)
Bonaire	*bonairensis*	-[7]		1.21 (0.74-1.78)	7.22 (5.10-9.59)
Blanquilla	*blanquillanus*	-[7]		0.60 (0.33-0.91)	7.22 (5.10-9.59)
bimaculatus series				22.1 (16.8-27.8)	43.6 (34.8-52.6)
St Martin Bank	*gingivinus*	37	Briden et al 1979, Maury et al 1990	*	14.5 (9.91-20.0)
Saba	*sabanus*	0.4	Roobol & Smith 2004	*	2.12 (1.42-2.92)
Kitts Plus Nevis bank	*bimaculatus*	3.4	Maury et al 1990	*	14.5 (9.91-20.0)
Antigua Barbuda Bank	*Leachi*	40	Briden et al 1979	*	19.6 (14.9-24.6)
Redonda	*nubilis*	<1.5	Maury et al 1990	*	5.96 (4.21-7.97)
Montserrat	*lividus*	4.4	Briden et al 1979, Maury et al 1990	*	9.37 (6.95-12.0)
I D Saintes	*terraealtae*	4.7	Maury et al 1990	*	13.6 (10.1-17.3)
Marie Galante	*ferreus*	[8]		*	12.0 (8.87-15.2)
Guadeloupe (minus Saintes & Marie Galante)	*marmoratus*[9]			6.91 (5.12-8.74)	7.61 (5.55-9.81)
Grande Terre + East BT + Desirade	*marmoratus* [9]			5.74 (4.12-7.37)	6.91 (5.12-8.74)
Desirade	*marmoratus* [9]	mesozoic	Maury et al 1990	*	5.74 (4.12-7.37)
Grande Terre +eastern BT)	*marmoratus*[9]			4.40 (3.10-5.77)	5.74 (4.12-7.37)
Basse Terre	W Basse Terre[9]	4-6	Maury et al 1990	3.62 (2.48-4.82)	6.91 (5.12-8.74)

Dominica	*oculatus*	<5	Maury et al 1990, Martin-Kaye 1969	3.98 (2.85-5.18)	13.6 (10.1-17.3)

Legend

Estimate of island and species age from densely sampled island species (see online Table 1 for all island species and details). Species = nominal species or allospecies. Island age = geological island age in million years from literature (see online table 1). Within = within Series/species divergence with 95% HPD in brackets, * = sampling inadequate for meaningful estimate. Among = among Series/species with 95% HPD in brackets. [1] These are allospecies of the nominal *roquet* complex *sensu* Thorpe et al (2015). [2] The range of the Central Martinique form also includes the Caravelle peninsula which is Oligocene (ca <34mybp). [3] Central and South Martinique include some low elevation areas which may have been under water until recently, and there is no strong phylogeographic structure. Hence these “Within” dates may be underestimates due to bottlenecking. [4] Martinique includes precursor islands from both the younger and older arcs. [5] Barbados is ancient rocks with some more recent limestone capping suggesting recent emergence, but the deep well-structured phylogeography suggests this species has been diverging in-situ for longer (Thorpe et al 2005). [6] In the south the younger arc is superimposed on the older arc so cited geological dates may reflect either young arc (St Vincent, Grenada) or older arc (St Lucia) volcanicity. [7] Bonaire and Blanquilla are old islands with younger limestone without sufficient data to confidently indicate a date of origin or emergence, although on the latter, low-elevation island populations may have been bottlenecked. [8] Marie Galante is mid Miocene overlain by more recent deposits (Martin-Kaye 1969). [9] The range of the nominal species *marmoratus* includes both Basse Terre (younger arc), and Grande Terre, together with some allopatric populations on islands that can be very ancient (e.g., La Desirade). Moreover, Grande Terre may be Lower to Mid Miocene (Martin-Kaye 1969), but it thought to have emerged more recently (Maury et al 1990). Dating the range of the nominal species is therefore meaningless, and here we just consider the younger arc island, Basse Terre, with its main lineage distributed over the centre and west of the island. One specimen among several, for both localities 2 and 7 in western Basse Terre (maBT02_08 and maBT07_39 respectively), are outliers (Tree Fig N), outside of the western Basse Terre clade. In other comparable phylogeographic analyses (Thorpe et al 2015) they group, compatible with their geographic position, with the other individuals from those localities in the western Basse Terre clade. Consequently, they are excluded from the dating process.

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