

University of Groningen

Identifying summary statistics for approximate Bayesian computation in a phylogenetic island biogeography model

Xie, Shu; Valente, Luis; Etienne, Rampal S.

DOI:

[10.1101/2023.10.13.562305](https://doi.org/10.1101/2023.10.13.562305)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version

Early version, also known as pre-print

Publication date:

2023

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Xie, S., Valente, L., & Etienne, R. S. (2023). *Identifying summary statistics for approximate Bayesian computation in a phylogenetic island biogeography model*. (BioRxiv). BioRxiv.
<https://doi.org/10.1101/2023.10.13.562305>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

1 **Identifying summary statistics for approximate Bayesian**
2 **computation in a phylogenetic island biogeography model**

3 Shu Xie^{1*}, Luis Valente^{1,2}, Rampal S. Etienne¹

4 1 Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9700CC,
5 Groningen, the Netherlands

6 2 Naturalis Biodiversity Center, 2333 CR Leiden, the Netherlands

7

8 **CORRESPONDING AUTHOR**

9 *Shu Xie*

10 *Email:* s.xie@rug.nl

1 **Abstract**

2 Estimation of parameters of evolutionary island biogeography models, such as
3 colonization and diversification rates, is important for a better understanding of island
4 systems. A popular statistical inference framework is likelihood-based estimation of
5 parameters using island species richness and phylogenetic data. Likelihood
6 approaches require that the likelihood can be computed analytically or numerically,
7 but with the increasing complexity of island biogeography models, this is often
8 unfeasible. Simulation-based estimation methods may then be a promising alternative.
9 One such method is approximate Bayesian computation (ABC), which compares
10 summary statistics of the empirical data with the output of model simulations.
11 However, ABC demands the definition of summary statistics that sufficiently describe
12 the data, which is yet to be explored in island biogeography. Here, we propose a set of
13 summary statistics and use it in an ABC framework for the estimation of parameters of
14 an island biogeography model, DAISIE (Dynamic Assembly of Island biota through
15 Speciation, Immigration and Extinction). For this model, likelihood-based inference is
16 possible, which gives us the opportunity to assess the performance of the summary
17 statistics. DAISIE currently only allows maximum likelihood estimation (MLE), so we
18 additionally develop a likelihood-based Bayesian inference framework using Markov
19 Chain Monte Carlo (MCMC) to enable comparison with the ABC results (i.e., making the
20 same assumptions on prior distributions). We simulated phylogenies of island
21 communities subject to colonization, speciation, and extinction using the DAISIE
22 simulation model and compared the estimated parameters using the three inference
23 approaches (MLE, MCMC and ABC). Our results show that the ABC algorithm performs
24 well in estimating colonization and diversification rates, except when the species
25 richness or amount of phylogenetic information from an island are low. We find that
26 compared to island species diversity statistics, summary statistics that make use of
27 phylogenetic and temporal patterns (e.g., the number of species through time)
28 significantly improve ABC inference accuracy, especially in estimating colonization and
29 anagenesis rates, as well as making inference converge considerably faster and
30 perform better under the same number of iterations. Island biogeography is rapidly
31 developing new simulation models that can explain the complexity of island
32 biodiversity, and our study provides a set of informative summary statistics that can
33 be used in island biogeography studies for which likelihood-based inference methods
34 are not an option.

35
36 **Keywords:** island biogeography, Approximate Bayesian Computation, summary statistics,
37 phylogenetic analysis, parameter inference

38

39

40

1 **Introduction**

2 Islands provide great opportunities for evolutionary and biogeographical studies. Their
3 geographical isolation makes it easier to make inferences on their unique ecological and
4 evolutionary processes, because of their well-defined boundaries. It also promotes
5 endemism, providing opportunities to study speciation and diversification. The field of
6 island biogeography is particularly concerned with understanding how island
7 characteristics shape colonization, extinction and speciation rates, and how these affect
8 species richness on islands (MacArthur & Wilson, 1963; Warren et al., 2015). Present-day
9 island biogeography integrates ecological dynamics with evolutionary processes, and
10 considers the disequilibrium of the islands affected by geological ontogeny over time
11 (Whittaker et al., 2008; 2017). In recent years, advances in molecular biology and
12 computational methods have allowed researchers to incorporate phylogenetic
13 information into evolutionary models (Rabosky and Glor 2010; Ronquist, 2011; Valente
14 et al., 2015), allowing a greater understanding of the evolutionary history and
15 relationships in island biotas. Key parameters in island biogeography that can potentially
16 be estimated from island phylogenetic and diversity data include rates of dispersal,
17 colonization, speciation, extinction, island carrying capacity, the strength of ecological
18 interactions, as well as rates of co-evolution and trait evolution (Patiño et al., 2017).
19 However, the application of phylogenetic information to estimate parameters in island
20 biogeography has remained relatively rare (Lim & Marshall, 2017; Valente et al., 2018).

21
22 Accurately estimating rates of colonization and diversification (speciation minus
23 extinction) in island biogeography models is essential for testing hypotheses on the
24 macroevolution and biogeography of island species and predicting future patterns.
25 Maximum likelihood and Bayesian estimation are widely used approaches for parameter
26 inference in a phylogenetic context (Ellison 2004; Sanmartín et al. 2008). Maximum
27 likelihood estimation is asymptotically unbiased and efficient, and also allows for
28 straightforward model comparison (Akaike, 1973). However, the estimation approach
29 can be sensitive to the choice of initial values, which could lead to local rather than global
30 likelihood maxima (Rogers and Swofford, 1999). Bayesian inference is an alternative
31 probabilistic approach that requires specifying a prior probability distribution reflecting
32 the prior knowledge of the parameters. The posterior distribution is updated using Bayes'
33 theorem incorporating the likelihood and the prior. Compared with a single point
34 estimation obtained through maximum likelihood, Bayesian inference can be more
35 informative, providing a distribution of possible parameter values, and allowing for an
36 escape from local maxima. Markov Chain Monte Carlo (MCMC) is a typical method used
37 in the Bayesian inference framework. MCMC has been particularly developed for cases
38 when only the likelihood ratio or the likelihood of an augmented data set is available, but
39 here we use it with the full likelihood function. While efficiently computing the likelihood
40 or likelihood ratio can be done for simple models of island biodiversity dynamics, the
41 increasing complexity of models in island biogeography and the resulting increase in

1 parameters to be estimated makes it unfeasible. Thus, there is a need for likelihood-free
2 parameter estimation methods.

3
4 A promising approach to overcome this challenge is approximate Bayesian computation
5 (ABC), a likelihood-free simulation-based Bayesian method. The ABC algorithm estimates
6 model parameters by simulating data, and accepts the parameters which can generate
7 simulations close enough to the observations according to summary statistics and
8 distance measures (Beaumont et al., 2002; Toni & Stumpf, 2009). The ABC approach
9 originated in the context of population genetic analysis with a basic ABC rejection
10 algorithm (Beaumont, 2010). However, this algorithm can be inefficient with a low
11 acceptance rate in complex models, especially when the prior distribution is difficult to
12 specify (Sadegh and Vrugt, 2014). In the past decade, Monte Carlo algorithms, such as
13 Markov chain Monte Carlo (MCMC) or sequential Monte Carlo (SMC), have been
14 incorporated in ABC and have been applied to infer diversification rates in ecological or
15 evolutionary models (Jabot & Chave, 2009; Rabosky, 2009; Bokma, 2010; Slater et al.,
16 2012; Janzen et al., 2015). The ABC-SMC algorithm has become a popular method as it
17 allows for tackling large and complex systems.

18
19 The computational efficiency and performance of the ABC algorithm are largely
20 determined by the choice of summary statistics (Janzen et al., 2015; Jiang et al. 2017). In
21 macroevolutionary studies, potentially informative statistics are those describing the
22 species richness and the endemism of the extant species of interest. In addition, summary
23 statistics that quantify the phylogenetic relationships between species and branching
24 times may also be important. In island biogeography, phylogenetic data provide
25 information on whether island species are derived from single or multiple independent
26 colonization events. Furthermore, phylogenies also help to identify the biogeographic
27 regions from which island colonizers originated, and can provide information on the role
28 of dispersal or vicariance in shaping the distributions of island lineages. In a likelihood
29 context, the inference accuracy of island colonization, speciation and extinction rates has
30 been shown to be improved by adding temporal phylogenetic information on the pattern
31 of accumulation of species on island, particularly the colonization times of island lineages,
32 but also cladogenetic branching times (Valente et al. 2018). Hence identifying summary
33 statistics capturing phylogenetic information seems a promising strategy.

34
35 Phylogenetic diversity (PD) and mean pairwise distance (MPD) are widely used statistics
36 in phylogenetic analysis (Tsirogiannis & Sandel, 2016). Another promising summary
37 statistic, the normalized Lineage Through Time (nLTT), was proposed to assess the
38 similarity between any two phylogenetic trees (Janzen et al., 2015). It was shown that
39 nLTT performs better than traditionally used statistics (PD, tree size and gamma statistic)
40 in estimating diversification rates in birth-death, time-dependent and diversity-
41 dependent speciation models (Janzen et al., 2015). The good performance of this statistic
42 can be explained by the fact that it has been shown to be a sufficient statistic for the

1 estimation of speciation and extinction rates in a constant-rate or time-dependent birth-
2 death model of diversification (Louca & Pennell, 2020). Furthermore, while PD and MPD
3 statistics are calculated based on binary trees, in which all the species evolved from the
4 same ancestor, (a variant of) the LTT statistic can also be used for analyzing phylogenies
5 of multiple independent clades (Neves et al., 2022). This is relevant in island
6 biogeography models, where the focus is often on the diversity dynamics of the entire
7 island community, that is, the phylogenetic trees composed of the clades descending from
8 multiple independent colonization events.

9
10 The ABC approach has been used in island biogeography on population genetic analyses
11 (Patiño et al., 2015), but remains relatively underutilized in macroevolutionary models.
12 Island biogeography is rapidly developing new models that can better explain the
13 complexity of island biodiversity, for example incorporating geodynamics (Borregaard et
14 al 2015, Neves et al., 2022), trait evolution (Xie et al., 2023), or both (Sukumaran et al.,
15 2016). It is thus essential to identify general but efficient summary statistics, particularly
16 for phylogenies of island species and communities, in order to be able to use ABC
17 approaches to estimate parameters in complex island biogeography models (which are
18 not amenable to likelihood methods). In this study, we develop an ABC-SMC framework
19 and test its inference ability on simulations with the island biogeography model, DAISIE
20 (Dynamic Assembly of Island biotas through Speciation, Immigration and Extinction)
21 (Valente et al., 2015) by comparing with the results using likelihood-based methods.
22 DAISIE integrates phylogenetic information into island biogeography. It allows
23 estimation of the rates of colonization, extinction and speciation (CES) from phylogenetic
24 data, and can be used to simulate these processes for given rates. The DAISIE simulation
25 framework was expanded into various directions incorporating island ontogeny and sea-
26 level change (Neves et al., 2022) and trait effects (Xie et al., 2023). However, computing
27 the likelihood is often not possible for these extended models, and thus a likelihood-free
28 ABC algorithm is necessary for parameter estimation. To facilitate comparison with the
29 ABC results (i.e., making the same assumptions on prior distributions), here we also
30 develop a likelihood-based Bayesian inference framework using Markov Chain Monte
31 Carlo (MCMC). We simulated a variety of island biogeography scenarios with the DAISIE
32 simulation model and compared the estimated values using the three inference
33 approaches: MLE, ABC and MCMC. We asked the following questions by comparing the
34 estimation performance: 1) Can the ABC algorithm accurately estimate parameters in
35 phylogenetic island biogeography models (as accurately as MLE or MCMC)? 2) If not,
36 under what conditions are estimations poor? 3) Which summary statistics are most
37 relevant and efficient for ABC island biogeography studies? 4) Are phylogenetic summary
38 statistics more informative than statistics of the tips of the tree (e.g. species richness)?

39
40
41
42

1 **Methods**

2 ***Simulation model and scenarios***

3 Our focal system is a community of extant species living on an island, for which one would
4 like to estimate rates of colonization, speciation and extinction based on diversity and
5 phylogenetic data. Hence, we used as observations island diversity and phylogenetic data
6 simulated in the DAISIE framework. The species richness on the island is determined by
7 the colonization rate γ , anagenesis rate λ^a , cladogenesis rate λ^c and extinction rate μ .
8 Cladogenesis and colonization rates can be diversity-dependent, declining linearly with
9 an increasing number of species on the island. The simulation output is a set of
10 phylogenies of island species each resulting from an independent colonization event of
11 the island. Some phylogenies may have multiple species (e.g. island radiation), and others
12 may have just a single island species (e.g., non-endemic species that have not had time to
13 speciate or endemic singleton species with no close relatives on the island). To mimic
14 empirical studies in which it is difficult to obtain complete extinction information, we
15 pruned all extinct species from the simulations and used as data entries the reconstructed
16 trees containing all species that are extant on the island at the end of the simulation. We
17 used the standard DAISIE simulation code implemented in the R package DAISIE (Etienne
18 et al., 2023). We do not consider extensions of the original model (such as trait-
19 dependence or area-dependence of rates) because there are currently no likelihood
20 methods for these more complex models. The simulated data produced in this way are
21 hereafter referred to as observed data, as they are meant to mimic empirical data, and to
22 distinguish them from the simulations performed in the ABC analysis.

23
24 We used a total of 16 parameter combinations (Table 1) to simulate observed islands
25 (composed of one or more phylogenetic trees, each representing a lineage descending
26 from a colonization event). We ran 10 replicates for each parameter combination, thus
27 obtaining 160 simulated islands in total as observed data that were used for the
28 subsequent inference using different estimation methods. We set the island age as 5
29 million years in all the simulations. We tested the estimation performance in a diversity-
30 independent (DI) model with no upper bound for the species richness on the island.

31
32 Table 1. Parameter space used to generate the observed data used in ABC-SMC and MCMC algorithms.
33 In total, 16 parameter combinations were used.

Parameters	Meaning	Parameter values
λ^c	Cladogenetic speciation rate	0.4, 0.7
μ	Extinction rate	0, 0.3
γ	Colonization rate	0.003, 0.009
λ^a	Anagenetic speciation rate	0.1, 1.0

34

35

1 **Maximum likelihood estimation**

2 A likelihood computation method already exists in the DAISIE framework (Valente et al.,
3 2015). The method allows estimating colonization, speciation and extinction rates using
4 maximum likelihood, based on the phylogenetic information of colonization and
5 branching times, as well as the endemism status of species (endemic or not endemic to
6 the island). The code for parameter estimation is implemented in the R package DAISIE
7 (Etienne et al., 2023).

8 **Metropolis-Hastings MCMC algorithm**

9 We developed and performed a Metropolis–Hastings Markov chain Monte Carlo (MCMC,
10 Metropolis et al. 1953; Hastings 1970) analysis to obtain our reference estimates on the
11 observed data using the analytical likelihood (Valente et al. 2015). In Bayesian MCMC, a
12 sequence (chain) of parameter values is generated using Monte Carlo sampling, where
13 each step in the chain only depends on the previous step (Markov property). The chain is
14 designed such that the distribution of the generated parameter values converges to the
15 posterior distribution of the parameters. We ran 1,000,000 iterations for the MCMC chain,
16 with a discarded burn-in phase of 100,000 at the beginning, and the chain was thinned
17 by sampling every 400th iteration, with low autocorrelation coefficient values (< 0.15).
18 In order to reduce the influence of the prior distribution, we chose uniform distributions
19 as the prior distributions for each parameter, using two sets of prior distributions with
20 different ranges (Table 2) to evaluate the effect of the choice of the prior.
21
22
23

24 Table 2. The ranges of the two uniform prior distributions used in ABC-SMC and MCMC algorithms.

Parameters	Prior distribution 1	Prior distribution 2
λ^c	[0, 1]	[0, 2]
μ	[0, 0.5]	[0, 2]
γ	[0, 0.02]	[0, 0.02]
λ^a	[0, 1.5]	[0, 2]

25

26

27 **ABC-SMC algorithm**

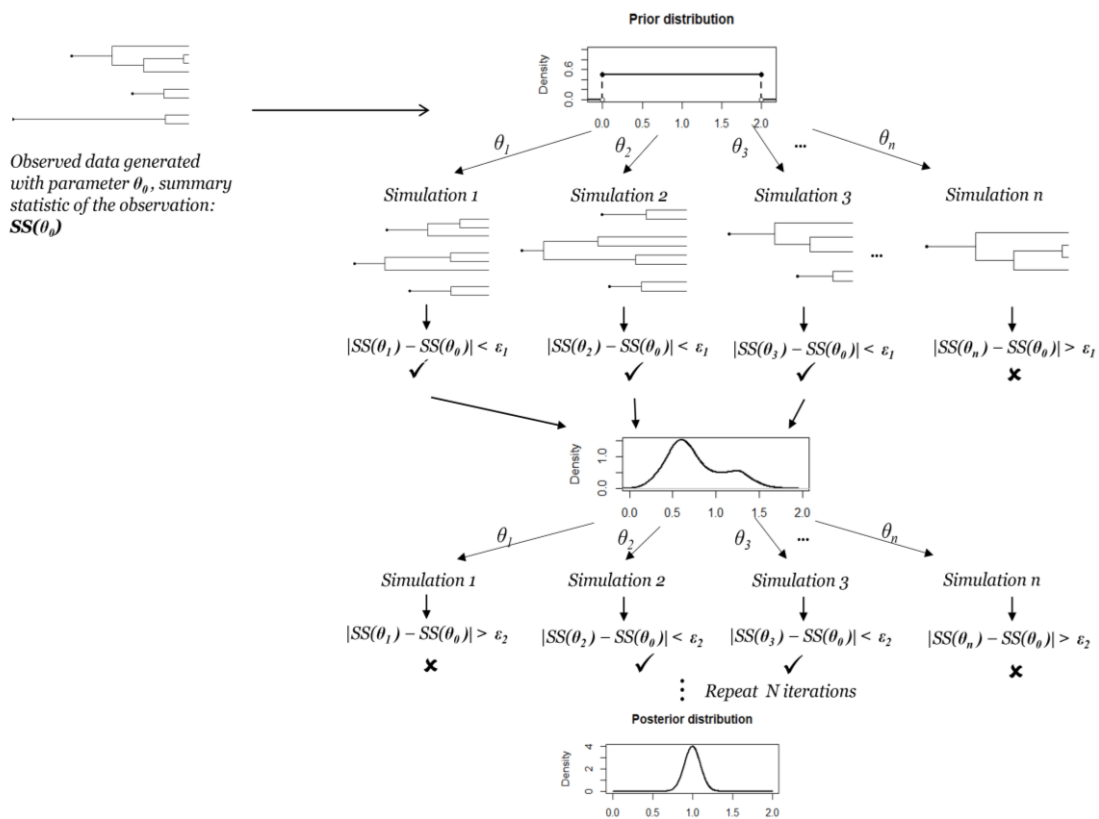
28 We applied a likelihood-free ABC-SMC algorithm to the observed data to estimate
29 parameters (Toni et al., 2009). ABC-SMC uses a sequential sampling approach that
30 generates a series of intermediate distributions with narrowing-down scales (Fig 1). In
31 our ABC-SMC algorithm, we first sample a group of parameters (collectively called
32 *particle*) from the prior and perturb the parameters using a normal distribution with zero
33 mean and a standard deviation of 0.05, and then we use these to simulate islands with
34 the DAISIE simulation model. The similarity between the observed data and the
35 simulated data is assessed with the distance between vectors of summary statistics. The
36 particles are accepted when the distance for each summary statistic between the two

1 datasets is smaller than a predefined threshold ε . Otherwise, the particle should be
 2 resampled from the prior distribution until accepted. When a sufficient number of
 3 particles (set beforehand at 500 in our simulations) is accepted, then a new iteration
 4 starts, where again particles are sampled, but now from the previous parameter
 5 population. Then the above processes of simulating datasets and accepting particles is
 6 repeated (Fig 1). The threshold decreases with each new iteration ($\varepsilon_1 > \varepsilon_2 > \dots > \varepsilon_n$), where
 7 we use the median values of the summary statistic distances as the new thresholds in the
 8 following iteration. The algorithm stops when the acceptance rate is lower than 0.002
 9 (one accepted particle in every 500 simulation steps), and we assume that the particles
 10 have converged. The population of the samples in the last iteration are regarded as the
 11 posterior, which is used to compare with the other approaches.

12

13 To be comparable, we used the same observed data and the same prior distributions as
 14 in the MCMC algorithm (Table 2). In the ABC simulations, we kept the same island age (5
 15 million years) as in the observed island dataset, but the number of species and the
 16 number of colonists present on the island can vary stochastically. We also pruned extinct
 17 species from each ABC-simulated island dataset.

18



19

20

21 Figure 1. Illustration of the ABC-SMC algorithm. $\theta_1, \theta_2, \dots, \theta_n$ indicate n particles sampled from the prior
 22 distribution, and $SS(\theta)$ is the summary statistic of the particle (a single simulation). ε is the distance
 23 threshold for each iteration, which decreases with each iteration.

24

1 We selected eight summary statistics that describe the number of extant species on
 2 islands, the phylogenetic relationships between species as well as the timing of
 3 accumulation of species (times of colonization and branching times) (Table 3). We
 4 evaluated the ABC performance using four groups of summary statistics, a) ABC diversity,
 5 with three statistics with island species richness and endemism information but without
 6 information on evolutionary history: the total number of extant species on the island
 7 (N_{total}), the number of endemic species (N_{end}), and the number of non-endemic species
 8 ($N_{non-end}$); b) ABC NLTT, with three LTT statistics with temporal information: the total
 9 number of species on the island through time ($NLTT_{total}$), the number of singleton
 10 endemic species through time ($NLTT_{singleton-end}$), the number of non-endemic species
 11 through time ($NLTT_{non-end}$); c) ABC phylogenetic, with five statistics consisting of the
 12 three temporal statistics in the ABC NLTT group plus two additional phylogenetic
 13 statistics: the standard deviation of colonization time (SD-CT), and the standard deviation
 14 of clade size (SD-CS); d) ABC all, the combination of all eight statistics. Phylogenetic
 15 information allows us to determine whether an endemic island clade is composed of a
 16 single endemic species (singleton endemic) or of multiple endemic species (radiation). In
 17 the three groups of summary statistics that use phylogenetic information (ABC NLTT,
 18 ABC phylogenetic and ABC all), we used the NLTT of singleton endemic species
 19 ($NLTT_{singleton-end}$) instead of NLTT of all the endemics, because it is more informative on
 20 anagenetic speciation (e.g., if there are fewer endemic singleton clades than endemic
 21 clades with multiple species, this suggests that cladogenesis is more frequent than
 22 anagenesis). We do not lose information, because the number of endemics in a radiation
 23 can be calculated from the total number of species, the number of non-endemics and the
 24 number of singleton endemics. We calculated NLTT statistics using the R package *nLTT*
 25 on CRAN, which is also available on GitHub (<https://github.com/thijsjanzen/nLTT>). The
 26 code used to perform the MCMC and the ABC-SMC analyses was implemented in the R
 27 package *DivABC* on GitHub (<https://github.com/xieshu95/DivABC>).

28

29 Table 3. Summary statistics used for the ABC algorithm. We consider statistics 1-3 to be diversity-
 30 related statistics (ABC diversity), 4-6 to be temporal/phylogenetic statistics (ABC NLTT), and 7-8 to
 31 be phylogenetic statistics (ABC phylogenetic).

	Summary statistics	Description	Category
1	N_{total}	Total number of extant species on the island	Diversity-related
2	N_{end}	Number of endemic island species	Diversity-related
3	$N_{non-end}$	Number of non-endemic island species	Diversity-related
4	$NLTT_{total}$	Number of island lineages through time	Phylogenetic (NLTT)
5	$NLTT_{singleton-end}$	Number of singleton island endemics through time	Phylogenetic (NLTT)
6	$NLTT_{non-end}$	Number of non-endemic island species through time	Phylogenetic (NLTT)
7	SD-CT	Standard deviation of colonization time among island clades	Phylogenetic
8	SD-CS	Standard deviation of clade size among island clades	Phylogenetic

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41

Results

We compared the performance of the parameter estimation using the MLE, ABC and MCMC approaches. We found that MLE performs the best. The ABC algorithm performs well in estimating the colonization, extinction and speciation (CES) rates when the colonization rate is high, and thus the observed data contain more clades and species on the island. For most of the parameter sets we tested in this study, using phylogenetic statistics in the ABC approach results in higher estimation accuracy than using only diversity-related statistics. Furthermore, for all three methods (MLE, MCMC and ABC), we find that the inference error and the standard deviation decrease as the species richness and the number of clades increase.

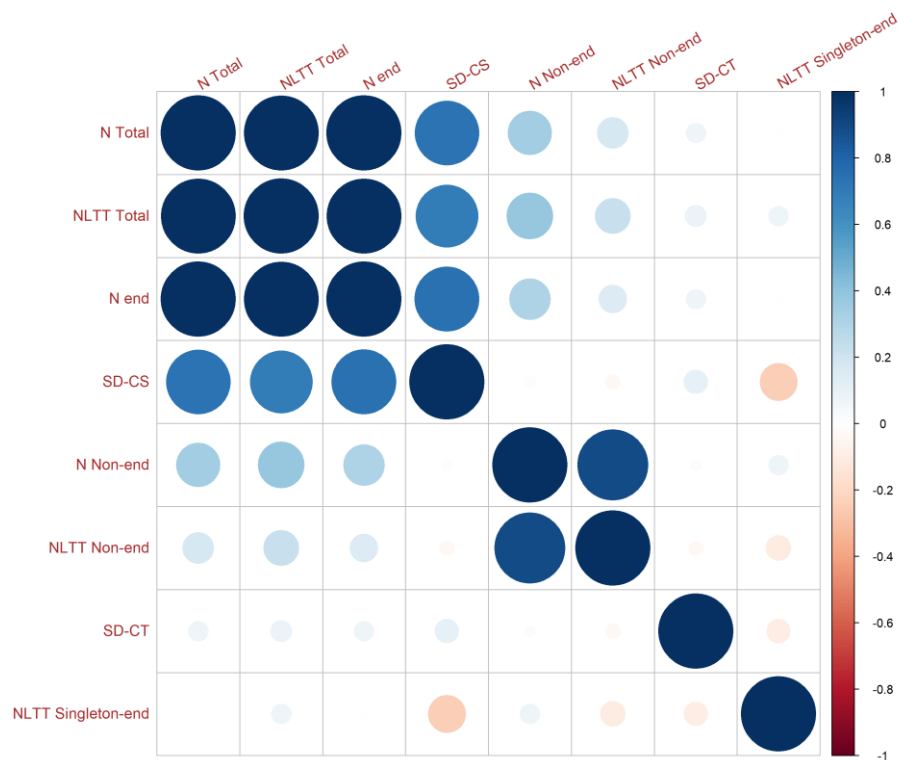
Observed data

The island datasets generated with different parameter sets show large differences in the total species diversity and the number of clades present on the island (Table 4). As for the endemism status, the number of non-endemics differs less than the number of endemic species (Table S1). High cladogenesis ($\lambda^c = 0.7$) and colonization ($\gamma = 0.009$) rates can cause some islands to have more than 500 extant species in total, with the largest recorded clade containing 129 species (Table S1). The smallest island dataset we obtained in this study has just seven species distributed over five clades, which was obtained under conditions of low colonization ($\gamma = 0.003$) and speciation rates ($\lambda^c = 0.4$), and a high extinction rate ($\mu = 0.3$). Although such highly diverse or very species-poor islands may not be common in empirical studies, we nevertheless wanted to evaluate the inference power in those extreme cases. We calculated the summary statistics of all the observations used in this study, and evaluated the correlations between the statistics with a heatmap (Fig 2). There are strong one-to-one correlations between the diversity-related statistics (N_{total} , $N_{non-end}$) and the temporal NLTT statistics ($NLTT_{total}$, $NLTT_{non-end}$), which indicates a high overlap of the information provided by these statistics. N_{end} is independent from $NLTT_{singleton-end}$, but is positively correlated with N_{total} . However, $SD-CT$, which is a statistic to measure the colonization time variance, is independent of other statistics, as is evident from a low correlation coefficient (Fig 2).

1 Table 4. Statistics of the observed datasets. We show the mean (standard deviation) of the 10
 2 replicates for each parameter set.

Scenario	λ^c	μ	γ	λ^a	Number of clades	Total species richness	Largest clade
1	0.4	0	0.003	0.1	14 (4)	44 (15)	13 (5)
2	0.7	0	0.003	0.1	14 (3)	134 (58)	52 (28)
3	0.4	0.3	0.003	0.1	9 (3)	19 (10)	7 (3)
4	0.7	0.3	0.003	0.1	11 (5)	47 (21)	17 (7)
5	0.4	0	0.009	0.1	44 (6)	138 (30)	20 (9)
6	0.7	0	0.009	0.1	41 (8)	352 (124)	56 (22)
7	0.4	0.3	0.009	0.1	30 (5)	64 (16)	11 (4)
8	0.7	0.3	0.009	0.1	32 (6)	159 (41)	35 (17)
9	0.4	0	0.003	1	17 (4)	52 (18)	14 (9)
10	0.7	0	0.003	1	16 (2)	127 (40)	42 (19)
11	0.4	0.3	0.003	1	8 (3)	15 (6)	5 (2)
12	0.7	0.3	0.003	1	13 (3)	55 (22)	16 (7)
13	0.4	0	0.009	1	42 (6)	155 (39)	22 (13)
14	0.7	0	0.009	1	44 (6)	389 (124)	71 (28)
15	0.4	0.3	0.009	1	30 (4)	60 (15)	9 (4)
16	0.7	0.3	0.009	1	32 (5)	152 (47)	27 (10)

3



4

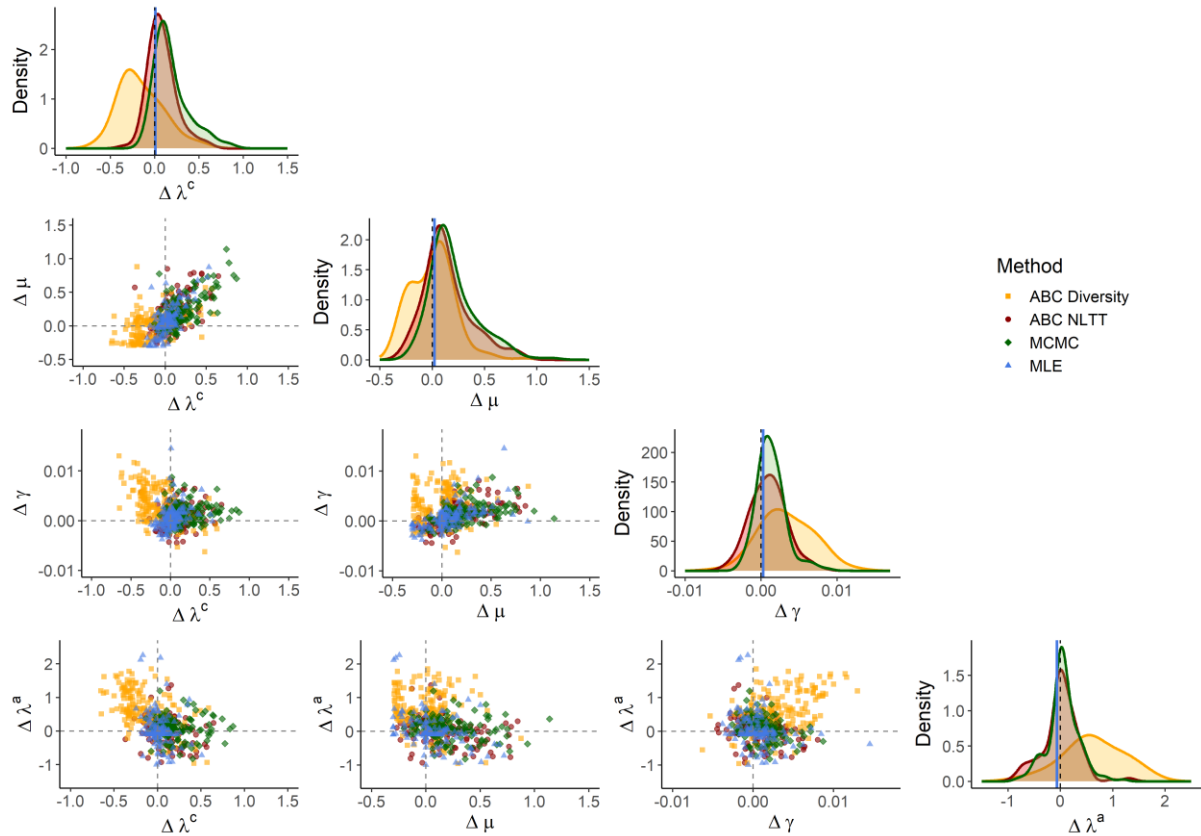
5 Figure 2. Correlation heatmap between summary statistics of all the observations that were used in
 6 the ABC algorithm. Red indicates a negative correlation between two statistics, and blue a positive
 7 correlation. The size and color of the circle show the strength of the correlation.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Inference comparison between ABC, MCMC and MLE

To facilitate comparison between the methods across various parameter combinations used as generating values, we calculated the relative difference between the generating (“true”) rates and the estimated rates, and compared the differences (Δ -rate) between methods. As for the choice of the prior distribution, we find that the ABC estimation performs better under the narrower prior (Fig S1 and S2), with relatively less bias and variance than under the broader prior (Fig 4 and 5), but with the same bias patterns (overestimation or underestimation). Because speciation and extinction rates can often be high on islands (Warren et al., 2015), and because researchers are unlikely to have sufficient information to specify narrow priors, here we discuss the parameter estimations under the broader prior distribution, and we show the estimation results under the narrow prior distribution in supplementary Figure S1 and S2.

Overall, the MLE approach showed the highest accuracy in estimating parameters in the DAISIE framework (Figs 3 and 5), with median Δ values closest to zero for most of the parameter sets. The MCMC and the ABC estimations (except when using diversity-related statistics) have similar performance with minor difference, but both show relatively larger bias in estimating cladogenesis and extinction rates when the generating rate of colonization is low (Fig 5). In addition, because the MCMC and the ABC are Bayesian algorithms producing a distribution as posterior, the standard errors are relatively larger than for the MLE.



1

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

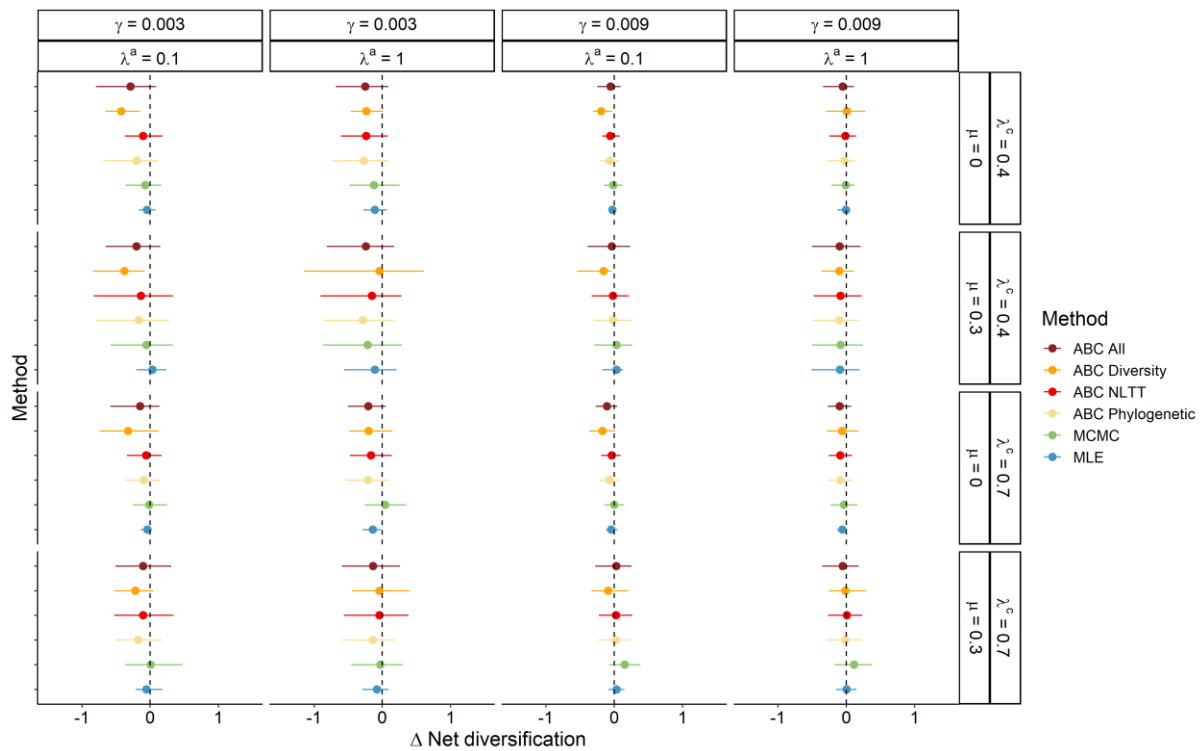
21

22

23

Figure 3. Inference of **cladogenesis, extinction, colonization and anagenesis rate** parameters across all 160 parameter sets. The ABC results are from the analyses using the **broader prior** (See Table 2). Plots show the Δ -rate, that is, the difference between the estimated value and the true value used for generating the observed simulations. The diagonal shows density distributions of the estimations using MCMC (green), ABC with diversity-related (orange) or NLTT (red) statistics. The dashed line is the baseline at zero, and the blue solid line is the median of all MLE estimations across all the parameter sets. The scatter plots in the lower triangle show the Δ -rates for different parameter combinations: the point estimation of MLE (blue triangles), the median value of the posterior distribution using MCMC (green diamonds) and ABC (orange squares and red circles). The gray dashed lines are the baseline, which intersect at zero. ABC Diversity - three diversity-related statistics; ABC NLTT - three NLTT statistics; MLE - maximum likelihood estimation; MCMC - Markov Chain Monte Carlo; γ - colonization rate; μ - extinction rate; λ^c - cladogenesis rate; λ^a - anagenesis rate.

1
2



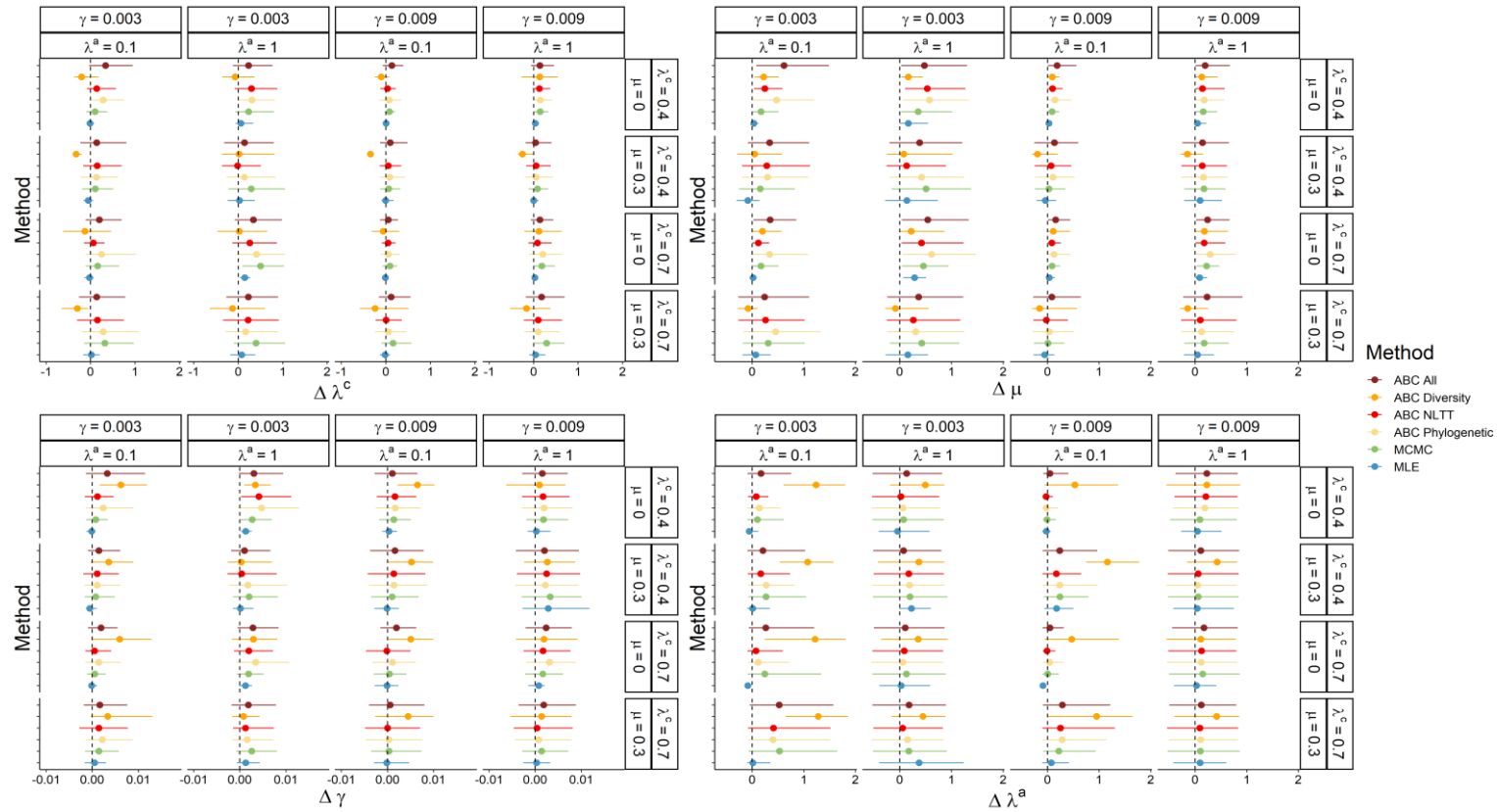
3

4 Figure 4. Results of inference of the **net diversification** rate (rate of cladogenesis minus rate of
5 extinction) using MLE, MCMC and ABC. Lines show 95% confidence intervals, dots the median value.
6 The ABC results are from the analyses using the **broader prior** (See Table 2). Plots show the Δ -net
7 diversification rate, that is, the difference between the estimated value and the true value used for
8 generating the observed simulations. The true values are shown at the top of each column and to the
9 right of each row. The distribution for each method combines the 10 replicates for each parameter set.
10 For MLE, these replicates result in 10 data points, whereas for MCMC and ABC these replicates result
11 in 10 posterior distributions combined. In the case of ABC-SMC, the posterior distribution for each
12 replicate is based on 500 particles from the last iteration step of the algorithm. ABC All - all statistics;
13 ABC Diversity - three diversity-related statistics; ABC NLTT - three NLTT statistics; ABC Phylogenetic
14 - five phylogenetic statistics; MLE - Maximum likelihood estimation; MCMC - Markov Chain Monte
15 Carlo; γ - colonization rate; μ - extinction rate; λ^c - cladogenesis rate; λ^a - anagenesis rate.

16

17

18



1

2 Figure 5. Inference of the **cladogenesis, extinction, colonization and anagenesis rates** using MLE, MCMC and ABC. Lines show 95% confidence intervals,
3 dots the median value. The ABC results are from the analyses using the **broader prior** (See Table 2). Plots show the Δ -rate, that is, the difference between
4 the estimated value and the true value used for generating the observed simulations. The true values are shown at the top of each column and to the right of
5 each row. The distribution for each method combines the 10 replicates for each parameter set. For MLE, these replicates result in 10 data points, whereas for
6 MCMC and ABC these replicates result in 10 posterior distributions combined. In the case of ABC-SMC, the posterior distribution for each replicate is based
7 on 500 particles from the last iteration step of the algorithm. ABC-All – all eight statistics; ABC Diversity – three diversity-related statistics; ABC-NLTT – three
8 NLTT statistics; ABC-Phylogenetic – five phylogenetic statistics; MLE – maximum likelihood estimation; MCMC – Markov chain Monte Carlo; γ – colonization
9 rate; μ – extinction rate; λ^c – cladogenesis rate; λ^a – anagenesis rate.

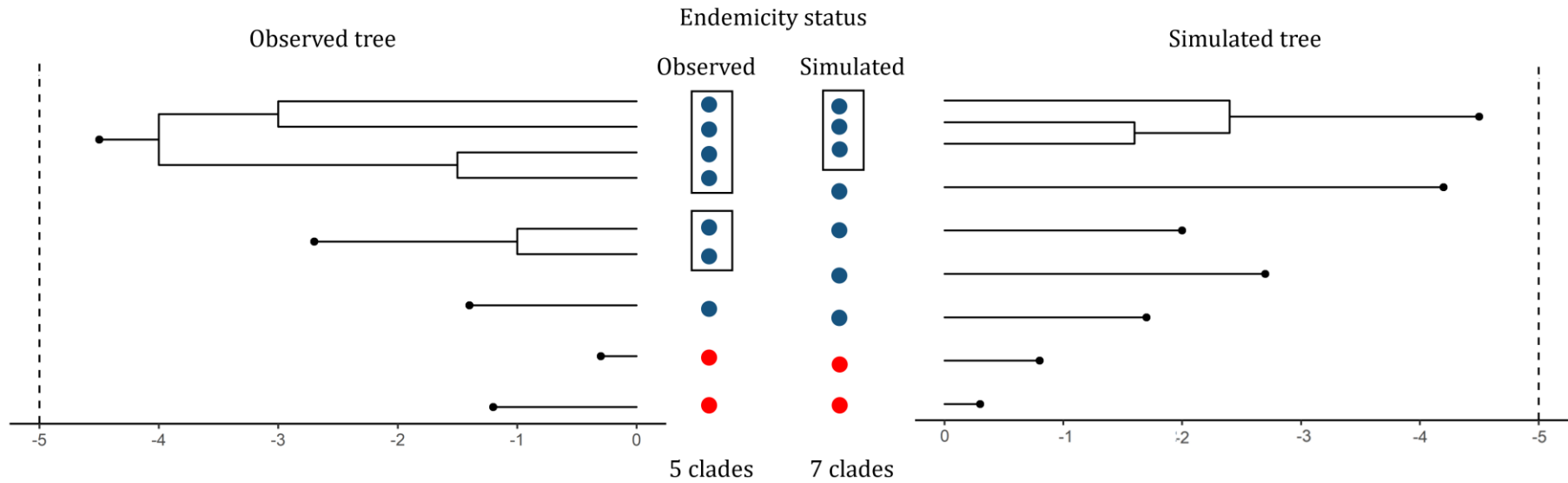
1 **Summary statistics**

2 When comparing the posterior distribution of the last ABC iteration we find that, overall,
3 the estimation using phylogenetic statistics (ABC-phylogenetic and ABC-NLTT) appears
4 to be more accurate and stable than that using diversity-related statistics (ABC-diversity),
5 especially when estimating colonization and anagenesis rates (Figs 3-5). We do note that
6 the ABC algorithm with phylogenetic statistics tends to overestimate the cladogenesis
7 and extinction rates when the colonization rate is low ($\gamma = 0.003$) (Fig 5). The bias in the
8 extinction rate is larger than that of the cladogenesis rate, therefore resulting in
9 underestimated net diversification rates (Fig 4). The estimations of anagenesis and
10 colonization are accurate for most of the parameter scenarios (Fig 5).

11
12 The ABC approach using only diversity-related statistics produces large inference bias.
13 Cladogenesis and extinction rates tend to be underestimated, especially when the
14 generating rate of extinction is non-zero ($\mu = 0.3$) (Figs 3 and 5). In addition, colonization
15 and anagenesis rates are largely overestimated for most of the parameter sets (Fig 3), and
16 are more biased when the generating rate of anagenesis is low ($\lambda^a = 0.1$) (Fig 5). Unlike
17 phylogenetically-informed statistics, diversity-related statistics cannot determine how
18 extant species are divided among clades, or whether an endemic species is in a singleton
19 or in a radiation clade. Therefore, anagenesis rates are difficult to estimate, and tend to
20 be uniformly distributed across the posterior distribution, leading to larger bias. Under
21 the same total number of species and endemic species as in the observed data, an
22 overestimated anagenesis rate may cause more singleton endemic clades and fewer
23 radiations in the ABC simulation (Fig 6), which in turn tends to result in an overestimated
24 colonization rate (Fig 5) and an underestimated net diversification rate. (Fig 4).

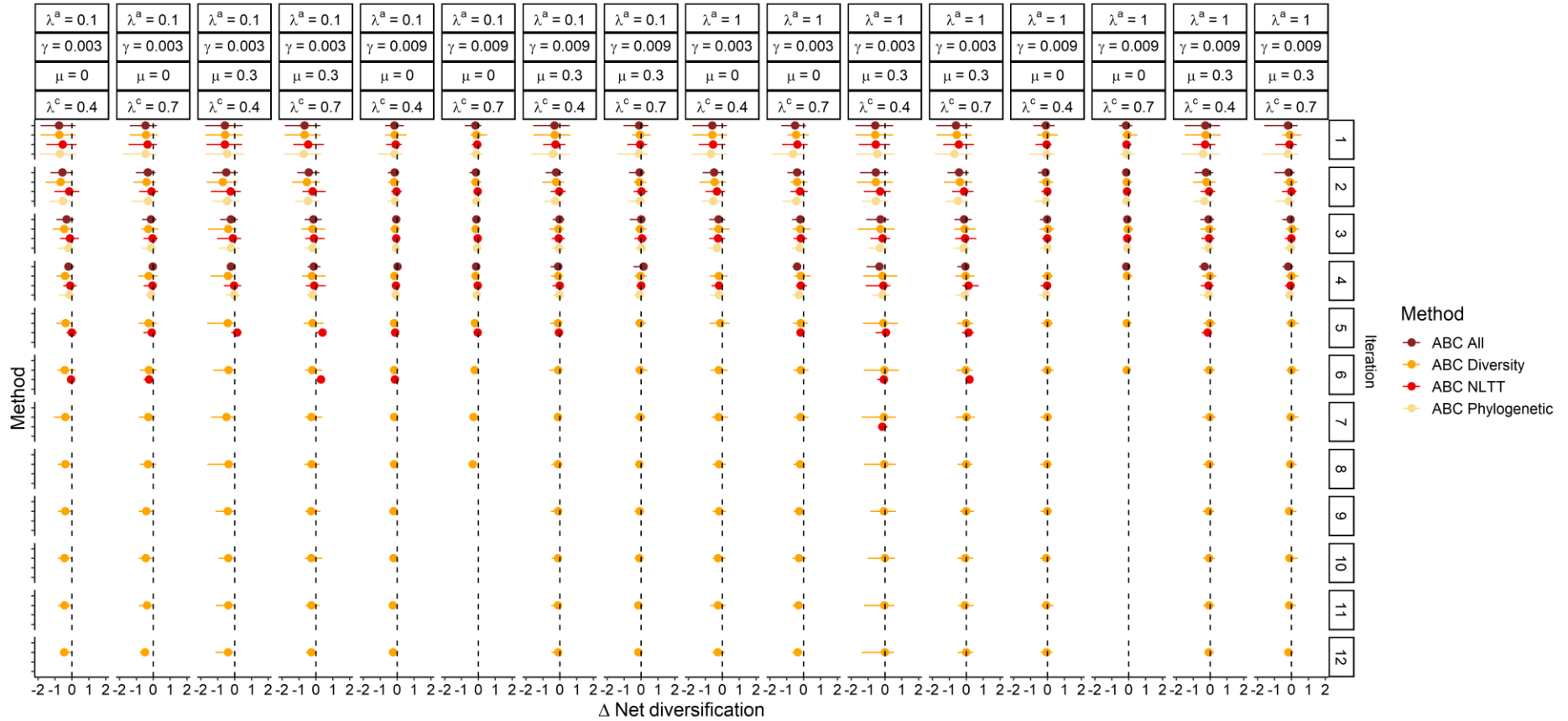
25
26 If we zoom in on each single replicate (the estimation of each observed dataset), the
27 estimation using diversity-related statistics (ABC-diversity) is more likely to converge to
28 an extremely deviating value (Figs S3 and S4). Furthermore, comparing the estimations
29 under the same iterations, we observe that using phylogenetic statistics always
30 converges faster, which means higher efficiency in estimation (Figs 7 and S5-S8). In
31 addition, estimations with NLTT statistics (ABC-NLTT) contain the least bias and
32 variance comparing the distributions under the same iteration. Adding SD-CS and SD-CT
33 to the three NLTT statistics (ABC-phylogenetic) or combining all the summary statistics
34 (ABC-all) does not provide significant improvement over using only the ABC-NLTT
35 statistics.

1
2



3

4 Figure 6. Illustration of how the ABC method with only diversity-related statistics may cause bias in estimating parameters, highlighting the importance of including
5 phylogeny-related statistics. The phylogenetic tree on the left side is an example of an observed dataset, and the tree on the right side is an example of a simulated tree.
6 The two columns in the middle show the endemicity status of the extant species for both observed and simulated data, with non-endemic in red and endemic species in
7 blue. Species inside rectangles are endemic species from the same clade (radiation). The simulated tree has the same total number of species, endemic species and non-
8 endemic species as the observed tree, but a different distribution of species between clades and the number of clades, with many more endemic singletons than the
9 observed data.

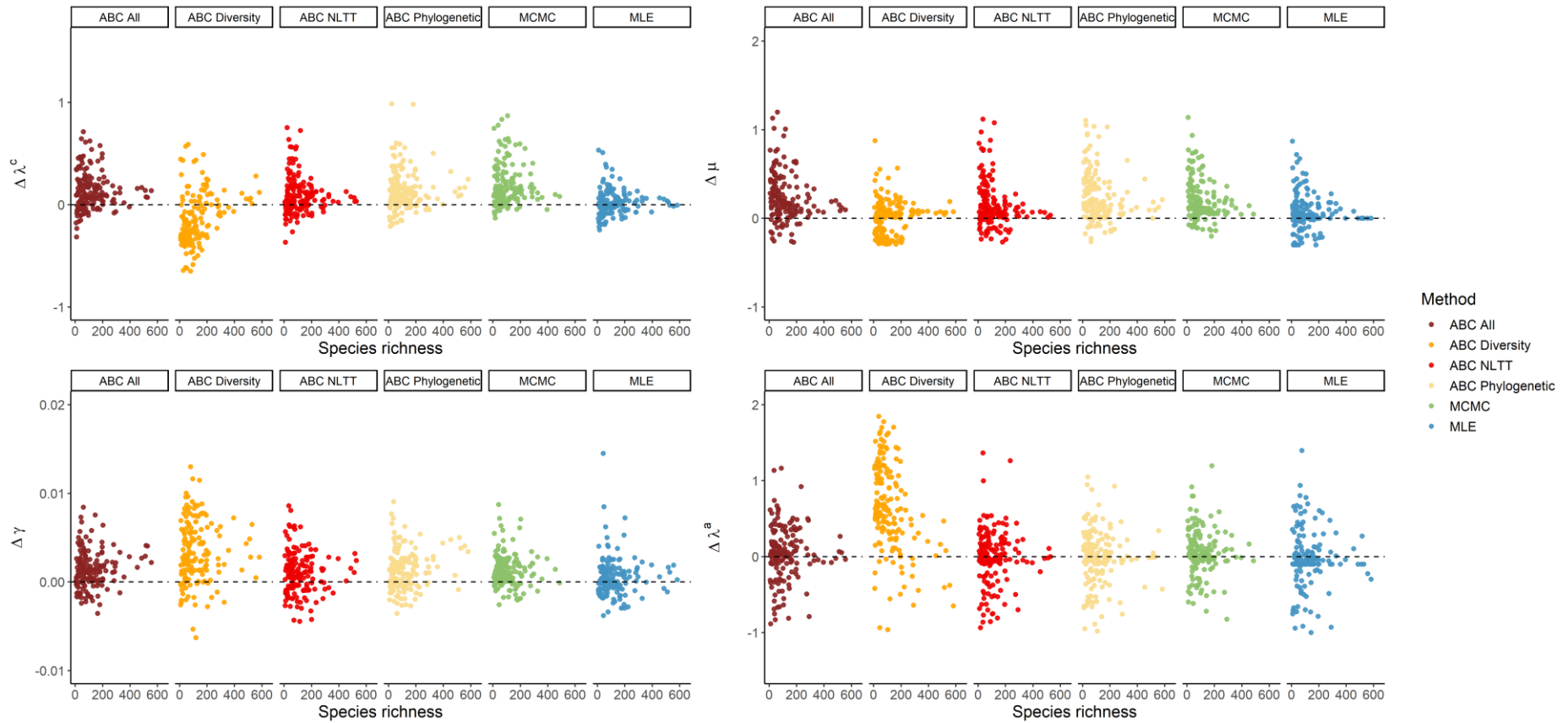


1
2 Figure 7. Results of inference of the **net diversification rate** (rate of cladogenesis minus rate of extinction) through **iterations** using ABC with different
3 groups of summary statistics. The ABC results are from the analyses using the broader prior scale (Table 2). Plots show the Δ -net diversification, that is, the
4 difference between the estimated values and the true values used for generating the observed data. The true values are shown at the top of each column. The
5 right of each row shows the number of the ABC iteration. The distribution for each method combines the replicates for each parameter set at a specific
6 iteration. ABC All - all statistics; ABC Diversity - three diversity-related statistics; ABC NLTT - three NLTT statistics; ABC Phylogenetic - five phylogenetic
7 statistics; γ - colonization rate; μ - extinction rate; λ^c - cladogenesis rate; λ^a - anagenesis rate.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

Correlation between observed dataset properties and estimation

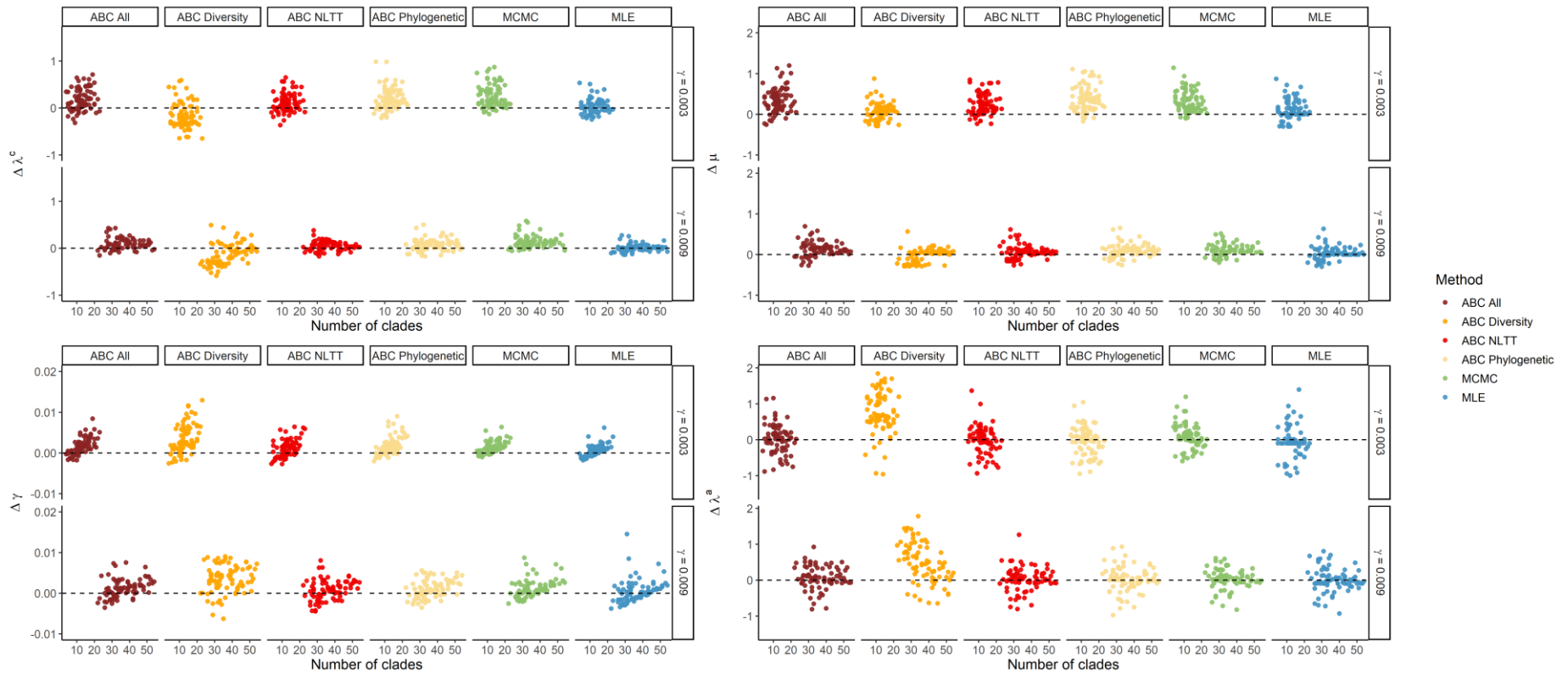
As we found that the generating value of colonization rate plays an important role in estimating parameters, and that colonization rate can affect both the species richness and the number of island clades, we investigated how the parameter estimations depend on properties of the observed data. We used three property metrics to describe the observed datasets: species richness (total number of species on the island), the number of clades, and size of the largest clade. We fitted the relationships between the metrics (median and standard deviation) and the parameter estimations (median) for each observation, and find that all the estimation methods have the same trend: datasets with fewer species and smaller size of the largest clade are likely to cause larger inference and standard errors (Figs 8, and S9, S10 and S11). However, the relationship between the number of clades and the parameter estimations shows two clusters according to the generating colonization rate (Figs 9 and S12). The datasets with higher generating colonization rate contain more clades and have significantly lower bias, especially in estimating cladogenesis and extinction rates.



1

2 Figure 8. The relationship between the **species richness** of the whole island community and the relative difference in estimating **CES rates**. Different colors
 3 indicate different estimation methods. The points show the point estimation of MLE or the **median** value of the posterior distribution using MCMC and ABC.

4



1

2 Figure 9. The relationship between **the number of clades** present on the island and the relative difference in estimating **CES rates**. Different colors indicate
 3 different estimation methods. The points show the point estimation of MLE or the **median** value of the posterior distribution using MCMC and ABC. The points
 4 are clustered based on the generating rates of colonization.

5

1 **Discussion**

2 We developed and tested the use of ABC inference in estimating colonization, speciation
3 and extinction rates in an island biogeography model. We compared the estimation
4 performance of the likelihood-free ABC approach with the MCMC and MLE approaches,
5 and evaluated the ABC performance with different sets of summary statistics. Our results
6 indicate that, overall, the performance of the ABC method with phylogenetic statistics is
7 comparable to the likelihood-based methods (especially for MCMC), as the median values
8 of the distributions show minor differences. However, the accuracy of the ABC estimation
9 is sensitive to the generating colonization rate, which is associated with the properties of
10 the observed data (e.g., species richness, the number of clades in the whole island
11 community) (Figs. 8-9 and S9-S12). Furthermore, adding phylogenetic information
12 significantly improves the estimation accuracy and efficiency in the ABC algorithm.

13
14 In ABC algorithms, the selection of the prior distribution and the summary statistics
15 significantly affect the power of the estimation (Aeschbacher et al., 2012; Burr &
16 Skurikhin, 2013). We found that a broader prior distribution exacerbates the bias when
17 the observation provides limited information with poor species richness, which was also
18 found in the MCMC results. In this case, higher colonization and cladogenesis than
19 expected (true) rates are more likely to be sampled from broad prior distributions, and
20 can be balanced by high extinction rates to reach the target number of species on the
21 island. However, in the island biogeography context, the extinction or speciation rate
22 could be high in some clades, and from the phylogenetic data one cannot easily extract a
23 suitable prior distribution. Therefore, a broader distribution is necessary to cover the
24 potential true values. In this study, we used uniform distributions as priors. A popular
25 alternative is using the exponential prior distribution for estimating diversification rates
26 (Scarpino et al., 2014). The advantage of using the exponential distribution is to avoid
27 setting boundaries, and always obtain positive values. However, the choice of prior
28 distribution is more important in shaping the posterior when the likelihood function is
29 not highly informative. In this case, using an exponential prior distribution tends to shape
30 the posterior to an asymmetric distribution with low values, which may not be
31 problematic for estimating colonization rates, but could have a significant impact on
32 extinction rates in island biogeography models.

33
34 The robustness of the inference on extinction rates is a topic of debate, because of the
35 difficulty in high-precision extinction estimation for single lineages and the lack of
36 information on extinctions (Burin et al., 2019; Louca and Pennell, 2021). However, in the
37 DAISIE framework the likelihood-based approaches can more accurately estimate
38 extinction rates likely because DAISIE works on multiple clades instead of a single lineage.
39 Independent clades can be regarded as multiple replicates, which can be informative for
40 providing almost unbiased estimations (Valente et al., 2015; 2017; 2018). In our study,
41 we also found that the MLE approach can accurately estimate extinction rates for most of

1 the parameter sets (Fig 5). However, because we use pruned phylogenetic trees (both
2 observed and simulations in the ABC algorithm) which exclude extinction events, the ABC
3 algorithm is apparently more sensitive than MLE or MCMC to how much information can
4 be gained from the extant phylogenies (Fig 5), leading to larger inference error in smaller
5 trees. Therefore, the choice of efficient summary statistics, which contain more
6 information on evolutionary dynamics is crucial.

7
8 The NLTT statistic is regarded as a powerful statistic that contains evolutionary
9 information as well as the species richness existing at the tips (Janzen et al., 2015;
10 Saulnier et al., 2016; Richter & Wit, 2021). In our study, we find that NLTT statistics are
11 more efficient than diversity-related statistics, with fewer iterations required to reach
12 convergence and less bias (Figs 3-6). In island biogeography, NLTT statistics include the
13 information of colonization time and branching time of each extant clade on the island.
14 When species richness and endemic status are the same, different branching times can
15 lead to variations in NLTT accumulation over time, and the additional phylogenetic
16 information can improve parameter estimation by controlling the temporal variance (Fig
17 6). This is similar to the conclusions in studies that have shown higher inference accuracy
18 incorporating phylogenetic information (Valente et al., 2018; Antonelli et al., 2018).
19 According to our results, the most efficient combination of the summary statistics in
20 island biogeography modelling is that of NLTT statistics of total species, singleton island
21 endemism and non-endemic species. Including additional statistics does not always
22 result in higher inference accuracy, because they are highly correlated and hence
23 relatively redundant (Fig 2).

24
25 The ABC method is considered a good alternative to maximum likelihood estimation,
26 especially when the model is computationally complex. There are a few ABC related R
27 packages implementing ABC algorithms (Csilléry et al., 2012; Jabot et al., 2013), and ABC
28 has been used in a large number of ecological and evolutionary studies (Beaumont, 2010).
29 However, ABC algorithms are rarely used in estimating parameters in macroevolutionary
30 studies in island biogeography. Furthermore, it is rare to find studies comparing the
31 estimation performance between maximum likelihood and ABC when it is possible to
32 analytically calculate the likelihood. This study has identified useful summary statistics
33 to be used for inference in island biogeography models and their extensions. However,
34 more complex summary statistics may be needed for these models. For example, in trait-
35 dependent island biogeography models, trait-related summary statistics will still be
36 required.

37
38
39
40
41

1 **References**

- 2 Aeschbacher, S., Beaumont, M. A., & Futschik, A. (2012). A novel approach for choosing
3 summary statistics in approximate Bayesian computation. *Genetics*, *192*(3), 1027–
4 1047. <https://doi.org/10.1534/GENETICS.112.143164/-/DC1>
- 5 Akaike, H. (1973). Maximum likelihood identification of gaussian autoregressive moving
6 average models. *Biometrika*, *60*(2), 255–265.
7 <https://doi.org/10.1093/biomet/60.2.255>
- 8 Antonelli, A., Zizka, A., Carvalho, F. A., Scharn, R., Bacon, C. D., Silvestro, D., & Condamine,
9 F. L. (2018). Amazonia is the primary source of Neotropical biodiversity.
10 *Proceedings of the National Academy of Sciences of the United States of America*,
11 *115*(23), 6034–6039. <https://doi.org/10.1073/pnas.1713819115>
- 12 Beaumont, M. A. (2010). Approximate Bayesian computation in evolution and ecology.
13 *Annual Review of Ecology, Evolution, and Systematics*, *41*, 379–406.
14 <https://doi.org/10.1146/annurev-ecolsys-102209-144621>
- 15 Beaumont, M. A., Zhang, W., & Balding, D. J. (2002). Approximate Bayesian computation
16 in population genetics. *Genetics*, *162*(4), 2025–2035.
17 <https://doi.org/10.1093/genetics/162.4.2025>
- 18 Bokma, F. (2010). Time, species, and separating their effects on trait variance in clades.
19 *Systematic Biology*, *59*(5), 602–607. <https://doi.org/10.1093/sysbio/syq029>
- 20 Burin, G., Alencar, L. R. V., Chang, J., Alfaro, M. E., & Quental, T. B. (2019). How Well Can
21 We Estimate Diversity Dynamics for Clades in Diversity Decline? *Systematic*
22 *Biology*, *68*(1), 47–62. <https://doi.org/10.1093/sysbio/syy037>
- 23 Burr, T., & Skurikhin, A. (2013). Selecting summary statistics in approximate bayesian
24 computation for calibrating stochastic models. *BioMed Research International*,
25 *2013*. <https://doi.org/10.1155/2013/210646>
- 26 Csilléry, K., François, O., & Blum, M. (2012). Approximate Bayesian Computation (ABC)
27 in R: A Vignette. *202.162.217.53*, 1–21.
28 <ftp://202.162.217.53/CRAN/web/packages/abc/vignettes/abcvignette.pdf>
- 29 Jabot, F., & Chave, J. (2009). Inferring the parameters of the neutral theory of
30 biodiversity using phylogenetic information and implications for tropical forests.
31 *Ecology Letters*, *12*(3), 239–248. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2008.01280.x)
32 0248.2008.01280.x
- 33 Jabot, F., Faure, T., & Dumoulin, N. (2013). EasyABC: performing efficient approximate
34 Bayesian computation sampling schemes using R. *Methods in Ecology and Evolution*,
35 *4*(7), 684–687. <https://doi.org/10.1111/2041-210X.12050>
- 36 Janzen, T., Höhna, S., & Etienne, R. S. (2015). Approximate Bayesian Computation of
37 diversification rates from molecular phylogenies: introducing a new efficient
38 summary statistic, the nLTT. *Methods in Ecology and Evolution*, *6*(5), 566–575.
39 <https://doi.org/10.1111/2041-210X.12350>
- 40 Lambert, J. W., Neves, P. S., Bilderbeek, R. L. C., Valente, L., & Etienne, R. S. (2022). The
41 effect of mainland dynamics on data and parameter estimates in island
42 biogeography. *BioRxiv*, 2022.01.13.476210.
43 <http://biorxiv.org/content/early/2022/01/15/2022.01.13.476210.abstract>

- 1 Lim, J. Y., & Marshall, C. R. (2017). The true tempo of evolutionary radiation and decline
2 revealed on the Hawaiian archipelago. *Nature*, *543*(7647), 710–713.
3 <https://doi.org/10.1038/nature21675>
- 4 Louca, S., & Pennell, M. W. (2020). Extant timetrees are consistent with a myriad of
5 diversification histories. *Nature*, *580*(7804), 502–505.
6 <https://doi.org/10.1038/s41586-020-2176-1>
- 7 Louca, S., & Pennell, M. W. (2021). Why extinction estimates from extant phylogenies
8 are so often zero. *Current Biology*, *31*(14), 3168–3173.e4.
9 <https://doi.org/10.1016/j.cub.2021.04.066>
- 10 MacArthur, R. H., & Wilson, E. O. (1963). An Equilibrium Theory of Insular
11 Zoogeography. *Evolution*, *17*(4), 373. <https://doi.org/10.2307/2407089>
- 12 Patiño, J., Carine, M., Mardulyn, P., Devos, N., Mateo, R. G., González-Mancebo, J. M., Shaw,
13 A. J., & Vanderpoorten, A. (2015). Approximate Bayesian Computation Reveals the
14 Crucial Role of Oceanic Islands for the Assembly of Continental Biodiversity.
15 *Systematic Biology*, *64*(4), 579–589. <https://doi.org/10.1093/SYSBIO/SYV013>
- 16 Patiño, J., Whittaker, R. J., Borges, P. A. V., Fernández-Palacios, J. M., Ah-Peng, C., Araújo,
17 M. B., Ávila, S. P., Cardoso, P., Cornuault, J., de Boer, E. J., de Nascimento, L., Gil, A.,
18 González-Castro, A., Gruner, D. S., Heleno, R., Hortal, J., Illera, J. C., Kaiser-Bunbury,
19 C. N., Matthews, T. J., ... Emerson, B. C. (2017). A roadmap for island biology: 50
20 fundamental questions after 50 years of The Theory of Island Biogeography.
21 *Journal of Biogeography*, *44*(5), 963–983. <https://doi.org/10.1111/jbi.12986>
- 22 Rabosky, D. L. (2009). Ecological limits and diversification rate: alternative paradigms
23 to explain the variation in species richness among clades and regions. *Ecology*
24 *Letters*, *12*(8), 735–743. <https://doi.org/10.1111/J.1461-0248.2009.01333.X>
- 25 Richter, F., & Wit, E. C. (2021). *D ETECTING PHYLODIVERSITY - DEPENDENT*
26 *DIVERSIFICATION WITH A GENERAL PHYLOGENETIC INFERENCE FRAMEWORK*. 1–
27 19.
- 28 Ronquist, F. (2011). Phylogenetic methods in historical biogeography. *Annual Review of*
29 *Ecology, Evolution, and Systematics*, *42*. [https://doi.org/10.1146/annurev-ecolsys-](https://doi.org/10.1146/annurev-ecolsys-102209-144710)
30 [102209-144710](https://doi.org/10.1146/annurev-ecolsys-102209-144710)
- 31 Santos Neves, P., Lambert, J. W., Valente, L., & Etienne, R. S. (2022). The robustness of a
32 simple dynamic model of island biodiversity to geological and sea-level change.
33 *Journal of Biogeography*, *49*(11), 2091–2104. <https://doi.org/10.1111/jbi.14519>
- 34 Saulnier, E., Gascuel, O., & Alizon, S. (2016). *Assessing the accuracy of Approximate*
35 *Bayesian Computation approaches to infer epidemiological parameters from*
36 *phylogenies*. <https://doi.org/10.1101/050211>
- 37 Scarpino, S. V., Levin, D. A., & Meyers, L. A. (2014). Polyploid formation shapes flowering
38 plant diversity. *American Naturalist*, *184*(4), 456–465.
39 <https://doi.org/10.1086/677752>
- 40 Slater, G. J., Harmon, L. J., Wegmann, D., Joyce, P., Revell, L. J., & Alfaro, M. E. (2012).
41 FITTING MODELS OF CONTINUOUS TRAIT EVOLUTION TO INCOMPLETELY
42 SAMPLED COMPARATIVE DATA USING APPROXIMATE BAYESIAN COMPUTATION.
43 *Evolution*, *66*(3), 752–762. <https://doi.org/10.1111/J.1558-5646.2011.01474.X>
- 44 Sukumaran, J., Economo, E. P., & Lacey Knowles, L. (2016). Machine learning

- 1 biogeographic processes from biotic patterns: A new trait-dependent dispersal and
2 diversification model with model choice by simulation-Trained discriminant
3 analysis. *Systematic Biology*, 65(3), 525–545.
4 <https://doi.org/10.1093/sysbio/syv121>
- 5 Toni, T., & Stumpf, M. P. H. (2009). Simulation-based model selection for dynamical
6 systems in systems and population biology. *Bioinformatics*, 26(1), 104–110.
7 <https://doi.org/10.1093/bioinformatics/btp619>
- 8 Toni, T., Welch, D., Strelkova, N., Ipsen, A., & Stumpf, M. P. H. (2009). Approximate
9 Bayesian computation scheme for parameter inference and model selection in
10 dynamical systems. *Journal of the Royal Society Interface*, 6(31), 187.
11 <https://doi.org/10.1098/RSIF.2008.0172>
- 12 Tsirogianis, C., & Sandel, B. (2016). PhyloMeasures: a package for computing
13 phylogenetic biodiversity measures and their statistical moments. *Ecography*,
14 39(7), 709–714. <https://doi.org/10.1111/ECOG.01814>
- 15 Valente, L., Etienne, R. S., & Dávalos, L. M. (2017). Recent extinctions disturb path to
16 equilibrium diversity in Caribbean bats. *Nature Ecology and Evolution*, 1(2), 1–7.
17 <https://doi.org/10.1038/s41559-016-0026>
- 18 Valente, L. M., Phillimore, A. B., & Etienne, R. S. (2015). Equilibrium and non-equilibrium
19 dynamics simultaneously operate in the Galápagos islands. *Ecology Letters*, 18(8),
20 844–852. <https://doi.org/10.1111/ele.12461>
- 21 Valente, L., Phillimore, A. B., & Etienne, R. S. (2018). Using molecular phylogenies in
22 island biogeography: it's about time. *Ecography*, 41(10), 1684–1686.
23 <https://doi.org/10.1111/ecog.03503>
- 24 Warren, B. H., Simberloff, D., Ricklefs, R. E., Aguilée, R., Condamine, F. L., Gravel, D.,
25 Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernández-
26 Palacios, J. M., Hengl, T., Norder, S. J., Rijdsdijk, K. F., Sanmartín, I., Strasberg, D.,
27 Triantis, K. A., ... Thébaud, C. (2015). Islands as model systems in ecology and
28 evolution: Prospects fifty years after MacArthur-Wilson. *Ecology Letters*, 18(2),
29 200–217. <https://doi.org/10.1111/ele.12398>
- 30 Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K., & Triantis,
31 K. A. (2017). Island biogeography: Taking the long view of nature's laboratories.
32 *Science*, 357(6354). <https://doi.org/10.1126/science.aam8326>
- 33 Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic
34 island biogeography. *Journal of Biogeography*, 35(6), 977–994.
35 <https://doi.org/10.1111/j.1365-2699.2008.01892.x>
- 36 Xie, S., Valente, L., & Etienne, R. S. (2023). Can we ignore trait-dependent colonization
37 and diversification in island biogeography? *Evolution*, 77(3), 670–681.
38 <https://doi.org/10.1093/EVOLUT/QPAD006>
39