

Detecting evolutionarily significant units above the species level using the generalised mixed Yule coalescent method

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Summary

1. There is renewed interest in inferring evolutionary history by modelling diversification rates using phylogenies. Understanding the performance of the methods used under different scenarios is essential for assessing empirical results. Recently, we introduced a new approach for analysing broadscale diversity patterns, using the generalised mixed Yule coalescent (GMYC) method to test for the existence of evolutionarily significant units above the species (higher ESUs). This approach focuses on identifying clades as well as estimating rates, and we refer to it as clade-dependent. However, the ability of the GMYC to detect the phylogenetic signature of higher ESUs has not been fully explored, nor has it been placed in the context of other, clade-independent approaches.

2. We simulated > 32 000 trees under two clade-independent models: constant-rate birth-death (CRBD) and variable-rate birth-death (VRBD), using parameter estimates from nine empirical trees and more general parameter values. The simulated trees were used to evaluate scenarios under which GMYC might incorrectly detect the presence of higher ESUs.

3. The GMYC null model was rejected at a high rate on CRBD-simulated trees. This would lead to spurious inference of higher ESUs. However, the support for the GMYC model was significantly greater in most of the empirical clades than expected under a CRBD process. Simulations with empirically derived parameter values could therefore be used to exclude CRBD as an explanation for diversification patterns. In contrast, a VRBD process could not be ruled out as an alternative explanation for the apparent signature of hESUs in the empirical clades, based on the GMYC method alone. Other metrics of tree shape, however, differed notably between the empirical and VRBD-simulated trees. These metrics could be used in future to distinguish clade-dependent and clade-independent models.

4. In conclusion, detection of higher ESUs using the GMYC is robust against some clade-independent models, as long as simulations are used to evaluate these alternatives, but not against others. The differences between clade-dependent and clade-independent processes are biologically interesting, but most current models focus on the latter. We advocate more research into clade-dependent models for broad diversity patterns.

Key-words: birth-death, clade-dependent, clade-independent, diversification, phylogenetic clustering, rate shift, relative extinction rate, simulation

Introduction

There is currently widespread interest in understanding the evolutionary history of clades by inferring diversification dynamics from phylogenetic trees. Of particular interest has been identifying shifts in net diversification rates (Rabosky 2006; Alfaro *et al.* 2009) or rapidly diversifying clades (e.g.

Hughes & Eastwood 2006; Valente, Savolainen & Vargas 2010) that might be associated with a particular trait or region (Maddison, Midford & Otto 2007; Goldberg, Lancaster & Ree 2011). Recent advances have focussed on making the widely used birth-death model (Nee, May & Harvey 1994) more flexible, allowing rates to vary more generally over time (Morlon, Parsons & Plotkin 2011), as a function of standing diversity (Etienne *et al.* 2012) or among lineages, to identify clades undergoing adaptive radiation (Etienne & Haegeman 2012) or with shared evolutionary dynamics (Rabosky 2014).

What processes could cause sharing and decoupling of rates among lineages? Recently, we proposed a model of evolutionarily significant units above the level of species (Barraclough

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2010; Humphreys & Barraclough 2014). This model assumes that (i) species within a wider clade occupy a range of geographical regions and/or ecological zones; (ii) there are separate limits on the number of species within each geographical region or ecological zone; (iii) species turnover occurs through ongoing speciation and extinction and (iv) transitions between geographical regions or ecological zones are rare, meaning that closely related species tend to occupy the same region and/or zone. If these conditions are met, then species will fall into a set of clades, each of which occupies a separate geographical region or ecological zone, which we call higher evolutionarily significant units (hESUs; Fig. 1). Because of ongoing species turnover, species within a hESU share evolutionary fate as well as history (Barraclough & Humphreys 2015). This means that any event influencing the likelihood of lineages speciating or going extinct will be shared among species within but not among hESUs; hence, diversification rates are shared within and decoupled among hESUs.

The hESU model thus provides an explanation for diversity patterns that focuses on identifying units (clades) as well as estimating diversification rates. We therefore refer to it as a clade-dependent model (Fig. 1). The phylogenetic signature of hESUs is a significant increase in the rate of lineage accumulation towards the present. However, such a pattern may equally result from a clade-wide increase in diversification rates caused, for example, by a rebound from a mass extinction event (Crisp & Cook 2009) or a burst following environmental change (Stadler 2011). In other words, the pattern of an increase in branching rate, predicted to arise with hESUs, could also result from a uniform change in diversification rate, acting across an entire clade or independently of clade membership (clade-independent model, Fig. 1). Indeed, distinguishing alternative models for diversification is

challenging because several processes can lead to indistinguishable patterns (Barraclough & Nee 2001; Rabosky 2009; Morlon, Potts & Plotkin 2010; Moen & Morlon 2014). Understanding the performance of the models used to study these patterns is therefore necessary if we are to have confidence in empirical inferences.

Here, we use simulations to explore error rates of the generalised mixed Yule coalescent (GMYC; Pons *et al.* 2006) method, used to define hESUs, when trees actually derive from clade-independent processes. The GMYC method analyses waiting times between branching events in a time-calibrated phylogeny, where tips represent species, densely sampled (Humphreys & Barraclough 2014) for a broader clade, to identify significant shift(s) in the rate of branching. The approach uses a null model that no shift has occurred and that a single process is sufficient to describe phylogenetic branching across the entire clade. The alternative model finds one (single-threshold version, ST) or more (multiple-threshold version, MT) shifts in branching rate towards the present (Pons *et al.* 2006; Fontaneto *et al.* 2007; Monaghan *et al.* 2009; Fujisawa & Barraclough 2013), denoting the transition from among to within hESU branching. In its current formulation, the alternative model thus uses two branching parameters, λ , to explain the distribution of waiting times, one within and one among hESUs. In addition, the GMYC algorithm includes one (null) or two (ST, MT) scaling parameters, p , that allow the net branching rate to depart from a constant-rate process ($p = 1$), to either accelerate ($p > 1$) or decelerate ($p < 1$) towards the present.

Several studies have assessed the factors that influence the performance of the GMYC method applied at the species level (e.g. Papadopoulou *et al.* 2008; Reid & Carstens 2012; Fujisawa & Barraclough 2013; Tang *et al.* 2014), the main factor

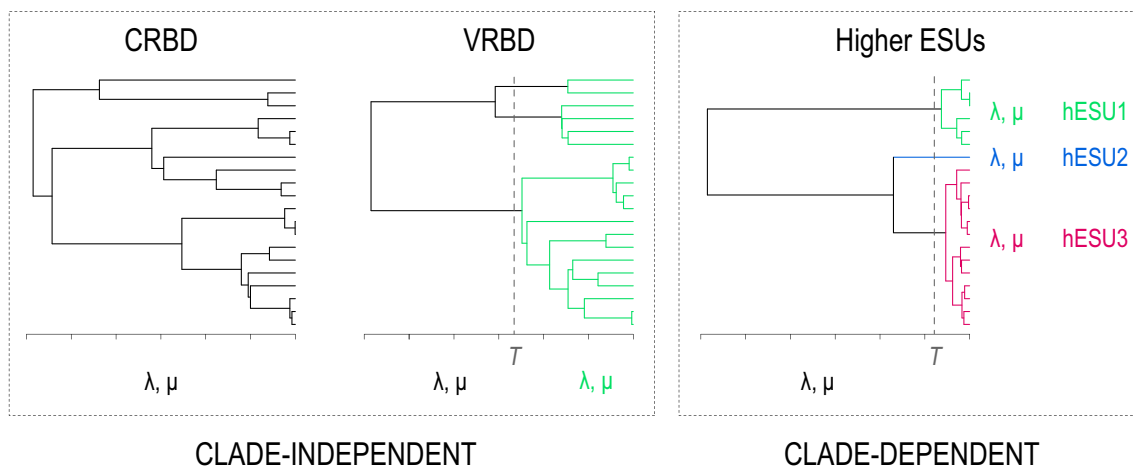


Fig. 1. Models of sharing and decoupling of speciation and extinction rates over time and among clades. In clade-independent models, these parameters apply across the entire clade and may be constant (CRBD) or variable (VRBD) over time. If variable over time, any rate shift that occurs at a given time, T , will affect all lineages equally, irrespective of clade membership. In contrast, in clade-dependent models, speciation and extinction parameters will vary over time as well as being decoupled among clades, due to occupation of different geographical or ecological zones. Turnover through ongoing speciation and extinction will operate independently among such clades, referred to as higher evolutionarily significant units (hESUs). In this class of model, the threshold time, T , denotes the timing of the shift from among to within clade processes. However, T does not denote the timing of any particular event in the past, only the age of the most recent common ancestor of the oldest hESU, which depends on the rate of turnover in that hESU. CRBD = constant-rate birth-death; VRBD = variable-rate birth-death.

being the level of variation within species relative to divergence times among species (Fujisawa & Barraclough 2013). For analyses of higher clades, we previously recorded high error rates for trees simulated under a particular clade-independent model (with constant extinction rates), but found that empirical signatures of hESUs in were significantly stronger than expected under that model (Humphreys & Barraclough 2014). We build on these results here to assess error rates for a broader range of clade sizes, extinction rates and diversification processes. We examine the performance of the GMYC approach on empirical trees and trees simulated under two different clade-independent processes that might generate similar phylogenetic patterns to the hESU model: constant-rate birth-death (CRBD) and variable-rate birth-death (VRBD) with a tree-wide shift in diversification rate. The CRBD model, commonly used for macroevolutionary analyses, generates an upturn in apparent branching rate towards the present when extinction rates are high (Nee *et al.* 1994). This might artefactually lead to the detection of hESUs using the standard GMYC method. Simulated trees were therefore used to estimate the rate of incorrect detection of hESUs for data generated using a CRBD model. More challenging still, the VRBD model generates a simultaneous increase in branching rate across an entire clade. This pattern should be indistinguishable from the predictions of hESUs as detected using the ST version of GMYC. There is no reason, however, to expect simultaneous transition times for all hESUs in a clade-dependent model, and therefore, the MT version of the GMYC might still reveal stronger evidence for hESUs than a VRBD model.

To focus our investigation on real data sets, we ran the simulations using parameter values estimated for nine empirical clades. We then compared the significance of hESUs in each clade relative to the standard GMYC null model, to trees simulated assuming a CRBD model and to trees simulated assuming a VRBD model. Empirical trees yielded higher likelihoods under the alternative GMYC model than did trees simulated under the CRBD model, indicating that inferences of hESUs are robust to the effects of constant extinction rates on tree shapes. The likelihoods of empirical trees under the GMYC model were not, however, higher than expected under the VRBD model, even using the MT version. Additional measures of tree shape or of ecological trait variation are necessary to distinguish a signal of clade-dependent hESUs from a VRBD model.

Materials and methods

PHYLOGENETIC TREES FOR EMPIRICAL DATA

Empirical analyses were performed for nine clades, defined as representing at least one order and a manageable number of species (≤ 1000 species), for which densely sampled (~70–80% species; Humphreys & Barraclough 2014), time-calibrated phylogenies were available or could be generated using published data. Such phylogenies were available for three clades of mammals (Carnivora, Euungulata and Lagomorpha; Humphreys & Barraclough 2014), birds (Afroaves (*sensu* Jarvis *et al.* 2014), nightbirds (except owls), swifts and

hummingbirds (*sensu* Ericson *et al.* 2006; hereafter 'nightbirds') and core waterbirds plus pigeons and cuckoos (hereafter 'waterbirds'; Jetz *et al.* 2012; Text S1) and conifers (Leslie *et al.* 2012). Phylogenies for cycads and Gnetales were generated using standard protocols from published matK, rbcL, 18S and, for cycads, PHYC sequences (Rydin & Korall 2009; Nagalingum *et al.* 2011; Hou *et al.* 2015; Text S2). Overall, all orders, families and genera in these clades were sampled and on average 80–90% of the species (Table S2).

GENERALISED MIXED YULE COALESCENT ANALYSES FOR EMPIRICAL TREES

Null, ST and MT GMYC models were fitted to each bird and gymnosperm maximum clade credibility tree using the *R* (R Development Core Team 2011) package *splits* (Ezard, Fujisawa & Barraclough 2014). The null model has two parameters (λ , p) and the alternative models four (λ_{among} , p_{among} , λ_{within} , p_{within}). The inferred threshold time does not constitute a model parameter but a constraint to model search space (Fujisawa & Barraclough 2013). Model inferences were summarised across the 95% confidence set of models. Mammal results were obtained from Humphreys & Barraclough (2014).

SIMULATING BIRTH-DEATH TREES WITH EMPIRICAL PARAMETER VALUES

To study the behaviour of GMYC models under alternative scenarios, CRBD trees (Nee, May & Harvey 1994) with the properties of each of the nine empirical clades [number of tips, speciation (λ) and extinction (μ) rates] were simulated. Parameter values were estimated using the birth-death function in the *R* package *ape* (Paradis, Claude & Strimmer 2004), applied to 500 trees for all data sets except conifers, where a single tree was used. Five hundred CRBD trees were simulated using λ and relative extinction ($\mu/\lambda = \epsilon$) rates sampled randomly from across the range of estimates for each clade using *sim.bd.taxa* in *TreeSim* (Stadler 2012) and *drop.extinct* in Geiger (Harmon *et al.* 2008). The estimate of ϵ for Gnetales was always 1.00 (Table S3) so trees were simulated with this parameter sampled between 0.98 and 0.99 to speed up the simulations. For the conifer CRBD trees, parameters were sampled from the same range as for cycads because the point estimate for conifers was identical to the median estimate for cycads. This resulted in 9×500 CRBD trees of varying size, λ and ϵ (Table S3). Finally, null, ST and MT GMYC models were fitted to each simulated tree and the difference in fit between null and alternative models determined using likelihood ratio (LR) tests. Error rates for CRBD trees were recorded as the proportion of trees in each set for which the null model was rejected. Note these are not type I error rates, but errors due to the null model being rejected in favour of the GMYC model when in fact a third model is true (i.e. CRBD).

SIMULATING BIRTH-;DEATH TREES WITH GENERAL PARAMETER VALUES

To test the GMYC performance above the species more generally, trees were simulated under a pure birth model ($\epsilon = 0$; Yule 1925) and CRBD models with $\epsilon = 0.1, 0.3, 0.5, 0.7$ and 0.9 . Pure birth trees were simulated using the *tree.bd* function in *diversitree* (FitzJohn 2012), 'low' ϵ trees ($\epsilon = 0.1, 0.3$) using *sim.bdtree* in Geiger and 'high' ϵ trees ($\epsilon = 0.5, 0.7, 0.9$) using *sim.bd.taxa* in *TreeSim* and *drop.extinct* in Geiger. The speciation rate was set to 1.0 for all simulations. For each rate of ϵ , 500 trees were simulated, each with 100, 500 and 1000 tips. From these, sets

of trees with 100%, 75% and 50% sampling were generated. Removing tips changes the shape of the lineages-through-time (LTT) plot, generating trees with an excess of early branching events ('slowdown') or, under high rates of ϵ , a less severe 'pull of the present' effect. The sets of pruned trees therefore allowed assessing GMYC performance under departures from CRBD. In all, this resulted in 9×500 trees for each level of ϵ , that is, a total of 54×500 CRBD trees of varying size, ϵ and branching process. Null, ST and MT GMYC models were fitted to each tree in turn and error rates recorded as above.

SIMULATING BIRTH-DEATH TREES WITH A CLADE-WIDE SHIFT IN RATES

To generate the phylogenetic signature of a clade-wide shift in rates and test the performance of the GMYC method under this scenario, VRBD trees were simulated using the empirically estimated shift position (T , threshold time in absolute time) and ratio of within:among hESU branching rate ($\lambda_{\text{within}}:\lambda_{\text{among}}$, interpreted as pre-shift and post-shift diversification rates, respectively, starting at the present and going back in time), scaled to match rates expected under a CRBD process (Text S3). Trees were simulated using `sim.rateshift.taxa` in `TreeSim` and nine combinations of parameters and tree characteristics obtained from the empirical clades (Table S4). Parameters were as follows: λ_{among} , λ_{within} and ϵ , randomly sampled from the estimates across 500 trees. Tree characteristics (constraints to reconstructed tree space; Stadler 2011) were as follows: clade size (number of extant tips) and location of the rate shift, expressed in absolute time and sampled randomly from the range of mean threshold times retained among the confidence set of GMYC models for each data set. This resulted in 9×100 VRBD trees of varying size, overall λ , ϵ and position and severity of the rate shift. Null, ST and MT GMYC models were fitted to each tree in turn as above and the proportion of trees for which (i) the null was rejected in favour of the ST GMYC, (ii) the correct empirical position of the rate shift was recovered, and (iii) fit of the MT GMYC was significantly better than ST GMYC [$\Delta\text{AIC} \geq 5$; a somewhat conservative cut-off (Burnham & Anderson 2002), due to known sensitivity of MT GMYC (Fujisawa & Barraclough 2013)] was recorded.

TREE CHARACTERISTICS

Clade size, root age, ϵ , clade imbalance and tree stemminess were recorded for each empirical and simulated tree to assess to what extent the simulated process captured other features of the empirical trees and what affects performance of the GMYC method. Tree imbalance was estimated using Colless' (Ic; Colless 1982; Heard

1992) and Sackin's (Is; Shao & Sokal 1990) indices because they have been found to perform well compared to other measures (Agapow & Purvis 2002). The former uses the difference in the number of nodes arising from the sister clades of each node and the latter the number of nodes that separates each tip from the root. In general, more imbalanced trees have a higher value under both indices. To enable comparison among data sets, they were normalised using a Yule model (Blum, François & Janson 2006). Tree stemminess was estimated using the non-cumulative stemminess index (St_N ; Rohlf *et al.* 1990). Stemmier trees, that is those that have longer unbranched edges, have a higher value. However, values also tend to increase with increasing clade size so St_N was only compared among trees within each size set. Each index was calculated using `apTreeshape` (Ic and Is; Bortolussi *et al.* 2012) and customised R scripts (St_N ; Text S4). Tree characteristics were correlated against error rates using linear regressions and generalised additive models (Hastie & Tibshirani 1990) using the R package `mgcv` (Wood 2000, 2011).

Results

GENERALISED MIXED YULE COALESCENT RESULTS FOR EMPIRICAL CLADES

The GMYC null model was rejected in favour of the ST model for all clades except waterbirds and in favour of the MT model for all clades (Table 1). Only MT models were retained in the 95% confidence set of models for euungulates, conifers, Afroaves and nightbirds; both ST and MT models were retained for carnivores, lagomorphs, cycads and Gnetales, and for waterbirds, the null was included as well. Based on the confidence set of models, hESUs date to the Miocene [mean threshold: 5.65 Ma (Gnetales)–16.4 Ma (conifers); Table 1, Fig. S1] and correspond to traditionally named genera (gymnosperms, mammals), families (mammals) or clades of subfamilial, generic or subgeneric rank (birds; Fig. S2).

CONSTANT-RATE BIRTH-DEATH SIMULATED TREES

As suspected, the standard GMYC method often erroneously detected hESUs from CRBD trees. Error rates for CRBD trees based on empirical parameter estimates ranged from 6.6% to 56.8% for ST and from 21.1% to 88.9% for MT GMYC, being lowest in trees simulated using carnivore parameter

Table 1. Fit of null, single (ST) and multiple (MT) threshold GMYC models for empirical clades and inferences across the confidence set of models

Clade	Lh (Null)	Lh (ST)	Lh (MT)	Models in 95% confidence set	hESUs	Mean threshold (Ma)
Carnivores	319.46	326.05***	328.17***	6 × MT, 8 × ST	20 (17–24)	14.1 (13.1–15.4)
Euungulates	475.90	487.52***	491.87***	7 × MT	24 (18–29)	12.7 (11.2–15.5)
Lagomorphs	42.89	48.76**	49.35**	3 × MT, 8 × ST	6 (2–11)	8.36 (5.53–13.5)
Conifers	738.5	756.5***	761.7***	9 × MT	83 (75–90)	16.4 (14.9–17.4)
Cycads	318.8	367.5***	369.4***	2 × MT, 1 × ST	14 (12–16)	6.83 (6.34–7.63)
Gnetales	11.2	15.1*	16.0**	4 × MT, 25 × ST	17 (7–31)	5.65 (2.70–19.1)
Afroaves	3230.72	3238.98***	3262.43***	6 × MT	76 (71–81)	14.4 (14.1–14.8)
Nightbirds	1181.56	1186.08**	1201.13***	5 × MT	64 (60–66)	11.1 (10.8–11.5)
Waterbirds	2445.82	2447.45	2448.83*	5 × MT, 41 × ST, Null	42 (1–1027)	33.3 (79.0–0.00)

Lh, log likelihood; Ma, million years; GMYC, generalised mixed Yule coalescent. Asterics denote significance compared to the null at $P = 0.05$ (*), $P = 0.01$ (**) and $P \leq 0.001$ (***).

Table 2. Performance of the GMYC applied to CRBD trees simulated using empirical parameter values for each study clade: the LR difference in fit between null and alternative models for empirical (LR_{obs}) and simulated trees (LR_{sim}) and error rate (rejection of the null)

Clade	N	ST			MT		
		LR _{obs}	LR _{sim} (95%, 99%) ¹	Error rate (%)	LR _{obs}	LR _{sim} (95%, 99%) ¹	Error rate (%)
Carnivores	235	13.2	6.95, 10.3	6.64	17.50	10.2, 13.0	21.1
Euungulates	302	23.4	9.58, 13.0	9.50	31.94	12.5, 18.4	31.1
Lagomorphs	71	11.7	9.22, 14.9	12.1	12.92	13.2, 19.4	31.9
Conifers	489	36.0	17.9, 22.5	56.8	46.4	24.2, 29.1	88.9
Cycads	204	97.4	11.6, 17.6	30.8	101.2	19.9, 26.1	68.3
Gnetales	72	7.80	12.5, 16.5	33.0	9.60	15.6, 10.7	63.4
Afroaves	1132	16.5	9.51, 13.0	12.2	63.4	12.4, 14.5	44.9
Nightbirds	556	9.04	10.2, 12.4	16.1	39.1	16.4, 21.3	54.6
Waterbirds	1028	3.26	8.45, 10.4	10.7	6.02	10.4, 13.6	36.5

ST, single-threshold GMYC method; MT, multiple-threshold GMYC method; N, number of tips in phylogeny; LR, likelihood ratio; GMYC, generalised mixed Yule coalescent; CRBD, constant-rate birth-death.

¹95th and 99th percentiles.

values and highest in those based on conifers (Table 2). There is no effect of clade size on error rates (linear regression ST: $F = 0.28$ on 7 d.f., $P = 0.61$; MT: $F = 0.02$ on 7 d.f., $P = 0.89$) but error rates increase with increasing ϵ (linear regression ST: $F = 24.4$ on 7 d.f., $P = 0.0017$, $R^2 = 0.78$; MT: $F = 29.1$ on 7 d.f., $P = 0.0010$, $R^2 = 0.81$). There is no interaction between clade size and ϵ , and the relationship is stronger for MT than ST GMYC (slope = 49 and 26, respectively; Fig. 2).

Results for CRBD trees simulated with general parameters confirm these results (Fig. 2). Error rates increased nonlinearly for all data sets except MT GMYC with 100% sampling. For the other sets of trees, error rates remained around 10% (ST) and 30% (MT) until $\epsilon = 0.3$, when they increased, nonlinearly. The best regression model is a Gaussian process, which is indistinguishable from a quadratic polynomial model, based on AIC values (Table S5). Overall, error rates were higher for MT GMYC and for higher levels of sampling. This is not because clades with more complete sampling are larger but because they have LTT plots with a more pronounced upturn (Fig. S3; the effect of sampling was marginally significant for the MT results when all clades were analysed together, $P = 0.047$).

Despite these effects, the empirical results are generally not explained by incorrect rejection of the null model due to constant-rate birth-death processes: the LR difference in fit between null and alternative GMYC models is much greater for empirical trees than CRBD-simulated trees for both ST and MT models and for all clades except Gnetales and waterbirds (Table 2). Thus, the evidence for hESUs is robust with respect to an alternative CRBD model.

VARIABLE-RATE BIRTH-DEATH SIMULATED TREES

The ST GMYC detected a shift in $\geq 94\%$ of trees for all data sets except those based on carnivore (47%) and lagomorph (75%) parameter values (Table 3). The simulated position of the shift was correctly inferred on average (estimated threshold time overlaps with range of threshold times under which trees were simulated) for all clades except those based on Afroaves

values (Fig. S4). Fit of MT GMYC was indistinguishable from ST GMYC for the cycad-based trees and possibly those simulated using Gnetales parameter values (94% and 90% of simulated trees, respectively) but significantly better for all other data sets (in 14–67% of simulated trees; Table S6).

The likelihood of the GMYC model for the empirical trees, however, was not greater than expected from VRBD-simulated trees, for either ST or MT versions. Indeed, for both versions, the empirical LR between null and alternative GMYC models was lower for the empirical trees than for the simulated VRBD trees (Table 4).

CHARACTERISTICS OF SIMULATED VS. EMPIRICAL TREES

The root height of the CRBD trees encompassed the root height of the empirical trees for all data sets except those based on euungulate and lagomorph parameter estimates, where simulated trees were too young (Fig. S1). The shape of the CRBD trees differed from the empirical trees by having too few deep lineages (carnivores, euungulates, conifers and all three bird clades), a less severe upturn in branching rate (lagomorphs, cycads and Gnetales) and by being more balanced and/or stemmy (Table S7). Exceptions are simulated trees based on carnivore, lagomorph and cycad parameter values, which were indistinguishable from empirical trees for both balance and stemminess.

The root height for VRBD trees was extremely old for all simulated trees, except those based on carnivore (overlapped empirical trees) and Afroaves (younger than empirical trees) parameter estimates (Fig. S4). The shape of the VRBD trees approximated that of the empirical tree for carnivore-based trees but differed in various ways for the other data sets. For example, VRBD conifer-based trees had too few surviving old lineages compared to the empirical tree, a completely different shape for all three sets simulated based on bird parameter values and were generally more balanced and/or stemmy than empirical trees (Table S7). Exceptions are trees based on carnivore and lagomorph parameter values, which were

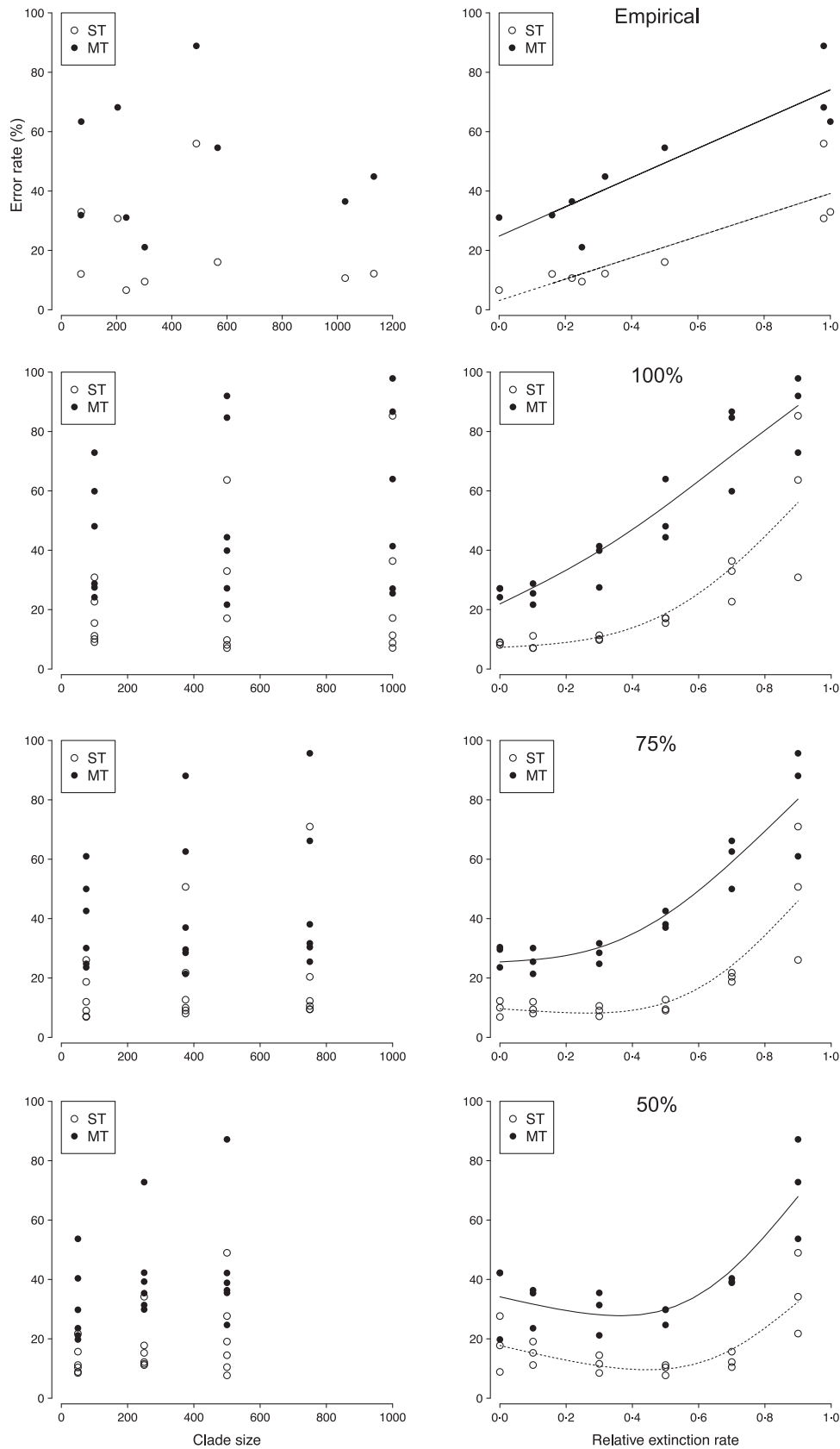


Fig. 2. Error rates of the GMYC method applied above the species vs. clade size (left) and relative extinction rate (ϵ , right). Top row: Results for CRBD trees simulated using parameter values estimated from the empirical clades. Rows 2–4: Results for CRBD trees simulated using general parameter values, with 100%, 75% and 50% of the species retained.

Table 3. Median and 95% CI ST GMYC inferences for VRBD-simulated trees where the null was rejected

Clade	$P \leq 0.05^1$	hESUs	Threshold (Ma)	Relative depth of shift	λ_{between}	λ_{within}	$\lambda_{\text{within}}/\lambda_{\text{between}}$	P_{between}	P_{within}
Carnivores	47.4%	13 (2–28.9)	18.3 (13.4–45.6)	0.39 (0.20–1.00)	0.065 (2.0e–05–0.38)	0.31 (0.059–0.55)	4.77	0.87 (0.00 to 12.7)	0.41 (0.23–0.64)
Euungulates	100%	19 (1.1–34)	15.1 (12.0–21.9)	0.08 (0.047–0.16)	0.019 (0.0041–0.11)	0.33 (0.20–0.50)	17.37	0.86 (0.056 to 1.52)	0.43 (0.33–0.52)
Lagomorphs	74.5%	4 (2–12.4)	7.52 (4.92–11.3)	0.02 (0.33–0.0042)	5.6e–04 (6.1e–08–4.7e–02)	0.50 (0.25–1.54)	892.86	2.36 (–0.93 to 17.3)	0.45 (0.14–0.64)
Conifers	100%	29 (8.50–49.1)	28.0 (15.5–82.2)	0.031 (0.012–0.12)	0.0016 (0.00054–0.021)	0.071 (0.012–0.13)	44.38	1.34 (0.063 to 1.78)	0.84 (0.69–1.01)
Cycads	100%	28 (11–46)	6.79 (5.99–16.2)	0.00032 (0.00013–0.00099)	7.11e–05 (1.41e–05–9.81e–04)	0.32 (0.16–0.57)	4500.70	1.64 (0.94 to 2.35)	0.68 (0.41–0.88)
Gnetales	94%	6 (3–31.4)	6.59 (0.83–20.6)	0.0081 (0.0013–0.079)	7.35e–04 (4.48e–08–0.19)	0.24 (0.060–0.44)	326.53	1.76 (–0.31 to 12.9)	0.78 (0.048–1.16)
Afroaves	100%	49 (31–66)	31.4 (28.8–34.7)	0.60 (0.49–0.69)	0.088 (0.04–0.22)	0.85 (0.67–1.27)	9.66	0.98 (0.69 to 1.24)	2.22e–08 (1.03e–09–1.56e–07)
Nightbirds	100%	87 (63–112.1)	14.5 (11.7–15.5)	0.050 (0.031–0.076)	0.014 (0.0042–0.029)	0.32 (0.19–0.47)	22.86	1.00 (0.78 to 1.33)	0.41 (0.26–0.56)
Waterbirds	99%	15 (6.5–24)	40.2 (32.7–55.3)	0.20 (0.12–0.42)	0.015 (0.0050–0.092)	0.13 (0.096–0.19)	8.67	0.87 (0.000082 to 1.56)	0.50 (0.45–0.55)

CI, confidence interval; VRBD, variable-rate birth-death; Ma, million years; GMYC, generalised mixed Yule coalescent.

¹Proportion of trees where single-threshold (ST) GMYC detects a shift in diversification rate.

Table 4. Performance of the GMYC applied to VRBD trees simulated using empirical parameter values for each study clade: the LR difference in fit between null and alternative models for empirical (LR_{obs}) and simulated trees (LR_{sim})

Clade	ST		MT	
	LR_{obs}	LR_{sim} (95%, 99%) ¹	LR_{obs}	LR_{sim} (95%, 99%) ¹
Carnivores	13.2	15.5, 23.5	17.50	21.3, 29.7
Euungulates	23.4	84.6, 92.7	31.94	90.5, 100.2
Lagomorphs	11.7	80.0, 106.0	12.92	80.8, 106.3
Conifers	36.0	96.3, 107.6	46.4	100.9, 109.7
Cycads	97.4	332.1, 391.9	101.2	337.1, 395.7
Gnetales	7.80	62.9, 82.1	9.60	61.8, 83.9
Afroaves	16.5	319.3, 326.8	63.4	469.4, 498.6
Nightbirds	9.04	149.1, 153.3	39.1	156.2, 164.5
Waterbirds	3.26	85.4, 90.3	6.02	87.0, 93.8

ST, single-threshold GMYC method; MT, multiple-threshold GMYC method; LR, likelihood ratio; GMYC, generalised mixed Yule coalescent.

¹95th and 99th percentiles.

indistinguishable from empirical trees for both balance and stemminess.

Discussion

Our results show that the standard GMYC method is sensitive to high rates of extinction (above approximately 30% of the speciation rate) in CRBD models. Although the scaling parameters, p , were developed to allow for departures from a pure birth model, a constant extinction rate produces a recent upturn in branching rates rather than a gradual increase through the whole tree (Nee *et al.* 1994). This problem becomes more severe with increasing extinction rates but is relatively unaffected by clade size and ameliorated by incomplete sampling (c.f. Fujisawa & Barraclough 2013).

One solution, however, is to use a critical value for significance obtained from simulations (e.g. Maddison, Midford & Otto 2007; FitzJohn, Maddison & Otto 2009; Humphreys & Barraclough 2014). This entails comparing the LR difference in fit between null and alternative models for simulated data to that estimated from the empirical data. Using our CRBD simulations for this purpose reveals that the difference in fit between null and alternative models is significantly greater for empirical than simulated trees for all clades except Gnetales and waterbirds ($P < 0.01$; for lagomorphs, $P = 0.05$). For the other seven clades, the CRBD model can be excluded. We therefore recommend use of simulations with empirical parameter values to judge significance of the GMYC model against alternative, clade-independent models. Based on the clades analysed here, a general rule of thumb seems to be that a $LR \geq 15$ (ST) and ≥ 20 (MT) compared to the null model is indicative of empirical results that differ significantly from those expected under a BD process at $P = 0.05$ (Table 2). It is also possible to use specific estimates of the LR difference needed for significance for a given extinction rate, ϵ (Fig. 3).

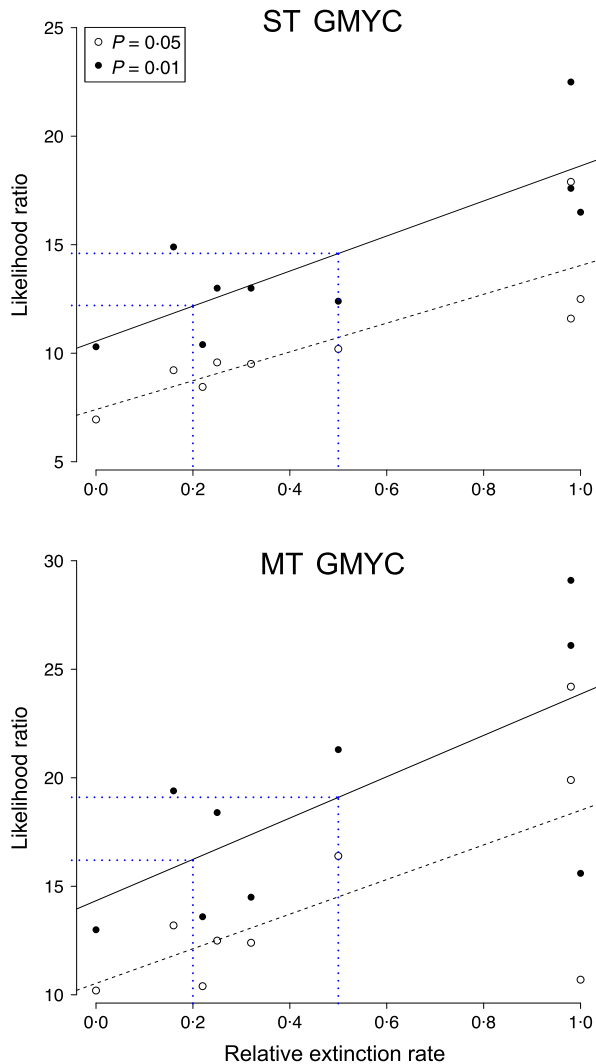


Fig. 3. Rule-of-thumb likelihood ratio (LR) values needed for significance against a CRBD model based on relative extinction rate (ϵ) for the single-threshold (ST, top) and multiple-threshold (MT, bottom) version of the GMYC, at $P = 0.05$ (dashed line, open circles) and $P = 0.01$ (solid line, filled circles; LR values from Table 2). Fitted linear models: $y = 6.6x + 7.4$ (ST, $P = 0.05$); $y = 8.1x + 10.6$ (ST, $P = 0.01$); $y = 8.0x + 10.5$ (MT, $P = 0.05$); $y = 9.5x + 14.3$ (MT, $P = 0.01$). For example, a clade with average $\epsilon = 0.2$ would need a LR ≥ 16.2 to reject the null in favour of the MT GMYC at $P = 0.01$ and a clade with average $\epsilon = 0.5$ would need a LR ≥ 19.1 (blue lines).

In contrast, and as expected, the GMYC model could not discriminate clade-dependent hESUs from a clade-independent VRBD model, where the whole clade experienced a single shift in diversification rate (e.g. due to a change in environmental conditions). In some circumstances, the GMYC model might still be able to distinguish these scenarios: for example, if origination of hESUs is staggered in time so that the most recent among-unit branching event postdates the most ancient within-unit branching event (Monaghan *et al.* 2009; Fujisawa & Barraclough 2013), but not in the clades analysed here.

How might we refine comparison of these alternatives, which are biologically interesting? The GMYC approach focuses on waiting intervals between branching events, but

other features of tree shape might discriminate clade-dependent and clade-independent models. One possibility for improving model discrimination in future is to include additional metrics in model evaluation. We found that the clade-independent models analysed here do a poor job at capturing features of real (empirical) phylogenies. For instance, the root height of VRBD trees is generally ridiculously old, for example on average 13.7 billion years for cycads, ~ 900 Ma for conifers and Gnetales and ~ 500 Ma for lagomorphs. In addition, there is a tendency for both CRBD and VRBD trees to be more balanced and stemmy than empirical trees but VRBD trees differ more from the empirical trees than do the CRBD trees, despite being simulated to more closely capture the LTT pattern of the empirical trees. The finding that CRBD models do not capture the shape of empirical trees is not new (Moore & Heard 1997; Nee 2006) but less is known about VRBD models in this respect. Beyond this, and rather than comparing just one null and alternative model, a broad array of models could in principle be fitted to identify a confidence set of plausible models and parameter estimates consistent with the data.

Other considerations argue for biological relevance of the detected hESUs, whether those units result from a clade-dependent or clade-independent VRBD process. The hESUs correspond to various taxonomic ranks, revealing taxonomic inconsistencies among groups that are not surprising (e.g. Avise & Johns 1999; Holt & Jönsson 2014). However, the correspondence of hESUs with traditionally named taxa is striking for both mammals (families and genera) and gymnosperms (genera), suggesting that future efforts to understand diversification dynamics in these groups should focus on these ranks. There is less correspondence of bird hESUs with named higher taxa, although these results might be premature because the phylogenies analysed here are based on data for two-thirds of the species only (Jetz *et al.* 2012). Intriguingly, the average age of hESUs in each bird, mammal and gymnosperm clade dates to the Miocene. In theory, this does not necessarily mean that anything special happened at that time (Fig. 1, and see Barraclough & Humphreys 2015) but might suggest similar, average turnover rates across clades. Previous analyses of birds and conifers have identified high rates of species turnover in regions characterised by climate fluctuations during the Neogene, including high latitude regions of the Northern Hemisphere and mountainous regions (Jetz *et al.* 2012; Leslie *et al.* 2012). Our results suggest not only general rules governing turnover rates among regions but that different types of organisms occupying these regions might be similarly affected by these rate-governing processes. Further research is needed to determine the causality and generality of these findings.

In conclusion, we have shown how inferences of hESU using the GMYC method are robust against some clade-independent models (CRBD), as long as simulations are used to evaluate these alternatives, but not against others (VRBD) that generate very similar patterns in waiting intervals between branching events. The differences between clade-dependent and clade-independent models are biologically interesting, however, and additional metrics either of tree shape or evaluation of ecological trait distributions

(Humphreys & Barraclough 2014) are needed to discriminate these alternatives. We suspect that clade-dependent models, focussing both on diversification rates and the units within which they operate, will prove important for explaining broadscale diversity patterns and encourage more research on this class of models.

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Data accessibility

The R code used to calculate the non-cumulative stemminess index (St_N) is provided as online supporting information (Text S4). Trees simulated using empirical parameter values have been deposited in the Dryad Data Repository (<http://dx.doi.org/10.5061/dryad.3rt26>), as have the Gnetales and cycad trees (Humphreys et al. 2016). Mammal trees can be found in TreeBASE (study ID S15307; Humphreys & Barraclough 2014).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Text S1. Selection and definition of bird clades.

Text S2. Phylogenetic analyses for cycads and Gnetales.

Text S3. Scaling GMYC rates to match those of the birth–death process.

Text S4. R code used to calculate the non-cumulative stemminess index (St_N).

Table S1. Topological constraints and age priors for cycad and Gnetales Beast analyses.

Table S2. Taxonomic diversity and sampling of empirical clades.

Table S3. Parameter values for CRBD simulations based on empirical estimates.

Table S4. Parameter values for VRBD simulations based on empirical estimates.

Table S5. Models explaining the relationship between relative extinction rate (ϵ) and error rates in CRBD trees simulated using general parameter values.

Table S6. Fit of the MT GMYC model to VRBD trees.

Table S7. Tree characteristics of empirical and simulated trees of each size set.

Fig. S1. Lineages-through-time plots for trees simulated under CRBD models and the MCC tree for each empirical clade.

Fig. S2. Taxonomic rank of hESUs for mammals, gymnosperms and birds.

Fig. S3. Lineages-through-time plots for trees simulated under CRBD models with general parameter values.

Fig. S4. Lineages-through-time plots for trees simulated under VRBD models and the MCC tree for each empirical clade.