BayesReef: A Bayesian inference framework for modelling reef growth in response to environmental change and biological dynamics

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Abstract

Estimating the impact of environmental processes on vertical reef development in geological time scales due to complex models and data with missing information is a very challenging task. This paper provides a Bayesian framework called BayesReef, based on PyReef-Core, for the estimation and uncertainty quantification of environmental processes and factors which impact the depth distribution of communities of corals and coralline algae (coralgal assemblages) found in fossil reef drill cores. PyReef-Core is a deterministic, carbonate stratigraphic forward model designed to simulate the key biological and physical processes that determine vertical accretion and assemblage changes in reef drill cores. The results show that explicitly accounting for the temporal structure of the reef core, as opposed to only the depth structure, increases accuracy in parameter estimation. BayesReef provides insights into the complex posterior distributions of parameters in PyReef-Core and provides the groundwork for future research in this area.

Keywords: Coral Reefs, Bayesian Inference, Stratigraphic Forward Modelling, Multinomial Likelihood, Markov Chain Monte Carlo

1. Introduction

Developing realistic models of reef evolution is challenging because the complexity of the process often exceeds the amount of available data necessary to estimate this complexity. Reef-building processes are determined by the interaction between many environmental factors such as water chemistry, light availability, sedimentation and hydrodynamic energy [2], yet the data from the geological record is sparse. As a result, limited work has been done in modelling reef evolution. While some software and models of long-term interactions of organisms in a marine ecosystem exist [3], only recently has a specific software for coral reef modelling has been created [1,2].

PyReef-Core [1] is a forward model that captures a number of important ecological dynamics in coral reef systems and is the first model to constrain hydrodynamic energy and sediment input exposure thresholds for coralgal assemblages on a geological timescale. It is a deterministic, one-dimensional (1-D) carbonate stratigraphic forward model (SFM) that simulates the vertical (and not lateral, hence 1-D) coral growth patterns observed in a drill core. PyReef-Core has a number of parameters representing external environmental factors which impact reef development. Examples of these factors include sea level changes and the relationship between sediment input and depth. It also has parameters describing the response of coralgal assemblage growth to these environmental factors, such as water flow and parameters for internal population dynamics such as the Malthusian parameter. Figure 1 shows the workflow of PyReef Core.

The identification of the initial conditions and optimal pathway, which lead to observed or simulated outcomes in forward models of geoscientific phenomenon, rarely have a unique solution [5,6]. For example, different combinations of a range of environmental parameters such as water flow and parameters for internal population dynamics may give rise to the same observed reef stratigraphy. This is known in the geological modelling literature as non-uniqueness [7]. Stratigraphic forward models (SFMs) produce a set of solutions that represent multiple and competing hypotheses regarding geological system evolution [8,9]. However, the explicit temporal structure simulated by PyReef-Core presents an opportunity to increase the likelihood of obtaining unique solution.

PyReef-Core simulates both the depth and temporal structure of communities of corals and coralline algae (coralgal assemblages) at a geological timescale. By depth structure, we refer to the thickness and type of coral coralgal assemblages at varying depths. By temporal structure, we refer to the thickness and type of sediment and/or coralgal material laid down at varying points in time. We use this feature of PyReef Core to show how incorporating the time series structure reduces the number of possible outcomes.
In addition to the uncertainty which results from a lack of uniqueness, there are several other sources of variability [10]. Even if we manage to constraint the number of possible solutions to be unique, there is still uncertainty surrounding that unique solution. For example, we may estimate the community interaction parameter between different assemblages to be -0.5. However, we need to be able to make a probabilistic statement which expresses our uncertainty of this estimate, such as the statement that the parameter lies between [-0.55 and -0.47] with probability 0.90. To make such statements, we need a logically consistent framework which fully accounts for different sources of uncertainty [10].

Bayesian inference is a method for estimating a parameters and for quantifying the uncertainty surrounding that estimate. It is a principled manner in which to incorporate information from multiple sources [11]. Information from prior research, and expert opinion, or knowledge of the physical processes, can be incorporated via a set of prior beliefs. Information from observed data is used to update these prior beliefs via the likelihood function. The prior and likelihood are combined via Bayes’s theorem to give the posterior distribution, which is the basis for Bayesian inference. In the case of environmental problems, Bayesian inference for uncertainty quantification has been deployed for a number of problems [12].

This paper provides a Bayesian framework for the estimation and uncertainty quantification of environmental processes and factors which impact the depth and temporal distribution of communities of corals and coraline algae (coralgal assemblages) found in fossil reef drill cores. This investigation is the first of its kind to use Bayesian inference for understanding the evolution of reefs over geological timescales. We show how the Bayesian framework can be used as a tool for quantifying uncertainty which arises from several sources of incomplete information. We extend the usefulness of PyReef-Core model, to estimate parameters that affect long-term biological and geological reef-building processes. We call this framework BayesReef and implement it using Markov Chain Monte Carlo (MCMC) sampling methodology. We choose PyReef-Core to demonstrate the idea since it is the only tool for available for the problem, however, the framework is general and can be adapted for other models. BayesReef provides estimation and uncertainty quantification for complex processes with sparse data makes four major contributions to the literature.

First, we extend PyReef-Core, which is a deterministic forward model, to a probabilistic one, BayesReef, by placing probability distributions over the initial conditions, informed from previous knowledge of the system. These distributions, are examples of prior distributions, referred to earlier, and explicitly encode all assumptions. For example, we can say that our prior belief regarding water flow velocity is that it should be greater than 0, and less than 0.3 meters(m)/seconds (s) [13]. Constraining the set of possible values of unknowns is crucial in obtain-
Second, we use the Bayesian framework to fuse various sources of information in a logically consistent manner. Expert opinion and the results of previous studies can be incorporated in the prior, while simulated data from the pyReef-Core source of information in a logically consistent manner. Expert code our assumptions. Thus we can measure the sensitivity of our results and inference to those assumptions by altering them.

Third, we use BayesReef to constrain the number of solutions that represent the unique palaeo-environmental history of the reef core by incorporating knowledge of the time structure as well as the depth structure of reef drill cores embedded in PyReef-Core.

Fourth, we make the methodology and its implementation available as software tool BayesReef for other researchers in the embedded in PyReef-Core, area [14]. This software can be used to make inference about evolution of reefs over time, to make predictions from PyReef-Core and to quantify the uncertainty of that prediction.

The rest of the paper is outlined as follows: Section 2 provides background and related work while Section 3 presents the methodology and techniques used, including the multinomial likelihood function. Section 4 presents experiments and results. Sections 5 and 6 conclude the paper with a discussion of results and of areas of future research.

2. Background

2.1. Coral reef evolution

The ability of corals to vigorously grow and build reef structures is dependent upon favourable environmental conditions [16]. Three related environmental factors examined in pyReef-Core are key in influencing coral reef evolution on multi-decadal to centennial timescales. They are water depth (accommodation), hydrodynamic energy and autochthonous (reef-derived) sediment input.

Accommodation is the vertical space in the water column above the substrate within which corals can grow. Accommodation affects hydrodynamic energy and sediment flux. Wave energy and water flow decrease with depth, such that corals growing in shallower water experience increased hydrodynamic energy [17]. At the organism level, currents, water flow and oscillatory motion induced by waves are critical in modulating physiological processes in coral and thus influence coral growth rates [18,19]. Similarly, fluxes of reef-derived carbonate sediments typically increase with depth as they are less disturbed by currents and settle on corals [20]. Sediment input inhibits coral reef growth and even causes mortality via turbidity, reducing light and the ability of corals to meet energy requirements via photosynthesis [21,22], and via smothering and abrasion [23].

Environmental threshold functions control how the rate of vertical accumulation for different coral assemblages can be enhanced or limited by environmental factors (Figures 1 and 4). The environmental threshold functions in this version of PyReef-Core measure assemblages’ sensitivity to sediment input exposure and exposure to the velocity of water flow (i.e. hydrodynamic energy). In PyReef-Core, four values define each exposure threshold, where the outer two values indicate the absolute minimum and maximum values of the environmental stressor which are known to be tolerable to an assemblage and beyond which, the effects of exposure are lethal [21]. The remaining two values within the minimum and maximum bounds indicate where flow velocity or sediment input begin to restrict growth [1]. During each time step, flow velocity and sediment input will intersect different points of the threshold curves for each assemblage. The environmental factor, $F_{env}$, that limits growth during each time step is found by taking the minimum of all threshold functions (i.e. $f_{depth}$, $f_{sed}$ and $f_{flow}$: Figure 2). This is multiplied by the maximum vertical accretion rate for each assemblage to limit growth according to environmental exposure (Fig. 1).

While there are clear theoretical relationships between the duration and rates of sedimentation and flow velocity on coral mortality [21,28], determining these thresholds quantitatively as inputs into pyReef-Core remain difficult to estimate. Using a data fusion approach, the existing state of knowledge can be employed within a Bayesian framework to estimate the values of these unbounded parameters.

Over geological timescales, these environmental disturbances are important determinants of the composition of coral assemblages and their spatial distribution in specific environmental niches across the reef and with depth [24,25,26,27].
2.3. Bayesian Inference

We use Bayesian framework to provide estimates of model parameters and quantify the uncertainty surrounding these parameters. It is common to denote these parameters generically by $\theta$, if there is only one parameter, or by $\boldsymbol{\theta}$ if we are interested in a vector of parameters. In the Bayesian paradigm, a prior belief about $\theta$ is updated from information contained in an observed data point via the likelihood, and inference about $\theta$ proceeds via the posterior distribution. The relationship between these three functions, the prior, the likelihood and the posterior is given by Bayes Theorem

\[ P(\theta|D) = \frac{P(D|\theta)P(\theta)}{P(D)} \]  

where $D$ is the data, $P(D|\theta)$ is the likelihood, $P(\theta)$ is the prior and $P(\theta|D)$ is the posterior. Unfortunately this posterior distribution is rarely available in closed form. This is particularly true for nonlinear inverse problems in geophysical models like pyReef-Core, where no analytical expression for the forward relation between data and model parameters is available [29]. In situations such as these sampling based methods such as Markov Chain Monte Carlo (MCMC) methods are used to approximate the posterior, [30]. Loosely speaking, this involves proposing draws of the quantity of interest from some proposal distribution, and accepting these draws with a probability which ensures that the Markov chain is reversible [31, 32].

MCMC methods are well established in many areas of geoscience, with applications to modelling geochronological ages [33], modelling the effect of climate changes in land surface hydrology [34], inferring sea-level and sediment supply from the stratigraphic record [35] and inferring groundwater contamination sources [36]. However, Bayesian inference has seldom been applied to reef modelling, despite evidence of their usefulness when handling models with complex, interrelating parameters [37, 38].

3. Methodology

In this section, we present the BayesReef methodology to demonstrate how heterogeneous sources of information can be combined to estimate key parameters which govern coral vertical accumulation in PyReef-Core and quantify the uncertainty surrounding them. We assess the performance of our method by creating a synthetic core ground truth and compare the predictions, parameter estimates and associated uncertainties of BayesReef with that ground truth. We first discuss the creation of the synthetic core and then we present our methodology.
Figure 3: Graphs of the boundary conditions established for sea level (left) water flow velocity (centre) and sediment input (right) used to create the synthetic ground truth (Figure 1) and in all subsequent BayesReef experiments.

Figure 4: Graphs of the environmental threshold functions for the shallow (upper), moderate-deep (centre) and deep (lower) assemblages characteristic of an exposed reef margin, interpreted from Dechnik et al. 2015. The x-axis indicates the limitation on maximum vertical accretion for conditions outside the optimal, 100% maximum growth window, indicated for clarity (blue translucent boxes) for the hydrodynamic energy threshold for all assemblages. Note that maximum vertical accretion rates are defined in Table 1, which were used to create the synthetic ground truth in Figure 1.

Table 1: Summary of free and fixed parameter values used in BayesReef experiments. True values of free parameters are used to obtain the synthetic ground truth (Figure 1). Note that true values of the hydrodynamic energy and sediment input exposure thresholds for each assemblage are graphically represented in Figure 4. Fixed parameters remain constant across all experiments including the creation of the synthetic ground truth dataset.

### 3.1. Creation of synthetic ground truth

A synthetic ground truth is created that represents an idealised shallowing-upward fossil reef sequence representing a catch-up growth strategy consistent with the Holocene evolution of several reefs globally (Figure 2A). Given some true initial conditions, chosen to be consistent with the literature, we use the deterministic model PyReef-Core to produce the synthetic ground truth. This ground truth is a single drill core which records the whether a coralgal assemblage is present. If it is present, then the type of coralgal assemblage is recorded, otherwise PyReef-Core produces sediment.

The information from the drill core is represented in two ways, which we refer to as the depth-structure and the time-structure. The depth structure representation records the ground truth as the coralgal assemblage present at various depths in the drill core. The time structure representation of the data records the time at which the ground truth coralgal assemblage in the drill core was formed. Both of these representations are available from PyReef Core.

PyReef Core is a complex forward model depending upon many factors, see Figure 1. The values of the factors, which we refer to as parameters, appear in Table 1 for these three assemblages, which were used to create the synthetic ground truth in Figure 1.

The simulated time for the synthetic ground truth and all subsequent experiments run from 8.5 thousand years ago (ka), where water depth was likely 5 metres below sea level (mbsl), to present day. The initiation time 8.5 ka is within the take-off envelope for Holocene growth for outer-platform reefs, which ranges ∼8.6-6.6 ka. The initial reef surface is 30 mbsl, which is consistent with the base of shallowing-upward sequences exhibited in drill cores from the Great Barrier Reef (GBR) and Indo-Pacific reefs.

The synthetic experiment simplified accommodation (i.e., the vertical space available for potential reef accumulation) by simulating it as a function of Holocene sea-level changes and ver-
tical coral reef growth only. The Holocene relative sea-level (RLS) curve for the Australian East Coast is used as the sea-level boundary condition, presented in Figure 3 [19]. The data indicates a RLS characteristic by a mid-Holocene highstand of 1.8 m at ~4 ka before returning slowly to present sea-level.

We assume that flow velocity and related hydrodynamic energy is an exponentially decreasing function of depth (Figure 5). Flow varies from extremely low, laminar flow (<4 cm/sec) on the deep forereef (>30 m depth) to mean flow speeds of 20-30 cm/sec in <1 m depth [13]. This relationship has been validated by lab and field studies [22, 43, 44]. The maximum flow velocity reached in any PyReef-Core are restricted to 30 cm/sec based on these studies.

Simulations in PyReef-Core use a depth-dependent sediment input function to approximate the spatial variation in sedimentation rate resulting from hydrodynamic conditions. Following the same approach as for the definition of the hydrodynamic energy, we use a sedimentation-depth relationship conceptualised by Chappell [20] to simulate sediment deposition in this study (Figure 6).

The coralgal assemblages produced by PyReef-Core can take on one of three types, shallow, moderate deep and deep. These three types are consistent with those found on southern GBR reefs and capture the full extent of the shallowing-upward sequence in a high-energy, exposed setting (Figure 5) [15]. The maximum vertical accretion (VA) rates for the three assemblages are defined based on a full analysis of all Indo-Pacific reef drill cores [17, 15] (Table 1).

Environmental threshold functions for the ground truth depicted in Figure 4 entail the growth response of coralgal assemblages to changing depth, sediment input and hydrodynamic energy. The pyReef-Core model is constructed so that maximum VA rates for assemblages are only reached under optimal conditions. Elsewhere, growth is proportional to the environmental factor determined by exposure threshold functions [11] (Figure 4).

The depth exposure thresholds for each coralgal assemblage are well-defined in the literature [15, 55], however there is little to no data on the optimal growth environments or assemblages in relation to other environmental factors; not at the species level and certainly not on greater-than-decadal timescales. Therefore, the threshold functions for sediment input and hydrodynamic energy have been manually estimated for the creation of the synthetic ground truth (Figure 4). This manual estimation is done largely by trial and error, until the desired shallowing-upward sequence is obtained that accurately reflects the expected shift from deep to moderately-deep assemblages at ~15–20 mbsl, and from moderately-deep to shallow assemblages at ~6 mbsl [46, 15] (Figure 2).

Temporal and vertical evolution of the produced synthetic core are obtained at user-defined intervals and depend on each assemblage production rate that varies based on aforementioned input parameters.

3.2. BayesReef: Likelihood and Priors

To demonstrate the technique, we consider the synthetic ground truth as the observed coralgal assemblages, $y^o = (y^o_1, \ldots, y^o_T)$, where $y^o_d$ is the type of coralgal assemblage at depth $d$, for $d = 1, \ldots, D$. The superscript $o$ is for observed, while the subscript $D$ is to denote that the data has a depth structure, i.e. the observations record the coralgal assemblage at a particular depth.

If we can identify the date at which the coralgal assemblage was formed, then we denote the data as $y^o = (y^o_{1,1}, \ldots, y^o_{T,1})$, where the subscript $T$ is to denote that the data has a time structure, and $y^o_{d,t}$ is the type of coralgal assemblage observed at time $t$, for $t = 1, \ldots, T$. We note that there are many time structures which give rise to the same depth structure, but not vice-versa. Thus the time structure contains more information than the depth structure. Indeed there is only a one-to-one correspondence between the two if the rate of coralgal growth is constant over the entire time period in question. We show how using this knowledge of the time structure allows us to constrain the parameter space.

For conciseness we will now drop the subscripts $D$ and $T$ and develop the general model for the data, but we return to this in the discussion of the results.

The observations $y^o$ are the data referred to in Equation (1). Given the data, $y^o$, inference about the unknown parameters, $\theta$, proceeds via the posterior distribution, $p(\theta|y^o)$. The denominator in Equation (1) is just a normalizing constant and does not depend upon $\theta$, so that Equation (1) is often expressed as

$$p(\theta|y^o) \propto p(y^o|\theta) \times p(\theta).$$

where $p(\cdot)$ represents a probability density function, $p(y^o|\theta)$ is the likelihood function and $p(\theta)$ is the prior distribution.

In this paper the parameters of interest, denoted by $\theta$, are; the Malthusian parameter, denoted by $\epsilon$; the elements of the assemblage interaction matrix (AIM), denoted by the matrix $A$; four critical points that define the hydrodynamic energy exposure threshold function for each assemblage, $f_{flow} = (f^1_{flow}, \ldots, f^4_{flow})$, where $i$ denotes the assemblage type $i$; and four critical points defining the exposure threshold function of sediment input $f_{sed} = (f^1_{sed}, \ldots, f^4_{sed})$. So the vector of parameters on which we wish to make inference is $\theta = (\epsilon, A, f_{flow}, f_{sed})$. Details about the “true” value of these parameters used in obtaining the synthetic ground truth, $y^o$, appear in Table 1.

### Likelihood

Likelihoods are probabilistic models of the data-generating process given some parameters $\theta$. They are used to describe how likely the observed data are if we knew the true value of $\theta$. The existence and type of coralgal assemblage that grows at various points in time are random variables that take on a discrete number of outcomes; either coral grows or it does not (in which case we observe sediment), and if it does, then the assemblage type is either shallow, moderate-deep or deep and any likelihood function should reflect the discrete nature of these outcomes.
In this example we choose a multinomial likelihood. There is no explicit expression for the quantity $p(y^o|\theta)$, however we use the output from PyReef Core to compute this function.

Given values of $\theta$, PyReef Core produces the proportion of various assemblage types at equally spaced points in time, denoted by $\Pi = (\pi_1, \ldots, \pi_T)$, where $\pi^m_k = (\pi^m_{k1}, \ldots, \pi^m_{kK})$, for $t = 1, \ldots, T$, and $k = 1, \ldots, 4$ with $\sum_{k=1}^K \pi_{tk} = 1$. These proportions are time-varying, but the manner in which they change over time cannot be explicitly written. Instead these changes are embedded in the PyReef Core forward model.

It is important to note that there is a deterministic relation relationship between $\theta$ and $\Pi$, and therefore $p(y^o|\theta) = p(y^o|\Pi)$. We consider the elements of the $T \times K$ matrix $\Pi$, namely, $\pi_{tk}$, to be the probability that assemblage $k$ is present at time $t$, and use these probabilities as inputs for the multinomial likelihood. So that

$$\Pr(y^o|\theta^*) = \prod_{t=1}^T \prod_{k=1}^K \pi_{tk}^{z_{tk}}$$

where $z_{tk} = 1$ if $y_t = k$, and $z_{tk} = 0$ otherwise.

The observations are the coralgal assemblages in the synthetic core $y^o$.

### 3.3. Priors

#### 3.3.1. Priors for $\epsilon$ and $A$

In order to make the algorithm computationally feasible, some simplifications were made to the PyReef-Core model to reduce the total amount of free parameters in BayesReef. First, the value of the Malthusian parameter, $\epsilon$, is assumed apriori to be equal for all coralgal assemblages. We place an uninformative prior on $\epsilon$, so that $p(\epsilon) \sim U[0, 0.15]$. Second, the AIM $A$, is assumed to be symmetric and block diagonal with equal diagonal elements, so that

$$A = \begin{bmatrix} \alpha_m & \alpha_s & 0 \\ \alpha_s & \alpha_m & \alpha_s \\ 0 & \alpha_s & \alpha_m \end{bmatrix}$$

The zeros in the matrix indicate conditional independence between two assemblages that are not close together in space, [47]. The prior for $p(\alpha_m)$, $p(\alpha_s)$ is $U[-0.15, 0]$. There are additional restrictions imposed upon combinations of $\epsilon$ and $A$. The numerical ordinary differential equation (ODE) solver we use, the Runge-Kutta-Fehlberg of order (4,5) (RKF-45) method, becomes linearly unstable when the magnitude of the difference between $\epsilon$ and $\alpha_m$ or $\alpha_s$ is too great. This is
because it uses adaptive stepsizes, which has limited stability when dealing with stiff equations \[48\]. One way to address this is to pick a ODE solver that does not have adaptive stepsize, however this reduces accuracy of solutions. To ensure stability, the range of $\epsilon$, $\alpha_s$ and $\alpha_a$ are limited to $0.15$ and $-0.15$ respectively (Table $2$).

### 3.3.2. Priors for $f_{flow}$ and $f_{sed}$

Parameters that define the sediment input exposure threshold function, $f_{sed}$, and the hydrodynamic energy exposure threshold function, $f_{flow}$, serve as constraints that restrict vertical growth to only occur within a range of values for these environmental stressors. There are four parameters for each assemblage that define the exposure threshold function to hydrodynamic energy, $f_{flow}$, for three assemblages, so that there are a total of $24$ parameter; $12$ for $f_{flow}$ and another for $12$ $f_{flow}$.

Based on the sediment-depth and flow-depth relationships established in Section $3.1$, the maximum flow velocity is $0.3$ m/sec and the maximum sediment input is $0.005$ m/yr. The limits on these environmental factors have been informed by physics and prior knowledge of reef systems. Prior distributions for all elements of $f_{flow}$ and $f_{sed}$ ensure an ordering. For example, $f_{flow} = (f^1_{flow}, f^2_{flow}, f^3_{flow})$ has a prior distribution such that

$$P(f_{flow}) = P(f^1_{flow}) \times \prod_{j=2}^4 P(f^j_{flow}/f^{j-1}_{flow})$$

with $f^j_{flow} \sim U(f^{j-1}_{flow}, 0.3]$.

Table 2: Prior distributions and the proposal standard deviation $\sigma$ for the Metropolis-Hasting kernel in the MCMC scheme for the free parameters in BayesReef. Note that proposal standard deviation is $1\%$ of the width of the absolute range of the prior.

| Parameter | Priors | $\sigma$, Stepsize in RWMH |
|-----------|--------|-----------------------------|
| $f_{flow}$ | $P(f_{flow}) \times \prod_{j=2}^4 P(f_{flow})/f^{j-1}_{flow}$ | $0.00300$ |
| $f_{sed}$ | $P(f_{sed}) \times \prod_{j=2}^4 P(f_{sed})/f^{j-1}_{sed}$ | $0.00005$ |
| $\epsilon$ | $U[0.05, 0.15]$ | $0.00150$ |
| $\alpha_s$ | $U[-0.15, 0.00]$ | $0.00150$ |
| $\alpha_a$ | $U[-0.15, 0.00]$ | $0.00150$ |

There is little to no quantitative data collected on the growth response of coral species (let alone coral assemblages) to different flow and sediment regimes. As such, we cannot incorporate more information into the prior. The relaxed constraint we chose gives the best chance for coracal vertical accetration to be simulated in the model by avoiding situations where a threshold is too narrow to allow growth to occur at all. Therefore, they formally express the state of limited knowledge regarding long-term effect of hydrodynamic energy and sediment flux regimes on coral growth. Details regarding their corresponding prior distributions appear in Table $2$.

### 3.4. Estimation via Bayesian Inference

We take a Bayesian approach and use the posterior distribution, $p(\theta|y^*)$, to estimate and make inference regarding $\theta$. We obtain the predictive distributions of an assemblage at time $T+1$ to be $p(y^*_{T+1}) = p(y^*_{T+1}|y^*)$, where the notation $y^*$ denotes an unobserved prediction, by integrating over all possible values of $\theta$.

$$Pr(y^*_{T+1}|y^*) = \int Pr(y^*|y^*, \theta)p(\theta|y^*)d\theta \quad (3)$$

Then the integral in $\eqref{3}$ is approximated by,

$$Pr(y^*_{T+1}|y^*) \approx \frac{1}{M} \sum_{j=1}^M Pr(y^*_{T+1}|y^*, \theta^j) \quad (4)$$

where $\theta^j \sim Pr(\theta|y^*)$. We use a Random Walk Metropolis-Hasting (RWMH) transition kernel for the proposal distribution $q(.)$ in Algorithm $1$.

The BayesReef framework for estimation and inference is shown in Figure $5$ which highlights the MCMC sampling for inference of free parameters in the $py$-Reef $Core$ model.

#### Alg. 1 BayesReef algorithm

Initialise $\theta = \theta^{[0]}$, by drawing $\theta^{[0]}$ from the joint prior distribution $\theta^{[0]} = \sim p(\theta) i = 1 : M$

1. Propose a value $\theta^{[i]}|\theta^{[i-1]} \sim q(\theta^{[i-1]})$, where $q(.)$ is the proposal distribution, which we choose to be normal with mean $\theta^{[i-1]}$ and diagonal covariance matrix, $\Sigma$, with diagonal entries equal to the square of $\sigma$ in Table $2$.
2. Using the forward model $py$-Reef-$Core$, with $\theta^{[i]}$ as the initial conditions, compute the set of parameters need to evaluated the likelihood, $\Pi^{[i]}$ and $\Pi^0$.
3. Calculate:

$$P_{accept} = \min \left\{ \frac{p(y|\Pi^{[i]})p(\theta^{[i]})}{p(y|\Pi^{[i-1]})p(\theta^{[i-1]})}, \frac{q(\theta^{[i-1]}|\theta^{[i]})}{q(\theta^{[i]}|\theta^{[i-1]})} \right\}$$

where $p(y|\Pi)$ is given by Equation $2$.

4. Generate $u \sim U(0, 1)$ and set $\theta^{[i]} = \theta^{[i]}$ if $P_{accept} < u$. Otherwise, set $\theta^{[i]} = \theta^{[i-1]}$.

We note that although this paper uses a random walk for the proposal $q(.)$, BayesReef is a general framework and hence other proposal distributions such as the NUTS algorithm in Hamiltonian MCMC $[49]$ can be used.

**Software availability:** The source code and installation package of BayesReef can be downloaded from the $py$Reef-model Github repository at: https://github.com/pyReef-model/BayesReef.

### 4. Experimental Design and Results

We investigate the performance of BayesReef using the multinomial likelihood function outlined in Section $3.2$ when the time structure is the basis of prediction and when the depth structure is the basis of prediction. The performance of
BayesReef is measured in two ways: by its ability to recover the time structure and depth structure of coralgal assemblage compositions and transitions of the ground truth; and the estimation accuracy of the parameters used to create the ground truth core. Note that these two performance measures are related but not the same. It may be that the same coralgal assemblage is predicted by different combinations of input parameters.

The technique’s relative performance of the time structure vs depth structure was examined in two settings. In the first setting the super-/sub-diagonal parameter of the AIM (\(\alpha_s\)) and the Malthusian parameter (\(\varepsilon\)) are free to vary while the remaining parameters are fixed. In the second setting, the four parameters that comprise the hydrodynamic energy exposure threshold function \(f_{\text{flow}}\) for the moderate-deep assemblage are free to vary. The number of MCMC iterations in the first setting was 10,000 samples, while the corresponding number in the second setting was 20,000 samples Both have a 10% burn-in. Each experiment takes ~11-22 hours to run using an Intel Core i7-8700 Processor (6 Cores, 12 MB cache, 4.6 GHz).

### 4.1. Two-parameter experiment results

Figure 6 presents the results of experiment in the first setting. Panels(a) to (c) present the results for the time structure while Panels(d) to (f) present the results for the depth structure. We observe that with time-based inference the parameter estimates are highly accurate. The posterior distributions of \(\alpha_s\) and \(\varepsilon\) contain the true values, with the mean and modes nearly centered on the true values (Figures 6a and 6b, Table 3). In contrast the posterior distributions of \(\alpha_s\) and \(\varepsilon\), using depth-based inference, (Figures 6c and 6d) are wider, reflecting greater uncertainty and in the case of \(\varepsilon\), it is unlikely that the histogram estimates approximates the posterior distribution at all, Figure 6d. The trace plots suggest that the MCMC chain has not converged to the posterior distribution of \(\varepsilon\).

The mean predictions and the 5% and 95% prediction intervals for the time-based and depth-based estimation are presented in Figures 6c and 6f respectively. These figures display the 90% credible interval (CI) of BayesReef predictions and the true depth and time structures of the ground truth core. Figure 6c shows that the predictions using the time-based estimation are remarkably accurate at estimating both the time and depth structures of the data. In contrast, while predictions of the depth structure using the depth-based data are accurate, predictions of the time structure are not, Figure 6f. The estimate predicts that the shallow assemblage developed earlier and ceased growth earlier in time, with a longer period of sedimentation between ~3000-4500 yrs of the simulation. This is in line with the observation that many different time-based structures can lead to very similar depth-based structures.

Figure 7 displays the time-based, panel (a), and depth-based, panel (b), log of the likelihood surface as a function of \(\alpha_s\) and \(\varepsilon\). Figure 7a shows one distinct peak that is centered near the true values of \(\alpha_s\) and \(\varepsilon\) (-0.03 and 0.08 respectively). In contrast, Figure 7b shows a flat likelihood surface indicating that an area of equally likely combinations of \(\alpha_s\) and \(\varepsilon\).

### 4.2. Four-parameter experiment results

We present results with four free parameters to investigate the ability of BayesReef to handle a higher-dimensional problem. In this setting the four flow parameters of the medium-depth assemblage were allowed to vary, while the remaining parameters were held constant. Figure 8 summarizes the results. Panel (a) shows that the parameters \(f_2\) and \(f_4\) are well estimated by the model with time-based structure, but \(f_2\) and \(f_4\) are not. The trace plots for \(f_2\) and \(f_4\) in Figure 8, panel (b), show a high degree of autocorrelation in the iterates and suggests that the MCMC scheme may not have converged. Although we note that the 90% credible intervals do contain the true values of these parameters. A similar story emerges for the results of depth-based structure; \(f_2\) and \(f_4\) are well estimated but not as well as the time-based structure, while \(f_2\) and \(f_4\) are not, and a high degree of autocorrelation for \(f_2\) and \(f_4\). The estimates of the actual depth structure for both time-based and depth-base, Figure 8, left side of panels (e) and (f), are comparable to estimates for the two free parameter setting. However, in the four free parameter setting, a 0.5 m package of the shallow assemblage at ~17 m depth is not captured by the time or depth based models. The estimates of the actual time structure are well approximated by the time-based model but, consistent with the two free parameter setting, not so well captured by the depth-based model, Figure 8, right side of panels (e) and (f).

The loglikelihood surfaces, as a function of \(f_2\) and \(f_4\) are shown in Figure 9 panel (a) for the time-based inference; and panel (b) for depth-based inference. Panel (a) shows a marked peak for \(f_2 = 0.05\), but this log-likelihood value is the same across a range of values for \(f_4\), show by the ridge at \(f_4 = 0.05\). This peak is not as pronounced for the depth-based structure.

| Parameter | True value | Time structure | Depth structure |
|-----------|------------|----------------|----------------|
| \(\alpha_s\) | -0.03 | 0.08 | 0.172 | 0.185 |
| \(\varepsilon\) | 0.08 | -0.029 | -0.081 | 0.091 |

Table 3: Summary statistics for parameter estimates from time structure and depth structure experiments with two and four free parameters. AR is acceptance rate.

5. Discussion

The results show that BayesReef provides a reliable prediction of the synthetic ground truth data in the majority of cases.
Figure 6: Density histograms of parameter estimates and mean model predictions from experiments with only two free parameters, $\alpha_s$ and $\epsilon$. Time structure predictions are in Panels (a) to (c), and depth structure predictions are in panels (d) to (f). Panels (a,b) and (d,e) give histogram estimates of posterior distributions (upper) and trace plots (lower) for the free parameter. The solid, black line in the histograms indicates the true values used to generate the ground truth. Panels (c) and (f) are model estimates and measures of uncertainty in prediction on the basis of the (c) time structure and (f) depth structure of the ground truth core. Note that we present the mean predictions from the perspective of both the depth and time structure of the core. The credible interval and mean of the model estimation is compared to the ground-truth (black line).

Moreover, the estimated parameters provide an accurate prediction of the reef-core when compared to the synthetic reef-core data which demonstrates convergence. BayesReef provides the groundwork for an insight into the complex posterior distributions of parameters in pyReef-Core. As expected time-based inference produces more accurate predictions than dept-based inference, and also has less uncertainty associated with this prediction. With the exception of $f_{f,lm}^3$ and $f_{f,lm}^4$, the posterior distributions of free parameters after a maximum of 20,000 iterations appeared to have converged. The 90% credible intervals contained the true parameter value using time-based inference in both settings. Moreover, mean estimations for the parameters were almost exact replicas of the time and depth-structure of the synthetic ground truth. In contrast, depth-based inference was unable to replicate the time structure of the synthetic core in neither setting.
We constrained the number of dimensions in the experiments to investigate how BayesReef performs with a low-dimensional (two-parameter) model, and a high-dimensional (four parameter) model. The results show that time-based inference had equally-accurate predictions in low and high-dimensional experiments. This promotes confidence in this technique in achieving accurate predictions with higher-dimensional problems. Depth-based inference, on the other hand, produced comparative accuracy in the two and four-parameter experiments in depth structure only. Time structure predictions were marginally better in the four-parameter experiment, however, using depth-based inference showed greater uncertainty in reef-core predictions in all the experiments. However, regardless of using time or depth-based inference, four-parameter experiments could not constrain the two upper parameters of the hydrodynamic energy exposure threshold ($f_{\text{low}3}$ and $f_{\text{low}4}$) (Figures 8a and 8b). The large uncertainty around mean estimates for $f_{\text{low}3}$ and $f_{\text{low}4}$ highlight how a broad range of values can achieve the equivalent core prediction (Figures 8a and 8b). Similarly, the bivariate likelihoods for $f_{\text{low}3}$ and $f_{\text{low}4}$ in Figure 9 show that, beyond a certain point, any values of $f_{\text{low}3}$ and $f_{\text{low}4}$ produce equivalent high-likelihood results. This indicates that there is not have enough information available to constrain these parameters. Therefore, informative priors or reef-core data containing more information may be able to constrain and pinpoint the upper threshold of hydrodynamic energy for the moderate-deep assemblages.

Alternatively, the result may actually reflect the environmental sensitivity of the moderate-deep assemblage. As the lower limit of fluid flow is better constrained, we may understand moderate-deep coral assemblages can tolerate extremely low flow ≤5 cm/sec (Figure 8a). In addition the lack of constraints regarding the maximum tolerable fluid flow may indicate that the moderate-deep assemblage is robust to turbulent water flow (Figure 9). Moreover, this may lead us to investigate factors other than hydrodynamic energy that prevent the assemblage from colonising in shallow water environments. Therefore, the results provide insight into the influence of hydrodynamic energy on coral assemblage accretion.

Similarly, we infer from log-likelihood surface that $\varepsilon$ has a marginally greater control on the population dynamics of assemblages than $\alpha$, (Figure 7). The Malthusian parameter ($\varepsilon$) governs the intrinsic rate of growth and decline of coral populations, whereas the sub-diagonal assemblage interaction matrix parameter ($\alpha$) governs the intensity of the competition between coral assemblages. The inference is that the competition between assemblages is less important than the rate of population growth in determining biological interactions between assemblages.

In summary BayesReef has enabled greater insight into the importance of the Malthusian parameter and assemblage interaction matrix parameters. Furthermore, it is demonstrably useful in quantifying unobservable parameters such as a coral assemblage’s response function to long-term hydrodynamic energy exposure.

### 5.1. Non-unique solutions and multimodality

The results show that reef-core predictions are better using a time rather than a depth based likelihood. This is best highlighted by the log-likelihood of $\alpha$ and $\varepsilon$ (Figure 7). We observe only a narrow peak in maximum likelihood using time-based likelihood, and a large plateau of maximum likelihood using depth-based likelihood (Figure 9). The flat surface of the depth-based likelihood indicates a variety of combinations of population dynamics parameters can give similar observed stratigraphy. Therefore, the depth structure of pyReef-Core simulations may be considered to have no unique solution.

In some cases, we observed that BayesReef cannot reliably estimate the true parameter values, while at the same time produce accurate prediction of the drilled cores which implies multi-modality which is also visible by the likelihood surface. Such cases of multi-modality also appear in other geoscientific problems such as landscape evolution models where different combinations of parameters such as precipitation and landscape...
Figure 8: Summary of results for a BayesReef experiment with four free parameters governing the hydrodynamic threshold of the moderate-deep assemblage. Panels (a), (c) and (e) use a time-dependent likelihood and panels (b), (d), and (f) use a depth-dependent likelihood. Panels (a) and (b) are the hydrodynamic energy exposure threshold composed of four parameters ($f_{low}^1$, $f_{low}^2$, $f_{low}^3$, $f_{low}^4$, left-to-right in the figure), which function as coordinates. They are visualised to represent how coral growth is limited according to the shape of these functions. The black line represents the initial thresholds used to create the synthetic data. The blue line presents the modal estimates of each parameter with an envelope that represents the 90% credible interval. Associated traces of MCMC chains for $f_{low}^1$, $f_{low}^2$, $f_{low}^3$, $f_{low}^4$ are in panels (c) and (d). Panels (e) and (f) are the mean model estimates.
erodibility have shown to produce similar topography evolution [50]. Non-uniqueness in solutions in forward models such as pyReef-Core makes it difficult to disentangle the different process parameters (i.e., environmental parameters and population dynamics parameters) that produced a particular stratigraphy and consequently several competing hypotheses regarding the dominant controls on reef development [51, 4]. Reef geologists get a limited understanding of the temporal evolution of reefs based on the composition and depth structure of a drill core alone. Drill cores must have core samples radiometrically dated to be able to constrain the timing of reef accretion, the rates of coral growth and the rates of sedimentation. With BayesReef, we are able to constrain the environmental conditions that elicit growth responses from corals over time, and thus are better to understand the dominant controls on reef development and compare competing hypotheses of reef evolution (e.g., [52, 53]). In this way, we can isolate the far-fewer parameter combinations that produce a particular time series of reef-growth events and hiatuses. Not only is pyReef-Core a useful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution, but BayesReef is a powerful tool for reef geologists who wish to understand a reef’s temporal evolution.

5.2. Implications and extensions

Using time-based inference, the reef-core predictions from two-parameter experiments were of equivalent quality and accuracy compared to the four-parameter experiments. To eliminate all assumptions, 27 free parameters would need to be estimated for a pyReef-Core problem with 3 assemblages, and an even greater number of parameters with increasing number of assemblages. We note that the experiments which considered only four free parameters with 10,000 samples took more than 12 hours of computational time. With added dimensionality, we can expect greater complexity in the posterior distribution which cannot be explored efficiently with a canonical Metropolis-Hastings MCMC algorithm. A greater number of samples will be required when the parameter increases and hence the sampling could suffer from the curse of dimensionality. In future experiments, we hope to use parallel tempering which is more suited for multi-modal distributions and also can be implemented using a multi-core architecture for high performance computing in order to address the computational requirements when the number of parameters increases. Such implementations have shown to be very useful for inference of landscape evolution models [54].

The use of a multinomial likelihood produces accurate predictions, however one can argue that it does not fully convey the nature of reef-building processes since it assumes independence of observations. In other words, deposition of an assemblage in the past is independent of deposition in the present. In reality, the substrate composition of a reef is a strong predictor of which assemblage will colonise it since corals tend to grow vertically on their skeletons and populate areas where assemblages of their type flourish [55]. A degree of dependence between observations is captured by the deterministic model pyReef-Core, where assemblage ‘populations’ depend on the relative abundance of their same assemblages. Nevertheless, future developments of BayesReef must account for the dependence of observations through time to better capture the nature of biological reef-building processes.

6. Conclusion and Future Work

We have presented BayesReef which is a comprehensive Bayesian framework that incorporates multiple sources of information including forward models, priors and empirical data from geological reef-cores. The methodology solves geologi-
cal inverse problem posed by unobserved environmental conditions and non-unique pathways to reef stratigraphies. The results show that the methodology estimates and provides uncertainty quantification of the parameters that represent environment and ecological conditions in PyReef-Core using the (posterior) probability distribution.

In future work, it would be useful to incorporate robust sampling methods such as parallel tempering in conjunction with high performance computing in order to address the computational requirements when the number of parameters increases. Moreover, it is possible to visualize joint posterior likelihoods of parameters, providing insight into the nature of parameter interactions.

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