An integrated model of population genetics and community ecology

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Abstract
Aim: Quantifying abundance distributions is critical for understanding both how communities assemble, and how community structure varies through time and space, yet estimating abundances requires considerable investment in fieldwork. Community-level population genetic data potentially offer a powerful way to indirectly infer richness, abundance and the history of accumulation of biodiversity within a community. Here we introduce a joint model linking neutral community assembly and comparative phylogeography to generate both community-level richness, abundance and genetic variation under a neutral model, capturing both equilibrium and non-equilibrium dynamics.

Location: Global.

Methods: Our model combines a forward-time individual-based community assembly process with a rescaled backward-time neutral coalescent model of multi-taxon population genetics. We explore general dynamics of genetic and abundance-based summary statistics and use approximate Bayesian computation (ABC) to estimate parameters underlying the model of island community assembly. Finally, we demonstrate two applications of the model using community-scale mtDNA sequence data and densely sampled abundances of an arachnid community on La Réunion. First, we use genetic data alone to estimate a summary of the abundance distribution, ground-truthing this against the observed abundances. Then, we jointly use the observed genetic data and abundances to estimate the proximity of the community to equilibrium.

Results: Simulation experiments of our ABC procedure demonstrate that coupling abundance with genetic data leads to improved accuracy and precision of model parameter estimates compared with using abundance-only data. We further demonstrate reasonable precision and accuracy in estimating a metric underlying the shape of the abundance distribution, temporal progress towards local equilibrium and several key parameters of the community assembly process. For the insular arachnid assemblage, we find the joint distribution of genetic diversity and abundance approaches equilibrium expectations, and that the Shannon entropy of the observed abundances can be estimated using genetic data alone.

Main conclusions: The framework that we present unifies neutral community assembly and comparative phylogeography to characterize the community-level distribution of both abundance and genetic variation through time, providing a resource that should greatly enhance understanding of both the processes structuring ecological communities and the associated aggregate demographic histories.
1 INTRODUCTION

The species abundance distribution (SAD) is a classic summary of the structure of ecological communities (McGill et al., 2007), which is gaining increasing interest in areas of applied ecology and biodiversity management (Matthews & Whittaker, 2015), community assembly (Fattorini, Rigal, Cardoso, & Borges, 2016) and biogeography in general (Matthews, Borges, Azevedo, & Whittaker, 2017). However, unbiased comparative species abundance data are often challenging to obtain (Cardoso, Erwin, Borges, & New, 2011). Standardized sampling protocols can be implemented to improve comparability within studies (e.g. Emerson et al., 2017), but these do not account for idiosyncratic phenological or microhabitat differences among species that may affect sampling probability, potentially skewing estimates of relative abundance. Genetic sequence data retain a record of population size changes through time (Griffiths & Tavare, 1994), yet this axis of information has rarely been exploited by community ecologists (Laroche, Jarne, Lamy, David, & Massol, 2015; Vellend, 2005), and never at the scale of the full community. Therefore, a model linking abundance and effective population size at the community scale could enable a new way to characterize abundance distributions using genetic data alone. Additionally, rather than sampling more individuals to increase resolution of community assembly inference, sampling sequences may allow discrimination between assembly models that are known not to be identifiable with current abundance data alone (Rosindell, Hubbell, He, Harmon, & Etienne, 2012; but see Al Hammad, Alonso, Etienne, & Cornell, 2015). Such rapid and cost-effective estimation of SADs could greatly enhance understanding of the structure of ecological communities, with potential to aid in the design of conservation strategies, and to improve forecasts of changes in aggregate population dynamics in the context of global climate change.

The accumulation of sequence data for non-model organisms from over two decades of comparative phylogeographic studies (Avise, Bowen, & Ayala, 2016), large-scale DNA barcoding initiatives (e.g. Bucklin, Steinke, & Blanco-Bercial, 2011) and forthcoming community-scale genome-wide data (Garrick et al., 2015) presents an exciting opportunity for linking abundances and aggregate population genetic data. However, we lack a flexible joint model that links existing models in comparative phylogeography (Satler & Carstens, 2017; Xue & Hickerson, 2017) with existing biogeographical models of community assembly (Rosindell & Harmon, 2013; Rosindell et al., 2012).

Despite the potential of comparative phylogeography to leverage the power of aggregated demographic histories to answer fundamental questions about community assembly and macroecology (Avise et al., 1987, 2016; Hickerson et al., 2010), such approaches have generally neglected the growing body of theory from community ecology that seeks to accommodate the relative importance of deterministic (Maire et al., 2012; Tilman, 2004) and stochastic processes (Hubbell, 2011; MacArthur & Wilson, 1963; Rosindell et al., 2012) governing the assembly of communities. For instance, comparative phylogeographic approaches that do incorporate community assembly have tended to focus on general models of shared demographic histories (Burbrink et al., 2016; Satler & Carstens, 2017), rather than models that are explicitly parameterized from ecological community assembly theory (but see Bunnefeld, Hearn, Stone, & Lohse, 2018).

Ecological theory has been fundamental for understanding processes underlying spatial patterns of biodiversity as typically quantified by regional SADs and species–area relationships (McGill et al., 2007). However, ecological models of community assembly tend to view communities as static pools with an ahistorical focus on equilibrium expectations (Weiher et al., 2011). Although there have been efforts to incorporate non-equilibrium history in models of community assembly (Clark & McLachlan, 2003), as well as a long tradition of incorporating phylogenetic information (Jabot & Chave, 2009; Webb, Ackerly, McPeek, & Donoghue, 2002) that also accommodates non-equilibrium historical dynamics (Manceau, Lambert, & Morlon, 2015; Pigot & Etienne, 2015), there has only been limited, yet promising, effort in considering intraspecific genetic polymorphism within a dynamic non-equilibrium assembly framework (Laroche et al., 2015; Vellend et al., 2014) or within statistical models of macroecology (Pelletier & Carstens, 2018; Smith, Seeholzer, Harvey, Cuervo, & Brumfield, 2017). These efforts in bridging the gap between ecological models and population genetics have focused on characterizing the correlation between species diversity and genetic diversity in ecological communities (the species–genetic diversity correlation: Laroche et al., 2015; Papadopoulou et al., 2011; Vellend, 2005; Vellend et al., 2014), while other efforts have looked at the relationships between adaptive genetic diversity and community dynamics (Becks, Ellner, Jones, & Hairston, 2010; Hughes, Inouye, Johnson, Underwood, & Vellend, 2008; Schoener, 2011).

Despite these important efforts to unify our understanding of ecological and evolutionary dynamics, a community-scale model linking species abundances and genetic diversities under a dynamic model of assembly has yet to be proposed. Here we describe, test and demonstrate a joint inferential framework that bridges ecological neutral theory with population genetics in order to make joint predictions of community-wide distributions of species abundances.
genetic diversities and genetic divergences under a dynamic non-equilibrium model of assembly. The unified framework we present combines a forward-time model of community assembly with a backward-time coalescent model, linking abundance and colonization history with aggregated population genetic samples from multiple taxa.

We use simulation experiments to validate the power and accuracy of our method using an approximate Bayesian computation framework (ABC; Csilléry, François, & Blum, 2012) for estimating model parameters. Similar to Jabot and Chave (2009), who used phylogenetic information to estimate parameters of a neutral community assembly model with ABC, we merge population genetics and a similar neutral ecological model in an ABC context. After using simulations to validate the method, we demonstrate an application to a sample of community-wide mitochondrial DNA sequence data and corresponding densely sampled abundance estimates obtained from an assemblage of 57 spider species from the island of Réunion (Emerson et al., 2017). Using only the sequence data, we accurately estimate the Shannon entropy of the observed SAD and additionally obtain an estimate of the equilibrium state of the community. The joint model, implemented in Python, and all Jupyter notebooks for reproducing simulations and analysis are freely available on GitHub: https://github.com/isaacovercast/gimmeSAD.

2 | MATERIALS AND METHODS

2.1 | Model overview

First, forward-time community assembly simulations are performed using an island/mainland metacommunity model following Rosindell and Harmon (2013). This individual-based neutral model unifies MacArthur and Wilson’s equilibrium theory of island biogeography (ETIB) with Hubbell’s unified neutral theory of biodiversity (UNTB) to generate time-dependent non-equilibrium and equilibrium predictions of local richness and abundances (Hubbell, 2011; MacArthur & Wilson, 1963). We use these predicted temporal changes in abundance distributions and colonization times to parameterize a multipopulation model of aggregate population genetic data backwards in time under the coalescent (Rosenberg & Nordborg, 2002). The former allows for inference about the time series progression of community change while the latter links predicted changes in community population genetic data to this community assembly process (see Figure 1 & Box S1).

![Figure 1](https://wileyonlinelibrary.com)  Schematic version of the model parameters, processes and response variables. Directed acyclic graph (DAG) depicting the conditional dependencies underlying the joint model’s set of adjustable parameters, response variables, data and associated summary statistics (under model configuration $M_{abc}$). For simplicity, the components of the source metacommunity are elided from the figure, but are described fully in the text [Colour figure can be viewed at wileyonlinelibrary.com]
2.2 | Forward-time model

Forward-time simulations of community assembly follow the spatially implicit neutral model of Rosindell and Harmon (2013) that unifies the ETIB with the UNTB whereby abundance distributions, and immigration and extinction rates proceed under a birth/death/colonization process in the biogeographical context of a focal local community and a regional source pool (metacommunity). In this model, the carrying capacity \( K \) of the local community is fixed and of finite size. The colonization rate is modelled as a single parameter \( c \) that specifies the probability of a colonization event. Colonizing species are sampled from a metacommunity composed of species with abundances that are independently and identically distributed according to the log series distribution (Fisher, Corbet, & Williams, 1943), and which is static with respect to the time-scale of local assembly. At each time-step, one individual is randomly sampled for removal from the local community. With probability 1−\( c \), this individual is replaced by the offspring of a randomly sampled individual from the local community. With probability \( c \), the individual is replaced by a randomly sampled member of the metacommunity, where the probability of sampling from any given species is weighted by the relative metacommunity abundance \( A_{\text{meta}} \) (Table S1 in Appendix S1).

Given that the forward-time process follows a Moran model, we will refer to one birth/death event as a time-step, with one generation encompassing \( K \) time-steps. Information about the state of the community in the forward-time simulation model is recorded at regular time intervals of arbitrary length, with the default interval length being equal to 100,000 time-steps. Model state can be described by a vector of \( T_i = \{\tau_1, \ldots, \tau_{\text{final}}\} \) containing the time since colonization (in generations) for species \( i \) in the local community as well as a jointly associated vector \( A_i = \{A_{1i}, \ldots, A_{N_{\text{meta}}i}\} \) that contains the associated abundances for species \( i \) in the local community. The history of abundance changes for species \( i \) going back in time \( \tau \) generations is contained by a \( A_i^j = \{A_i^{j,0}, \ldots, A_i^{j,-\tau}\} \) such that \( j = \tau - 0 \) decreases going back in time at prior time intervals until \( \tau - \tau \). The counts of post-colonization migration events are accumulated per species in the vector \( M = \{M_1, \ldots, M_{N_{\text{meta}}}\} \) (Table S1 in Appendix S1).

Two emergent pseudo-parameters (model response variables) are then \( c' \) (effective colonization rate) and \( \dot{\tau} \) (effective extinction rate) which are defined as the realized number of colonization and extinction events per generation, respectively (Table S2 in Appendix S1).

2.3 | Scaling forward-time model to backward-time coalescent model

For the \( i \)-th local species that is extant at the \( j \)-th time interval with an abundance of \( A_i^j \), there exists the history of changes in abundance over time since colonization \( \tau_i \) from a source species in the metacommunity. To relate raw sample-based abundances with the effective population sizes that parameterize the backward-time coalescent process of the gene tree lineages, we make the assumption of a random spatial distribution of individuals that is predicted to lead to a simple scaling relationship whereby the sample-based and regional-based abundance distributions have the same functional form (Green & Plotkin, 2007). To approximate this expectation, we incorporate a rescaling that is based on the assumption that the observed local abundances from direct sampling are proportional to regional abundances and thus current effective population sizes.

To this end, we rescale the time-dependent abundance of each species \( A_i^j \) into a time-dependent effective population size \( N_i^j \) using the scaling factor \( \sigma \) such that \( A_i^j = N_i^j \sigma \). This is equivalent to assuming that the abundance counts \( A_i^j \) actually record the number of demes, each of size \( \sigma \), over time per species. Across all species sampled genetically at the \( j \)-th time interval, this yields time-dependent vectors of the effective population sizes for species \( i \) \( \{N_i^j\} \), the associated times since colonization in units of generations \( T_i = \{\tau_1, \ldots, \tau_{\text{final}}\} \) and temporally static effective population size vectors for the corresponding source metacommunity species \( \{N^j_{\text{meta}}\} \). Under this assumption, each local species consists of a metapopulation consisting of \( A_i^j \) demes of size \( \sigma \) with strong migration conditions that reduce to the temporally dynamic predictions of a panmictic effective population size \( A_i^j \sigma \). Under this assumption, the "collecting phase" is predicted to dominate the entire history of ancestry, thereby approaching the standard panmictic coalescent expectations of a time-dependent effective population size \( A_i^j \sigma \) as the number of demes become large (Wakeley, 2001, 2004; Wakeley & Aliacar, 2001). Importantly, this rescaling is based on the assumption that the observed abundances from direct sampling are proportional to actual abundances and current effective population sizes, although these relationships are known to be complex (Luikart, Ryman, Tallmon, Schwartz, & Allendorf, 2010). However, how \( \sigma \) changes the time-scale of both forward and backward processes is not determined in our model, and therefore, it is critical to determine if a chosen \( \sigma \) value results in a model that can generate the observed data. As a check, one should assess the ability of the model to generate the data by statistical goodness-of-fit tests or model evaluation (Gelman, 2003; Lemaire, Jay, Lee, Csilléry, & Blum, 2016). Alternatively, \( \sigma \) could be treated as an unknown parameter and estimated given the data.

Given the parameters of the backward-time model (Tables S1 & S2 in Appendix S1), we use the msprime coalescent simulator program (Kelleher, Etheridge, & McVean, 2016) to generate genetic polymorphism data matching an arbitrary sampling regime of the local and/or metacommunity species pair sample sizes (with respect to numbers of individuals sampled at a mtDNA locus of length \( L \)). Instead of parameterizing the coalescent simulations of the \( i \)-th species following the \( \tau^i \) stochastic changes in effective population sizes since colonization according to \( N_i = \{N_i^{j,0}, \ldots, N_i^{j,-\tau}\} \), we use \( N_{\dot{\tau}} \), the harmonic mean of each species’ effective population size across all time-steps indicated by the \( \tau^i \) elements within \( N_i \) (Karlin, 1968; Pollak, 1983). One gene genealogy is simulated for each sampled species pair corresponding to a 570 bp segment of the mitochondrial COI gene, and mutations are applied under an infinite-sites model given an assumed invertebrate mitochondrial divergence rate (1.1% per species per million years; e.g. Brower, 1994).
2.4 | Initial conditions

Our initial conditions simulate a volcanic island origin which slightly deviates from that of Rosindell and Harmon (2013). At time zero, Rosindell and Harmon (2013) assume that one initial colonizing lineage consumes all available space in the community, thereby saturating K. In our model, we select the most abundant species in the metacommunity and introduce one individual into the unpopulated local community. This initial condition is both biologically more realistic and also avoids the assumption that volcanic island carrying capacity is saturated at time zero, which could generate unrealistic quantities of genetic diversity in the initial colonizing lineage.

2.5 | Quantifying equilibrium

Equilibrium is commonly defined as the dynamic balance between colonization and extinction rates that emerges over time, eventually leading to a stationary distribution where the two rates are expected to be equal (MacArthur & Wilson, 1963). However, under certain conditions, species richness and abundances may fail to equilibrate simultaneously, in which case the classic definition of equilibrium is insufficient (see Rosindell & Harmon, 2013). To address the need for a more robust concept, we follow Rosindell and Harmon (2013) in defining equilibrium as the point at which the starting conditions of the model are no longer detectable in the state of the system. In addition to colonization/extinction rate balance, this auxiliary definition guarantees that both richness and the SAD have reached their expected equilibrium values. Here we define a new term to measure the fraction of this equilibrium obtained by the community and treat it as an emergent parameter that can be estimated by sampling the prior and posterior distribution (\(\lambda\); Table S2 in Appendix S1). This quantity is defined as \(\Lambda = \sum_{i=1}^{K} E_i / K\), where K is the carrying capacity and E is the Boolean vector of length K such that \(E_i = 1\) for \(i = 1, ..., K\) indicates the colonization status of each individual in the local community. The value of \(\Lambda\) therefore ranges from 0 to 1 with small values indicating early assembly history, and larger values indicating later assembly history and approach to equilibrium. When all individuals present in the local community are descended from a lineage that colonized during the simulation, then \(\sum_{i=1}^{K} E_i = K\) and \(\Lambda = 1\). Our model of community assembly is inherently stochastic, so the amount of time for any given simulation to reach equilibrium is a random variable given the distribution under the model. For each forward-time simulation, we track elapsed time, local community composition (both abundances and richness), and colonization times for all local species. We are interested in equilibrium and non-equilibrium dynamics, so we poll this information at regular intervals of arbitrary duration.

2.6 | Summary statistics

At each time interval, we extract the simulated sequences from a sample of the local community and calculate nucleotide diversity as the average number of pairwise differences (\(\pi\); Tajima, 1983) within the local community for each sampled species given \(S_{local} = \{x_1, ..., x_n\}\). We then summarize the distribution of genetic variation by constructing a one-dimensional histogram (\(\pi\)) of local community genetic diversity such that:

\[ S_{local} = \sum_{i=1}^{k} f_i \]

where \(k\) is the number of bins (with \(k = 10\) for all simulation and empirical analyses), and bin width \(\max(x_i)/k\). We term this summary of local community diversity the one-dimensional species genetic diversity distribution (1D- SGD; Figure S1 in Appendix S1). Next, we calculate absolute divergence (\(D_{xy}\); Nei, 1987) between samples from each local-metacommunity sister pair (\(D_{xy} = \sum_{i=1}^{\infty} \frac{D_{xy,i}}{D_{xy,i}}\)). The values of \(x_i\) and \(D_{xy,i}\) are aggregated across all species-pairs sampled from the community within each time point and summarized as a \(k \times k\) joint frequency histogram (X) with equal-width bins such that:

\[ S_{local} = \sum_{i=1}^{k} \sum_{j=1}^{k} X_{ij} \]

The upper bound for each dimension of the histogram is fixed to the maximum values of \(x\) and \(D_{xy}\) within a given simulation. We term this joint summary of community diversity/divergence as the two-dimensional species genetic diversity distribution (2D- SGD; Figure S2 in Appendix S1). The 1D and 2D- SGD are simple histograms that collapse the full distribution of community genetic diversity into a summary representation. Additionally, at each time interval, we record the rank abundance curve (RAC), the SAD, and Shannon entropy calculated for the community (\(H'^{'}\); Boltzmann, 1872; Shannon, 1948; Hill, 1973), which is:

\[ \sum_{i=1}^{n} p_i \log(p_i) \]

where \(p_i\) is the proportional abundance of species \(i\). Given an observed sample of \(S_{local}\) species sampled from an empirical community, the simulated summary statistics are filtered to match the observed sampling configuration. As an additional method of comparison with the \(H'^{'}\) derived from the SAD, we also calculated the Shannon entropy derived for both the 1D- SGD (\(\alpha\)) and distribution of \(D_{xy}\) per sampling time point and notate this as \(H'^{'} \alpha\) and \(H'^{'}_{Day}\) respectively.

2.7 | Simulation study design

To characterize the joint temporal dynamics of the SAD and 2D- SGD under non-equilibrium and equilibrium community assembly, we simulated assembly histories under a range of parameter values using a range of local community sizes (\(K = 1,000, 5,000, 10,000\)) and colonization rates (\(c = 0.0001, 0.001, 0.01\)). We generated 10,000 replicated simulations for each combination of local community size and colonization rate, resulting in 180,000 total simulated community histories. All forward-time simulations were run for twice the mean time to turnover equilibrium (\(\lambda\)) for the largest local community with the smallest colonization rate (5 × 10⁶ generations). We then summarized the temporal changes in \(H'^{'}\), \(\pi\), \(D_{xy}'\), \(H'^{'} ≠\) and \(H'^{'}_{Day}\) by calculating the
mean and standard deviation of each of these metrics for each parameterization across replicate sets of simulations at five values of $\Lambda$ (0.1, 0.25, 0.5, 0.75, 1). For this initial set of exploratory simulation experiments, we calculated $H'$ on the entire set of species, while $\pi$, $D_{xy}$, $H'_{xy}$, and $H'_{Day}$ were likewise calculated on this entire set of $S_{local}$ species given samples of 10 individuals per species in the local community and associated metacommunity source populations.

2.8 | Bias and accuracy in estimating parameters

Next, we evaluated the suitability of $H'$ and the relative bin magnitudes of the SGD as summary statistics for parameter estimation using ABC by conducting a suite of leave-one-out cross-validation experiments under various configurations (Table 1) whereby parameters of known values are estimated (Cisillery et al., 2012). We focus on evaluating accuracy and precision in estimating the following community-wide model parameters and pseudo-parameters: local community size ($K$), parameterized colonization rate ($c$), fraction of equilibrium ($\Lambda$), realized colonization rate ($c'$), extinction rate ($\dagger$) and Shannon entropy ($H'$).

We additionally explored estimation of community-wide parameters given various sequence and abundance data availability configurations (see Table 1). For example, given only the DNA sequence data sampled from a focal local community, the relative bin magnitudes of the observed 1D-SGD can be used as the summary statistic vector and both $H'$ and $\Lambda$ can be estimated, along with the other model parameters such as $c$, and $\dagger$ (ABC configuration $M_2$; Table 1).

To construct the reference table for the cross-validation analyses, we performed 1,000,000 community assembly simulations, sampling parameter values of $K$, $c$ and $\Lambda$ according to uniform prior distributions ($K = \sim U(1,000–10,000)$, $c = \sim U(0.0001–0.01)$ and $\Lambda = \sim U(0, 1)$; see Table S1 in Appendix S1 for all simulation parameters).

We then conducted ABC leave-one-out cross-validation using the ‘cv-4abc’ function of the ‘abc’ R package (Cisillery et al., 2012). For the ABC procedure, we used simple rejection sampling and a tolerance sufficient to retain 1,000 samples from the prior to construct the posterior estimate for each parameter of interest. We performed 100 leave-one-out cross-validation replicates per data configuration for each estimated parameter, and quantified accuracy of parameter estimation by calculating root-mean-square error (RMSE) and the coefficient of determination ($R^2$) for sampled and estimated parameter values.

2.9 | Empirical application

Following our simulation experiments demonstrating that the ABC model can effectively estimate parameters, we perform an empirical analysis on a published dataset from a community of spiders from the island of Réunion, an overseas department of France located in the Indian Ocean approximately 900 km east of Madagascar. In the original study, using a standardized protocol spiders were sampled from 10 lowland rain forest plots distributed across the island and sorted into 57 presumed biological species using a protocol combining morphological sorting and mtDNA sequencing (570 bp cytochrome oxidase c subunit I; Emerson et al., 2017). The dense and standardized sampling allows us to use both the $c$ calculated from the observed SAD as well as the 1D-SGD calculated from the observed sequence data for estimating assembly model parameters. Therefore, we use model configuration $M_1$ to estimate $H'$, and $M_2$, $M_3$, and $M_4$ to alternatively estimate $\Lambda$ (Table S1 in Appendix S1).

Under all model configurations, we estimate parameters $c'$ and $\dagger$. For the ABC inference procedure, we simulated 1,000,000 samples by drawing parameter values from the same prior distribution used for the cross-validation analysis, and used the same rejection method to accept the closest 1,000 datasets to sample from the posterior distribution. When calculating $\pi$ for each island taxon, we used sample sizes with respect to numbers of individuals matching the observed spider data exactly with respect to numbers of individuals and length of DNA sequence. Simulations for the empirical analysis were run on a 40 core Intel Xeon 2.20 GHz workstation with 256 GB of main memory and were completed in approximately 1 week.

We evaluated the overall goodness-of-fit of our posterior estimate to the observed data in two ways. First, we quantified the absolute Euclidean distances between the retained and observed summary statistics. Additionally, we performed a prior predictive check by projecting the retained simulated SGD, along with the observed SGD into principal component (PC) space. A good fit of the model to the data should generate simulated summary statistics sufficiently similar to those of the observed data as to be indistinguishable in the PC analysis.

3 | RESULTS

3.1 | The joint SAD and SGD through time

The classically lognormal-like shape of the SAD, with most species of low abundance, is mirrored by the distribution of genetic diversities (Figure 2). The shape of the joint spectrum of community genetic
Joint distribution of genetic diversity/divergence through time

![Joint distribution of genetic diversity/divergence through time](image)

FIGURE 2 Joint distribution of genetic diversity/divergence through time. (Panel 1) Summed aggregations of the 2D-SGD across $1 \times 10^4$ replicated simulations at varying stages of community assembly. All simulations were conducted with intermediate values of community size and colonization rate ($K = 5,000$, $c = 0.03$). Each point in the plot is a joint frequency bin for values of local nucleotide diversity ($\pi$) and absolute divergence between the local community and the metacommunity ($D_{xy}$). The colour of each bin indicates the number of species it contains, with cooler colours signifying fewer species and warmer colours signifying more species. Panel (2) Corresponding rank abundance plots of the $1 \times 10^4$ simulated communities. Values of $\Lambda$ depicted capture multiple stages of community assembly from early ($0.05$, $0.1$), through middle ($0.25$, $0.5$), to late ($0.75$, $1$) [Colour figure can be viewed at wileyonlinelibrary.com]

2) Rank abundance through time

![Rank abundance through time](image)

FIGURE 2 Rank abundance through time. (Panel 1) Summed aggregations of the 2D-SGD across $1 \times 10^4$ replicated simulations at varying stages of community assembly. All simulations were conducted with intermediate values of community size and colonization rate ($K = 5,000$, $c = 0.03$). Each point in the plot is a joint frequency bin for values of local nucleotide diversity ($\pi$) and absolute divergence between the local community and the metacommunity ($D_{xy}$). The colour of each bin indicates the number of species it contains, with cooler colours signifying fewer species and warmer colours signifying more species. Panel (2) Corresponding rank abundance plots of the $1 \times 10^4$ simulated communities. Values of $\Lambda$ depicted capture multiple stages of community assembly from early ($0.05$, $0.1$), through middle ($0.25$, $0.5$), to late ($0.75$, $1$) [Colour figure can be viewed at wileyonlinelibrary.com]
accrue with time as $\Lambda$ progresses. On the other hand, time has a reduced impact on the distribution of $D_{xy}$, which obtains the lognormal-like shape even at very early stages of assembly, although with greater variability, as expected given that the final waiting times in the larger ancestral population will predict a large variance in this summary statistic, regardless of colonization time (Takahata & Nei, 1985).

Different colonization rates and local community sizes leave different signatures through time on both the SAD and the 2D-SGD (Tables S3 & S4 in Appendix S1). Overall, higher colonization rates tend to increase the species richness in the community, predominantly by increasing the proportion of rare species, as well as species with lower $\pi$. Higher colonization also increases local extinction rates and this increase in turnover decreases average divergence times, with a subsequent reduction in both $\pi$ and $D_{xy}$. In a similar fashion, under reduced colonization rates, turnover is lower, the proportion of rare species is reduced, divergence times are longer on average, and $\pi$ is increased on average. Additionally, the correlation between $\pi$ and abundance is dependent on $\Lambda$, increasing as $\Lambda$ increases and finally becoming strong as $\Lambda$ approaches 1. A powerful feature of our joint model is that it does not assume this correlation between genetic variation and abundance, and indeed, the dynamics of how this correlation changes over time provides some of the information for the estimation of model parameters.

### 3.2 Bias and accuracy in estimating parameters

Broadly speaking, cross-validation indicated reasonable accuracy and limited bias in estimating all parameters under all ABC model
3.3 Estimating parameters for the Réunion spider community

For an empirical application, we chose to use only the 1D-SGD as observations to estimate $H^\prime$ calculated from the observed SAD ($M_j$). In this configuration, the bin magnitudes of the 1D-SGD are treated as the summary statistic vector, and $H^\prime$ is treated as the parameter to be estimated. However, we also have the observed $H^\prime$ calculated from the samples for direct comparison to the estimate of $H^\prime$ under the ABC configuration $M_j$. In this case, our ABC mode estimate of $H^\prime = 1.816$ (Figure 5a; 95% HPD: 1.171–2.822) came remarkably close to the observed $H^\prime$ of 2.246 calculated from the sampled abundance data. This good fit of the posterior estimate to the observed $H^\prime$ indicates that the observed distribution of genetic diversity contains sufficient information about the community history of effective population size trajectories across island species with regard to predictions of the contemporary SAD under a neutral model of assembly (Figure 4). Our simulation study demonstrates this possible dynamic as both $H^\prime$ and the SGD are predicted to increase over time under most conditions, such that our ABC model could potentially estimate the former with the latter given the strongly temporal features of our assembly model. Given the coupled dynamic of $H^\prime$ and the SGD as a progressive function of time in our simulation study, it follows that our ABC procedure has potential to estimate the degree of equilibrium parameter ($\Lambda$), as shown in our cross-validation experiments. We estimated $\Lambda$ for the spider community using three different ABC model configurations representing different combinations of $H^\prime$ and the 1D-SGD as summary statistics ($M_A$, $M_I$, and $M_M$). Given $M_A$, the mode estimate of $\Lambda$ was 0.51 but with a diffuse posterior distribution (Figure 5b; 95% HPD: 0.05–0.93). In sharp contrast, ABC configurations $M_M$ and $M_I$ yielded mode estimates and HPDs that were both relatively clustered around high values of $\Lambda$ (Figure 5c,d; posterior mean 0.89; 95% HPD: 0.69–1). Additionally, ABC estimates of $c^\prime$ (Figure 5e; posterior mean 0.001; 95% HPD: 0.0007–0.0017) and $\dagger$ (Figure 5f; posterior mean 0.001; 95% HPD: 0.0009–0.0012) under model $M_A$ were broadly concordant. More formal goodness-of-fit analysis with both the prior predictive check with principal components and Euclidean distances between retained and observed summary statistics corroborate the good fit of the model (Figures S8 & S9 in Appendix S1).

4 DISCUSSION

Similar to efforts that merge phylogenetic frameworks with community assembly models (Jabot & Chave, 2009; McPeek, 2008; Webb et al., 2002), recent important progress has been made towards linking community ecology models with population genetics (Baselga, Gómez-Rodríguez, & Vogler, 2015; Laroche et al., 2015; Vellend, 2005). However, current theory either lacks an explicit population genetic foundation (Vellend, 2005) or considers...
genetic variation only of a focal taxon (Laroche et al., 2015). A focus on genetic diversity at the community scale offers an opportunity for ecological theory to further incorporate the potentially powerful dimension of flexible comparative phylogeographic models (Satler & Carstens, 2017; Xue & Hickerson, 2017). This should be facilitated by the increasing availability of genome-scale phylogeographic data that allows exploration of evolutionary models of increasing complexity and explanatory power (Schraiber & Akey, 2015), yet such approaches have seen limited use to infer the temporal and spatial dynamics at play at the community level (but see Bunnefeld et al., 2018). On the other hand, while many classic comparative phylogeographic studies attempted to infer

**Figure 5** ABC posterior estimates of colonization/extinction rates, $H'$, and $\Lambda$ for the Réunion island spider community. ABC posterior estimates of colonization and extinction rates, and $H'$ and $\Lambda$ for the spider community dataset from the island of Réunion. (a) Using only the 1D-SGD as the summary statistic vector ($M_I$), the mode estimate of $H'$ was 1.816 (95% HPD: 1.171–2.822; red dashed lines). The true value of $H'$ as calculated from the observed abundance data was 2.246 (red solid line). Posterior estimates of $\Lambda$ using three different model configurations: (b) only $H'$ as data ($M_{H}$); (c) only the 1D-SGD as data ($M_I$); and (d) both $H'$ and the 1D-SGD as data ($M_{AI}$). Posterior estimates of colonization rate and extinction rate using model $M_{AI}$ are depicted in panels (e) and (f), respectively. In all panels, the red dashed lines indicate the 95% HPD, and the blue line illustrates the prior distribution [Colour figure can be viewed at wileyonlinelibrary.com]
histories of Pleistocene community assembly and diversification (Bermingham & Moritz, 1998; Hewitt, 2000) by examining combined results of multiple single-taxon phylogeographic studies within a region (Emerson, Cicconardi, Fanciulli, & Shaw, 2011), most of these endeavours were not grounded in ecological assembly theory.

Even the comparative phylogeographic models that globally operate at the assembly level have yet to be grounded in ecological theory that can account for stochastic and deterministic forces underlying community assembly (Gehara et al., 2017; Prates et al., 2016). Fortunately, the community assembly models that generate expectations for temporally dynamic SADs (Missa, Dytham, & Morlon, 2016) and speciation/colonization rates (Rosindell & Harmon, 2013) could have an identifiable relationship with population genetic parameters like divergence times, admixture, expansion, colonization times and changes in effective population sizes. Unifying the parameters of these two modelling frameworks could provide a new way of testing an array of competing assembly models with genetic data as well as estimating the relative strength of various deterministic forces underlying the assembly models such as niche filtering and competition. By linking ecological and micro-evolutionary processes whose dynamics and equilibrium expectations can occur on different time-scales, our new joint approach potentially allows for improved resolution and statistical power for estimating parameters as well as improved potential for testing and fitting a number of different neutral and non-neutral community assembly models. Likewise, understanding whether or not communities tend towards stable equilibria remains an unanswered question (Harmon & Harrison, 2015; Rabosky & Hurlbert, 2015; Valente et al., 2017) that can now be addressed with our joint approach that makes generative predictions of richness, abundance and the spectrum of genetic diversity under both ecological and evolutionary time-scales.

4.1 Assembly of the Réunion spider community

The joint data of mitochondrial polymorphism and abundance structure from >50 spider species on the volcanic island of Réunion afford us the opportunity to compare the estimate of the Shannon entropy ($H'$) using only the genetic data (i.e. ABC model configuration $M_j$) with the $H'$ calculated from the observed abundance distribution. In this case, the posterior distribution of $H'$ under $M_j$ was able to successfully recover the observed $H'$. If this is a general feature of our approach, it would be encouraging given that estimating species abundances directly from field surveys can be difficult and problematic for some taxa (Kunin, Hartley, & Lennon, 2000; Petrovskaya, Petrovskii, & Murchie, 2012).

Using the distributions of abundance and genetic diversity jointly ($M_{jg}$) also allowed us to gain insight into the stage of progression towards equilibrium of this spider assemblage under our ecologically neutral model, yet the distribution of genetic diversity alone may have been sufficient ($M_j$). This was not the case of using the distribution of abundances alone ($M_{gj}$), indicating there is little information about equilibrium state ($\Lambda$) in $H'$. This result is in agreement with the ABC cross-validation findings suggesting that estimation under ABC configuration $M_{jg}$ improves accuracy and reduces bias in the estimation of $\Lambda$. It is notable that both ABC configurations including local genetic data ($M_j$ and $M_{jg}$) strongly indicate that this isolated spider community is consistent with an ecologically neutral assembly that is approaching or has reached equilibrium. Additionally, this assessment is supported by the similar mode estimates and largely overlapping HPD of $c'$ and $\gamma$ which hews to the more traditional consideration of equilibrium as the dynamic balance of colonization and extinction. Indeed, Réunion island emerged from a classic volcanic hotspot formation approximately 5 Ma (Lénat, Gibert-Malengreau, & Galdéano, 2001), and this is likely sufficient time for equilibrium expectations of species richness, and community-wide distributions of abundance and genetic diversity to have accumulated.

4.2 Outlook

The simple neutral model we introduce can be used as a candidate null hypothesis against which to test comparative population genomic/phylogeographic data, while the flexibility of the framework can accommodate various particular ecological contexts. For example, the model could incorporate in situ local speciation either as instantaneous events or as a protracted process (Rosindell, Cornell, Hubbell, & Etienne, 2010). Furthermore, it could incorporate non-neutral processes by including trait parameters for differential niche filtering or dispersal limitation across species that result in variable colonization rates. In this case variation in colonization, probabilities would be a proxy for non-neutral processes such as trait-dependent environmental filtering (Pigot & Etienne, 2015). Along these lines, the model could also accommodate deterministic processes such as resource-limited colonization probabilities or priority effects while retaining the stochastic dynamics of ecological drift underlying our joint model in the spirit of stochastic assembly theory (Tilman, 2004). In this case, the magnitude of deviation from neutral expectations of colonization time, abundances and genetic diversities could be modelled as a free parameter within our joint assembly model.

The increased complexity of these different modelling strategies would all benefit from the increased information content of higher resolution data types such as RADseq (Andrews, Good, Miller, Luikart, & Hohenlohe, 2016), or whole genomes (Bunnefeld et al., 2018). Additionally, the widespread availability of mitochondrial and environmental DNA data also makes our approach amenable to model the assembly of complex microbial systems (Li & Ma, 2016) with time series information (Ridenhour et al., 2017). Such time series data could introduce an additional axis of information allowing increased power to test hypotheses about the process of community assembly within a historical perspective.

From a practical standpoint, our model makes it possible to fit assembly models and estimate abundances from a sample of DNA sequence data from a community for which comparable abundance data could be logistically challenging to collect. Taxa with high dispersal potential such as spiders are ideally suited for the estimation of SADs because their genetic samples are more likely to have arisen...
from a panmictic coalescent process. While taxa with elevated levels of population structure or more complex assembly histories might be more challenging for parameter estimation under our simple model, it could potentially be extended to explicitly model spatial processes, or the more complex assembly histories which may be inherent on real island systems. Our model thus provides a flexible framework that can, even in the absence of comparable species abundance data, allow researchers to use the vast amounts of available mitochondrial DNA sequence data to test competing models of island community assembly.

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DATA ACCESSIBILITY

No new data were generated for this study. The joint model implemented in Python, and all ipython notebooks for reproducing simulations and analysis are freely available on GitHub: https://github.com/isaacovercast/gimmeSAD.

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BIOSKETCHES

Isaac Overcast is interested in investigating the interaction between ecological and evolutionary processes across spatial and temporal scales, from the level of single species to whole communities. Brent Emerson has complementary interests in the geology and biodiversity of oceanic islands, and the application of molecular data to understand the origin and maintenance of species and communities of species. Michael J. Hickerson is interested in comparative population genomics within the context of biogeography.

Author contributions: I.O. and M.J.H. conceived the study and designed the model. I.O. coded the simulations, analyses and produced the figures. I.O. wrote the manuscript with the assistance of M.J.H. B.C.E. contributed empirical data and helped writing the manuscript. All authors reviewed the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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