

1 **Title:** Identifying Models of Trait-Mediated Community Assembly Using Random Forests and
2 Approximate Bayesian Computation

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21 **Statement of Authorship:** MR, DCT, and LJH developed research concept. BW contributed to
22 the creation of the non-neutral assembly models and KP collected all empirical data. MR

23 developed CAMI, performed all analyses, and wrote the manuscript. All authors contributed to
24 critiques of the analysis and subsequent revisions of the text.

25 **Data Accessibility Statement:** All code for the R package CAMI is available at
26 github.com/ruffleymr/CAMI. All scripts for each analysis, along with the output data, can be
27 found in github.com/ruffleymr/CAMI/vignettes and github.com/ruffleymr/CAMI/data,
28 respectively.

29 **Abstract**

30 Ecologists often use dispersion metrics and statistical hypothesis testing to infer
31 processes of community formation such as environmental filtering, competitive exclusion, and
32 neutral species assembly. These metrics have limited power in inferring assembly models
33 because they rely on often-violated assumptions. We adapt a model of phenotypic similarity and
34 repulsion to simulate the process of community assembly via environmental filtering and
35 competitive exclusion, all while parameterizing the strength of the respective ecological
36 processes. We then use random forests and approximate Bayesian computation to distinguish
37 between these models. We find that our approach is more accurate than using dispersion metrics
38 and accounts for uncertainty. We also demonstrate that the parameter determining the strength of
39 the assembly processes can be accurately estimated. This approach is available in the R package
40 CAMI; Community Assembly Model Inference. We demonstrate the effectiveness of CAMI
41 using an example of plant communities living on lava flow islands.

42

43 **Introduction**

44 Though methods to infer community assembly vary, many approaches share a central
45 idea based on phylogenetics: the pattern of shared evolutionary history between species that
46 coexist provides insight into the historical processes that assembled the community (Brooks and
47 McLennan 1991; Losos 1996; Grandcolas 1998; Webb 2000; Thompson *et al.* 2001; Webb *et al.*
48 2002). To gain insight into the assembly process, a collection of metrics have been used to
49 characterize the patterns of diversity in a community using species/genus ratios and other higher
50 taxonomic diversity metrics (Magurran 1988; Faith 1992; Weiher & Keddy 1995; Gotelli &
51 Colwell 2001). Though informative, these patterns often provide little information about the
52 processes that generated them (Peters 1991). Functional traits provide information about
53 diversity and niche space within a community (Macarthur & Levins 1967; Weiher *et al.* 1999;
54 McGill *et al.* 2006), and have long been used to understand resource partitioning between
55 species, as well as coexistence (Cornwell *et al.* 2006; Kraft *et al.* 2007, 2015; de Bello *et al.*
56 2009). Though the collection and dimensionality of trait data is at times insurmountable, turning
57 to phylogenetic information as a proxy for functional traits was, and is, a viable alternative.
58 Measures of phylogenetic diversity and dispersion, which carry more information than higher
59 taxonomic categories and hopefully, encompass trait information, have become widely used in
60 community ecology to infer community assembly processes (Webb 2000; Webb *et al.* 2002a,
61 2008; Cavender-Bares *et al.* 2006; Kembel *et al.* 2010; Miller *et al.* 2017). These metrics focus
62 on identifying alternative models of community assembly, environmental filtering and
63 competitive exclusion. Environmental filtering occurs when the abiotic properties of an
64 environment physically keep a species from existing there (Bazzaz 1991). Competitive exclusion
65 describes when species that share the same or similar niche space compete for resources resulting

66 in some species being excluded from the community altogether, also referred to as limiting
67 similarity (MacArthur & Levins 1967). To determine whether non-neutral processes have
68 predominantly influenced assembly patterns, Phylogenetic dispersion metrics, such as mean
69 pairwise distance (MPD) and mean nearest-taxon distance (MNTD) – which can be calculated
70 using phylogenetic branch lengths, number of nodal distances, and phenotypic distances – are
71 used to compare observed community dispersion to null expectations (Webb 2000; Gotelli &
72 Colwell 2001; Webb *et al.* 2002a, 2008; Kembel *et al.* 2010).

73 Inferences of the assembly process using dispersion metrics are determined in a statistical
74 hypothesis testing framework using several randomly generated null models (Conner &
75 Simberloff 1979; Gotelli & Graves 1996). Commonly, the standard effect size of dispersion
76 metrics, commonly known as net relatedness index (NRI) for MPD and nearest taxon index
77 (NTI) for MNTD (Webb 2000), are used as the test statistic to measure significance of the
78 observed community compared to null expectations of community dispersion if the community
79 were assembled randomly or neutrally. However, inference is conditional on the assumption that
80 the relevant phenotypes for the environment or competition are phylogenetically conserved
81 amongst the species in the community, or harbor strong phylogenetic signal within the
82 community of focus. If this assumption is true, and environmental filtering has predominately
83 impacted the assembly process, the phylogenetic data are expected to be significantly clustered,
84 or under-dispersed, in the local community. Likewise, when considering a community assembled
85 by competitive exclusion, we expect to see significantly less shared evolutionary history as
86 compared to null expectations, or significant phylogenetic over-dispersion (Weiher & Keddy
87 1995; Webb 2000; Cavender-Bares *et al.* 2006).

88 The dubious assumption of strong phylogenetic signal between the phylogeny and
89 phenotypes is a main critique of these approaches. Kraft *et al.* (2007) showed via simulations
90 that when the assumption of phylogenetically conserved traits was even mildly violated,
91 phylogenetic dispersion metrics were inadequate to infer community assembly processes.
92 Furthermore, this violation of assumptions can, in fact, lead to patterns contrary to those
93 expected for a given assembly process (Weiher & Keddy 1995; Cavender-Bares *et al.* 2009;
94 Mayfield & Levine 2010; HilleRisLambers *et al.* 2012; Gerhold *et al.* 2015). To circumvent this
95 issue, one can assess whether or not functional traits of interest for the community are
96 phylogenetically conserved, and then use that information to guide the inference procedure
97 (Kraft 2007, Kembel *et al.* 2010). Though, if functional trait information is available, it is
98 typically used in consort with phylogenetic information because using phenotypic information
99 alone relies on expectations for how the phenotypes should be distributed in the community to
100 infer non-neutral processes (de Bello *et al.* 2009; Graham *et al.* 2012). While in many instances
101 both phylogenetic dispersion and phenotypic dispersion are measured and analyzed in a similar
102 framework (HilleRisLambers *et al.* 2012), an approach that integrates both to simultaneously
103 estimate support for alternative assembly models is lacking.

104 Finally, the inference procedure using dispersion metrics relies on statistical hypothesis
105 testing, and therefore, on how well the null model represents neutral expectations. Currently,
106 there exists an extensive number of null models that can be used to infer assembly processes,
107 ranging from simple null models based on random shuffling of taxon labels (Gotelli & Graves
108 1996; Webb *et al.* 2002; Cornwell *et al.* 2006; Kembel *et al.* 2010), to incredibly dynamic null
109 models (Pigot & Etienne 2015) and analytical frameworks (Stegen *et al.* 2013) that incorporate
110 macroevolutionary processes such as speciation, dispersal, and extinction. There also exist

111 simulation software (Münkemüller & Gallien 2015) to simulate the process of assembly with
112 trait information mediating which species enter the community. However, even with more
113 dynamic null models and simulation power, relying on statistical hypothesis testing and passing a
114 significance threshold to infer an assembly processes is problematic. In part due to the sensitivity
115 between p-values and sample size and how we interpret “significance”, but also because each
116 analysis of a particular data type and test statistic result in a measure of significance. Researchers
117 are then responsible for integrating across a suit of hypothesis tests, some that may be significant
118 while others are not, in order to draw an inference. Arguably, a model-based inference procedure
119 is necessary to incorporate all data at once, rank models of community assembly by their relative
120 support, and importantly, incorporate uncertainty in model inference. In this model-based
121 inference procedure, we can simultaneously weigh the support for each community assembly
122 model while also considering both phylogenetic and phenotypic data in the regional and local
123 community. When each model garners a portion of support given the data, we are able to
124 understand when a dominant signal of non-neutrality or neutral is present in the data, whether
125 two process are acting simultaneously (*i.e.* split support between models). or when the data lack
126 signal to identify a dominant process (*i.e.* relatively equal support across all models).

127 Several approaches have implemented model-based inference procedures for community
128 assembly already (Van Der Plas *et al.* 2015; Munoz *et al.* 2018; Pontarp *et al.* 2019), paving the
129 way to measuring the relative impact of different processes on community assembly. However,
130 we still lack a method that integrates both phylogenetic and phenotypic information in a species-
131 based model where the strength of the non-neutral processes can be estimated. Here, we develop
132 a stochastic algorithm to simulate communities assembled under environmental filtering and
133 competitive exclusion processes by adapting coevolutionary phenotypic matching and repulsion

134 models. In doing this, we avoid having to make any assumptions about how the traits have
135 evolved along the phylogeny. Our approach simultaneously considers the phylogenetic and
136 phenotypic information from species in the local and regional communities and parameterizes
137 the relative strength of the assembly processes realizing strong to mild non-neutral assembly.
138 Finally, we implement a model-selection inference procedure by using two approximate
139 approaches, random forests (RF; Breiman 2001; Breiman & Cutler 2007) and approximate
140 Bayesian computation (ABC; Csilléry *et al.* 2010). While we acknowledge these processes are
141 often happening simultaneously in nature, when investigating a targeted trait hypothesized to
142 play a role in the non-neutral assembly of a particular community, the model selection inference
143 procedure holds power to detect the most conspicuous process, if applicable. We are using both
144 model selection approaches because, though RF has been used for model selection in other
145 contexts, it has not been used to distinguish between community assembly models like ABC has
146 (Van Der Plas *et al.* 2015; Munoz *et al.* 2018; Pontarp *et al.* 2019); thus we document a
147 comparison and collaboration of the two here.

148 We make our approach available as an R package, CAMI, Community Assembly Model
149 Inference (github.com/ruffleymr/CAMI). To demonstrate the effectiveness of CAMI, we use
150 power analysis to show that our approach more accurately infers models of community assembly
151 compared to hypothesis testing using dispersion metrics. We also show that the parameter
152 governing the strength of the assembly processes can be accurately estimated using ABC.
153 Finally, we demonstrate community assembly model inference and parameter estimation using
154 CAMI, with an empirical example from the plant communities that exist on lava flow islands in
155 Craters of the Moon National Monument and Preserve.

156

157 **Methods**

158 *1.0 Community Assembly Models*

159 We focus on three community assembly models: neutral, environmental filtering, and
160 competitive exclusion. For all models, we assume communities are assembled from a regional
161 pool of species where each species in the regional pool is equally likely to colonize the local
162 community. We also assume the phylogenetic relationships between all species are known and
163 that there is continuous trait information for all species. We simulate the assembly of a local
164 community under one of the three models. Under the neutral model of assembly, all species in
165 the regional community have an equal probability of persisting in the local community (Hubbell
166 2001; Rosindell *et al.* 2012). The probability that a given species survives, or persists, in a non-
167 neutrally assembled community, however, is not equal for all species, and these varying
168 probabilities of persistence drive the alternative models of community assembly.

169 To model environmental filtering, we adapted an approach from coevolutionary models
170 (Nuismer *et al.* 2013; Nuismer & Harmon 2015) to relate trait interactions between species and
171 their environment with the probability of surviving in a community. For interactions between
172 species and their environment, we implement a phenotypic matching mechanism where the
173 probability, $P(z_i, z_E)$ of a species persisting in the local community increases when the
174 phenotype of the species z_i and the optimal phenotype of the environment z_E are more similar:

$$175 P(z_i, z_E) = \text{Exp} \left[-\frac{1}{t_E} (z_i - z_E)^2 \right] \quad (1)$$

176 The probability a species with phenotype, z_i , persists in an environment with a phenotypic
177 optimum, z_E , also depends on the strength of the environmental filtering, t_E . When t_E is large,
178 filtering has a mild effect in that species are less penalized for having phenotypes dissimilar to

179 the environmental optimum; whereas when t_E is small, the filtering effect is stronger because
180 species are heavily penalized for phenotypes dissimilar to the optimum.

181 To model competitive exclusion, the probability, $P(z_i, \bar{z})$, of a species persisting in the
182 local community increases as the phenotype of the species z_i and the mean phenotype of the
183 local community \bar{z} are more dissimilar.

$$184 \quad P(z_i, \bar{z}) = 1 - \text{Exp} \left[-\frac{1}{t_C} (z_i - \bar{z})^2 \right] \quad (2)$$

185 Here, the probability a species with phenotype, z_i , persists in a community with mean
186 phenotypic, \bar{z} , depends on the strength of competition between species, t_C . When t_C is large,
187 competition has a strong effect in that species are heavily penalized for having phenotypes
188 similar to the mean phenotype of the local community. When t_C is small, competition is weaker
189 in that species are less penalized for having a phenotype similar to the mean phenotype of the
190 community.

191

192 *2.0 Data Simulation*

193 For a single simulation of community assembly, first, a regional community phylogeny is
194 simulated under a constant birth-death process with speciation, λ , and extinction, μ , parameters,
195 until the desired number of regional species, N , is reached (Fig. 1; Stadler 2011). Traits are
196 evolved on the regional phylogeny, one for each species, (Revell 2012) under either a Brownian
197 Motion (BM; Felsenstein 1985) or Ornstein-Uhlenbeck (OU) model of trait evolution (Hansen
198 1997; Butler & King 2004) characterized by the rate of character change, σ^2 , and, for OU
199 models, the “strength of pull” to the trait optimum, α (Fig. 1). BM evolves traits in a way that
200 mimics drift over macroevolutionary timescales and OU does the same only it includes a
201 selective regime in which traits are “pulled” toward a phenotypic optimum. We simulate under

202 these different models of trait evolution because they do not enforce the assumption that trait
203 differences are correlated to phylogenetic differences and create more variability in how the data
204 behave under the assembly models. Once the regional community exists with phylogenetic
205 relationships and trait information, the assembly of the species in the local community can begin.

206 The assembly process uses the probabilities of species persisting in local communities,
207 $P(z_i, z_E)$ for environmental filtering and $P(z_i, \bar{z})$ for competitive exclusion, and a rejection
208 algorithm to stochastically assemble the local community. When simulating under a competition
209 model, the strength of competition between species, t_C , parameterizes the assembly process.
210 Likewise, under an environmental filtering model, the strength of the environmental filter, t_E ,
211 along with the environmental phenotypic optimum, z_E , parameterizes the assembly process. For
212 the investigative simulations, the phenotypic optimum is determined by a random value drawn
213 from the simulated traits of the regional community, and it remains constant throughout an entire
214 simulation. When a species colonizes the community, the probability of persistence is calculated,
215 and the species is included in the local community if that probability is greater than a uniform
216 random number between 0 and 1 (Fig. 1). Otherwise, the species is rejected from being in the
217 local community. This stochasticity included in the algorithm is more apparent in the emergent
218 data when the ecological strength parameter is imposing weak non-neutral assembly. When a
219 species is rejected from entering the community, it remains in the regional pool and is still able
220 to colonize the local community again. In this case, the probability of persistence is recalculated,
221 and the species has another chance to pass the rejection algorithm. As in the neutral model, the
222 assembly process ends when the local community has reached species richness capacity, n .

223 All parameters mentioned are either fixed or drawn from a prior distribution. Information
224 regarding the default prior distributions and fixed values for each parameter can be found in

225 Supplemental Table 1 or in the help documentation for the R package ‘CAMI’
226 (github.com/ruffleymr/CAMI). Any parameter mentioned, along with prior distributions, can
227 also be set by the user. In simulations described here, the default prior distributions were used
228 unless otherwise stated.

229

230 *3.0 Inference Procedure*

231 For a single simulation of community assembly, a regional and local phylogeny and a
232 regional and local distribution of trait values is returned. This information is summarized in 30
233 different summary statistics that capture information about the phylogeny, trait distributions, and
234 phylogenetic signal within the traits of the local community (Komsta & Novomestky 2015,
235 Janzen *et al.* 2015; Pennell *et al.* 2015; Deevi *et al.* 2016, Kendall *et al.* 2018, Paradis & Schliep
236 2018; Supplemental Table 2). These summary statistics are then used for model selection and
237 parameter estimation.

238 To predict model probabilities from empirical data, we used two model selection
239 approaches. The first approach uses a machine learning classification algorithm, random forests
240 (RF; Breiman 1999; Liaw & Wiener 2002) to build a ‘forest’ of classification trees using the
241 simulated summary statistics as predictor variables and the community assembly models as
242 response variables. As a classifier is being built, RF is simultaneously measuring the ‘Out of
243 Bag’ (OoB) error rates of the classifier by cross-validating each classification tree with a subset
244 of the original data that was not used to make the tree in question. The OoB error rates measure
245 how often the data are incorrectly classified. Additionally, RF quantifies the effect of including
246 each summary statistic on the accuracy of the classifier through two variable importance

247 measures, Mean Decrease in Accuracy (MDA) and Mean decrease in Gini Index (GINI)
248 (Breiman 2002).

249 RF is generally robust to noisy and/or overpowering predictor variables because each tree
250 in the forest is constructed with only a subset of the data and multiple predictor variables are
251 used at each node (Breiman & Cutler 2007). Our second approach, ABC, relies on the Euclidean
252 distance between observed and simulated summary statistics to accept simulations into the
253 posterior probability distribution of the models given the data (Csilléry *et al.* 2010). The support
254 for each model then comes from the proportion of simulations from each model accepted into the
255 posterior probability distribution. If there are summary statistics included that add a lot of noise
256 to the classification process, ABC will lose power in distinguishing support between models. RF
257 is able to measure which summary statistics are the most influential in distinguishing between
258 the models, through importance measures such as MDA and GINI, thus we used this information
259 to select a subset of 10 summary statistics to use in ABC model selection. ABC then predicts
260 model probabilities using those statistics, a rejection algorithm, and a tolerance of 0.001 (Csilléry
261 *et al.* 2012). The performance of ABC in classifying the data can be measured using a leave-one-
262 out cross validation approach for model selection which results in model misclassification rates
263 for each model.

264

265 *4.0 Power Analyses*

266 We compared the accuracy of three approaches in identifying community assembly
267 models from the data simulated under the three community assembly models in CAMI. The first
268 approach follows previous work and uses dispersion metrics, such as MPD and MNTD
269 (standardized as NRI and NTI), in statistical hypothesis testing to infer the community assembly

270 process from phylogenetic and phenotypic information, separately (Webb 2000; Cornwell *et al.*
271 2006; Kembel *et al.* 2010; Kraft & Ackerly 2010). For MNTD calculated using phenotypic
272 information, the nearest neighbor is the species closest in trait space (Ricklefs & Travis 1980;
273 Graham *et al.* 2012; Swenson *et al.* 2012).

274 The second and third inference approaches are approximate model selection techniques
275 used in CAMI, RF (Breiman 1999; Liaw & Wiener 2002) and ABC (Toni *et al.* 2009; Csilléry *et*
276 *al.* 2010, 2012). We measured the power of each approach in correctly classifying community
277 assembly data (see sections 1.0 and 2.0) through the OoB error rates for RF and cross validations
278 for ABC. We performed these power analyses for a range of community sizes to assess whether
279 the power of any of the approaches increased with sample size of the regional/local community,
280 which in this case is species richness. For data to classify, we simulated 1,000 datasets in CAMI
281 under each community assembly model for 20 different regional community sample sizes
282 ranging from 50 to 1000, increasing by increments of 50, with the local community always half
283 the size of the regional. For more details on each of the model identification techniques, refer to
284 supplemental methods section 2.

285 We also investigated whether RF and ABC can be used to accurately infer the model of
286 community and trait evolution simultaneously. For this, we performed the power analysis as
287 described above, only here we classified six models (neutral, filtering, and competition models
288 under both BM and OU models of trait evolution) rather than just the three community assembly
289 models.

290

291 *5.0 Parameter Estimation*

292 We measured the ability of this approach to estimate the strength of the assembly
293 process, t_E and t_C , under non-neutral models of community assembly, environmental filtering
294 and competitive exclusion. For both models, we attempted parameter estimation when the traits
295 were simulated under a BM and an OU model of trait evolution. We also attempted parameter
296 estimation for two sizes of regional communities, 200 and 800, with corresponding local
297 community sizes of 100 and 400. We simulated 50,000 community assembly datasets under each
298 condition to serve as the reference dataset for parameter estimation. For details on these
299 simulations, reference the supplemental methods section 3.

300 We simulated 100 datasets each for 13 different values of t_E and t_C , ranging from 1 to 60
301 in increasing increments of 5 (see supplemental methods section 3 for other parameter details).
302 These simulated datasets would serve as the “observed” datasets to use for parameter estimation,
303 in which case we know what the true value of t_E and t_C are. To measure not only how accurately
304 t_E and t_C are estimated, but whether all values can be estimated accurately, we performed
305 parameter estimation for each of the simulated datasets. For this, we assumed that data simulated
306 under environmental filtering and competitive exclusion models were correctly classified as
307 those models. We repeated this procedure increasing the sample size of the regional and local
308 community to measure whether t_E and t_C estimates improved with increased sample size.

309

310 *6.0 Empirical System*

311 Craters of the Moon National Monument and Preserve (CRMO) is a volcanic landscape
312 in southern Idaho. The overlapping basalt lava flows formed along vents in the Great Rift
313 between 2 – 15 KYA (Kuntz *et al.* 1982, 1986). Within the lava flows are kipukas – islands of
314 vegetation that are completely surrounded by uninhabitable lava (Vandergast & Gillespie 2004).

315 Given their isolated nature and recent colonization, the plants on kipukas are an ideal system for
316 studying community assembly. We opted to use height as our functional trait of interest because
317 it is known to be an important proxy for resource partitioning and competitive ability in plants
318 (Westoby 1998; Weiher *et al.* 1999; Cornwell *et al.* 2014).

319 The regional phylogeny was constructed for 113 species that occur in the CRMO by
320 dropping non-CRMO species (79,768) from a Spermatophyta phylogeny (Smith & Brown 2017).
321 Likewise, the local community phylogeny was constructed by dropping non-kipuka community
322 species from the regional phylogeny, resulting in 63 local species (Supplemental Table 8). If a
323 particular species was not in the Spermatophyta phylogeny, we used a random relative in the
324 same genus (Qian & Jin 2016). In addition to the total local species pool on the kipukas, we also
325 investigated eight kipukas individually, kipukas that consisted of 18-20 species from the local
326 community (Supplemental Table 10) Maximum vegetative height data for all species in the
327 regional and local community were gathered using a combination of herbarium records, species
328 descriptions, and floras (*e.g.* Hitchcock & Cronquist 2018).

329 To assess whether an assembly process has structured the plant community on kipukas,
330 we used NRI and NTI calculated from both phylogenetic and phenotypic (maximum vegetative
331 height) information, separately, and CAMI using RF and ABC to perform model selection. We
332 also performed parameter estimation using ABC to understand what the influence of t_E or t_C was
333 on the assembly processes in either the filtering or competition models, should they be highly
334 supported. For more details regarding the empirical data analysis, including plant collections and
335 data simulated for the analysis, refer to the supplemental methods sections 4.

336

337 **Results**

338 *4.0 Power Analysis*

339 The average proportion of misclassified simulations using the standard approach of
340 phylogenetic dispersion metrics for all regional/local community sizes was 56 % (Table 1),
341 decreasing from 63.3 to 52.9 % with increasing sample size (Fig. 2, Supplemental Table 3). For
342 each of the community assembly models, the average misclassification rate for each model was
343 consistent between MPD and MNTD (Table 1) when using phylogenetic information. When
344 calculating these metrics from phenotypic information, the average misclassification rate varied
345 depending on whether MPD or MNTD was being used, with MPD having a very low error rate,
346 4.9 %, and MNTD a high error rate, 48 % (Table 1; Supplemental Table 4).

347 Average error rates for both of our model selection approaches were substantially lower.
348 The average random forests OoB error rate when classifying community assembly models was
349 3.6 %, ranging from 16.7% for small communities to 1.5 % for large communities (Fig. 2). The
350 average OoB error rates for each community assembly model with RF were 4.8%, 3.0 %, and 2.9
351 % for neutral, filtering, and competition models, respectively (Table 1). The average ABC model
352 misclassification rate was 8.47 % (Table 1), ranging from 20.9 % for small communities to 5.9 %
353 at large communities (Fig. 2). The average ABC error rates for each community assembly model
354 were 5.4%, 13.6%, and 6.32 % for neutral, filtering, and competition models, respectively (Table
355 1).

356 Using RF and ABC to classify models of community assembly and trait evolution
357 simultaneously resulted in overall higher error rates compared to inferring community assembly
358 alone (Supplemental Fig. 1). On average, the average OoB error rate for RF was 23.2%, ranging
359 between 45.7% and 16.2% from small to large communities (Supplemental Table 5), and the

360 overall error rate for ABC was 30.7 %, ranging between 50.8 % and 23.5 % from small and large
361 communities (Supplemental Table 6).

362 *5.0 Parameter Estimation*

363 For all models, the simulations with larger community sizes better estimated the true
364 value of t_E and t_C compared to communities of smaller size (Fig. 3). Regardless of sample size,
365 t_C was overestimated when of smaller value. In both filtering and competition models, t_E and t_C
366 are slightly underestimated when of larger value – though this is due to the true value of
367 t_E and t_C being at the upper bound of the prior distribution, which if extended would not be
368 apparent.

369 *6.0 Empirical System*

370 Several dispersion metrics used from phylogenetic and phenotypic information identified
371 significant under-dispersion, or clustering, amongst plant species in the kipukas, suggesting a
372 community assembly pattern of environmental filtering. When calculating NRI and NTI using
373 phylogenetic information from all plants in the kipukas, the resulting p-value was 0.02 for MPD
374 and 0.29 for MNTD. When calculating the same metrics from phenotypes, the resulting p-value
375 for each test statistic was 0.03 and 0.01, respectively (Supplemental Table 7). For the eight
376 separate kipuka communities, only MPD using phylogenetic information identified two other
377 community as significantly under-dispersed (Supplemental Table 7).

378 We constructed two RF classifiers to make predictions about empirical data. One
379 classifier was built with simulations from both trait models and the other classifier was built with
380 data simulated only under an OU trait model. This OU models-only RF classifier was built
381 because the trait data for the kipuka plants better fit an OU model of trait evolution compared to
382 a BM model (see supplemental methods 4). The OoB error rates for these two classifiers were

383 25.50 and 23.61 %, respectively. We also estimated the error rate when using ABC in the same
384 way as with RF. For these, the error rate for each cross-validation was 33.20 and 30.40 %. Using
385 these data and approaches, we predicted the model of community assembly for the empirical data
386 with RF and ABC, and saw a majority of support for environmental filtering, with the second
387 highest support for the neutral model (Table 2 OU model-only prediction, Supplemental Table
388 11 for OU and BM model predictions).

389 We performed parameter estimation of t_E for the environmental filtering model for each
390 dataset under an OU model of trait evolution (Supplemental Table 12). Each time 100
391 simulations were accepted as from the posterior distribution of t_E (Fig. 4). We also compared the
392 amount of model support for the environmental filtering models with the median estimated of
393 t_E (Supplemental Fig. 2, Supplemental Table 12).

394

395 **Discussion**

396 *Performance of CAMI*

397 Using CAMI, we can correctly classify models of community assembly and importantly,
398 quantify the uncertainty associated with community assembly model inference. This approach
399 improves upon current methods in community phylogenetics by harnessing the critical
400 information present in the phenotypic and phylogenetic data that directly relate observed patterns
401 to processes. Our approach is successful, in part, because over and under-dispersion in the
402 phylogenetic and trait data are emergent properties of the community assembly models
403 described. Through our method, we can control the processes that directly impact the amount of
404 over and under-dispersion in the phenotypic data, along with their degree of association with the

405 phylogenetic information. Furthermore, our inference pipeline is unique in allowing users to
406 gauge or rank evidence for both neutral and non-neutral assembly processes.

407 The performance of RF and ABC are comparable in that they both accurately classify the
408 community assembly models. A benefit to RF is that all of the summary statistics from the
409 simulated data can be used without compromising the power or computational speed of the
410 method. Additionally, RF measures how important each summary statistic is for classifying the
411 data accurately. While we don't use this information for any additional community assembly
412 inferences here, there is potential to ask which summary statistics play an important role in these
413 assembly processes, and further, whether there are any biological implications to gain from that
414 information. The main advantage of using ABC is that parameter estimation is straight forward
415 using simulated data, and this is particularly relevant for estimating the strength of non-neutral
416 assembly via t_E and t_C , though parameter estimation using RF is increasingly common.

417 The predictive approaches outlined here are not meant to replace dispersion metrics, but
418 rather to be used as an additional tool in making inferences about community assembly. We have
419 shown here, as others have (Kraft *et al.* 2007), that dispersion metrics are not reliable in
420 determining models of community assembly with phylogenetic information alone. When using
421 phenotypic data, though MPD proved to be comparable in accuracy at distinguishing community
422 assembly models to RF and ABC; MNTD still had very high error rates (Table 1).

423 Though CAMI is currently implemented using one trait, the analyses do not necessarily
424 need to be limited to one trait. If there are several traits of interest in a particular community,
425 data dimension reduction techniques could be used, such as principle components or linear
426 discriminate analysis, to associate each species with a singular value representing where they fall
427 in trait space with respect to other species in the community. Though we do not explore the

428 power of inferring models of community assembly from several traits defined in one composite
429 dimension through simulations, we expect, to some degree, that the method will behave as
430 presented above in the single-trait case. Using multiple traits in a true multivariate framework,
431 which we have not implemented, could make for an even more powerful inference, as many
432 factors influencing community structure could be measured at once (Weiher *et al.* 1998; Herben
433 & Goldberg 2014; Kraft *et al.* 2015). However, if multiple traits are being considered, there also
434 need be the consideration that there could be multiple phenotypic optima or complex routes of
435 competition between species, and here we consider the presence of only a single optimum and
436 equal competition amongst species (Weiher *et al.* 1998).

437 While we feel CAMI will continue to make progress in advancing our understand of
438 community ecological patterns globally, there are still many aspects of community ecological
439 theory yet to be incorporated (Belyea & Lancaster 1999; Weiher *et al.* 2011). The assembly
440 models defined here could be made more powerful by considering other community dynamics
441 such speciation, colonization, and extinction during the assembly process (Rosindell & Harmon
442 2013), as well as co-occurring and structured non-neutral processes (Keddy & Shipley 1989)
443 where the relative importance can be measured (as in Van Der Plas *et al.* 2015; Munoz *et al.*
444 2018). These aspects may be more or less relevant depending on the taxonomic scale of the
445 community being investigated (Weiher *et al.* 2011). Furthermore, the performance could also
446 improve by making it an individual-based model of community assembly (Rosindell *et al.* 2015;
447 Pontarp *et al.* 2019), where individuals can diverge to speciate and harbor intraspecific diversity
448 amongst phenotypes (Jung *et al.* 2010, 2014) while tracking abundance distributions and
449 population demographics (HilleRisLambers *et al.* 2012; Overcast *et al.* 2019). A spatially
450 explicit model (see Pontarp *et al.* 2019) could also allow for the exploration of how geography,

451 or even local topography, impacts the assembly process. Ultimately, we believe this approach
452 has the capability of being extended to incorporate more complexities known to influence and
453 emerge from the assembly process.

454

455 *Inferring the Strength of the Assembly Process*

456 Parameterizing the strength of the assembly process provides an additional mode of
457 inference for the relative strength of the non-neutral community assembly processes,
458 environmental filtering, t_E , and competitive exclusion, t_C . We have shown that ABC can be an
459 appropriate tool to estimate both t_E and t_C accurately (Fig. 3) for their respective community
460 assembly models. We have also shown that empirical data, from different communities, do
461 indeed bear some signal to indicate different magnitudes of t_E (Fig. 4). Additionally, we also
462 show that the estimate of t_E has a relationship with the amount of support the corresponding
463 non-neutral model receives, in this case, the environmental filtering model. We know that for
464 filtering models, the smaller the value of t_E , the stronger the effects of filtering, thus the smaller
465 the estimate of t_E , the greater the model support for environmental filtering (Supplemental Fig.
466 2). Having this measure that can quantify the influence of the assembly process at play opens the
467 door for comparisons of communities globally that have been assembled by the same mechanism
468 (Götzenberger *et al.* 2012). Prior to now, if multiple communities were inferred to be assembled
469 via environmental filtering, there was no way to ask whether one environment's pressure was
470 stronger relative to the other, while t_E and t_C now permits these questions.

471

472 *Models of Trait Evolution*

473 Identifying models of community assembly alone was much more successful than when
474 trying to simultaneously identify models of trait evolution, as shown by the increase in error rates
475 (Supplemental Fig. 1). When the model of trait evolution is identifiable, as in many BM and OU
476 cases, simulating under both models is not necessary and drastically decreases the amount of
477 simulations needed. Information about the best fit trait model, including parameter estimates, can
478 be used to directly inform parameters used to simulate community assembly data in CAMI (as in
479 the empirical study). However, we do show that considering both models of trait evolution
480 simultaneously versus only one at a time does not drastically change the community assembly
481 inference (Supplemental Table 11). Thus, should one be unable to properly, or with confidence,
482 estimate the true model of trait evolution, the combined inference procedure in CAMI is
483 appropriate, and this may be especially useful for early-burst or multi-optima OU models of trait
484 evolution (Slater & Pennell 2013; Uyeda & Harmon 2014). We should note here that a model of
485 trait evolution fit to community data, phylogenetic and phenotypic, involves excluding many
486 taxa from the tree and trait distributions. This means the parameter estimates cannot be tied to
487 the entire evolution of a particular trait, but rather its evolution amongst a certain set of species.

488

489 *Empirical Inference*

490 When using CAMI to distinguish models of community assembly, we reliably see a
491 majority of support go to the environmental filtering model when considering the entire local
492 kipuka community, with some support given to the neutral model (Table 2). When looking at the
493 eight separate kipuka communities, we see that while environmental filtering does still receive a
494 majority of the support, there is a lot of support garnered for the neutral model as well, and
495 sometimes even for the competitive exclusion model (Table 2). Conveniently though, when

496 comparing the model probability estimates with the t_E estimates, we get a better understanding
497 of why the model support is where it is for a particular kipuka and that the t_E parameter is being
498 estimated appropriately (Supplemental Figure 2).

499 When using dispersion metrics to distinguish models of community assembly, the
500 reliability is less apparent. Many of the observed dispersion metrics fall at the lower ends of the
501 random distribution of dispersion indices, and subsequently result in low p-values. However, one
502 of the caveats of hypothesis testing is that there is a sort of arbitrary cutoff between when
503 something is significant and when it is not. In this case, technically the cutoff is 0.025 and so
504 only four out of 36 metrics were significant. These issues are generally overcome with intuition
505 because it is obvious some of the p-values are still very low, but they do highlight problems with
506 hypothesis testing and relying on p-values for marks of biological significance.

507 For each kipuka species pool, the strength of the filtering process was estimated quite
508 differently. For the entire species pool of the kipukas, the t_E estimate was a relatively moderate
509 value, 15.4, given the prior range of 1 to 60, where values near 1 imply strong filtering, and
510 values closer to 60 imply weak filtering. For other kipuka communities though, t_E was often a
511 moderate estimate, falling somewhere in the middle of the prior distribution, though sometimes
512 the estimate was very low (Fig. 4D-E) and other times, quite high (Fig. 4I). We recognize though
513 that any interpretation of t_E is challenging because the parameter has never before been
514 measured using any community or trait before. Thus, we expect with continued investigations of
515 community data using CAMI will decipher a sharper picture on how t_E behaves across many
516 natural communities. We feel these estimates are a good start to that investigation given their
517 correspondence with the model probabilities (Supplemental Fig. 2). We should note that in the
518 case of these t_E estimates, the rate of character change is so low that a strong effect of filtering

519 with that little phenotypic variation may be harder to detect than if more variation were present.
520 Similarly, the estimates of t_E are be less reliable when the community size is small (Fig. 3),
521 which is true in the case of these kipukas.

522 One anecdotal explanation for the support for the environmental filtering assembly
523 model lies in the structure of the kipukas. Lava flow builds up on the edges of the habitable land
524 forming a sort of “bowl,” with the plant community inside the bowl. Species that generally grow
525 taller than the bowl edges are less protected from heavy wind speeds common in the area and
526 may be more likely to be filtered from the environment. Likewise, with high wind speed comes a
527 likely increase in dispersal ability for some species in the regional pool, which may explain the
528 support of the neutral model. However, even though we can speculate on the cause for the
529 support of an environmental filtering model acting on height in the kipukas, we still lack
530 evidence of the true cause of the support.

531 While vegetative height has been hypothesized to play an important role in community
532 structure, as a functional phenotype and a proxy for other important traits (Cornwell *et al.* 2014),
533 because we only take into account a single functional trait, we recognize the potential limitations
534 to these inferences. The CAMI framework does permit the testing of multiple traits
535 independently and using the evidence of how each trait influenced community assembly to better
536 understand the historical and contemporary assembly processes (Herben & Goldberg 2014).
537 Additionally, each trait, if influencing community assembly in a non-neutral way, will be
538 associated with an estimate of t_E or t_C , which will also provide insight into the degree that each
539 trait influences the assembly process for a particular community.

540

541 *Conclusion*

542 CAMI is a new approach able to estimate the probability of neutral and non-neutral
543 community assembly models given observed phylogenetic and phenotypic information. By
544 harnessing the power of simulations and approximate approaches for model selection, such as RF
545 and ABC, we can quantify uncertainty in community assembly inferences. Additionally, new
546 parameters described here, t_E and t_C , govern the strength of environmental filtering and
547 competition, respectively, and are estimable with data. Defining the non-neutral assembly
548 models and parametrizing the processes to mimic strong to mild assembly dynamics will add to
549 what we know about assembly processes globally and communities that have been assembled via
550 the same mechanisms. While there are other approaches that infer community assembly in a
551 model-based framework (Van Der Plas *et al.* 2015; Munoz *et al.* 2018; Pontarp *et al.* 2019),
552 CAMI also offers a unique opportunity to use information that is readily available in
553 phylogenetic community ecology. Given these data are common for community assembly
554 studies, this framework could be readily applied to many existing systems and provide more
555 information about the differences in community ecology globally.

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750

751 **Fig. 1.** Outline of data simulation process. (1.1) Simulate the regional phylogeny using
752 associated parameters. (1.2) Simulate trait evolution along the regional phylogeny under
753 associated parameters. (1.3) Simulate the assembly of the local community by sampling species
754 at random from the regional species pool and calculating the probability of persistence for each
755 sampled species. These probabilities are calculated differently depending on the model of
756 assembly being simulated, and if a species' probability of persistence is greater than a randomly
757 generated probability, then that species survives in the local community.

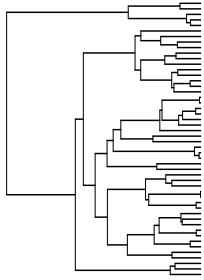
758 **Fig. 2.** Error rates, or proportion of incorrectly classified simulations, when classifying
759 community assembly models compared to the size of the local community used. Four model
760 identification approaches are summarized here. The first is the average error rate when using
761 dispersion metrics (MPD and MNTD) from phylogenetic information (dotted). The second is the
762 average error rate when using dispersion metrics from functional trait information (big dashed).
763 The final two are model selection approaches employed in CAMI, ABC (gray), and RF (small
764 dashed).

765 **Fig. 3.** Estimation of t_E and t_C under their respective non-neutral models of community
766 assembly, coupled with one of two models of trait evolution. In each graph, the individual
767 boxplots represent the median values of either t_E or t_C from 100 independent attempts at
768 parameter estimation, thus they are not posterior distributions, but rather a distribution of median
769 parameter estimates. The light gray boxes represent datasets with regional/local community sizes
770 of 200/100 and the dark gray boxes represent regional/local community sizes of 800/400. The
771 dotted line in each plot represents a 1:1 correlation between estimated and true values of
772 either t_E or t_C . A. Environmental filtering community assembly with a BM model of trait
773 evolution. B. Competitive exclusion community assembly with a BM model of trait evolution. C.

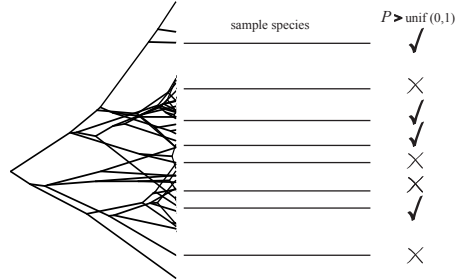
774 Environmental filtering community assembly with an OU model of trait evolution. D.
775 Competitive exclusion community assembly with an OU model of trait evolution.
776 **Fig. 4.** left) Regional phylogeny of species in the Craters of the Moon National Monument and
777 Preserve, coupled with each species' maximum vegetative height in meters represented by the
778 filled bar plots by each species. Species only present in the regional community have their trait
779 bars colored white, while species that are also present in the local community have their trait bars
780 colored black. The bars are truncated at 6 meters, as only the four trees in this study are larger
781 than 6 meters, and those species and their heights are available in supplemental table 8. right)
782 Nine panels displaying the prior (light gray) and posterior (dark gray) probability distributions of
783 t_E under an environmental filtering model and OU model trait evolution. The dotted line
784 represents the median estimate of t_E . A) Estimate from the entire local kipuka plant species pool.
785 B-I) Estimates from the separate eight kipuka communities.
786

1. Data Simulation

1.1 Regional community
phylogeny: N, λ, μ



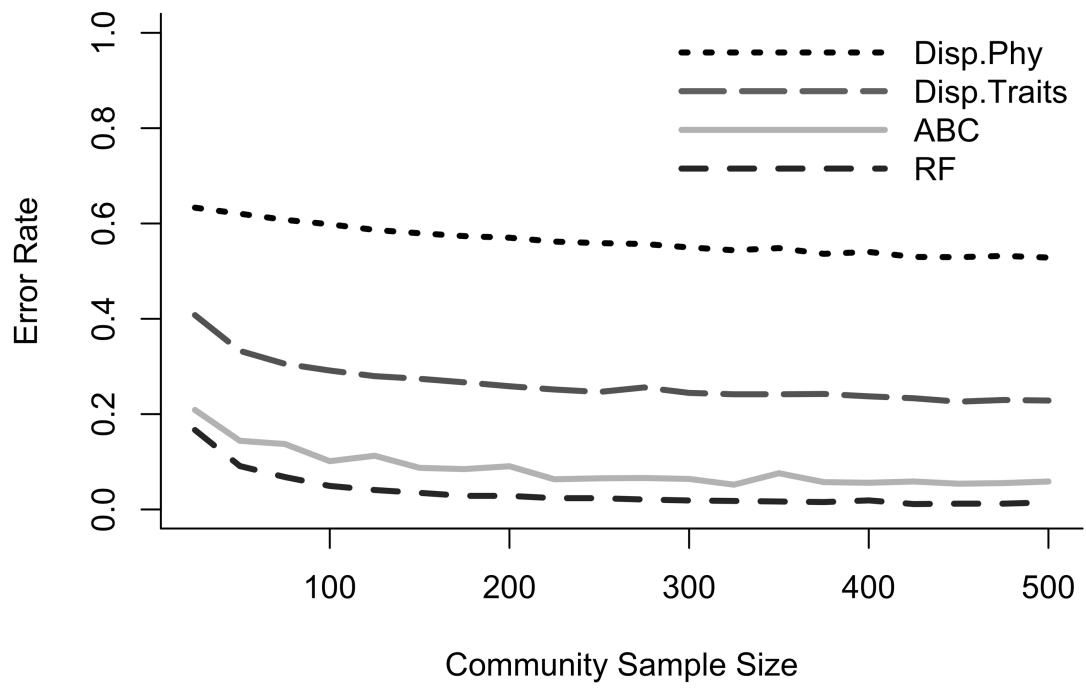
1.2 Trait evolution:
 σ^2, α



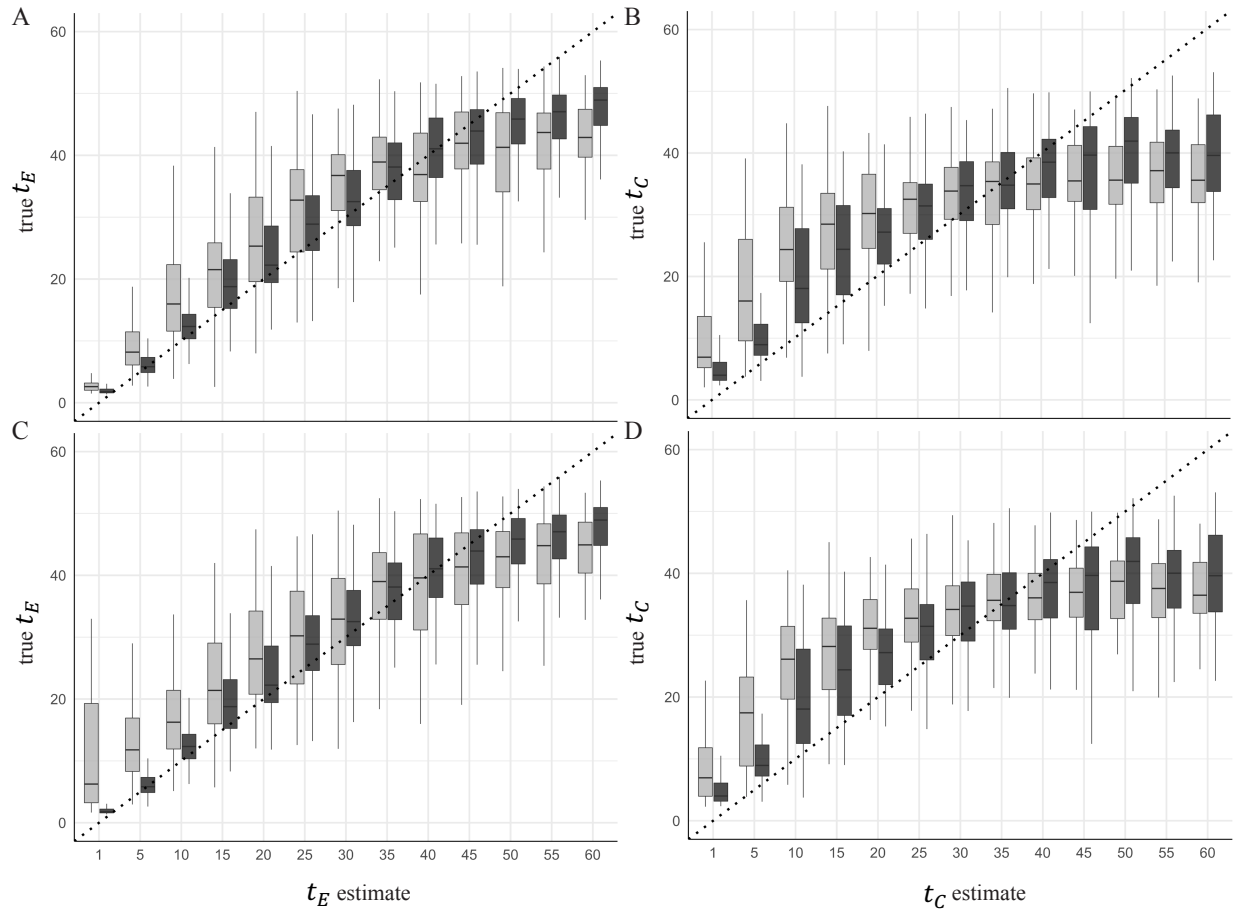
1.3 Local community
assembly: n, t_E, t_C

N	regional species pool
λ	speciation rate
μ	extinction rate
σ^2	rate of character change
α	strength of constraints (OU only)
n	local species pool
t_E	effect of environmental filtering
t_C	effect of competitive exclusions

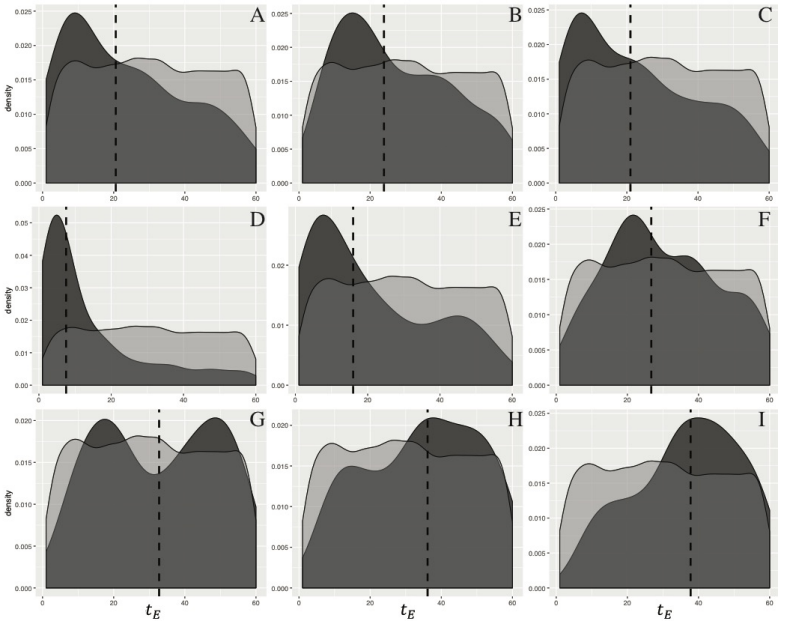
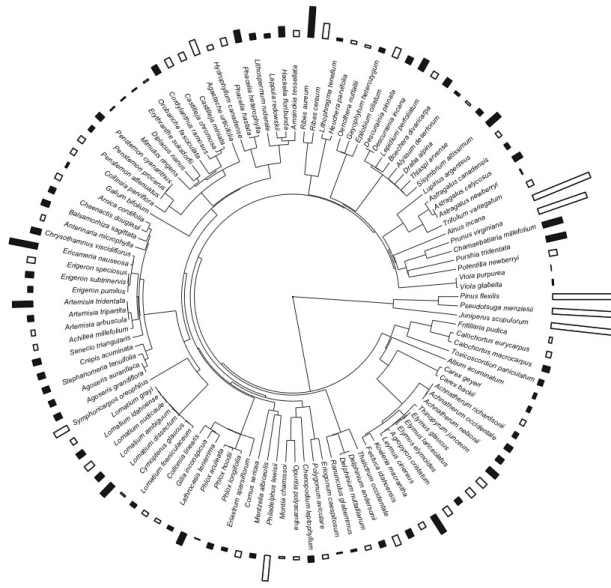
787 **Fig. 1**



788 Fig. 2



789 **Fig 3.**



790

791 **Fig. 4**

792 **Table 1.** Average error rates for model classification approaches in classifying each of the three
 793 community assembly models, as well as overall classification error.

		Neutral	Filtering	Competition	Mean
Phylogenetic	MPD	4.810	72.590	90.845	56.082
	MNTD	4.930	66.000	99.390	56.773
Phenotypic	MPD	4.741	7.940	2.130	4.937
	MNTD	4.911	39.855	99.465	48.077
	RF	4.845	3.013	2.855	3.571
	ABC	5.440	13.640	6.320	8.467

794
 795

796 **Table 2.** Community assembly model predictions from RF and model posterior probabilities
 797 from ABC for all local kipuka plant species and eight individual kipuka communities. All
 798 predictions were made with simulations using an OU model of trait evolution.

	RF			ABC		
	Competition	Filtering	Neutral	Competition	Filtering	Neutral
ALL	-	0.64	0.36	-	0.82	0.18
B	0.06	0.54	0.40	-	0.35	0.65
C	0.06	0.60	0.34	-	0.50	0.50
D	0.07	0.61	0.32	-	0.92	0.08
E	0.06	0.58	0.36	-	0.67	0.33
F	0.02	0.46	0.52	-	0.47	0.53
G	0.05	0.52	0.43	-	0.60	0.40
H	0.04	0.52	0.44	0.02	0.47	0.52
I	0.08	0.48	0.45	0.32	0.25	0.43

799