

1 **Disentangling metacommunity processes using multiple metrics in space and time**

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56 **Disentangling metacommunity processes using multiple metrics in space and time**

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58 **Keywords:** Metacommunity ecology, simulation study, random forests

59

60 **Abstract**

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62 Metacommunity ecology has focused on using observational and analytical approaches
63 to disentangle the role of critical assembly processes, such as dispersal limitation and
64 environmental filtering. Many methods have been proposed for this purpose, most
65 notably multivariate analyses of species abundance and its association with variation in
66 spatial and environmental conditions. These approaches tend to focus on few emergent
67 properties of metacommunities and have largely ignored temporal community dynamics.
68 By doing so, these are limited in their ability to differentiate metacommunity dynamics.
69 Here, we develop a ‘virtual ecologist’ approach to evaluate critical metacommunity
70 assembly processes based on a number of summary statistics of community structure
71 across space and time. Specifically, we first simulate metacommunities emphasizing
72 three main processes that underlie metacommunity dynamics (density-independent
73 responses to abiotic conditions, density-dependent biotic interactions, and dispersal). We
74 then calculate a number of commonly used summary statistics of community structure in
75 space and time, and use random forests to evaluate their utility for understanding the
76 strength of these three processes. We found that: (i) time series are necessary to
77 disentangle metacommunity processes, (ii) each of the three studied processes is

78 distinguished with different descriptors, (iii) each summary statistic is differently sensitive
79 to temporal and spatial sampling effort. Some of the most useful statistics include the
80 coefficient of variation of abundances through time and metrics that incorporate variation
81 in the relative abundances (evenness) of species. Surprisingly, we found that when we
82 only used a single snapshot of community variation in space, the most commonly used
83 approaches based on variation partitioning were largely uninformative regarding
84 assembly processes, particularly, variation in dispersal. We conclude that a combination
85 of methods and summary statistics will be necessary to understand the processes that
86 underlie metacommunity assembly through space and time.

87

88 **Introduction**

89 A perennial goal amongst ecologists is to be able to infer processes that influence
90 the emergent ecological patterns of interest. For example, in metacommunity ecology
91 —the study of sets of local communities linked by the movement of organisms— a large
92 body of work has focused on using statistical analyses to understand the relative
93 importance of underlying processes in structuring community assembly (overviewed in
94 Logue et al. 2011, Soininen 2014, Leibold and Chase 2017, Ovaskainen et al. 2019). Most
95 notably, these processes include species interactions and environmental filtering that
96 have dominated ‘niche-based’ thinking (e.g., Tilman 1982, Chase and Leibold 2003), as
97 well as aspects of stochasticity and dispersal limitation inherent to ‘neutral-based’
98 perspectives (e.g., Hubbell 2001).

99 Unfortunately, following initial promise, it has become clear that inference-based
100 analyses can suffer from statistical biases (e.g. Gilbert & Bennett, 2010) and that analyses
101 of metacommunities at a single point in time (snapshot) are often insufficient to
102 differentiate among multiple ecological processes. For example, early interest in using
103 the shape of the species abundance distribution (SAD) alone for differentiating neutral
104 theory from niche-based alternatives (Hubbell 2001, Volkov et al. 2003, McGill 2003)
105 quickly gave way to the realization that multiple processes could produce a similar SAD
106 shape (Chave et al. 2002, Wilson et al. 2003, Chisholm and Pacala 2010). Likewise,
107 neutral theory's predicted species-area and distance-decay relationships are also readily
108 predicted from other metacommunity models (Condit et al. 2002).

109 Later, emphasis for disentangling metacommunity processes from patterns shifted
110 to multivariate analyses of species composition and its spatial variation (i.e.,
111 beta-diversity) and how that is associated with variation in spatial (S) and environmental
112 conditions (E). For example, Cottenie (2005) used multivariate variation partitioning
113 (Borcard et al. 1992) to link empirical patterns of observed community structure
114 (specifically, the fractions of variation explained by S vs. E) to four classic metacommunity
115 archetypes. The strength of the relationship between environmental features and
116 community composition was assumed to indicate the relative importance of
117 environmentally driven species sorting processes, while the strength of the relationship
118 between spatial features and community composition was assumed to indicate the
119 degree to which communities were structured by dispersal (see also e.g., Legendre
120 2008, Soininen 2014, 2016). While this approach became widely used, the explicit

121 connection between the metacommunity theories and this variation partitioning
122 approach is weak. For example, a number of features can reduce the fraction of
123 composition explained, including unmeasured spatial and environmental variables, biotic
124 interactions, and temporal changes in environmental conditions (Gilbert and Bennett
125 2010, Smith and Lundholm 2010, Tucker et al. 2016, Leibold and Chase 2017). Indeed,
126 most syntheses of these patterns show only a small amount of the variation in most
127 metacommunities is explained (Cottenie 2005, Soininen 2014).

128 As a result of the limitations of the original multivariate partitioning,
129 metacommunity ecologists have continued to develop more refined analytical tools. For
130 example, some of the issues with the variation partitioning approach have been dealt
131 with by including latent variables to account for unmeasured environmental variables
132 (Peres-Neto and Legendre 2010), by correcting spurious correlations caused by
133 autocorrelated environmental variables (Clappe et al. 2018), by improving the fit of
134 environmental responses using tree-based machine learning (Viana et al. 2019), and/or
135 by accounting for species co-occurrence patterns in the context of joint species
136 distribution models (JSDM) (e.g. Ovaskainen et al. 2017). Other approaches include the
137 use of multiple diversity indices (sometimes including functional and phylogenetic
138 information), selected according to simulation models with known underlying dynamics
139 (virtual ecologist approach) to assess possible echoes of different processes in complex
140 empirical patterns (Münkemüller et al. 2012, Ovaskainen et al. 2019).

141 The approaches used to analyse metacommunity structure so far have mostly
142 relied on analysis of spatial pattern alone, without considering temporal dynamics, and

143 are only able to explain a relatively small amount of the variation observed in real
144 metacommunities (Jabot et al. 2020). Temporal dynamics clearly play a critical role in
145 many classic metacommunity models, and without considering time, it can be impossible
146 to discern among processes. For example, communities that arise from neutral processes
147 can lead to quite similar patterns of spatial compositional turnover compared to those
148 that arise from priority effects (the order and timing of species arrival in a community), but
149 their patterns diverge when temporal dynamics are considered (Tucker et al. 2016,
150 Leibold and Chase 2017).

151 Here, we use a pluralistic, process-based approach to get closer to the ultimate
152 goal of deriving process from pattern in community assembly and metacommunity
153 dynamics (Figure 1). We build on a recent framework developed by Thompson et al.
154 (2020), which leaves behind the idea that real metacommunities can be understood by
155 comparing them to a set of discrete archetypes bound by restrictive assumptions (e.g.,
156 species sorting vs. mass effects vs. neutral). Instead, this framework emphasizes how a
157 broad continuum of metacommunity dynamics can arise via the interplay of three key
158 processes (building on e.g., Loreau et al. 2003, Gravel et al. 2006, Vellend 2010, 2016,
159 Fournier et al. 2017): 1) density-independent responses to abiotic conditions (i.e. the
160 fundamental abiotic niche), 2) density-dependent biotic interactions (e.g. competition),
161 and 3) dispersal. Stochasticity is incorporated as the probabilistic realization of the first
162 three core processes (Shoemaker et al. 2020) (Figure 1 - arrows i and ii).

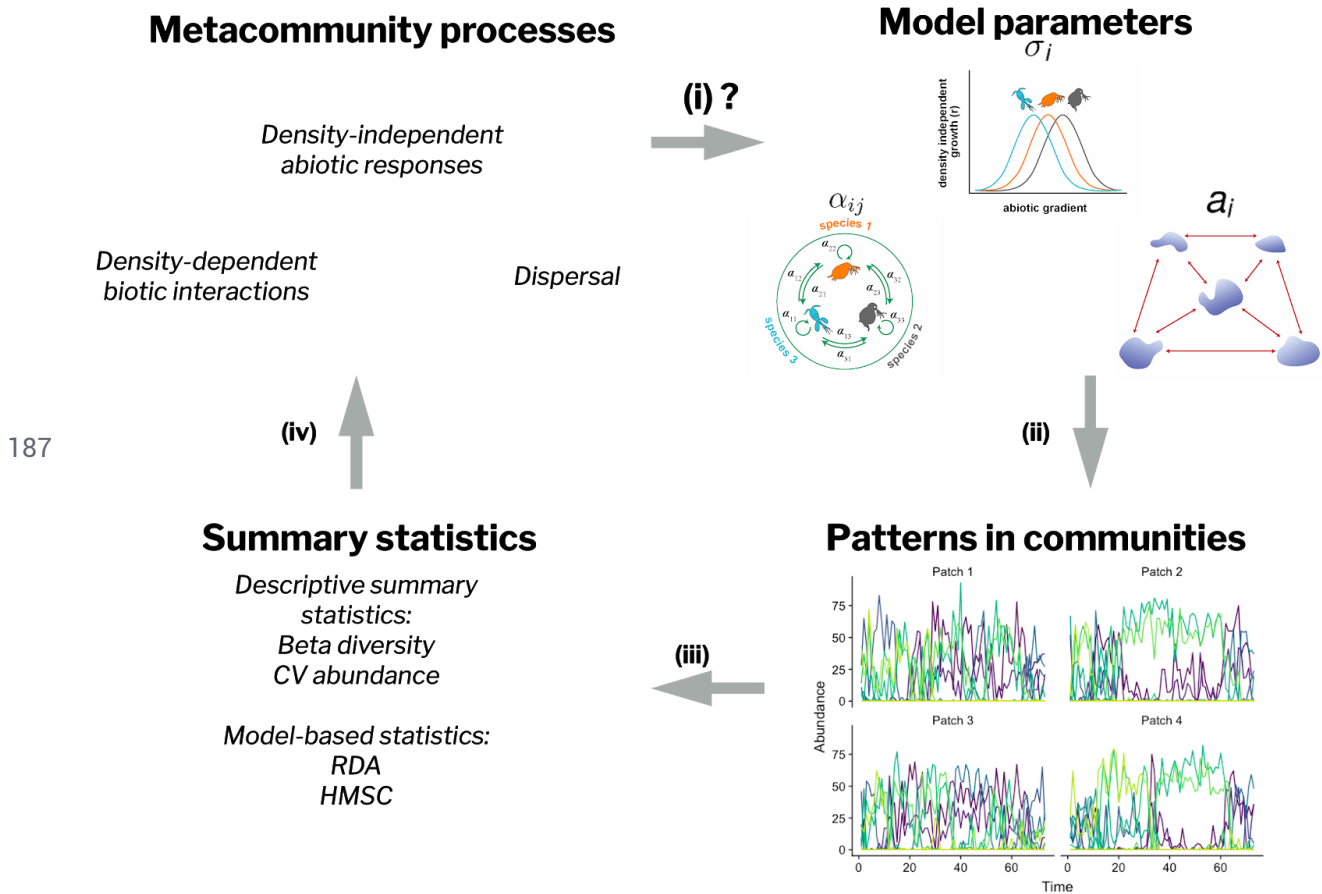
163 We use the model presented in Thompson et al. (2020), which simulates a wide
164 range of metacommunity dynamics by changing the strength of each process. From

165 simulated metacommunities, we estimate spatial and temporal variation in patterns of
166 relative abundance, diversity and composition, to better capture the dynamic nature of
167 metacommunity patterns (Figure 1 - arrow iii). We then use a suite of summary statistics –
168 patterns and model-based statistics – in random forest models (non-parametric learning
169 algorithms commonly used for regression and classification problems (Breiman 2001)) to
170 predict the parameters of the simulation model that generated the metacommunity
171 dynamics. This allowed us to identify the summary statistics that were most informative
172 for distinguishing variation in each of the three underlying metacommunity processes
173 (Figure 1 - arrow iv). Using these random forests we compared the performance of
174 combinations of summary statistics and established the minimal set of summary statistics
175 required to predict the metacommunity processes. As a final step, we examine the
176 influence of sampling effort in time and space on the summary statistics.

177

178 Our results highlight that deriving pattern from process requires a pluralistic
179 approach. That is, we find that there is no single ‘magic bullet’ parameter or analysis,
180 but that a number of metacommunity statistics and analytical approaches may be
181 required to assess the relative importance of the underlying processes. Finally we show
182 which parameters are sensitive to data resolution by reducing the number of time points
183 or patches, and conclude that most empirical studies may be severely undersampling
184 their metacommunities to the point that reliable metrics cannot be obtained to infer
185 metacommunity processes.

186



187

188 **Figure 1:** Workflow for finding summary statistics that distinguish patterns resulting from different

189 metacommunity processes. (i) The different strengths of the processes result in different metacommunity

190 dynamics. (ii) We adjusted key model parameters – abiotic niche breadth parameter (σ_j), inter and intra

191 competition strengths (α_{ij}), and the probability of dispersal parameter (a_i) – to change the strength of the

192 density-independent, density-dependent, and dispersal processes in the simulations. (iii) We used

193 descriptive statistics and model-based statistics to summarise the dynamics observed across the

194 metacommunity through the time series (here we present some examples of summary statistics, for the full

195 list see Table 1). (iv) Using random forests, we identified which of the summary statistics are most useful at

196 distinguishing the three different model parameters.

197

198 **Methods**

199

200 *Simulations*

201 Our goal with the simulations was to produce time series of metacommunity
202 dynamics that varied in the three core processes in the model (abiotic niche breadth,
203 density-dependent biotic interaction structure, and dispersal). Simulated metacommunity
204 dynamics were generated using the model of Thompson et al. (2020) with replicate
205 simulations (Model overviewed in Box 1). We used similar simulations presented in
206 Thompson et al. (2020).

207 The metacommunities were composed of 100 patches and a starting regional
208 richness of 50 species. We ran each simulation for 2200 time steps, including an
209 initialization (200 time steps) and burn-in period (800 time steps), which were
210 subsequently discarded. Following the burn-in period, we retained every 20th time step
211 to keep the size of the simulated data manageable, leaving a total of 60 retained time
212 steps per simulation.

213 To change the density-independent responses to abiotic heterogeneity, we
214 adjusted the abiotic niche breadth parameter (σ_i) from a weak response to the
215 environment (10) to a strong response to the environment (0.001). To change the
216 density-dependent biotic responses, we adjusted the inter and intra competition
217 strengths in four different scenarios (for details see Thompson et al. 2020): equal
218 competition ($\alpha_{ij} = \alpha_{ii}$), stabilizing competition ($\alpha_{ij} < \alpha_{ii}$), mixed competition (α_{ij} can be
219 less than or greater than α_{ii}) and competition colonization tradeoff (30% of species are
220 competitively dominant ($\alpha_{ij} > \alpha_{ii}$) but their dispersal rates are an order of magnitude

221 lower, 70% of species are subdominant and have stabilizing competitive interactions).
222 Finally to change dispersal, we adjusted the probability of dispersal parameter (a_i)
223 ranging from metacommunities that were effectively disconnected (0.0001) to fully
224 connected (0.464).

225 The abiotic environment in any given patch varies between 0 and 1 and is spatially
226 and temporally autocorrelated. The mean value across time and space is 0.5.

227 We ran 660 combinations of dispersal rates, abiotic niche breadth and
228 competition scenarios for 15 randomly generated replicate landscapes which varied in
229 the location of the patches and the environmental conditions experienced. Landscapes
230 were created by drawing xy coordinates in geographic space for each habitat patch from
231 the range [1:100] and then converting these coordinates into a torus to avoid edge
232 effects. Overall this resulted in 9900 simulation runs. Many of these combinations
233 yielded no persistence in the metacommunity (2020 simulation runs) (Thompson et al.
234 2020). We define persistence as abundance greater than 0 after the initial burn in time.
235 Lack of persistence mostly occurred when dispersal was low and responses to
236 environmental variation were strong. We only considered simulations where the entire
237 metacommunity (i.e., gamma diversity) had more than one species, and where the
238 number of replicates that consistently showed persistence was greater than 10 out of 15.
239 This ensured that parameter combinations that were not well replicated did not drive the
240 patterns when we compared across parameter estimates.

241

242 *Summary statistics*

243 We calculated 85 summary statistics from each simulation run. These included
244 descriptive statistics (e.g, diversity metrics) as well as model-based statistics from
245 commonly used methods to analyse metacommunity dynamics (e.g., variation partitioning
246 fractions) (see Table 1 for the main description of the statistics and Table S1 for a full tally
247 of all the statistics we used).

248 First, we calculated statistics that describe patterns of relative abundances (i.e.,
249 relative species commonness and rarity) that determine the shape of the SAD, including
250 Hill number ratios based on either abundance or occupancy. These were based on the
251 ratio of the Hill numbers, which reflect a measure of evenness while controlling for
252 species richness (Hill 1973, Chao et al. 2014). We use two main ratios ${}^1D/{}^0D$ and ${}^2D/{}^0D$
253 to capture evenness. 2D is the inverse Simpson's diversity, a measure of dominance in
254 the community. 1D is the exponent of Shannon's diversity and 0D is species richness.
255 When a community is exactly even, 2D or 1D approximates 0D and therefore the ratio
256 of these values is closer to 1. However, when the community is very uneven, then 2D or
257 1D will be much lower than 0D and the ratios of ${}^1D/{}^0D$ and ${}^2D/{}^0D$ will be much
258 smaller.

259 Second, we calculated the coefficient of variation of local and regional abundance
260 across all species through time. This statistic measures the stability of communities by
261 providing a standardized index of variation in abundance through time (Tilman 1996,
262 Loreau et al. 2003).

263 Third, we calculated beta diversity and its decomposition into richness differences
264 and replacement components (Podani and Schmera 2011). Beta diversity measures

265 compositional heterogeneity between habitat patches (spatial beta diversity) or time
266 points (temporal beta diversity) (Tuomisto 2010), and it can be partitioned into species
267 replacement and richness differences. Species replacement indicates the turnover of
268 species among samples, for example due to environmental filtering or competition
269 (Legendre 2014). On the other hand, richness differences may reflect the different
270 coexistence parameters in different locations and/or dispersal limitation independently of
271 species replacement (Schmera et al. 2020). Nestedness, for example, is a type of
272 richness difference characterized by subsets of species from the richer site (Legendre
273 2014). Both species replacement and richness differences can be evaluated through time
274 or through space.

275 Finally, we calculated the proportion of patches occupied for each species, and
276 then calculated the mean, minimum, and maximum across species. Low occupancy can
277 be a sign of dispersal limitation or the strength of competition, whereas high occupancy
278 could point to mass effects (Ehrlén and Eriksson 2000).

279 For the model-based statistics, we used two families of statistical models to
280 determine how the amount of variation in species' abundances explained by time, space
281 and environment are related to the processes that shape metacommunity structure. First,
282 we performed a classical variation partitioning based on redundancy analysis (RDA)
283 (Borcard et al. 1992) to quantify the amount of variation in community composition
284 explained by the environment, space and time. We did this for data taken only at the final
285 time point, using environment and space as predictors, and for data taken across the
286 entire time series, using environment, space and time as predictors. For both models, we

287 calculated the spatial component using distance-based Moran's eigenvector maps
288 (MEMs) calculated using the *dbmem* function from the *adespatial* package (Dray et al.
289 2019). The MEMs were calculated across all patches and the same set reused for all the
290 simulations using the same landscape. We used all positively autocorrelated MEMs in the
291 analysis, as selecting specific MEMs does not fully account for spatial autocorrelation in
292 the residuals (Peres-Neto and Legendre 2010). While we recognize that using a selection
293 procedure of MEMs can yield better results for individual simulation runs, we decided to
294 keep the number of MEMs consistent across simulation runs so they are more easily
295 comparable. We calculated the temporal component using asymmetric eigenvector maps
296 (AEMs) calculated using the *aem.time* function from the *adespatial* package (Blanchet et
297 al. 2008, Dray et al. 2019).

298 Second, we used Hierarchical Modelling of Species Communities (HMSC)
299 (Ovaskainen et al. 2017), which is a hierarchical Bayesian joint species distribution model
300 that uses fixed environmental predictors and spatiotemporal random effects to make
301 community-level inference of assembly processes. We used species abundance with an
302 assumed Poisson distribution as the response variable. The environmental variable was
303 included as a fixed linear and quadratic effect to fit the Gaussian-shaped response of
304 species to the abiotic environment. The spatial and temporal structures of the data were
305 modelled through autocorrelated spatial, temporal, and spatiotemporal random factors.
306 The spatial random effect was modelled using the x and y coordinates. The temporal
307 random effect was modelled using timestep as a random temporal coordinate. The
308 spatiotemporal random effect was modelled using the x, y, and time coordinates. We

309 used the nearest-neighbour Gaussian process with 10 neighbours for the spatial and
310 spatiotemporal random effects to reduce computation time (Tikhonov et al. 2020). We
311 also restricted each random effect to a single latent factor to make the analysis
312 computationally feasible. Although additional variation may be explained by allowing for
313 more latent factors, it is unlikely to be large as there are no unmeasured environmental
314 variables in our simulation model. The summary statistics we used in the Random Forest
315 consisted of partitioned explained variation according to all fixed and random effects:
316 environment, space, time, spacetime. We used both the raw variation fractions and
317 standardized fractions by total $T_{\text{jur}}R^2$ to also account for differences in the amount of
318 residual variation across simulations. In addition to the variation fractions, we used the
319 estimates of species associations aggregated into statistics such as the proportion of
320 positive or negative associations (Ovaskainen et al. 2019). HMSC was run across 4
321 chains, each with 1000 samples and a transient period of 5000 steps. Sensitivity
322 analyses suggest that while this length of MCMC sampling does not lead to full
323 convergence, it is sufficient to provide estimates of the summary statistics that we use in
324 our analysis (Figure S7). Furthermore, restricting our analysis in this way was necessary to
325 make it computationally feasible (following Ovaskainen et al. 2019). Thus, our results for
326 the HMSC analysis should be comparable across the range of parameters in our
327 simulations, but are conservative for the potential performance of HMSC in assessing
328 metacommunity processes. HMSC was implemented using the HMSC-R package
329 (Tikhonov et al. 2019).

330

331 **Table 1** - Main types of summary statistics investigated as candidate descriptors of
 332 metacommunity dynamics.

A - Descriptive statistics				
Name	Equation	Equation parameters	Variants	Ref
Abundance and occupancy ratios - Local scale (α) metacommunity scale (γ)	Hill numbers given by: ${}^qD = \left(\sum_{i=1}^S p_{ix}^q \right)^{1/(1-q)}$ Abundance ratio given by: ${}^1D/{}^0D$ and ${}^2D/{}^0D$	p_i is the relative abundance of species i in patch x . S is the total number of species. q determines the sensitivity to the relative frequencies	1. Abundance ratios - Local scale (α). 2. Occupancy ratios - Local scale (α) where p_i is the relative occupancy. 3. Abundance ratios - metacommunity scale (γ) where p_i is the relative abundance of species i across all patches and time points.	(Hill 1973)
Coefficient of variation	$CV = CV_t \left(\sum_{i=1}^S N_i \right)$	N_i is the abundance of	1. At local scale the abundance is	(Tilman 1996)

in total community abundance		species i . S is the total number of species.	summed at each patch. 2. At metacommunity scale the abundance is summed across all patches.	
Beta diversity	${}^qD_{\beta} = \frac{{}^qD_{\gamma}}{{}^qD_{\alpha}}$	${}^qD_{\gamma}$ is the diversity index at the metacommunity scale and ${}^qD_{\alpha}$ is at the local scale. We used q as either 0, 1 or 2.	1. Beta diversity through space. 2. Beta diversity through time.	(Tuomis to 2010)
Beta diversity decomposition in space or time using	$BD_{Total} = \sum_{h=1}^{n-1} \sum_{i=h+1}^n \frac{D_{hi}}{[n(n-1)]}$ $BD_{Total} = Repl_{Total} + RichDiff_{Total}$	D_{hi} is the dissimilarity between sites h and i .	1. Beta diversity and all of the decompositions in space. 2. Beta diversity and	(Legendre 2014)

Jaccard-based indexes			all of the decompositions in time.	
Proportion of patches occupied across species	$p_i = s_i/s_{Total}$	s_i is the number of patches occupied by species i and s_{Total} is the total number of patches sampled.	<ol style="list-style-type: none"> 1. Mean proportion of patches occupied across species. 2. Minimum 3. Maximum 	(Ehrlén and Eriksson 2000)
B- Model-based statistics				
Name	Predictors		Outputs	Ref
Variation partitioning only in space	MEMs, Environmental variables		Variation explained by space and environment and all of the shared fractions for the final time step	(Borcard et al. 1992)

Variation partitioning in time and space	MEMs, Environmental variables, AEMs	Variation explained by space, time and environment and all of the shared fractions	(Blanch et al. 2008)
Hierarchical modelling of species composition (HMSC)	<p><i>Fixed effects:</i></p> <p>Environment (2nd degree polynomial)</p> <p><i>Random effects:</i></p> <p>Space x Time</p> <p>Space</p> <p>Time</p>	<p>Mean variation explained by space, time and environment and space x time.</p> <p>Summaries of species associations.</p>	(Ovaskainen et al. 2017)

333

334

335

Box 1 - Model

The dynamics of the metacommunity are governed by a Beverton-Holt (Beverton and Holt 1957) growth dynamics with generalized Lotka-Volterra competition:

$$N_{ix}(t + 1) = \hat{N}_{ix}(t + 1) - E_{ix}(t) + I_{ix}(t) \quad (1)$$

where $\hat{N}_{ix}(t + 1)$ is the population size at time t before accounting for dispersal.

$$\hat{N}_{ix}(t + 1) = \text{Poisson}\left(\max\left\{N_{ix}(t) \frac{r_{ix}(t)}{1 + \sum_{j=1}^s \alpha_{ij} N_{jx}(t)}, 0\right\}\right) \quad (2)$$

where $\hat{N}_{ix}(t + 1)$ is the expected abundance of species i in patch x at time $t + 1$, α_{ij} is the per capita interaction effect of species j on species i , and S is the total number of species. Stochasticity in local demographic outcomes is incorporated through the Poisson draw in equation 2. $r_{ix}(t)$ is the density-independent growth rate of species i in patch x at time t which is given by:

$$r_{ix}(t) = e^{-\left(\frac{z_i - env_x(t)}{2\sigma_i}\right)^2} \quad (3)$$

where z_i is the environmental optimum of species i , $env_x(t)$ is the environmental condition in patch x at time t , and σ_i is the abiotic niche breadth.

The number of emigrants $E_{ix}(t)$ was determined as the outcome of $N_{ix}(t)$ draws of a binomial distribution, each with a probability equal to a_i . The destination of each of these emigrants is determined through a random draw of the patches, with their probabilities determined by:

$$\hat{I}_{ix}(t) / \sum_{x=1}^M E_{ix}(t) \quad (4)$$

$\hat{I}_{ix}(t)$ is the expected number of individuals that immigrate from species i in patch x at time t and it is given by:

$$\hat{I}_{ix}(t) = \sum_{y \neq x}^M E_{iy}(t)^{-L_i d_{xy}} \quad (5)$$

where M is the total number of patches, $E_{iy}(t)$ is the number of immigrants of species i from another patch y , L_i is the strength of exponential decrease of dispersal with distance and d_{xy} is the distance between patches x and y .

336

337 *Random Forests*

338

339 We identified the summary statistics that were the most effective in discriminating
340 among the metacommunity processes using random forests (Breiman 2001). We used
341 random forests because they can be used both for regression and classification
342 problems (dispersal and abiotic niche breadth parameters are continuous, while the
343 competition scenario is a categorical parameter). Further, random forests are
344 non-parametric, allowing any relationship between predictor and response, and can be
345 used to rank the importance of the predictors (Breiman 2001).

346 We built 21 random forest models (7 classes of models for 3 predictors separately
347 see Table 2) for each process separately to determine which summary statistics were
348 better at predicting each process across all simulations (Table 2). Across all models, we
349 ran 500 trees for each random forest. In random forests, the variable importance is
350 determined by observing how much the prediction error increases when each variable is
351 permuted, while the other variables remain the same (Breiman 2001, Liaw and Wiener
352 2002).

353

354 **Table 2** - Random forests were used to compare the performance of sets of summary
 355 statistics at explaining variance in each of the three metacommunity processes:
 356 density-dependent biotic interactions, dispersal, density-independent responses to
 357 abiotic conditions. We set up 7 different types of models depending on the types of
 358 summary statistics for each of the three processes for a total of 21 random forests.
 359

Model	Summary statistics used as predictors in model	N	Classification/ R² Density - dependent biotic interactions	Classification/ R² Dispersal	Classification/ R² Density - independent responses to abiotic conditions
1 - Spatial descriptive statistics	Beta diversity in space and the partitioning of beta diversity in space	6596	69.78%	57.51%	32.48%
2 - Temporal and spatial descriptive statistics	All of the statistics presented in Table 1A	6596	83.29%	85%	48.39%
3 - RDA Variation partitioning only in space	All of the statistics in Table 1B- Variation partitioning in space	5613	32.99%	0%	35.6%
4 - RDA Variation partitioning	All of the statistics in Table 1B-	6590	49.71%	59.05%	49.14%

in space and time	Variation partitioning in time and space				
5 - HMSC	All of the statistics in Table 1B-HMSC	5728	78.6%	63.85%	51.33%
6 - All summary statistics	All of the summary statistics presented in Table 1, including both model based and descriptive	5185	90.24%	85.88%	61.78%
7 - Minimal model	The minimal model was done using recursive feature elimination from model 6	5185	90.55%	86.77%	62.49%

360

361

362 Because some simulations were discarded (see above), the maximum number of

363 simulations we analyzed was 6596 (Table 2) for the simple metacommunity descriptors.

364 For metacommunity descriptors derived from models (i.e. RDA or HMSC), we only ran

365 random forests for metacommunities that had persistence of at least two species for

366 more than 3 time points. In addition, some of the model-based statistics yielded NA

367 values (e.g. when calculating species covariance involving transient species that

368 occurred in only one time step). We removed the simulation results that had missing

369 values. As a result, the number of simulations used in the random forest for the HMSC
370 and all summary statistics was lower (5728 and 5185, respectively).

371

372 The minimal model was selected using recursive feature elimination and a 10-fold
373 cross-validation procedure. This algorithm first partitions the data into test and training
374 sets. The model is fit with all of the predictors to the training data and tested with the
375 held-back samples, where each predictor gets an importance value. The algorithm then
376 keeps only the 'n' most important variables, re-fits the model and tests it again with the
377 held-back samples. This procedure is repeated for 10 to 50 'n' number of predictors
378 (Figure S1). The algorithm determines the best number of predictors and the best
379 predictors based on the prediction accuracy (with the held-back samples). The whole
380 procedure is repeated 10 times (Ambroise and McLachlan 2002, Svetnik et al. 2004).

381

382 *Sensitivity analysis to spatial and temporal sampling effort*

383

384 The summary statistics, with the exception of the spatial-only variation partitioning, were
385 calculated on the entire simulation time series (after burn-in) of the metacommunity.
386 However, empirical data are inevitably limited in the number of samples that can be
387 obtained in space and time. Therefore, we investigated the effect of limited sampling by
388 running our analyses on a subset of all existing patches and time points, as is typically
389 the case in empirical studies. For this, we used a simulation that had stabilizing
390 competition ($\alpha_{ij} < \alpha_{ii}$), intermediate levels of density-independent responses to abiotic

391 conditions (4.64159) and intermediate levels of dispersal (0.00215). We chose these
392 parameter values because they yielded gamma diversity above 1 for all simulations and
393 they were intermediate values of dispersal and abiotic conditions. Then, we randomly
394 sampled m of 100 patches where $m = 4, 8, 12, 16, \dots, 100$. This sampling was repeated
395 1000 times to cover spatial variation in the subsamples. We also sampled t of our 60 time
396 points, where $t = 4, 8, 12, 16, \dots, 60$. This sampling was not repeated, as the number of time
397 points included was sequential. We subsampled time and space factorially (i.e., few time
398 points and few patches, few time points and many patches, many time points and few
399 patches, and many patches and time points).

400

401 All of the code for our simulations and analyses can be found on GitHub:

402 https://github.com/lmguzman/disentangling_metacommunities, and will be mirrored at

403 Zenodo upon acceptance.

404

405 **Results and Discussion**

406

407 Overall, we found that jointly addressing time and space is necessary for distinguishing
408 metacommunity dynamics. Including statistics that are measured through time increased
409 the explanatory power of the random forests by up to 59% when compared to cases
410 where only spatial variation was considered. This was the case when temporal variation
411 was incorporated in the descriptive statistics (Table 2 - Model 1 vs Model 2) and in the
412 RDA variation partitioning (Table 2 - Model 3 vs Model 4). These results suggest that a

413 simple snapshot of communities at a certain moment in time is not sufficient, and neither
414 substituting space for time in observational studies to understand spatio-temporal
415 dynamics. Additionally, we found that different summary statistics are complementary
416 and can capture different aspects of metacommunity dynamics. For instance, including
417 both descriptive and model-based summary statistics increased the explanatory power of
418 the random forests by up to 22% (Table 2 - Model 6 and 7).

419

420 For all processes, descriptive statistics were more informative than model-based
421 statistics, even with fewer predictors (Table 2 - Model 2 vs Model 5). Model 2 included
422 statistics that described communities through space *and* time. These statistics capture
423 more variation in metacommunity dynamics than redundancy analysis or HMSC. For
424 example, the variation of community biomass through time and the ratios of occupancy
425 (evenness) are important statistics in the random forest (Figure 2). These statistics
426 capture a real pattern in metacommunity variation, while variation partitioning (either RDA
427 or HMSC) represent a model fit. Measures of temporal variability and the SADs are also
428 important at distinguishing metacommunity processes. However, we emphasize that
429 rather than using them in isolation, as had been the focus previously (e.g., distinguishing
430 niche vs. neutral processes (Hubbell 2001, Volkov et al. 2003, McGill 2003, Chisholm and
431 Pacala 2010), these statistics are much more informative when combined with other
432 statistics such as beta diversity metrics (Table S1).

433

434 Despite its continued historic popularity, RDA based variation partitioning using only
435 spatial data (Model 3) had the lowest performance to distinguish metacommunity
436 dynamics (Table 2). This is likely because variation partitioning does not take into account
437 species interactions and partly due to model misspecification (Viana et al. 2019). In
438 addition, using a single snapshot in time does not capture the spatio-temporal dynamics
439 of dispersal. While it is rather surprising that the random forest that included only spatial
440 descriptive statistics performed better than the RDA-based variation partitioning in space,
441 using metrics that describe community dynamics themselves rather than model-fits
442 seems to be more informative for the random forest. Thus, despite the fact that this has
443 been a very popular approach to infer potential metacommunity mechanisms, our
444 analysis shows that this approach is prone to yield misleading interpretations.

445

446 Once we included temporal dynamics, the RDA based variation partitioning performed
447 better in classifying and explaining the variation of the underlying processes (Table 2 -
448 Model 4). Including time in the variation partitioning model increased the classification
449 success for different types of biotic interactions to 50%, and explained more variation in
450 dispersal (59%) and in responses to abiotic conditions (49%). It is especially remarkable
451 that the amount of variation explained in dispersal was particularly sensitive to the
452 inclusion of time, as it increased from 0% to 59% when time was included. Dispersal is a
453 spatio-temporal process that affects the dynamics of local populations. Thus, it does not
454 seem that surprising that including the effect of time, instead of the commonly used
455 "snapshot" of the metacommunity, increases our predictive ability. Likewise, the random

456 forest for biotic interactions and abiotic responses are more successful in inferring
457 processes once we include time. As such, it seems clear that including sampling in both
458 time and space is necessary for disentangling metacommunity processes, and that
459 relying on snapshots in time for disentangling dynamic systems is insufficient.

460

461 Hierarchical modelling of species composition (HMSC) had a greater predictive power of
462 metacommunity processes than redundancy analysis with time (Table 2 - Model 5 vs
463 Model 4). The best improvement was in the classification of the biotic interactions
464 (success rate 79% for model 5 vs. 50% for model 4). This is because the HMSC approach
465 explicitly estimates positive or negative interspecific associations via species covariance
466 *after* accounting for the effect of (environmental) covariates (Ovaskainen et al. 2017).
467 Although the utility of using species associations for inferring the importance of actual
468 species interactions is still widely debated (Blanchet et al. 2020), our results nevertheless
469 suggest that these model based statistics increase our ability to distinguish the type of
470 biotic interactions, even if the pairwise species interaction coefficients cannot be reliably
471 recovered.

472

473 All statistics together, including descriptive and model-based statistics (Model 6),
474 performed better for all three processes than using only one type of statistic alone.
475 Several statistics provided complementary information that was useful at discriminating
476 metacommunity processes (Table 2). However, this random forest included up to 85
477 predictors (All predictors in Table S1) and very little predictive ability was lost when we

478 reduced it to a minimal model through backwards selection (Table 2). These minimal
479 models included a subset of statistics depending on the random forest used to infer each
480 of the processes (Figure 2). The best number of predictors was 50 for the
481 density-dependent biotic interactions, 32 for dispersal and, 29 for density-independent
482 responses to abiotic conditions (Figure S1). The most informative statistics selected by
483 the random forest were those having the smallest variance at each parameter value, but
484 exhibited most variation across parameter space (Figure 3a,e,i vs Figure 3c,d,h). In what
485 follows, we describe the minimal model for each process.

486

487 *Density-dependent biotic interactions*

488

489 The minimal model to distinguish different types of biotic interactions had a classification
490 success of 90.68%. Stabilizing competition was easiest to distinguish with the available
491 summary statistics (3.32% error rate), while the competition-colonization trade-off was the
492 hardest to separate from the other types (19.97% error rate). The most important summary
493 statistic that helped to distinguish biotic interactions was the coefficient of variation of
494 abundance at the local scale (Figures 2 and S2). This was lowest under stabilizing
495 competition, increased with equal competition and mixed competition, and was highest
496 with competition-colonization trade offs (Figure 3a). Under stabilizing competition, local
497 diversity is higher (see also Thompson et al. 2020), which stabilizes overall community
498 abundance through insurance and portfolio effects (Doak et al. 1998, Yachi and Loreau
499 1999). The increased variability in the other scenarios is due to the stronger competitive

500 effects (Chesson 2000), which reduce diversity, and can result in abrupt compositional
501 transitions with greater temporal variability in community abundance (Thompson et al.
502 2020).

503

504 The second most important summary statistic was the proportion of spatial beta diversity
505 due to richness differences. We found the lowest richness differences under equal
506 competition and stabilizing competition, moderate richness differences with mixed
507 competition and highest richness differences with competition-colonization trade offs.
508 With stabilizing and equal competition, richness differences accounted for a smaller
509 proportion of the total spatial beta diversity, meaning that patches often have a similar
510 number of species and species replace each other across the landscape. On the other
511 hand, with competition-colonization trade-offs, richness differences accounted for a
512 higher proportion of spatial beta diversity (Thompson et al. 2020).

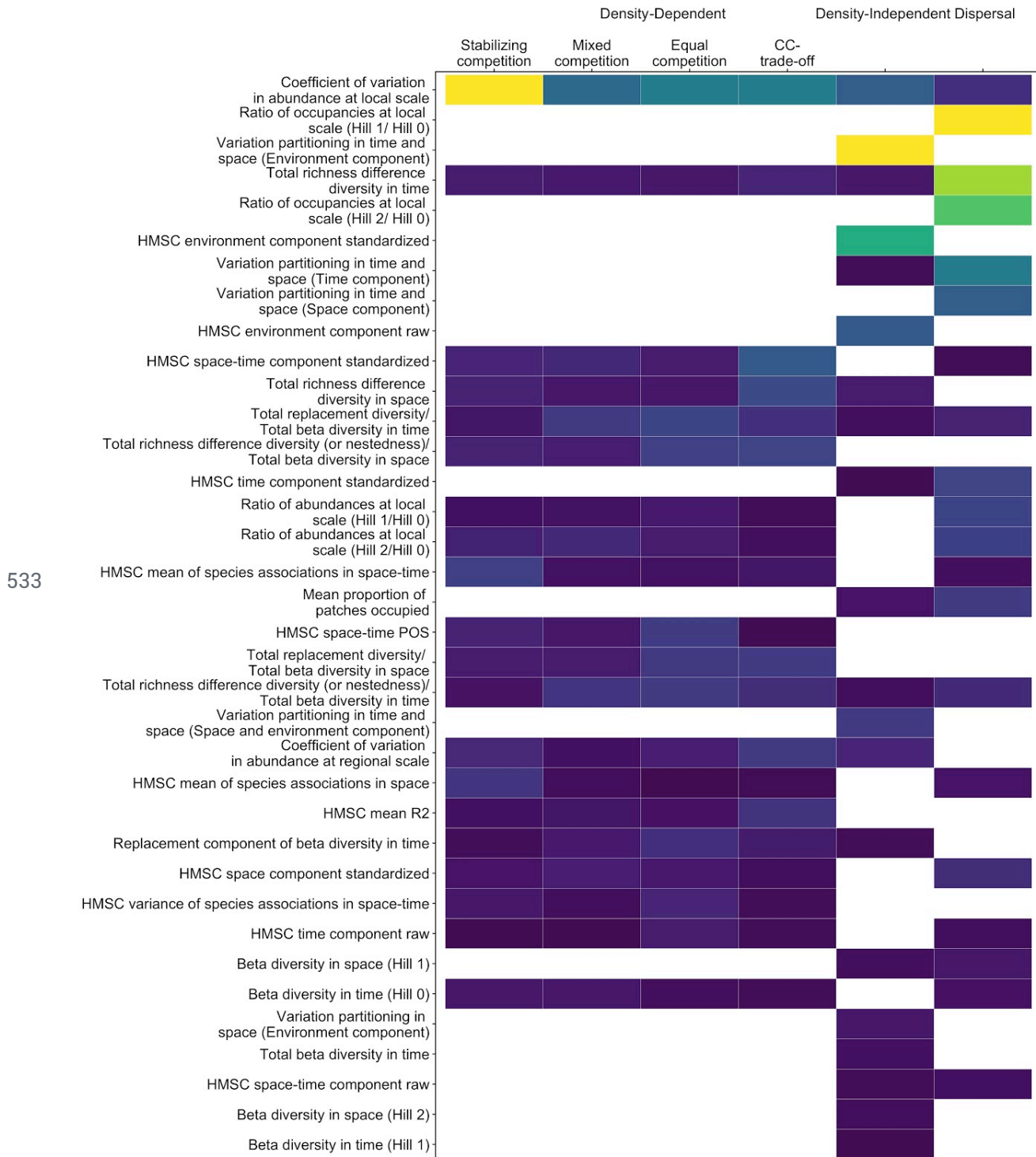
513

514 *Dispersal*

515

516 The minimal model explained 86.77% of the variation in dispersal in the simulated
517 metacommunities (Table 2). Here, community evenness—captured by the ${}^1D/{}^0D$
518 occupancy ratio—emerged as the most important summary statistic (Figure 2 and S3).
519 This statistic has a U-shaped relationship with dispersal (Figure 3e). Low dispersal results
520 in a relatively high evenness, which suggests that most species occupy a relatively
521 similar number of patches, despite considerable variation in occupancy. At intermediate

522 levels of dispersal, species mostly track environmental conditions, i.e. we find most
523 effective species sorting. High dispersal again results in a relatively high evenness,
524 suggesting that most species are distributed evenly across the landscape, pointing at
525 mass effects (Figure 3e). The second important summary statistic was the total richness
526 difference between time points (Figure 2 and S3, Table 1). We observed another
527 U-shaped relationship with dispersal. When dispersal is low, species are largely
528 constrained to their initial patches with little ability to move and are more likely to go
529 extinct when environmental conditions change, leading to higher richness differences
530 through time. As dispersal increases, species are maintained locally and less likely to go
531 extinct, and therefore the richness differences between time points decreases (Leibold et
532 al. 2004).



534 **Figure 2:** The best 20 performing summary statistics ordered from top to bottom by their overall

535 importance in the minimal random forest model (model 7). The importance of the summary statistics

536 decreases from top to bottom of the graph and from yellow (most important) to purple (least important).

537 Blank areas are variables that were not selected in the minimal models. The most important summary

538 statistic to differentiate between the four types of local interactions is the coefficient of variation in

539 abundance at a local scale, the most important summary statistic for dispersal is the portion of total

540 richness difference of beta diversity in time, and the most important summary statistic for the

541 density-independent responses to abiotic conditions is the environmental component of the variation

542 partitioning in time.

543

544 *Density-independent responses to abiotic conditions*

545

546 The minimal model to explain variation in the strength of density independent

547 environmental filtering in the simulated metacommunities captured only 62.5% of the

548 variation, even with all the summary statistics available. The most important summary

549 statistic for the responses to abiotic conditions was the environmental component of the

550 variation partitioning through time and space (Figure 2 and S4). This component has a

551 hump-shaped relationship with the strength of abiotic conditions (Figure 3i) and this

552 relationship may be biological or statistical in nature. When species respond strongly to

553 abiotic conditions (i.e. σ_i - niche breath- is small), the environmental component explains

554 very little variation in community composition, because species will not be able to persist

555 in their patches when the environment changes. As the responses to the abiotic

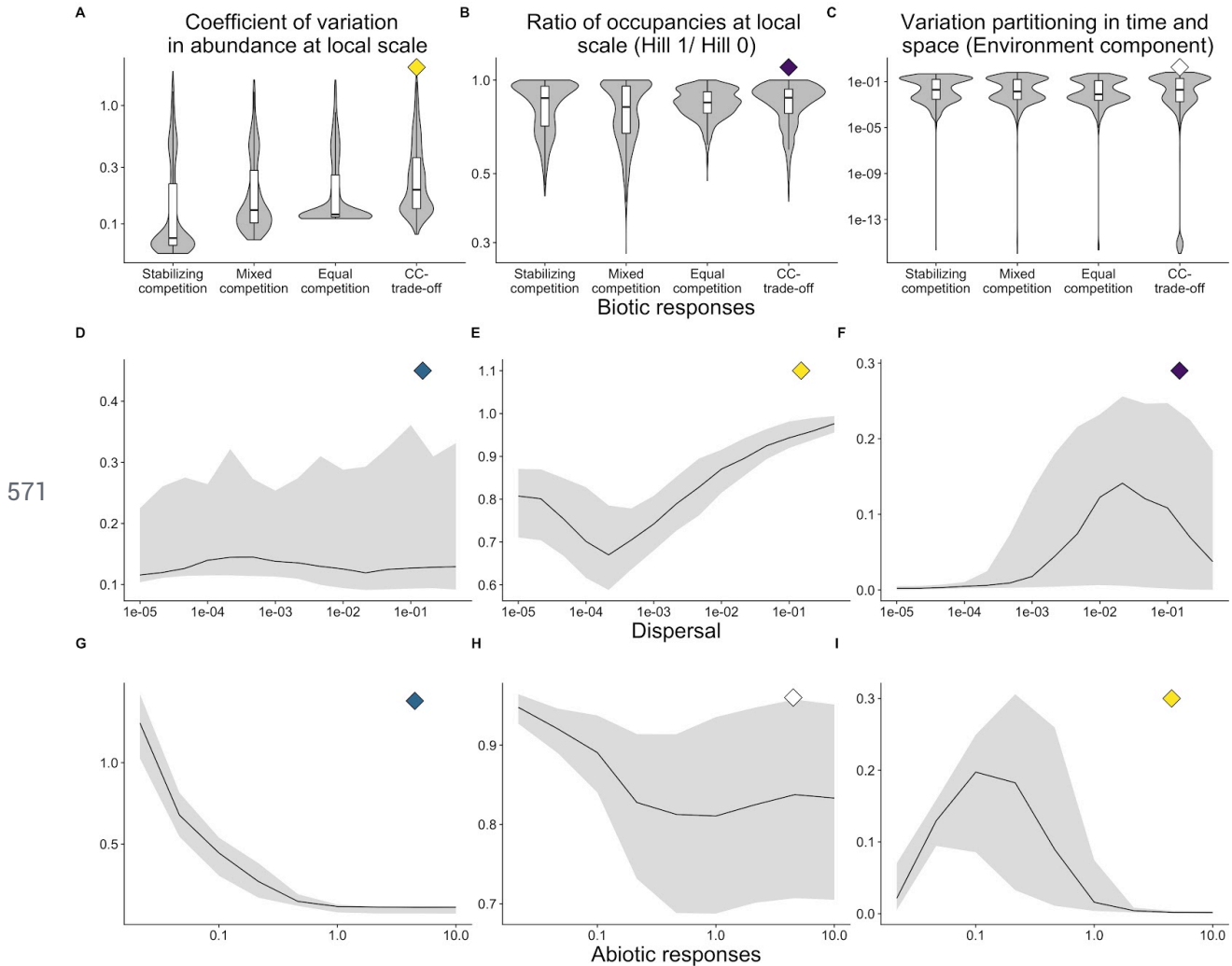
556 conditions weaken (i.e. intermediate σ_i), the environmental component explains the most

557 variation in community composition. Under such conditions, species can respond to

558 environmental variation by moving to suitable patches and not driven extinct by changes

559 in environmental conditions before moving. Finally, when the responses to abiotic
560 conditions are very weak (i.e. σ_i is large), the amount of variation explained by the
561 environmental component is again low, as variation in environmental conditions does not
562 lead to changes in community composition (Figure 3i). In addition, when niche breadth is
563 very narrow (i.e. strong abiotic response), the models used here (both the E component
564 generated via partial RDA or HMSC) may not be able to fit the environmental response
565 (eg. RDA fits linear responses), but when the niche is wider, then the models are better
566 able to fit the species response to the environment (either fitting the unimodal
567 relationship like in HMSC or linear responses in RDA are more suitable). When the niche
568 breath is too wide, environmental variation does not explain variation in species
569 composition.

570



572 **Figure 3:** The three most important summary statistics for predicting the underlying metacommunity
 573 processes (density-dependent biotic interactions - top row; dispersal - middle row; and
 574 density-independent responses to abiotic conditions - bottom row) as determined by the minimal random
 575 forest model (model 6): 1) the coefficient of local scale variation in community abundance (left column), 2)
 576 ratio of occurrence at local scale (Hill 1/ Hill 0) (middle column), and 3) the environmental component of
 577 variation partition through time and space; right column. The color of the diamonds in the top right of each
 578 panel corresponds to the colour in Figure 2 and shows the relative importance of each summary statistic
 579 for explaining that metacommunity process. The error lines in the bottom two rows represent the 1st and 3rd
 580 quartiles of the values of the summary statistic, while the lines represent the median values of the summary

581 statistic. The top row represents the distribution of the data using violins and boxplots within those violins
582 represent the 1st and 3rd quartiles and the median of the summary statistics.

583

584 *Sensitivity analysis*

585

586 When we reduced sample completeness to be more realistic for empirical studies, the
587 summary statistics were not equally affected (Figure 4). We evaluated the error half-life of
588 the summary statistics when time was fully sampled but patches were not, and
589 vice-versa. The error half life is the minimum number of patches or sequential time points
590 needed to reduce the ‘error’ in the summary statistic by half. Not surprisingly, we found
591 that some summary statistics are more sensitive to the loss of patches while some
592 summary statistics are more sensitive to the reduced coverage in time. Here, we
593 describe the error half life for the number of patches when time is fully sampled, which is
594 clear in the simulations, but less clear in empirical studies. Empiricists will have to
595 determine what full sampling time means for their study system depending on the
596 organisms studied. When time is fully sampled, total beta diversity in time, beta diversity
597 in space (Hill 1 and 2), replacement diversity in time and richness differences in time, as
598 well as all of the temporal and environmental components of variation partitioning, are
599 robust to a reduced number of sampled patches. These statistics needed less than 8% of
600 patches sampled to reduce the error rate by half. On the other hand, the spatial
601 component of variation partitioning is very sensitive to the loss of patches, and reaches
602 half the error at 72% of patches remaining (Table S2, Figure S5). When space is fully
603 sampled, the minimum and maximum proportion of patches occupied, the space-time

604 component of variation partitioning, beta diversity in space and time (Hill 1 and 2), and
605 the coefficient of variation in abundance at the local scale are very robust to the loss of
606 time points, where only 8% of the time points are needed to reduce the error rate by half.
607 On the other hand, the space-environment shared component of variation partitioning,
608 and replacement and richness differences through time need more than 80% of time
609 points to reduce the error rate in half (Table S3, Figure S6).

610

611 Some statistics are sensitive to the loss of both time points and patches. For example, the
612 coefficient of variation in abundance at a local scale, which is critical for detecting biotic
613 interactions, is not very sensitive to the number of time points, but the variance is higher
614 with fewer patches sampled (Figure 4a). Richness differences through time is highly
615 sensitive to the number of time points sampled. In addition, when the number of patches
616 sampled is low, the variance around the summary statistics was much larger than when
617 more patches were sampled (Figure 4b). Finally, the mean proportion of patches used by
618 species is more sensitive to the loss of patches than time points. When the entire (100
619 patches) metacommunity is sampled, only 30% of the time points need to be sampled to
620 obtain the true summary statistic. But if few patches are sampled, then even complete
621 temporal sampling of the metacommunity will lead to large discrepancies between
622 estimated values and true values (Figure 4c).

623

624 Multiple studies have shown that sampling effort can have large consequences for the
625 inferences made on metacommunity processes (Gilbert and Bennett 2010, Ovaskainen et

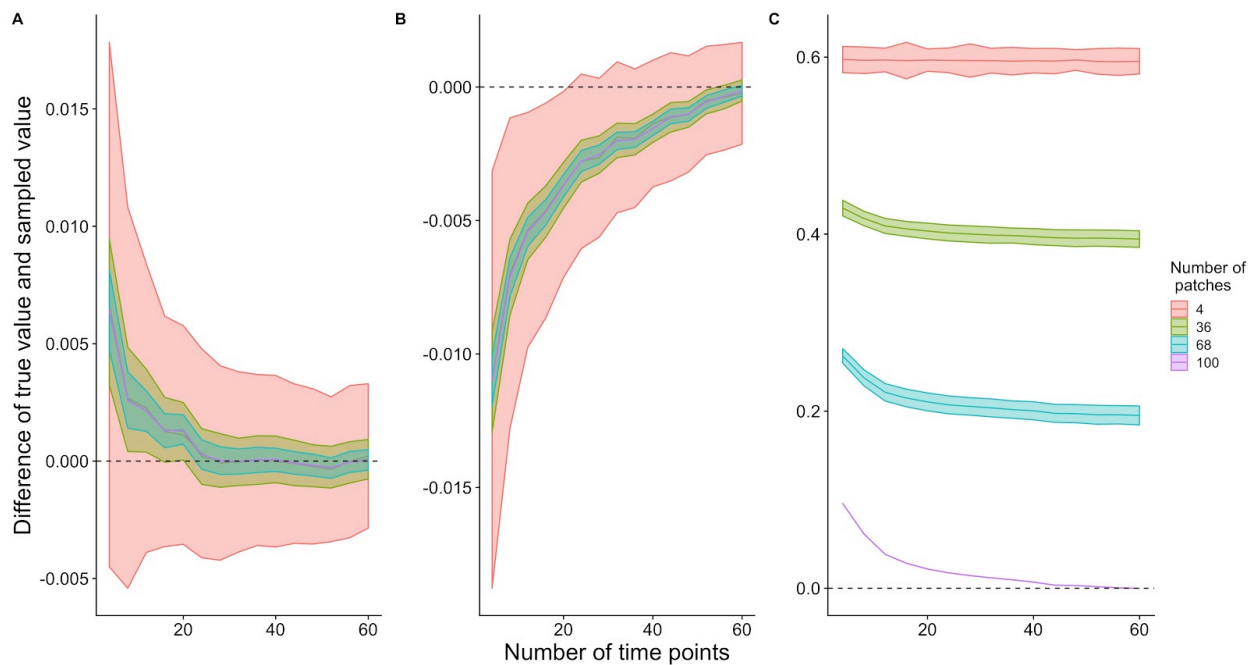
626 al. 2019, Viana and Chase 2019). We add to this by showing how the undersampling of
627 the temporal series also affects the robustness of inferences. The coefficient of variation
628 in abundance at a local scale was important for both biotic and abiotic processes. If
629 space is fully sampled, only a few time points are needed to capture this statistic.
630 Similarly, the environmental component of variation partitioning in space and time was a
631 very important statistic for abiotic processes. We suggest that depending on the
632 processes of interest, space or time may be prioritized to capture the appropriate
633 dynamics given sampling constraints.

634

635

636

637



638 **Figure 4:** Sensitivity analysis showing how the number of time points and the number of patches sampled
639 can increase the difference between an estimated summary statistic and its true value. Different summary

640 statistics are more or less sensitive to the incomplete sampling of patches or time points. We present the
641 sensitivity as the difference between the true value (i.e. the value of the summary statistic when the
642 metacommunity was fully sampled) and the value of the summary statistic with the presented number of
643 time points and patches. The coefficient of variation in abundance at a local scale (A) is insensitive to the
644 number of time points or patches. The richness differences through time is very sensitive to the lack of time
645 points (B). The mean proportion of patches occupied is more sensitive to the number of patches (C).

646

647 *General discussion and caveats*

648

649 The relative importance of the summary statistics depends on the assumptions made in
650 the simulation model. For example, in the model used here, we assumed that all the
651 species had the same dispersal rate, though this can be changed for future studies.
652 Interspecific variation in dispersal rates will likely reduce the degree to which observed
653 patterns can be used to assess dispersal processes. In addition, by forcing all species to
654 have the same dispersal rate might explain why our simulations result with empty
655 metacommunities. We make a similar assumption for niche breadth, where all the species
656 have the same breath but different optima and that all patches have the same size. For
657 example, the latter assumption has consequences for the observed colonization and
658 extinction rates (MacArthur and Wilson 1967), as well as community size and spatial
659 environmental heterogeneity within the patch, which can weaken the relationship
660 between dispersal rate and the summary statistics identified. By modifying different
661 assumptions, we can identify how robust the relationship between the processes and the
662 summary statistics will be. This approach allows us to generate hypotheses about the

663 links between patterns and processes in metacommunities, which can then be tested via
664 experiments and controlled observational work.

665

666 In this model we assumed that all species were governed by the same metacommunity
667 dynamics. Empirical metacommunities may not adhere to this assumption and in fact,
668 empirical metacommunities may have different sub-assemblages of functionally different
669 taxa governed by different metacommunity dynamics (Thompson et al. 2017). However,
670 this type of analysis can be useful for sets of competitors with similar dispersal abilities. In
671 addition, we did not incorporate the complexity of trophic metacommunities (Guzman et
672 al. 2019), but this type of workflow can be used to investigate trophic metacommunities.

673

674 While we show that the classical partitions of “E” and “S” from RDA-based variation
675 partitioning may not be informative for inferring metacommunity processes, E and S may
676 still be informative when we want to understand species responses to global change or
677 to develop management actions by knowing whether the community patterns are
678 governed more by environmental (be it indirectly through species interactions) or spatial
679 (be it due to unmeasured environmental gradients). In addition, the comparison of S or E
680 components between datasets or species may provide useful information (De Bie et al.
681 2012).

682

683 Our analysis also suggests why most empirical metacommunity analysis have such low
684 explanatory power — dramatic undersampling in space and time. Our sensitivity analysis

685 shows that while some of the metrics are robust to low sample size in space or time, very
686 few are robust when both space and time are undersampled. If empirical metacommunity
687 studies only sample few of the relevant patches or time points, trying to understand the
688 processes that structure metacommunities might not be possible.

689

690 **Conclusions and future directions**

691

692 As a next step forward, we suggest that one can use the summary statistics identified
693 here in an Approximate Bayesian Computation (ABC) framework (Slater et al. 2012,
694 Pontarp et al. 2019). Recent studies have also used a random forest approach to reduce
695 dimensionality for an ABC framework (Hauenstein et al. 2019). Such a framework would
696 use simulated models and summary statistics to determine the posterior distribution of
697 parameters of interest (e.g., dispersal rate) based on the distance between empirical data
698 and summary statistics. This method can be used with an absolute model fit to assess
699 how well the simulation model explains empirical data (Pennell et al. 2015).

700

701 Overall, we highlight two main take-home messages from our study. First, although the
702 majority of studies of metacommunities focus on static (snapshot) patterns of species
703 abundances and distributions in space, we showed that considering temporal dynamics
704 is key for distinguishing the processes driving metacommunity dynamics. By doing so,
705 our ability to explain variation in density-dependent, density-independent and dispersal
706 processes improved by up to 60%. These results suggest that we cannot substitute

707 space for time (or vice-versa) when we want to study metacommunity dynamics. Second,
708 although there can never be a one-to-one matching of pattern to process, we show that it
709 is essential to use multiple summary statistics simultaneously in order to disentangle
710 among the fundamental processes driving metacommunity dynamics. Model based
711 statistics in addition to descriptive statistics were needed to have the highest
712 performance in the random forest models.

713

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