Full title: Multivariate methods for testing hypotheses of temporal community dynamics

Running header: Testing hypotheses of temporal community dynamics

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ABSTRACT

For ecological research to make important contributions towards understanding and managing temporally-variable global change processes, such as responses to land-use and climatic change, we must have effective and comparable ways to quantify and analyse compositional change over time in biological communities. These changes are the sum of local colonisation and extinction events, or changes in the biomass and relative abundance of taxa within and among samples. We conducted a quantitative review of currently available methods for the analysis of multivariate datasets collected at temporal intervals. This review identified the need for the application of quantitative, hypothesis-based approaches to understand temporal change in community composition, particularly for small datasets with less than 15 temporal replicates. To address this gap, we: (1) conceptually present how temporal patterns in community dynamics can be framed as specific, testable hypotheses; (2) provide three fully-worked case-studies, complete with R code, demonstrating multivariate analysis methods for temporal hypothesis testing and pattern visualisation; and (3) present a road map for testing specific, quantitative hypotheses relating to the underlying mechanisms of temporal community dynamics.

KEYWORDS

Beta diversity, biodiversity, community variation, compositional change, multivariate analysis, species turnover, temporal change, temporal variability, time series, zeta diversity

INTRODUCTION

A key task for ecologists is to monitor, quantify, analyse, and predict temporal changes in the structure of ecological communities as a function of ongoing changes in climate, land use, and other environmental drivers. Ecological communities comprise populations of multiple taxa. The structure of communities—the number of taxa (‘richness’) and their relative abundance (‘composition’)—changes through time because of fluctuations of individual

38 populations and local colonisations and extinctions of taxa (Micheli et al. 1999, Legendre and
39 Gauthier 2014). These temporal dynamics are governed by both intrinsic factors, including
40 intraspecific and interspecific interaction, colonisation, and extinction, and extrinsic factors,
41 which are processes that relate to periodic disturbances and directionally changing
42 environmental conditions (Connell and Slatyer 1977, Brown and Lawson 2010).
43 Understanding the temporal dynamics of community structure can illuminate fundamental
44 ecological processes, including effects of individual life histories on rates of ecosystem
45 change, the relative importance of biotic and abiotic factors in determining community
46 structure, or how taxa and the networks in which they are embedded respond to
47 environmental change (Tilman 1999, Hobbs et al. 2007, Kampichler et al. 2012). Temporal
48 changes in taxon richness and composition also can provide both simple summaries of
49 ecosystem change and information that can be translated rapidly into action, either to protect
50 and restore declining taxa, or to staunch unsustainable growth of unwanted organisms.

51 Representations of community structure as multivariate datasets that include
52 information on multiple taxa can be more sensitive to changes in explanatory or predictor
53 variables (e.g., pH, temperature, soil type), than univariate summary statistics, such as taxon
54 richness, diversity, or biomass (Micheli et al. 1999, Chao et al. 2014), and hence more
55 informative about causal processes. However, quantitative methods for investigating and
56 testing hypotheses about temporal dynamics of multivariate measures of community structure
57 (henceforth 'community dynamics') also are more complex than methods used for univariate
58 data (Schaefer et al. 2005, Legendre and Legendre 2012). To date, methods for the analysis
59 of spatial multivariate community structure data (e.g., Whittaker 1960, Legendre and
60 Legendre 2012) have received far more attention than methods for analysis of temporal
61 multivariate data. Well-known concepts used to describe spatial changes in community
62 structure—grain, extent, nestedness, beta diversity, taxonomic turnover—have been

transferred to the temporal domain (Azeria and Kolasa 2008, Anderson et al. 2011, Legendre and Gauthier 2014), and some well-developed multivariate methods for large spatial datasets have been used to detect temporal changes in community structure (Legendre and Gauthier 2014). However, although temporal studies of compositional change are commonly undertaken, it is not always clear which analytical methods are appropriate or available for any given research question, data type, or community structure; indeed, there may not be one ideal method for all situations and a range of methods may be required to answer a given question (Whittaker 1960). Comparisons of multivariate ecological data through time pose unique, non-trivial challenges because these analyses must also account for spatial variation in these data, (Philippi et al. 1998, Micheli et al. 1999, Collins et al. 2000, Schaefer et al. 2005).

In this paper, we: (1) review empirical studies that have undertaken analyses of multivariate temporal community datasets, to gain insight into how researchers have been applying analysis methods over the past several decades, (2) provide recommendations for the greater use of quantitative methods for testing specific temporal hypotheses, and (3) provide guidance for researchers, including those new to community dynamics research, in analysis decisions, particularly for small temporal datasets (fewer than 15 temporal replicates).

How to use this paper

This paper does not necessarily need to be read from start to finish; we suggest readers identify the section(s) most appropriate for their interests. The remainder of this paper is structured into five main sections: (A) a review of the recent literature; (B) a conceptual description of the types of hypotheses that can be addressed in analyses of temporal community dynamics data; (C) three worked case study examples illustrating hypothesis-driven analyses of temporal community data, including code for the software programme ‘R’

(R Core Development Team 2017) to allow readers to easily implement methods described in this paper; (D) A "road map" to analysing temporal community data, including descriptions, and how to identify and present, analyses appropriate for testing particular hypotheses; (E) A brief discussion of recent advances in multivariate analysis of community dynamics.

A. LITERATURE REVIEW

DATA COLLECTION AND ANALYSIS

We reviewed and described the multivariate analyses of community dynamics in studies published up until September 2017 to provide an overview of available methods, their benefits and drawbacks, and what they can reveal about community dynamics. Specifically, we asked: Are data collected from different taxonomic groups, habitats, spatial extents, and time-scales analysed in particular (or different) ways, i.e., are there consistencies in analysis approaches due to discipline-specific preferences?

We searched the literature for studies investigating changes in ecological communities over time. We searched the ISI Web of Science Core Collection on 5 September 2017 for articles using the following search statement: ["temporal" AND "composition*" AND "communit*" AND ("community dynamic*" OR "temporal dynamic*" OR "temporal community varia*" OR "community change" OR "compositional change")]. We refined this search to include only document types listed as 'articles' and published in 'English'. This search yielded 692 articles for review. Of these, we excluded 241 papers that lacked community data (i.e. those that included fewer than three taxa), had no temporal replication or pooled all temporal data, used only artificial communities or simulated datasets, or used space-for-time substitution (e.g., using chronosequences) to infer community ages. Although we did not constrain the temporal search window, our search terms only returned papers after 1990, indicating that the specific terms we used were not part of the compositional change literature prior to the 1990s.

We extracted and collated key attributes relating to each study in the remaining 451 papers from the ISI database (e.g., publication year, number of citations). Specific study attributes were determined from the body text of each manuscript, including information on (i) habitat type (e.g., estuarine); (ii) habitat location (e.g., U.S.A.); (iii) taxonomic identity (e.g., vertebrate; fish); (iv) manipulation (e.g., natural variation, experimental resource manipulation); (v) spatial extent (e.g., local, global); (vi) temporal grain and extent (e.g., minutes, months); (vii) how composition was measured (e.g., presence-absence, relative abundances of taxa); (viii) how time was included in each analysis (i.e., explicitly as a predictor variable, or where other variables represent time, e.g., climatic factors recorded at different times); and (ix) the key perceived research question (e.g., exploration of yearly dynamics) (Data S1). We categorised organisms being studied into the following taxonomic groups: plants (Kingdom Plantae); vertebrates (Phylum Chordata); invertebrates (Phyla Annelida, Arthropoda, Cnidaria, Ctenophora, Echinodermata, Mollusca, Platyhelminthes, or Porifera); microeukaryotes (algae and Kingdoms Fungi and Protista); prokaryotes (Domains Bacteria and Archaea); and viruses (non-cellular pathogenic organisms). The data types collated and included papers are provided in the supplementary material (Data S1).

LITERATURE REVIEW RESULTS AND DISCUSSION

The 451 papers identified by our search, when compared by year to the number of papers in community ecology, showed that every year since 1990, publications on temporal community dynamics consistently have comprised approximately 24% of studies within community ecology. Thus, studies on temporal dynamics have increased from less than five publications per year in the early 1990s to more than 30 per year in the last five years (Appendix S1: Fig. S1). Few of the 451 reviewed publications (20 papers; 4% of those reviewed) contained more than one independent dataset; those instances were treated as multiple studies that were analysed as separate data points (increasing our total sample size *n* to 475). The majority of

138 studies (70%) were conducted within North America and Europe (Fig. 1), likely reflecting the
139 relative availability of research funding and resources.

140 Reviewed studies generally focused on organisms, scales, and habitats that were
141 conducive to studying temporal community dynamics. For instance, prokaryotes and
142 invertebrates were studied most frequently (Fig. 1), being relatively dynamic and easy to
143 study over smaller temporal and spatial scales; by contrast, research on plants and vertebrate
144 fauna together accounted for less than one-third of all studies of community dynamics.
145 Although studies spanned a broad range of habitat types, taxa, spatial, and temporal scales,
146 there were two-to-three times more studies at small spatial extents (micro, point sample, and
147 local scales) across the 14 habitat categories identified from the articles (Appendix S1: Fig.
148 S2A). Similarly, the most common temporal extent (i.e., the time between the collection of
149 the first and last samples) of individual studies was years, and only a minority of studies on
150 plant and vertebrate communities extended for a decade or more (Appendix S1: Fig. S2B).
151 Smaller organisms were often measured at finer temporal resolutions (grain) than larger
152 organisms, and many studies on short-lived prokaryote and viral communities lasted more
153 than one year. The temporal grain of sampling generally was smaller for communities of
154 microorganisms than for communities of vertebrate animals and plants, for which the most
155 common grain for repeated sample collection was years rather than months or seasons
156 (Appendix S1: Fig. S2B).

157 Researchers frequently used a range of different analytical methods, even within one
158 study, to enable them to understand the complexities of observed temporal changes. Up to
159 eight different analytical methods were used (Fig. 2A), with about two-thirds of the studies
160 applying ≤ 3 methods, and most using two. Although the number of studies addressing
161 community dynamics have increased dramatically since the 1990s and have begun to
162 incorporate more computationally-complex methods over time (Appendix S1: Fig. S3A),

163 descriptive methods (i.e., visual, non-statistical comparisons) and ordination have remained
164 the most commonly-used analyses, comprising 33% and 22% of all applied methods,
165 respectively (Fig. 2B). In fact, 134 out of 451 studies (30%) used only descriptive approaches
166 to "analyse" their datasets, while another 35% of studies used descriptive methods in addition
167 to at least one other method. We suspect that the overall ease of use of descriptive and
168 ordination methods, their accessibility via readily-available software programs, and their
169 focus on visually-presenting complex multivariate data, together have driven this trend. The
170 use of the raw dissimilarity values (18%), time-lag analysis (9%), and cluster analysis (7%)
171 comprised the next most common types of methods; the remaining 12 methods were used
172 infrequently (Fig. 2B). Several methods captured by this review were not multivariate (see
173 Appendix 2), including univariate linear methods, temporal stability (*a.k.a.* coefficient of
174 variation), frequency change (testing for significant changes in the frequency of individual
175 taxa over time), and multiplicative change (percent cover change statistic for a single taxon or
176 taxon group used in subsequent regression analyses). Since 2005, the use of raw dissimilarity
177 methods has increased considerably. In the same decade, a steady stream of alternative
178 methods that incorporate time explicitly have been applied, albeit with poor uptake across the
179 wider literature in this area. These methods often are 'one-off' analyses that have been
180 applied only a handful of times; we refer to these as 'minor' methods (Appendix S1: Fig. S3).
181 Preferred ordination methods changed from detrended correspondence analysis (DCA) and
182 principal components analysis (PCA) in the early 1990s, to canonical correspondence
183 analysis (CCA) in the late 1990s, and, since the early 2000s, to non-metric multidimensional
184 scaling (NMDS) (Appendix S1: Fig. S3B).

185 Three-quarters of all analyses compiled were from observational studies aimed at
186 describing patterns of community change or related to monitoring community composition,
187 rather than exploring environmental effects or studying the effects of biotic processes or

188 interactions (Appendix S1: Fig. S4). In fewer cases, researchers were interested in the effect
189 of environmental change, such as seasonality or climatic cycles over longer time periods.

190 Our review also shows how common it is for researchers to analyse datasets with low
191 temporal replication. Across research aims and for most methods, most time series had fewer
192 than 15 observations (mean = 14.9, median = 7, mode = 4; Fig. 3); the few studies that used
193 network analyses and machine-learning methods used 50 or more observations taken through
194 time. Overall, neither the number of temporal replicates, nor any other study attributes we
195 extracted during our review (e.g., habitat, taxonomic group), appeared to explain well the
196 differences in how researchers analysed their data or their motivations for doing so.

197 Typically, researchers will have some notion of how their communities of interest
198 might be changing, which motivated them to undertake temporal sampling in the first place
199 (Bestelmeyer et al. 2011). In some cases, long-term datasets exist because previous
200 researchers began data collection with a rationale and method that is different from the
201 current research questions, and so we can sometimes be limited by past sampling designs.
202 Nonetheless, our review highlights that most studies describe temporal community dynamics
203 within their studied communities without explicit, quantitative hypotheses and specific,
204 testable predictions about the expected drivers of observed community changes (Appendix
205 S1: Fig. S4). Clearly, there are many benefits to entering the analysis pathway with a strong *a*
206 *priori* prediction of the compositional pattern(s) expected and the biological hypotheses that
207 underpin those predictions.

208 **B. HYPOTHESES OF TEMPORAL COMMUNITY DYNAMICS**

209 Quantitative and specific predictions of the nature and variability in temporal community
210 dynamics allows deeper understanding of the patterns and processes involved. However, to
211 achieve this, *a priori* expectations of change need to be developed and paired with the
212 appropriate analytical method(s) to achieve rigorous tests. Here, we describe in detail the

213 possible observed changes in community composition (taxon presence or abundance) in one
214 sampling unit (site, host, etc.) over time (Fig. 4) or in a set of sampling units over time (Figs.
215 5-7) and what some of the ecological research questions are that may underpin such
216 hypotheses. In each case, we give predictions for how pairwise dissimilarity values, the basis
217 for most of the commonly-used quantitative measures of compositional change identified in
218 the literature review, would change. Many of these hypotheses are not mutually exclusive
219 although some could be used as multiple alternatives to be tested simultaneously, depending
220 on the research question(s) of interest. Note that 'dissimilarity measures', also called
221 'distance measures' or 'beta-diversity', are the inverse of 'similarity measures'. These
222 metrics quantify the compositional distance between two samples (pairwise dissimilarity).
223 *Simple predictions for a single sample unit: Persistence and directional change*
224 Aside from the 'null' prediction of no change in composition ('persistence'; Fig. 4b), one of
225 the simplest predictions of compositional dynamics is that of 'directional' change, whereby
226 certain taxa either increase or decrease so that the dissimilarity of a sampling unit to itself at
227 previous sampling occasions increases (or decreases) over time (Fig. 4c); when composition
228 turns over as taxa are replaced, the magnitude of change in dissimilarity can be high. Such a
229 hypothesis could arise from many ecological processes, e.g., has the community undergone
230 'succession', whereby there is a predictable replacement of individual or groups of taxa over
231 time; has it undergone 'degradation', whereby rare taxa are lost from the system over time;
232 has it had an 'invasion' event, where the relative dominance of one taxon or functional group
233 increases; is it changing in composition in response to a changing biotic or abiotic variable,
234 such as predation or temperature?
235 *Simple patterns for multiple sample units: Directional change, divergence and convergence*
236 Where a set of sample units are all undergoing the same directional changes in composition
237 over time, pairwise 'spatial' dissimilarity among that set of sampling units, would not change

238 significantly over time, because all sampling units are moving in the same direction at the
239 same rate in compositional space because the same taxa are changing in the same ways (Fig.
240 5b). We also might ask whether sample units are becoming more dissimilar to each other, due
241 to interactions between the changing factors described above and characteristics of the
242 community, such as initial composition or differences in habitat conditions. In this case
243 'divergence' represents the hypothesis where a set of sampling units are all becoming more
244 dissimilar in their composition, so that their pairwise dissimilarities increase over time; this
245 term therefore does not apply to change within one sampling unit (Fig. 5c).

246 Two very similar patterns predict decreasing pairwise dissimilarity values over time.
247 In contrast to 'divergence', under 'convergence' taxonomic composition of two or more
248 sampling units becomes more similar over time (Fig. 5e) in a predictable way because of
249 increases or decreases in taxon presence or abundance; this is also called 'homogenisation'
250 (Fig. 5e), where there is a concurrent decrease in diversity and dissimilarity becomes
251 relatively low. In contrast, convergence simply implies that between sample-unit dissimilarity
252 declines over time, but not necessarily to a very low level. In the cases where taxa are lost,
253 the predicted overall decline in dissimilarly is large. These hypotheses of change would be
254 relevant if we are interested in the effects of an experimental treatment designed to increase
255 the growth of a particular set of taxa, or under invasion, such as the biotic homogenisation of
256 cities due to urbanisation, or loss of native taxa due to competition with the invading taxa.
257 Note that the predicted effect of invasion on dissimilarity values depends on whether we are
258 considering the trajectory of one sample unit (divergence) or many sample units
259 (convergence) and the among-sample unit variation in other interacting factors.

260 *More complex temporal patterns: Perturbations, resilience, and cyclical change*

261 More complex patterns in temporal dynamics involve compositional shifts that change in
262 their magnitude or direction over time. Natural or manipulative experiments asking questions

263 about the effects of disturbance on community composition can lead to complex predictions
264 of change. 'Perturbation' is a pattern for which the change in composition is initially high but
265 lessens over time and can be detected by comparison to undisturbed treatments or areas (Fig.
266 6a). The perturbation can occur as either a 'press perturbation' (Fig. 6b), such as the removal
267 of a predator or a continuous nutrient addition treatment, or a 'pulse perturbation' (Fig. 6c),
268 such as a disturbance event or a population density reduction; these two perturbations result
269 in different rates of change in pairwise temporal dissimilarities. Post-perturbation, a
270 community either could remain in a state that is dissimilar to un-perturbed sample units
271 ('tipping point'), or could return to its previous state over time ('resilience'). The prediction
272 of a 'pivot point' or 'threshold' can be used to test for a significant compositional shift for
273 one or more sampling units over a relatively short period of time, meaning that temporal
274 pairwise dissimilarity among times for each sampling unit is low before, and also after, the
275 pivot point, but is high for temporal pairs across the pivot point (Fig. 6c).
276 Questions about the scale of temporal dynamics in a community, such as the presence
277 of seasonal cycles, lead to predictions of 'cyclical' change or 'periodicity', which represent
278 shifts in composition that repeatedly diverge and re-converge back to a previous state;
279 dissimilarity increases at short temporal scales but decreases at larger temporal scales, and
280 will alternate between high and low at increasing temporal scales that correspond to some
281 cyclical process, e.g., warming events (Fig. 4d).
282 *Predictability of change: Instability and stabilisation*
283 Questions about the predictability of compositional changes over time resulting from
284 interactions between causal-change processes, such as temperature shifts throughout a year,
285 and biotic or abiotic differences among sampling units, could also lead to hypotheses
286 regarding the variability in relative compositional change. For instance, 'instability' predicts
287 significantly increasing temporal variation in dissimilarity for a set of sampling units because

288 relative increases and decreases among taxa are not correlated or consistent; change is not
289 directional although mean dissimilarity would also likely increase with the variance (Fig. 5d).
290 In contrast, 'stabilisation' predicts the opposite: significantly decreasing temporal variation in
291 dissimilarity as initially significant compositional change lessens over time; pairwise
292 dissimilarity is initially high at short temporal scales (the opposite of Fig. 5d).

293 *Taxon dynamics: Synchronicity*

294 In many cases, we are interested in asking if different components of the community are
295 responding in similar or different ways over time. Where individual taxa, or particular groups
296 of taxa (e.g., functional groups), change in similar ways at the same time ('synchronicity'),
297 we can detect this because among-taxon-group dissimilarity increases, but within-taxon-
298 group dissimilarity does not change (this involves comparing the pairwise sampling unit
299 dissimilarities separately for different taxonomic subsets) (Fig. 7a). Synchronicity may result
300 in directional or other types of compositional dynamics patterns within one sampling unit or a
301 set of sampling units (Fig. 7b).

302 Hypotheses of biological processes causing dynamics may be very specific, such as a
303 decrease in certain prey taxa in response to a predator, or more general, such as a shift
304 towards a grassland community in response to fire disturbance of a woodland or an increase
305 in annual plant taxa in spring compared to winter. More specific and directional (increases or
306 decreases) hypotheses lead to more powerful tests of compositional change; we strongly
307 encourage researchers to generate such hypotheses *a priori* and to pair these with predictions
308 that are as quantitative as possible, e.g., define the predicted timescales of variation.

309 C. WORKED CASE STUDY EXAMPLES

310 Here, we provide three worked examples to demonstrate the hypothesis-testing approach we
311 advocate for different types of community dynamics. We used open-access datasets to test
312 for: (1) significant divergence in temporal community dynamics among disturbance

313 treatments imposed upon plant communities in experimental grasslands, (2) neutral
314 community dynamics for a fully-censused forest plot, and (3) seasonal (cyclical) temporal
315 dynamics in marine aquatic bacterial communities. We present a brief description of each
316 dataset and describe the results and interpretation for the relevant exploratory data analysis
317 (EDA; see section 'D. Road map for analysing temporal community dynamics') and
318 hypothesis-testing analyses. More detailed descriptions, explanations and R code for each
319 case study are provided as supporting information (Data S2-4).

320 **TESTING FOR DIVERGENT COMMUNITY DYNAMICS WITHIN A CONTROLLED EXPERIMENT**

321 Porensky et al. (2016a, 2016b) measured plant species composition annually from 2007 to
322 2014 in quadrats on 24 transects to which six grazing treatments were applied since 1982
323 (four transects in each treatment): none (exclosure), light, moderate, heavy, heavy-to-light
324 (lightly grazed since 2007; 'new light') and heavy-to-none (new exclosure since 2007). They
325 calculated the mean cover in 25 quadrats for each species on transects. We tested the
326 hypothesis that increasing grazing intensity causes increasing divergence (directional change;
327 as detailed in section B) in species composition relative to the control (no-grazing) treatment.

328 EDA (as described in section D)) showed that the 24 transects were dominated across
329 all measurements by ten common species out of a total of 92 species (Data S2: row and
330 column summaries, relative abundance plots and rank abundance curves). Species turnover
331 (section D 4.0) through time was high; mostly 30% or greater for time period-treatment
332 combinations (Fig. 8). Principal coordinates analysis (PCoA; section D 1.4 Ordination)
333 suggested that the main compositional differences corresponded to the grazing treatments,
334 and that transect composition changed over time, but not markedly (Data S2: PCoA analysis
335 and figure). PERMANOVA (section D 1.4a) showed that transects were significantly
336 compositionally distinct and changed significantly over time in different ways (Data S2:
337 PERMANOVA outputs – all three coefficients for a two-way PERMANOVA with transect,

338 year and their interaction were significant $P < 0.05$). Partitioning spatial and temporal beta
339 diversity (section D 1.2) showed that two of the control (exclosure) treatments differed
340 significantly (Fig. 9). Principal Response curves (section D 1.4b) showed that the grazed
341 treatments differed from the control and that the relative abundances of four species in
342 particular were influential in driving these differences among treatments, but did not show
343 increasing divergence over time (Fig. 10). This result is consistent with the analysis of
344 temporal coherence (icc = -0.04; see section D 1.4a and Data S2 for detailed description of
345 this statistic), which showed that transects were not synchronous in their temporal changes
346 (Data S2: temporal coherence analysis). Thus, we conclude that treatment differences in
347 turnover and shifts in composition were not consistent or directional and so we reject our
348 hypothesis that increasingly grazed transects diverged more over time relative to the control.

349 **TESTING FOR NEUTRAL COMMUNITY DYNAMICS ACROSS SPATIAL SCALES**

350 The 50-ha forest census plot on Barro Colorado Island, Panama, has been censused eight
351 times between 1982 and 2015 (Condit 1998, Hubbell et al. 1999,
352 http://ctfs.si.edu/webatlas/datasets/bci/, 2005). This plot was established in part to test for
353 neutral community dynamics (Hubbell 1979) by fully censusing all woody stems greater than
354 1 cm diameter at breast height every five years. Under this hypothesis, we expected to see no
355 directional or other patterns in temporal community dynamics ('persistence'; as described in
356 section B.). EDA showed that the dataset consisted of 324 species generating a highly right-
357 skewed abundance distribution (most species were rare) (Data S3: EDA analyses and section
358 D). A line graph plot of species' abundance values over time showed very little change in
359 total abundance over time (Data S3: line graph of abundance; Appendix S2: Univariate linear
360 methods). Two analyses that allowed us to test for stability in community composition in
361 time, i.e., change in species composition is lower than expected if individual trees were
362 randomly distributed in time (keeping their spatial positions fixed), showed that change in

363 species composition was lower than expected: (1) Zeta diversity analysis (Data S3: zeta
364 diversity and section D 2.0) showed that the presence of species across census times was
365 more consistent than expected (Fig. 11) and (2) total turnover in species abundances (Data
366 S3: total turnover rates analyses and section D 4.0) at each of the seven time periods was
367 lower than expected (Fig. 12), particularly when the plot data were at larger spatial scales.
368 Thus, we conclude that the observed lack of pattern is consistent with our hypothesis of
369 neutral community dynamics.

370 **TESTING FOR SEASONAL COMMUNITY DYNAMICS**

371 Gilbert et al. (2012) measured bacterial taxonomic composition monthly over six years using
372 pyrosequencing of the 16S rRNA gene for water samples from a single site off the coast of
373 Plymouth, United Kingdom (source data can be obtained from the journal's online
374 supplementary file). We tested the hypothesis that subsets of the community would show
375 cyclical patterns of temporal change due to seasonality. EDA (section D) showed that the
376 dataset consisted of 74 operational taxonomic units (OTUs) across 62 temporal samples.
377 Most taxa were common through time. Proportional turnover between temporal samples
378 varied from 4% to 48% (Data S4: turnover calculation and section D 4.0), which is relatively
379 low, and was consistent with the detrended correspondence analysis (DCA) result showing a
380 short gradient length of 1.8 for axis 1 (Data S4: DCA and section D. EDA). Similarly, PCoA
381 graphs (section D. EDA) showed little consistent change within years (Fig. 13). However, 13
382 of the OTUs were deemed to be highly variable in that they changed by more than 500 reads
383 across the sampling period (mean number of reads = 296 ± 829 S.D..; Data S4: row and
384 column summaries, relative abundance distributions and abundance plots and section D.
385 EDA).

386 Time-lag analysis (section D 1.3) showed that although there was a significant
387 increase in dissimilarity within increasing time lag, variability was high, showing that

temporal changes did not occur in a simple divergence over time pattern (Fig. 14). Temporal synchrony analysis (sensu Loreau and de Mazancourt 2008) showed that some subsets of OTUs in the community were significantly changing in similar ways (Synchrony = 0.27; $P < 0.05$; Data S4: temporal synchrony analysis and section D 3.0). When patterns in these variable taxa were examined through time using zeta diversity analysis (Hui and McGeoch 2014) (Data S4: zeta diversity analysis; section D 2.0), which is based on the presence of species in samples, winter samples shared significantly more species across sets of temporal samples than autumn, spring and summer (Fig. 15; ANOVA, $P < 0.01$; Appendix S2: Univariate linear methods). Further analysis of the most variable taxa using the raw dissimilarity values based on abundance data calculated for temporal samples within seasons showed clear cyclical patterns (Fig. 16; Data S4; section D 1.1). Thus, we conclude that the patterns are consistent with our hypothesis of seasonal dynamics in community composition, largely driven by a small subset of OTUs that varied in their abundance, rather than presence, over time.

D. ROAD MAP FOR ANALYSING TEMPORAL COMMUNITY DYNAMICS

The two most common sets of methods seen in our review of the temporal community dynamics literature were descriptive (mostly tables and figures that show changes in taxon presence or abundance) and ordination-based methods. Although these techniques are useful for illustrating temporal trends and qualitatively exploring patterns in the data, they are used less often for testing specific quantitative hypotheses of patterns and processes in community dynamics. We recommend that researchers augment such descriptions with methods that quantify temporal dynamics in taxonomic composition in more powerful ways, thus allowing more quantitative and potentially comparable descriptions of spatiotemporal patterns and explicit hypothesis-testing of mechanisms underlying observed patterns in community dynamics.

413 Once the hypotheses to be tested have been generated, we suggest that researchers
414 undertake five steps: (Step 1) perform exploratory data analysis (EDA), (Step 2) choose
415 multivariate methods that can test the *a priori* temporal hypotheses, (Step 3) test for statistical
416 significance, (Step 4) report on the analysis workflow, and (Step 5) consider how to present
417 the results of the selected methods in the text and in figures.

418 **STEP 1: EXPLORATORY DATA ANALYSIS (EDA)**

419 As with any data analysis, the first step in the analysis of temporal community dynamics is an
420 exploratory data analysis (EDA) phase (Zuur et al. 2010). This generates basic information
421 that can be used to both error-check the data and to gain an understanding of key aspects of
422 the dataset (Table 1). R code for the relevant EDA steps is provided in three worked
423 examples, described previously (Data S2-4).

424 ***a. Count the number of taxa, the number of samples and the number of empty***
425 ***samples and missing data points***

426 The ratio of the number of taxa and samples is an important consideration because some
427 multivariate methods are more susceptible than others to the influence of rare taxa (Lepš and
428 Šmilauer 2003) and these may be of more or less interest, depending on the research
429 hypotheses. Whilst long-term data and monitoring are highly valued (e.g., Hobbs et al. 2007),
430 it is unfortunately common for long-term datasets to contain missing values; these values
431 should be denoted as missing (i.e., 'NA' in R) and not given zero or other numerical values.
432 The importance of missing values and how to deal with them during data analysis depend on
433 the number of missing data points and how they are distributed across the dataset.
434 Multivariate analyses based on compositional dissimilarities, e.g., some ordination methods,
435 cannot be applied to datasets containing samples where no taxa are present (McCune and
436 Grace 2002). However, empty samples may be important for analyses where we are

437 interested in understanding responses to disturbance and local extinctions. The ratio of the
438 number of explanatory variables to the number of independent replicates is also important for
439 temporal analyses because it affects the degrees of freedom available for statistical testing
440 (Johnstone and Titterington 2009).

441 ***b. Examine taxon frequency distributions and response curves***

442 Some multivariate analyses assume specific frequency distributions of taxa (a histogram of
443 the number of individuals or their relative abundance across samples for each taxon), e.g.,
444 CCA assumes that taxa have optima along environmental gradients ('unimodal' responses).
445 Examining the shapes of taxon frequency distributions is necessary for determining whether
446 taxa are responding strongly to environmental gradients in the dataset and whether their
447 distributions conform to analysis assumptions. Where many taxa are involved, the common
448 ones should be examined.

449 ***c. Determine the ratio of temporal to spatial variation in composition***

450 The degree of spatial and temporal replication is important in determining the method of
451 analysis because few sites with many measurements over time would be analysed differently
452 from many sites measured only a few times. If the data have a nested structure, e.g., samples
453 are nested within sites, this needs to be accounted for in the analysis, particularly if one wants
454 to report significance values. For example, if plant species composition was recorded in
455 quadrats that were nested within transects that were nested within sites, then quadrats are not
456 fully independent replicates. Similarly, information from technical replicates (such as PCR
457 products) should be kept separate at this stage because they provide useful information about
458 variability at different scales in the dataset. It is inadvisable to average or pool data until the
459 significant sources of variation are understood. For instance, if we want to test hypotheses of
460 temporal dynamics, but there is a high degree of spatial variation among samples in the

461 dataset, this can alter analysis choices or how results are presented and interpreted (Thrush et
462 al. 2008). The relative amount of change in taxonomic composition can be estimated from the
463 differences in sample scores on DCA ordination axes, e.g., the 'gradient length' statistic
464 quantifies the turnover in taxonomic composition (Lepš and Šmilauer 2003); this relatively
465 descriptive analysis would ideally be conducted as part of the EDA process prior to selecting
466 an analysis pathway appropriate for testing a quantitative hypothesis of temporal dynamics,
467 such as divergence or convergence.

468 ***d. Determine the optimal dissimilarity measure***

469 A community dataset may be an abundance matrix (number of individuals), relative
470 abundance matrix (e.g., percent cover, sequence abundances), rank-abundance matrix
471 (ordinal abundance ranks), or a taxon-occurrence (presence-absence) matrix. These different
472 response variables can influence the choice of analysis methods, including which distance
473 measure to use to calculate pairwise community dissimilarity values for samples (see
474 Magurran 2004, or Legendre and Legendre 2012 for a comprehensive description). To ensure
475 that abundance data from different taxa are comparable using dissimilarity, data should be
476 standardised prior to analysis if they are measured on different scales (Legendre and
477 Legendre 2012). For example, taxon abundance values within each sample can be divided by
478 the total abundance within the sample, or can be standardised across all samples so that each
479 taxon has a mean of zero and standard deviation of one (Borcard et al. 2011). Alternatively, a
480 distance measure that incorporates a standardisation can be used, e.g., Hellinger distance
481 (Legendre and Gallagher 2001, Anderson et al. 2011, Legendre and Legendre 2012). The
482 commonly-used Euclidean distance measure is not usually appropriate for taxon abundance
483 data, which are often characterised by non-linear relationships among taxa, abundance values
484 measured on different scales, or by the 'double-zero problem', which is the idea that samples
485 that are missing the same taxa and therefore, have lower dissimilarity when using this

distance measure (Borcard et al. 2011). Comparing results based on presence-absence data with those generated using relative abundance data allows us to evaluate the role of taxon abundances in generating temporal patterns (e.g., Angeler and Johnson 2012). Estimating abundances of each population within the community has its own important considerations, i.e., variation in taxon detection probabilities, which have been addressed elsewhere (e.g., animals: Gaston and McArdle 1994, metagenomics data: Amend et al. 2010). Many distance measures cannot be computed if there are empty samples or missing values. Deleting entire rows or estimating missing data so that the dataset can be analysed may be an option in some cases (McCune and Grace 2002). However, other measures, such as the Gower coefficient, can be calculated while ignoring comparisons among samples with missing data (Legendre and Legendre 2012; coefficient S15: 278).

STEP 2: CHOOSE ANALYSES FOR TESTING HYPOTHESES OF TEMPORAL DYNAMICS

In this section, we describe a range of methods for testing hypotheses of community dynamics, including their outputs, highlighting in each case, the relevant ecological questions and the kinds of hypotheses that those analyses can be used to address: pairwise dissimilarity-based methods (section 1, below), zeta diversity (section 2), synchrony (section 3), turnover rates (section 4) and multivariate regression modelling (section 5). Further, each of the described methods has been cross-referenced with (i) which hypotheses it is best suited to test; (ii) whether or not it allows the identification of individual taxon effects on, or responses to, temporal change; (iii) whether or not explanatory and spatial variables can be explicitly incorporated; (iv) the type of statistical testing normally used; and (v) any requirements for the length of the time series (number of temporal samples) (Fig. 17). The selection of an appropriate analytical method also can be influenced by the kind of output desired (Table 2). For instance, some analyses result in outputs that require more effort to interpret than others, whilst others show differences in taxon responses or generate outputs that can be added to a

511 geographic map. Further, as our literature review highlighted, in many cases several different
512 analytical methods often are appropriate for asking questions about temporal dynamics and
513 presenting the results at the desired level of complexity; it is also the case that many analyses
514 can be used to test a wide range of hypotheses, so our focus is on describing the strengths of
515 each analysis method and the minimum requirements for use, rather than on making explicit
516 recommendations. Thus, we recommend that, at this point, readers use Tables 2 and 3 to help
517 identify the methods of interest and then refer to the relevant sub-sections of section C that
518 describe those particular methods.

519 Our literature review revealed that in numerous cases, researchers performed and
520 compared separate analyses on their community matrices from each sample time, e.g.,
521 separate nestedness analyses at each sample time (Azeria et al. 2006); we do not specifically
522 address these applications here in any depth because these methods do not explicitly evaluate
523 community dynamics through time. We also focus on methods that are truly multivariate
524 rather than methods that are applied separately to abundances of individual taxa; however, if
525 less than ten taxa are of interest, it may be that hypothesis testing via univariate approaches
526 (e.g., separate linear regressions of taxon abundances) will be adequate for drawing synthetic
527 conclusions about community change. In the supplementary material (Appendix S2), we
528 summarise univariate methods that were commonly used in the literature review articles:
529 univariate linear methods, temporal stability (*a.k.a.* coefficient of variation), frequency
530 change, multiplicative change, and Markov chain modelling. A few studies used alternative
531 methods such as cluster analysis and network analysis; however, we excluded those because
532 we think the methods presented here provide equally good, or better, alternatives, but we
533 nonetheless provide an explanation of them (Appendix S2) because they appeared in our
534 literature review. Some of the analytical methods described below can be implemented in
535 several different software packages (e.g., PC-ORD, PRIMER, CANOCO), but, for simplicity

536 and widest accessibility, we illustrate their implementation in R (Data S2-4), except for
537 Moran's Eigenvector Maps (MEMs), which is given in Legendre & Gauthier (2014), and
538 Multivariate Autoregressive State Space modelling (MARSS), which is presented in the
539 documentation associated with the R package 'MARSS' (Holmes et al. 2012).

540 **1. Methods based on pairwise dissimilarity values**

541 Pairwise dissimilarity methods can be used to test nearly the full range of questions and
542 hypotheses in community dynamics (Anderson et al. 2011; Figs. 4-7). Pairwise dissimilarity
543 methods are the most frequent way ecologists quantify the difference in the identities of taxa
544 occurring in two samples. The result is a single number that measures the distance in
545 compositional space between the two samples. Dissimilarity can also be represented as
546 similarity, i.e., 1 − dissimilarity (Whittaker 1960, Anderson et al. 2011, Magurran 2013).
547 When applied to multiple samples, it results in a matrix of all possible comparisons (a
548 triangular dissimilarity matrix). For example, Collins (1992) measured the between-year
549 percent change in plant species composition for grassland plots that had been repeatedly
550 measured over a nine-year period. Dissimilarity methods are more desirable than univariate
551 methods, which analyse the abundance of each taxon separately, because they consider the
552 entire community at once and directly quantify change in community structure.

553 The development of dissimilarity indices is an active area of research. Magurran
554 (2013) is a useful general discussion of dissimilarity measures, Anderson et al. (2011)
555 provides a practical guide to selecting an appropriate index and issues of importance, such as
556 whether to include joint absences in the calculation. Different authors often use different
557 names for the same dissimilarity measure, so we recommend using a comprehensive and
558 consistent guide, such as Legendre and Legendre (2012; Table 7.4: 324). Legendre and De
559 Cáceres (2013) also provide comprehensive descriptions of most dissimilarity measures and

560 rationales for choosing one. Several recent advances are specifically relevant to temporal data
561 (e.g., Podani and Schmera 2011, Baselga 2012, Shimadzu et al. 2015) and some contributions
562 aid in improving dissimilarity measures for use in certain circumstances, such as imperfect
563 detection of taxa (e.g., Chao et al. 2006) or which indices are most appropriate for calculating
564 dissimilarity (Legendre and De Cáceres 2013). For example, the unique fraction (UniFrac)
565 dissimilarity metric was designed for microbial communities where phylogenetic information
566 is available from sequencing that has been used to determine taxa in samples (Lozupone and
567 Knight 2005, Lozupone et al. 2007). This metric measures phylogenetic distance between
568 samples as the fraction of branch lengths leading to descendants from each sample. UniFrac
569 can be used with abundance data, which weights the branch lengths prior to calculating
570 distances (weighted UniFrac), or with presence-absence data (unweighted UniFrac Lozupone
571 et al. 2007).

572 In the context of temporal community dynamics, dissimilarity is calculated in two
573 different ways: (1) separately among spatial samples at each of a series of time points or (2)
574 among samples taken at different times at the same location(s). Dissimilarity matrices are the
575 basis for several methods recommended in our guide, including ordination analyses and
576 Moran's Eigenvector Maps (MEMs). It is important to realise that it is not easy to use such
577 methods to simultaneously assess both temporal and spatial variation in the same analysis;
578 however, temporal and spatial dissimilarity can be computed and assessed in parallel to test
579 hypotheses and make inferences about spatiotemporal community dynamics (e.g., Legendre
580 and Gauthier 2014, Lamy et al. 2015).

581 *1.1. Using the raw dissimilarity values*

582 There are two ways in which raw dissimilarity values for samples are typically used.
583 Either of these approaches could be used for different taxonomic subsets of the community to
584 test hypotheses of taxonomic variation in dynamics. First, compositional dissimilarity can be

585 calculated among samples taken at different locations to obtain a measure of spatial
586 heterogeneity in community composition. To use these values to analyse temporal
587 community dynamics, pairwise dissimilarity (spatial dissimilarity) must be calculated
588 separately for each sampling time, and the means of these spatial dissimilarity values can
589 then be compared across time visually in a table (e.g., Collins 1992), graph (e.g., Barros et al.
590 2014), or using a correlation or regression analysis where time is the predictor variable and
591 amount of spatial variability at each site is the response (e.g., Barros et al. 2014). The mean
592 dissimilarity can be divided by the number of taxa to generate an independent measure of
593 compositional change (Cleland et al. 2013). Such comparisons over time could be done
594 separately for different groups of samples, such as different experimental treatments, to test
595 for predictors of differences in temporal change in composition. Bagchi et al. (2017) illustrate
596 predictions of how temporal differences in dissimilarity can include non-linear patterns and
597 thus how applying linear and non-linear regression modelling to pairwise dissimilarity values
598 can be used to test more complex hypotheses of temporal dynamics. Regression approaches
599 can also include mixed-effects models that account for nesting and other types of non-
600 independence in the data, or non-linear models (e.g., generalised additive models) that may
601 be useful to predict cyclical or threshold patterns in community dynamics (e.g., Shenhav et
602 al. 2017). However, these modelling methods will apply well only in situations with longer
603 time series (i.e., greater than 25 temporal replicates) and the more complex the prediction of
604 temporal change, the greater replication is likely required. Alternatively, a Mantel test can be
605 used to compare pairs of dissimilarity matrices computed at different times and to test for
606 significant difference over time (see section in the main text 'Test for statistical
607 significance'). This approach is only useful for a small number of spatiotemporal
608 observations (i.e., ten or fewer) because the comparisons are pairwise.

Second, if a set of samples were all taken at the same site at different times, 'temporal heterogeneity' can be calculated using the mean dissimilarity of the entire sequence of temporal samples to obtain a single measure of within-site temporal variability (Collins and Smith 2006). If multiple sites are sampled through time, this method can be applied at different spatial scales (Collins 1992, Collins and Xia 2015) to examine spatial scale-dependent temporal dynamics (Collins and Smith 2006). Regression approaches that relate mean temporal dissimilarity values to other explanatory variables for sites or samples could be used to explore spatial variability in temporal change. Alternatively, the 'dissimilarity-overlap' method, first described by Bashan et al. (2016) and further explained by Kalyuzhny and Shnerb (2017), can be applied to raw dissimilarity values to test for similarity among samples in community dynamics. This method uses the relationship between the pairwise dissimilarity values and the proportion of individuals in pairs of samples that overlap taxonomically to detect if changes in taxonomic composition (degree of overlap) alters relative abundances in a consistent way across samples (dissimilarities). It can be used for very large numbers of samples and taxa and could be applied to different groups of taxa to test for synchronicity.

1.2. Beta diversity decomposition

'Beta diversity' is term used for several different types of measures in ecology, e.g., (Whittaker 1960, Baselga 2010, Legendre and De Cáceres 2013), including as a synonym for compositional dissimilarity. It always describes some measure of how taxonomic composition changes across a set of samples. A number of recent advances in the calculation of beta diversity have illustrated that, if calculated in particular ways, it can be 'partitioned' into different components that relate to different predictions of how taxa or their abundances change in space or time (Baselga 2010, Ellison 2010, Legendre and De Cáceres 2013). Beta diversity decomposition methods can be applied to testing almost any hypothesis of

634 compositional change (Fig. 17). The outputs are focussed on species replacement and
635 whether samples are subsets of each other (Table 2), so detecting patterns such as
636 convergence or divergence is very easy. However, depending on what subsets of the data are
637 used in separate calculations, beta diversity decomposition is equally able to detect rapid
638 shifts in composition, e.g., perturbation, tipping point, or increases or decreases in temporal
639 variability, e.g., 'instability' or 'stability'. Two approaches so far have been usefully applied
640 to quantifying community dynamics measured in the field (Baselga 2010, Baselga and Orme
641 2012, Legendre and De Cáceres 2013, Lamy et al. 2015).

642 First, when among-sample dissimilarity is measured as Sørensen's dissimilarity [(b +
643 c)/2a + b + c), where a is the number of shared presences and b and c are the number of
644 unshared presences in each of the two samples], the Simpson's dissimilarity index (also
645 known as 'species turnover': b / (b + a)) can be subtracted from this value, resulting in a
646 measure of 'nestedness' (Baselga 2010, 2012, Baselga and Orme 2012). This measure of
647 nestedness reflects the degree to which the species composition of smaller samples (lower
648 species richness) is encompassed by the species composition of larger samples (higher
649 richness); samples may differ in space or time. In contrast, 'species turnover' measures the
650 degree to which samples do not share species: how the identities of species differ among
651 samples. It is useful to separate these two components (nestedness and turnover) to obtain a
652 more informative quantification of beta diversity that reflects differences in the underlying
653 processes. Such separation can be done either pairwise or for multiple sets of samples
654 (Baselga 2010, 2017), and has been used to decompose temporal beta diversity in tests of
655 hypotheses unique to temporal data (e.g., Baselga and Orme 2012).

656 Second, and in contrast, Legendre & De Cáceres (2013) defined beta diversity as the
657 sums of squares in the variation of taxon abundance (or presence) corrected for the number of
658 samples. They partitioned this measure of beta diversity into two different components:

659 ‘Species contribution to beta diversity’ (SCBD) and ‘local contribution to beta diversity’
660 (LCBD), which describe, respectively, the relative contributions of different taxa and sites to
661 overall beta diversity (Table 2; Legendre and Gauthier 2014). This method allows for tests of
662 predictions of patterns in temporal community dynamics related to different taxa in the
663 dataset. For example, Lamy et al. (2015) decomposed beta diversity (based on Bray-Curtis
664 dissimilarity) of fish communities at each of 13 reef sites into contributions from biomass
665 replacement and biomass differences over time. They demonstrated that total biomass in the
666 community changed little, but that the observed significant temporal changes in fish
667 composition resulted from differential changes in the relative biomass of species.
668 Spatiotemporal patterns in the two components of fish community beta diversity were
669 visualised using principal coordinates analysis (PCoA).

670 *1.3. Time-lag analysis*

671 A time-lag analysis involves relating the amount change in composition to the amount of
672 change in time across increasing temporal distances, called ‘lags’ (Table 2). For example,
673 Collins & Xia (Collins and Xia 2015) compared plant species composition of repeatedly-
674 measured grassland transects across all time lags between 1989-2008 (from a 1- to 19-year
675 difference). There are two ways of assessing the time-lag effect on community dissimilarity:
676 graphically (‘time-decay curve’) and statistically (time-lag regression analysis). For
677 meaningful inference, time-lag graphs require at least five samples and statistical time-lag
678 analysis requires at least ten samples for each temporal sequence. For both approaches, the
679 pairwise compositional dissimilarity (temporal beta diversity) among temporal samples is
680 calculated first.

681 To generate a time-decay curve, pairwise temporal dissimilarity values are plotted
682 against temporal distance between samples (time lag; pairwise Euclidean distances in sample
683 times) to show how community dissimilarity changes as samples become further apart in time

684 (Collins 2000, Collins et al. 2000, Hallett et al. 2016). This graph can be then used to visually
685 assess whether community composition is converging (becoming more similar) or diverging
686 (becoming less similar) over time (e.g., Collins 2000). For example, Bar-Massada & Hadar
687 (2017) plotted temporal beta diversity (as Bray-Curtis dissimilarity) of plants in grazed and
688 ungrazed treatments in Mediterranean herb communities, revealing that composition diverged
689 over time, regardless of grazing treatment. Alternatively, temporal community dissimilarity
690 can be graphed against dissimilarity in environmental variables (rather than time), if the
691 primary research focus is on response of the community to environmental change rather than
692 time *per se*.

693 Time-lag regression analysis was developed specifically for data with greater than ten
694 time points to assess directional, cyclic or stochastic changes within communities (Collins
695 2000, Collins et al. 2000) and has been evaluated against other temporal analysis methods
696 (Angeler et al. 2009). For time-lag regression analysis, the pairwise compositional distances
697 are plotted against the square-root of the time lag, which reduces the bias that results from
698 having fewer data points at larger time lags (Collins 2000, Collins et al. 2000). A regression
699 line is then fitted to determine the pattern of compositional change. A significantly positive
700 relationship indicates that compositional changes in communities is directional, because
701 sampling points that are further apart in time are more dissimilar than those that are closer
702 together in time (i.e., Fig. 2 in Collins 2000). A negative slope shows that some convergence
703 towards the taxonomic composition at one of the earlier time points has occurred, because
704 measurements close together in time are more dissimilar in composition compared to those
705 further apart in time. No slope, or a non-significant regression, implies stochastic changes in
706 the community over time. Non-linear regressions also can be used to describe more complex
707 temporal patterns (Magalhães et al. 2007).

A robust measure of significance in time-lag regression analysis can be determined by running Mantel tests on the dissimilarity matrix and the matrix of pairwise distances among samples in time, with Monte Carlo permutations (Bêche and Resh 2007, Day et al. 2017). Time-lag regression analysis is appealing because it is intuitive, produces one statistic (the regression coefficient), and can be easily visualised (e.g., freshwater macroinvertebrates: Bêche and Resh 2007, gut bacteria: Dimitriu et al. 2013, and plants: Collins and Xia 2015). However, time-lag analysis only provides one value for each sampling unit, so further analyses may be required to investigate changes within treatments or groups.

1.4. Ordination

Ordination summarises multivariate community data by optimising relationships between high-dimensional samples and taxa in low-dimensional space to detect important ecological gradients in communities (Table 2). This dimensionality reduction means that they are not especially useful for directly testing, or visualising, complex changes in community composition over time, such as tipping points, cyclical patterns or synchronicity. However, more simple patterns, such as divergence or convergence, can be more easily detected. Ordinations are either unconstrained, meaning that they do not incorporate explanatory variables, or constrained, which assess the effect of explanatory variables, including time (e.g., Kent 2012, Legendre and Legendre 2012, Palmer 2019). Ordination methods, including constrained ordination and using the ordination scores from an unconstrained ordination in a regression model (e.g., general linear model, mixed-effects model) are only appropriate for testing hypotheses of community dynamics in cases where EDA shows that the ordination axes used strongly represent temporal compositional change and therefore explain a substantial proportion of the variation. This is because the amount of temporal compositional variation represented by the ordination axis scores will be low if there is not a strong temporal gradient along the axes. Ordination methods allow only weak inference of the

733 relationship between taxa and community dynamics if the temporal pattern is complex
734 relative to the ordination axes because some ordinations, e.g., DCA, only provide an
735 ordination axis score for taxa, and others do not provide 'species scores' at all, e.g., PCoA
736 and NMDS. PCoA can be used to calculate the amount of variance explained by the
737 ordination axes, which is important if a time-series analysis is to be performed using the axis
738 scores. Where species scores are not provided, weighted averaging can be used to plot points
739 for each taxon on the ordination diagrams to relate differences in site composition to
740 differences in taxon presence or relative abundance if you wish to examine the associations
741 between samples and taxa (McCune and Grace 2002). One advantage of PCoA is that the
742 first PCoA axis represents the gradient explaining the greatest amount of variation in
743 composition, followed by the second axis that explains the next greatest amount, and so on;
744 this is not the case for NMDS (McCune and Grace 2002). Therefore, it is recommended that
745 NMDS scores are not used in community dynamics analyses unless the amount of variation
746 explained by each axis is clearly stated in order to validate their use in further analyses. 'Co-
747 inertia analysis' can be coupled with ordination in a 'partial triadic analysis' to investigate
748 community dynamics in relation to environmental variables. This method may be particularly
749 useful when testing for temporal stability (Kidé et al. 2015).

750 a. Using ordination site scores to assess compositional change

751 Ordination axis scores for samples taken at different times can be used to quantify and test
752 hypotheses of compositional change. Ordination diagrams are visually appealing, but for
753 illustrating compositional change through time, it is difficult to interpret the magnitude and
754 significance of temporal dynamics without statistical testing, such as permutational analysis
755 of variance (PERMANOVA: Anderson 2001), unless temporal trends in the data are very
756 strong along the ordination gradients in composition. This difficulty is amplified if there are
757 many samples or if the sampling design includes a large number of sites, environmental

factors, or temporal replicates. Note that PERMANOVA requires the assumption of homogeneity of dispersion to be met (this can be tested using the "betadisper" function in the R package vegan; Oksanen et al. 2017). Further, ordination diagrams and their statistics computed for different matrices (different sets of taxa or sites) are not comparable; results of individual ordinations cannot be compared among them. The partial exception to this is Procrustes analysis, which can measure the distortion, or 'lack of fit' between two ordinations, or dissimilarity matrices (Jackson 1995, Peres-Neto and Jackson 2001). It can be used to identify which taxa are most important in differentiating between the two ordination patterns.

A more quantitative, and often more flexible, approach is to use the ordination axis 'site' scores in linear models with time and other explanatory variables of interest entering as predictor variables (e.g., Berthon et al. 2014, Broadway et al. 2015). For example, Cotton et al. (2015) used DCA scores as a response variable in a linear mixed model to investigate the importance of carbon dioxide, ozone, and time on arbuscular mycorrhizal fungal community composition. This is like doing a constrained ordination, such as RDA, dbRDA, or CCA, where time is used as a constraining explanatory variable in the ordination; these methods will test the significance of time and any other explanatory variables. However, it is more difficult within a constrained ordination to test for non-linear, cyclical or other complex temporal patterns, and in this case, using the ordination axis scores in a more complex model may be more useful.

Ordination axis scores for samples can be used to quantify temporal changes in other ways. For example, Quinn et al. (1991) developed a 'malleability index' by regressing the pairwise Euclidean distances between the first three dimensions of ordination space for temporal samples, against environmental variables. One potential problem with this method is caused by the tendency of ordinations to distort the relative distances (dissimilarity)

783 between samples, depending on, for example, differences in the number of rare taxa, and so
784 values from distance-based indices may not be comparable, even in different parts of the
785 same ordination.

786 Temporal coherence measures the degree to which a response variable is similarly
787 variable in time across a set of sites. In the case of measuring temporal coherence in
788 community composition, the multivariate response variable is taxonomic composition in the
789 form of ordination axis site scores (Angeler and Johnson 2012). Temporal coherence
790 compares the amount of temporal variation in the ordination axis site scores across a set of
791 sites by using statistics generated by an ANOVA of the site scores (using year and site as
792 factors) to calculate the 'intra-class correlation coefficient', which ranges from $-1/(n-1)$ to
793 $+1$, where n is the number of sites sampled, given that $n > 1$ (for calculation details see Zar
794 1996 pp 398, Rusak et al. 1999). High positive values of this metric indicate increased
795 coherence of the different sites in composition over time. The measure can be recalculated
796 while dropping each time in sequence (an ordered jackknife) to determine the relative effect
797 of each time on the overall value (Rusak et al. 1999). Different sets of sites or treatments can
798 be compared using a Fisher's *Z* test (Angeler and Johnson 2012) or randomisation test in the
799 case of low sample sizes (Rusak et al. 1999).

800 b. Principal Response Curves (PRC)

801 The method of principal response curves (PRC) was first developed by van den Brink & ter
802 Braak (1999) for comparing compositional change in treatment sites relative to a control site.
803 It is similar to redundancy analysis (RDA) in that a multivariate regression is performed on
804 the sample × taxon matrix constrained by variables of interest, but PRC is explicitly
805 constrained by time (Lepš and Šmilauer 2003, ter Braak and Šmilauer 2015). It was
806 developed to eliminate the need for cluttered biplots that make it difficult to see temporal
807 trends within and between treatments. To overcome this problem, PRC uses a single axis,

plotted against time, to express trajectories of compositional change (Lepš and Šmilauer 2003: 145); further axes can be calculated if they are of interest. Taxon weights also can be calculated and plotted for each PRC to show the change in the relative abundance (e.g., percent cover) of each taxon in the treatments relative to the control. The significance of the PRC is tested using Monte Carlo simulations (Van den Brink and Ter Braak 1999). As with RDA, PRC yields a measure of the percent variance explained for the overall taxonomic composition and how much is attributable to each variable (treatment and time). For example, Sugiura et al. (2013) used PRC to show that plant invasion in forests on a small island in the north-western Pacific had little effect on the temporal dynamics of invertebrate communities. The potential drawbacks of this method include its requirement for a 'baseline' or 'control' treatment level to be set for comparison, an attribute that many observational datasets will not have. Furthermore, PRC allows for only one 'treatment' variable and each analysis focusses on the change at one site, relative to the control site. However, Auber et al. (2017) have recently generalised this method so that it can be used to analyse compositional change at multiple sites, relative to a baseline or control, but this application removes the ability to consider an environmental or treatment effect. Thus, a principal response curve analysis yields a line graph showing the relative change in taxonomic composition for each 'treatment' along one compositional gradient relative to a control (Table 2).

1.5. Moran's eigenvector maps (MEMs)

Moran's eigenvector maps (MEMs; also known as 'principal coordinates of neighbour matrices', PCNM) is a method designed to characterise the spatial scales of variation in univariate or multivariate data (Borcard and Legendre 2002, Dray et al. 2006, Legendre and Gauthier 2014). However, MEMs have recently been applied to detect temporal scales of variation in communities (Angeler et al. 2009, Caruso et al. 2013, Legendre and Gauthier 2014). For instance, if a cyclical pattern in compositional change, such as seasonality, was

833 detected as significant for a dataset, this can be illustrated using line graphs showing the
834 temporal pattern (Table 3; Legendre and Gauthier 2014). This method is particularly useful
835 for detecting very complex temporal patterns, such as seasonality (periodicity), cyclical
836 changes or tipping points, but requires relatively large temporal sample sizes (Fig. 17). For
837 example, Kampichler et al. (2014) used MEMs to detect temporal patterns in multiple
838 datasets that had at least 20 annual measurements of bird communities.

839 First, a distance matrix is generated. Then, to focus on neighbour relationships, a
840 threshold value is chosen (see Borcard et al. 2011 for advice). For values below this
841 threshold, the distance value is retained; values above this threshold are assigned an
842 arbitrarily large value. Legendre & Gauthier (2014) recommend using one time interval as
843 the threshold for regular time series or the length of the longest lag for irregular series. A
844 PCoA is then applied to this modified distance matrix to generate a large number of
845 eigenvectors that describe a wide range of temporal scales of variation.

846 The eigenvectors from the PCoA can be used as explanatory variables, most often in a
847 redundancy analysis (RDA) or multiple regression. Combined with RDA, MEMs can be used
848 to determine whether there is cyclic or synchronised temporal change in composition and
849 which taxa, or taxon groups, are the drivers of it (Fig. 17). MEMs-RDA scores also can be
850 plotted as a function of time to assess visually the intervals of fluctuating community
851 dynamics (Angeler et al. 2009, Kampichler et al. 2014). In a comparison of different methods
852 to assess community dynamics, Angeler et al. (2009) observed that MEMs-RDA consistently
853 explained a greater proportion of variation in data with low taxonomic richness and linear
854 changes in time relative to time-lag regression analysis, Mantel tests, or RDA. However,
855 power was higher for taxon-rich communities because there was a greater probability of more
856 taxa fitting the temporal models. As a scale-detection method, MEMs could be applied to
857 determining the relevant time intervals for community monitoring. This method can be

858 combined with variance partitioning to show the relative variance in composition explained
859 by temporal, spatial and other explanatory variables (Legendre and Gauthier 2014).

860 *1.6. Compositional pivot days*

861 Compositional pivot days is a dissimilarity-based method developed by, and unique to,
862 Lellouch et al. (2014). This method is appropriate for situations where we want to test for the
863 occurrence of fast changes in taxonomic composition across one point in time, such as the
864 application of an experimental treatment or the effects of a rapid change in environmental
865 conditions (Table 2). It works by comparing pairwise distance values for pairs of temporal
866 observations taken at the same sample location to identify the time points where rapid shifts
867 in composition occurred. A 'pivot day' is a sampled time point that is identified by pairwise
868 similarities being low before and after that time point, but relatively higher across it.
869 Compositional pivot days are identified either visually from the pairwise distance matrix plot,
870 or using clustering (see Lellouch et al. 2014 for details). This method may be a good option
871 for a preliminary identification of thresholds or rapid shifts in community structure, but does
872 not provide a statistical test for the significance of the threshold relative to background. The
873 power of this analysis will increase as the number of sampled time points increases relative to
874 the number of pivot days.

875 *1.7. Community trajectory analysis*

876 Community trajectory analysis quantitatively compares the temporal change in multivariate
877 compositional dissimilarity space among samples using geometric calculations (de Caceres et
878 al. (2019). These comparisons are based on the relative amounts, rates, and directions of
879 sample movement in compositional space, thus, the method allows flexible testing of a wide
880 range of very specific, quantitative hypotheses of change, such as the divergence or
881 convergence of samples over time. This method is especially useful for a small number of

spatial replicates because the output can be graphical; plots use arrows on an ordination diagram to show how samples have moved in compositional space over time; however, larger numbers of samples could be graphed separately. We do not illustrate this method here because comprehensive R code and explanations are presented in the R package 'vegeclust' (De Cáceres et al. 2010) and demonstrative examples are given in de Caceres et al. (2019).

2. Zeta diversity

Zeta diversity, a measure of similarity, analyses change in community composition among samples in the dataset by calculating the average number of taxa that are shared between samples that are grouped in pairs, triples, quadruples, etc. (Table 3). The method was developed and introduced by Hui & McGeoch (2014), extended to temporal data by McGeoch et al. (2017), and comes with its own R package, 'zetadiv' (Latombe et al. 2017b). Zeta diversity estimates compositional turnover from multiple ($n \geq 2$) samples, rather than the pairwise comparisons used to estimate beta diversity. What is obtained by the method is a series of zeta values (similarity) for different orders of zeta: zeta_1 to zeta_n, where n is the total number of time points. Each of these values represents the average of the number of taxa shared by each set of times in the dataset. For example, zeta_2 (zeta order 2) represents the average number of taxa shared by all possible pairs of samples in the dataset (equivalent to 1 − beta diversity or mean similarity), zeta_3 represents the average number of taxa shared by all possible subsets of three samples, and so on. Zeta_1 (zeta order 1) represents the average alpha diversity (taxon richness) of all the samples in the dataset.

If there is complete turnover in community composition in time, at some point, zeta_i (where $i \neq 1$) will equal zero when there are no taxa shared by a given sized subset of samples. In contrast, if community composition never changes through time, $\text{zeta}_n = \text{zeta}_1$. Therefore, the rate of decline in zeta with increasing 'zeta order' tells us about the rate of

change in community composition in time ('zeta decline'). 'Zeta decay' can be considered analogous to time-lag graphs and time-lag regression analyses, which we described earlier for pairwise dissimilarity measures (Table 3). This means it experiences the same issue of few time points at higher lags, and thus higher uncertainty. The temporal scale(s) of community dynamics can be illustrated by plotting the change in sample zeta diversity of a particular zeta order against the temporal lag of samples, meaning that this method is useful for detecting both directional changes and cyclical patterns. For instance, if a multi-year time series in composition is cyclical (e.g., shows seasonality), zeta would seasonally decrease and then increase. These analyses can be done for different sets of samples to make spatial or temporal comparisons and, if necessary, zeta values can be normalised using the gamma diversity (total number of taxa in the dataset) to account for differences in taxon richness across samples (McGeoch et al. 2017). Further, different methods of creating the subsets for calculating zeta can be used, such as nearest neighbours or relative to a time-zero sample, further facilitating hypothesis testing (McGeoch et al. 2017). Latombe et al. (2017a) used zeta diversity to extend generalised dissimilarity modelling (Ferrier et al. 2007). This enables the user to assess taxonomic turnover at different orders of zeta and understand drivers of turnover in rare and common taxa (Latombe et al. 2017a). This method could be extended to assess temporal turnover at different orders of zeta by adding time as an environmental variable.

3. Synchrony

Although other methods can be performed on taxonomic subsets to look for similarities and differences in the temporal dynamics among groups of taxa ("synchronicity"), a useful measure of the 'temporal synchrony' in multivariate taxon abundances was developed by Loreau & Mazancourt (2008) and comes with its own R package, 'synchrony' (Gouhier and Guichard 2014). This standardised value measures how closely changes in taxon abundances

931 within a community track one another in time. It varies between zero (complete asynchrony
932 of taxon abundances in the community) and one (perfect synchrony; all taxon abundances
933 changing in the same way) and, by exploring different sized 'time windows', can be used to
934 detect scales of temporal variation. Overall significance tests of synchronicity in community
935 change can be obtained by performing null model analysis (e.g., Pedersen et al. 2017).

936 A similar method (Houlahan et al. 2007) uses the sum of the temporal variances and
937 pairwise covariances of all taxa in the community to distinguish if the community shows
938 'compensatory dynamics' over time. This method results in either a positive, negative or zero
939 community-level covariance value, indicating that taxa are increasing or decreasing in
940 synchrony (positive community covariance), some taxa are increasing, but this is
941 compensated for by decreases in other taxa (negative community covariance), or that no
942 change is evidence (zero community covariance) (Houlahan et al. 2007, Hallett et al. 2016).

943 **4. Turnover Rates**

944 The degree of temporal variation in community composition can be assessed by calculating
945 the turnover rate of the community (a.k.a. 'temporal turnover' or 'species turnover'), which is
946 a measure of the rate of change in taxonomic composition for a 'site' over time (e.g., Aguirre
947 et al. 2003). Turnover rates can be computed to measure the magnitude of compositional
948 change, but in a way that does not result in an understanding of the direction of change or the
949 taxa involved in compositional shifts. This method can detect when, and how rapidly,
950 temporal shifts occur in a temporal sequence to detect complex temporal patterns such as
951 perturbations, tipping points and pivot points (Fig. 17). Turnover rates are calculated using
952 combinations of colonisation, immigration, extinction, mortality, recruitment, and survival.
953 One of the commonly used methods is that of Diamond (1969) where the percentage turnover
954 rate, T, is calculated as $T = 100 \times (E + C) / (S1 + S2)$, where E is the number of taxa that went

955 extinct between two time points, *C* is the number of taxa that colonised between the same two
956 time points, *S*1 is the number of taxa present at time 1 and *S*2 is the number of taxa present at
957 time 2. *T* gives the percent change in taxon identities over the time period and varies from 0,
958 representing no turnover, to 1, indicating complete turnover (Diamond 1969). This measure
959 can be calculated only for a single location at two time points; pairwise turnovers must be
960 calculated separately for datasets with multiple time periods or multiple sites. *T* values can be
961 compared through time, at different time intervals, or at different spatial scales (e.g.,
962 Boulinier et al. 2001, Tworek 2004). They also can be used in a regression-style analysis to
963 assess the effects of a treatment variable or other explanatory factor on compositional
964 turnover (e.g., Aguirre et al. 2003, Tworek 2004). These methods are only useful for
965 communities that have relatively high rates of temporal turnover in taxa. The degree of
966 compositional turnover also is tied to the temporal extent of the study for the given system
967 and the average lifespan of taxa. For example, complete turnover in prokaryotes can be
968 observed over a period of days (e.g., Kara and Shade 2009), whilst many decades may be
969 required to detect any species turnover in some plant communities (e.g., Kardol et al. 2010).
970 However, because it can be standardised by the number of taxa in the community, *T* is a
971 potentially comparable measure of compositional change among different datasets, if they are
972 on similar timescales and encompass communities with a similar distribution of life-histories.

973 **5. Multivariate regression modelling**

974 Multivariate autoregressive state-space models (MARSS) are multivariate linear regression
975 methods that model the stochastic temporal dynamics in matrices of species' abundances in
976 relation to abiotic or biotic covariates, while accounting for potential observation
977 (measurement) error (Hampton et al. 2013). The models are autoregressive in that previous
978 measurements in time are assumed to be correlated to future measurement, and these

autocorrelations are formalised by modelling the current values of the response matrix as a weighted linear sum of previous values at a specified temporal lag (Penny and Harrison 2006). MARSS models can be used to disentangle temporal variation in species abundances into the relative contributions of inter- and intraspecific interactions, abiotic variations, and of demographic stochasticity (Mutshinda et al. 2009). Effect sizes of these different components are estimated from the multivariate model structure through the use of conditional least-squares, maximum-likelihood, or Bayesian estimation methods (Hampton et al. 2013). Observation errors, and other complexities such as spatially-replicated time series and non-uniform sampling, can be formally modelled within the state-space framework (Holmes et al. 2012). Further, MARSS models can be used to compute several metrics that indicate the degree to which communities are possibly becoming less stable over time (Ives et al. 2003). This level of flexibility means that they are able to test for even the most complex temporal patterns in communities, and can simultaneously reveal similarities and differences among taxa, and account for environmental factors or other covariates. However, they do require relatively long time series (ideally more than 25 temporal replicates), and, like any statistical model, more independent replication is required for more complex models. There are several examples of the use of MARSS models in freshwater and marine ecology, particularly in terms of estimating aquatic food web dynamics (Beisner et al. 2003, Hampton et al. 2008, Thibaut et al. 2012); there have been relatively few applications for terrestrial communities (e.g., Yamamura et al. 2006, Mutshinda et al. 2009). The 'MARSS' R package (Holmes et al. 2012) enables the fitting of MARSS models and includes a range of ecological examples, so we have not included example code in this paper.

Multispecies N mixture models and joint species distribution models are other regression methods that can be used to model explicit, quantitative hypotheses of community change, with a focus on interactions among taxa (e.g., Dorazio et al. 2015, Ovaskainen et al.

2017). These methods can allow for useful additions, such as accounting for uncertainty in the detection of taxa; however, due to their complexity and high computational requirements, they have yet to be implemented for datasets with large numbers of species.

STEP 3: TEST FOR STATISTICAL SIGNIFICANCE

Whichever multivariate analysis has been selected, most ecologists interested in community dynamics seek a way to determine if the changes that they see over time in the results of those analyses are greater than, or less than, they would expect by chance alone. Some of the methods presented above have their own built-in significance tests, often based on randomisations of the community matrix. Commonly-used randomisation tests include the Mantel test (Legendre and Legendre 2012) and permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, Legendre and Legendre 2012). Null models, whereby community matrices are randomised under sensible criteria (Gotelli and Graves 1996, Gotelli 2000, 2001, Gotelli and Entsminger 2001, Ulrich and Gotelli 2007, 2010), can be used to test the significance of any observed change in compositional dissimilarity, and can easily be incorporated into analyses described above including zeta diversity. The primary consideration in applying any randomisation test is what assumptions are being made about taxon niches and whether they are valid. If the interest is in testing the effects of interactions among taxa on their co-occurrence, but the randomisation procedure (null model) allows taxa to occur in samples where they are unable to occur for other reasons, such as habitat differences, a difference among samples may be falsely detected (an inflated Type I error rate). Thus, if strong inferences are to be made about compositional differences, we must be sure that the differences among the groups of sites that we are testing are the only difference. Similarly, the sample size needs to be high enough to allow the detection of differences among sets of sites for the given level of compositional variability (Type II error rate).

1029 Schaefer, et al. (2005) introduced a novel method for detecting significant shifts in
1030 community composition using randomisations under null models of taxon mean abundances
1031 through time. They demonstrate that this approach, which uses both compositional distance
1032 (pairwise dissimilarities) and the coefficient of variation (CV), could detect significant
1033 dynamics in community composition, even where only small amounts of change had
1034 occurred. In this method, temporal changes in communities are assessed by using a
1035 compositional distance measure that is selected by the user. This quantifies the multivariate
1036 distance between the randomly generated communities (null model randomisations) and
1037 observed 'reference' samples (e.g., 'Time 0' samples, compared to randomisations of 'Time
1038 1' samples). If the observed distance is greater than under randomisation, then we can infer
1039 statistically significant temporal change. Because this can be done in an ordination context,
1040 increases and decreases of particular taxa driving the change can be determined from the
1041 ordination plots. Limitations of this method are that it requires a relatively large degree of
1042 temporal change in the data compared to spatial variation (i.e., more temporal, than spatial,
1043 variation) and it is relatively computationally intensive; however, we provide the R code for a
1044 worked example in the supplementary material (Data S2).

1045 **STEP 4: REPORT ON THE ANALYSIS WORKFLOW**

1046 Our literature review suggested a lack of consistent reporting of critical aspects of the data
1047 analysis workflow. Such reporting of ensures that the results are robust, represent the
1048 variation deemed important for the research aim and are reproducible. The number of taxa,
1049 samples, and independent replicates in space and time all should be clearly reported in the
1050 Methods or Results section of the paper (see Hurlbert 1984 for guidance on statistical
1051 independence). The dissimilarity measure selected, and the rationale and procedures used to
1052 arrive at that decision, should be reported in the Methods section of the paper. We encourage
1053 researchers to refer to a specific source, such as Legendre & Legendre (2012), or to give the

formula applied to maximise the repeatability and transparency of their research; these indices can be inherent in particular methods or built-in as defaults in software, but nevertheless should still be reported. Different methods of dissimilarity or ordination (or other analysis types) that were compared, e.g., in the EDA phase, should be listed in the Methods section of the paper stating that their results were consistent with each other. The choice of dissimilarity or ordination method is subjective, but rules of thumb can be used for assessing different methods, so that the method selected optimises the reduction of dimensionality in the data and thus maximises the variation accounted for by the analysis (see McCune and Grace 2002 for comprehensive advice).

STEP 5: PRESENT TEMPORAL PATTERNS AND RESULTS

Some of the analysis methods that we describe in this paper do not produce simple visual outputs that clearly show temporal trends in community datasets and visualising temporal dynamics can be difficult for species-rich datasets or complex sampling designs. However, there are a variety of useful methods that can be used to complement a hypothesis-driven analysis (Table 3). Many descriptive methods work best where a small group of taxa is measured only a few times. However, there are examples of descriptive methods being used effectively for larger, more complex examples. Pereira et al. (2017) used a heat map to show compositional changes of 808 bacterial genera, at a single location, sampled 24 times over two years. Certain descriptive methods are useful for only specific types of temporal patterns, e.g., ‘time cores’ is a method that identifies ‘core’ groups of taxa that remain present over time (Vallès et al. 2014). Others, such as Venn diagrams and measures of overlap in composition, are useful only for small numbers of temporal comparisons. We recommend and provide R code (Data S2) for time cores and Venn diagrams because these methods are suitable for assessing hypotheses of taxon replacement while specifically identifying the taxa driving compositional shifts (Tables 2 and 3). Relative abundance distributions (RADs, *a.k.a.*

1079 ‘rank abundance curves’), can provide relatively sophisticated visualisations of community
1080 dynamics, and rank abundances can be used to quantitatively measure the shift in taxon ranks
1081 within samples taken at different time points (Hallett et al. 2016). RADs are plots of the
1082 relative abundances (on the *y*-axis) of all species in a community ranked (on the *x*-axis) from
1083 highest to lowest. They are closely related to *k*-dominance curves, in which species ranks are
1084 shown on the *x*-axis, but cumulative proportional abundance (dominance) is plotted on the *y*-
1085 axis (Lambshead et al. 1983). If samples taken at different times are plotted separately, the
1086 set of RADs can illustrate changes in community structure over time. RADs also can be used
1087 to explore community dynamics if a dissimilarity measure, such as Bray-Curtis, is calculated
1088 for the species’ ranks at each time point. The resulting temporal dissimilarity of the RADs
1089 can be explored by plotting rank dissimilarity against time lag or by ordinating rank
1090 dissimilarities in the same way that spatial compositional dissimilarities are examined. For
1091 example, temporal changes in RAD dissimilarity can illustrate changes in species evenness
1092 over time as might be expected if compositional homogenisation and a decline in evenness
1093 occurs because of invasion by an increasingly dominant species (Ruhl 2008).

1094 **E. DISCUSSION**

1095 There is an ever-expanding set of analyses that use a wide variety of multivariate and
1096 univariate methods to quantitatively address temporal questions about communities that
1097 continue to be developed (e.g., De Cáceres et al. 2019). One of the key reasons for the
1098 proliferation of methods appears to be variability in the length of the time series. For
1099 example, if the time series is long enough, methods such as temporal MEMs could be used;
1100 however, consistent with other reviews (e.g., Vaughn and Young 2010) and databases
1101 (Dornelas et al. 2018), most datasets captured by our literature had relatively few temporal
1102 measurements (mean = 14.9, median = 7, mode = 4), requiring very different methods. In
1103 other cases, the ability to implement some methods in temporal community ecology still

1104 requires development, such as the application of time-ordered and time-aggregated network
1105 analysis for spatiotemporal community datasets (Blonder et al. 2012).

1106 Some analysis types are well established for spatial data, but can be applied easily to
1107 temporal data, potentially yielding useful and comparable results for explicit temporal
1108 analyses. Further research is required to generate standard extensions and approaches using
1109 such methods for temporal data. For example, nestedness (*sensu* Patterson and Atmar 1986)
1110 is usually applied to spatial data and the analysis is repeated for different time points;
1111 however, there is no reason that we cannot apply this method across times to look at whether
1112 sites are becoming more or less nested over time. For instance, if younger sites were nested
1113 within older sites, this may indicate that sites were becoming more homogeneous over time.

1114 Our understanding of temporal dynamics in biological communities, and the methods
1115 we use to investigate them, have improved greatly over the past 25 years, probably because
1116 of increases in computational power and in dataset size. We can continue to improve our
1117 understanding by moving away from merely describing community changes, to linking these
1118 changes to understanding and testing the processes driving community change and
1119 biodiversity; that is, moving from hypothesis-generating methods towards hypothesis-testing
1120 methods enabled by well-defined research questions with specific, testable hypotheses that
1121 result in clear predictions for observed temporal patterns (e.g., Figs 4-7). Even for
1122 exploratory studies of compositional variation through time, we emphasise the benefits of
1123 making *a priori* predictions for how we think composition should change through time.

1124 Interactions between community composition and environmental or other factors
1125 across space and time are complicated. For example, Brown (2003) showed that temporal
1126 variability in species composition of stream invertebrates was reduced by high spatial
1127 heterogeneity, which may be because there are increased niches or refugia in changing
1128 environmental conditions. Manipulative experiments are useful, but not always possible,

1129 especially for long-lived taxa. Therefore, combining current knowledge of intrinsic and
1130 extrinsic factors controlling community change into null models and simulations may be the
1131 way forward (Brown and Lawson 2010). Carefully considering sample sizes and appropriate
1132 replication of particular factors are also important if we are to properly test hypotheses of
1133 species coexistence over time (Philippi et al. 1998). There is a need for us to make useful
1134 predictions about how communities may continue to respond to ecosystem disturbances, such
1135 as climate change, invasive species, and habitat fragmentation (Hobbs et al. 2007,
1136 Kampichler et al. 2012). Many methods commonly used to analyse temporal community
1137 dynamics are not quantitative, meaning conclusions can only be narrative descriptions, rather
1138 than clear tests of hypotheses. Many of the methods presented here push us to quantitatively
1139 assess dynamics, which naturally leads to clearer hypothesis testing.

1140 There is a wide variety of methods available for analysing temporal dynamics of
1141 biological communities; however, many studies in our literature review using these methods
1142 are descriptive, showing that a large body of literature in community ecology is not focussed
1143 on testing quantitative hypotheses of change. Surprisingly few studies in our review
1144 presented hypotheses that were more complex than simply predicting that composition would
1145 have changed in some way over time, instead of specifying predictions of quantitative and
1146 directional patterns of change in community composition. Even additional searching beyond
1147 our original search terms that included more specific terminology for compositional change
1148 (succession, turnover, synchron*, resilience, homogenization, divergence, convergence)
1149 revealed few empirical papers that tested specific, quantitative hypotheses. This search
1150 resulted in an additional 1,514 papers of which we read 10% (151 papers). Of these, 60
1151 papers met the inclusion criteria of our original review and only 13 papers tested hypotheses
1152 that were more sophisticated than the simple prediction that composition would have changed

in some way over time, e.g., directional change or that the abundances of some taxa would change more than others.

This lack of specific, quantitative hypothesis testing is not surprising because to predict change in composition in a quantitative way, we require an in-depth understanding of a system and how different components of the diversity differ in their ecology or other factors that could cause directional, cyclical, or other differential change in time. In many cases, particularly in the observational, rather than experimental, community ecology literature, this is not the situation. This means that, although such studies may state hypotheses, these hypotheses are not very specific or quantitative. In most cases, they predict some change in response to time or another factor that is correlated with time (such as disturbance or pollution), but the types of temporal change (divergence, convergence, synchrony, etc.) are not specified. We strongly recommend that researchers generate *a priori* hypotheses of compositional change (e.g., Figs. 4-7; Bagchi et al. 2017). These predictions should be used to select appropriate quantitative data analysis methods (Fig. 17). The comprehensive description and hypothesis testing of temporal community patterns requires the use of multiple data analysis methods, but by using standard exploratory data analysis methods followed by testing *a priori* hypotheses, the methods selected can be explicitly focussed on the most appropriate tests for the situation. We hope that this synthesis will allow researchers to make informed decisions about their choice of data analysis for their research question and pave the way for more uniformity in reporting of these analyses and/or innovation in comparability. Our understanding of patterns and drivers of changes in species communities would benefit by having more longer-term and fine-scale studies.

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SUPPORTING INFORMATION

Data S1. Description of attributes, and associated data, extracted from papers in the literature review.

Data S2. Example R code for plant community dataset

Data S3. Example R code for BCI dataset

Data S4. Example R code for marine bacterial community dataset (from high throughput sequencing)

Appendix S1. Supplementary figures from the literature review.

Appendix S2. Descriptions of methods encountered in the literature review that are not included in the main text.

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1632 **TABLES**

1633

1634 **Table 1**: Recommended steps for exploratory data analysis (EDA) of community data prior to selecting analysis methods for temporal data. R

1635 code for the methods is provided in the supplementary materials Data S2-4.

Step	Description	Rationale	Methods
1	Count the number of taxa, the number of samples and the number of empty samples	Some ordination methods are influenced by rare taxa; identify empty samples; determine replication for significance testing against explanatory variables	Row and column totals of the sample × taxon matrix. Plot the relative abundance distributions.
2	Examine taxon frequency distributions and response curves	Some ordination methods assume either unimodal or linear pattern of frequency distribution	Plot the abundance of species across time or other explanatory variables.

3	Determine the ratio of temporal to spatial variation in composition	If temporal change is to be detected within different spatial sampling locations, the analysis must adequately tease apart the variation in time and space. Where little spatial variation exists, spatial samples could be averaged at each time.	Mean spatial and temporal turnover should be calculated following Collins et al. (2000) to allow a 'global' comparison of the amount of compositional variability among samples from each time and among times (see Hallett et al. 2016 for details); it can be calculated for different subsets of samples or times for which different predictions about temporal dynamics have been made, e.g., different experimental treatments. Ordination approaches, such as DCA (ter Braak and Šmilauer 2015), can be used to quantify spatiotemporal variation and to identify 'outliers', i.e., samples that are very different to other spatial or temporal replicates.

4	Determine the optimal dissimilarity measure and whether data should be standardised	The dissimilarity measure selected depends on the response variable type (presence data, relative abundance data, etc.) This choice of appropriate distance measure and/ or standardisation determines the degree of emphasis of sample richness, composition or relative abundances in the resulting distance matrix, and thus may also relate to the research question (Anderson et al. 2011).	Possible dissimilarity measures to compare samples should be selected using criteria listed in sources such as Anderson et al. (2011), Legendre & Legendre (2012) and Legendre & Cáceres (2013). Principal coordinates analysis or non-metric multidimensional scaling (NMDS) of the different dissimilarity matrices can be compared. The distance measure that gives the greatest spread of points in a few dimensions and, therefore better discrimination among the samples, should be selected. If NMDS is used, the stress values associated with the different distance measures can be compared, because lower stress values show that the ecological distances between samples are being better represented in ordination spaces.

1636

1637 **Table 2**: Descriptions of the outputs obtained from analysis methods for temporal change in community composition with example from the
1638 literature. LCBD refers to 'Local Contributions to Beta Diversity' and SCBD refers to 'Species Contributions to Beta Diversity'. * Venn
1639 diagrams and time cores are specifically useful for detecting taxon replacement over time, and are described in the section "Visualising temporal
1640 patterns".

Method (text section)	Description of outputs	Key paper(s) using each method
Beta diversity decomposition (nestedness, turnover) (D 1.2)	Beta diversity values for nestedness and turnover that can be used in subsequent graphs (e.g., time lag) or analyses of explanatory variables.	Baselga & Orme (2012)
Beta diversity decomposition (SCBD, LCBD) (D 1.2)	List of relative contributions of taxa to the overall compositional variation. Matrix of LCBD values showing the relative contribution of each sample-time combination to the overall compositional variation. Values can be used in subsequent graphs or analyses of explanatory variables.	Legendre & De Cáceres (2013); Legendre & Gauthier (2014); Lamy et al. (2015)

Beta or zeta diversity time-lag graph (D 1.2 or 2.0)	Graph showing the relationship between temporal diversity and time lag (distance in time). In the case of zeta and multi-site dissimilarity, time-lag graphs are specific to each number of samples in the subset (e.g., zeta order).	Hui & McGeoch (2014); McGeoch et al. (2017)
Beta or zeta time lag regression (D 1.2)	Regression statistics indicating the significance of the relationship between temporal diversity and time lag (distance in time). In the case of zeta and multi-site dissimilarity, time-lag analyses are specific to each number of samples in the subset (e.g., zeta order).	McGeoch et al. (2017)
Community trajectory analysis (D 1.7)	Principal coordinates analysis diagram with trajectories showing the relative change in species composition of samples through time. Trajectory statistics, including shape, size and direction are also obtained.	De Cáceres et al. (2019)

Multivariate regression modelling (D 5.0)	Multivariate regression models quantifying the relative effects of species (or species groups) interactions, environmental covariates, spatial structure, and observation error on relative abundances through time. Effects can also be output as estimated trajectory plots. Options exist to produce metrics of community stability.	Hampton et al. (2013)
Mean dissimilarity (D 1.1)	Mean dissimilarity values for data subsets. Values can be used in subsequent graphs, analyses or maps.	Collins (1992)
Mean dissimilarity as response in regression (D 1.1)	Regression statistics indicating the significance of the relationship between mean dissimilarity and explanatory variables, which includes time if dissimilarity is calculated for different spatial samples, or will only include change in non-time explanatory variables, if dissimilarity is calculated across time.	Collins (1992); Barros et al. (2014)

Moran's eigenvector maps (MEMs) with db-RDA (D 1.5)	MEMs results in a matrix of uncorrelated temporal variables that characterize scales of temporal variation in composition that can be used in the db-RDA. The RDA results in a table of ordination statistics, an RDA ordination diagram, and if paired with variance partitioning, a Venn diagram showing the amount of variance explained by each component.	Legendre & Gauthier (2014)
Ordination (constrained) (D 1.4)	Ordination diagram and table of statistics (see the text section 'Ordination' for more details and other possible outputs).	Anderson & Willis (2003); http://ecology.msu.montana.edu/labdsv/R/
Ordination site scores in glm or non-linear regression (D 1.4a)	Regression statistics indicating the significance of the relationship between species composition and explanatory variables.	Day & Buckley (2013)
Pivot days (D 1.6)	A list of time points are identified at which significant shifts in composition have occurred.	Lellouch et al. (2014)

Principal response curves (D 1.4b)	Principal response curve diagram comparing trajectories in compositional space of different sites or samples over time relative to the baseline or control.	Auber et al. (2017)
Raw dissimilarity values (D 1.1)	Various, depending on the method. For example, the dissimilarity-overlap method results in a graph of pairwise dissimilarity values against the proportion of individuals that taxonomically overlap; overlaid on this is a non-parametric, non-linear regression line, the slope of which indicates whether or not samples are changing in similar ways or not; this is compared to a null hypothesis of zero slope.	Bashan et al. (2016)
Synchrony (D 3.0)	A single value representing the degree to which taxa are changing in a similar way over time, calculated for a given sample by species matrix across a set of times. Can be compared for different time windows or different subsets of samples (e.g., experimental treatments).	Loreau & Mazancourt (2008); Gouhier & Guichard (2014)

Temporal coherence (D 1.4a)	A single value representing the degree of consistency in temporal change among samples for the dataset or subset considered (see the text section 'Ordination' for more details).	Rusak et al. (1999); Angeler & Johnson (2012)
Turnover rates (D 4.0)	Percent change in species composition between time points.	Diamond (1969)
Venn diagrams, overlap and time cores*	Venn diagram showing the number of taxa shared and unshared between two or more subsets of samples. Lists of shared and unshared taxa. Time cores results generate lists of taxa that occur consistently through time for a set of samples.	Vallès et al. (2014); O'Sullivan et al. (2015)
Zeta diversity (D 2.0)	Zeta diversity values for each zeta order (number of samples in subsets) that can be used in subsequent graphs (e.g., zeta diversity vs. order) or analyses of explanatory variables.	Hui & McGeoch (2014); McGeoch et al. (2017)

1641

1642 **Table 3**: Data visualisation methods and considerations for their use in temporal community dynamics studies.

1643

Methods	Description and example references	Considerations
Ordination axis samples scores	Symbols (e.g., Noll et al. 2005), envelopes (e.g., Rayner et al. 2009), or trajectories (e.g., Rojas-Sandoval et al. 2012) can be added to ordination diagrams to display the relative compositional change among temporal samples.	Can be used to show convergence, divergence, or in/stability of sets of samples. Useful for many samples and taxa. Ordination sample scores can also be used in other graphs or maps to display spatiotemporal compositional variation.
Relative abundance distributions	Plot the relative abundance of all taxa in the community (Lambshead et al. 1983, Stead et al. 2003, Ruhl 2008).	Shows changes in evenness over time where separate relative abundance distributions are plotted for each time. Useful only for small numbers of comparisons, e.g., two or three sampling times.

Venn diagrams	Displays the overlap in species composition among samples (e.g., O'Sullivan et al. 2015).	Suitable for visualising taxon replacement while specifically identifying the taxa driving compositional shifts. Useful only for small numbers of temporal replicates.
Time cores	Identify 'core' groups of taxa that remain present over time (Vallès et al. 2014).	Useful for visualising synchronicity in compositional shifts.
Heat maps	A grid representing spatial and/or temporal samples where cells are coloured by a gradient representing relative abundances, ordination sample scores, or compositional change (e.g., Pedersen et al. 2017, Pereira et al. 2017).	Useful for representing change between time points across sample space, even in the case of complex patterns.
Geographic maps	Grid cells or other geographic polygons displaying numeric values representing relative abundances, ordination sample scores, or compositional change (e.g., Clavero and Garcia-Berthou 2006).	Useful for representing change between time points where variation in geographic space is also important. Useful for relatively few time points.

Abundance graphs	Bar graphs, boxplots, scatterplots, or pie charts showing relative abundance of different taxa at different times (e.g., Xiong et al. 2014, Chapman and McEwan 2016, Franca et al. 2016).	Can show complex temporal dynamics such as non-linearities in species' responses and synchronicity among different taxa, but useful only for a small number of taxa.
Relative abundance tables	Relative abundance or percent dominance values across time (e.g., Shertzer et al. 2009).	Useful only for a small number of taxa and spatiotemporal samples.
Photographs of gels or electropherograms	Show the relative frequencies of characteristic taxon identifiers (e.g., Shi et al. 2016).	Useful only for a small number of taxa and spatiotemporal samples.

FIGURES

Figure legends

Fig. 1. Number of studies identified by our search criteria from each continent. Numbers of studies were: Global (*n* = 5), Oceanic (*n* = 5), Africa (*n* = 20), Antarctica (*n* = 6), Asia (*n* = 47), Australia (*n* = 18), Europe (*n* = 166), North America (*n* = 161), Oceania (*n* = 8) and South America (*n* = 39). Darker colours indicate more studies have been conducted within those continents, including Oceania. Pie charts show the taxonomic focus of study data from each continent as being on (●) plants, (●) vertebrate animals, (●) invertebrate animals, (●) microeukaryotes, (●) prokaryotes, (●) viruses, or (●) mixed taxonomic groups.

Fig. 2. The frequency of use of different temporal community dynamics analysis methods across all reviewed studies. Specifically: (a) the number of different analyses applied in each study; (b) the percent of uses of each analysis type across all studies and times. Descriptions of analysis types are detailed in either S1 or S2 Text.

Fig. 3: The relative distribution of the mean number of independent temporal samples across different research aims and temporal analysis methods. ‘Minor methods’ include compositional pivot days, frequency change, Markov chain modelling, multiplicative change, Moran's eigenvector maps (MEMs), nestedness analysis, and synchrony. Descriptions of analysis types are detailed in Section D ‘Road map for analysing temporal community dynamics’ in the text. Research aims vary from understanding compositional dynamics at fine, medium and coarse temporal scales, to investigating the effect on species composition over time of species interactions, environmental conditions, and ecological disturbance, to understanding successional change in communities.

Fig. 4. Conceptual figure illustrating the different patterns in (a) temporal community dynamics for a single sample unit expected under different hypotheses of community change, visualised as how pairwise dissimilarities (*D*), e.g., Bray-Curtis, would change over different time lags: (b) the null hypothesis of no change ('persistence'), (c) 'directional' change, and (d) 'cyclical change'/ 'periodicity'. Points represent individual pairwise comparisons of across eight sampling occasions and the error envelope is the standard deviation (absent for the largest lag because there is only one comparison at that scale).

Fig. 5. Conceptual figure illustrating the different patterns in (a) temporal community dynamics for a set of sample units (Sample units *A*-*C*) expected under different hypotheses of community change, visualised as how pairwise dissimilarities (*D*), e.g., Bray-Curtis, would change over eight sampling occasions (Time 0-8): (b) the null hypothesis of no change ('persistence) or 'directional', whereby all sampling units are moving at the same direction and speed in compositional space, (c) 'divergence', (d) 'instability', and (e) 'convergence' (blue line)/ 'homogenisation' (red line). Points represent individual pairwise comparisons for three sample units at eight sampling occasions, and the error envelope is the standard deviation of the three values.

Fig. 6. Conceptual figure illustrating the different patterns in (a) temporal community dynamics for a set of experimental sample units in two treatments (*X* and *Y*) expected under different hypotheses of community change, visualised as how pairwise dissimilarities calculated between treatment pairs (*D*), e.g., Bray-Curtis, would change over eight sampling occasions (Time 0-8): (b) a 'press perturbation' that occurs at Time 0 or a (c) a 'pulse perturbation' that creates a 'pivot point' or 'threshold' that occurs at Time 3. Both pulse and press perturbations can generate either a 'tipping point' (red line) or 'resilience' (blue line)

type response. Points represent individual pairwise comparisons for three sample units at eight sampling occasions, and the error envelope is the standard deviation of the three values.

Fig. 7. Conceptual figure illustrating the idea of ‘synchronicity’, whereby different functional or taxonomic subsets of a community are changing differently from other subsets (but the taxa within those respective groups are changing synchronously). In this case, (a) pairwise dissimilarities are calculated separately for the different subsets and (b)any possible differences in changes over time between the two subsets can be observed, e.g., one functional group might be becoming more homogeneous (blue), whereas another might be changing directionally (red). Points represent individual pairwise comparisons for two different functional groups (red and blue) from three sample units at eight sampling occasions, and the error envelope is the standard deviation of the three values.

Fig. 8: Changes in compositional turnover over time for data from the Porensky et al. (2016a, b) case study. Four transects were subjected to one of six grazing treatments and were sampled annually from 2007 to 2014. Note that “exclosure” treatment is the control (no grazing). The different lines represent different transects.

Fig. 9: Local contributions to beta diversity (LCBD) for each transect at each sampling time for data from the Porensky et al. (2016a, b) case study. Plot shows the relative contributions of the different transects and times to the overall beta diversity. Symbol size is proportional to the LCBD value and significance is indicated by the red, outlined circles; blue circles are not significant. Transects had a grazing treatment and were established in one of two replicate pastures (1 or 2) and were either north-facing (f) or south-facing (s). Grazing treatments

were: none (exclosure), light, moderate, heavy, heavy-to-light (lightly grazed since 2007; 'new light') and heavy-to-none (new exclosure since 2007).

Fig. 10: Principal response curve analysis of data from the Porensky et al. (2016a, b) case study. Results show that treatments differed in plant species composition from the control (exclosure; grey line) but the differences between treatments were inconsistent over time. Treatments were: new exclosure (since 2007; dark blue), continuous light (red), new light (since 2007; light blue), continuous moderate (green), and continuous heavy (black). Four particularly influential species where either lower (BOGR = *Bouteloua gracilis*) or higher (PASM = *Pascopyrum smithii*, STCO = *Hesperostipa comata*, and BRTE = *Bromus tectorum*) in abundance than in the control (black horizontal lines represent the abundance of each species relative to the control).

Fig. 11. Zeta diversity analysis, based on the number of species shared by a set of temporal samples from the Barro Colorado Island case study. Results show that the woody forest community in the 50-ha forest census plot on BCI has been significantly more stable over time than random expectation, particularly at large spatial scales where richness is higher. Maps show for 1 - zeta diversity calculated for quadrats of increasing sizes (20 × 20 m, 50 × 50 m, 125 × 125 m, 250 × 250 m and 500 × 500 m) and for between 2 and 7 orders of zeta (the number of temporal samples compared): (A) the observed values, (B) observed - expected values under a null model of random change in species composition in quadrats over time, and (C) significance of the observed values. Results are given as 1 - zeta so that they are comparable to the turnover results in that higher values represent higher dissimilarity in species composition.

Fig. 12. Turnover analysis results for the seven time intervals for the Barro Colorado Island forest community. Results show that the proportion of species turning over each measurement interval was significantly lower than under random expectation, particularly at large spatial scales where richness is higher and composition is more stable: Maps show proportion of species turnover calculated for quadrats of increasing sizes (20 × 20 m, 50 × 50 m, 125 × 125 m, 250 × 250 m and 500 × 500 m) across the seven time intervals: (A) the observed values, (B) observed - expected values under a null model of random change in species composition in quadrats over time, and (C) significance of the observed values.

Fig. 13. Principal coordinates analysis of 74 marine bacterial OTUs across 62 temporal samples from the Gilbert et al. (2012) case study. Results show no visible consistency in compositional change by season (coloured points) within or between years for the single site analysed. Black lines link samples taken consecutively within years.

Fig. 14. Time lag analysis of 74 marine bacterial OTUs across 62 temporal samples at one site off the coast of Plymouth, United Kingdom from the Gilbert et al. (2012) case study. Results show high variability in pairwise Bray-Curtis dissimilarity values with slight divergence occurring over time. The blue line is a linear regression line. The high variability suggests that there is not consistent, directional temporal change at this site.

Fig. 15. Zeta diversity analysis of the 13 marine bacterial OTUs that were most variable in abundance across 62 temporal samples from the Gilbert et al. (2012) case study. Results show that spring samples were more diverse than winter or summer samples. Zeta order represents the number of temporal samples compared and so each point on the graph shows the mean number of OTUs shared among these different numbers of temporal samples.

1770

1771 Fig. 16. Change in the mean Bray-Curtis dissimilarity values calculated for temporal samples
1772 (n = 62) grouped by season from the Gilbert et al. (2012) case study. Results are for the 13
1773 most variable marine bacterial OTUs at the one site analysed, showing cyclical community
1774 dynamics. The blue line is a polynomial regression line with 16 terms. Multiple comparisons
1775 from an analysis of variance showed that samples taken in spring were significantly less
1776 similar to other spring samples than were samples taken in summer, autumn, or winter ($P <$
1777 0.001). Samples taken in summer were significantly less similar to other summer samples
1778 than were samples taken in autumn ($P < 0.05$).

1779

1780 Fig. 17. Potential methods that are appropriate for testing different predictions of temporal
1781 patterns in community dynamics indicating the required temporal sample size and whether:
1782 environmental variables can be included in the analysis (Env.); the analysis can be made
1783 explicitly spatial to account for temporal samples being clustered in different sites by
1784 including spatial variables (Spatial); or the role of individual taxa are identified in the
1785 analysis (Taxa), and the type(s) of significance testing (Sig.) that are used for the analysis
1786 (Rnd. = randomisations, Reg. = regression statistics, None = significance testing is not
1787 normally applied, Mtl. = Mantel test). Note that the null hypothesis for each of these
1788 predictions is that there is no change over time in either taxon presence or abundance
1789 ('persistence'). Cell shading indicates the number of temporal samples in the time series for
1790 which each analysis method is appropriate (note that some hypotheses require more temporal
1791 samples than others): No shading—method applies well to time series of any length; cross-
1792 hatched pattern—method only applies well for few measures in a time series (< 5 temporal
1793 samples); Light grey—only applies well for ≥ 5 temporal samples; Mid-grey—only applies
1794 well for ≥ 10 samples; Darkest grey—only applies for ≥ 20 samples, but many more than 20

spatial and temporal replicates may be required, depending on the number of explanatory variables in the regression model; note that a time series of at least 20 temporal samples are required for calculating Moran's eigenvector maps (MEMs).（✓）indicates that although these statistics are not explicitly spatiotemporal analyses, they can be calculated for spatiotemporal subsets of sample units and therefore, such groupings could be used to compare variation in both space and time. + Requires a strong gradient in composition that is well represented by the ordination axis scores for samples. ++ Weak inference from species' positions on biplot. # Zeta diversity modelling can be combined with generalised dissimilarity modelling (Ferrier et al. 2007) to assess the effect of environmental variables. ## PRC requires a 'baseline' or a 'control' treatment level against which other samples are compared through time. Beta diversity decomposition refers to nestedness, turnover, and 'Local Contributions to Beta Diversity' (LCBD). * Venn diagrams and time cores are specifically useful for detecting taxon replacement over time, and are described in the section "Visualising temporal patterns". Numbers in parentheses next to each method refer to the text section that gives a detailed description of each method.

Figure 1

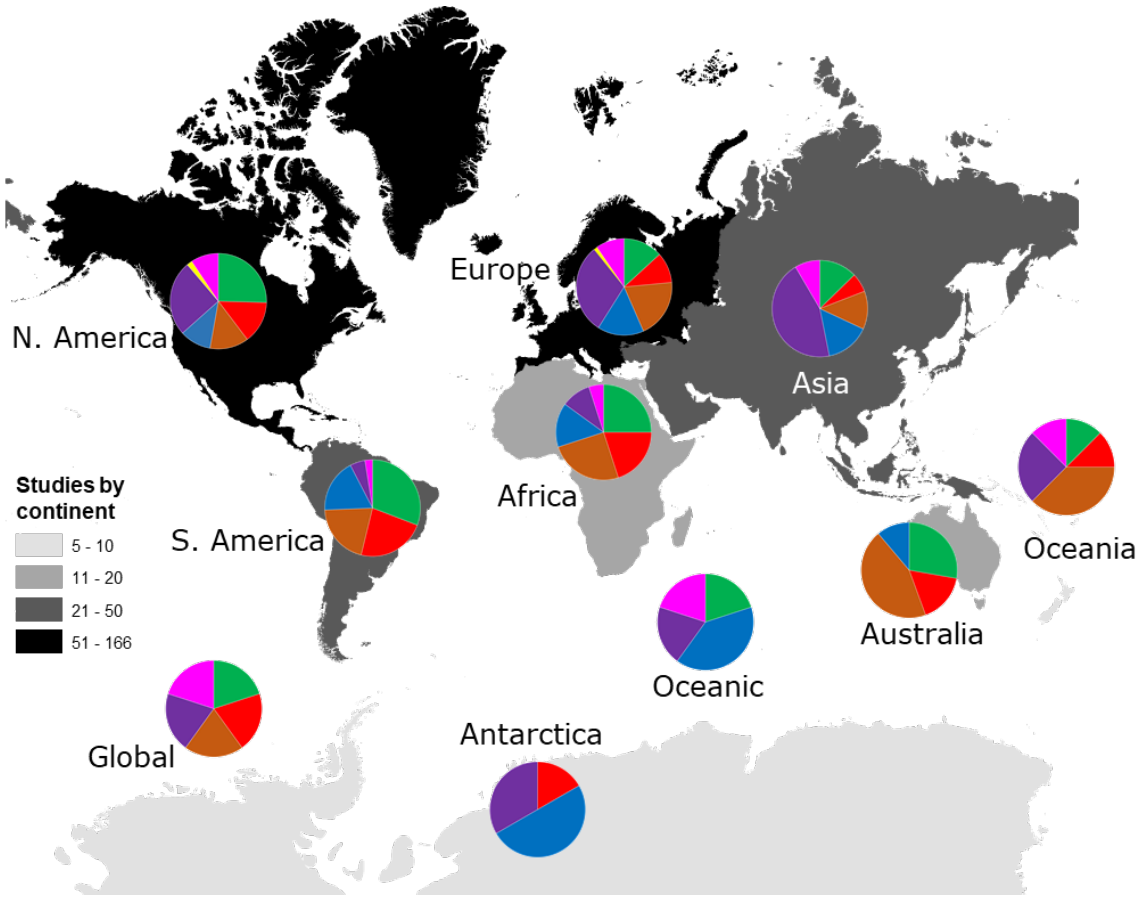
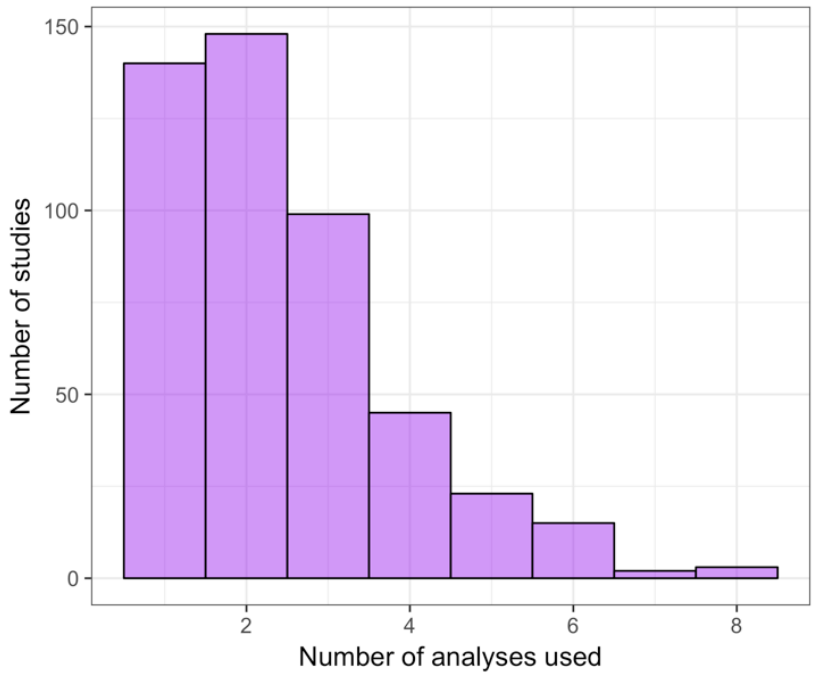

Europe
N. America
Asia
Africa
Studies by continent
5 - 10
11 - 20
21 - 50
51 - 166
S. America
Oceania
Australia
Oceanic
Global
Antarctica

Figure 2

(a)


150
100
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0
Number of studies
2
4
6
8
Number of analyses used

(b)

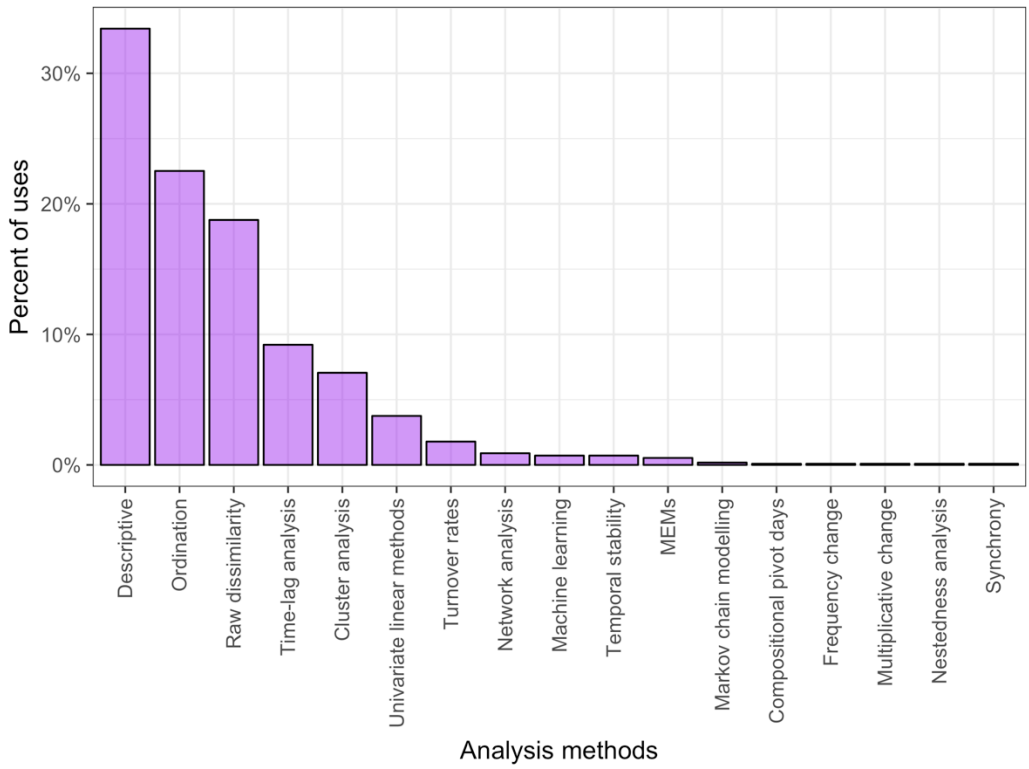
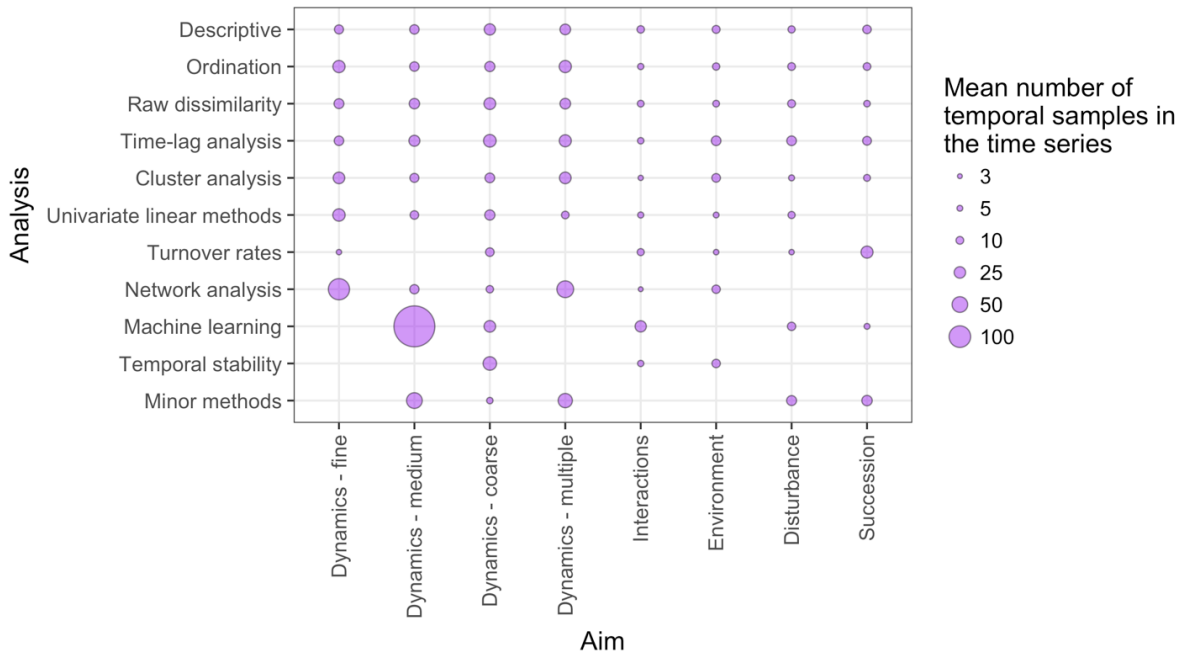

30%
20%
10%
0%
Percent of uses
Descriptive
Ordination
Raw dissimilarity
Time-lag analysis
Cluster analysis
Univariate linear methods
Turnover rates
Network analysis
Machine learning
Temporal stability
MEMs
Markov chain modelling
Compositional pivot days
Frequency change
Multiplicative change
Nestedness analysis
Synchrony
Analysis methods

Figure 3


Descriptive
Ordination
Raw dissimilarity
Time-lag analysis
Cluster analysis
Univariate linear methods
Turnover rates
Network analysis
Machine learning
Temporal stability
Minor methods
Analysis
Dynamics - fine
Dynamics - medium
Dynamics - coarse
Dynamics - multiple
Interactions
Environment
Disturbance
Succession
Aim
Mean number of temporal samples in the time series
3
5
10
25
50
100

1827
1828 Figure 4

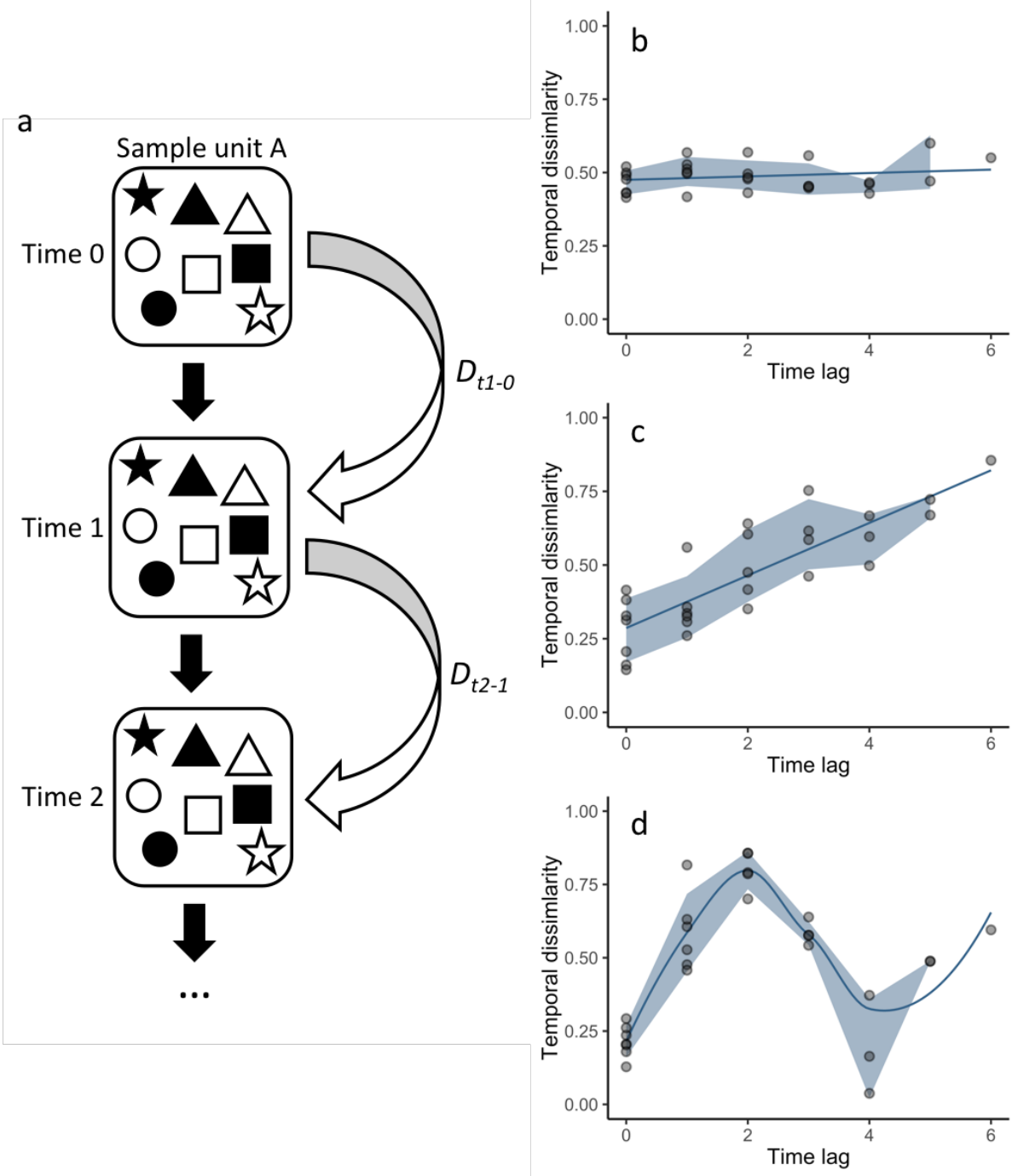


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Figure 5

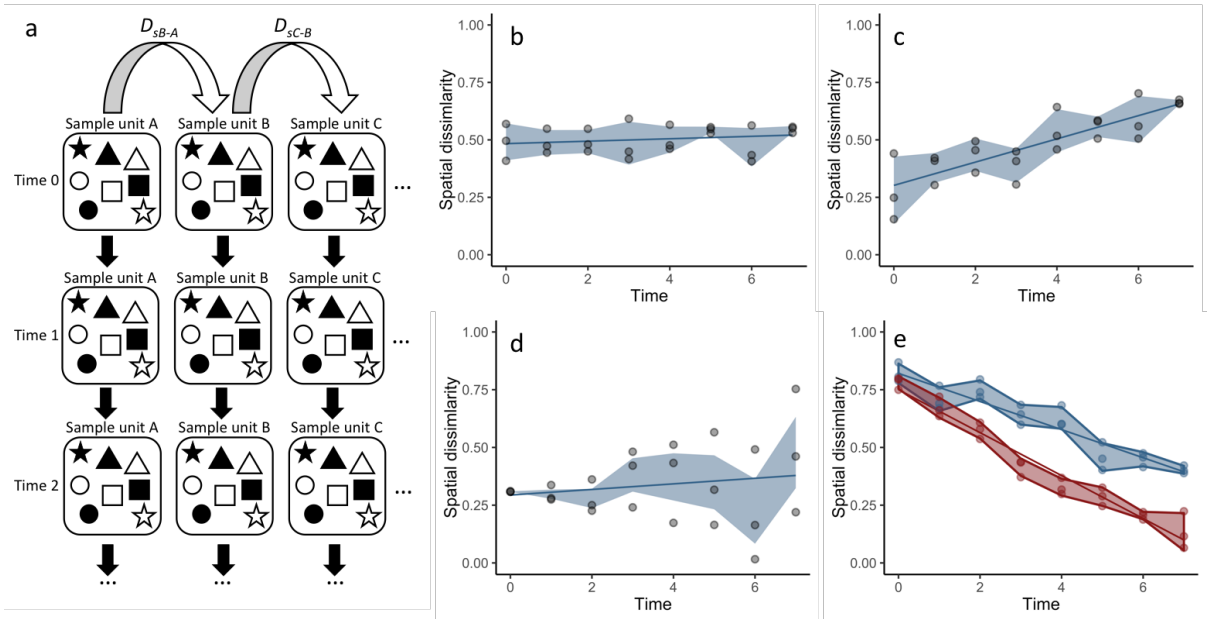

a
D_{sB-A}
D_{sC-B}
Sample unit A
Sample unit B
Sample unit C
Time 0
Time 1
Time 2
b
c
d
e
Spatial dissimilarity
Time
1.00
0.75
0.50
0.25
0.00
0
2
4
6

Figure 6

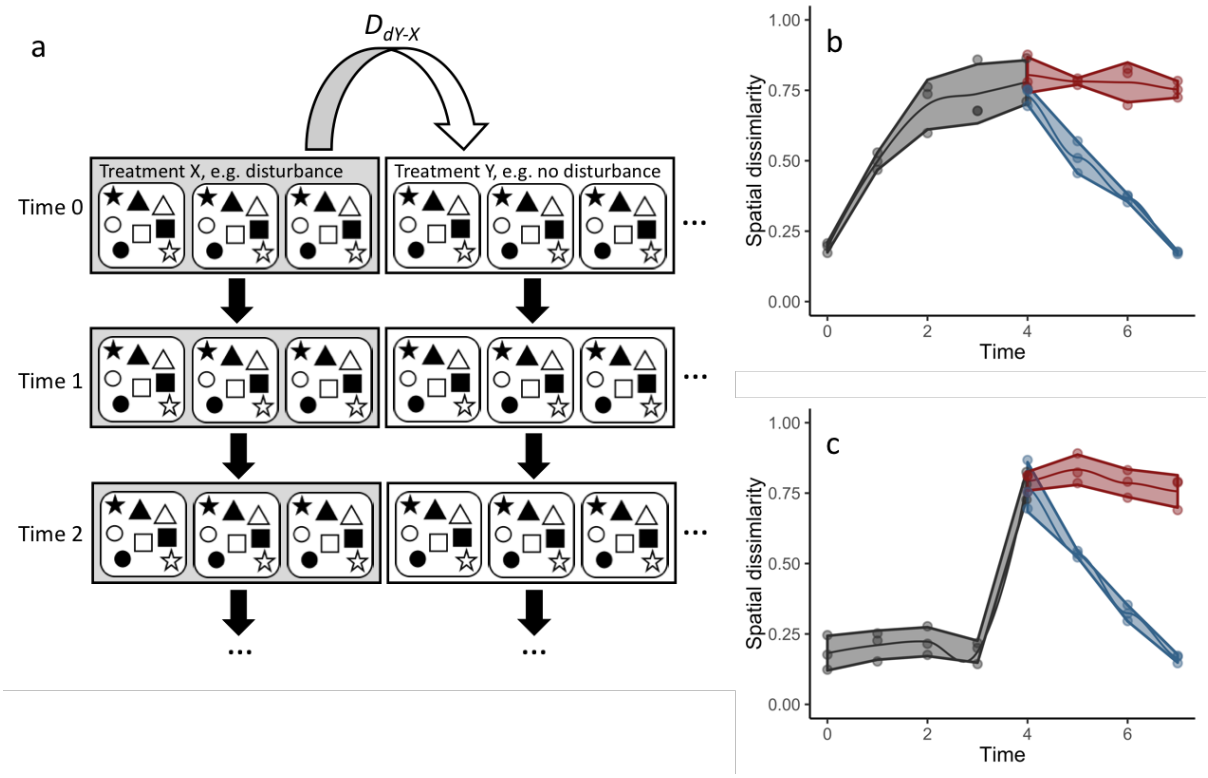

a
$D_{dY\text{-}X}$
Treatment X, e.g. disturbance
Treatment Y, e.g. no disturbance
Time 0
Time 1
Time 2
b
c
Spatial dissimlarity
Time
1.00
0.75
0.50
0.25
0.00
0
2
4
6

Figure 7

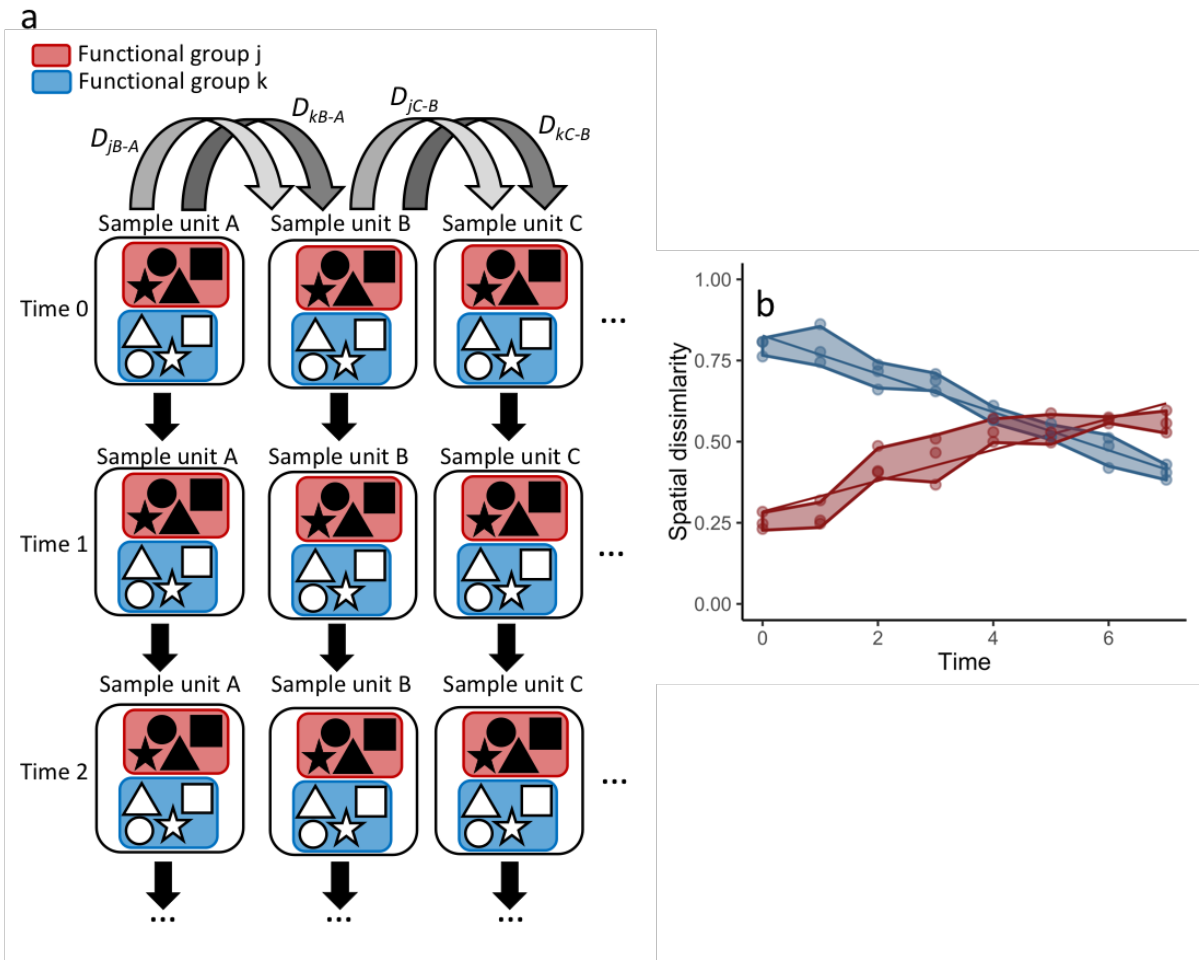

a
Functional group j
Functional group k
D_{jB-A}
D_{kB-A}
D_{jC-B}
D_{kC-B}
Sample unit A
Sample unit B
Sample unit C
Time 0
Time 1
Time 2
b
Spatial dissimlarity
1.00
0.75
0.50
0.25
0.00
0
2
4
6
Time

Figure 8

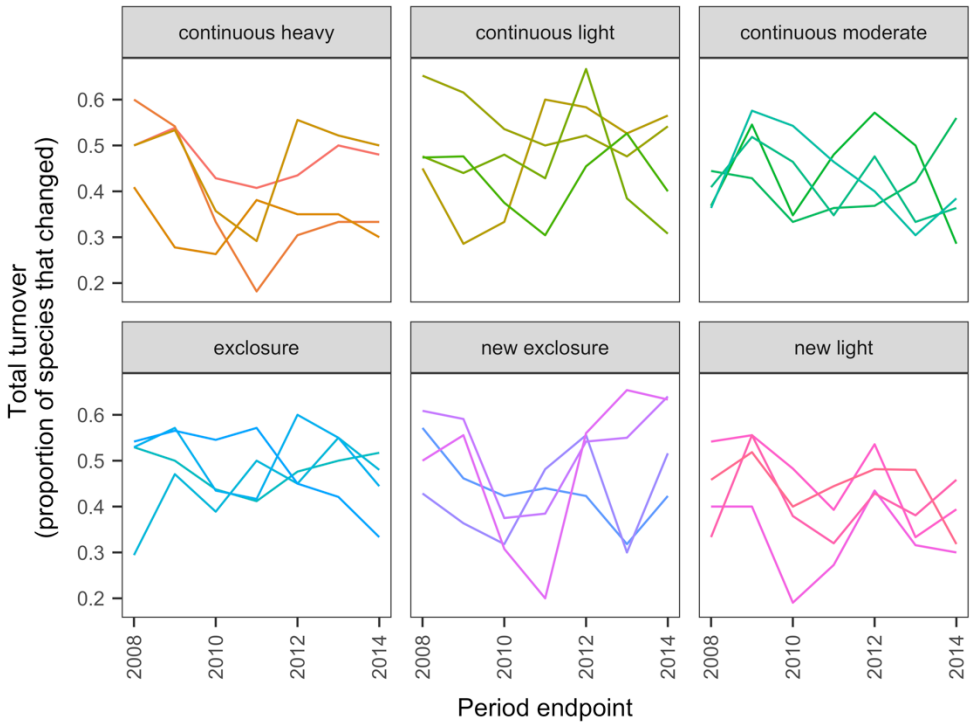

continuous heavy
continuous light
continuous moderate
exclosure
new exclosure
new light
Total turnover
(proportion of species that changed)
0.6
0.5
0.4
0.3
0.2
2008
2010
2012
2014
Period endpoint

Figure 9

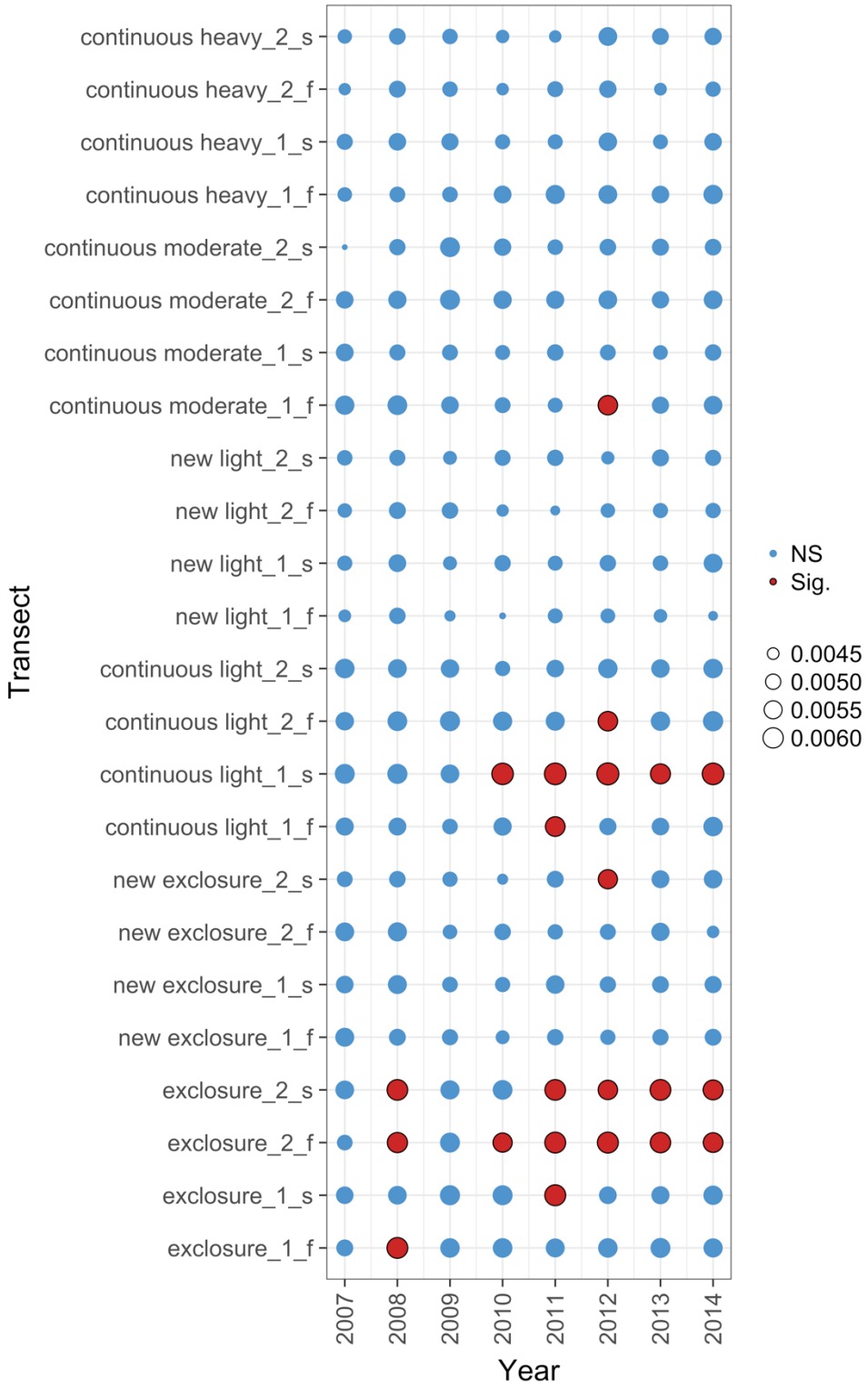

continuous heavy_2_s
continuous heavy_2_f
continuous heavy_1_s
continuous heavy_1_f
continuous moderate_2_s
continuous moderate_2_f
continuous moderate_1_s
continuous moderate_1_f
new light_2_s
new light_2_f
new light_1_s
new light_1_f
continuous light_2_s
continuous light_2_f
continuous light_1_s
continuous light_1_f
new exclosure_2_s
new exclosure_2_f
new exclosure_1_s
new exclosure_1_f
exclosure_2_s
exclosure_2_f
exclosure_1_s
exclosure_1_f
Transect
2007
2008
2009
2010
2011
2012
2013
2014
Year
NS
Sig.
0.0045
0.0050
0.0055
0.0060

Figure 10

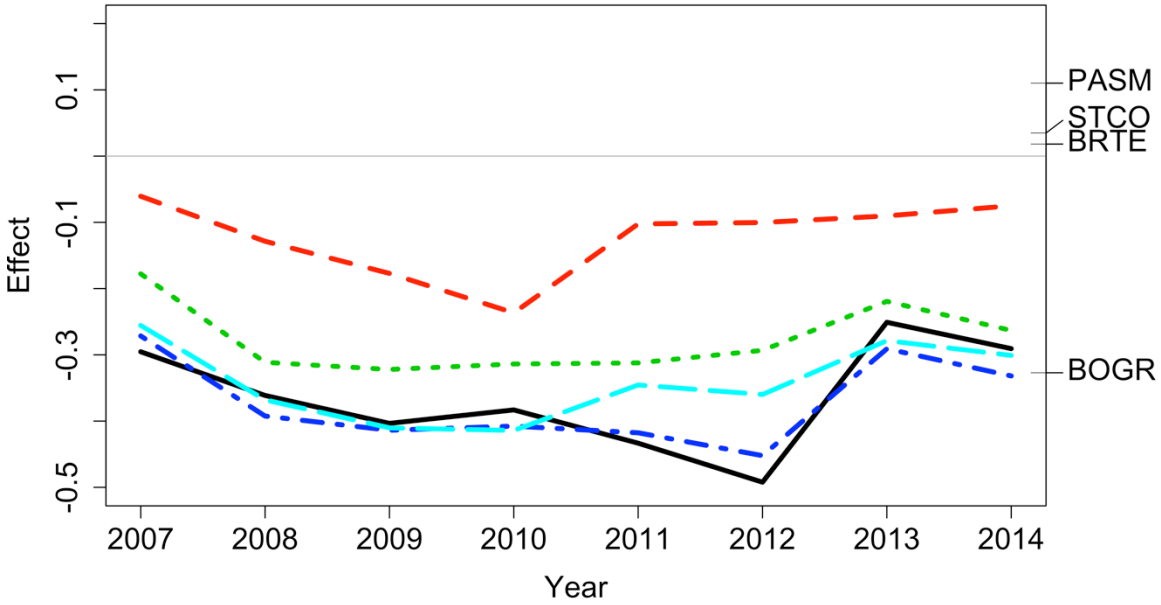
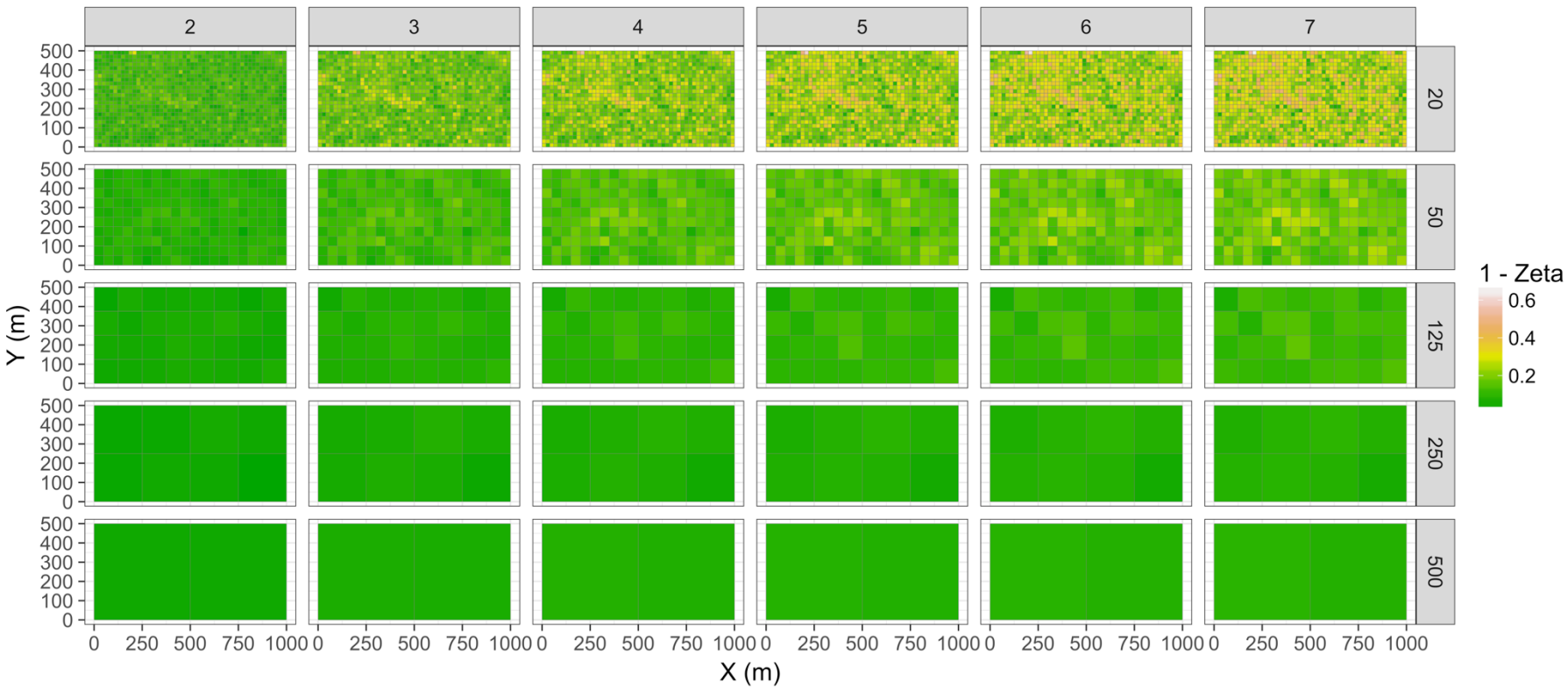
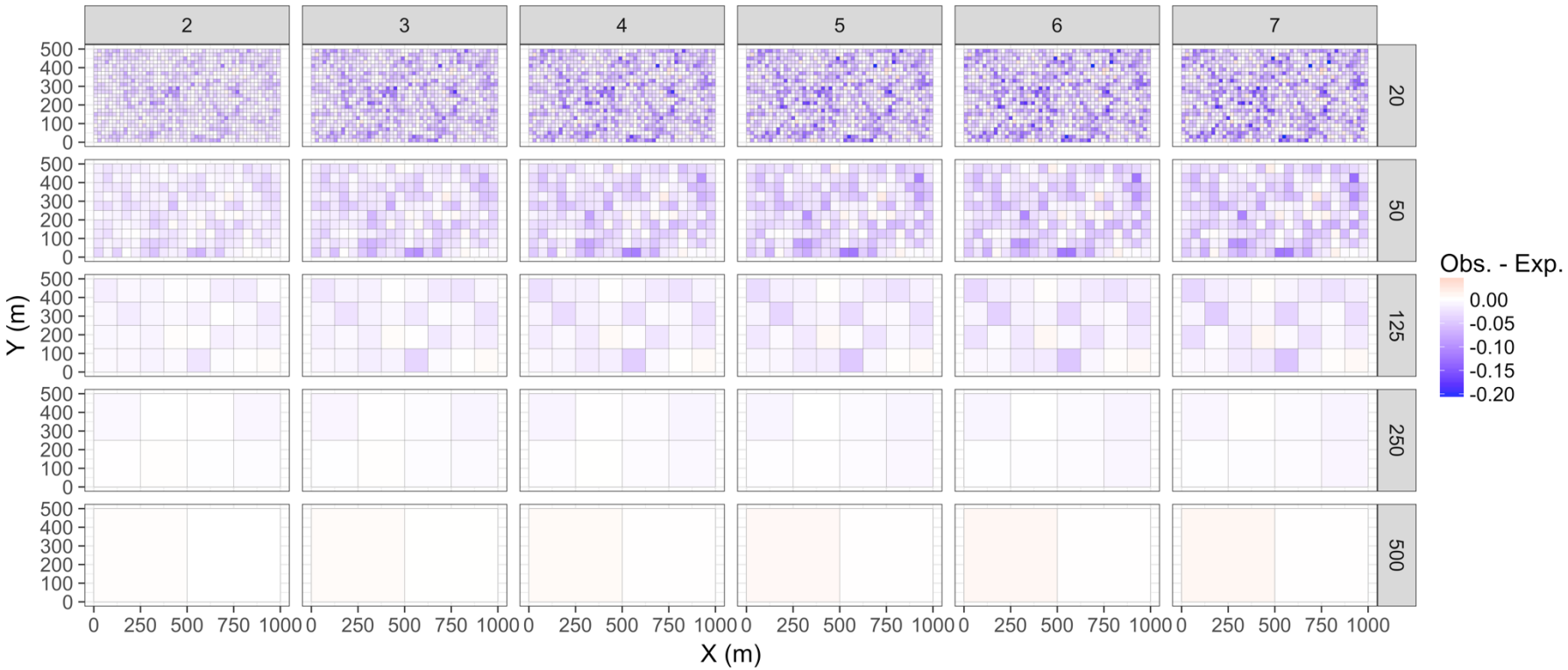

PASM
STCO
BRTE
BOGR
Effect
0.1
-0.1
-0.3
-0.5
2007
2008
2009
2010
2011
2012
2013
2014
Year

Figure 11

(A)


2
3
4
5
6
7
20
50
125
250
500
Y (m)
X (m)
0
100
200
300
400
500
0
250
500
750
1000
1 - Zeta
0.6
0.4
0.2

(B)


2
3
4
5
6
7
20
50
125
250
500
Y (m)
X (m)
0
100
200
300
400
500
0
250
500
750
1000
Obs. - Exp.
0.00
-0.05
-0.10
-0.15
-0.20

(C)

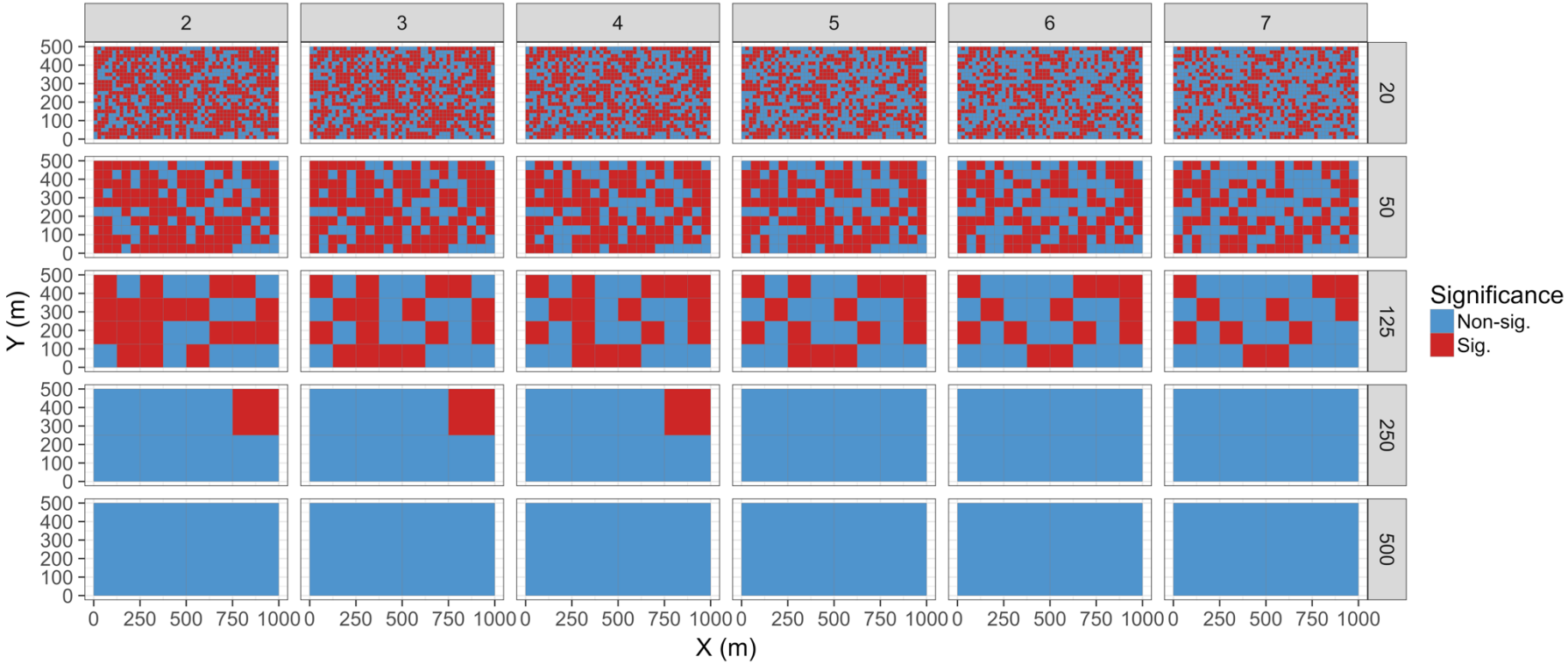
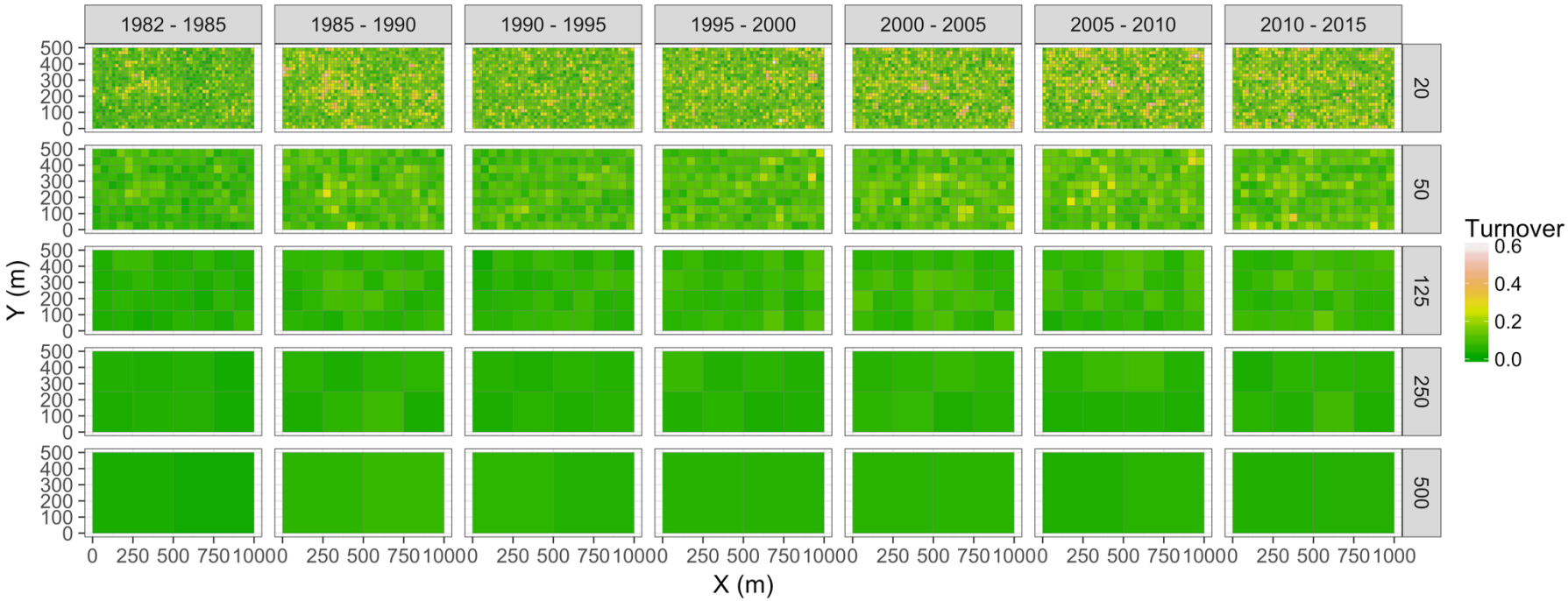
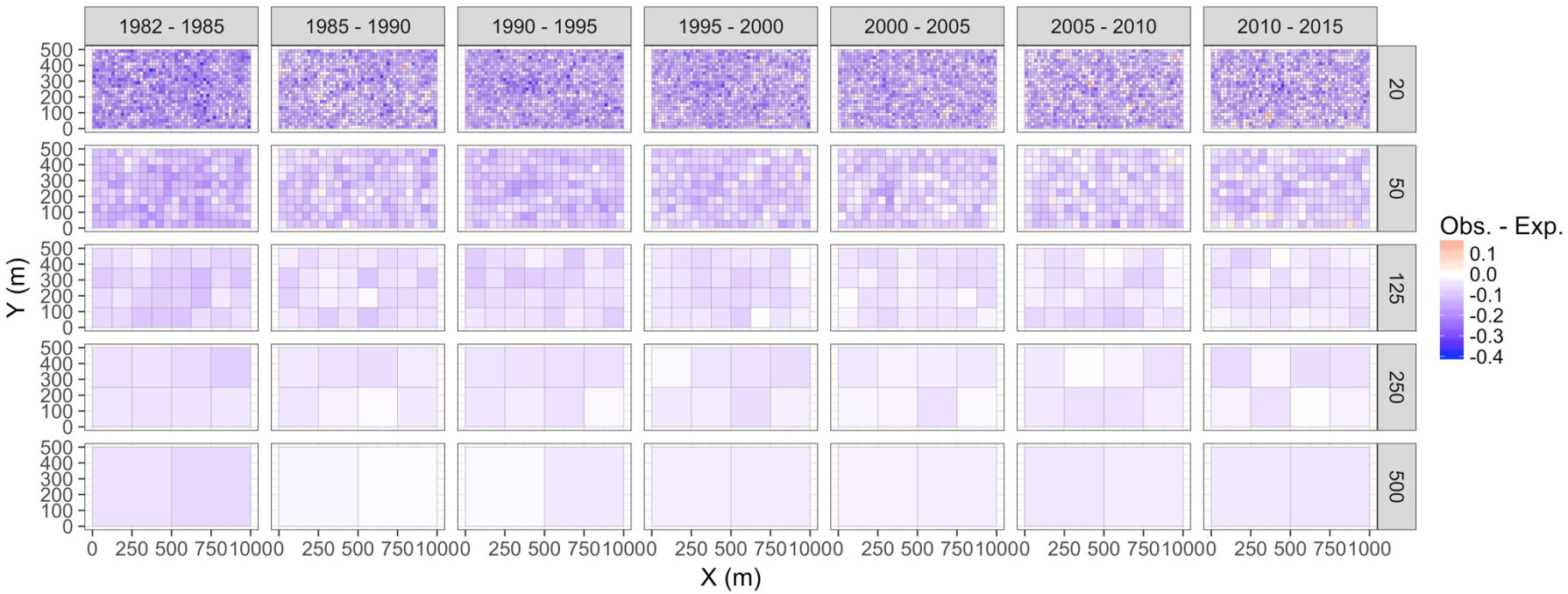

2
3
4
5
6
7
20
50
125
250
500
Y (m)
X (m)
0
100
200
300
400
500
0
250
500
750
1000
Significance
Non-sig.
Sig.

Figure 12

(A)


1982 - 1985
1985 - 1990
1990 - 1995
1995 - 2000
2000 - 2005
2005 - 2010
2010 - 2015
20
50
125
250
500
Y (m)
X (m)
Turnover
0.6
0.4
0.2
0.0

(B)


1982 - 1985
1985 - 1990
1990 - 1995
1995 - 2000
2000 - 2005
2005 - 2010
2010 - 2015
20
50
125
250
500
Y (m)
X (m)
Obs. - Exp.
0.1
0.0
-0.1
-0.2
-0.3
-0.4

(C)

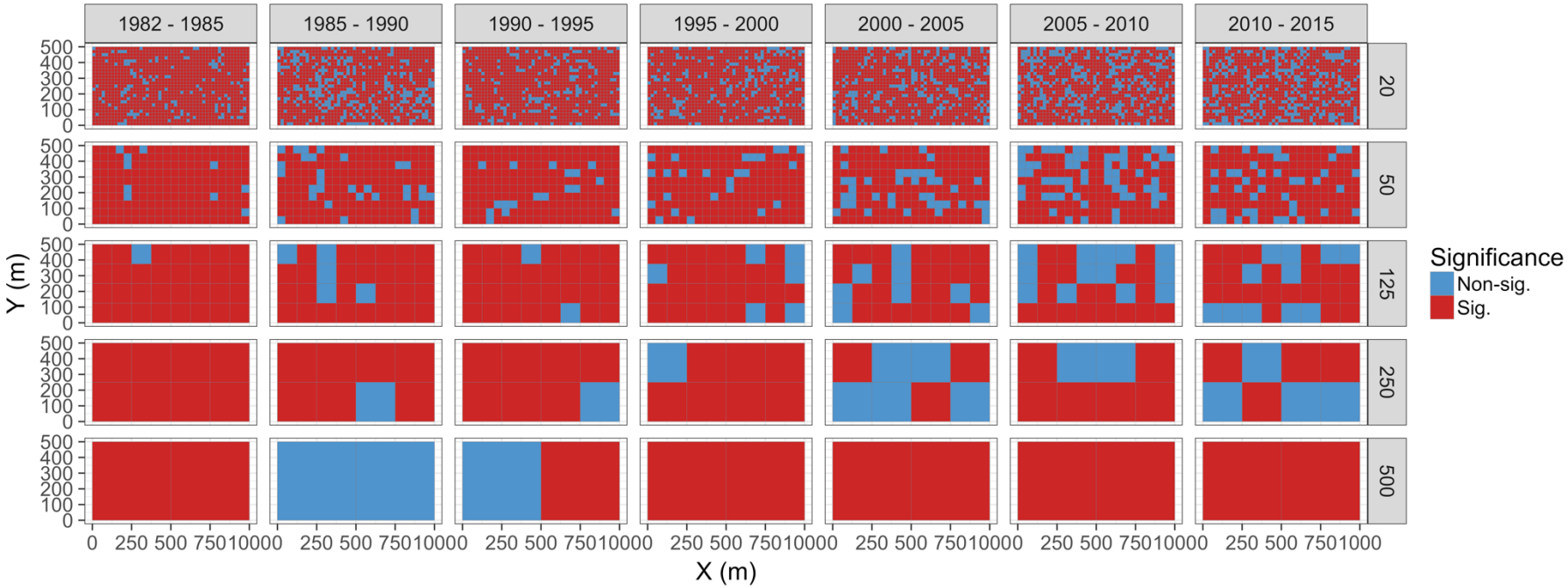

1982 - 1985
1985 - 1990
1990 - 1995
1995 - 2000
2000 - 2005
2005 - 2010
2010 - 2015
20
50
125
250
500
Y (m)
X (m)
Significance
Non-sig.
Sig.

Figure 13

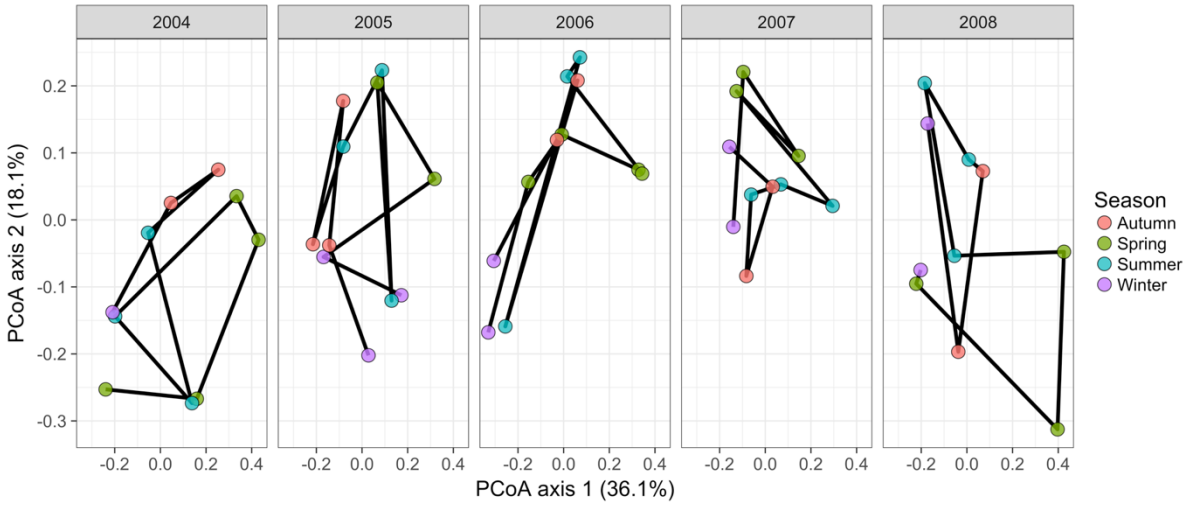

2004
2005
2006
2007
2008
PCoA axis 2 (18.1%)
PCoA axis 1 (36.1%)
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.2
0.0
0.2
0.4
Season
Autumn
Spring
Summer
Winter

Figure 14

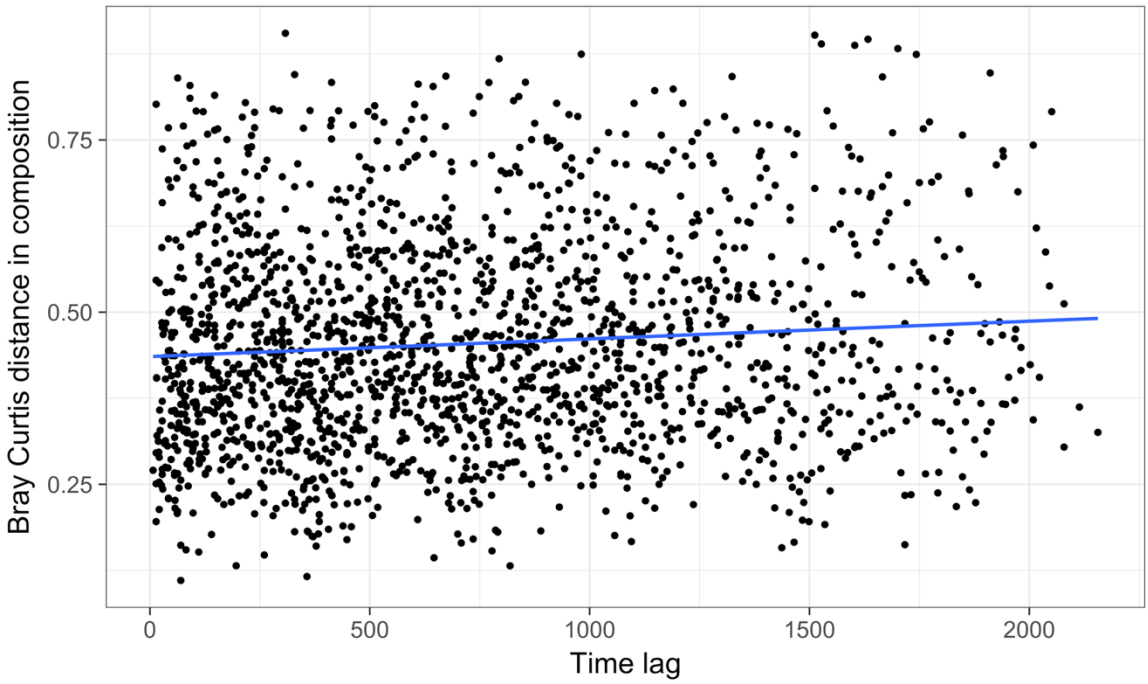

Bray Curtis distance in composition
0.75
0.50
0.25
0
500
1000
1500
2000
Time lag

Figure 15

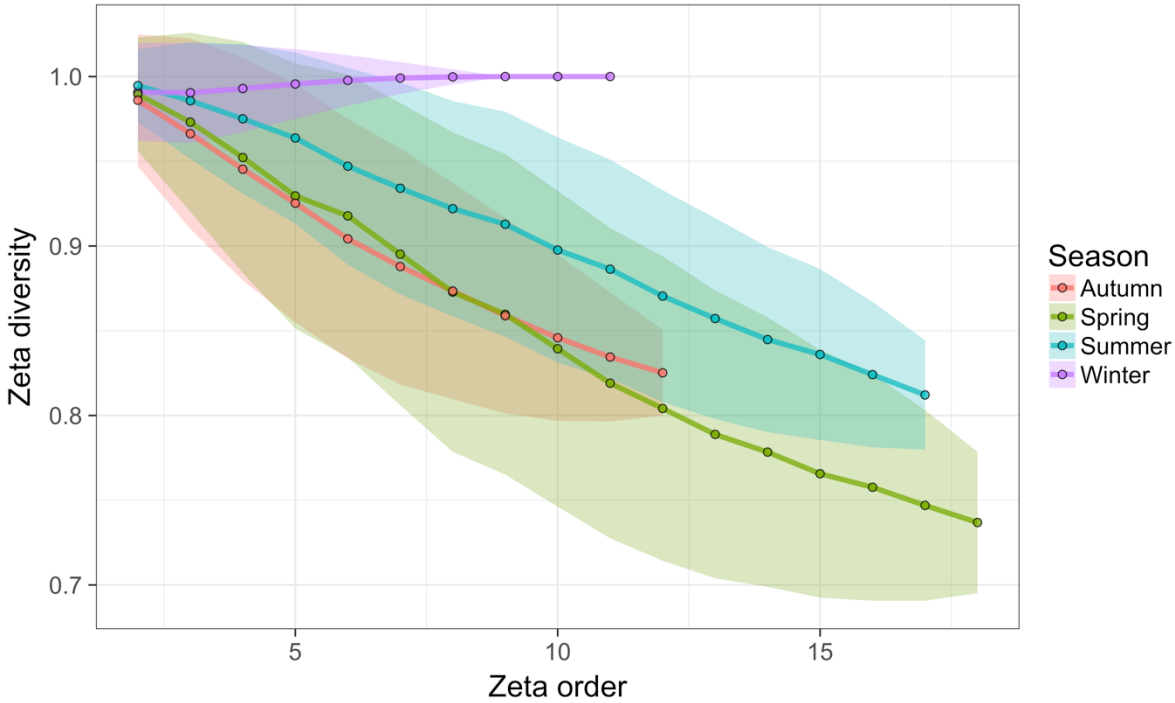

1.0
0.9
0.8
0.7
Zeta diversity
5
10
15
Zeta order
Season
Autumn
Spring
Summer
Winter

Figure 16

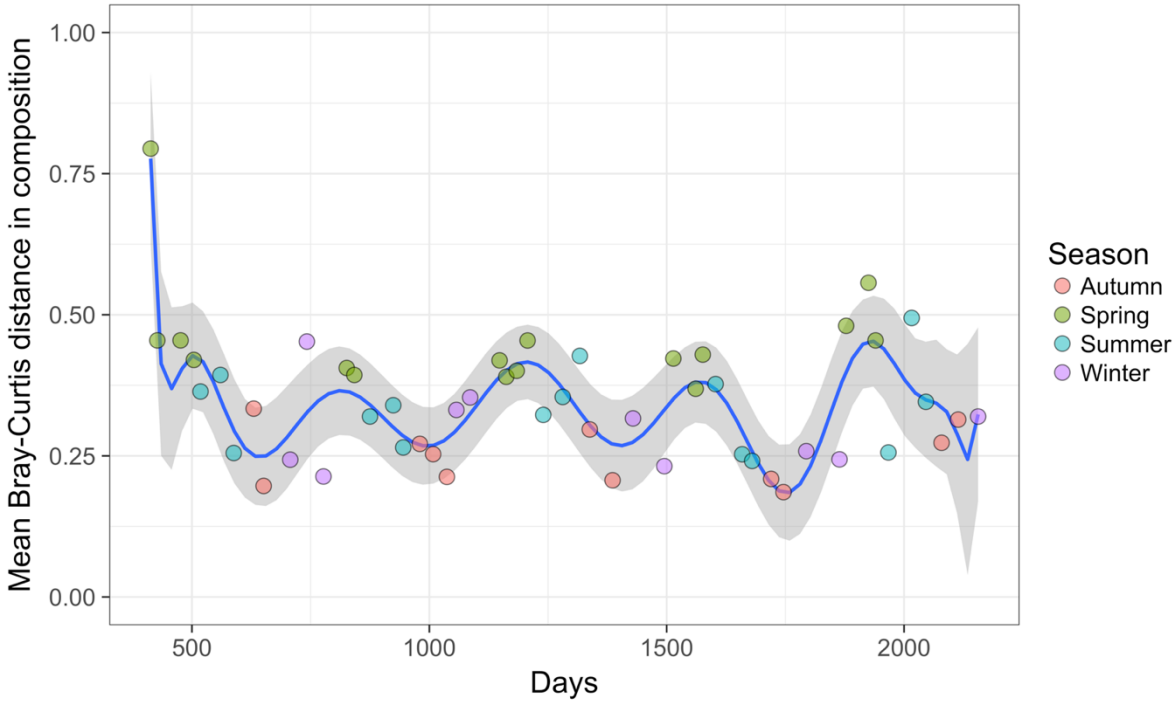

Mean Bray-Curtis distance in composition
1.00
0.75
0.50
0.25
0.00
500
1000
1500
2000
Days
Season
Autumn
Spring
Summer
Winter

Figure 17.

	Also interested in?			Hypotheses of temporal community dynamics					
Method (text section)	Env.	Spat.	Taxa	Directional Succession Invasion Divergence Convergence Homogenisation Degradation	Periodicity Cyclical	Instability Stabilisation	Perturbation Pivot point Tipping point Threshold Resilience	Synch-ronicity	Sig. test type
Mean dissimilarity (D 1.1)		(✓)		✓	✓	✓	✓	✓	Rnd.
Beta diversity decomposition (D 1.2)		(✓)	✓	✓	✓	✓	✓	✓	Rnd.
Zeta diversity (D 2.0)	#	(✓)		✓	✓		✓	✓	Rnd.
Synchrony (D 3.0)		(✓)						✓	Rnd.
Turnover rates (D 4.0)		(✓)		✓			✓		Rnd./ Reg.
Community trajectories (D 1.7)		(✓)		✓	✓	✓	✓		Rnd.
Venn diagrams and time cores*		(✓)	✓	*					None
Time lag graph or regression (D 1.3)		(✓)		✓	✓	✓	✓	✓	Mtl/ Rnd.
Pivot days (D 1.6)		(✓)					✓		Rnd.
Multivariate regression (D 5.0)	✓	✓	✓	✓	✓	✓	✓	✓	Rnd./ Reg.
Regress mean dissimilarity (D 1.1)	✓	✓		✓	✓	✓	✓	✓	Reg.
MEMs with db-RDA (D 1.5)	✓	✓	✓	✓	✓	✓	✓	✓	Rnd.
Constrained ordination (D 1.4)	✓	✓	++	+					Rnd.
Ordination site scores (D 1.4a)	✓	✓	++	+	+	+		+	Reg.
Temporal coherence (D 1.4a)		(✓)		+				+	Rnd.
PRC (D 1.4b)##	✓	✓	✓	+	+			+	Rnd.

← Increasing sample size required ←

1890

Appendix S1

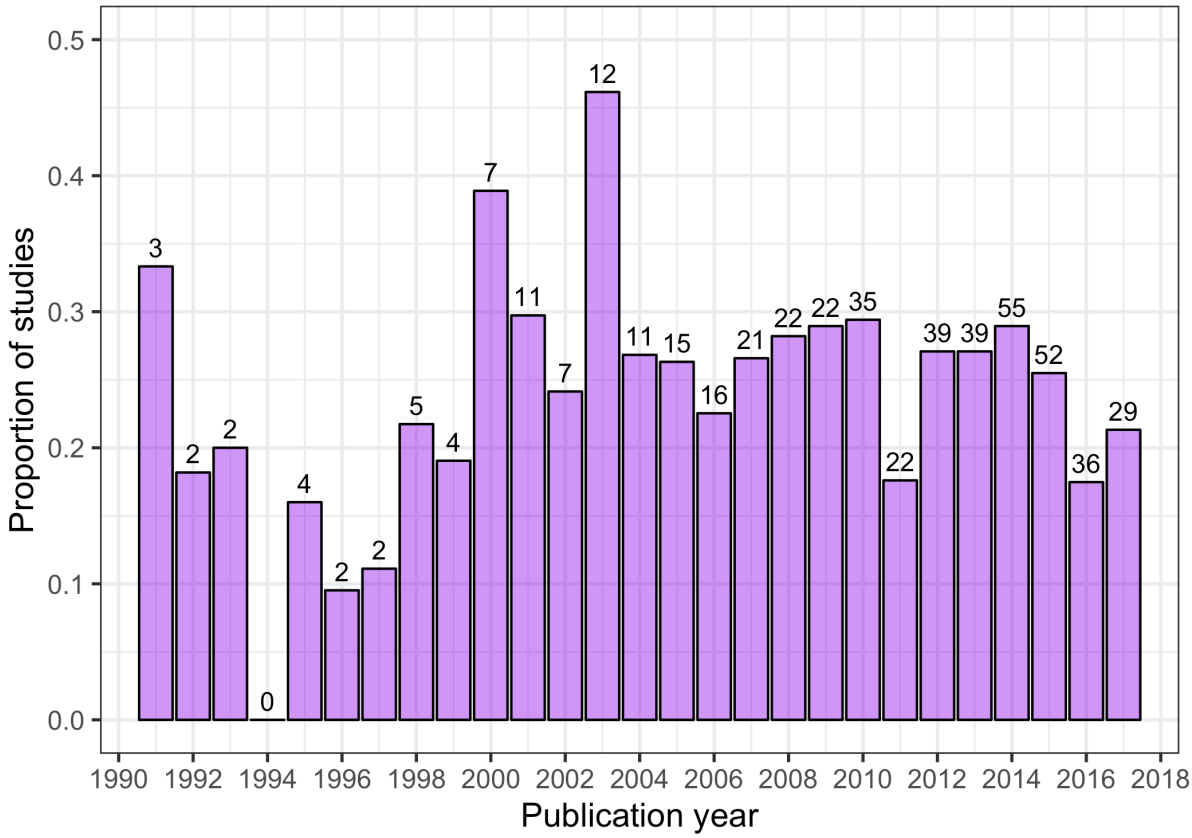
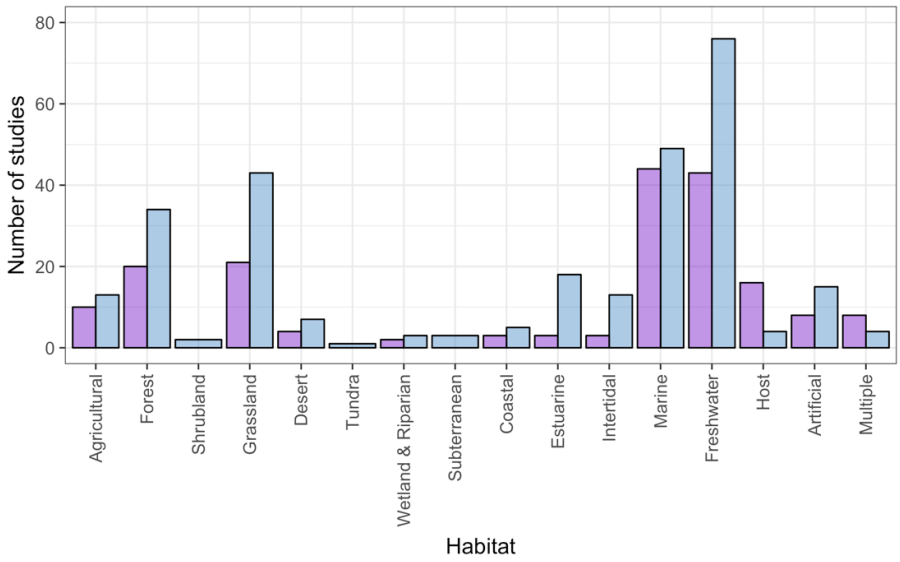


Figure S1. Proportion of studies identified using our search terms that were published each year until September 2017. No studies prior to 1991 were captured by our search terms. The total number of studies in each year is the value above the bars.

(A)



(B)

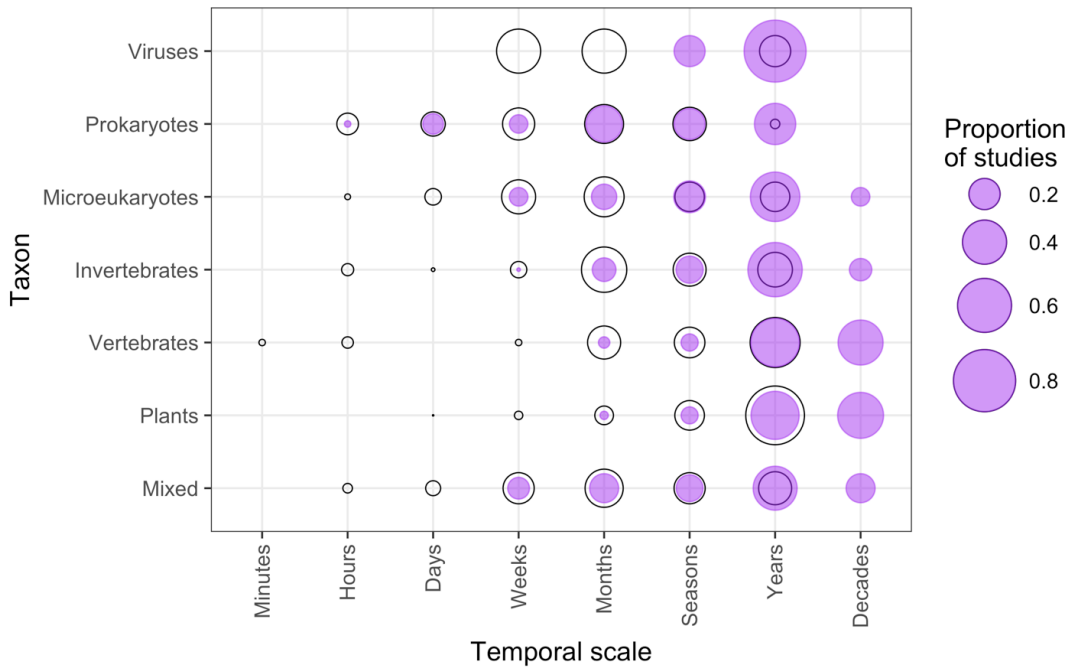


Figure S2. (A) The numbers of small and large spatial scale studies by habitat category. Small spatial scale (blue bars) studies were considered to be those carried out at micro, point sample, and local scales, while large spatial scale studies (purple bars) were those at regional, continental, or global scales. (B) The proportion of studies of different taxa within categories defined by the temporal grain (black circles) and extent (purple dots). Temporal grain is the minimum time between sampling events within the study and the temporal extent is the maximum time between sampling events within the study.

(A)

(B)

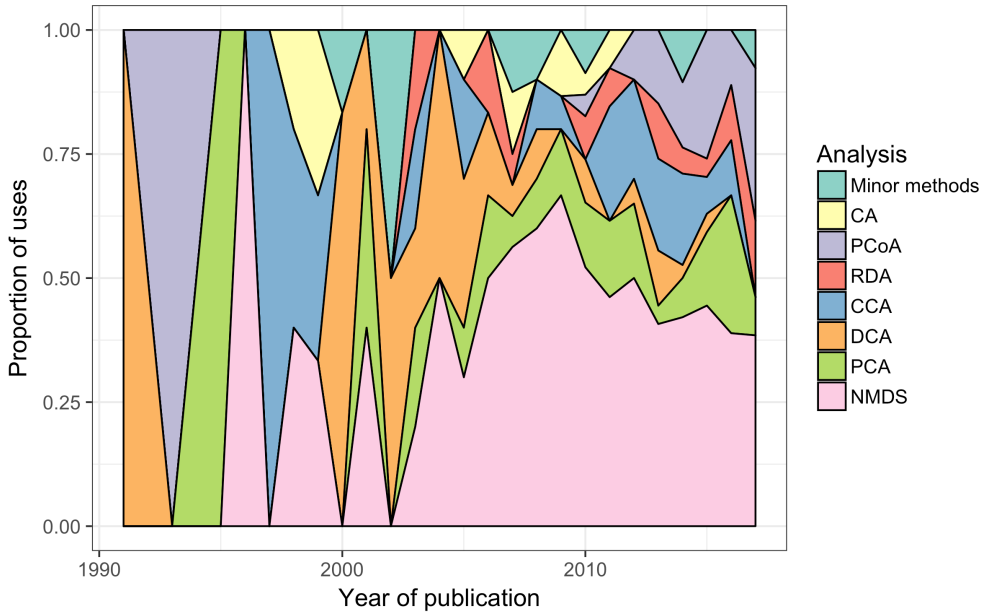


Figure S3. (A) The proportion of uses of each type of analysis across all sampled publications between 1990 and 2017. 'Minor methods' include compositional pivot days, frequency change, Markov chain modelling, multiplicative change, Moran's eigenvector maps (MEMs), Nestedness analysis, and synchrony. (B) The popularity of the different ordination methods used across the 27 years. 'Minor methods' are: dbRDA, DCCA, pCCA, pRDA, Procrustes, RA and multiple co-inertia analysis. Descriptions of analysis types are detailed the S1 Text supplementary material.

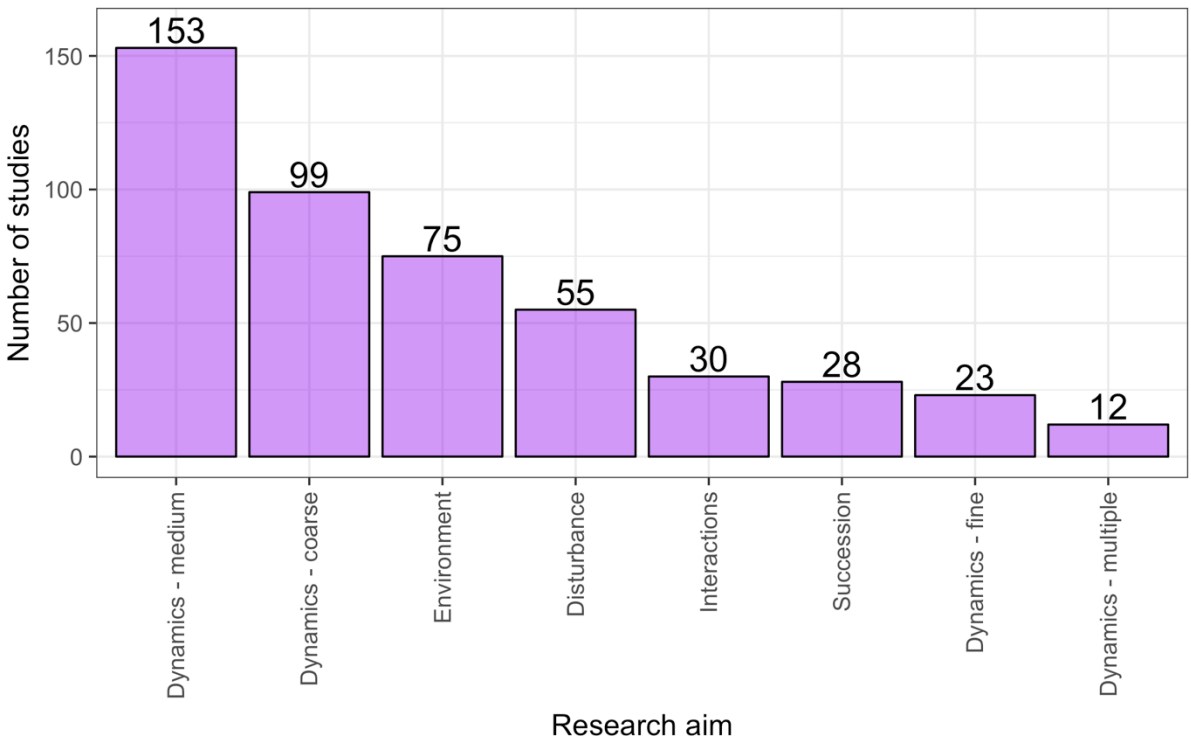


Figure S4. The distribution of studies across the different research aims. Research aims vary from understanding compositional dynamics at fine, medium and coarse temporal scales, to investigating the effect on species composition over time of species interactions, environmental conditions, and ecological disturbance, to understanding successional change in communities. Scales of temporal dynamics were classified as fine (days), medium (weeks, months, or seasons), and coarse (annual, years, or decades).

Appendix S2. Other methods encountered in the literature review, not explained in the text

UNIVARIATE LINEAR METHODS

Univariate linear methods, including analysis of variance (ANOVA), analysis of covariance (ANCOVA), repeated measures ANOVA (rmANOVA), simple correlation (e.g., Pearson's and Spearman's correlation coefficients), and regression (linear regression, generalised linear models, generalised linear mixed effects models, logistic regression, *etc.*), are used to examine temporal changes in a univariate response (dependent) variable. The independent variable is either time, or an environmental variable that changes over time, and the response variable usually is the (relative) abundance of a focal taxon or functional group.

Univariate linear methods are applied most frequently to community dynamics by constructing separate models for each species. These methods of assessing compositional dynamics are limited because multiple analyses, conducted in parallel on selected taxa, are required to make inferences regarding composition. For even modest numbers of taxa, these multiple analyses can become unwieldy and require *P*-value corrections for multiple tests (Benjamini and Hochberg 1995, Zar 1996). For example, Bugalho et al. (2013) used repeated-measures mixed-effects modelling to assess the effects of deer exclusion over time on the abundance of seedlings and saplings of forest tree species. In this case, the univariate modelling approach was usefully applied because fewer than ten species were analysed. Alternatively, abundance can be analysed for all species in the same model as long as there are enough degrees of freedom in the model to include species as a fixed or random effect term (e.g., Buckley and Freckleton 2010); see Harrell (2001) for a rule of thumb stating that we should have at least ten independent samples for each predictor variable in our model. Generalised linear models are more flexible in that they can handle designs with unbalanced data and nested sampling (e.g., plots within sites) (Bolker et al. 2009, Zuur et al. 2009). R code is provided in Appendix S4.

CLUSTER ANALYSIS (A DISSIMILARITY BASED METHOD)

Cluster analysis is a catch-all term applied to dissimilarity-based methods that either group samples together (agglomerative methods) or split all samples into sub-groups (divisive methods); the clustering is based on the distances between clusters (Legendre and Legendre

2012). There are two approaches for using cluster analysis to assess community dynamics: (1) identifications of transitions between clusters over time, and (2) examination of differences of clusters of repeated observations. In the first approach, a separate cluster analysis is computed for each temporal sample of community data (e.g., Day and Buckley 2013). In the second approach, all samples taken at different times are included in a single cluster analysis (e.g., Araujo et al. 2008). If compositional shifts are small relative to the total compositional variation in the dataset, the first approach will not be able to detect temporal differences. However, if compositional shifts are relatively large, it yields a clear way of showing shifts in 'community types': groups of samples of similar composition that can be characterised using a method such as indicator species analysis (e.g., Day and Buckley 2013). The first method can potentially be applied to a larger number of time points if all that is desired is to report the percent of sites that changed cluster groups each time. For example, cluster analysis of 34 phytoplankton species in Laoshan Bay, China revealed distinct groups of species occurred at different times over a six-month period (Xu et al. 2010).

TEMPORAL STABILITY (A.K.A. COEFFICIENT OF VARIATION)

The coefficient of variation (CV) is used to measure temporal stability of the abundance or biomass of an individual taxon, or group of taxa, across all times (not space); this is not a multivariate method (Grossman et al. 1990, Brown and Lawson 2010, Hector et al. 2010). The CV is the ratio of the standard deviation to the mean, and often is multiplied by 100 to obtain a percentage. The mean of the CV values for all taxa (e.g., abundance or biomass) is used as an aggregate measure of temporal stability for a whole community; smaller values imply greater stability. Because the CV is a ratio, changes in community composition can be compared even if there are differences in total abundances among taxa or in taxon richness among taxon groups. Such values are often presented in tables or the text as a measure of variation or are sometimes used as a response variable against other (spatial) variables of interest (e.g., Doxa et al. 2012). For example, CV can be calculated for disturbed and undisturbed communities to assess if the disturbance has resulted in a more temporally variable community. Grossman et al. (1990) categorised particular values of CV to assess stability of freshwater fish communities: a community was 'highly stable' if it had a CV < 25%, 'moderately stable' if 25% < CV < 50%, 'moderately fluctuating' if 50% < CV < 75% or 'highly fluctuating' if CV > 75%. The statistical significance of CV values could be obtained by comparing the observed values to those from communities generated using

randomisations under sensible null models. Note that temporal CV is necessarily be measured on a per site basis to exclude spatial variation.

FREQUENCY CHANGE

Changes in the frequency of individual taxa within a community over time can be assessed by subtracting their frequency at each sampling occasion from a prior sampling occasion; this is not a multivariate method. Permutation tests can be used to test the significance of these changes in frequencies (Kapfer et al. 2011). Community samples (with their given taxon frequencies) are randomised among sampling times and the change in taxon frequency recalculated with each permutation. A significant change in the observed taxon frequency is inferred if the observed change is greater than the 95th percentile change from the permutations. Permutations should be spatially restricted so that only samples from homogeneous habitat types are compared; otherwise the chance of spuriously detecting change is greatly increased. The outcome of these tests is a list of taxa that had significant increases or decreases in frequencies, and the amount, between sampling times. For example, Kapfer et al. (2011) used permutation tests to assess changes in frequencies of 85 plant species from two time points 50 years apart. This method could be used on data from multiple sampling occasions, but would quickly become cumbersome with many temporal observations. It can only be used to compare individual taxa over time, does not apply to rare taxa (taxa need to occur in enough sites to make the calculations tractable), and results in a (potentially) large table of taxa with significant (or not) changes, therefore, it has limited applicability to taxon-rich datasets where changes in rare taxa are of interest.

MULTIPLICATIVE CHANGE

The change in percent cover of a taxon, or group of taxa, at a single site can be used to obtain a ‘growth rate’ using a linear regression equation; this is not a multivariate method (Debinski et al. 2010, Collins and Xia 2015). This rate of change can then be used in a regression or ANOVA to assess predictors of change for each species (‘multiplicative change’). For example, different sites or sets of sites, can be compared in their relative change in the percent cover of different functional groups (Debinski et al. 2010), as long as communities consist of taxa with similar ecology and life-histories, e.g., grassland plant communities in different moisture regimes. This method appears to be most useful for studies where (1) there is little temporal replication, or at least where differences among temporal replicates are not

of interest, because the growth rate is calculated using only two temporal samples, and (2) few species, species groups, are of interest because a different analysis must be performed for each. However, it would be possible to calculate the change in percent cover for different time periods within the overall study, if one was interested in investigating finer-scale trends.

MARKOV CHAIN MODELLING

Markov chain modelling uses a series of transition probabilities (a 'Markov chain'), which describe how the occupancy of a taxon or functional group in a site changes from time t to time $t + 1$ (Hill et al. 2004). The user varies these probabilities in space and/or time to create a set of different hypothesis-driven models that predict the observed occupancy. The model set can then be evaluated against the observed data using log-linear modelling and AIC model selection to determine the influential and significant processes on taxon site occupancy through time (Hill et al. 2004). Community dynamics usually are examined by comparing predicted changes in individual taxa, making the method easier to apply to communities of few taxa (or groups of taxa). Because models often are parameterised using the modelled data, dependence of samples needs to be dealt with through sampling design or post-hoc statistical analyses (Hill et al. 2004). This method is most appropriate for sessile communities where patch occupancy is easy to replicate and define (e.g., Hill et al. 2004, Pueyo and Beguería 2007). It best describes directional dynamics, such as secondary succession (e.g., Baasch et al. 2010, Jiménez-Franco et al. 2011) and it is relatively computationally difficult. However, it makes detailed, taxon-level predictions that can be useful for the analysis of experimental studies where researchers want to explore specific predictions from multiple scenarios, such as taxon extinctions (e.g., Wootton 2004) or restoration manipulations (Baasch et al. 2010).

MACHINE LEARNING AND DATA MINING METHODS

Machine learning is branch of computer science that deals with the development of learning algorithms that are used to explore large, multivariate datasets, and has the primary aim of generating accurate, predictive models (Carbonell et al. 1983). Common machine-learning methods include artificial neural networks and decision-tree methods which can be used with either univariate or multivariate response variables, and Bayesian versions can incorporate prior knowledge (Cutler et al. 2007, Olden et al. 2008). Whilst the field of machine learning focusses on making predictions from data, many of its methods also are used in a data-mining

capacity to discern spatiotemporal patterns from complex and noisy datasets and can be used for classification, regression, clustering, and data reduction (Olden et al. 2008).

Machine-learning methods are attractive because they do not have many of the restrictive assumptions, such as linearity or data normality, that underpin many traditional statistical methods (Olden et al. 2008). Thus, machine-learning methods are becoming increasingly popular for exploratory and predictive analyses of community dynamics (e.g., Kampichler et al. 2010). For example, Vallès et al. (2014) used self-organising maps, an implementation of artificial neural networks (Kohonen 1982), to show that complex microbial communities sampled from infants' guts formed distinct clusters at each of five sample times (based on relative abundance data), suggesting that successional processes were occurring within the first year of these infants' lives. Sheaves et al. (2010) used a multivariate classification and regression tree analysis (De'ath 2002) to investigate spatial and temporal differences in fish assemblages; results showed that despite considerable spatial variation in community structure among different estuaries, there nonetheless were clear patterns of temporal change in species' abundances and assemblage composition. These methods are very flexible and can handle both univariate and multivariate input datasets with large numbers of predictor variables, including space and time, allowing simultaneous investigation of spatial and temporal community dynamics. Standardised approaches for characterising different types of temporal patterns and causal processes in community datasets will hopefully emerge from further research. R code is not provided, but R packages are available (the MultivariateRandomForest package: Rahman 2017, and rpart package: Therneau and Atkinson 2018).

NETWORK ANALYSIS

Ecological network analysis enables the investigation of the complex associations among species, and among species and their environment, through space and time (Newman 2010, Blonder et al. 2012). This method recognises that an ecological community is a complex biological system comprised of interconnected units whose associations can be modelled mathematically using constructs such as vertices (representing taxa) and edges, which are the connections between the vertices (representing ecological interactions) (Blonder et al. 2012). In the context of investigating community dynamics, patterns of species' associations and community memberships are most typically visualised as a topological network diagram created from taxon abundance data collected at multiple time points (*sensu* "time-aggregated

networks" (Blonder et al. 2012). From the network topology, a variety of statistics can be calculated that measure variability in community composition and interactions at particular times, which can then be compared. This method is most applicable for multi-trophic communities or where interaction networks can be clearly defined for the community; it is less useful where a single trophic level is of interest and interactions are not quantified, e.g., a plant community, but see Cram et al. (2015) for an example of spatiotemporal microbial networks. In R, the package 'timeordered' is the easiest way to implement a network analysis of community dynamics data. R code is not provided.

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