Temporal β diversity – a macroecological perspective

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Abstract

Issue: Biodiversity change, that is how the taxonomic identities and abundances of species in ecological systems are changing over time, has two facets: temporal α diversity and temporal β diversity. To date, temporal α diversity has received most attention even though compositional shifts in assemblages exceed expectations based on ecological theory. Growing concern about the state of the world's biodiversity highlights the need for better understanding of the extent, and consequences, of compositional reorganization in ecological systems.

Challenges: Most methods of measuring β diversity have been developed in a spatial context. We discuss the additional challenges involved in the assessment of temporal change, summarize existing methodological approaches, highlight the importance of establishing relevant baselines, and identify the need for appropriate null models of temporal β diversity. Given considerable potential for research on the macroecology of temporal β diversity we suggest future directions and challenges.

Conclusions: Although data availability remains the main impediment to improved quantification of temporal β diversity at macroecological scales, there are substantial opportunities for improved methodology and theory. Taxonomic β diversity has received most attention, but other dimensions of diversity, including functional and phylogenetic, should be part of integrated assessments of biodiversity change. Future approaches need to be ecologically meaningful and interpretable as well as statistically robust.

The 2019 Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Global Biodiversity Assessment (Brondizio, Settele, Díaz, & Ngo, 2019; Pereira et al., 2010; Tittensor et al., 2014) argues that, in many cases, anthropogenic pressures on nature in the second half of the 20th century exceeded those that had occurred over the entire course of preceding human history. To protect these ecosystems in the Anthropocene it is imperative to understand how and why biodiversity is changing over time. Many of the headline treatments of contemporary biodiversity change concern the fate of iconic species. When attention has focussed on ecological systems, such as assemblages, investigations of temporal change in α diversity (such as species richness) have dominated the discussion (Brondizio et al., 2019). However, substantial and ongoing change in the compositional make up of assemblages around the world is also a pressing, (e.g. Blowes et al., 2019; Dornelas et al., 2014; Gotelli et al., 2017) but less appreciated, problem. Meta-analyses suggest that contemporary rates of temporal β diversity are greater than ecological theory predicts (Gotelli et al., 2017). The consequences of these shifts for community resilience and ecosystem functioning are unclear. To understand, and potentially ameliorate, rapid biodiversity change, effective methods of measuring temporal β diversity are needed. The goal of this paper is to examine current approaches used to quantify temporal β diversity, identify the challenges and opportunities involved, and map out some future directions. Although our focus is on contemporary assemblages, many of the same considerations apply to the analysis of palaeontological systems (e.g. Tomašových & Kidwell, 2009) albeit with additional challenges such as the fragmented nature of fossil data.

It is now well appreciated that the measurement of biodiversity requires careful planning; different metrics capture different aspects of community structure, some more effectively than others, and practical considerations such as the type and intensity of sampling can have a marked influence on the conclusions drawn (Gotelli & Colwell, 2001; Magurran, 2004; Southwood & Henderson, 2000). These considerations apply equally to the quantification of biodiversity change (Anderson et al., 2011; Dornelas et al., 2014; Dornelas et al., 2013; Hillebrand et al., 2017; Santini et al., 2017), which is an expression of change over time in the size and structure (α diversity), <u>and</u> the composition (β diversity) of assemblages; in the case of temporal β diversity, however, the field is still evolving with little consensus, as yet, on the best way to proceed. We start by briefly defining how we use the terms temporal β diversity and temporal turnover, in the discussion that follows. We next examine methods of quantifying temporal β diversity, and consider the role that null models can play in judging meaningful shifts in this form of diversity. We begin by reflecting on the types of compositional changes that can occur in assemblages, to provide context on the aspects of biodiversity change that temporal β diversity measures need to capture.

Temporal β diversity
We define temporal β diversity as the shift in the identities and/or the abundances of named taxa in a specified assemblage over two or more time points. Whereas temporal α diversity is agnostic to species identities, temporal β diversity tracks changes attributed to species composition. In the same way that change in α diversity needs to be interpreted in relation to the approach (e.g. species richness) used to quantify it, temporal β diversity will be a product of the metric used to track change in assemblage composition. Our focus here is on taxonomic diversity, but we recognise that other dimensions of diversity, including

functional and phylogenetic diversity, are also important, and touch on these later on. Temporal turnover is a related concept. It can be used either in a broad sense, and treated as synonymous with compositional change (e.g. McGeoch et al., 2019), or in a narrow sense to refer to the contribution that strict species replacement makes to a dissimilarity measure (e.g. Baselga, 2010). These different usages mean that it is important to define turnover when the term is used. In what follows we use turnover in its broad sense, except when stated otherwise.

Assemblages consist of the species that co-occur at a given place and time, and are often (but not always) delimited by phylogeny and/or by the sampling methodology used during surveys. There is a popular misapprehension that ecological communities resemble museum collections, in that the same species (like exhibits) will be reliably found in the same place, year after year. Yet, all natural systems undergo constant compositional change (Darwin, 1859). Indeed, foundational ecological theory, including MacArthur & Wilson's *theory of island biogeography* (MacArthur & Wilson, 1967), and Hubbell's *unified neutral theory of biodiversity and biogeography* (Hubbell, 2001), take temporal β diversity as given.

Temporal change in assemblage composition can involve different types of species shuffling (Figure 1). For example, some species could be replaced over time, on a one for one basis. Alternatively, local colonisations and extinctions may change the size of the species list. The abundances of the species present will vary, while the order in which taxa are ranked in the species abundance distribution may also be subject to change (Collins et al., 2008). Dominant species (Shi et al., 2015; Song et al., 2019) could be most influential in community reorganisation in some cases, with rare species playing an important role in others (Christensen, Harris, & Ernest, 2018). Alterations in the identities of the persistent and transient species are another possibility (Magurran & Henderson, 2003). The challenge in measuring β diversity, then, is to capture the ongoing temporal changes in assemblage composition in a way that reflects the ecological processes, and the ecosystem functions, that are involved.

Whittaker (1960, 1972) introduced the α, β, γ framework to relate regional (γ) diversity to compositional heterogeneity (β diversity) amongst units of local (α) diversity. Tuomisto (2010a, 2010b), provides a comprehensive and thoughtful overview of β diversity (in its spatial context), in which she stresses the need to use terms carefully while being critical of the use of 'β diversity' to cover a range of approaches that lie outside the precise methodology she outlines. Nonetheless, and in line with its original definition by Whitaker 1960 ('the extent of change of community composition, or degree of community differentiation'), we have retained 'temporal β diversity' in this paper as an overarching term for the different methods of quantifying compositional change through time. This also reflects usage in recent publications (e.g. Dornelas et al., 2014). We agree with Anderson et al. (2011) that the careful application of different methods of evaluating β diversity can yield insightful advances, particularly in the context of macroecology, where there are still many unanswered questions.
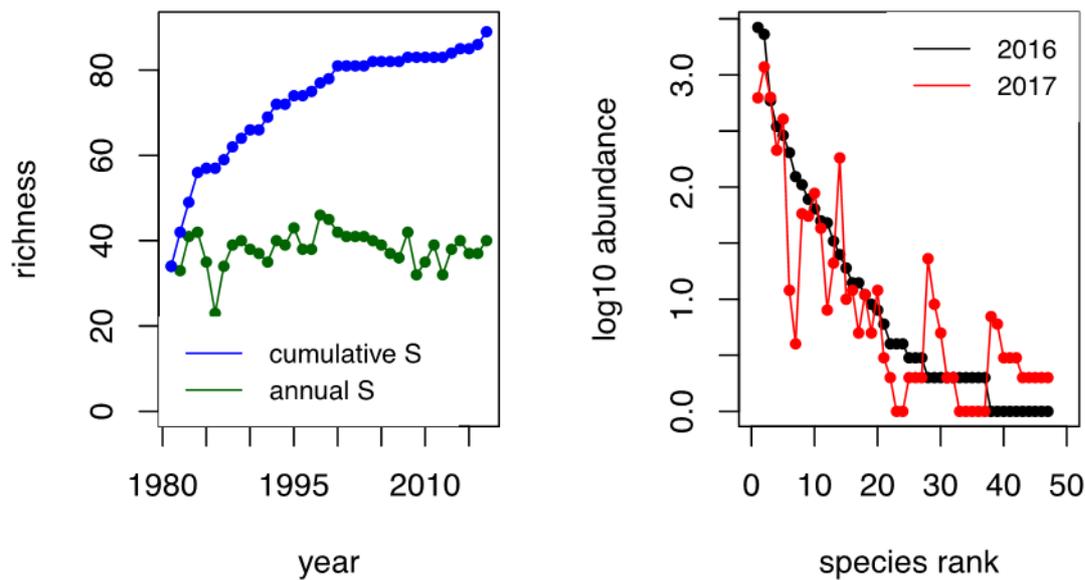
Figure 1: Estuarine fish, in the UK's Bristol Channel (Henderson, 2007; Magurran & Henderson, 2018) have been sampled using consistent methodology for 37 years. This figure illustrates the types of structural and compositional change in assemblage time series that measures of temporal β diversity may seek to capture. A. Annual and cumulative richness. The number of species present in the system in each year is untrending, with an average of S=38 species. Of these S=12 species are present every year, with S=34 species found in at least half of the years. The species accumulation curve exhibits a rising but flattening trend to the current total of S=89 species. B. Rank abundance plots for a pair of years (2016 and 2017) reveal the different elements of the temporal turnover within this system. Abundances for both years are ranked by species abundances in 2016. Richness increases from 2016 to 2017 (S=37 to S=40) but overall numerical abundance is almost halved (N=7006 to N=3625). Ten species are gained and seven lost with S=30 species present in both years. The dominant species in 2016 (Sprattus sprattus) experiences a 76% decrease in abundance and becomes the third most dominant species in 2017. There is also marked shuffling in ranks of other taxa between years.

β diversity – time versus space

Methods of assessing β diversity developed with spatial questions in mind can be adapted to measure temporal change but, as for diversity more broadly (Dornelas et al., 2013), there are a number of things to consider. First, as already noted, ecological communities experience constant compositional turnover and shifts in species abundances. Null models can be used to take account of this 'baseline change'. Second, time is unidirectional. Successional change is a classic case of a system undergoing directional change in composition. Less obviously, because population dynamics can be asymmetric, for example when populations take longer to grow than decline (Ginzburg & Inchausti, 1997), as well as due to processes such as density dependence (Henderson & Magurran, 2014), the arrow of time runs in a single direction even in assemblages that appear to be in a 'steady state' (Gotelli et al., 2017). Moreover, since an individual cannot exist in two places at once, but can persist in the same habitat over time, there may be greater scope for temporal

autocorrelation than for spatial autocorrelation. While the level of autocorrelation is related to individual ranges in space, generation times affect temporal autocorrelation. Third, and following this last point, while α diversity and β diversity are relatively easy to translate from a spatial to a temporal context, the same is not true of γ diversity. A pool of γ species is used to construct null models in tests of spatial dissimilarity (Chase, Kraft, Smith, Vellend, & Inouye, 2011) but species pools are not static. For example, invasive species are potential colonists of a local community only after they have joined the species pool. Identifying the 'correct' species pool is a noted challenge in assessments of spatial β diversity (Anderson et al., 2011); it is substantially greater in the temporal context.

Measuring temporal β diversity

As with α diversity, it is essential that analyses involving β diversity metrics are grounded in fair comparisons and not biased by differences in sampling effort or sampling method. Sample based rarefaction is often appropriate in such circumstances as (unlike most traditional approaches to individual based rarefaction) it preserves species identities (Gotelli & Colwell, 2001, 2011). There is a range of options for quantifying temporal β diversity. The key here, as in all ecological analyses, is that the methodology adopted is explicit and clear, as well as appropriate for the questions posed. In part this will depend on the aspect of temporal change under scrutiny, and the hypothesis (if any) that has been articulated. Here it can be helpful to think of 'pattern' and 'process'.

Questions to do with pattern focus on documenting the magnitude and direction of the compositional change taking place, as revealed by the measure of choice. A given measure might suggest no discernible temporal β diversity but since assemblages can be reorganised in different ways (see Figures 1 and 2), other metrics could be responsive to the changes involved. As such, assessments of temporal β diversity cannot be disassociated from the metric used to produce them.

Process questions link this documented change to some putative cause or mechanism such as disturbance (Supp & Ernest, 2014), invasive species (Buckley & Catford, 2015) or climate change (Sgardeli, Zografou, & Halley, 2016). In this context it is worth noting that 1) temporal analysis are particularly well suited to attribution (because of the unidirectional arrow of time), 2) temporal analysis can and should consider the possibility of lagged responses, and 3) some fraction of observed temporal β diversity will be baseline change. Pattern and process questions are overlapping ones. An effective metric can shed light on the underlying reasons for temporal β diversity as well as reporting the magnitude of the compositional rearrangement.

Next, we briefly review the main approaches into quantifying temporal β diversity. The starting point is typically an assemblage time series, in which species identities (and ideally species abundances) have been recorded using the same methodology. The first choice for measuring temporal β diversity is often a (dis-)similarity measure. (Dis-)similarity is typically computed using pairwise comparisons, and includes metrics that consider only compositional change (these are measures such the Jaccard index (Jaccard, 1908; Magurran, 2004) in which every species has the same weight) as well as those that additionally evaluate change in species abundances (e.g. the Morisita-Horn index (Magurran, 2004; Morisita, 1959)). (Similarity measures are usually scaled between 0 and 1 where 1 is perfect similarity, but can be recast as dissimilarity measures in which 1 is perfect dissimilarity.) Many metrics are possible, and many of the statistical considerations that apply to their usage in spatial contexts (Jost, Chao, & Chazdon, 2011) are relevant in temporal ones as

well. The relative contributions of species replacement (narrow sense turnover) and change in richness to dissimilarity can be obtained from an additive partition; here we note the ongoing debate about the most appropriate partitioning methods (Baselga, 2010, 2013; Cardoso et al., 2014; Carvalho, Cardoso, Borges, Schmera, & Podani, 2013).

One straightforward way of adapting these approaches to a time series is to compute the slope of (dis-)similarity values (e.g. Figure 2A&E), based on a plot in which a start point is compared with each successive time step (Dornelas et al., 2014), bearing in mind that the slope is not β-diversity itself, but rather an expression of its temporal dependence. Compositional differences can also be calculated between successive pairs of samples, as running averages, or between all possible time periods.

Zeta diversity, the number of species shared by different assemblages, or by the same assemblage at different time points (Hui & McGeoch, 2014; Latombe, McGeoch, Nipperess, & Hui, 2018; McGeoch et al., 2019; McGeoch et al., 2017) is a different and conceptually-appealing way of quantifying temporal β diversity. Because it provides a measure of turnover (based on similarity) for a given combination of i sites or times, the constraints of dealing only with pairwise comparisons are reduced. Another advantage is that the contributions of rare and common species to turnover can be examined. Directional (such as along a gradient) and non-directional options are possible, to allow the user flexibility in dealing with temporal dependence. Zeta diversity (McGeoch et al., 2019) can be expressed as zeta decline (the change in number of species shared as more time periods are included in the comparison – e.g. Figure 2B&F) and/or as zeta decay (change in the number of species shared as the time interval between comparisons increases. The resulting patterns shed light on ecological mechanisms and enable hypothesis testing. Zeta diversity can additionally be expressed in a form equivalent to measures such as Jaccard and Sørensen indices, as well as being partitioned into species replacement and richness components (McGeoch et al., 2019).

Other methods include total turnover (sensu Hallett et al., (2016) after Diamond and May (1977)) – the rate at which species join and leave an assemblage (e.g. Figure 2C&G), and metrics based on rank (Collins et al., 2008). The mean rank shift statistic (Collins et al., 2008; Hallett et al., 2016) compares the relative rank (by abundance) of species i at time t and time t+n (e.g. Figure 2D&H), and can pinpoint temporal change that is overlooked by other methods. For example, Jones et al. (2017) found that compositional change in an arid system was related to the reordering of species abundances rather to than species replacements. Community dynamics, such as immigration, local extinctions and population (and rank) change, can also be examined in a modelling framework where the goal is to identify which species and which environmental factors have the strongest influence on temporal β diversity (e.g. Shimadzu, Dornelas, & Magurran, 2015). Multivariate approaches (Legendre & Gauthier, 2014) are a further option. For example, cluster analysis and non-metric multidimensional scaling were used to identify climate-related shifts in the composition of a Norwegian inshore fish assemblage over 8 decades (Barceló, Ciannelli, Olsen, Johannessen, & Knutsen, 2016), while machine learning helped uncover assemblage reorganisation in a desert rodent community (Christensen et al., 2018).
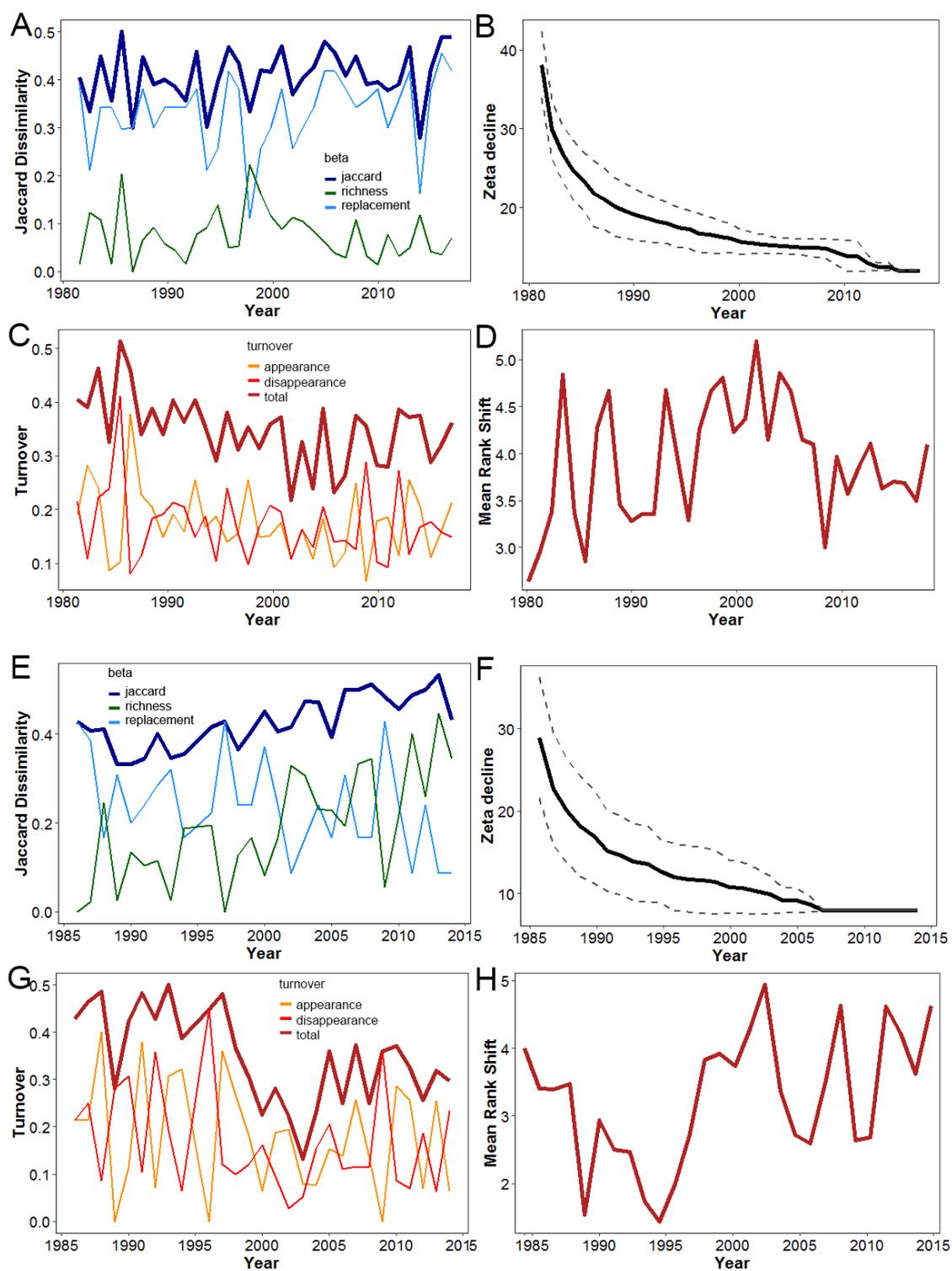
Figure 2:Different methods of quantifying temporal β diversity reveal different aspects of compositional change in assemblages.

(A-D). Temporal β diversity in the Bristol Channel assemblage time series shown in Figure 1. All metrics, computed in R (RCoreTeam, 2015), are relative to the assemblage composition in year 1. A). Jaccard dissimilarity shows no clear trend through time, and is dominated by species replacement (narrow sense turnover), (computed using the function beta.pair in the R package betapart (Baselga

et al., 2018)). B) Zeta decline (the decrease in average number of shared species), computed using R code in McGeoch et al. (2019). In this assemblage zeta decline is initially marked, but then reduces. C) Total turnover, plus species appearances and disappearances, computed using the function turnover in the R package codyn (Hallett et al., 2016). Overall turnover (broad sense turnover) moderates over the time series, and appearances and disappearances are balanced. D) Mean rank shift, computed using function mean_rank_shift in the R package codyn (Hallett et al., 2016). Mean rank shift fluctuates and is most pronounced in the early 2000s.

(E-H). The marine fish assemblage occurring in the 59˚ latitudinal band to the NW Scotland exhibits a different pattern of temporal β diversity. Although (like the Bristol Channel fish) there is no temporal trend in richness (Magurran et al., 2015), Jaccard dissimilarity (E) increases over time. Species replacement (narrow sense turnover dominates in the first part of the time series while change linked to richness becomes relatively more important in the second part. Zeta decline (F) is more abrupt than in the Bristol Channel, species appearances and disappearances are elevated and overall turnover (broad sense turnover) undergoes a step change in the late 1990s. Mean rank shift increases at the same time. These data are provided by ICES (DATRAS, 2013; see also Magurran et al., 2015)

Figure 2 illustrates how different approaches to quantifying temporal β diversity can shed light on different aspects of compositional dynamics. The Bristol Channel estuarine fish time series exhibits relative constancy over time in many assemblage properties – something that may be attributable to spatial and temporal niche partitioning (Henderson & Bird, 2010; Henderson & Magurran, 2010; Magurran & Henderson, 2012; Shimadzu, Dornelas, Henderson, & Magurran, 2013). In contrast, the same analyses performed on a marine fish assemblage to the West of Scotland, surveyed over a similar time frame, indicate substantial rearrangements of community composition even though, as in the Bristol Channel, temporal α diversity is untrending.

Null models and the nature of change

Baseline temporal change will reflect a combination of features including species detectability (Buckland, Studeny, Magurran, & Newson, 2011), demographic stochasticity (i.e. ecological drift (Sgardeli et al., 2016)) and species interactions. At present there is considerable lack of clarity about what baseline change is, particularly when the goal is to uncover the extent of change attributable to anthropogenic impacts; this is an important topic for future work, especially given the phenomenon of shifting baselines. Shifting baselines, as Pauly (1995) noted, alter perceptions of how much biodiversity change has occurred, and even what a pristine environment is. Null models of spatial β diversity typically set out to distinguish sampling effects from ecological mechanisms such as dispersal limitation or environmental filtering, and also factor in variation in species abundance and species occurrence (Socolar, Gilroy, Kunin, & Edwards, 2016). Socolar et al's (2016) discussion of strengths and limitations (e.g. with regard to deducing scaling relationships) of null models of spatial β diversity identifies some of the issues that need to be considered in the development of their temporal equivalents. Geometric considerations relating to the spatial and temporal scaling of β diversity (e.g. Šizling, Kunin, Šizlingová, Reif, & Storch, 2011) have a vital role to play in null models of compositional change in relation to predictions about temporal grain size, and in terms of articulating baseline change.

In light of evidence that assemblage size is often in a steady state (Brown, Ernest, Parody, & Haskell, 2001; Gotelli et al., 2017; Storch, Bohdalková, & Okie, 2018), and assuming that the community of interest is not undergoing directional change, such as succession, a reasonable null expectation for temporal α diversity might be a non-significant slope in a plot of a diversity metric (such as richness or Shannon diversity, e.g. Figure 1) against time (Dornelas et al., 2014). Other views are that biodiversity loss (Mace et al., 2018), or even biodiversity gain (Buckley & Catford, 2015), are valid null expectations. The existence of alternative null expectations reinforces the need to set out the reasoning for the predictions in each study.

How should change in temporal β diversity be judged? Here there is even less agreement than with temporal α diversity. Dornelas et al. (2014) used two approaches, both drawing on ecological theory - a species-level stochastic colonisation-extinction model based on the MacArthur & Wilson equilibrium model, and a set of null expectations informed by Hubbell's neutral model. In each case observed temporal β diversity, as measured using the Jaccard index, was substantially greater than the expected values. For instance, neutral model simulations predicted levels of compositional change two orders of magnitude below the observed values. This result suggests that anthropogenic pressures are strongly influencing the dynamics of the world's assemblages while underlining the need for ecological theory able to accommodate biodiversity change during the Anthropocene. Sgardeli et al. (2016) also drew on the neutral model of biodiversity to estimate baseline ecological drift in a Greek butterfly assemblage and concluded that the observed shift in community composition was linked to temperature rise.

Dornelas et al's (2014) null models were informed by assumptions about mechanism (Gotelli & Ulrich, 2011). Another option is to take the baseline shuffling that characterises all systems as given, and randomise observed values to produce the null (Gotelli & Graves, 1996; Gotelli & McGill, 2006; Gotelli & Ulrich, 2011). Such randomization tests are constrained by the data themselves. There has been a long discussion on how best to design and implement such null models, much of it focused on spatial questions, and much of it involving species x sites matrices. Temporal change raises additional questions, particularly as temporal autocorrelation within populations means that a completely free temporal permutation may be ecologically unrealistic. One option is to employ a cyclic-shift permutation (Hallett et al., 2014; Hallett et al., 2016; Harms, Condit, Hubbell, & Foster, 2001), which preserves within-species temporal autocorrelation, but breaks cross-correlations between species. It does this by randomising the start time of each species in the time series. Magurran et al. (2018) used a cyclic shift permutation to evaluate both temporal α diversity and temporal β diversity in diatoms, benthic invertebrates and fish in streams of Trinidad's Northern Range mountains, and showed that temporal β diversity was the dominant signature of biodiversity change in these systems.

The 'top down' approaches described above capture trends in overall temporal β diversity (and/or in its species replacement and richness components). A 'bottom up' approach (i.e. examining trends in the constituent parts of an assemblage) is also possible. Here the user decomposes assemblages *a priori* into components or events that are predicted to shed light on the dynamics that underpin temporal β diversity, and asks how these components combine to produce overall change. One example would be a core-transient decomposition (Coyle, Hurlbert, & White, 2013; Magurran & Henderson, 2003; Snell Taylor, Evans, White, & Hurlbert, 2018). Dornelas et al. (2019) also decomposed assemblages to identify colonisations and extinctions, and used population trends to

identify species that are 'winning' and those that are 'losing' in terms of abundance. Their study uncovered significantly accelerating extinction and colonisation rates. Overall about 15% of species showed significant trends in abundance with an approximate balance in species gained and species lost, and between winners and losers. The fraction of taxa involved may be small, but substantial temporal β diversity can still result.

Research challenges

It is clear that the world's ecosystems are undergoing substantial reorganisation, and that ecologists are only just beginning to probe the nature and extent of this change. The focus to date on 'biodiversity loss' (Brondizio et al., 2019), which has dominated the popular reporting of contemporary ecosystems, has directed attention away from the extensive rearrangements and compositional shifts that are ongoing. Indeed, these compositional rearrangements may play a key role in stoking up the extinction debt (Jablonski, 2001) (the idea that populations are in disequilibrium due to habitat transformation or other impacts, with the result that their persistence is in doubt) that will ultimately leverage extensive biodiversity loss. Although temporal β diversity is increasing both local and probably also at global levels (McGill, Dornelas, Gotelli, & Magurran, 2015), considerable uncertainty about the pattern of change at meta-community and biogeographic scales remains. Resolving these spatial patterns and understanding the processes that underpin them is an important macroecological challenge.

Emerging evidence points towards higher rates of temporal β diversity in the oceans than on land (Blowes et al., 2019). In both realms compositional change is dominated by species replacement (i.e. narrow sense temporal turnover) rather than by shifts in richness. However, there is also heterogeneity across assemblages (e.g. Baeten et al., 2012; Magurran, Dornelas, Moyes, Gotelli, & McGill, 2015), and particularly amongst latitudes (Blowes et al., 2019), in the pattern of change. For example, as regression tree analysis (Figure 3) of BioTIME data (Dornelas et al., 2018) shows, the relative importance of richness or species replacement in compositional change measured by Jaccard dissimilarity depends on both taxon and latitude. Species poor assemblages that lie above 41˚N exhibit change dominated by richness, whereas turnover has a greater influence in the richer ones. Regression trees make decisions based on data mining rather than responding to the user's expectations about where a separation point might lie, and are sensitive to different combinations of input variables and data. It is nonetheless intriguing that independent meta-analyses, this time with a focus on spatial β diversity, and using different data, also identify latitudinal breakpoints (Castro-Insua, Gómez-Rodríguez, & Baselga, 2016; Soininen, Heino, & Wang, 2018), including, in the case of Soininen et al. (2018), a breakpoint at 41˚. Ecosystem reorganisation is particularly marked in some biomes such as the tundra (Bjorkman et al., 2018); linking temporal β diversity with geographically variable environmental change will be one of the biggest macroecological challenges in the next few years. Improved data availability, better methodological tools and conceptual advances are needed to meet this goal.

Data
The sparsity of biodiversity data, particularly quality assemblage time series data, from under represented regions and latitudes, has been highlighted many times before, but the fact that this is not a novel comment does not mean it is an unimportant one. While it is impossible to go back in time and sample taxa and localities that have never been studied,

in many cases suitable data do exist but are contained in personal notes or private repositories, and risk being lost when the collector dies or loses interest. The current practice of publishing, as open-access, the data used for a paper is commendable, but there is still considerable scope for collating and crediting data not currently in the public domain. In addition, maintaining time series, and providing continuity between data sets if taxonomy or sampling methods change (Magurran et al., 2010), is a priority.
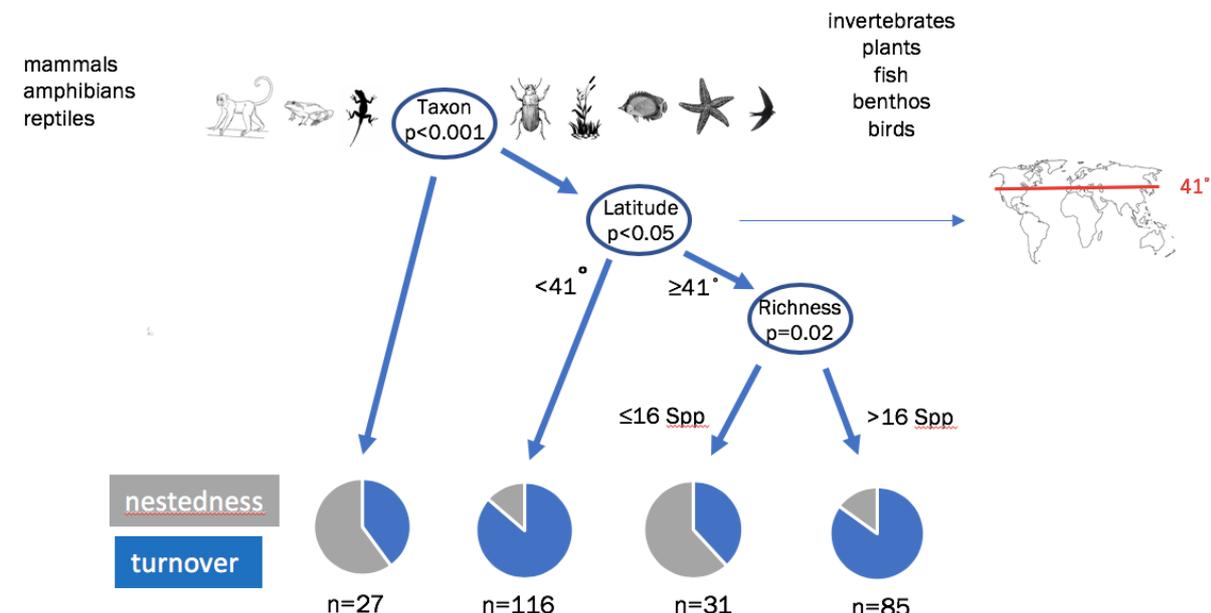
Figure 3: Regression tree analysis of BioTIME assemblage data (Dornelas et al., 2018) to assess the variables that predict whether temporal compositional change (measured as the slope of Jaccard dissimilarity) is dominated by nestedness or species replacement (turnover) Partitions were computed using the betapart package (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2013), while binary recursive partitioning used the party package (Hothorn, Hornik, & Zeileis, 2006) with default settings for the ctree function. All analyses were in R (RCoreTeam, 2015). The input variables were: median richness; total richness; realm; climate; biome; taxon; number of data points; start year; central latitude; area in km^2. Data available at BioTIME website (http://biotime.st-andrews.ac.uk) and Zenodo repository (https://zenodo.org/record/1095627); downloaded 21 June 2018.

Emerging technologies, including eDNA (e.g. Thomsen & Willerslev, 2015), and advances in the analysis and interpretation of palaeoecological data (e.g. Tomašových & Kidwell, 2009), are likely to play a much greater role in providing informed baselines against which current biodiversity change can be judged. Here the challenge will be to establish continuity between these data types and 'classical' biodiversity studies that report the identities and abundances of species recorded using conventional sampling methods (e.g. Fisher, Corbet, & Williams, 1943).

As noted earlier, this paper has focussed on taxonomic β diversity. Temporal change in the phylogenetic structure and diversity of assemblages, and in their functional diversity, are equally valid research challenges, but ones that have, as yet, received less attention. Better resolution of phylogenies, combined with improved information on functional traits, where possible measured in the field in parallel with the recording of taxonomic data, is thus also vital, and will contribute substantial added value to biodiversity analyses. Recently,

Chao et al., (2019) have been developing a new approach to provide an integrated assessment of taxonomic, phylogenetic and functional β diversity. At present the focus is on spatial comparisons but these methods have considerable potential in the quantification of temporal β diversity.

Methodology

Methodological innovations, both in terms of data collection and data analysis, have an important influence on the ability of macroecologists to advance understanding of biodiversity change. State-of-the-art methodologies for handling and analysing 'big data' (e.g. De Cáceres et al., 2019; Farley, Dawson, Goring, & Williams, 2018; Sirén, Lens, Cousseau, & Ovaskainen, 2018) make macroecological analyses more tractable, and have the potential to yield new insights. Yet, however powerful these analyses, the ecology that underpins them should not be forgotten. Sampling effort, for instance, cannot be ignored in biodiversity assessment. Inconsistent sampling effort, or highly variable species densities, can lead to misconceptions about the underlying pattern of diversity (Gotelli & Colwell, 2001). Estimates of species richness are notoriously vulnerable to these sampling effects but all diversity metrics (both α and β) are affected in one way or another (Magurran, 2004). Until now, rarefaction has been the recommended solution, with the downside that some data are discarded in the process of ensuring fair comparisons. However, there has been remarkable progress in recent years, much of it led by Chao and her colleagues, in extending existing approaches to take account of 'unseen' species. Extrapolation methods were initially applied to α diversity measures, including Hill numbers (Hill, 1973; Hsieh, Ma, & Chao, 2016) but have application in tests of β diversity (e.g. Cayuela, Gotelli, & Colwell, 2015).

It is clear that null models have a crucial role to play in assessments of temporal β diversity as they do in evaluating other diversity patterns (Cayuela et al., 2015) but, as discussed above, we are a long way from a settled view on what the best null models should be. Accommodating spatial and temporal scaling in these null models will be a particular challenge for macroecologists (Šizling et al., 2011).

Conceptual advances

One thing that has become evident in recent analyses of biodiversity change is that current ecological theory is inadequate for predicting the nature and extent of community reorganisation that the natural world is experiencing (Gotelli et al., 2017). This is perhaps the greatest challenge for the future.

The traditional perception of the measurement of β diversity is that metrics are – or should be – independent of species richness (Wilson & Shmida, 1984). In practice, however, β diversity (whether spatial or temporal) is linked to α diversity (Magurran, 2004). Recognition of this point is the motivation for partitions of measures into components influenced by species replacement and species richness. Linkage between α and β diversity is inevitable because all assemblages take the form of a species abundance distribution (SAD) in which some species are common, and many are rare (May, 1975; McGill et al., 2007), and because the amount of life any assemblage can support has an upper limit (Brown, 2014; see also Storch et al., 2018; Taylor, 1978). The shape of the SAD can provide insights into the types of compositional rearrangements likely to prevail in a given system. For example, if an assemblage has a long tail of rare species, but remains in a steady state

in terms of its overall structure, the replacement component of compositional change may be elevated, since many of these rare taxa will be transient (Magurran & Henderson, 2003). This could contribute to the predominance of species replacement rather than richness change already reported in many assemblage time series (Blowes et al., 2019). If, on the other hand, a SAD has a large fraction of persistent species, rank shifts may be the main form of change. In addition, any factors that lead to changes in the shape of a SAD, such as gains and losses of species as climate waxes and wanes, will influence the richness component of temporal β diversity. Thus, by focussing on the SAD, and the way it changes through time, it should be possible to develop a framework that predicts the relative importance and magnitude of replacement, richness, and rank shifts in temporal β diversity, under a range of scenarios, and deduce the consequences of these compositional changes for ecosystem function. Given current understanding of community ecology, this predictive framework is achievable.

There are a number of methodological and conceptual innovations that make explicit linkages between temporal α and temporal β diversity, and in doing so stand poised to substantially advance understanding of biodiversity change. One promising direction would be an extension of the MoB (measurement of biodiversity) approach (McGlinn et al., 2019) used to assess the relative contributions of the spatial arrangement of individuals, density, and the species abundance distribution, to trends in species richness. Another is the metapopulation approach developed by O'Sullivan et al. (2019) in which regional dynamics are modelled using Lotka-Volterra competition equations. This method makes no *a priori* assumptions about spatial structure and the distribution of abundance yet can reproduce ubiquitous patterns such as the species abundance distribution and species area relationships. It also predicts a steady state in species richness alongside substantial species turnover. Finally, as Jackson & Blois (2015) note, ecological processes occurring over time periods of millennia are not fully integrated into community ecology. Better appreciation of diversity dynamics over both short and long time periods will advance understanding of biodiversity change.

Conclusions
The 2019 IPBES Global Assessment has done much to focus attention on the state of the world's biodiversity, and the pressures it is under. However, it is challenging to quantify biodiversity change, and to do so in a way that uses meaningful benchmarks, recognises uncertainty, is statistically robust, and widely understandable. On the one hand, recent advances in ecological statistics have extended the methodological toolkit for quantifying biodiversity, and how it is changing over space and time. At present the main constraint on quantification of biodiversity change, including temporal β diversity, on macroecological scales, is data availability rather than metrics or computing power. On the other hand considerable disagreement remains on how best to measure biodiversity change, particularly its temporal β component, though we note the range of views even in the case of species richness (Primack et al., 2018) - usually considered the most intuitive temporal α biodiversity metric. Much more work on the quantification of temporal β diversity is needed before there is consensus on the most effective approaches, as well as the best way of reporting this component of biodiversity change. Such methods need to consider the different dimensions of diversity – taxonomic, functional and phylogenetic – without becoming intractable or losing their ecological relevance. Perhaps this consensus will never happen. Southwood (1978) observed that the history of biodiversity measurement is

characterised by papers that decry existing methods before introducing a new metric. Nonetheless, if ecologists work together, difficult problems, such as the quantification of change in species richness over spatial scales, can be tackled (Chase et al., 2019). Future work on temporal β diversity offers similar challenges and opportunities.

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