

PRIMARY RESEARCH ARTICLE

Long-term changes in temperate marine fish assemblages are driven by a small subset of species

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Abstract

The species composition of plant and animal assemblages across the globe has changed substantially over the past century. How do the dynamics of individual species cause this change? We classified species into seven unique categories of temporal dynamics based on the ordered sequence of presences and absences that each species contributes to an assemblage time series. We applied this framework to 14,434 species trajectories comprising 280 assemblages of temperate marine fishes surveyed annually for 20 or more years. Although 90% of the assemblages diverged in species composition from the baseline year, this compositional change was largely driven by only 8% of the species' trajectories. Quantifying the reorganization of assemblages based on species shared temporal dynamics should facilitate the task of monitoring and restoring biodiversity. We suggest ways in which our framework could provide informative measures of compositional change, as well as leverage future research on pattern and process in ecological systems.

One-sentence summary: Only a small subset of species in an ecological assemblage makes large contributions to long-term changes in species composition.

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KEYWORDS

baseline, biodiversity, long-term monitoring, marine fish assemblages, species composition, temporal beta diversity

1 | INTRODUCTION

The biodiversity crisis is one of the greatest challenges we currently face (Brondizio et al., 2019). To date, most headline reports have emphasized species loss (Ceballos et al., 2017; Tittensor et al., 2014). However, the compositional reorganization of ecological assemblages is an equally important, but much less well understood, component of this ongoing biodiversity change (Hillebrand et al., 2018). This reorganization is occurring at rates that have little precedent in historical times (Jonkers et al., 2019) and that exceed the predictions of current ecological theory (Blowes et al., 2019; Dornelas et al., 2014; Lu et al., 2019). To improve our ability to determine the causes and predict the consequences of biodiversity change, we need to identify the species that play disproportionate roles in reshaping assemblage composition. A focus on species-level change is critical because contributions to ecosystem function, stability, and services are often unequal amongst species. This knowledge is also key to the development of new monitoring methods to track compositional change that will be needed to support the 2050 Vision for Biodiversity (www.cbd.int/).

2 | MATERIALS AND METHODS

In spite of widespread interest in identifying the species most responsible for compositional change (Ovaskainen et al., 2017), most analyses summarize assemblage-level change as a single numeric index of biotic dissimilarity (but see Shimadzu et al., 2015; Tatsumi et al., 2021). To understand how the temporal dynamics of individual species contribute to long-term compositional change, we devised a canonical classification system based on the ordered sequence of presences and absences that each species contributes to an assemblage time series. Each species is assigned uniquely to one of the seven categories of change (Figure 1), based on three criteria: its frequency of occurrence in early versus late years of the study (contingency test), its frequency of colonization and extinction transitions throughout the time series (runs test), and its status in the baseline year of the study (present or absent; Materials and methods and additional details are available as supplementary materials at the Global Change Biology website).

Three of the categories ((1) no change; (2) recurrent change; and (3) random change) can affect year-to-year changes in species composition but are unlikely to contribute to sustained long-term change. Category 1 (no change) includes the small fraction of species that were present in each census in the series. Category 2 (recurrent change) includes those species in which the number of runs of consecutive presences or consecutive absences is statistically small

(one-tailed runs test). In these cases, a species that arrives persists for an unusually long number of years before disappearing and then reappearing, conditioned on the total number of presences or absences in the sequence. The random change category includes those species whose temporal sequence cannot be distinguished statistically from an equiprobable reshuffling of the observed sequence of presences and absences.

Species in the remaining four categories ((4) converging increasing; (5) converging decreasing; (6) diverging increasing; and (7) diverging decreasing) are the potential drivers of long-term compositional change. They are distinguished by whether the incidence of the species is significantly changing through time (increasing or decreasing) and whether that change is contributing to a return toward the baseline species composition (converging), or a departure away from it (diverging; Materials and methods and additional details are available as supplementary materials at the Global Change Biology website; Table S3). To test whether a species was significantly increasing or decreasing through time, we first split the entire time series into an early and late sequence, and used a contingency table analysis of the resulting 2×2 table (present/absent; early/late). If the species was present in the baseline year, a statistical pattern of increasing incidence in later years was classified as converging increasing (category 4) because this species would contribute to composition becoming more similar to the baseline in later years. Conversely, if the species was present in the baseline year, a statistical pattern of decreasing incidence in later years was classified as diverging increasing (category 6) because this species would contribute to composition becoming less similar to the baseline in later years. Similar logic was used to define the categories of converging decreasing (category 5) and diverging decreasing (category 7).

To assess how these categories of species dynamics contribute to long-term compositional change, we selected from the BioTIME data base (Dornelas et al., 2018) 280 data sets for assemblages of temperate marine fishes, each of which included at least 20 years of standardized annual samples and 10 or more species (average = 51 species per assemblage) that were recorded in one or more annual censuses (Materials and methods and additional details are available as supplementary materials at the Global Change Biology website; Figure 2a; Table S1; Figure S1).

3 | RESULTS

For each data set, we first calculated Jaccard's dissimilarity index (Keil, 2019) between each year's assemblage and the baseline assemblage, which was operationally defined as the species composition in the first year of the survey. The slope of a simple linear

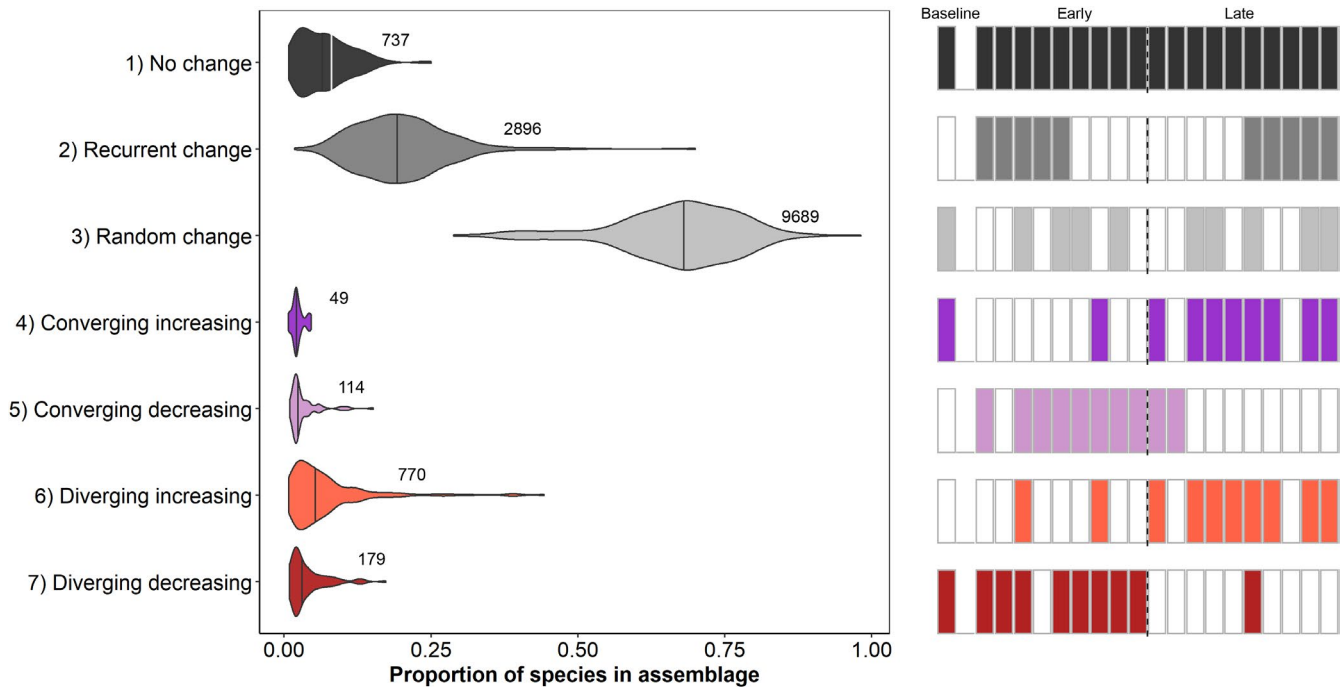


FIGURE 1 Classification scheme of species temporal dynamics. The classification comprises three categories of non-directional change: no change (category 1), recurrent change (category 2), and random change (category 3); and four categories of directional change: converging increasing (category 4), converging decreasing (category 5), diverging increasing (category 6), diverging decreasing (category 7). Violin plots illustrate the relative frequencies of species in each category for 14,434 trajectories of species of marine fishes in the 280 assemblages analyzed. The numbers next to each violin plot are the total number of trajectories recorded in each category among all assemblages. The right-hand figure is a schematic representation of an ordered species incidence sequence for each category (one per row). Filled cells indicate a species is present in a particular year, and empty cells indicate a species is absent. The first survey in each time series is designated as the baseline year. For each assemblage, the time series is split evenly into early and late periods for a 2×2 contingency analysis to detect increasing or decreasing incidence trends. If this contingency test is significant, the species is assigned to one of the four directional change categories, depending on whether it is increasing or decreasing in incidence, and whether the species was present or absent in the baseline year. If the contingency test is not significant, an additional runs test is used to assign the species to the recurrent change category or to the random change category

regression of dissimilarity versus time (Figure 2b) is an unbiased estimator of the rate of change in species composition for each assemblage (Chandler & Scott, 2011). Among assemblages, 90% of these slopes were positive (54% statistically significant), indicating a long-term increase in dissimilarity and a divergence through time in species composition compared with the baseline year. (Figure 2a). Only 10% of the slopes were negative (1% statistically significant), indicating that few assemblages converged in the long-term toward the baseline composition.

Across all assemblages, we then classified each of the 14,434 individual species trajectories into the seven categories above (Figures 1 and 2c). Random change (67%) and recurrent change (20%), were the most common patterns, whereas only 8% of the species trajectories were classified in categories of directed change. Within the four categories of directed change (categories 4–7), 6.7% of the species trajectories led to divergence from the baseline, and only 1.3% led to convergence. This result is consistent with the observation that 90% of the assemblages showed a long-term increase in species dissimilarity (Figure 2a).

To quantify the contribution of the different species categories to the overall dissimilarity trend, we used a simple randomization

procedure in which we equiprobably reshuffled the incidence sequence of each species within a particular category (Materials and methods and additional details are available as supplementary materials at the Global Change Biology website). Applying this randomization separately to the subset of species in each of the seven categories isolates the effects of that group on the overall slope of the relationship between dissimilarity and time (Figure 3). For each time series and temporal dynamic category, we kept the incidence patterns of species in all the other categories as observed, but within the focal category we reshuffled the incidence of each species across time (so that group is now random) and asked how different the new slope is when that groups' signal is, thus, removed.

The no change category (1) had an effect size of 0 for every assemblage because the incidence pattern (present in every census) is not changed by randomization. For the random change and recurrent change categories, the average change in the assemblage dissimilarity slopes did not differ significantly from zero. In contrast, three of the four directed change categories significantly changed the dissimilarity slopes toward convergence or divergence (Figure 4a). Although the numbers of species in the four directed change categories (4–7) were small, the average per capita effect sizes were

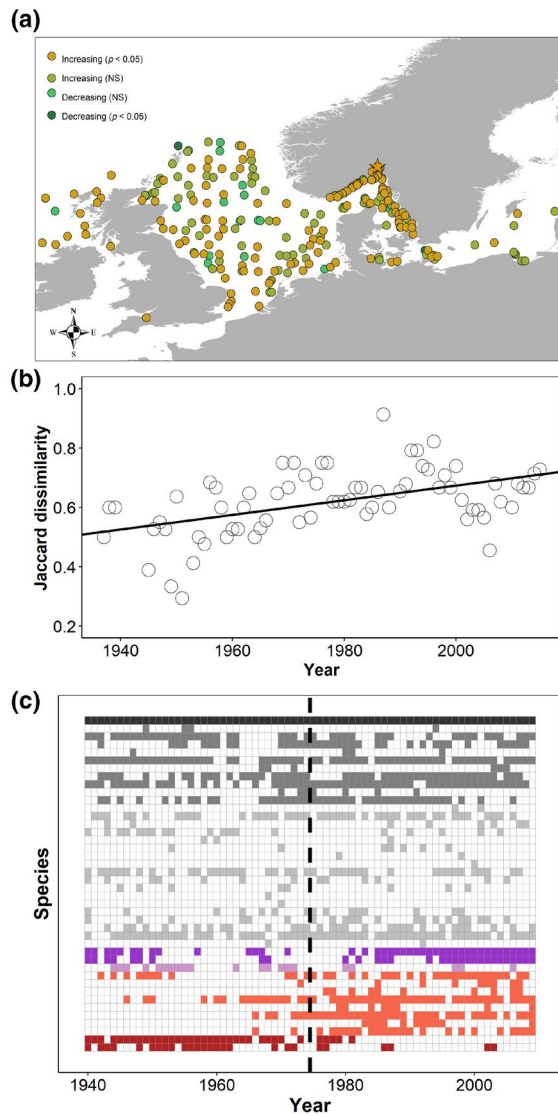


FIGURE 2 Study site map and measurements for a single assemblage data set. (a) Locations of sites in the North Sea area where marine fish assemblages were surveyed each year for 20 or more years (see Figure S1 for complete global maps with all 280 assemblages). The color of each symbol represents strength and direction of the linear slope of the relationship between dissimilarity and time. The star indicates the location of one survey used for illustrating patterns in (b) and (c; BioTIME site ID = 428_3630, surveyed between 1937 and 2015, with a total of 43 species and 5264 individuals). (b) Temporal trends in species dissimilarity for the assemblage at the starred site in (a). In each timestep, dissimilarity is calculated in comparison with the baseline year. The slope of this regression line is then used to calculate the effect size for each of the species categories shown in (c; see Figure 3 for these effect sizes for all assemblages). (c) Species \times Year incidence matrix used to classify species and calculate the temporal trend in Jaccard's dissimilarity in (b). Each row is a species, each column is a year, and the cells indicate the presence (filled) or absence (empty) of each species in a particular year. The very first year of the survey is designated as the baseline, and the vertical dashed line breaks the series into an early and late period for a test of trends in species incidences. Each species is classified into one of seven unique categories of incidence dynamics over time, using the same color codes as in Figure 1

larger than those of the three undirected change categories (1–3; Figure 4b).

Moreover, the assemblages with the greatest amount of compositional change had greater proportions of species in the diverging directional change categories, whereas the proportions of species in the three undirected change categories were not significantly correlated with the amount of compositional change (Figure S7). Our results were generally robust to sampling variability (Table S2; Figure S2), detection errors (Figure S4), trends in total abundance (Figure S5), the choice of the particular baseline assemblage (Table S4; Figure S3), and variation among assemblages in total species richness and other assemblage-level covariates (Figure S6). Finally, our randomization for quantifying effect size generated a more consistent signal of biodiversity change than an alternative method based on species deletions (Figure S8).

We do note that the results are sensitive to the quantification of cumulative compositional change relative to the baseline year of each assemblage. If compositional change is instead calculated as dissimilarity between each consecutive year of the survey, the effect size differences for the species categories disappear (Figure S9). This result reflects the fact that the four diverging and converging categories are conditional on the presence or absence of each species in the baseline year, but the baseline year only contributes one observation to the time series of adjacent differences.

4 | DISCUSSION

For these marine fish assemblages, three novel patterns emerge from our analyses. First, on average, fewer than 10% of the species in an assemblage are contributing strongly to long-term trends in species compositional change. Second, 1.3% of species trajectories are driving the pattern back toward the baseline assemblage, potentially reducing patterns of divergent change. Third, 81% of species trajectories contributing to long-term divergence in species composition were initially absent in the baseline year, but increased in incidence in the later decades of the surveys (diverging increasing). Only 19% of species trajectories contributing to divergence were initially present but decreased in incidence over time (diverging decreasing). These patterns are consistent with the observation for high-latitude assemblages that environmental change, including extreme climate events, is often associated with the arrival of novel or infrequently seen species (Diez et al., 2012), including non-native and invasive species (Winder et al., 2011), as well as species expanding their ranges toward the poles in response to climate change (Lenoir et al., 2020; Poloczanska et al., 2016). The diverging decreasing category may also represent species whose ranges are shifting, and that may be at eventual risk of local or regional extinction (Sánchez-Bayo & Wyckhuys, 2019; Tilman et al., 2017).

We recognize that the majority of assemblages in our study come from one geographic area, namely the NE Atlantic, with the North Sea providing most of the data we analyze. Spatial bias in investigations of

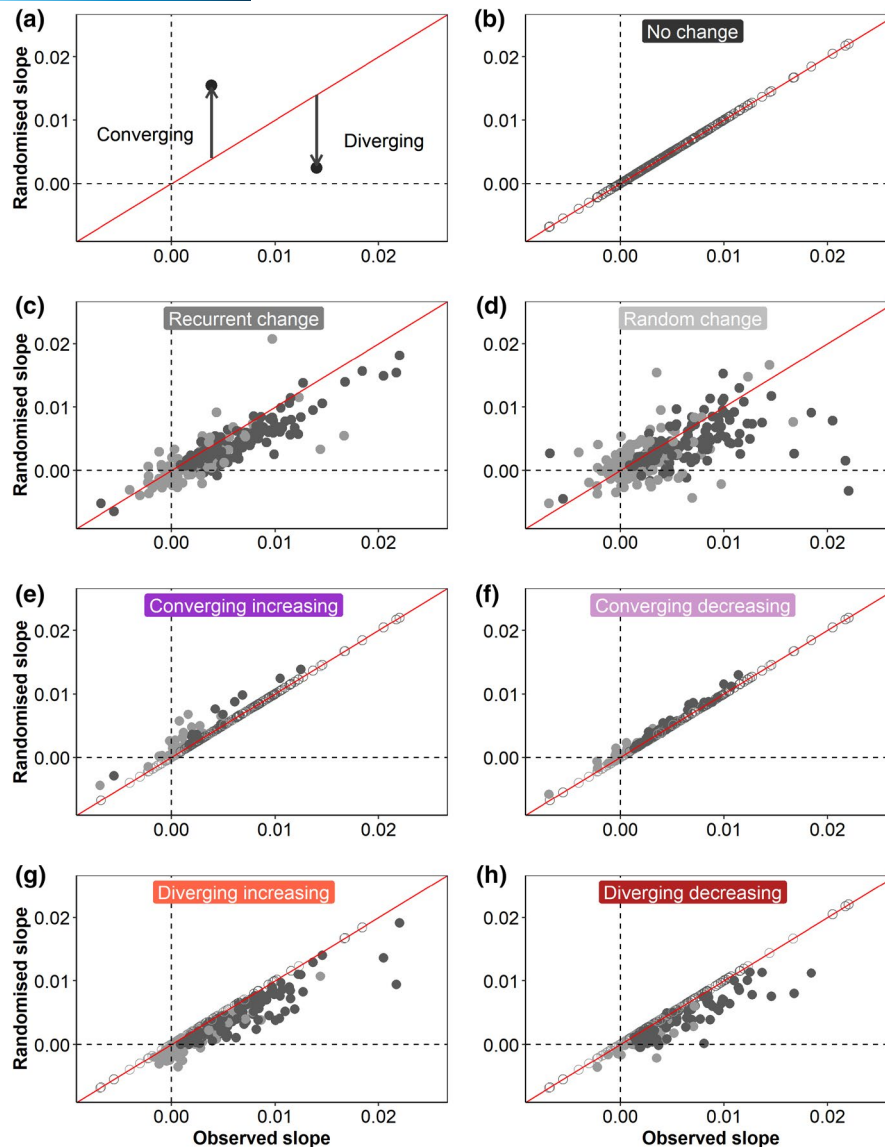


FIGURE 3 Measurement of effect sizes for the seven categories of species temporal incidence dynamics. (a) Schematic illustrating data points for two assemblages. The x-axis is the observed slope of the regression of dissimilarity versus time (as in Figure 2b). The y-axis is the recalculated slope after randomly reshuffling among years the observed incidence for each species in the indicated category; only a single reshuffling is used, and species in the six other categories are not reshuffled (label colors as in Figures 1 and 2c). Each point is a different assemblage, and the line of equality (in red) is the expected value when there is no change in the dissimilarity slope. The length of the arrow is strength of the signal for the group of interest, which is removed by reshuffling species occurrences within that group. This effect size may be positive, negative, or zero for each category (as illustrated in [a]). Negative deviations indicate divergence in species composition from the baseline year, and positive deviations indicate convergence in species composition toward the baseline year. (b–h) Effect sizes for each assemblage in the seven categories in Figure 1. Dark gray points are those assemblages for which there is a significant temporal trend in compositional dissimilarity (one-tailed $p \leq 0.05$). Light gray points are those assemblages for which the temporal trend is not significant. Open circles are those assemblages for which the particular category of species is not present, so the effect size is zero. In (b), all assemblages are indicated with open circles, because the effect size for this no change category is always zero

biodiversity change is already well recognized (Di Marco et al., 2017; Trimble & van Aarde, 2012). Although progress is being made toward better global data coverage (Froese & Pauly, 2019; GBIF, 2015), the pressing need to understand how ecological communities are being reorganized in the contemporary world makes it imperative to make best use of the information we do have. Indeed, recent work has shown that existing data can uncover hitherto unappreciated

change in ecosystems, such as elevated compositional rearrangements (Blowes et al., 2019; Dornelas et al., 2014). The North Sea is exceptional in providing high-quality data over an extended period, and these data have played a pivotal role in the development of quantitative fisheries models (Beverton & Holt, 1957), as well as informing population ecology and the modelling of multispecies systems (May et al., 1979). It, thus, represents an informative setting in which to

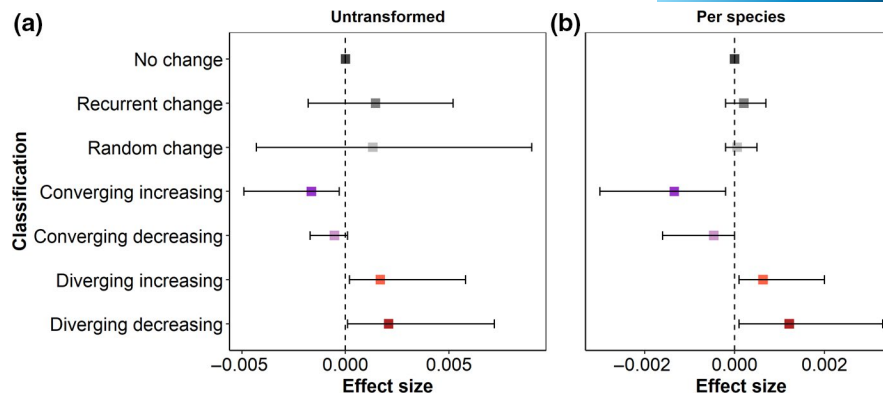


FIGURE 4 Average effect sizes across assemblages with 95% interquartile distribution (confidence interval) for the seven species change categories. (a) Untransformed effect sizes, which include zeroes for assemblages with missing categories. (b) Per species effect sizes, which exclude missing categories and divide the total effect size for each assemblage by the number of species in the category. Interquartile distributions are calculated directly from the histogram of simulated slope differences, with one reshuffling used to estimate the effect size for each assemblage (Figure 3)

develop our new approach to quantifying temporal change in ecological assemblages.

This classification scheme represents a new way to think about the organization of communities, and it complements traditional classifications that are based on shared traits, levels of abundance, or phylogenetic relatedness (Magurran & McGill, 2011). Although the analysis is presented here for long-term temporal monitoring, it can be easily extended to spatial analysis for plots that can be ordered along any one-dimensional gradient, such as productivity, disturbance, latitude, or elevation (Tylianakis & Morris, 2017). As the pace of environmental change continues to accelerate, the shift from univariate metrics of compositional change to short lists of species in critical categories should facilitate the task of monitoring, forecasting, and restoring biodiversity.

Until now nearly all the concern about the state of biodiversity, particularly in popular writing, has focused on alpha diversity, with species richness and/or species loss often used as the headline metric. Yet, as ecologists are aware, species richness is strongly influenced by sampling effort (Gotelli & Colwell, 2001). Moreover, even when appropriate sampling and statistical methods have been implemented to ensure fair evaluations, neither an increase in species richness in local assemblages over time due, for example, to the presence of invasive species (Kortz & Magurran, 2019) or because of local warming (Steinbauer et al., 2018) nor the absence of systematic change in richness (Dornelas et al., 2014) can be taken as evidence that an ecosystem is in good health.

However, perceptions are shifting and, as a recent IPBES-IPCC workshop on “Biodiversity and Climate Change” (IPBES-IPCC, 2021) makes clear, there is increased recognition of the need to understand and monitor compositional change. At present there is no consensus on how to quantify compositional change in ecological assemblages, or on which compositional change metrics have most utility in the context of conservation or environmental management. The framework we have introduced in this paper, which makes explicit links between the extent of compositional reorganization in an

assemblage and the contribution of different categories of species to that change, provides scope for a novel approach.

We suggest that the fraction of species in an assemblage that contribute to compositional change (taking account of the balance between those associated with diverging directional change versus converging directional change) could be an informative metric; future work should probe the behavior of this metric (alongside the overall partition) across systems, and test its performance in relation to anthropogenic drivers (Bowler et al., 2020). In addition, the decomposition of assemblages into species with different contributions to compositional reorganization has the potential to advance theory and improve practice.

For example, information on the characteristics of species that contribute disproportionately to compositional change such as their functional role, or population dynamics, could shed new light on the processes that shape biodiversity change. Similarly, knowing whether the species that are reshaping assemblage composition are of conservation priority, or invasive, will aid policy decisions. In summary, the new framework introduced in this paper not only is timely, with a role to play in improving assessments of biodiversity change in our rapidly changing world, but also provides a stepping-stone to further investigations with the goal of a better understanding of temporal dynamics in ecological assemblages.

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AUTHOR CONTRIBUTIONS

Conceptualization: Nicholas J. Gotelli, Anne E. Magurran with additional input from Faye Moyes, Laura H. Antão, Shane A. Blowes, Maria Dornelas, Brian J. McGill, Amelia Penny, Aafke M. Schipper Hideyasu Shimadzu, Sarah R. Supp, Conor A. Waldock; Methodology: Nicholas J. Gotelli, Anne E. Magurran, Faye Moyes, Maria Dornelas, Hideyasu Shimadzu, Shane A. Blowes, Sarah R. Supp; Interpretation

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DATA AVAILABILITY STATEMENT

The time series used in this analysis (see File S1) come from the published BioTIME data set (Dornelas et al., 2018) or other publicly available sites BioTIME data are open access and can be accessed on Zenodo (<https://doi.org/10.5281/zenodo.2602708>) or through the BioTIME website (<http://biotime.st-andrews.ac.uk/>). The four studies not included in the BioTIME database are accessible via the references and sources listed in Data S1 (metadata_for_marine_fish_assemblages.xlsx). The BioTIME level studies were subset into grid cells to maintain spatial extent throughout; information on this process can be found in the supplementary materials and in the supplement for Blowes et al. (2019). Code for this process is available on Zenodo at <https://zenodo.org/record/3367444#.YJku9LVKjIU>. Other code used in the current work can be found in the Data S2 (Appendix_code_functions.html).

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