Species contributions to biotic homogenisation and differentiation

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Running title: Species contributions to homogenisation

ABSTRACT

Aim

Homogenisation (decreasing beta-diversity) among biological assemblages is often interpreted as being caused by already-widespread species increasing. The link between individual species level trends and homogenisation between assemblages however, has not been fully addressed with most studies focused solely on either assemblage level or species level changes. Here we aim to test the widely held hypothesis that homogenisation is driven by the decrease of localised species and increase of those already widespread using species contribution to beta-diversity.

Location

North America, Europe, South Africa

Time Period

1970 to 2019, 1966 to 1996, 11,700 years ago to present, 2011 to 2021, 1960 to 2016

Major Taxa Studied

Birds, plants, benthos, mammals

Methods

Here, we consider individual species contributions to spatial beta-diversity and how these change over time. We focus on the relative contributions of localised and widespread species across five case studies, to determine which are contributing most to homogenisation.

Results

Species occurring in around half of sites provided the greatest contributions to beta-diversity at a given time, but not through time. The most widespread species (>0.75 of sites) contributed little to beta-diversity change with this most apparent in highly nested assemblages. In contrast, localised species (initially in <0.25 of sites) contributed most to both homogenisation (when declining) and differentiation (when increasing) regardless of nestedness.

Main Conclusions

This challenges the hypothesis that widespread generalist species are the main drivers of homogenisation, underlining the importance of rare species and of nestedness to patterns of beta-diversity change. Conservation interventions to increase localised species occurrence would do more to limit homogenisation than attempts to control already-widespread species or prevent others becoming widespread, especially when assemblages are highly nested.

Keywords: biotic homogenisation, beta-diversity, species trends, dissimilarity, species contributions to beta-diversity, rare, widespread

Data availability statement: All data is publicly available from the sources cited (birds: https://doi.org/10.5066/P97WAZE5 , plants: https://biotime.st-andrews.ac.uk/ , benthos: https://doi.org/10.25829/idiv.3503-jevu6s and mammals: https://catalogue.ceh.ac.uk/id/ab61349e-c055-477c-9872-22a4f7cc2473). Pollen data were

obtained from the Neotoma Paleoecological Database (http://www.neotomadb.org) and its constituent databases (in particular, the European Pollen Database and the Alpine Pollen Database, Table S3). The work of data contributors, data stewards, and the Neotoma community is gratefully acknowledged. Analysis code is available from Zenodo https://doi.org/10.5281/zenodo.17734387

1 Introduction

One of the most widely reported changes to biodiversity in the Anthropocene is biotic homogenisation of the global biosphere (McKinney & Lockwood, 1999), the increasing similarity of the composition of biological assemblages in different locations (McGill *et al.*, 2015). This pattern of change is supported by a considerable amount of evidence (Newbold *et al.*, 2018; Lewthwaite & Mooers, 2022; Staude *et al.*, 2022). The most widely supported hypothesis explaining this pattern is that homogenisation is being driven by common and rapidly expanding species (including invasives) becoming even more widespread while localised species are disappearing (Finderup Nielsen *et al.*, 2019; Petsch *et al.*, 2022). However, homogenisation is not observed in all circumstances (Kramer *et al.*, 2023; Gordon *et al.*, 2024), and a more complex picture is emerging (Rolls *et al.*, 2023). The manner in which the changing distributions (frequencies of occurrence in samples) of species are contributing to declines (homogenisation) and increases (differentiation) in beta-diversity across entire regions and for different taxonomic groups is complex and not fully understood (Blowes *et al.*, 2024). This implies a gap in understanding of a key component of biodiversity and biodiversity change, required knowledge if environmental management aims to address reported biotic homogenisation.

Homogenisation is normally regarded as occurring when species with relatively low occurrence are replaced by those with relatively high occurrence (Rolls *et al.*, 2023). This is based on the idea that a small number of species who are already generalist, adaptable and widespread are able to increase in human modified areas whereas localised and rare species often decrease and disappear from these human modified spaces (Newbold *et al.*, 2018). It has long been known that the influence of individual species on overall biodiversity patterns is related to their rarity. Common species typically dominate richness patterns, largely, but not completely as a consequence of the greater information encapsulated in their occurrence patterns (Lennon *et al.*, 2004; White *et al.*, 2023). Beta-diversity is intrinsically tied to occupancy across species (Arita *et al.*, 2008). The idea that common species also drive beta-diversity trends has been prevalent. Recent work has however found that although a weak homogenisation trend exists due to increases in widespread species this is mostly seen at larger scales and over longer durations (Blowes *et al.*, 2024). At smaller temporal and spatial scales, in particular, Blowes *et al.* (2024) found a mix of homogenisation trends resulting from the loss of low occupancy species, the gain of high occupancy species and both in combination (replacement) with differentiation resulting from opposite patterns.

Work focused on species has found that population and distribution trends can vary right across the range size spectrum; localised species may either decline or spread, and widespread species do not inevitably increase (Daskalova *et al.*, 2020). Studies of European and North American birds, as well as terrestrial insects, for example, have found that some of the largest population declines have been in relatively common and widespread species (Inger *et al.*, 2015; Rosenberg *et al.*, 2019; van Klink *et al.*, 2024). Both increases and decreases across the localised-to-widespread spectrum mean that it is far from obvious which species changes are contributing most to community differentiation and homogenisation with substantial variation across locations, taxa, time and scale (Blowes *et al.,* 2024). Although range size and measures of frequency of occurrence and occupancy are not directly analogous (Crisfield et al., 2024), we would expect these to be reasonably correlated at larger spatial extents

One of the major challenges in reconciling these apparently conflicting observations is that homogenisation is measured at the level of the ecological assemblage, whereas the interpretation is often focused on the fates of individual species or species groups without directly linking this with which species are most important in maintaining beta-diversity. One way to reconcile and unite community and species perspectives is to analyse the influences of individual species within an assemblage on the movement of that assemblage towards homogenisation or differentiation, by calculating species contributions to beta-diversity (Legendre & De Cáceres, 2013). Species with declining contributions to beta-diversity cause homogenisation whereas species with increasing beta-diversity contributions contribute to differentiation. By assessing the contributions of individual localised and widespread species to beta-diversity, we can gain a better understanding of which types of species are driving inter-assemblage homogenisation and differentiation.

In this study, we evaluate how individual species, which vary in their frequencies of occurrence, contribute to the spatial dissimilarity of ecological assemblages, for a variety of taxonomic groups and geographic regions. We consider the contributions of the individual taxa to beta-diversity at single time periods and also how they contribute to changes in beta-diversity between time periods. We also consider co-occurrence structure, directly and via consideration of the two components of beta-diversity - nestedness (changes in species richness) and turnover (species replacement). Although species contributions to beta-diversity have been examined before, knowledge of contributions to change and incorporation of co-occurrence structure and particularly nestedness are so far lacking. This means that our aims here are vital for a fuller understanding of biotic homogenisation. Co-occurrence structure is important to beta-diversity as species occurring in locations or sets of locations not favoured by the majority of other species will contribute more to variation and hence spatial beta-diversity. The ratio of nestedness to turnover is important as it is linked to the co-occurrence structure of assemblages. In systems with high nestedness the most common species are always found in the locations that are most species rich and the same species are usually found together as assemblages are nested subsets of one another. This should limit the variation in the beta-diversity contributions of widespread species. Based on the literature (McKinney & Lockwood, 1999; Newbold *et al.*, 2018; Staude *et al.*, 2022) and the fact that widespread species are known to contribute disproportionately to turnover patterns globally (Gaston *et al.*, 2007), we predicted that increases in *widespread* species would have a disproportionate effect in driving biotic homogenisation over time, with additional contributions from decreases in *localised* species. We in fact find that it is the balance of increases and decreases among rare species that has the clearest effect with little consistency around the effects of the most widespread species.

2 Materials and methods

2.1 Species data

We consider here a sample of 5 datasets all with more than 40 spatially distinct sampling locations, surveyed in at least two time periods, representing a variety of taxa, locations and durations of change (Table S1, Figure S1). The datasets selected are as follows: North American breeding birds (Ziolkowski, Jr. *et al.*, 2022), UK mammals (Crawley *et al.*, 2023), South African plants (Thuiller *et al.*, 2007; Dornelas *et al.*, 2018), Pacific ocean benthos (Santa Barbara Coastal LTER *et al.*, 2014; Sagouis *et al.*, 2023) and European Holocene pollen records (Fyfe *et al.*, 2009; Williams *et al.*, 2018; Gordon *et al.*, 2024). Time periods were selected based on data availability, subsequently aiming to maximise both the spatial and temporal span of the data by choosing the period that allowed for the most locations to be included without substantial reductions in the temporal span. For the North American Breeding Bird Survey we chose the time periods 1970 to 1974 and 2015 to 2019 due to the lower number of routes prior to 1970 and the Covid-related cancellation of surveys in 2020. This provided a total of 642 routes and 482 species (see supplementary methods for more details). For South African plants we used a set of 63 quadrats that had been surveyed twice, once in 1966 and then re-surveyed in 1996 with a total species pool of 418 plant species (Taylor, 1984; Privett *et al.*, 2001; Thuiller *et al.*, 2007). For the European pollen data (pollen records from individual sites, Table S3) we chose two time periods chosen to span the vegetation changes that took place during the Holocene: at the start of the Holocene (11,700 to 10,000 cal yr BP) separated by 8,000 years from more recent samples (2,000 - 0 cal yr BP; see supplementary methods for more details). This gave us a total of 41 sites and 505 pollen types. Pacific coast benthos data was from 44 permanent transects in the Santa Barbara channel. We used survey data from 2011 and 2021. This time span allowed us to maximise the number of sampled transects and provided occurrence data on 83 taxa. The UK mammal atlas covers 3,004 10 km grid squares for the two time periods: 1960 to 1992 and 2000 to 2016. We included the 40 species of terrestrial non-volant mammals. We refer to species throughout but in the case of pollen and benthos aggregates are included.

In order to test how rarity influences species contributions to beta-diversity, we calculated the proportion of survey sites occupied by each species in each time period. From this we were also able to measure changes in the proportion of sites occupied between the two time periods. A flow chart of our methods is provided as Figure S2.

2.2 Beta-diversity contributions and co-occurrence patterns

In order to compute total beta-diversity for each dataset we compiled species by site tables detailing the presence or absence of each species at each location in each time period. We then calculated the total variance of these species by site tables (following Hellinger transformation) as our measure of beta-diversity from which individual species contributions were partitioned (Legendre & De Cáceres, 2013). This was done using the R package '*adespatial*' (Dray *et al.*, 2022). We also calculated the relative contributions of nestedness (richness differences) and turnover (species replacement) to beta-diversity based on the Podani decomposition (Podani *et al.*, 2013). The Podani decomposition used Sørensen dissimilarity rather than Hellinger transformation as Sørensen allows for the proper decomposition of total beta-diversity into nestedness and turnover components (Legendre, 2014) but, unlike Hellinger transformation, the contribution of individual species cannot be identified from Sørensen dissimilarity using the total variance methodology (Legendre & De Cáceres, 2013). Both methods retain the desirable qualities of a beta-diversity metric (Legendre & De Cáceres, 2013) and the total beta-diversity values from the two methods were highly correlated when compared across each dataset-time period combination (Spearman's rank correlation coefficient = 0.95, $p < 0.01$, $n=10$ [2 time periods for 5 datasets]). We used Hellinger transformation for our main beta-diversity metrics, allowing for the estimation of species contributions and used Sørensen distances for the decomposition of total spatial beta-diversity. Although only one of many methods of beta-diversity calculation, the total variance of an appropriately transformed species by site matrix has a number of advantages. The total variance relates strongly to the concepts of homogenisation and differentiation which aim to quantify if assemblages are becoming more similar (lower variance) or less similar (higher variance). Examination of the matrix as a whole also avoids non-independence issues that arise from multiple pairwise distance comparisons. In addition, variance partitioning is very common and flexible allowing species and site attribution as well as summing across groups.

To test whether species with distinctive distribution patterns (i.e. dissimilar from the distributions of most other species) had higher beta-diversity contributions, we calculated metrics relevant to species co-occurrence. For each species, we calculated the correlation of its occurrence with overall species richness using a Spearman’s rank correlation. This showed how the patterns of occurrence of an individual species correlated with the rest of the community. For example a negative correlation indicates that a species occurs at sites with few other species whereas a positive correlation indicates a species is more likely to occur at species-rich sites.

Temporal change in all metrics was calculated for each case study comparing the two time periods.

2.3 Influence of nestedness and turnover

To test how the relative amounts of nestedness and turnover contained within our beta-diversity measure influence the relationship between rarity and species contributions we decomposed beta-diversity into the two components. As highlighted above this was done first for our five empirical datasets. We also took this further investigating the importance of the relative contribution of nestedness and turnover to the estimated species beta-diversity contributions using a simulation. We produced a community table representing complete nestedness (all differences between sites are due to different species richness). Species occurrence proportions were fixed to range between 0.02 and 1.00. From this fully nested set of assemblages we generated a series of eight further sets that reduced in nestedness proportion by 0.2 from the original (1.0) to 0.2. We did this by first randomly selecting a column (species) and then randomly selecting two rows (sites). We then swapped the values in these cells and repeated the process until the desired proportion of nestedness was achieved. We used these randomly generated assemblages of known nestedness to produce species beta-diversity contributions plots analogous to those produced for the empirical case studies.

3 Results

The total spatial beta-diversity between sites showed a minor decrease between the two sample periods for all of these studies (birds = 0.49 to 0.48; plants = 0.73 to 0.72; pollen = 0.50 to 0.49; benthos = 0.57 to 0.56; mammals = 0.49 to 0.46) indicating little change for the taxa, regions and durations considered. Assemblages did, however, differ in the proportion of the total beta-diversity attributable to nestedness, varying between 0.19 for North American birds and 0.63 for UK mammals in time period 2 (Figure 1 legend).

3.1 Species contributions to spatial beta-diversity

For a single time point we found that individual species contributions were greatest for species found in half of sites (Figure 1; although see the influence of nestedness below). This was relatively consistent across taxa, locations and time periods and is consistent with mathematical expectations and drivers of species richness patterns, being the occurrence frequency at which information content is maximised (Figure 2; Koleff *et al.*, 2003; Lennon *et al.*, 2004). This demonstrates that our chosen datasets are representative of wider ecological patterns. We found that other factors also influence this relationship. Co-occurrence structure also had an influence, with the species with distributions that were poorly correlated with overall richness having comparatively higher contributions to beta-diversity for their given occurrence frequency (Figure 1).

Co-occurrence structure relates to nestedness because a completely nested set of communities does not include any species that are more frequent in species-poor communities. With higher levels of nestedness, species contributions to beta-diversity begin to plateau for species with occurrence frequencies in excess of 0.5, rather than displaying the curved reduction seen in assemblages with high turnover. This can be seen in the empirical data where UK mammals have the highest nestedness and show the least signs of a curve whereas North American birds have the lowest nestedness and clearly display a curve centred around 0.5 frequency of occurrence (Figure 1). Assemblages generated randomly but with specified occurrence frequency and nestedness structure also showed this pattern (Figure 2; note that a measurement uptick occurs at extremely high occurrence in near completely nested communities, but this falls outside the empirical species/community parameter space). Overall, species contribute most to beta-diversity at a given time if they occur in ~0.5 of sites, with species occupying over 0.5 of sites also contributing strongly to beta-diversity in highly nested assemblages. In a perfectly nested set of assemblages, the most common species represent a high proportion of the species in low diversity communities, with these low diversity communities making disproportionate contributions to beta-diversity.

3.2 Species contributions to temporal change in spatial beta-diversity

Just as the contributions of species to spatial patterns of beta-diversity depend on occurrence, we found that species' contributions to temporal change in beta-diversity also depend on initial occurrence frequency (Figure 3). This is because the contribution of a species to a *change in beta-diversity* depends on the *gradient* of the beta-diversity curve at its position during time period 1 (panels in the left-hand column of Figure 1), whether it increases or decreases in frequency of occurrence between time periods, and by how much. Therefore the species with a frequency of occurrence >0.25 (where the curve in Figure 1 is steep) contribute strongly to beta-diversity change. The same is true for species with a frequency of >0.75 (but only for taxa with low nestedness).

Beta-diversity is therefore increased (differentiation) by species with initially low frequency of occurrence (<0.25) increasing to more sites approaching a frequency of occurrence of 0.5. In principle, beta-diversity increases can also result from the most widespread species (here classed as those with occurrence frequencies >0.75), declining to approach 0.5 occurrence, but as noted, only in taxa with low nestedness (Figures 1, 3). Beta-diversity decreases (homogenisation) between time periods if the opposite is true - low occurrence species decreasing and high occurrence species increasing. For declining beta-diversity there is however a third contributor - species with initial occurrence frequencies around 0.5. For these species both increases and decreases in status will result in declines in beta-diversity as they move away from the position with maximum individual contribution. Thus, the species that contribute most to beta-diversity at a given time (occurring ~0.5 of sites at time period 1) typically cause declines in beta-diversity when their status changes.

However, as is widely known, assemblages do not contain species equally spaced along a rarity spectrum with most assemblages containing a disproportionate amount of rare species (Figure S3). This means that it is important to consider the net summed effect across groups. When this is done it can be seen that species occurring in less than 0.25 of sites make the greatest contributions to differentiation collectively (blue points in Figure 4 left column), their importance increased by the high number of rare species (Figure S3). Across all datasets this group generally made the greatest contribution to homogenisation (decreasing species) and differentiation (increasing species) with the net contribution being the largest net contribution to differentiation (Figure 4). The largest net contributions to homogenisation came from species with an original occurrence frequency ~ 0.5 with the 0.25 - 0.5 and 0.5 to 0.75 groups having the largest net differentiation contribution depending on the dataset. The results for species with very high frequency of occurrence were far less conclusive with differences between the datasets analysed. For the most widespread species (initial occurrence frequency > 0.75) most changes in status were relatively modest (often declining rather than increasing), and few species had such high frequency of occurrence; hence they individually and collectively had limited impact on changes to total beta-diversity (Figures 3, 4).

4 Discussion

We found that ‘species’ that differed in the overall proportion of sites they occupied contributed in quite different ways to beta-diversity at a given time, and to how beta-diversity changes through time. The nestedness of the assemblages also has a strong influence on the role of widespread species, decreasing their influence on beta-diversity change at high levels of nestedness. Species occurring in around 0.5 of sites provide the greatest contributions to differentiation at a given time, but act as a homogenising force if they either increase or decrease - an important distinction from the perception that homogenisation is caused primarily by increases in a few of the most widespread species (McKinney &

Lockwood, 1999). In the most nested assemblages however, increases and decreases in these widespread species had little effect. Regardless of nestedness it should also be noted that given the relatively small range of species contribution values and the fact that most species in ecological communities are rare, it is unlikely that the numerically few common species can have a major direct effect. In contrast it was the net effect of increases and decreases in rarer species that substantially accounted for the overall pattern of biotic homogenisation (decreased spatial beta-diversity) through time, but in five different datasets covering a wide range of taxa and ecosystems the net changes were relatively minor.

As noted by others (Gaston *et al.*, 2007; Xia *et al.*, 2022), localised species do not make important contributions to spatial beta-diversity during a given census period. In contrast to other studies, however, we also consider beta-diversity change, leading us to conclude that localised species are important to the temporal dynamics of homogenisation and differentiation. This is due to the steep gradient of the occurrence-beta contribution curves for species at low occurrence (Figures 1, 2), a feature consistent even in highly nested assemblages. Hence, small changes to the status of large numbers of low-frequency species (species/taxa typically occur in a low proportion of all sites; Figure S3) can result in considerable changes in total species contributions to beta-diversity. Thus, localised species generated the greatest increases *and* declines in beta-diversity change across our datasets (Figures 3, 4). The dynamics of localised species did not, however, generate net community level homogenisation across the study systems considered here as would be expected if most of the localised species had declined - one of the hypotheses suggested as a driver of community homogenisation (McKinney & Lockwood, 1999). This was because increased frequencies of some localised species (i.e. those with < 0.25 occurrence frequency in the first time period) generated greater differentiation, in total, than the homogenisation caused by declines in other localised species (Figures 3, 4). This held for all five of the datasets considered here. Thus, the dynamics of localised species had a net differentiating rather than homogenising effect. The magnitude and sign of the net effect will depend on the ratio and relative magnitudes of localised species increasing and decreasing in response to environmental change. If the majority of localised species respond negatively or positively to a particular driver of change, then that driver of change will have a large influence on beta-diversity through its effects on localised species. If, however, the responses of localised species are highly variable, with equivalent numbers increasing while others decrease, the overall effect of localised species will be negligible. In some circumstances, they may simply ‘cancel out’ to produce a near zero net contribution.

In contrast to localised species, the species that occur in around half of sites contribute the most individually to beta-diversity at a given time. The slope of the occurrence frequency-beta contribution relationship is however, shallow in this area (Figures 1, 2). Therefore, occurrence increases or decreases of any one of these species need to be relatively large to produce substantial changes in their individual contributions to beta-diversity. Collectively though, as any movement away from occurring in half of sites reduces the beta-diversity contribution of a species, species that occur in around half of sites at the beginning of any period under consideration can in sum have a large net homogenising impact whether they increase or decrease (Figure 4). The net summed effects of the most widespread species (>0.75) were generally small (Figure 4). This in combination with our results for rarer species and those in around 0.5 of sites suggests little overall support for widespread species driving homogenisation patterns as we hypothesised.

One of our most novel findings regarded the nestedness of assemblages and the contributions of common species. We would expect the datasets with the greatest extent to have the largest amount of turnover (Soininen *et al.*, 2018) and indeed the datasets with the greatest extents (North American birds and European pollen) are among the datasets with relatively high proportional turnover. We expected more turnover relative to nestedness to produce more variability in the beta-diversity contributions of the more common species. Indeed these studies show the clear unimodal beta contribution curve, with the highest slopes for localised and widespread species whereas datasets with higher proportional nestedness show a far shallower curve for the more widespread species (Figure 1). Our study also extended beyond our five empirical datasets to explore nestedness in randomly generated assemblages providing the additional insight that at high levels of nestedness the species richness of sites in which a species occurs also becomes very important. In a fully nested assemblage, species that occur in the most sites are also the only species occurring in species poor sites, bolstering the beta-diversity contribution of these species (Figure 2). Our results regarding nestedness have two major implications. Firstly, as hypothesised widespread species as a group show more consistency in beta-diversity when nestedness proportion is high (flatter curve above 0.5), showing the influence of nestedness on contribution patterns. Secondly, as in proportionally more nested communities the curve is flatter for the upper half of occurrence frequency, changing in the occurrence frequency will have less of an effect on beta-diversity change than in datasets with proportionally higher turnover. Thus the influence of common species on beta-diversity change is reduced substantially when the assemblages are highly nested.

Our empirical examples showed however that there are multiple factors. For UK mammals (the most nested set of assemblages), increasing frequency of already fairly-common (here classes as those with 0.5-0.75 occurrence frequency) species contributed most to homogenisation. This is the only dataset that is consistent with the hypothesis that homogenisation is driven by common species (0.5-0.75 occurrence frequency) becoming more widespread. Of the five species contributing most to homogenisation, three had an initial occurrence frequency of ~0.7, which increased by the second time period (Figure 3 bottom-right panel). These were the Eurasian Otter (*Lutra lutra*), European Badger (*Meles meles*) and Red Fox (*Vulpes vulpes*). The fact that the UK mammals dataset did not follow the pattern that we would have expected looking at low gradients for common species seen from a single time period can be attributed to the earlier identified factor - the number of low frequency species. The UK mammals dataset has a high mean frequency of occurrence (across species) compared to our less nested datasets (Figure S3). This again highlights how our results show the importance of the homogenising role played by both increases *and* decreases of species in the middle of the range size distribution, which has been hitherto under-emphasised. However, these patterns need further exploration beyond the case studies presented here. Although testable in randomly generated communities the distribution of species occurrences and site richnesses still places some constraints on the possible range of other properties such as nestedness. In real world data these constraints are likely to further be amplified by ecological processes.

The three key factors influencing whether assemblages will experience homogenisation or differentiation as a consequence of temporal changes in species occurrence can therefore be summarised as: the frequency of occurrence distribution across species, how consistently frequency of occurrence change is based on its original value (do all rare species decrease?) and the proportion of beta-diversity between assemblages attributable to nestedness patterns. Firstly, the distribution of frequency of occurrence in the dataset matters (Figure S3). If there are many species with occurrence frequencies around 0.5 at the beginning of a period of change, their change in occurrence will nearly always contribute to beta-diversity reductions, and hence homogenisation is difficult to avoid. If on the other hand there are very many localised species, the impact of this group can offset or surpass that of the species with occurrence frequencies around 0.5. This brings us to the second factor - consistency of response for a given frequency of occurrence. If there are many localised species but the number of them increasing and decreasing is relatively balanced then their net contribution to changes in beta-diversity will be small at the community level, as seen in South African plants (Figure 4). If a sizable majority of localised species are increasing then this will provide a large net increase in beta-diversity potentially able to offset or surpass reductions elsewhere. For the most widespread species (>0.75 occurrence frequency), the net effect of changing distribution is close to zero if there are similar numbers of increases and decreases, as seen for North American bird species (Figures 3, 4). The final factor is the degree of nestedness which predominantly influences the shape of the relationship between beta-diversity contribution and occurrence frequency at the mid to high end of the occurrence frequency axis (Figure 1, 2).

One group of species often seen as a homogenising force are introduced species. Our results show that beta-diversity contribution to homogenisation or differentiation is highly scale dependent. From an introduced population of a few individuals at a few locations newly introduced species would need to crest the contributions curve and occupy more than half of sites to become a homogenising force. This might not even be enough if the assemblages in the region have a high degree of nestedness. For illustration, the three widespread and range-expanding British mammal species that generated the most community-level homogenisation (above) were native species with distributions increasing following reductions in species control and conservation measures, especially for the Otter (Crawley *et al.*, 2020). In contrast, the only introduced mammal species contributing substantially to a decline of beta-diversity was the House Mouse (*Mus musculus*) which declined from 0.37 to 0.23 occurrence. The species contribution most to homogenisation in the North American avifauna included the Red Tailed Hawk (*Buteo jamaicensis*) and Turkey Vulture (*Cathartes aura*), raptors increasing following alleviation of past pressures (Rosenberg *et al*., 2019) as well as declining natives such as the Loggerhead Shrike (*Lanius ludovicianus*). For South African plants the largest contributors to homogenisation involved declining endemics *Berzelia abrotanoides* and *Lachnea densiflora*. The largest contributors to homogenisation for the Pacific benthos were declining species such as *Pisaster brevispinus*. For European Holocene plants the species contributing to homogenisation included the increasing Alder *Alnus glutinosa* type and Oak Quercus robur type pollen.

An alternative route by which non-native species might result in homogenisation would be through their effects on localised species. If newly introduced species reduce the occurrence of localised species, this would contribute to homogenisation. The combined reduced combinations of localised species however would need to outweigh the increased contributions of the new species as it increases in occurrence from a low value to 0.5. Once an introduced species passes 0.5 occurrence then it is likely to be a directly homogenising force unless it subsequently declines. This again emphasises the complexity of direct species effects on beta-diversity.

Our study provides key insights into the process of biotic homogenisation and differentiation. It details a methodological framework for combining changes at the species level with those recorded for assemblages. There are clearly, however, a wide range of ecological and methodological factors that influence observed patterns linking rarity and spatial biodiversity (White *et al.*, 2023). There are also a number of different ways in which to conceptualise rarity. Here we have focused on site level occurrence but there are also local abundance and geographic range extent aspects (Crisfield *et al.*, 2024). The total variance approach employed here is also only one approach for quantifying beta-diversity with discussion of the desirable properties of a species contributions derivations and additional methods required for a fuller picture. In addition other facets of biodiversity beyond taxonomic composition, namely phylogenetic and functional diversity are becoming increasingly accessible for this area of research (White *et al.*, 2023). We suggest that the methodology presented here, combining species level trends with species contributions to inter-assemblage level changes, provides a framework for further investigating these questions.

5 Conclusions

Our results demonstrate that it is the species that occur in around half of sites that contribute most individually to beta-diversity in a single time point and they are also the species contributing most to homogenisation between time periods. It is generally localised species that are increasing their contributions to beta-diversity. If a high enough proportion of localised species are increasing (and most species are localised) their differentiating effect could be great enough to offset or surpass the homogenising effect of changes to the distributions of more common species. However, the net increases in differentiation generated by localised species were not sufficient in any of the datasets analysed here to offset the beta-diversity declines exhibited by species with higher frequencies of occurrence (>0.25), and hence the communities experienced modest levels of biotic homogenisation. This research also brings into question the focus on widespread species (here those with frequencies of occurrence >0.75) that are expanding in the homogenisation literature, as a strongly homogenising effect was not detected consistently for these species and is unlikely to occur directly unless the dataset has high levels of species turnover. While improving our understanding of how occurrence based spatial beta-diversity patterns are generated, this research also has implications for conservation and management strategies aimed at preventing increasing biotic homogenisation. Focusing on preventing declines in distribution of localised species and reversing this trend is likely to contribute more than a focus on controlling or containing the spread of already-widespread species. Hence, conservation measures that focus on increasing the range sizes of as many localised species as possible make the greatest contributions to increasing beta-diversity. Here we provide a useful framework for investigating beta-diversity patterns and unveil a number of complexities that will likely continue to develop as research expands both geographically and taxonomically.

References

Arita, H.T., Christen, J.A., Rodríguez, P. and Soberón, J. (2008) Species diversity and distribution in presence-absence matrices: mathematical relationships and biological implications. *The American Naturalist*, **172**(4), 519-532.

Blowes, S.A., McGill, B., Brambilla, V., Chow, C.F.Y., Engel, T., Fontrodona-Eslava, A… Chase, J.M. (2024) Synthesis reveals biotic homogenisation and differentiation are both common. *Science Advances*, **10**(8), p.eadj9395.

Crawley, D., Coomber, F., Kubasiewicz, L., Harrower, C., Evans, P., Waggitt, J… Mathews, F. (2020) *Atlas of the mammals of Great Britain and Northern Ireland*, (ed. by D.

Crawley, F. Coomber, L. Kubasiewicz, C. Harrower, P. Evans, J. Waggitt, B. Smith, and F. Mathews) Pelagic Publishing, Exeter.

Crawley, D., Coomber, F., Kubasiewicz, L., Harrower, C., Evans, P., Waggitt, J… Mathews, F. (2023) Occurrence data at 10km resolution for terrestrial mammals in Great Britain and Northern Ireland, 1960-1992 and 2000-2016 v2. *EIDC*.

Crisfield, V.E., Guillaume Blanchet, F., Raudsepp-Hearne, C. & Gravel, D. (2024) How and why species are rare: towards an understanding of the ecological causes of rarity. *Ecography*, **2024**, e07037.

Daskalova, G.N., Myers-Smith, I.H. & Godlee, J.L. (2020) Rare and common vertebrates span a wide spectrum of population trends. *Nature Communications*, **11**, 4394.

Dornelas, M., Antão, L.H., Moyes, F., Bates, A.E., Magurran, A.E., Adam, D… Zettler, M.L. (2018) BioTIME: A database of biodiversity time series for the Anthropocene. *Global Ecology and Biogeography*, **27**, 760–786.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guénard, G… Legendre, P., Madi, N. & Wagner, HH. (2022) adespatial: Multivariate Multiscale Spatial Analysis.

Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M. & Bruun, H.H. (2019) More is less: net gain in species richness, but biotic homogenization over 140 years. *Ecology Letters*, **22**, 1650–1657.

Fyfe, R.M., de Beaulieu, J.-L., Binney, H., Bradshaw, R.H.W., Brewer, S., Le Flao, A., Finsinger, W., Gaillard, M.-J., Giesecke, T., Gil-Romera, G., Grimm, E.C., Huntley, B., Kunes, P., Kühl, N., Leydet, M., Lotter, A.F., Tarasov, P.E. & Tonkov, S. (2009) The European Pollen Database: past efforts and current activities. *Vegetation History and Archaeobotany*, **18**, 417–424.

Gaston, K.J., Davies, R.G., Orme, C.D.L., Olson, V.A., Thomas, G.H., Ding, T.-S., Rasmussen, P.C., Lennon, J.J., Bennett, P.M., Owens, I.P.F. & Blackburn, T.M. (2007) Spatial turnover in the global avifauna. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 1567–1574.

Gordon, J.D., Fagan, B., Milner, N. & Thomas, C.D. (2024) Floristic diversity and its relationships with human land use varied regionally during the Holocene. *Nature Ecology & Evolution*, 1–13.

Inger, R., Gregory, R., Duffy, J.P., Stott, I., Voříšek, P. & Gaston, K.J. (2015) Common European birds are declining rapidly while less abundant species' numbers are rising. *Ecology Letters*, **18**, 28–36.

van Klink, R., Bowler, D.E., Gongalsky, K.B., Shen, M., Swengel, S.R. & Chase, J.M. (2024) Disproportionate declines of formerly abundant species underlie insect loss. *Nature*, **628**, 359–364.

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, **72**, 367–382.

Kramer, J.M.F., Zwiener, V.P. & Müller, S.C. (2023) Biotic homogenization and differentiation of plant communities in tropical and subtropical forests. *Conservation Biology*, **37**, e14025.

Legendre, P. (2014) Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, **23**, 1324–1334.

Legendre, P. & De Cáceres, M. (2013) Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology Letters*, **16**, 951–963.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2004) Contribution of rarity and commonness to patterns of species richness. *Ecology Letters*, **7**, 81–87.

Lewthwaite, J.M.M. & Mooers, A.Ø. (2022) Geographical homogenization but little net change in the local richness of Canadian butterflies. *Global Ecology and Biogeography*, **31**, 266–279.

McGill, B.J., Dornelas, M., Gotelli, N.J. & Magurran, A.E. (2015) Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution*, **30**, 104–113.

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, **14**, 450–453.

Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y… Purvis, A. (2018) Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLOS Biology*, **16**, e2006841.

Petsch, D.K., Bertoncin, A.P. dos S., Ortega, J.C.G. & Thomaz, S.M. (2022) Non-native species drive biotic homogenization, but it depends on the realm, beta diversity facet and study design: a meta-analytic systematic review. *Oikos*, **2022**.

Podani, J., Ricotta, C. & Schmera, D. (2013) A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. *Ecological Complexity*, **15**, 52–61.

Privett, S.D.J., Cowling, R.M. & Taylor, H.C. (2001) Thirty years of change in the fynbos vegetation of the Cape of Good Hope Nature Reserve, South Africa. *Bothalia*, **31**, 99–115.

Rolls, R.J., Deane, D.C., Johnson, S.E., Heino, J., Anderson, M.J. & Ellingsen, K.E. (2023) Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. *Biological Reviews*, **98**, 1388–1423.

Rosenberg, K.V., Dokter, A.M., Blancher, P.J., Sauer, J.R., Smith, A.C., Smith, P.A… Marra, P.P. (2019) Decline of the North American avifauna. *Science*, **366**, 120–124.

Sagouis, A., Blowes, S.A., Xu, W.-B. & Chase, J.M. (2023) Metacommunity surveys: A large synthesis dataset of metacommunity time series for the Anthropocene (Version 1.0).

Santa Barbara Coastal LTER, Reed, D.C. & Miller, R.J. (2014) SBC LTER: Reef: Annual time series of biomass for kelp forest species, ongoing since 2000 ver 11.

Soininen, J., Heino, J. & Wang, J. (2018) A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, **27**, 96–109.

Staude, I.R., Pereira, H.M., Daskalova, G.N., Bernhardt-Römermann, M., Diekmann, M., Pauli, H… Baeten, L. (2022) Directional turnover towards larger-ranged plants over time and across habitats. *Ecology Letters*, **25**, 466–482.

Taylor, H.C. (1984) A vegetation survey of the Cape of Good Hope Nature Reserve. I. The use of association-analysis and Braun-Blanquet methods*. *Bothalia*, **15**, 245–258.

Thuiller, W., Slingsby, J.A., Privett, S.D.J. & Cowling, R.M. (2007) Stochastic Species Turnover and Stable Coexistence in a Species-Rich, Fire-Prone Plant Community. *PLOS ONE*, **2**, e938.

White, H.J., McKeon, C.M., Pakeman, R.J. & Buckley, Y.M. (2023) The contribution of geographically common and rare species to the spatial distribution of biodiversity. *Global Ecology and Biogeography*, **32**, 1730–1747.

Williams, J.W., Grimm, E.C., Blois, J.L., Charles, D.F., Davis, E.B., Goring, S.J… Takahara, H. (2018) The Neotoma Paleoecology Database, a multiproxy, international, community-curated data resource. *Quaternary Research*, **89**, 156–177.

Xia, Z., Heino, J., Yu, F., He, Y., Liu, F. & Wang, J. (2022) Spatial patterns of site and species contributions to β diversity in riverine fish assemblages. *Ecological Indicators*, **145**, 109728.

Ziolkowski, Jr., D.J., Lutmerding, M., Aponte, V.I. & Hudson, M.-A.R. (2022) *North American Breeding Bird Survey Dataset 1966 - 2021*, U.S. Geological Survey.

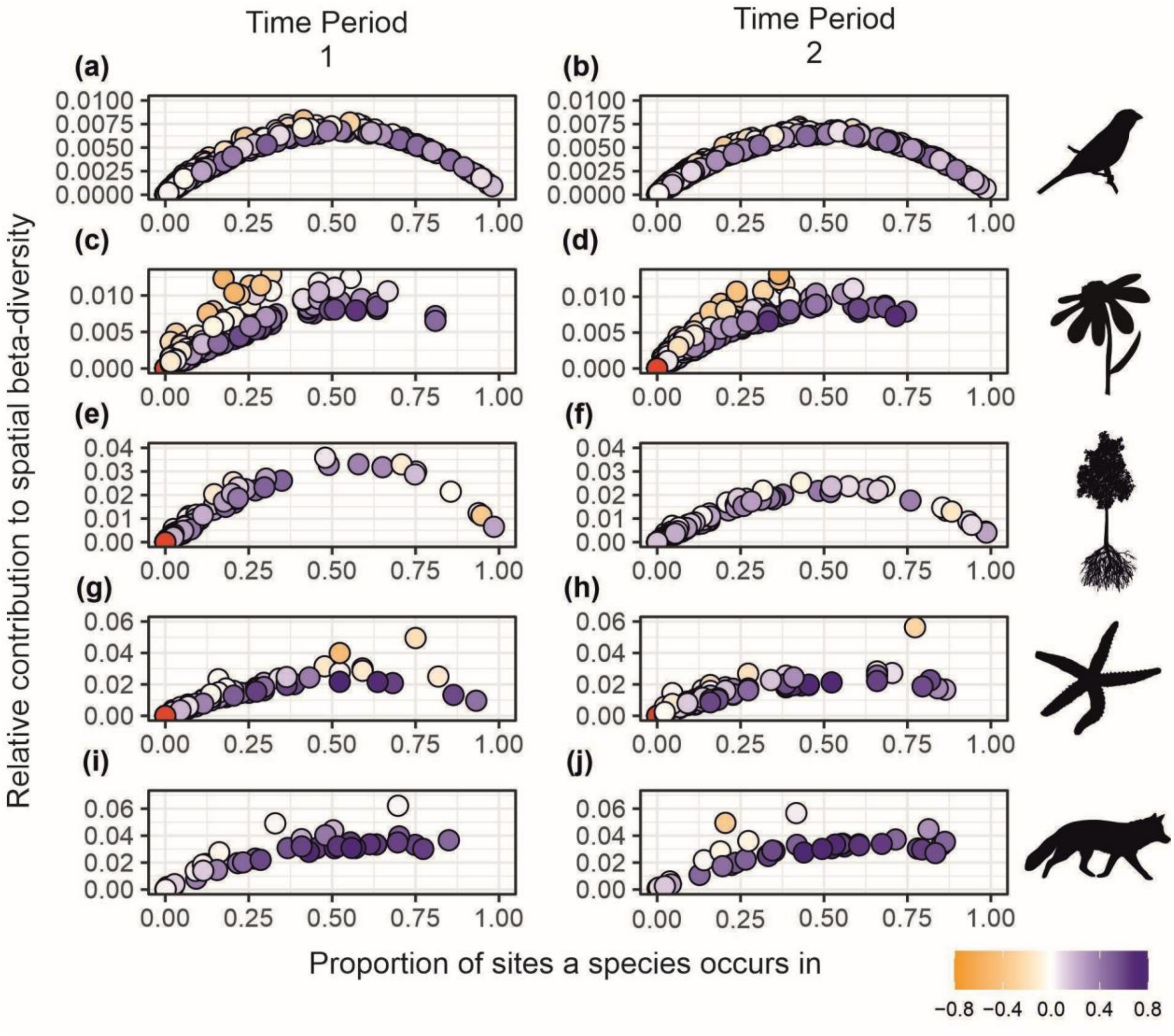

Figure 1 - Relative contributions of each species to spatial beta-diversity (Hellinger transformed total variance) in the two time periods compared to the proportion of sites each species was recorded in. Data shown for North American birds, South African plants, European pollen samples, Pacific coastal benthos and UK mammals. Colours indicate the correlation between the occurrence of each species and overall richness. Red points indicate species not present in the time period that are present in the other time period (gains and losses). The five analyses are ordered from the least community nestedness - birds showed the least nestedness at 0.22 and 0.19 (time periods 1 and 2 respectively), followed by plants (0.35 and 0.29), pollen (0.39 and 0.36), benthos (0.40 and 0.48) and then mammals with the greatest nestedness (0.59 and 0.63).

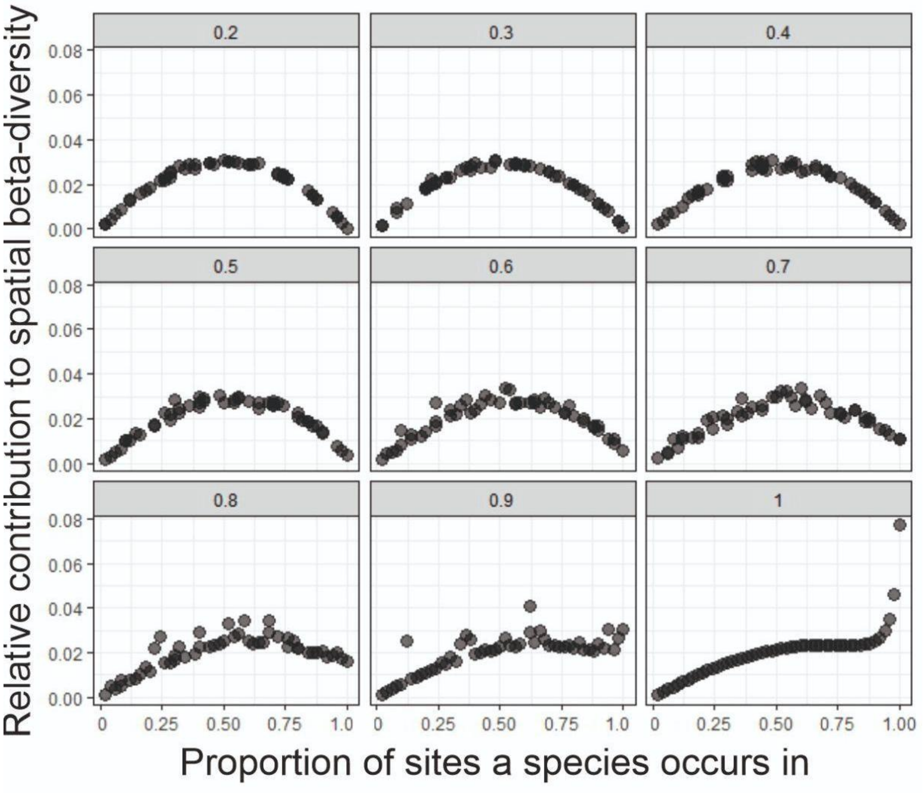

Figure 2 - Species contributions to beta-diversity in randomly generated assemblages. Each figure is arranged from low (top left panels) to high (bottom right) levels of nestedness. Panel headings indicate the proportion of the total beta-diversity attributed to nestedness (species richness differences) as opposed to turnover (replacement of species).

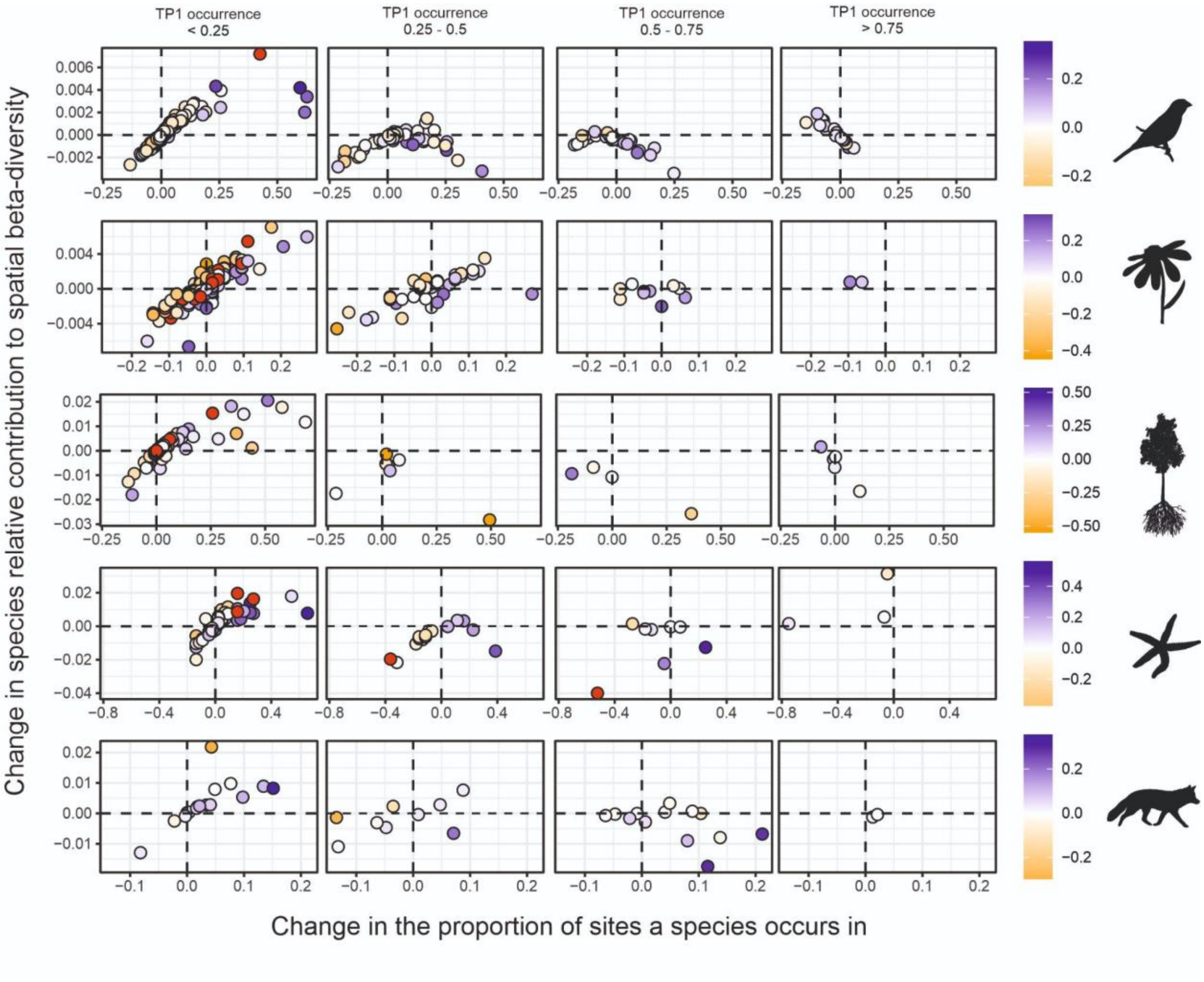

Figure 3 - Difference in species contributions to spatial beta-diversity between the two time periods compared to change in the proportion of sites a species occurs in (time period 2 - time period 1). Negative values indicate that values in time period 2 are lower than those in time period 1. Dotted lines show zero change. Data shown for North American birds, South African plants, European pollen samples, Pacific coastal benthos and UK mammals. Species are split based on the proportion of sites they occur in during the first time period. Colour scale indicates change in correlation of the occurred values of an individual species and site richness. Red points indicate species only found in one time period hence these species only have a single correlation value (no change value) and other differences are from 0.

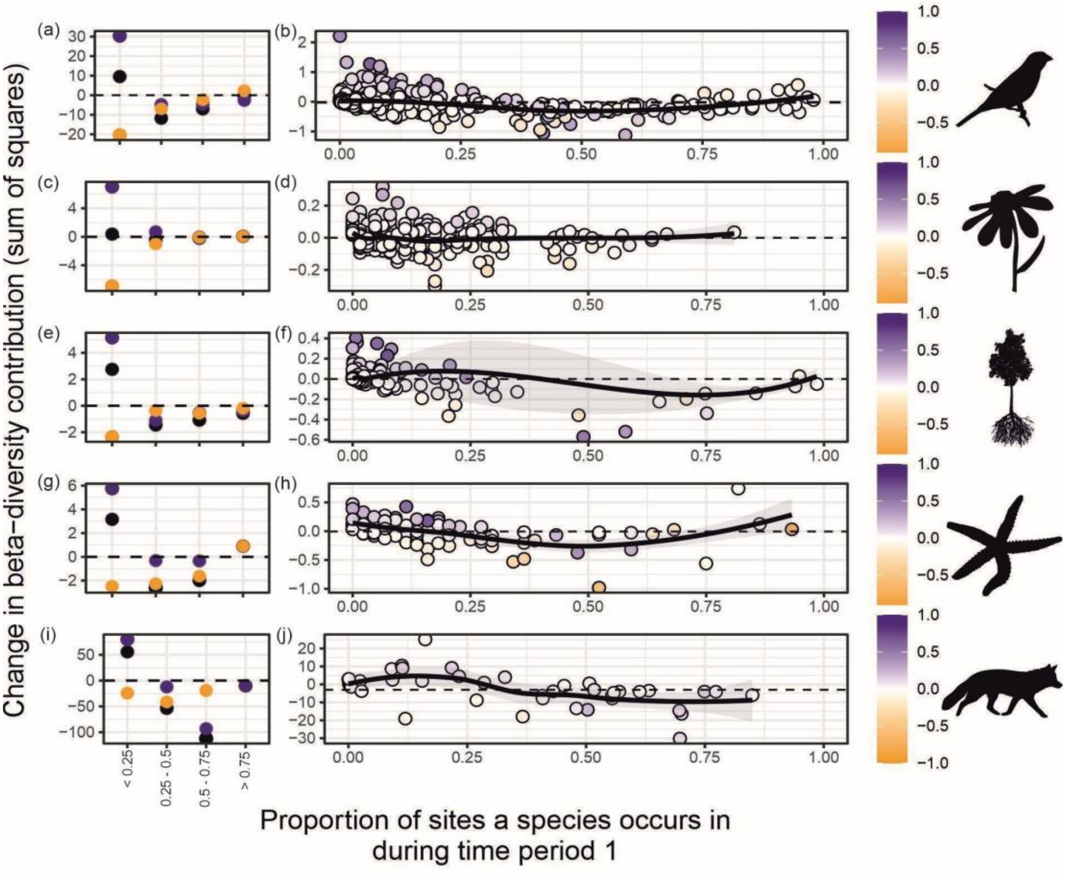

Figure 4 - Sum of squares change in species contributions to spatial beta-diversity between time periods totalled by occurrence frequency at TP1 group (first column) and for individual species (second column). In the first column species sum of squares values are totalled based on quartiles of the proportion of sites they occur in during time period 1, with black points indicating the net change for each occurrence frequency group, blue points for only the species that increased in occurrence and orange points for only the species that decreased in occurrence. The vertical dotted line indicates no net change. In the second column individual species sum of squares values are shown with points coloured by occurrence change. The horizontal dotted line indicates the average change across all species. The solid line indicates a moving average with 95% standard error shading. The colour scale shown for points in the second column indicates change in occurrence frequency between time points with orange values indicating a decrease from TP1 to TP2 and blue an increase. Data shown for North American birds, South African plants, European pollen samples, Pacific coastal benthos and UK mammals.