

Dominance structure of assemblages is regulated over a period of rapid environmental change

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Abstract

Ecological assemblages are inherently uneven, with numerically dominant species contributing disproportionately to ecosystem services. Marked biodiversity change due to growing pressures on the world's ecosystems is now well documented. However, the hypothesis that dominant species are becoming relatively more abundant has not been tested.

We examined the prediction that the dominance structure of contemporary communities is shifting, using a meta-analysis of 110 assemblage timeseries. Changes in relative and absolute dominance were evaluated with mixed and cyclic-shift permutation models. Our analysis uncovered no evidence of a systematic change in either form of dominance, but established that relative dominance is preserved even when assemblage size (total N) changes. This suggests that dominance structure is regulated alongside richness and assemblage size, and highlights the importance of investigating multiple components of assemblage diversity when evaluating ecosystem responses to environmental drivers.

Keywords: Dominance, timeseries, assemblage, biodiversity

Introduction

The substantial threat to ecosystems posed by the global biodiversity crisis [1] underlines the urgent need to understand how habitats and ecosystems react to change. A number of studies have reported species richness (S) loss, particularly in habitats that have been extensively transformed [2], while other investigations have found no evidence of declining trends [3][4][5]. One explanation for the apparent stasis in species richness in many ecosystems, even in the face of compositional reorganisation, is that assemblages are regulated in terms of their S and total abundance (N). A recent study uncovered evidence for widespread regulation of S and N, where regulation was defined as the assemblage time series returning towards its long term mean following a perturbation [6]. However, the fact that S and N are regulated in many instances does not mean that other attributes of assemblages, such as dominance structure, follow suit. Indeed, we already know that untrending S can be accompanied by marked temporal turnover in species composition [3]. This raises the question of whether or not relative abundance patterns are regulated.

One of the few universal patterns in ecology is that, while most species are rare, a handful of very common species dominate assemblages [7]. These numerically dominant species can contribute disproportionately to ecosystem services, so even a small change in their relative or absolute abundance could have large consequences for ecosystem functioning and sustainability[8].

Dominance patterns may be shifting as a consequence of ongoing environmental changes [9] [10], particularly as dominant species may be generalist species better able to adapt to change [11], but this has not yet been tested.

To explore how dominance patterns are changing in the Anthropocene, we undertake a meta-analysis of change in the numerical abundance of dominant species in consistently monitored assemblages across the globe. We first pose the question: 'are there systematic temporal changes in dominance?'. Next, we ask if dominance changes as a by-product of shifts in N. If dominance is regulated by the same processes that regulate N, any changes in the abundance (not identity) of the dominant species will be in proportion to change in N. In this scenario, absolute dominance will track changes in assemblage size, but relative dominance will not. On the other hand, a shift in the relative abundance of the dominant taxon (with or without change in absolute dominance) would suggest that assemblages are being restructured as they change in size.

Methods

We used the BioTIME database of monitored local species assemblages[12]. This database contains both animal and plant time series data from around the globe, between 1900 and the present. We selected the 110 assemblages that had at least 10 sample years to avoid artefacts due to short time series duration, and chose only assemblages where abundance had been quantified as numbers of individuals. Of these assemblages, 50 were marine, 49 were terrestrial, and 11 were freshwater.

We applied sample-based rarefaction [3] to each assemblage to account for sampling differences. Analysis was undertaken in R [13]. To focus on long-term trends, we exclude seasonality by summing the abundance of each species each year within each assemblage.

We defined the dominant species as the most numerically abundant taxon in a given year. Note that we are interested only in the abundance of this species, not its identity (which can change between years). Where two species were equally dominant in a year, we selected the first species listed in the dataset. In each year, we computed the following values: assemblage size - the summed abundance of all species in the assemblage (N); absolute abundance of the dominant species - the number of individuals recorded for that species (D_a); relative abundance of the dominant species $D_r = D_a/N$.

To assess whether there was a systematic increase in dominance, we constructed two mixed models using the package lme4 [14] (*Equation S1*). For D_a , \log_2 abundance was regressed against mean centred year, with assemblage identity included as a random effect with varying intercept and slope. Similarly, D_r , the relative dominance of the dominant species each year, was regressed against mean centred year, with assemblage identity included as a random effect with varying intercept and slope. We then computed the overall rate of change (slope) for both models.

To explore whether observed trends in dominance differ from what would be expected by chance (assuming realistic population dynamics), we next employed a cyclic-shift null model (*sensu* Hallet *et al.* [15], see *Fig. S4*) which preserves within species temporal autocorrelation, but breaks species cross correlations in abundance. To do this we shuffled every assemblage 1000 times using the random shift permutation and calculated its rate of change in both D_a and D_r on each run using the same mixed models as for the observed data above; this gave us a null distribution of 1000 slopes per assemblage. We then asked where the observed slope of dominance change lay relative to the null distribution for that metric and assemblage; observed values below the 2.5% or above the

97.5% quantile were assumed to exhibit a significant shift. We recognise that this analysis does not take account of multiple testing, but note that any correction for this would have the effect of decreasing the number of studies departing from the null expectation.

To examine how D_a and D_r change in relation to assemblage size (*Fig. S5*) we first estimated rates of change of assemblage size using a mixed model of \log_2 assemblage size regressed against mean centred year, with assemblage identity included as a random effect with varying intercept and slope (*Equation S2*). We then used model fitting to assess whether including assemblage size change as a fixed effect that interacts with mean centred year (*Equation S3*) improved model fit in either the absolute or relative dominance models. We also used Pearson's Correlation to assess the relationship between Z scores of the assemblage size model and the two dominance variables, as calculated from the null model results.

Results

We detected no systematic change in either D_a (slope = 0.006, SE = 0.009) or D_r (slope = -0.04, SE = -0.05) (*Fig. 1*). There were no marked differences in rates of change for realms (terrestrial/freshwater/marine) or taxa (*Figures S6 & S7*). The cyclic-shift null model supported this overall result, but uncovered heterogeneity in the pattern of change. Cases of positive and negative change were slightly less balanced for D_a (decrease in dominance relative to the null expectation: 17 (15%) studies; increase: 33 (33%) studies; no change 60 (54%) studies) than for D_r (decrease: 45 (41%) studies; increase: 33 (30%) studies; no change: 32 (29%) studies (*Fig. S8*).

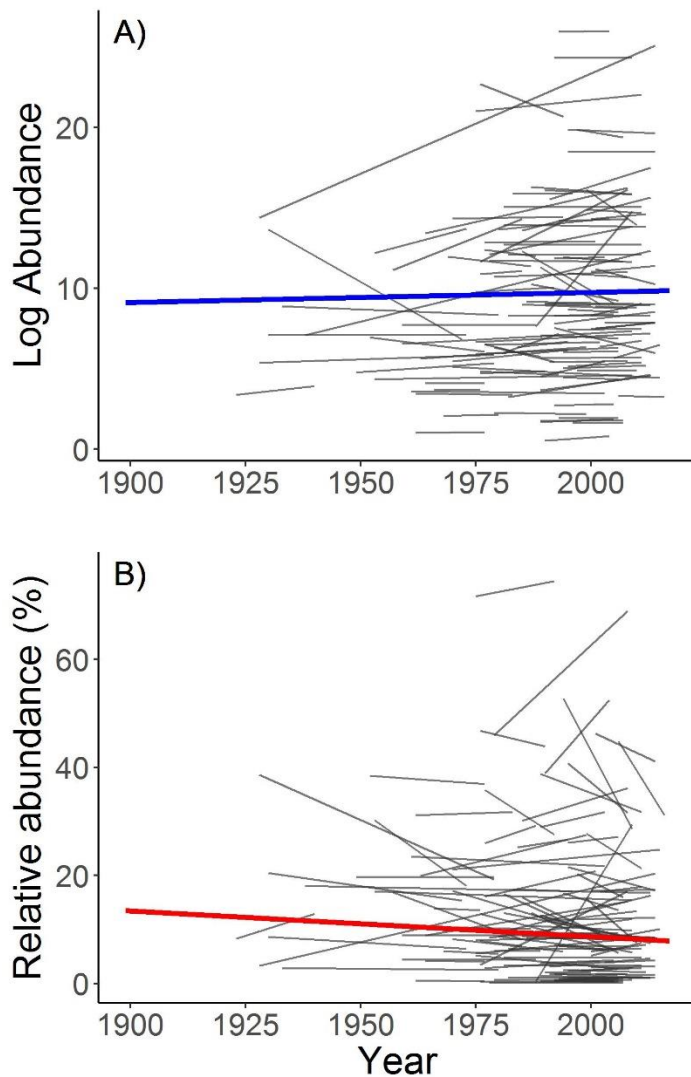


Figure 1. Rates of change of (A) absolute and (B) relative dominance. Each thin grey line represents the trend in dominance within a single assemblage as calculated by the random slopes in the mixed model. The bold lines across both plots show the overall model trend lines.

There was no systematic change in N over time (slope = 0.0069, SE = 0.0070; Fig. S9), but this overall trend was also underlain by temporal variation in numerical abundance within and among assemblages. D_r on average represents less than 20% of N in the majority (86) of assemblages (Fig. S10). At the assemblage level, Z scores of changes in D_a were correlated with Z scores of changes in total N ($r = 0.67$; Fig. 2a). Including rate of change in N , and its interaction with time, improved the fit of the D_a model ($p < 0.001$), supporting a positive relationship between change in absolute dominance and change in assemblage size.

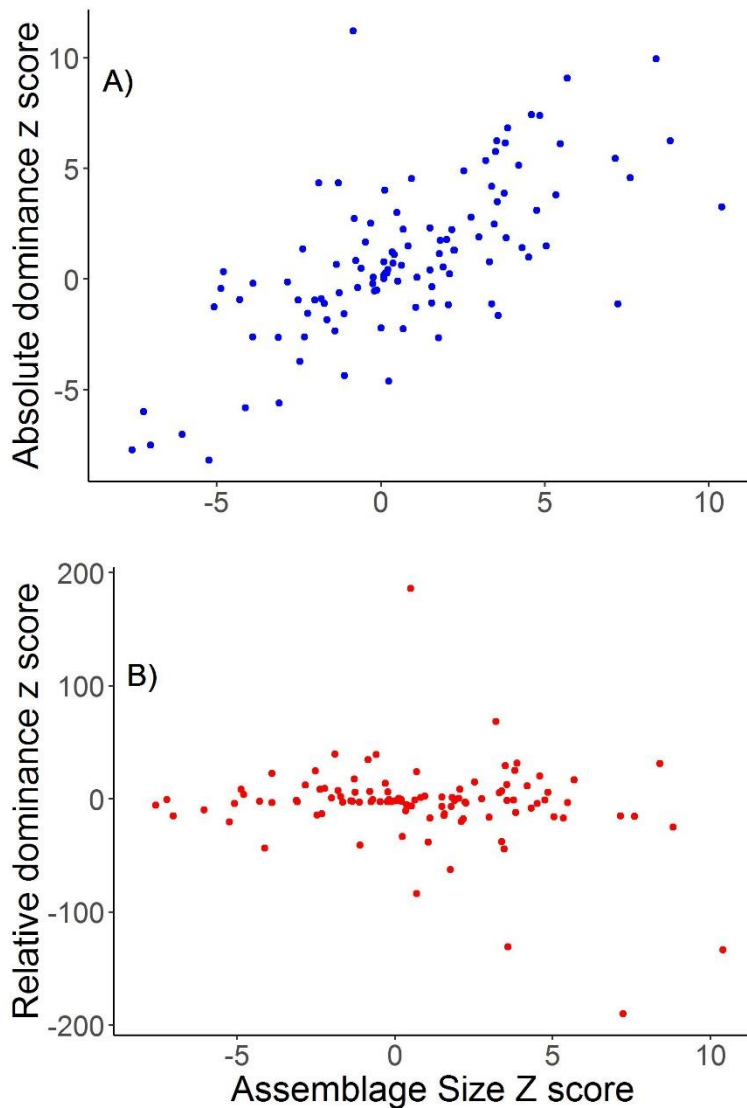


Figure 2. Z scores from the assemblage size change model against both the absolute (A) and relative (B) dominance change models. A positive relationship is evident for absolute dominance but not relative dominance.

There was, conversely, no relationship between Z scores of changes in N and changes in D_r ($r = -0.21$; Fig. 2b). Including rate of change of N in the D_r change model did not improve model fit ($p = 0.3$).

Discussion

Although dominance and species richness components of assemblages contain orthogonal information on biodiversity [16] there has, until now, been only limited understanding of how dominance structure changes through time. Despite predictions of widespread assemblage restructuring [16] we found no evidence of a systematic increase in dominance. However, shifts in dominance were present and generally tracked changes in overall assemblage size. In other words, dominant species continued to account for roughly the same fraction of the assemblage even when it contracted or expanded in size. As a result, there is little support for the idea that common species are increasingly dominating ecosystems.

Many different external drivers, such as climate change [17], pollution [18] and land use intensity [10], have the potential to alter the patterns of dominance. Nonetheless, our analyses show that in the assemblages we studied, dominance structure is not undergoing any directional change. This suggests that dominance is being regulated alongside S and N [6]. The potential mechanisms underlying this phenomenon are numerous, and include niche and fitness differences (see HilleRisLambers *et al.* [19] for further discussion).

The abundance and identity of a species combine to shape its influence on ecosystem functioning [20]. Indeed, the identity of the dominant species is the main driver in influencing biomass production, community composition and functioning [21]. As such, there could be shifts in ecosystem functioning despite no change in dominance structure. Elucidating these shifts is a key challenge in building a predictive framework of biodiversity change in a rapidly changing world [22].

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Author contributions

FJ undertook analysis, AEM supervised analysis. Both authors wrote the manuscript. Both authors agree to be held accountable for the content therein and approve the final version of the manuscript.

Data accessibility

Data in Dornelas *et al* [12]. Full details in *Table S1*.

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Competing interests

The authors have no competing interests.

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