Synchronous or compensatory community dynamics? Insights from a long-term bird study at multiple temporal and taxonomic scales

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1 Introduction

Ecological theory suggests that within rich communities where a number of species have similar functions, due to their proximity in morphological or phylogenetic space, they might exhibit compensatory dynamics [1], i.e., species within the same guild should swap places to some extent, whenever there is a space or resource constraint combined with temporal environmental variability. Which species "win" at any particular point in time may then depend on the fine-grained temporal environmental variation, or just on random exclusion processes (e.g., who gets there first). Whatever the cause of compensatory dynamics, its main consequences for ecosystem functioning is therefore that the community as a whole exhibits lower biomass variation than its constituent species (REFS), and is therefore more stable in the sense of lower variation.

Early investigations of synchronous vs compensatory dynamics focused on the variance ratio, that is, the variance of the sum of the community biomass divided by the sum of the variance of the component species biomasses. Unfortunately, this approach is not appropriate for communities subjected to community-wide environmental forcing (REFs), because one main environmental driver (e.g., temperature or light) may synchronize all the species abundances or growth rates. Further research has therefore focused on specific timeframes where compensatory dynamics may be found (e.g., below the seasonal scale where temperature fluctuation tends to synchronize species, Vasseur ref).

Despite this effort to make temporal scales more precise, temporal compensation has been surprinsingly elusive in the field (REFs). Most datasets used to evaluate temporal compensation vs synchrony involve planktonic organisms (REFs) or terrestrial plants (; though see). Here, we take advantage of a long-term bird time series record at the monthly scale (XX years), in a natural reserve, that allows us to dig deeper into patterns of synchrony between species at various time and taxonomic scales.

Indeed, taxonomic scale should be a main modulator of synchrony/compensation, a factor of variation that has been somewhat negelected for now. On the one hand, one could argue that compensation should be higher between similar species, because functional and phylogenetic differences being generally correlated. If species A and B are two duck species that share almost the same food niche and share many traits, it makes little difference to the rest of the community whether one species gets replaced by the other (functional compensation, [1]). On the other hand, it could be argued as well that more dissimilar groups of species - within the same trophic level nonetheless - could exhibit compensation exactly because they have different environmental preferences and the environment varies (e.g., groups of species preferring more open vs more closed habitats replacing each other as a function of changes in vegetation height). Surprisingly, this aspect has been relatively less well explored even though there is some empirical evidence for this [2].

Our dataset is ideally suited to tackle how synchronous are bird communities at different temporal and taxonomic scale given that (i) it is a highly temporally resolved time series with respect to the species typical generation times and (ii) the reserve where the data has been collected was subjected to a major management change c. 2006 (change in water levels), favouring different types of wetland birds (so that over long timescales, there is a potential for changes in community composition).

2 Material and Methods

2.1 Data

The monthly time series used for the statistical analyses have been collected at the Teich Ornithological Reserve, Arcachon Bay, France ([coordinates here]). The reserve is constituted of XX ha of wetlands , and the data have been aggregated at the reserve scale by using for each species the maximum observed abundance over a month, which provide a "monthly snapshot" of the bird community. In the statistical analyses, we use both the monthly data and aggregates at the seasonal scale. We defined two seasons in the following manner XXXX (see Appendix S1 for alternative choices of season definition).

2.2 Statistical Analyses

We used the synchrony index defined by [3], which writes

$$\eta = \frac{1}{n} \sum_i \mathrm{Corr}(P_i, \sum_{j \neq i} P_j) \tag{1}$$

The index described in eq. 1 varies between -1 (compensation, total biomass is constant) and 1 (synchrony), while 0 represents a case where all populations fluctuate independently. Contrary to previous indices (see, for instance, **(author?)** 4), this index is independent from the richness of the community and its overall stability **(author?)** [5]. We computed synchrony indices at the seasonal scales using the codyn package in R **(author?)** [6]. We used two definitions of the season. The first one was based on official months: winter corresponded to the three months between January and March, until autumn which was defined as the months between October and December. The second definition was based on observations of bird presence related to temperature: we defined a 'cold season' as the months between November of the previous year and February, and a 'warm season', from May to August. In both cases, we averaged bird abundances over the season and computed the synchrony index from one year to another. We also differentiated three periods: before and after 2006, where management chance ocurred, and a period including all years, ignoring the change in 2006. We computed the statisticial significance of the synchrony values obtained with Monte Carlo randomizations **(author?)** [7]. For each sets of time series (each season), we kept the auto-correlation of the species time-series but removed the cross-correlation between species by shifting each time series by a random lag **(author?)** [8]. We obtained 100 sets of randomized time series for each season and period of time considered and computed the corresponding synchrony index. We then compared the observed values to the values obtained with the randomized time-series. Independence of species was rejected at the 5% threshold. threshold.

In addition to time-series analysis, we focused on the wader community for a further frequency-based analysis. Based on the work by **(author?)** [9], we used the wavelet transform of the time series to measure the coherency between time series

$$\rho(t,s) = \frac{\Lambda_{t,s}(|\sum_k w_k(\tau,s)|)}{\Lambda_{t,s}(\sum_k |w_k(\tau,s)|)} \tag{2}$$

where $w_k(\tau, s)$ is the continuous Morlet wavelet transform of species k at time τ for scale s, $\Lambda_{t,s}(\centerdot) = \int_{-\infty}^{+\infty} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2}(\centerdot)d\tau$ and $|\centerdot|$ is the modulus of the complex number. The numerator corresponds to the total biomass variation while the denominator corresponds to the variations of each species. This index is close to 0 when species compensate and reaches 1 when they are synchronous. As before, the significance of each value was tested at the 5%, Bonferroni-corrected, threshold by 100 phase-randomizations of each species time series, and computation of the corresponding ρ values.-

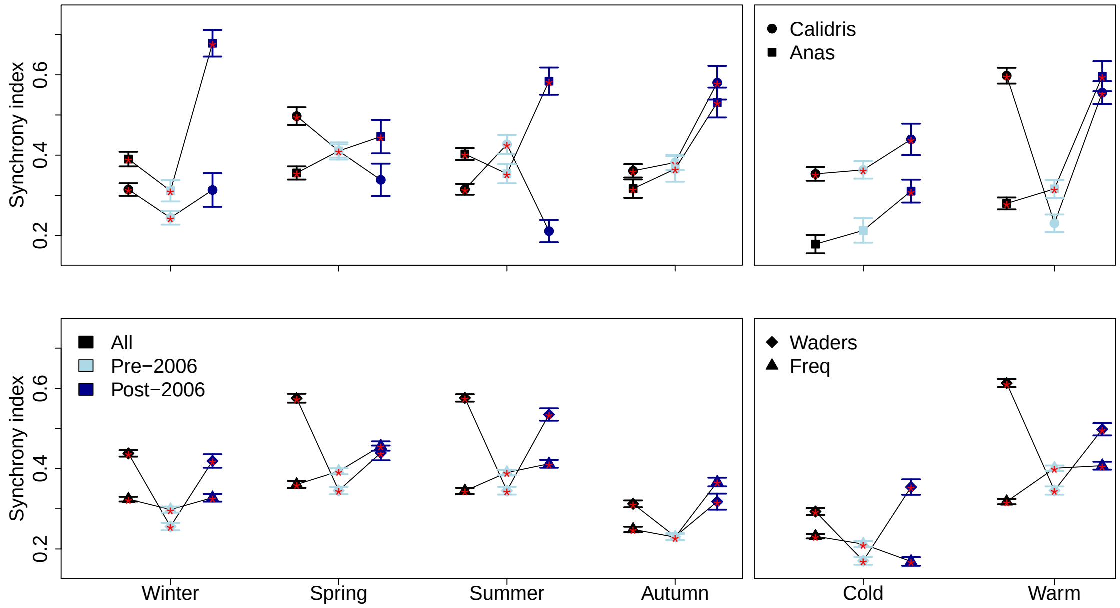

Figure 1: Gross' synchrony index as a function of the season (official season, left, or cold and warm season, right), calculated on different functional (frequent birds, waders, bottom) or taxonomic (Anas, Calidris, top) groups. Indices were computed on the whole dataset (black) or with the same dataset separated in two periods: before and after 2006 (light and dark blue), when a management change occurred. Red stars correspond to synchrony values significantly different from the null model (independent species), at the 5% threshold.

3 Results

Figs 1-2-3

4 Discussion

Compensatory dynamics are still rare even a short frequencies among taxonomically or functionally close species, i.e. there is no functional compensation. Yet, accross contrasted guilds can change in frequency in the long run (in this case, due a change in management). We therefore suggest that compensation should be searched for more often between rather within functional groups, and on relatively long timescales above that of the dominant driver (e.g., seasonality).

References

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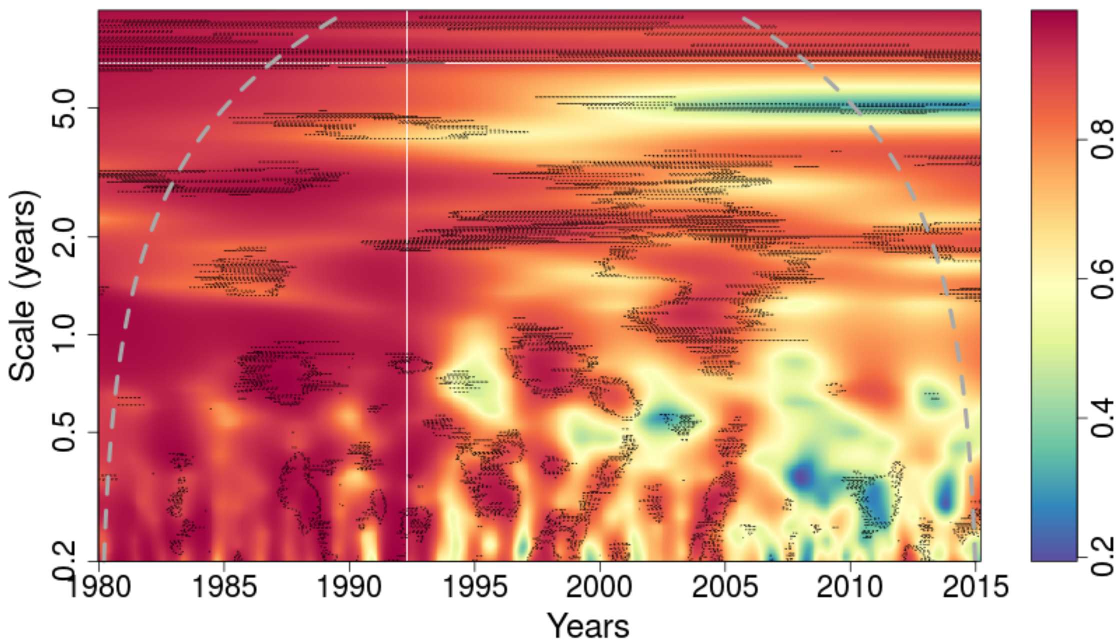

Figure 2: Wavelet modulus ratio for the wader community, scaling from 0 (compensation) to 1 (synchrony). Dashed black lines delineate regions significantly different from the null model with a false discovery rate controlled at the 5% level.

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