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 at the same trophic level, where a number of species can 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 can swap places to some extent. This is particularly likely to occur when 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 having lower temporal variability. By contrast, synchrony occurs when all species fluctuate in phase, and therefore the biomass of the community does not fluctuate less than its constituent parts.

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 (Ranta et al.), because one main environmental driver (e.g., temperature or light) may synchronize 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 2014 ref).

Despite this effort to look for more meaningful temporal scales, 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 (for 35 years[1]), in a natural reserve, that allows us to dig deeper into patterns of synchrony between species at several temporal 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 are generally correlated. For example, if species A and B are two duck species that share almost the same food niche as well as 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

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[1] If we consider only the years we use. Otherwise, the dataset begins in 1973

of changes in vegetation height). Surprisingly, this aspect has been 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 (44.64°N / -1.02°E). The reserve is constituted of 120 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 provides 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 based on observations of bird presence related to temperature. We defined a 'cold season' as the months between November and February of the following year, and a 'warm season', from May to August. This makes sense from an ecological viewpoint, as we separate wintering birds from summer residents, and these two communities have different needs and a shifting composition (though they partially overlap). (see Appendix S1 for alternative choices of season definition).

Fig. 1 shows the patterns in abundance for key groups in the Teich reserve bird community.

2.2 Statistical Analyses

We used the synchrony index defined by Gross et al. [3], which is defined as the mean cross-correlation between each species and the rest of the community (eq. 1).

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

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, Loreau and de Mazancourt [4]), this index is independent from the richness of the community and its overall stability [5, 6]. This is important here, as we will perform analyses at different taxonomic scales and therefore with a different number of groups.

We computed synchrony indices at the seasonal scale using the codyn package in R [6].

We averaged monthly bird abundances, for each species, over the season duration, and computed the synchrony index using the year as our statistical unit. We also differentiated before and after 2006,give that a management change occurred within the reserve in 2006., We considered both the synchrony inside a given group (e.g., among the *Anas* genus) or between groups (e.g., between *Anas* and *Calidris*). In the latter case, we summed species together before seasonal averaging. We also examined the specific case of Cormorant, Egret and Heron, the first one displaying dynamics opposed to the later two.

We computed statisticial significance of synchrony index values using Monte Carlo randomizations [7]. For each set of time series (each combination years × 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 [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. .
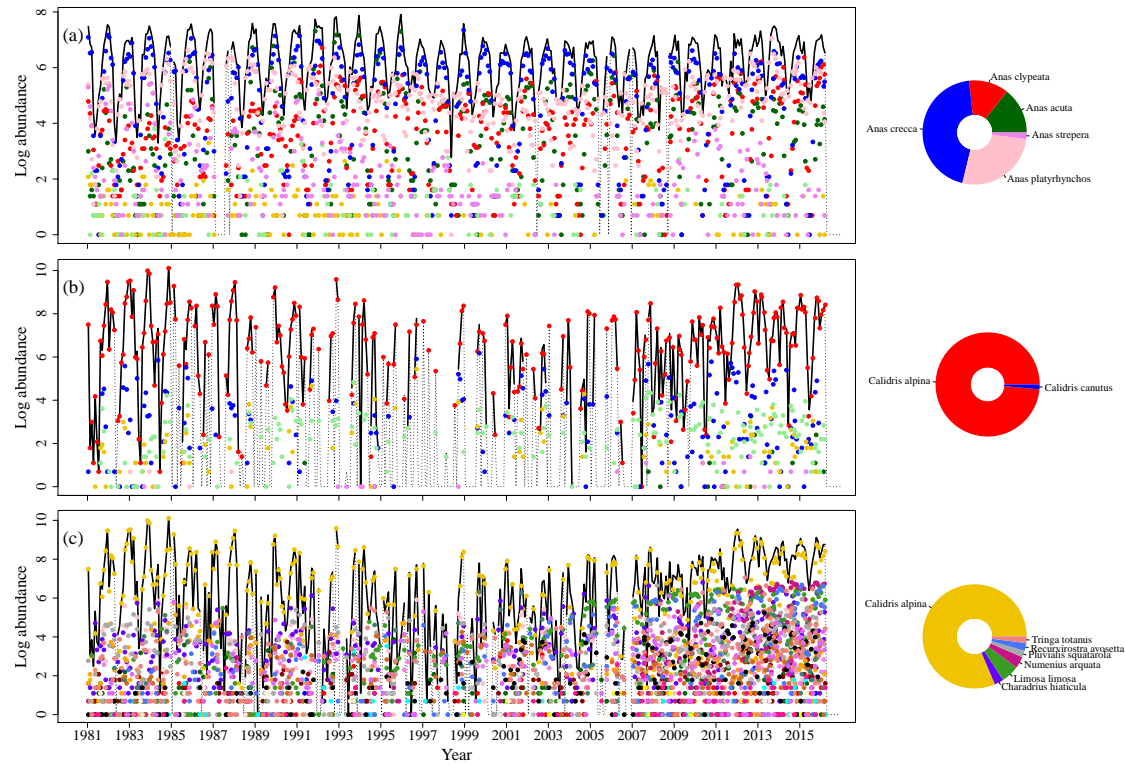
Figure 1: Temporal trends for ducks (a, *Anas* genus), calidrids (b, *Calidris* genus), and all waders (c, including calidrids). The filled black lines represent trends in summed abundances for each guild, thin dotted lines putative trends (when some species are absent). The coloured symbols below the curves represent each species abundances, with species composition on the right side on the donut plots for the most abundant species.

In addition to the time-domain analyses above, we focused on the rich wader community for a frequency-domain analysis. Based on the work by Keitt [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, $\Lambda_{t,s}(.) = \int_{-\infty}^{+\infty} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2}(.)d\tau$ and $|.|$ 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.-

3   Results

Using a taxonomic classification (Calidris and Anas), we can see that within-genus synchrony indices are always positive, i.e. there is no compensation within a genus (Fig. 2). The synchrony tend to be lower during the cold season, and to be lower during the pre-2006 period as well (during which water levels were higher). These changes are somewhat matched by the functional classification, for waders at least.

Even though there is no community-wide or genus-wide compensation using the year (differentiating the seasons) as the baseline temporal unit, there could be compensation at finer temporal scales, e.g. a month or two, or larger, over several years. The wavelet plot (3), that allows to consider a time-varying strength of synchrony vs. compensation, suggests that there is synchrony even at a fine temporal scale throughout most of the time series. However, post-2006, there seems to be a possibility for overcompensation on a scale around 5 years or around 3-4 months.

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, across contrasted guilds, community composition 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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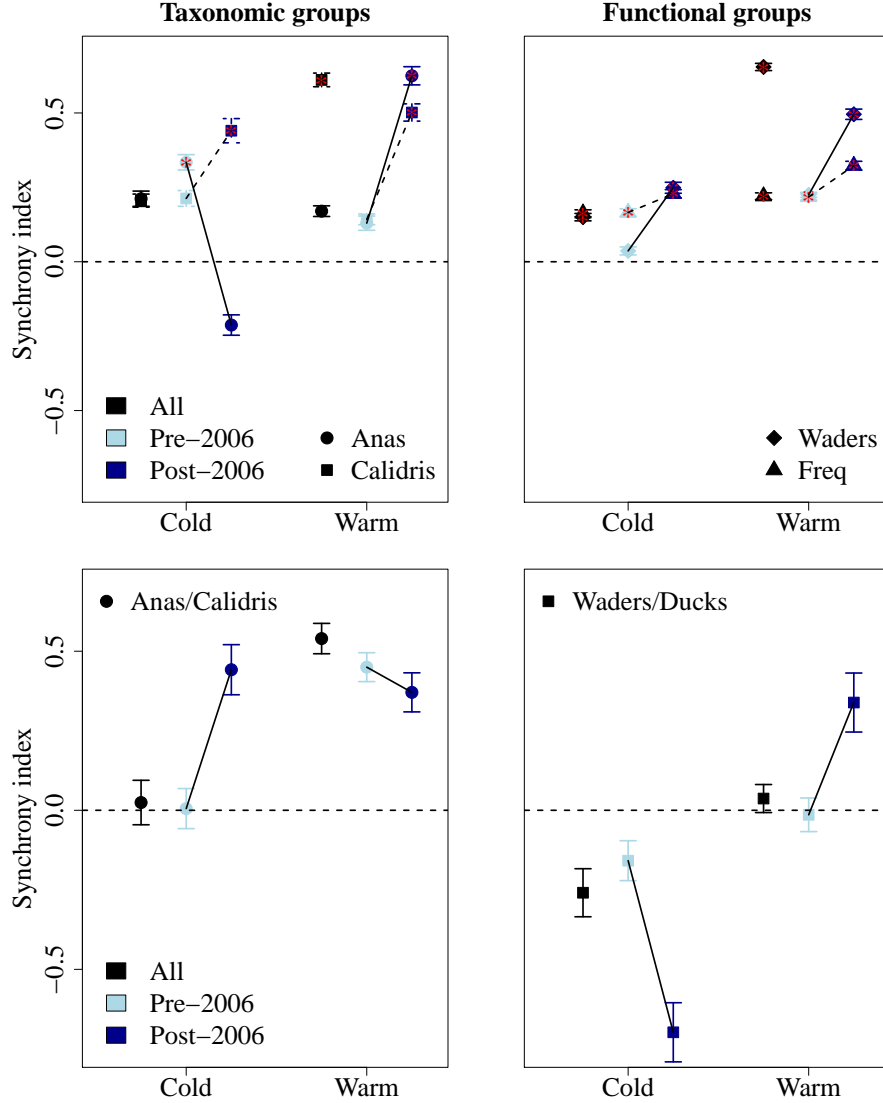
Figure 2: Gross' synchrony index as a function of the season (cold and warm seasons,), calculated among (top) and between (bottom) different functional groups (all frequent birds, waders, right) or taxonomic groups (Anas, Calidris, leftf) groups. Indices were computed on the whole dataset (black) or 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.
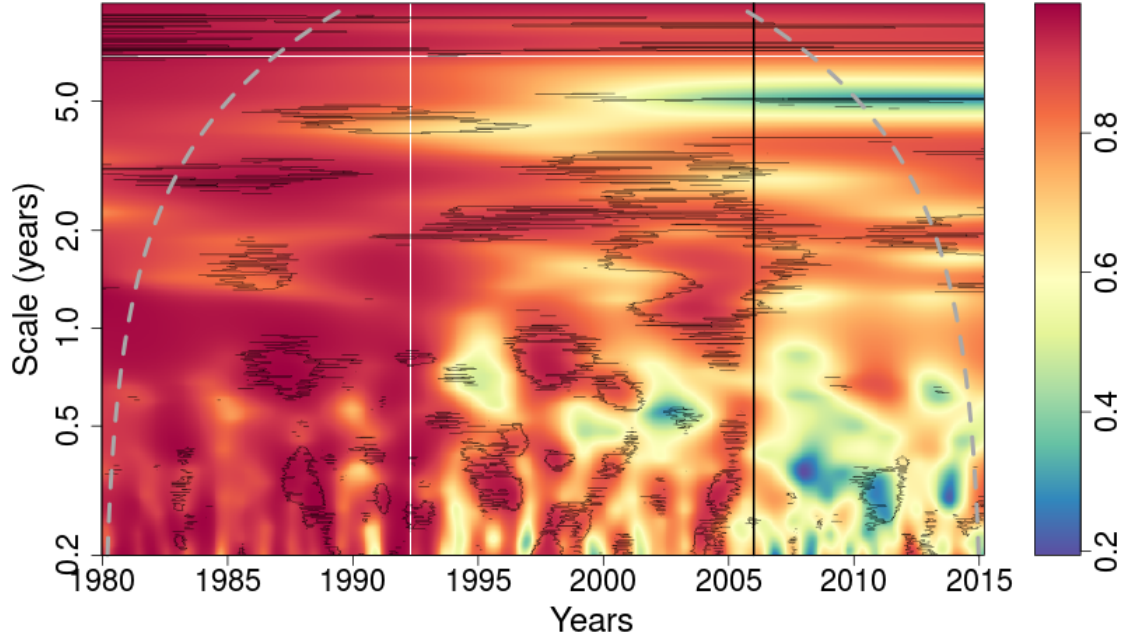
Figure 3: Wavelet modulus ratio for the wader community, scaling from 0 (compensation) to 1 (synchrony). Dashed black lines delineate regions significantly different from the null model with a false discovery rate controlled at the 5% level.
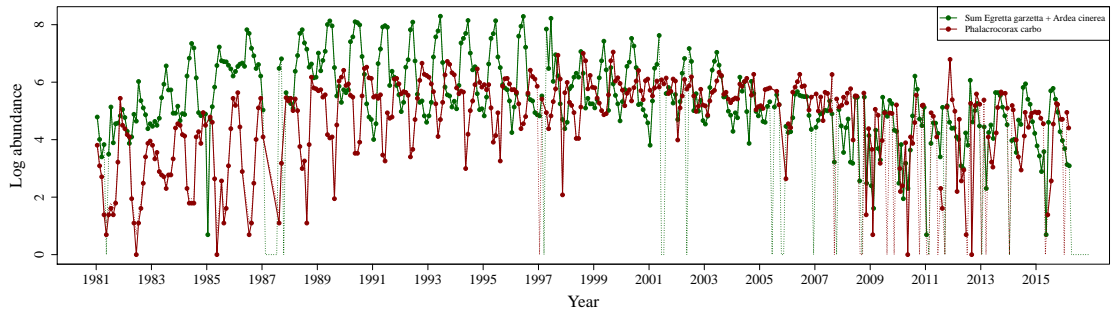

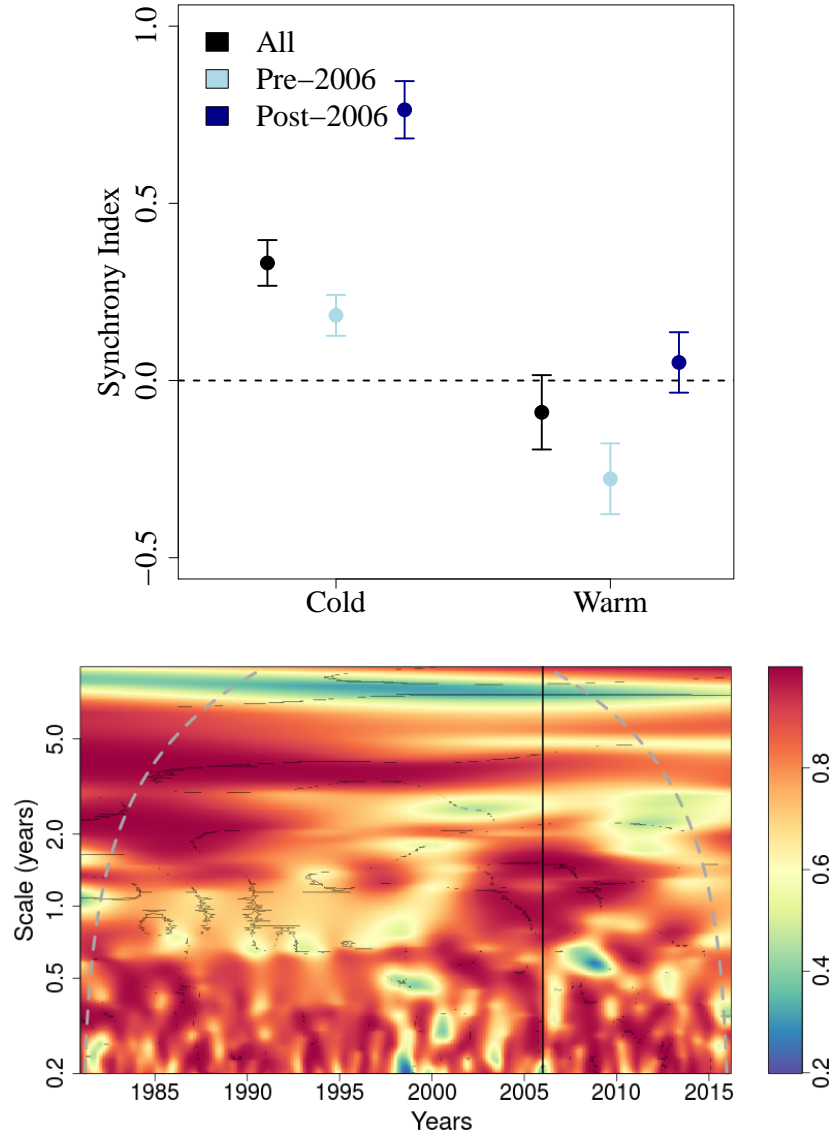Figure 4: Time series of Cormoran, Heron and Egret

Figure 5: Time (top) and frequency (bottom) -based synchrony analysis of the group formed by Cormorant, Egret and Heron

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