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 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 2, 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 ([3]), 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, [4]).

Despite this effort to look for more meaningful temporal scales, temporal compensation has been surprisingly elusive in the field ([5]). Most datasets used to evaluate temporal compensation vs synchrony involve planktonic organisms (Vasseur & Gaedke, 4) or terrestrial plants (5, 2 ; 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 or functional scales.

Indeed, taxonomic scale should be a main modulator of synchrony/compensation, a factor of variation that has been somewhat neglected 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 compensation between dissimilar guilds [6]. We explore different ways to cluster the community, along either taxonomic or functional classifications.

Our dataset is ideally suited to tackle how synchronous bird communities are at different temporal and taxonomic/functional 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 the 'cold season' as the months between November and February of the following year, and a 'warm season', from May to August. From an ecological viewpoint, we separate wintering birds from summer residents, as these two communities have different requirements and there is a large shift in composition (though winter and summer communities partially overlap due to a number of shared species).

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. [2], which is defined as the mean cross-correlation between each species and the rest of the community (eq. 1).

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

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 [7]), this index is independent from the richness of the community and its overall stability [8, 9]. 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 (that is, for a given cold or warm season each year) using the codyn package in R [9]. 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 periods before and after 2006, given that a management change occurred within the reserve in 2006. We considered both the synchrony inside a given group (e.g., within species of the *Anas* genus) or between groups (e.g., between the summed abundances of all species of genus *Anas* and the sum of all *Calidris* species). In the latter case of between-groups comparisons, we summed species together before seasonal averaging.

We used both taxonomic classifications of the species (between and within genera) and functional classifications of the species (e.g., wader versus ducks) as we suspected that a functional classification may allow to partition better the abiotic requirements of the species.

We also "zoomed in" on a group of species that were known to exhibit potentially compensatory dynamics (through competition for nesting sites): the Great Cormorant *(Phalacrocorax carbo)*, the little Egret (*Egretta garzetta*) and the Grey Heron (*Ardea cinerea*).
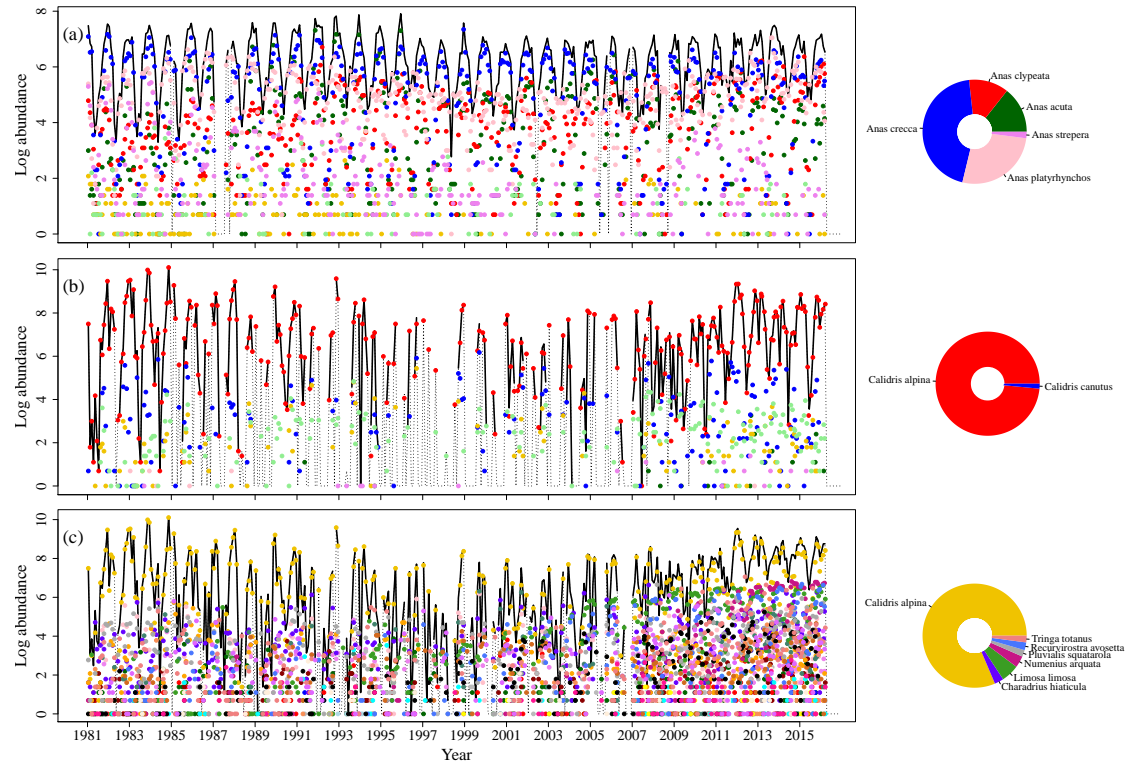
Figure 1: Time series of counts for ducks of the genus *Anas* (a), calidrids (b, *Calidris* genus), and all waders (c, including calidrids). The solid black lines represent trends in summed abundances for each guild, thin dotted lines represent putative trends (when some species are absent). The coloured symbols below the curves represent each species abundances, with species composition on the right side on the donut plots for the most abundant species (over 1% of the community we consider).

We computed statisticial significance of synchrony index values using Monte Carlo randomizations [10]. 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 [11]. 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 of η to the values obtained with the randomized time-series. Independence of species was rejected at the 5% threshold. .

In addition to the time-domain analyses above, we performed frequency-domain analyses, in particular for analyzing synchrony within the rich wader community, as well as the group formed by the Great cormorant, grey heron and little egret. Based on the work by Keitt [12], 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, $\Lambda_{t,s}(\textbf{.}) = \int_{-\infty}^{+\infty} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2}(\textbf{.})d\tau$ and $|\,\textbf{.}\,|$ 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 at the seasonal scale are always positive whenever significantly different from the null (no temporal correlation between species), i.e. there is no compensation within a genus (Fig. 2). This matches the patterns obtained within the entire wetland bird community (Appendix X).

For the cold season, Calidris and Anas exhibit opposite trends in synchrony in response to the managment change in 2006, but these are not statistically significant. However, for the warm season, the management change, which consisted in lowering the water levels, creates more synchronous communities of species within the *Anas* and *Calidris* genera.

This increase in synchrony after 2006 is matched by the functional group classification. Using the functional group classification, we see that pre-2006, there was some compensation within the waders, though not very pronounced.

Even though there is no widespread community-wide or genus-wide compensation at the yearly timescale (differentiating the seasons) , there could be compensation at finer temporal scales, e.g. a month or two, or broader scales, over several years. The wavelet plot (3), that allows to consider a time-varying and scale-dependent strength of synchrony, 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.

There are therefore relatively contrasted results regarding the effect of the management change on synchrony within the wader community. At the yearly (season) timescale, it seems to increase the synchrony (though the Gross index and wavelets provide slightly different answers). At shorter timescales though, it seems to decrease it.

More clear-cut can be found when we examine the synchrony vs. compensation between functional groups (Fig. 2d). Since we consider only two functional groups, the Gross index is a simple correlation. Waders and ducks are negatively correlated during the cold season and positively correlated during the warm season. The patterns are not clear using taxonomic classification (Fig. 2c).

Fig. 5 demonstrates that synchrony between Cormorants and Egret+Heron is the rule, but over long temporal scales [~6 years) there seems to be some compensation, traducing a progressive change within the community. There might be some compensation over very short timescale as well (within
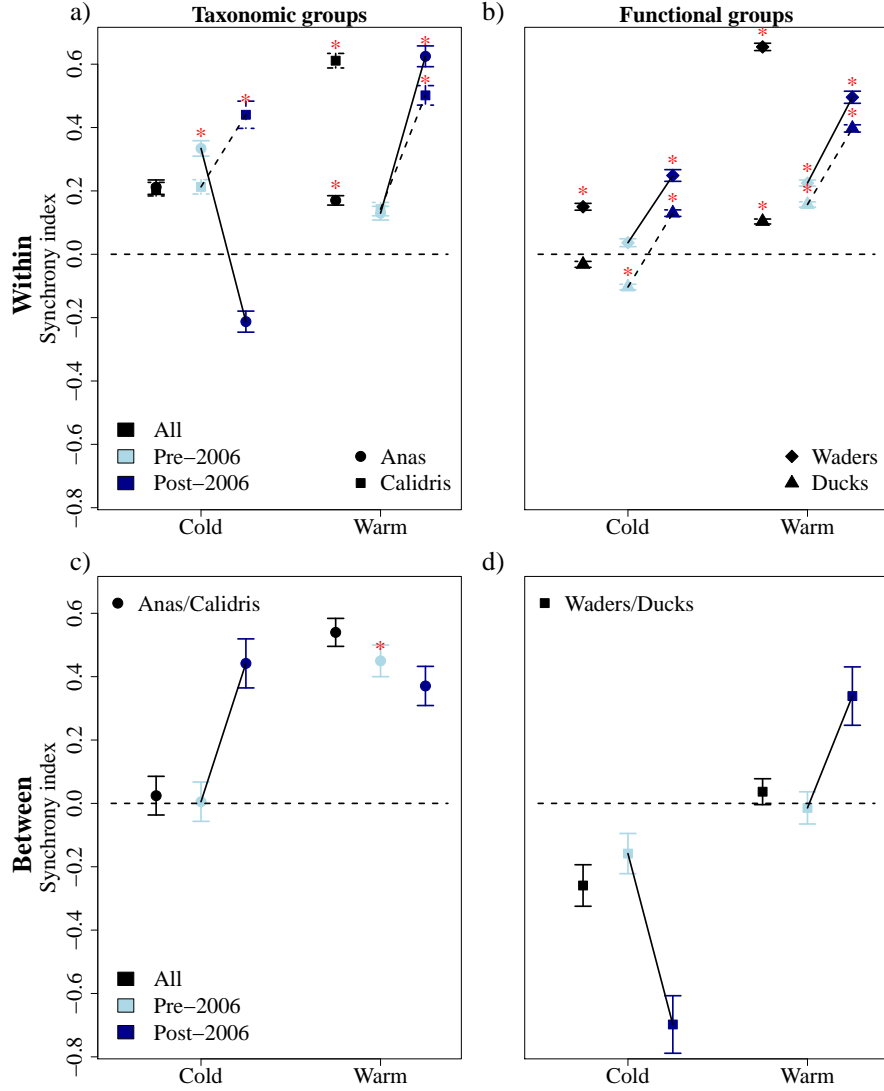
Figure 2: Gross' synchrony index as a function of the season (cold and warm seasons,), calculated among (top) and between (bottom) different functional groups (ducks, waders, right) or taxonomic groups (Anas, Calidris, leftf) groups. Indices were computed on the whole dataset (black) or with the same 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.
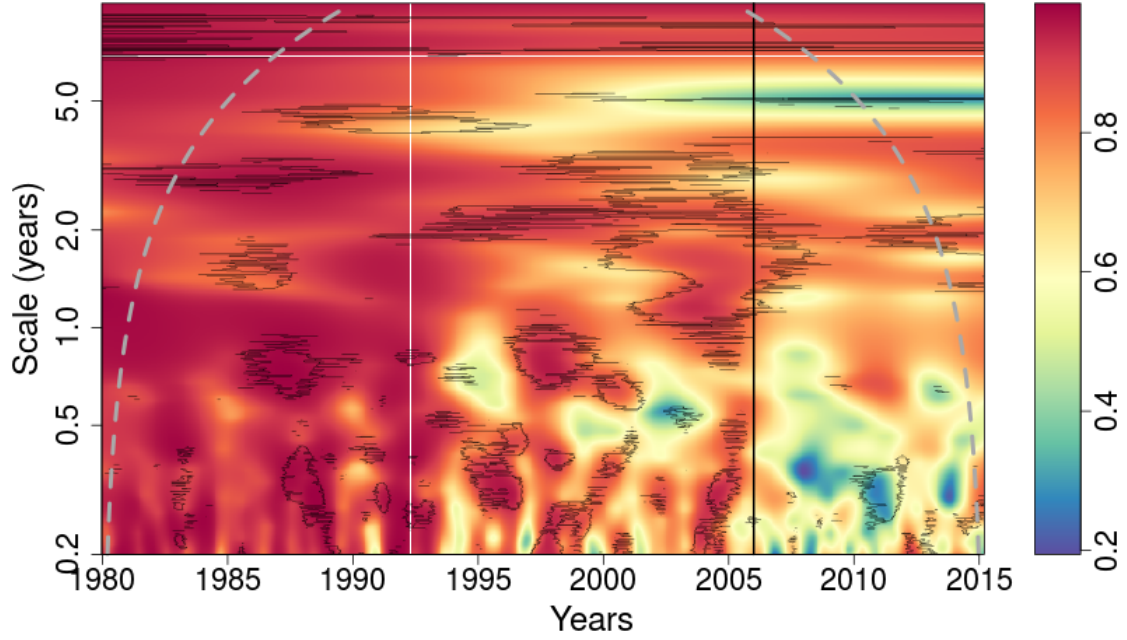
Figure 3: Wavelet modulus ratio for the wader community, scaling from 0 (compensation) to 1 (synchrony). Dashed black lines delineate regions significantly different from the null model with a false discovery rate controlled at the 5% level.
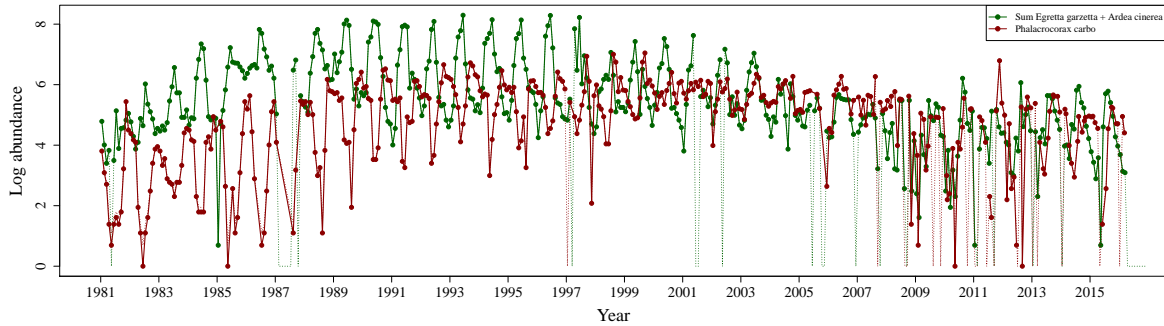

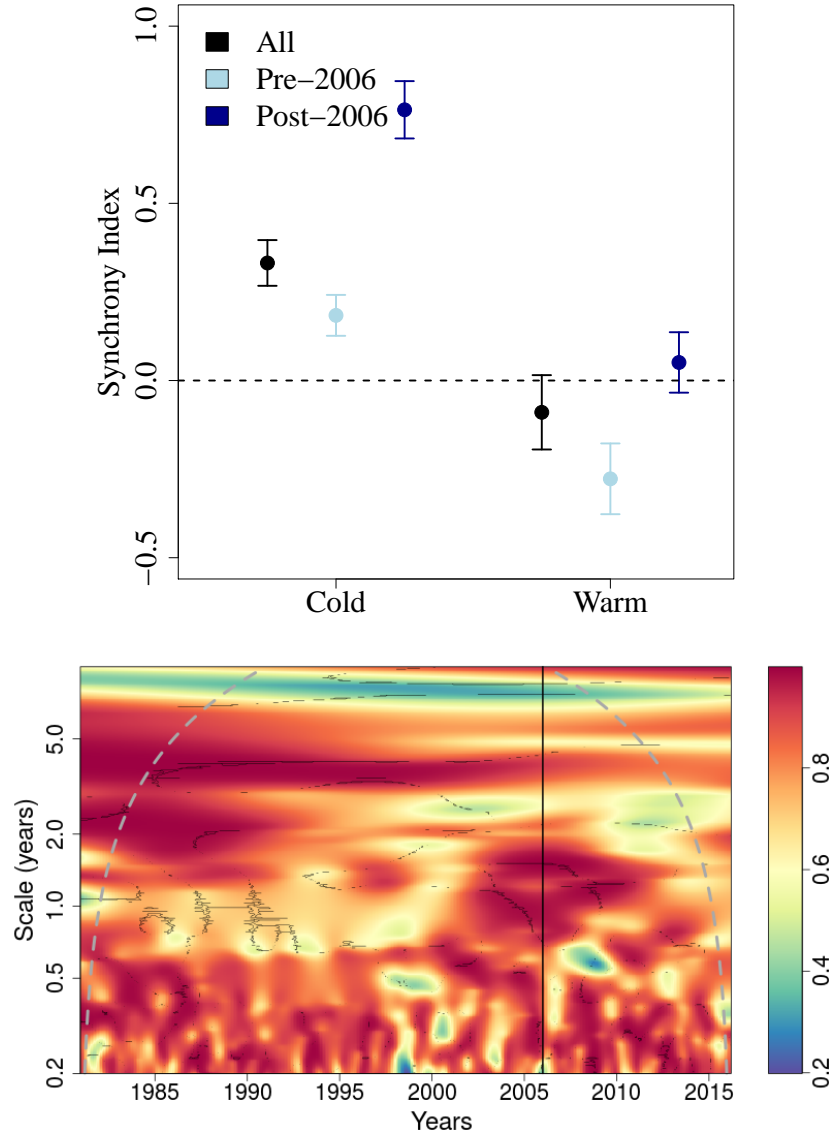Figure 4: Time series of Great Cormoran, Grey Heron and Little Egret

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

the season), but this is less clear and the biological mechanisms for this are unclear since these species compete through nesting (which usually occurs throughout the season).

4   Discussion

Compensation was very rare at the yearly timescale (differentiating between the cold and warm season). At short timescales (below the season) among taxonomically or functionally close species, some compensation could be found but only at certain periods. In other words, there was no widespread functional compensation within genera or guilds at the annual scale or below .

Yet, across contrasted guilds, community composition can change in frequency in the long run. We used correlation between the summed abundances of closely related species (species within Anas genus vs. species within the Calidris genus) or the summed abundances of functionally similar species (waders vs. ducks). The functional group classification was more relevant in this respect. We expected to see compensation at that "functional scale" irrespective of the season, but here waders and ducks correlate negatively only during the cold (wintering) season. This may be because the summer seems a broad inflow of birds including non-breeding individuals. It may be better to say that we detected "compensation" rather than "compensatory dynamics" between those species [1] as these changes (more waders, less ducks) might be due to an increase inflow of birds preferring low water levels and outflow of birds preferring high water levels, under an overall space constraint. In other words, the shift in community dynamics is likely not due to birth and deaths. However, we did not restrict compensation to near constant total biomass [1], but instead we considered negative covariation between system components (species or groups of species).

Comparing the Great Cormorant with Heron and Egrets, we find that compensation mostly occurs above the annual temporal scale, and predominantly in summer as well as before 2006. This occurs because a long-term shift due to competition for resting sites in the summer season, which mostly occurred before 2006.

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). This goes against calls to search for compensation at very short timescales 1: we suspect that because many species share common abiotic drivers at that scale 7, compensation is bound to very rare.

In many ways, searching for compensation using biodiversity time series data is searching for needles in a haystack: only some specific temporal and functional/taxonomic scales allow to see compensation whilst numerous confounding factors make the community co-vary positively at all other scales. Although the knowledge of specific biological mechanisms increasing the densities of some species at the expense of others can help (here, a change in management favouring waders over ducks, competition for nests between cormorants and herons), synchrony will likely dominate community-level time series data. This is true even in cases of known competition or shifts in community composition due to abiotic changes as in this study.

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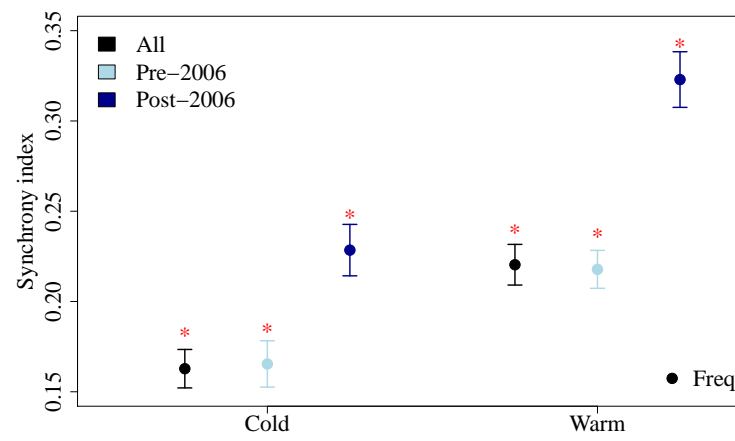
Figure 6: Gross synchrony index for frequent birds, not including waders