

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

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Abstract

Compensatory dynamics, during which community composition shifts despite a total community size that stays near constancy, are usually rare and synchronous dynamics prevail in natural communities. This is a puzzle for ecologists because of the key role of this phenomenon to explain the relation between biodiversity and ecosystem functioning. Early studies suggested that this rarity may be due to the use of temporal scales at which a key abiotic driver such as temperature can synchronize the whole community. New ideas and techniques have then been put forward to look at compensation vs synchrony at varied temporal scales, which we apply here. We take advantage of a long-term wetland bird biodiversity time series of 35 years in a natural reserve, where we suspected that compensation might be possible due to changes in water levels and known trends in some species. We find that compensatory dynamics are still rare, likely due to the synchronizing influence of climate on birds, even after considering several temporal scales of covariation (during cold or warm seasons, above or below the season). Negative covariation in abundance at the community level did appear, however, but only after a management change in the reserve, and at the scale of a few months or several years. Although a lot of attention has been focused on temporal scale, we remark the potential for compensation to vary with taxonomic and functional scale too: we find that compensation appears more frequently between guilds rather than within guilds, and it does so at long temporal scales (several years). This suggests that, in contrast to suggestions to search for very fine grained compensation within communities, perhaps compensation has more potential to emerge between classes, families or broad functional groups.

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]. Compensation occurs when individuals of some species replace individuals of another species, either because of explicit competitive processes or shifts in some environmental driver that change selection pressures. 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 (i.e., 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]. Compensation is therefore intertwined with community-level stability, at least when stability is understood as the reciprocal of variability. By contrast, another very frequent outcome on biodiversity time series is synchrony [3, 4]. Synchrony occurs when all species fluctuate in phase, and therefore the biomass of the community may not fluctuate less than its constituent parts.

Early investigations of the frequency 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 [5, 1]. Unfortunately, this metric is not appropriate for communities subjected to community-wide environmental forcing [6], because one main environmental driver (e.g., temperature or light) may synchronize species abundances or growth rates at some scale, and yet the species could have strongly competitive dynamics. 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, [7]).

Despite this effort to look for more meaningful temporal scales, temporal compensation has been surprisingly elusive in the field ([5, 7], ; but see [8, 9]). Most datasets used to evaluate temporal compensation vs synchrony involve planktonic organisms ([10, 7]) or terrestrial plants ([5, 2] ; though see [11]). Here, we take advantage of a long-term bird time series record at the monthly scale (for 35 years¹), 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 varia-

¹Considering only the years used in our analysis. Otherwise, the dataset begins in 1973.

tion that has been somewhat neglected for now. On the one hand, one could argue that compensation should be higher between closely related 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, *sensu* [1]), and priority effects could dominate. On the other hand, it could be argued as well that the two similar duck species will precisely respond in similar ways to environmental variables, and only exhibit competition at some specific times or places. Under the latter scenario, more dissimilar species or groups - within the same trophic level nonetheless - could exhibit compensation exactly because they have different environmental preferences and the environment varies over time (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 - compensation between guilds - has been less well explored, even though there is some empirical evidence for compensation between dissimilar guilds [12]. We therefore 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 scales 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 Au-

gust. From an ecological viewpoint, this seasonal classification separates wintering birds from summer residents. This makes sense biologically because the two communities have different requirements and respond differentially to abiotic drivers. This also makes sense from a more statistical perspective, as there is a shift in composition between the seasons, 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, showing the marked signature of seasonality.

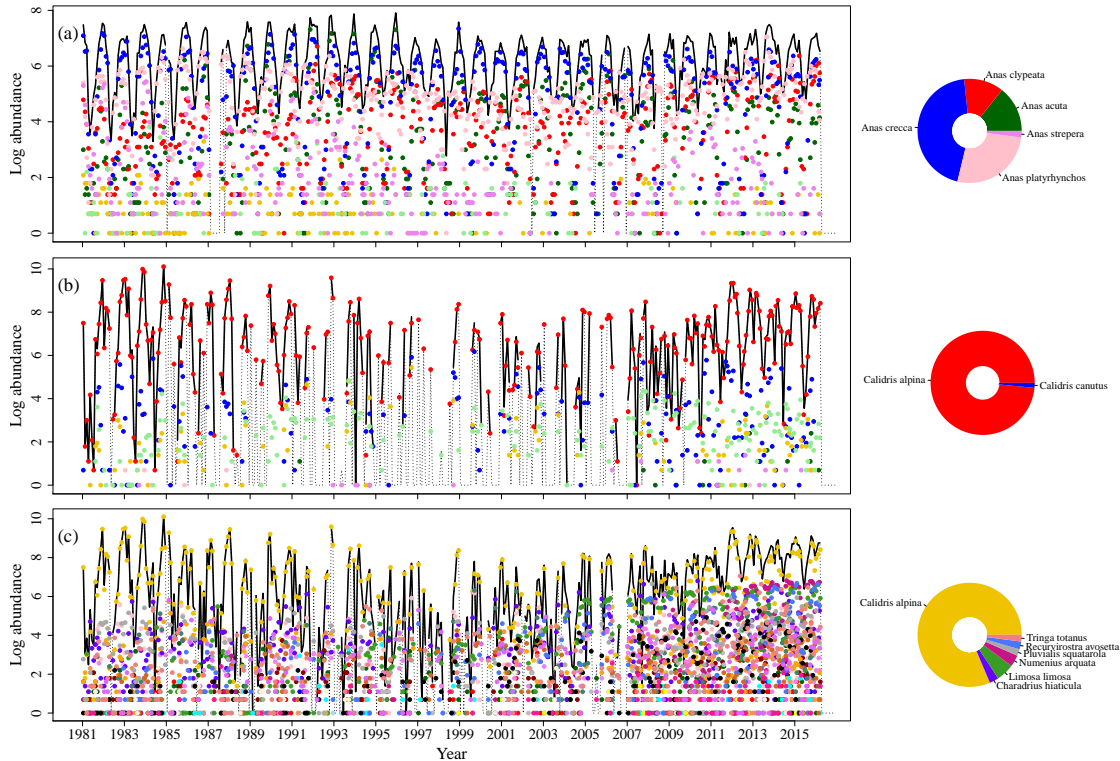


Figure 1: Time series of counts for ducks of the genus *Anas* (a), calidrids (b, *Calidris* genus), and all waders (c, including calidrids). The solid black lines represent trends in summed abundances for each guild, thin dotted lines represent putative trends (when some species are absent). The coloured 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).

2.2 Statistical Analyses

We used for yearly analyses 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).

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

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 [13]), this index is independent from the richness of the community and its overall stability [14, 15]. 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 year \times season scale (that is, for a given cold or warm season each year) using the *codyn* package in R [15]. 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., among species of the *Anas* genus) or between groups (e.g., between the summed abundances of the 9 species of genus *Anas* and the sum of the 12 *Calidris* species). In the latter case of between-groups comparisons, we summed species together before seasonal averaging, to consider seasonal averages of the group density.

We used both taxonomic classifications of the species (between and within genera) and functional classifications of the species (e.g., 30 species of waders versus 34 species of 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*). The little egret and the grey heron abundances were summed because of their similar requirements (i.e., they form a small functional group).

We computed statistical significance of synchrony index values using Monte Carlo randomizations [16]. For each set of time series (each combination year \times 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 [17]. 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 Bonferroni-corrected 10% threshold.

In addition to the time-domain analyses above, we performed frequency-domain analyses, in par-

119 ticular for analyzing synchrony within the rich wader community, as well as the group formed by the
 120 great cormorant, grey heron and little egret. Based on the work by Keitt [18], we used the wavelet
 121 transform of the time series to measure the coherency between time series

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

122 where $w_k(\tau, s)$ is the continuous Morlet wavelet transform of species k at time τ for scale s , $\Lambda_{t,s}(\cdot) =$
 123 $\int_{-\infty}^{+\infty} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2}(\cdot)d\tau$ and $|\cdot|$ is the modulus of the complex number. The numerator corresponds to
 124 the total biomass variation while the denominator corresponds to the variations of each species. This
 125 index is close to 0 when species compensate and reaches 1 when they are synchronous. As before,
 126 the significance of each value was tested at the 5%, Bonferroni-corrected, threshold by 100 phase-
 127 randomizations of each species time series, and computation of the corresponding ρ values.

128 3 Results

129 Using a taxonomic classification of the community (focusing on the genera *Calidris* and *Anas*), we can
 130 see that within-genus synchrony indices at the seasonal scale are always positive whenever significantly
 131 different from the null (no temporal correlation between species), i.e. there is no compensation within
 132 a genus (Fig. 2). This matches the patterns obtained within the entire wetland bird community (Fig
 133 A1 in ESM1[F: **Actually now we have a problem as with the reintroductions of the waders**
 134 **as the graph shows some slight compensation that does not seem to match Fig. 2 - we**
 135 **need to solve this...]).**

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

140 This increase in synchrony after 2006 is matched by the functional group classification. Using the
 141 functional group classification, we see that pre-2006, there was some compensation within the waders
 142 [F: this shows a little here, and perhaps more in Fig. A1], though not very pronounced, which later
 143 disappeared.

144 Even though there is no widespread community-wide or genus-wide compensation at the yearly
 145 timescale (differentiating the seasons), there could be compensation at finer temporal scales, e.g. a

146 month or two, or broader scales, over several years. The wavelet plot (Fig. 3), that allows to consider
 147 a time-varying and scale-dependent strength of synchrony, suggests that there is synchrony even at
 148 a fine temporal scale throughout most of the time series. However, post-2006, there seems to be a
 149 possibility for overcompensation on a scale around 5 years or around 3-4 months.

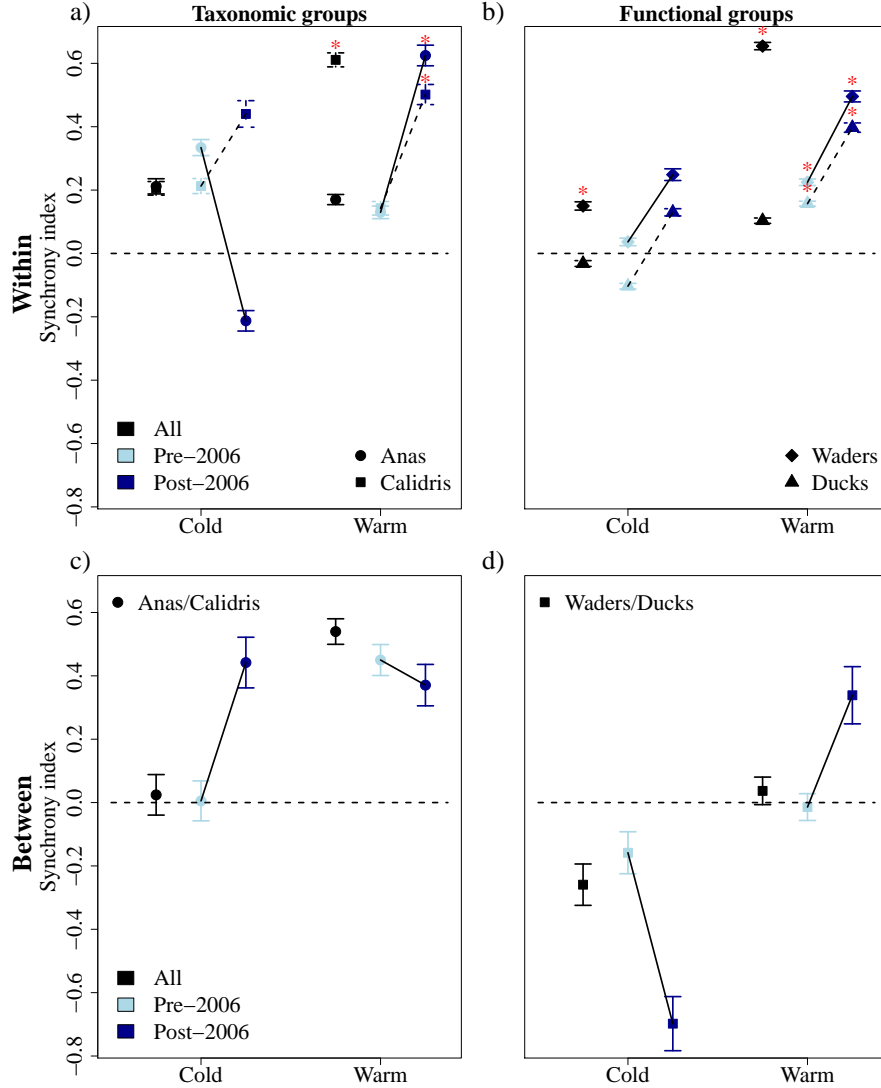


Figure 2: Gross' synchrony index as a function of the season (cold and warm seasons), calculated among (top, a-b) and between (bottom, c-d) groups. The groups considered were different functional groups (ducks vs. waders, right b-d) or taxonomic groups (*Anas* genus, *Calidris* genus, left a-b) groups. The index was computed in each panel on the whole dataset (black) or using two periods: before and after 2006 (light and dark blue), the year of the change in water level management. Red stars correspond to synchrony values significantly different from the null model (independent species), at the 5% threshold.

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 results 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 reduces to a simple correlation². 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).

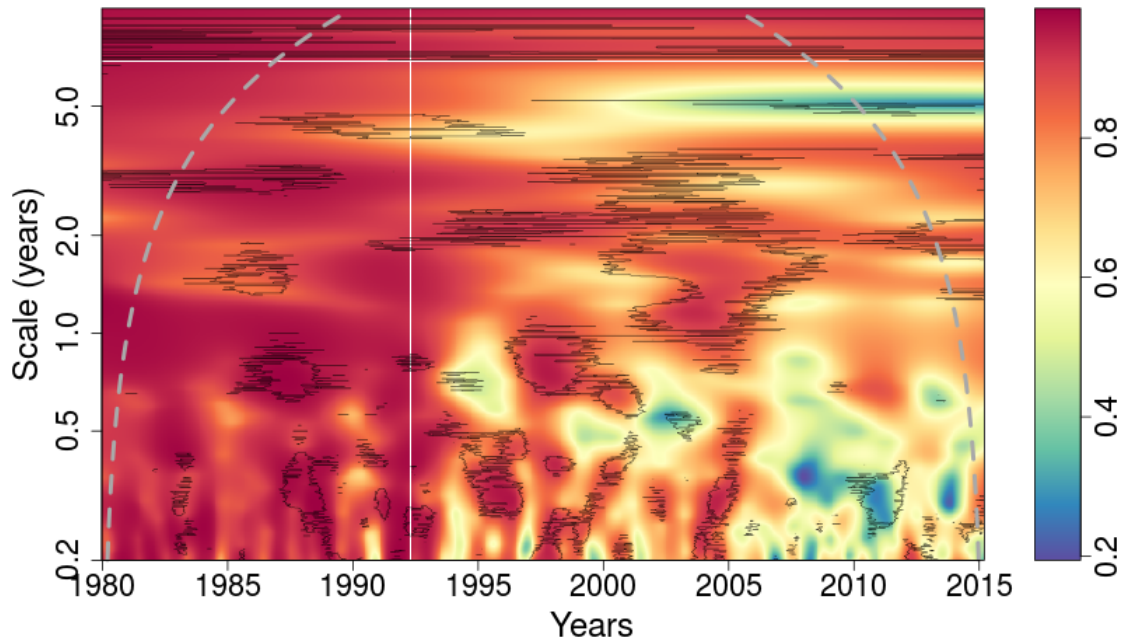


Figure 3: Wavelet modulus ratio for the wader community, scaling from 0 (compensation, blue color) to 1 (synchrony, red color). Dashed black lines delineate regions significantly different from the null model with a false discovery rate controlled at the 5% level.

²It should be noted that with more species, the Gross index has been specifically designed so as to be able to take the value -1 when there is a zero-sum dynamics, i.e., perfect compensation, unlike the classical correlation coefficient.

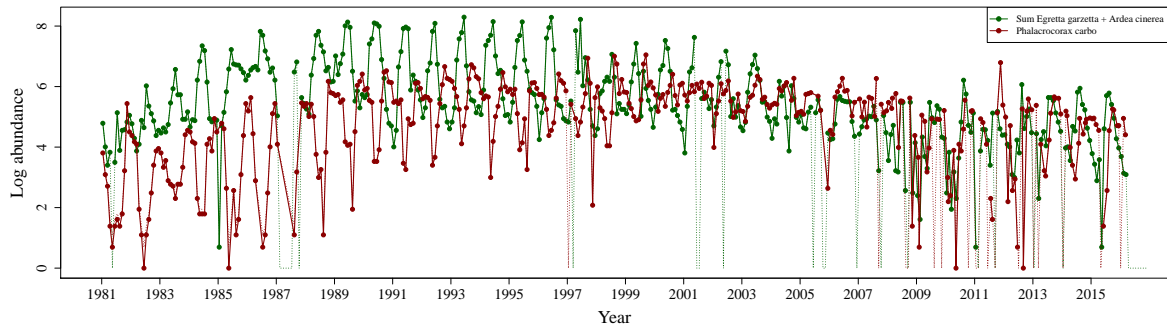


Figure 4: Time series of Great Cormoran abundance, as well as summed abundances of Grey Heron and Little Egret (logarithmic scale).

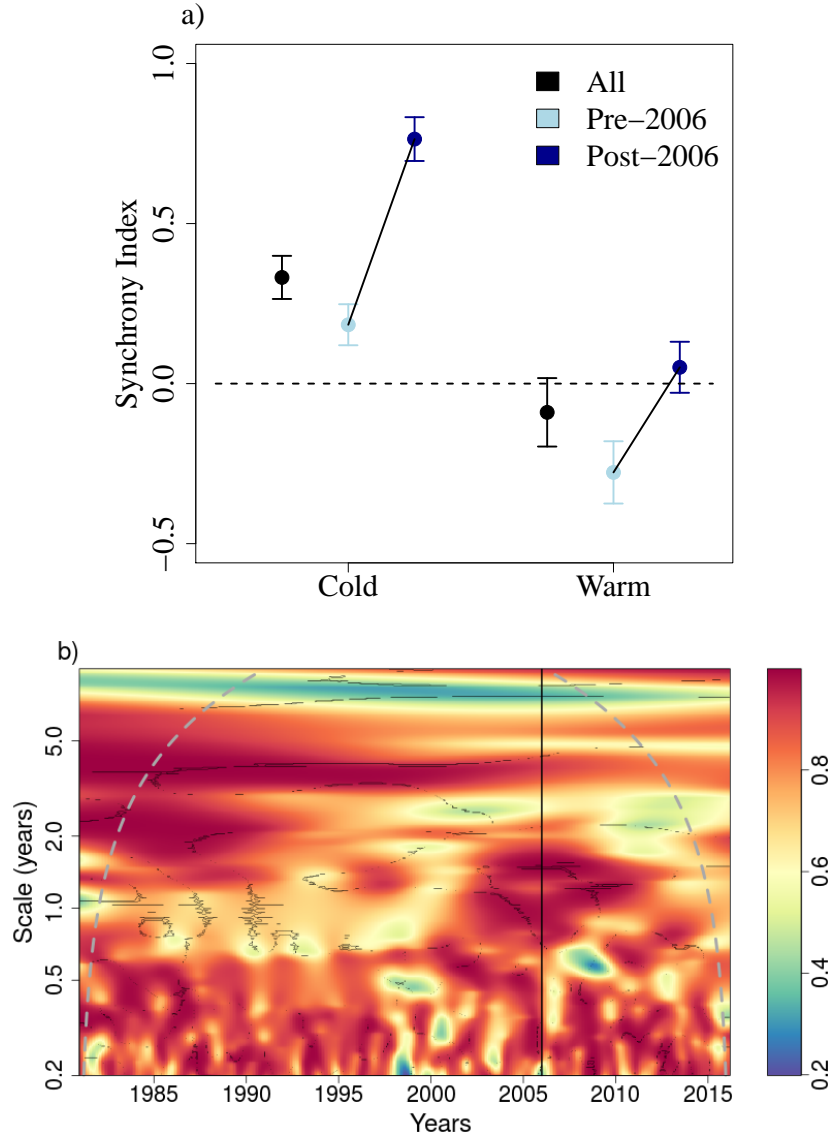


Figure 5: Time-domain (top) and frequency-domain (bottom) synchrony analyses of the group formed by cormorant, egret and heron

While compensation can be expected upon visual inspection of the time series of the two groups formed by cormorant on the one hand, and egret plus heron on the other hand (Fig. 4), we see on Fig. 5 that synchrony is in fact the rule. However, over long temporal scales (~ 6 years) there seems to be some compensation, traducing a progressive change in composition within this small community module, that was already visible on the time series plot (Fig. 4). There might be some compensation over very short timescale as well (within the season), but this is less obvious and the biological mechanisms for this are unclear since these species compete for roost sites (and the choice

165 of the roost site usually last through a season).

166 4 Discussion

167 Compensation was very rare at the yearly timescale (differentiating between the cold and warm sea-
168 son). At short timescales (below the season) among taxonomically or functionally close species, some
169 compensation could be found but only at certain periods. In other words, there was no widespread
170 “functional compensation” (sensu [1]) *within* genera or guilds at the annual scale or below.

171 Yet, summing species abundances and comparing the “biomass sums” of contrasted guilds, com-
172 munity composition did change in frequency in the long run; in other words, there was compensation
173 *between* guilds. We used correlation between the summed abundances of closely related species (species
174 within the *Anas* genus vs. species within the *Calidris* genus) or the summed abundances of functionally
175 similar species (waders vs. ducks) to uncover this. The functional group classification produced more
176 clearly compensation. We expected to see compensation at that “functional scale” irrespective of the
177 season, but here waders and ducks were found to correlate negatively only during the cold (wintering)
178 season. This may be because the summer is characterized by a broad inflow of birds, including non-
179 resident individuals that somehow add random variation to the community dynamics (though other
180 explanations are possible).

181 It may be better to say that we detected “compensation” rather than “compensatory dynamics”
182 between bird species [1] as the observed long-term changes in species composition (more waders, less
183 ducks) might be due to an increased inflow of birds preferring low water levels and outflow of birds
184 preferring high water levels, under an overall space constraint. In other words, the shift in community
185 dynamics is likely not directly due to birth and deaths. However, despite the importance of movements
186 and habitat preference to the local community dynamics, there is certainly also an influence of the
187 regional changes in births and deaths on the local dynamics.

188 Zooming in on the cormorant-heron-egret module, we find that compensation mostly occurs above
189 the annual temporal scale, and predominantly in summer as well as before 2006. This occurs because
190 of a long-term shift due to competition for resting/roosting sites in the summer season, which mostly
191 occurred before 2006.

192 Overall, our results suggest to search for compensation more often *between* rather than *within* func-
193 tional groups, and over relatively long timescales above that of the dominant driver (e.g., seasonality).
194 This goes against calls to search for compensation at very short timescales [10, 1]. Although searching

for compensation at temporal scales below the seasonal abiotic driver (e.g., temperature) was partly motivated by studies on plankton whose community dynamics are much faster, we could have expected compensation to manifest also that scale here (e.g., monthly): movement of birds can certainly occur at that scale. We suspect instead that because many species share common abiotic drivers at short temporal scales [13], compensation is bound to be very rare below the dominant temporal scale of the environment.

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 [7] Although the knowledge of specific biological mechanisms increasing the densities of some species at the expense of others can help, synchrony will likely dominate community-level time series data for closely related species, even in species that compete strongly [6]. This is true even in cases of known mechanisms of competition or shifts in community composition due to abiotic changes as in this study. We suggest that “zooming out” taxonomically (considering summed abundances of dissimilar functional groups) and temporally (temporal scales above the dominant driver) may often be the best strategy to see the compensation that will inevitably manifest if the community-level abundance is maintained within bounds.

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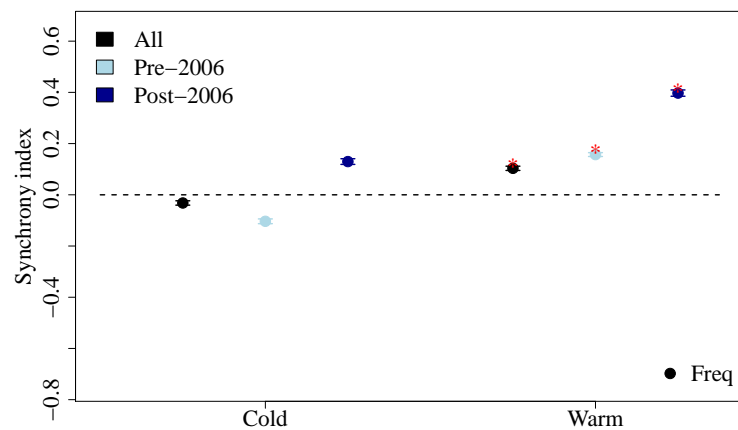


Figure A1: Gross' synchrony index as a function of the season (cold and warm seasons), calculated among the 60 most frequent species in the Teich reserve. The index was computed in each panel on the whole dataset (black) or using two periods: before and after 2006 (light and dark blue), the year of the change in water level management. Red stars correspond to synchrony values significantly different from the null model (independent species), at the 5% threshold.

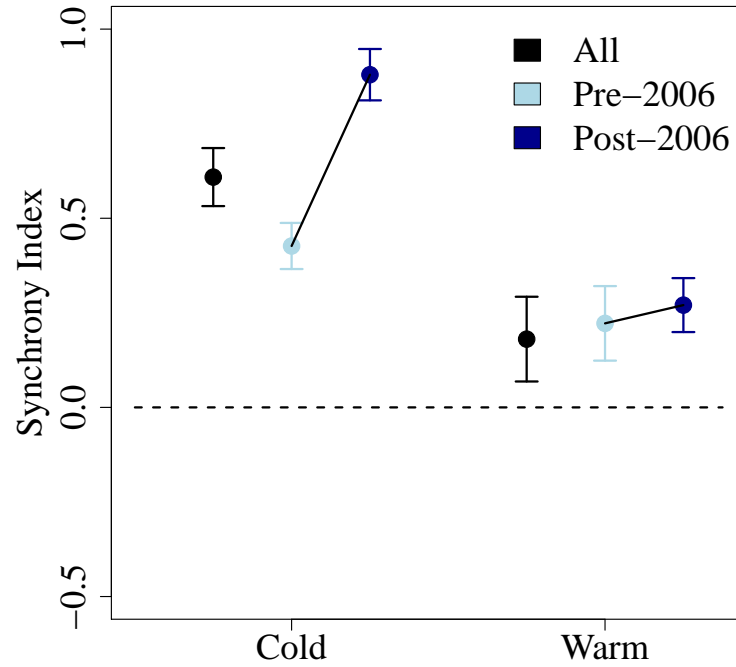


Figure A2: Gross' synchrony index as a function of the season (cold and warm seasons), calculated on log-transformed abundance data for the two groups formed by cormorant and heron+egret. The index was computed in each panel on the whole dataset (black) or using two periods: before and after 2006 (light and dark blue), the year of the change in water level management. No value was deemed significant.

268 We noted on Fig. 4 that cormorants, herons and egrets seemed to compensate each other, at least
 269 for the first period of the time series. This compensation was even more conspicuous on a log scale.
 270 We thus wondered if log-transforming the abundance would affect the values of the synchrony index
 271 observed for this group. It appears that synchrony values are higher with log-transformed abundances.

272

273 **How does the whole community synchrony index vary with the number**
 274 **of species, richness of the community, and effect of the environment?**

275 Starting from the model developped by (author?) [2] (Appendix D), we explored the effect of a
 276 common environmental driver on a community formed by two groups reacting oppositely to this driver.
 277 Keeping the same number of species per group, we also increased the total size of the community to
 278 examine the evolution of η with the overall richness.

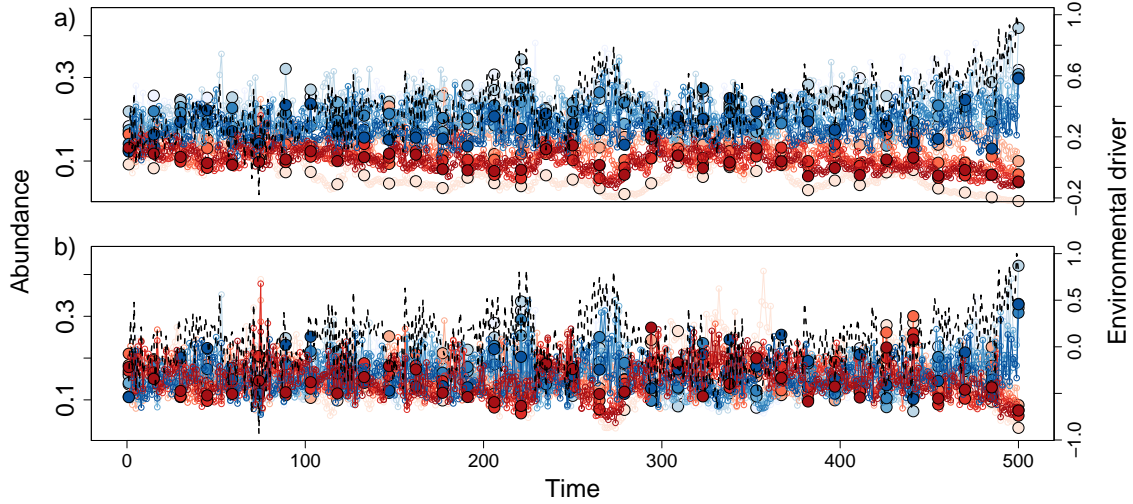


Figure A3: Time series for a community of 10 species, a strong effect of the environment ($b=0.75$, see eq. 3) and a time series of 500 time steps. Open circles represent all points of the time series while filled circles correspond to the sub-sampling of the time series to keep only 35 points. Cold colors indicate species which react positively to the environmental signal and warm colors indicate species which have a negative reaction to the same signal. The environmental signal is shown in black, dashed lines, and indexed on the right axis. This signal either follows an increasing trend (a), or just an autocorrelated signal (b).

279 Assuming that the environmental driver $U(t)$ is an autocorrelated signal, the dynamics of the
 280 species follow the equation:

$$x_i(t+1) = x_i(t) \exp \left(r_i \left(1 - \frac{x_i(t) + \sum_{j \neq i}^n \alpha x_j(t)}{K} \right) + b_i U(t) + \epsilon_i(t) \right) \quad (3)$$

281 where the community is formed by $N = 2n$ species, with 2 groups of n species who have exactly
 282 opposite reaction to the environmental driver, that is $\forall i \in [1, n], \exists j \in [1, n], b_j = -b_i = b$. The
 283 growth rate r_i follows a normal distribution with mean 1 and standard deviation 0.25. All interaction
 284 coefficients α are set to 0.5 and $K = \frac{1+\alpha(N-1)}{N}$. The noise $\epsilon_i(t)$ is normally distributed, centered on 0

285 with a standard deviation of 0.1.

286 We compared results for time series of length 35 (the length of our data set), 100 and 500, to
 287 represent realistic time series. For all experiments, dynamics are first run for 500 time steps as a burn-
 288 in. To take into account different experimental design, we either take the first 35 or 100 time steps
 289 of the following 500-time steps series, or subsample this time series to have the right amount of data.
 290 We also considered different community richness (10, 30, 60 and 100 species), and different strength
 291 of the environmental signal ($b=[0.1, 0.5, 0.75]$). For each combination of parameters, we computed 10
 292 repetitions.

293 We considered different type of environmental driver

- 294 • $U_t = u_t$ where u_t is an autocorrelated signal ; and we do not subsample the data

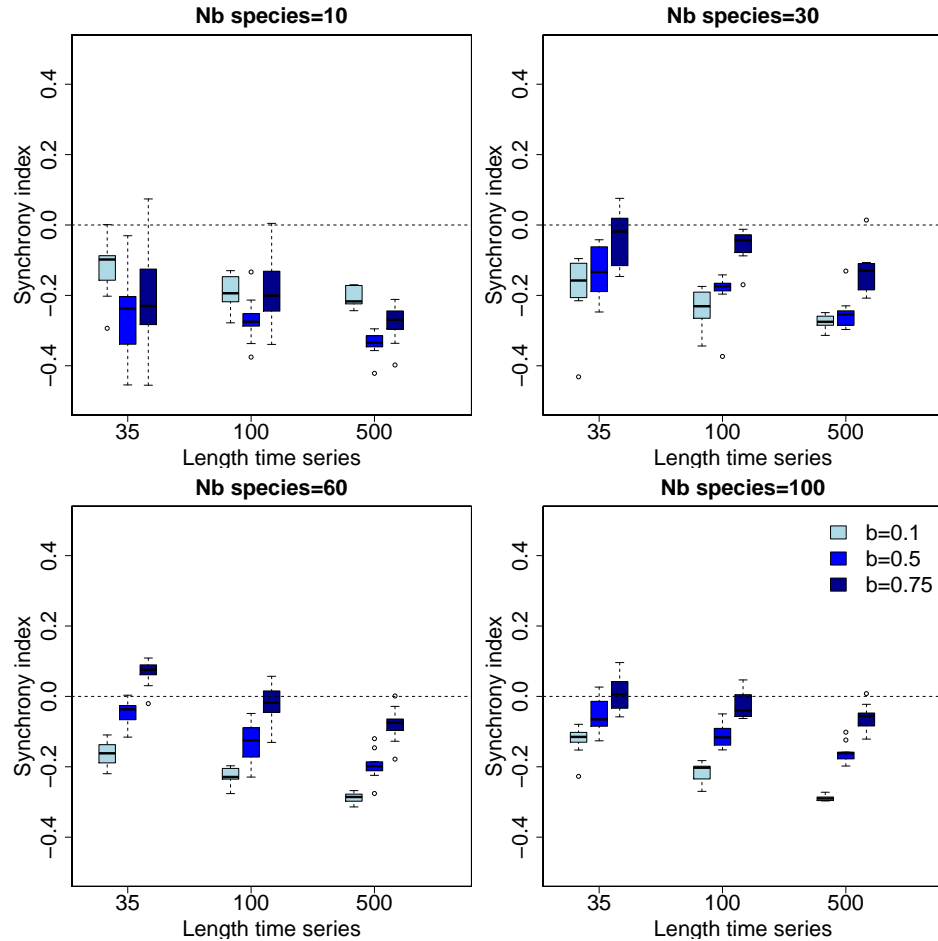


Figure A4: Evolution of Gross' synchrony index for different time series length and number of species in the community, in simulations where there is no trend in the environmental signal and the data is not subsampled, keeping the autocorrelation of the environment in the dynamics of the species.

- $U_t = u_t$ and we subsample the data

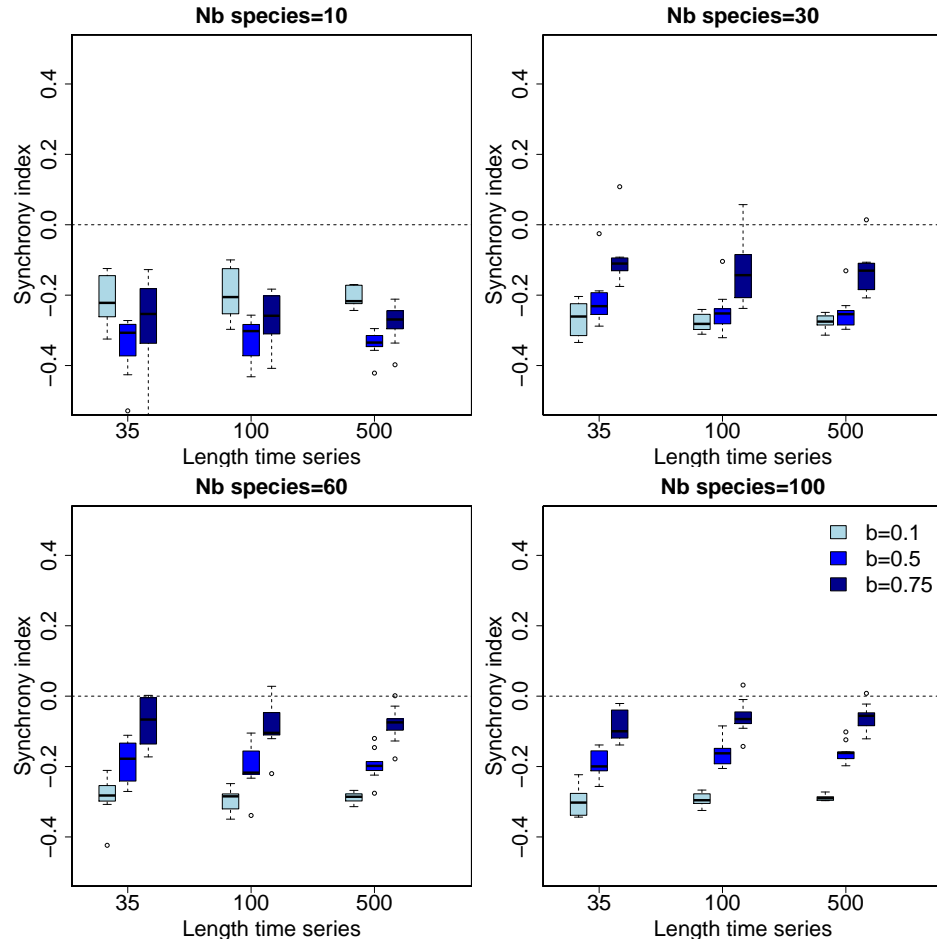


Figure A5: Evolution of Gross' synchrony index for different time series length and number of species in the community, in simulations where there is no trend in the environmental signal and the data is subsampled (for 35 or 100 time steps), removing the autocorrelation of the environment in the dynamics of the species.

- $U_t = u_t + x_t$ where x_t follows an increasing trend ; and we subsample the data

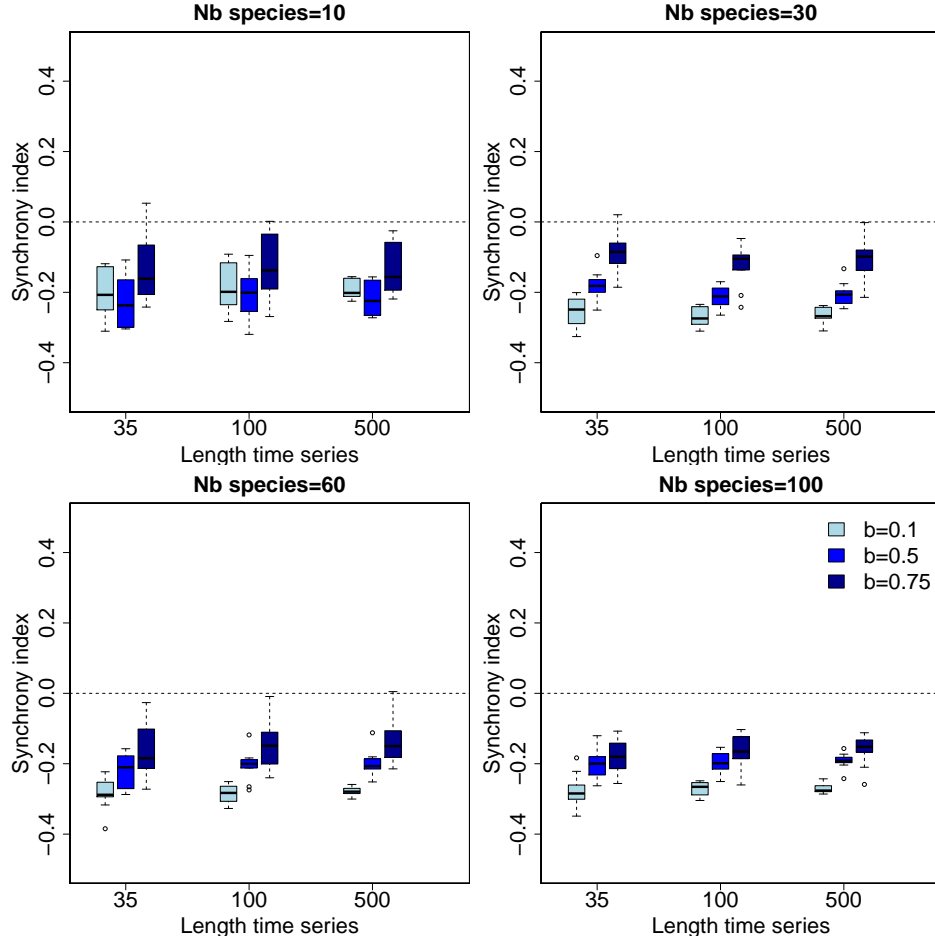


Figure A6: Evolution of Gross' synchrony index for different time series length and number of species in the community, in simulations where there is an increasing trend in the environmental signal and the data is subsampled (for 35 or 100 time steps), removing part of the autocorrelation of the environment in the dynamics of the species

297 We first confirm that unless there is a high autocorrelation in the driver (as in Fig. A4), if we
 298 consider two groups which have opposite reactions to the same driver, the Gross index is not sensitive
 299 to the length of the time series or the number of species in the community. For larger communities
 300 (over 10 species), synchrony is higher when the response to the driver is stronger. For our data, we
 301 can assume that the more the birds are sensitive to the change in management, the less we can expect
 302 compensation in the community due to this change.

303 The negative or low positive values we obtain in our data set may indicate that species share the
 304 same response to the environment.