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 near-constant total community size, are usually rare: synchronous dynamics prevail in natural communities. This is a puzzle for ecologists, because of the key role of compensation 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 community time series of 35 years in a natural reserve, where we suspected that compensation might occur 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 seasonal scale). Negative covariation in abundance at the whole community level did only appear 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 the temporal scale of compensation, we remarked the potential for compensation to vary with taxonomic and functional scale too: compensation appeared here more frequently between guilds rather than within guilds, and it did so at long temporal scales (several years). This suggests that, in contrast to suggestions to search for very fine-grained compensation within communities organised as species list, perhaps compensation has more potential to emerge between classes, families or broad functional groups.

1 Introduction

Ecological theory suggests that within rich communities, 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 other 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 priority effects (i.e., who gets there first). Whatever the cause of compensatory dynamics, its main consequences for ecosystem functioning is 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 observed 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 a main environmental driver (e.g., temperature or light) may synchronize species abundances or growth rates at some scale, creating large variance in community-wide biomass, in spite of 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 fluctuations tend to synchronize species dynamics, [7]).

Despite this effort to look for more meaningful temporal scales in biodiversity time series, temporal compensation has remained surprisingly elusive in the field ([5, 7]; but see [8, 9]). Most datasets used so far 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 (over 35 years[1]), in a natural reserve, that allows us to dig deeper into patterns of synchrony, at several temporal and taxonomic or functional scales.

Indeed, taxonomic scale should be a main modulator of synchrony/compensation, an explanatory factor that has been somewhat neglected for now. On the one hand, one could argue that compensation should be

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

higher between closely related species, because functional and phylogenetic differences are generally corre-
lated. 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 that these two similar duck species will precisely respond in similar ways to environmen-
tal variables, which tends to obfuscate compensation. Under the latter scenario, more dissimilar species or
groups of species - within the same trophic level nonetheless - could compensate each other within the whole
community, precisely 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, compensation between guilds has been less well explored than
within guilds, even though there is actually some empirical evidence for compensation between dissimilar
guilds [12]. We therefore explore different ways to cluster the bird community, within or between guilds,
along either taxonomic or functional classifications.

Our objective is therefore to examine how synchronous or compensatory bird communities are at different
temporal and taxonomic (or functional) scales. Our dataset is ideally suited to the task given that (i) it is a
highly temporally resolved time series with respect to the species typical generation times, but it also extends
well beyond generation time (35 years) 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 real 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), by the staff of the Teich reserve. The reserve comprises
120 ha of wetlands, and the data have been aggregated at the reserve scale. We use for each species the
maximum observed abundance over a month, which provides a "monthly snapshot" of the bird abundance. In
the statistical analyses, we use both the original monthly data and seasonal averages. We defined two seasons
based on observations of bird presence. We defined a 'warm season', from May to August, and a 'cold season'
as the months between November and February of the following year. From an ecological viewpoint, this
seasonal classification separates wintering birds from summer residents (some of whom are breeding). This

makes sense biologically because the two communities have different requirements and respond differentially to abiotic drivers. It is also useful 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.
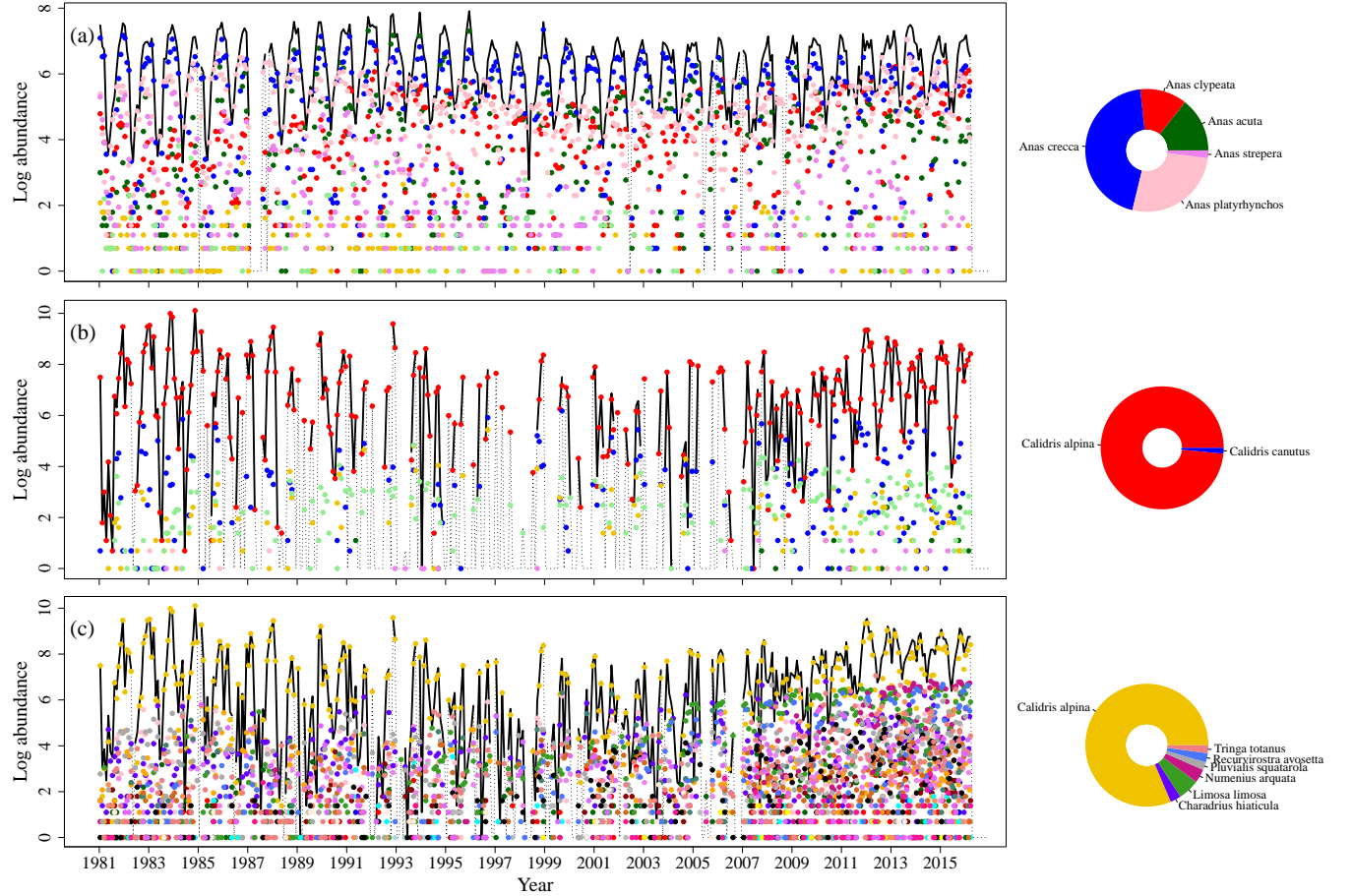

Figure 1: Time series of counts for ducks of the genus *Anas* (a), calidrids (b, *Calidris* genus), and all waders (c, including calidrids). The solid black lines represent trends in summed abundances for each guild, thin dotted lines represent putative trends (when some species are absent). The coloured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

2.2 Statistical Analyses

We used for yearly analyses the synchrony index η defined by Gross et al. [2], which is constructed as the mean cross-correlation between each species biomass and the summed biomasses of the rest of the community

88 (eq. 1).

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

89 where P_i is the abundance or biomass of species i in a community of n species. This synchrony index

90 described in eq. 1 varies between -1 (perfect compensation, total biomass is constant) and 1 (complete

91 synchrony), while 0 represents a case where all populations fluctuate independently. Contrary to previous

92 indices (see, for instance, Loreau and de Mazancourt ϕ [13, 14]), this index is independent from the richness

93 of the community (or more generally the number of system components) and its overall stability [15, 14]. This

94 is important here, as we will perform analyses at different taxonomic scales and therefore with a different n

95 in eq. 1.

96   We computed synchrony indices at the year × season scale (that is, for a given cold or warm season

97 each year) using the codyn package in R [14]. We averaged monthly bird abundances, for each species,

98 over the season duration, and computed the synchrony index using the year as our statistical unit. We also

99 differentiated periods before and after 2006, given that a management change occurred within the reserve

100 in 2006. We considered both the synchrony inside a given group (e.g., among species of the *Anas* genus) or

101 between groups (e.g., between the summed abundances of the 9 species of genus *Anas* and the sum of the

102 12 *Calidris* species). In the latter case of between-groups comparisons, we summed species together before

103 seasonal averaging, to consider seasonal averages of the monthly group density.

104   We used both taxonomic classifications of the species (i.e., between and within genera) and functional

105 classifications of the species (e.g., 30 species of waders versus 34 species of ducks) as we suspected that a

106 functional classification may allow to partition better the abiotic requirements of the species. We use "duck"

107 as a shorthand for the larger functional group of herbivorous divers, because the birds in that category are

108 mostly ducks: this group includes nonetheless all anatids (geese and swans in particular) as well as the

109 common coot *(Fulica atra*, an abundant species here).

110   We also "zoomed in" on a group of species that were known to exhibit potentially compensatory dynamics

111 (through competition for roosting sites): the great cormorant *(Phalacrocorax carbo)*, the little egret (*Egretta*

112 *garzetta*) and the grey heron (*Ardea cinerea*). The little egret and the grey heron abundances were summed

113 because of their similar requirements (i.e., they form a small functional group).

114   We computed statistical significance of synchrony index values using Monte Carlo randomizations [16].

115 For each set of time series (each combination year × season), we kept the auto-correlation of the species

116 time-series, but removed the cross-correlation between species by shifting each time series by a random lag

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[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 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 [18] and follow-up by Vasseur et al. [7], 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 10%, 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 of the community (focusing on the genera *Calidris* and *Anas* as two key examples of contrasted birds), 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 (Fig A1 in ESM1).

For the cold season, *Calidris* and *Anas* exhibit opposite trends in synchrony in response to the management change in 2006. However, for the warm season, the management change, which consisted in lowering the water levels, created more synchronous communities of species within the *Anas* and *Calidris* genera. This increase in synchrony after 2006 is matched by the functional group classification.

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 coarser scales, over several years. The wavelet plot (Fig. 3), that allows to consider a time-varying and scale-

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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.
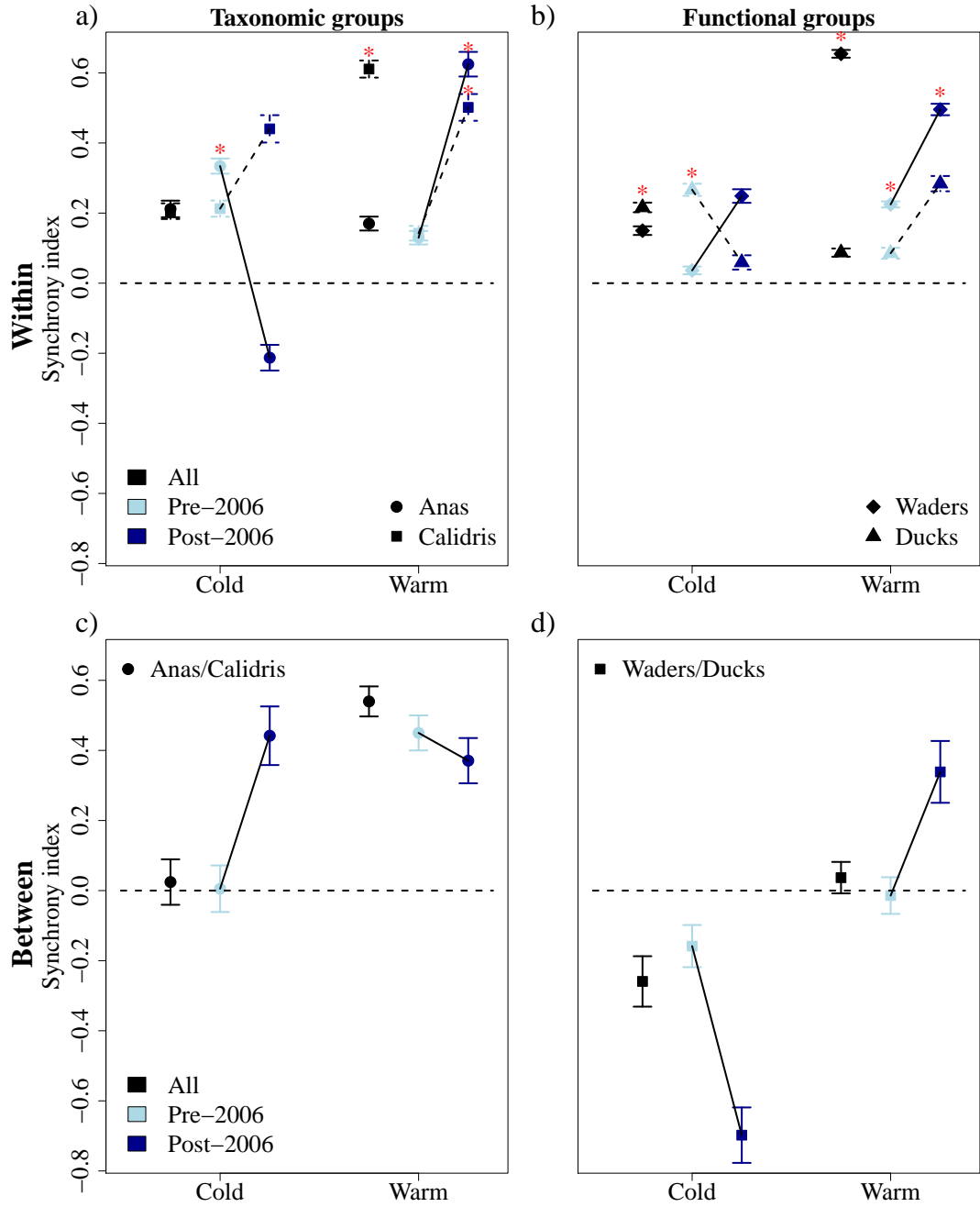
Figure 2: Gross' synchrony index (η) as a function of the season (cold and warm seasons), calculated within (top, a-b) and between (bottom, c-d) groups. The groups considered were different functional groups (ducks vs. waders, right b-d) or taxonomic groups (*Anas* genus, *Calidris* genus, left a-b) 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 10% threshold.

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There are therefore relatively contrasted results regarding the effect of the management change on short-term 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 even 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 correlation[2]. Waders and ducks are negatively correlated during the cold season and positively correlated during the warm season. These patterns are in contrast unclear when using a taxonomic classification (no compensation, Fig. 2c).
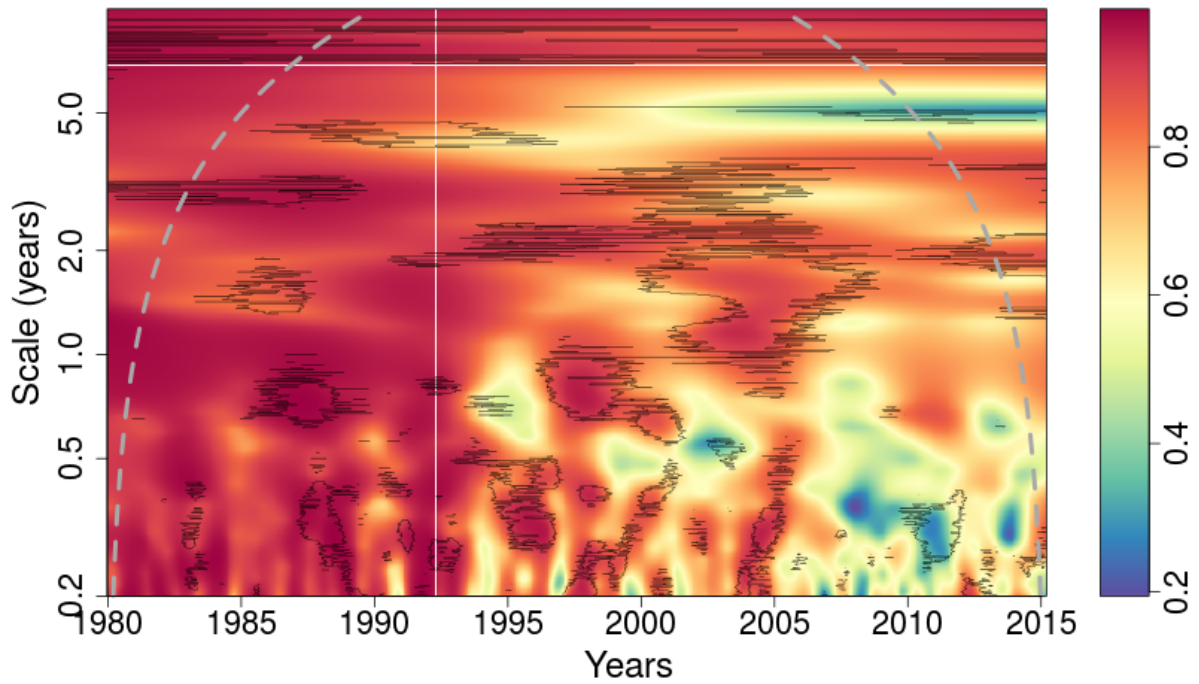

Figure 3: Wavelet modulus ratio for the wader community, scaling from 0 (compensation, blue color) to 1 (synchrony, red color). Dashed black lines delineate regions significantly different from the null model with a false discovery rate controlled at the 10% threshold.

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[2]It should be noted that with more species, the Gross et al. [2] 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.
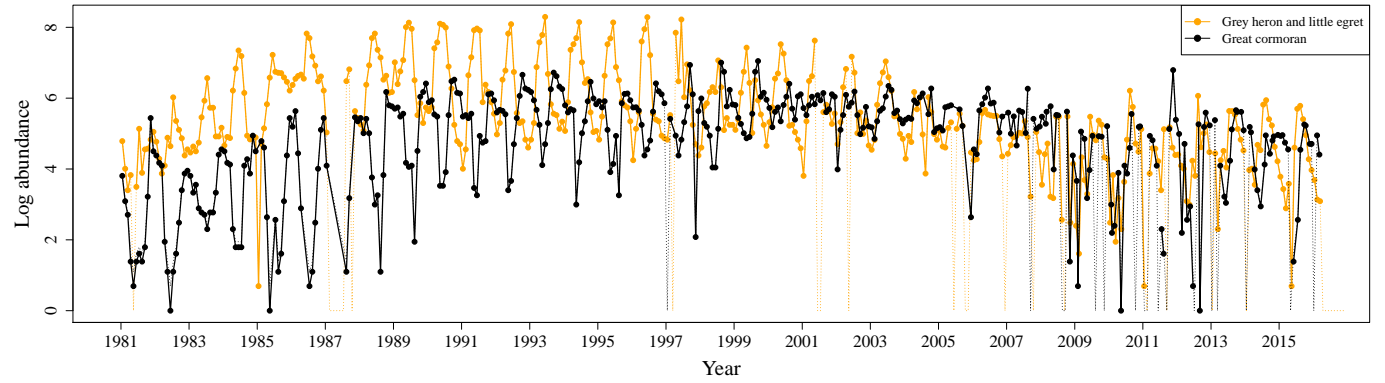
Figure 4: Time series of great cormoran abundance, as well as summed abundances of grey heron and little egret (logarithmic scale).
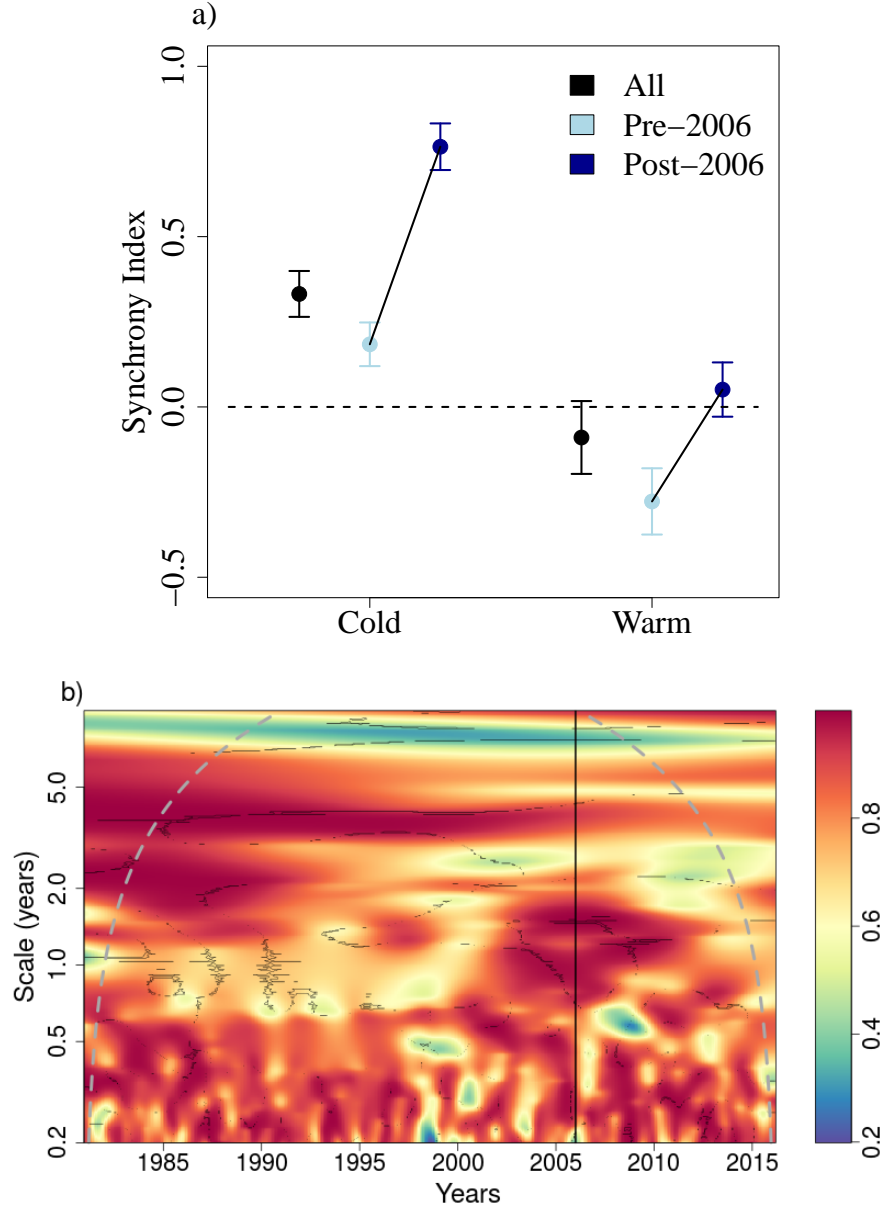
Figure 5: Time-domain (a) and frequency-domain (b) synchrony analyses of the group formed by cormorant, egret and heron

¹⁵⁶ While compensation could be expected upon visual inspection of the time series of the two groups formed
¹⁵⁷ by cormorant on the one hand, and egret plus heron (summed as a small functional group) on the other
¹⁵⁸ hand (Fig. 4), we see on Fig. 5 that synchrony is in fact the rule around the annual scale and below, when
¹⁵⁹ considering the wavelet index. We wondered if the patterns in Fig. 4 were caused by the use of a log scale,
¹⁶⁰ but we found that in fact the correlation was higher rather than lower on the log scale (ESM 2). However,

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over long temporal scales ($\sim$ 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 at very specific times and the biological mechanisms for this are unclear since these species compete for roost sites, a process that it unlikely to manifest at such very short timescales.

4   Discussion

Compensation was overall very rare at the yearly timescale (differentiating between the cold and warm season). At short timescales (below the season), and 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" (sensu [1]) *within* genera or guilds at the annual scale or below.

Yet, summing species abundances within a guild and comparing the "biomass sums" of contrasted guilds, community composition did change in frequency in the long run; in other words, there was compensation *between* guilds. We used correlation between the summed abundances of closely related species (species within the *Anas* genus vs. species within the *Calidris* genus) or the summed abundances of functionally similar species (waders vs. ducks) to uncover this.

Given that we compare the level of synchrony/compensation within guilds (with many species) and between guilds (with only a handful of groups), we checked in ESM 3 whether changing the number of "compartments" (n) in the Gross η index could affect its value: it did not. However, we found that if two groups respond in opposite ways to a shared driver, the stronger the response to the driver, the lesser the compensation indicated by η at the whole community level. This might explain the low levels of compensation that we found at the overall wetland bird community level (ESM 1), in spite of the clear presence of two groups reacting in opposite way to shared driver (here, water levels). Analyses at several taxonomic/functional scales are therefore warranted to be conclusive about compensation.

The functional group classification produced much more clearly compensation between guilds than the taxonomic classification. We expected to see compensation at that "functional scale" irrespective of the season, because the requirements of these birds are different, but here waders and ducks were found to correlate negatively only during the cold (wintering) season. This may be because the summer is characterized by a broad inflow of birds, including non-resident individuals that somehow add random variation to the community dynamics (though other explanations are possible).

It may be better to say that we detected "compensation" rather than "compensatory dynamics" between

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bird species [1] as the observed long-term changes in species composition (more waders, proportionally less ducks; ESM4) might be due to an increased 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 directly due to birth and deaths. However, despite the importance of movements and habitat preference to the local community dynamics, there is certainly also an influence of the regional changes in births and deaths on these local dynamics.

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

Overall, our results suggest to search for compensation more often *between* rather than *within* functional groups, and over relatively long timescales above that of the dominant driver (e.g., above 5 years if the main driver is a seasonal climate). This goes against calls to search for compensation at very short timescales [10, 1] in order to filter out the effect of the main seasonal driver. 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 as well (e.g., monthly). Movement of birds reacting to food availability can certainly occur that fast, and wetlands certainly have a carrying capacity, which could promote short-term compensation. We suspect that instead, because many species share common abiotic drivers at short temporal scales [13], compensation is bound to be quite 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 or functionally (considering summed abondances of dissimilar functional groups) and temporally (considering temporal scales well 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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Acknowledgements

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Supplementary Material

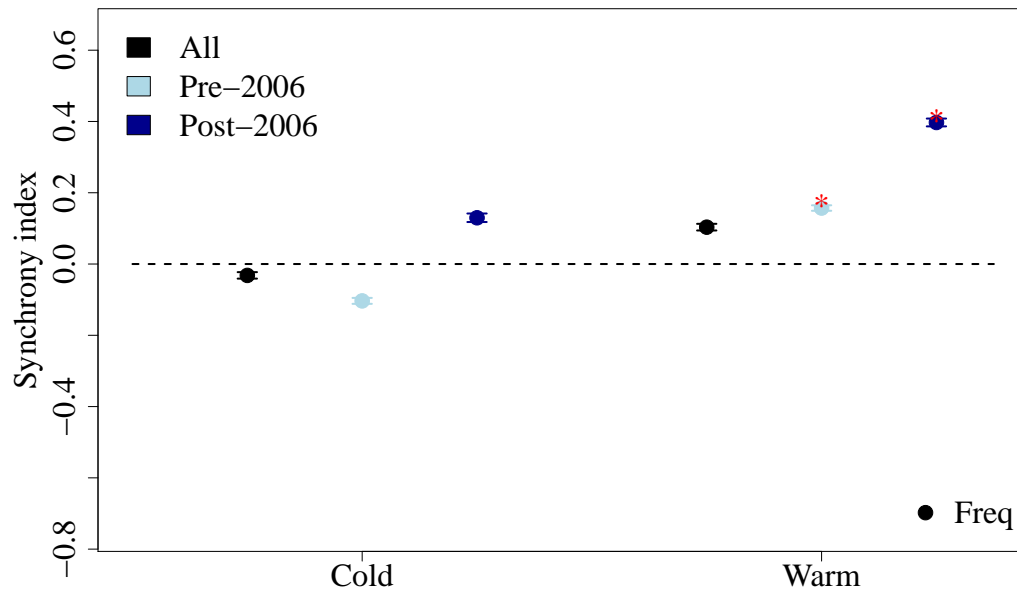## ESM 1 - Gross synchrony index at the whole community level

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 Bonferroni-corrected 10% threshold.

ESM 2 - Correlation in log-scale betwen cormorant and heron+egret
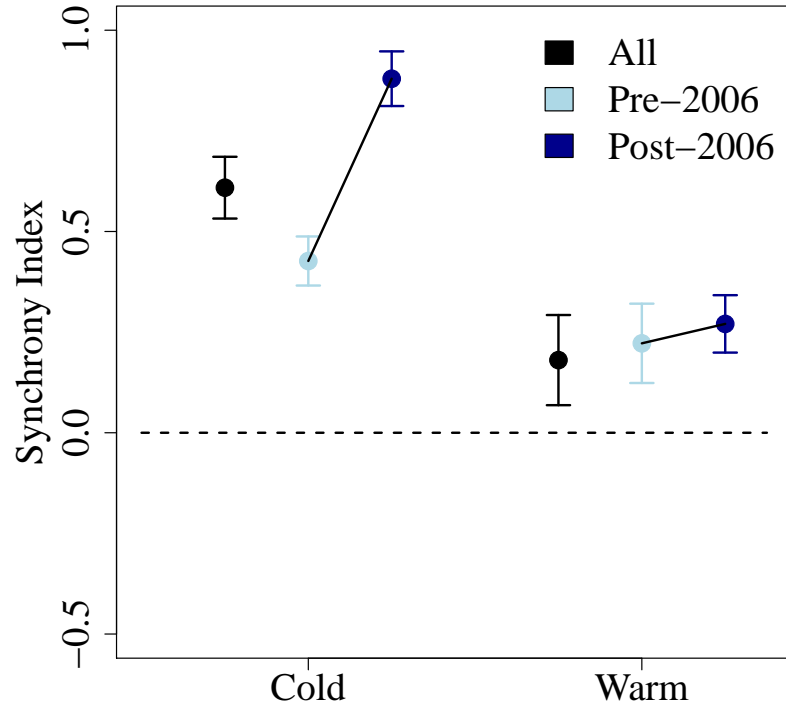

Figure A2: Gross' synchrony index as a function of the season (cold and warm seasons), calculated on log-transformed abundance data for the two groups formed by cormorant and heron+egret. The index was computed in each panel on the whole dataset (black) or using two periods: before and after 2006 (light and dark blue), the year of the change in water level management.

282 We noted on Fig. 4 that cormorants, herons and egrets seemed to compensate each other, at least for the

283 first period of the time series. This compensation was seen on a log scale, and seemed conspicuous on that

284 scale. We thus wondered if log-transforming the abundance would affect the values of the synchrony index

285 observed for this group, and make compensation more likely. It appears to be the reverse: synchrony values

286 are higher with log-transformed abundances.

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ESM 3 - Properties of the Gross whole community synchrony index when two
groups react in opposite ways

290 Here, we make η vary with the number of species, richness of the community, and the strength of the effect

291 of the environment. Starting from the model developped by Gross et al. [2] (developed in their Appendix

292 D), we explored the effect of a common environmental driver on a community formed by two groups reacting
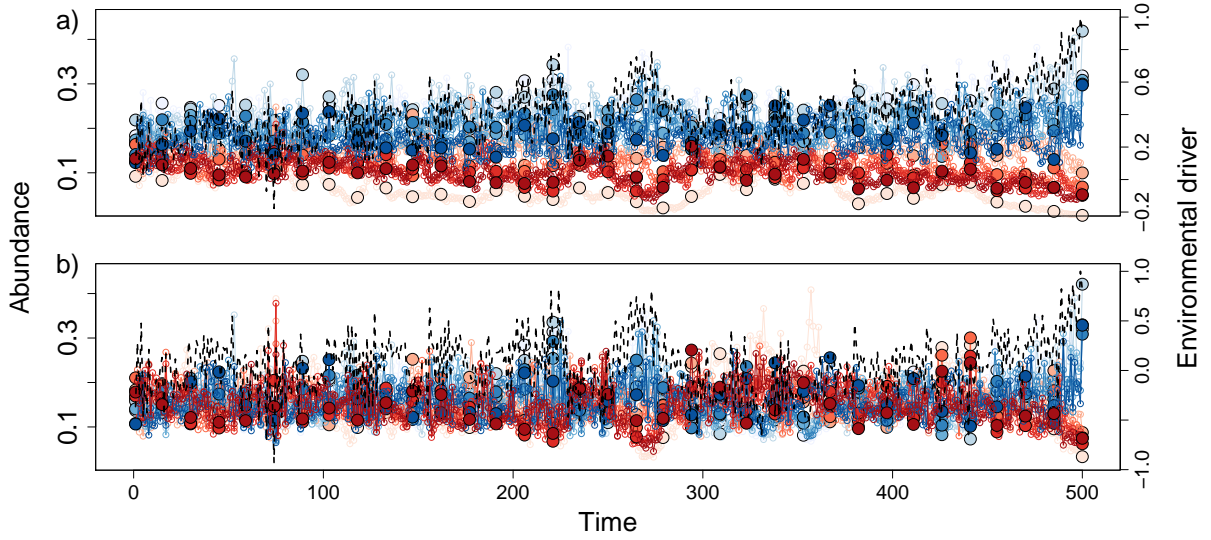
293 oppositely to this driver.

Figure A3: Time series for a community of 10 species, with 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 large filled circles correspond to the sub-sampling of the time series (keeping 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).

294 We assume that the environmental driver $U(t)$ is an autocorrelated signal (see below for details).

295 The dynamics of species i then follows the equation 3:

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

296 where the whole community is formed by $N = 2n$ species, with 2 groups of n species who have exactly

297 opposite reaction to the environmental driver, that is $\forall i \in [1,n], \exists j \in [1,n], b_j = -b_i = b$. The growth rate

298 r_i follows a normal distribution with mean 1 and standard deviation 0.25. All interaction coefficients α are

299 set to 0.5 and $K = \frac{1+\alpha(N-1)}{N}$, to keep the model in other ways exactly similar to Gross et al. [2]. The noise

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$\epsilon_i(t)$ is normally distributed, centered on 0 with a standard deviation of 0.1.

We compared results for time series of length 35 (the length of our data set), 100 and 500. For all simulation experiments, dynamics are first run for 500 time steps as a burn-in. To take into account different observational designs, we either take the first 35 or 100 time steps of the following 500-time steps series, or subsample the time series after burn-in. We also considered several community richness (10, 30, 60 and 100 species), and several strengths of the response to the environmental signal ($b =$[0.1, 0.5, 0.75]). For each combination of parameters, we computed 10 repetitions (i.e., replicates).

We considered different types of environmental driver, crossed with subsampling / no subsampling. We considered in total three scenarios, and present below the results for all three:

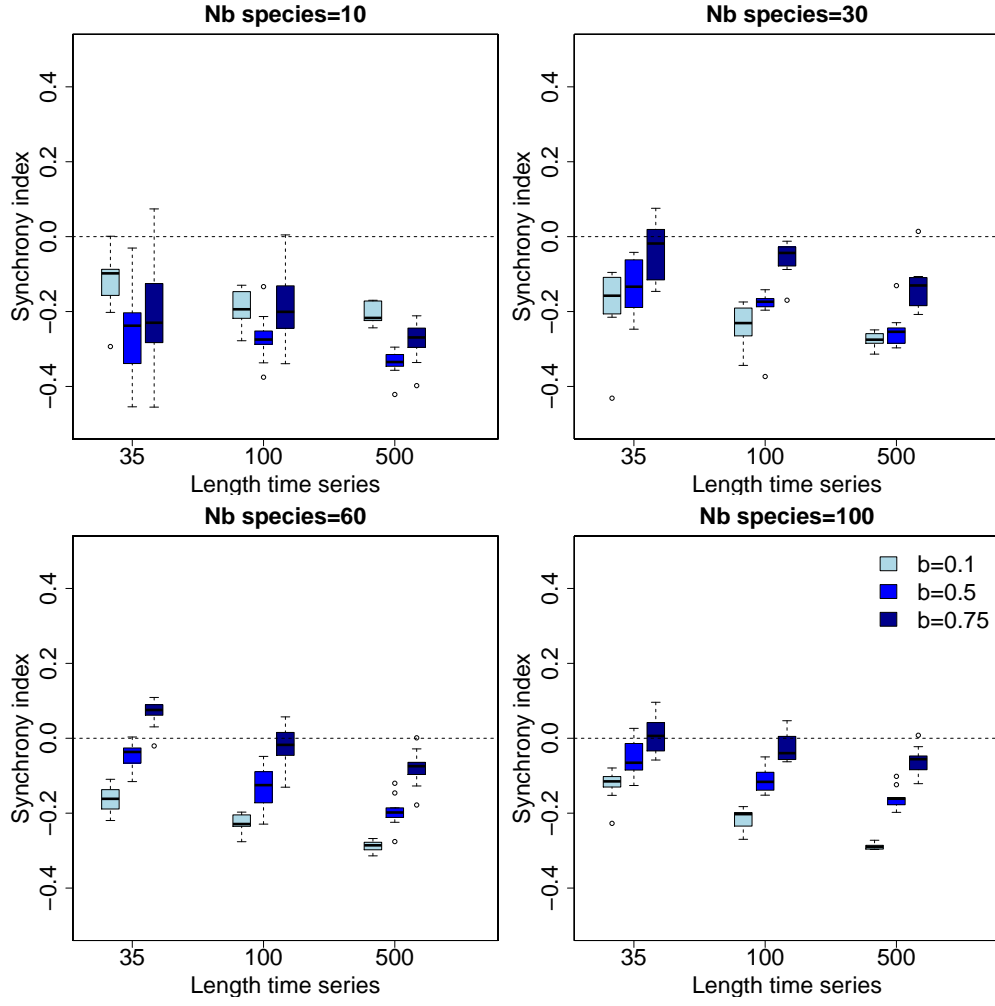- Scenario 1: $U_t = u_t$ where u_t is an autocorrelated signal (standardized); no subsampling of the data

Figure A4: Evolution of Gross' synhrony 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.
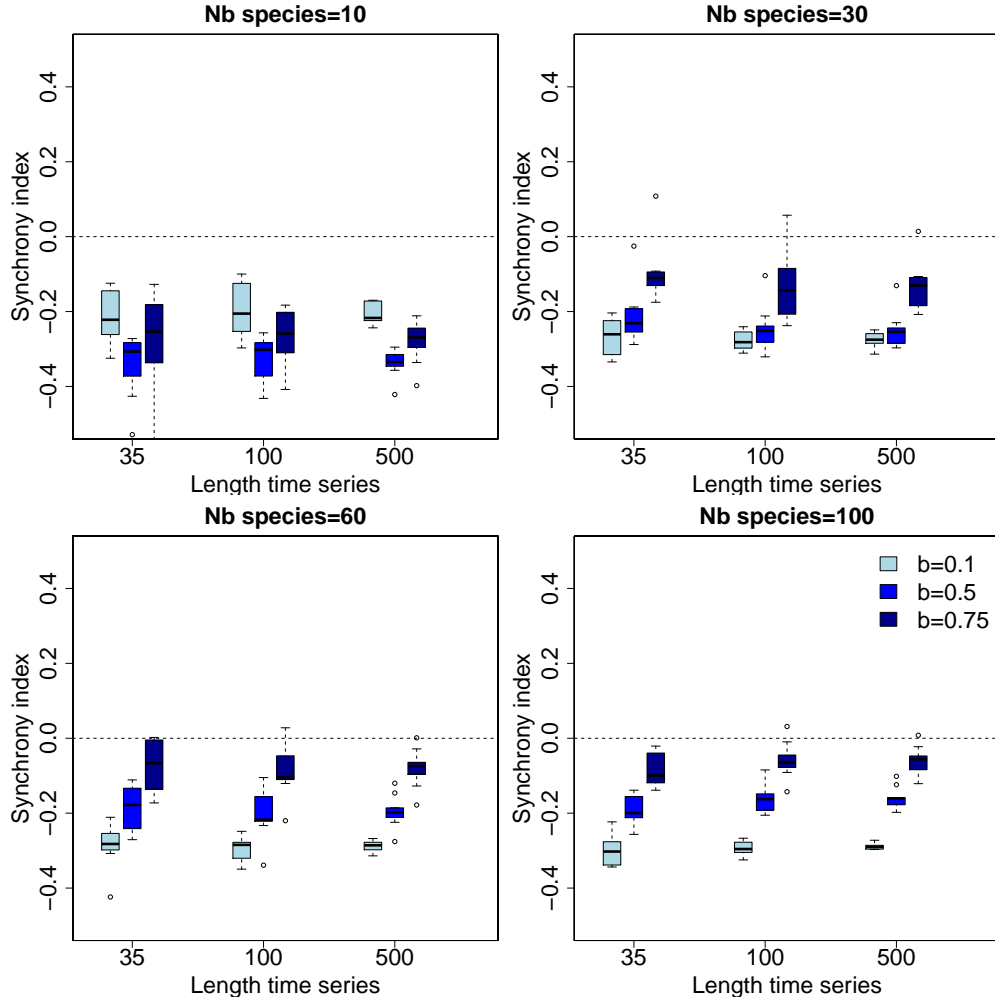
- Scenario 2: $U_t = u_t$; data subsampling

Figure A5: Gross' synhrony 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 (keeping 35 or 100 time steps), removing in effect the autocorrelation of the environment.

- Scenario 3: $U_t = U_{\min} + (U_{\max} - U_{\min})(u_t + x_t)/2$ where $x_t \in [0, 1]$ follows an increasing trend; data subsampling
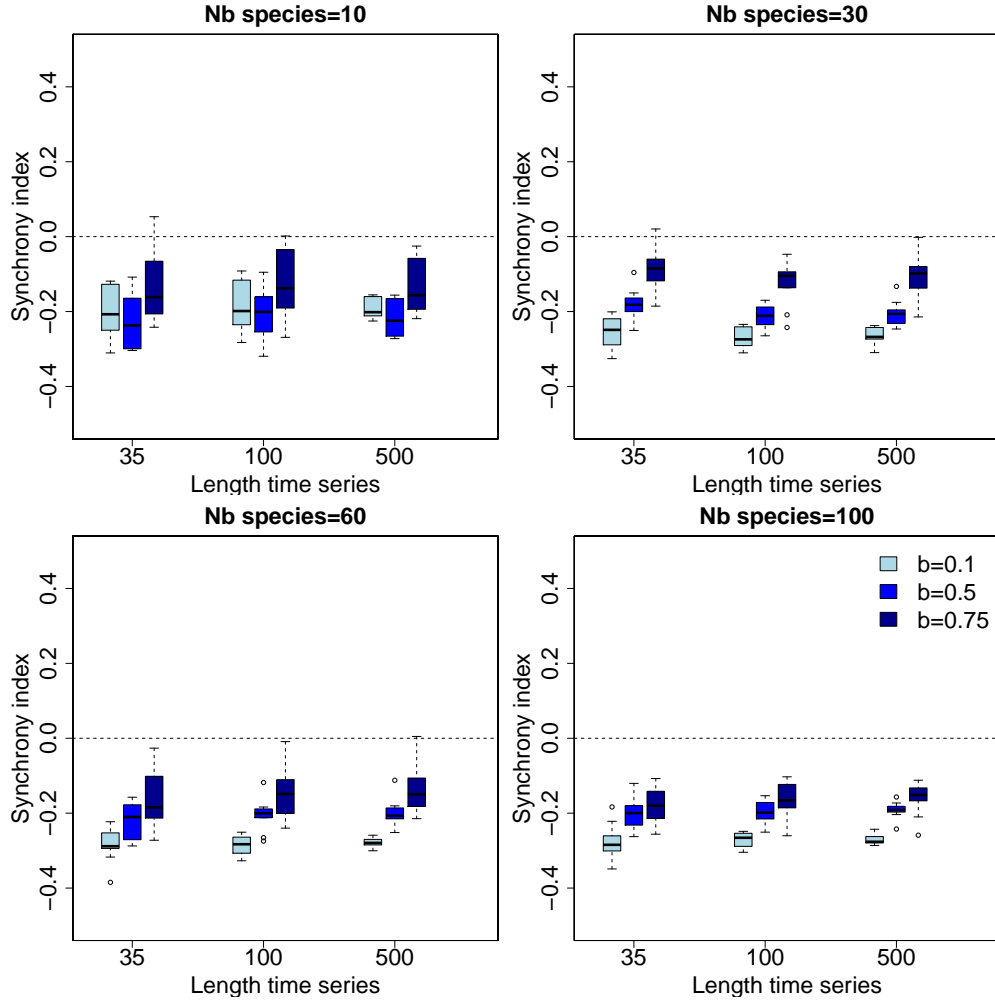
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Figure A6: Gross' synchrony index for different time series length and number of species in the community, in simulations where there is an increasing trend in the environmental signal and the data is subsampled (for 35 or 100 time steps), removing part of the autocorrelation of the environment in the dynamics of the species

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

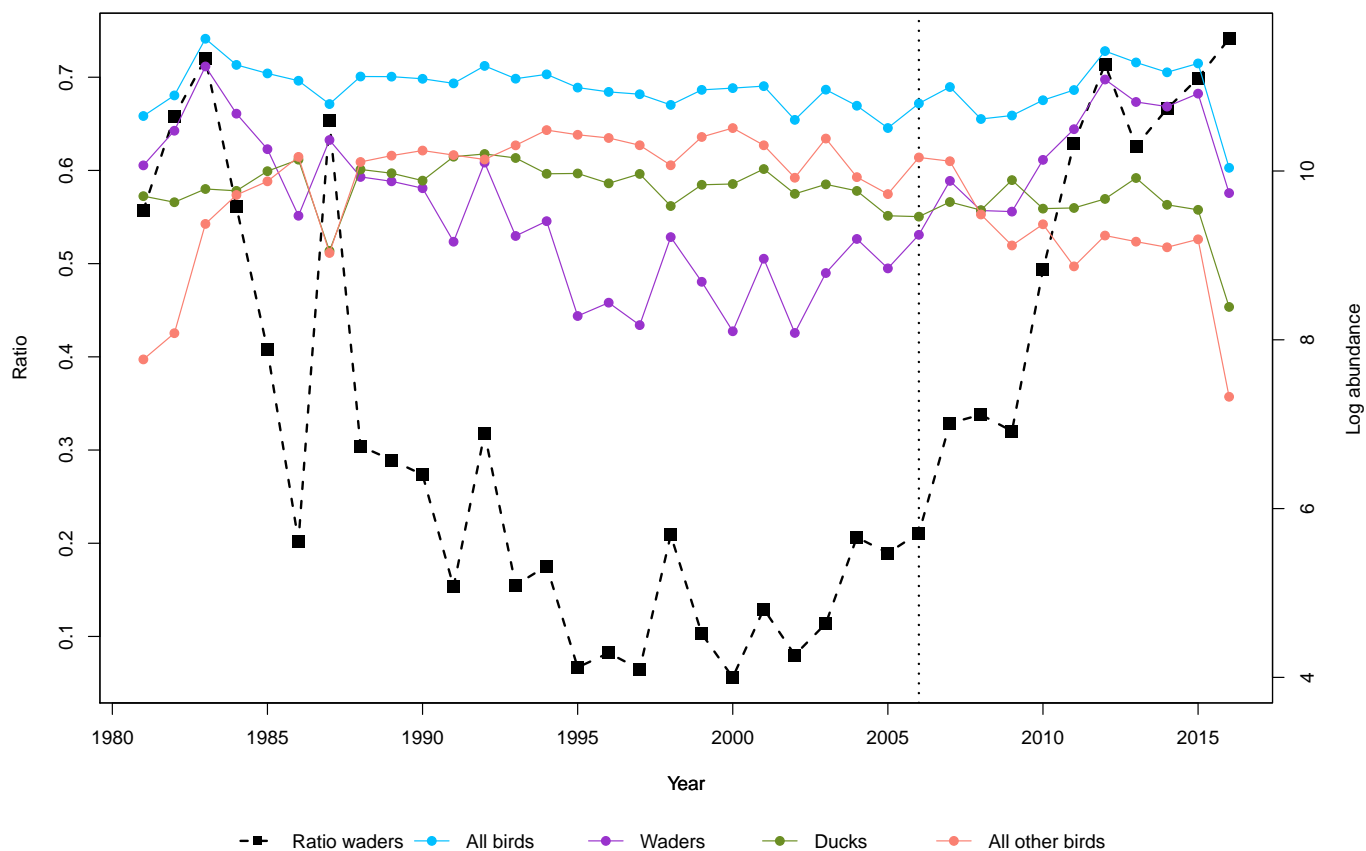**ESM 4 - Temporal patterns of functional groups in the Teich bird community**

Figure A7: Temporal trends in the abundance of all birds and the main functional groups (waders and ducks). The duck category actually includes all species functionally similar to ducks (i.e., anatids and the common coot).