

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

Frédéric Barraquand^{1,2,*}, Coralie Picoche¹, Christelle Aluome^{1,3}, Laure Carassou^{1,4} & Claude Feigné⁵

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¹ University of Bordeaux, Integrative and Theoretical Ecology, LabEx COTE Bât. B2 - Allée Geoffroy St-Hilaire, 33615 Pessac, France

² CNRS, Institute of Mathematics of Bordeaux 351 Cours de la Libération, 33405 Talence, France

³ ISPA, Bordeaux Sciences Agro, INRA, 33140, Villenave d'Ornon, France

⁴ Irstea, UR EABX, 50 Avenue de Verdun, 33612 Cestas, France

⁵ PNR Landes Gascognes, Teich Ornithological Reserve, Rue du Port BP 11 33470 Le Teich, France

* Corresponding author. Email: frederic.barraquand@u-bordeaux.fr

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 biodiversity 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 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 the temporal scale of compensation, we remark the potential for compensation to vary with taxonomic and functional scale too: compensation appears here 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 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 (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, an explanatory

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

factor 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 that the two similar duck species will precisely respond in similar ways to environmental variables, and although they might compete, this might be visible in their dynamics only at some specific times or places. 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, 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 bird 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, but it also extends well beyond these 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 in species respond differently).

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 aggregates at the seasonal scale. We defined two seasons based on observations of bird presence. 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, 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.

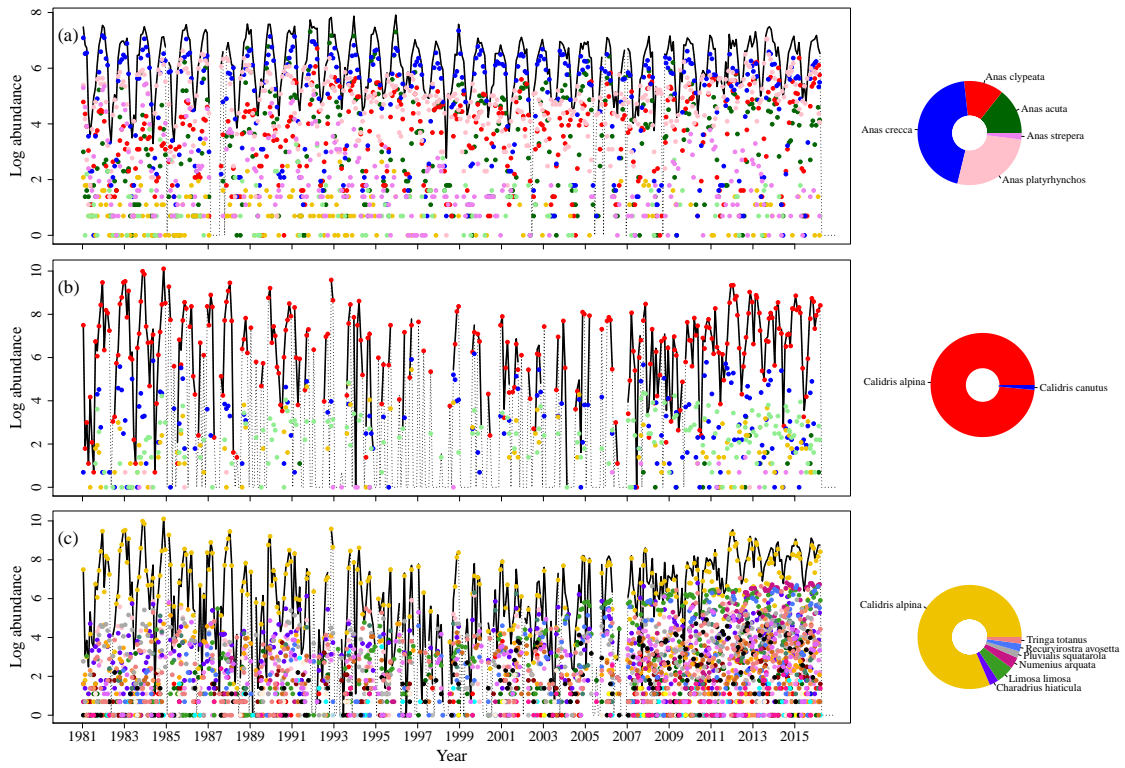


Figure 1: Time series of counts for ducks of the genus *Anas* (a), calidrids (b, *Calidris* genus), and all waders (c, including calidrids). The solid black lines represent trends in summed abundances for each guild, thin dotted lines represent putative trends (when some species are absent). The coloured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

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

where P_i is the abundance or biomass of species i in a community of n species. 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 ϕ [13, 14]), this index is independent from the richness of the community and its overall stability [15, 14]. 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 [14]. 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.

120 In addition to the time-domain analyses above, we performed frequency-domain analyses, in par-
 121 ticular for analyzing synchrony within the rich wader community, as well as the group formed by the
 122 great cormorant, grey heron and little egret. Based on the work by Keitt [18], we used the wavelet
 123 transform of the time series to measure the coherency between time series

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

124 where $w_k(\tau, s)$ is the continuous Morlet wavelet transform of species k at time τ for scale s , $\Lambda_{t,s}(\cdot) =$
 125 $\int_{-\infty}^{+\infty} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2}(\cdot)d\tau$ and $|\cdot|$ is the modulus of the complex number. The numerator corresponds to
 126 the total biomass variation while the denominator corresponds to the variations of each species. This
 127 index is close to 0 when species compensate and reaches 1 when they are synchronous. As before,
 128 the significance of each value was tested at the 10%, Bonferroni-corrected, threshold by 100 phase-
 129 randomizations of each species time series, and computation of the corresponding ρ values.

130 3 Results

131 Using a taxonomic classification of the community (focusing on the genera *Calidris* and *Anas* as two
 132 key examples of contrasted birds), we can see that within-genus synchrony indices at the seasonal scale
 133 are always positive whenever significantly different from the null (no temporal correlation between
 134 species), i.e. there is no compensation within a genus (Fig. 2). This matches the patterns obtained
 135 within the entire wetland bird community (Fig A1 in ESM1).

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, created 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 though not very pronounced and not significant statistically, which later disappeared.

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

147 a fine temporal scale throughout most of the time series. However, post-2006, there seems to be a
 148 possibility for overcompensation on a scale around 5 years or around 3-4 months.

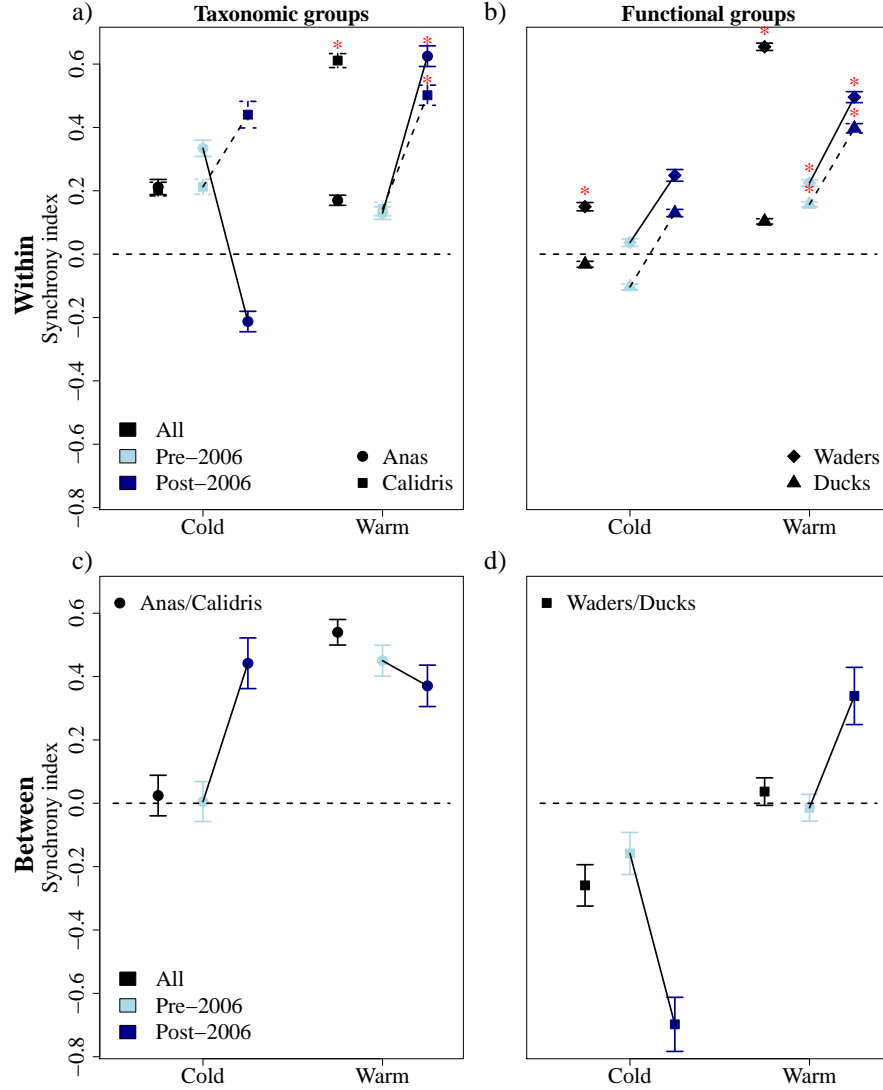


Figure 2: Gross' synchrony index as a function of the season (cold and warm seasons), calculated among (top, a-b) and between (bottom, c-d) groups. The groups considered were different functional groups (ducks vs. waders, right b-d) or taxonomic groups (*Anas* genus, *Calidris* genus, left a-b) groups.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

149 There are therefore relatively contrasted results regarding the effect of the management change
 150 on short-term synchrony within the wader community. At the yearly (season) timescale, it seems to

151 increase the synchrony (though the Gross index and wavelets provide slightly different answers). At
 152 even shorter timescales though, it seems to decrease it.

153 More clear-cut results can be found when we examine the synchrony vs. compensation between
 154 functional groups (Fig. 2d). Since we consider only two functional groups, the Gross index reduces to a
 155 simple correlation². Waders and ducks are negatively correlated during the cold season and positively
 156 correlated during the warm season. These patterns are in contrast unclear when using a taxonomic
 157 classification (no compensation, Fig. 2c).

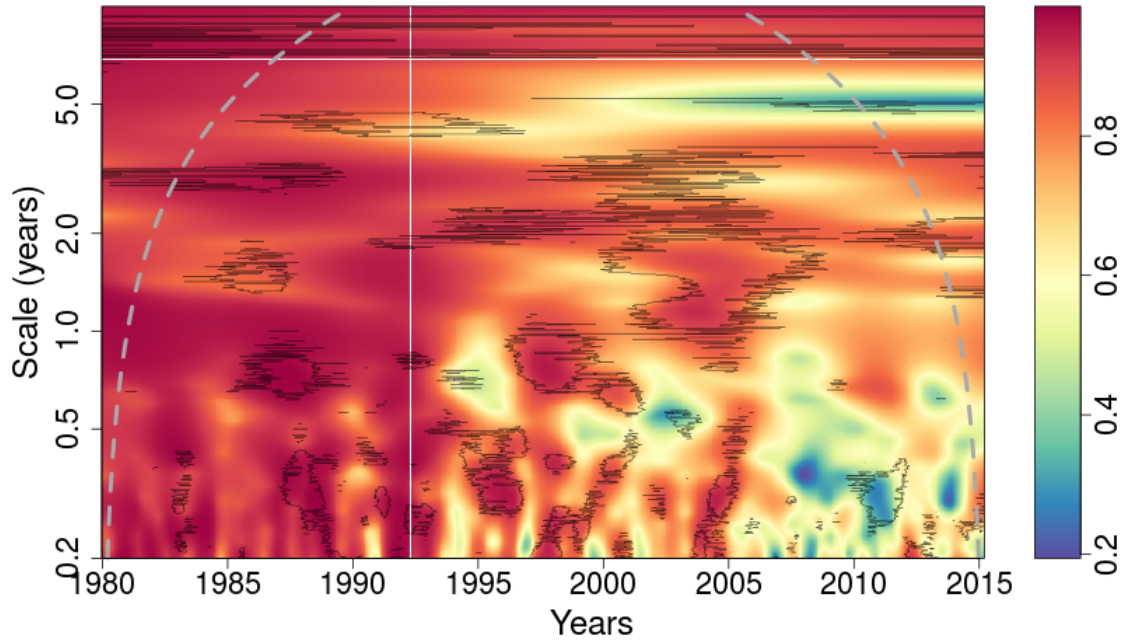


Figure 3: Wavelet modulus ratio for the wader community, scaling from 0 (compensation, blue color) to 1 (synchrony, red color). Dashed black lines delineate regions significantly different from the null model with a false discovery rate controlled at the 5% level.

²It should be noted that with more species, the (author?) [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.

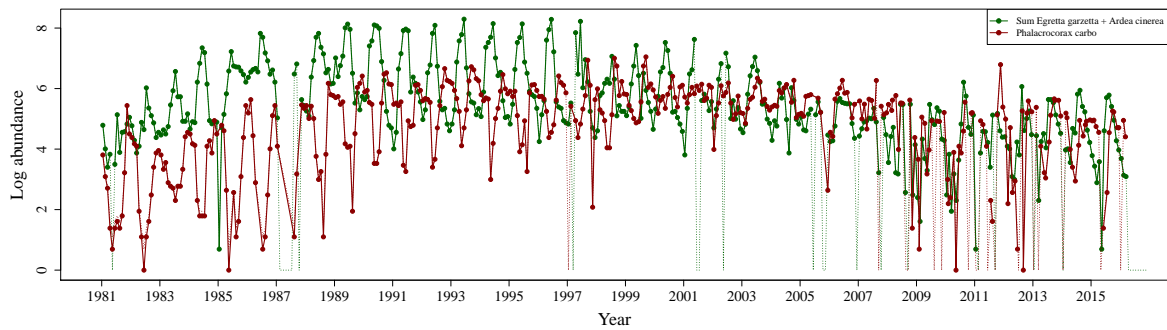


Figure 4: Time series of great cormoran abundance, as well as summed abundances of grey heron and little egret (logarithmic scale).

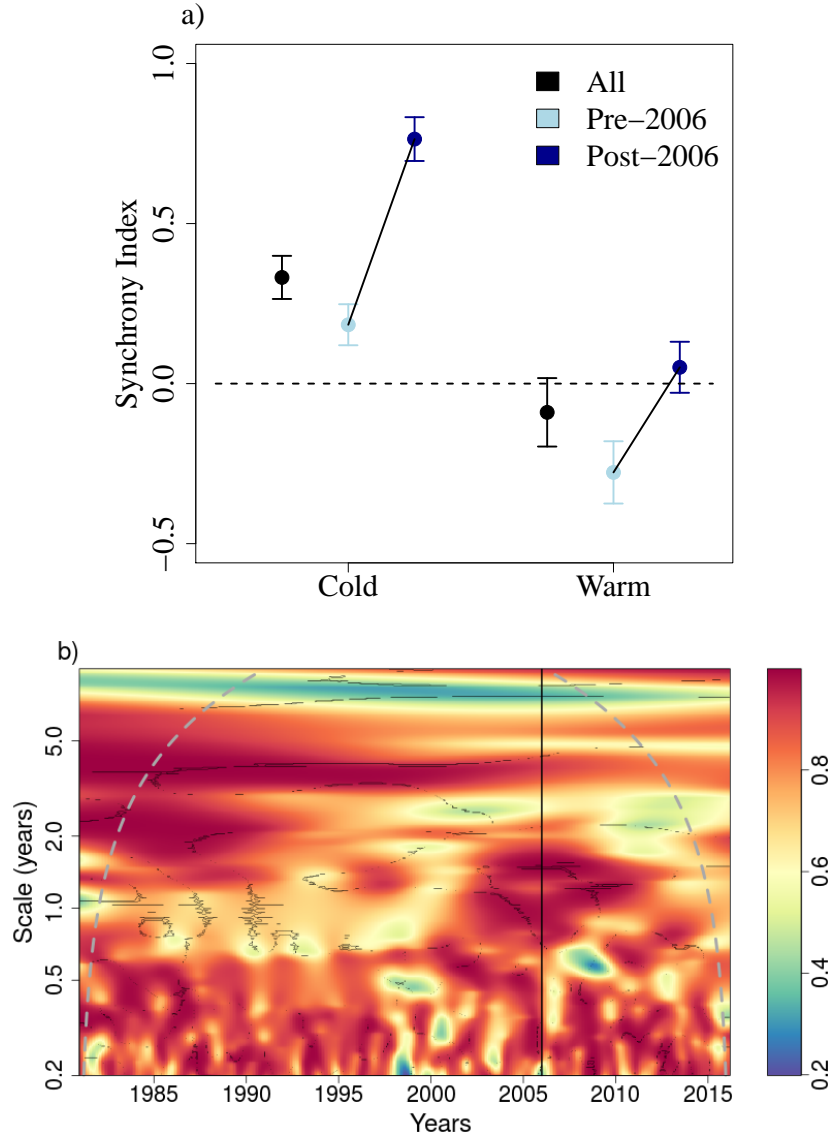


Figure 5: Time-domain (top) and frequency-domain (bottom) synchrony analyses of the group formed by cormorant, egret and heron

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

165 might be some compensation over very short timescale as well (within the season), but at very specific
166 times and the biological mechanisms for this are unclear since these species compete for roost sites , a
167 process that it unlikely to manifest at such very short timescales.

168 4 Discussion

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

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

178 Given that we compare the level of synchrony/compensation within guilds (with many species)
179 and between guilds (with a handful of groups), we checked in ESM 3 whether changing the number
180 of “compartments” in the Gross η index could affect its value: it did not. However, if two groups
181 respond in opposite ways to a shared driver, we found nonetheless that the stronger the response to
182 the driver, the lesser the compensation using η at the community level. This might explain the low
183 levels of compensation that we found at the overall wetland bird community level (ESM 1), in spite of
184 the presence of two groups reacting in opposite way to shared driver (here, water level).

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

191 It may be better to say that we detected “compensation” rather than “compensatory dynamics”
192 between bird species [1] as the observed long-term changes in species composition (more waders, less
193 ducks) might be due to an increased inflow of birds preferring low water levels, and outflow of birds
194 preferring high water levels, under an overall space constraint. In other words, the shift in community

195 dynamics is likely not directly due to birth and deaths. However, despite the importance of movements
196 and habitat preference to the local community dynamics, there is certainly also an influence of the
197 regional changes in births and deaths on the local dynamics.

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

202 Overall, our results suggest to search for compensation more often *between* rather than *within*
203 functional groups, and over relatively long timescales above that of the dominant driver (e.g., season-
204 ality). This goes against calls to search for compensation at very short timescales [10, 1] in order to
205 filter out the main seasonal driver. Although searching for compensation at temporal scales below the
206 seasonal abiotic driver (e.g., temperature) was partly motivated by studies on plankton whose com-
207 munity dynamics are much faster, we could have expected compensation to manifest also that scale
208 here (e.g., monthly): movement of birds reacting to food availability can certainly occur that fast. We
209 suspect instead that because many species share common abiotic drivers at short temporal scales [13],
210 compensation is bound to be very rare below the dominant temporal scale of the environment.

211 In many ways, searching for compensation using biodiversity time series data is searching for needles
212 in a haystack: only some specific temporal and functional/taxonomic scales allow to see compensation
213 whilst numerous confounding factors make the community co-vary positively at all other scales [7].
214 Although the knowledge of specific biological mechanisms increasing the densities of some species at
215 the expense of others can help, synchrony will likely dominate community-level time series data for
216 closely related species, even in species that compete strongly [6]. This is true even in cases of known
217 mechanisms of competition or shifts in community composition due to abiotic changes as in this study.
218 We suggest that “zooming out” taxonomically (considering summed abundances of dissimilar functional
219 groups) and temporally (considering temporal scales well above the dominant driver) may often be the
220 best strategy to see the compensation that will inevitably manifest if the community-level abundance
221 is maintained within bounds.

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224 ecological communities. *Annu. Rev. Ecol. Evol. Syst* **40**, 393–414.

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277 Supplementary Material

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

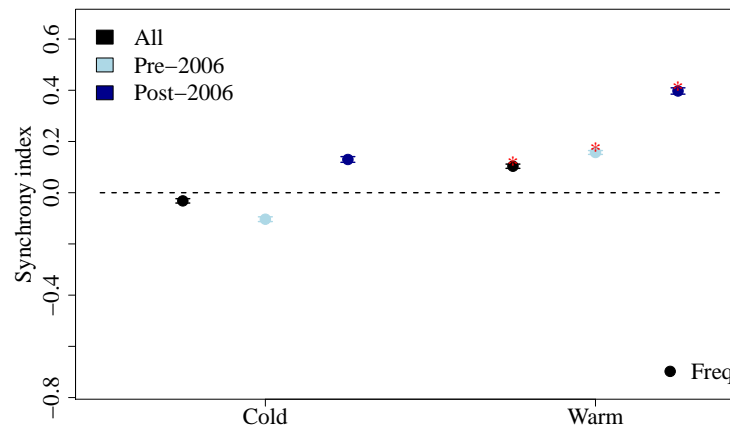


Figure A1: Gross' synchrony index as a function of the season (cold and warm seasons), calculated among the 60 most frequent species in the Teich reserve. The index was computed in each panel on the whole dataset (black) or using two periods: before and after 2006 (light and dark blue), the year of the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

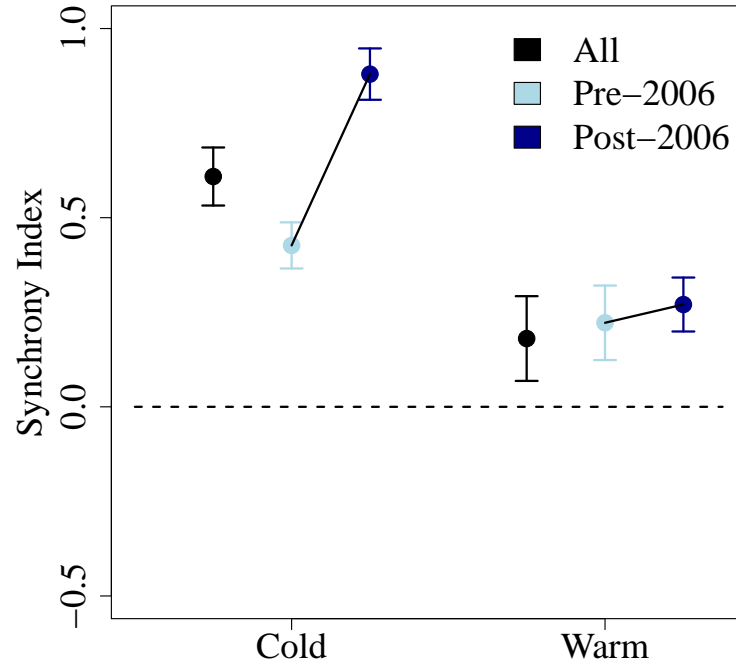


Figure A2: Gross' synchrony index as a function of the season (cold and warm seasons), calculated on log-transformed abundance data for the two groups formed by cormorant and heron+egret. The index was computed in each panel on the whole dataset (black) or using two periods: before and after 2006 (light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

280 We noted on Fig. 4 that cormorants, herons and egrets seemed to compensate each other, at least for
 281 the first period of the time series. This compensation was seen on a log scale, and found conspicuous.
 282 We thus wondered if log-transforming the abundance would affect the values of the synchrony index
 283 observed for this group, and make compensation more likely. It appears to be the reverse: synchrony
 284 values are higher with log-transformed abundances.

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

Here, we make η vary with the number of species, richness of the community, and the strength of the effect of the environment. Starting from the model developed by Gross et al. [2] (developed in their Appendix D), we explored the effect of a common environmental driver on a community formed by two groups reacting oppositely to this driver.

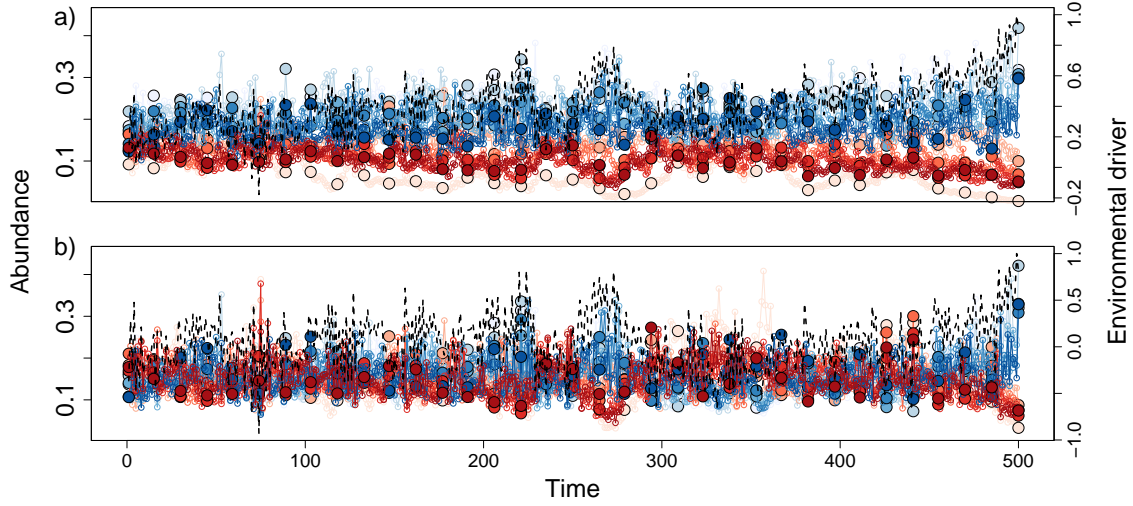


Figure A3: Time series for a community of 10 species, with a strong effect of the environment ($b=0.75$, see eq. 3) and a time series of 500 time steps. Open circles represent all points of the time series while large filled circles correspond to the sub-sampling of the time series (keeping only 35 points). 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).

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

The dynamics of species i then follows the equation 3:

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

where the whole community is formed by $N = 2n$ species, with 2 groups of n species who have exactly 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 r_i follows a normal distribution with mean 1 and standard deviation 0.25. All interaction coefficients α are 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 $\epsilon_i(t)$ 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:

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

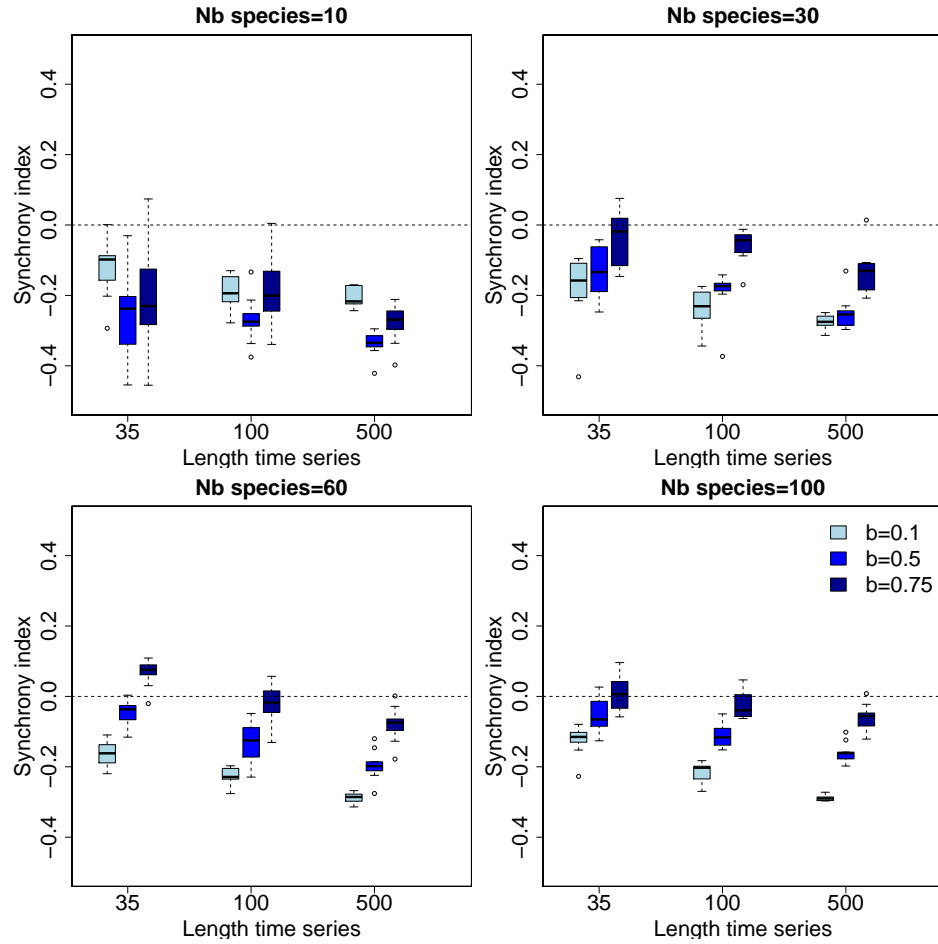


Figure A4: Evolution of Gross' synchrony index for different time series length and number of species in the community, in simulations where there is no trend in the environmental signal and the data is not subsampled, keeping the autocorrelation of the environment.

- $U_t = u_t$ and we subsample the data

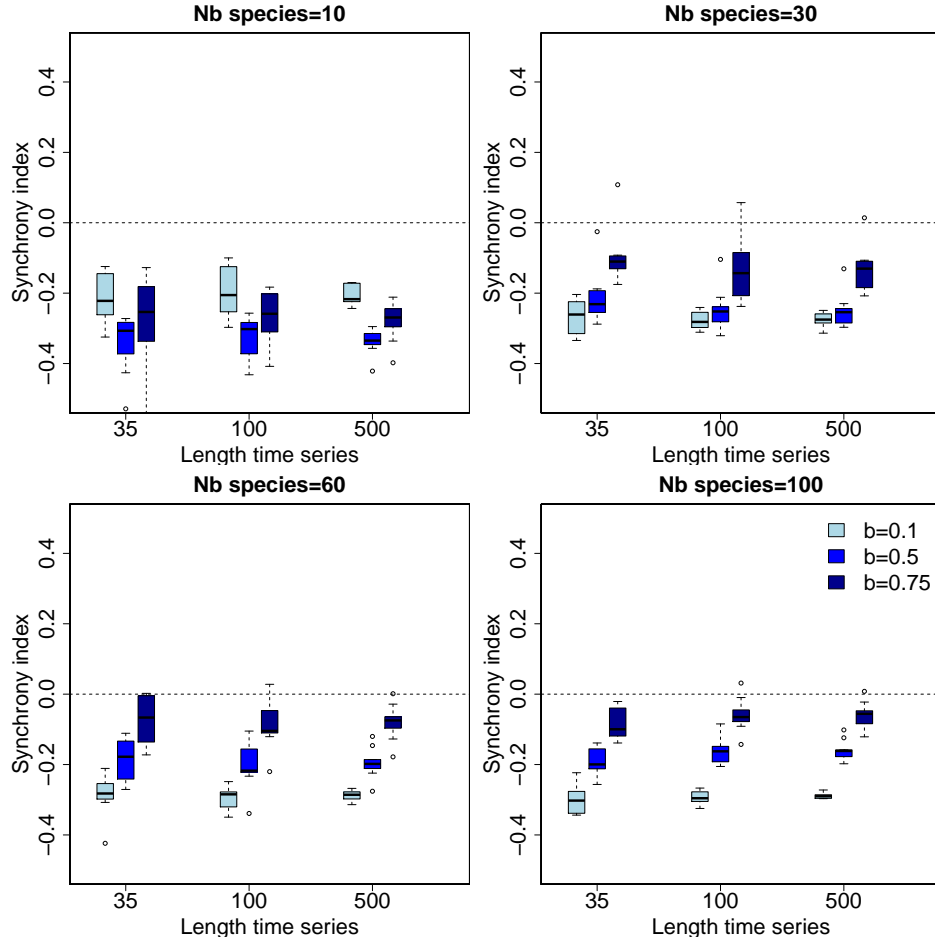


Figure A5: Gross' synchrony index for different time series length and number of species in the community, in simulations where there is no trend in the environmental signal and the data is subsampled (keeping 35 or 100 time steps), removing in effect the autocorrelation of the environment.

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

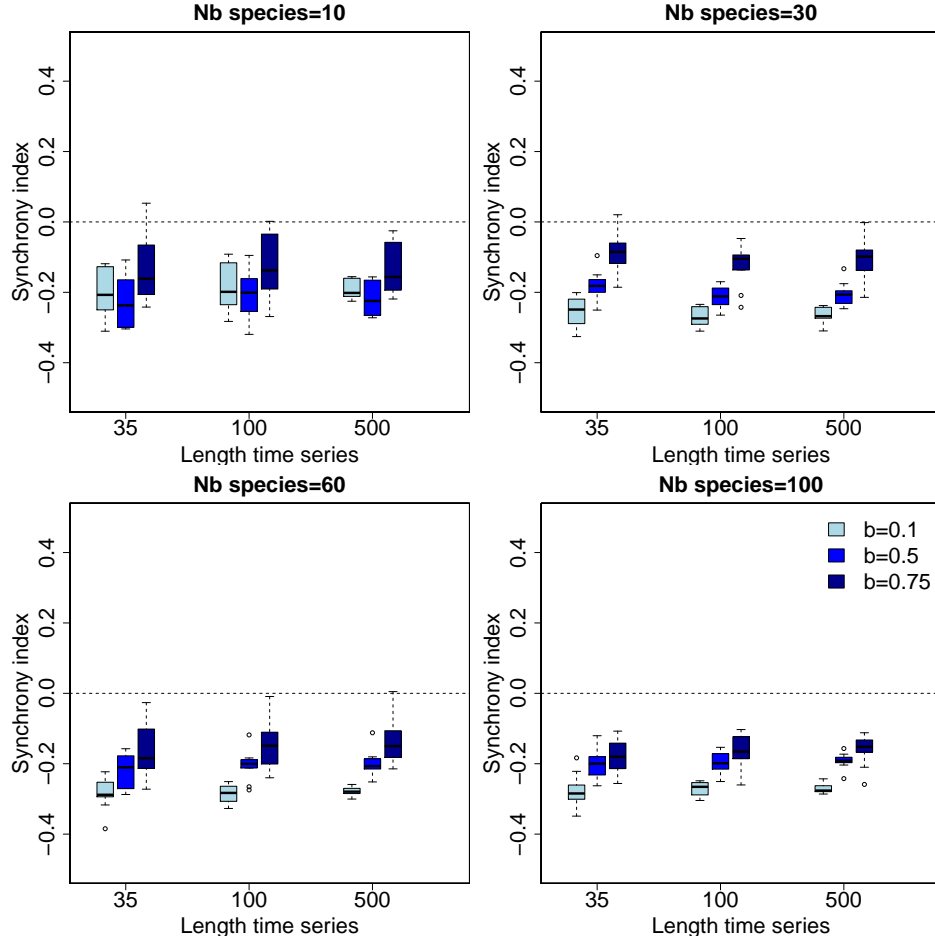


Figure A6: Gross' synchrony index for different time series length and number of species in the community, in simulations where there is an increasing trend in the environmental signal and the data is subsampled (for 35 or 100 time steps), removing part of the autocorrelation of the environment in the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

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