Looking for compensation at multiple scales in a wetland bird community

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Abstract

1. 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.

2. However, most studies so far have considered compensation in either plants or planktonic organisms, so that evidence for the generality of such synchrony is limited. Here, we extend analyses of community-level synchrony to wetland birds.

32. ~~We take~~Taking advantage of ~~a long-term wetland bird community time series of~~a monthly survey for 35 years, ~~where~~in a bird community where ~~–~~we suspected that compensation might occur - due to changes in water levels and known trends -, we perform both yearly and monthly analyses of community synchrony, applying yearly indices and wavelet-based synchrony measures to time series.~~.~~

4. 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 either 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. We also found that compensation varies with taxonomic and functional scale: compensation appeared more frequently between rather than within guilds.

5. Although most research has focused on the temporal scale of compensation vs synchrony, our results suggest that ~~we found that compensation varies with taxonomic and functional scale too: compensation appeared more frequently between rather than within guilds. This suggests that~~ compensation has more potential to emerge between broad functional groups rather between species.

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 (Gonzalez and Loreau, 2009). 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.

Understanding why environmental variation may lead to compensation is relatively easy, provided species performances respond to that environmental variation: if species have some environmental preference (e.g. thermal optima), and the environment changes over time, different species will be most fit at different points in time. As a consequence, relative abundances will shift over time even though the community biomass as a whole may remain relatively stable (Gonzalez and Loreau, 2009). However, the conditions for compensation to happen depend on the particulars of the interactions between and within species in the community.

~~This~~Compensation is particularly likely to occur when such temporal environmental variation combines ~~there is~~with a space or strongly limiting resource constraint, so that individuals compete in a zero-sum game (sensu Hubbell, 2001 or lottery-style models, Chesson, 1994). When the total community size is constant over time, and the composition fluctuates, negative covariation between abundances then emerges by design (Loreau and de Mazancourt, 2008) since no species can increase without another species decreasing in abundance. Outside of this zero-sum scenario, in models where Lotka-Volterra competition is combined with temporal environmental variability, theoretical research has revealed that increased interspecific competition might not increase species compensation (Ives et al. 1999) and might even decrease it (i.e., increase species synchrony instead, Loreau and de Mazancourt, 2008), though this depends on the fluctuation regime. Thus, in a world where total community size varies, predicting whether compensatpry (asynchronous) dynamics can occur is intrinsically

difficult.

Some scenarios with either zero-sum (lottery-style) or Lotka-Volterra competition are, however, likely to always yield compensatory dynamics, such as a dependence of the strength of competition itself on the value of the environmental signal: a negative covariance between competitive strength and environmental variation is at the heart of the temporal storage effect (Chesson, 1994; Ellner et al., 2016), which is essentially a temporal partitioning of the niche. Although rarely the only driver of coexistence, the temporal storage effect is though to be common (e.g., Usinowicz et al., 2017) and lead to compensatory dynamics (Gonzalez and Loreau, 2009). Other ways to create compensation arise when considering the regional dynamics, which creates interaction between temporal environmental variation, competition, and dispersal. Dispersal can then create a spatial insurance effect, generating asynchrony at the regional level (Loreau et al. 2003), or generate compensation locally, e.g., by re-colonization after disturbances combined with priority effects (Fukami, 2015), which allows one of several near-equivalent species to "take over", but with temporal variation in the identity of the winner. Compensatory dynamics can therefore arise from a variety of ecological processes combining to different degrees competition and diverging responses to environmental variables.

Whatever the cause(s) of compensatory dynamics, its main consequences for ecosystem functioning is that the community as a whole exhibits lower biomass variation than its constituent species (Gross et al., 2013). Compensation is therefore intertwined with community-level stability, at least when stability is understood as the reciprocal of variability. By contrast, ~~another very frequently~~the most frequently observed outcome on biodiversity time series is community-level synchrony (Vasseur et al., 2014)~~. Synchrony occurs when~~ with all species that 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 (Houlahan et al., 2007; Gonzalez and Loreau, 2009). Unfortunately, this metric is not appropriate for communities subjected to community-wide environmental forcing (Ranta et al., 2008), 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~~during which –compensatory dynamics may be found (e.g., below the seasonal scale ~~where~~at which -temperature fluctuations tend to synchronize species dynamics, Vasseur et al., 2014).

Despite ~~this~~ efforts to look for more meaningful temporal scales in community-level time series, temporal compensation has remained surprinsingly elusive in the field (Houlahan et al., 2007; Vasseur et al., 2014); but see Ernest et al. (2008); Christensen et al. (2018). Most datasets used so far to evaluate temporal compensation vs synchrony involve planktonic organisms (Vasseur and Gaedke, 2007; Vasseur et al., 2014) or terrestrial plants (Houlahan et al., 2007; Gross et al., 2013; though see Bell et al. 2014). 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~~allowing 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, and this explanatory 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

[1]Considering only the years used in our analysis. Otherwise, the dataset begins in 1973. [[CP : Can't we remove this footnote?]]

the other (functional compensation, *sensu* Gonzalez and Loreau 2009) so that individuals from species A or B would experience similar competition. Priority effects and chance events could then determine whether duck species A or B dominates. On the other hand, it could be argued that these two similar duck species will precisely respond in similar ways to environmental 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. This should occur because more dissimilar species are more likely to 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, such compensation *between* guilds has been less well explored than within guilds, even though there is actually some empirical evidence for compensation between dissimilar guilds (e.g. Sinclair et al., 2013). In this paper, we explore different ways to cluster the bird community, within or between guilds, along either taxonomic or functional classifications. Although a functional classification might appear more intuitively more appealing, it is important to keep in mind that our description of functions through traits (e.g., body size, feeding relations) are necessarily partial and imperfect, so that a taxonomic description can sometimes yield a better explanation of performances (Clark, 2016) ~~[REF Clark]~~.

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), favoring different types of wetland birds (so that over long timescales, there is a real potential for changes in community composition).

Material and Methods

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, over the whole study period. The reserve comprises 120 ha of wetlands, and the counts have been aggregated at the reserve scale (summed over ~~XX~~18 sectors where the counts are actually performed, using binoculars). We use for each species the maximum observed abundance over a month, which provides a "monthly snapshot" of the bird abundance, that has been used to monitor the reserve since its inception. When abundance values are missing for certain species and months, we replace them by 0s. Given the sustained observation effort (all sectors are patrolled multiple times throughout the month by the staff, amateur ornithologists visiting the reserve daily and signalling their findings to the reserve staff), we consider that the absence of ~~information proves that the~~counts for a given ~~-~~species ~~was indeed missing in the reserve~~signals its true absence from the reserve. This creates some zero abundances for rare species at the monthly scale. We have not attempted to "correct" those zeroes (e.g., inferring the "missing" data with a model assuming that our reserve is a subsample of a regional population) because doing so would have compromised the patterns of local synchrony/compensation. However, we do check below that having such zeroes in the monthly time series cannot affect our conclusions. ~~Reconstructing time series based on the assumption that birds are always present in the region and that abundances should not be null, as would be done with Bayesian methods[REF] or GLM [REF], might hide local changes in the behaviour (e.g., specific avoidance) of these species. Moreover, the timescale that we analyse (seasons or long-term trends) is barely affected by monthly missing values [[Do we talk about ESM5 here or in the wavelet part?]]~~. In the statistical analyses, we use ~~both the original monthly data and~~ seasonally ~~-~~averaged abundances~~s~~ (plotted in Fig. 1), as well as the original

monthly data (presented in Appendix S1). 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.

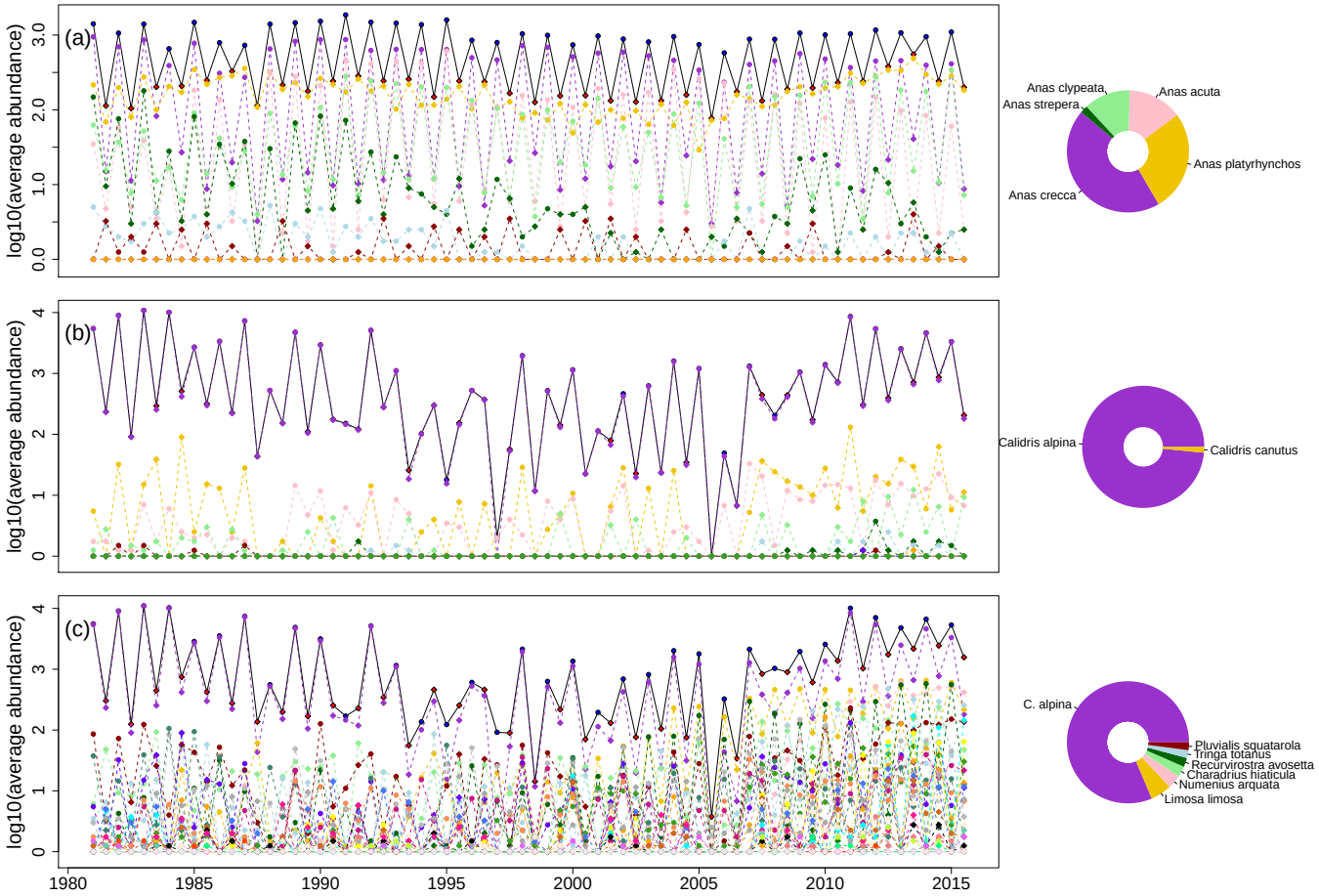

Figure 1: Time series of seasonal ~~average~~ly averaged abundance for ducks of the genus *Anas* (a), calidrids (b, *Calidris* genus), and all waders (c, including calidrids). The solid black lines represent the summed average abundances for each guild, dotted lines represent average abundance for each species. Circles represent the cold season and diamonds, the warm season. 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).

Statistical Analyses

Yearly analyses

We used for yearly analyses the synchrony index η defined by Gross et al. (2013), which is constructed as the mean cross-correlation between each species biomass and the summed biomasses of 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. This synchrony index described in eq. 1 varies between -1 (perfect compensation, total biomass is constant) and 1 (complete synchrony), while 0 represents a case where all populations fluctuate independently. Contrary to other indices (e.g., Loreau and de Mazancourt (2008)'s ϕ), this index is independent from the richness n of the community (or more generally the number of system components) and its overall stability (Blüthgen et al., 2016; Hallett et al., 2016). This is particularly important here as we perform analyses at different taxonomic scales, and therefore with a different n in eq. 1.

We computed synchrony indices at the year × season scale ~~(that is, for a given cold or warm season each year)~~ using the codyn package in R (Hallett et al., 2016). That is, we constructed two community-level time series where each year is associated to a vector of species abundances, one for the cold season and one for warm season. To do so, w~~W~~e averaged monthly bird abundances, for each species, over the season duration.~~, and~~We then ~~-~~computed the synchrony index for both cold and warm seasons using the year as our statistical unit. In follow-up analyses, w~~W~~e 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 monthly group density.

We ~~used both~~ considered taxonomic classifications of the species (i.e., between and within genera) and functional classifications of the species (e.g., 30 species of waders vs 34 species of ducks) as we suspected that a functional classification may allow to partition better the

abiotic requirements of the species. We use "duck" as a shorthand for the larger functional group of herbivorous divers, because the birds in that category are mostly ducks: this group includes nonetheless all anatids (geese and swans in particular) as well as the common coot *(Fulica atra*, an abundant species here).

We also "zoomed in" on a group of species that were known to exhibit potentially compensatory dynamics (through competition for roosting 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 (Gouhier and Guichard, 2014). 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 (Purves and Law, 2002). 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 (a Bonferroni correction is needed here because multiple comparisons across 2 seasons and 3 periods).

Wavelet analyses

In addition to the time-domain analyses above, we performed frequency-domain analyses for a range of temporal scales ranging from a few months to years. ,This was done -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.-All wavelet analyses take as input the monthly time series data.

Based on the work by Keitt (2008) and follow-up by Vasseur et al. (2014), we used the

wavelet transform of the time series to measure the coherency between time series

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

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.

All datasets and statistical analyses are available in a GitHub repository `https://github.com/fbarraquand/BirdTimeSeries_Teich`[2].

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 hypothesis (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 Appendix 1).

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

[2] Will be ~~M~~made public upon acceptance and archived in Zenodo

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. When we consider the wavelet plot (Fig. 3), that is a time-varying and scale-dependent strength of synchrony, we can see 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.

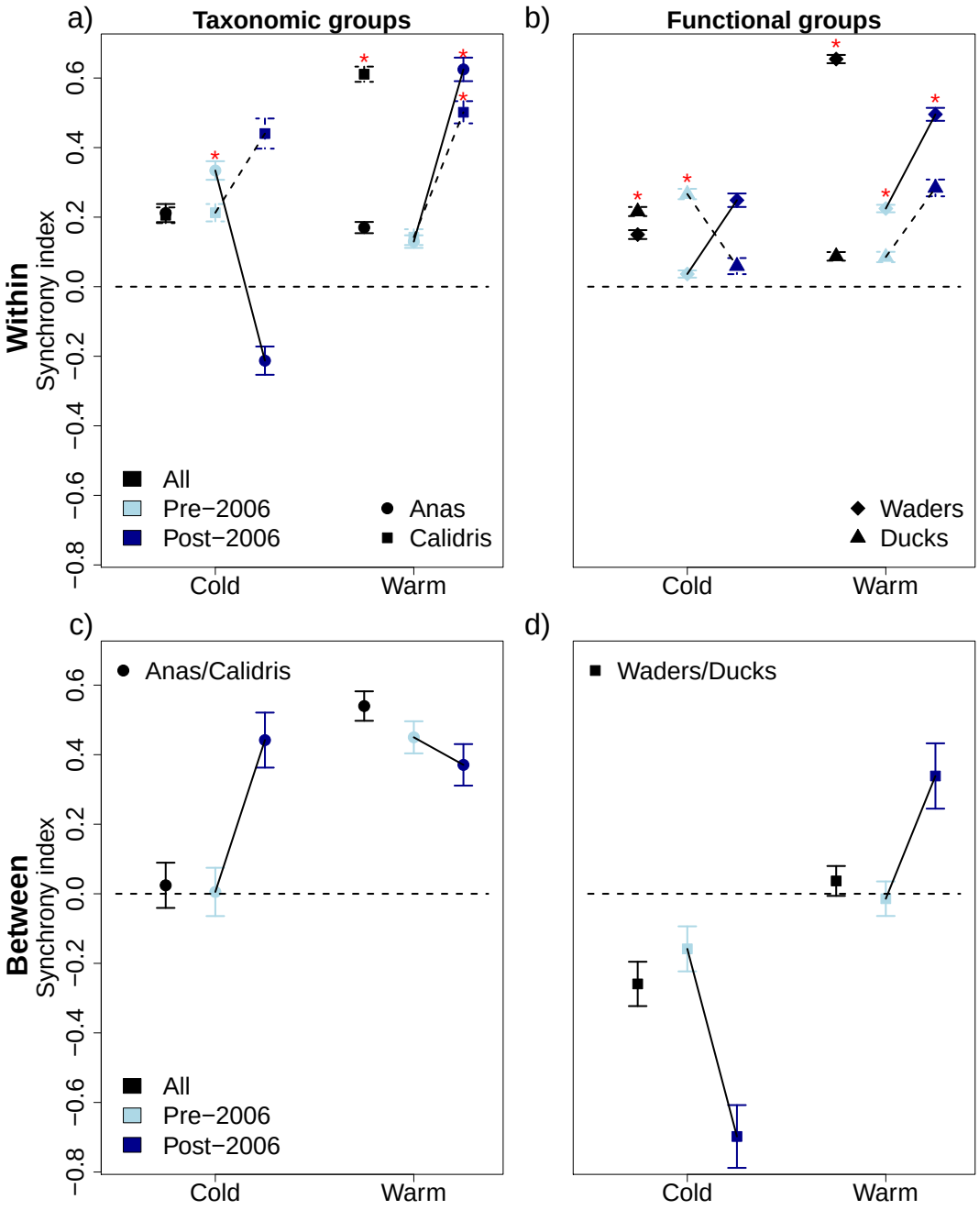

Figure 2: Gross' synchrony index (η) as a function of the season (cold and warm seasons), calculated within (top, a-b) and between (bottom, c-d) groups. The groups considered were different functional groups (ducks vs waders, right b-d) or taxonomic groups (*Anas* genus, *Calidris* genus, left a-b) groups.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

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. 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).

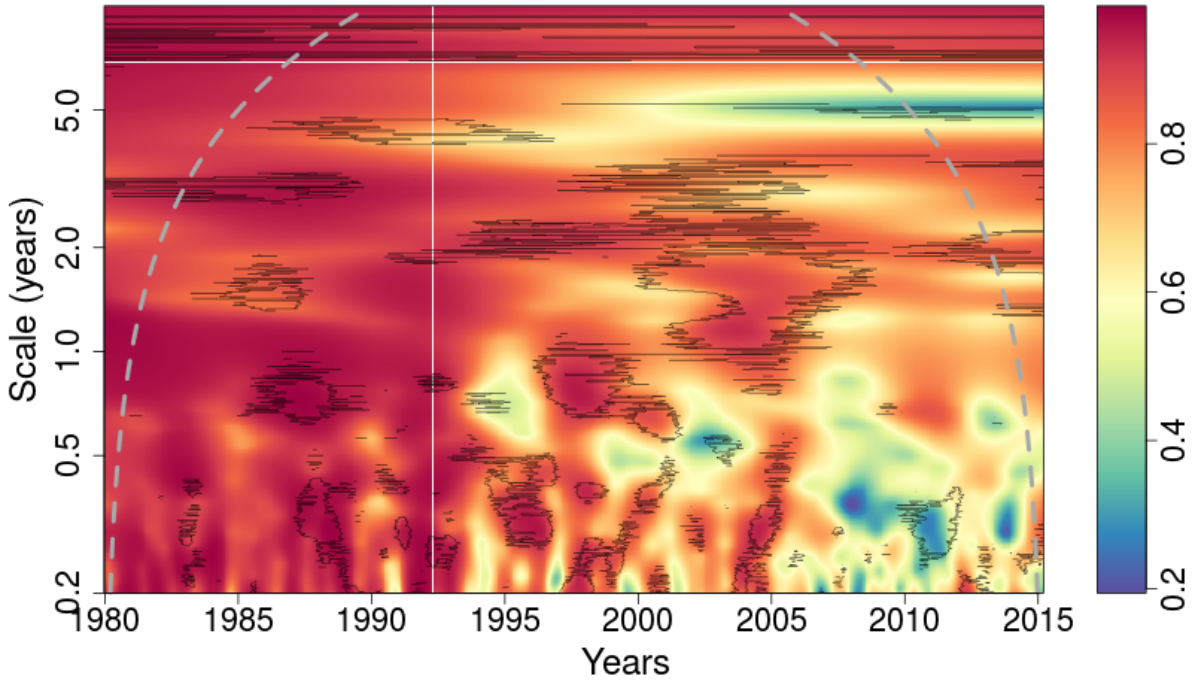

Figure 3: Wavelet modulus ratio for the wader community, scaling from 0 (compensation, blue color) to 1 (synchrony, red color). Dashed black lines delineate regions significantly different from the null model (independently fluctuating species) with a false discovery rate controlled at the 10% threshold.

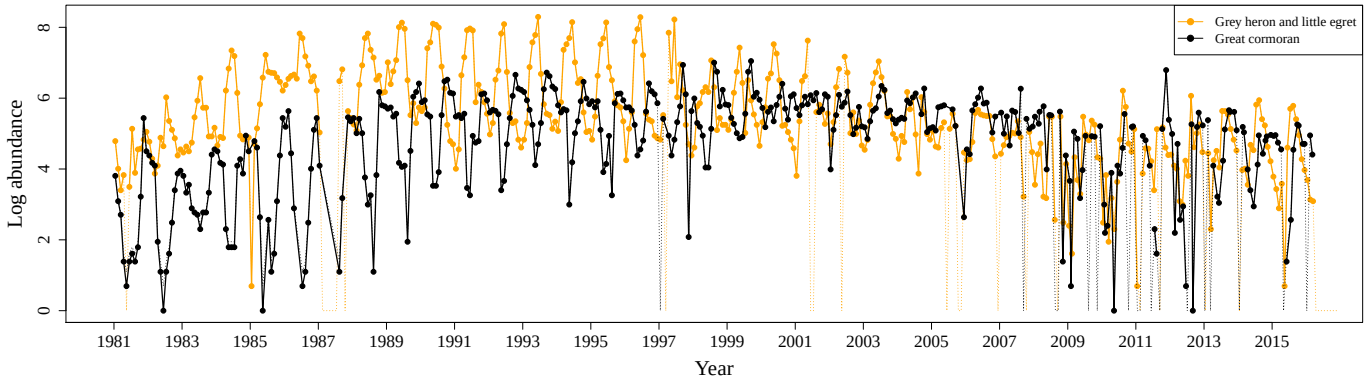

Figure 4: Time series of great cormoran abundance, as well as summed abundances of grey heron and little egret (logarithmic scale).

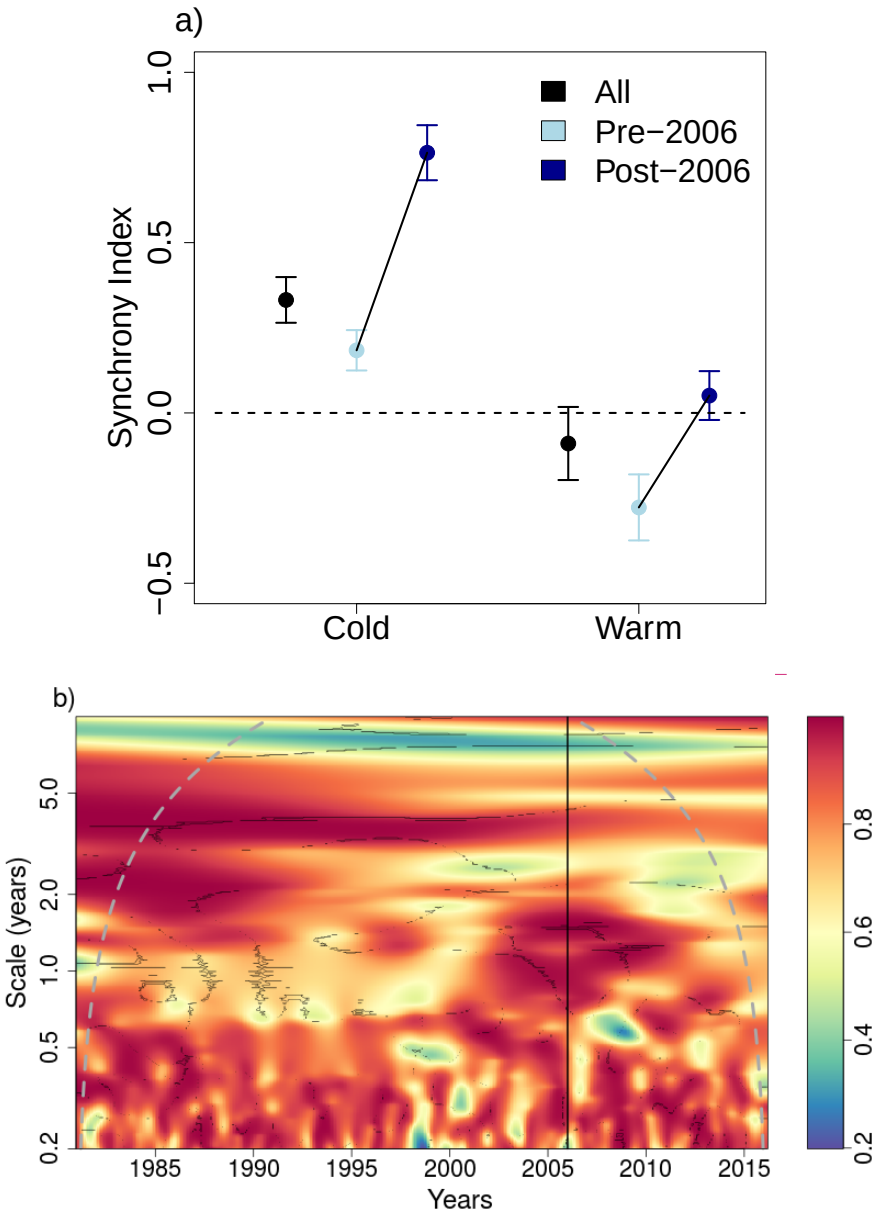

Figure 5: Time-domain (a) and frequency-domain (b) synchrony analyses of the group formed by cormorant, egret and heron (see the captions of Fig. 2 and Fig. 3 for symbol interpretation)

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 is in fact the rule around the annual scale and below, when considering the wavelet index. We wondered

if the patterns in Fig. 4 were caused by the use of a log scale, but we found that in fact the correlation was higher rather than lower on the log scale (Appendix 2). However, over long temporal scales ($\sim$ 6 years) there seems to be some compensation, which may indicate 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.

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* Gonzalez and Loreau 2009) *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 some compensation *between* guilds.

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 Appendix 3 if 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 (Appendix 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.

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 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 bird species (Gonzalez and Loreau, 2009) as the observed long-term changes in species composition (more waders, proportionally less ducks; Appendix 4) 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, it would be incorrect to conclude that such local compensation is disconnected from regional-scale community dynamics: ~~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.~~which species are present in the reserve affects ~~[?? missing a word ??]~~ their reproductive success, which feeds back into regional-scale dynamics, and in turn, regional-scale dynamics influences which species are locally settling and competing.

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 slow replacement of species 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 the typical temporal autocorrelation ~~at~~ 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 (Vasseur and Gaedke, 2007; Gonzalez and Loreau, 2009), below the timescale of the main synchronizing seasonal environmental driver, –in order to filter out ~~the~~its synchronizing –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 and generation times are much lower, we could have expected compensation to manifest also that scale here as well (e.g., monthly). ~~M~~Indeed, movement of birds reacting to food availability can certainly occur ~~that fast~~within the season, and wetlands have a finite carrying capacity, which could promote such short-term compensation. We suspect that instead, because many species share common abiotic and biotic drivers ~~at short temporal scales (Loreau and de Mazancourt, 2008), compensation is bound to be quite rare~~even below the dominant temporal scale of the environment, 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 (Vasseur et al., 2014). 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 (Ranta et al., 2008). 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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