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 more 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.

3. We analyze a 35-year monthly survey of a community where we suspected that compensation might occur due to changes in water levels, favouring birds with different habitat preferences, and potential competition. We perform both yearly analyses by season, using a synchrony index, and monthly analyses using wavelet-based measures allowing for scale-dependence. We analyse synchrony both within and between guilds, with guilds defined either through phylogeny or more functional groups.

4. We find that abundance compensation is 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 synchrony varies with taxonomic and functional scale: the rare cases where compensation appeared consistently were *between* rather than *within* guilds, using functional groups.

5. Although most research has focused on viewing compensation vs synchrony across temporal scales, because synchrony is guaranteed at the temporal scale of the dominant environmental forcing, our results suggest that compensation can be masked as well at some taxonomic or functional scales. We suggest that abundance compensation may have more potential to emerge between broad functional groups, rather between species.

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Introduction

Density compensation occurs when individuals of a given species replace individuals of other species within a community, either because of explicit competitive processes or shifts in environmental drivers that change selection pressures (Gonzalez and Loreau, 2009). The community as a whole then exhibits lower biomass variation than its constituent species (Gross et al., 2013): some degree of compensation or asynchrony is therefore a prerequisite to stabilization at the community level (Loreau and de Mazancourt, 2013).

Understanding why environmental variation may lead to compensation is relatively easy,: if species have different 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 also depend on the particulars of the interactions between and within species in the community.

Compensation is particularly likely to occur when such temporal environmental variation combines with a space or strongly limiting resource constraint, so that individuals are close to competing 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, 2013), though this depends on the fluctuation regime. Thus, in a world where total community size varies, predicting whether compensatory (asynchronous) dynamics can occur is intrinsically

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68 difficult (van Klink et al., 2019)

69 Early investigations of the frequency of synchronous vs compensatory dynamics focused
70 on the variance ratio, that is, the variance of the sum of the community biomass divided
71 by the sum of the variance of the component species biomasses (Houlahan et al., 2007;
72 Gonzalez and Loreau, 2009). Unfortunately, this metric is not appropriate for communities
73 subjected to community-wide environmental forcing (Ranta et al., 2008), because a main
74 environmental driver (e.g., temperature or light) may synchronize species abundances or
75 growth rates at some scale, creating large variance in community-wide biomass, in spite of
76 strongly competitive dynamics. Further research has therefore focused on specific timeframes
77 during which compensatory dynamics may be found (e.g., below the seasonal scale at which
78 temperature fluctuations tend to synchronize species dynamics, Vasseur et al., 2014).

79 Despite efforts to look for more meaningful temporal scales in community-level time series,
80 temporal compensation has remained surprisingly elusive in the field (Houlahan et al., 2007;
81 Vasseur et al., 2014); but see Ernest et al. (2008); Christensen et al. (2018). Most datasets
82 used so far to evaluate temporal compensation vs synchrony involve planktonic organisms
83 (Vasseur and Gaedke, 2007; Vasseur et al., 2014) or terrestrial plants (Houlahan et al., 2007;
84 Gross et al., 2013; though see Bell et al. 2014 in fishes and van Klink et al., 2019 in beetles).
85 Here, we take advantage of a long-term bird time series record at the monthly scale (over 35
86 years), in a natural reserve, allowing us to dig deeper into patterns of synchrony, at several
87 temporal and taxonomic or functional scales.

88 Indeed, taxonomic and functional scales should be main modulators of synchrony/compensation.
89 On the one hand, compensation can be high between similar and closely related species. If
90 two species of ducks A and B share almost the same niche, individuals from either species
91 experience similar competition from species A or B, and should feel the effects of other species
92 in the community identically. This favours priority effects (Fukami, 2015), with chance due
93 to movement events determining whether species A or B locally dominates, which can then

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provide compensation at the landscape level (Loreau et al., 2003). 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. Hence, more dissimilar species or groups (within the same trophic level nonetheless) could exhibit more compensation (Morin et al., 2014; van Klink et al., 2019) because they are more likely to respond to the environment in an asynchronous manner (sensu Loreau and de Mazancourt, 2013). Surprisingly, such compensation *between* guilds has been less well explored empirically than *within* guilds, even though there is actually some empirical evidence for compensation between dissimilar guilds (e.g., Roscher et al., 2011; Sinclair et al., 2013; van Klink et al., 2019). In this paper, we explore the level of compensation/synchrony within or between guilds of a wetland bird community, along either taxonomic or functional classifications. Although a functional classification might appear intuitively more appealing, our knowledge of functional traits is necessarily partial and imperfect, so that a taxonomic description can sometimes be preferable (Clark, 2016).

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. A species list of the frequent birds is provided in SI Appendix S1. The reserve comprises 120 ha of wetlands, and the counts have been aggregated at the reserve scale (summed over 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 communicating their findings to the reserve staff), we consider that the absence of counts for a given species 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 sub-sample of a regional population) because doing so would have compromised the patterns of local synchrony/compensation. However, we did check below that having such zeroes in the monthly time series cannot affect our conclusions. In the statistical analyses, we use seasonally averaged abundances (plotted in Fig. 1), as well as the original monthly data (presented in SI Appendix S2). 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

₁₄₀ respond differentially to abiotic drivers. It is also useful from a more statistical perspective, as

₁₄₁ there is a shift in composition between the seasons, though winter and summer communities

₁₄₂ partially overlap due to a number of shared species.

₁₄₃ Fig. 1 shows the patterns in abundance for key groups in the Teich reserve bird commu-

₁₄₄ nity, showing the marked signature of seasonality.

Figure 1: Time series of seasonally averaged abundance for ducks of the tribe *Anatini* (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).

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Bird taxonomic and functional groups

The reserve is dominated by waders and waterfowl (ducks, geese and swans). These two functional groups collectively represent 68% of the total number of observed birds over the years and are always present on site. Two fairly common phylogenetic groups, both in abundance and occurrence, are members of the *Anatini* tribe (corresponding previously to the *Anas* genus, Gonzalez et al., 2009) in ducks and members of the *Calidris* genus in waders. Waders and ducks have different environmental preferences, with ducks (and waterfowl more generally) preferring water levels allowing them to dive, while waders usually forage on mudflats. A list of all birds found frequently in the reserve is presented in SI Appendix S1; aside from waders and waterfowl, other common species includes herons, egrets and cormorants (see below). Among the fish eaters, grebes and gulls were also present; a few raptors as well.

To examine compensation *between* and *within* the waders and waterfowl categories, we contrasted analyses using a taxonomic classification of the species (i.e., between and within phylogenetic groups such as genera) and a functional classification of the species (26 species of waders vs 17 species of waterfowl). The waterfowl group includes all anatids (ducks, geese and swans in particular) as well as the common coot *(Fulica atra*, an abundant species here, which is a Rallidae but as all coots, resembling a duck in morphology and foraging habits; hence its inclusion).

In addition to our main analyses on waders and waterfowl, we also "zoomed in" on a set 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).

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).

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

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 $\times$ season scale 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, we averaged monthly bird abundances, for each species, over the season duration. We then computed the synchrony index for both cold and warm seasons using the year as our statistical unit. In follow-up analyses, 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 *Calidris* genus) or between groups (e.g., between the summed abundances of the 7 species of tribe *Anatini* and the sum of the 7 *Calidris* species). In the latter case of between-groups comparisons,

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we summed species together before seasonal averaging, to consider seasonal averages of the monthly group-level abundance.

We computed the statistical significance of the synchrony index by comparing the observed values to the distribution of η under the null hypothesis (Gouhier and Guichard, 2014), which amounts to zero cross-correlations between species abundances (or guild-level abundances when considering functional groups). The challenge to construct such null hypothesis is to remove all cross-correlations while keeping the exact same autocorrelation in each individual time series. Therefore, for each set of time series (each combination year × season for a given community), we constructed 100 "surrogates" in which we kept auto-correlations but removed cross-correlations between time series. There are multiple ways to erase cross-correlations depending on the resolution of the considered community. Within communities, we shifted the time-series (Purves and Law, 2002) while between communities, we used a frequency-based approach (Iterated Amplitude-Adjusted Fourier Transform or IAAFT, see Schreiber and Schmitz, 2000). We first explain the shift-based approach: the suite of abundance values (after seasonal averaging) is displaced by a random temporal lag τ, so that a value y_t is now found at $y_{t+\tau}$. At the boundary (the end of the time series), remaining points are displaced towards the beginning of the time-series, which implements a toroidal shift. This methods works well when comparing many times series corresponding to the multiple species. However, when computing synchrony across –only two groups ("between guilds"), , spurious cross-correlations could emerge with a shift-based approach as the number of possible combinations is more limited. Therefore, to test for synchrony between the summed abundances of two guilds or taxonomic units, we used the more refined IAAFT method (Schreiber and Schmitz, 2000), which retains the frequency spectrum of the time series while randomizing its values. We obtained 100 sets of randomized time series for each computed synchrony index. We then compared the number of η_{H0} values which exceeded or were inferior to the observed value to compute the p-value according to North et al. (2002) (i.e., using the ratio $(r + 1)/(n + 1)$

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₂₁₇ where r is the number of surrogate values that are $\geq \eta_{obs}$ (respectively $\leq \eta_{obs}$) and n is the

₂₁₈ number of surrogates). Independence of species was rejected at the 10% threshold with a

₂₁₉ Benjamini-Hochberg correction, as we compare across 2 seasons and 3 periods, with partially

₂₂₀ overlapping data. This was found satisfactory based on simulated data, although power is low

₂₂₁ for detecting compensation (i.e., the null cannot always be rejected) when only two groups

₂₂₂ are compared.

₂₂₃ **Wavelet analyses**

₂₂₄ In addition to the time-domain analyses above, we performed frequency-domain analyses for

₂₂₅ a range of temporal scales ranging from a few months to years. This was done in particular

₂₂₆ for analyzing synchrony within the rich wader community, as well as the group formed by the

₂₂₇ great cormorant, grey heron and little egret.All wavelet analyses take as input the monthly

₂₂₈ time series data. Based on the work by Keitt (2008) and follow-up by Vasseur et al. (2014),

₂₂₉ we used the wavelet transform of the time series to measure the coherency between time

₂₃₀ series

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

₂₃₁ where $w_k(\tau,s)$ is the continuous Morlet wavelet transform of species k at time τ for

₂₃₂ scale s, $\Lambda_{t,s}(\bullet) = \int_{-\infty}^{+\infty} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2}(\bullet)d\tau$ and $|\bullet|$ is the modulus of the complex number. The

₂₃₃ numerator corresponds to the total abundance variation while the denominator corresponds

₂₃₄ to the fluctuations of each species. This index is close to 0 when species compensate and

₂₃₅ reaches 1 when they are synchronous. As before, the significance of each value was tested

₂₃₆ at the 10%, Benjamini-Hochberg corrected, threshold by 100 phase-randomizations of each

₂₃₇ species time series, and computation of the corresponding ρ values. The robustness of the

₂₃₈ wavelet approach to the presence of exactly zero values is tested in SI Appendix S7 [I guess

₂₃₉ we may have to change it to S2 and re-order all of them accordingly later on].

All datasets and statistical analyses are available in a GitHub repository `https://github.com/fbarraquand/BirdTimeSeries_Teich`[1].

Results

Synchrony within phylogenetic or functional groups

Using a taxonomic classification of the community, focusing on the genera *Calidris* and *tribe Anatini* (formerly *Anas*) as two key examples of taxonomic units with contrasted preferences, we can see that within-genus synchrony dominates at the seasonal scale. Using functional groups (waders and waterfowl), synchrony within functional groups was also prominent. The Gross synchrony indices are indeed mostly positive, and always positive whenever significantly different from the null hypothesis (no temporal correlation between species). Therefore, there is no compensation within guilds (Fig. 2a and b) at the annual scale. This matches the patterns obtained within the entire wetland bird community (Fig A1 in Appendix S3): synchrony dominates when abundances are computed at the species level.

For the cold season, abundances within *Calidris* and *Anatini* display opposite changes in synchrony values in response to the management change in 2006, with species within *Anatini* becoming less synchronous over time, although we should mention that these changes are not statistically significant. For the warm season, the management change, which consisted of lowering the water levels, created little change in communities of species within the *Anatini* and *Calidris*: they are all synchronous.

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

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[1]Will be made public upon acceptance

₂₆₃ can see that there is synchrony even at a fine temporal scale throughout most of the time

₂₆₄ series. However, post-2006, there seems to be a possibility for compensation on a temporal

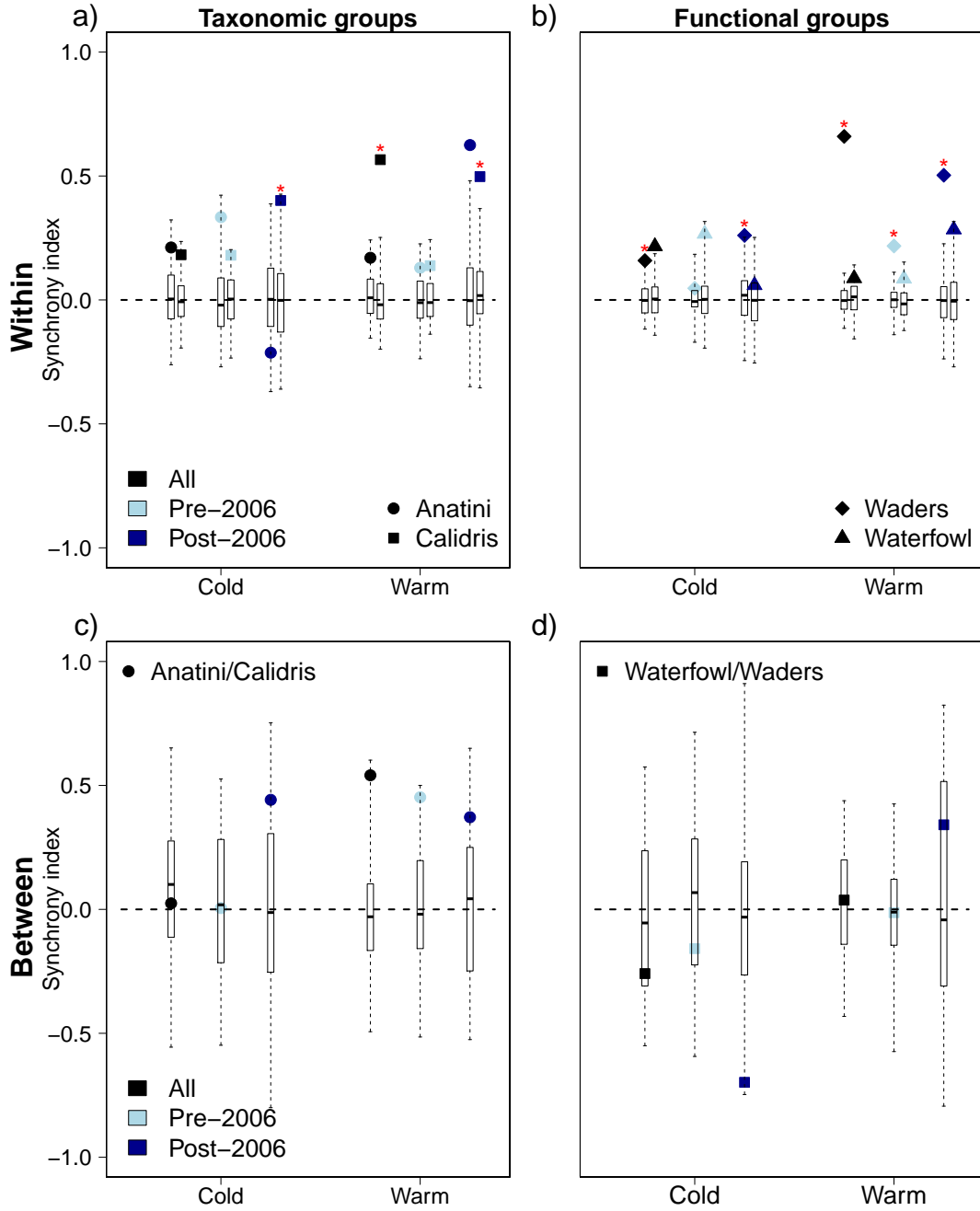₂₆₅ scale of approximatively 5 years or 3-4 months.

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 (waders vs waterfowl, right b-d) or taxonomic groups (*Anatini*, *Calidris*, left a-b). 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. Boxplots indicate the distribution of η under the null hypothesis (independent species) and filled symbols correspond to the observed values. Red stars correspond to synchrony values significantly different from the null model, at the 10% threshold with a Benjamini-Hochberg correction.

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There are therefore contrasted results regarding the effect of the management change on –synchrony within guilds or within the whole bird community. At the yearly (season) timescale, the results are unclear for both guilds. At shorter (a few months) and longer (several years) timescales though, the management change may decrease synchrony and even promote compensation.
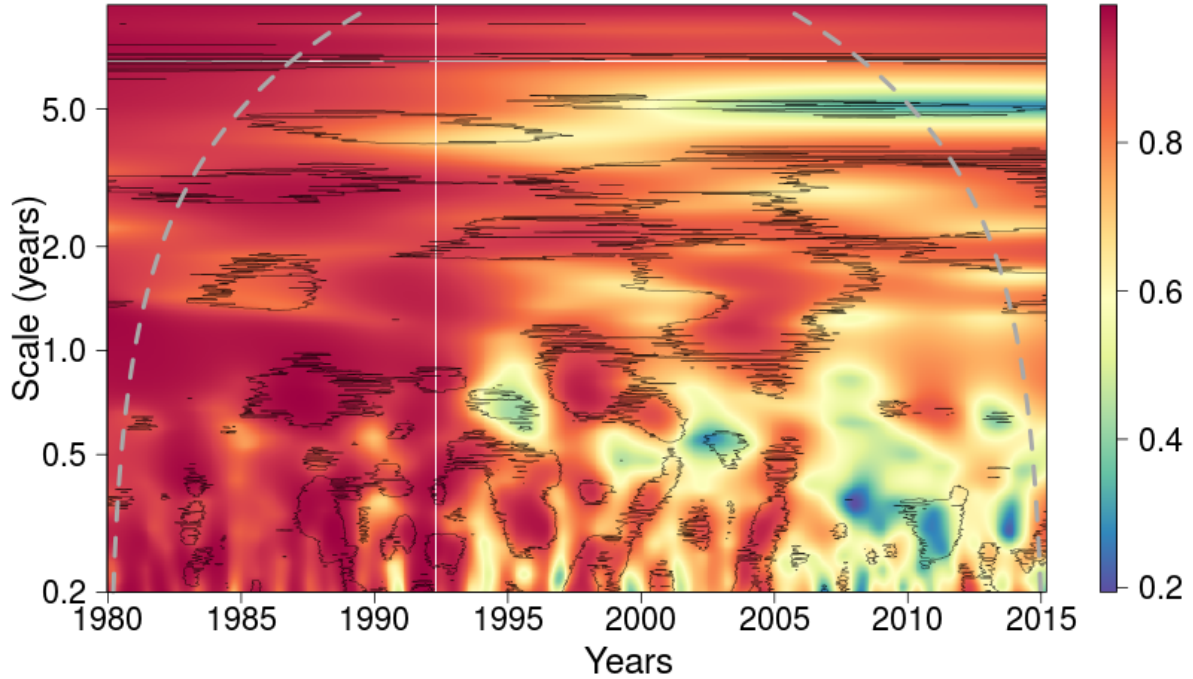

Figure 3: Wavelet modulus ratio for the wader community, scaling from 0 (compensation, blue color) to 1 (synchrony, red color). Dashed black lines delineate regions significantly different from the null model (independently fluctuating species) with a false discovery rate controlled at the 10% threshold.

Synchrony between phylogenetic or functional groups

More interpretable results can be found when we examine the synchrony vs compensation between functional groups (Fig. 2d). Since we consider only two functional or phylogenetic groups, the Gross index reduces to a simple correlation between two groups. *Anatini* and *Calidris* are positively correlated in the warm season (for all periods), and have unclear

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correlations during the cold season (Fig. 2c). In contrast, waders and waterfowl are negatively correlated during the cold season and positively correlated during the warm season (Fig. 2d). Although the negative correlation is not statistically significant, it is consistent for both pre- and post-2006 periods. .

Synchrony in a small module with known competition

Compensation could be expected upon visual inspection of the time series of the two groups formed by cormorant on the one hand, and little egret plus grey heron (summed as a small functional group) on the other hand (Fig. 4, though see SI Appendix S4 for alternative representations). However, 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 could correspond to the progressive change in composition within this small community module, that was already visible on the abundance 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.
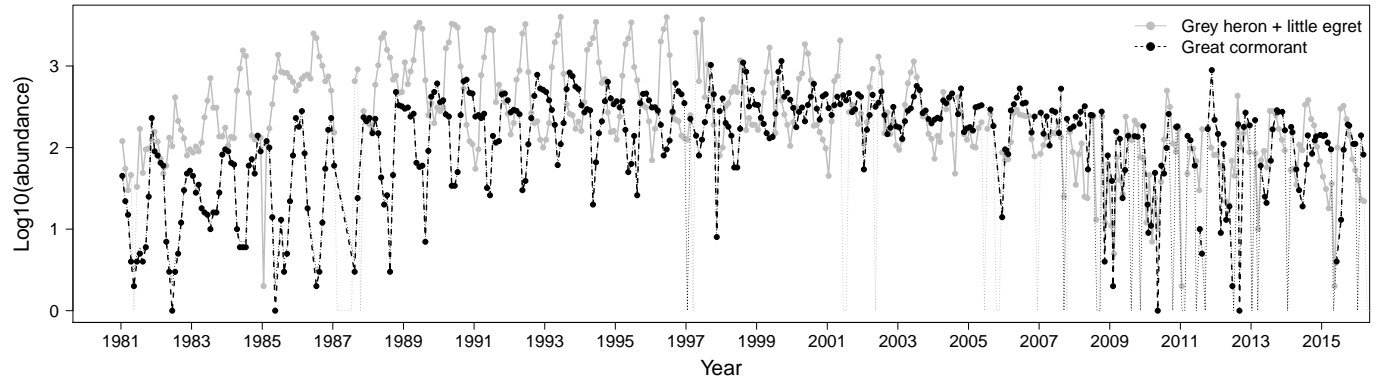
Figure 4: Time series of great cormorant abundance (dash-dotted black line), as well as summed abundances of grey heron and little egret (solid grey line).
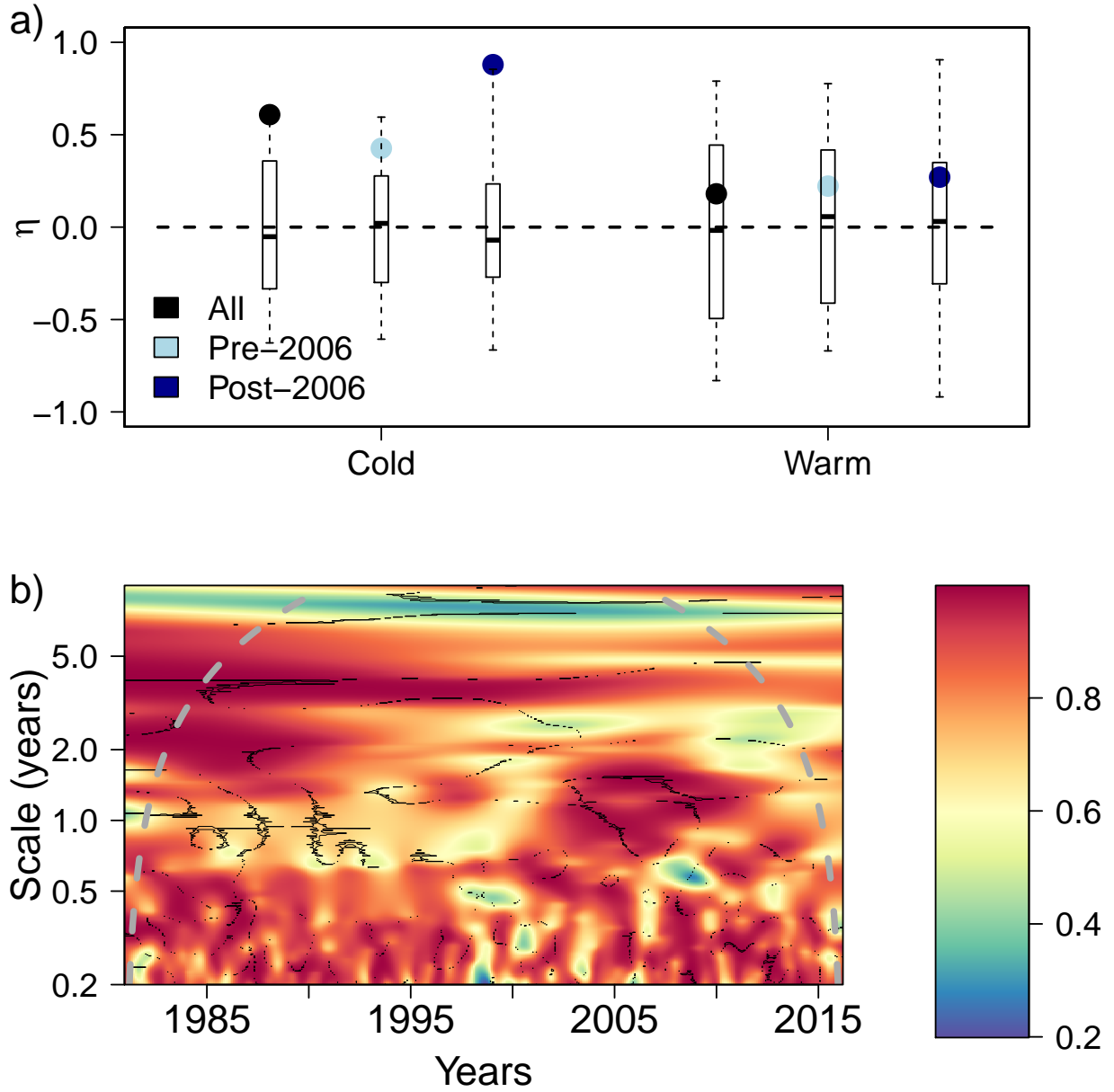
Figure 5: Time-domain (a) and frequency-domain (b) synchrony analyses of the group formed by cormorant, egret and heron (see the captions of Fig. 2 and Fig. 3 for symbol interpretation)

Discussion

Compensation was overall very rare at the yearly timescale (differentiating between the cold and warm season), with synchrony between species being the rule. 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 total abundance of contrasted guilds, it was possible to find some compensation (although the null hypothesis of no correlation could not be rejected); in other words, there was some compensation *between* guilds. A zoom on a module of three species with known competition also revealed compensation at scales above 5 years. Similar results have been obtained using biomass in place of abundance (SI Appendix S5). We elaborate below on these findings.–

Synchrony *within* or *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 S6 if changing the number of "compartments" (n) in the Gross η index could affect its value: it did not have marked effects, unless the number of compartments is equal to 2, in which case, significance is hard to achieve and some compensatory dynamics can be missed with weak environmental response. However, we found that if two guilds 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 S2), in spite of the clear presence of two guilds (waders and waterfowl) reacting in opposite way to shared driver (here, water levels). Analyses at several taxonomic/functional scales are therefore warranted to be conclusive about compensation.

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We used correlation between the summed abundances of closely related species (species within the *Anatini* tribe vs species within the *Calidris* genus) or the summed abundances of functionally similar species (waders vs waterfowl) to uncover compensation. The functional group classification produced some compensation between guilds while the taxonomic classification did not, despite the contrasted habitat preferences of these two phylogenetic groups. Using functional group produced more logical results, although as we stressed above, the null hypothesis of no compensation at the yearly scale is still plausible as well.

We expected to see compensation at the "functional group scale" irrespective of the season, because the requirements of these birds are different, but waders and waterfowl were found to correlate negatively only during the cold (wintering) season. This can be explained by a broad inflow of birds in the summer, including non-resident individuals that 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 waterfowl; SI Appendix S2) might be due to an increased inflow of birds preferring low water levels (waders), and outflow of birds preferring high water levels (waterfowl), 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: which species are present in the reserve affects their reproductive success, which feeds back into regional-scale dynamics, and in turn, regional-scale dynamics influences which species are locally settling and competing.

Effect of the change in management on synchrony

Although we performed analyses throughout the whole time series, in which there is a progressive change in composition (Appendix S1), a marked change in management occured

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around 2006, after which the water levels were kept at a lower level. We have therefore also performed yearly analyses pre- and post-2006. These showed very little differences during either the warm or cold season. However, in the wavelet analyses, we see at monthly or 5-year timescales more compensation after 2006. Since the water levels are on average more appropriate for waders and their overall proportion has increased, it may be tempting to interpret this as a consequence of the community becoming saturated with waders, but we caution that it is difficult to make any strong conclusion based on a single synchrony index. Similar analyses on beetle communities by van Klink et al. (2019) found little effect of disturbances on synchrony patterns, even though in theory such disturbances should promote synchrony. In fact, like us, they might have found a little less synchrony after disturbance, but the results were not clear cut. We now describe a case where the biological processes at hand are better understood.

Synchrony in a small module with known competition

Zooming in on the cormorant-heron-egret module, for which we knew beforehand that competition for resting/roosting sites in the summer season occurs between on the one hand, cormorants, and on the other hand, little egrets and grey herons (C. Feigné, pers. obs.). Abundance time series suggested some negative correlation, but it was not found on the annual scale for which synchrony (or an absence of relation) dominates. Instead, we find that compensation mostly occurs above the annual temporal scale, approximatively on a scale of 6 years, much above the annual scale. . This may indeed be a consequence of the slow shift in frequencies cormorants and little egrets / grey herons.

Conclusion and perspectives for theory

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 autocorre-

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lation of the dominant driver (e.g., above 5 years if the main driver is a seasonal climate). This rejoins the recent findings of van Klink et al. (2019) who found that increased functional differences between species tend to decrease synchrony. Our suggestion goes against calls to search for compensation within closely related species but 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 its synchronizing effect. 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, with much shorter generation times, we could have expected compensation to manifest also at that scale here as well (e.g., monthly). Indeed, movement of birds reacting to food availability can certainly occur within the season, and wetlands have a finite carrying capacity, so that there is competition for space, which could promote short-term compensation. We suspect that instead, because many species share common abiotic and biotic drivers (e.g., disturbances due to nearby hunting) even below the yearly timescale, their dynamics are bound to be synchronized to some degree even below the yearly scale.

The attractor of community dynamics, i.e., the shape of community trajectories in phase space, seems to be more or less an annual cycle here: the dominant species fluctuate seasonally, but even though there are shifts in some species dynamics, no abundant species seem to exhibit violent multi-year oscillations. If we had to describe our community mathematically, a dynamical model with a stable fixed point forced by seasonality and some noise would probably work nicely. This mild fluctuation scenario somehow constrasts with the dynamics of other communities, such as insect pests, that have quite often multi-year cycles (on top of seasonal cycles, for multivoltine species), with possibly strong indirect interactions between similar species mediated by predators and parasitoids (Murdoch et al., 2003). In this latter context of internally-generated variability ("Endogenous compensatory cycles" in Gonzalez and Loreau, 2009), compensation is quite likely as well. Klapwijk et al. (2018)

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recently reported only transient synchrony between species of moths, so that compensation could occur more frequently for more strongly oscillating species. Therefore, compensation could be more likely for those groups at the yearly timescale. Whether or not these findings have some generality remains to be investigated by examining multi-species synchrony for more varied animal taxa.

In many ways, searching for abundance 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; Loreau and de Mazancourt, 2008). This is true even in cases of known mechanisms of competition for space or shifts in community composition due to abiotic changes affecting differentially species preferences, as in this study. We therefore suggest that "zooming out" functionally (considering summed abondances of dissimilar functional groups) and temporally (considering temporal scales well above the periodicity of the dominant abiotic driver) may often be the best strategy to see the compensation that will inevitably manifest if the community-level biomass is to be maintained within bounds in the long run.–

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