Looking for compensation at multiple scales in a wetland bird community

Journal:	*Ecology*
Manuscript ID	Draft
Wiley - Manuscript type:	Reports
Date Submitted by the Author:	n/a
Complete List of Authors:	Barraquand, Frédéric; University of Bordeaux, Picoche, Coralie; University of Bordeaux, Aluome, Christelle; INRA ISPA Carassou, Laure; Irstea Centre de Bordeaux, Waters; University of Bordeaux Labex Cote, Integrative Theoretical Ecology chair Feigné, Claude; PNR Landes Gascognes
Substantive Area:	Community Ecology < Substantive Area, Community Analysis/Structure/Stability < Community Ecology < Substantive Area, Disturbance < Community Ecology < Substantive Area, Species Interactions < Community Ecology < Substantive Area, Niche Relationships/Resource Partitioning < Species Interactions < Community Ecology < Substantive Area, Regional Studies < Ecosystems < Substantive Area, Statistics and Modeling < Theory < Substantive Area, Reserves/Protected Areas < Management < Substantive Area, Data < Substantive Area
Organism:	Birds (specify type in field below) < Vertebrates < Animals
Habitat:	Wetlands/Swamps/Bogs < Freshwater < Aquatic Habitat < Habitat
Geographic Area:	Western Europe < Europe < Geographic Area
Additional Keywords:	compensation, synchrony, wavelets, biodiversity, time series
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. We take advantage of a long-term wetland bird community time series of 35 years, where we suspected that compensation might occur due to changes in water levels and known trends. We find that compensatory dynamics are still rare, likely due to the synchronizing influence of climate on birds, even after considering several temporal scales of covariation (during cold or warm seasons, above or below the seasonal scale). Negative covariation in abundance at the whole community level did only appear after a management change in the reserve, and at the scale of a few months or several years. Although most research has

| | focused on the temporal scale of compensation vs synchrony, 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. |
| | |

Looking for compensation at multiple scales in a wetland bird community

Frédéric Barraquand[1,2,*], Coralie Picoche[1], Christelle Aluome[1,3], Laure Carassou[1,4] & Claude Feigné[5]

October 27, 2018

[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

1

1 **Abstract**

2   Compensatory dynamics, during which community composition shifts despite a
3 near-constant total community size, are usually rare: synchronous dynamics prevail
4 in natural communities. This is a puzzle for ecologists, because of the key role of com-
5 pensation to explain the relation between biodiversity and ecosystem functioning. We
6 take advantage of a long-term wetland bird community time series of 35 years, where
7 we suspected that compensation might occur due to changes in water levels and known
8 trends. We find that compensatory dynamics are still rare, likely due to the synchro-
9 nizing influence of climate on birds, even after considering several temporal scales of
10 covariation (during cold or warm seasons, above or below the seasonal scale). Negative
11 covariation in abundance at the whole community level did only appear after a manage-
12 ment change in the reserve, and at the scale of a few months or several years. Although
13 most research has focused on the temporal scale of compensation vs synchrony, we
14 found that compensation varies with taxonomic and functional scale too: compensa-
15 tion appeared more frequently between rather than within guilds. This suggests that
16 compensation has more potential to emerge between broad functional groups rather
17 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. This is particularly likely to occur when there is a space or resource constraint combined with temporal environmental variability. Which species "win" at any particular point in time may then depend on the fine-grained temporal environmental variation, or just on priority effects (i.e., who gets there first). Whatever the cause of compensatory dynamics, its main consequences for ecosystem functioning is that the community as a whole exhibits lower biomass variation than its constituent species (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 observed outcome on biodiversity time series is synchrony (Vasseur et al., 2014). 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 (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 compensatory dynamics may be found (e.g., below the seasonal scale where temperature fluctuations

3

tend to synchronize species dynamics, Vasseur et al., 2014).

Despite this effort 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 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 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

---

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

69 as a function of changes in vegetation height). Surprisingly, such compensation *between* guilds

70 has been less well explored than within guilds, even though there is actually some empirical

71 evidence for compensation between dissimilar guilds (e.g. Sinclair et al., 2013). In this paper,

72 we explore different ways to cluster the bird community, within or between guilds, along

73 either taxonomic or functional classifications.

74   Our objective is therefore to examine how synchronous or compensatory bird communities

75 are at different temporal and taxonomic (or functional) scales. Our dataset is ideally suited

76 to the task given that (i) it is a highly temporally resolved time series with respect to the

77 species typical generation times, but it also extends well beyond generation time (35 years)

78 and (ii) the reserve where the data has been collected was subjected to a major management

79 change c. 2006 (change in water levels), favoring different types of wetland birds (so that

80 over long timescales, there is a real potential for changes in community composition).

Material and Methods

Data

83 The monthly time series used for the statistical analyses have been collected at the Teich

84 Ornithological Reserve, Arcachon Bay, France (44.64°N / -1.02°E), by the staff of the Teich

85 reserve. The reserve comprises 120 ha of wetlands, and the counts have been aggregated at

86 the reserve scale. We use for each species the maximum observed abundance over a month,

87 which provides a "monthly snapshot" of the bird abundance. In the statistical analyses, we

88 use both the original monthly data and seasonal averages. We defined two seasons based on

89 observations of bird presence. We defined a 'warm season', from May to August, and a 'cold

90 season' as the months between November and February of the following year. From an eco-

91 logical viewpoint, this seasonal classification separates wintering birds from summer residents

92 (some of whom are breeding). This makes sense biologically because the two communities

5

93 have different requirements and respond differentially to abiotic drivers. It is also useful from

94 a more statistical perspective, as there is a shift in composition between the seasons, though

95 winter and summer communities partially overlap due to a number of shared species.

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

97 nity, showing the marked signature of seasonality.

Statistical Analyses

99 We used for yearly analyses the synchrony index η defined by Gross et al. (2013), which

100 is constructed as the mean cross-correlation between each species biomass and the summed

101 biomasses of the rest of the community (eq. 1).

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

102 where P_i is the abundance or biomass of species i in a community of n species. This syn-

103 chrony index described in eq. 1 varies between -1 (perfect compensation, total biomass is

104 constant) and 1 (complete synchrony), while 0 represents a case where all populations fluc-

105 tuate independently. Contrary to other indices (e.g., Loreau and de Mazancourt (2008)'s ϕ),

106 this index is independent from the richness n of the community (or more generally the num-

107 ber of system components) and its overall stability (Hallett et al., 2016). This is particularly

108 important here as we perform analyses at different taxonomic scales, and therefore with a

109 different n in eq. 1.

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

111 warm season each year) using the codyn package in R (Hallett et al., 2016). We averaged

112 monthly bird abundances, for each species, over the season duration, and computed the

113 synchrony index using the year as our statistical unit. We also differentiated periods before

114 and after 2006, given that a management change occurred within the reserve in 2006. We

6

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 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 ran-
domizations (Gouhier and Guichard, 2014). For each set of time series (each combination
year × 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 con-
sidered and computed the corresponding synchrony index. We then compared the observed
values of η to the values obtained with the randomized time-series. Independence of species
was rejected at the Bonferroni-corrected 10% threshold. In addition to the time-domain anal-
yses above, we performed frequency-domain analyses, in particular for analyzing synchrony
within the rich wader community, as well as the group formed by the great cormorant, grey

141 heron and little egret. Based on the work by Keitt (2008) and follow-up by Vasseur et al.

142 (2014), we used the wavelet transform of the time series to measure the coherency between

143 time series

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

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

145 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

146 numerator corresponds to the total biomass variation while the denominator corresponds to

147 the variations of each species. This index is close to 0 when species compensate and reaches

148 1 when they are synchronous. As before, the significance of each value was tested at the 10%,

149 Bonferroni-corrected, threshold by 100 phase-randomizations of each species time series, and

150 computation of the corresponding ρ values.

151 All datasets and statistical analyses are available in a GitHub repository `https://github.`

152 `com/fbarraquand/BirdTimeSeries_Teich`[2].

Results

153

154 Using a taxonomic classification of the community (focusing on the genera *Calidris* and *Anas*

155 as two key examples of contrasted birds), we can see that within-genus synchrony indices at

156 the seasonal scale are always positive whenever significantly different from the null hypothesis

157 (no temporal correlation between species), i.e. there is no compensation within a genus (Fig.

158 2). This matches the patterns obtained within the entire wetland bird community (Fig A1 in

159 Appendix 1). For the cold season, *Calidris* and *Anas* exhibit opposite trends in synchrony in

160 response to the management change in 2006. However, for the warm season, the management

161 change, which consisted in lowering the water levels, created more synchronous communities

---

[2]Made public upon acceptance and archived in Zenodo

162 of species within the *Anas* and *Calidris* genera. This increase in synchrony after 2006 is

163 matched by the functional group classification.

164 Even though there is no widespread community-wide or genus-wide compensation at the

165 yearly timescale (differentiating the seasons), there could be compensation at finer temporal

166 scales, e.g. a month or two, or coarser scales, over several years. When we consider the

167 wavelet plot (Fig. 3), that is a time-varying and scale-dependent strength of synchrony, we

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

169 series. However, post-2006, there seems to be a possibility for overcompensation on a scale

170 around 5 years or around 3-4 months.

171 There are therefore relatively contrasted results regarding the effect of the manage-

172 ment change on short-term synchrony within the wader community. At the yearly (season)

173 timescale, it seems to increase the synchrony (though the Gross index and wavelets provide

174 slightly different answers). At even shorter timescales though, it seems to decrease it.

175 More clear-cut results can be found when we examine the synchrony vs compensation

176 between functional groups (Fig. 2d). Since we consider only two functional groups, the

177 Gross index reduces to a simple correlation. Waders and ducks are negatively correlated

178 during the cold season and positively correlated during the warm season. These patterns are

179 in contrast unclear when using a taxonomic classification (no compensation, Fig. 2c).

180 While compensation could be expected upon visual inspection of the time series of the

181 two groups formed by cormorant on the one hand, and egret plus heron (summed as a small

182 functional group) on the other hand (Fig. 4), we see on Fig. 5 that synchrony is in fact the

183 rule around the annual scale and below, when considering the wavelet index. We wondered

184 if the patterns in Fig. 4 were caused by the use of a log scale, but we found that in fact

185 the correlation was higher rather than lower on the log scale (Appendix 2). However, over

186 long temporal scales ($\sim$ 6 years) there seems to be some compensation, which may indicate

187 a progressive change in composition within this small community module, that was already

9

188 visible on the time series plot (Fig. 4). There might be some compensation over very short

189 timescale as well (within the season), but at very specific times and the biological mechanisms

190 for this are unclear, since these species compete for roost sites, a process that it unlikely to

191 manifest at such very short timescales.

192 Discussion

193 Compensation was overall very rare at the yearly timescale (differentiating between the cold

194 and warm season). At short timescales (below the season), and among taxonomically or

195 functionally close species, some compensation could be found but only at certain periods. In

196 other words, there was no widespread "functional compensation" (*sensu* Gonzalez and Loreau

197 2009) *within* genera or guilds at the annual scale or below. Yet, summing species abundances

198 within a guild and comparing the "biomass sums" of contrasted guilds, community composi-

199 tion did change in frequency in the long run; in other words, there was some compensation

200 *between* guilds.

201   Given that we compare the level of synchrony/compensation within guilds (with many

202 species) and between guilds (with only a handful of groups), we checked in Appendix 3 if

203 changing the number of "compartments" (n) in the Gross η index could affect its value: it

204 did not. However, we found that if two groups respond in opposite ways to a shared driver,

205 the stronger the response to the driver, the lesser the compensation indicated by η at the

206 whole community level. This might explain the low levels of compensation that we found at

207 the overall wetland bird community level (Appendix 1), in spite of the clear presence of two

208 groups reacting in opposite way to shared driver (here, water levels). Analyses at several

209 taxonomic/functional scales are therefore warranted to be conclusive about compensation.

210   We used correlation between the summed abundances of closely related species (species

211 within the *Anas* genus vs species within the *Calidris* genus) or the summed abundances of

10

₂₁₂ functionally similar species (waders vs ducks) to uncover compensation. The functional group

₂₁₃ classification produced much more clearly compensation between guilds than the taxonomic

₂₁₄ classification. We expected to see compensation at that "functional scale" irrespective of the

₂₁₅ season, because the requirements of these birds are different, but here waders and ducks were

₂₁₆ found to correlate negatively only during the cold (wintering) season. This may be because

₂₁₇ the summer is characterized by a broad inflow of birds, including non-resident individuals

₂₁₈ that somehow add random variation to the community dynamics (though other explanations

₂₁₉ are possible).

₂₂₀ It may be better to say that we detected "compensation" rather than "compensatory dy-

₂₂₁ namics" between bird species (Gonzalez and Loreau, 2009) as the observed long-term changes

₂₂₂ in species composition (more waders, proportionally less ducks; Appendix 4) might be due

₂₂₃ to an increased inflow of birds preferring low water levels, and outflow of birds preferring

₂₂₄ high water levels, under an overall space constraint. In other words, the shift in community

₂₂₅ dynamics is likely not directly due to birth and deaths. However, despite the importance of

₂₂₆ movements and habitat preference to the local community dynamics, there is certainly also

₂₂₇ an influence of the regional changes in births and deaths on these local dynamics. Zooming

₂₂₈ in on the cormorant-heron-egret module, we find that compensation mostly occurs above the

₂₂₉ annual temporal scale, and predominantly in summer as well as before 2006. This occurs

₂₃₀ because of a slow replacement of species due to competition for resting/roosting sites in the

₂₃₁ summer season (C. Feigné, pers. obs.), which mostly occurred before 2006.

₂₃₂ Overall, our results suggest to search for compensation more often *between* rather than

₂₃₃ *within* functional groups, and over relatively long timescales above that of the dominant

₂₃₄ driver (e.g., above 5 years if the main driver is a seasonal climate). This goes against calls

₂₃₅ to search for compensation at very short timescales (Vasseur and Gaedke, 2007; Gonzalez

₂₃₆ and Loreau, 2009) in order to filter out the effect of the main seasonal driver. Although

₂₃₇ searching for compensation at temporal scales below the seasonal abiotic driver (e.g., tem-

perature) was partly motivated by studies on plankton whose community dynamics are much faster, we could have expected compensation to manifest also that scale here as well (e.g., monthly). Movement of birds reacting to food availability can certainly occur that fast, and wetlands have a finite carrying capacity, which could promote short-term compensation. We suspect that instead, because many species share common abiotic drivers at short temporal scales (Loreau and de Mazancourt, 2008), 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.

Acknowledgements

12

References

Bell, R., M. Fogarty, and J. Collie, 2014. Stability in marine fish communities. *Marine Ecology Progress Series* **504**:221–239.

Christensen, E., D. Harris, and S. Ernest, 2018. Long-term community change through multiple rapid transitions in a desert rodent community. *Ecology* **99**:1523–1529.

Ernest, S. M., J. H. Brown, K. M. Thibault, E. P. White, and J. R. Goheen, 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. *The American Naturalist* **172**:E257–E269.

Gonzalez, A. and M. Loreau, 2009. The causes and consequences of compensatory dynamics in ecological communities. *Annu. Rev. Ecol. Evol. Syst* **40**:393–414.

Gouhier, T. C. and F. Guichard, 2014. Synchrony: quantifying variability in space and time. *Methods in Ecology and Evolution* **5**:524–533.

Gross, K., B. J. Cardinale, J. W. Fox, A. Gonzalez, M. Loreau, H. Wayne Polley, P. B. Reich, and J. van Ruijven, 2013. Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *The American Naturalist* **183**:1–12.

Hallett, L. M., S. K. Jones, A. A. M. MacDonald, M. B. Jones, D. F. B. Flynn, J. Ripplinger, P. Slaughter, C. Gries, and S. L. Collins, 2016. codyn: An r package of community dynamics metrics. *Methods in Ecology and Evolution* **7**:1146–1151.

Houlahan, J. E., D. J. Currie, K. Cottenie, G. S. Cumming, S. M. Ernest, C. S. Findlay, S. D. Fuhlendorf, U. Gaedke, P. Legendre, J. J. Magnuson, and others, 2007. Compensatory dynamics are rare in natural ecological communities. *Proceedings of the National Academy of Sciences* **104**:3273–3277.

13

Keitt, T. H., 2008. Coherent ecological dynamics induced by large-scale disturbance. *Nature* **454**:331–334.

Loreau, M. and C. de Mazancourt, 2008. Species Synchrony and Its Drivers: Neutral and Nonneutral Community Dynamics in Fluctuating Environments. *The American Naturalist* **172**:E48–E66.

Purves, D. W. and R. Law, 2002. Fine-scale spatial structure in a grassland community: quantifying the plant's-eye view. *Journal of Ecology* **90**:121–129.

Ranta, E., V. Kaitala, M. S. Fowler, J. Laakso, L. Ruokolainen, and R. O'Hara, 2008. Detecting compensatory dynamics in competitive communities under environmental forcing. *Oikos* **117**:1907–1911.

Sinclair, A., K. L. Metzger, J. M. Fryxell, C. Packer, A. E. Byrom, M. E. Craft, K. Hampson, T. Lembo, S. M. Durant, G. J. Forrester, et al., 2013. Asynchronous food-web pathways could buffer the response of serengeti predators to el niño southern oscillation. *Ecology* **94**:1123–1130.

Vasseur, D. A., J. W. Fox, A. Gonzalez, R. Adrian, B. E. Beisner, M. R. Helmus, C. Johnson, P. Kratina, C. Kremer, C. de Mazancourt, E. Miller, W. A. Nelson, M. Paterson, J. A. Rusak, J. B. Shurin, and C. F. Steiner, 2014. Synchronous dynamics of zooplankton competitors prevail in temperate lake ecosystems. *Proceedings of the Royal Society B: Biological Sciences* **281**:20140633–20140633.

Vasseur, D. A. and U. Gaedke, 2007. Spectral analysis unmasks synchronous and compensatory dynamics in plankton communities. *Ecology* **88**:2058–2071.

307 # Figure legends

Figure 1: Time series of counts for ducks of the genus *Anas* (a), calidrids (b, *Calidris* genus), and all waders (c, including calidrids). The solid black lines represent trends in summed abundances for each guild, thin dotted lines represent putative trends (when some species are absent). The coloured symbols below the curves represent each species abundances, with species composition on the right side on the donut plots for the most abundant species (over 1% of relative abundance in the group considered).

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.

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)
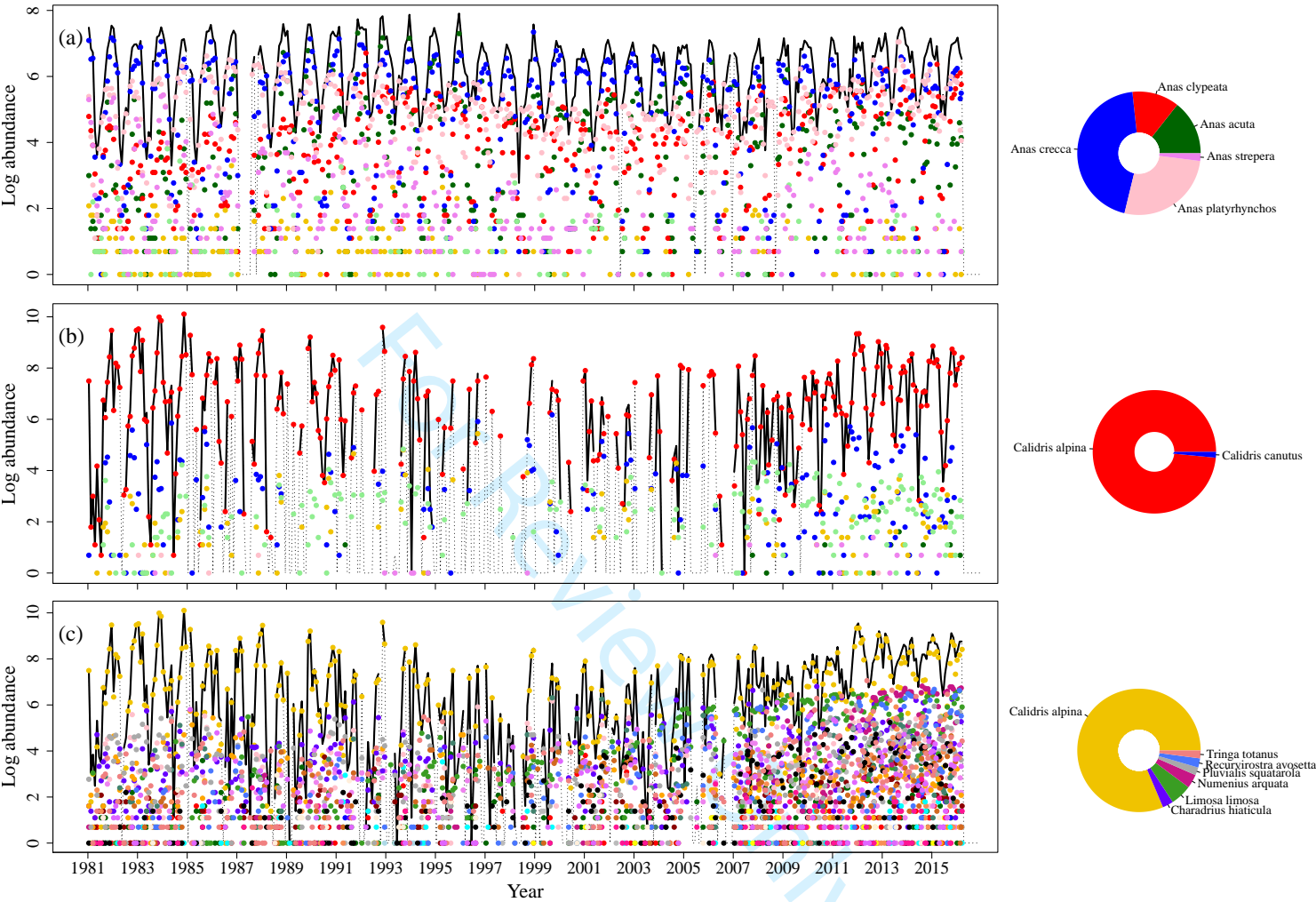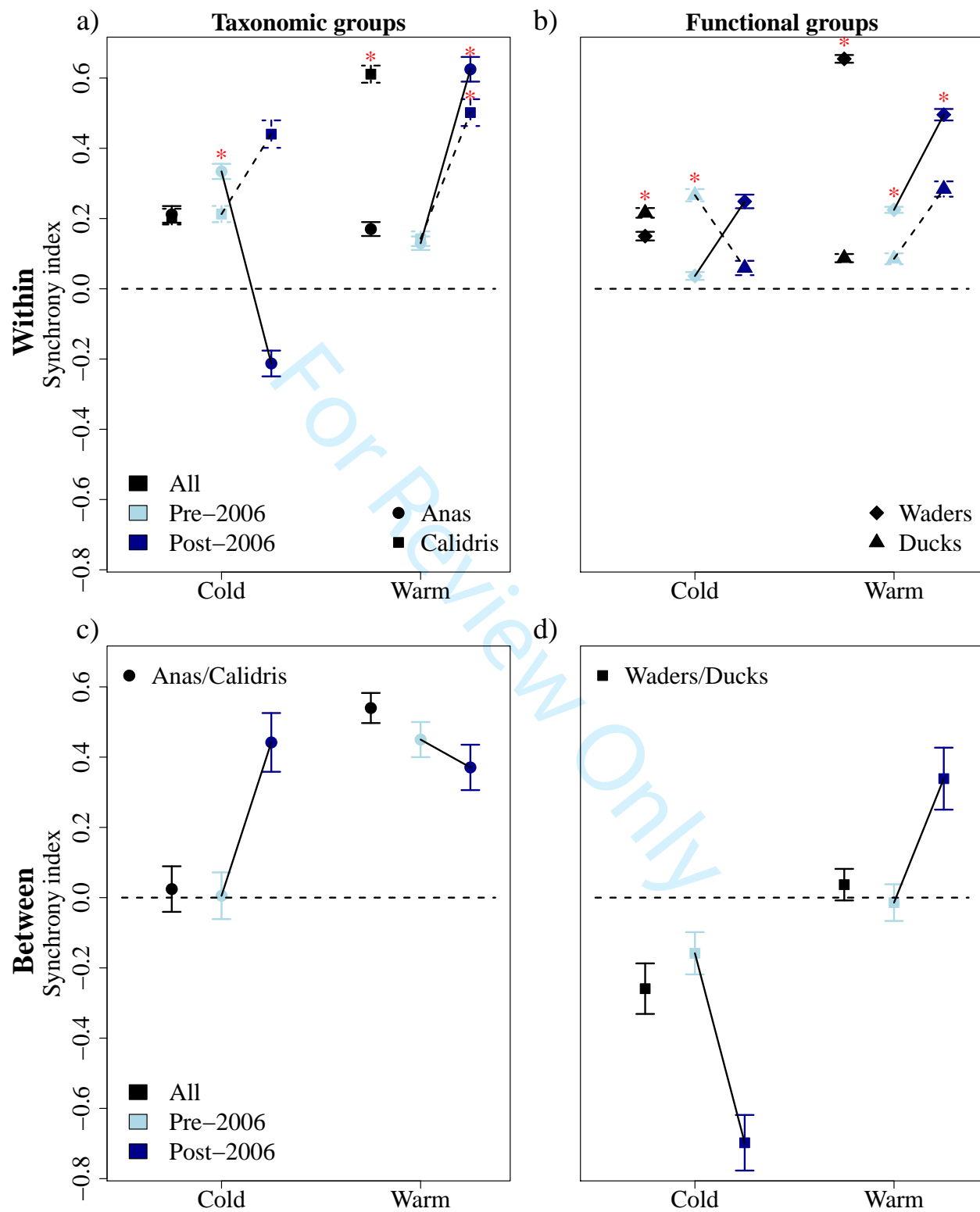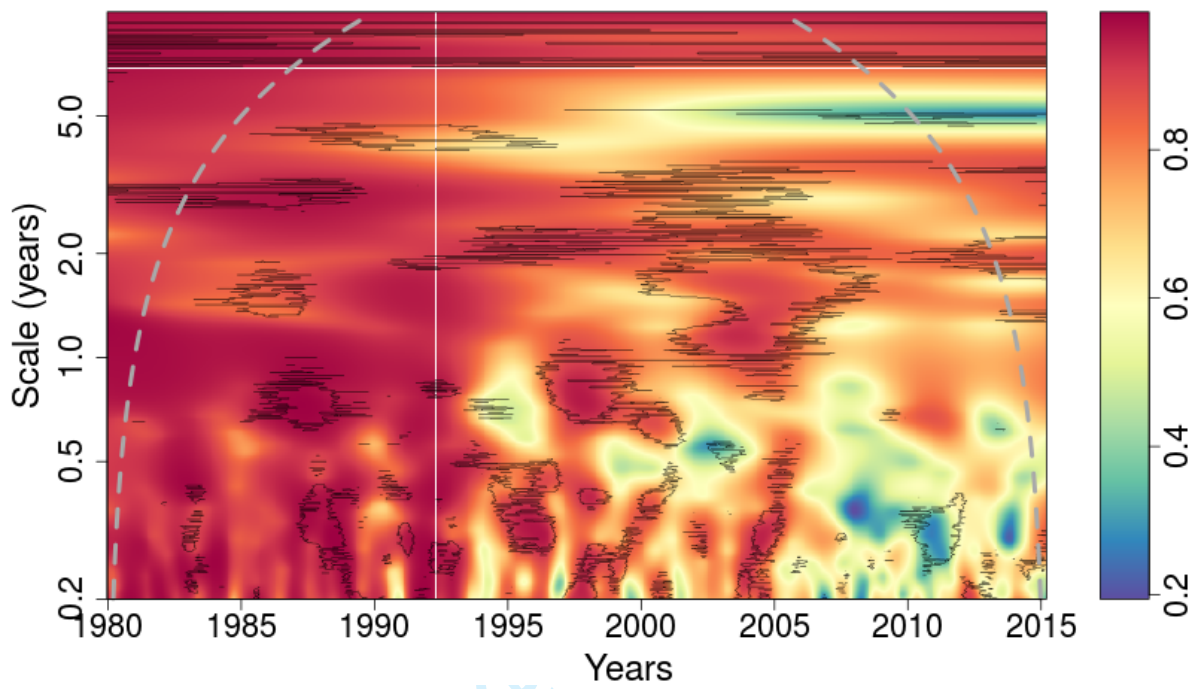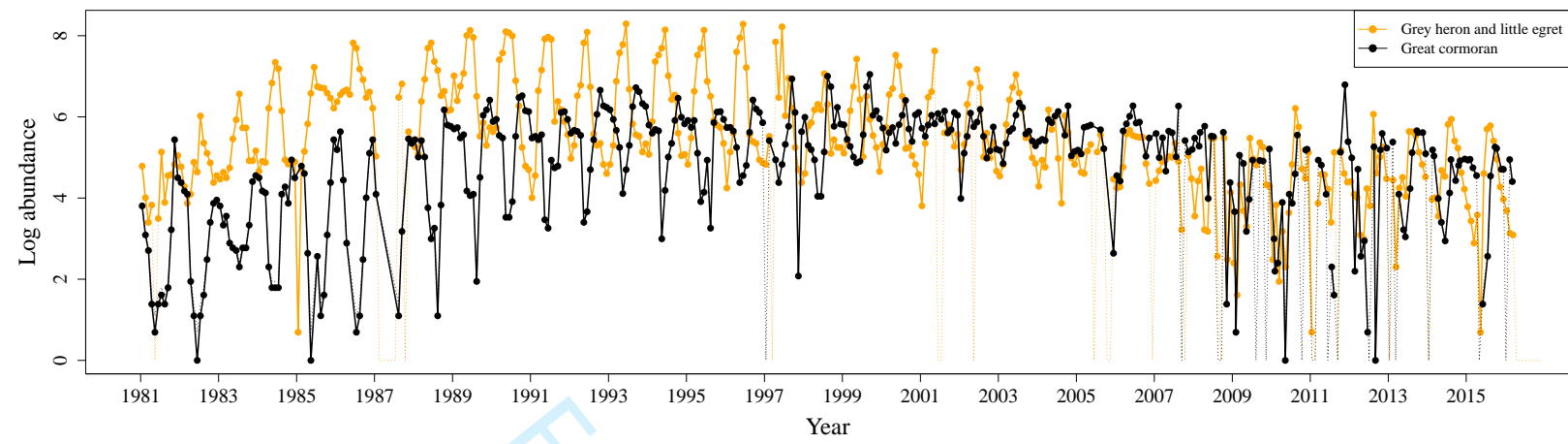
15

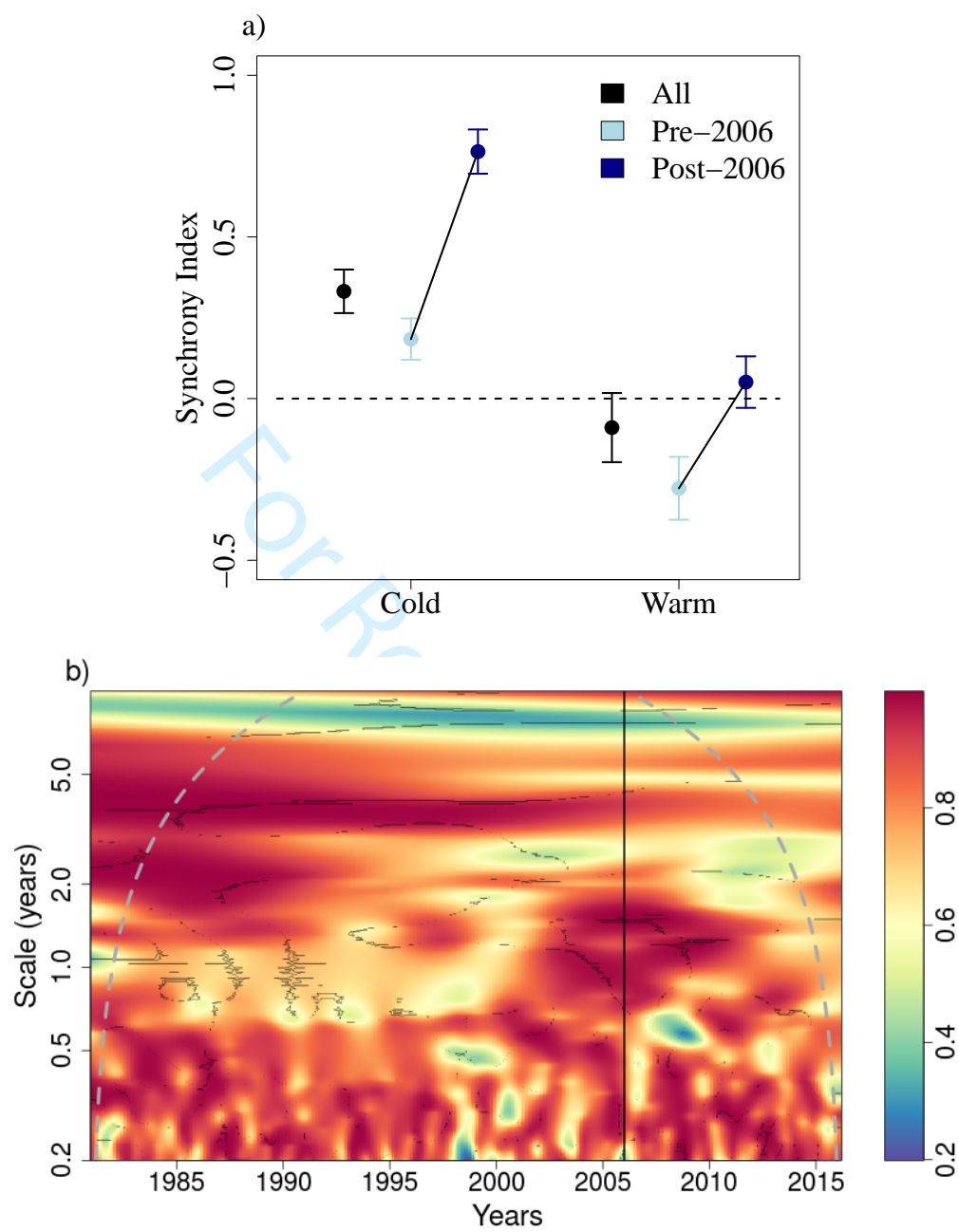308 **Figures**

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Online Supplementary Material

Appendices to *Looking for compensation at multiple scales in a wetland bird community.* Barraquand F., Picoche C., Aluome C., Carassou L., and Feigné C.

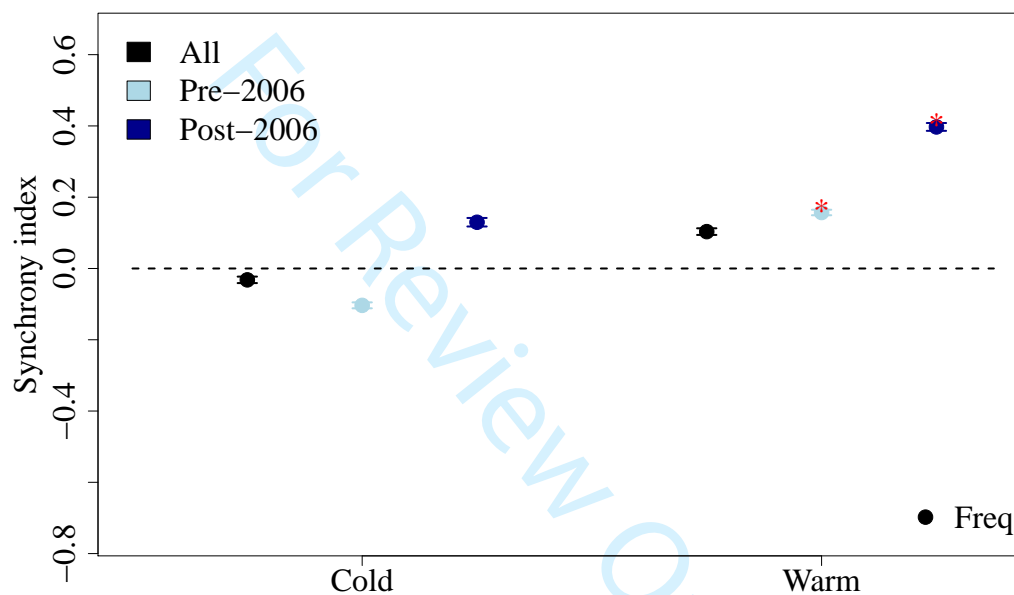## Appendix 1 - Gross synchrony index at the whole community level

Figure A1: Gross' synchrony index as a function of the season (cold and warm seasons), calculated among the 60 most frequent species in the Teich reserve. The index was computed in each panel on the whole dataset (black) or using two periods: before and after 2006 (light and dark blue), the year of the change in water level management. Red stars correspond to synchrony values significantly different from the null model (independent species), at the Bonferroni-corrected 10% threshold.

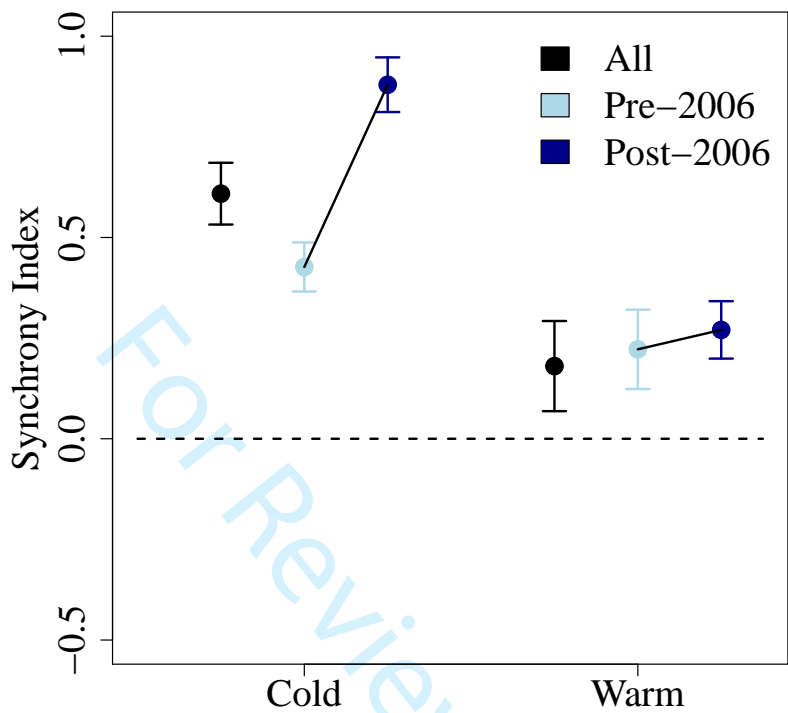## Appendix 2 - Correlation in log-scale betwen cormorant and heron+egret

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

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

Appendix 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 developped by Gross et al. [1] (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.
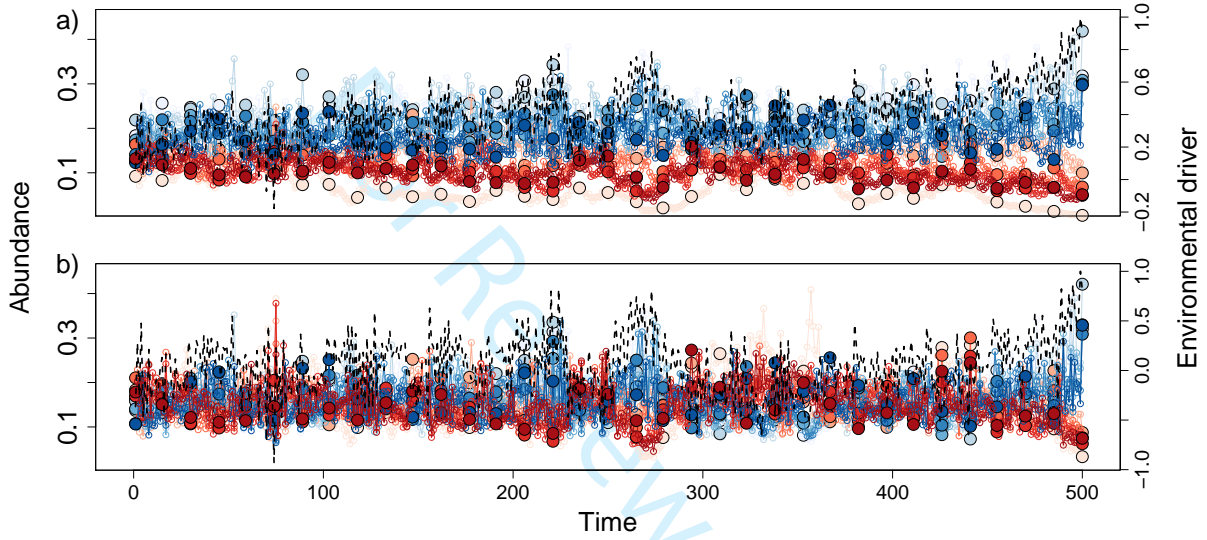

Figure A3: Time series for a community of 10 species, with a strong effect of the environment (b=0.75, see eq. 1) and a time series of 500 time steps. Open circles represent all points of the time series while large filled circles correspond to the sub-sampling of the time series (keeping only 35 points). 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 1:

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

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. [1]. The noise

3

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

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

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

- Scenario 1: $U_t = u_t$ where u_t is an autocorrelated signal (standardized); no subsampling of the data
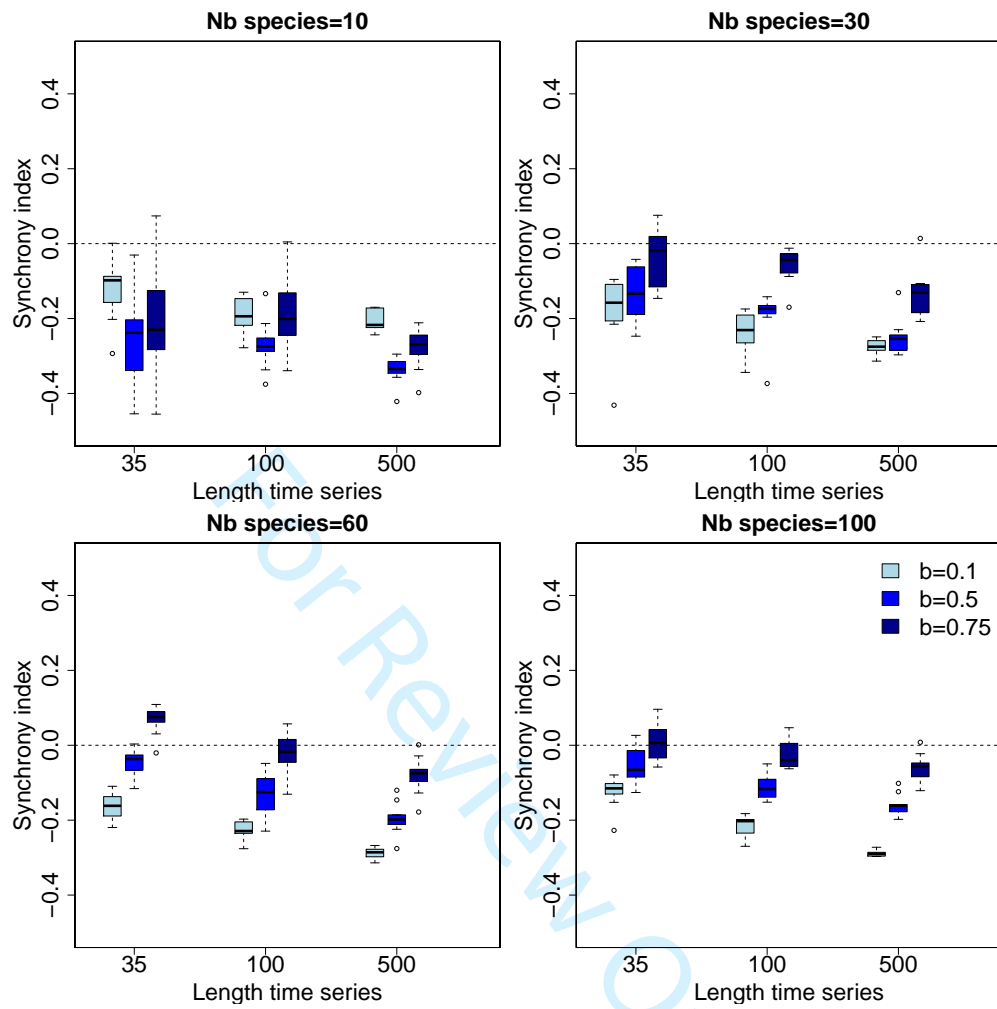
Figure A4: Evolution of Gross' synchrony index for different time series length and number of species in the community, in simulations where there is no trend in the environmental signal and the data is not subsampled, keeping the autocorrelation of the environment.
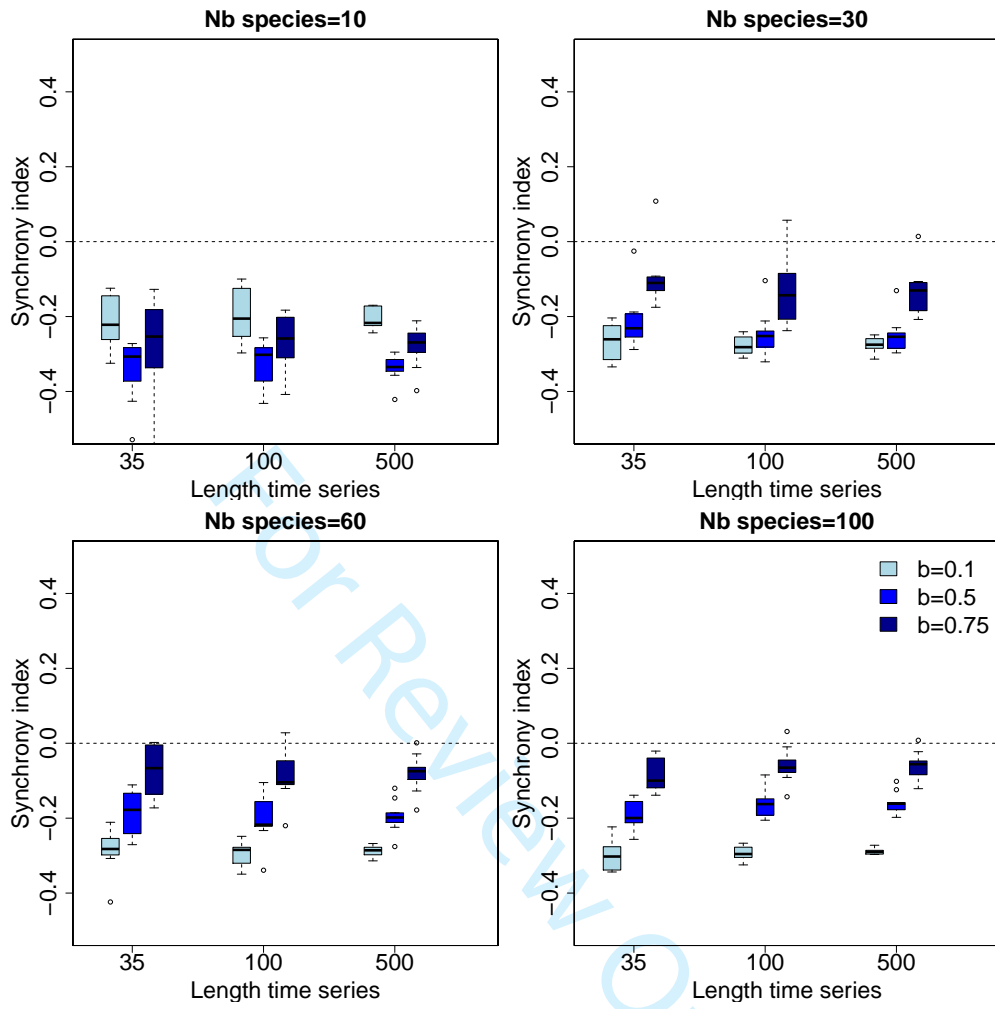
- Scenario 2: $U_t = u_t$; data subsampling

5

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.

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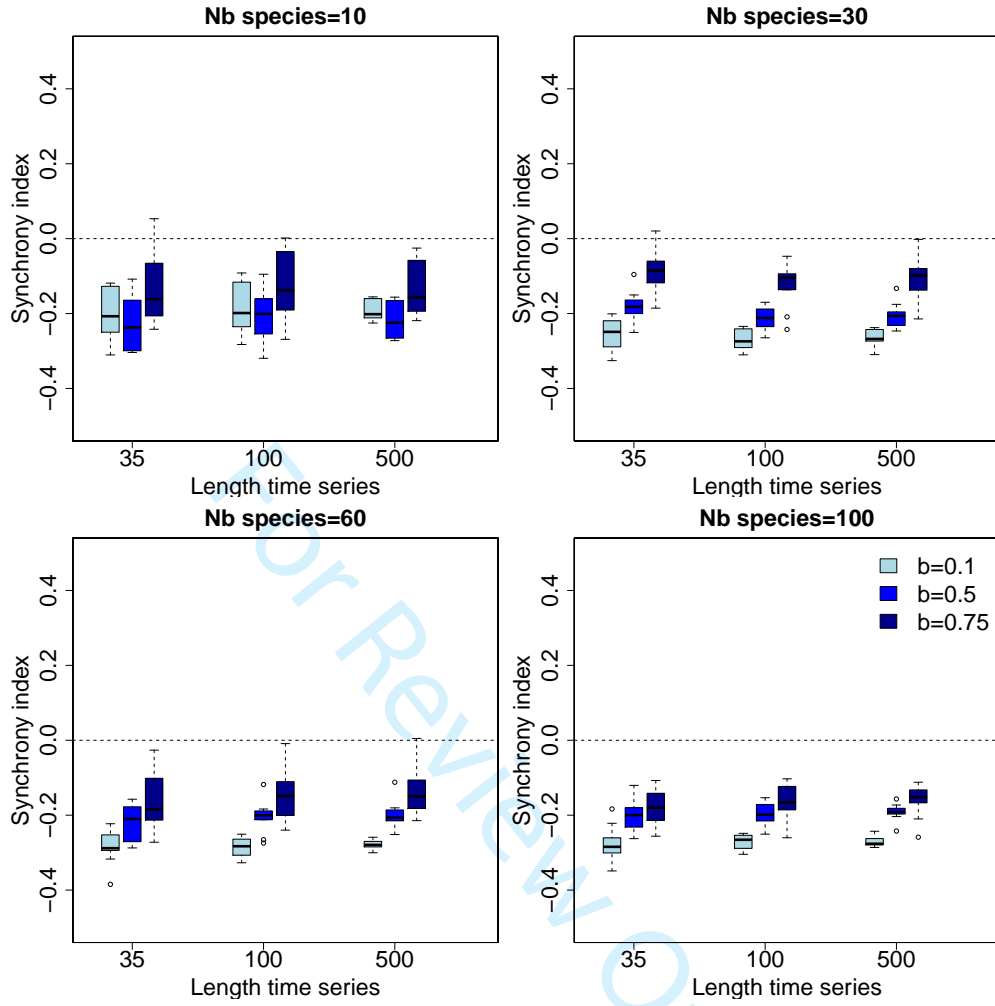
Figure A6: Gross' synchrony index for different time series length and number of species in the community, in simulations where there is an increasing trend in the environmental signal and the data is subsampled (for 35 or 100 time steps), removing part of the autocorrelation of the environment in the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

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

7

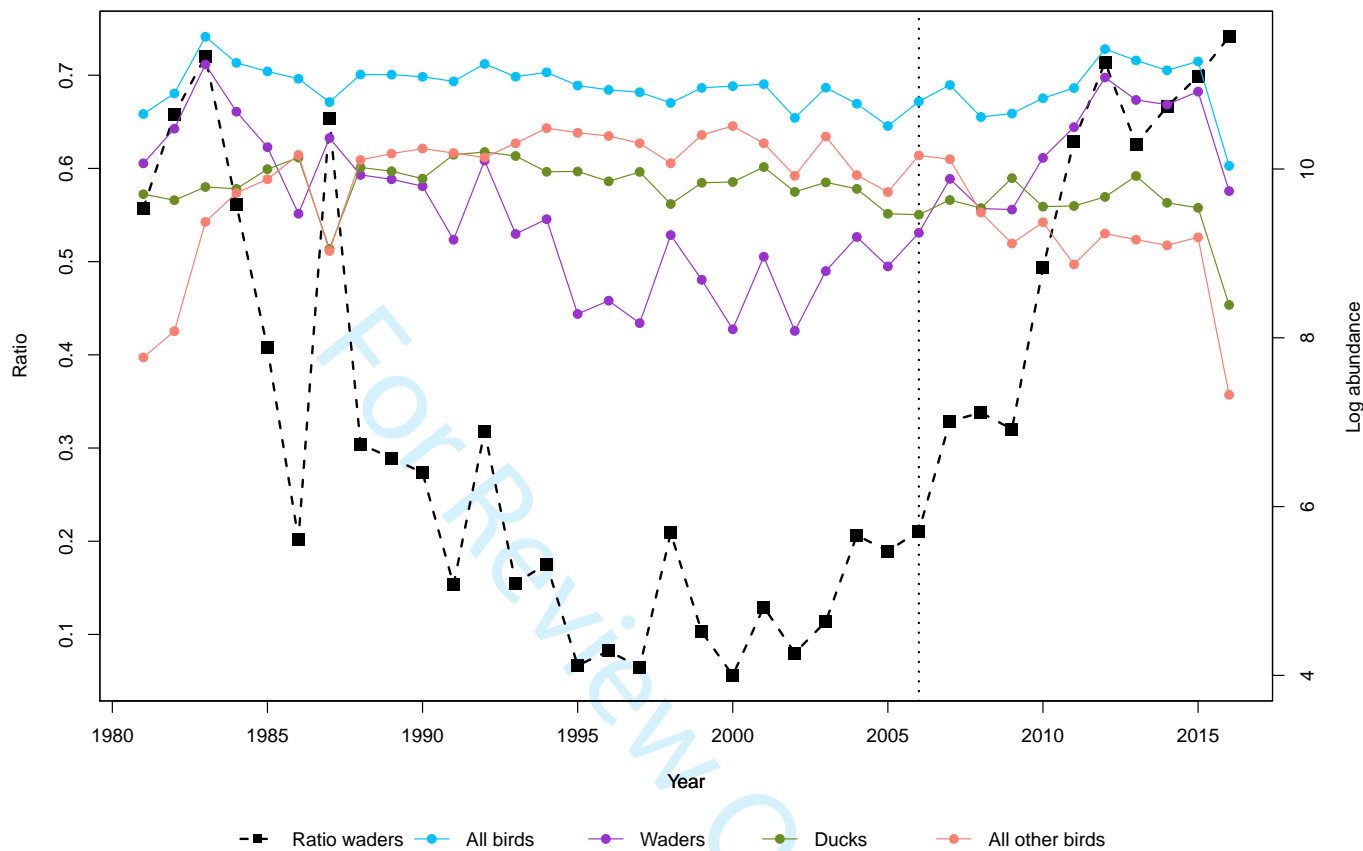**ESM 4 - Temporal patterns of functional groups in the Teich bird community**

Figure A7: Temporal trends in the abundance of all birds and the main functional groups (waders and ducks). The duck category actually includes all species functionally similar to ducks (i.e., anatids and the common coot). The dashed line presents the ratio of wader individuals in the whole community, which changes over time.

References

[1] Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., Wayne Polley, H., Reich, P. B. & van Ruijven, J., 2013 Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *The American Naturalist* **183**, 1–12.