

On wavelet analyses with the `mvcbwt` package, issues, and technical fixes

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To study synchrony, Keitt (2008) presents the wavelet modulus ratio, i.e. $\rho(s, t) = \frac{\Lambda_{s,t}(|\sum_k w_k|)}{\Lambda_{s,t}(\sum_k |w_k|)}$ where $\Lambda_{s,t}$ is an operator weighting a function $f(s, t)$ of both location in time and scale, defined by $\Lambda_{s,t}(f) = \int_{-\infty}^{+\infty} \frac{1}{\sqrt{2\pi}} e^{-\frac{1}{2}(\frac{t-\tau}{s})^2} \times f(s, \tau) d\tau$. In the numerator, $f(s, \tau) = |\sum_k w_k(\tau, s)|$ (community-level fluctuation amplitude), and in the denominator $f(s, \tau) = \sum_k |w_k(\tau, s)|$ (sum of species-level amplitudes), if the computation is done for multiple species within a community (it can be performed for functional groups rather than species). The signal $w_k(\tau, s)$ is the continuous wavelet transform of species k abundance, with mother Morlet wavelet. The package `mvcbwt` is meant to compute this index, and works as follows:

1. the function `mvcbwt` takes a table of dates and time series and computes the corresponding Morlet wavelet for each scale and location required. By default, the number of locations L is the number of dates, and is equal to the number of scales S .
2. the function `wmr.boot` takes the wavelets and computes the wavelet modulus ratio (`wmr`) of the observed time-series. It then computes R surrogates to provide the quantiles corresponding to the observed value at each scale and location.
 - (a) it first computes the observed `wmr` (called `z`)
 - (b) for each scale s , the function shifts the phase of the observed wavelets for the number of surrogates required. In total, there are therefore $S \times R$ bootstrapped wavelets.
 - (c) for each scale, the function compares the value of the observed `wmr` at location t to the distribution of the index obtained from the surrogates. There are therefore $S \times L$ comparisons to a distribution made of R samples. This is performed with the `ecdf` function (Fig. 2) which returns $Pr(X \leq x)$. The table made of $S \times L$ $Pr(X \leq x_{obs})$ is called `z.boot`.
3. the function `image.mvcbwt` takes an object from `wmr.boot` (or `wmr`, which contains only the observed values of the index, `z`). It first plots the values in `z` as an image ; then uses `z.boot`. We describe first the way this function was originally implemented, and then the modifications we made.
 - (a) the function first computes $1 - |1 - 2 * Pr(X \leq x_{obs})|$. This formulation corresponds to the usual two-sided p-value, that is $p_{val} = 2 \min(Pr(X \leq x_{obs}), Pr(X \geq x_{obs}))$.
 - (b) the function then computes the adjusted p-value $p_{val,adj}$ with a Benjamini-Yekutieli false discovery rate.
 - (c) the function finally plots the contour for p_{val} and $p_{val,adj}$ at the chosen α level (0.05 by default).

What we changed

There were several adjustments we made to the `image.mvcbwt` function. The first ones were only cosmetic. Panels were created to be able to plot a `wmr` image as well as other plots on the same figure, add a colorbar and increase

the size of certain labels. We also changed the Benjamini-Yekutieli False Discovery Correction (FDR) to Benjamini-Hochberg following the suggestion of Referee 2 in Revision 1 (who actually only suggested that we changed from Bonferroni to something else).

We also differentiated between low values and high values of the observed wmr. To do so:

1. we first compute p_{val} and $p_{val,adj}$
2. for each z.boot value, we check if $Pr(X \leq x_{obs}) < Pr(X > x_{obs})$ (x_{obs} has a low value and might therefore indicate compensation) or $Pr(X \leq x_{obs}) > Pr(X > x_{obs})$ (x has a high value and might therefore indicate synchrony).
3. we draw a contour at the alpha level with the following code: red for each p_{val} (or $p_{val,adj}$) where $Pr(X \leq x_{obs}) > Pr(X > x_{obs})$ and blue for each p_{val} (or $p_{val,adj}$) where $Pr(X \leq x_{obs}) < Pr(X > x_{obs})$.

What were the issues?

There were several issues (theoretical, probably not due to the package itself) that we discovered after implementing the suggestions of Referee 1 and 3 in Revision 2.

- We first implemented, using the changes mentioned above, a visualization of significantly low (blue) and significantly high (red) synchrony zones, as suggested by referee 1 (Fig. 1). This revealed that the significance contours were not always logically located (blue lines should be around low values of the index).
- Increasing the number of surrogates from 100 (Fig. 1) to 1000, as suggested by referee 1, most of the significant zones disappeared. As the number of surrogates increased, we could assume that the distribution of actually sampled values increased in breadth, with more and more observed values closer to the tail of the distribution, causing this behaviour (i.e., a sampling effect on the tails due a too low number of surrogates). This, however, was not clear when empirical cumulative distributions are plotted (Fig. 2). We actually do not know what causes this discrepancy, as the same technique seemed to be less sensitive to the number of surrogates for simulated data (not shown).

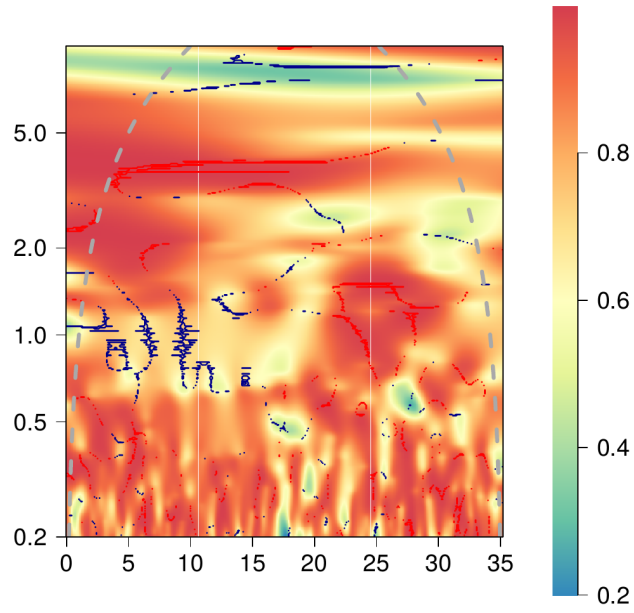


Figure 1: Reference wavelet analysis for the Cormoran/Heron/Egret case with 100 surrogates, Benjamini-Hochberg false discovery correction and a fine grid (423×423)

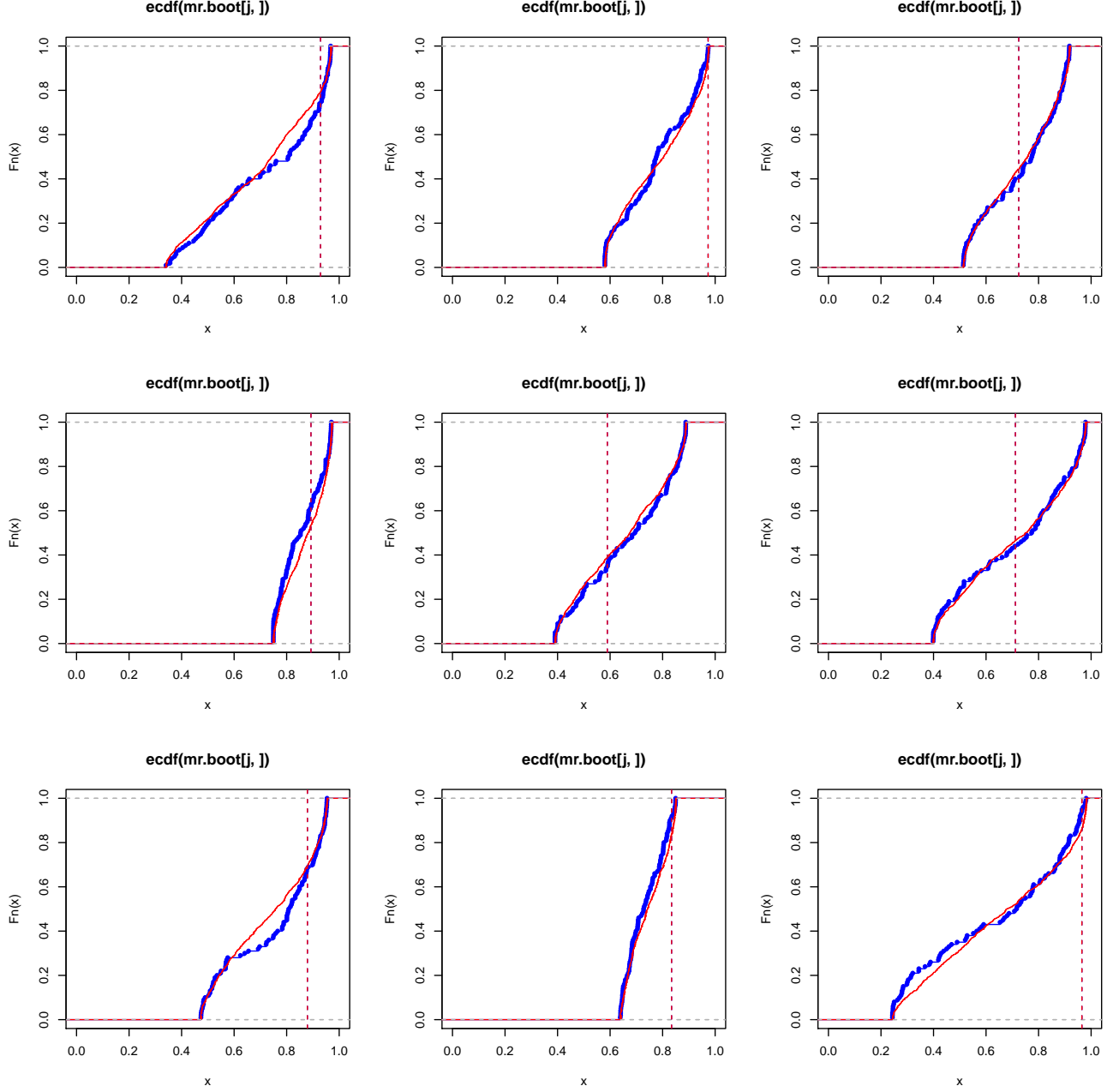


Figure 2: Empirical cumulative distribution of $\rho(s, t)$ for several randomly chosen s and t with 100 (blue) and 1000 (red) surrogates. Observed values are indicated by vertical dashed lines.

- the Benjamini-Hochberg-adjustment of p-values led from 12% $p\text{-values} < 0.1$ to 2% $p\text{-values} < 0.1$ in the Cormoran/Heron/Egret case with 100 surrogates and from 11% to 0.2% with 1000 surrogates. The important reduction in significant values after correction could perhaps come from the large number of comparisons due to the size of the grid. Indeed, when using a fine-scaled image grid, there was 178929 ($423 \text{ scales} \times 423 \text{ locations}$) comparisons. It appeared that only the p-values equal to 0 when not adjusted became eventually significant with this FDR (False Discovery Rate) correction (Fig. 3), which raises some questions as to the usefulness of the whole FDR-correction process. The FDR correction appears of dubious utility here, since it is essentially equivalent to picking exactly zero p-values rather than highlighting zones with low p-values.

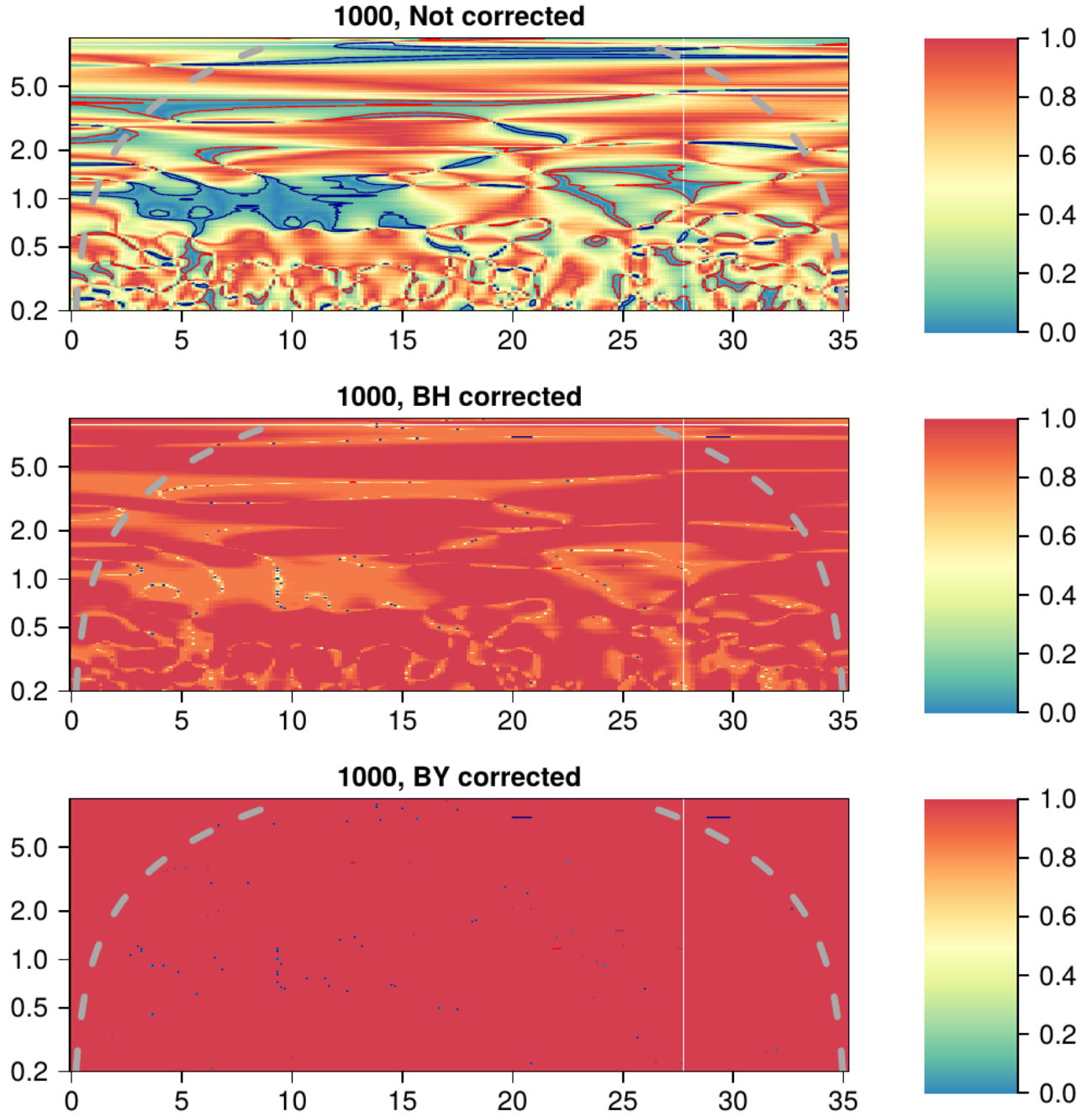


Figure 3: P-value images (i.e., each pixel in the grid is a p-value) for 1000 surrogates without FDR correction (top), with the BH (Benjamini-Hochberg) correction (middle), and with the BY (Benjamini-Yekutieli) correction (bottom) as recommended by Keitt (2008). Red is high probability, close to 1, blue is low probability, close to 0. The bottom and middle panel show “scattered significance” through the blue dots, rather than contours of high- and low-value wmr.

- Standardizing $((x - \text{mean}) / \text{sd})$ the time-series also led to a change in observed wmr values (see for instance the wavelet/wader wavelet plots in which the synchronizing effect of 2006 is much stronger with the scaled time-series). However, this suggestion was not a mere technical fix but rather implied a change in the meaning of the index. Normalised wavelet modulus ratios are not comparable to the Gross index and the notion of compensation they examine has no ecosystem-level meaning (i.e., rare species have equal weight than common species in normalised analyses, while common species are actually the species that matter most for

compensation in real systems). Thus these normalised analyses have not been retained.

What we also checked and eventually decided

- The line contours that are drawn in the wmr plots do correspond well to small p-values; see Fig. 3: these are not a mere plotting bug.
- While removing the FDR correction (but still using Keitt 2008’s method), we changed the number of scales (from 423 to 100) and locations (from 423 to 212) to limit the number of p-value computations. This had the benefit of reducing the noise in significance contours (as well as the size of the images), see Fig. 4. However, illogical contours still appeared in Fig. 4, in the sense that a zone with index value around 0.5 was found to be of significantly low synchrony, which essentially suggested that there was an issue with the null hypothesis (i.e., we can reject too easily the null in places we should not be able to).

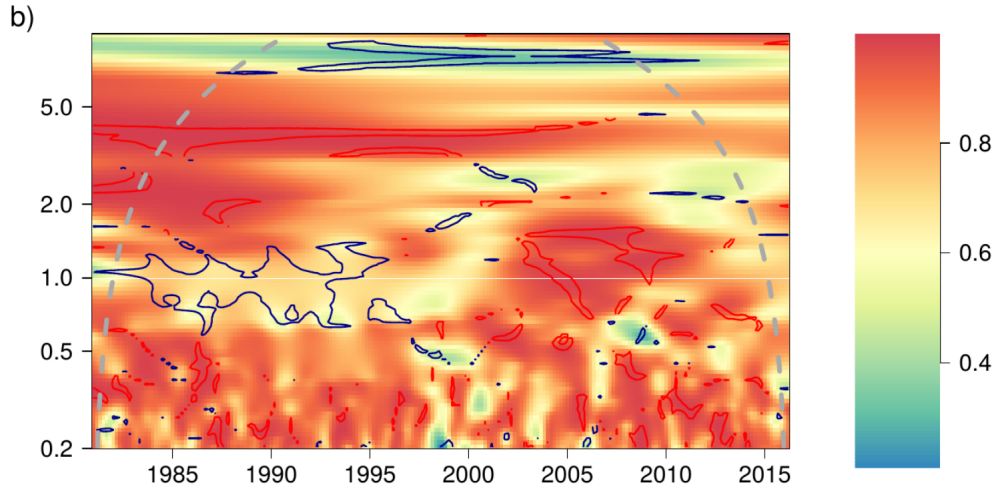


Figure 4: Wavelet analysis on a coarse grid, with 1000 surrogates from Keitt (2008) and no FDR-correction

- To fix the problems of null hypotheses and associated p-values, that could not be fixed by simply changing the grid size or changing the FDR correction, we constructed an entirely new null hypothesis. Instead of phase-randomization of the wavelets sensu Keitt (2008), we built new time series with the IAAFT method (Schreiber & Schmitz, 2000) and then built the p-values using each image pixel’s surrogate distribution. Each surrogate $\rho_j(s, t)$ is therefore obtained through wavelet transformation and wavelet modulus ratio computation of the IAAFT-obtained time series. In theory, this could have led to less significant zones than alternative methods (Cazelles *et al.*, 2014), but we found that it provided a suitable and easily understandable null hypothesis: the Fourier spectrum is conserved for each species while all cross-correlations between species are lost. In Fig. 5, the number of significant pixels has not changed markedly, but all significant $\rho(s, t)$ are now in one block of obvious compensation instead of being spread out throughout the image as scattered points, which is obviously desirable behaviour. In Fig. 5, we kept the Benjamini-Hochberg FDR correction but we eventually removed that correction, which is in general not considered in wavelet analyses Cazelles *et al.* (2014). The graphs presented in the paper and the response letter/revision folder, on both real and simulated data, were found to be satisfactory when using 1000 rather than 100 surrogates and an absence of the FDR-correction¹.

¹Upon reflection, strictly FDR-correcting such p-values images might make little theoretical sense: we do not count / sum over significant pixels to determine how much of the image shows compensation or synchrony. Contiguous high or low synchrony zones that are deemed significantly away from the null are interpreted “as a whole”, e.g., there’s a low-synchrony band near 8 years.

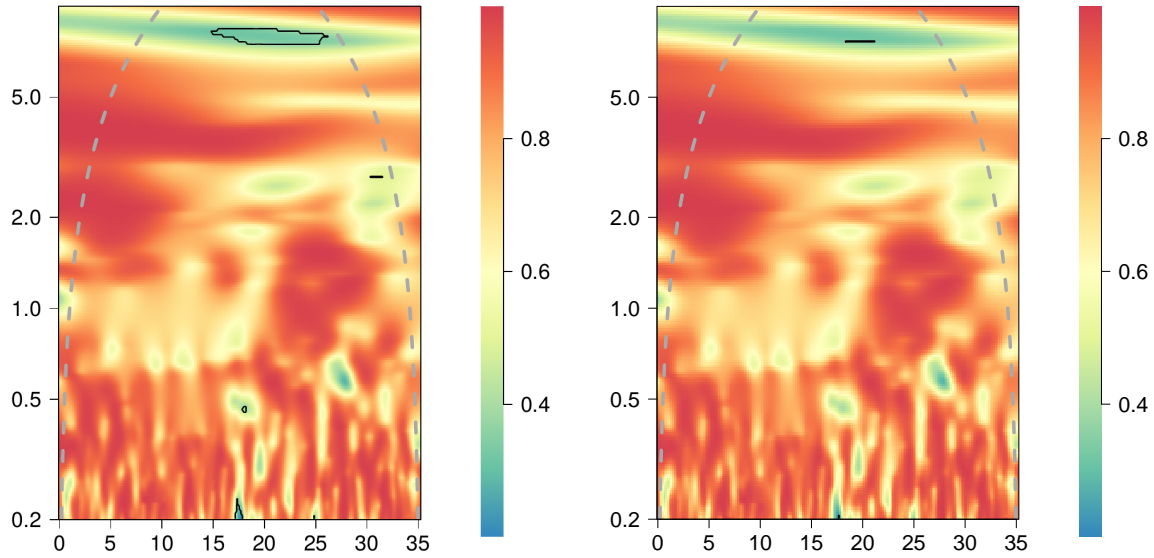


Figure 5: Wavelet analysis with 100 IAAFT surrogates (left) and 1000 IAAFT surrogates (right). These graphs include a BH-correction for the false discovery rate.

Conclusion

Although the null hypothesis testing proposed by Keitt (2008) does seem to provide sensible results in some cases, with hindsight it was both difficult to

- fully understand the biological meaning of this null hypothesis
- make it produce meaningful results on our data

We have therefore used instead the well-known IAAFT procedure which has a clearly defined null hypothesis and provided sensible results on both simulated and real data.

References

- Cazelles, B., Cazelles, K. & Chavez, M. (2014) Wavelet analysis in ecology and epidemiology: impact of statistical tests. *Journal of the Royal Society Interface* **11**, 20130585.
- Keitt, T.H. (2008) Coherent ecological dynamics induced by large-scale disturbance. *Nature* **454**, 331–334.
- Schreiber, T. & Schmitz, A. (2000) Surrogate time series. *Physica D: Nonlinear Phenomena* **142**, 346–382.